UNIVERSITY OF CALIFORNIA
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Quantifying the effects of spatial environmental variation and soil microbes on plant community dynamics

A dissertation submitted in partial satisfaction
of the requirements for the degree Doctor of Philosophy
in Biology

by

Gaurav S. Kandlikar

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ABSTRACT OF THE DISSERTATION

Quantifying the effects of spatial environmental variation and soil microbes on plant community dynamics

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Doctor of Philosophy in Biology

University of California, Los Angeles

Professor Nathan Kraft, Chair

Understanding the processes that determine the diversity and dynamics of plant communities is a longstanding challenge in ecology. Many studies have inferred the role of demographic processes by studying patterns of functional trait variation in natural communities, but studies explicitly linking such functional trait differences to demographic processes are lacking. There has also been a growing realization that the dynamics of plant communities are also influenced by the composition of the soil microbial community, but despite hundreds of empirical studies, predicting the influence of soil microbes on the diversity and dynamics of natural plant communities remains a challenge. In my dissertation I couple ecological theory with field and greenhouse experiments to build a more complete and generalizable understanding of the processes that control plant biodiversity.

In Chapter One, I ask whether community-wide shifts in three key plant functional traits across an environmental gradient reflect variation in the trait-performance relationship across the landscape. To address this question I coupled observational data of variation in plant composition and functional with experimental data on species performance

across the same landscape. I asked whether observed trait-environment interactions in the experimental data match observed patterns of trait variation. I found that shifts in community-weighted mean traits generally reflect the direction of trait-environment interactions. But on the whole, the interactions we found were weak, and by themselves might not be sufficient to explain community-wide shifts. This supports the value of plant functional traits for predicting species responses to environmental variation, and highlights a need for more detailed evaluation of how trait-performance relationships change across environments to improve such predictions.

Chapters Two and Three focus on how soil microbes can influence diversity in plant communities. Chapter Two begins with a re-analysis of a classic framework that has been extensively used to study how feedbacks between plants and soil microbes can influence species coexistence. A great deal of existing theoretical and empirical work has shown that soil microbes can promote plant coexistence when they generate stabilizing feedback loops, or can drive exclusion when they generate destabilizing feedback loops. I applied insights from modern coexistence theory to show that existing work has largely neglected another avenue by which plant-soil feedbacks can mediate plant coexistence, by driving average fitness differences between plants. This chapter also extends classic models of plant-soil feedback to include more biological detail to show how the effects of plant-soil feedback on plant coexistence depends critically on how plants interact with each other through other processes like resource competition.

In the final chapter of my dissertation, I applied the insights from Chapter Two to ask how plant-soil feedbacks influence diversity in southern California annual grassland communities. I conducted a greenhouse experiment to quantify microbially mediated stabilization and fitness differences among fifteen pairs of annual plants. We found that soil microbes frequently generate negative frequency-dependent dynamics that stabilize plant

interactions, but they simultaneously generate large average fitness differences between species. The net result is that if the plant species are otherwise competitively equivalent, soil microbes would often drive exclusion among the focal species. This work illustrates the importance of quantifying microbially mediated fitness differences, and points to important avenues for future studies on how soil microbes shape plant diversity.

The dissertation of Gaurav S. Kandlikar is approved.

Priyanga Amarasekare

Jennifer Martiny

Lawren Sack

Felipe Zapata

Nathan Kraft, Committee Chair

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Acknowledgements

I am by nature more collectivistic than individualistic, which means I value working in groups with shared goals more than I value working alone. At times this has been at odds with academia's emphasis on individual ideas and achievements. Luckily, I have had the good fortune of developing a robust network of mentors, collaborators, and friends with whom I have chased scientific mysteries, celebrated milestones, and struggled through personal and professional difficulties. These relationships have been hugely important for helping me feel at home in science.

I first thank Nathan Kraft for being a terrific mentor and for building a lab group that has been a wonderful home for my intellectual and personal growth over the past few years. I have learned a great deal from Nathan about nearly every aspect of being a scientist. As any graduate advisor should, he has helped me learn how to formulate interesting and important questions, pursue their answers with creative experiments, and communicate their findings through papers and presentations. But Nathan's mentorship has gone beyond what I used to think was the role of a scientific advisor. He always seemed to have a knack for knowing exactly when to encourage me to pursue a vague interest that could lead to something valuable, and when to rein me in from diving into yet another deep rabbit hole that would likely result in a dead-end. Nathan has also been a great role model on the personal side of science. He has been patient when I needed time, and uplifting when I needed a push. Nathan has reminded me several times that his mentorship won't end after I finish graduate school, and for that I am very grateful. My dissertation has also improved greatly based on the valuable feedback from my committe members: Priyanga Amarasekare, Jennifer Martiny, Lawren Sack, and Felipe Zapata.

I am especially grateful for the mentorship I have received from Priyanga, who has

treated me as one of her own students throughout my time at UCLA. Starting from my first year at UCLA, Priyanga has helped me appreciate the value of combining biology and mathematics to uncover the elegent complexity of so many fundamental ideas in ecology and evolution. Priyanga was also incredibly helpful when I began to consider next steps after graduate school. She spent hours helping me think through what kinds of questions I wanted to pursue, and then helped review my application materials and wrote letters of support. I've also learned from Priyanga about using what power and privilage one has to advocate for justice in the community. I count this among the most important lessons I have learned in the past five years.

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and companion throughout my PhD. We have shared many laughs and frustrations, but above all I've been inspired by Marcel's boundless and contagious curiosity, thoughtful approach to science, and energy for lifting up unheard voices. Every young scientist would be lucky to have a friend like Marcel, from whom they can learn so much, and in whom they can confide their insecurities.

Throughout graduate school I've had the pleasure of pursuing various collaborative projects that are not included in my dissertation. I thank Nathan Kraft and Ned Fetcher for inviting me to join their project on the functional ecology of Melastomes in Costa Rica. I also thank Nathan, Ned, Marcel Vaz, German Vargas, and Ricardo Kreibel for helping draft a manuscript based on that work, which became my introduction to the world of scientific publishing. I'm very happy that I accepted Emily Curd's invitation to join a somewhat motley but definitely top-notch team dedicated to sorting out bioinformatics for the Cal-eDNA program. I greatly enjoyed learning about the virtues and challenges of eDNA with Emily, Zack Gold, and Jesse Gomer on the Anacapa pipeline, and with Maddi Cowen on ranacapa. Conversations with Will Petry about seed predation, spatial coexistence, and the human side of science have helped me understand my own scientific and personal priorities. I also thank Maddi Cowen, Kenji Hayashi, Rosa McGuire, Marcel Vaz, and Xinyi Yan for collaborating with me on EcoEvoAppsover the last few months, a project that I had wanted to pursue since my first semester in graduate school.

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Many of the ideas I have pursued during graduate school, as well as the confidence to pursue these ideas despite setbacks, came about thanks to the tremendous mentorship I received during my undergaduate training at the University of Minnesota. It was in George Weiblen's lab that I first appreciated the value and joy of pursuing a scientific inquiry of nature. I will always be grateful to George for inviting me into his lab and for entrusting me to simultaneously work at the sequencing bench, help assemble a book of trees in Wanang (Papua New Guinea), and process herbarium specimens from all over the world. These experiences have given me a much wider picture of ecology and natural history. I also learned a great deal from my graduate mentor Erin Treiber, who patiently trained me in the sequencing process, but more im-

portantly gave me lots of insights into the ups and downs of life as a graduate student. (Among other important lessons, I learned from Erin that it is essential to keep a pair of chopsticks at one's office desk, in case one needs to eat Cheetos while working at the computer). Time flew by so quickly when I was working in the Weiblen lab, and this helped me feel that I had found an intellectual home in plant biology.

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I will always look back on my years in graduate school with a mix of joy and sadness. During these years I've made many enriching friendships (as I hope is evidenced by these acknowledgements), but it is also during graduate school that I lost an original best friend – my father – who had been a source of inspiration and strength throughout my life. If I manage to move through my own life expressing even just a fraction of the curiousity, kindness, and fearlessness that my father expressed on a daily basis, I will

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Curriculum Vitæ

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Education

2015-20	Ph.D. in Ecology and Evolutionary Biology (Expected), University of California, Los Angeles. Advisor: Dr. Nathan Kraft
2014-15	Graduate Program in Behavior, Ecology, Evolution, and Systematics, University of Maryland (College Park) (Moved to UCLA in 2015 with Kraft lab)
2010-13	B.S. in Ecology, Evolution, and Behavior and Plant Biology, University of Minnesota (Twin Cities)

Publications

10) Kandlikar, G.S., Yan, X., Levine, J.M., and Kraft, N.J.B. Soil microbes generate stronger fitness differences than stabilization among California annual plants. In press at *The American Naturalist*. Pre-print available on BioRXiv.

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Fellowships and Awards

2020 Murray F. Buell Award for Excellence in Ecology, Ecological Society of America

2019 Student Research Award, American Naturalist Society

2019 Student Research Award, La Kretz Center for Conservation Science

2019 Scherbaum Award for excellence in graduate research, UCLA EEB Dept.

2019 Special Faculty Award for outstanding service, UCLA EEB Dept.

2019 Josephine Reich Quarter Fellowship and Travel Award, UCLA EEB Dept.

2017 Vavra Research and Travel Grants Awards, UCLA EEB Dept.

2015 Graduate Research Fellowship, National Science Foundation

Teaching

Instructor of Record for MCDB 495, a Graduate-level course at UCLA on Teaching in the Life Sciences

Guest Lectures: "Coexistence in plant communities" for upper-division Plant Ecology course; "From taxon tables to biological understanding" for Lower-division course on modern approaches to studying biodiversity; "Soil microbes and the coexistence of California annual plants" for upper-division course on environmental soil microbiology.

Graduate student writing mentor at the UCLA Graduate Writing Center (2018-2020).

Graduate Mentor for "Calculus for Life Sciences" for UCLA PEERS program

Teaching Assistant for Plant Physiology, Plant Ecology, Practical Computing for Biology, Calculus for Life Sciences, Principles of Molecular Biology, Principles of Ecology.

Service

Founder of "Hacky Hours", a Graduate student and Postdoc co-working space at the Dept. of Ecology and Evolutionary Biology, UCLA.

Graduate student representative on Faculty search committee for Quantitative Microbial Ecology/Evolution position, Dept. of Ecology and Evolutionary Biology and Institute for Quantitative and Computational Biology, UCLA. 2018.

Graduate student representative on Department seminar committee, Dept. of Ecology and Evolutionary Biology, UCLA. 2016-2017.

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Peer reviewer for Annals of Botany, Ecology, Ecology Letters, Functional Ecology, Oecologia, and Journal of Ecology.

Dedicated to the memory of my father, Sunil Kandlikar

and to the women whose sacrifices have made it possible for me to pursue this work:

वर्षा कांडलिकर, शरयू शेजवलकर आणि राधा कांडलिकर

Things are similar: this makes science possible.

Things are different: this makes science necessary.

Richard Levins and Richard Lewontin

Dialectics and Reductionism in Ecology

Introduction to the thesis

Biological systems are complex. They comprise huge numbers of entities whose organization, dynamics, and interactions are governed by processes that operate at various spatial and temporal scales. Understanding how component entities and process interact with the dynamics of the whole system is a fundamental theme across the life sciences. The goal of the research presented in this dissertation is to advance our understanding of a few processes that structure plant communities, the biological system at the energetic base of all terrestrial ecosystems on Earth.

The same properties that make plant communities so enthralling – the incredible diversity of form and function within and between species, the mix of antagonistic and mutualistic interactions, the various interactions between life and the abiotic environment – also make the search for general explanations very challenging. How then do we build our understanding of what shapes plant community dynamics? The approach I have adopted[1] has been to make careful assumptions that let us build tractable but only partial mental pictures of how nature works, and cautiously extend the insights build on these abstractions to describing nature.

[1] I thank the many thoughtful philsophers of science whose work has helped me develop an internal framework for conducting science, but is not cited in this dissertation. Jay Odenbaugh's work has been especially helpful, and the approach of dialectical materialism developed in Levins and Lewontin (1980) most closely matches my current perspective on ecological research.

Figure 1: Photographs of the annual grassland at the University of California Sedgwick Reserve (Santa Barbara County, CA, USA). Panel (A) shows the landscape, with a serpentine hummock in the foreground. Panel (B) shows *Lasthenia californica* (yellow flowers) and *Plantago erecta* (white) growing together on a serpentine hummock. Both photographs were taken in March 2016.

In the chapters that follow, I attempt to apply this approach to study how spatial abiotic variation and interactions between plants and soil microbes influence plant communities. I address two of these questions (Chapters One and Three) in an annual grassland in coastal southern California (Fig. 1). As is characteristic of Mediterranean climate ecosystems, the grasslands in this region are incredibly species-rich, and the growing season of the annual plants is restricted to the mild, rainy winters that separate the hot, dry summers. In California, the grasslands occur over complex edaphic backgrounds, encompassing a great deal of variation in soil physical and chemical properties. It is thus an ideal system in which to study how various processes structure diverse plant communities. In Chapter One, I focus on how plant functional traits – physiological characteristics that capture plant ecological strategies – influence species responses to environmental variation. Specifically, I ask whether

observed shifts in the average physiological characteristics of whole plant communities reflect differences in how individual species respond to the gradient. For example, if average leaf size decreases in soils with fewer nutrients, does this in fact mean that smaller-leaved plant species are less sensitive to nutrient stress? If community-wide patterns of trait turnover can serve as reliable proxies for how individual species with different trait values respond to the gradient, then observed correlations between environmental gradients and the traits of dominant plants can serve as the basis for predictions about the relative performance of different plant species across environmental gradients. Accurately predicting of how species might respond to environmental variation is of especial importance as human activity rapidly changes the climate and other physical condition that plant species experience, and the results from this chapter highlight both the value and potential dangers of making such predictions on the basis of existing trait-environment relations.

In Chapters Two and Three, I turn my attention to interactions between plants and other living components of their environment. Over the past few decades, our growing awareness of the ubiquity of microbial life and its influence on large-scale processes has challenged many branches of life sciences to revise existing paradigms (Gilbert et al. 2012). But the fact that microbes can control the dynamics of larger organisms has not been as much of a revalation for the botanical sciences, which has a long history of studying the role of symbioses, especially in the forms of rhizobia and mycorrhizae. What *has* been a revalation is that we are now developing rigorous conceptual frameworks that let us organize and interpret the variety of effects soil microbes have on plant dynamics, and ever-improving technologies that allow us to more precisely characterize these effects. Chapter Two presents a critical re-evaluation of Bever et al. (1997)'s classic theoretical framework for how soil microbes influence plant

coexistence. This framework considers the interactions between two plant species that differ only in the soil microbial communities they cultivate, and in how their growth is influenced by these cultivated communities. Numerous empirical studies inspired by this framework that have shown that soil microbes can have important consequences for plant community structure in various ecosystems (Crawford et al. 2019). But our re-evaluation identified important gaps in existing studies and generated three key insights.

The first key insight is that previous work has left us with an incomplete understanding of the range of effects that soil microbes can have on plant species interactions, in part because the potential for soil microbes to drive average fitness differences between species has been largely ignored. My coauthors and I derived a new metric that quantifies this microbially mediated fitness difference, and showed how this metric can be parameterized empirically. Next, we showed that the effects of soil microbes on plant diversity in species rich communities might not be easily predicted from studies of plant-soil feedback among species pairs. Using simple examples, we show how in systems with three plant species, soil microbes might promote diversity even when they drive species exclusion in any single pairwise interaction, or might hinder diversity even when they stabilize each pairwise interactions. Previous empirical studies suggest that such dynamics may be common among naturally interacting plants. Finally, we showed that studying how soil microbes influence plant diversity in isolation of other processes like resource compatition may obscure the role of soil microbes in promoting (or hindering) plant diversity. Together, these results solidify the theoretical foundation for plant-soil feedback studies, and identify several priority research areas for this field.

Building on the first insight from Chapter Two, we conducted a greenhouse ex-

periment to evaluate the degree to which soil microbes mediate pairwise stabilization and fitness differences among 6 annual plant species that co-occur in southern California grasslands, including at Sedwgick Reserve. This experiment forms the basis of Chapter Three. As expected based on studies of plant-soil feedback in other grassland communities, we found that species tend to grow more vigorously when their soil microbial community was cultivated by individuals of a different species than by individuals of their own species. As a result, soil microbes generally generate negative frequency dependence among the plant species. However, by parameterizing the new metric derived in Chapter Two, we found that soil microbes also generate large average fitness differences among the plants in this experiment. This result highlights the potential for microbially mediated fitness differences to be a critical driver of microbial effects on plant diversity, an effect that has been largely neglected by previous studies. Quantifying microbially mediated fitness differences across ecosystems, and asking whether they do so in a way that primarily exaggerates or reduces other competitive asymmetries, is ripe for further research.

As is true of most ecological research (Holt 2007), the studies in this dissertation generate new understanding and suggest avenues for future research, but also serve as reminders of old lessons. Chapter One reminds us of the many-to-one mapping between properties of individual species and properties of a community. In this case, various combinations of how individual species' demography changes across an environmental gradient can give rise to the observed shifts in community-weighted means across the gradient. One implication is that we cannot easily use patterns of variation in community properties across gradients to infer the responses of individual species, but our study highlights the value of combining experiments and observational studies to show when plant functional traits are good predictors of how species may respond

to environmental gradients. Chapters Two and Three remind us that as organisms grow, they are simultaneously responding to and actively modifying the environment they inhabit. More specifically, these chapters show that how plants modify the soil microbial community (and how the microbes in turn affect plant performance) can mediate the outcome of competitive interactions in ways that have received little empirical attention. Our results point to the value of studies that contextualize plant-microbe interactions relative to other processes that simultaneously govern plant diversity.

As a whole, the results of my dissertation suggest that as the volume of information available to plant ecologists expands, and questions of how plant communities are structured become ever more important, a pluralistic approach that incorporates relationships between what have been largely studied as distinct processes may be key to addressing fundamental gaps in our understanding of ecological communities.

Chapter 1

Variation in community-weighted mean traits across environments reflects shifts in trait optima in a California grassland

This chapter is in preparation for submission as Kandlikar, G.S., Kleinhesselink, A.,and Kraft, N.J.B. Variation in community-weighted mean traits across environments generally reflects shifts in trait optima in a California grassland.

GSK conceived the problem with NJBK and AK. GSK and AK led the data collection, and GSK led the analysis. GSK wrote the manuscript and all authors contributed revisions.

Abstract

Turnover in species composition and community-wide functional traits across environmental gradients is a ubiquitous pattern in ecology, but the processes that give rise to these patterns remain unclear. We asked whether shifts in the community-weighted means of three key plant functional traits across an environmental gradient in a southern California grassland reflect variation in the trait-performance relationship across the landscape. We planted seeds of 17 annual plant species in cleared patches with no competitors, and quantified the lifetime seed production of 1632 individuals. We then asked whether models that included trait-environment interactions help explain interspecific variation in demographic responses to the environment. This allowed us to evaluate whether observed shifts in community-weighted mean traits matched the direction of any trait-environment interactions detected in the plant performance experiment. Our results indicate that commonly-measured plant functional traits help explain variation in species responses to the environment - for example, the performance of high-SLA species was more sensitive to soil Ca:Mg levels than that of low-SLA species. We also found that shifts in community-weighted mean traits generally reflect the direction of trait-environment interactions, but the interactions we found are not strong enough by themselves to drive community-wide shifts. Our results support the value of plant functional traits for predicting species responses to environmental variation, and highlight a need for more detailed evaluation of how trait-performance relationships change across environments to improve such predictions.

Introduction

Understanding how environmental variation shapes the diversity and dynamics of plant communities is a fundamental challenge in ecology (Schimper 1898), made even more compelling by rapid anthropogenic changes to environmental heterogeneity (McKinney and Lockwood 1999). In addition to variation in species composition (Whittaker 1960; Janzen 1967), turnover in the functional traits of plant communities across abiotic gradients has emerged as a ubiquitous pattern across ecosystems (Cavender-Bares et al. 2004; Hulshof et al. 2013; Bjorkman et al. 2018; Jardine et al. 2020). These functional traits reflect key physiological and life history strategies of plants, which ultimately determine variation in plant fitness across different environments (Grubb 1998; Violle et al. 2007). Although shifts in the functional traits of plant communities across environmental gradients is well-documented, the demographic processes driving this pattern remains unclear.

One of the most common ways for plant ecologists to study trait-environmental relationships has been to quantify variation in community-weighted mean (CWM) of functional traits across landscapes. CWM trait values are calculated as species' trait values weighted by their relative biomass or cover, and reflect the functional properties of the dominant plant species growing in a community (Grime 1998; Garnier et al. 2004). Across ecosystems, communities with less harsh abiotic conditions (e.g. lower drought stress, higher resource availability) tend to be dominated by plants with functional traits that generally reflect resource-acquisitive strategies (e.g. higher specific leaf area or leaf N concentrations, Wright et al. (2004)), and vice-versa in environments that are more restrictive for plant growth. Such shifts in CWM traits are often assumed to reflect variation in trait optima across gradients, with species whose traits closely match CWM expected to have highest fitness (Ackerly 2003; Shipley et al. 2006;

Enquist et al. 2015).

Despite our thorough understanding of CWM trait shifts across environmental gradients, predicting how variation in species functional traits drives variation in community composition – one of the key promises of functional trait ecology (McGill et al. 2006)– remains a challenge. For example, Muscarella and Uriarte (2016) found that a substantial portion of tree species in a tropical forest were more abundant in sites where their traits were more dissimilar from the site's CWM, contrary to predictions of the hypothesis that CWM shifts reflect shifts in trait optima. Part of the challenge is that we lack a clear understanding of whether CWM trait shifts reflect variation in the relationship between functional traits and the vital rates (e.g. germination rate, fecundity, sensitivity to competitors) that determine species performance across landscapes (Shipley et al. 2016). In one of the few studies that has investigated whether CWM trait shifts reflect variation in trait optima, Laughlin et al. (2018) found CWM shifts in leaf, root, and reproductive functional to be unreliable predictors of how traits influence survival rates across gradients, also contradicting the predictions of the idea that CWM trait shifts reflect shifting trait optima.

One path to building a clearer understanding of whether CWM trait shifts across environmental gradients reflect shifting trait-performance relationships is to compare observed shifts in CWM traits to models that directly test whether trait-environment interactions drive variation in species' fitness across the same landscape (Laughlin and Messier 2015). It is important for such analyses to quantify species fitness based on their vital rates or population growth rates rather than species abundance measured at a single time point, which can be influenced multiple abiotic and biotic processes (e.g. dispersal, competition, natural enemies) and is thus a poor proxy for intrinsic fitness (e.g. Fox 2012; Benning et al. 2019).

Comparing CWM trait shifts to trait-environment interactions driving variation in species performance across landscapes can have a wide range of results, some of which are illustrated in Fig. 1.1. If trait-performance relations remain constant across an environmental gradient (Fig. 1.1B), any observed CWM trait shifts likely reflect the effects of species interactions or other processes rather than shifting trait optima. Trait-performance relationships may differ in magnitude but not in sign across a gradient in a way that matches observed shifts in CWM traits (Fig. 1.1C). Such trait-performance relationships with the same sign across the environmental gradient would not by themselves result in differential distribution of traits across the landscape, but provide weak support that CWM trait shifts reflect shifting trait optima. The strongest evidence that CWM trait shifts reflect shifting trait optima would be if the sign of the trait-performance relationship changes across the gradient in a way that is consistent with the CWM trait patterns (Fig. 1.1D). It is also possible that we find strong trait-environment interactions when looking at the vital rates even when there are no observed CWM trait shifts. This might indicate that other processes obscure underlying trait-performance relationships. A major challenge in testing for concordance between CWM trait shifts and variation in trait-performance relationships is that quantifying how trait variation influences species demography across landscapes is very data-intensive, requiring plant performance data across large temporal and spatial gradients. Short-lived plant communities thus offer an ideal system in which to test for concordance between trait-performance relationships and CWM trait shifts. Here we ask whether CWM trait shifts reflect variation in trait optima in a serpentine annual grassland community in southern California. We surveyed the plant community at sites that captured a wide range of variation in soil Ca:Mg, sand content, and depth, three axes of abiotic variation that are known to be important in such serpentine communities. To capture various dimensions

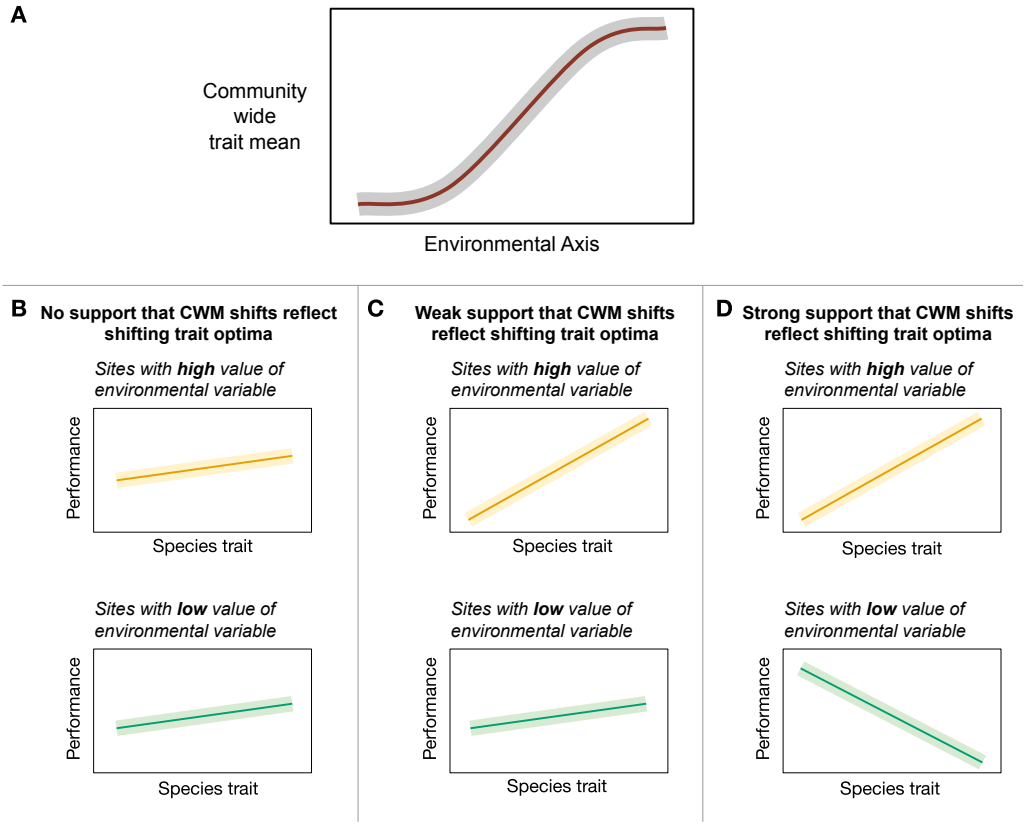

Figure 1.1: A) Variation in community-weighted mean (CWM) functional traits across gradients is a common pattern in plant communities, though whether or not such variation in CWM traits reflects shifts in trait optima across environmental gradients. Here we evaluate whether CWM shifts in plant functional traits reflect shifts in trait-performance relationships across key environmental gradients. Panels B-D illustrate how trait-performance relationships might vary across environments. B) The trait-performance relationship may be identical at opposite ends of the environmental gradient, indicating that other factors (e.g. dispersal limitation) might drive observed shifts in CWM traits. We interpret this as a lack of evidence that CWM trait-environment relationships reflect variation in trait optima across the environment C) The trait-performance relationship may change across the environmental gradient in a direction that is consistent with observed CWM shifts, but the sign of the trait-performance relationship may be the same at either end of the gradient. We interpret this as providing weak evidence that CWM shifts reflect changing trait optima. D) The sign of the trait-performance relationship may change across the gradient, such that species with low trait values have a relative advantage at the low end of the environmental gradient, and vice versa at the high end of the gradient. We interpret this as strong evidence that CWM shifts reflect changing trait optima.

of plant ecological strategies, we quantified community-wide variation in one leaf trait (specific leaf area), one root trait (specific root length), and one whole-plant trait (maximum height). In a parallel experiment, we quantified the intrinsic fitness (lifetime fecundity of individuals growing without competitors, w_i[1]) of 17 annual plant species that naturally occur in this community and that capture a wide range of functional variation. We then asked whether observed CWM trait shifts reflect trait-environment interactions that shape variation in species' fecundity across this gradient. Our results show that shifts in CWM traits can provide valuable information into how trait optima shift across gradients, but also caution against predicting species responses to environmental variation on the basis of shifts in CWM traits alone.

Methods

Study system

We studied trait-environment relations in the annual grassland community at the University of California Sedgwick Reserve in southern coastal California. This region experiences a Mediterranean climate characterized by cool, wet winters and long, dry summers. Plant phenology in this system is driven largely by the rainfall regime. Seeds of annual plants germinate with early-season rain storms. Plants begin to senesce and reproduce with the onset of summer droughts, though there is substantial variation in the timing of reproduction among species (Godoy and Levine 2014; Kraft et al. 2015). The reserve encompasses significant topographic and edaphic hetereogeneity, including oak-savanna, coastal sage scrub, and California grassland communities. Our study focused on a part of the reserve with serpentine-derived soils that are dominated

[1]This term is denoted elsewhere as λ (e.g. Levine and HilleRisLambers (2009); Kraft et al. (2015)), but as λ is also frequently used to denote the discrete population growth rate (i.e. N_{t+1}/N_t), we follow Law and Watkinson (1987) in symbolizing the fecundity of plants without competitors as w.

by invasive *Avena* and *Bromus* spp. In this area, rocky serpentine outcrops ("hummocks") are embedded within a matrix of deep, clay soil. The outcrops are considerably less vegetated than the matrix soils, and act as spatial refuges for several native plant species (Gram et al. (2004)). We studied trait-environment interactions at 16 sites on this landscape, with 10 sites located on hummocks and 6 in the matrix.

Quantifying species performance across the landscape

In November 2015, before the first major rain storm of the season, we cleared any existing vegetation at our 16 focal sites and sowed six sub-plots with seeds of our 17 focal species. Five sub-plots were sowed as replicate "no-competition" plots, in which we sowed the equivalent of 20-60 viable seeds each focal species (Table 1.1) on a grid with 15 cm spacing between each point. The sixth sub-plot was a mixture plot, in which we sowed a high density of seeds (equivalent of 100-200 viable seeds/focal species), spread homogeneously across the sub-plot so that plants were growing in competition . All seeds were collected in the spring prior to this study from hundreds of plants growing across Sedgwick Reserve, and were homogenized within species to ensure that local adaptation (Rajakaruna and Bohm 1999) or maternal effects (Germain and Gilbert 2014) did not drive variation in plant performance across sites in our experiment.

In February 2016, we counted the number of germinants at each grid point in our no-competition plots, and thinned each grid point to leave only two individuals of the focal species. In March, we further thinned each no-competition plot, leaving only a single individual of each focal species growing without any competitors in a 15cm radius. Between April-June 2016, we quantified the seed output of each focal individual in the no-competition plots and of up to five individuals of each focal species

Table 1.1: Species used in the performance experiment, and their mean values for the focal traits of our analysis.

Family	Species	Species code	SLA (cm^2/g)	SRL (m/g)	Max height (cm)
Asteraceae	*Agoseris heterophylla*	AGHE	253.40	313.51	30.25
	Centaurea melitensis	CEME	202.73	145.36	83.65
	Chaenactis glabriuscula	CHGL	142.76	32.85	13.97
	Hemizonia congesta	HECO	215.21	232.98	70.60
	Lasthenia californica	LACA	206.55	253.27	13.75
	Micropus californica	MICA	248.11	65.82	27.33
Boraginaceae	*Amsinckia menziesii*	AMME	203.87	218.95	58.75
Euphorbiaceae	*Euphorbia spathulata*	EUSP	208.23	224.07	20.00
Fabaceae	*Acmispon wrangelianus*	ACWR	128.49	203.59	23.50
	Medicago polymorpha	MEPO	237.77	271.43	11.50
Lamiaceae	*Salvia columbariae*	SACO	132.26	195.46	42.25
Onagraceae	*Clarkia bottae*	CLBO	177.35	247.74	32.45
	Clarkia purpurea	CLPU	205.70	266.02	58.50
Plantaginaceae	*Plantago erecta*	PLER	143.81	135.51	13.66
Poaceae	*Bromus madritensis*	BRMA	269.49	96.31	10.40
	Hordeum murinum	HOMU	276.38	60.92	16.80
	Vulpia microstachys	VUMI	146.22	85.89	15.25

from the "competition" plots at each site, for a total of 1632 individuals tracked across the environment (see Appendix S1 for details on how seed output was quantified). This design let us quantify three vital rates for each species at each site: germination rate, per-germinant seed production in the absence of competitors ("low-density seed production", w_i), and sensitivity to competitors. Each of these vital rates is know to be an important determinant of annual plant demography in this community (Levine and HilleRisLambers 2009), but we focus only on the low-density seed production as a measure of species performance in the remainder of this study.

Measuring compositional turnover across the landscape

In Spring 2017, we surveyed five replicate undisturbed plots (1x1m) adjacent to each of our 16 experimental sites to quantify vascular plant community composition. Plots

were genearlly arranged linearly, parallel to cleared plots in which we had experimentally quantified plant performance. We ensured that the community composition plots were generally located on similar soils as the experimental plots (e.g. if the experimental site was in the matrix but near a hummock, all community composition plots were located in the matrix). In each plot, we visually estimated the relative cover of each of species using 5% cover classes.

Functional trait measurement

Kraft et al. (2015) had previously measured 11 functional traits that are known to capture ecologically important variation in leaf, root, whole-plant, and reproductive functioning of plant species for most (12/17) species in our demography experiment. In Spring 2016, during our plant performance experiment, we supplemented this dataset with additional measurements of four leaf traits (leaf size, leaf dry matter content, specific leaf area (SLA), mass-based leaf [N]), two belowground traits (rooting depth and specific root length (SRL)), two abovegroud whole-plant traits (maximum height and canopy shape index), and two reproductive traits (flowering phenology and seed mass) for the five species in our experiment that were not part of Kraft et al. (2015)'s study (*Bromus madritensis*, *Chaenactis glabriuscula*, *Hordeum murinum*, *Micropus californica*, and *Vulpia microstachys*.). For these five species, all traits were measured from 5-8 individuals growing in an additional plot adjacent to one of the matrix sites in the performance experiment. In spring 2017, we measured the same set of functional traits on all species encountered within the community composition plots. Our trait sampling followed standard protocols (Pérez-Harguindeguy et al. 2013), as detailed in Kraft et al. (2015).

Based on a principal component analysis (PCA) of the functional traits measured

for this study (Fig. S1.1), we identified specific leaf area (SLA), specific root length (SRL), and maximum height as three biologically relavent and largely uncorrelated axes of trait variation in our study. SLA, the ratio of leaf area to dry mass, is a key trait that is strongly linked to species' position along the leaf economics spectrum (Wright et al. 2004) and that is positively correlated to photosynthesis and growth rates (Adler et al. 2014). SRL, the ratio of fine root length to dry mass, reflects the area over which roots can uptake resources relative to biomass investment, is an important component of the belowground root economics spectrum (Laliberté 2016; Weemstra et al. 2020). At both a global scale (Weemstra et al. 2016) and within our study (Fig. S1.1), SRL is largely uncorrelated with SLA. Species with higher SRL tend to have superior nutrient acquisition, especially for phosphorus (Laliberté et al. 2014), but are generally more susceptible to attack by pathogenic microbes (Eissenstat 1992). Maximum height is a globally relavent trait (Díaz et al. 2016) that integrates across various dimensions of ecological strategy and can indicate the ability of adult plants to pre-empt and intercept light (Westoby et al. 2002). In the plant community at Sedgwick Reserve, maximum height is also correlated with the reproductive phenology of species, with large statured species generally growing later into the summer drought and having later flowering phenology [Kraft et al. (2015); Fig. S1.1]. The 17 focal species of our performance experiment reflected a wide range of variation observed across the plant community for these three traits (Fig. S1.2)

Environmental sampling

We quantified various soil chemical and physical characteristics to identify the primary axes of environmental variation among our study sites. We measured gravimetric water content ((weight of fresh soil - weight of dry soil)/weight of dry soil) in the early- and mid- growing season (March and April, respectively), and summarized across

these measurements to estimate the average soil moisture at each site. We collected soil for analysis by A&L Western Agricultural Laboratories (Modesto, CA) for a range of soil chemical and physical properties: soil organic matter, P (Weak Bray and Olsen methods), K (ppm), Mg (ppm), Ca (ppm), Na(ppm), pH, CEC, NO_3, SO_4, NH_4, and soil texture (sand, silt, and clay content). At each site, we collected a small volume of soil at three points arranged in between the six sub-plots, and homogenized within site prior to analysis. We also used iButtons (Maxim Integrated) programmed to log temperature at 2-hr intervals to quantify the average daily maximum temperature at each site. To avoid direct solar radiation on iButtons, we placed them in anchored PVC tubes with holes for airflow. Based on a PCA of all environmental variables (Fig. S1.3), we identified soil Ca:Mg, soil sand content, and soil depth as biologically relavent and largely uncorrelated environmental variables that captured the primary axes of abiotic variation among our study sites.

Analysis

Quantifying community-weighted trait turnover across the landscape

We used the community composition and trait data to calculate the community-weighted mean (CWM) trait values, which represent the mean trait value of all species growing at a site, weighted by the species' relative cover. We calculated the CWM for each trait (t) at each of our 16 sites (s) by averaging across the CWM of the five sub-plots p at each site as follows: $CWM_{t,s} = \frac{1}{5}\sum_{p=1}^{5}\sum_{i=1}^{n} t_i c_{i,p}$, where n is the number of species found in each subplot, t_i is the mean trait value of species i, and $c_{i,p}$ is the relative cover of species i in the sub-plot p. We then evaluated whether CWM traits vary across the environmental gradient in our study with simple bivariate linear regressions between each of the three focal traits and each of the four focal environmental characteristics. We also tested for evidence of nonlinear trait-environment

relations by including a quadratic term in the predictor (environmental) variables, but we found very little evidence for such relations (Table S1.1).

Evaluating variation in species responses to the environment

The ultimate goal of our analysis was to evaluate whether shifts in CWM traits across environmental gradients are driven by shifts in trait optima. We began by simply evaluating whether the low-density seed production of each focal species in our demography experiment varied across hummock and matrix sites. To do so, we used the glmmTMB package (Brooks et al. 2017) to fit generalized linear mixed models with a negative binomial distribution and log link function.[2] We tested whether the number of seeds produced by each species varied as a function of the site type (hummock or matrix), and included site number as a random effect to account for nonindependance of the samples. The models also included a zero-inflation term to account for the fact that many species failed to produce seeds, especially in hummock sites. The zero-inflation parameter was allowed to vary as a function of site type (hummock or matrix). Models with zero-inflation terms did not converge for two species that had high seed output throughout all sites (PLER and VUMI) and for two species that failed to make seeds at nearly every site in our study (CLBO and CLPU), so we exluded the zero-inflation terms for these species.

Quantifying the functional trait basis for variation in species responses to the environment

After evaluating whether species vary in their demographic responses to hummock vs. matrix sites, we next asked whether functional traits explain variation in species' responses to the environmental gradients in our study. To do so, we

[2]We chose a negative binomial rather than Poisson distribution because comparing the AICs of models fit with either the Poisson or Negative Binomial distribution always favored the Negative binomial models with ■AIC > 2.

built two sets of models that regressed seed production against species traits, the local site environment, and a random effect of species identity. The first set of models included only additive effects of species traits and environment (e.g. Number of seeds $\sim$ γ Species identity + β_1 Ca : Mg + β_2 SLA), while the second set of models also included an interaction between the trait and environment terms (e.g. β_3 Ca : Mg $*$ SLA). The models also included a term that allowed the zero-inflation parameter to vary as a function of the environmental variable and species identity. As in the previous analysis, these models used a negative binomial distribution with log link function. For tractability we modeled each trait-environment interaction in a separate model. We took ■AIC > 2 in favor of the model with the trait-environment interaction term as evidence that variation in functional traits helps explains variation in species' responses to the environmental gradient. We scaled the environmental variables to help with model convergence, and used log-transformed trait values for improved linearity and normality of residuals.

When model comparisons supported a trait-environment interaction, we assessed whether the direction of the interaction term matched the expectation based on shifts in CWM traits across the gradient. We then used `ggeffects` (Lüdecke 2018) to calculate the slope of the trait-performance relationship in sites with the highest and lowest value of the focal environmental gradient measured in our study (averaged over the species random effects), and asked whether the sign of the trait-performance relationship changed across the environmental gradient. We considered trait-environment interactions that were supported by the ■AIC approach, but whose slope did not change sign across the environmental gradient, as weak evidence that CWM trait shifts reflect shifts in trait optima across the landscape (Fig. 1.1C). If the

sign of the trait-performance sign shifted in the direction predicted by CWM trait shifts, we considered this as strong evidence that CWM trait shifts reflect shifts in trait optima across the landscape (Fig. 1.1D).

Results

Community-wide trait turnover at Sedgwick

The plant species in our study system vary considerably in their leaf functional traits. Across the 55 species recorded in our focal community, we observed 3 fold variation in SLA (5th percentile = 124.83cm^2/g, 95th percentile = 433.8cm^2/g), 9 fold variation in SRL (5th percentile = 32.26cm^2, 95th percentile = 290.67cm^2), and 10 fold variation in Maximum Height (5th percentile = 11.38 mg/g, 95th percentile = 108.7mg/g). Although all sites in our study had a strong serpentine character (Ca:Mg ratio was well under 1 in all plots; min = 0.118 and max = 0.327), our study captured substantial environmental variation. Our focal sites ranged in soil depth ranged from 12.8 - 45cm, and sand content ranged from 19 to 71%.

Even though all of the soils in our study had a strong serpentine character, we found considerable variation in plant functional traits among our focal sites. Hummocks were on average dominated by plant species with lower specific leaf areas (SLA) than plant communities growing in the matrix between hummocks (Fig. 1.2A). When we regressed community-weighted mean traits against continuous environmental variables, we found that CWM SLA increased significantly with soil Ca:Mg ratio and depth, but did not vary significantly with soil sand content (Fig. 1.4). CWM SRL did not vary significantly between hummock and matrix plots (Fig. 1.2B), but did vary significantly with sand content, with sandier sites being dominated by

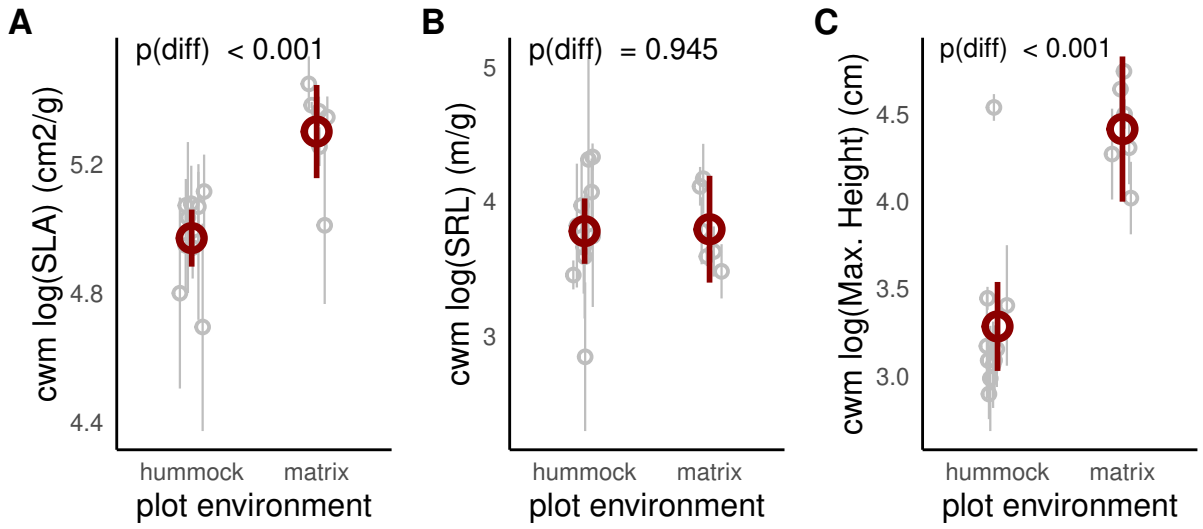

Figure 1.2: Plant communities on matrix soils tend to be characterized by higher values of community-weighted mean SLA (panel A) and maximum height (C) than plant communities on serpentine hummocks. Small grey points and errorbars indicate mean CWM at each site $\pm$ 2 standard error of the mean; large red points and error bars represent estimates and 95% confidence intervals from linear models regressing CWM by site environment.

plants with higher SRL (Fig. 1.5). Finally, CWM maximum height differed significantly between hummock and matrix sites (Fig. 1.2C) and was significantly positively associated with soil depth (Fig. 1.6).

Variation in species' low-density seed production across the landscape

The species in our demography experiment varied considerably in their low-density seed production rate across the landscape. In GLMMs that regressed the number of seeds produced against site type (hummock vs. matrix), the mean low-density per-capita seed production (w_i) of three species (AMME, CLBO, CLPU) was predicted to be less than 1 seed in either environment, indicating strong environmental filtering of these species from the focal serpentine grassland community. Two species (MEPO

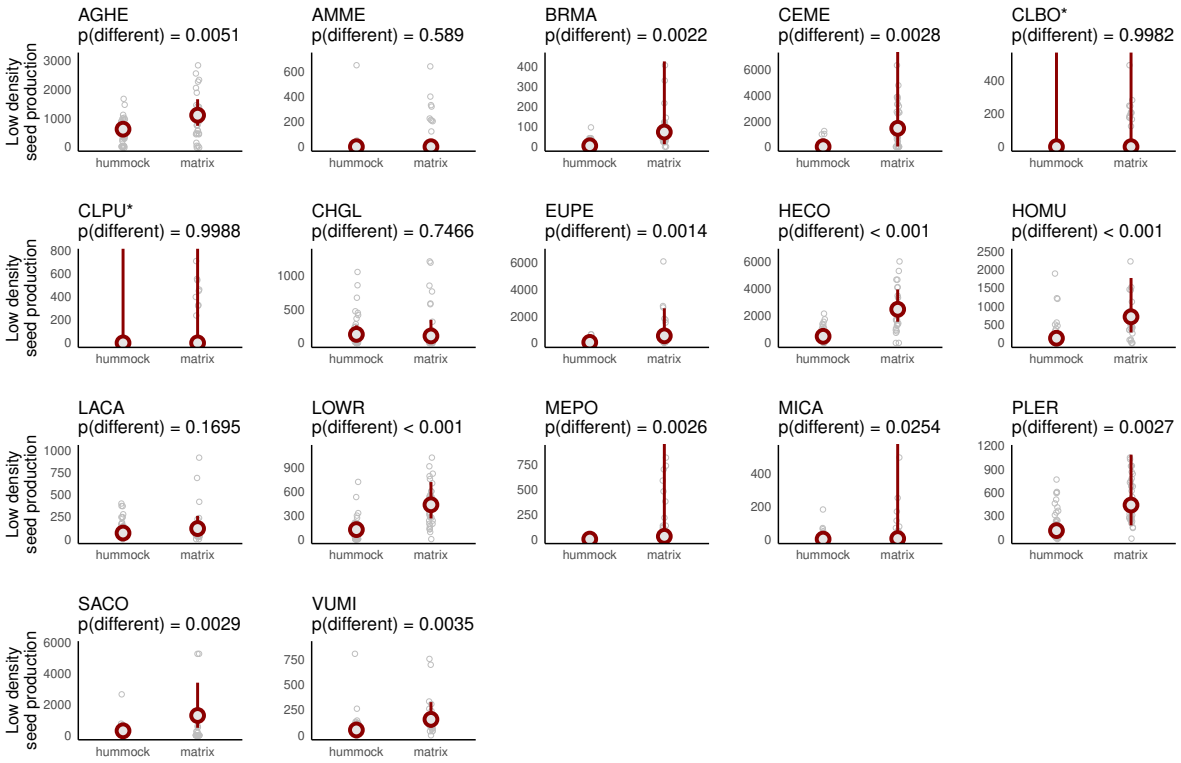

Figure 1.3: Variation in species' demographic responses to the environment. Small grey points indicate field-measured seed production; large red points and errorbars represent the predicted w_i and 95% confidence interval from GLMM regressing seed production by site environment and site number as a random effect. * *Large error bars are due to issues with model convergence in the SE parameter.*

and MICA) had predicted $w < 1$ on hummocks but had a significantly higher w in matrix sites, indicating that environmental filtering excludes these species from the hummocks but not the matrix. Apart from the three species predicted to make no seeds regardless of plot type, w_i for two additional species (CHGL and LACA) did not vary significantly between hummock and matrix sites. Most species (12/17) were predicted to have significantly lower w_i on hummocks than in matrix sites (Fig. 1.3).

Do shifts in CWM traits match changes in trait optima across environmental gradients?

Having verified that the performance of our focal species varies across the environmental gradient in which we documented shifts in CWM traits, we next asked whether variation in species' functional traits explains variation in their performance in different environments. Comparing any such trait-environment interactions to observed shifts in CWM traits across environments allowed us to address the core question of our study: do shifts in CWM traits reflect shifts in trait optima across environments (Fig. 1.1)?

Our GLMM analyses indicated that the effect of SLA on plant performance varies with soil Ca:Mg levels (■AIC = 4.2 in favor of model with trait-environment interaction, Table 1.2). Evaluating the trait-performance relations at the low- and high-ends of the Ca:Mg gradient in our study, we found that lower SLA species have higher w_i than high-SLA species in low Ca:Mg environments, but there is very little effect of SLA on w_i in high Ca:Mg sites (Fig. 1.4). Following Fig. 1.1, we interpret this as weak evidence that the observed shifts in CWM-SLA across soil Ca:Mg reflects shifts in the optimal SLA along this gradient. We also found a significant increase in CWM SLA with soil depth, but found no evidence that this pattern reflects variation in the effects of SLA on w_i across soil depth gradients (Fig. 1.4). Finally, we did not observe shifts in CWM SLA across soil sand content, and did not observe any variation in the SLA-performance relationship across this gradient.

The effect of SRL on plant performance varies with soil sand content (■AIC = 10.6 in favor of model with trait-environment interaction, Table 1.2). Higher-SRL species are predicted to have higher w_i than lower-SRL species at all points across the gradient, but the negative interaction term in this model indicates more positive SRL-performance

relationships in less sandy soils (and a less positive relationship in sandier soils) (Fig. 1.5F). This provides weak evidence that the observed significant decrease in CWM SRL in sandier sites (Fig. 1.5E) reflects variation in SRL optimum across this gradient. We found no evidence that CWM SRL shifts monotonically with soil Ca:Mg, and similarly did not find that the SRL-performance relationship varies along these gradients. We found that CWM SRL varies non-linearly with Ca:Mg, with CWM SRL maximized at intermediate values of Ca:Mg (Table S1.1), but were not able to test for non-linear shifts in trait-performance relations in our demography dataset.

Finally, we found that that the effect of Maximum Height on plant performance varies with soil depth (■AIC = 5.4 in favor of model with trait-environment interaction, Table 1.2). Taller species outperform shorter species at all points across the soil depth gradient in our study, though the relationship is stronger in deeper than shallower soils (Fig. 1.6D). This provides weak evidence that the observed increase in CWM maximum height with soil depth reflects variation in trait optima across the gradient (Fig. 1.6C). We did not observe shifts in CWM maximum height across soil Ca:Mg or sand content, and did not observe any variation in the maximum height-performance relationship across this gradient.

Discussion

Variation in the physiological characteristics of plant communities across environmental gradients is a ubiquitous pattern in nature. However, whether such community-wide shifts in functional traits reflect shifts in trait-performance relations across environmental gradients remains poorly understood (Muscarella and Uriarte 2016; Shipley et al. 2016). As a result, predicting plant species' demographic responses to environmental variation on the basis of their functional traits remains challenging (Laughlin

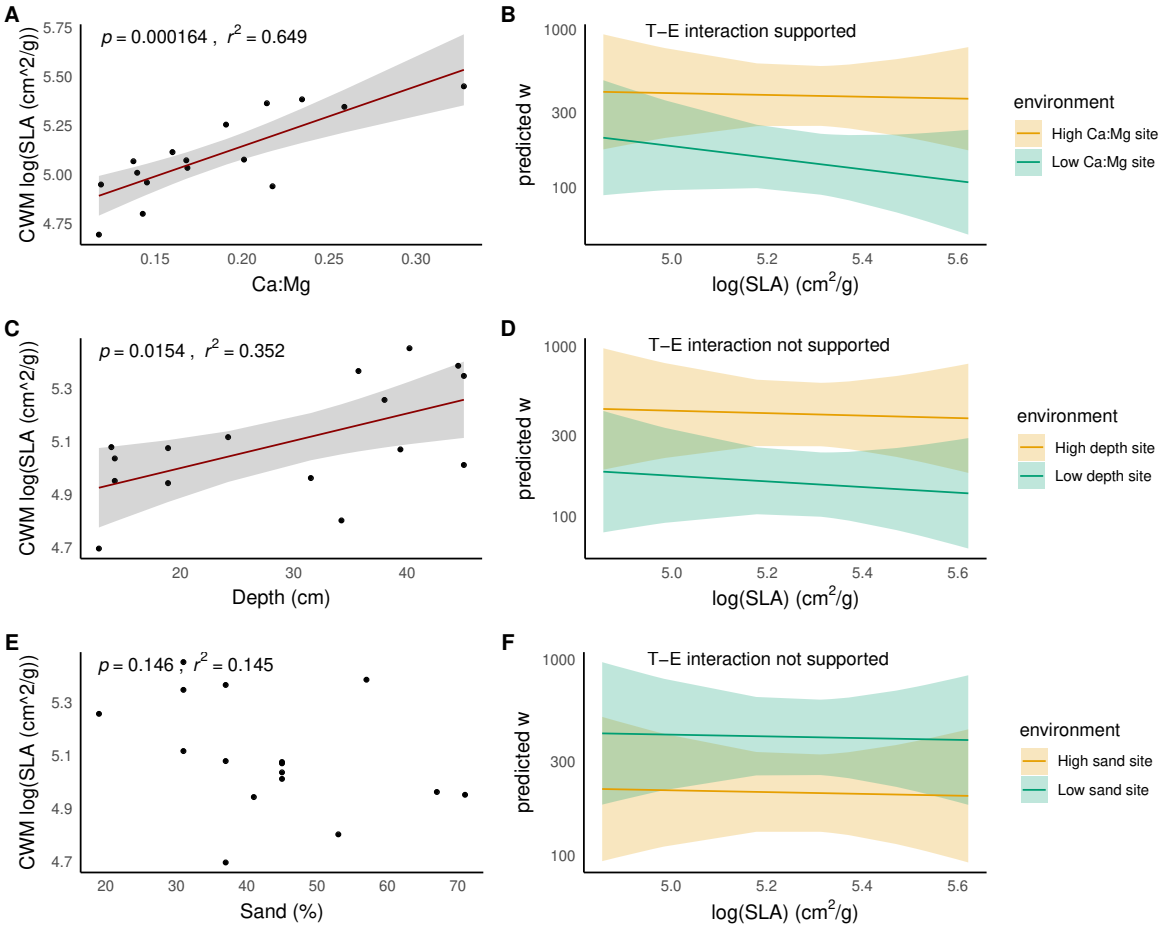

Figure 1.4: CWM turnover in SLA across environmental gradients often reflects variation in trait optima across environments (but not for soil depth)

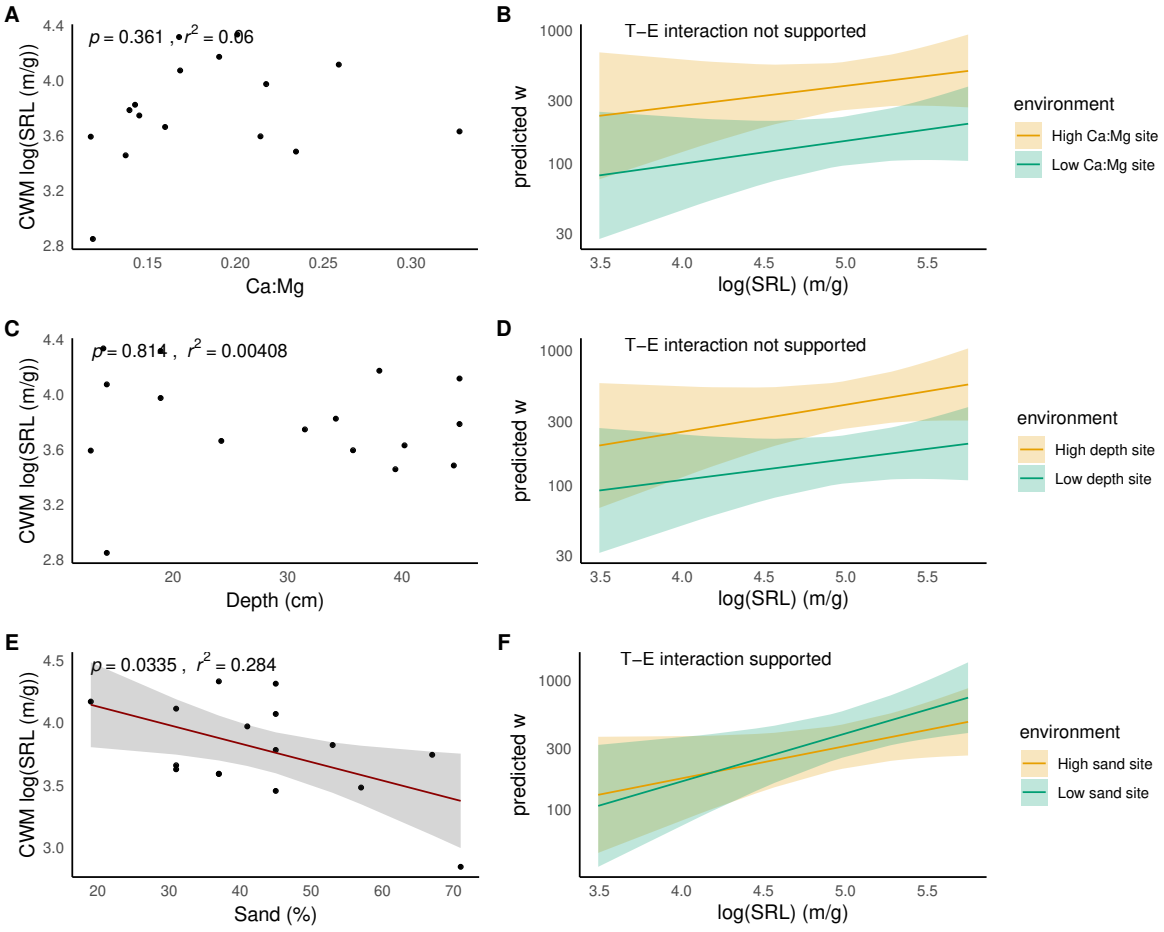

Figure 1.5: CWM turnover in SRL across environmental gradients often reflects variation in trait optima across environments (but not for Ca [ppm])

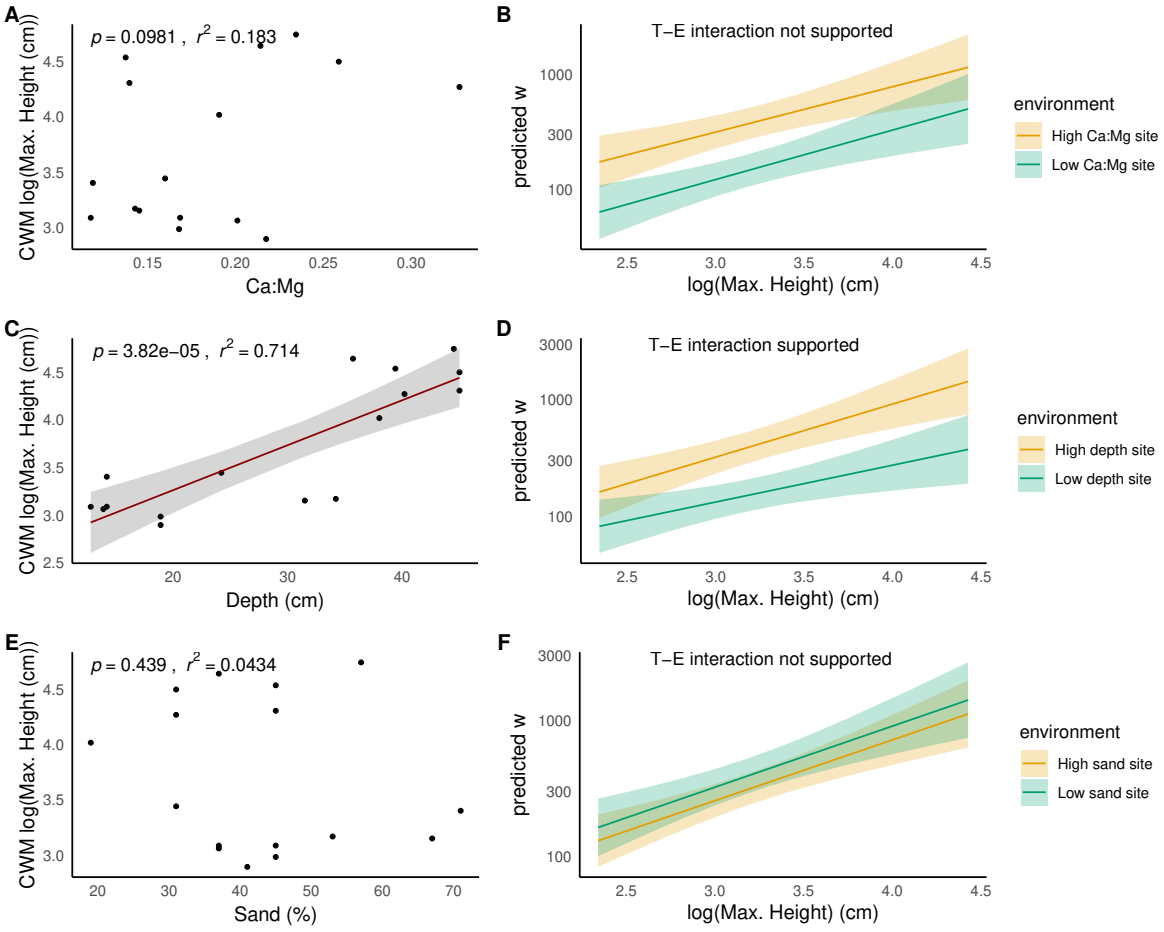

Figure 1.6: CWM turnover in leaf size across environmental gradients often reflects variation in trait optima across environments (but not for Ca [ppm] or soil depth)

Table 1.2: Concordance between CWM trait-environment relations in the observational vs. experimental study. ■AIC > 2 in favor of the model including a trait:environment interaction term was taken as evidence that the trait-performace relationships changes over the landscape.

Trait	Environment	CWM turnover?	■AIC between models		Evidence that CWM turnover is adaptive[1]
			No trait-environment interaction	With trait-environment interaction	
SLA	Ca:Mg	**Yes**	4.199	**0**	Weak
	Depth	**Yes**	**0**	1.429	None
	Sand	No	**0**	2.119	-
SRL	Ca:Mg	No	**0**	1.935	-
	Depth	No	**0**	1.087	-
	Sand	**Yes**	10.612	**0**	Weak
Max. Height	Ca:Mg	No	**0**	1.594	-
	Depth	**Yes**	5.447	**0**	Weak
	Sand	No	**0**	2.114	-

[1] Strength of supporting evidence evaluated as described in Fig. 1

et al. 2018). Quantifying trait-performance relations across environmental gradients at the community level is a key step in improving our ability to project how plant communities will respond to environmental change. A clearer understanding of how trait-performance relations across gradients shape community-weighted mean (CWM) trait shifts is a key step in advancing our ability to make informed predictions of species- and community-level responses to environmental variation. Here, we asked whether patterns of turnover in three key plant functional traits reflect variation in the relationship between these traits and plant species' intrinsic demographic responses to environmental variation in a southern California serpentine grassland community. We found that the effects of species traits on their performance depends on the environmental gradients in a direction that is generally consistent with observed CWM shifts in these traits (Figs. 1.4-1.6). However, shifts in trait-performance relations were generally weak (Fig. 1.1B) and CWM trait shifts likely reflect the combined effects of pro-

cesses other than the trait-performance relations quantified in our study. Quantifying how traits mediate species' demographic responses across their life remains a key step in improving our ability to use functional traits to predict plant community responses to environmental variation.

Variation in species demography across the landscape

A necessary condition for variation in CWM to be driven by shifting trait optima across the gradient is that species' vital rates respond differently to the underlying abiotic environment. This condition was met in our system. Most species (12/17) in our experiment had significantly higher low-density seed production (w_i) in matrix sites than on hummocks. This finding is consistent with the expectation that the lower Ca:Mg ratio of soils in serpentine hummocks, in conjunction with lower levels of macronutrients in these soils (Fig. S1.3), present a severe abiotic stress for many plant species (Kruckeberg 1951; Huenneke et al. 1990). However, although most species had higher w_i in matrix than hummock sites, not all species were equally sensitive to the harsher conditions of the hummocks (ratio of predicted w_i in matrix vs. hummock sites ranged from 1.8-630 among these 12 species, Fig 1.3).

Although most species in our experiment were predicted to have substantially higher w in matrix sites than on hummucks, in our surveys of the naturally occurring plant community on this landscape, we found individuals of these 12 species much more frequently on hummocks than in matrix sites. This is likely due to competition at the seedling stage between the species in our experiment and the invasive European grasses that dominate the matrix habitat (primarily *Avena* and *Bromus* sp.), which prevents establishment of the focal species in the matrix sites (DiVittorio et al. 2007). The mismatch between the environments that maximize species' intrinsic performance and the ones in which they are most common supports the idea that variation in abundance

is a poor proxy for species' fitness in different environments (Fox 2012; Muscarella and Uriarte 2016).

Functional drivers of variation in species performance

The finding that plant species differ in their demographic responses to the landscape leads to the question of whether species functional traits help explain this variation. At the community level, we found strong correlations between each of the focal traits and at least one environmental gradient in our study. The positive correlations between CWM SLA and soil Ca:Mg and soil depth are generally consistent with the expectation that high-SLA species tend to have a suite of leaf traits that helps them dominate less harsh abiotic conditions (Reich 2014). We found a negative correlation between CWM SRL and soil sand content, which is consitent with results from some systems (e.g. Hogan et al. 2019) but not others (e.g. Laughlin et al. 2018). We also found evidence for a non-linear relationship between CWM SRL and soil Ca:Mg, such that CWM SRL is maximized at intermediate levels of Ca:Mg, contrary to the general expectation that SRL patterns are generaly coordinated with patterns in SLA (Reich 2014). In general, how SRL and other root traits are coordinated with aboveground traits, and how they influence plant growth over soil chemical and physical gradients remains an open question (Kramer-Walter et al. 2016; Weemstra et al. 2020). Finally, we found a positive correlation between CWM Max. height and soil depth, consistent with the hypothesis that the higher water retention of deeper soils may sustain the growth of larger statured species, which can in turn exclude shorter-statured species by pre-emtping light and other nutrients (Freckleton and Watkinson 2001; Kraft et al. 2015).

Most importantly for the central question of our study (Fig. 1.1), pairing our observational study of the plant community at Sedgwick reserve with an experiment to quantify trait-performance relations across this landscape allowed us to evaluate

whether community-wide patterns accurately reflect shifts in trait optima across the landscape. The observed increase in CWM SLA with soil Ca:Mg (Fig. 1.4A) appears to be at least in part driven by the less negative SLA- w_i relationship in high-Ca:Mg than low Ca:Mg sites (Fig. 1.4B). Lower CWM-SRL in sandier soils (Fig. 1.5E) is consistent with the result that the demographic advantage to high-SRL species diminishes in sandier soils (Fig. 1.5F). Finally, higher CWM maximum height in deeper soils (Fig. 1.6C) is consistent with the more positive maximum height- w_i relationship in deeper vs. shallower soil (Fig. 1.6D). However, we did not find any evidence that increase in CWM SLA with soil depth (Fig. 1.4C) reflects shifts in the SLA- w_i relationship, showing that CWM shifts are not always evidence for shifting trait optima across the landscape. On the other hand, there was no instance in which a trait-environment interactions was detected in our experimental data but not in the natural plant community, indicating that strong trait-environment relations are likely to manifest in CWM trait turnover across the gradient. Taken together, we interpret our findings as providing consistent but weak and imperfect evidence that the observed shifts in CWM traits reflect variation in the trait-performance relationships in this landscape.

It is important to note that we did not find that the sign of any trait-w_i relationship changes across the extent of the gradient in our study. As a result, the shifts in trait-w_i relations identified in our analysis would not, by themselves, lead to the observed shifts in CWM traits across the gradient. However, if traits affect other vital rates in the same direction as they do w_i, (e.g. if high-SLA species have lower w_i in low-Ca:Mg sites, as we found, and are also suppressed more by competitors in such conditions), then the interactive effects of traits on multiple processes may build on the trait-w_i relationship we found here to influence CWM traits. This result is qualitatively similar to those of Laughlin et al. (2018)'s analysis of whether shifts in CWM traits reflect shifts in trait-

survival relations in a pine forest community. We echo their call for future studies that quantify how functional traits influence all the vital rates that determine population-level performance across environmental gradients.

Future directions for improving predictions of plant performance across gradients

Predicting the performance of organisms in different environmental contexts is a long-standing challenge, and plant ecologists' ability to do so will determine the efficacy of future efforts to conserve and restore natural communities in a dynamic environment. Our results support the value of cautiously applying trait-environment relations in developing such predictions, but also suggest several avenues for future research. First, we were unable to account for the possibility that intra-specific variation driven by local adaptation, phenotypic plasticity, or material effects – processes known to be important in serpentine systems (Rajakaruna and Bohm 1999; Baythavong 2011; Germain and Gilbert 2014) and elsewhere – mediate plant functional and demographic responses to environmental variation. However, our findings that trait-performance relationships change over environmental gradients generate predictions for how such intraspecific trait variation (ITV) might be structured. For example, our results (Fig. 1.4B) predict that plants growing in high-Ca:Mg sites should have higher SLA than plants of the same species growing in lower Ca:Mg soils. Understanding how the spatial structure of ITV differs between species may be critical for predicting variation between species in their demographic responses to environmental gradients.

Another important aspect of our study was that we were able to quantify CWM traits across gradients, and also conduct a separate experiment that allowed us to quantify a key vital rate (seed production in the absence of competitors, w_i) for 17 species that occur in this community. This dual approach allowed us to evaluate whether CWM trait shifts reflect shifting trait-performance relationships in this system, but ex-

perimentally quantifying vital rates across environmental gradients is a difficult task in most systems. A promising approach to build on our results and better understand the trait-performance relationships in longer-lived, more diverse, or less accessible ecosystems may be to rely on statistical methods that use time series data to disentangle the direct effects of environmental variation from the indirect effects of species interactions (e.g. Seyednasrollah and Clark 2020). Coupling long-term monitoring data, which are becoming increasingly abundant for various ecosystems (e.g. Anderson-Teixeira et al. 2014), with such statistical methods, may allow for more robust understanding of how plant traits mediate species responses to the environment at various scales.

Conclusion

Understanding and forecasting how species and communities respond to environmental variation is a fundamental challenge in ecology. Predicting variation in species-level demographic processes based on patterns in trait turnover across whole communities is a promising approach, but most methods to do so have relied on the assumption that variation in community-weighted mean (CWM) traits reflect shifts in trait optima over landscapes. Our study found consistent but weak evidence that variation in CWM traits across environmental gradients reflect the effects of changing trait-performance relationships, but they also caution against inferring likely demographic responses of plants to environments on the basis of CWM traits alone. Future efforts that link plant traits to variation in population growth rates will help build towards more predictive trait-based models of plant community dynamics.

Acknowledgements

We acknowledge the Tongva/Gabriellino and Chumash peoples as the traditional land caretakers of the ecosystem studied in this project. We thank Mirjam von Rutte, Renato Guidon, Mary Van Dyke, Xinyi Yan, Anmol Dhaliwal, Clare Camilleri, and Aoefe Galvin for help in the field and lab, and Kate McCurdy and other staff at Sedgwick Reserve for help in the field. We thank Kenji Hayashi, Mary Van Dyke, and Marcel Vaz for comments on the analysis and manuscript. This work was funded by the National Science Foundation DEB-1644641.

Chapter 1 Supplementary Materials

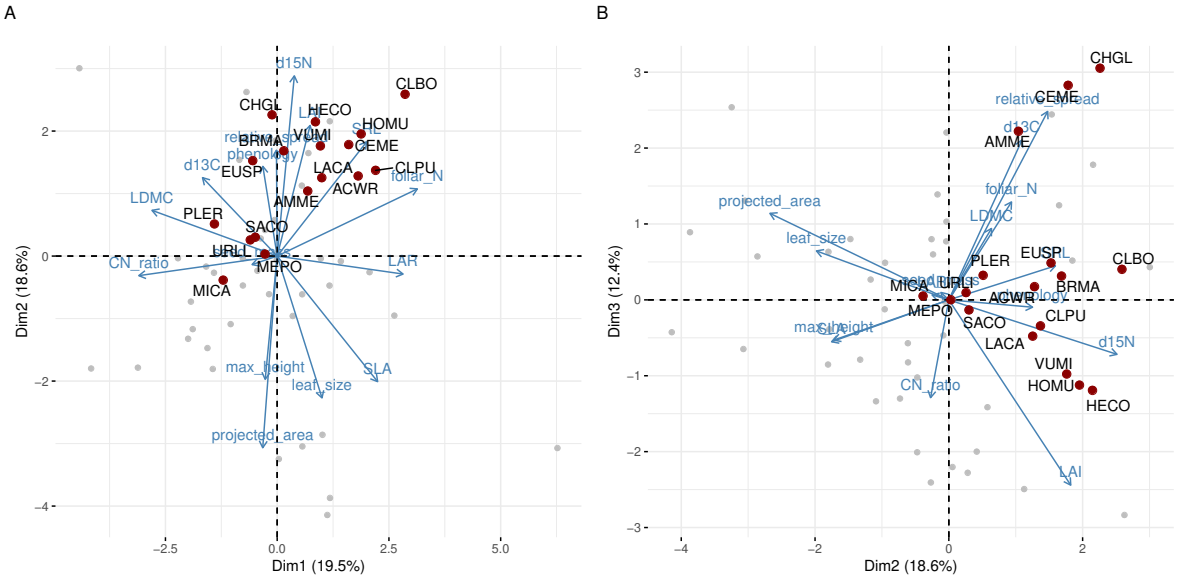

Figure S1.1: Biplots of axes 1/2 (Panel A) and axes 2/3 (Panel B) from a PCA of the functional traits measured for this study. Light grey points indicate the position of the species found across the community (N = 55), and red points indicate the position of each of the focal species of the demography experiment (N = 17)

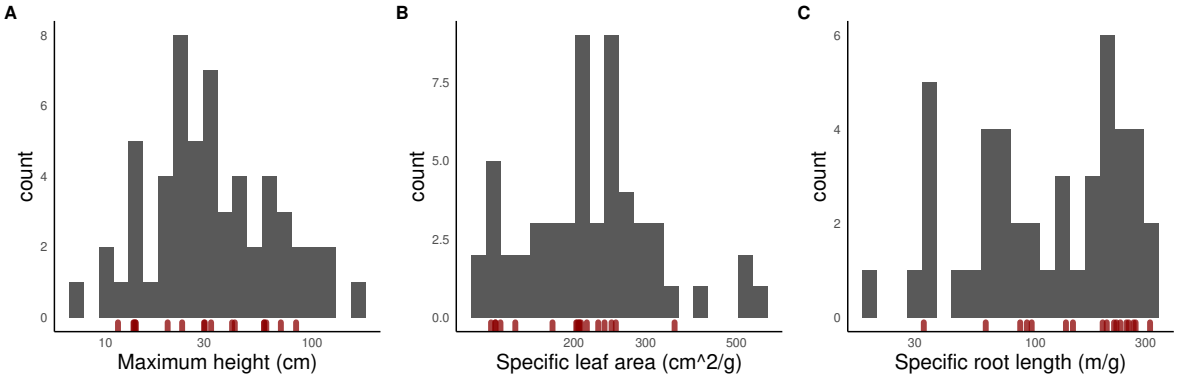

Figure S1.2: Histograms of the three focal functional traits for all species encountered in the Serpentine grassland at Sedgwick Reserve. Each red line at the bottom of the histograms indicates the trait value for one of the focal species in the demography experiment. Note the log-transformed X-axis in each panel.

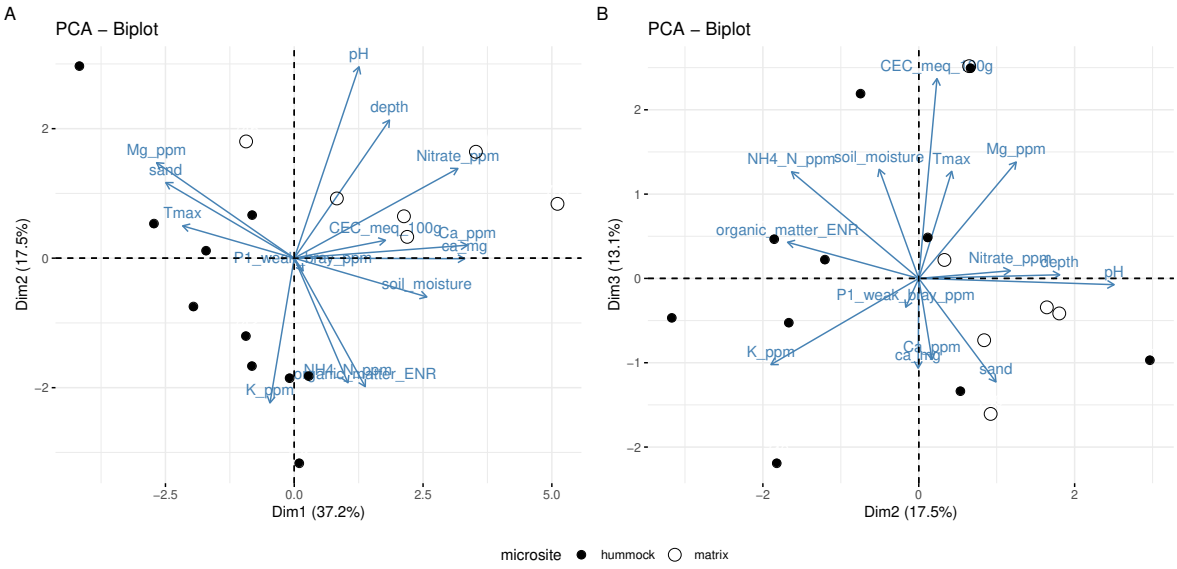

Figure S1.3: Biplots of axes 1/2 (Panel A) and axes 2/3 (Panel B) from a PCA of the environmental gradients measured for this study.

Table S1.1: We tested for quadratic relationships between CWM traits and environment and only found support for a non-linear relationship between CWM SRL and soil Ca:Mg ratio

trait	environment	term	estimate	std.error	statistic	p.value
SLA	Ca:Mg	Intercept	4.1710630	0.3810	10.9473	0.0000
SLA		Linear	6.7997132	3.7945	1.7920	0.0964
SLA		Quadratic	-8.8295749	8.8486	-0.9978	0.3366
SLA	Depth	Intercept	4.8685302	0.3669	13.2676	0.0000
SLA		Linear	0.0039068	0.0296	0.1322	0.8968
SLA		Quadratic	0.0001119	0.0005	0.2187	0.8302
SLA	Sand	Intercept	5.6767840	0.5039	11.2652	0.0000
SLA		Linear	-0.0211202	0.0225	-0.9375	0.3656
SLA		Quadratic	0.0001628	0.0002	0.6820	0.5072
SRL	Ca:Mg	Intercept	1.3091538	0.9470	1.3824	0.1901
SRL		Linear	24.1034774	9.4310	2.5558	0.0239
SRL		Quadratic	-53.0592298	21.9926	-2.4126	0.0313
SRL	Depth	Intercept	3.7116730	0.8014	4.6316	0.0005
SRL		Linear	0.0093611	0.0645	0.1450	0.8869
SRL		Quadratic	-0.0001975	0.0011	-0.1768	0.8624
SRL	Sand	Intercept	3.6723606	0.7948	4.6207	0.0005
SRL		Linear	0.0207823	0.0355	0.5849	0.5686
SRL		Quadratic	-0.0003831	0.0004	-1.0175	0.3275
Max. Height	Ca:Mg	Intercept	2.9756663	1.9356	1.5373	0.1482
Max. Height		Linear	2.8657993	19.2769	0.1487	0.8841
Max. Height		Quadratic	5.5585773	44.9527	0.1237	0.9035
Max. Height	Depth	Intercept	3.4516879	0.7104	4.8586	0.0003
Max. Height		Linear	-0.0486766	0.0572	-0.8508	0.4103
Max. Height		Quadratic	0.0016727	0.0010	1.6891	0.1150
Max. Height	Sand	Intercept	4.4618081	1.7386	2.5663	0.0235
Max. Height		Linear	-0.0246015	0.0777	-0.3165	0.7566
Max. Height		Quadratic	0.0001513	0.0008	0.1837	0.8571

Appendix 1.1: Converting field measurements of reproductive output to estimates of seed count per individual

For this study we quantified the seed output of 1632 plants in the field. When possible we directly counted the number of seeds on each focal individual when plants were at their maximum reproductive output, but for time constraits had to measure proxies of reproductive output (e.g. diamater of flower head) for several species. In this Appendix we describe how we converted these proxy measurements of reproductive output into estimates of seed counts for each of the species in our experiment.

For AMME, BRMA, CEME, EUPE, HECO, HOMU, MICA, PLER, and VUMI we could simply count the number of seeds on each focal plant in the field. For AGHE, LOWR, and MEPO, we counted the number of seed heads or fruits per individual in the field. We separately counted the number of seeds in 40 mature seed heads or fruits, and multiplied the fruit or seed head count by the mean count of seeds per fruit to estimate the number of seeds made by each plant in the field (Fig S1.4). For CHGL, LACA, SACO, we measured the diamater of each flower head in the field. We separately built a regression between the area of seed heads (calculated assuming the seed head was circular) and number of seeds (Fig S1.5), and used the regression equation to estimate the number of seeds produced by each species in the field. For CLBO and CLPU, we measured the length of each fruit in the field, and again used a regression equation between fruit length and number of seeds per fruit to calculate the seed production of focal individuals (Fig S1.5). We rounded each calculated seed count down to the nearest integer. When a focal individual was too large to count every seed, fruit or flower head, we counted the reproductive units on a quarter or half of the plant, and multiplied as appropriate for a whole-plant estimate.

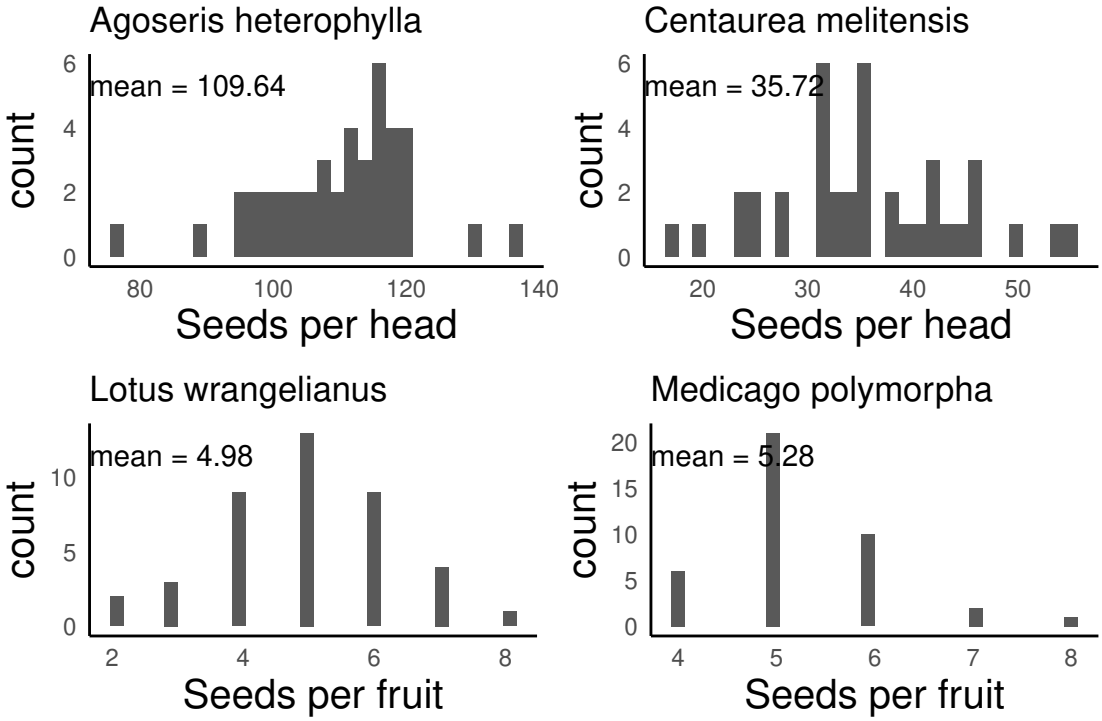

Figure S1.4: Histogram of the number of seeds per flower head (or fruit) for Agoseris heterophylla, Centaurea melitensis, Lotus wrangelianus, and Medicago polymorpha

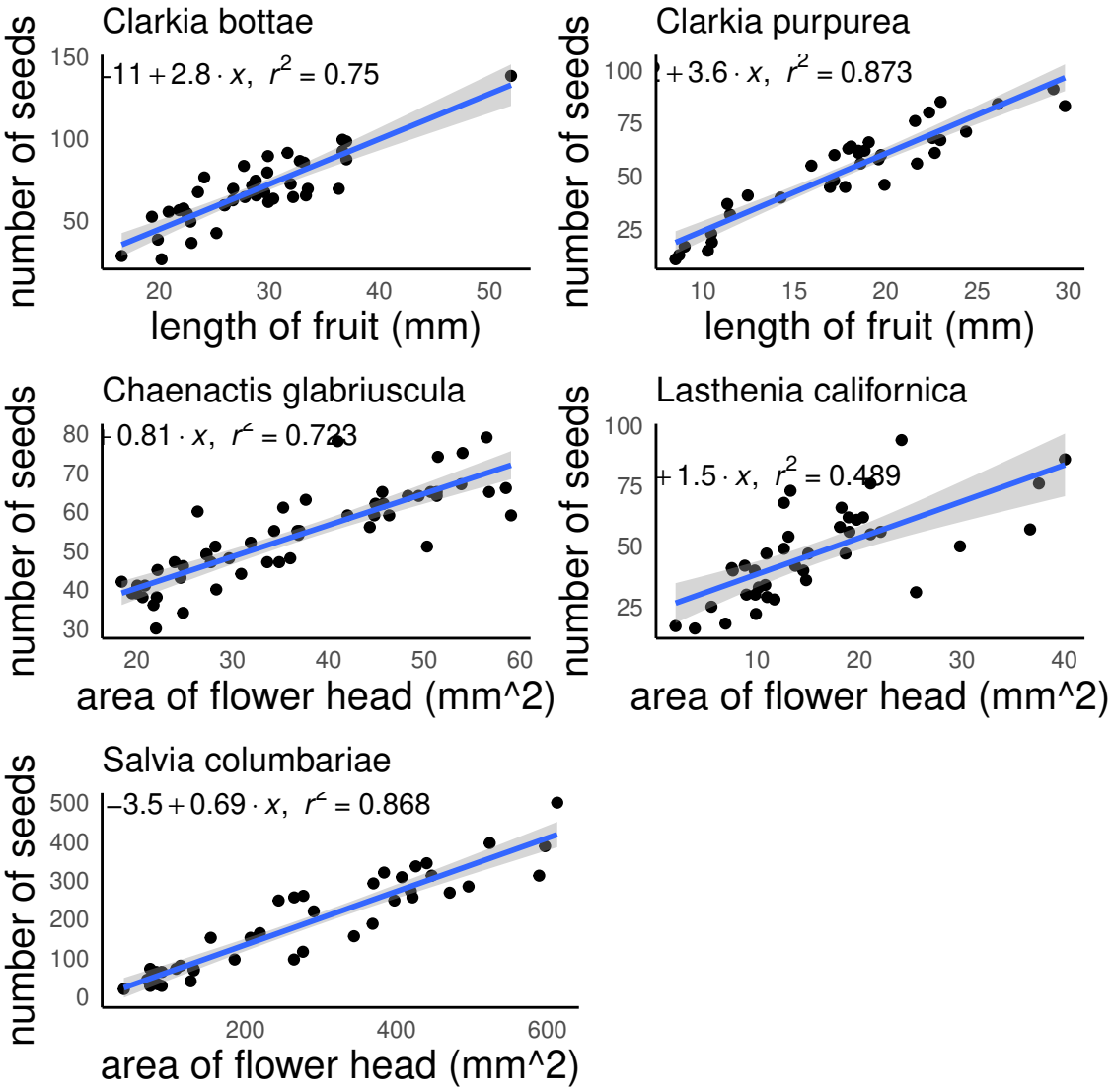

Figure S1.5: Regressions of seed count as a function of flower head or fruit size for Clarkia bottae, Clarkia purpurea, Chaenatcis glabriuscula, Lasthenia californica, and Salvia columbariae

Chapter 2

Winning and losing with microbes: how microbially mediated fitness differences influence plant diversity

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GSK conceived the problem with NJBK and JML. GSK led the research with JML and all authors provided input. GSK wrote the manuscript with JML and all authors contributed revisions.

Abstract

Interactions between plants and soil microbes can strongly influence plant diversity and community dynamics. Soil microbes may promote plant diversity by driving negative frequency-dependent plant population dynamics, or may favor species exclusion by providing one species an average fitness advantage over others. However, past empirical research has focused overwhelmingly on the consequences of frequency-dependent feedbacks for plant species coexistence and has generally neglected the consequences of microbially mediated average fitness differences. Here we use theory to develop metrics that quantify microbially mediated plant fitness differences, and show that accounting for these effects can profoundly change our understanding of how microbes influence plant diversity. We show that soil microbes can generate fitness differences that favor plant species exclusion when they disproportionately harm (or favor) one plant species over another, but these fitness differences may also favor coexistence if they trade off with competition for other resources or generate intransitive dominance hierarchies among plants. We also show how the metrics we present can quantify microbially mediated fitness differences in empirical studies, and explore how microbial control over coexistence varies along productivity gradients. In all, our analysis provides a more complete theoretical foundation for understanding how plant-microbe interactions influence plant diversity.

Introduction

Interactions between plants and soil microbes are widespread and consequential for plant performance (Selosse et al. 2015; Peay 2016). Over the past two decades, ecologists have begun to quantify the complex ways in which these interactions can influence plant competition and community dynamics (van der Putten et al. 1993; van der Heijden et al. 2008; Bever et al. 2012). The soil microbial community has been implicated in regulating a number of ecological processes. Negative frequency dependent growth in plant populations driven by the soil microbial community can help maintain plant diversity in various communities including old fields (Pendergast et al. 2013), Mediterranean shrublands (Teste et al. 2017), and tropical forests (Mangan et al. 2010). Spatial variation in the soil microbial community can lead to variation in plant productivity (van der Heijden et al. 2008) and can influence the outcome of plant restoration (Wubs et al. 2016). Interactions between plants and soil microbes have also been shown to influence plant succession and species invasions (Inderjit and van der Putten 2010). Nevertheless, predicting the influence of soil microbes on the diversity and dynamics of natural plant communities remains a challenge.

Empirical research has highlighted two general avenues by which soil microbes can modify plant community dynamics. First, differential responses of plant species to soil microbes can contribute to negative frequency dependent plant population dynamics that can promote diversity (Mangan et al. 2010; Bever et al. 2015). Many studies find that plants grow less vigorously in soil harboring a microbial community cultivated by conspecific individuals than in soil harboring a microbial community cultivated by heterospecific individuals (reviewed in Kulmatiski et al. 2008). Moreover, plant species that experience more negative microbial effects in greenhouse experiments tend to be less abundant in natural communities (Klironomos 2002; Mangan et

al. 2010; Kempel et al. 2018, but see Maron *et al.* 2016), suggesting a link between the strength of these interactions and plant abundance. Our ability to project the influence of plant-microbe interactions in stabilizing coexistence has been both facilitated and motivated by a theoretical framework developed in Bever et al. (1997) and Bever (2003) (Box 1) which summarizes the effect of microbial feedbacks in a metric termed I_S. In the context of modern coexistence theory (Chesson 2000), plant-microbe interactions that generate frequency-dependent feedback loops have a "*stabilizing*" (negative feedbacks) or "*destabilizing*" (positive feedbacks) effect on the plant community.

The second avenue through which the soil microbial community can influence plant community dynamics is by driving the replacement of plant species, especially during succession or invasion. In a seminal study, for example, van der Putten et al. (1993) found that succession in foredune communities might be driven by the low susceptibility of late-succession plant species to the pathogenic microbes that accumulate in soils colonized by early-succession plants. Plant-microbe interactions can similarly exacerbate plant invasions when invasive species are less susceptible than native plant species to soil-borne pathogens in the exotic range (Reinhart et al. 2003; Callaway et al. 2004; Inderjit and van der Putten 2010). While in all of these examples, the plant-microbe interactions will inevitably cause some frequency dependent dynamics, if one averages over the range of plant species frequencies in these systems, one species (often the late-succession or invasive species) is on average less sensitive to the harmful effects of cultivated soil biota than the other. Following Chesson (2000), we term such average differences among plants in their susceptibility to soil-borne pathogens or in the benefits they accrue from belowground mutualists as "*microbially mediated fitness differences*". Importantly, in Chesson's framework, these fitness differences are an abstraction, analogous to competitive ability, that reflect species performances across the

full range of conditions they can experience; they are not per-capita growth rate differences as might be expected from conventional uses of the term "fitness" (Chesson 2018).

The net effect of soil microbes on plant diversity depends both on the extent to which they stabilize or destabilize plant interactions due to frequency-dependent feedbacks, and on the extent to which they give one species an average fitness advantage. In the extreme, microbial interactions that have stabilizing effects on plant coexistence can nonetheless drive species exclusion if they also generate plant fitness differences to an extent that exceeds their stabilizing influence. A similar result was shown by Bever et al. (1997), who found that plant species pairs whose interactions are stabilized by microbes (negative I_S) could fail to coexist if the microbial communities overwhelmingly favor one plant species (Box 1). Still, the original analysis in Bever et al. (1997) and subsequent theoretical analyses and extensions of the model (Bever 2003; Kulmatiski et al. 2011; Revilla et al. 2013; Eppinga et al. 2018) focus primarily on the frequency-dependent stabilizing or destabilizing effects of microbes, with less attention paid to microbially mediated fitness differences.

Box 1

Bever's model of pairwise plant-soil feedback

Here we summarize the pioneering plant-soil feedback framework developed Here we summarize the pioneering plant-soil feedback framework developed in Bever et al. (1997) and Bever (2003), and briefly summarize its use in empirical research. The Bever framework considers the effects of microbes in a system in which each of two plant species 1 and 2 cultivates a particular microbial community denoted A and B respectively. The aggregate soil microbial community

depends on the relative abundance and influence of each plant species. These interactions can generate a frequency-dependent plant-soil feedback via a two-step process. First, as a plant population grows in proportion, the microbial community becomes more similar to that plant's characteristic community. Second, the altered soil community influences the performance of both plant species at a rate m. The effects of each microbial community on the plant species that cultivates it (i.e. the effect of microbe community A on plant 1 and of microbe community B on plant 2, denoted m_{1A} and m_{2B} respectively) are termed "direct feedbacks". The effects of each microbial community on the other plant (i.e. the effect of microbe A on plant 2 (m_{2A}) and of microbe B on plant 1 (m_{1B})) are termed "indirect feedbacks" (Fig. 1). Bever et al. (1997) showed that microbes can stabilize plant dynamics when they exert more negative (or less positive) direct feedbacks than indirect feedbacks, resulting in a negative value for the metric they termed I_S. Bever (2003) extended the framework to show that microbial feedbacks could dictate the outcome of community dynamics even when there is simultaneous plant competition.

Bever et al. (1997) show that the degree to which the system is stabilized (negative frequency dependent dynamics between the plant species) or destabilized (positive frequency dependence) is given by the following:

$$I_S = m_{1A} - m_{2A} - m_{1B} + m_{2B}$$

This term measures the degree to which the microbial community cultivated by each plant harms the competitor more than the cultivating plant (or favors the cultivating plant over its competitors). Negative I_S causes negative frequency de-

pendent dynamics (tendency towards coexistence), while positive I_S means positive frequency dependent dynamics (tendency towards priority effects). Bever et al. (1997) also showed that in addition to a negative I_S, stable coexistence requires that the microbes cultivated by each plant species influence the cultivating species more negatively (or less positively) than the other plant species ($m_{1A} < m_{2A}$ and $m_{2B} < m_{1B}$). Revilla et al. (2013) later developed a metric termed J_S, which generalizes I_S to describe the sign of microbial feedbacks when the plant species are unequal competitors.

Part of the reason behind the lasting influence of the plant-soil feedback theory is that Bever (1994) and Bever et al. (1997) outlined a two-phase experimental approach to estimate the microbial effects relevant to I_S that remains a gold-standard (Pernilla Brinkman et al. 2010; Bever et al. 2012). In the first phase of these experiments, plants of each focal species are grown in sterilized soil containing a field-collected inoculum. In the second phase, plants from all focal species are grown in sterilized soil that is inoculated with a microbial community cultivated either by conspecifics or by one of the other focal species. The biomass of plants grown on previously cultivated soils is generally used to estimate the four m terms to calculate I_S for each species pair (e.g. Fitzsimons and Miller 2010; Smith and Reynolds 2015; Bauer et al. 2017).

Although I_S incorporates the effects of both microbial communities on both plant species, relatively few empirical studies motivated by Bever's framework quantify all four components of the pairwise stabilization term directly (Smith-Ramesh and Reynolds 2017). Considerably more plant-soil feedback studies evaluate individual (rather than pairwise) negative feedbacks by measuring the growth of one or a few focal plant species in soil harboring a

conspecific-cultivated microbial community and in soil harboring a microbial community cultivated by other plant species. For example, negative values of a log-response ratio ($\ln(\frac{\text{biomass}_{\text{conspecific microbes}}}{\text{biomass}_{\text{heterospecific microbes}}})$) indicate lower plant growth in soils with conspecific-cultivated microbial communities than in soils with heterospecific-cultivated microbial communities (corresponding to $m_{1A} - m_{1B} < 0$ in Bever's framework), resulting in negative individual feedback for the focal species (Reinhart 2012; Baxendale et al. 2014; Pfennigwerth et al. 2017; Teste et al. 2017). Although it is true that all else being equal, a more negative individual feedback suggests a diversity-maintaining role for microbes, it should be clear that assessing the net stabilizing effects of plant-microbe interactions on plant diversity requires simultaneously assessing their effects across both plant species. Moreover, as we show in the main text, focusing only on the stabilizing effects of plant microbe interactions and not comparing these stabilizing effects to microbially mediated plant fitness differences can lead to false conclusions regarding the influence of soil microbes on plant diversity.

Empirical studies have also tended to emphasize the positive or negative frequency-dependency arising from plant-microbe interactions and have typically ignored the effects of microbially mediated fitness differences (reviewed in Ke and Miki 2015; but see Chung and Rudgers 2016; Siefert et al. 2019). It is therefore difficult to draw inferences regarding the total or net effects of soil microbes on plant species diversity from many empirical plant-soil feedback studies. Part of the problem relates to our lack of a theoretically justified metric for the microbially mediated fitness differences, analogous to the metric I_S for quantifying frequency-dependent effects. Only with such a metric can we more accurately infer the effects of microbial interactions on plant species diversity by analyzing the interplay between their (de)stabilizing

effects and the fitness differences they generate. Here, we use theory to explore how plant-microbe interactions can generate fitness differences between competitors, and derive a metric essential for quantifying the effect of such interactions on plant diversity. To do so, we first define the microbially mediated fitness differences in Bever's classic plant-soil feedback model, a difference that favors one plant over the other and thereby counterbalances the stabilizing or destabilizing effects of soil microbes. We then explore the biological processes that can contribute to these fitness differences by expanding the classic plant-soil feedback model to include a greater range of soil microbial dynamics. Through a series of scenarios, we illustrate how not accounting for microbially mediated fitness differences can lead to erroneous conclusions about how microbes influence plant diversity. Lastly, we show how our model relates to a much larger body of work in coexistence theory that allows us to predict, for example, how the importance of plant-microbe interactions changes along productivity gradients. In the discussion we explain how the fitness differences identified here can be quantified in empirical studies and propose avenues of research to give a more complete picture of how soil microbes shape plant diversity.

Microbes drive a fitness difference between plants in the classic plant-soil feedback model

We begin by analyzing the model of plant-soil feedbacks among competing plants from Bever (2003) to develop a metric that quantifies microbially mediated fitness differences. The following analysis also applies to the original competition-implicit model in Bever et al. (1997) (Appendix S1). Bever (2003) models two plant species N_1 and N_2 that interact via Lotka-Volterra competition and via their effects on soil microbial communities A and B. With some minor notational changes from Bever (2003), the

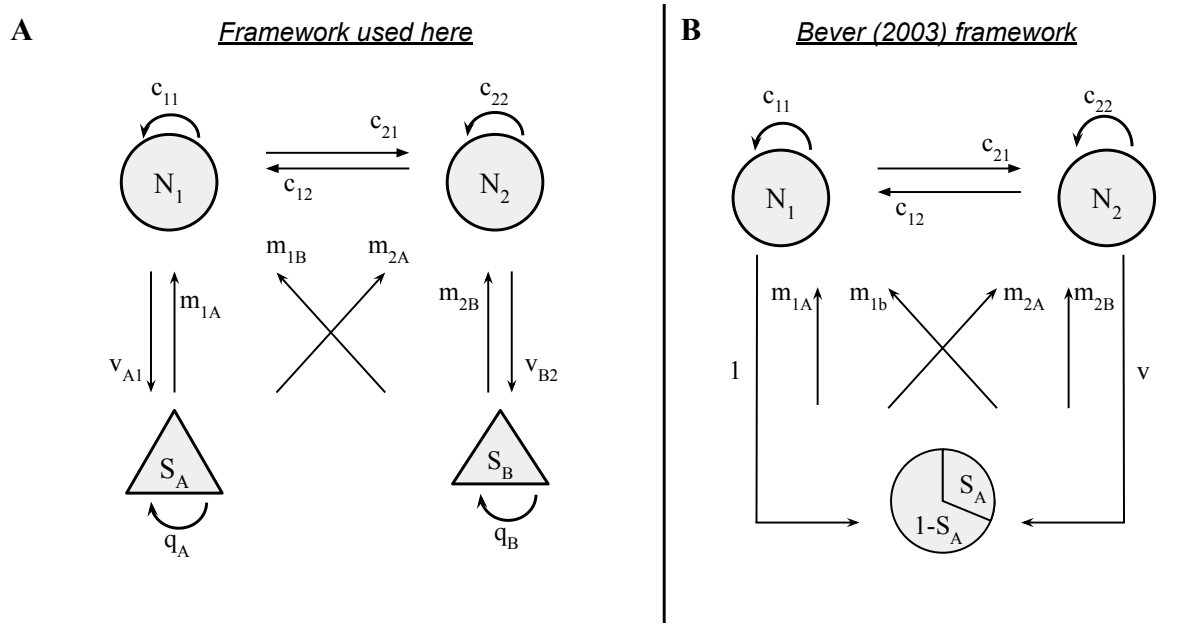

Figure 2.1: A) A schematic of the framework we use to model plant-microbe interactions. Plants N_1 and N_2 compete via Lotka-Volterra competition (c's) and via their interactions with microbes A and B. As in Bever's classic plant-soil feedback models, plant species 1 cultivates soil microbial community A, and plant species 2 cultivates microbial community B. In this model, S_A and S_B denote the density of microbes A and B respectively. Plants 1 and 2 cultivate microbial communities A and B at a per-capita rate v_{A1} and v_{B2}, respectively, and each microbial community has a per-capita effect on each plant species (m terms). B) The classic framework for plant-microbe interactions occuring among competing plant species as described in Bever (2003). Plants compete via Lotka-Volterra competition (c's) and via their interactions with soil microbes. Microbes A represent the microbial community characteristic of plant 1's soil, and microbes B represent the microbial community characterstic of plant 2's soil. S_A and S_B denote the proportion of of microbes A and B in the soil, so that $S_A + S_B = 1$. The rate at which plant 2 cultivates microbes B, relative to the rate at which plant 1 cultivates microbes A, is denoted v.

dynamics of plant densities N are as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = g_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}S_B) \qquad \text{(Eqn. 2.1)}$$

where g_1 represents the intrinsic growth rate of plant species 1 in the absence of competitors and microbial effects, and c_{11} and c_{12} represent the intra- and interspecific per-capita competitive effects on plant 1, respectively. The microbial community characteristic of plant 1's soil is denoted A, and the microbial community characteristic of plant 2's soil is denoted B. S_A denotes the proportional effect of plant 1 on the composition of the soil microbial community, and the proportional effect of plant 2 on the soil microbial community, denoted S_B, is equal to $1 - S_A$. m_{1A} is the growth of species 1 on soil containing only microbial community A minus its growth on uncultivated soil (Bever et al. 1997); an analogous definition exists for m_{1B}. Positive values of m_{1A} or m_{1B} indicate higher plant performance in the presence of cultivated microbes, while negative values of m_{1A} or m_{1B} indicate lower plant performance in the presence of cultivated microbes. The proportions S_A and S_B therefore scale the microbial effects on plant growth.

In Bever's model, the rate of change in S_A depends on the relative frequency of plants 1 and 2, and on the relative degree to which plant 2 versus plant 1 cultivate their characteristic soil microbial community, with this relative degree denoted v:

$$\frac{\mathrm{d}S_A}{\mathrm{d}t} = S_A(1 - S_A)\left(\frac{N_1}{N_1 + N_2} - v\frac{N_2}{N_1 + N_2}\right) \qquad \text{(Eqn. 2.2)}$$

We focus on the effects of plant-microbe interactions on plant dynamics by assuming that the intra- and inter-specific competitive effects of each plant species are equal (i.e. $c_{12} = c_{22}$ and $c_{21} = c_{11}$; see Appendix S1 for the coexistence criteria when this as-

sumption is violated). With this assumption, the per-proportion growth rate of plant species 1 when invading a system with plant species 2 at equilibrium, denoted IGR_1, is as follows (see Appendix S1 for derivation):

$$\mathrm{IGR}_1 = g_1(m_{1B} - m_{2B})$$

This shows that the invasion growth rate of plant 1 is determined by the relative effect of the resident plant 2's soil microbial community (i.e. microbial community B) on each plant species. Note that g_1, the growth in the absence of microbes, simply scales the relative effects of the resident microbial community on the two plant species. Assuming g_1 is positive, it has no effect on the sign of the invasion growth rate and is therefore irrelevant to the mutual invasibility condition. Following Chesson (2000), we can express the scaled (IGR_1/g_1) invasion growth rate $\mathrm{IGR}_1^{'}$ as the sum of the microbially mediated fitness difference and the stabilizing effects of plant-microbe interactions:

$$\mathrm{IGR}_1^{'} = (\mathrm{fitness}_1 - \mathrm{fitness}_2) + \mathrm{stabilization}$$

As Bever et al. (1997) have shown, microbial interactions stabilize plant coexistence when microbes more strongly suppress (or more weakly promote) the growth of their cultivating plant species than of the other plant. In the Chesson-type decomposition of the invasion growth rate, the stabilization due to microbes, which contributes to both species' invasion growth rates, is as follows (Appendix S1):

$$\mathrm{stabilization} = -\frac{1}{2}I_S = -\frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B}) \qquad \text{(Eqn. 2.3)}$$

Recall that m_{1A} is the difference between species 1's growth with soil microbial community A and its growth in uncultivated soil. Given that m_{1B} is the difference between species 1's growth with microbial community B and its growth on the same uncultivated soil, $m_{1A} - m_{1B}$ is independent of growth on uncultivated soil (Appendix S1). Thus, as noted by Bever et al. (1997), the degree to which microbes stabilize plant interactions is not affected by the growth of plants in uncultivated soils, simplifying experimental parameterizations of I_S. This result also makes intuitive sense, since I_S describes the average consequences of plants growing with soil microbes cultivated by one plant species versus another; growth on uncultivated soil is irrelevant to this problem. As in Bever's past work, negative frequency dependent dynamics (negative I_S) increase invasion growth rates, and positive frequency dependent dynamics (positive I_S) decrease invasion growth rates. However, as we explain next, the net effect of plant-microbe interactions on plant diversity will depend on whether their stabilizing effect exceeds the fitness difference they generate.

The microbially mediated average fitness of plant 1 is determined by the average degree to which the two microbial communities A and B benefit or harm plant 1 (Appendix S1):

$$\text{fitness}_1 = \frac{1}{2}(m_{1A} + m_{1B}) \qquad \text{(Eqn. 2.4)}$$

An analogous expression exists for plant 2. When microbial communities A and B are on average more pathogenic or less mutualistic towards one plant species than another, they generate a fitness difference:

$$\text{fitness difference} = \frac{1}{2}(m_{1A} + m_{1B} - m_{2A} - m_{2B})$$

Importantly, proper parameterization of the microbially mediated fitness differ-

ence requires measuring the plant growth on uncultivated soil, something that is not required for determining the stabilizing effect (I_S). Following from the definition of each m term as the growth G on cultivated (subscripted A or B) versus uncultivated (subscripted O) soils (e.g. $m_{1A} = G_{1A} - G_{1O}$, Bever et al. (1997)), the fitness difference can be calculated as follows:

$$\text{fitness difference} = \left(\frac{1}{2}(G_{1A} + G_{1B}) - G_{1O}\right) - \left(\frac{1}{2}(G_{2A} + G_{2B}) - G_{2O}\right) \qquad \text{(Eqn. 2.5)}$$

The fitness difference can therefore be interpreted as the difference between species 1 and 2 in how much their growth benefits or suffers, on average, from the soil microbial community cultivated by the two competitors. This benefit or harm is measured with reference to growth on uncultivated soil (G_{1O} or G_{2O}, depending on the focal plant species).

In the absence of stabilization, the invasion growth rate is positive for only one species, and coexistence is impossible. When microbial stabilization of plant dynamics is sufficiently large to overcome the fitness disadvantage of the weaker plant, microbial interactions can cause both plants to have positive invasion growth rates and therefore coexist. This condition is equivalent to the feasibility criteria from Bever et al. (1997) stating that stable coexistence is possible when I_S is negative and the effects of each microbial community are more negative (or less positive) on the species that cultivates it than on the other plant (i.e. $m_{1A} < m_{2A}$ and $m_{2B} < m_{1B}$; Appendix S1). In sum, soil microbes enhance plant coexistence with negative values of I_S, but also mediate an average fitness difference that favors the exclusion of one plant species.

A closer evaluation of microbial effects on plant fitness differences

A deeper understanding of the microbial interactions that drive plant fitness differences can come from a fuller exploration of the dynamics of soil microbes. Following Eppinga et al. (2006), we expand the microbial population dynamics in Bever's framework to model the density (rather than frequency) of the two soil microbial communities. Increasing the range of microbial dynamics possible in the model admittedly makes the theory less easily parameterized with soil training experiments, but allows us to include a greater range of soil microbial dynamics that can favor one plant over another. We can then see how these dynamics are encapsulated within the inter- and intra-specific competitive coefficients underlying coexistence or exclusion, and what assumptions need to be made to yield versions of the model that are more easily parameterized. Moreover, by removing some of the constraints on microbial dynamics in the original formulation of the plant-soil feedback model, we can derive stabilization and fitness difference terms that integrate the effects of both plant competition and microbial feedbacks, and formally link the model to broader coexistence theory. As we show in the final section of this paper, doing so allows us to explore, for example, how resource availability influences the importance of plant-microbe interactions for competitive outcomes.

In our expanded model, plant dynamics still follow Eqn. Eqn. 2.1, but we now model the density S of soil microbial communities A and B that are cultivated by plant species 1 and 2 respectively, and suffer from density-dependent mortality:

$$\frac{1}{S_A}\frac{\mathrm{d}S_A}{\mathrm{d}t} = v_{A1}N_1 - q_A S_A \qquad \text{(Eqn. 2.6)}$$

An analogous equation exists for S_B. This model assumes that species 1 cultivates soil microbial community A at a constant per-capita rate v_{A1}, and that the density of A declines due to density-dependent mortality, q_A (Stevens and Holbert 1995; Woody et al. 2007). Following classic plant-soil feedback theory, S_A and S_B denote densities of the unique microbial communities cultivated by plant species 1 and 2 respectively. In this framework, the densities S_A and S_B can vary independently of each other– they are no longer proportions constrained to sum to 1, and S_B can no longer be expressed as $1 - S_A$. Although the two microbial communities S_A and S_B may directly interact with each other in natural systems, we assume in the main text that these interactions do not significantly affect the overall microbial dynamics (see Appendix S2 for a model that includes microbial competition). As this model is coupled to the plant dynamics in Eqn. Eqn. 2.1, the m terms in the plant dynamics equation are now interpreted as the per-capita effect of each microbial community on plant growth. The units and definitions of the parameters are summarized in Table S2.1.

These changes to the microbial dynamics equations can increase the range of behavior the model is capable of producing relative to the original Bever models, but they inevitably make the model less coupled to the two-phase experiments that so nicely parameterize Bever's model (Box 1). However, as we show in the following scenarios and in the discussion, many insights provided from the model developed here apply regardless of whether one begins with a frequency-based framework or our extended version.

To evaluate microbial effects on plant dynamics in terms of fitness differences that favor one plant over the other, and niche differences that stabilize their interaction by favoring species that drop to low density, we assume that microbial dynamics operate on a faster time scale than the plants. This assumption is consistent with the general

expectation that microbes have shorter generation times and faster dynamics than their plant hosts (Bever et al. 2012; but see Treseder and Lennon 2015). With this separation of timescale assumption, the per-capita effect of plant j on plant i, which is used to calculate the degree of niche overlap and the magnitude of the fitness difference, is termed α_{ij} and is expressed as follows (see Appendix S2 for derivation):

$$c\alpha_{ij} = \left(c_{ij} - \frac{m_{iX} v_{Xj}}{q_X} \right) \quad \text{(Eqn. 2.7)}$$

where $X = A$ when $j = 1$, and $X = B$ when $j = 2$. This expression shows that two processes influence the per capita effect of plant j on plant i. First, plant j harms plant i through direct competition (c_{ij}) independent of the soil microbial community. Second, plant j can cultivate a microbial community X that affects plant i's population growth. The sign of this effect depends on whether the microbial community cultivated by plant j is on average beneficial for plant i (with positive m's that weaken the total per capita suppression) or suppressive (with negative m's that increase the per capita suppression). The strength of this effect is determined by how strongly the microbes grow with plant j (v_{Xj}), how strongly the microbes affect plant i (m_{iX}), and how well the microbes survive in the soil (q_X). The effect of plant j on plant i due to competition alone or due microbial interactions alone can be assessed by setting the other mechanism equal to zero. For example, in the absence of competition ($c_{ij} = 0$), the per capita suppression of plant species i by species j is simply determined by the degree to which plant species j promotes a microbial community that harms species i.

When the cultivated microbial community has a net positive effect on a plant species ($\frac{m_{iX} v_{Xj}}{q_X} > 0$), there is the potential for net facilitation ($\alpha_{ij} < 0$). For example, plant 2 may facilitate plant 1 when the microbial community it cultivates (community B) is more beneficial for plant 1 than plant 2's competitive suppression of plant 1

(i.e. $c_{12} < \frac{m_{1A}v_{B2}}{q_B}$, resulting in $\alpha_{12} < 0$). Such interspecific facilitation generally makes coexistence a non-issue. When only one plant species is facilitated, coexistence simply requires that the species being facilitated limits itself more than it limits the other species ($\alpha_{21} < \alpha_{11}$ in this example). When both plant species facilitate one another, coexistence is assured. We therefore focus the remainder of this paper on cases where the net effects of plants on neighbors are negative, meaning interspecific competition is stronger than any microbially mediated interspecific facilitation (i.e., $c_{12} > \frac{m_{1B}v_{B2}}{q_B}$ and $c_{21} > \frac{m_{2A}v_{A1}}{q_A}$). Similarly, because species can never indefinitely facilitate themselves (which would lead to unbounded growth), we also assume net negative intraspecific interactions. These conditions are automatically satisfied when microbe effects (m_{iX}) are themselves negative.

The relative strength of interspecific and intraspecific suppression determines the degree of niche overlap ρ as follows (Chesson 2012):

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \qquad \text{(Eqn. 2.8)}$$

This term reflects the degree to which the two plant species limit heterospecifics versus conspecifics. There is complete niche overlap ($\rho = 1$) when each plant species equally affects the growth of con- and heterospecifics. The niche difference is simply the complement of the niche overlap ($1 - \rho$). In this model, two types of biological differences can stabilize coexistence by reducing niche overlap. First, species differences that drive stronger intra- than interspecific competition ($c_{11} > c_{21}$ and $c_{22} > c_{21}$) can stabilize coexistence. Second, microbial interactions can stabilize coexistence when the microbial community cultivated by each plant is on average more harmful (or less beneficial) to the cultivating species than to the other plant. The stabilization due to competition alone (ρ^{comp}) or due to microbial interactions alone (ρ^{micr}) can be assessed by setting the

microbial or competition terms, respectively, equal to zero in **??**. Assuming symmetry in all parameters except the microbial effects on plants, the niche overlap term ρ has a nearly identical interpretation to I_S in Bever's framework: strong conspecific and weak heterospecific microbial suppression drive a negative plant-soil feedback indicated by negative values of I_S, and they drive low niche overlap ($\rho < 1$) in our framework.

Whether species coexist is determined both by the degree of niche overlap, and by their average fitness differences. The ratio of the two species' geometric mean suppression by intraspecific and interspecific individuals determines their fitness difference κ_2/κ_1 as follows (Godoy and Levine 2014):

$$\frac{\kappa_2}{\kappa_1} = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}} \qquad \text{(Eqn. 2.9)}$$

The fitness difference reflects the relative degree to which each species is influenced by competition and microbial interactions, irrespective of which plant cultivates the microbes. Fitness differences are large when species differ in their sensitivity to competition, as explained in Chesson (2000) and Godoy and Levine (2014), or when they differ in their sensitivity to the microbial community. As above, the fitness differences generated by competition alone (${\kappa_2/\kappa_1}^{comp}$) or by microbial interactions alone (${\kappa_2/\kappa_1}^{micr}$) can be calculated by setting the other process equal to zero in **??**.

Coexistence depends on small niche overlap (a large niche difference) relative to the fitness differences as follows:

$$\rho < \frac{\kappa_2}{\kappa_1} < \frac{1}{\rho} \qquad \text{(Eqn. 2.10)}$$

Algebra shows that this inequality is equivalent to the well-known condition from two-species coexistence in Lotka-Volterra competition models, which requires that in-

traspecific competition is stronger than interspecific competition (i.e. $\alpha_{21} < \alpha_{11}$ and $\alpha_{12} < \alpha_{22}$, Appendix S2, and the two species equilibrium exhibits the same stability properties). Species with large fitness differences (κ_2/κ_1 further from 1) can coexist only when there is low niche overlap ($\rho \to 0$); conversely when species have high niche overlap, coexistence is only possible if the two species have very similar ecological fitness (κ_2/κ_1 close to 1, Fig. 2.2A). Microbial interactions can also drive positive frequency dependence leading to a priority effect when they cause net intraspecific suppression to be weaker than interspecific suppression, resulting in $\rho > 1$; stable coexistence is impossible in such cases.

It is important to note here that the terms describing plant-microbial interactions are essential to determine the interaction terms α, which in turn determine both niche overlap and fitness difference. Thus, the microbial influence on plant species diversity will result from effects on both the niche overlap and the fitness difference.

Why microbially mediated fitness differences matter

We now elaborate three scenarios that demonstrate why quantifying microbially mediated fitness differences is important for understanding how soil microbes influence plant coexistence. Rather than forging new theoretical results (see Bever 2003; Revilla et al. 2013; Eppinga et al. 2018), each of these scenarios aims to make obvious for empiricists measuring only I_S that the microbially mediated fitness difference is an equally important metric for inferring microbial effects on coexistence.

Our three scenarios include one in which microbes favor exclusion even when they cause negative plant-soil feedback, one in which microbes favor coexistence even when they cause no plant-soil feedback, and one in which microbes promote diver-

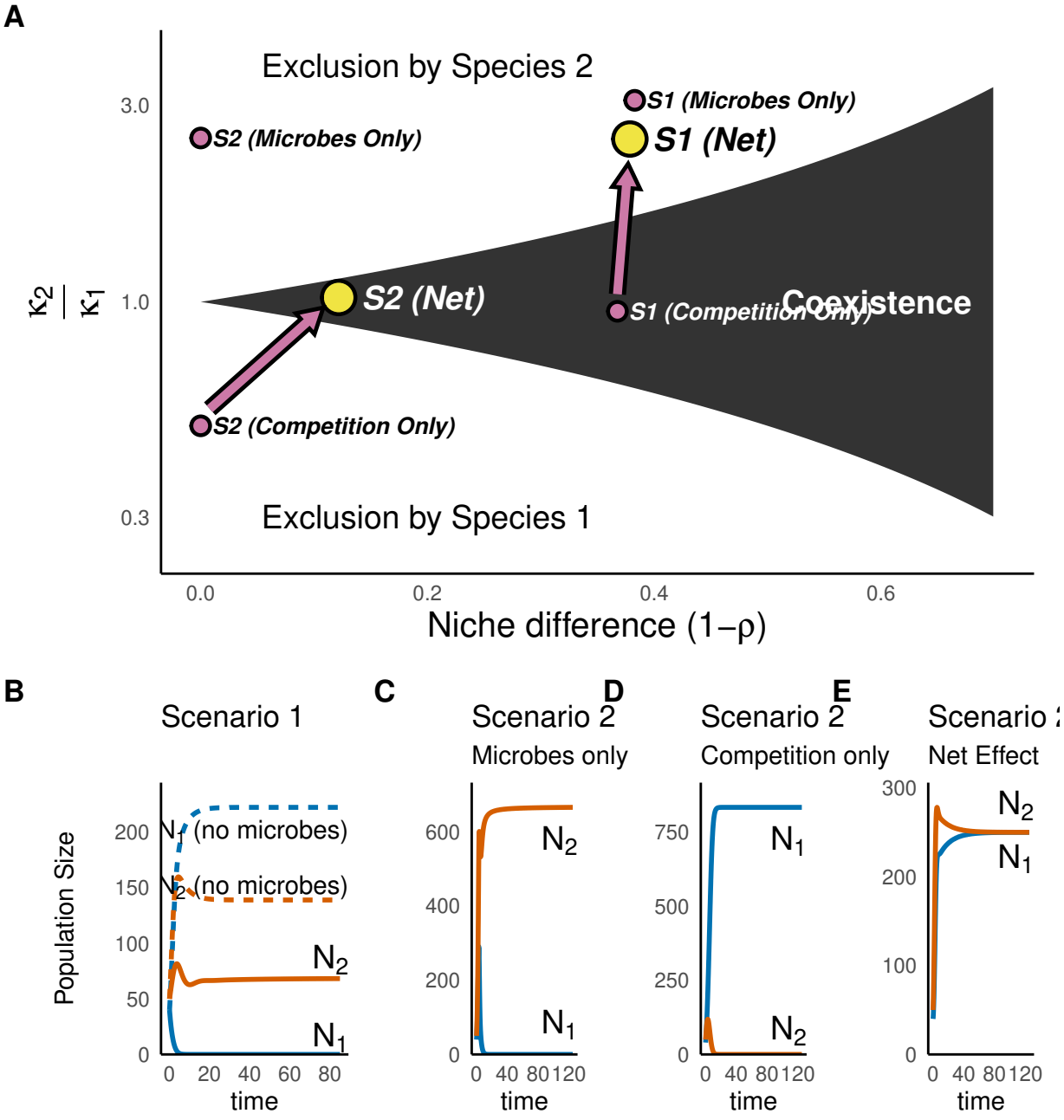

Figure 2.2: Outcomes of coexistence in the microbe density model. A) Coexistence is possible when stabilizing effects between species are stronger than the fitness difference between them, i.e. when the inequality $\rho < \kappa_2/\kappa_1 < 1/\rho$ is satisfied. Arrows indicate the change in net fitness and niche differences due to plant-microbe interactions. B) In Scenario S1, plants coexist when microbial effects are set to zero (dashed lines). The plant-interactions further stabilize this interaction; however, the net effect of microbes is to drive the exclusion of N_1 (solid lines) due the large fitness difference they generate. C-E) In Scenario S2, neither competition nor microbial interactions alone stabilize coexistence among the plant species (C, D). However, when both mechanisms occur simultaneously, they promote coexistence both by equalizing fitness and driving a niche difference (E).

sity in multi-species plant communities despite favoring exclusion among pairs. The parameter values used in each of these scenarios are presented in Appendix S3.

Scenario 1: Microbes favor exclusion even when they cause negative plant-soil feedback

We first consider a scenario (**S1** in Fig. 2.2A) where measuring the microbially mediated fitness difference would be key to properly inferring that the net effect of microbes is to favor plant species exclusion. The results of this scenario also follow from the feasibility criteria of Bever et al. (1997), though this earlier result was not expressed in terms of microbially mediated fitness differences. We consider a plant species pair that can coexist in the absence of microbial effects due to stronger intraspecific than interspecific competition (dashed lines in Fig. 2.2B). The plant-microbial interactions in this scenario further stabilize the system ($\rho^{micr} = 0.617$).

However, in this scenario, microbes also have the effect of more strongly suppressing plant 1 than plant 2, causing a substantial fitness difference ($(\kappa_2/\kappa_1)^{micr} = 3.086$) that overcomes their stabilizing effect. Indeed, when competition and plant-microbe interactions act together, plant 1 is excluded from the system because its microbial interactions give it such low fitness. Thus, contrary to the conclusion from analyzing microbe effects on niche differentiation alone, properly predicting that the net effect of microbial interactions is to drive the exclusion of species 1 (solid lines in Fig. 2.2B) requires measuring the microbially mediated fitness difference as well.

Scenario 2: Microbes promote coexistence even without generating negative plant-soil feedback

Next, we consider a scenario (**S2** in Fig. 2.2A) that highlights how measuring microbially mediated fitness differences is key to inferring the interactive effects of competition and plant-microbe interactions. The model developed here and its associated measure of the niche difference (Eqns. **??** and Eqn. 2.9) not only allows us to more precisely define the basis of microbially mediated fitness and niche differences, but also to quantify the effects of new stabilizing mechanisms that are more difficult to resolve under the Bever framework. For example, it is well known that a competition-defense trade-off can create opportunities for plant coexistence beyond the stabilizing opportunities from each mechanism alone (Holt et al. 1994; Mordecai 2011). This tradeoff can also involve plant-microbe interactions (Laliberté et al. 2014; Bever et al. 2015; Lekberg et al. 2018).

We consider a system in which plant species differences in their sensitivity to competition drive a competitive fitness difference in favor of plant 1 (${\kappa_2/\kappa_1}^{comp} = 0.5$), and there is no competition-mediated stabilization ($\rho^{comp} = 1$). Thus, in the absence of microbial interactions, competition would cause the exclusion of plant 2, the inferior competitor (Fig. 2.2C). However, there is a tradeoff such that plant 1, the stronger competitor, is more sensitive to pathogenic soil microbes. By also assuming that the two plants have complete microbial niche overlap, microbes drive a fitness difference in favor of plant 2 (${\kappa_2/\kappa_1}^{micr} = 2.5$) and provide no stabilization ($\rho^{micr} = 1$). Thus, independent of competition, plant-microbe interactions simply favor the exclusion of plant 1 (Fig. 2.2D).

However, when the effects of competition and plant-microbial interactions are considered simultaneously, it becomes clear that microbes in fact promote coexistence

in this system (Fig. 2.2A, 2E). Two processes contribute to this outcome. First, competitive and microbial interactions jointly equalize plant fitness (${\kappa_2/\kappa_1}^{net} = 1.025$), as species 1 has superior competitive ability but suffers more from microbes, and vice-versa for species 2. Second, competitive and microbial interactions reduce net niche overlap from 1 to $\rho^{net} = 0.878$ (Fig. 2.2A). In other words, although plant-microbial interactions alone do not create a negative plant-soil feedback that stabilizes plant coexistence in this scenario, their interplay with plant competition provides an additional axis for niche differentiation that promotes species diversity in this system (Chesson and Kuang 2008). This scenario provides another example of how the total effects of soil microbes on diversity in natural plant communities can only be understood by studying microbially mediated stabilization and fitness differences relative to those caused by other ecological process like competition.

Scenario 3: Microbially mediated fitness differences can help maintain plant diversity in multispecies systems through indirect effects among competitors

As in the previous two scenarios, most theoretical and empirical plant-soil feedback research has focused on the effects of plant-microbial interactions on pairwise plant competition (but see Eppinga et al. (2018) for an n-species version of I_S that incorporates the structure of the feedback network). Our next scenario illustrates that while inferring the effects of soil microbes from the pairwise stabilization and fitness differences they generate might obscure their role in influencing plant diversity in systems of more than two species, this role can be understood from the network of pairwise fitness differences. To explore such a multispecies system, we extend Eqns Eqn. 2.1 and Eqn. 2.6 to model the interactions between three plant species and the microbial communities they each cultivate (Appendix S3). Importantly, the inequality in Eqn. 2.10

(or the equivalent condition that each species suppress itself more than it suppresses the other) no longer fully explains coexistence in this multispecies model (Barabás et al. 2016), though lower values of α_{ij}/α_{jj} generally favor diversity (Chesson 2018). In other words, evaluating the stabilization and fitness differences that microbes mediate between each species pair might not predict whether they promote plant diversity across the entire system, because the outcome of any given pairwise interaction can be modified by the indirect effects of microbes cultivated by other plant species.

For this scenario, we examine a system of three species where microbially mediated pairwise fitness differences can promote multispecies coexistence by creating an intransitive dominance hierarchy (i.e. no single species has a fitness advantage over all others, May and Leonard 1975; Soliveres et al. 2018), a condition which was recently explored by Eppinga et al. (2018). We parameterize the system such that each plant's microbial community gives the cultivating species a fitness advantage over one other species in the system. Specifically, the interactions with soil microbes generate an ecological "rock-paper-scissors" dynamic (Allesina and Levine 2011; Gallien et al. 2017) in which plant 1 has an advantage over plant 2, plant 2 an advantage over plant 3, and plant 3 an advantage over plant 1. In this scenario, microbial interactions also stabilize the interaction between each pair, but this stabilizing effect is not sufficient to overcome any of the pairwise fitness differences they generate (Fig. S3.1). Thus, for any given plant species pair, the microbially mediated fitness differences drive exclusion (Fig. 2.3B-D). Nonetheless, by evaluating the dynamics of this system when all three plant species are present, it becomes clear that the indirect effects of the microbially mediated fitness differences in this scenario in fact create an intransitive loop that allows coexistence of all three species (Fig. 2.3A). In the present parameterization, all three plant species coexist even when the soil microbial community drives exclusion

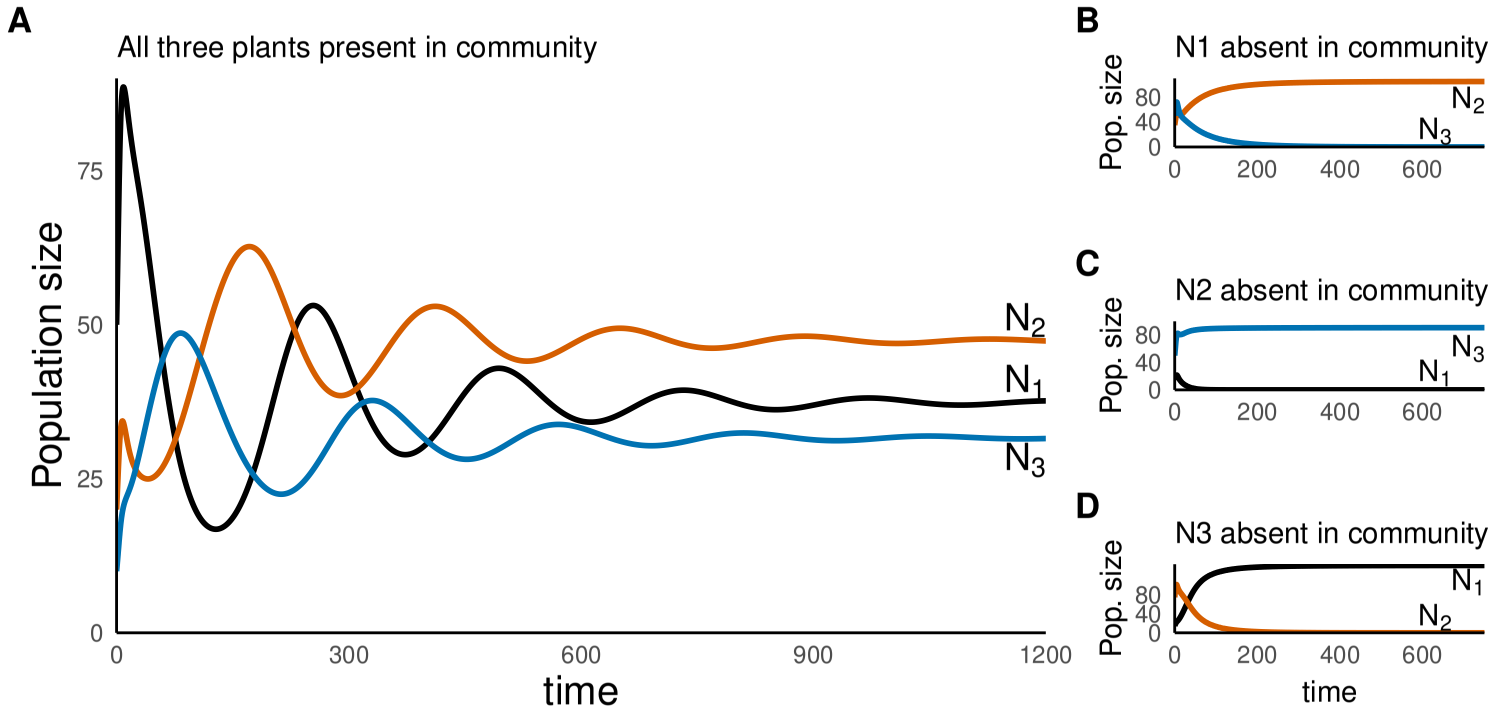

Figure 2.3: When plant-microbe interactions drive intransitive dominance hierarchies among plants, they can promote diversity in multispecies plant communities (panel A) even when they do not allow any species pair to coexist (panels B-D). The position of the three species pairs in the fitness difference/niche difference landscape is presented in Fig. S2.1 (Appendix S3).

among any given pair, but one can also construct scenarios in which the network of microbially mediated fitness differences reduces diversity in multispecies systems even when microbial stabilization allows each individual species pair to coexist (Appendix S3). In general, accurately predicting whether soil microbes favor or hinder plant diversity in speciose systems from studies of pairwise plant interactions is a difficult task, one that will be made more tractable by interpreting microbial effects on the stability of plant interaction networks in diverse communities (Barabás et al. 2016; Levine et al. 2017; Eppinga et al. 2018).

Integrating plant-microbe interactions into broader coexistence theory generates useful predictions

As demonstrated in the three scenarios of the prior section of this paper, the plant-microbe interaction model developed here allows us to integrate our work into a large body of theory regarding the coexistence of species competing for resources and interacting via organisms at other trophic levels. This allows us to model a wide range of ecological scenarios– for example, one can modify the multispecies model used in Scenario 3 to decompose the effects of the soil microbial community as a whole into the effects of particular microbial taxa or guilds (Appendix S4). As the last section of this paper, we demonstrate the value of integrating plant-microbe feedbacks with broader coexistence theory by considering a model of explicit resource competition and plant-microbe interactions that we use to make theoretically justified predictions regarding the relative importance of microbial interactions across a productivity gradient.

Recent advances in coexistence theory have made it clear that the effects of density dependence arising from trophic interactions are symmetric to those of resource

competition, and that the relative importance of each mechanism to determining the diversity of a given guild depends on a variety of ecological conditions (Chesson and Kuang 2008). These insights can be extended to provide a theoretical basis for understanding the relative importance of plant-microbe interactions and competition in natural communities. To do so, we unite the effects of explicit resource competition and plant-microbe interactions into a single model with plants as the focal guild consuming resources and interacting with microbes (Fig. 2.4A). For simplicity, the effects of microbes on plant growth in our model operate independently of plant resource uptake; models in which plant-microbe interactions directly influence the nature of plant resource uptake also yield valuable insights (Umbanhowar and McCann 2005; Jiang et al. 2017). The plant-microbe interactions in this model follow exactly from the previous model (Eqns Eqn. 2.1 and Eqn. 2.6). Following MacArthur (1970) and Chesson and Kuang (2008), we model resources l that accumulate logistically with a low-density growth rate of r_l until they reach a resource carrying capacity of $1/s_l$. Plants consume resources at a rate u and convert resources into plant population growth. Equations and analyses for this model are presented in Appendix S5.

Assuming that both resource and microbe dynamics occur more rapidly than plant dynamics (MacArthur 1970; Chesson and Kuang 2008), the per-capita suppression of plant species i by species j in this model (α'_{ij}) is as follows (see Appendix S5 for derivation):

$$\alpha'_{ij} = \left(\overbrace{\sum_l \frac{u_{il}u_{jl}}{s_l r_l}}^{\text{resource competition effect}} - \overbrace{\frac{m_{iX}v_{Xj}}{q_X}}^{\text{microbe effect}} \right) \qquad \text{(Eqn. 2.11)}$$

where $X = A$ when $j = 1$ and $X = B$ when $j = 2$. The left term in α'_{ij} shows that the

strength of resource competition depends on the rate of resource consumption (u's) and on the nature of resource dynamics in the system (s_l and r_l). When plants i and j consume entirely distinct resources, the left term is equal to zero, and plant j's interaction with plant i is determined only via the effect of the soil microbial community it cultivates. However, when plant species overlap in resource consumption, their overall interaction is determined jointly by resource competition and the microbial community each plant cultivates. As in the interaction term for the previous model (**??**), the sign and strength of microbial effects is determined by the rate at which plant j cultivates microbes that affect the growth of plant i. The niche overlap ρ and fitness differences κ_2/κ_1 in this model are calculated in the same way as in the previous analysis (Eqns. Eqn. 2.8 and Eqn. 2.9 respectively) (Chesson 2012). Importantly, this model, a simple extension of Chesson and Kuang (2008), can be used to make theoretically justified predictions regarding the relative contribution of resource competition and plant-microbe interactions to the outcome of plant competition as a function of site productivity (r_l). In this model formulation, the interspecific interaction parameters α', and ultimately the net niche overlap ρ, are more strongly driven by the degree to which plants overlap in their resource use in low-productivity communities (i.e. low values of r_l). By contrast, in productive communities (high r_l), species interactions are more strongly influenced by the soil microbial communities, and these interactions strongly determine the net niche overlap (Fig. 4B). A similar result can be derived for the fitness differences (Fig. S5.1 in Appendix S5). Moreover, the qualitative result that microbial niche differences more strongly influence net niche overlap at high resource levels than at low resource levels also holds in systems in which microbial effects on plants (i.e. the m terms) themselves shift from being mutualistic in low-resource environments, to pathogenic in high-resource environments (Revillini et al. 2016, Figure S5.2). This result is not due to changes in resource niche overlap along the gradient– in

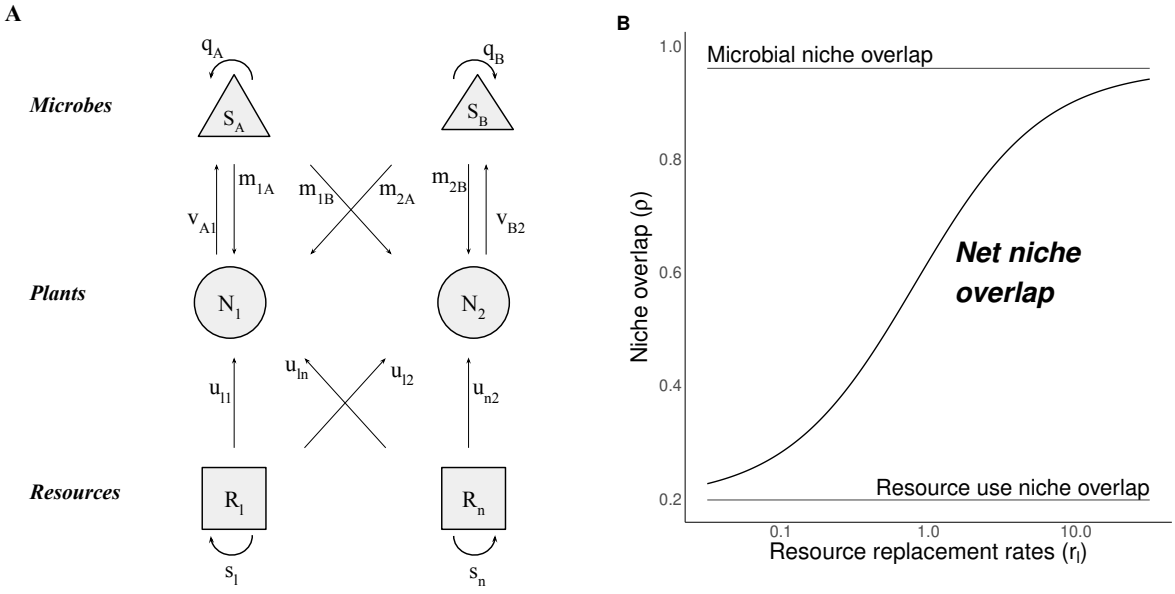

Figure 2.4: A) Schematic of a model with explicit resource competition. Plant-microbe interactions (top two trophic levels) are modeled as in Fig. 1A. Populations of plants 1 and 2 grow as they take up resources l. The u terms denote the per-capita resource uptake rates of each resource by each plant. Resources are modeled as experiencing logistic growth with a low-density growth (replacement) rate of r_l until they are saturated at the carrying capacity $1/s_l$. See Appendix S5 for dynamics equations. B) The net niche overlap between plants represents the joint influence of the niche overlap due to shared resource consumption and the niche overlap due to shared microbial interactions. The resource use niche overlap exerts a relatively strong influence on the net *ho* when resource replacement rates are low; at higher levels of resource replacement rate, the net *ho* is more strongly influenced by the niche overlap due to microbial interactions.

our analysis, the niche overlap due to resource competition is just as high in productive sites as in low-productivity sites. Rather, this model predicts that when resources are less limiting, resource competition more weakly affects plant community dynamics. It is important to note that this result is in part due to our formulation of a model in which the direct microbial effects on plant-plant interactions operate separately from plant resource uptake (i.e. microbes do not directly change plant resource uptake dynamics), as a result of which the productivity term r_l appears only in the denominator of the resource competition component of Eqn. 2.11.

Discussion

Plant-microbe interactions can drive a fitness difference that provides one plant species an average fitness advantage over the other in pairwise competition. These fitness differences arise from differences in plant species' ability to tolerate the pathogenic soil microbes or benefit from the mutualistic soil microbes cultivated by different plant species. We show that ignoring microbially mediated fitness differences and only considering the stabilizing or destabilizing effects of plant-microbe interactions, as is frequently done in empirical analyses, can lead to erroneous conclusions regarding the total effects of soil microbes on plant diversity. With an extension of Bever et al. (1997)'s pioneering theoretical framework of plant-soil feedbacks, we show that the degree to which soil microbes can drive plant coexistence or exclusion is influenced by the relative sensitivity of each plant to the microbial communities, as well as the rate at which each plant influences the growth of persistent soil microbial communities. Finally, we show that modeling microbial dynamics in terms of their density allows us to organize, interpret, and predict the effects of microbes in light of a large body of coexistence theory that considers the drivers of coexistence among consumer-resource communities.

We focus our discussion on the implications of our theoretical results for empirical work testing how interactions between plants and soil microbes influence plant diversity. To do so, we first show how microbially mediated plant fitness differences can be quantified in typical plant-soil feedback experiments. We then discuss some limitations to the standard experimental approach used in these studies. Last, we suggest avenues for future research to integrate insights from our theoretical work and develop a more complete understanding of how soil microbes influence plant diversity.

Empirically measuring the microbially mediated plant fitness difference

Our plant-soil feedback model with microbial density dynamics showed that microbial effects on plant diversity depend on microbe dynamics terms that are difficult to measure in two-phase plant-soil feedback experiments (e.g. the v and q terms in Eqn. 2.6). Thus, we expect that until it becomes more feasible to quantify these microbial dynamics parameters, most empirical studies of plant-soil feedback will continue to use the two-phase approach (Box 1) to parameterize Bever's microbe frequency-based framework. Nevertheless, the conceptual insights from our microbial density-based model apply to the interpretation of these empirical studies. Moreover, our analysis suggests that variation in microbial community dynamics can be consequential to determining the effects of soil microbes on plant diversity, and that empirically testing assumptions regarding microbial dynamics that are implicit in the standard two-phase experimental approach should help refine our understanding of how plant-microbial interactions influence plant species diversity. For example, assumptions about how each plant species favors its microbial community can be tested with greenhouse ex-

periments capturing the temporal dynamics of plant-soil feedbacks (e.g. Hawkes et al. 2012; Wubs and Bezemer 2017; Bezemer et al. 2018) and with more refined measurements of microbial population dynamics now possible with advances in DNA sequencing and cell counting technologies (e.g. Quantitative Microbiome Profiling (Vandeputte et al. 2017)).

Regardless of whether one begins with the model of Bever (2003) (or Bever et al. (1997)) or a more complex version like the one we develop here, our analyses show that empirically quantifying the microbially mediated fitness difference is an essential step for understanding the full effects of soil microbes on plant coexistence. Doing so is rather straightforward following Eqn. Eqn. 2.5. One simply needs the growth of both plant competitors on soils cultivated by both plants and on a reference uncultivated soil, as noted in the text before Eqn. 2.5. Thus, at a minimum, soil feedback experiments following the two-phase approach with an additional uncultivated soil treatment during the second phase provide the necessary empirical data for parameterizing both the stabilization term and the microbially mediated fitness difference. With such information, one can compare the magnitude of the stabilization term ($-\frac{1}{2}I_S$) to the microbially mediated fitness difference (Eqn. 2.5).

Recommendations for future empirical plant-soil feedback studies

One limitation of the classic plant-soil feedback experimental design (Box 1) is that the coexistence consequences of soil microbes are not clear without contextualizing microbially mediated fitness differences within those generated by competition or other ecological processes. For example, soil microbes can favor plant diversity (reduce the degree of niche differentiation required for coexistence) even when they generate no negative frequency dependence if they simply give a fitness advantage to a weak re-

source competitor. Indeed, in Scenario 2, the joint effect of competition and plant-microbe interaction was to stabilize plant interactions even when neither mechanism alone promotes coexistence. Similarly, whether microbially mediated fitness differences quantified in soil feedback studies actually reduce diversity in nature will depend on whether they ameliorate or augment fitness differences based on plant competitive ability. Although this competitive information is not frequently quantified in empirical plant-soil feedback studies, evidence is accumulating that plant species experience trade-offs between competitive ability and susceptibility to soil pathogens or mutualists (Laliberté et al. 2014; Lekberg et al. 2018). This suggests that soil microbes might indeed frequently promote plant diversity in nature by equalizing competitive fitness differences.

We therefore echo recent calls (Smith-Ramesh and Reynolds 2017; Lekberg et al. 2018) for experiments that explicitly investigate the joint effects of plant-microbe interactions and resource competition in nature. The niche and fitness difference terms we derive from our density-based model of plant-microbe interactions (Eqns. **??**–Eqn. 2.9) provide a foundation for future studies that couple population dynamics models with greenhouse and field experiments (Hart et al. 2018) to more thoroughly assess the influence of soil microbes on plant diversity.

When should microbes most strongly influence plant diversity?

The final goal of our analysis was to show that modeling microbial population dynamics in terms of their absolute abundance can allow us to apply insights from a vast body of ecological theory to understanding the role of plant-microbial interactions in shaping plant diversity. Specifically, we explored how the relative importance of plant-microbe interactions and resource competition changes along a productivity

gradient, a topic for which a number of authors have recently posed hypotheses (van der Putten et al. 2016; Smith-Ramesh and Reynolds 2017; Lekberg et al. 2018). These hypotheses are generally motivated by empirical observations of variation in the effect sizes of competition and plant-microbe interactions on the growth of individual plants at different sites. However, the consequences of such variation in plant growth for the population dynamics of competing species are difficult to evaluate without a theoretical model (Chesson and Huntly 1997; Chase et al. 2002; Hart and Marshall 2013). Our analysis of one such model shows that even when the strength of competitive and microbial interactions is held constant, the relative importance of plant-microbe interactions for plant dynamics increases with productivity (Fig. 2.4B, Fig. S5.1). We encourage future modeling efforts to incorporate observed variation in the direction and strength of plant-microbe interactions across productivity gradients into plant population dynamics models, as well as the potential for microbes to directly mediate plant resource uptake. Such models and associated empirical studies will refine our understanding of the relative importance of soil microbes in shaping natural plant communities.

While tremendous progress has been made by treating the soil microbial community cultivated by plants as a black box, our ability to predict the consequences of plant-microbe interactions to the dynamics of natural plant communities will also improve with a more mechanistic understanding of how the population dynamics and effects of individual components of the microbial community (e.g. pathogens, mutualists, saprophytes) vary across environments (van der Putten et al. 2016; Bennett and Klironomos 2018; Lekberg et al. 2018). A growing number of studies are building this understanding by performing experiments that involve modifying targeted components of the microbial community across resource gradients (e.g. Jiang et al. 2018), but

it is difficult to evaluate results from these studies in the context of plant-soil feedback theory and the paired two-phase experimental approach, which focus on the effects of the whole microbial community cultivated by each plant species.

In this paper we followed classic plant-soil feedback theory to define the soil communities A and B in our density-based model as the unique microbial communities cultivated by plants 1 and 2. However, the modeling framework we use here can be easily extended to evaluate the coexistence consequences of particular groups of microbes. To do so, one can define the S terms in Eqn. Eqn. 2.5 as the density of individual microbial taxa or guilds, and extend the model to any n number of such microbial groups. Such models can be used, for example, to evaluate the coexistence consequences of mutualistic microbes that can be cultivated by any plant species but to which plant species vary in their response (Appendix S4). Parameterizing such models is challenging, and beyond the elegant simplicity of the two-phase feedback experimental approach. Integrating the dynamics and effects of particular components of the microbial community to better understand when these interactions can most strongly influence plant community dynamics will require studies that combine careful experimental methods and modern molecular technology to embrace the complex nature of these plant-microbial interactions.

Conclusion

Ecologists have learned a great deal regarding the importance of soil biota for plant coexistence since the pioneering work of Bever et al. (1997). Here, we have identified the conditions under which microbes can favor one plant species over others, and this simple result has important implications for how we interpret the results of empirical

investigations of feedbacks between plants and the soil microbial community. Analyzing empirical data in ways that quantify both the stabilizing effects of plant-microbe interactions and their effect on frequency-independent fitness differences should be a top priority to improve our understanding of how soil microbes influence plant diversity. In addition, along with Eppinga et al. (2018), our work also suggests that the focus on pairwise approaches in the plant-soil feedback literature might obscure an important role for soil microbes in maintaining diversity in multispecies plant communities. More generally, we expect that our understanding of the net effects of microbes on plant diversity will improve with future studies that couple experimental approaches to population dynamics models capturing the many ways soil microbes can influence plant diversity.

Chapter 2 Supplementary Materials

Appendix 2.1: Deriving the niche and fitness difference due to microbes in Bever's classic plant-soil feedback model

In this Appendix we analyze the effects of microbial interactions in Bever (2003) in terms of the fitness difference and stabilization they generate.

Bever (2003) models growth of plant species that are interacting via Lotka-Volterra competition and via cultivating soil microbial communities that affect plant performance (Eqn. 2.1, Fig 2.1B in main text), given by:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = g_1 N_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}(1 - S_A)) \qquad \text{(Eqn. S2.1)}$$

For clarity we write the model from Bever (2003) with some notational changes. First, we index the plant species as N_1 and N_2 rather than N_A and N_B, and denote their intrinsic growth rates independent from any competitive or microbial effects as g_1 and g_2 rather than r_A and r_B. Second, we denote the per-proportion effect of microbes as m rather than α and β. Third, we express the self-limitation of a species in terms of intraspecific competition parameters c_{11} and c_{22}, and not in terms of their carrying capacity. Fourth, recognizing that the relative influence of plant 2 on the soil microbial community (S_B in Bever (2003)) is always equal to 1 minus the proportion representing plant 1's effects, we we use the expression $(1 - S_A)$ in place of S_B. The definitions of all parameters are provided in the main text and in Table S2.1 (Appendix S2).

Bever's framework models the relative influence of plant species 1 on the soil microbial community (S_A) as a function of the relative frequency of plants 1 and 2, and

on the strength of plant influence on microbial community as follows:

$$\frac{\mathrm{d}S_A}{\mathrm{d}t} = S_A(1 - S_A)\left(\frac{N_1}{N_1 + N_2} - v\frac{N_2}{N_1 + N_2}\right) \quad \text{(Eqn. S2.2)}$$

As microbial effects depend only on the relative frequency of each microbial community, which in turn relies on the relative frequency of each plant species, we can write a single expression to account for the frequency of plant species A and B. We define F_1 as the relative frequency of plant species 1:

$$F_1 = \frac{N_1}{N_1 + N_2}$$

Now, we apply the quotient rule to Eqn. S2.1, and model the change in F_1 according the following equation:

$$\begin{aligned}\frac{\mathrm{d}F_1}{dt} = \frac{\mathrm{d}\frac{N_1}{N_1+N_2}}{\mathrm{d}t} = \frac{1}{(N_1 + N_2)^2} * (N_1 + N_2)(g_1N_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}(1 - S_A))) \\ -N_1(g_1N_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}(1 - S_A)) \\ +g_2N_2(1 - c_{21}N_1 - c_{22}N_2 + m_{2A}S_A + m_{2B}(1 - S_A)))\end{aligned} \quad \text{(Eqn. S2.3)}$$

We can simplify this expression to the following:

$$\begin{aligned}\frac{\mathrm{d}F_1}{dt} = \frac{1}{(N_1 + N_2)^2}(N_1N_2)(g_1N_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}(1 - S_A)) \\ -g_2N_2(1 - c_{21}N_1 - c_{22}N_2 + m_{2A}S_A + m_{2B}(1 - S_A)))\end{aligned} \quad \text{(Eqn. S2.4)}$$

Which can be rearranged as follows:

$$\frac{dF_1}{dt} = \frac{N_1}{N_1+N_2}\frac{N_2}{N_1+N_2}(g_1N_1(1-c_{11}N_1-c_{12}N_2+m_{1A}S_A+m_{1B}(1-S_A)) \\ -g_2N_2(1-c_{21}N_1-c_{22}N_2+m_{2A}S_A+m_{2B}(1-S_A))) \quad \text{(Eqn. S2.5)}$$

Recognizing that $\frac{N_1}{N_1+N_2} = F_1$ and $\frac{N_2}{N_1+N_2} = 1-F_1$, we can express the per-proportion rate of change in F_1 as:

$$\frac{1}{F_1}\frac{dF_1}{dt} = (1-F_1)(g_1N_1(1-c_{11}N_1-c_{12}N_2+m_{1A}S_A+m_{1B}(1-S_A))- \\ g_2N_2(1-c_{21}N_1-c_{22}N_2+m_{2A}S_A+m_{2B}(1-S_A))) \quad \text{(Eqn. S2.6)}$$

We can now determine the conditions under which species 1 increases in frequency when it is invading an equilibrium community of species 2 (i.e. the invasion growth rate of species 1). When plant 1 is absent from the system (i.e. $N_1 = 0$), the community only consists plants of species 2 (i.e. $F_1 = 0$) and the microbial community is only influenced by plant 2 (i.e. $S_A = 0$). From an analysis of species 2's population growth equation, the population size of plant 2 at its single-species equilibrium can be expressed as $N_2^* = (1+m_{2B})/c_{22}$. Substituting these values into Eqn. S2.1 gives the invasion growth rate of species 1 as the following:

$$\text{IGR}_1 = g_1\left(1-\frac{c_{12}}{c_{22}}(1+m_{2B})+m_{1B}\right) \quad \text{(Eqn. S2.7)}$$

Following Bever (2003), we focus on the contribution of microbes to the invasion growth rate by setting aside species competitive differences. To do so we assume equal competition among species ($c_{12} = c_{22}$), an assumption we relax below in the section "Coexistence when plants are unequal competitors". With the assumption that plants have equal intra- and intraspecific competitive effects, Eqn. S2.7 can be

simplified as follows:

$$\text{IGR}_1 = g_1(m_{1B} - m_{2B}) \qquad \text{(Eqn. S2.8)}$$

Note that g_1, the growth in the absence of microbes, simply scales the relative effects of the resident microbial community on the two plant species. Assuming g_1 is positive, it has no effect on the sign of the invasion growth rate and is therefore irrelevant to the mutual invasibility condition. We show below that this is identical to the invasion growth rate in the exponential growth rate model used in Bever et al. (1997). Following Eqn. 3 of Chesson (2000), the scaled (IGR_1/g_1) invasion growth rate $\text{IGR}_1^{'}$ can be decomposed into the effect of each species' average ecological fitness and the effect of niche stabilization in the system: $\text{IGR}_1^{'} = ((\text{fitness}_1 - \text{fitness}_2) + \text{stabilization})$.

The average microbially mediated fitness of each plant species can be calculated as its average growth rate over all possible soil states (Chesson 2018):

$$\text{fitness}_1 = \frac{\int_0^1 m_{1B} + (m_{1A} - m_{1B})S_A dS_A}{\int_0^1 dS_A} = m_{1B}S_A + \frac{(m_{1A} - m_{1B})}{2}{S_A}^2|_0^1 = \frac{m_{1A} + m_{1B}}{2}$$

In other words, the microbially mediated average fitness of each plant species is equal to the arithmetic mean of its response to each microbial community. Using this expression of fitness, we can express the invasion growth rate as the sum of the fitness difference and the stabilization as follows (Chesson 2000, 2018):

$$\text{IGR}_1^{'} = (m_{1B} - m_{2B}) = \left(\frac{1}{2}(m_{1A} + m_{1B}) - \frac{1}{2}(m_{2A} + m_{2B})\right) + \text{stabilization} \qquad \text{(Eqn. S2.9)}$$

Algebra shows us that the stabilization term is as follows:

$$\text{stabilization} = -\frac{1}{2}I_S = \frac{1}{2}(m_{1B} + m_{2A} - m_{2B} - m_{1A}) \qquad \text{(Eqn. S2.10)}$$

Stabilization is also related to Revilla et al. (2013)'s J_S measure of plant soil feedback as follows:

$$\text{stabilization} = -\frac{1}{2}(J_S + m_{1B}m_{2A} - m_{1A}m_{2B})$$

As Bever et al. (1997) have shown, negative values of I_S stabilize coexistence, whereas positive values of I_S create positive frequency dependence that destabilizes coexistence. Bever et al. (1997) also show that, following the definition of m_{1A} as the growth of plant 1 with microbial community A minus the growth of plant 1 in uncultivated soils (i.e.$m_{1A} = G_{1A} - G_{1O}$) the degree to which microbes stabilize plant interactions is not affected by the growth of plants in uncultivated soils:

$$\begin{aligned}\text{stabilization} =& \frac{1}{2}((G_{1B} - G_{1O}) + (G_{2A} - G_{2O}) - (G_{2B} - G_{1O}) - (G_{1A} - G_{1O})) \\ =& \frac{1}{2}(G_{1B} + G_{2A} - G_{2B} - G_{1A})\end{aligned}$$

The net effect of microbes is to promote coexistence when they generate sufficient stabilizing niche differences to allow the weaker competitor to persist in the system, i.e. when the following inequality is satisfied:

$$\frac{1}{2}I_S < \text{fitness}_1 - \text{fitness}_2 < -\frac{1}{2}I_S \qquad \text{(Eqn. S2.11)}$$

Algebra shows that this inequality is consistent with the feasibility condition derived in Bever et al. (1997). The left hand side of Eqn. S2.11 can be written as follows:

$$\frac{1}{2}I_S < \text{fitness}_1 - \text{fitness}_2$$

$$\frac{1}{2}(m_{1A} - m_{1B} + m_{2B} - m_{2A}) < \frac{1}{2}(m_{1A} + m_{1B} - m_{2A} - m_{2B})$$

$$(m_{1A} - m_{1B} + m_{2B} - m_{2A}) < (m_{1A} + m_{1B} - m_{2A} - m_{2B})$$

$$(m_{2B} - m_{1B}) < (m_{1B} - m_{2B})$$

$$2(m_{2B} - m_{1B}) < 0$$

$$(m_{2B} - m_{1B}) < 0$$

$$m_{1B} > m_{2B}$$

Through a similar analysis of the right hand side of Eqn. S2.11, we find that the second condition for stable coexistence is that $m_{2A} > m_{1A}$.

Coexistence when plants are unequal competitors

In the derivation of the fitness difference and stabilization metrics above, we assumed that the two plant species have equal intra- and interspecific competitive effects, i.e. $c_{12} = c_{22}$ and $c_{21} = c_{11}$. Recall that without this assumption, the invasion growth rate of species 1 is given by Eqn. S2.7. Species 1 can invade from rarity provided that the term in the parentheses is greater than zero, i.e.

$$\left(1 - \frac{c_{21}}{c_{22}}(1 + m_{2B}) + m_{1B}\right) > 0$$

Rearranging this inequality shows that the invasion condition for species 1 is as follows:

$$\frac{c_{22}}{c_{12}} > \frac{(1 + m_{2B})}{(1 + m_{1B})}$$

Similarly, the invasion condition for species 2 is that $\frac{c_{11}}{c_{21}} > \frac{(1+m_{1A})}{(1+m_{1B})}$. Multiplying these two inequalities yields the following condition for mutual invasibility:

$$\frac{c_{22}c_{11}}{c_{21}c_{12}} > \frac{(1+m_{1A})(1+m_{2B})}{(1+m_{2A})(1+m_{1B})}$$

This inequality, which is equivalent to Eqn 5 of Bever (2003) and to Eqn 10 of Revilla et al. (2013), shows that mutual invasibility is favored by higher intra-specific than interspecific competition, which increases the left hand side of the inequality, and more negative (or less positive) intra-specific microbial effects than interspecific microbial effects, which decreases the right hand side of the inequality.

Invasion growth rate in Bever et al. (1997)'s exponential growth model

In Bever et al. (1997)'s framework, the two plant species do not compete with each other- instead, they are assumed to grow exponentially at a rate determined by their interactions with the soil microbial community as follows:

$$\frac{dN_1}{dt} = N_1(m_{1A}S_A + m_{1B}(1-S_A)) \qquad \text{(Eqn. S2.12)}$$

The parameter definitions are the same as in Eqn. S2.1. The microbial community is modeled in the same way as in Eqn. S2.2. As in the analysis of Bever (2003) above, we define F_1 as the relative abundance of N_1 and use the quotient rule to rewrite Eqn. S2.12 as follows:

$$\begin{aligned}\frac{dF_1}{dt} = \frac{d\frac{N_1}{N_1+N_2}}{dt} = \frac{1}{(N_1+N_2)^2} * [(N_1+N_2)N_1(m_{1A}S_A + m_{1B}(1-S_A)) \\ -N_1(N_1(m_{1A}S_A + m_{1B}(1-S_A)) + N_2(m_{2A}S_A + m_{2B}(1-S_A)))]\end{aligned} \qquad \text{(Eqn. S2.13)}$$

This equation can be simplified as follows:

$$\frac{dF_1}{dt} = \frac{(N_1 N_2)[(m_{1A}S_A + m_{1B}(1 - S_A)) - (m_{2A}S_A + m_{2B}(1 - S_A))]}{(N_1 + N_2)^2} \quad \text{(Eqn. S2.14)}$$

Eqn. S2.14 can be rewritten as follows:

$$\frac{dF_1}{dt} = \frac{N_1}{N_1 + N_2}\frac{N_2}{N_1 + N_2}((m_{1A}S_A + m_{1B}(1 - S_A)) - (m_{2A}S_A + m_{2B}(1 - S_A)))$$

Recognizing that $\frac{N_1}{N_1+N_2} = F_1$ and that $\frac{N_2}{N_1+N_2} = 1 - F_1$, we rewrite this as follows:

$$\frac{dF_1}{dt} = F_1(1 - F_1)((m_{1A}S_A + m_{1B}(1 - S_A)) - (m_{2A}S_A + m_{2B}(1 - S_A))) \quad \text{(Eqn. S2.15)}$$

To calculate the invasion growth rate of plant 1 (IGR_1), we set $F_1 = 0$ and $S_A = 0$. Thus, as in Eqn. S2.8, the invasion growth rate is simply equal to the difference in how the soil microbes of the resident species 2 (i.e. microbes B) influence the invading species:

$$\text{IGR}_1 = m_{1B} - m_{2B} \quad \text{(Eqn. S2.16)}$$

Note that there is no term that describes innate growth in the Bever et al. (1997) model, there is no need to scale the invasion growth relative as we had done in the previous analysis.

Appendix 2.2: Deriving interaction parameters in the microbe density model

In this appendix, we first describe the derivation of the interspecific interaction terms α_{12} (**??** in main text) in our microbe density model. Then, we derive the same interaction term for a model in which the two microbial communities A and B compete with each other. Finally, we present the dynamics equations for a multispecies extension of the plant and microbe population dynamics, which we parameterize in Scenario 3 of the main text.

Recall from the main text (Eqn. 2.1) that we model plant population dynamics according to the following differential equation:

$$\frac{1}{N_A}\frac{\mathrm{d}N_A}{\mathrm{d}t} = g_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}S_B) \qquad \text{(Eqn. S2.17)}$$

and that we model density S of soil microbial communities A and B, which are cultivated by plant species 1 and 2 respectively, and suffer from density-dependent mortality (Eqn. 2.6 of the main text):

$$\frac{1}{S_A}\frac{\mathrm{d}S_A}{\mathrm{d}t} = v_{A1}N_1 - q_A S_A \qquad \text{(Eqn. S2.18)}$$

An analogous equation exists for microbial community B, which is cultivated by plant 2. The definitions of all parameters are provided in the main text and in Table S2.1.

To analyze this model, we follow the approach of Chesson and Kuang (2008) and assume that microbes operate on a much faster timescale than the plants. In other words, the microbial population density immediately equilibrates to the density of the two plants in the system. This assumption allows us to express the equilibrium

microbial density at any time as follows:

$$S_A^* = \frac{v_{A1} N_1}{q_A} \qquad \text{(Eqn. S2.19)}$$

A corresponding equation exists for S_B. We can substitute these expressions into Eqn. S2.17 to express plant dynamics as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = g_1 \left(1 - c_{11}N_1 - c_{12}N_2 + \frac{m_{1A}v_{A1}N_1}{q_A} + \frac{m_{1B}v_{B2}N_2}{q_B}\right)$$

which can be rearranged as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = g_1 \left(1 - \left(c_{11} - \frac{m_{1A}v_{A1}}{q_A}\right) N_1 - \left(c_{12} - \frac{m_{1B}v_{B2}}{q_B}\right) N_2\right) \qquad \text{(Eqn. S2.20)}$$

Evaluating Eqn. S2.20 at Species 2's single-species equilibrium (i.e. when $N_1 = 0$ and $N_2 = N_2^* = \frac{1}{c_{22} - (m_{2B}v_{B2})/q_B}$ shows that the invasion growth rate of species 1 is as follows:

$$\mathrm{IGR}_1 = g_1 * \left(1 - \frac{c_{12} - \frac{m_{1B}v_{B2}}{q_B}}{c_{22} - \frac{m_{2B}v_{B2}}{q_B}}\right) \qquad \text{(Eqn. S2.21)}$$

Note that unlike the invasion growth rate expression in Bever (2003) (Eqn. S2.7), IGR_1 in this model is influenced not only by the competitive effects of species 2 and the microbial effect on species 1, but also by the microbial population dynamics themselves (the v and q terms).

We now collect the per-capita inter-specific effects of competition and microbial interactions in Eqn. S2.20 into a single term α_{12}, which describes the effect of an indi-

vidual of species 2 on the dynamics of species 1 (**??** in the main text):

$$\alpha_{12} = \left(c_{12} - \frac{m_{1B} v_{B2}}{q_B}\right) \quad \text{and} \quad \alpha_{21} = \left(c_{21} - \frac{m_{2A} v_{A1}}{q_A}\right) \tag{Eqn. S2.22}$$

Likewise, we can collect the per-capita intra-specific effects of competition and microbial interaction into a single term α_{22} as follows:

$$\alpha_{11} = \left(c_{11} - \frac{m_{1A} v_{A1}}{q_A}\right) \quad \text{and} \quad \alpha_{22} = \left(c_{22} - \frac{m_{2B} v_{B2}}{q_B}\right)$$

These α terms, together with the invasion growth rate expression in Eqn. S2.21, show that both species can invade when rare (i.e. satisfy the mutual invasibility criterion and therefore coexist) provided that $\alpha_{12} < \alpha_{22}$ and $\alpha_{21} < \alpha_{11}$, which is the standard invasion criterion for two-species Lotka-Volterra competition models.

With the α terms thus defined, it becomes clear that in our framework, the plant population dynamics equation (Eqn. S2.20) parallels a standard two-species Lotka-Volterra competition model, with the α terms reflecting the effects both of competition and of microbial interactions:

$$\frac{1}{N_A}\frac{\mathrm{d}N_A}{\mathrm{d}t} = g_1(1 - \alpha_{11}N_1 - \alpha_{12}N_2)$$

Following Chesson (2012) the niche overlap ρ for this model can be expressed as follows:

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} = \sqrt{\frac{(c_{12} - \frac{m_{1B} v_{B2}}{q_B})(c_{21} - \frac{m_{2A} v_{A1}}{q_A})}{(c_{11} - \frac{m_{1A} v_{A1}}{q_A})(c_{22} - \frac{m_{2B} v_{B2}}{q_B})}} \tag{Eqn. S2.23}$$

Following Godoy and Levine (2014), the fitness difference is expressed as follows:

$$\frac{\kappa_2}{\kappa_1} = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}} = \sqrt{\frac{(c_{11} - \frac{m_{1A}v_{A1}}{q_A})(c_{12} - \frac{m_{1B}v_{B2}}{q_B})}{(c_{22} - \frac{m_{2B}v_{B2}}{q_B})(c_{21} - \frac{m_{2A}v_{A1}}{q_A})}} \quad \text{(Eqn. S2.24)}$$

As explained in Eqn. 2.9 of the main text, species can coexist when the strength of stabilization exceeds the fitness difference as follows (Chesson and Kuang 2008):

$$\rho < \frac{\kappa_2}{\kappa_1} < \frac{1}{\rho} \quad \text{(Eqn. S2.25)}$$

Algebra shows that this condition is equivalent to the standard coexistence criterion in two-species Lotka Volterra competition model, in which stable is coexistence is possible when each species limits itself more than it limits the competitor. The left hand side of the inequality in Eqn. S2.25 can be expressed as follows:

$$\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} < \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}}$$

Or equivalently,

$$\frac{\alpha_{21}}{\alpha_{11}} < \frac{\alpha_{11}}{\alpha_{21}}$$

Which requires that $\alpha_{21} < \alpha_{11}$. Simplifying the right hand side of the coexistence inequality similarly leads to the requirement that $\alpha_{12} < \alpha_{22}$.

Interaction terms in a model with microbe competition

In the main text we assume that interactions between the microbial communities cultivated by plants 1 and 2 are weak and do not impact the dynamics of S_A and S_B, an

assumption we relax here. In this model we maintain plant dynamics as in Eqn. 2.1 of the main text, and model the plant dynamics as follows:

$$\frac{1}{S_A}\frac{dS_A}{dT} = v_{A1}N_1 - q_{AA}S_A - q_{AB}S_B$$

where q_{AA} represents the density-dependent mortality rate due to competition within S_A, and q_{AB} represents the density-dependent competitive effects of S_B on microbial community A.

As in the analysis above, we assume that microbial dynamics operate faster than plant dynamics, and derive an expression for the equilibrium value of S_A:

$$S_A^* = \frac{v_{A1}N_1 - \frac{q_{AB}}{q_{BB}}v_{B2}N2}{q_{AA}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)}$$

Similarly, the equilibrium value of S_B is as follows:

$$S_B^* = \frac{v_{B2}N_2 - \frac{q_{BA}}{q_{AA}}v_{A1}N_1}{q_{BB}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)}$$

Substituting the above expressions for S_A and S_B into Eqn. 2.1 of the main text yields the following dynamics equation for the focal plant populations:

$$\frac{1}{N_1}\frac{dN_1}{dT} = g_1\left(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}\left(\frac{v_{A1}N_1 - \frac{q_{AB}}{q_{BB}}v_{B2}N_2}{q_{AA}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)}\right) + m_{1B}\left(\frac{v_{B2}N_2 - \frac{q_{BA}}{q_{AA}}v_{A1}N_1}{q_{BB}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)}\right)\right)$$

As in the previous analysis, we can collect the per-capita inter-specific effects via competition and microbial interactions into a single term α_{12}, which describes the effect of an individual of species 2 on the dynamics of species 1:

$$\alpha_{12} = c_{12} + \frac{m_{1A}\frac{q_{AB}}{q_{BB}}v_{B2}}{q_{AA}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)} - \frac{m_{1B}v_{B2}}{q_{BB}\left(1 - \frac{q_{AB}q_{BA}}{q_{AA}q_{BB}}\right)}$$

The niche and difference terms for this model can then be derived as in the previous analysis.

Mapping our microbe density-based model onto Bevers' frequency-based framework

Although fully parameterizing our extended plant-soil feedback model, which models microbial dynamics in terms of their density rather than their frequency, requires a detailed understanding of microbial population dynamics that may be difficult to achieve in many natural systems, making some assumptions regarding these microbial dynamics shows that the insights our extended framework projects onto Bever (2003)'s model. We redefine the m terms as the per-capita effects of microbes on plants, scaled by the degree to which plants cultivate their microbial community and the persistence of the microbial community, i.e. $m'_{1A} = (m_{1A}v_{A1})/q_A$ and $m'_{1B} = (m_{1B}v_{B2})/q_B$. As empirical studies rarely quantify microbial dynamics, these rescaled m terms are more representative of the microbial effects measured in these studies. With this simplifications to our model equations, can rewrite Eqn. S2.20 as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = g_1\left(1 - \left(c_{11} - m'_{1A}\right)N_1 - \left(c_{12} - m'_{1B}\right)N_2\right) \qquad \text{(Eqn. S2.26)}$$

Following the logic in the main text, we focus our analysis on cases when plants have net negative effects on their neighbors, i.e. $c_{11} - m'_{1A} > 0$ and $c_{12} - m'_{1B} > 0$. Evaluating Eqn. S2.26 at the single-species equilibrium of N_2 shows that the invasion growth rate of N_1 is as follows:

$$\text{IGR}_1 = g_1 \left(1 - \frac{(c_{12} - m'_{1B})}{(c_{22} - m'_{2B})}\right)$$

An analogous expression exists for the invasion growth rate of N_2. N_1 has a positive growth rate provided that $(c_{12} - m'_{1B}) < (c_{22} - m'_{2B})$. Assuming that both species are equal competitors (i.e. $c_{12} = c_{22}$, as was done in our analysis of the Bever (2003) model, Appendix S1), $\text{IGR}_1 > 0$ if $m'_{1B} > m'_{2B}$. N_2 can similarly invade when rare (i.e. there is mutual invasibility, and stable coexistence is possible) if $m'_{2A} > m'_{1A}$. This is the identical coexistence criterion from our analysis of the Bever (2003) model (Appendix S1).

Multispecies extension of the Lotka-Voterra competition/microbial interaction model

We now describe the generalized Lotka-Volterra model of competition and plant-microbial interactions that is used to model Scenario 3 in the main text. To do so we extend Eqns. 1 and 5 from the main text to model plant-microbe interactions in multispecies plant communities by developing a more generalized Lotka-Volterra model with plant dynamics modeled as follows:

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = g_i(1 - \sum_j c_{ij}N_j + \sum_k m_{ik}S_k) \qquad \text{(Eqn. S2.27)}$$

As before, the growth of each microbe k is influenced by the effects of all plants j:

$$\frac{1}{S_k}\frac{\mathrm{d}S_k}{\mathrm{d}t} = \sum_j v_{kj}N_j - q_k S_k \qquad \text{(Eqn. S2.28)}$$

Table S2.1: Parameter definitions in Bever's model and our extension

Term	Units and Definition in Bever (2003) model	Units and Definition in our extended model
N_i	Number [of plants]; Population size of plant i	*same as in Bever (2003)*
S_A	Dimensionless; proportion of soil community that reflects the microbes cultivated by plant species 1	Number [of microbes]; Abundance of microbial community A
S_B	Dimensionless; proportion of soil community that reflects the microbes cultivated by plant species 2 (constrained to equal $1 - S_A$)	Number [of microbes]; Abundance of microbial community B
g_i	T^{-1}; intrinsic rate of growth for plant species i	*same as in Bever (2003)*
c_{ij}	(Number [of plants])$^{-1}$; per-capita competitive effect of species j on species i	*same as in Bever (2003)*
m_{ij}^1	T^{-1}; Effect of soil microbial community j on plant species i	(Number of microbes)$^{-1}$; per-capita effect of microbial community j on plant species i
v	Dimensionless; rate at which plant species 2 cultivates its microbial community, relative to the rate at which plant species 1 cultivates its microbial community	NA
v_{ij}	NA	(Number [of plants])$^{-1}$; per-capita rate at which plant species j cultivates microbial community i
q_i	NA	(Number [of microbes])$^{-1}$; Density-dependent mortality rate of microbial community i
f_i	NA	Intrinsic growth rate of microbial community i (set to zero in all analyses in the main text)

[1] Bever et al. (1997) define m_{ij} as the growth of plant i with microbial community j minus growth of plant i on uncultivated soil

Although the coexistence criteria from the two-species model does not apply in this multispecies extension (Barabás et al. 2016; Chesson 2018), parameterizing this model with multiple plant and microbe communities can yield insight into dynamics of natural communities (see Appendix S4). In the Scenario 3 of the main text, we parameterize this model such that each pairwise interaction between plants results in exclusion of the weaker competitor, but the intransitive/rock-paper-scissors dynamic generated by the microbes permits stable coexistence of all three species. The parameter values used for this scenario are provided in Table S3.2.

Appendix 2.3: Parameter values used in main text scenarios

In this Appendix, we first list the parameter values used in the Main Text scenarios S1, S2 and S3 (Tables 2.2 and 2.3). Then, in Fig S2.1, we show how the three species pairs from Scenario 3 map on to the plot of niche and fitness differences. Finaly, we present an additional scenario using the multispecies model to show that the network of microbially mediated fitness differences can cause exclusion in multispecies communities even when microbes stabilize each pairwise plant interaction.

Parameter values used in the three scenarios of the Main Text

Table S2.2: Parameter values used in Scenarios 1-2 from the main text. In addition to the parameters in the table, $g_1 = g_2 = 1$ in both scenarios

	Competition coefficients				Microbe effects on plant				Microbe cultivation rates				Net outcome		Outcome due to microbes alone		Outcome due to competition alone							
	c_{11}	c_{12}	c_{21}	c_{22}	m_{1A}	m_{1B}	m_{2A}	m_{2B}	v_{A1}	v_{A2}	v_{B1}	v_{B2}	ρ	κ_2/κ_1	ρ^{micr}	κ_2/κ_1^{micr}	ρ^{comp}	κ_2/κ_1^{comp}	ρ	κ_2/κ_1	ρ^{micr}	κ_2/κ_1^{micr}	ρ^{comp}	κ_2/κ_1^{comp}
Scenario 1	3e-03	0.0024	0.002	0.004	-0.050	-0.040	-0.01	-0.021	0.005	0	0	0.005	0.62146	2.48582	0.61721	3.08607	0.63246	0.94868	0.62146	2.48582	0.61721	3.08607	0.63246	0.94868
Scenario 2	5e-04	0.0010	0.001	0.002	-0.025	-0.025	-0.01	-0.010	0.005	0	0	0.005	0.87831	1.02470	1.00000	2.50000	1.00000	0.50000	0.87831	1.02470	1.00000	2.50000	1.00000	0.50000

Table S2.3: Parameter values used in Scenario 3 from the main text. In addition to the parameters in the table, the following parameters were used for the scenario: all competition coefficients $c_{ij} = 0.002$; $g_1 = g_2 = g_3 = 0.2$; $q_A = q_B = q_C = 0.01$

Microbe effects on plant 1			Microbe effects on plant 2			Microbe effects on plant 3			Microbe cultivation by plant 1			Microbe cultivation by plant 2			Microbe cultivation by plant 3		
m_{1A}	m_{1B}	m_{1C}	m_{2A}	m_{2B}	m_{2C}	m_{3A}	m_{3B}	m_{3C}	v_{A1}	v_{B1}	v_{C1}	v_{A2}	v_{B2}	v_{C2}	v_{A3}	v_{B3}	v_{C3}
-0.006	-0.005	-0.0133333	-0.0065	-0.0085	-0.0075	-0.00375	-0.009	-0.01	0.01	0	0	0	0.01	0	0	0	0.01

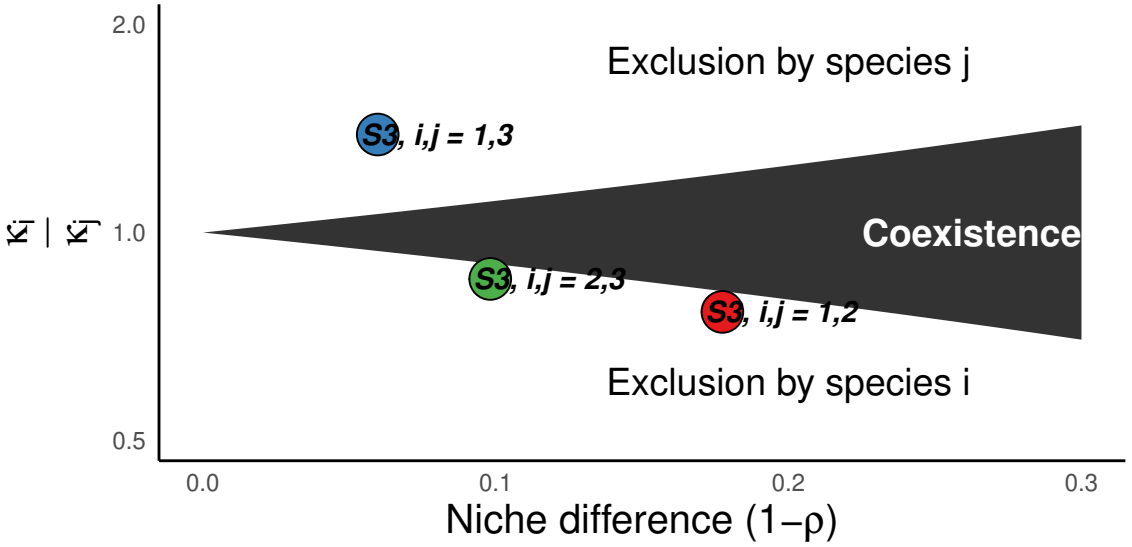

Figure S2.1: In Scenario 3 of the main text, microbially mediated stabilization is insufficient to overcome microbially mediated plant fitness differences in all three species pairs; however, because each species has an advantage over exactly one other species (specifically, Species 1 over Species 2; Species 2 over Species 3; and Species 3 over Species 1), all three can coexist in a three-species community.

Microbially mediated fitness differences can cause exclusion in multispecies systems

Here we parameterize a scenario (Scenario S3.b) with the multispecies extension of our plant-soil feedback (see Appendix S2) such that microbes stabilize coexistence between three plant species pairs that have complete competitive niche overlap (i.e. all c's are equal, Table S3.3). In this system , microbially mediated stabilization is stronger than the fitness differences in any given species pair, such that each two-species combination can coexist (Fig. S2.2B-D; Fig. S2.3). However, plant species 3 is on average inferior to both plants 1 and 2, and when all three plants are present in the system, the microbially mediated fitness differences drive the exclusion of plant species 3 (Fig. S2.2A).

Microbe effects on plant 1			Microbe effects on plant 2			Microbe effects on plant 3			Microbe cultivation by plant 1			Microbe cultivation by plant 2			Microbe cultivation by plant 3		
m_{1A}	m_{1B}	m_{1C}	m_{2A}	m_{2B}	m_{2C}	m_{3A}	m_{3B}	m_{3C}	v_{A1}	v_{B1}	v_{C1}	v_{A2}	v_{B2}	v_{C2}	v_{A3}	v_{B3}	v_{C3}
-0.0075	-0.005	-0.005	-0.005	-0.0065	-0.005	-0.007	-0.006	-0.006	0.01	0	0	0	0.01	0	0	0	0.01

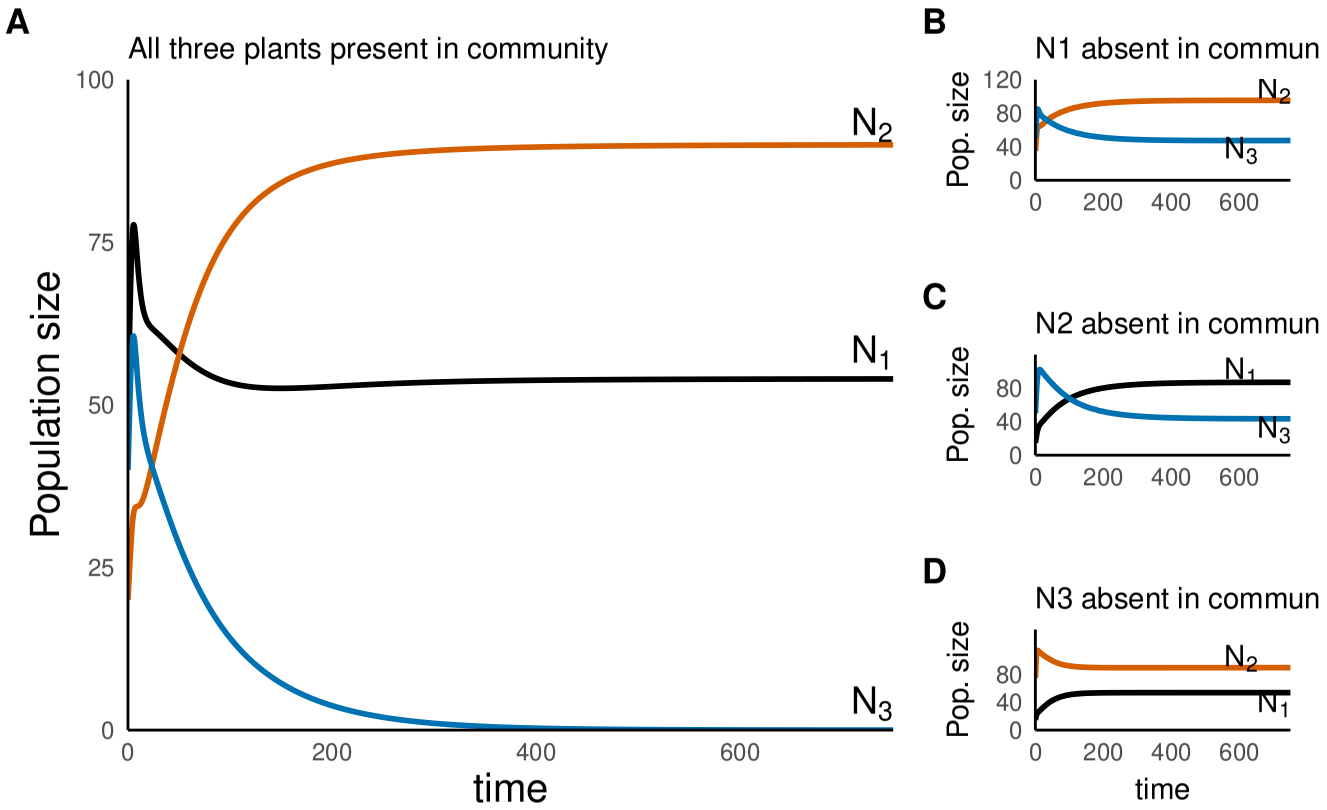

Figure S2.2: Trajectories for the scenario S3.b described above. Microbially mediated fitness differences can result in the exclusion of a species in multispecies communities (panel A) even when any single species pair can stably coexist (panels B-D).

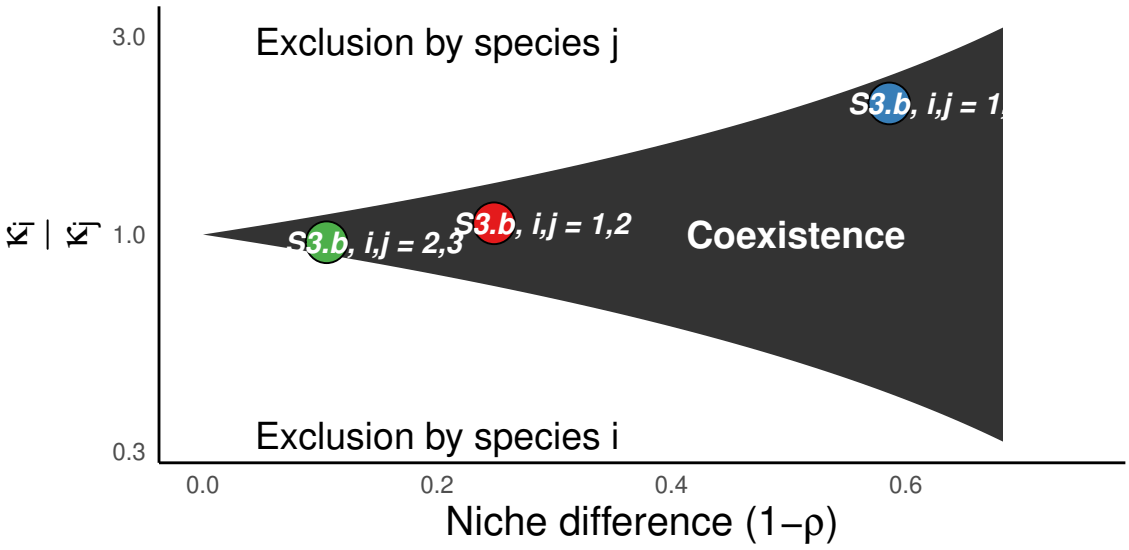

Figure S2.3: Each species pair in Scenario S3.b above can stably coexist according to the pairwise fitness and niche differences.

Appendix 2.4: Connecting plant-microbe interactions to classic apparent competition models

The plant microbe interaction model developed here allows comparisons with other consumer resource models and extensions to any number of microbes or microbial community subsets. For example, we may wish to investigate the consequences of particular microbial species or community of interest (e.g. an emergent pathogen or decomposing fungi as a guild) on plant diversity. This is difficult to conceptualize with the classic plant-soil framework, which requires there to be as many distinct microbial community types as there are plant species. However, we can extend the framework we use here to divide the microbial community into as many guilds or species as are of interest in any given study (Eqn. S2.27-Eqn. S2.28 in Appendix 2). For example, we may wish to study the effects of plant-microbial interactions on plant diversity in a system in which plants interact with specialist soilborne pathogens and a generalist mutualist community (e.g. Figure S2.4A), a scenario that is quite likely in natural communities (Smith and Read 2008; Sarmiento et al. 2017). We demonstrate the ability to consider such a case in our framework using the multispecies extension in Appendix 2. We parameterize a scenario in which the specialist pathogens of two plant species create enough niche differentiation to stabilize coexistence (Fig. S2.4B, S2.4C). We add a third microbe in this scenario that has a mutualism with both plant species. If the mutualist microbe provides a stronger benefit to one plant species than the other, as it does here, the mutualist microbe can create a fitness difference that is stronger than the stabilizing effects of specialist pathogenic interactions (Fig S2.4B, S2.4D). The ability to explicitly model the effects of particular microbes or microbial guilds may provide a framework for unifying empirical work on plant-soil feedback with other major branches of research on the effects of particular groups of soil microbes in plant com-

munities, such as the effect of ectomycorrhizal fungi in driving monodominance in tropical tree communities (Hart et al. 1989; Corrales et al. 2016).

Table S2.4: Parameter values used in Figure S2.4. In addition to the values in the table, the following parameters were used: all competition coefficients $c_{ij} = 0.01$; $g_1 = g_2 = 1$, $q_A = q_B = 0.01$; $q_C = 0.005$

	m_{1A}	m_{1B}	m_{1C}	m_{2A}	m_{2B}	m_{2C}	v_{A1}	v_{A2}	v_{B1}	v_{B2}	v_{C1}	v_{C2}
Pathogens Only	-0.02	0	-	0	-0.01	-	0.001	0	0	0.001	-	-
All microbes	-0.02	0	0.001	0	-0.01	0.02	0.001	0	0	0.001	0.001	0.001

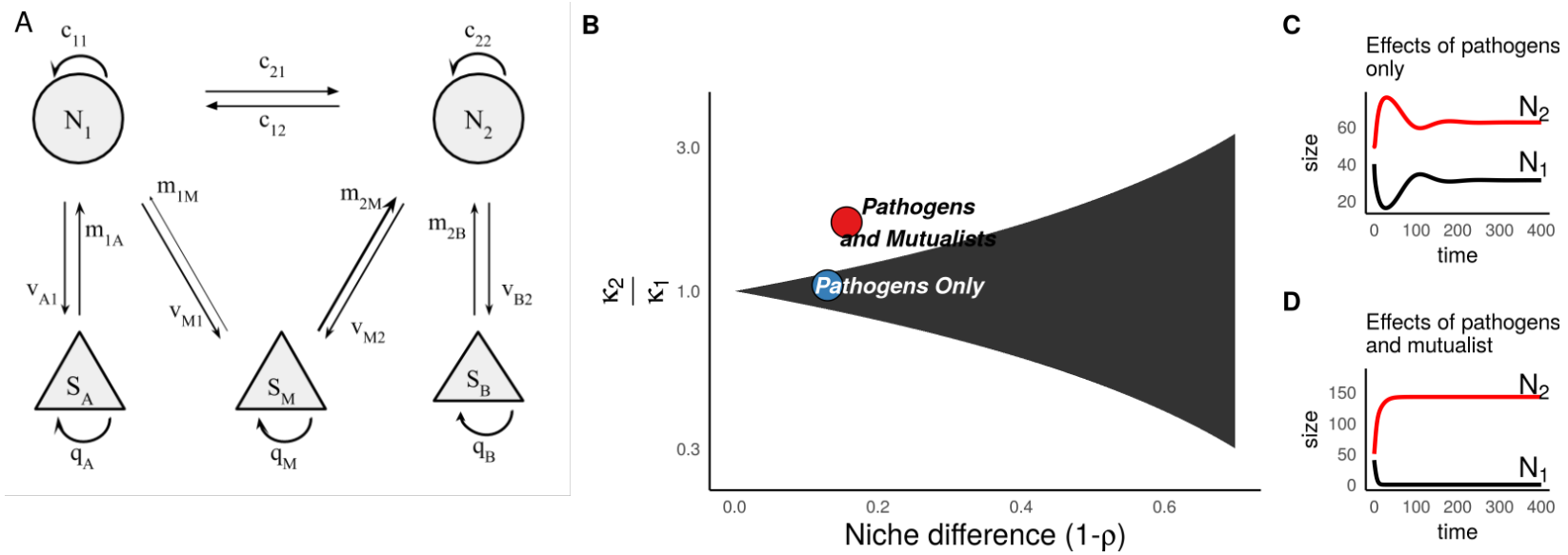

Figure S2.4: The effects of the soil community on plant diversity can be decomposed into the effects of particular microbial species or guilds under our framework. We consider a scenario in which the net effect of the microbial community is to drive the exclusion of plant 1; however, this outcome is primarily due to the effect of a generalist mutualist that favors plant 2 more than plant 1. In the absence of this mutualist, the specialist pathogen communities of both plants promote their coexistence

Appendix 2.5: Deriving interaction parameters in the resource competition model

In this appendix we derive the expressions for niche and fitness differences for the mechanistic resource competition model. In this system, we model the populations of plants N_1 and N_2, which grow by consuming resources R_l at a rate u. Plants have a maintenance cost μ, and convert excess resources into plant population growth.

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = \sum_l u_{1l}R_l + \sum_A m_{1A}S_A - \mu_1 \qquad \text{(Eqn. S2.29)}$$

Resources have logistic growth with an intrinsic rate of growth r_l until a carrying capacity of $1/s_l$. The resource pool is depleted as it gets consumed by plants 1 and 2:

$$\frac{1}{R_l}\frac{\mathrm{d}R_l}{\mathrm{d}t} = r_l(1 - s_l R_l) - u_{1l}N_1 - u_{2l}N_2 \qquad \text{(Eqn. S2.30)}$$

Following Chesson (1990) and Chesson and Kuang (2008), we analyze this model in terms of fitness and niche differences by assuming that nutrient dynamics operate faster the dynamics of plant communities. This allows us to express the equilibrium of the resource pool at any given plant abundance as follows:

$$R_l^* = \frac{r_l - u_{1l}N_1 - u_{2l}N_2}{s_l r_l} \qquad \text{(Eqn. S2.31)}$$

Microbial dynamics and their effects on plant growth remain the same as in the main text Eqns. 1 and 3. Thus, we can substitute the equilibrium abundance of microbes from Eqn. S2.19 (Appendix 2) and the equilibrium resource concentration from Eqn. S2.31 (this appendix) into the plant growth model (Eqn. S2.29) to express plant dy-

namics as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = \sum_l \frac{u_{1l}}{s_l} - \sum_l \frac{u_{1l}^2 N_1}{s_l r_l} - \sum_l \frac{u_{1l}u_{2l}N_2}{s_l r_l} + \frac{m_{1A}v_{A1}N_1}{q_A} + \frac{m_{1B}v_{B2}N_2}{q_B} - \mu_1 \tag{Eqn. S2.32}$$

We can now collect all the terms that describe the effect of species 2 on the growth of species 1 into a single term that accounts for the effects via resource competition and via microbial feedbacks. We denote this term $\alpha_{12}^{'}$ to distinguish it from the interaction coefficient in the earlier model.

$$\alpha_{12}^{'} = \frac{\sum_l \frac{u_{1l}u_{2l}}{s_l r_l} - \frac{m_{1B}v_{B2}}{q_B}}{\sum_l \frac{u_{1l}}{s_l} - \mu_1} \tag{Eqn. S2.33}$$

Note that the denominator in this expression of α_{12} is required to make the term have the same units as the interaction parameters in the Lotka-Volterra model, i.e. the proportional reduction in the intrinsic growth rate of species 1 due to species 2 (Godoy and Levine 2014).

We now use the interaction term in Eqn. S2.33 to define niche overlap as follows (Chesson 2012):

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} = \sqrt{\frac{\left(\sum_l \frac{u_{1l}u_{2l}}{s_l r_l} - \frac{m_{1B}v_{B2}}{q_B}\right)\left(\sum_l \frac{u_{2l}u_{1l}}{s_l r_l} - \frac{m_{2A}v_{A1}}{q_A}\right)}{\left(\sum_l \frac{u_{1l}^2}{s_l r_l} - \frac{m_{1A}v_{A1}}{q_A}\right)\left(\sum_l \frac{u_{2l}^2}{s_l r_l} - \frac{m_{2B}v_{B2}}{q_B}\right)}} \tag{Eqn. S2.34}$$

The fitness difference is written as follows (Godoy and Levine 2014):

$$\kappa_2/\kappa_1 = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{21}\alpha_{22}}} = \frac{\sum_l \frac{u_{2l}}{s_l} - \mu_2}{\sum_l \frac{u_{1l}}{s_l} - \mu_1}\sqrt{\frac{\left(\sum_l \frac{u_{1l}^2}{s_l r_l} - \frac{m_{1A}v_{A1}}{q_A}\right)\left(\sum_l \frac{u_{1l}u_{2l}}{s_l r_l} - \frac{m_{1B}v_{B2}}{q_B}\right)}{\left(\sum_l \frac{u_{2l}u_{1l}}{s_l r_l} - \frac{m_{2A}v_{A1}}{q_A}\right)\left(\sum_l \frac{u_{2l}^2}{s_l r_l} - \frac{m_{2B}v_{B2}}{q_B}\right)}} \tag{Eqn. S2.35}$$

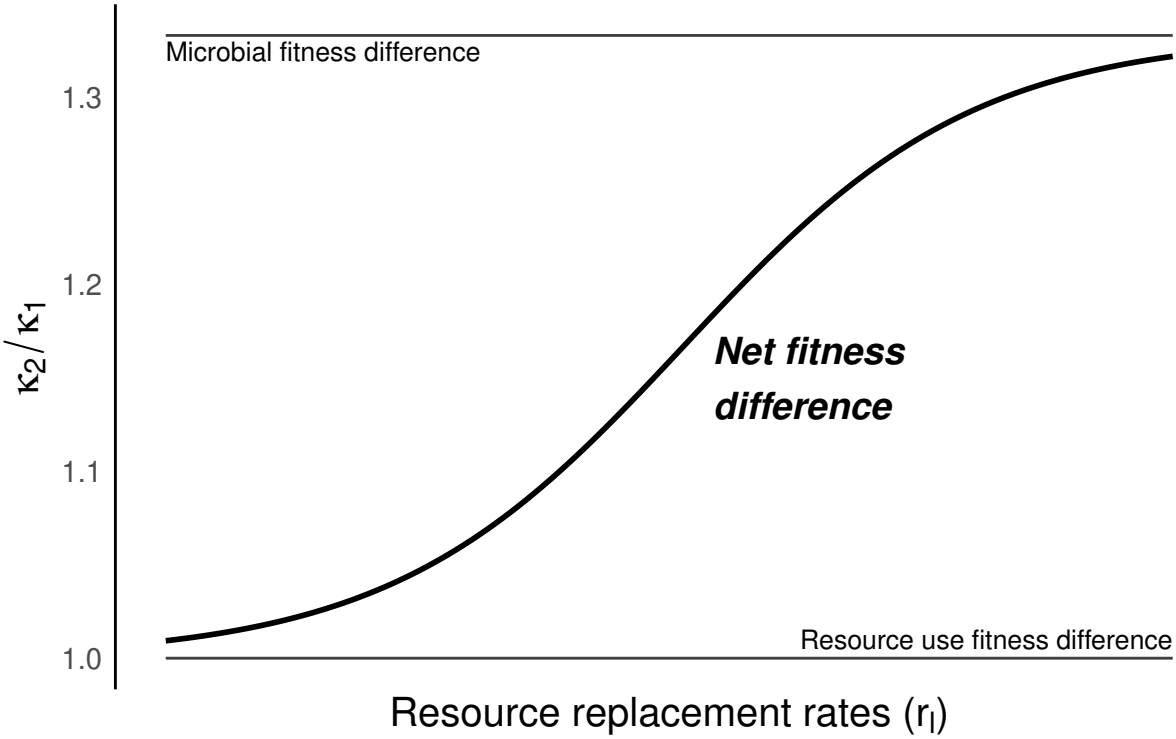

Figure S2.5: The net fitness difference is more strongly influenced by the microbially mediated fitness differences when resource replacement rates are high

The relative influence of microbial interactions on plant fitness differences increases with site productivity

In the Main Text (Fig. 2.4B) we show that the net niche overlap between competing plant species is more strongly determined by the strength of their microbial niche overlap than by their resource-mediated niche overlap at highly productive sites, and vice-versa at low productivity sites. Fig. S2.5 shows that a similar result holds for plant fitness differences:

Varying microbial effects with resource replacement rates

In the model analysis in the main text, we make predictions regarding the relative contribution of plant-microbe interactions and resource competition to niche differences while keeping the per-capita effect of microbes on plant performance constant across the resource gradient. Our modeling approach allows us to relax this assumption, for example to consider a scenario in which the microbial effects on plant performance switch from primarily mutualistic (positive m terms) at low resource sites (low values of r_l) to primarily pathogenic (negative m terms) at high resource sites (Revillini et al. 2016; van der Putten et al. 2016). To do so, we maintain the plant, resource, and microbe dynamics equations as above, and simulate a system in which the m terms are linear functions of the the resource replacement rate (r_l). We parameterize the scenario such that at low r_l, the net effects of microbes on plants are positive, whereas at high r_l, the net effects of microbes on plants are negative (Figure S2.6A).

We find that allowing the m terms to be negative linear function of the resource replacement does not change our result that the influence of microbial niche overlap on net niche overlap grows with inreasing resource replacement rates (Figure S2.6B). Interestingly, we find in this simulation that in low resource environments, positive effects of microbes on plants can cause the net plant niche overlap to be *lower* than the niche overlap predicted by resource competition alone, a result that is not possible if plant-microbe interactions are constant across the resource gradient.

Abiotic resource model

We now show that qualitative results from our model analysis hold when resource dynamics are modeled following an abiotic resource model (Stewart and Levin 1973; Tilman 1977). In this model, microbial and plant dynamics remain the same as in Eqns.

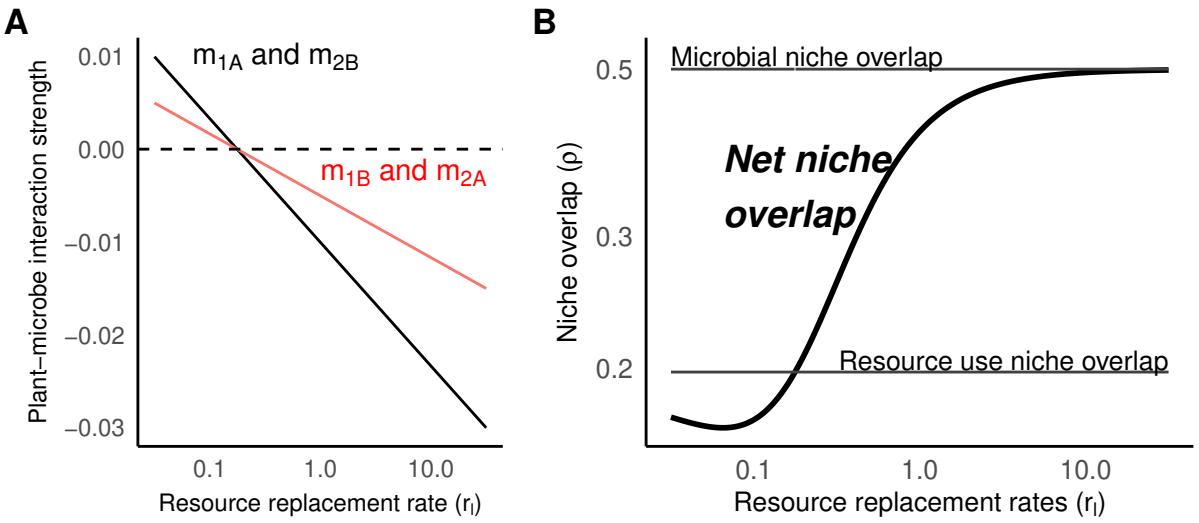

Figure S2.6: Microbes more strongly drive net pairwise stabilization when resource replacement rates are high, even when microbial effects vary along the resource gradients

1 and 3 from the main text. Resource dynamics are now dictated by a chemostat model in which resources enter the system until they are at a maximum I, and as before, are depleted as they are consumed by plants:

$$\frac{\mathrm{d}R_l}{\mathrm{d}t} = I_l - R_l - u_{1l}R_lN_1 - u_{2l}R_lN_2 \qquad \text{(Eqn. S2.36)}$$

Again following the separation of timescales assumption, the equilibrium resource concentration R_l is as follows:

$$R_l^* = \frac{I_l}{1 - u_{1l}N_1 - u_{2l}N_2} \qquad \text{(Eqn. S2.37)}$$

We use the Taylor series approximation that $\frac{a}{b+c} \approx \frac{a}{b}(1-c)$ to rewrite Eqn. S2.37 as follows:

$$R_l^* = I_l - u_{1l}N_1I_l - u_{2l}N_2I_l \qquad \text{(Eqn. S2.38)}$$

We can now substitute the equilibrium abundance of microbes from Eqn. B3 (Appendix B) and the equilibrium resource concentration from Eqn. E8 into the plant growth model (Eqn. E1) to express plant dynamics as follows:

$$\frac{1}{N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} = \sum_l u_{1l} I_l - \sum_l u_{1l}^2 I_l N_1 - \sum_l u_{1l} u_{2l} N_2 I_l + \frac{m_{1A}}{q_A}(v_{A1} N_1 + v_{A2} N_2) - \mu_1 \quad \text{(Eqn. S2.39)}$$

We can group the effects of species 2 on species 1 to express α_{12} as follows:

$$\alpha_{12}^{'} = \frac{\sum_l u_{1l} u_{2l} I_l - \frac{m_{1B} v_{B2}}{q_B}}{\sum_l u_{1l} I_l - \mu_1} \quad \text{(Eqn. S2.40)}$$

The niche and fitness differences can now be calculated as above (Eqn. S2.34 and Eqn. S2.35).

Chapter 3

Soil microbes generate stronger fitness differences than stabilization among California annual plants

This chapter is in press as Kandlikar, G.S., Yan, X., Levine, J.M., and Kraft, N.J.B. Soil microbes generate stronger fitness differences than stabilization among California annual plants. *The American Naturalist* (expected to be published in Volume 197, 2021). It is also available as a pre-print on BioRXiv (Kandlikar et al. 2020).

GSK conceived the problem with NJBK and JML. GSK led the research with XY and all authors provided input. GSK wrote the manuscript and all authors contributed revisions.

Abstract

Soil microorganisms influence a variety of processes in plant communities. Many theoretical and empirical studies have shown that dynamic feedbacks between plants and soil microbes can stabilize plant coexistence by generating negative frequency-dependent plant population dynamics. However, inferring the net effects of soil microbes on plant coexistence requires also quantifying the degree to which they provide one species an average fitness advantage, an effect that has received little empirical attention. We conducted a greenhouse study to quantify microbially mediated stabilization and fitness differences among fifteen pairs of annual plants that co-occur in southern California grasslands. We found that although soil microbes frequently generate negative frequency-dependent dynamics that stabilize plant interactions, they simultaneously generate large average fitness differences between species. The net result is that if the plant species are otherwise competitively equivalent, the impact of plant-soil feedbacks is to often favor species exclusion over coexistence, a result that only becomes evident by quantifying the microbially mediated fitness difference. Our work highlights that comparing the stabilizing effects of plant-soil feedbacks to the fitness difference they generate is essential for understanding the influence of soil microbes on plant diversity.

Introduction

The dynamics of plants and soil microorganisms are tightly intertwined. The composition of soil microbial communities responds strongly to different plant species, in large part due to variation in plant species' root exudate profiles and immune responses (Berg and Smalla 2009). Soil microorganisms in turn influence the growth of plant species, with the direction and magnitude of their effect determined both by the composition of the microbial community and by the genetic and functional characteristics of the plants (Laliberté et al. 2014; Keller and Lau 2018). These plant-soil feedbacks can have important consequences for various processes in plant communities (van der Putten et al. 2016), including species coexistence.

The effects of soil microorganisms on plant species coexistence are typically studied in the context of a theoretical framework developed by Bever et al. (1997). This framework isolates the effects of soil microbes by modeling the dynamics of plant species that differ only in the soil microbial communities they cultivate and in how their growth is influenced by these cultivated communities. Bever et al. (1997) showed that the soil microbial community stabilizes plant interactions when the microbial community cultivated by each plant species limits the growth of the cultivating plant species more (or benefits it less) than that of the other plant species in the system. When this condition is satisfied, the microbial community generates a relative advantage in favor of species that decline to low abundances as opposed to those that remain abundant, thereby generating negative frequency-dependent plant population dynamics that should promote species coexistence. Alternatively, plant-soil feedbacks can destabilize plant interactions if they create positive feedback loops that favor abundant species over species that are rare. Results from numerous empirical studies motivated by this framework indicate that plant-soil feedbacks often drive such frequency-

dependent plant population dynamics. Feedbacks most strongly stabilize interactions among distantly related plant species that associate with similar mycorrhizal guilds and interact with one another in their native range (reviewed in Crawford et al. (2019)).

Although plant-soil feedback research has revealed the potential for these interactions to influence species diversity in plant communities, we still lack a general understanding of whether soil microbes generally favor plant coexistence or species exclusion. This is in part because inferring the coexistence consequences of plant-soil feedbacks from their stabilizing or destabilizing effects alone is incomplete. More specifically, theoretical and empirical studies of plant-soil feedback have emphasized the potential stabilizing or destabilizing effects of soil microbes, but have largely neglected the potential for soil microbes to mediate an average fitness difference between competing plants (but see Chung and Rudgers 2016; Siefert et al. 2019). Not comparing the (de)stabilizing effects to the degree to which soil microbes mediate an average fitness difference between plant species can lead to false conclusions about how soil microbes influence plant diversity (Chesson 2000; Kandlikar et al. 2019). This microbially mediated fitness difference reflects plant species' variation in their average sensitivity to the pathogenic or mutualistic soil microbes cultivated by both conspecifics and heterospecifics. In the classic plant-soil feedback model (Bever et al. 1997), species coexistence is only possible when the stabilizing effects of plant-soil feedbacks exceed the microbially mediated fitness difference, while soil microbes drive species exclusion when they mediate larger fitness differences than stabilization (Kandlikar et al. 2019). In more complex models that incorporate other competitive asymmetries among plants, microbially mediated fitness differences can accelarate species exclusion if they exaggerate competitive asymmetries, but could also promote species coexistence if they favor the otherwise weaker competitor (Bever 2003; Kandlikar et al. 2019; Ke and Wan

2019).

Empirically quantifying microbially mediated stabilization and fitness differences simply requires data from a standard two-phased feedback experiment (Bever et al. 2010), with an additional treatment in the second phase to quantify plant growth in a reference uncultivated soil microbial community (Kandlikar et al. 2019). The reference soil community should reflect the field soil microbial community when the focal plant species are absent (or very rare) in the system, i.e. the microbial community of field soil that has not been conditioned by any of the focal plant species. Though the two-phased feedback design has been used to study plant-soil feedbacks among hundreds of plant species pairs (Crawford et al. 2019), the reference soil experimental treatment is excluded in most studies of plant-soil feedback. Microbially mediated fitness differences can also be quantified by parameterizing population growth models with data from more complex experiments that vary both the soil microbiota and the relative frequency of focal species (e.g. Chung and Rudgers 2016; Siefert et al. 2019), though such experiments are less common because they require manipulations that are not possible in many systems. Moreover, while previous studies have identified microbially mediated fitness differences, it has not been done in a way that allows easy quantitative comparison to the (de)stabilizing effects of soil microbes documented in a majority of the plant-soil feedback literature, as is possible with the modified two-phased feedback design (Kandlikar et al. 2019).

To evaluate the influence of microbially mediated stabilization and fitness differences on plant coexistence, we conducted a two-phased experiment (Bever et al. 2010) in which we first grew monocultures of six plant species to cultivate their characteristic soil microbial community, and then measured the growth of each species in soils inoculated with a distinct microbial community – including a field-collected microbial

inoculum that was not cultivated by any of the focal species. We used these data to estimate the key parameters from Bever et al. (1997)'s model of plant-soil feedback. Then, we quantified the degree to which soil microbes stabilize or destabilize pairwise plant interactions and the degree to which they drive average fitness differences using metrics derived in Kandlikar et al. (2019). Our study shows that even when plant-soil feedbacks stabilize species interactions, their net effect can be to favor species exclusion if they simultaneously drive strong fitness differences between plant species.

Methods

Study system

We studied the effects of plant-soil feedbacks on the pairwise interactions of six annual plant species: *Acmispon wrangelianus* (Fabaceae), *Festuca microstachys* (Poaceae), *Hordeum murinum* (Poaceae), *Plantago erecta* (Plantaginaceae), *Salvia columbariae* (Lamiaceae), and *Uropappus lindleyi* (Asteraceae). These species co-occur in the winter annual plant community in the University of California Sedgwick Reserve in Santa Barbara County, California, USA (34 41' N, 120 02' W, 290-790m above sea level). This region experiences a Mediterranean climate of cool, wet winters (October-May mean temperature = 13.5°C, mean monthly precipitation = 164mm) and hot, dry summers (June-September mean temperature = 20°C, mean monthly precipitation = 3.7mm). Seeds of the annual plants in this system germinate after rainstorms begin early in the winter, and plants complete their life cycle before the onset of the summer drought. The focal species of this experiment commonly grow together near outcrops of serpentine soil that are characterized by a low Ca:Mg ratio (Gram et al. 2004). As is common across southern California grasslands, large portions of the reserve are dominated by invasive annual grasses, especially *Avena* and *Bromus* species (Gram et al. 2004; D'Antonio

et al. 2007).

Experiment Phase 1: Cultivating species-specific microbial communities

To cultivate the microbial community characteristic of each species' soil, we grew five replicate high-density monocultures (8g viable seed/m^2) of each species in sterilized 3.6L pots. These pots were filled with 3L greenhouse soil (18.75% sand, 18.75% loam, 37.5% peat moss, 12.5% perlite, and 12.5% vermiculite) that we had autoclaved twice for 2 hours each, with a 1-day rest period. To this sterile background we added 0.35L of field-collected inoculum, and capped this layer with 0.15L of sterilized greenhouse soil. This resulted in 10% v/v of live inoculum:sterile soil. We collected the inoculum soil in Sedgwick reserve 1 week prior to the experiment and stored it at 0°C until planting. To ensure that the microbial community of this field soil was not pre-conditioned by any of the species in our experiment, we ensured that there were no individuals of our six focal species growing in a 1m radius around the five distinct points at which we collected the soil (the dominant plant around these points was the invasive grass *Avena fatua*, which is one of the most abundant plant species in this landscape).

We grew plants from seeds collected in Sedgwick reserve in the spring prior to the experiment. We surface-sterilized these seeds by soaking in 0.785% bleach for 3 minutes and washing in DI water twice for 1 minute each. After planting seeds, we stored the pots at 0°C for one week to trigger germination. We began this phase of the experiment in February 2019 and allowed plants to grow in standard greenhouse conditions for 11 weeks. At the end of Phase 1, we harvested the aboveground biomass from each pot and homogenized the soil from the five replicate monocultures of each species to serve as the inoculum for the following phase of the experiment. We also saved soil samples from each replicate monoculture of *Plantago erecta* to use as the inoculum in a parallel experiment aimed to assess whether homogenizing across repli-

cate cultivations influences the effects of cultivated soils on plant growth, described in Supplement S2.

Experiment Phase 2: Quantifying plant responses to soil microbial communities

In the second phase of the experiment, we grew individuals of each of the six focal species in 125mL Deepots (Stuewe & Sons, Inc.) filled with 108mL greenhouse soil, autoclaved as for Phase 1, and 12mL of soil inoculum. This again resulted in 10% v/v of live inoculum, a proportion that is consistent with other studies of plant-soil feedback (Crawford et al. 2019) and that minimizes abiotic differences among treatments. The inoculum for each pot came from one of eight sources: a control treatment of autoclaved greenhouse soil, the same live field soil that was used to inoculate Phase 1 pots (and stored at 0°C during the first phase of the experiment), or soil cultivated by one of the six focal species during Phase 1 of the experiment (see Supplement S1 for graphical schematic of the experimental design). We grew 10 replicate individuals of each species in each soil background, for a total of 480 pots (6 species*8 soil sources*10 replicates), arranged in a randomized block design. We added three germinants of surface-sterilized seeds into each pot, and after 1 week thinned each pot to a single plant. We added an additional seedling in pots that had no surviving germinants after 1 week. Six pots had no surviving plants 2 weeks after initial planting; we excluded these pots from analyses. This phase of the experiment began in May 2019, and we harvested aboveground biomass after 8 weeks of growth, before the plants began to senesce and lose aboveground biomass. We weighed the aboveground biomass of each individual after drying for 72H at 60°C.

Data analysis: Quantifying pairwise stabilization and fitness differences

We used the log-transformed aboveground biomass of plants at the end of Phase 2 to calculate the degree of microbially mediated stabilization and fitness differences. Fol-

lowing Kandlikar et al. (2019), we calculated the degree to which plant-soil feedbacks stabilize each species pair by comparing growth in conspecific-cultivated soil community to growth in the heterospecific-cultivated community:

$$\text{stabilization}_{1,2} = -\frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B}) \qquad \text{(Eqn. 3.1)}$$

Each m_{ix} term represents the growth of plant species i with microbial community x, minus the plant species' growth in the reference (uncultivated) field soil (e.g. $m_{1A} = \ln(\text{biomass}_{\text{sp 1, soil A}}) - \ln(\text{biomass}_{\text{sp 1, uncultivated soil}})$). Due to arithmetic, plant growth on field soil cancels out of this equation and is not required to calculate microbially mediated stabilization (Bever et al. 1997, see Supplement S1). Positive values of stabilization indicate that soil microbes generate negative frequency-dependent feedback loops that stabilize species interactions, whereas negative values indicate that plant-soil feedbacks drive positive frequency-dependent feedback loops that destabilize interactions and lead to loss of plant diversity through exclusion or priority effects. The stabilization metric in Eqn. 3.1 is equal to negative one half of I_S, the stabilization metric originally derived by Bever et al. (1997), and it allows for direct comparison with the microbially mediated fitness difference (Kandlikar et al. (2019); see Eqn. 3.3). This stabilization term is also equal to negative one half of the sum of the two species' log response ratios (i.e. $-\frac{1}{2}\left(ln\left(\frac{\text{biomass}_{1A}}{\text{biomass}_{1B}}\right) + ln\left(\frac{\text{biomass}_{2B}}{\text{biomass}_{2A}}\right)\right)$), a metric commonly calculated in plant-soil feedback studies (Pernilla Brinkman et al. 2010; Crawford et al. 2019).

Inferring the net effects of plant-soil feedbacks requires also quantifying the microbially mediated fitness difference, which is calculated as the difference between the two species' average response to cultivated soil microbial communities (Kandlikar et al. 2019):

$$\text{fitness difference}_{1,2} = \frac{1}{2}(m_{1A} + m_{1B}) - \frac{1}{2}(m_{2A} + m_{2B}) \qquad \text{(Eqn. 3.2)}$$

Although growth in the reference field soil is not required for calculating the degree of microbially mediated stabilization, this information *is* required for calculating the fitness difference. For simplicity, we always define species 1 in any given pair to be the fitness superior in this study.

Comparing the degree of microbially mediated stabilization and fitness difference allows us to infer the net effect of plant-soil feedbacks on species coexistence in the classic plant-soil feedback model (Bever et al. 1997). Specifically, assuming that plant species are otherwise equal competitors, differences in plant responses to soil microbial communities result in species coexistence when stabilization is stronger than the microbially mediated fitness difference, or species exclusion when fitness differences mediated by microbes are larger than their stabilizing effects (Kandlikar et al. 2019):

$$\text{fitness difference}_{1,2} < \text{stabilization} \qquad \text{(Eqn. 3.3)}$$

This condition in Eqn. 3.3 is equivalent to the feasibility criteria presented of Bever et al. (1997) and Eppinga et al. (2018), which states that plant-soil feedbacks allow coexistence provided that they cause a negative I_S *and* that the relative frequency of each species at equilibrium, calculated as $\hat{P}_1 = \frac{m_{2B} - m_{1B}}{I_S}$ and $\hat{P}_2 = \frac{m_{1A} - m_{2B}}{I_S}$, is between 0 and 1 (see Supplement S3). To assess whether the microbially mediated fitness differences are weaker or stronger than the degree of stabilization, we calculated the stabilization and fitness difference metric within each replicate Phase 2 block, and summarized across blocks to calculate the mean and standard error.

We conducted all analyses in `R` v. 3.6.2 (R Core Team 2019). All data and code to recreate analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5068/D1B688 (Kandlikar et al. 2020).

Results

Do the effects of cultivated soil microbial communities differ across species?

The influence of the soil microbial community on plant growth varied across plant species (Two-factor ANOVA, focal species x soil source interaction term $F_{35} = 14.07$, P < 0.001). Each plant species achieved its maximum biomass when growing with the field-collected reference soil, and five out of six focal species grew larger in sterile soils than when inoculated with soil cultivated by any species in Phase 1 (Fig. 3.1). Only one species (*Acmispon wrangelianus*) grew more poorly in sterile soil than in soil containing any live inoculum (88.9% lower biomass in sterile soil than average biomass with any live inoculum, Fig. 3.1).

Do plant-soil feedbacks favor coexistence or exclusion among the focal species?

Plant species' distinct responses to soil microbial communities resulted in complex coexistence outcomes for the species in this study. Plant-soil feedbacks tended to drive negative frequency-dependent feedback loops that stabilize the interaction for most (14/15) species pairs in our study (mean value of stabilization > 0), though species pairs differed in the strength of this effect. The mean stabilization $\pm$ 2*SEM overlapped zero for 9 of these pairs, meaning that only 5 pairs show strong (significant) stabilization. For a single species pair (*Salvia/Plantago*), microbial effects tended to drive positive frequency-dependent feedback loops that destabilize the pairwise interaction (mean value of stabilization < 0, but mean $\pm$ 2*SEM overlaped zero). Each species' interaction with at least one other species was strongly stabilized by plant-soil feedbacks (Table 1).

Soil microbes also drove a strong fitness difference in 9 out of the 15 species pairs in our study (mean fitness difference $\pm$ 2*SEM does not overlap zero). These micro-

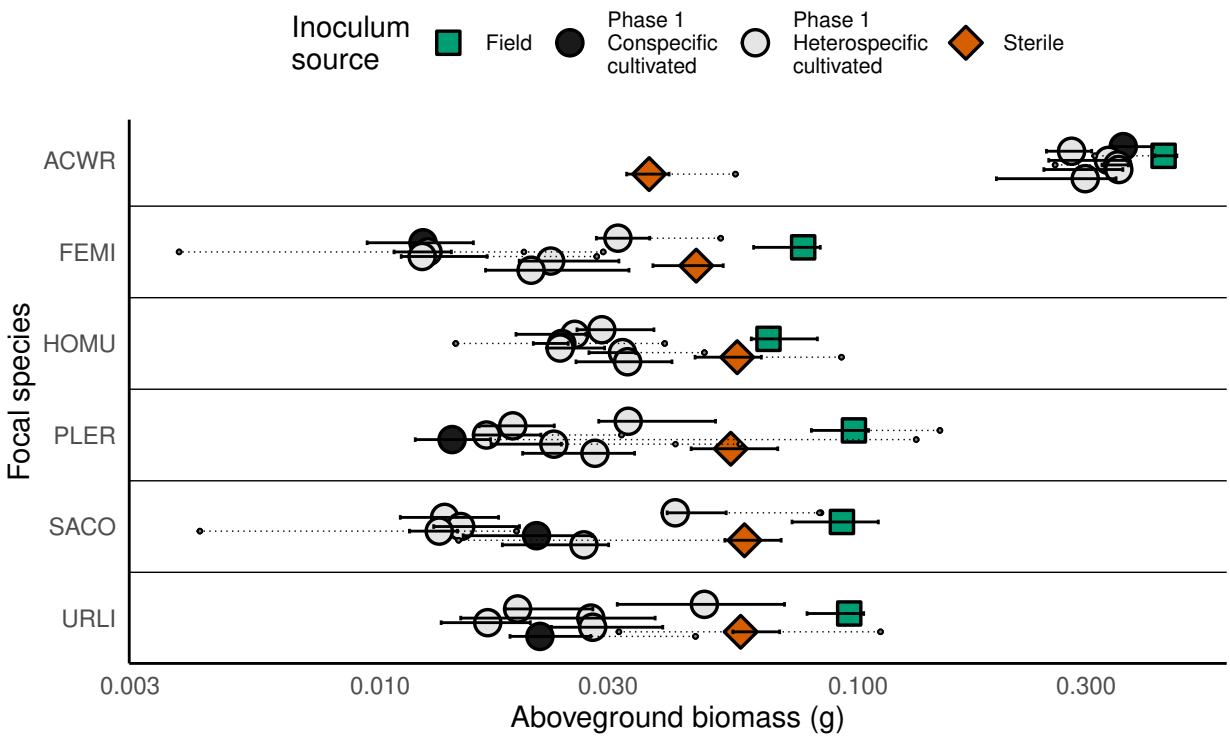

Figure 3.1: Aboveground biomass of each focal species growing with inocula of sterile greenhouse soil, live field-collected soil, or soil conditioned during phase 1. Large points indicate median biomass, and the solid error bars extend to the lower and upper quartiles. Small points and dashed lines show outliers, which were identified as points that were more than (1.5*IQR) away from the lower or upper quartile. Note the log-transformed X-axis.

bially mediated fitness differences favored certain species and harmed others. In particular, the legume *Acmispon wrangelianus* gained a fitness advantage due to microbial feedbacks in its interactions with each of the other five species in our experiment. Similarly, the grass *Hordeum murinum* gained a fitness advantage over all other species except *A. wrangelianus*.

Most importantly, using Eqn. 3.3 to compare the magnitude of microbially mediated stabilization and fitness differences reveals whether plant-soil feedbacks generally promote plant species coexistence or exclusion in the classic plant-soil feedback model (Bever et al. 1997). We found that soil microbes tended to promote species coexistence in three pairs in our study (*Plantago/Festuca*, *Salvia/Uropappus*, and *Uropappus/Festuca*). For these pairs, the mean stabilization estimate was larger than the mean microbially mediated fitness difference (Fig. 3.2), though the confidence intervals around the stabilization estimates overlaps those of the fitness difference (Table 1). By contrast, for a majority of the species pairs in our study (11/15), we found larger microbially mediated fitness differences than stabilization (Fig. 3.2). There is especially strong evidence that soil microbes favor exclusion in six of these pairs, for which the lower bound of the fitness difference estimate was greater than the upper bound of the stabilization estimate (Table 1). The fitness differences that drive exclusion in the Bever et al. (1997) model can also favor diversity in nature if they benefit plant species that are otherwise weak competitors.

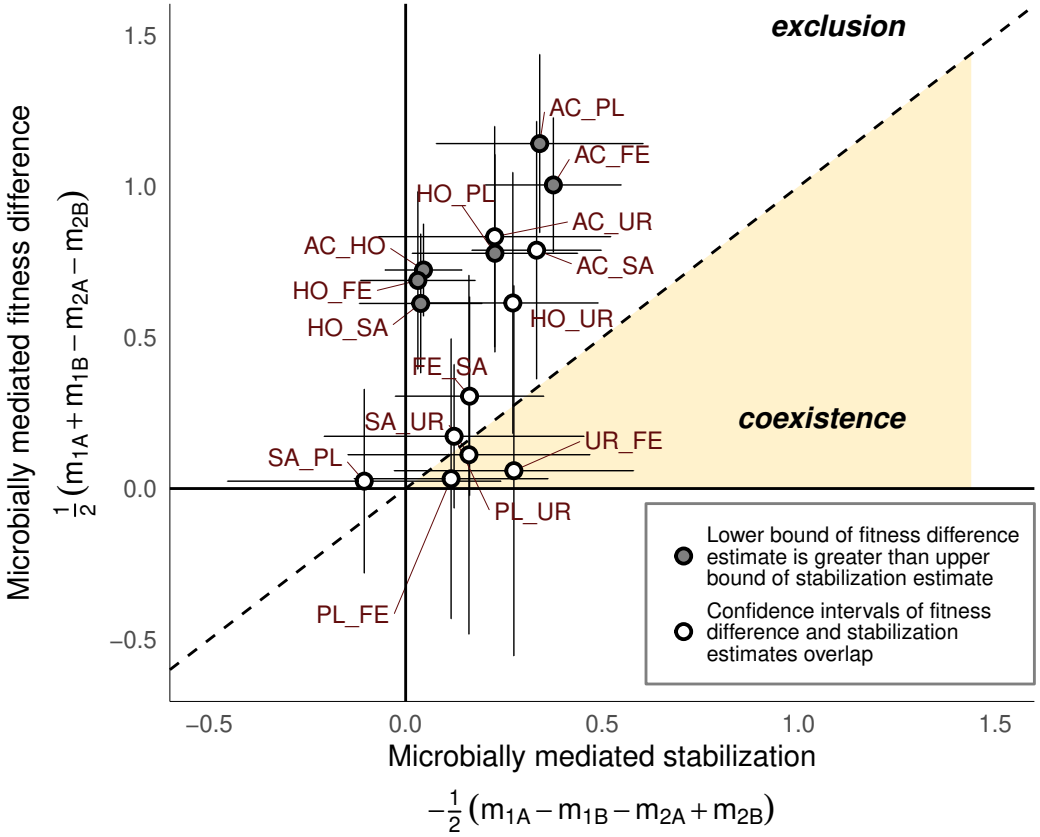

Figure 3.2: In the classic plant-soil feedback model (Bever et al. 1997), soil microbes favor species coexistence in the species pairs that fall below the dashed line, and exclusion in the pairs that fall above the dashed line. The microbially mediated fitness differences that always drive exclusion Bever et al. (1997)'s model may promote plant diversity in more complex models that incorporate other interactions between plant species if they benefit the otherwise inferior competitor (see Discussion). Error bars show mean $\pm$ 2*SEM.

Table 3.1: Microbially mediated stabilization and fitness differences among the fifteen species pairs in our study. Bold terms indicate those values whose confidence intervals do not overlap zero. The net effect of plant-soil feedbacks reflects the relative magnitude of stabilization vs. fitness differences in Bever et al. (1997)'s plant-soil feedback model (Eqn. 3), though microbially medaited fitness differences may promote diversity by equalizing fitness differences in more complex models.

Species pair	Code	Stabilization	Fitness Difference	Net effect of PSF in Bever et al. (1997) model
Plant-soil feedbacks tend to promote coexistence (stabilization > fitness difference)				
P. erecta/ *F. microstachys*	PL_FE	0.116 (-0.13–0.362)	0.032 (-0.432–0.58)	coexistence
U. lindleyi/ *F. microstachys*	UR_FE	0.275 (-0.029–0.579)	0.059 (-0.555–0.889)	coexistence
S. columbariae/ *U. lindleyi*	SA_UR	0.161 (-0.147–0.469)	0.112 (-0.482–0.755)	coexistence
Plant-soil feedbacks tend to promote exclusion (fitness difference > stabilization)				
A. wrangelianus/ *S. columbariae*	AC_SA	**0.333** (0.169–0.497)	**0.789** (0.363–0.759)	exclusion
A. wrangelianus/ *U. lindleyi*	AC_UR	0.227 (-0.069–0.523)	**0.834** (0.468–0.593)	exclusion
F. microstachys/ *S. columbariae*	FE_SA	0.163 (-0.027–0.353)	0.306 (-0.024–0.493)	exclusion
H. murinum/ *U. lindleyi*	HO_UR	**0.273** (0.055–0.491)	**0.614** (0.182–0.705)	exclusion
P. erecta/ *U. lindleyi*	PL_UR	0.123 (-0.207–0.453)	0.173 (-0.065–0.361)	exclusion
Strong evidence that plant-soil feedbacks promote exclusion (lower bound fitness difference estimate > upper bound of stabilization estimate)				
A. wrangelianus/ *F. microstachys*	AC_FE	**0.376** (0.204–0.548)	**1.005** (0.781–0.6)	**exclusion**
A. wrangelianus/ *H. murinum*	AC_HO	0.045 (-0.053–0.143)	**0.724** (0.57–0.199)	**exclusion**
A. wrangelianus/ *P. erecta*	AC_PL	**0.341** (0.077–0.605)	**1.142** (0.846–0.637)	**exclusion**
H. murinum/ *F. microstachys*	HO_FE	0.031 (-0.115–0.177)	**0.689** (0.395–0.325)	**exclusion**
H. murinum/ *P. erecta*	HO_PL	**0.227** (0.017–0.437)	**0.779** (0.451–0.555)	**exclusion**
H. murinum/ *S. columbariae*	HO_SA	0.038 (-0.118–0.194)	**0.613** (0.383–0.268)	**exclusion**
Plant-soil feedbacks tend to destabilize plant interactions (stabilization < 0)				
S. columbariae/ *P. erecta*	SA_PL	-0.105 (-0.453–0.243)	0.024 (-0.28–0.199)	exclusion or priority effect

Discussion

Theoretical and empirical studies have shown that plant-soil feedbacks can influence whether a pair of species coexists if they drive stabilizing feedback loops that favor species that decline in abundance and disadvantage more abundant species (or destabilizing loops that favor more abundant species and disadvantage rare ones) (Bever et al. 1997; Crawford et al. 2019). However, recent theoretical advances have clarified that species coexistence is also determined by the degree to which soil micobes mediate an average fitness difference that gives one species a demographic advantage over its competitor, regardless of its abundance in the system (Chesson 2000; Kandlikar et al. 2019). Here, we show that empirically quantifying the microbially mediated fitness difference and comparing it to the degree of microbial stabilization in Bever et al. (1997)'s classic model of plant-soil feedback is essential for understanding how soil microbes shape plant species coexistence. Specifically, we found that even though soil microbes stabilize pairwise interactions by generating negative frequency-dependent dynamics in nearly all pairs in our study, they often drive substantial fitness differences that overwhelm their stabilizing effects.

That plant-soil feedbacks drive stabilization but also strong average fitness differences is determined by the particular arrangement of interspecific differences in species' response to soil communities cultivated by conspecifics and heterospecifics. In our experiment, species generally performed better with a soil community cultivated by heterospecifics than with a soil community cultivated by conspecifics (across all species, growth with conspecific-cultivated microbes was on average 13% lower than growth with heterospecific microbes). Thus, the effect of plant-soil feedbacks is generally to stabilize rather than destabilize plant interactions (Fig. 3.2), a result which is consistent with meta-analyses of similar experiments among grassland species (Kul-

matiski et al. 2008; Crawford et al. 2019). Inferring the influence of plant-soil feedbacks from this result alone might lead us to conclude that soil microbes generally favor plant diversity in this system. However, a novel aspect of our experiment is that we can compare the stabilizing effects of soil microbes to the fitness difference they generate to more fully assess their effects on plant coexistence. This comparison is possible because we also measured plant growth with the microbial community of field-collected soil that had not been directly influenced of any focal species in our experiment, a treatment has been omitted from most studies of plant-soil feedbacks.

All six species in our experiment grew less vigorously with microbes cultivated during Phase 1 than when grown with the microbial community of uncultivated field soil (Fig. 3.1). It is possible that this result is driven by slightly higher nutrient levels in pots inoculated with a reference vs. cultivated soil inoculum, though we aimed to minimize this possibility by adding only a small volume (10%) of inoculum soil into a common sterile background (see Fig. S1). Assuming that variation in species' growth during the second phase of the experiment is primarily driven by differences in soil microbes, our results indicate that greenhouse-grown high-density monocultures of the focal species might harbor more pathogenic (or fewer mutualistic) soil microbes than field-collected reference soils. However, this effect was weak for *Acmispon wrangelianus* – the only Fabaceae species in our experiment – which grew more similarly with microbes cultivated during Phase 1 as with the field-collected reference microbial community (*A. wrangelianus* growth was 28% lower with cultivated microbes than with the reference field inoculum, vs. 71% lower growth on average for all other species). This result, as well as our finding that *A. wrangelianus* grows much more vigorously when inoculated with any live microbial community than in sterile soil (Fig. 3.1), is consistent with other studies showing that growth of *A. wrangelianus* benefits from

the presence of many strains of nitrogen-fixing soil bacteria in the genus *Mesorhizobium*, strains likely present in our field soil inoculum (Porter et al. 2016, 2019). As a consequence of the differences in species' response to the microbial communities cultivated by the focal species, plant-soil feedbacks generate a fitness advantage in favor of *A. wrangelianus* in its pairwise interaction with each of the other species in our experiment (Table 1). Although empirical studies of plant-soil feedback have rarely explicitly quantified microbially mediated average fitness differences, ours is one of a growing number of studies finding that complex, diverse soil microbial communities benefit Fabaceae species that associate with N-fixing bacteria more than plants of other functional groups (van der Heijden et al. 2015; Teste et al. 2017). This indicates that plant-soil feedbacks may frequently drive a fitness advantage in favor of these legume species.

The microbially mediated stabilization and fitness differences quantified in our study and other two-phase feedback experiments are determined by the soil microbes cultivated by focal plant species from the soil community of the reference inoculum. This raises the question of what the appropriate reference inoculum is for plant-soil feedback experiments, a question that has not been highlighted by previous studies because growth in the reference soil is not essential for calculating the stabilization metric that has been the focus of most existing research. The unconditioned soil inoculum should generally reflect the field soil's microbial community when the soil has not been conditioned by the focal species in the experiment (Bever et al. 1997). Ideally, this reference inoculum captures the state of the soil microbial community when all focal plant species are absent from the system (and the remainder of the plant community is at equilibrium). In practice, soil that has been previously conditioned by the dominant plant species in the field may be an obvious first choice for reference

soil, especially in systems that lack extensive spatial structure. When there is no clear choice of a reference soil, or when the focal species in the experiment are themselves dominant in the community, collecting multiple reference inocula (e.g. from individuals of several dominant plant species, or from several locations on a spatial grid) and quantifying the microbially mediated stabilization and fitness differences separately from each of the reference inocula would be an ideal approach to evaluate the range of possible coexistence consequences of soil microbes. For our experiment we collected the reference soil near the invasive grass *Avena fatua* because *Avena* has long been one of the dominant plants throughout southern California grasslands (D'Antonio et al. 2007), including at our field site. We therefore expect that the focal species in our experiment often interact with each other in soils previously cultivated by *Avena* or other non-native annual grasses. Our conclusions about effects of plant-soil feedbacks on plant coexistence in this system may have been different had we used soil collected near native California grassland species as the reference, because the soil communities of non-native plants in this ecosystem are often different from those of the native species (Batten et al. 2007; Vogelsang and Bever 2009). Using the two-phased experimental design with the additional reference soil treatment to evaluate the variation in plant-soil feedback effects based on the microbial composition of reference inocula will be an important priority for future research.

Although the two-phased feedback experiment design isolates the effect of soil microbes on plant interactions, more thoroughly evaluating the consequences of soil microbes on plant diversity requires also considering other processes like resource competition that simultaneously influence species interactions (Bever 2003; Kandlikar et al. 2019). Specifically, although stabilizing plant-soil feedbacks should promote species coexistence regardless of other processes, the microbially mediated fitness dif-

ferences that drive exclusion in Bever et al. (1997)'s model may in fact favor plant diversity in nature if they benefit the otherwise weaker competitor. Indeed, in a previous field experiment among annual plants in the same system that motivated our study, *A. wrangelianus* was predicted to be excluded in pairwise interactions with three other focal species in our experiment (*Plantago erecta*, *Salvia columbariae*, and *Uropappus lindelyi*) (Kraft et al. 2015, note that *A. wrangelianus* was *Lotus wrangelianus* and *U. lindelyi* was *Agoseris heterophylla* in that study). In that study, *A. wrangelianus* was grown with competitors in live field soil, and the outcome reflects the joint effects of resource competition, plant-soil feedback, and other processes operating in nature. Thus, the microbially mediated fitness advantage in favor of *A. wrangelianus* that we identified appears to simply improve the performance of a weak competitor, though the relative boost to *A. wrangelianus'* performance due to the microbially mediated fitness advantage appears to be insufficient to overcome other competitive asymmetries. Similarly, Siefert et al. (2018) found that soil microbes are more likely promote coexistence of two highly co-occurring species of *Trifolium* by reducing their competitive fitness differences than by generating negative density-dependent dynamics between the two species. More generally, if soil microbes drive observed trade-offs between plant species' ability to compete for limiting resources and their sensitivity to natural enemies (Bever et al. 2015; Peay 2016), microbially mediated fitness differences might often promote plant diversity by reducing the degree of niche differentiation required for stable coexistence. Future empirical studies designed to quantify how microbially mediated stabilization and fitness difference change the outcome of other competitive asymmetries (e.g. using the designs proposed by Ke and Wan (2019)) will help clarify the interplay between plant-soil feedback and other processes that influence plant species coexistence in nature.

Our study highlights the potential for plant-soil feedbacks to simultaneously stabilize pairwise interactions and also drive average fitness differences that always favor one species over the other, but our results have some important caveats. First, we mixed the soils cultivated by replicate Phase 1 monocultures of each species to create the soil inoculum for Phase 2. This is a common step in many plant-soil feedback studies (e.g. Klinerová and Dostál (2020); Cortois et al. (2016)), but it can result in falsely precise or inflated estimates of the soil microbial community's effect on plant growth (Reinhart and Rinella 2016). When we assessed the consequence of soil homogenization by comparing growth in soil homogenized across replicate monocultures vs. growth with soil from a single monoculture (Fig. S2.1), we found that this homogenizing across monocultures is unlikely to have significantly influenced the results of our main experiment. In general, however, we agree with Reinhart and Rinella (2016) that more careful study of the variable nature of plant-microbe interactions will be a fruitful avenue for future research.

A second limitation of our study is that it did not account for the fact that the composition and dynamics of soil microorganisms in Mediterranean ecosystems are also influenced by the length and intensity of the summer droughts that separate the annual plant community's growing seasons (Barnard et al. 2014). By not accounting for the possibility that the cultivating effects of plant species on soil microbial communities erode over the six-month dry season, our experiment might have overestimated the long-term effects of plant-soil feedbacks on species coexistence in this annual plant system. Future studies that adapt the standard two-phase design of plant-soil feedback experiments to capture relevant biological idiosyncrasies of focal plant communities will be important for contextualizing our understanding of how soil microorganisms shape plant diversity in natural systems (Smith-Ramesh and Reynolds 2017).

In conclusion, we have demonstrated that dynamic feedbacks between plants and soil microorganisms can have important consequences on plant coexistence. Existing research has emphasized the potential for such feedbacks to stabilize or destabilize plant interactions by generating negative or positive frequency-dependent dynamics. Here we conducted a two-phase feedback experiment with annual plants that co-occur in southern California grasslands and showed that inferring the net effects of soil microbes by evaluating only their (de)stabilizing effects and not comparing these to the microbially mediated fitness difference can lead to false conclusions regarding soil microbes' effects on plant diversity. Comparing the strength of microbially mediated stabilization and fitness differences in a wide range of ecosystems and plant functional types should be a priority for future plant-soil feedback research. Ultimately, translating the consequences of plant-soil feedbacks into predictions for how soil microbes mediate diversity in nature will require contextualizing the effects of soil microbes relative to those of competition and other processes that affect the dynamics of plant and soil microbial communities.

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Chapter 3 Supplementary Materials

Appendix 3.1: Modifying the standard two-phase design of plant-soil feedback experiments to quantify microbially mediated fitness differences

Most studies that use a two-phase experimental design to study the coexistence consequences of plant-soil feedbacks only grow plants with cultivated soil microbial communities in the second phase of their experiment, and not with an uncultivated, reference soil community. This is because quantifying microbially mediated stabilization, which is the focus of most such studies, does not require measuring plant growth with uncultivated microbes. Specifically, Bever et al. (1997) showed that following the original definitions of the m_{ix} terms as growth of plant i with microbes x minus the growth of plant i with uncultivated microbes ($m_{ix} = G_{ix} - G_{iO}$), growth with uncultivated microbes is irrelavent for quantifying the stabilization metric I_S. Following the same logic, growth with uncultivated microbial communities also cancels out of the equation for the stabilization metric derived in Kandlikar et al. (2019):

$$\begin{aligned}
\text{stabilization} &= -\frac{1}{2}(m_{1A} + m_{2B} - m_{1B} - m_{2A}) \\
&= -\frac{1}{2}((G_{1A} - \cancel{G_{1O}}) + (G_{2B} - \cancel{G_{2O}}) - (G_{1B} - \cancel{G_{1O}}) - (G_{2A} - \cancel{G_{2O}})) \\
&= -\frac{1}{2}(G_{1A} + G_{2B} - G_{1B} - G_{2A})
\end{aligned} \tag{Eqn. S3.1}$$

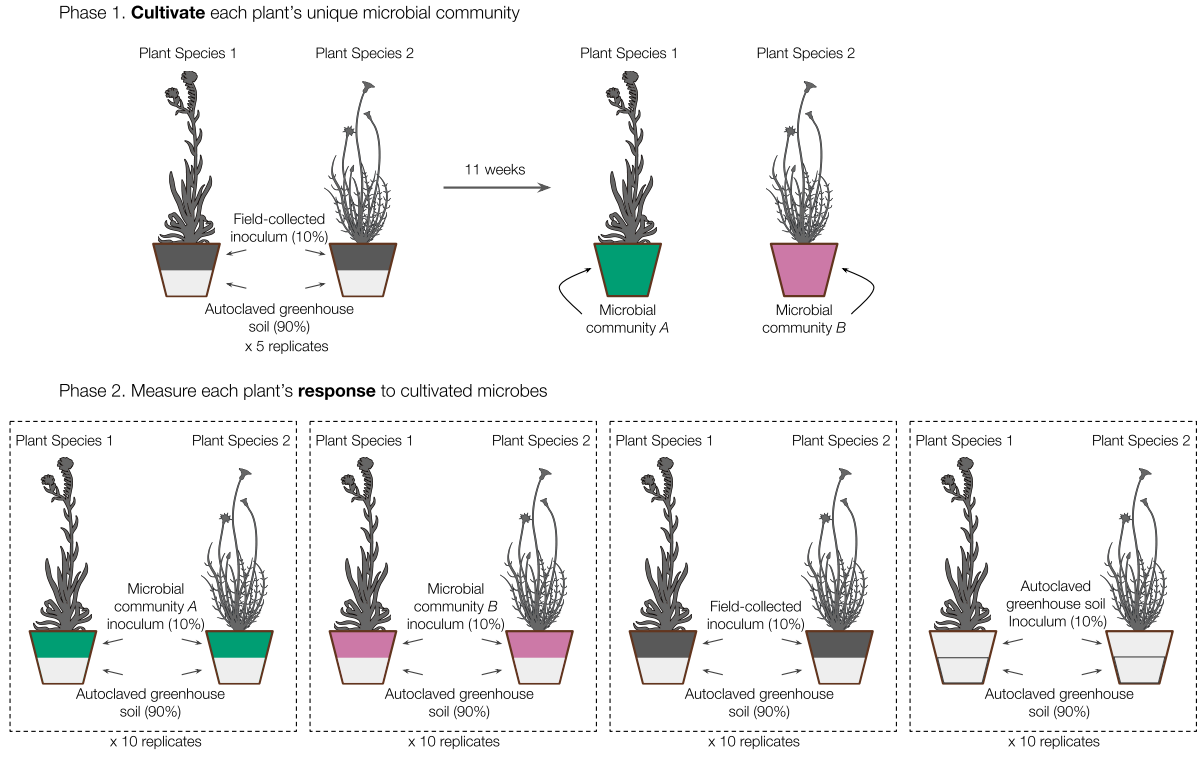
However, growth with uncultivated microbes *is* relevant for quantifying the microbially mediated fitness difference:

$$
\begin{aligned}
\text{fitness difference}_{1,2} &= \frac{1}{2}(m_{1A} + m_{1B}) - \frac{1}{2}(m_{2A} + m_{2B}) \\
&= \frac{1}{2}((G_{1A} - G_{1O}) + (G_{1B} - G_{1O})) - \frac{1}{2}((G_{2A} - G_{2O}) + (G_{2B} - G_{2O})) \\
&= \left(\frac{1}{2}(G_{1A} + G_{1B}) - G_{1O}\right) - \left(\frac{1}{2}(G_{2A} + G_{2B}) - G_{2O}\right)
\end{aligned}
\tag{Eqn. S3.2}
$$

Thus, simply using the standard two-phase design of plant soil feedback experiments with an additional treatment of growth in uncultivated reference soil in the second phase (see Fig. S1.1), gives all the measures required to quantify both the stabilization and fitness difference mediated by soil microbes in Bever et al. (1997)'s model of plant-soil feedback. In the Discussion section of the main text, we lay out general guidelines for how to choose an appropriate reference soil community, and explain how we chose the reference soil for our experiment.

It is important to note that although plant growth with the uncultivated (reference) inoculum cancels out of the stabilization metric, the composition of the reference soil microbial community can nevertheless influence the quantification of microbially mediated stabilization in plant-soil feedback experiments. For example, a two-phase feedback experiment might under-estimate stabilization if the unconditioned inoculum is missing a host-specific pathogen that would otherwise proliferate in phase 1 and suppress conspecific growth in phase 2. Thus, choosing an appropriate reference community that the focal plant species would be likely to experience when they are absent from the community is important even for plant-soil feedback studies that only aim to quantify the degree of microbially mediated stabilization.

Figure S3.1: A schematic of experimental design. Note that plants were grown as high-density monocultures (8g seed/m2) for the first (cultivation) phase, but shown as a single plant here for simplicity. Plants were grown as single individuals in pots for the second (response) phase of the experiment. Soils across the five replicate Phase 1 cultivations were homogenized to create the inocula for the second phase of the experiment (but see Supplement 2 for results from a parallel experiment in which we tested the effects of each Plantago-cultivated soil separately). Our experiment included six focal species; we show only two here for clarity.



Appendix 3.2: Evaluating the effects of homogenizing replicate Phase 1 cultivations

Homogenizing soils from across the replicate Phase 1 cultivations to create the inocula for the second phase, a common step in plant-soil feedback experiments (Gundale et al. 2018) that we adopt in this study, makes such experiments more feasible but can lead to biased and falsely precise results (Reinhart and Rinella 2016). To explore the variation in the effects of the replicate Phase 1 cultivations, we set up a parallel experiment in which we grew ten replicate individuals of *Plantago erecta* and *Festuca microstachys* in soils cultivated by each of the five *Plantago* Phase 1 monocultures (2 species * 5 soil inocula * 10 replicates = 100 pots). Although this approach does not quantify the variation in each focal species' cultivation, it can yield insight into the potential consequences of pooling across replicate Phase 1 monocultures on plant growth. As in Phase 2 of the feedback experiment, we planted germinants from surface-sterilized seeds into 125mL Deepots that contained 10% v/v live inoculum, and added an additional seedling in pots that had no surviving germinants after 1 week. Two pots had no surviving plants 2 weeks after initial planting; we excluded these pots from analyses. We harvested aboveground biomass after 8 weeks of growth, and weighed after drying for 72H at 60°C.

Results: The biomass of *Plantago erecta* and *Festuca microstachys* grown with an inoculum that came from a single *Plantago* phase 1 monoculture did not differ significantly from their biomass when grown with an inoculum made by combining soil from each of the five *Plantago* monocultures (one-factor Anova; Plantago: $F_{5,55} = 1.16$, $p > 0.05$; Festuca: $F_{5,52} = 1.78$, $p > 0.05$, Fig. S3.2). Whether the inoculum was sourced from a single Phase 1 monoculture or was homogenized across replicate monocultures also did not influence the variance in aboveground biomass (Levene's test; Plantago

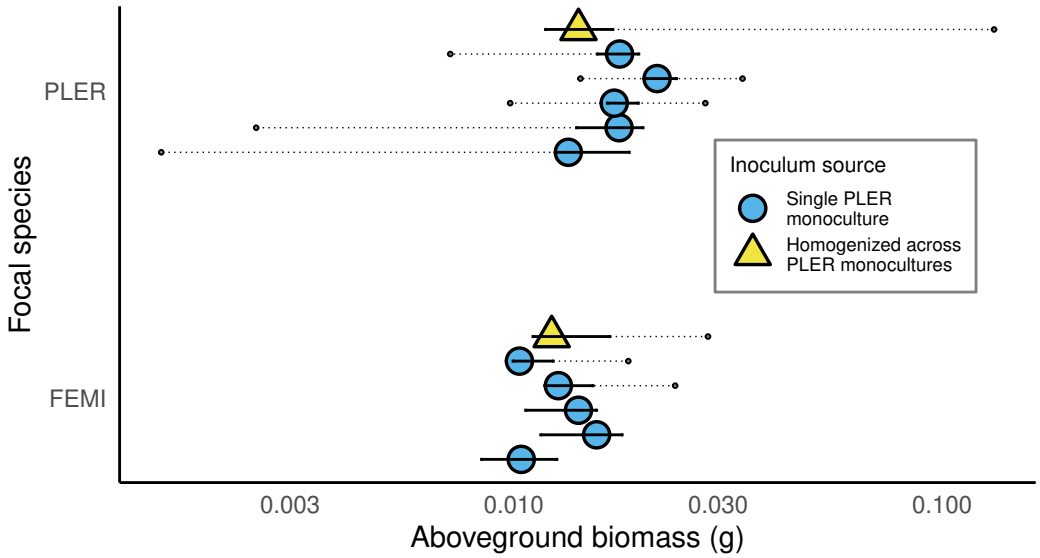


Figure S3.2: Results from a parallel experiment to explore the effect of homogenizing soil from replicate Phase 1 monocultures on growth of two plant species. Aboveground biomass of Plantago erecta and Festuca microstachys grown with a soil inoculum that was sourced either from a single Plantago phase 1 monoculture (blue circles) or with an inoculum created by homogenizing soil from all five repilicate monocultures (yellow triangles), as was done for the main experiment. Large points indicate median biomass, and the solid error bars extend to the lower and upper quartiles. Small points and dashed lines show outliers, which were identified as points that were more than (1.5*IQR) away from the lower or upper quartile. Note the log-transformed X-axis.

$F_{5,55} = 0.82,\ p > 0.05$; Festuca $F_{5,52} = 0.44;\ p > 0.05$).

Appendix 3.3: Comparing predictions of coexistence derived by comparing strength of stabilization and fitness differences to predictions made via Bever et al. (1997)'s feasibility analysis

Our approach of inferring coexistence in terms of microbially mediated stabilization and fitness differences using our experimental data yields conclusions that are consistent with the feasibility analysis originally presented in Bever et al. (1997) (for an algebraic explanation of this equivalence, see Appendix S1 of Kandlikar et al. (2019)). In Bever et al. (1997)'s analysis of the plant-soil feedback model, soil microbes stabilize plant interactions when they result in a negative value for the stabilization metric I_S, calculated as $I_S = m_{1A} + m_{2B} - m_{1B} - m_{2A}$. Importantly, negative I_S is a *necessary* condition for plant coexistence, but it is not *sufficient*: stable coexistence of plant species also requires that both plants have a positive frequency at equilibrium, with this equilibrium frequency $\hat{P}$ calculated as $\hat{P}_1 = \frac{m_{2B} - m_{1B}}{I_S}$ for species 1, and $\hat{P}_2 = \frac{m_{1A} - m_{2A}}{I_S}$ for species 2. In other words, plant-soil feedbacks result in stable coexistence provided three conditions are satisfied (Bever et al. 1997; Eppinga et al. 2018):

$$I_S < 0; \quad 0 < \hat{P}_1 < 1; \quad 0 < \hat{P}_2 < 1 \qquad \text{(Eqn. S3.3)}$$

In Table S3.1 below we show, for each species pair in each block, that analyzing experimental data in terms of Eqn S3.1 above or the inequality in Eqn. 3.3 (from the Main Text) yields the same conclusions regarding coexistence vs. exclusion.

Table S3.1: Evaluating the coexistence consequences of soil microbes via microbially mediated stabilization and fitness differences vs. via comparing I_S to p^* yield identical results

rep	pair	m_{1A}	m_{1B}	m_{2A}	m_{2B}	I_S	$\hat{p_1}$	$\hat{p_2}$	outcome (feasibility)	stabilization	fitness difference	outcome (IGR)
1	AC_FE	-0.410	-0.219	-0.721	-1.720	-1.191	1.260	-0.260	exclude	0.596	0.906	exclude
2	AC_FE	-0.242	-0.346	-1.035	-2.290	-1.151	1.689	-0.689	exclude	0.575	1.369	exclude
3	AC_FE	-0.193	-0.743	-1.155	-2.224	-0.519	2.854	-1.854	exclude	0.259	1.222	exclude
4	AC_FE	-0.282	-0.275	-0.687	-1.628	-0.949	1.426	-0.426	exclude	0.475	0.879	exclude
5	AC_FE	-0.231	-0.488	-1.060	-1.914	-0.597	2.387	-1.387	exclude	0.299	1.127	exclude
6	AC_FE	-0.186	-0.360	-0.604	-2.499	-1.721	1.243	-0.243	exclude	0.861	1.278	exclude
7	AC_FE	-0.165	-0.667	-0.842	-1.901	-0.557	2.215	-1.215	exclude	0.278	0.955	exclude
8	AC_FE	0.447	-0.390	-1.117	-1.637	0.316	-3.942	4.942	exclude	-0.158	1.405	exclude
9	AC_FE	0.052	-0.645	-0.012	-1.146	-0.437	1.146	-0.146	exclude	0.218	0.282	exclude
10	AC_FE	-0.280	-0.521	-0.552	-1.506	-0.713	1.382	-0.382	exclude	0.356	0.629	exclude
1	AC_HO	-0.410	-0.532	-1.133	-0.887	0.368	-0.965	1.965	exclude	-0.184	0.539	exclude
2	AC_HO	-0.242	-0.171	-0.976	-1.088	-0.183	5.003	-4.003	exclude	0.092	0.826	exclude
3	AC_HO	-0.193	-0.849	-0.665	-1.463	-0.142	4.307	-3.307	exclude	0.071	0.542	exclude
4	AC_HO	-0.282	-0.016	-0.724	-0.843	-0.385	2.147	-1.147	exclude	0.193	0.635	exclude
5	AC_HO	-0.231	-0.398	-1.144	-1.570	-0.260	4.515	-3.515	exclude	0.130	1.042	exclude
6	AC_HO	-0.186	-0.276	-0.749	-1.138	-0.299	2.879	-1.879	exclude	0.150	0.712	exclude
7	AC_HO	-0.165	-0.820	-0.711	-0.955	0.411	-0.329	1.329	exclude	-0.205	0.341	exclude
8	AC_HO	0.447	0.131	-0.829	-0.914	0.232	-4.506	5.506	exclude	-0.116	1.160	exclude
9	AC_HO	0.052	-0.325	-0.592	-1.192	-0.223	3.892	-2.892	exclude	0.111	0.755	exclude
10	AC_HO	-0.280	-0.204	-0.750	-1.101	-0.427	2.101	-1.101	exclude	0.213	0.683	exclude
1	AC_PL	-0.410	-0.375	-0.795	-1.422	-0.662	1.582	-0.582	exclude	0.331	0.716	exclude
2	AC_PL	-0.242	-0.165	-1.225	0.324	1.472	0.332	0.668	exclude	-0.736	0.247	exclude
3	AC_PL	-0.193	-0.213	-0.887	-1.486	-0.579	2.198	-1.198	exclude	0.290	0.983	exclude
4	AC_PL	-0.282	-0.343	-1.321	-2.242	-0.862	2.205	-1.205	exclude	0.431	1.469	exclude
5	AC_PL	-0.231	-0.094	-0.959	-1.570	-0.748	1.972	-0.972	exclude	0.374	1.102	exclude
6	AC_PL	-0.186	-0.164	-1.166	-1.843	-0.700	2.399	-1.399	exclude	0.350	1.330	exclude
7	AC_PL	-0.165	-0.361	-0.685	-2.069	-1.188	1.437	-0.437	exclude	0.594	1.114	exclude
8	AC_PL	0.447	0.076	-1.262	-2.291	-0.659	3.594	-2.594	exclude	0.329	2.038	exclude
9	AC_PL	0.052	-0.251	-0.322	-2.326	-1.701	1.220	-0.220	exclude	0.850	1.224	exclude

10	AC_PL	-0.280	-0.688	-0.881	-2.485	-1.197	1.502	-0.502	exclude	0.598	1.199	exclude
1	AC_SA	-0.410	-0.147	-0.237	-0.915	-0.942	0.816	0.184	coex	0.471	0.297	coex
3	AC_SA	-0.193	-0.642	-0.842	-1.961	-0.670	1.969	-0.969	exclude	0.335	0.984	exclude
4	AC_SA	-0.282	-0.895	-0.455	-1.112	-0.045	4.820	-3.820	exclude	0.023	0.195	exclude
5	AC_SA	-0.231	-0.166	-1.117	-1.421	-0.369	3.397	-2.397	exclude	0.185	1.070	exclude
7	AC_SA	-0.165	-0.332	0.107	-1.624	-1.565	0.826	0.174	coex	0.782	0.510	coex
8	AC_SA	0.447	0.157	-1.409	-2.156	-0.458	5.056	-4.056	exclude	0.229	2.085	exclude
9	AC_SA	0.052	-0.717	-0.421	-1.439	-0.249	2.903	-1.903	exclude	0.124	0.598	exclude
10	AC_SA	-0.280	-0.191	-0.474	-1.144	-0.760	1.255	-0.255	exclude	0.380	0.573	exclude
1	AC_UR	-0.410	-0.320	-1.118	-1.695	-0.668	2.061	-1.061	exclude	0.334	1.042	exclude
2	AC_UR	-0.242	-0.382	-0.093	-1.189	-0.956	0.844	0.156	coex	0.478	0.329	coex
4	AC_UR	-0.282	-0.855	-0.875	-2.639	-1.191	1.498	-0.498	exclude	0.596	1.189	exclude
5	AC_UR	-0.231	-1.003	-0.295	-1.480	-0.414	1.155	-0.155	exclude	0.207	0.271	exclude
6	AC_UR	-0.186	-0.206	-0.935	-2.162	-1.207	1.620	-0.620	exclude	0.604	1.352	exclude
7	AC_UR	-0.165	-0.269	-2.090	-1.314	0.880	-1.188	2.188	exclude	-0.440	1.485	exclude
8	AC_UR	0.447	-1.386	-0.330	-0.956	1.206	0.356	0.644	exclude	-0.603	0.174	exclude
9	AC_UR	0.052	-0.224	-0.390	-1.441	-0.775	1.570	-0.570	exclude	0.388	0.830	exclude
1	FE_HO	-1.720	-1.456	-0.782	-0.887	-0.369	-1.542	2.542	exclude	0.185	-0.754	exclude
2	FE_HO	-2.290	-1.844	-1.190	-1.088	-0.344	-2.196	3.196	exclude	0.172	-0.928	exclude
3	FE_HO	-2.224	-2.023	-0.842	-1.463	-0.822	-0.682	1.682	exclude	0.411	-0.971	exclude
4	FE_HO	-1.628	-1.537	-1.395	-0.843	0.461	1.505	-0.505	exclude	-0.231	-0.464	exclude
5	FE_HO	-1.914	-2.039	-1.066	-1.570	-0.380	-1.233	2.233	exclude	0.190	-0.658	exclude
6	FE_HO	-2.499	-2.690	-1.375	-1.138	0.428	3.628	-2.628	exclude	-0.214	-1.338	exclude
7	FE_HO	-1.901	-1.805	-1.103	-0.955	0.051	16.530	-15.530	exclude	-0.026	-0.824	exclude
8	FE_HO	-1.637	-1.676	-0.918	-0.914	0.043	17.627	-16.627	exclude	-0.022	-0.741	exclude
9	FE_HO	-1.146	-0.577	-1.444	-1.192	-0.316	1.946	-0.946	exclude	0.158	0.457	exclude
10	FE_HO	-1.506	-2.082	-1.149	-1.101	0.624	1.571	-0.571	exclude	-0.312	-0.669	exclude
1	FE_PL	-1.720	-1.656	-1.506	-1.422	0.020	11.631	-10.631	exclude	-0.010	-0.224	exclude
2	FE_PL	-2.290	-1.966	-1.801	0.324	1.800	1.272	-0.272	exclude	-0.900	-1.389	exclude
3	FE_PL	-2.224	-1.856	-1.335	-1.486	-0.519	-0.714	1.714	exclude	0.259	-0.630	exclude
4	FE_PL	-1.628	-1.288	-2.260	-2.242	-0.322	2.965	-1.965	exclude	0.161	0.793	exclude
5	FE_PL	-1.914	-2.020	-1.251	-1.570	-0.214	-2.106	3.106	exclude	0.107	-0.557	exclude
6	FE_PL	-2.499	-1.583	-2.160	-1.843	-0.600	0.434	0.566	coex	0.300	-0.040	coex

7	FE_PL	-1.901	-1.826	-1.508	-2.069	-0.635	0.383	0.617	coex	0.318	-0.075	coex
8	FE_PL	-1.637	-1.749	-1.660	-2.291	-0.519	1.044	-0.044	exclude	0.260	0.283	exclude
9	FE_PL	-1.146	-0.609	-1.723	-2.326	-1.139	1.507	-0.507	exclude	0.570	1.147	exclude
10	FE_PL	-1.506	-2.026	-1.779	-2.485	-0.186	2.466	-1.466	exclude	0.093	0.366	exclude
1	FE_SA	-1.720	-0.827	-1.043	-0.915	-0.766	0.116	0.884	coex	0.383	-0.294	coex
3	FE_SA	-2.224	-1.377	-1.848	-1.961	-0.960	0.608	0.392	coex	0.480	0.104	coex
4	FE_SA	-1.628	-1.151	-2.361	-1.112	0.771	0.051	0.949	exclude	-0.386	0.347	exclude
5	FE_SA	-1.914	-1.201	-2.142	-1.421	0.007	-29.649	30.649	exclude	-0.004	0.224	exclude
7	FE_SA	-1.901	-1.698	-1.930	-1.624	0.103	0.714	0.286	exclude	-0.052	-0.022	exclude
8	FE_SA	-1.637	-1.042	-2.137	-2.156	-0.614	1.814	-0.814	exclude	0.307	0.807	exclude
9	FE_SA	-1.146	-0.391	-2.407	-1.439	0.213	-4.917	5.917	exclude	-0.107	1.154	exclude
10	FE_SA	-1.506	-0.912	-1.527	-1.144	-0.211	1.101	-0.101	exclude	0.105	0.127	exclude
1	FE_UR	-1.720	-0.543	-1.864	-1.695	-1.009	1.143	-0.143	exclude	0.504	0.648	exclude
2	FE_UR	-2.290	-3.403	-0.983	-1.189	0.907	2.440	-1.440	exclude	-0.454	-1.760	exclude
4	FE_UR	-1.628	-1.454	-1.067	-2.639	-1.746	0.679	0.321	coex	0.873	0.312	coex
5	FE_UR	-1.914	-1.498	-1.562	-1.480	-0.335	-0.052	1.052	exclude	0.168	-0.185	exclude
6	FE_UR	-2.499	-1.247	-1.431	-2.162	-1.984	0.461	0.539	coex	0.992	-0.077	coex
7	FE_UR	-1.901	-0.952	-1.730	-1.314	-0.532	0.680	0.320	coex	0.266	0.096	coex
8	FE_UR	-1.637	-1.642	-1.079	-0.956	0.128	5.352	-4.352	exclude	-0.064	-0.622	exclude
9	FE_UR	-1.146	-0.341	-2.276	-1.441	0.031	-35.453	36.453	exclude	-0.016	1.115	exclude
3	HO_PL	-1.463	-0.965	-1.564	-1.486	-0.420	1.241	-0.241	exclude	0.210	0.311	exclude
4	HO_PL	-0.843	-0.659	-1.896	-2.242	-0.530	2.984	-1.984	exclude	0.265	1.318	exclude
5	HO_PL	-1.570	-1.472	-1.398	-1.570	-0.271	0.362	0.638	coex	0.135	-0.037	coex
6	HO_PL	-1.138	-1.108	-1.699	-1.843	-0.174	4.229	-3.229	exclude	0.087	0.648	exclude
7	HO_PL	-0.955	-1.201	-2.395	-2.069	0.572	-1.516	2.516	exclude	-0.286	1.154	exclude
8	HO_PL	-0.914	-0.959	-1.922	-2.291	-0.324	4.110	-3.110	exclude	0.162	1.170	exclude
9	HO_PL	-1.192	-0.864	-1.255	-2.326	-1.399	1.045	-0.045	exclude	0.700	0.762	exclude
10	HO_PL	-1.101	-1.034	-1.462	-2.485	-1.090	1.331	-0.331	exclude	0.545	0.905	exclude
1	HO_SA	-0.887	-0.500	-1.406	-0.915	0.103	-4.043	5.043	exclude	-0.051	0.467	exclude
3	HO_SA	-1.463	-0.940	-1.540	-1.961	-0.944	1.082	-0.082	exclude	0.472	0.549	exclude
4	HO_SA	-0.843	-0.538	-1.590	-1.112	0.172	-3.340	4.340	exclude	-0.086	0.661	exclude
5	HO_SA	-1.570	-1.115	-1.656	-1.421	-0.220	1.391	-0.391	exclude	0.110	0.196	exclude
7	HO_SA	-0.955	-1.076	-1.809	-1.624	0.306	-1.788	2.788	exclude	-0.153	0.701	exclude

8	HO_SA	-0.914	-0.651	-1.977	-2.156	-0.442	3.404	-2.404	exclude	0.221	1.285	exclude
9	HO_SA	-1.192	-0.513	-1.679	-1.439	-0.439	2.110	-1.110	exclude	0.219	0.706	exclude
10	HO_SA	-1.101	-1.138	-1.770	-1.144	0.662	-0.009	1.009	exclude	-0.331	0.337	exclude
1	HO_UR	-0.887	-0.551	-2.919	-1.695	0.888	-1.289	2.289	exclude	-0.444	1.588	exclude
2	HO_UR	-1.088	-1.016	-0.910	-1.189	-0.351	0.490	0.510	coex	0.175	-0.003	coex
4	HO_UR	-0.843	-0.666	-1.634	-2.639	-1.182	1.669	-0.669	exclude	0.591	1.382	exclude
5	HO_UR	-1.570	-1.118	-1.212	-1.480	-0.720	0.503	0.497	coex	0.360	0.002	coex
6	HO_UR	-1.138	-0.903	-1.735	-2.162	-0.663	1.900	-0.900	exclude	0.331	0.928	exclude
7	HO_UR	-0.955	-0.824	-1.068	-1.314	-0.377	1.299	-0.299	exclude	0.188	0.301	exclude
8	HO_UR	-0.914	-0.450	-1.130	-0.956	-0.290	1.746	-0.746	exclude	0.145	0.361	exclude
9	HO_UR	-1.192	-0.660	-1.123	-1.441	-0.850	0.919	0.081	coex	0.425	0.356	coex
1	PL_SA	-1.422	-1.175	-1.914	-0.915	0.752	0.346	0.654	exclude	-0.376	0.116	exclude
3	PL_SA	-1.486	-1.721	-2.055	-1.961	0.329	-0.730	1.730	exclude	-0.164	0.404	exclude
4	PL_SA	-2.242	-1.653	-1.497	-1.112	-0.204	-2.653	3.653	exclude	0.102	-0.643	exclude
5	PL_SA	-1.570	-1.229	-1.692	-1.421	-0.070	2.742	-1.742	exclude	0.035	0.157	exclude
7	PL_SA	-2.069	-1.878	-1.680	-1.624	-0.135	-1.873	2.873	exclude	0.068	-0.322	exclude
8	PL_SA	-2.291	-0.963	-1.977	-2.156	-1.507	0.792	0.208	coex	0.754	0.440	coex
9	PL_SA	-2.326	-0.882	-2.238	-1.439	-0.645	0.863	0.137	coex	0.322	0.234	coex
10	PL_SA	-2.485	-1.749	-1.925	-1.144	0.045	13.419	-12.419	exclude	-0.023	-0.582	exclude
1	PL_UR	-1.422	-1.637	-2.164	-1.695	0.684	-0.085	1.085	exclude	-0.342	0.400	exclude
2	PL_UR	0.324	-1.311	-1.309	-1.189	1.756	0.070	0.930	exclude	-0.878	0.755	exclude
4	PL_UR	-2.242	-2.046	-1.677	-2.639	-1.158	0.512	0.488	coex	0.579	0.014	coex
5	PL_UR	-1.570	-0.674	-1.518	-1.480	-0.858	0.939	0.061	coex	0.429	0.377	coex
6	PL_UR	-1.843	-1.516	-1.794	-2.162	-0.695	0.929	0.071	coex	0.348	0.299	coex
7	PL_UR	-2.069	-1.125	-1.592	-1.314	-0.666	0.284	0.716	coex	0.333	-0.144	coex
8	PL_UR	-2.291	-1.333	-2.371	-0.956	0.457	0.825	0.175	exclude	-0.229	-0.148	exclude
9	PL_UR	-2.326	-1.316	-1.863	-1.441	-0.588	0.213	0.787	coex	0.294	-0.169	coex
1	SA_UR	-0.915	-0.645	-1.493	-1.695	-0.473	2.220	-1.220	exclude	0.237	0.814	exclude
4	SA_UR	-1.112	-0.644	-1.304	-2.639	-1.803	1.106	-0.106	exclude	0.902	1.093	exclude
5	SA_UR	-1.421	-1.394	-1.188	-1.480	-0.320	0.270	0.730	coex	0.160	-0.073	coex
7	SA_UR	-1.624	-1.709	-1.217	-1.314	-0.012	-32.707	33.707	exclude	0.006	-0.401	exclude
8	SA_UR	-2.156	-1.223	-0.755	-0.956	-1.135	-0.235	1.235	exclude	0.567	-0.834	exclude
9	SA_UR	-1.439	-1.671	-1.814	-1.441	0.604	0.380	0.620	exclude	-0.302	0.073	exclude

Colophon

This document is set in EB Garamond, Source Code Pro and Lato. The body text is set at 11pt with *TeXGyrePagella*(0).

It was written in R Markdown and LaTeX, and rendered into PDF using gauchodown and bookdown.

This document was typeset using the XeTeX typesetting system, and the University of Washington Thesis class class created by Jim Fox. Under the hood, the University of Washington Thesis LaTeX template is used to ensure that documents conform precisely to submission standards. Other elements of the document formatting source code have been taken from the Latex, Knitr, and RMarkdown templates for UC Berkeley's graduate thesis, and Dissertate: a LaTeX dissertation template to support the production and typesetting of a PhD dissertation at Harvard, Princeton, and NYU

The source files for this thesis, along with all the data files, have been organised into an R package, xxx, which is available at `https://github.com/xxx/xxx`. A hard copy of the thesis can be found in the University of Washington library.

This version of the thesis was generated on 2020-09-10 17:26:08. The repository is currently at this commit:

The computational environment that was used to generate this version is as follows:

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