

Plant species coexistence in variable landscapes

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Good morning everyone, thanks all for being here and for being on my dissertation committee. I look forward to sharing my research agenda with you and for your feedback. I will with some background on myself and proposal to research how species' ecological strategies and their interactions with soil microbes shape the coexistence of plants.

Introduction

Slide 2-4

I grew up in India with a love for the diversity of tropical rainforests, I enjoyed learning the local names and uses of all the tree species near my grandparent's farm, and was often struck by how many names there were to remember! As my childhood love for nature matured into a scientific interest in how diversity is generated and maintained, I came to realize that there are fundamental physical and biological phenomena structuring plant diversity- in systems as varied as coastal dune communities of annual forbs, and deserts home to beautifully adapted succulents. There's a lot of similar processes taking place in all of these systems, and one emergent phenomenon common to all of these communities is the co-occurrence of many species of plants.

Slide 5-13

The structure of these communities is influenced by many processes. Among them are evolution, which shapes the regional species pool and drives a lot of broad biogeographic patterns;

seed dispersal- and here I mean both dispersal within a community that might influence the local occurrence of species and the longer-range dispersal that determines which members of the regional species pools end up in the community;

multi-trophic interactions- here I am showing a deer to indicate herbivory, but these could also be mutualistic interactions, for example between acacia plants and the ants that inhabit their domatia and protect them from herbivores;

local environmental variation- here indicated by a gradient of orange dots in the soil, but can also be a temporal variation; interspecific interactions between the plant species- we generally focus on competition here but mutualisms may also be at play;

variation within species- here I am indicating that with a slightly brown individual of this species;

feedbacks between plants and the abiotic environment- in other words, plants can use up resources or release allelopathic chemicals to change soil chemistry or structure;

and finally, feedbacks between plants and the soil biotic environment, namely the microbial community. I want to spend some time on this interaction because although humankind has kind of known about it for a while and used it as the basis of crop rotation, the role of this interaction in community ecology has really emerged quite recently, in the last two decades or so. In a recent review paper Noah Fierer highlighted that a single hectare of soil often house more than a thousand kilograms worth of microbial biomass- so these are really quite ubiquitous. And they might have profound effects on plant communities- for example in 2010, Mangan et al. suggested that the strength of plant-soil feedbacks for six tropical tree species could actually explain variation in those species' abundance in the forest plot at Barro Colorado Island.

Slide 14-15

Of these interactions, I aim to focus on these four aspects- and specifically, I propose to do research that can help us understand how to examine the importance of these processes in any given community, rather than focusing on their importance in a given community. Therefore, I mainly aim to do experimental and theoretical work that can be interpreted in light of ecological first principles. I aim to do so by studying these four interactions in the context of modern coexistence theory, which, although it's a be-all, end-all for explaining community structure, provides us a nice framework to investigate the influence of each of these mechanisms.

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Contemporary coexistence theory, inspired in large part by the work of Peter Chesson, frames coexistence as an outcome of two types of differences between species. First are the so-called "Fitness differences"- these are differences that confer one species a density-independent advantage over the other. Tolerance of a generalist predator is an example- all else being equal, the less susceptible species is expected to win over the species that is more susceptible to the predator. The second type of differences are called "stabilizing niche differences" - these are differences between species that cause a species to limit its own population growth more than that of its competitor. Differences in the timing of resource use, for example, can drive stabilizing niche

differences.

The key insight here is that for a pair of species to coexist, the stabilizing niche differences between them must overcome any fitness differences.

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What determines the magnitude of niche and fitness differences? We can ask this question for any pair of species and ask- what are the niche and fitness differences between these two forbs? or between these two trees? or between these two yuccas? Obviously, it is hard to achieve generality in this way. One way to bring generality is to investigate species coexistence as a consequence of species ecological strategies, as summarized by their functional traits. For example, do differences in root structure drive niche differences because species with dissimilar roots access distinct resource pools? Do differences in leaf size drive fitness differences because larger-leaved species can intercept more light for photosynthesis than smaller-leaved species? This generality is the promise of trait based ecology, but such links as I just described are only recently starting to emerge.

Since variation in space is thought to be an important driver of coexistence, I specifically aim to test whether functional trait differences between species helps us understand whether their coexistence is stabilized by spatial environmental variation.

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As our understanding of this question develops, an important detail is to understand how much intra-specific variation in these traits influences the outcome of coexistence. The real power in trait-based ecology lies in being able to sample individuals from a species and infer community level understanding, so this is a core issue.

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Interactions between soil microbes and plants can also influence fitness and stabilizing niche differences. In nature, interactions between plants and microbes play out simultaneously with the resource competition dynamics that are the traditional focus of plant ecology.

However, in the literature, the two mechanisms are generally considered independently. To make sense of which processes are important in structuring natural communities, we need to better understand the relative importance of these two mechanisms, and that will be the focus of my final chapter.

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This leads me to the three questions I hope to address with my dissertation:

1. How do differences in species functional traits relate to their demographic variation in patchy landscapes?
2. How does intra-specific trait variation influence competitive dynamics?
3. How can we jointly consider the consequences of resource competition and plant-microbe interactions in a unified framework?

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To address the first two questions I am doing field research in Sedgwick Reserve, a UC-NRS site in the Santa Ynez valley of Central Coastal California. Sedgwick boasts a diverse community of annual plants that occur over a heterogeneous landscape encompassing variation in topology and edaphic properties. For question 3 I propose to take a step back from empirical work and frame the relative effects of microbes and resource competition in the competition-predation framework of Chesson & Kuang 2008 and review existing plant-microbe literature in this framework.

Slide 23- Question 1

Understanding the links between species traits and their demography is a crucial link in using traits to understand competitive dynamics and reach the full predictive potential of trait-based ecology.

Slide 25-27

Nature is often strikingly patchy in space, and theoretical and empirical observations suggest that variation in how species respond demographically to that variation is an important driver of coexistence. Although the mathematical requirements for spatial variation to stabilize coexistence are quite complex, we can focus on one empirically and intellectually straightforward component: the requirement that for spatial variation to drive coexistence, species must have idiosyncratic demographic responses to the same environmental variation. If two species have an identical response- in other words, if the sites good for one species are good for the other, and vice-versa, then spatial variation alone is unlikely to drive their coexistence.

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Therefore, to understand how functional traits influence competitive dynamics in a spatially heterogeneous community, we can ask these two questions to explore whether species functional traits are predictive of how their demography changes across environments.

1. Which environmental factors drive variation in species responses to spatial heterogeneity?
2. Which traits mediate species response to the environmental drivers?

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These are the question we sought to address in an experiment we conducted in the 2015-2016 growing season to quantify the demography of 17 annual plant species at 24 experimental plots within sedgwick.

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We planted the experiment in a way that allowed us to parameterize a simplified model of annual plant population growth. Specifically, at each site, we planted seeds in a spaced out grid that let us estimate germination rate and allowed an individual to complete its life cycle without competitors, and also planted seeds in a mixed community of competitors.

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In this model, populations grow as a function of how well a species survives as seeds in the seedbank, how well it germinates, and how well each germinant performs in the absence of competition. The rate of population growth is decreased by the number of competitors each germinant faces at a site and how sensitive it is to competition.

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The seventeen species list we used in this experiment came from eight families and seven orders from across the tree of life, including several Asteraceae in the top row, and several Poaceae in the bottom row.

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The 24 plots we worked in were spread across the reserve, with a cluster of 16 plots in the north edge of the reserve. The plots we worked in varied in NMDS axis 1 in their chemistry, ranging from plots with very high calcium to magnesium ratios and also high nitrate levels,

to those with very low ratios. That makes sense, because some of the plots are on serpentine soils characterized by low Ca:Mg ratio.

We also wanted to know whether there is turnover in the soil microbial community across our sites to which the plants might be responding. To characterize this axis of variation, we extracted total DNA, and PCR amplified 16s, ITS, and 18s regions to characterize the bacterial, fungal, and small eukaryote communities.

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To determine which plant traits mediate species response to environmental variation, we measured a set of traits that are commonly measured in the plant functional ecology literature. At one site, my advisor Nathan Kraft had measured a suite of leaf, root, seed, and whole-plant functional traits on twelve of the seventeen species used in this experiment. I rounded out the dataset by measuring the same traits on the five remaining species. In addition I am measuring leaf osmotic potential, which is a strong predictor of the leaf drought tolerance, on all of the non-grass species in the experiment, and will measure this trait on the grasses in the coming growing season.

These traits generally relate to the plant's ecological strategy, especially on the leaf economics spectrum. Globally, plants with higher SLA tend to also have higher maximum photosynthetic and respiration rates, and lower SLA are characteristic of slower growing or stress tolerant species. There are reasons to expect these traits to predict how species respond to environmental variation- for instance we might expect that species with more drought tolerant leaves have a competitive advantage in drier sites but fare poorly in sites with more available water, assuming that there is a tradeoff between drought tolerance and maximum growth rate.

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For spatial environmental variation to matter for coexistence, species there needs to be variation in how species respond to environmental variation. To test for this I calculated the correlation coefficient between species performance- here measured as germination rate, and here I am plotting a histogram of those correlations - a negative number would mean that the two species in a pair perform best at opposite sites, a correlation of 1 means that both species do well at the same sites and poorly at the others, and an intermediate value means that there is some idiosyncrasy to the species responses. We found that species pairs tended to be uncorrelated in how they respond to environmental variation- this means that we have satisfied one ingredient for spatial variation to promote species coexistence.

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To ask which components of environmental variation drive variation in species demography and which traits mediate those responses, I propose to perform Generalized linear mixed models adapted from the Jamil et al. 2012, in which performance is modeled as a function of species, the species' traits, the environmental conditions of a site, and an interaction between the species traits and how they respond to the environment.

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This model lets us address the two questions I had posed up front- q1 with the environment term,

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and q2 with the interaction term.

Results from preliminary analyses hint at some trait-based drivers of species response. For instance, four of the five smallest seeded species germinate better in soils that are sandier and shallower, whereas all other species have higher germination rates in deeper, clay-er soil.

Slide 39 -42

In summary, in this chapter I will experimentally explore which are the environmental parameters that drive demographic variation, and which traits mediate species responses. Although the drivers of selection will undoubtedly vary across different communities, this study will help the field think about how to interpret patterns of trait turnover in natural communities and which traits to focus on when only a few can be sampled.

Slide 43

So far in my Chapter 1, and in the field of plant trait ecology generally, functional traits are typically used to summarize ecological strategies at the species level. But we know that there is variance in trait values within species. In this chapter, I propose to study how such intraspecific trait variation (which I might call ITV) influences coexistence outcomes.

Slide 44-46

There can be substantial variation of functional traits within a species. Such ITV has many sources. For example, shade leaves tend to be larger and thinner than sun-exposed leaves of the same individuals. Population genetic differences within a species may cause species to have different traits in different environments.

In a meta-analysis, Siefert et al. recently reported that on average a quarter of the variation in traits within communities is driven by ITV.

As the demographic properties that are at the heart of coexistence emerge from interactions between individuals, it is important to consider how intra-specific trait variation, or ITV, can influence coexistence of species.

Slide 47-49

Some authors have suggested that traits of individuals may shift in ways that minimize fitness differences or maximize niche differences so that coexistence is promoted, as in the black arrows here.

On the other hand, Hart et al. recently developed a theoretical model that accounts for individual-level variation in demographic traits and showed that such ITV can act to promote competitive exclusion of species due to nonlinear averaging. This was a very compelling result, but Hart et al.'s study had two important limitations. First, they work with variation in demographic rates such as the sensitivity of an individual to competitors, whereas most empiricists measure variability in functional traits. Second, Hart et al. assumed a well-mixed community in which there was no structure to the trait variation- in other words, the traits of an individual were randomly drawn from a species distribution. This is unlikely to occur in nature, as we know that traits tend to change predictably. Therefore, the consequences of observed ITV in natural communities still remains murky.

As most trait based studies of community ecology rely on the validity of the assumption that species mean traits are predictive of competitive dynamics that play out between individuals, it is important for the field to have a better understanding of how (if at all) ITV in functional traits influences coexistence.

As Kraft et al. have developed trait-based models of niche and fitness differences for the Sedgwick annual plant community, it is an ideal community in which to ask the following questions.

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1. What is the structure of trait variation across the environmental gradient over which we work at Sedgwick? In other words, do traits vary randomly across the landscape, or are there patterns to how traits change within a species? and 2) How do traits respond to competitive neighborhoods, and how might this influence coexistence outcomes? In other words, do plants shift their ecological strategies based on their competitive neighborhood to change the outcome of their interaction?

Slide 51-52

To address these questions we planted seeds of 20 species at the same 24 plots we had used for the Chapter 1 experiments. At each site seeds were planted 15cm away from each other so that plants were growing at a very low density of competitors. Additionally, at one site, we planted the same set of species in high-density competition plots.

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We measured the leaf size, specific leaf area, and leaf dry matter content of three leaves from each individual, measured the height and canopy shape index of each individual, and stored washed fine roots of in ethanol for analysis this fall to measure their specific root lengths. We chose these traits because they are known to vary across environmental gradients both within and between species, and because they are commonly measured on large numbers of individual due to their relative ease of measurement.

For this study we have to-date processed over 800 individual plants and over 2400 leaves for an average sampling of 40 individuals per species.

Slide 54-55

To test for the effects of our treatments on traits, I plan to again fit GLMM models with a similar structure as in Chapter 1. Here, trait values will be modeled as a function of species identity, environmental parameters, and an interaction term. If species have idiosyncratic responses to the environment, then we expect this environmental term to be significant and have strong effect sizes.

Slide 56

As a preliminary test of this second question, I conducted a two-way ANOVA to test for the influence of species identity, competitive den-

sity, and their interaction on the leaf functional traits measured for this study.

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For the next few slides I will show graphs showing the shift in SLA in response to competition. Here we see that the SLA of LACA shifts to be lower- in other words, a slightly more “resource conservative” leaf, for this species.

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But for another species, Euphorbia, we see that SLA goes up in response to competition. For this species pair we’re getting higher trait differences when measured in competition.

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If we consider a third species, Plantago erecta, we see that the trait difference between plantago and lasthenia is diminished when measured in competition.

Slide 60

Obviously I can take up your whole day if I keep doing these pairwise comparisons so I’m going to show the trait responses all at once, and although it’s kind of a busy graph, the thing to keep in mind is that there is considerable variance in these slopes. That there is variance in the slopes is captured by the significance of the interaction term of the ANOVA.

Slide 61

And in fact we see that the interaction term is significant in the ANOVA for all three leaf traits measured for this study.

From here, we need to take these differences and feed them into the models of pairwise fitness and niche differences built by Kraft et al for the Sedgwick system, and that’s what I exactly what I plan to do.

Slide 62-64

As a summary, in this chapter I plan to experimentally tackle the important question of whether individual variation in functional traits can change the magnitude of fitness or niche differences to change the outcome of competition.

Slide 66

The dynamics of natural communities are complex, being influenced by multiple mechanisms at once. Plant ecologists have recently realized that microbes can effect dramatic changes in plant community dynamics, and in my third chapter, I propose to demonstrate how we can consider the effects of this mechanism in conjunction with the effects of plant competition.

Slide 67

Microbes are ubiquitous and can have dramatic impacts on plant communities. As a dramatic example, in 2002, Redman showed that panic grass can withstand sustained soil temperatures greater than 50 degrees Celsius, but only if its roots are colonized by fungi in the genus *Curvularia*. As the grass is commonly found growing in geothermal soils near volcanoes in the Western US, this microbial interaction is critical to explaining its distribution. Microbes can also effect profound changes on plant community dynamics through much subtler mechanisms. In a seminal paper that came out about 20 years ago, van der Putten et al. suggested that primary succession in coastal foredune communities could be the dynamics between plants and microbes.

Slide 68

Twenty years ago, Bever et al. showed with a theoretical model that interactions between plants and the soil microbes they cultivate may promote the coexistence of plant species. The key insight was that plant species coexistence was possible when the soil microbial community cultivated by one species had more negative impacts on population growth of the same species than of the competitor. In the parlance of Modern Coexistence Theory, Bever et al. were proposing a new mechanism for stabilizing niche differences.

The PSF framework has stimulated considerable empirical research. Numerous studies have been conducted, often in greenhouses, and have found that PSFs may promote, destabilize, or not affect coexistence outcomes. But as I see it, there is tremendous scope to call on the insights of this framework and Modern Coexistence theory to have a more holistic view of how microbes can affect coexistence.

For instance, this framework doesn't account for the fact that microbes may also drive fitness differences; second, studies in this framework test the impacts of plant-soil feedbacks independently of the plant competition dynamics that have long been the focus of traditional plant ecology.

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Furthermore, MCT can bring some quantitative rigor that I think can address some of the ambiguities in the PSF literature right now. For example, two recent review papers have proposed competing hypotheses regarding the importance of PSFs in natural studies. Smith-Ramesh and Reynolds suggested that PSFs should be less important in nutrient-rich communities than in nutrient-poor communities because plants might have stronger defence capabilities when nutrients are abundant, whereas van der Putten et al. 2016 suggested that PSFs should be most important in nutrient-rich communities where pathogen loads are higher.

Slide 70

For the third chapter of my dissertation, I propose to demonstrate how PSFs can be considered under the modern coexistence theory using a competition-predation framework developed by Chesson and Kuang in 2008. This framework addresses the two shortcomings I mentioned on the previous slide: first, it accounts for contribution of plant-microbe interactions to fitness differences, and second, it calculates both niche and fitness differences as a consequences of the joint effects of natural enemies and resource competition.

Slide 71

Chesson and Kuang propose a system in which they model the dynamics of focal species, the resources they consume, and their enemies

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The system is fairly straight forward, and I'm happy to discuss parameters later.

From these, Chesson and Kuang derive equations for the niche and fitness differences between the focal species.

Slide 73

Here I am showing the equations for niche and fitness differences from Chesson and Kuang's framework. I'd like to highlight that the consequences of microbes, highlighted in red, and those of resources, highlighted in blue, feature in both equations. We can assess the relative importance of one mechanism by tweaking its parameters and keeping the others constant.

Slide 74

As an example of how this framework can be useful to the field of plant soil feedbacks, we can revisit the competing predictions I had brought up earlier about whether PSFs are more important in nutrient-rich communities or nutrient-poor ones. We can keep all parameters constant except for those that determine the availability of resources

Slide 75

This theory tells us that the relative importance of plant-soil feedbacks - in other words, the contribution of plant-soil feedbacks- is higher in nutrient-rich communities than in nutrient-poor ones. The insight is that in high nutrient communities, plants aren't being restricted by nutrients, so the parameters that govern community dynamics are those related to the microbes.

Slide 76-78

For my Chapter 3, I plan to further explore this model and reframe plant soil feedbacks in this framework. Investigating this model will mean, for example, studying not only the steady state dynamics but also the transient dynamics that ensue after changing certain state parameters, because those are the variables that are most frequently tested in empirical studies. Another extension I propose to do is to consider the effects of net-positive plant-microbe interactions. This can be done by tweaking the attack rate parameter to be a negative number, so that the plant population benefits from interacting with the microbes. I then conduct a review of the PSF literature in light of which parameters of coexistence have been quantified by experiments to date and highlight the parameters which the theory suggests might be important ones to further investigate. Finally, I will propose and conduct experiments to quantify the parameters and test the predictions of this framework.

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In summary, I plan to use modern coexistence theory as a tool to investigate the diversity of natural communities in my PhD. In Chapters 1 and 2, I propose to extend how we use functional traits, which summarize plant ecological strategies, to understand coexistence in variable environments. In chapter 3 I consider the effects of microbes, a mechanism of biodiversity maintenance that has yet to receive sufficiently close scrutiny. I hope that this will give me better insight into the diversity I have grown to love.

Acknowledgements