

Species interactions 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.

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

Additional collaborators: Andy Kleinhesselink (UCLA); Jonathan Levine (ETH-Zurich); Emily Curd (UCLA/Cal eDNA)

In the intro, write about microbial community as an environmental variable

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).

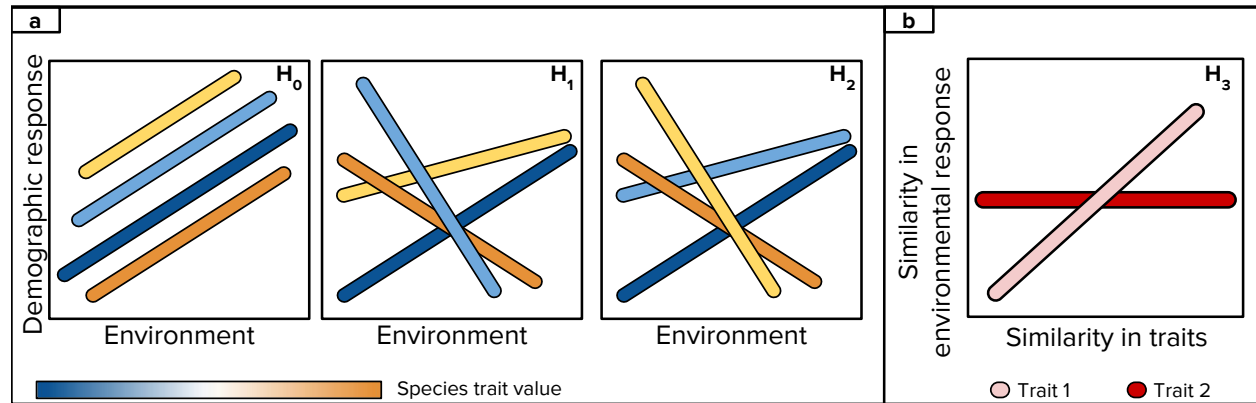


Figure 1: Test

Methods

Demographic response: In 2015-2016, I 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 ??) were measured for twelve of the annual plant species in this experiment by Kraft et al. (2015). I will measure the same set of traits for the five remaining species according to the same protocols 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 environmental variables at each of our experimental sites during the 2015-16 growing season. Soil physical and chemical properties were analysed by A&L Western Labs. 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. The gravimetric water content was measured for each plot on 1 April 2016 (corresponding to the peak growing season for the majority of species that have an earlier phenology) and on 1 May 2016 (corresponding to peak growing season for a suite of 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 sampled on 1 April 2016 and pooled from three equally spaced points within each experimental plot into a single sterilize 15 mL tube. Samples were 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.

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), models species performance across a landscape ($p_{i,j}$) as a function of species traits z , environmental properties x , and crucially, an interaction term

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 wrangelensis
Poaceae	Bromus madritensis
Poaceae	Hordeum murinum
Poaceae	Vulpia microstachys
Lamiaceae	Salvia columbariae
Plantaginaceae	Plantago erecta

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 $\hat{\sigma}_b$ between 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 ??a), suggests against H_{10} . 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 $[Ca^{2+}]:[Mg^{2+}]$ ratio and in soil texture and depth (Figure ??b).

The soil microbial community also varied across our landscape (currently running scripts to get an NMDS plot f

The species in this experiment span a wide range of functional diversity, with leaf size ranging from XXX to XXX and SLA ranging from XXX to XXX (Figure ??c). 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 (Figure ??d).

Modeling variation in plant response to environment according to the GLMM framework above will address a fundamental gap of trait-based plant ecology: the assumption 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, root and seed traits that directly link to species' belowground ecological strategies may be more relevant to explaining variation in species response in our system than traits that primarily inform aboveground strategies. Alternatively, traits that have direct links to plant physiology that clearly link to an environmental axis (e.g. 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 the models (Snyder & Ellner, *in prep*). A number of studies have also documented 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. Armed with a better understanding of the link function between traits and fitness, trait-based plant ecology can move towards its potential to be a predictive science in a rapidly changing world (McGill et al. 2006)

Chapter 2: How might trait plasticity in response to abiotic environment and competitors shape species' demographic responses to environment?

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Methods

Preliminary results

What results might mean

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

Additional collaborators: Emily Curd (Cal eDNA Consortium)

- There is mounting evidence that interactions between plants and microbes have the potential to influence plant community dynamics (van der Putten et al. 2016). Microbes can have positive or negative impacts on plant performance.
- In an extreme case, Redman (2002) showed that the Panic grass *Dichanthelium lanuginosum* was able to withstand sustained soil temperatures of 50 C when its roots were colonized by endophytic fungi in the genus *Curvularia*, but suffered 100% mortality when grown alone. As the grass naturally occurs in geothermal sites whose soils frequently reach >50 C in Yellowstone and Lassen Volcanic National Parks, it was shown that this microbial interactions was critical to determining plant performance in the field.
- Soil microbes also have the potential to severely harm plants. 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), which continues to have profound impacts on the community and ecosystem dynamics in those systems (Cobb et al. 2013).
- These above interactions are fundamentally about the plant response to their environment; in other words, these only consider the consequences of the environment on plant performance and not the impacts of plants on the soil microbiota.
- Feedbacks between plants and soil microbes may also have subtler mechanisms for affecting profound impacts on plant community dynamics. For example, van der Putten et al. (1993) suggest that plant succession in foredune communities is driven by the relative promotion of later-successional plant species in soil that are colonized by microbial communities cultivated by earlier-successional species.
- In short, plant-microbe interactions have tremendous potential to influence the outcomes of species interactions and community assembly (Bever et al. 2015).
- Bever et al. (1997) developed a fruitful theoretical framework to describe the consequences of plant-soil feedbacks on plant populations that has been extended by many subsequent theoretical and empirical studies (Bever 2003, Eppinga et al. 2006, Aguilera 2011). Here, I

present the fundamentals of this framework, highlight important results, and argue that considering plant-microbe interactions in the modern coexistence framework (Chesson 2000) will help us better understand these interactions in realistic environmental contexts.

Plant-soil feedbacks

- PSFs operate when plant species “culture” a soil microbial community that in turn influences the performance of plants growing in that soil.
- The field of PSFs blossomed with two seminal studies in the early 1990s.
- First, Bever (1994);
- Second van der Putten et al. (1993)
- Bever et al. (1997) proposed a theoretical framework to investigate these interactions in the classic Lotka-Volterra framework for a pair of competitively equivalent species. Bever (2003) built upon this framework to describe the role of PSFs in a system of unequal competitors
- A key insight to emerge from Bever et al. (1997) was that PSFs could promote coexistence of plant species when each plant species cultivated a soil community that had a greater negative impact on conspecifics than heterospecifics
- Phenomenologically, this is analogous to the coexistence criteria that a pair of species can coexist when net intraspecific competition exceeds net interspecific competition in the system.
- However, a great many of these experiments are conducted in highly controlled greenhouse settings, translating the outcomes from these experiments to the realized drivers of community assembly in the field remains a challenge (Casper and Castelli 2007, van der Putten et al. 2016, Smith-Ramesh and Reynolds 2017)
- Review of the many outcomes that have been documented from studies of “How do PSF strength relate to competition strength” and “How do PSFs predict species abundances”
- Greater integration of PSFs into the burgeoning modern coexistence framework (Chesson 2000) offers a promising way to organize the many ways in which PSFs may also influence the fitness differences to either promote coexistence and consider the joint effects of multiple drivers of community assembly:
 - At the local scale, PSFs may promote coexistence if performance of the competitive superior is curbed due to a buildup of microbes that have a more negative effect on the superior than the inferior competitor.
 - PSFs may also promote exclusion at the local scale if the soil microbial community confers a fitness independent advantage to one of the species

- In heterogeneous environments, variation in soil microbes may promote coexistence if that variation contributes to variation in species' site preference
- On the other hand, soil microbes may hinder coexistence if they have greater negative effects on the competitive inferior plant species in its preferred environments than the negative effects on competitive superior in its preferred environments (i.e. soil microbial communities may reduce the strength of *covEC*)
- Lau and Lennon (2012) showed that plants suffered less in drought conditions when the soil harbored a microbial community adapted to droughts- so, plant species growing in drier sites may suffer less in drought years.
- While the theoretical framework of Bever et al. (1997) allows us to consider the role of microbes in driving stabilizing niche differences, it does not allow for microbes to drive equalizing differences between plant species.
- A promising route for integration is to model plant-microbe interactions under the apparent competition models of Chesson and Kuang (2008), which builds on the apparent competition framework of (???)

Summary of Chesson 2008

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

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

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

- The microbial community cultivated by each species can be modeled as a single “predator” species- an important implication is that this allows the predator to have species-specific impacts on the focal plant species. Cases in which a microbial community has a net positive fitness impact on a plant species can be modeled by setting a_{jm} to a negative value.

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Methods

Preliminary results

What results might mean

Timeline

Academic Year	Quarter	Plan
2017-18	Fall-Winter	
2017-18	Spring-Summer	
2018-19	Fall-Winter	
2018-19	Spring-Summer	
2019-20	Fall-Winter	

Supplement

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