

Consequences of plant functional traits and plant-microbe interactions on species coexistence in heterogeneous landscapes

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Abstract:

How do interactions between organisms and their environment influence the dynamics of ecological communities? Ecologists have long understood that species performance can be impacted by both their response to the abiotic variation and by their interactions with other organisms. In my dissertation I aim to experimentally investigate how species coexistence is impacted by plant resource use strategies (as summarized by functional traits) and species-specific interactions with soil microorganisms in an annual plant community in coastal California. A longstanding assumption has been that the coexistence of species with dissimilar functional traits is stabilized due to their distinct responses to environmental heterogeneity (Adler et al. 2013). For Chapter 1 I plan to test this assumption using recent advances in coexistence theory that decompose the outcome of species interactions in patchy landscapes into coexistence-promoting stabilizing niche differences and fitness differences that drive competitive exclusion (Chesson 2000). Specifically, I propose to test whether functional trait differences are predictive of the similarity in the functional responses of species to environmental gradients. Another striking observation from nature is that individuals within a species can have vastly different phenotypes. Despite considerable interest, the consequences of this variation on species coexistence remain largely unclear (Violle et al. 2012, Turcotte and Levine 2016). For Chapter 2, I aim to investigate how intra-specific variation in functional traits might influence community dynamics beginning from understanding of how trait differences influence species coexistence generally. Over the past two decades, a great deal of research has also highlighted the role of soil microorganisms in shaping terrestrial plant communities (Bever et al. 2015). A key insight to emerge from this line of inquiry is that plant species coexistence can be promoted when plants cultivate a soil microbial community that has more negative impacts on plants of the same species than on plants of other species, which is in agreement with traditional coexistence theory (Chesson 2000, Bever 2003). Although these biotic interactions influence plant community dynamics in nature in conjunction with abiotic factors, their effects are generally considered independently of one another (van der Putten et al. 2016). For Chapter 3, I aim to demonstrate how the relative contributions of plant-plant competition and plant-microbe interactions can be jointly considered under the established coexistence framework of Chesson and Kuang (2008) via a critical review of existing plant-soil feedback literature. This thesis will involve novel applications of recent advances in theoretical ecology to plant community and integrate the historically disjunct fields of plant competition and plant-microbe interactions.

Background

Overall introduction will go here. I plan to give a broad introduction to species coexistence, describe the benefits of the trait-based approach, and describe how recent advances in microbial ecology have been relevant to plant ecology (1-1.5 pages?).

Chapter 1: How do functional traits relate to species responses to variable environments?

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A foundational principle of trait-based ecology is that traits are functional to the extent that they influence population demography by directly influencing growth, survival, and reproduction (Vielzeuf et al. 2007). As variation in demographic properties is at the heart of species coexistence (Chesson 2000), understanding the links between species traits and their demography is a critical step in using traits to understand coexistence. Although ecologists have long understood that trait differences can reduce the niche overlap between species to promote coexistence (MacArthur and Levins 1967), recent advances have shown that trait differences can also promote competitive exclusion (Adler et al. 2013, Kraft et al. 2015). As nature is often strikingly patchy in space and as species often have clumped distributions on landscapes, spatial variation is thought to be an important driver of coexistence in plant communities (Chesson 2000). Therefore, traits likely influence species coexistence by their effect on species' demographic responses to variable environments.

Despite being fundamental to interpreting patterns of trait variation in nature, the links between trait differences and species' demographic responses remain largely unresolved (Shipley et al. 2016, but see Adler et al. (2014) and Wright et al. (2010) for counter-examples). Many studies have shown non-random associations between trait values and the environment (Cornwell and Ackerly 2009, Dray et al. 2014, Fortunel et al. 2014). However, it is difficult to interpret these results in the context of the demographic drivers of coexistence. For example, an important limitation of these studies is that observed abundances are influenced not only by environmental variation but also by biotic variation between sites (Adler et al. 2013). Indeed, the most abundant species at a site need not have the traits that confer the highest fitness at that site (Fox 2012). Therefore, experimentally isolating the impact of environment while keeping the competitive environment constant is a critical step in building stronger links between functional trait differences and variation in species responses to variable environments (Adler et al. 2013). Interpreting these results in light of ecological first principles regarding trait-environment relationships can give generality to the findings.

In addition to the competitive neighborhood, the biotic interactions between plants and microbes may also change across space to influence plant performance. This turnover of soil microbes may have important effects on plant responses to abiotic environmental variation (Keymer and Lankau 2017). For example, Lau and Lennon (2012) found that the fruit production of *Brassica rapa* was less impacted by a drought treatment when the plants were grown with a drought-adapted soil microbial community than when grown with a soil microbial community that had not been previously exposed to drought. Therefore, the soil microbial community may function as an additional environmental variable that to date has received relatively little attention from plant ecologists. Recent advances in sequencing technology have made it feasible to characterize variation in soil microbial turnover, and we can begin to assess their role in driving plant environmental preferences.

To address these gaps, I propose to use experimental data to estimate the contribution of trait differences to species-specific demographic responses to environmental variation, including turnover in soil microbial communities, for the first chapter of my dissertation.

Chapter 1 hypotheses

H₀: Species may respond identically to environmental variation, irrespective of functional traits. We may expect this pattern if the environmental gradient spans a single stress gradient axis such that all species perform poorly at some sites and well at others (Figure 1a).

H₁: Species may have idiosyncratic responses to the environmental gradient, but the response may be unrelated to species functional traits. There may be potential for the storage effect to promote species coexistence, but the degree of stabilization would be uncorrelated to species' functional similarity (Figure 1a).

H₂: Variation in responses of species to environmental gradients may be explained by their functional traits. This pattern might arise if the functional traits are indicative of species' environmental preference along the gradient sampled (Figure 1a).

H₃: Species similarity in some traits may correlate with similarity in response to certain environmental variables. For example, species' similarity in drought tolerance may predict their response to an aridity gradient but not to a light gradient, and species similarity in seed size may predict their response to a soil texture gradient but not an aridity gradient (Figure 1b).

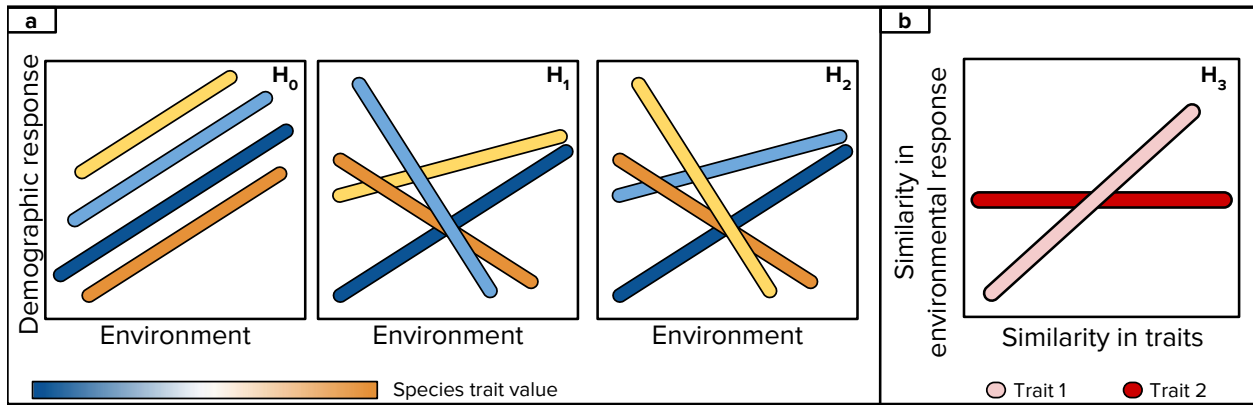


Figure 1: Potential ways in which trait differences may correlate with differences in species' demographic response

Methods

Demographic variation: In 2015-2016, we planted seeds of 17 annual plant species (Table 1) in a setup that allowed me to parameterize a simplified annual plant population growth model. Specifically, the population growth rate of species j at site x is modeled as a function of the germination rate $g_{j,x}$, a global seed-bank survival rate for each species s_j , low-density seed production $\lambda_{j,x}$, species response to competitors $r_{j,x}$, and the competitive neighborhood density η_x :

$$\frac{N_{t+1,j,x}}{N_{t,j,x}} = (1 - g_{j,x}) * s_j + \frac{g_{j,x} * \lambda_{j,x}}{1 + r_{j,x} * \eta_x}$$

In this framework, environmental response can be parameterized in three ways: germination rate, the per-capita seed production in the absence of competitors, and a composite index that yields the expected population growth rate in the absence of competitors.

Trait variation: A suite of leaf, root, seed, and whole-plant functional traits (*table to be inserted*) were measured for twelve of the annual plant species in this experiment by Kraft et al. (2015). I have measured the same set of traits for the five remaining species and will additionally measure leaf osmotic potential (Bartlett et al. 2012), stomatal index, and leaf vein density (Sack and Scoffoni 2013), all of which summarize components of leaf-level drought tolerance.

Abiotic environmental variation: We characterized various soil chemical and physical properties at each of our experimental sites during the 2015-16 growing season. Air temperature at each of the plots was measured with temperature data loggers (iButtons) that were placed inside PVC tubing to shield from solar radiation, and gravimetric water content was measured for twice for each plot - once each in the peak growing season for the early and later phenology species.

Biotic environmental variation: We characterized the variation in soil microbiota among our plots by using metagenomic sequencing to profile the diversity of bacteria, fungi, and small eukaryotes. Soil was pooled from three equally spaced points within each experimental plot into a single sterilize 15 mL tube and stored at -80°C until further processing. Total DNA was extracted using the MoBio Power Soil Extraction kit and PCRs were conducted using 16s rRNA primers for bacteria, fungal ITS primers, and 18s rRNA primers for small eukaryotes. Pooled samples were sequenced on the Illumina MiSeq platform at the UC-Berkeley sequencing facilities. Sequence data will be used to ordinate sites according to their soil microbial communities in multidimensional space.

Table 1: Species list for demography study

Family	Species
Asteraceae	Agoseris heterophylla
Asteraceae	Centaurea melitensis
Asteraceae	Chaenactis glabriuscula
Asteraceae	Hemizonia congesta
Asteraceae	Lasthenia californica
Asteraceae	Micropus californicus
Boraginaceae	Amsinckia menziesii
Onagraceae	Clarkia bottae
Onagraceae	Clarkia purpurea
Euphorbiaceae	Euphorbia peplus
Fabaceae	Medicago polymorpha
Fabaceae	Lotus wrangeliensis
Poaceae	Bromus madritensis
Poaceae	Hordeum murinum
Poaceae	Vulpia microstachys
Lamiaceae	Salvia columbariae
Plantaginaceae	Plantago erecta

Analyses: I propose to assess the influence of functional traits on the demographic responses of species to environmental gradients with a generalized linear mixed modeling (GLMM) framework modified from (Jamil et al. 2012). This framework, which was developed under the context of the fourth-corner problem (Legendre et al. 1997) to estimate trait-environment relationships, models species performance across a landscape ($p_{i,j}$) as a function of species traits z , environmental properties x , and crucially, an interaction term between the two:

$$p_{i,j} \sim \underbrace{a_0}_{\text{species effect}} + \underbrace{a_1 z_j}_{\text{trait effect}} + \underbrace{b_0 x_i}_{\text{environment effect}} + \underbrace{b_1 z_j x_i}_{\text{interaction}} + \underbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}_{\text{error terms}}$$

The species and site effect terms can be thought of as unmeasured species traits and environmental variables, respectively. The contribution of trait differences to interspecific variation in environmental response (i.e. the slope parameter β_1) can be quantified as a function of the variance explained $\hat{\sigma}_b$ by a model that includes a trait:environment term and one that lacks this interaction:

$$C_{\beta} = 1 - \frac{\hat{\sigma}_{\beta, \text{ no interaction term}}^2}{\hat{\sigma}_{\beta, \text{ with interaction term}}^2}$$

Preliminary results, implications, and further analyses

A large proportion of the species pairs had uncoupled demographic responses- in other words, most species pairs did not respond in the same way to the multivariate changes in environment across sites (Figure 2a), which suggests against \mathbf{H}_0 . Thus, variable responses of species to environmental heterogeneity may contribute to their coexistence in this landscape. The environmental variation stems primarily from differences in soil $[\text{Ca}^{2+}]:[\text{Mg}^{2+}]$ ratio and in soil texture and depth (Figure 2b). The species in this experiment differed primarily in leaf economics spectrum traits on the first axis of variation and on whole plant traits on the second axis of variation. Preliminary analyses conducted with simple linear regressions (not in the GLMM framework above) suggest that some trait differences may explain variation in species responses to environment. For example, four out of the five smallest-seeded species in this experiment responded positively to shallower and sandier soils, whereas all other species prefer deeper soils with higher clay content.

Modeling variation in demographic response to environment in this framework above will address a fundamental gap of trait-based plant ecology: the assumption that functional traits have direct and predictive relationships with measurable environmental gradients (Adler et al. 2013, Shipley et al. 2016). Due to strong separation of sites along axes of soil chemistry and physical structure, we may find that root and seed traits that directly link to species' belowground ecological strategies are more relevant to explaining variation in species response in our system than traits that primarily inform aboveground strategies. Alternatively, physiological traits with a clear link to an environmental axis (e.g. leaf osmotic potential to water availability) may show stronger links to plant performance than integrative traits like SLA that are related to various environmental axes. An important step will be to conduct a power analysis to assess the extent to which the potentially weak but important influences of individual traits (as might be expected for some of the integrative functional traits measured for this study) can be recovered given the probabilistic nature of many demographic models (Snyder & Ellner, *in prep*). A number of studies have also found phylogenetic structure in plant communities; therefore, incorporating evolutionary non-independence of our samples by using phylogenetically informed GLMMs (Ives and Helmus 2011) is another promising next step. I plan to interpret all results in light of ecological first-principles and in the framework of modern coexistence theory to yield generality to these findings. Armed with a more robust understanding of the link between traits and demography, trait-based plant ecology can move towards its potential to be a predictive science in a rapidly changing world (McGill et al. 2006)

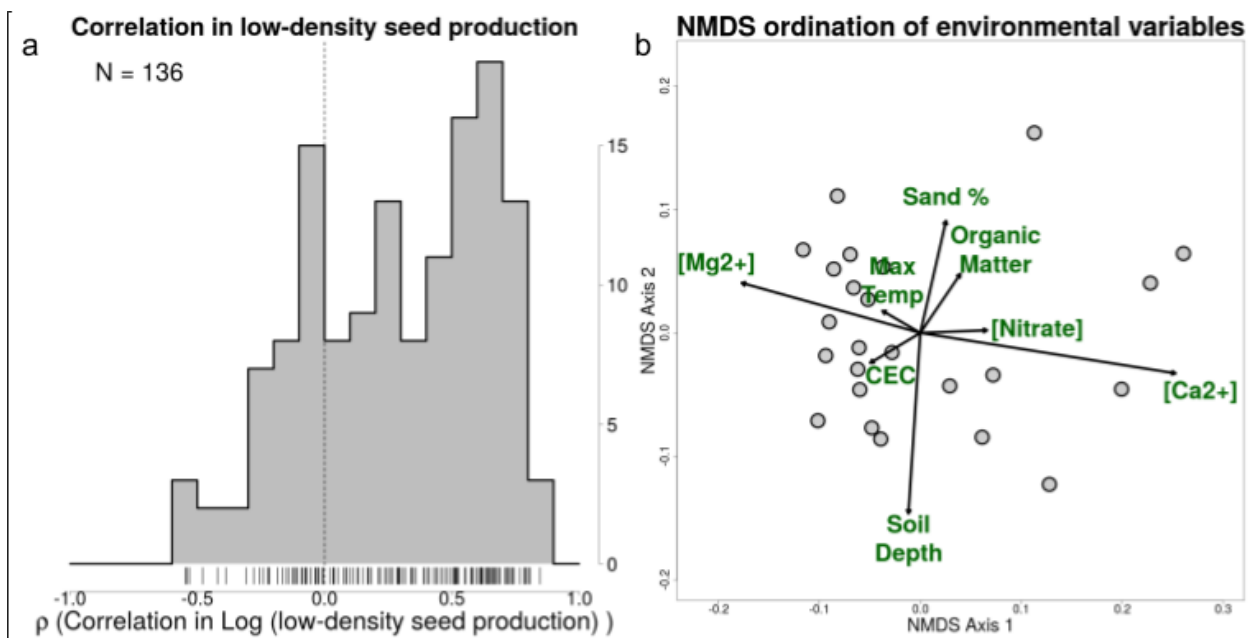


Figure 2: a) Species tended to show decoupled demographic responses (all pairwise correlations in species responses < 1). b) Soil chemical and physical properties were the primary axes of variation among sites. c) Species differed primarily in their leaf economics traits along PC axis 1 and primarily on whole-plant traits along PC axis 2. d) Four of the five smallest seeded species had a positive response to Environment axis 2, unlike all of the bigger seeded species. **This is a low-quality draft figure, will have better one later**

Timeline

Year	Season	Plan
2017	Fall- Winter	Finalize data collection and Analysis for Chapter 1; Literature reviews for Chapter 3
2018	Spring- Summer	Analysis and writeup for Chapter 1; Additional data collection for Chapter 2; Literature reviews & modeling for Chapter 3
2018	Fall- Winter	Submission for Chapter 1, Analysis for Chapter 2, Modeling & analysis for Chapter 3
2019	Spring- Summer	Writeup and Analysis for Chapter 2, Writeup for Chapter 3
2019	Fall- Winter	Writeup for Chapter 2; Submission for Chapter 3
2020	Spring	Submission for Chapter 2

Chapter 3: Considering the consequences of soil microbial communities on plant species dynamics under the modern coexistence framework

Microbes are ubiquitous in nature and can have dramatic impacts on the performance of larger organisms. Redman (2002) found that when colonized by endophytic fungi in the genus *Curvularia*, the Panic grass *Dichanthelium lanuginosum* could withstand sustained soil temperatures greater than 50°C. This interaction is critical to understanding the persistence of the grass in geothermal soils where few other plants occur. Conversely, microbes can severely harm plant populations. For instance, the oomycete *Phytophthora ramorum* caused dramatic declines in populations of tanoak (*Lithocarpus densiflorus*) and coast live oak (*Quercus agrifolia*) in coastal California and Oregon in the late 1990s (Rizzo et al. 2005). This severe bout of mortality continues to have profound impacts on the community and ecosystem dynamics in those systems (Cobb et al. 2013). Theoretical and empirical advances in the last two decades have highlighted that microbes can also have subtler mechanisms for effecting profound changes in plant communities. For example, van der Putten et al. (1993) suggested that plant succession in foredune communities is driven by the relative promotion of later-successional plant species in soils that harbor a microbial community cultivated by earlier-successional plants. In a generalized theoretical framework that has stimulated a great deal of research, Bever et al. (1997) showed how feedback loops between plants and soil microbes (“plant-soil feedbacks”, or PSFs) could permit the coexistence of competing plant species. In short, plant-microbe interactions have the potential to dramatically influence the outcomes of plant species interactions and community assembly.

But how important are these effects in comparison to the competitive effects that are the subject of traditional coexistence and community assembly theory? We cannot answer this question without a framework that simultaneously considers the effects of both mechanisms. For the third chapter of my dissertation, I propose to demonstrate that the effects of plant-microbe interactions can be considered jointly with the effects of resource competition under the competition-predation framework of Chesson and Kuang (2008) and critically review the empirical work conducted under the plant-soil feedback framework of Bever et al. (1997) in this new context. Fundamental to this reframing is the fact that microbes can influence plants in ways that are independent of any feedbacks (i.e. some microbial contexts always benefit or always harm plant species, regardless of plant species density), and via feedbacks (i.e. the impacts of some microbes on plant species may change with plant species density). Here I briefly review the state of PSF research, summarize Chesson and Kuang (2008)’s coexistence framework, and begin to show how the former can be integrated into the latter.

State of plant-soil feedback literature: Plants can alter both biotic and abiotic characteristics of the soil. Plants that later grow in those soils will be responding to the changes- this cyclical relationship is the basis of plant-soil feedbacks (PSFs). Bever et al. (1997) showed that if the effects of the soil community cultivated by a plant species *A* are more negative to the population growth rate of species *A* than the growth rate of plant species *B*, and vice-versa (i.e. more negative intra-specific effects than inter-specific effects), then PSFs can promote species coexistence. Alternatively, positive PSFs can drive competitive exclusion by preferentially promoting the performance of the abundant species. This framework has inspired many studies (a Web of Science search for titles containing “plant-soil feedback*” yielded 171 results overall and 73 in 2015-2017 alone) which have documented a diversity of positive, negative, and neutral effects of PSFs.

Despite such extensive experimentation, it remains difficult to predict the importance of PSFs: their impacts seem to be highly species- and environment-specific (van der Putten et al. 2016). For example, Smith-Ramesh and Reynolds (2017) predict that PSFs are less important for coexistence in higher nutrient sites where plants can have high immunity and produce more defence compounds, whereas van der Putten et al. (2016) predict that the higher performance of pathogens in higher nutrient sites will increase the importance of negative PSFs. Additionally, most experimental work is conducted under highly controlled greenhouse settings, and it is difficult to translate these results into the importance of PSFs in nature (van der Putten et al. 2016). Finally, an important limitation of these studies is that it ignores the potential for plants to respond to site-driven differences in soil microbes. Reframing the theoretical context of this work may highlight heretofore overlooked parameters and suggest avenues of research to start building generalities.

Overview of competition/predation framework: That shared natural enemies can change the outcome of strict resource competition has been long understood in ecology (Holt 1977). h

Many of these gaps can be addressed by reconsidering plant-microbe interactions in light of the competition-predation framework of Chesson and Kuang (2008). Soil microbes can be thought of as any other predator that decreases the population growth rate of the prey (here, the focal plants). Plant-microbe interactions with net positive feedbacks can be modeled by setting the effect of the predator on the prey to be positive.

Summary of Chesson 2008

$$\frac{1}{N_j} \frac{dN_j}{dT} = \sum_l c_{jl} v_l R_l - \sum_m a_{jm} P_m - \mu_j$$

$$\frac{1}{R_l} \frac{dR_l}{dT} = r_l (1 - \alpha_l R_l) - \sum_j N_j C_{jl}$$

$$\frac{1}{P_m} \frac{dP_m}{dT} = r_m (1 - \alpha_m P_m) + \sum_j W a_{jm} P_m$$

$$\rho = \frac{\sum_l \frac{C_{jl} V_l C_{kl}}{r_l^R \alpha_l^R} + \sum_m \frac{a_{jm} w a_{km}}{r_m^P \alpha_m^P}}{\sqrt{\left(\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} + \sum_l \frac{a_{jm}^2 w}{r_m^P \alpha_m^P} \right) \left(\sum_l \frac{c_{kl}^2 v_l}{r_l^R \alpha_l^R} + \sum_l \frac{a_{km}^2 w}{r_m^P \alpha_m^P} \right)}}$$

$$\kappa_j = \frac{\sum_l \frac{C_{jl} v_l}{\alpha_l^R} - \sum_m \frac{a_{jm}}{\alpha_m^P} - \mu_j}{\sqrt{\left(\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} + \sum_m \frac{a_{jm}^2 w}{r_m^P \alpha_m^P} \right)}}$$

Preliminary results, further analyses, and implications

Analysis of Chesson and Kuang (2008)'s model shows that the net impacts of plant-microbe feedbacks can be influenced by several parameters. For instance, the importance of PSFs to plant coexistence is not only a function of the relative impacts of the microbes on the two focal species, but also a function of the degree to which microbial populations are sustained by other species in the community. Specifically, the importance of PSFs is strongest when the microbes interact only weakly with species outside of the focal group (Table ??). Another key insight to emerge from this framework is that all else being equal, the relative importance of PSFs is higher in more fertile sites (those with higher resource replacement rates r^R , Table ??). This insight is in direct contradiction with the recent prediction of Smith-Ramesh and Reynolds (2017), who suggest that PSFs should be less relevant in more fertile sites but fail to consider the relative importance of PSFs and resource competition.

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