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THE SHIFTING IMPORTANCE OF COMPETITION AND FACILITATION ALONG DIVERSITY, ENVIRONMENTAL SEVERITY, AND PLANT ONTOGENETIC GRADIENTS

by

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ABSTRACT

THE SHIFTING IMPORTANCE OF COMPETITION AND FACILITATION ALONG DIVERSITY, ENVIRONMENTAL SEVERITY, AND PLANT ONTOGENETIC GRADIENTS

by

Alexandra Wright

The University of Wisconsin-Milwaukee, 2013
Under the Supervision of Professor Stefan A. Schnitzer

Ecological theory and empirical studies have focused heavily on the importance of competition in plant communities. Competition can help explain species coexistence, the maintenance of species diversity, and biological invasions. Competition for resources appears to be ubiquitous among coexisting organisms. This overwhelming focus on competition over the past one hundred years may have overshadowed the importance of positive interactions (facilitation). Growing near your neighbors involves competition for resources, but it also involves alteration of a shared microclimate. Neighboring plants have the capacity to increase shade, decrease air temperatures, increase humidity, and increase shallow soil moisture in their local environment. In severe environments – tundra, deserts, salt marshes – facilitation can outweigh the effects of competition. In periods of environmental severity, these benefits can prove essential. In this dissertation, I explore the importance of both competitive and facilitative interactions across gradients of environment severity, plant ontogeny, and productivity. I use an experimental manipulation of herbaceous plant diversity to manipulate the magnitude of competition and facilitation in a series of experiments in central Minnesota. I show that woody

encroachment into grasslands is influenced by both competitive and facilitative interactions related to decreasing local species diversity and increasing atmospheric CO_2 (Chapter 1). I show that diversity can ameliorate the microclimate to create local conditions that are cooler and more humid, and these effects can facilitate seedling growth and survival. I show that competition appears to increase as seedlings grow in size, but this size-structured change may be due more to decreasing facilitation rather than increasing competition (Chapter 2). Finally, plants may compete strongly for resources much of the time, but this can be outweighed by strong facilitation, and the interaction between the two processes can change on a day-to-day basis (Chapter 3). Finally, I use a modified Lotka-Volterra model to show how competition and facilitation may change as a function of environmental severity and productivity, and the implications of these relationships on individual plant performance and long-term community dynamics (Chapter 4). Nutrient availability, CO_2 concentrations, seasonal temperatures and precipitation will likely change independently in future climate change scenarios. It is therefore essential that we have a comprehensive understanding of the positive and negative components that underlie plant interactions, to better predict how plant communities will change in the future.

For my sisters.

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It turns out there are limits – limits to our intellectual capacity at any given point in time, limits to our emotional capacity, and limits to our physical capacity. Cyclists always tell me that to be a good cyclist you have to love the pain. You have to love the feeling of pushing yourself to a new point, absolutely hating it, feeling like you are going to die, and then getting to the other side and looking back with pride on the point where you broke it again. This is the nature of limits. They are constantly broken by pushing ourselves to the brink, and then just a little bit past it. So that the next time we approach the brink, it's a little bit further away, and we are a little bit stronger. Gross. I always thought I hated this idea. I hate physical pain. When I reach my threshold of physical pain while exercising, I just stop. And feel proud for what I accomplished up to that point. But not all limits are physical.

In November 2011, when I walked into my preliminary exam, my colleague Joe Mascaro told me: "don't worry Sasha, the point of the exam is for your committee to find the limits of your knowledge… and they *will* find them." There was something oddly comforting about that idea. I'm still not exactly sure what. Of course, they also demand you do it with confidence, accuracy, clarity, and the ability to sound interesting when you say you don't know the answer. That was the first time I realized what I might look like as a scientist. In the weeks leading up to that day I pushed myself to my limits in unknown ways, and in the moments after the exam I felt so exhilarated – there was my limit, I approached it, I cried a lot, I saw it again, I approached it, cried, and in the process kept surpassing my own expectations. I had such an intense feeling of satisfaction and accomplishment. Then, I went up to my lab to join my lab mate Katie Barry, and we celebrated. With tequila. And probably cried some more.

One of the things about me is that the process of pushing past my limits stresses me out. And this brings me to the brink of my own vulnerability, and my own emotional capacity. I could have never imagined what the explosion of my own emo-intellectual complex would look like. But I have to say, there is something cool about all of it.

That being said, I will admit that what I think is cool may not always be the most fun for those around me. Particularly when it involves tear bombs that explode all over your face. I have innumerable people to thank for helping me through this process. My mom, and a long line of women in my family, whose legacy makes it *very hard* to stop being a domineering matriarch who pursues her own dreams. My dad, for his self-deprecating sense of humor and loving support. My sisters who truly blazed the trail for me – I would have never thought any of this possible if they hadn't both shown me what smart women are capable of, and how attainable it can (sometimes) be. Stephanie for being brave to a fault. And Heather for being the strongest pillar of strength that exists in the entire world. Jordan Husney has seen me through some of these most recent dark moments, and even when I lash out with daggers, I thank him for his measured response. I also thank Sheila Mohn for six years of supporting me and helping me grow.

My adviser, Stefan Schnitzer, once infamously said, "there are no tears in Ecology." I really tried Stefan, but there appear to be tears in my Science. If I'm not crying, I think I might not be trying. Without Stefan I most certainly would not be here. Stefan's ability to boil ideas down to their most crystalized form is unparalleled. This process, no matter how freaking frustrating, is most certainly what made me into the scientist that I am today. Yaffa Grossman, my undergraduate adviser, saw something in me in August 2001 that has been playing out ever since. She is my most relied-upon professional adviser, and her advice, both spoken and unspoken, continues to shape my future. She has not failed me yet. Peter Reich is one of the most exciting, intelligent, and inspirational scientists I have ever had the privilege of knowing. His capacity to think broadly, as well as in clear detail, about the science of thousands of scientists around the world is something that I honestly can't comprehend. I am grateful for the constant personal and professional support from Jeff Karron, tireless input from a mathematical genius - at least to my Ecology brain - Gabriella Pinter, further amazing input from my committee members Emily Latch and Sara Hoot. My lab mates throughout the years have included a diverse group from Milwaukee to Minnesota: Joe Mascaro, Suzanne Rutishauser (Yorke), Ramesh Laungani, Eli Rodriguez, Sergio Estrada, Justin Becknell, Maga Gei, Joey Reid, Emily Peters, Kerrie Sendall, Laura Williams, Rebecca Montgomery, Jennifer Powers, Kally Worm, Susan Barrott, and ABSOLUTELY TIRELESS SUPPORT from the newly minted Katie Barry… I am so lucky to have such a collaborative and intelligent group of colleagues.

Finally, as Joe Mascaro loves to say: "no matter how much you love grad school, no one can survive it without a best friend." Well, for better or worse my friend, you were mine. Every time that it seemed like this was an insane idea designed for crazy people, he reassured me that: yes it was. That all of the manic productivity streaks, multi-day Netflix marathons, gaming addictions, loss of control, lack of self-confidence, meltdowns, and triumphs were normal. They were for crazy people, but yes, they were normal. Thanks friend, you saved me from giving up.

CHAPTER 1

Complex facilitation and competition in a temperate grassland: loss of plant diversity and elevated CO_2 have divergent and opposite effects on oak establishment

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Abstract

Encroachment of woody vegetation into grasslands is a widespread phenomenon that alters plant community composition and ecosystem function. Woody encroachment is often the result of fire suppression, but may also be related to changes in resource availability associated with global environmental change. We tested the relative strength of three important global change factors (CO_2 enrichment, nitrogen deposition, and loss of herbaceous plant diversity) on the first three years of Bur Oak (*Quercus macrocarpa*) seedling performance in a field experiment in central Minnesota, USA. We found that loss of plant diversity decreased initial oak survival but increased overall oak growth. Conversely, elevated CO_2 increased initial oak seedling survival and reduced overall growth, especially at low levels of diversity. Nitrogen deposition surprisingly had no net effect on survival or growth. The magnitude of these effects indicates that long-term woody encroachment trends may be most strongly associated with those few individuals that survive, but grow much larger in lower diversity patches. Further, while the CO_2

results and the species richness results appear to describe opposing trends, this is due only to the fact that the natural drivers are moving in opposite directions (decreasing species richness and increasing CO_2). Interestingly, the mechanisms that underlie both patterns are very similar, increased CO_2 and increased species richness both increase herbaceous biomass which (1) increases belowground competition for resources and (2) increases facilitation of early plant survival under a more diverse plant canopy; in other words, both competition and facilitation help determine community composition in these grasslands.

Introduction

Encroachment of woody vegetation into grassland communities and the resultant conversion of these communities into closed canopy forests is an increasingly common phenomenon (Archer 1989) and grassland-dominated landscapes are increasingly rare globally (Hoekstra et al. 2004). Species compositional shifts caused by woody encroachment into grasslands have important implications for community dynamics and ecosystem properties, such as carbon storage and nitrogen cycling (Post et al. 1982, Reich et al. 2001a, Jackson et al. 2002, McCulley et al. 2004, Knapp et al. 2008, Barger et al. 2011). While regional distributions of woody plants appear to be co-constrained by large-scale differences in precipitation and fire regimes (Staver et al. 2011), local success of woody plants in grasslands is strongly associated with a change in disturbance regime that favors woody plants over herbaceous species, such as fire suppression (Van Auken 2000, Roques et al. 2001, Silva et al. 2001) or increased grazing pressures by cattle (Archer et al. 1995, Brown and Archer 1999). However, recent evidence suggests that altered resource availability associated with global environmental changes (e.g. decreasing biodiversity and increasing atmospheric CO_2, and nitrogen deposition) may also drive woody encroachment into grasslands, but the role of these factors and their interactions remain poorly understood (Archer et al. 1995, Van Auken and Bush 1997, Davis et al. 1999, Polley et al. 2003, Dickie et al. 2007, Classen et al. 2010).

Increased global extinction rates and loss of biodiversity (e.g. Vitousek et al. 1997) may substantially alter grassland community composition. Specifically, loss of plant diversity at the patch scale may affect how plant species interact in positive (e.g. facilitation) and negative (e.g. competitive) ways; we outline these changes below.

Competition: The relationship between diversity and productivity is complex and feeds back on itself at different spatial scales (Naeem 2002). For example, macro-scale plant species richness patterns are a function of regional productivity gradients (Abrams 1995, Chase and Ryberg 2004, but see Adler et al. 2011). Conversely, at local scales, increasing levels of plant diversity drive increased production of biomass (Zhang et al. 2012). This is because higher diversity communities contain a larger number of species with unique traits (Reich et al. 2012) and competition strategies. As increasing numbers of species co-occur in an assemblage, their complementary resource acquisition strategies use overall resource pools more completely. This complementary resource use results in greater community-level biomass (Tilman et al. 1997a) and consequently, the community itself becomes less susceptible to colonization (Kennedy et al. 2002).

For the purposes of this study, we focus on the well-established positive relationship between local species richness and biomass production (Reich et al. 2001c, Tilman et al. 2001, Van Ruijven and Berendse 2003, Roscher et al. 2005, Isbell et al. 2011, Zhang et al. 2012). We predict, that when applied to woody encroachment into grasslands, declining levels of herbaceous species diversity associated with global change, can drive lower levels of biomass production (Schnitzer et al. 2011) and decreased competition for resources (Tilman et al. 1997a, 1997b). Decreased plant diversity may therefore lead to increased susceptibility to woody encroachment (Naeem et al. 2000, Kennedy et al. 2002, Fargione and Tilman 2005).

Facilitation: Loss of herbaceous species diversity may also alter facilitative interactions between plants. Survival rates of young plants tend to increase with increasing canopy cover, particularly in ecosystems that experience extreme abiotic conditions (Bertness and Callaway 1994, Miriti 2006, Cuesta et al. 2010, Farrer and Goldberg 2010, Bustamente-Sanchez et al. 2010). This facilitation effect is due to amelioration of the microclimate under higher density canopies (Callaway 1995, Callaway and Walker 1997, Cuesta et al. 2010, Bustamente-Sanchez et al. 2010). The strength of facilitation likely increases with increasing species diversity because higher-diversity assemblages usually have increased canopy cover (Tilman et al. 2001); although there is little empirical evidence to support a direct relationship between plant diversity and facilitation (but see (Bruno et al. 2003 and Bulleri et al. 2008 for theoretical discussion).

Other global change factors, such as increased CO_2 and N deposition also alter resource availability and can have interactive effects on woody encroachment into grasslands. For example, elevated atmospheric CO_2 appears to benefit woody seedlings grown alone in water-limited environments (Davis et al. 2007) and may help explain past woody range expansions (Kgope et al. 2009), particularly in the presence of fire (Bond and Midgley 2000). Elevated CO_2 increases plant water use efficiency (WUE), which should increase soil water availability (Polley et al. 2003, Adair et al. 2009, Reich 2009). Because woody plant establishment is often restricted by low soil water availability (Staver et al. 2011), an increase in soil moisture due to increased WUE may stimulate woody encroachment into grasslands. However, when soil water is limiting, increased soil water availability should also influence the growth of herbaceous species; but to our knowledge no study has assessed how CO_2 and herbaceous species richness simultaneously affect woody-herbaceous plant interactions. Finally, recent research has shown that past increases in atmospheric CO_2 concentrations may have strongly controlled woody encroachment into grasslands when atmospheric CO_2 was relatively low (180 ppm), but CO_2 may not be such a strong driver of woody success under current conditions (Kgope et al. 2009).

Nitrogen deposition often increases aboveground herbaceous productivity (Reich et al. 2001b, 2001c), and reduces both light and soil water availability in herbaceous vegetation (Tilman 1987). The effect of N deposition may limit oak establishment due to increased competition for light and/or water. Indeed, these indirect effects of nitrogen addition reduce woody plant growth and survival in grasslands in central Minnesota (Davis et al. 1998, 1999) and this effect depends on herbaceous productivity (Dickie et al. 2007). To date, most studies have examined woody encroachment into grasslands by manipulating only one or two factors in isolation, and the interacting effects of these global change factors, while potentially substantial, are largely unknown.

We examined the simultaneous roles of herbaceous species richness, elevated CO_2, and nitrogen enrichment on bur oak seedling survival and growth in Minnesota, USA. Bur oaks (*Quercus macrocarpa*) and pin oaks (*Quercus ellipsoidalis*) are common woody colonizers in grasslands in this region, and are therefore appropriate candidates to address general trends in woody encroachment. We tested the following four hypotheses: (1) Decreasing herbaceous species diversity decreases oak survival rates due to loss of the facilitative effects of a more diverse, higher canopy cover plant community; (2) Decreasing herbaceous diversity increases resource availability and therefore promotes oak growth due to lack of competition from neighboring plants; (3) CO_2 enrichment increases oak performance (both survival and growth) due to increased soil water availability; and (4) nitrogen deposition decreases oak performance by increasing herbaceous productivity and thus increasing competition for other limiting resources.

Materials and methods

Study Site and Experimental Design

We conducted this study in the biodiversity, CO_2, and nitrogen (BioCON) experiment at the Cedar Creek Ecosystem Science Reserve, located in central Minnesota. Soils at this site consist of nutrient-poor glacial outwash sand plain with low water- and nutrient-holding capacity (Reich et al. 2001c). Species richness levels in natural prairie communities at this field site range from approximately four species to sixteen species per 0.5 sq. m plot, and aboveground biomass ranges from approximately 50 g/m^2 to 150 g/m^2 (Knops 2006). Natural communities are dominated by *Schizachyrium* (C_4 grass, accounts for 69-76% of all aboveground biomass in prairies). Several other species of C_3 grasses are also common (*Poa pratensis, Panicum oligosanthes,* and *Agrostis scabra*); and *Rumex acetosella* (forb) and *Andropogon gerardii* (C_4 grass) can be found in high abundances (Knops 2006). Mean annual precipitation at Cedar Creek is 78 ± 7.5 cm (95% confidence intervals, 1982-2009), while mean annual precipitation over the course of our study (2001-2004) was 79.9 ± 12.9 cm (95% confidence intervals, no significant difference in rainfall from long-term average).

The BioCON experiment utilized six, circular, 20 m diameter plots; three are enriched to 560 $\mu mol\ mol^{-1}$ of CO_2, which is pumped from a ring of PVC tubes using a free air CO_2 enrichment system (FACE), while three control plots (hereafter referred to as “rings”) received approximately 370 μmol mol^{-1} of CO_2, which was the ambient atmospheric CO_2 level at the time of the experiment. The level of 560 μmol mol^{-1} of CO_2 was based on IPCC models for projected CO_2 concentrations by the year 2100. Nested within the rings are herbaceous species diversity and nitrogen treatments that subdivide the plots into 359 2 x 2 m square subplots. To manipulate species diversity, these plots were planted with 12 g m^{-2} of seed of 1, 4, 9, or 16 species in 1997. Herbaceous species composition in each of these diversity treatments was randomly assigned from a pool of 16 species, representing four species from each of four functional groups (four C_3 grasses, four C_4 grasses, four legumes, and four non-nitrogen fixing herbaceous plants). Species mixes were maintained with planted species only (although not re-seeded) using hand weeding. Within each ring, 21-22 subplots were planted using 1 species, 20-21 with 4 species, 10 subplots with 9 species, and 8 subplots with 16 species (total of 59-61 subplots per ring x 6 rings). For each diversity level, half of the plots had either nitrogen added in dry granules annually (4 g N $m^{-1}yr^{-1}$ as NH_4NO_3) or no nitrogen added.

In each of the 359 plots, we sampled herbaceous biomass (above and belowground) each June and August from 2001-2004. Aboveground biomass was clipped in 10 x 100 cm strips at the soil surface and never sampled less than 15 cm. from plot boundaries (to avoid edge effects). Belowground biomass was sampled to 100 cm using three 5-cm cores in the same area as the vegetation clip strips (see Reich et al. 2001b) for more details). Biomass sampling was conducted in different areas of plots for every sampling date of this study. We recorded soil volumetric water content monthly between May and October 2001-2004 using time domain reflectometry (TDR). We recorded percent light transmission below the canopy monthly between May and October

2001-2004 using a 1m integrated photosynthetically active radiation (PAR) sensor (Li-Cor Biosciences, Lincoln, Nebraska). In June and August of 2001 and 2002 we measured available soil nitrogen (in the forms of nitrate and ammonium) in each plot by collecting four soil cores at 0-20 cm depth, extracting nitrogen using 1 M KCl, and analyzing the nitrogen content using a Costech 4050 Element Analyzer (Dijkstra et al. 2005). All measurements taken over the course of this experiment (above- and belowground biomass, soil moisture, percent light transmission, and soil N) were averaged across all sampling dates in order to obtain a single plot-level average over time.

Oak performance

In October 2001, we collected and germinated recently fallen acorns from multiple local adult Bur Oak trees at the Cedar Creek Ecosystem Science Reserve. We combined and homogenized the acorns and planted three germinated seeds in each of the 359 2x2 m subplots. In June 2002, we recorded oak survival and the number of leaves per plant. In August 2002, we recorded plant survival, height, and the number of leaves per plant. In August 2004 we recorded survival, height, diameter, and the number of leaves per plant, and then harvested all surviving individuals. We estimated aboveground oak biomass over the course of the study using an allometric relationship that we derived using the field measurements and aboveground dry mass from the final harvest (June 2002 AGB in grams = -0.277 + (0.338 × leaves), $r^2 = 0.805$, $P<2.2e-16$, n=227, August 2002 AGB in grams = -0.837+ (0.112 × height) + (0.281 × leaves), $r^2=0.835$, $P<2.2e-16$, n=227).

Statistical Analysis

Base models: We analyzed oak survival using a generalized linear mixed-effects model (GLMM) for repeated measures with a multinomial distribution (SAS PROC GLIMMIX). In this model, each 4-m^2 plot was the experimental unit, and the probability of survival was based on the number of oak seedlings surviving in each plot (0-3 possible survivors). This base model included nitrogen addition, species richness, CO_2 enrichment, and all first order interactions as fixed effects, and ring nested within CO_2 as a random effect (follows (Reich et al. 2001c). The three sampling dates were treated as repeated measures, and each 4-m^2 plot was included as the subject. We analyzed growth (aboveground biomass of surviving seedlings per 4-m^2 plot) over time using a similarly structured mixed-effects model with a normal distribution (SAS PROC MIXED). Biomass was log-transformed to normalize residuals.

Covariate models: We evaluated the explanatory power of herbaceous biomass, percent light transmission below the herbaceous vegetation, soil moisture, and soil N concentrations on oak performance by including these measures as covariates. For both growth and survival, we constructed separate models including all covariates in isolation as well as all combinations of covariates. We compared these covariate models to the base models described above using Akaike Information Criteria (AIC).

We present AIC scores for all GLMM's in the online supplemental materials and only further report on the best-fit model throughout the results and discussion. We use frequentist statistical tools (p-values) to better interpret the contribution of each experimental main effect (N, CO_2, and species richness), as well as interactions between main effects and covariates in this best-fit GLMM. We use this mixed statistical approach as it best utilizes the statistical tools available while still making the results interpretable to the broadest possible audience (Bolker et al. 2009).

Results

There was only one significant pair-wise interaction between main effects in our analyses (CO_2 x species richness effect on oak growth). Hence we present results separately by treatments and discuss the CO_2 x species richness interaction at the end of the CO_2 results. There were no significant effects of N treatment on either survival (Table 1.1) or growth (Table 1.2), so no further results regarding this treatment are presented

Species Richness

The best main-effect predictor of both oak survival and growth was herbaceous species richness (Tables 1.1 and 1.2, respectively). Oak survival was lowest (34%) in the monoculture plots and highest (54% and 49%) in the most species rich plots (9- and 16-species, respectively) (Fig. 1.1; Table 1.1). These responses were evident within 8 months of planting the oaks (by June 2002) and did not change significantly between June 2002 and the harvest date in August 2004.

The surviving oak seedlings grew equally well across species richness levels during the first 8 months of the experiment; at which point seedlings in higher diversity treatments nearly stopped growing, while seedlings in single-species plots continued to grow (Table 1.2). By the final sampling date, oak growth (measured as total aboveground biomass per plant) was over four-times greater in herbaceous monoculture plots than in high species richness plots (averaged across CO_2 treatments; Fig. 1.2).

Elevated CO_2

Atmospheric CO_2 enrichment had an initial positive effect on oak survival in June 2002, but the strength of the effect was weak by August 2004, resulting in a significant CO_2 enrichment by time interaction on oak survival ($F_{2, 342} = 8.56$, $P = 0.0002$) (Table 1.1, Fig. 1.3). There were no interactions between CO_2 and any of the other main effects on oak survival.

CO_2 enrichment had no effect on oak growth rates averaged across sampling dates (Table 1.2). However, there was a significant CO_2 enrichment by time interaction ($F_{2, 205}=3.24$, $P=0.0412$) because seedlings grown in CO_2 enriched plots grew less than in ambient plots in the latter part of the study (Table 1.2). There was also a significant species richness x CO_2 enrichment interaction, driven mostly by the significantly greater growth of oaks in herbaceous monoculture plots under ambient CO_2 conditions (Table 1.2, Fig. 1.2). Further, the two-way interactions between species richness and time, CO_2 and time, and species richness and CO_2 indicate that the significantly greater growth in the monoculture plots (1-species) by August 2004 was almost exclusively due to older oaks growing in ambient CO_2 conditions (Fig. 1.2).

Covariate Models

Oak survival- the best-fit and most parsimonious model for oak survival was the base model that included only the manipulated factors, with no covariates included (AIC=18723.08, Appendix A). This finding indicates that none of the variables measured in the experiment added additional explanatory power beyond that already included by species richness and CO_2 enrichment, or better explain survival responses if these measures co-vary with treatments.

Oak growth- the best-fit and most parsimonious model for oak growth included soil moisture and extractable soil nitrate as covariates (AIC=-742.6; Appendix A). Soil nitrate explained the largest amount of growth variance, and the combination of reduced soil moisture and reduced soil nitrate explained the reduced oak growth found in high diversity plots, enriched CO_2 plots, and the CO_2 x time interaction (Table 1.2).

Discussion

Our results support the hypotheses that loss of plant diversity and atmospheric CO_2 enrichment influence woody encroachment into grassland ecosystems. Importantly, the CO_2 results and species richness results appear to describe opposing trends because the drivers are moving in opposite directions in the natural world (decreasing species richness and increasing CO_2); in fact the mechanisms that underlie both patterns are very similar, increased CO_2 and increased species richness both increase herbaceous biomass which (1) increases belowground competition for resources and (2) increases facilitation of early plant survival under a more diverse plant canopy.

Hypotheses 1 and 2: Decreased herbaceous species diversity limits early oak survival but promotes oak growth later in development

Our findings demonstrate that herbaceous species diversity facilitates early oak seedling survival. We suggest that this diversity effect is due to amelioration of plant stress under more diverse herbaceous canopies where temperature, humidity, and shallow soil moisture may be buffered by increased herbaceous cover. For the purposes of our experiment, we measured herbaceous biomass, and found that it did not directly explain a significant proportion of the growth response or the survival response (Appendix A).

Although we did not measure the micro-climate variables directly related to facilitation in 2001-2004, we measured some of them in 2010 in these same plots, to better understand these results. This more recent work demonstrated that increasing herbaceous diversity slightly increased surface soil moisture (0-6 cm) in 16-species plots compared with 1-species plots; and higher diversity plots were, on average, 1.7 C cooler than 1-sp plots. This interpretation (of amelioration of surface stress by higher diversity communities) is further corroborated by results from 2006 in BioCON, where during a dry summer, soil moisture at 0-17 cm was slightly higher in diverse plots than monocultures, whereas in deeper horizons, increasing diversity reduced soil moisture (Adair et al. 2011). Further work should be conducted in this area to show a direct causal relationship between micro-climate variables and plant facilitation at this site.

Positive facilitative relationships between aboveground cover and seedling survival have been documented in grasslands (Dickie et al. 2005, 2007), shrublands (Cuesta et al. 2010), and temperate forest gaps (Montgomery et al. 2010), although evidence for a relationship between herbaceous cover and shrub invasion in southwestern arid grasslands of the United States is varied (Van Auken and Bush 1997, Brown and Archer 1999, Van Auken 2000). In those examples where herbaceous biomass increases seedling survival, aboveground cover protects small seedlings from some type of environmental severity (e.g. extreme temperatures, increased surface soil drying, and increased rates of evapotranspiration). Aboveground cover may be particularly important for smaller/ younger seedlings, which tend to have less well-developed root systems, and less non-structural carbon reserves to survive short periods of stress (Niinemets 2010). As plants grow in size, their root systems become more developed, and they become less susceptible to short periods of extreme abiotic conditions. Indeed, we found a facilitative effect of herbaceous diversity for small oak survival, but following initial establishment, loss of plant diversity did not further decrease the survival of larger oak seedlings. We predict that this was likely because larger seedlings were less susceptible to environmental stressors.

Surviving oaks in low diversity plots grew rapidly after the first year, which was due to greater availability of soil nitrogen and soil moisture in the absence of strong competition from neighbors (Table 1.2). Indeed, soil moisture is one of the most important factors determining regional range limits for woody species (Staver et al. 2011, but see Brown and Archer 1999). In contrast, oaks in higher diversity plots grew very little after the first eight months because of intense competition for soil resources from herbaceous plants (Table 1.2). We propose that the increase in competition intensity with oak age is due to greater absolute resource requirements as oaks grow (and decreasing influence of resources from acorns, Ovington and MacRae 1960). Increased resource requirements as plants grow should result in increased growth limitations, which was evident for the oldest plants growing in the highest diversity plots. Soil nitrogen is the most limiting resource in grasslands at this field site (Tilman 1987) and limited availability of extractable soil nitrogen (nitrate) was the best covariate predictor of oak growth at each individual time point (Table 1.2). This resulted in little difference in oak growth between diversity levels at the beginning of the study, due to little need for nitrogen, but significantly less growth of oaks in high diversity plots over time.

This fits well with evidence that herbaceous species richness is positively related to biomass production in grasslands (Reich et al. 2001b, 2001c, Tilman et al. 2001, Van

Ruijven and Berendse 2003, Roscher et al. 2005, Isbell et al. 2011), and that this often leads to decreased availability of resources at higher levels of plant diversity (Tilman et al. 1996, Dijkstra et al. 2005, Reich 2009). Further, work on woody encroachment patterns in the semi-arid southwestern United States demonstrates a similar pattern between woody growth limitation and belowground competition for resources. While woody growth does not appear to be significantly affected by aboveground or overall competition in these systems (usually attributed to grazing, not diversity, Brown and Archer 1989, Van Auken and Bush 1997, Brown and Archer 1999), there is strong evidence that woody seedlings compete heavily with herbaceous species for belowground resources (Van Auken and Bush 1997) and that this may affect woody encroachment patterns.

Hypotheses 3 and 4: CO_2 enrichment increases oak performance due to increased soil water availability and N deposition decreases oak performance due to increased herbaceous productivity and competition for other limiting resources

Contrary to our original hypothesis, our data demonstrate that the effect of CO_2 enrichment on woody encroachment is not consistently positive, but instead also depends on oak ontogenetic stage. Atmospheric CO_2 enrichment had a positive effect on oak survival at the beginning of the study and a negative effect on growth of surviving oaks, especially at low levels of plant diversity. The positive effect of CO_2 enrichment on early oak survival may have been the result of higher herbaceous biomass in high CO_2 plots (12% higher than in ambient CO_2 plots, (Reich et al. 2001c) and amelioration of surface soil moisture in high CO_2 plots (Adair et al 2011). Although there was no direct effect of herbaceous biomass on oak survival or growth (Appendix A), increased herbaceous cover in elevated CO_2 plots may have reduced abiotic stress for the germinating oak acorns under the denser herbaceous canopy. This pattern also emerged early on in oak development when oaks were smaller and likely more vulnerable to abiotic stressors such as heat and drought (Niinemets 2010).

Subsequently, the positive CO_2 effect for survival transitioned to competition for resources as the oaks grew. CO_2 enrichment decreased longer-term oak growth rates because older seedlings in CO_2 enriched plots experienced more intense competition for resources, which limited oak growth over time. The enhanced oak growth effect was most evident in ambient CO_2 – monoculture plots, where competition intensity was lowest due to low competition from both low herbaceous diversity and lack of CO_2 fertilization (which in combination resulted in lower herbaceous biomass than in plots with higher diversity or elevated CO_2).

The negative effect of CO_2 enrichment on oak growth is surprising and important in the context of recent work on the singular effect of CO_2 enrichment on woody encroachment (Bond and Midgley 2000, Polley et al. 2003, Davis et al. 2007, Staver et al. 2011). This recent work suggests that CO_2 enrichment should have positive effects on overall trends in woody encroachment (Davis et al 2007) due to enhanced water use efficiency (Polley et al. 2003) and subsequent access to limiting soil moisture (Staver et al. 2011), and increased total carbon availability for woody species that need to invest large amounts of energy towards re-sprouting after fire (Bond and Midgley 2000). Our results suggest, that as oaks encroach into grasslands, herbaceous species may respond quickly to increased CO_2 enrichment and grow more due to the CO_2 fertilization effect.

When oaks arrive into higher biomass grasslands following increases in levels of atmospheric CO_2, they may be more limited by competition from greater herbaceous biomass than they are facilitated by CO_2 enrichment (e.g. Davis et al. 2007). We predict that while this has strong implications for how we interpret *future* trends of woody encroachment in grasslands, past trends in woody encroachment may have been more strongly controlled by increasing levels of atmospheric CO_2 due to greater response potential at lower levels of CO_2 (Kgope et al. 2009).

Also contrary to our original hypothesis, nitrogen addition had no detectable effect on oak survival or growth over time. The reason for this is unclear, but may be in part due to lower concentrations of nitrogen applied, compared with similar studies at this site (Davis et al. 1999), and the impact of these on the multiple resource factors that are important (light, water, and N). For example, the BioCON N addition strongly increased soil N pools, but also increased competition for those pools (Reich et al. 2001c, Reich 2009), while also slightly decreasing soil water supply (Reich 2009, Adair et al 2011) and increasing light transmission (through a compositional shift towards vertical grasses, Reich 2009). It is possible that increased root competition (Davis et al 1998, 1999; Reich 2009) and lower soil water content (Reich 2009, Adair et al 2011) offset possible positive impacts of greater soil N pools and higher light availability (Reich 2009), in terms of impacts on oak performance.

Synthesis

Woody encroachment into grassland communities is a widespread phenomenon that drives changes in community and ecosystem-level processes. Our findings demonstrate that the simultaneous loss of herbaceous plant diversity and increasing atmospheric CO_2

concentrations associated with global environmental change will affect oak encroachment into grasslands. Due to the divergent trajectories of species richness and atmospheric CO_2 concentrations (decreasing species richness and increasing CO_2concentrations) these results indicate that woody encroachment will be affected in divergent ways; and those divergent effects will themselves vary depending upon the oak life stage and process in question.

In this experiment, survival was 15-20% lower in herbaceous monoculture than in high diversity plots. Thus, if local plant diversity is driven to a low level, oak establishment may become increasingly rare. However, atmospheric CO_2 enrichment may counteract this trend; in our experiment a CO_2 doubling buffered the survival reduction in low diversity plots, and increased initial oak survival by ~14%. The magnitude of species loss paired with the degree of atmospheric CO_2 enrichment will determine the actual outcome of these trends for early oak establishment.

For oaks that establish, however, decreased plant diversity may prove beneficial. We found that surviving oaks grew twice as much in one-species plots than they did in sixteen-species plots. Oak growth was only modestly counteracted by a CO_2 doubling (17% growth reduction in lower diversity plots). Further, the actual conversion of these grasslands into closed canopy forests will depend heavily on oak growth: past research has shown that woody encroachment rates are strongly controlled by the ability of oaks to grow into larger size classes and eventually escape from under the herbaceous canopy (Bond and Midgley 2000). The strong growth advantage of oaks growing in lower diversity plots, regardless of CO_2 concentrations, suggests that loss of species richness may have an overall positive effect on woody encroachment in lower diversity grassland patches.

In a broader theoretical context, our findings support the idea that both competition and facilitation are operating in these plant communities. Young plants are particularly sensitive to severe environmental conditions, and thus benefit from the facilitative effects of higher total community biomass (which is positively related to both herbaceous richness and CO_2 concentrations), which can ameliorate harsh environmental conditions. As plants grow and become less susceptible to environmental stress in terms of survival, however, the positive effects of facilitation diminish and resource competition becomes a stronger determinant of plant growth, and hence longer-term plant performance. Thus, overall community composition in these grasslands may be structured by a balance that promotes establishment of colonizers in areas of high plant diversity through facilitation, but this higher diversity later limits overall growth through increased interspecific competition.

Acknowledgements

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Table 1.1 The effects of species richness, CO_2 addition, and nitrogen addition, as well as first and second order interactions on oak survival through time. This generalized linear mixed model was fit with a multinomial error distribution. All significant results are bold and marked with an asterisk.

Effect	d.f.†	F	P
Species Richness	3, 342	3.04	**0.0293**
CO_2	1, 4	5.43	0.0803
Nitrogen	1, 342	0.19	0.6623
Species Richness × CO_2	3, 342	1.18	0.3192
Species Richness × Nitrogen	3, 342	2.45	0.0637
CO_2 ×Nitrogen	3, 342	0.12	0.7330
Richness × CO_2 × Nitrogen	3, 342	0.49	0.6877
Time	2, 342	73.69	**<0.0001**
Time × Species Richness	6, 342	0.23	0.9681
Time × CO_2	2, 342	8.56	**0.0002**
Time × Nitrogen	6, 342	0.14	0.8703

† Denominator d.f. = 4 for the main effect of CO_2 and reflects the inclusion of CO_2 × ring as a random effect.

Table 1.2. The base model (without covariates) and the best-fit model (with covariates) examining the effects of species richness, CO_2 addition, and nitrogen addition on oak growth through time. All significant results are bold and marked with an asterisk.

		Without Covariates		With Covariates	
Effect	d.f.†	F	P	F	P
Species Richness	3, 205	8.60	**<0.0001***	1.85	0.1401
CO_2	1, 4	2.15	0.2168	0.28	0.6226
Nitrogen	1, 205	0.35	0.5559	0.25	0.6169
Species Richness × CO_2	3, 205	2.83	**0.0395***	2.57	0.0556
Species Richness × Nitrogen	3, 205	0.77	0.5118	1.25	0.2913
CO_2 ×Nitrogen	1, 205	0.10	0.7478	0.51	0.4755
Richness × CO_2 × Nitrogen	3, 205	0.90	0.4433	2.09	0.1032
Time	2, 205	39.9	<**0.0001***	40.59	<**0.0001***
Time × Species Richness	6, 205	8.28	**<0.0001***	7.98	**<0.0001***
Time × CO_2	2, 205	3.24	**0.0412***	2.82	0.0617
Time × Nitrogen	2, 205	0.52	0.5961	0.54	0.5808
Nitrate	1, 205	--	--	69.45	<**0.0001***
Moisture	1, 205	--	--	1.35	0.2468

† Denominator degrees of freedom are shown for the model including covariates. For the model not including covariates, denominator degrees of freedom for all effects other than $CO_2 = 207$. In both models, denominator d.f. = 4 for the main effect of CO_2 and reflects the inclusion of CO_2 × ring as a random effect.

Figure 1.1. Proportion of oaks surviving in 1-, 4-, 9-, and 16-species plots. Bars are means ± SE of the raw proportion survival measurement. Displayed results are averaged across sampling dates. Tukey tests for multiple comparisons between diversity levels were not possible using the GLMM with a multinomial distribution in SAS, for this reason letters indicating significance between groups are not displayed

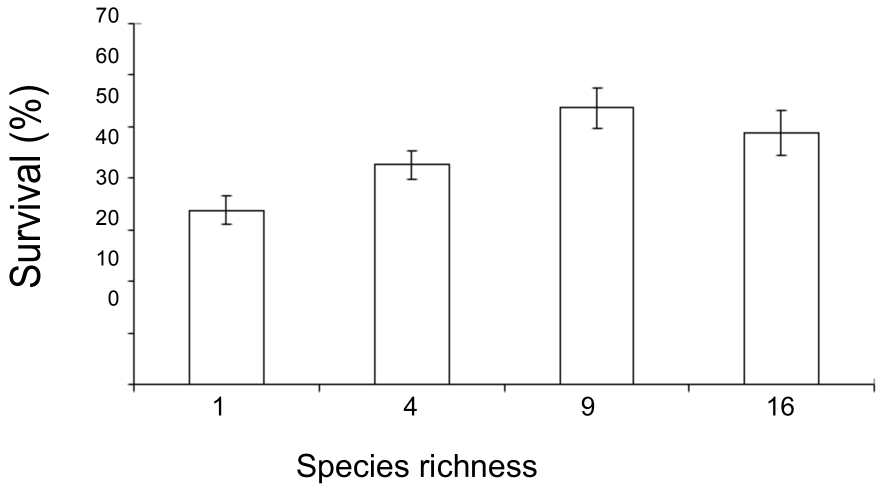


Figure 1.2. Final aboveground biomass of oak seedlings in relation to planted species richness at two CO_2 levels. Decreased oak growth due to herbaceous diversity was determined using Tukey-Kramer multiple comparisons and is denoted using letters (*a* vs. *b*). Due to significant interactions between CO_2 enrichment and species richness, differences in oak growth at different levels of CO_2 enrichment were also determined using Tukey-Kramer multiple comparisons and are denoted using stars (** vs. *)

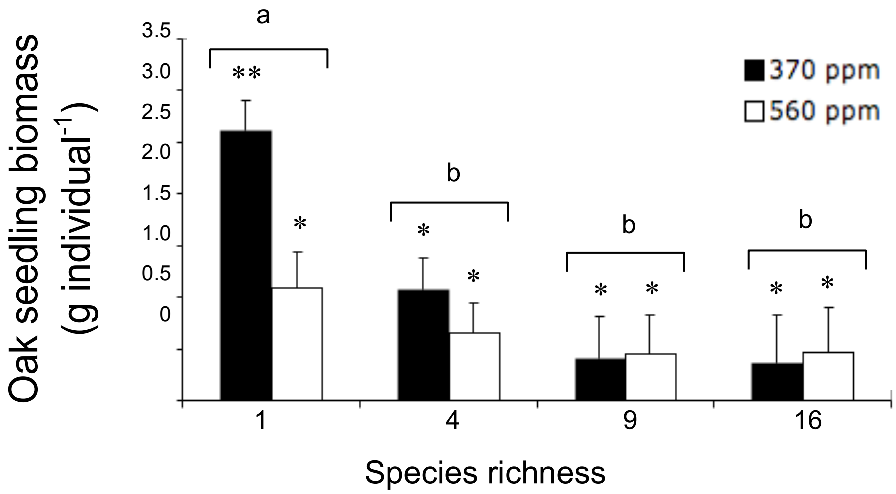
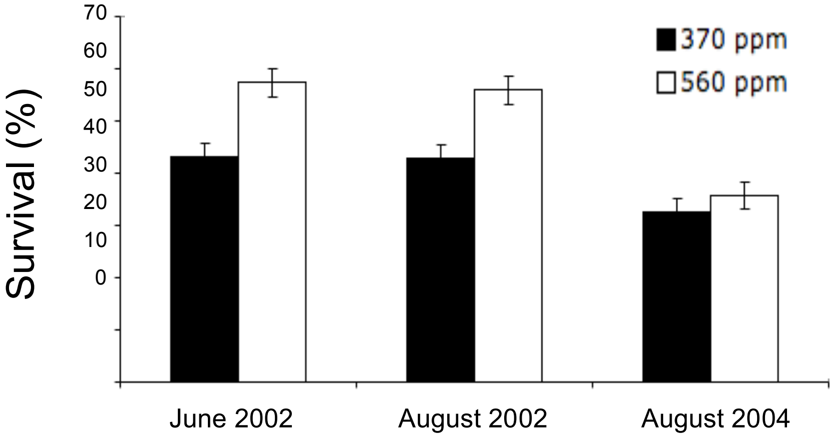


Figure 1.3. Oak survival at two CO_2 levels, averaged over the three sampling dates. Bars show mean ± SE of the raw proportion survival measurement. Tukey tests for multiple comparisons between different levels of CO_2 and time were not possible using the GLMM with a multinomial distribution in SAS, for this reason letters indicating significance between groups are not displayed



CHAPTER 2

Living close to your neighbors – the importance of both positive (facilitative) and negative (competitive) plant interactions

To be submitted with co-authors S.A. Schnitzer and P.B. Reich

Abstract

Competition has long been recognized as a fundamental process structuring plant communities. In contrast, positive interactions in plant communities (facilitation) have been largely overlooked until recent years. Facilitation may be particularly important in stressful environments, such as deserts, tundra, and salt marshes. Further, facilitation may be more important for colonizing seedlings when they are small, when mortality rates are higher, and when they are particularly susceptible to fluctuations in the environment. Indeed, both competition and facilitation may be operating simultaneously in many ecosystems, although it is difficult to determine the relative strength of both processes in experimental manipulations. When competition is the dominant mechanism, we conclude that the net effect of neighbor interactions is competitive, and miss any underlying variation in facilitation. To better understand the complexities of biotic interactions in plant communities, we manipulated seedling size in a biodiversity gradient in central Minnesota and measured seedling responses to co-occurring competition and facilitation. In experimental manipulations, higher diversity plant communities are more productive, and this may drive increased competition for resources – this may be particularly important

for larger seedlings. Conversely, increased aboveground biomass may drive increased facilitation due to microclimate amelioration. Microclimate amelioration may have strong effects on smaller seedling performance. We measured pine height and basal diameter every two weeks for two growing seasons. We compared biweekly relative growth rates to annual relative growth rates to assess the short-term effects of competition and facilitation, and how they both contribute to net long-term effects. We found strong evidence that competition is the dominant mechanism structuring these plant communities (over an annual period), but both competition and facilitation operate at shorter time scales (biweekly). Further, we found that net competition appeared to increase as plants grew in size, but this was primarily due to decreasing facilitation, not increasing competition.

Introduction

Over fifty years of ecological research has demonstrated that organisms compete for limiting resources in nearly every ecosystem (Hardin 1960, Connell 1961, Ricklefs 1977, Tilman 1977, Brokaw and Busing 2000, Coomes and Grubb 2000). In plant communities, neighboring plants utilize resources from a common pool (Casper et al. 2003). Increased competition for limiting resources results in reduced resource availability (Tilman et al. 1996), and ultimately leads to decreased performance at the individual plant level. When competition is strong, experimental removals of neighbor biomass result in increased growth and survival of intact individuals (Casper and Jackson 1997). In temperate grasslands, competition for nitrogen and soil water can help explain local successional trajectories (Tilman 1985), the positive relationship between biodiversity and productivity (Isbell et al. 2011), and woody encroachment patterns (Archer et al. 1995). Competition may occur in nearly every ecosystem (Tilman 1982), but overwhelming interest in competition experiments over the past fifty years may have obscured the co-occurring importance of positive interactions in plant communities (Bertness and Callaway 1994).

Positive interactions (facilitation) may sometimes promote increased growth and survival of plants growing near neighbors. Facilitation may be particularly relevant in severe environments where plants experience high levels of physiological stress that can be ameliorated by the microclimate of neighboring plants (Bertness and Callaway 1994). Specifically, plants can increase shade, reduce direct irradiance, reduce surface soil drying, reduce air and soil temperatures, increase relative humidity, and decrease vapor pressure deficit in their local microclimate (Holmgren et al. 1997, Classen et al. 2010, Montgomery et al. 2010). These direct effects of plants on the local microclimate (microclimate amelioration) can translate to increased performance of neighbors (facilitation). Facilitation is more common in severe environments where plants experience high levels of physiological stress and therefore benefit more from the microclimate amelioration effect (Callaway and Pennings 2000, Van Auken 2000, Brooker et al. 2008, Valladares et al. 2008). In fact, experimental removals of plant biomass in severe environments can result in decreased germination success, survival, and physiological performance – the exact opposite of what is predicted by competition.

The relative strengths of competition and facilitation may also change with plant ontogeny (Miriti 2006). During early ontogenetic stages, seedlings may be more vulnerable to abiotic stress and therefore facilitation may be particularly important (Miriti 2006). Smaller seedlings have relatively less access to deep soil water reserves, and less carbon available in storage organs, than larger plants (Niinemets 2010). They are consequently more vulnerable during environmentally stressful events (Cavender-Bares and Bazzaz 2000). Conversely, larger plants have deeper root systems and more carbon available in storage organs, and are thus more capable of surviving periods of environmental stress or low photosynthetic rates. Larger plants, however, also need increasingly greater quantities of resources to maintain basal metabolism, which may lead to increased resource limitation as they grow larger. Thus, the relative impact of facilitation may decrease with plant ontogeny, while competition intensity increases.

While empirical studies on facilitation are often focused on severe environments (tundra, deserts, salt marshes), more recent work indicates that facilitation may be more common than originally suggested by the stress gradient hypothesis (Dickie et al. 2005, Montgomery et al. 2010, Wright et al. 2012). Both competition and facilitation may be operating in all plant communities, but each may obscure the relative strength of the other. Thus, the outcome of plant interactions may be the sum of both competition for limiting resources and facilitation due to microclimate amelioration (Bruno et al. 2003). If one of the processes is stronger than the other over the course of a single study, the weaker processes will be overlooked and tacitly assumed to be absent. This assumption may be a serious oversight in the interpretation of plant-plant interaction experiments. For example, a positive effect of a neighbor removal on individual plant performance may be due to competitive release. However, neighbor removal may also increase physiological stress, due to the loss of protection from environmental extremes provided by the neighboring canopy. If release from competition has the strongest effect on overall growth (relative to growth lost during periods of physiological strain following neighbor removal), then competitive release will obscure the effect of facilitation, even if the facilitative effect is strong.

Here we test the overarching hypothesis that both competition and facilitation are important in plant communities. We planted three sizes of pine seedlings into an experimental herbaceous plant diversity gradient in central MN. We measured pine growth, nitrate availability, and microclimate conditions at two-week time scales over the course of two growing seasons. We tested three specific hypotheses:

1. Competition is most important when environmental conditions are mild, but biotic effects transition to facilitation when environmental conditions are severe
2. Competition increases with seedling size
3. Facilitation decreases with seedling size

Methods

Study Site and Experimental Design

We conducted this study at the Cedar Creek Ecosystem Science Reserve in central Minnesota, USA. Soils at this site consist of nutrient-poor glacial outwash sand plain with low water- and nutrient-holding capacity (Tilman 1982).

We utilized ambient treatment plots in the plant diversity gradient in the ongoing BioCON experiment at Cedar Creek (Reich et al. 2012). While several metrics have been proposed to measure the importance of plant diversity in the ecological literature, we use species richness as a proxy of plant diversity at this site. Hereafter, plant diversity and species richness are used interchangeably. The BioCON plots were established in 1997 by tilling and fumigating existing vegetation in six experimental blocks in an old-field. Plots were then seeded with herbaceous species that were selected randomly from a pool of 16 total species from four functional groups (four C_3 grasses, four C_4 grasses, four legumes, and four non-nitrogen fixing herbaceous plants). Seeds were divided equally among the species assigned to each plot and applied at a rate of 12 g m^{-2} of seed. Since 1997, species mixes were maintained using hand weeding to remove any species that migrated into the plot that were not planted in the original seed mix. Overall there were three plots maintained with no vascular plants, wherein all colonizing species were removed (hereafter bareground plots). In total, there were 32 plots with 1 species (with every monoculture represented twice), 32 plots with 4 species, 9 plots with 9 species, and 12 plots with 16 species (3+32+32+9+12=88 plots total).

In experimental manipulations of plant diversity, there is often a positive relationship between diversity and biomass production – higher diversity plots are more productive (Tilman et al. 2001, Reich et al. 2001, Van Ruijven and Berendse 2003, Roscher et al. 2005, Isbell et al. 2011, Reich et al 2012, Zhang et al. 2012). All else being equal, competition intensity usually scales with increasing neighbor density (Casper et al. 2003) and thus experimental manipulations of plant diversity may directly affect competition intensity (Kennedy et al. 2002). Conversely, biomass manipulations in severe environments demonstrate the importance of plant cover for amelioration of environmental conditions (irradiance, shallow soil moisture, air temperature, relative humidity) and consequent benefits conferred on seedling performance (Bertness and Callaway 1994). Increased biomass production in higher diversity communities may then also provide increased amelioration of environmental conditions for seedlings, and a positive relationship between experimental manipulations of plant diversity and facilitation (Wright et al. 2012).

In June and August of 2010 and 2011 we measured available soil nitrogen (in the form of nitrate) in each plot by collecting four soil cores at 0-20 cm depth, extracting nitrogen using 1 M KCl, and analyzing the nitrogen content using a Costech 4050 Element Analyzer. In each of the 88 plots we also sampled aboveground herbaceous biomass each June and August 2010-2011. Aboveground biomass was clipped in 10 x 100 cm strips at the soil surface and never sampled less than 15 cm. from plot boundaries (to avoid edge effects). Biomass sampling was conducted in different areas of plots for every sampling date of this study. From May- October in 2011 we measured air temperature and relative humidity (and calculated vapor pressure deficit, VPD) continuously at 5-minute intervals using Maxim iButton dataloggers (Maxim Integrated, San Jose CA). The iButton dataloggers were installed on wooden tent stakes approximately 20 cm above the ground surface and covered with plastic Dixie cups. The covers were painted white to reflect direct sunlight and guard from direct saturation by rainwater. The dataloggers were installed in a stratified subset of 55 plots, which included all monocultures represented once and at least 3 plots from each of the other species richness levels (assigned randomly within species richness level). Dataloggers were moved every month to capture microclimate conditions across a broader range of species combinations. We measured shallow soil moisture (0-6 cm) using an HH2 soil moisture meter (Dynamax Inc, Houston TX) every two weeks from May 2010- October 2010 and May 2011- October 2011.

Seedling growth

In June 2010 we planted 11 white pine (*Pinus strobus*) seedlings into each of the 88 plots described above. Plants were grown initially by Vans Pines Nursery (West Olive, MI) from locally sourced pine seed. In each plot we planted 3 large sized seedlings (>15cm), 3 medium sized seedlings (10-15cm), and 5 small sized seedlings (<5cm), as we predicted that survival rates of the smallest size class would be the lowest (Wright et al. 2012). We measured pine basal diameter and height every two weeks from June 16, 2010 to October 19, 2010 and again from May 10, 2011 to September 22, 2011, at which point all pines were harvested. For the pine harvest, we took care to preserve all aboveground biomass (AGB), but belowground biomass (BGB) was sacrificed for the sake of the long-term integrity of the experimental plots.

To estimate the relationship between measurements taken in the field (basal diameter and height) and plant biomass, we planted 10 large, 10 medium, and 20 small pine seedlings in a garden near the BioCON experiment. We harvested these seedlings throughout the first growing season and took care to preserve all aboveground and belowground biomass of all individuals. We pooled all samples (from the harvest garden and the BioCON final harvest) to calculate aboveground biomass from field measurements, and used the harvest garden data to estimate belowground biomass (as belowground biomass could not be harvested in the BioCON experiment, Table 2.1). Based on differences in seedling size and age, we fit a separate allometric relationship for the small size class, and one combined allometric relationship for the large and medium size classes, which formed a more continuous distribution (Table 2.1). We calculated relative growth rate (RGR) using the following equation: (ln(total final biomass)-ln(total initial biomass))/time interval.

Analysis

To address hypotheses one and two we analyzed the effects of herbaceous diversity on microclimate factors (shallow soil moisture, air temperature, relative humidity, and vapor pressure deficit) and soil nitrogen using a mixed-effects ANCOVA for repeated measures. Within the mixed-effects framework, the BioCON experimental block (“ring”) was included as a random effect. Species richness was considered a continuous fixed effect, and the environmental factors were included as continuous response variables. Time (year or biweekly interval) was included as a random effect to account for repeated measurements taken on the same plots over time.

We analyzed the effects of species richness and seedling size on pine RGR using a mixed-effects ANCOVA as described above (“ring” is a random effect). For these analyses, multiple pine seedlings were planted within each plot, so plot number was nested within “ring” to account for lack of independence among seedlings within a single plot (ring/plot). To examine the difference between net effects over the course of our study vs. underlying variation in competition and facilitation at bi-weekly time scales, we analyzed our dataset at two different time scales. Similar analyses were conducted for pine survival (Appendices B and C).

1. Coarse temporal scale: To test for the net effect of diversity on plant performance and size-specific differences in competition and facilitation, we calculated RGR over each individual year (June 4, 2010 – October 10, 2010 and June 1, 2011 – September 26, 2011). Sampling interval (year one and year two) was included in the model as a random effect to account for autocorrelation of measurements taken on the same plant over time, and to reduce error associated with between year differences.
2. Fine temporal scale: To determine the underlying variation in competition and facilitation over short time intervals, we used bi-weekly measurements of all individuals over the course of two years. For this analysis, bi-weekly census interval was included in the statistical model as a fixed effect. The inclusion of census interval allowed us to directly analyze whether the effects of diversity and size class changed over the course of the growing season (facilitation may change depending on environmental severity). To account for autocorrelation of measurements taken on the same plant over time, plant identity was nested in the random effects term described above (ring/plot/plantID).

Mechanisms - We conducted separate analyses to explore how soil nitrate and microclimate affect seedling growth, and how these mechanisms for competition and facilitation change with seedling size. Because soil nitrate was measured at the annual time scale, we assessed the effects of nitrate, size class, and interactions using a mixed-effects ANCOVA at the coarse temporal scale (number one above). We assessed the effects of VPD, soil moisture, size class, and interactions, using a mixed-effects ANCOVA at the fine temporal scale (number two above).

We also analyzed the effects of herbaceous aboveground biomass in a mixed-effects ANCOVA at the coarse temporal scale. We conducted this analysis to understand how pine growth was affected by between-plot variation in biomass production within species richness levels.

Results

Net effects and size structured effects

After two years, pines growing in higher diversity plots grew less than pines growing in lower diversity plots (Figure 2.2). In other words, the net effect of diversity on pine growth was competitive (Table 2.3). Smaller seedlings also grew relatively slower overall (in RGR terms) than larger seedlings (Table 2.3), but larger seedling growth was more negatively affected by diversity (Table 2.3). Specifically, small seedlings grew equally well across diversity treatments (Figure 2.3a), medium seedlings were slightly negatively affected by diversity (Figure 2.3b), and large seedling growth was strongly limited by diversity (Figure 2.3c). Herbaceous aboveground biomass explained only a small proportion of the above patterns in pine seedling growth (Table 2.3).

Soil nitrate and microclimate

Higher diversity plant communities (16-sp) had an average of 50% less soil nitrate than lower diversity communities ($F_{1,86}$=6.27, P=0.01). Increasing herbaceous species richness increased shallow soil moisture availability by 1% over the course of the growing season (Figure 2.1a) and reduced mean air temperature by 2°C (Figure 2.1b). Average relative humidity (for every 24 hr period over the course of the growing season) was 10% higher in high diversity plots (Figure 2.1c), and average vapor pressure deficit decreased to almost ¼ the bareground level in higher diversity plots (Figure 2.1d).

Competition and facilitation change with seedling size

When pine RGR was measured at bi-weekly temporal scales, to assess how competition and facilitation changed over shorter time periods, seedling growth was still most strongly affected by competition. However, seedling growth and biotic effects also changed significantly from one census to the next. The effect of diversity was sometimes positive (facilitative) and sometimes negative (competitive); within a single census interval the effects of diversity could be strongly competitive for large individuals and neutral for small individuals (similar to net effects above), or facilitative for small individuals and neutral for larger individuals (Figure 2.4).

There was an overall positive effect of nitrate availability on seedling RGR ($F_{1,71} = 7.66$, $P=0.007$); this effect did not change with seedling size ($F_{2,363} = 1.66$, $P=0.19$). All seedlings were equally limited by access to soil nitrate (Figure 2.5a). There was no overall effect of shallow soil moisture ($F_{1,276} = 0.49$, $P=0.48$) or vapor pressure deficit ($F_{1,262} = 0.07$, $P=0.80$) on seedling RGR (Table 2.5b). However, there was an interaction between seedling size and the effect of VPD on growth – small seedlings grew faster in plots where they didn't experience a large vapor pressure deficit, but larger seedlings were not affected by differences in VPD ($F_{2,1326} = 5.27$, $P=0.005$, Figure 2.5b).

Discussion

We found that both competition and facilitation influence growth rates of pine seedlings in this experimental grassland community. Competition for resources is intense in this community, and thus the importance of facilitation can be easily missed. By explicitly manipulating plant size, we found that growth of pines was limited in higher diversity plots, and this growth limitation increased with seedling size (Figure 2.6a). The most common interpretation of increasing growth limitation with increasing size may be increasing competition intensity (Figure 2.6b). However, competition for soil nitrate was not more intense for larger seedlings, meaning that larger seedlings may not have been more limited by competition (Figure 2.5a). An alternative explanation for increasing growth limitation with increasing seedling size is a decrease in facilitation intensity as seedlings grow larger (Figure 2.6c). Indeed, smaller seedlings experienced stronger facilitation in high diversity plots via microclimate amelioration and this effect decreased with seedling size (Figure 2.5b). While the net effect of plant interactions in this system may be competitive, both competition and facilitation help explain observed patterns.

Cedar Creek has a continental climate (warm summer and cold winters) and receives approximately 32.4 cm of precipitation during summer months (Davis et al. 2005, Peel et al. 2007). This is sufficient rainfall to be classified as a humid continental climate as opposed to arid or semiarid (Peel et al. 2007). In terms of plant desiccation stress, this system may not be particularly stressful in comparison to deserts and artic habitat. Past research at this site has demonstrated the importance of competition for community composition, succession, and overall plant diversity in both experimental (Tilman et al. 2001) and observational settings (Tilman et al. 1996). Annual pine RGR measurements in our experiment reflect similar patterns: when measured at coarse time scales, the only detectable pattern was decreased pine growth in higher diversity plots that became stronger with seedling size. Increased herbaceous plant diversity decreases resource availability and thus increases competition for limiting resources (Tilman et al. 1996). However, while competition may be stronger than facilitation in our experiment, the weaker effects of facilitation still help structure neighbor interactions. Further, because facilitation appears to be associated with environmental severity, we may expect it to change in the future as a result of climate change (He et al. 2013).

Facilitation is important for small seedlings because they are particularly sensitive to harsh environmental conditions. Small seedlings have reduced access to deep soil water reserves during periodic droughts, and have fewer non-structural carbohydrates available for maintaining plant metabolic activity during brief periods of stress (Niinemets 2010, Cavender-Bares and Bazzaz 2000). These physiological and physical constraints make smaller seedlings more vulnerable to environmental stressors, and therefore more dependent on facilitative microhabitat amelioration provided by neighbors. We found that the microclimate under the canopy of a high diversity community is cooler, more humid, and has higher soil water content at the soil surface than a lower diversity community. Our results demonstrate that small seedlings have increased vulnerability to environmental stress (Figure 2.5b), and that they benefit in higher diversity communities where there is increased amelioration of this environmental stress (Figure 2.1).

Facilitation at the seedling establishment phase may also help explain species coexistence. If the first filter for plant community composition relies heavily on protection from environmental severity, there may be a positive feedback for increased species diversity at the seedling establishment phase – high diversity may beget high diversity, particularly when environmental conditions are severe (Bertness and Callaway 1994, Brooker 2006). Overall community composition may be the result of strong facilitation at the establishment phase, leading to the highest diversity in the smallest seedling layer. Facilitation during initial plant establishment turns into competition for resources as plants grow (Wright et al. 2012), and thus larger plants may become limited by competition for resources.

Our data support the hypothesis that competition and facilitation are both operating between neighboring plants in plant communities (Bruno et al. 2003, Brooker 2006). When competition is the strongest type of interaction, positive interactions are overlooked, and assumed to be absent. In our study system, if the net effect of diversity were merely the result of competition, we may have observed little growth and establishment of the smallest pines and even stronger competition intensity for the largest pines. Instead we observed patterns that appear to reflect a combination of competitive effects and counteracting facilitative effects. If the observed neighbor interactions are the result of competition drivers (resource supply and demand) as well as facilitation drivers (environmental severity, temperature, drought) our expectations for community composition and diversity in the future may be very different from our current predictions (Brooker 2006).

Acknowledgements

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Table 2.1. Allometric relationships between pine seedling height and diameter for both aboveground biomass and belowground biomass. Different equations were used for small seedlings and medium/large seedlings.

Size Class	log(AGB)	r^2	log(BGB)	r^2	Total
Sml	-4.06 + 0.23*H + 10.20*D	**0.79**	-5.45 + (0.29*H) + (13.75*D)	**0.78**	AGB+BGB
Med/Lrg	-1.03 + 0.04*H + 3.07*D	**0.82**	-1.07 + (0.04*H) + (2.22*D)	**0.74**	AGB+BGB

Table 2.2. The effect of herbaceous species richness on four commonly described metrics of microclimate: air temperature, relative humidity, vapor pressure deficit, and shallow soil moisture.

Response Variable	d.f.†	F	P
Air Temperature	1, 50	24.67	**<0.0001***
Relative Humidity	1, 52	47.11	**<0.0001***
Vapor Pressure Deficit	1, 52	55.88	**<0.0001***
Shallow Soil Moisture	1, 84	11.30	**0.0012***

† This analysis took into account spatial variation associated with the blocked design ("Ring" in the BioCON framework). In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of spatial variation attributed to block differences, this is why denominator degrees of freedom are different depending on the metric described in this table.

Table 2.3. The effects of herbaceous species richness and seedling size class on seedling RGR. We conducted this analysis with and without herbaceous AGB. Results from both analyses are shown below as without herbaceous biomass (wo) and with herbaceous biomass (w).

Fixed Effect	d.f.† *wo/w*	F *wo/w*	P *wo/w*
Species Richness	1, 100/1, 99	30.0/24.9	**<0.0001*/<0.0001***
Size Class	2, 597/2, 595	40.0/39.5	**<0.0001*/<0.0001***
Sp Richness x Size Class	2, 603/2, 602	7.7/7.7	**0.0005*/0.0005***
Herbaceous AG Biomass	1, 98.1	0.65	0.42

† This analysis took into account spatial variation associated with the blocked design (“Ring” in the BioCON framework) as well as variation associated with taking measurements on multiple seedlings within plot (“plot”), and measurements on the same individuals over time. In the linear mixed effects model framework, denominator degrees of freedom “float” based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom are different depending on the metric described in this table.

Table 2.4. The effects of herbaceous species richness and seedling size class on seedling RGR for each individual 2-week census interval. In order to avoid pseudo-replication of measurements taken on the same individuals over time, seedling ID was included as a random effect in the statistical model.

Fixed Effect	d.f.†	F	P
Species Richness	1, 465	48.2	**<0.0001***
Size Class	2, 386	59.8	**<0.0001***
Census	15, 5967	69.7	<**0.0001***
Sp Rich x Size	2, 456	0.99	0.37
Sp Rich x Census	15, 6015	2.53	**0.001***
Size x Census	30, 5969	25.0	<**0.0001***
Sp Rich x Size x Census	30, 6022	3.97	<**0.0001***

† This analysis took into account spatial variation associated with the blocked design ("Ring" in the BioCON framework) as well as variation associated with taking measurements on multiple seedlings within one plot ("plot") and on the same individuals over time (seedling ID). In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom are different depending on the metric described in this table.

Table 2.5a. Mixed effects ANCOVA analyzing the effects of seedling size and available soil nitrate on seedling RGR. Interactions between seedling size and soil nitrate were used to test size structured competition.

Fixed Effect	d.f.†	F	P
Soil Nitrate	1, 71	7.66	**0.007***
Size Class	2, 359	24.78	<**0.0001***
Size Class x Nitrate	2, 363	1.66	0.19

† This analysis took into account spatial variation associated with the blocked design ("Ring" in the BioCON framework, and plot, based on the fact that many individuals were planted into each plot – plot was nested within ring), as well as variation associated with taking measurements on the same plot over time. Soil nitrate was measured twice per year and averaged on a per year basis. This analysis used the course time-scale measurement of pine RGR, based on year one and year two measurements, with year included in the analysis as a random effect. In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom differ for different factors above.

Table 2.5b. Mixed effects ANCOVA analyzing the effects of seedling size, shallow soil moisture, and VPD on seedling RGR. Interactions between seedling size and soil moisture or VPD were used to test size structured facilitation.

Fixed Effect	d.f.†	F	P
Vapor Pressure Deficit (VPD)	1, 263	0.07	0.80
Shallow Soil Moisture	1, 276	0.49	0.48
Size Class	2, 861	1.19	0.30
Size x VPD	2, 1326	5.27	**0.005***
Size x Shallow Moisture	2, 1426	1.14	0.32

† This analysis took into account spatial variation associated with the blocked design (“Ring” in the BioCON framework, and plot, based on the fact that many individuals were planted into each plot – plot was nested within ring), as well as variation associated with taking measurements on the same plots over time. All of these measurements were taken continuously or at least once per two weeks and averaged per two-week period. This analysis was done using the two-week pine RGR measurements. In the linear mixed effects model framework, denominator degrees of freedom “float” based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom are different depending on the metric described in this table.

Figure 2.1. Effects of herbaceous community diversity on microclimate conditions averaged for all 24-hour periods from May – Sept 2011 for air temperature, relative humidity, and VPD. And average per plot for 2010-2011 (May – Sept) for soil moisture. The four panels represent four commonly described micro-climate variables and how they relate to herbaceous species richness. Panel (a) demonstrates the relationship with shallow soil moisture, (b) temperature, (c) relative humidity, and (d) vapor pressure deficit. See Table 2 for statistics.

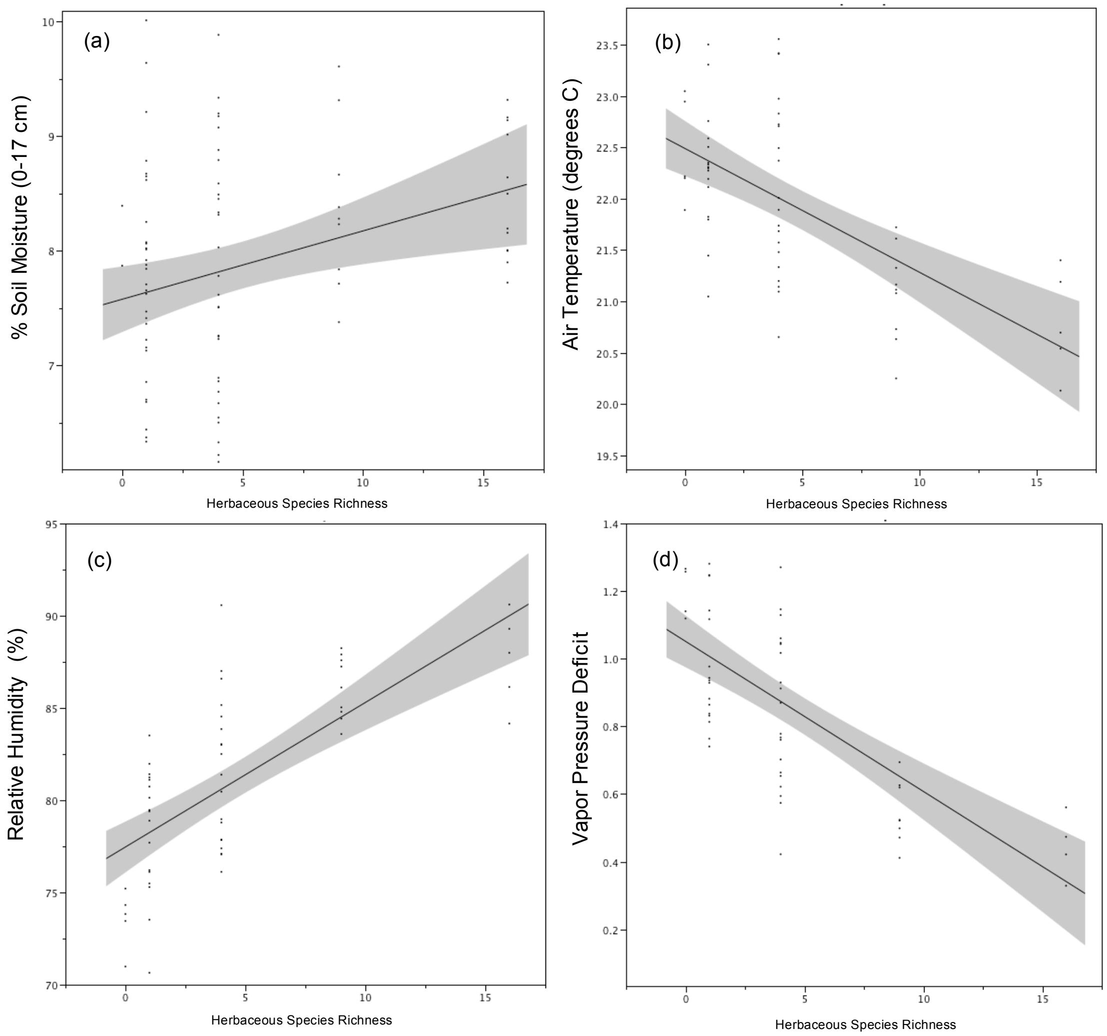


Figure 2.2. Course measurements of pine RGR (measured twice from May 2010 to October 2011) demonstrate that RGR declines with increasing herbaceous species richness.

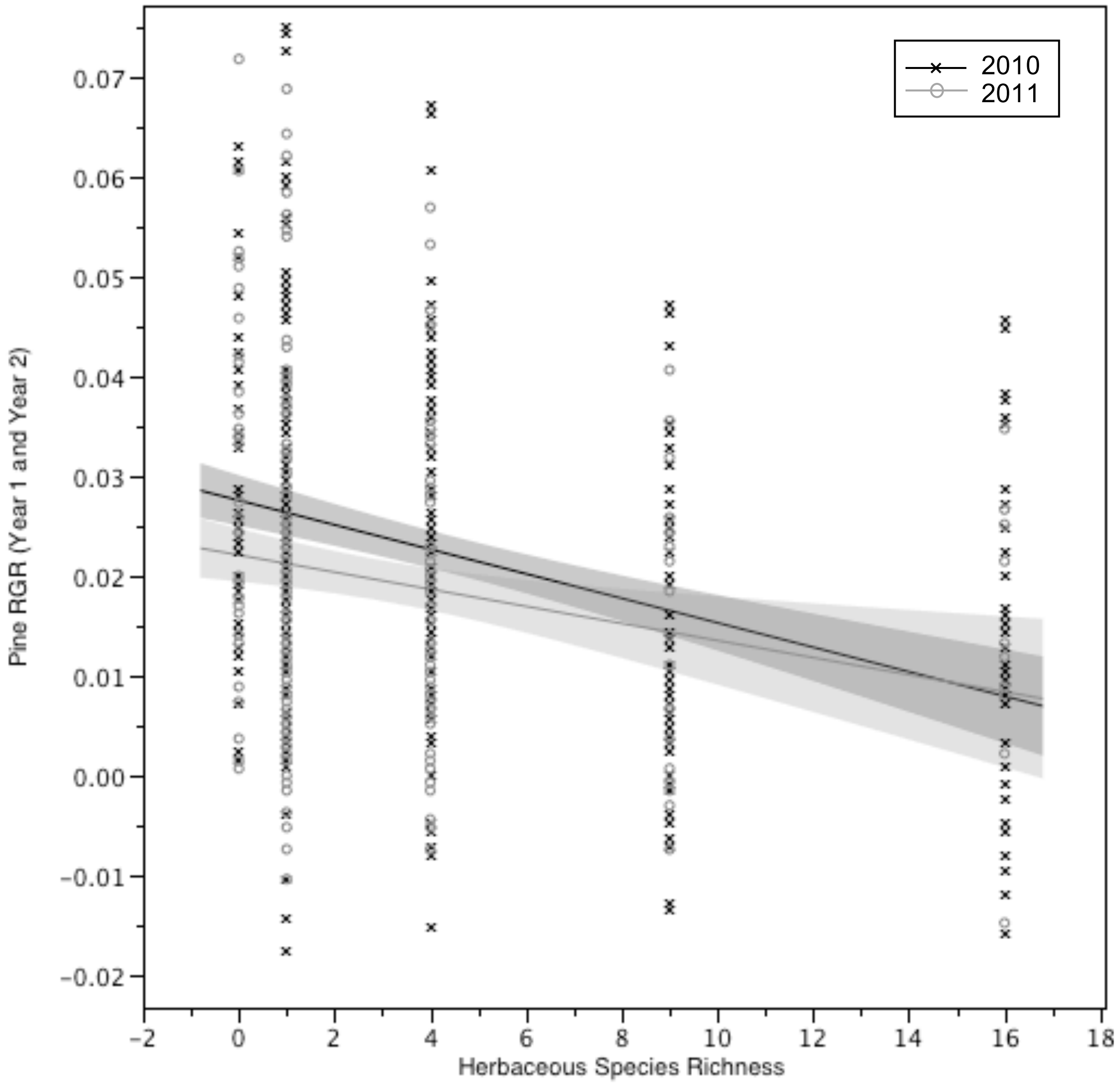


Figure 2.3. Course resolution measurements of pine RGR for both years. This demonstrates an interaction between species richness and pine size class, where larger pines are more strongly limited by herbaceous species richness.

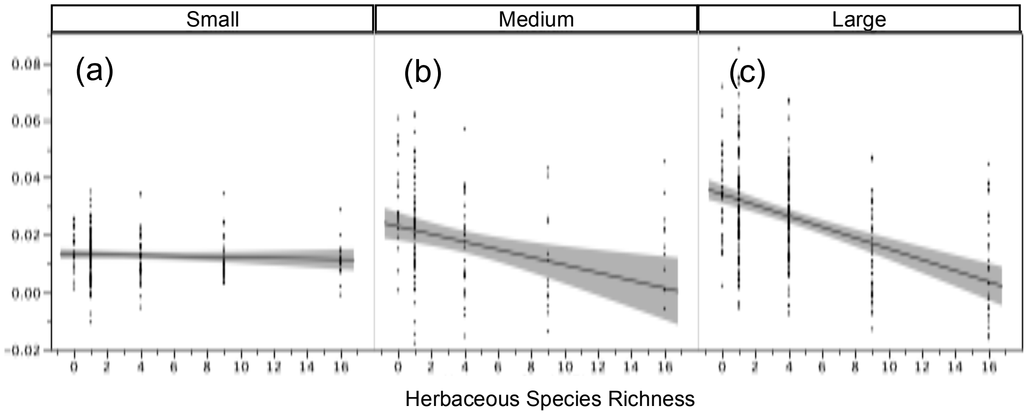


Figure 2.4. Finest scale measurements demonstrate that the effect of species richness on pine RGR depends on size class – and the magnitude and direction of this effect changes depending on census interval (there is a significant size x species richness x census interval interaction).

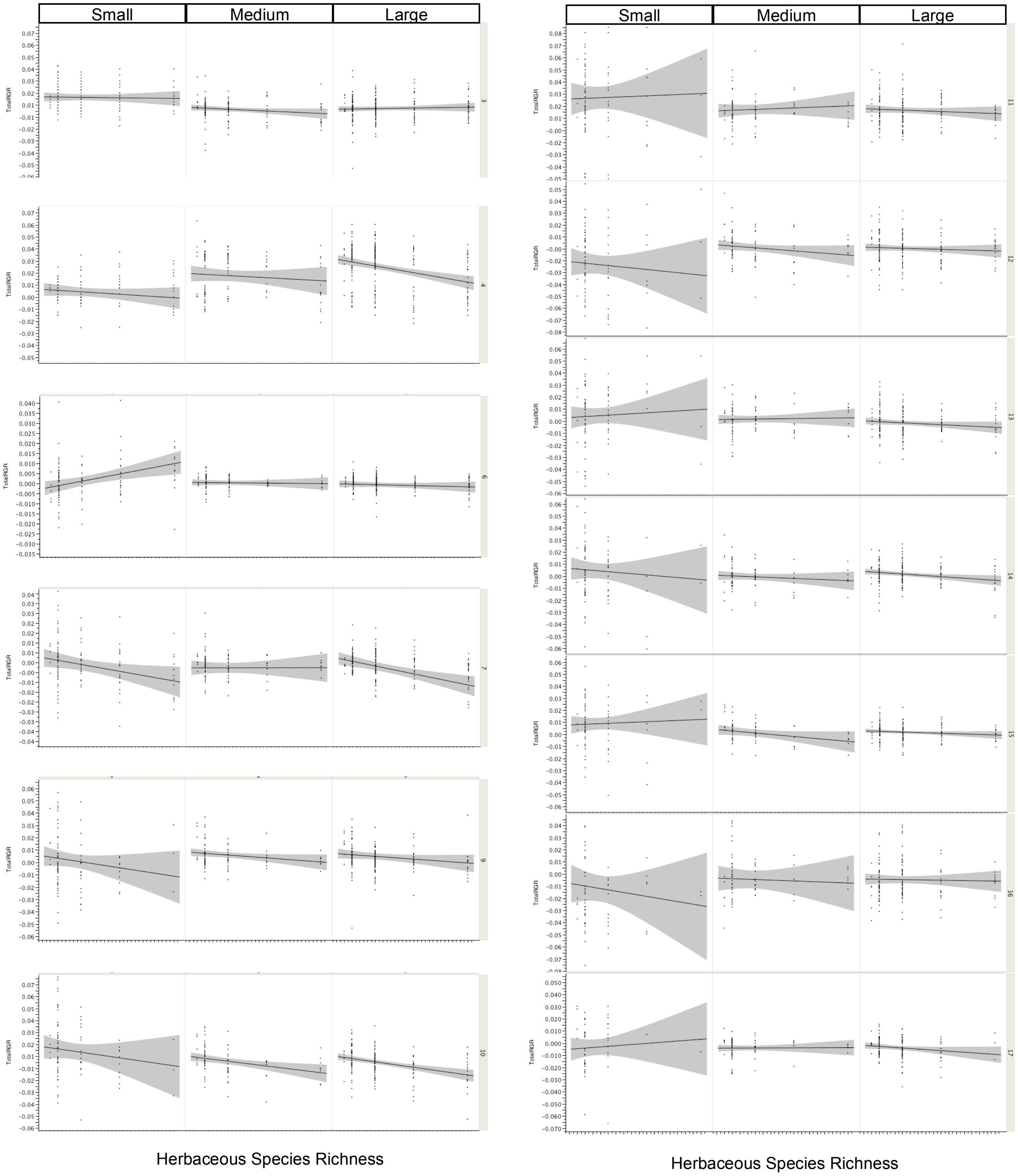


Figure 2.5. (a) RGR of all seedlings is equally limited by access to available soil nitrogen in the form of nitrate. Conversely, (b) there is a significant interaction between vapor pressure deficit and seedling size. Small individuals are strongly negatively affected by high vapor pressure deficit, whereas large and medium individuals are not significantly affected.

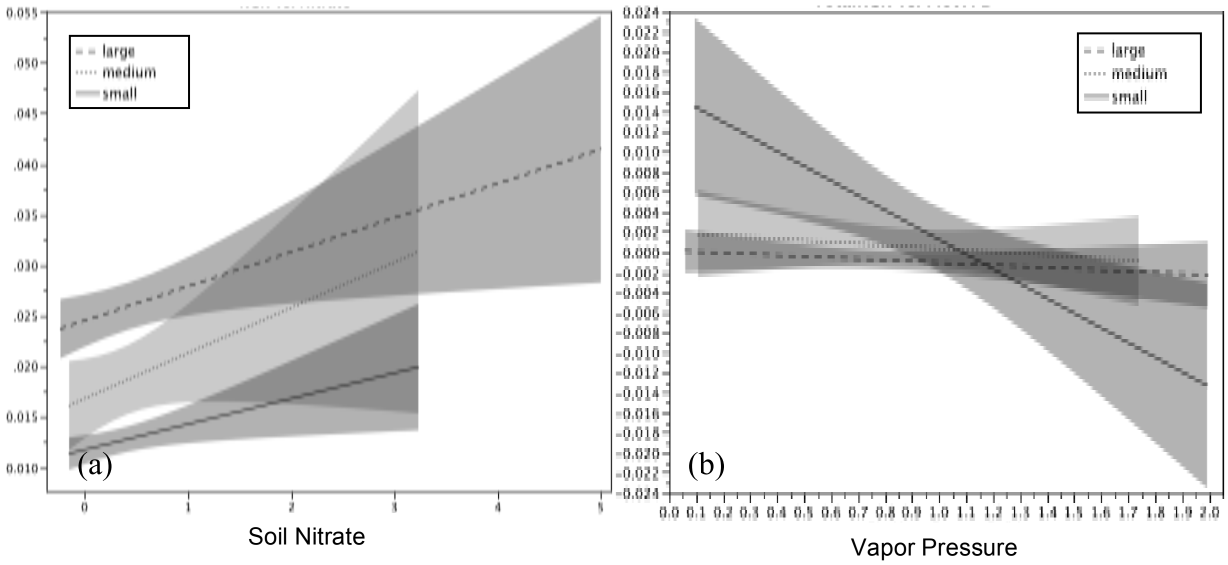
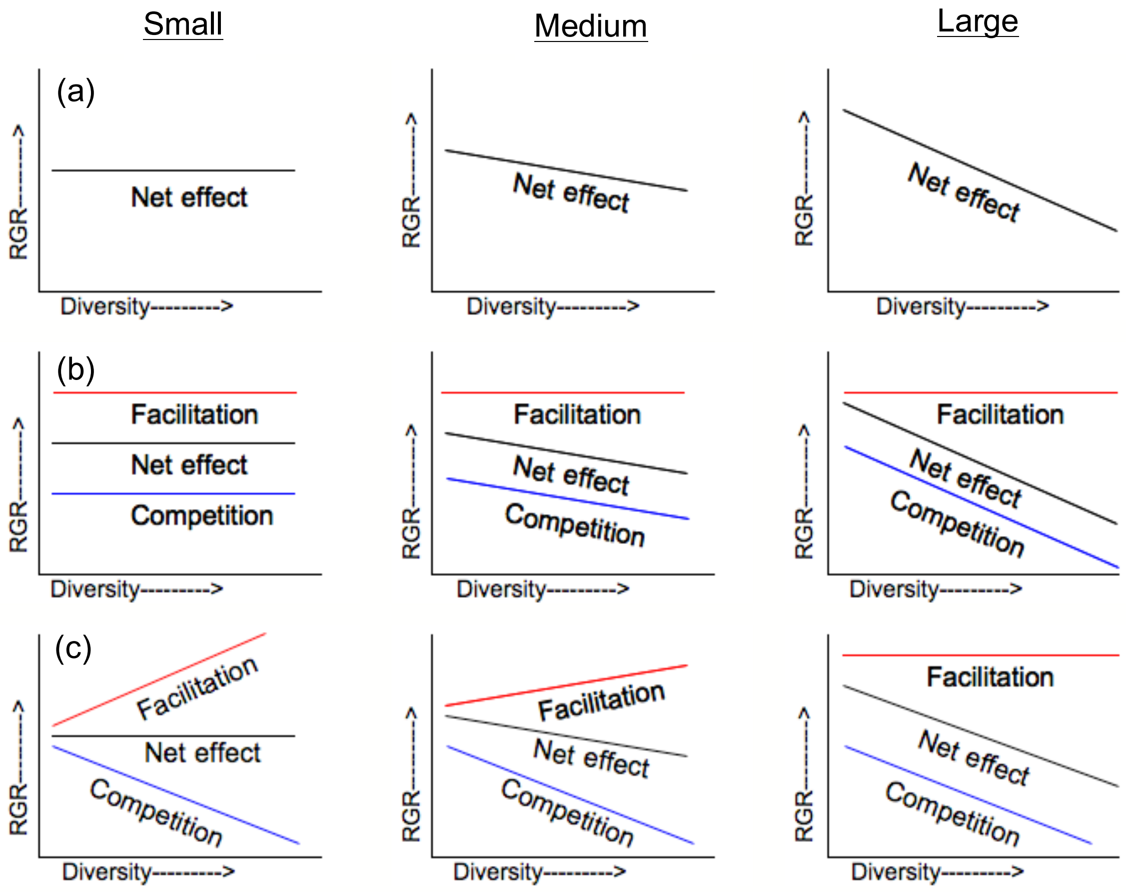


Figure 2.6. Conceptual diagram of net effects showing that observed effects of diversity on pine RGR may indicate increasing competition with increasing seedling size (a). However, underlying competition and facilitation may help explain these observation in several different ways. Competition intensity may increase with increasing seedling size (b). Or facilitation intensity may decrease with increasing seedling size (c).



CHAPTER 3

We need our neighbors when times are tough: seasonal weather patterns can drive the competition – facilitation balance

To be submitted with co-authors S.A. Schnitzer and P.B. Reich

Abstract

Plants compete for limiting resources. Resource limitation can decrease stomatal conductance, photosynthesis, growth, and survival. Conversely, positive interactions between neighboring plants (facilitation) can increase these same physiological processes. Facilitation is often mediated through abiotic conditions (temperature, wind, shade), and is therefore often related to environmental severity gradients. When environmental conditions are severe, the importance of facilitation often increases. The co-occurrence of both competition and facilitation among neighboring plants has made it difficult to tease them apart in plant communities. Here we tested the hypothesis that neighbor interactions can flip day-to-day from net negative to net positive depending on the conditions experienced by plants in a single growing season. We planted bur oak (*Quercus macrocarpa*) acorns into an experimental grassland diversity gradient in central MN. Plant diversity drives increased competition for resources, and may drive increased facilitation due to microclimate amelioration. We measured temperature, humidity, and soil moisture in these plots for two growing seasons. We also measured oak leaf water potential over a range of daily conditions. We found that that on cool days, competition

for soil water determines the net effect of plants on their neighbors. Conversely, on hot/dry days, facilitation of the microclimate near neighbors determines the net effect of plants on their neighbors. We posit that increased occurrence of extremely hot and dry days, one of the predictions of global change, will drive the increased importance of facilitation in the future.

Introduction

Plants compete for limiting resources and the outcome of competitive plant interactions can help explain community composition, global plant distributions (Bond et al. 2005) and species coexistence (Hardin 1960). At the individual plant level, neighbors competing for similar limiting resources can decrease interspecific and intraspecific growth rates (Ehleringer 1984, Gordon et al. 1989), and increase plant mortality (Davis et al. 1999). A key limiting resource in many ecosystems is soil water. Competition for soil water can result in a cascade of physiological changes for a plant, including increased water stress, decreased stomatal conductance, and decreased rates of photosynthesis and carbon gain (Bazzaz 1979, Gordon et al. 1989, Davis et al. 1999, Danner and Knapp 2003). When plants are water limited due to competition for soil water, they may close stomates to reduce water loss at the leaf surface. Stomatal closure due to limited soil water availability can lead to decreased plant growth and survival (Gordon et al. 1989).

Plants may also facilitate each other via amelioration of the local microclimate (Brooker et al. 2008). In fact, facilitation may underlie many plant interactions but it may be less common or often obscured by competitive interactions (Stachowicz 2001, Bruno et al. 2003). Plants can modify their local microclimate via shading, interception of direct irradiation, and evaporative cooling. The direct effect that plants have on their microclimate is called environmental amelioration. Environmental amelioration is a physical process, and may only result in facilitative effects for neighboring individuals when neighboring individuals are physiologically stressed, and therefore benefit from a cooler more humid environment. Thus, in severe environments, microclimate amelioration provided by neighboring plants is particularly important (the stress gradient hypothesis, Bertness and Callaway 1994). For example, plants growing in hot arid ecosystems are often clumped, due to an inability to germinate, grow, or survive in the harsh microclimate found away from other plants (Cuesta et al. 2010, Landero and Valiente-Banuet 2010, Jia et al. 2010, Armas et al. 2011). In arid systems, physiological constraints, related to water status, may be more important than competitive interactions. Plants may be limited by high rates of water loss at the leaf surface, due to high vapor pressure deficit in the microclimate, or directly, due to photoinhibition at high light levels (Valladares and Pearcy 1997). Facilitation may be dominant in these stressful abiotic conditions, but weaken and become subordinate to competition as environmental stress lessens (Callaway et al. 2002).

In the past decade, theoretical work has suggested that both competition and facilitation occur simultaneously in all plant communities (Bruno et al. 2003). We posit that, in terms of water status, the importance of facilitation relative to competition may be a function of daily differences in physiological stress (as measured by daily temperature and humidity), and therefore change on a daily basis. On days when environmental stress is low (cool humid days), facilitation may be weak and competition for soil water may dominate plant interactions. Conversely, on days when environmental stress is severe (hot/dry days), facilitation may be strong relative to competition and the positive effects of facilitation may dominate. The sum total of competitive and facilitative interactions may determine individual plant performance.

In 2012, we planted oaks into an experimental species richness gradient in central MN. We measured leaf water potential of oaks across a range of daily conditions at this site. We explored the relative importance of co-occurring competition and facilitation for plant water status, and how the balance of these two processes may change dynamically over the course of a growing season. We tested the hypothesis that both processes are operating, but that they tradeoff over short time periods depending on the relative severity of daily conditions. Specifically:

(1) *On cool days, competition for soil water is the dominant process driving plant water status*

(2) *On hot days, facilitation due to amelioration of the microclimate is the dominant process driving plant water status*

Methods

We conducted this study in 2011-2012 in the ambient treatment plots in the BioCON plant diversity experiment at the Cedar Creek Ecosystem Science Reserve in central Minnesota, USA. Cedar Creek has a continental climate, with cold winters and warm summers and an average of 660 mm of rainfall per year (Reich et al. 2001b). Daily 24-hour average temperatures during the growing season range from ~15°C - 30°C. Soils at this site are nutrient-poor glacial outwash sand plain with low water-holding capacity. The BioCON plots were established in 1997 by tilling and fumigating existing vegetation in six experimental blocks in an old-field grassland at the site. Plots were then seeded with randomly assigned herbaceous species (all native or naturalized) from a pool of 16 total species from four functional groups - four C_3 grasses, four C_4 grasses, four legumes, and four non-nitrogen fixing herbaceous plants (*Achillea millefolium, Agropyron repens, Amorpha canescens, Andropogon gerardi, Anemone cylindrica, Asclepias tuberosa, Bouteloua gracilis, Bromus inermis, Koeleria cristata, Lespedeza capitata, Lupinus perennis, Petalostemum villosum, Poa pratensis, Schizachyrium* *scoparium, Solidago rigida*, and *Sorghastrum nutans,*). There are 32 plots with 1 species (with every monoculture represented twice), 32 plots with 4 species, 9 plots with 9 species, and 12 plots with 16 species. Since 1997, species mixes have been maintained by hand weeding to remove any species that migrated into the plot that were not planted in the original seed mix.

We used species richness as a proxy for both competition and facilitation intensity (Wright et al. *in process*). Higher diversity plant communities have reduced resource availability and increased intensity of competition for colonizing plants (Tilman et al. 1996, Fargione and Tilman 2005). Increased biomass production in higher diversity communities (Naeem et al. 1995), may also be associated with increased protection from environmental conditions. Consequently, diversity may drive increased facilitation between plants due to amelioration of environmental extremes (Wright et al. 2012). In June and August 2012, we measured aboveground biomass production in all 85 ploys. Aboveground biomass was clipped in 10 x 100 cm strips at the soil surface at least 15 cm. from plot boundaries (to avoid edge effects).

We planted six bur oak (*Quercus macrocarpa*) acorns in all 85 plots described above in May 2010 and again in May 2012. Due to lack of emergence in the May 2012 crop, and consequently low sample size, age was not used as an independently manipulated variable in this study. Instead, seedlings used for leaf water potential measurements were selected randomly from the pooled group of all seedlings and seedling age was included in the analysis as a random factor. All seedlings were censused at the beginning of the growing season (May 28, 2012) and at the end of the growing season (Aug 27, 2012) to assess 2012 relative growth rates (RGR). We measured leaf number, seedling height, and seedling diameter of each seedling at each census date. We also censused seedling emergence at the beginning of the first growing season (July 1, 2010) and at the beginning of the 2012 growing season (May 28, 2012). We recorded survival of all seedlings that had emerged by August 27, 2012.

We simultaneously planted 37 oak seedlings in a nearby harvest garden and harvested them periodically between July 2010 and August 2011, to derive allometric equations for biomass. We used these measurements to derive equations for both aboveground biomass (AGB = 0.76 x diameter - 0.02 x height + 0.11 x leaves, r^2= 0.80) and belowground biomass (BGB = 6.5 x diameter - 0.12 x height + 0.14 x leaves, r^2= 0.35), though due to low r^2 values for BGB, we use AGB values to calculate RGR. We calculated aboveground RGR by taking ln(final AGB) – ln(initial AGB)/122 days.
We measured pre-dawn and mid-day leaf water potential in a stratified subset of 27-37 oak seedlings (depending on seedling availability as outlined below) across the diversity gradient, on six different sampling days (June 21, June 22, July 11, August 1, and August 14, and August 24). We chose sampling days based on forecast data of maximum daily temperatures at the site and an attempt to sample evenly across the range of previously observed temperatures (20-30°C). Oak leaves began to change color the week of Sept 10 so no further leaf water potential measurements were taken after August 24, 2012. We measured leaf water potential using a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Pre-dawn water potential (ψ_{pd}) was taken 2 hours before dawn each day (3:30-5:30), and mid-day leaf water potential (ψ_{md}) was taken at solar noon (12:00-2pm). All measurements were taken by wrapping leaves in Ziploc bags, excising leaves using a razor blade, and immediately transferring to the

pressure chamber. Plants were chosen based on having at least 3 oaks per herbaceous species richness level on each day, each oak having at least 3 leaves fully exposed at the time of sampling, and not sampling from the same plant two sampling dates in a row. When more than one plot, or more than one plant within plot, met the above requirements, the plant was chosen randomly from the subset of available plants. Mid-day measurements were taken on the same plants as pre-dawn measurements to assess daily changes in plant water stress at the individual plant level. We used a comparison between predawn (ψ_{pd}) and midday (ψ_{md}) leaf water potential (ψ_{md}- ψ_{pd}) to detect daily change in plant water status at the individual plant level.

From May- October 2011-2012 we measured plot-level air temperature and relative humidity (RH), and calculated vapor pressure deficit (VPD), continuously using Maxim iButton dataloggers logging every 5 minutes (Maxim Integrated, San Jose CA). Dataloggers were installed on wooden tent stakes at approximately 20 cm above the ground surface and covered with plastic Dixie cups. The covers were painted white to reflect direct sunlight and guard from direct saturation by rainwater. These dataloggers were installed in a stratified subset of 55 out of the 85 plots (maintaining at least 3 loggers per diversity level but assigning plot location within diversity treatment randomly). We collected site-level temperature, humidity, and vapor pressure deficit measurements from the Cedar Creek Ecosystem Science Reserve weather station. Finally, at 11am on the day of leaf water potential measurements (immediately prior to taking mid-day measurements) we measured shallow soil moisture within these plots approximately 0-6 cm below the soil surface using an HH2 soil moisture meter with theta probe (Delta-T Devices Ltd, Cambridge UK).

Analysis

We analyzed the effects of herbaceous diversity on microclimate (air temperature, relative humidity, and vapor pressure deficit) and whether the magnitude of these effects changed depending on daily environmental conditions. We calculated plot-level averages for all microclimate factors for each day of the study ("plot-level"). We also calculated daily averages for air temperature, relative humidity, and vapor pressure deficit data collected from the Cedar Creek weather station ("site-level"). We conducted three separate mixed effects ANCOVA's to assess the effects of weather (temperature, relative humidity, and vapor pressure deficit) on microclimate. These analyses included random effects for spatial variation associated with the BioCON block design, as well as plot variation associated with taking measurements on the same plots over time. These three ANCOVA's assessed: (1) fixed effects of daily average temperature at the site (taken from Cedar Creek weather station data), species richness, and their first order interaction effects on plot-level daily temperatures, (2) the same as above for site-level relative humidity effects on plot-level RH, and (3) the same as above for site-level VPD effects on plot-level VPD. We then included herbaceous aboveground biomass in these analyses to understand if variation in microclimate was mainly due to increased biomass production in higher diversity plots.

To assess the effects of daily and seasonal changes in weather, and species richness, on soil moisture, we conducted a mixed-effects ANCOVA as above, but with site-level temperature and day of year as fixed effects (to account for a correlation between soil moisture and day of year). We included ring and plot as random effects. We measured soil moisture in a 30-plot subset of the total plots used for this study, based on where leaf water potential measurements were taken on a given day. Consequently, statistical power was too low among species diversity levels on any single day to include random effects for ring and plot in the BioCON design. The models that included random effects failed to converge.

We analyzed the effects of species richness on aboveground oak seedling RGR and proportion survival (arcsine transformed) using a mixed-effects ANCOVA with plot nested in block, and seedling size included as random effects. Our sampling design was based specifically on forecast temperature conditions. We selected days based on equal representation across the range of 20-30°C. While relative humidity and vapor pressure deficit are both correlated with temperature, we focused on the effects of air temperature, as air temperature was the metric used to select days in our sampling design (our "fixed effect"). We conducted a mixed-effects ANCOVA (with block [plot], and seedling size included as random effects) to assess the daily effects of species richness, average daily temperature, and their interaction, on all measures of oak leaf water potential ($\psi_{pd,}$ ψ_{md}, ψ_{md}- $\psi_{pd,}$). After testing for the main effects of our models using ANCOVA, we performed a second set of ANCOVA's to assess the explanatory role of herbaceous aboveground biomass. Increased diversity plots have increased aboveground biomass. However, depending on species identity, some monocultures also have high biomass production (though none as high as 16-species mixtures). We assessed the effects of aboveground biomass to better understand the mechanisms for competition and facilitation in this system.

We conducted separate analyses to explore the mechanisms for competition and facilitation on three measures of oak leaf water status (ψ_{pd}, ψ_{md}, ψ_{md}- $\psi_{pd,}$). We assessed the effects of soil water, and plot-level vapor pressure deficit on predawn, midday, and daily differences in oak water potential using a mixed-effects ANCOVA. We treated daily soil moisture and plot VPD as continuous fixed effects, and spatial variation associated with experimental block and seedling identity as random effects (we never measured more than one seedling within a plot on a single day, so plot was not included as a random effect).

Results

Environmental Conditions

Annual temperatures in 2012 were the warmest on record in the United States (NCDC 2013). Mean air temperature at Cedar Creek was 8.1+/- 1.3°C (mean +/- 95% confidence intervals), which was statistically consistent with the 24-year average (6.9 +/- 1.2°C, Cedar Creek Ecosystem Science Reserve hourly climate data). Although July 2012 was the warmest month on record in the 24-year dataset at the Cedar Creek weather station (23.9°C, Figure 3.1). Annual precipitation was 495 mm, which was below the long-term average of 660 mm yr $^{-1}$ (Reich et al. 2001b), Figure 3.1).

Over the course of our six leaf water potential measurements, daily temperature was the highest on July 11 and August 24 and lowest on June 21 and August 14. Relative humidity was highest in early June and lowest in early July (Figure 3.2). There was no correlation between sampling date and temperature (Pearson product moment correlation coefficient, r=0.26, N=194) and no correlation between sampling date and relative humidity (r=0.08, N=194) – in other words, we didn't sample all cool/humid days in the spring and all hot/dry days in the late summer (Figure 3.2).

Microclimate and soil moisture

Higher diversity grassland plots were cooler, more humid, and had lower vapor pressure deficit than low diversity plots (Table 3.1a). The magnitude of the microclimate amelioration effect was stronger as daily weather conditions become hotter and drier (significant interaction term, Table 3.1a, Figure 3.3). There was a strong relationship between daily temperature conditions, species richness, and plot-level temperature (r^2=0.98, Figure 3.4). Conversely, both relative humidity and vapor pressure deficit appear to be controlled by additional factors (Figure 3.4). The microclimate amelioration effect was partially due to differences in herbaceous aboveground biomass (Table 3.1b), though even after accounting for differences in herbaceous aboveground biomass, the diversity – microclimate effect was significant (Table 3.1b). Soil moisture was lower in higher diversity plots, lower over the course of the season, and lowest in high diversity plots at the end of the season (Table 3.2, Figure 3.5).

Water stress, growth, and survival

Predawn leaf water potential values became more negative with increasing daily temperatures (Table 3.3a), indicating that the plants became more water stressed as temperature increased. Herbaceous species richness had an overall negative competitive effect on predawn leaf water potential (Table 3.3a) and an increasingly negative effect as daily temperatures increased (Figure 3.7). Overall predawn leaf water potential values were driven mostly by access to soil water, which experiences a seasonal dry down, where predawn leaf water potential was lowest when soil moisture was low (Table 3.4, Figure 3.9).

Midday leaf water potential values were more negative on hot days, but they did not vary with species richness (Table 3.3a, Figure 3.7). Species richness did not have a significant effect on midday leaf water potential values on any of the days we measured. Midday leaf water potential was more negative when soil moisture was low and when plot VPD was high (Table 3.4, Figure 3.9).

The difference between predawn leaf water potential (ψpd) and midday leaf water potential (ψmd) should reflect the change in water status of each oak experienced in a given day. By subtracting the predawn leaf water potential from the leaf water potential that is experienced during the time with the highest evaporative demand, we can partially remove the baseline water status that may be a legacy from the day before (or soil moisture differences), and focus on daily responses (although plant-level changes to stomatal conductance will still be affected by predawn values). There were no main effects of species richness or daily average temperatures on the daily change in leaf water potential (ψmd- ψpd). There was, however, a significant interaction between species richness and daily environmental conditions. Plants growing in high diversity plots on cool days experienced net competitive effects (more negative values of ψmd- ψpd in higher diversity plots). In contrast, plants growing in the same plots, on hot days, experienced net facilitation from neighbors (less negative values of ψmd- ψpd in higher diversity plots, Table 3.3a, Figure 3.8). The daily change in plant water status was driven by plot-level differences in vapor pressure deficit (Table 3.6, Figure 3.9).

All oaks grew less in higher diversity plots (N=430, $F_{1,60}$=16.46, P=0.0001), suggesting that, integrated across the entire growing season, competition was a stronger force on plant growth than facilitation. To isolate the ecological effects of diversity on oak growth (and exclude the effects of destructive leaf harvest) we excluded oaks that were destructively sampled for leaf water potential and found that the remaining oaks grew less in higher diversity plots (N=283, $F_{1,58}$=10.35, P=0.002, Figure 3.6). Growth rates of oaks that had leaves destructively sampled grew significantly less than oaks that weren't sampled (presumably due to artificial reduction in leaf number, $F_{1,409}$=54.48, P<0.001). However, there was no difference in the effect of species richness on oak RGR for harvested and unharvested oaks (interaction term, $F_{1,405}$=0.12, P=0.73) indicating that harvest did not have a unique effect on oak RGR depending on diversity level. Oak emergence was higher in higher diversity plots ($F_{1,82}$=15.75, P=0.0002), but survival of emerged seedlings was equal across the diversity gradient ($F_{1,82}$=2.02, P=0.16).

Discussion

Our data demonstrate that microclimate was ameliorated in higher diversity grassland plots, and this microclimate effect became more important for seedling water status when daily conditions were more severe, and plants were likely to be more physiologically stressed. This amelioration translated to a dynamic balance between competitive effects of neighbors on mild days, and facilitative effects of neighbors on stressful days. Daily changes in plant water status (ψmd- ψpd) depended heavily on species richness as well as daily average temperatures. There were a threshold set of environmental conditions associated with soil moisture availability, weather conditions, and the microclimate amelioration found in higher diversity plots that determined plant water status on any given day. The sum total of these interactions resulted in a dynamic balance between competition and facilitation (Figure 3.8). When environmental conditions were mild, plot-level VPD was low, and equal across diversity treatments. Consequently, midday water loss was also low, and changes in plant water status were mostly a reflection of competition for soil water. Conversely, on the hottest days, VPD was high and was strongly ameliorated in higher diversity plots. Consequently, while competition for soil water was also occurring, it may not have been as important as reduced water loss at the leaf surface (Figure 3.9).

Microclimate amelioration and diversity

The relationship between diversity and microclimate amelioration has only been explored briefly in the past (Wright et al. 2012) and is still poorly understood. We found that lower diversity plant communities were up to 6°C hotter, and 20% drier (in terms of relative humidity), resulting in nearly 3-times higher plot-level VPD on particularly hot and dry days. Conversely, on cool rainy days, temperature and humidity varied little across the diversity gradient (Figure 3.3). The stress gradient hypothesis predicts that facilitation is more important for plants in environmentally severe conditions (Bertness and Callaway 1994). When environmental severity is strong, plants experience increased physiological stress, and this translates to stronger benefits of growing near neighbors. The stress gradient hypothesis also predicts that when environmental conditions are mild, there may still be microclimate amelioration, but it may not translate to strong facilitation. We show that as the stress gradient hypothesis predicts, environmental amelioration may be most *important* for seedlings on hot and dry days. However, we also show that the magnitude of the actual microclimate amelioration that is occurring is greater (Figure 3.3).

The amelioration of the microclimate that we observed was due partially to increased biomass production in higher diversity plots. However, biomass did not fully explain the effect of plant diversity on habitat amelioration. One explanation for this finding is that higher diversity plots may be more likely to include particularly productive drought-resistant species that are capable of high photosynthetic rates, even on particularly hot/dry days (Tilman & Downing 1994). Increased photosynthesis, water loss, and evaporative cooling at the herbaceous leaf surface may help explain the cooling and humidifying effects of herbaceous diversity, apart from biomass effects on their own. A second potential explanation is that complementarity in leaf shape and plant architecture may lead to increased light interception in higher diversity plots that cannot be explained by biomass alone (Loreau and Hector 2001). Both explanations are non-mutually exclusive and may help explain the relationship between diversity and microclimate amelioration. It seems that plants are modifying their local microclimate via shading, interception of direct radiation, and evaporative cooling, and this is happening more in higher diversity plots. However, environmental amelioration is a physical process, and may only result in facilitative effects for neighboring individuals when neighboring individuals would otherwise by physiologically stressed and therefore benefit from a cooler more humid environment.

The competition – facilitation balance

Plant water status in most ecosystems is the result of a dynamic balance between competition for soil water (inputs) and facilitation in a moderated microclimate (outputs). The balance between the relative importance of each factor may be driven by daily changes in environmental conditions. Here we show that the balance between competition and facilitation can be teased out using three components of plant water status, and measuring these components across a range of daily conditions. Predawn leaf water potential reflected competition for soil water, midday leaf water potential reflected the counteracting effects of competition for soil water and facilitation in an ameliorated microclimate, and the daily change in plant water potential reflected the facilitative effects of reduced water loss at the leaf surface.

Predawn leaf water potential is often considered a close proxy for predawn soil water potential (Cavender-Bares et al. 2007). We found that soil moisture was lower in higher diversity plots, apparently due to competition for soil water. Seasonally, soil moisture appeared to be most strongly driven by a temporal dry down that occurred between early spring and fall. This underlying decrease in soil moisture over the course of the season drove decreasing predawn leaf water potential values. This relationship reflected the strong competitive components of living close to your neighbors in high diversity plots.

In general, midday leaf water potential is controlled by baseline values from the night before (predawn measurements), water loss at the leaf surface, access to soil water reserves, and plant-level physiological adjustments. We saw no net effect of diversity on midday leaf water potential, or interactions with daily conditions. The effects of competition for soil water may have counteracted the effects of amelioration of water loss at the leaf surface over the days we studied. In our experiment, plot-level VPD was lower in higher diversity plots (microclimate amelioration) even though soil moisture was also lower (resource competition). This decrease in plot-level VPD was related to less negative leaf water potential at midday (Figure 3.9). Furthermore, the decrease in soil moisture was also related to a decrease in midday leaf water potential (Figure 3.9). While both competitive mechanisms and facilitative mechanisms seem to drive midday leaf water potential values, the counteracting effects of competition and facilitation with increasing diversity may have driven the net neutral effects of diversity observed over the course of our study.

We treated the difference between predawn leaf water potential (ψpd) and midday leaf water potential (ψmd) as a reflection of the change in plant water status attributable to a specific day. We therefore predicted that daily changes in environmental conditions, and a shifting daily balance between competition and facilitation, would be reflected most strongly in daily changes in leaf water potential (ψmd - ψpd). Our data supported our hypotheses that daily changes in oak water status seemed to reflect competition on the coolest days – daily water potential values were more negative in higher diversity plots. Conversely, we found that daily changes in oak water status reflected facilitation on the hottest days – daily water potential values were less negative in higher diversity plots.

Less negative midday leaf water potential values in higher diversity plots on the hottest days may also be the result of reduced stomatal conductance in response to less soil water, which results from intense competition (Cavender-Bares and Bazzaz 2000). Oaks growing in higher diversity plots have less access to soil water. They may respond by closing their stomates earlier and consequently having less negative midday leaf water potential values. Stomatal conductance varies greatly among species (Davies and Kozlowski 1977, Johnson et al. 2009), and ontogenetic stages (Cavender-Bares and Bazzaz 2000), but can be comparatively consistent within a single species. Oaks are desiccation tolerant (Abrams 1990, Fotelli et al. 2000) compared to co-occurring species in our experiment, and past work has shown that threshold values for midday leaf water potentials that result in reduced stomatal conductance, are often lower than -2 MPa

(Abrams 1990, Johnson et al. 2009). Some oaks maintain over 50% of stomatal conductance at values as low as -3 MPa (Johnson et al. 2009). Our data indicate that soil moisture did not relate to midday leaf water potential as strongly as vapor pressure deficit, and daily differences (ψmd- ψpd) were not directly affected by soil moisture availability at all, but strongly controlled by plot-level VPD. If the pattern were driven by less access to soil water, and the closing of stomates in response to this soil water effect, we might expect daily changes in plant water status to be closely related to soil moisture. However, both stomatal conductance and VPD are likely important, and reduced stomatal conductance in higher diversity plots on the hottest days cannot be ruled out as a mechanism that helps explain midday water status.

Scaling up to seasonal oak growth and survival

We found that overall survival of oaks was equal across diversity treatments – stress related to plant water status may never be so high as to increase mortality rates in this species. However, water relations may be affecting growth rates. We found that oak growth rates were limited in higher diversity plots, but this may simply have been due to the balance between competition and facilitation, and net competitive effects experienced by oaks over the course of a growing season at this site.

Specifically, in terms of oak water status, competition between oak seedlings and the herbaceous plant community was strong below daily temperatures of ~24°C (Figure 3.8). Above 24°C; however, competition was outweighed by the facilitative effects of microclimate amelioration. During the 2012 growing season (May 15- Sept 31) there were only 15 days with average daily temperatures greater than 24°C. Based on our current dataset, this implies that oaks may experience predominant facilitative effects of diversity for 11% of the growing season, whereas competition will dominate for the remaining 89% of the time. This estimate does not account for competition for other limiting resources, such as nitrogen, which may further tip the competition/facilitation balance towards net competition. However, the potential for facilitation to drive increased photosynthetic rates in high diversity plots on the hottest days, means that an increased number of days with average daily temperatures greater than 24°C could potentially shift this balance in the future. A shift in this balance could mean increasing oak growth rates in higher diversity communities due to facilitation.

The future

As local and seasonal environmental conditions change in the future (IPCC 2007), it is increasingly important to tease out the relative roles of competition and facilitation and how we expect both processes to operate in an altered environmental (He et al. 2013). Intensity of competition is driven by supply and demand of limiting resources, whereas facilitation may be driven by the occurrence and persistence of environmental severity, which will likely increase with increasing drought and temperature (He et al. 2013). Furthermore, because both competition and facilitation are likely operating in nearly all plant communities, tests of competition may be missing underlying facilitation (11% of days in our experiment) due to stronger overall competitive effects (89% of days). Conversely, in more severe environments, the role of competition may be overshadowed by facilitation, possibly leading to the flawed conclusion that competition is not important in severe environments (Bruno et al. 2003). By determining the contribution of both competition and facilitation and how these processes change over gradients of plant diversity and plant ontogeny, we can begin to predict more accurate plant community responses to global environmental changes.

Acknowledgements

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Table 3.1a. Separate ANOVA's for the effects of daily temperature on microclimate temperature, daily RH on microclimate RH, and daily VPD on microclimate VPD.

			Plot Temp		Plot RH		Plot VPD	
Fixed Effect	d.f.†	R^2	F	P	F	P	F	P
Species Richness	1, 74	**0.98**	46.76	**<0.0001***				
Daily Temp	1, 13451		577337	**<0.0001***				
Sp Rich x Daily Temp	1, 13461		795.7	**<0.0001***				
Species Richness	1, 74	**0.92**			75.72	**<0.0001***		
Daily RH	1, 13029				120658	**<0.0001***		
Sp Rich x Daily RH	1, 13031				468.9	**<0.0001***		
Species Richness	1, 74	**0.88**					46.76	**<0.0001***
Daily VPD	1, 13045						78302	**<0.0001***
Sp Rich x Daily VPD	1, 13051						1508	**<0.0001***

† This analysis took into account spatial variation associated with the blocked design ("Block" in the BioCON framework). In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of variation attributed to random effects.

Table 3.1b. Separate ANCOVA's for the effects of daily temperatures on microclimate temperature, daily RH on microclimate RH, and daily VPD on microclimate VPD after accounting for aboveground biomass production.

			Plot Temp		Plot RH		Plot VPD	
Fixed Effect	d.f.†	R^2	F	P	F	P	F	P
Species Richness	1, 75	**0.98**	43.9	**<0.0001***				
Daily Temp	1, 13451		577702	**<0.0001***				
Sp Rich x Daily Temp	1, 13461		792.3	**<0.0001***				
Herbaceous AGB	1, 12836		13.3	**0.0003***				
Species Richness	1, 75	**0.92**			19.01	**<0.0001***		
Daily RH	1, 13028				120633	**<0.0001***		
Sp Rich x Daily RH	1, 13030				468.1	**<0.0001***		
Herbaceous AGB	1, 12661				0.09	0.77		
Species Richness	1, 74	**0.88**					48.6	**0.004***
Daily VPD	1, 13044						78356	**<0.0001***
Sp Rich x Daily VPD	1, 13050						1517	**<0.0001***
Herbaceous AGB	1, 12367						11.6	**0.0007***

† This analysis took into account spatial variation associated with the blocked design ("Block" in the BioCON framework). In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of variation attributed to random effects.

Table 3.2. The effects of daily temperatures, day of year, and interactions with species richness, on plot soil moisture.

Fixed effect	d.f.†	F	P
Date	1, 194	136	**<0.0001***
Species Richness	1, 194	9.21	**0.003***
Daily Temp	1, 194	33.9	**<0.0001***
Species Richness x Date	1, 194	3.14	0.08
Daily Temp x Date	1, 194	51.5	**<0.0001***

Table 3.3a. The relationship between daily average temperature, and species richness on oak leaf water potential. We conducted separate analyses for predawn, midday and daily changes (diff).

	Predawn (r^2=0.18)			Midday (r^2=0.09)			Diff (r^2=0.03)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 29.5	10.01	**0.004***	1, 33.7	0.008	0.93	1, 29.4	1.94	0.17
Daily Temp	1, 185.5	3.96	<**0.05***	1, 182.6	5.19	**0.02***	1, 187.7	2.68	0.11
Sp Rich x Daily Temp	1,180.1	11.48	**<0.001***	1, 184.4	0.92	0.34	1, 181.1	5.58	**0.02***

Table 3.3b. Effects of daily temperature differences after accounting for aboveground biomass production.

	Predawn (r^2=0.21)			Midday (r^2=0.1)			Diff (r^2=0.04)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 22	8.62	**0.008***	1, 27	0.08	0.77	1, 20	2.64	0.12
Daily Temp	1, 189	3.91	**<0.05***	1, 182	4.98	**0.03***	1, 183	2.31	0.13
Sp Rich x Daily Temp	1, 184	12.1	**0.0006***	1, 180	0.82	0.37	1, 180	5.62	**0.02***
Herbaceous AGB	1, 18	0.99	0.33	1, 20	2.98	0.10	1, 46	3.24	0.09

† These analyses took into account spatial variation associated with the blocked design ("Block" in the BioCON framework) and measurements taken on individuals in the same plots over time. In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of variation attributed to block differences, this is why denominator degrees of freedom are different depending on the metric described in this table.

Table 3.4. The relationship between soil moisture and vapor pressure deficit and predawn, midday, and daily change in leaf water potential

	Predawn			Midday			Diff		
Fixed Effect	d.f.	F	P	d.f.	F	P	d.f.	F	P
Soil Moisture	1, 170	46.9	<**0.0001***	1, 176	4.96	**0.03***	1, 172	0.02	0.89
Plot-level VPD	1, 108	1.32	0.25	1, 123	7.76	**0.006***	1, 110	8.92	**0.004***

Figure 3.1. Mean monthly temperature and precipitation data for Cedar Creek Ecosystem Science Reserve from May 2012 – September 2012. Dotted line shows precipitation and solid line show temperature.

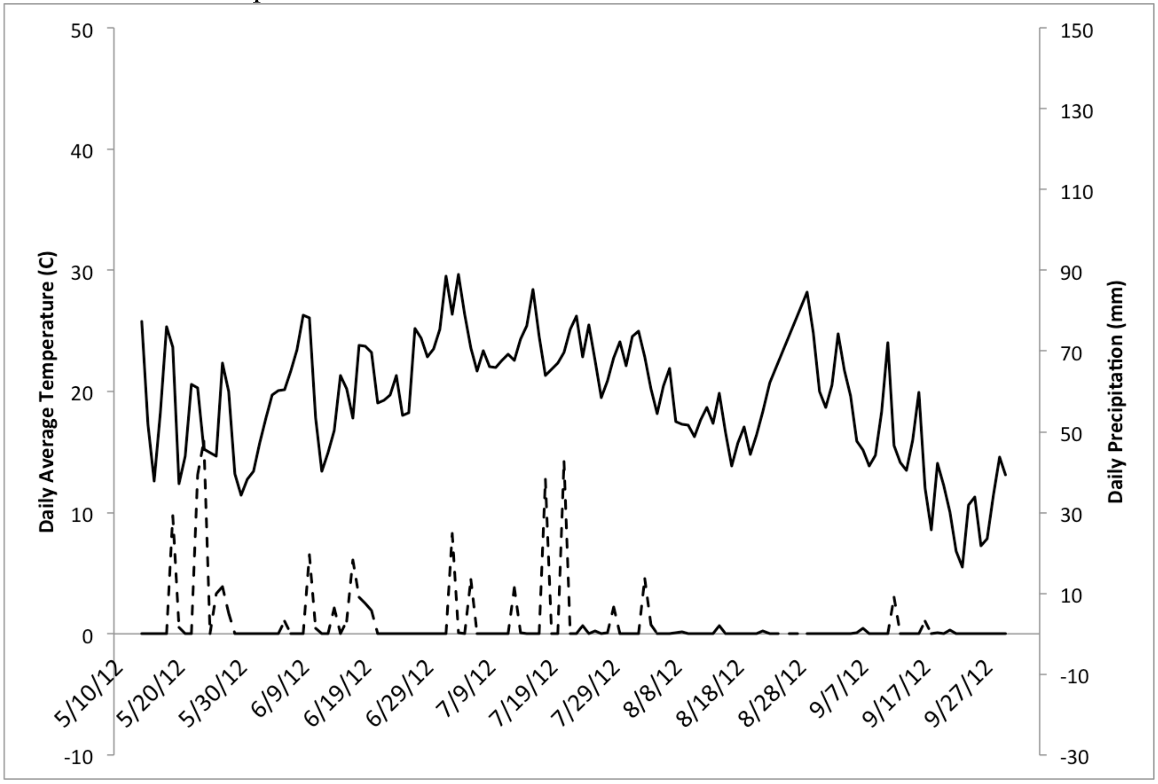


Figure 3.2. Relative humidity, daily average temperatures, calculated vapor pressure deficit and soil moisture conditions in plots where leaf water potential was measured during 2012 growing season.

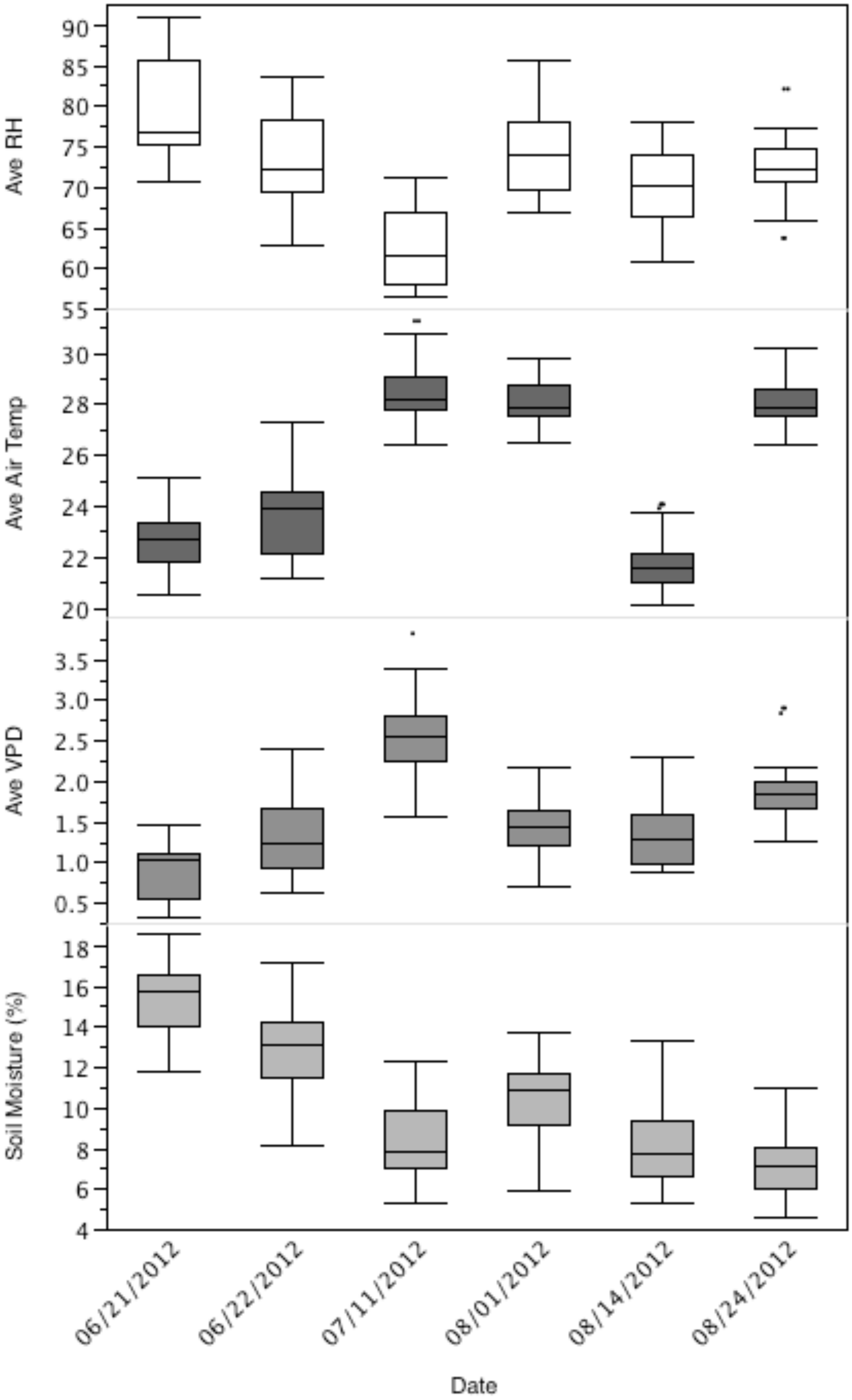


Figure 3.3. Daily average temperatures at Cedar Creek determine the magnitude of the effect of diversity on microclimate. Here we show the effects of temperature (RH and VPD are in the supplemental materials). (a) On cool days, the effect of diversity on air temperature is neutral, (b) on warmer days, higher diversity plots are slightly cooler than lower diversity plots, and (c) on hot days diversity has a strongly cooling effect on air temperature. When all days for the two years of measurement were analyzed, the effect of average daily temperature had a significant effect on how strongly diversity ameliorates the micro-climate (d).

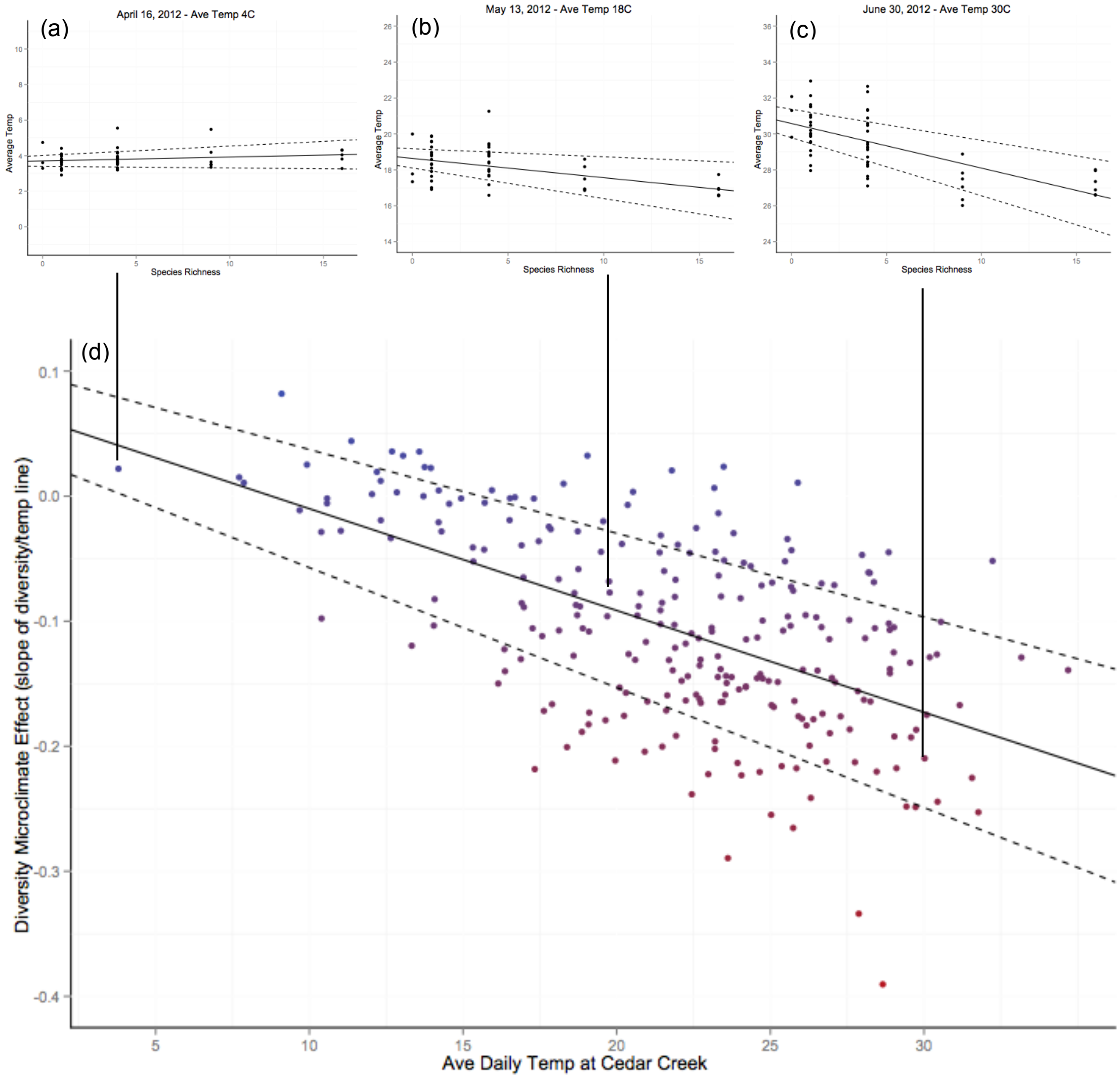


Figure 3.4. The predictive relationship between weather station data and species richness on plot-level (a) temperature, (b) relative humidity, and (c) vapor pressure deficit. These figures demonstrate the strength of the predictive relationship (actual vs. predicted).

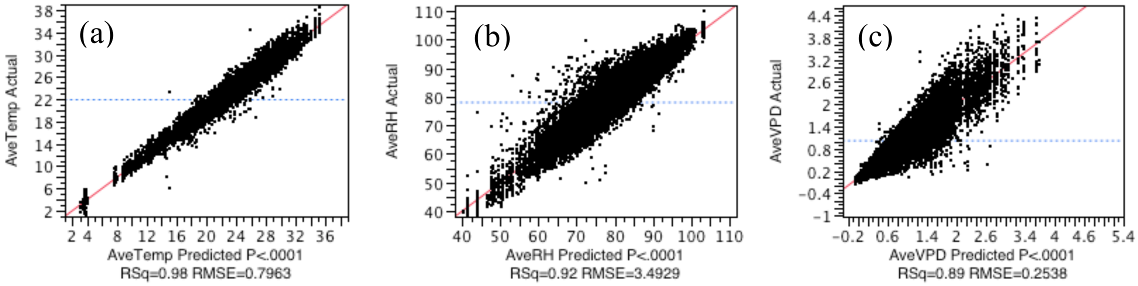


Figure 3.5. Soil moisture is lower in high diversity plots and increasingly limiting over the course of the season.

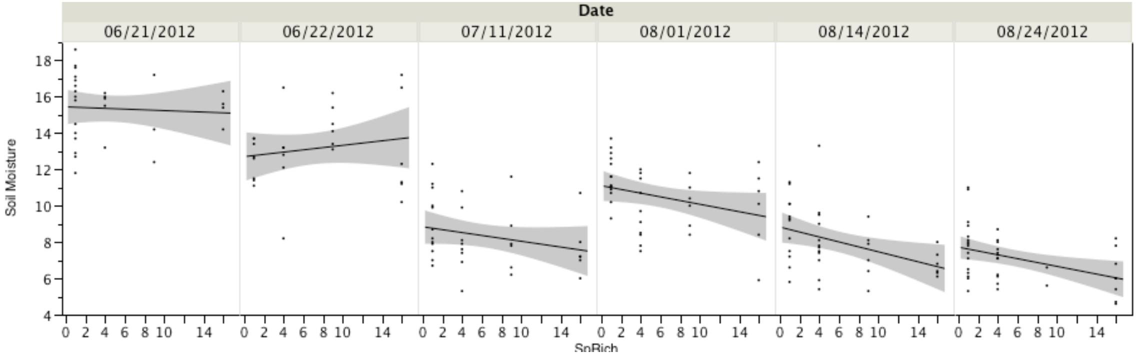


Figure 3.6. Oak growth was lower in higher diversity plots over the course of the 2012 growing season (May 28, 2012 – Aug 28, 2012).

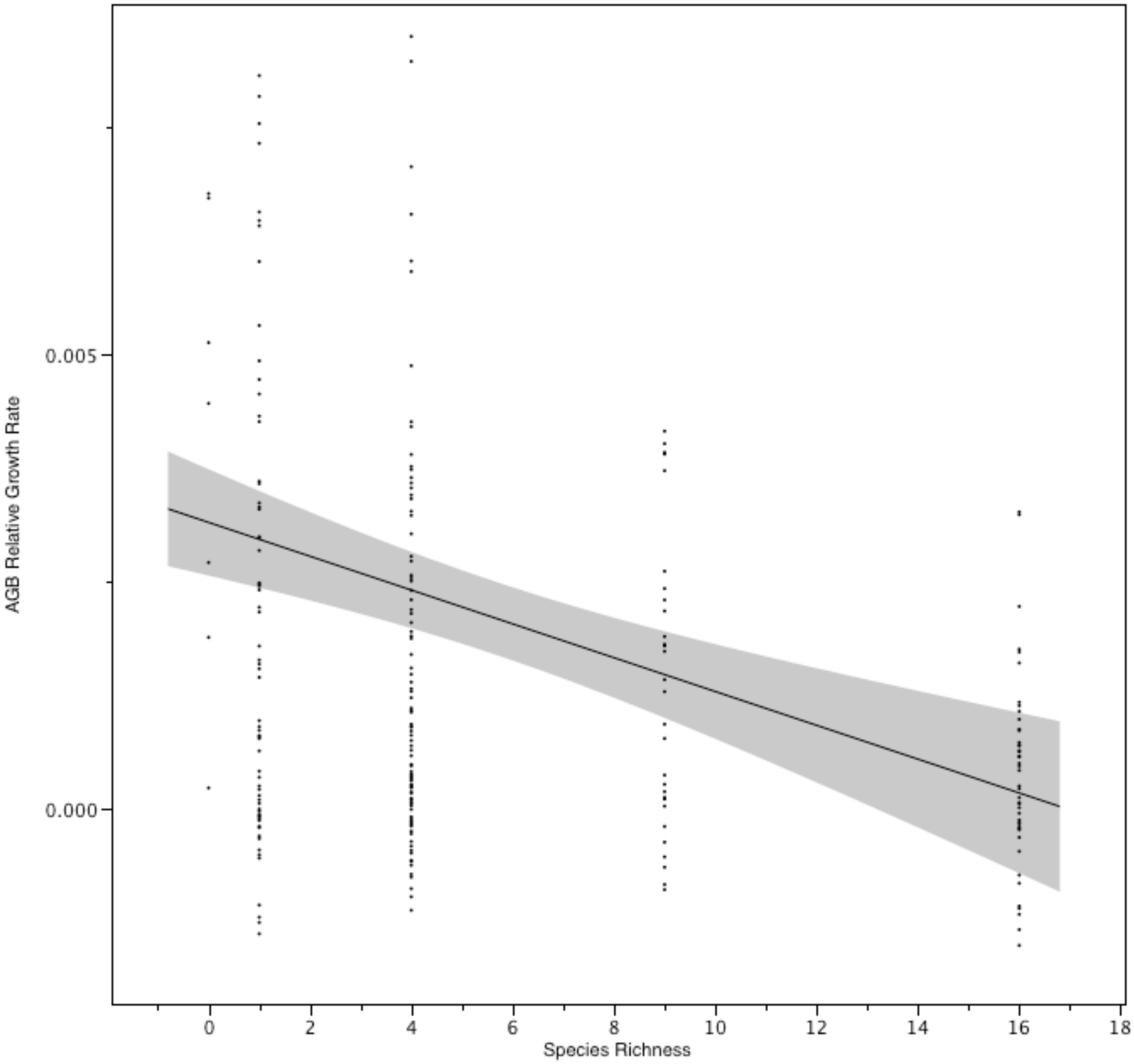


Figure 3.7. Predawn, midday, and daily difference in leaf water potential with increasing daily average temperatures. Lightest colored bars are 1-species plots, medium grey bars are 4-species plots, and for ease of visualization darkest grey bars are > 9 species (binned 9- and 16-species). The date is also displayed at the bottom for reference.

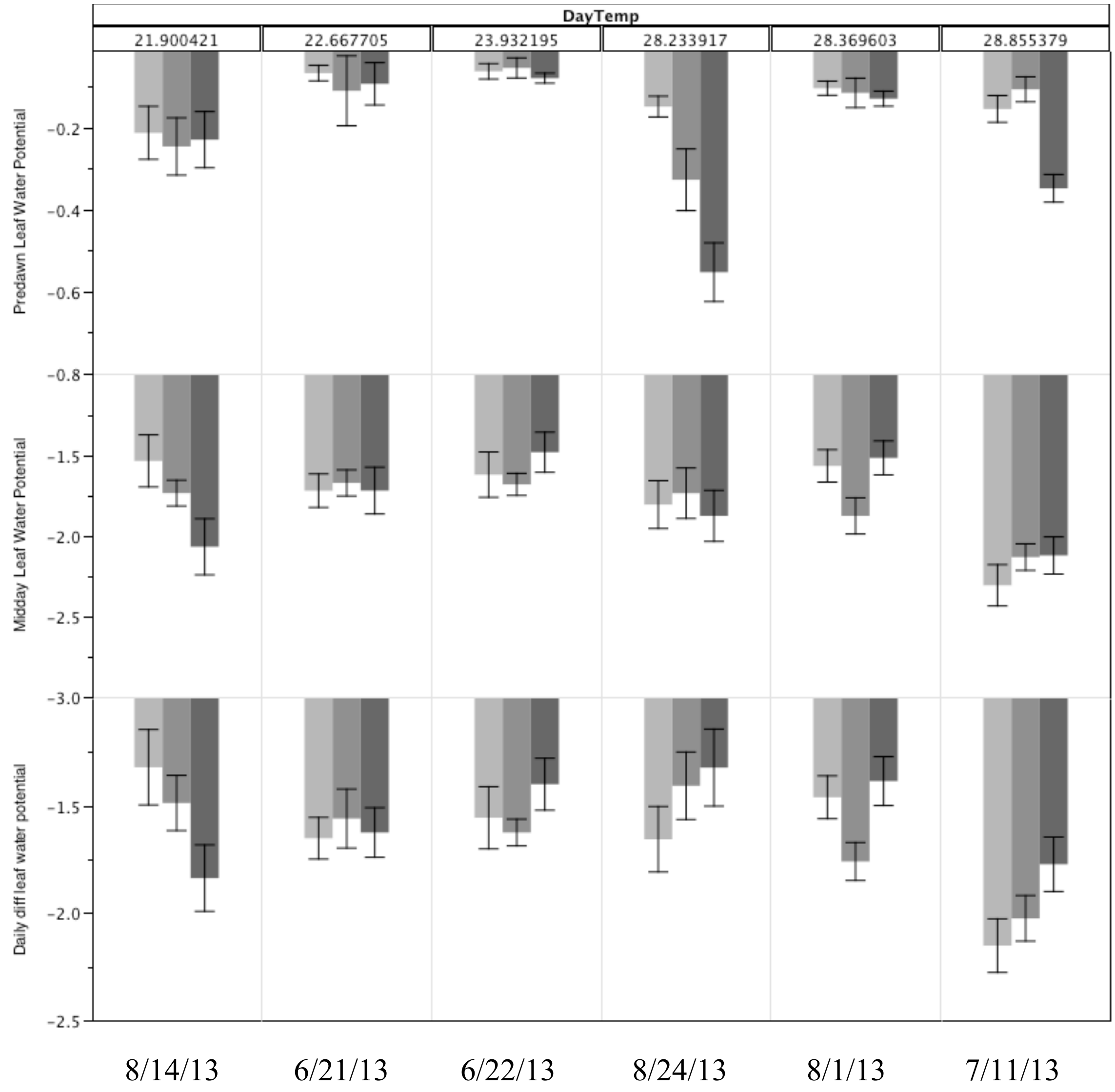


Figure 3.8. The effect of species richness on the daily difference in leaf water potential (ψmd- ψpd) depends on daily changes in average temperature.

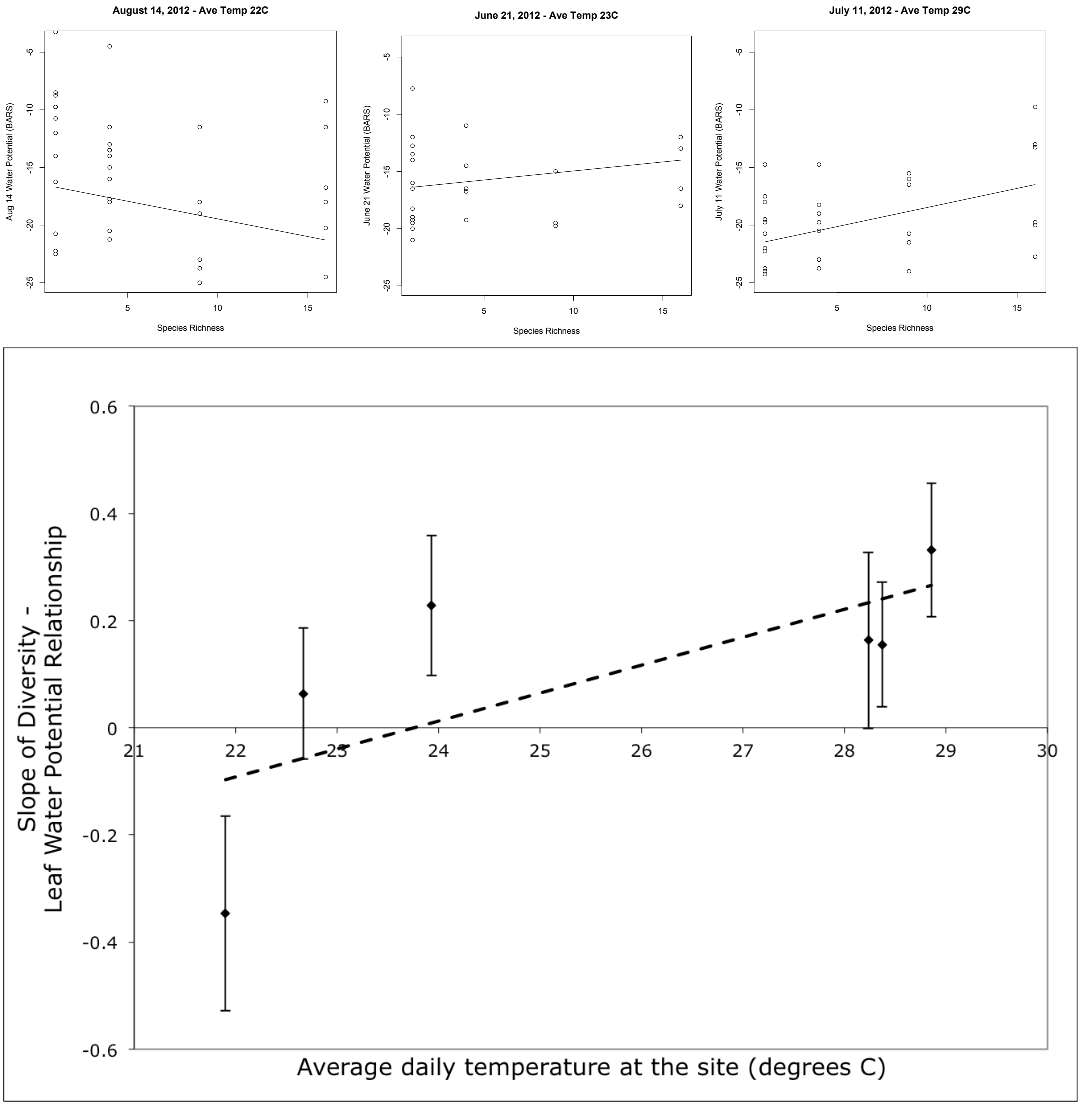
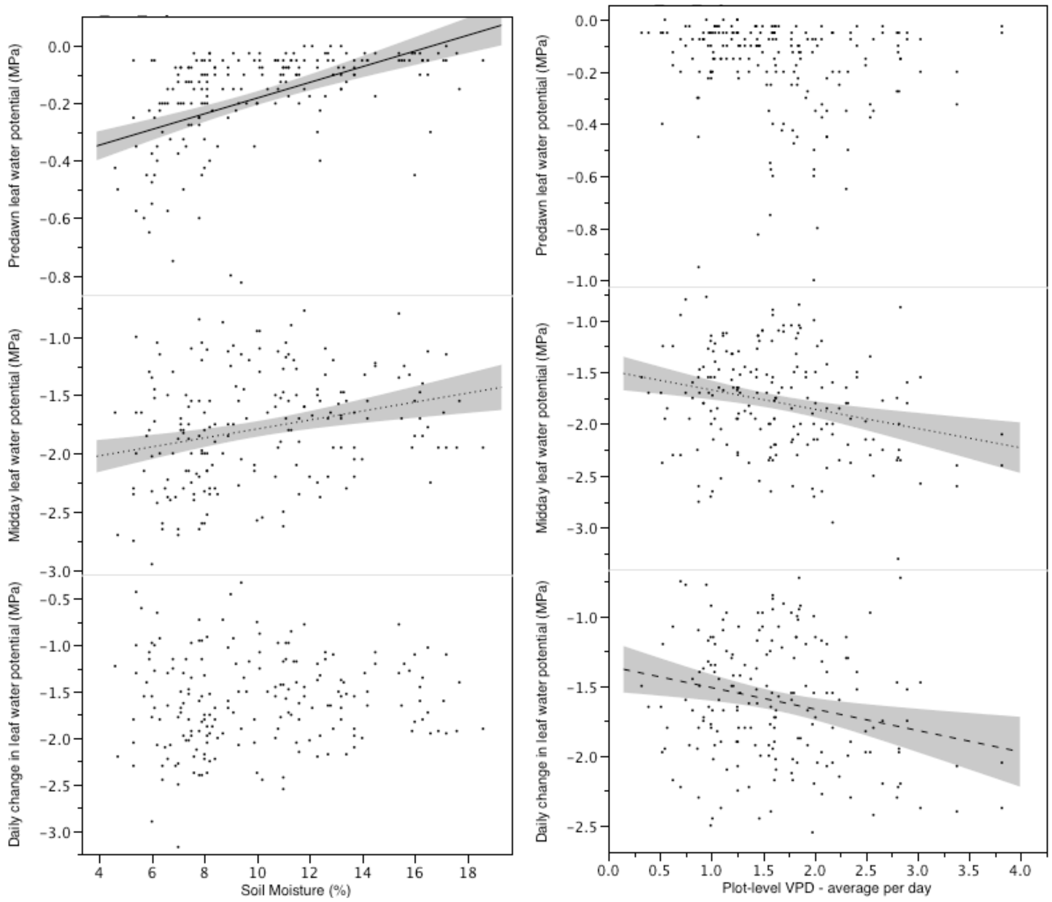


Figure 3.9. The relationship between soil water, vapor pressure deficit, and leaf water potential. Predawn leaf water potential is most strongly controlled by soil moisture, but daily change in leaf water potential is most strongly controlled by vapor pressure deficit. Lines indicate a significant relationship.



CHAPTER 4

An integrated Lotka-Volterra model for competition and facilitation: the importance of alpha

To be submitted with co-authors S. A. Schnitzer and G. Pinter

Abstract

Both competition and facilitation are important and co-occurring processes in plant communities. Competition intensity may increase with increasing productivity, whereas facilitation likely increases with increasing environmental severity. Ecologists have struggled to tease out the relative importance of competition and facilitation using experimental manipulations. Recent theoretical work predicts that there is underlying competition and facilitation in all plant communities, but whichever process is stronger may obscure the underlying contribution of the other. Here we modify a Lotka-Volterra model by manipulating the interaction term between two species (alpha) to represent varying levels of competition and facilitation. We use this model to show that well-established plant communities can facilitate colonizer growth in severe environments, but limit growth in mild environments. Further, we demonstrate that decreasing facilitation and increasing competition as plants grow, can explain long-term competitive effects observed in the vast majority of plant interaction experiments.

Introduction

Competition is one of the most well studied mechanisms in plant community ecology (Hardin 1960, Connell 1961, Tilman 1982, Goldberg and Barton 1992, Dybzinski et al. 2011). Plants compete for limiting resources and competition can be used to explain the maintenance of species diversity (Chesson 2000), competitive exclusion (Connell 1961), and biological invasions (Kennedy et al. 2002). One of the first mathematical representations of population and community level species interactions was based on competition for limiting resources (Lotka 1925), and this work has been tested extensively since its introduction. While species compete intensely for limiting resources, species coexistence can arise when unique species compete more intensely with themselves than with other species (Levine and Hille Ris Lambers 2009).

Competition intensity may vary among ecosystems and communities, but understanding the ecological drivers of competition has proven difficult. Competition may increase as a function of productivity (Grime 1977) and as a function of diversity (Fargione and Tilman 2005). Further, the relationship between diversity and productivity is complex, and may be bidirectional: productivity gradients may drive changes in species diversity (Adler et al. 2011) and increasing plant diversity may lead to increasing primary productivity (Tilman et al. 1996). While it is difficult to identify causal relationships between productivity and diversity in natural communities (Wardle et al. 2000, Jonsson and Wardle 2010, Adler et al. 2011), recent experimental manipulations have provided insight. Experimental work has consistently shown that when diversity is manipulated, primary productivity of the community increases, and this leads to increased competition intensity for plants invading higher diversity communities (Reich et al. 2001c, Tilman et al. 2001, Van Ruijven and

Berendse 2003, Roscher et al. 2005, Fargione and Tilman 2005, Isbell et al. 2011, Zhang et al. 2012). Here, we rely on theory, and data from several prominent ecological models, to develop a theoretical framework that assumes a causal relationship between productivity and competition intensity (Grime 1977, Grace 1991, Bruno et al. 2003, but see Tilman 1982) and between diversity and productivity (Tilman et al. 2001, Roscher et al. 2005, Isbell et al. 2011).

Positive interactions in plant communities (facilitation) may also help explain plant performance and community dynamics. Facilitation may occur in many systems, but be particularly important in severe environments, where plant physiological stress is strong (Bertness and Callaway 1994). In severe environments, protection from environmental stress, provided by the cool shaded microclimate of neighbors, outweighs the negative effects of competition for resources (Cuesta et al. 2010, Landero and Valiente-Banuet 2010, Jia et al. 2010, Armas et al. 2011). The stress gradient hypothesis has been tested conceptually using experimental plant removals and seed/seedling additions near neighbors across a range of environmental severity gradients (Callaway 1992, Bertness and Callaway 1994, Greenlee and Callaway 1996, Montgomery et al. 2010). However, the relationship between environmental severity, facilitation, plant performance, and community dynamics has been explored only briefly using mathematical models (Bruno et al. 2003, Bulleri et al. 2008, Chu et al. 2008).

The relative strengths of facilitation and competition may also vary as plants age and grow larger (Brooker et al. 2008). Facilitation may be a critical factor for the colonization of small plants in many environments, even those not considered to be particularly severe (Tielborger and Kadmon 2000, Miriti 2006, Cuesta et al. 2010, Farrer and Goldberg 2010, Bustamente-Sanchez et al. 2010). When colonizers are small, they are more vulnerable to water stress due to shallower root systems and relatively less carbon available in storage organs (Cavender-Bares and Bazzaz 2000, Niinemets 2010). Germination rates and early survival rates are higher in communities with greater vegetation cover when environmental conditions are severe (Cuesta et al. 2010, Farrer and Goldberg 2010, Bustamente-Sanchez et al. 2010). As colonizers grow deeper roots, they become less vulnerable to fluctuations in environmental conditions and consequently the relative importance of facilitative interactions decreases with plant size (Schiffers and Tielborger 2006). Conversely, larger plants consume greater quantities of resources per individual, and thus the relative role of competition likely increases as plants grow larger. Although demographic shifts are common in biology, and important for understanding species coexistence (Moll and Brown 2008), the shifting importance of competition and facilitation with plant ontogeny has not been explored in a modeling context.

Both facilitation and competition occur in nearly all ecosystems; however, because competition is slightly stronger in all but the harshest ecosystems, facilitation may often be overlooked (Bruno et al. 2003). Ecologists have largely ignored and otherwise struggled to tease out the relative contribution of each of these processes in experimental manipulations. Theoretical models that incorporate both competition and facilitation may provide insight into how these two processes fluctuate in natural ecosystems and contribute to individual plant performance.

Here we examine theoretical relationships between competition, productivity, facilitation, and environmental severity using a modification of a Lotka – Volterra (LV) model (Lotka 1925, Volterra 1930). Traditional implementation of LV models has been mostly restricted to understanding the importance of intra- vs. inter-specific competition over time. Intraspecific competition is represented using simple logistic growth models, where population growth rates (*r*) slow as they reach carrying capacity (*K*) due to intraspecific competition for a finite pool of resources (defined by *K*). Interspecific competition is represented by using a competition coefficient (α) to represent resource competition. A second species (N_2) has a unique growth rate (r_2), population size (N_2), and carrying capacity (K_2) and can negatively affect population growth of the first species (N_1) through positive values of α:

$$\frac{dN_1}{dt} = r_1 N_1(t)\left(1 - \frac{N_1(t) + \alpha_{21} N_2(t)}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2 N_2(t)\left(1 - \frac{N_2(t) + \alpha_{12} N_1(t)}{K_2}\right)$$

Here, we modify the alpha term to represent a range of plant – plant interactions, specifically the case where $\alpha < 0$. When α is negative, the presence of a second species ($N_{2,}$) can increase the carrying capacity of the original species (N_1), so that N_1 can grow larger than its original carrying capacity (Figure 4.1). This is a mathematical representation of facilitation – a mechanism that allows a species to grow more, or in previously inaccessible areas, due to the presence of a second species (Bruno et al. 2003). We use this theoretical framework to demonstrate two cases:

1. Productivity and diversity can facilitate plant performance when environmental conditions are severe, but limit performance when environmental conditions are mild.
2. Facilitation decreases and competition increases as plants grow in size. This leads to the increasing importance of net competition with increasing size.

Modified Lotka-Volterra interaction model

The model parameters

Traditional LV models calculate the change in population size over time between two species. For our model, we modified this conceptual framework, by considering an interaction between a single species (N_1, the colonizer) and the sum total of interactions of a community (N_2, the community). We considered the dynamics of plant biomass, as opposed to number of individuals, as plants can grow several orders of magnitude before reproductive maturity, and consequent changes in population numbers (Dybzinski and Tilman 2009). Therefore, r_1 was a species-specific intrinsic growth rate (growth – loss, instead of birth - death), N_1 was colonizer biomass, N_2 was community biomass, α_{12} represented the relative influence of the community on the colonizer, and α_{21} represented the relative influence of the colonizer on the community.

Alpha as competition/facilitation term

In traditional LV models, a positive alpha term for the effect of N_1 on N_2 (α_{12}) decreases the carrying capacity of N_2, thereby driving that group closer to carrying capacity at lower population numbers (fewer individuals can co-exist – effectively representing competition). In contrast, a negative alpha term for the effect of N_1 on N_2 allows N_2, to have a larger effective carrying capacity (more individuals can co-exist, effectively representing facilitation, Figure 4.1).

Alpha

To simplify the complex relationships that underlie plant – plant interactions we separated alpha into the sum of a series of simple and easily tractable relationships. The model treated alpha as a function of facilitative parts (α_f) and competitive parts (α_c) where

$\alpha=\alpha_c+\alpha_f$. The model treated the facilitative parts of alpha as a function of environmental severity and the competitive parts of alpha as a function of productivity.

Facilitation and severity (α_f)

We defined a relationship between facilitation (α_f) and environmental severity (s) where the absolute value of facilitation increased to a point, beyond which it decreased due to physiological constraints in the most severe environments (Figure 4.2): $b(s - \max)^2 - range$ (Holmgren and Scheffer 2010). Here, b was a scalar for the overall breadth of the curve, s was severity on the x-axis, *max* was the level of severity at which facilitation was maximized, and *range* was a measure of the depth of the curve between 0 and *max* (Figure 4.2).

Competition and productivity (α_c)

We represented competition with a simple increasing relationship between the intensity of competition (α_c) and productivity (Tilman et al. 1996), Figure 4.3). Productivity was scaled to 0-100% of total possible biomass. The relationship between competition and normalized biomass production (productivity) was a line with a y-intercept at 0, which increases with a slope of m: $\alpha_c = 0 + m * biomass$.

Community Biomass (N_2)

To model the specific scenario where an individual was colonizing a community that was at equilibrium, we incorporated community plant diversity into the model and used it to calculate potential standing biomass in an equilibrium community. Community biomass (N_2) was then treated as a static function of plant diversity (as was biomass in the competition – productivity relationship above). The traditional LV model considers two interacting populations that are changing over time (dN_1/dt and dN_2/dt from equations 1a and 1b in

Table 4.1). We substituted equation 1a (Table 4.1) with an equation that calculated equilibrium community biomass for each diversity level between 0 and 20 species: $N_2 = \frac{\max_{bio} \times d}{\theta + d}$. In this equation, N_2 was the biomass of the community, max_{bio} was the maximum biomass attained by any community in this system, d was the diversity of the community, and *theta* was the level of diversity at which half of the biomass has been produced (half saturation constant). Experimental manipulations of plant diversity have consistently demonstrated saturating relationships between diversity and productivity (Reich et al. 2001c, Tilman et al. 2001, Van Ruijven and Berendse 2003, Roscher et al. 2005), though recent analyses have demonstrated that this relationship may not saturate at such low levels over time (Reich et al. 2012). We used parameter values that were realistic for herbaceous biomass production, and a high half-saturation constant (*theta*), for a community that did not saturate over the range of diversity levels used in our simulation (Table 4.2). We then substituted Equation 1a (Table 4.1) for N_2 in the original LV model to reduce our system of equations to a single equation:

$$\frac{dN_1}{dt} = r_1 N_1(t)\left(1 - \frac{N_1(t) + \alpha_{21} * \frac{\max_{bio} \times d}{\theta + d}}{K_1}\right)$$

Colonizer age

We incorporated colonizer age as the third driver of plant interactions. We manipulated the alpha parameters above to represent decreasing facilitation and increasing competition with seedling age (Figure 4.4).

Model Parameterization

To address our first case, that productivity and diversity can facilitate plant performance when environmental conditions are severe, but limit performance when environmental conditions are mild, we parameterized our model using values for strong facilitation (α_f = -2 at 60% severity) and weak competition (α_c =1 at the highest level of productivity, Table 4.2). We ran a simulation for colonizers growing across a diversity gradient from 0 to 20 species, with a growth rate of r_1=0.1, a carrying capacity of 500 g/m^2, and an initial biomass of 0.01 g/m^2. We ran this simulation for 100 years to predict colonizer success across a range of diversity and severity conditions.

To address our second case, that competition increases and facilitation decreases over time (Tielborger and Kadmon 2000, Miriti 2006, Cuesta et al. 2010, Bustamente-Sanchez et al. 2010), we ran a 3-step simulation that involved:

(1) Alpha values representing the highest strength of facilitation/lowest competition (Figure 4.4a) for a colonizer planted at 0.01 g/m^2 (as above) for one-year, to simulate expected relationships with plant growth when seedlings are young.

(2) The biomass of the most facilitated individual (60% severity in high diversity plots) at the end of the first year, was 0.014 g/m.^{2} We used this biomass to start the simulations for years 1-3 following a model of increasing competition and decreasing facilitation with seedlings size (Figure 4.4b). We started the second simulation with an initial biomass of the most facilitated individual (0.014 g/m.^{2}), but this was only used as a comparison value to detect loss of biomass and mortality as described above. Again, when biomass after 3 years fell below the initial value (0.014), we interpreted the outcome of the simulation to be competitive exclusion.

(3) The biomass of the most facilitated individual was again used to start the simulation for the next 25 years of growth (0.0155 g/m^2).

Results and Discussion

Diversity can facilitate growth of colonizers in severe environmental conditions/ limit growth in mild environmental conditions

Using a modified version of a simple LV model, we can show how diversity can facilitate colonizer success under some conditions, but limit colonizer success under other conditions. Our model demonstrates that in conditions where competition outweighs facilitation (in mild environment, Figure 4.5a), diversity limits the success of colonizers, so that colonizers are excluded from communities. Colonizers can establish, with low growth rates, in communities of up to ~5 species (Figure 4.5). However, at all points where facilitation outweighs competition (severity > 10%), diversity facilitates colonizer growth and colonizers grow more in higher diversity communities. Further, at any single severity level, as diversity increases beyond a certain point, the competitive parts of alpha again outweigh the facilitative parts, and competition starts to limit colonizer growth (Figure 4.5). These relationships emerge from simple models of the relationship between facilitation, environmental severity, competition, productivity, and diversity.

Competition dominates as colonizers grow older

At the initial most facilitative stage of growth, we found that all colonizers, under all conditions, survived, except for seeds colonizing communities with >12 species in mild environmental conditions. These colonizers were competitively excluded from plots.

We found that following years one through three, colonizers in mild environments were competitively excluded from communities with >10 species, and even colonizers in moderate severity environments (20%) were excluded from higher diversity plots (>16 species). All colonizers in high severity environments persisted, but only experienced facilitation at intermediate levels of diversity. After that point, the competitive parts of diversity again outweighed the facilitative parts of the severe environment and we saw a humpbacked curve between increasing species diversity and colonizer growth.

We found that at the most competitive point in plant ontogeny (Figure 4.4c), which is likely the majority of the plant life cycle, all colonizers were excluded from all plots with > 8-10 species, regardless of environmental severity.

This three-step simulation shows that long-term trends may be controlled strongly by competition (Tilman et al. 1996) even if initial seedling establishment is facilitated by diversity in higher severity environments. However, it also indicates that at any given point in time, diversity/abundance of small seedlings could be higher than diversity/abundance of adults due to size-structured competition and facilitation. A decrease in abundance of stems with increasing age of the stand is consistent with successional patterns that predict a reduction in stem number with increasing stem basal area. This simulation introduces a potentially new fingerprint to detect interspecific facilitation in natural plant communities. If there is a pattern of decreasing diversity with increasing plant age, this may be due to high interspecific facilitation at the seedling stage that decreases over time. There is little evidence that this pattern would emerge based on current models of plant coexistence. While density dependent mortality predicts high diversity in the seedling layer of plant communities, due to immediate and strong susceptibility to species-specific pathogens at the smallest size classes (Hille Ris Lambers et al. 2002), there shouldn’t necessarily be a reduction in diversity beyond that stage.; although there may also be ecological drift driving the loss of rare species over time (Hubbell 2001). Further exploration of the unique role that strong facilitation in the youngest age class plays in age-structured diversity/abundance patterns, as well as overall diversity patterns, may prove a useful exploration of facilitation in the future.

From models to data: challenges with validation

We used these models as a first step in representing the underlying importance and variation in competition and facilitation along diversity and severity gradients. Experimental work has shown increased colonization success and growth near neighbors in severe environments, highlighting the importance of facilitation when environmental conditions are severe (Cuesta et al. 2010, Jia et al. 2010, Landero and Valient-Banuet 2010, Armas et al. 2011). We show here that a modified Lotka-Volterra model for competition and facilitation may be able to describe these patterns using our current knowledge of competition and facilitation in different types of environments.

The parameters that we chose for these simulations were rough estimates. For some values we based parameters on available data from long-term biodiversity experiments at Cedar Creek Ecosystem Science Reserve (Reich et al. 2012). However to make predictions using this model based on ecologically relevant values we would need access to data that is either impossible to obtain or could only be obtained using multi-decadal experiments that don’t exist. Specifically:

Long-term intrinsic growth rates (*r*) and carrying capacities (*K*) are species-specific and unknown for most species. Further, we would need the focal species to reach its carrying capacity to run robust maximum likelihood analyses to fit *K* and *r* to each species. For some herbaceous species this may be a few years, though recent data from biodiversity manipulations in grasslands indicate that carrying capacity may change over time due to nutrient concentrations in the soil that change as a function of species diversity (Tilman et al. 2012, Reich et al. 2012). For woody species it could be hundreds of years.

Parameterization of the facilitation and competition parts of alpha requires the isolation of the two parts using experimental manipulations that manipulate biodiversity and environmental severity independently in a full factorial design. In this way we could estimate how α changes as a function of diversity and environmental severity and infer underlying relationships with α_f, and α_c. But actual parameterization of α_f, and α_c would require the experimental isolation of the facilitative parts of alpha from competitive parts. An experiment of that sort does not currently exist. Finally, the carrying capacity of each colonizer likely changes as a function of environmental severity as well. Thus, long-term experiments measuring *K* of a single species across a range of environmental conditions for long periods of time may also be necessary.

Summary

Teasing apart the relative role of competition and facilitation in plant communities is exceedingly difficult. Both processes are likely operating in many communities, though measurement techniques make it difficult to tease apart the separate contributions of each, when one type of interaction likely dominates and overshadows the presence of the other (Bruno et al. 2003). This model demonstrates that diversity may limit invasion of individuals at later life history stages, but even where competition dominates, colonizer growth rates may be a reflection of both competition and facilitation. If the underlying processes that drive facilitation increase in occurrence or importance (drought, temperature events, other extreme weather events) we may expect a shift toward facilitation in future climates (Brooker 2006, He et al. 2013). The strength and importance of facilitative interactions may eventually outweigh and overshadow the importance of competition. Furthermore, we show that in scenarios where facilitation is outweighing the effects of competition, diversity can drive net increases in overall colonizer growth (Bruno et al. 2003). In scenarios where strong facilitation/weak competition persists over time, colonizer success would increase in higher diversity communities and there may be potential for a positive feedback between diversity and seedling recruitment in severe conditions (Eccles et al. 1999). As future climate change scenarios predict increasing drought, temperatures, and occurrence of extreme events (IPCC 2007), it may be important to consider these positive feedbacks between diversity and seedling establishment in the future.

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Table 4.1. Equations used in modified LV model

Name	Equation
1. Lotka-Volterra competition	a. $\frac{dN_1}{dt} = r_1 N_1(t)\left(1 - \frac{\boldsymbol{N_1(t)+\alpha_{21}N_2(t)}}{K_1}\right)$ b. $\frac{dN_2}{dt} = r_2 N_2(t)\left(1 - \frac{N_2(t)+\alpha_{12}N_1(t)}{K_2}\right)$
2. α_f	$b(s - \mathrm{max})^2 - range$
3. α_c	$0 + m * biomass$
4. α	$\alpha = \alpha_f + \alpha_c$
5. Biodiversity – productivity	$N_2 = \frac{\mathrm{max}_{bio} \times d}{\theta + d}$
6. Colonizer – community interaction	$\frac{dN_1}{dt} = r_1 N_1(t)\left(1 - \frac{\boldsymbol{N_1(t)+\alpha_{21}} * \frac{\mathrm{max}_{bio} \times d}{\theta + d}}{K_1}\right)$

Table 4.2. Parameter values for modified LV model

Parameter	Description	Value
b	*scalar for* α_f	0-1 yr = 0.00055 1-3 yr = 0.0003 >3 yr = 0.0001
max	*% severity at which facilitation is maximized*	0-1 yr = 60 1-3 yr = 70 >3 yr = 70
range	*range of variation in facilitation term*	0-1 yr = 2 1-3 yr = 1.5 >3 yr = 0.5
m	*rate at which competition increases with productivity*	0-1 yr = 0.001 1-3 yr = 0.0015 >3 yr = 0.0017
max_{bio}	*maximum biomass of the plant community*	2000
theta (θ)	*half saturation of diversity – productivity curve*	20 sp
r_1	*intrinsic growth rate of colonizer*	0.1
K_1	*carrying capacity of colonizer*	500
w0	*initial size of colonizer in model runs*	0.01

Figure 4.1. As in Figure 1, r_1 and r_2 are 0.3, K_1 and K_2 are 50, and the effect that species 2 has on species 1 (α_{21}) is 0.01. Here, to represent facilitation, the effect that species 1 has on species 2 is -0.5. A negative value of alpha causes the other species to grow beyond its original carrying capacity (50). Coexistence occurs for all negative/ facilitative values of alpha.

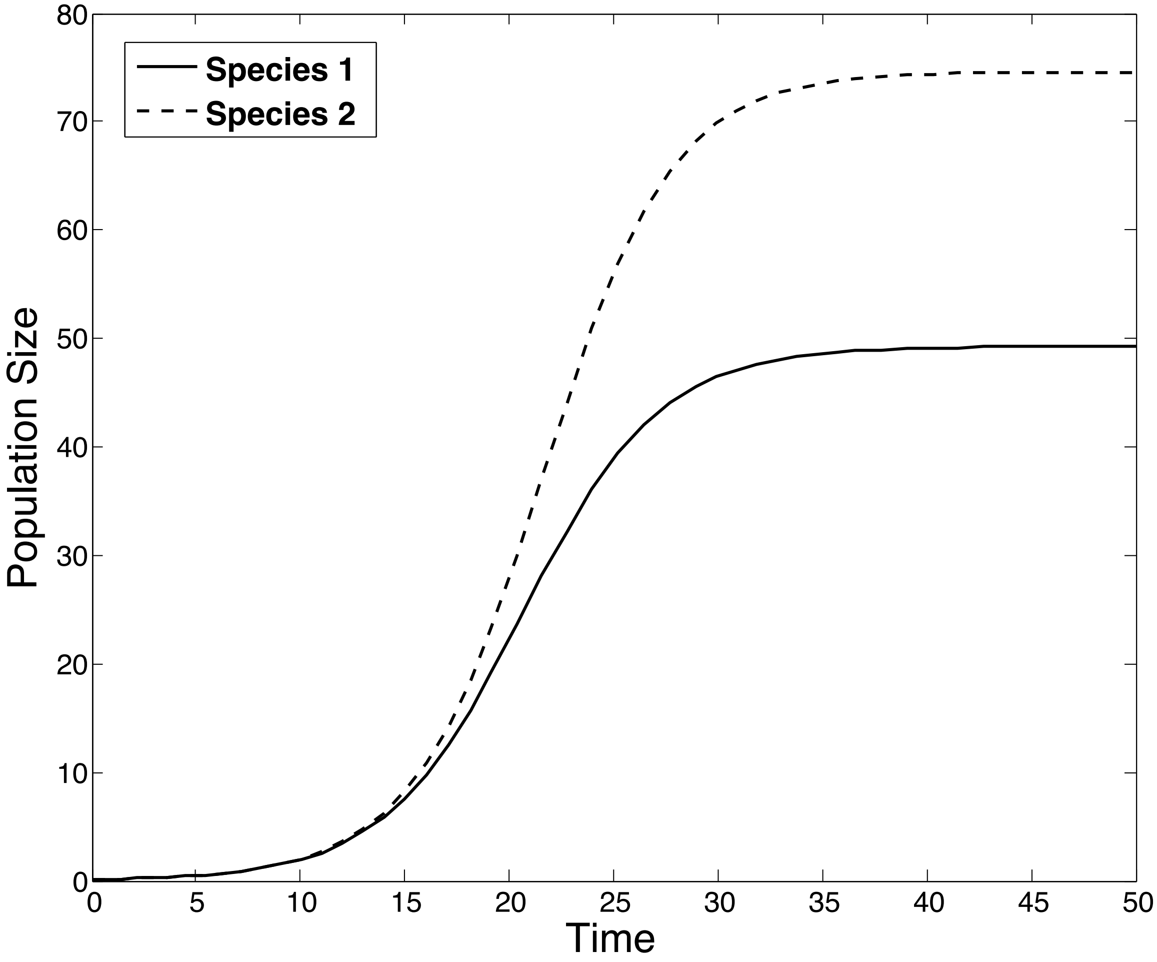


Figure 4.2. A quantitative representation of the relationship between facilitation (α_f) and environmental severity (s) where the absolute value of facilitation increases to a point, beyond which it decreases due to physiological constraints in the most severe environments. Severity is expressed as a percentage. This function is a potential representation, where b is a scalar for the overall breadth of the curve, s is severity on the x-axis, max is the level of severity at which facilitation is maximized, and range is a measure of the depth of the curve between 0 and max.

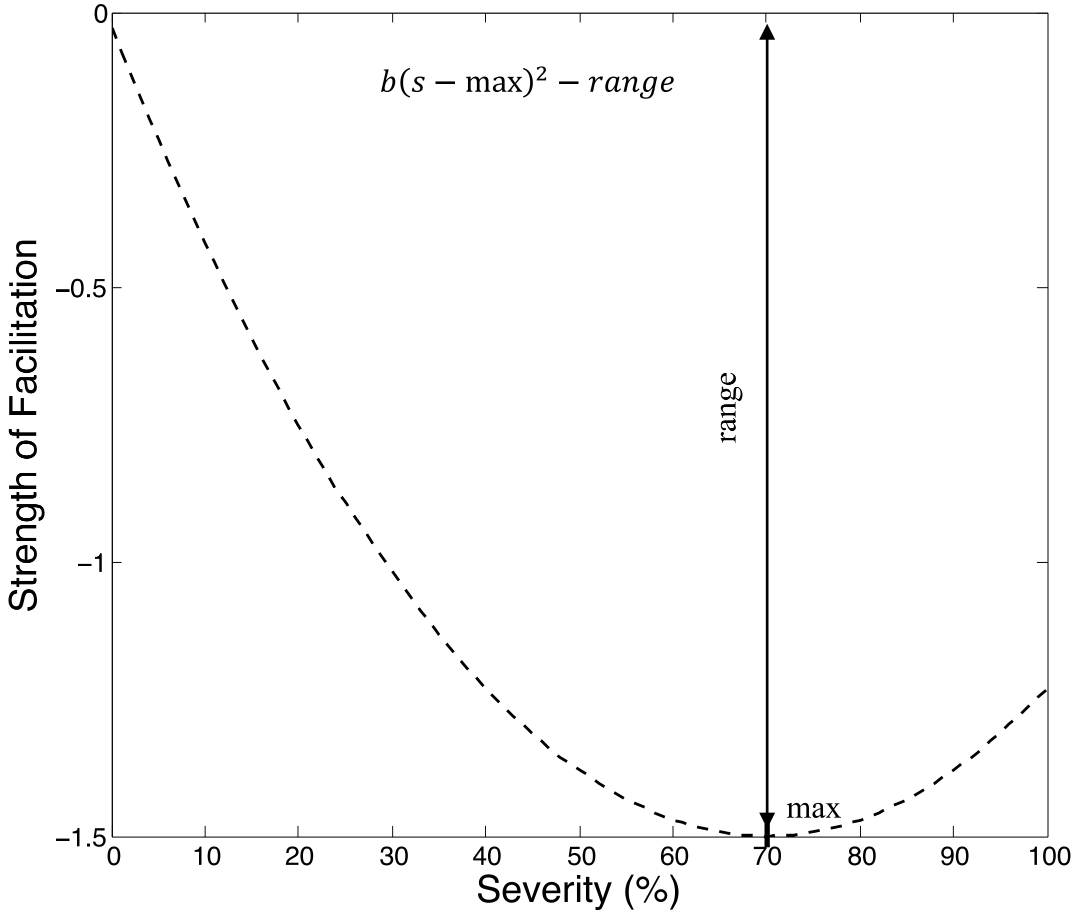
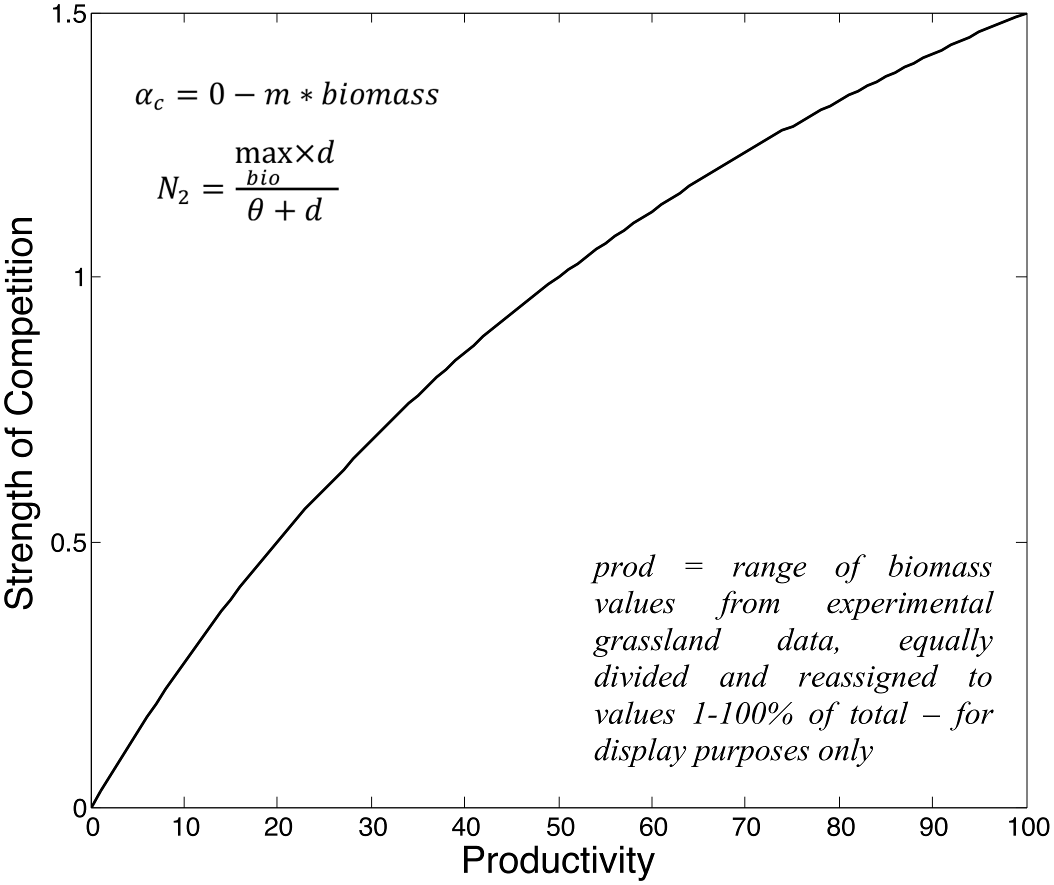


Figure 4.3. We started with a simple increasing relationship between the intensity of competition (α_c) and productivity. Productivity is scaled to 0-100% of total possible biomass (N_2). Biomass is itself a saturating function of diversity (d), defined by maximum biomass production (max_{bio}) and the level of diversity where biomass production is halfway to the maximum (*theta*). The relationship between competition and normalized biomass production (productivity) is a line with a y-intercept of 0 at 0 productivity, which increases at a rate (m).



prod = range of biomass values from experimental grassland data, equally divided and reassigned to values 1-100% of total – for display purposes only

Figure 4.4. For the purposes of demonstration, we scaled the x-axis to be increasing environmental severity from low to high, but decreasing productivity from high to low. While the exact relationship between productivity and environmental severity is unknown, we follow models from Bruno et al. (2003) for purposes of demonstration only. (a) represents strong facilitation and weak competition, (b) represents a growing colonizer with decreasing facilitation and increasing facilitation, and (c) represents the largest size class with the strongest competition and the weakest facilitation. The dotted line at 0 represents no interaction. Everything above 0 represents net competition, and everything below 0 represents net facilitation.

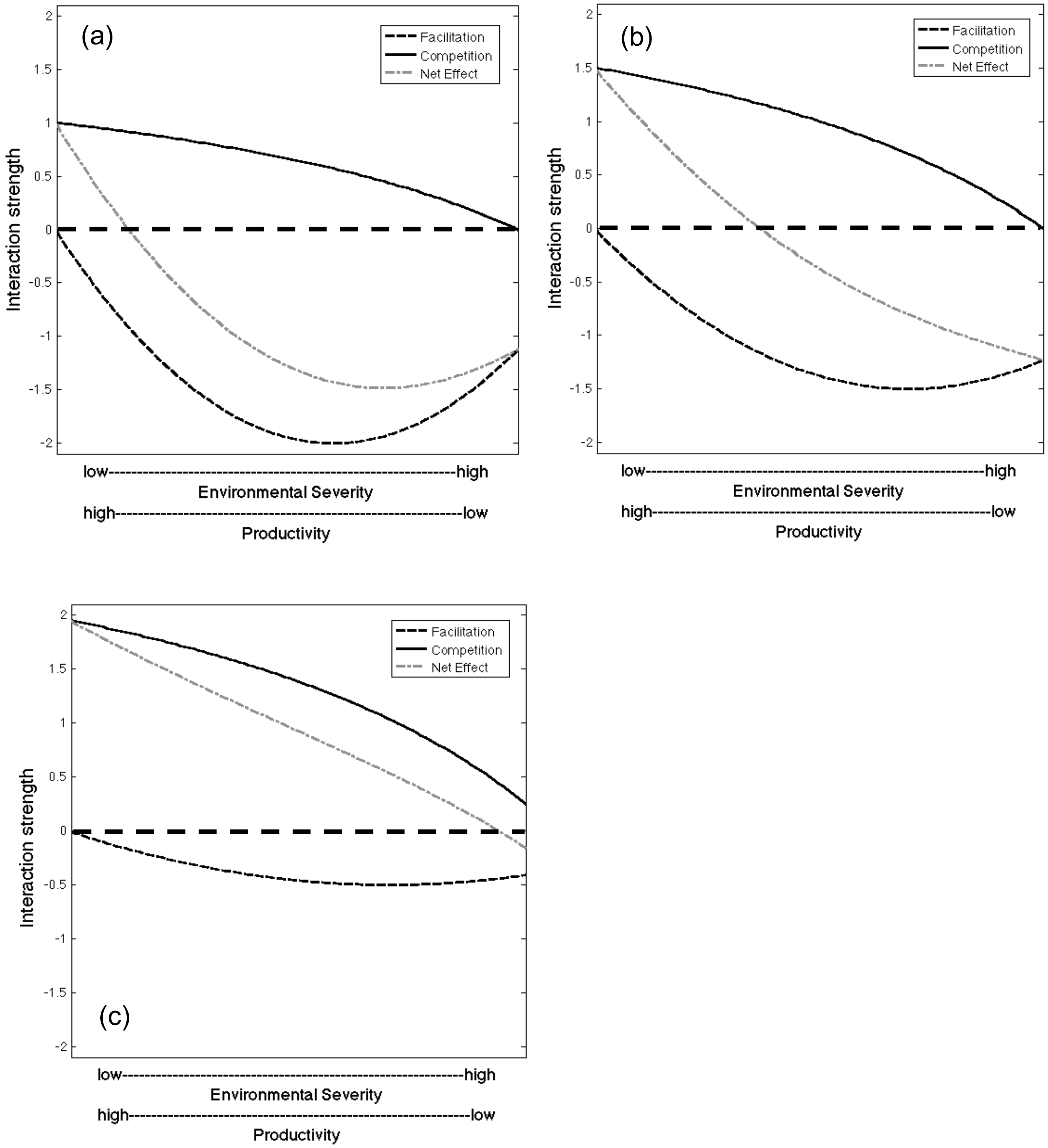


Figure 4.5. Colonizer growth increases in higher diversity plots in severe environments (up to 60%), but is limited by diversity in mild environments.

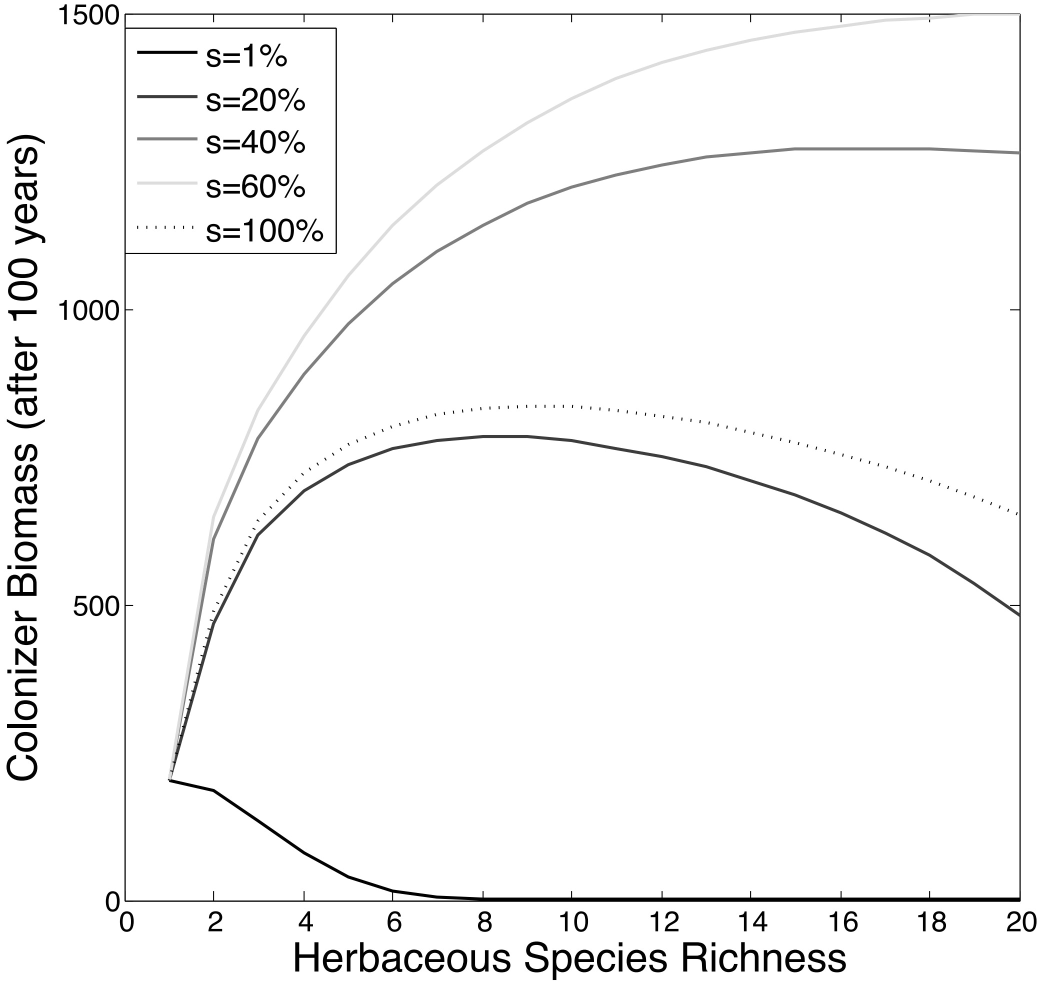
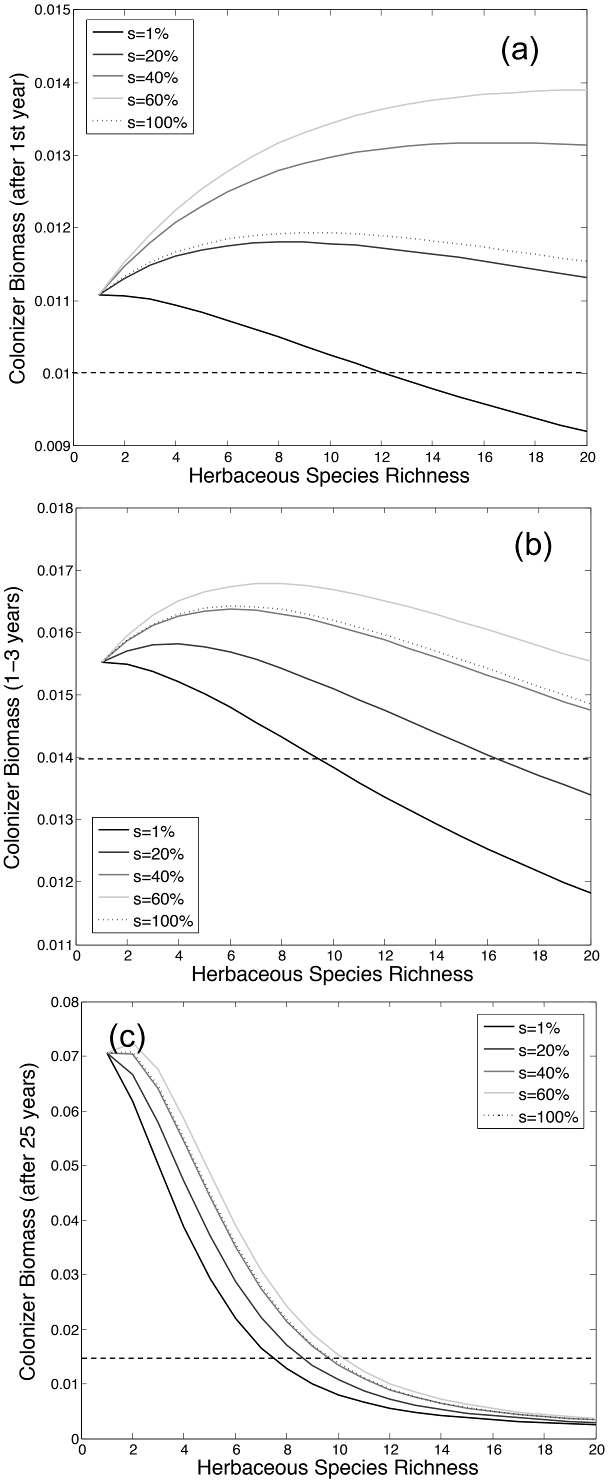


Figure 4.6. The importance of facilitation decreases and competition increases as seedlings grow in size for seedlings in their first year (a), in years 1-3 (b) and up to 25 years (c). We considered loss of biomass an indication of net loss in competition, and therefore considered those seedlings excluded. The line at which biomass was lost is indicated in all panels using a dashed line. Below that line colonizers were considered excluded.



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Appendix A. AIC scores for the base model that includes all of the main effects and interactions compared with all of the covariate submodels. The lowest AIC score represents the best-fit model. Survival AIC scores are on the left and growth AIC scores are on the right. The best-fit model is indicated with an asterisk and bold text.

Model	Akaike Information Criteria	
	Survival	Growth
Base Model	18723.08*	-688.9
Base model + total herbaceous biomass	18766.87	-681.9
Base model + BGB	18764.1	-693.1
Base model + AGB	18762.83	-680.7
Base model + percent light transmission	18753.95	-689.7
Base model + soil moisture	18753.84	-690.2
Base model + soil nitrate	18760.36	-741.6
Base model + soil ammonium	18760.31	-686.6
BM + total herbaceous + light	18795.48	-687.8
BM + total herbaceous + soil nitrate	18800.27	-722.3
BM + total herbaceous + soil ammonium	18802.98	-677.9
BM + total herbaceous + soil moisture	18796.67	-682.4
BM + BGB + light	18795.85	-692.6
BM + BGB + soil nitrate	18797.09	-724.4
BM + BGB + soil ammonium	18800.21	-688.2
BM + BGB + soil moisture	18793.94	-693.2
BM + AGB + light	18794.13	-676.4
BM + AGB + soil nitrate	18802.22	-728
BM + AGB + soil ammonium	18800.88	-677.4
BM + AGB + soil moisture	18794.27	-681.5
BM + light + soil nitrate	18797.62	-736.4
BM + light + soil ammonium	18793.88	-686.2
BM + light + soil moisture	18786.97	-690.1
BM + soil nitrate + soil ammonium	18794.58	-735.6
BM + soil nitrate + soil moisture	18787.44	-742.6*
BM + soil ammonium + soil moisture	18790.33	-687.7
BM + total herb + light + nitrate	18835.12	-717.4
BM + total herb + light + ammonium	18834.07	-682.5
BM + total herb + light + moisture	18827.68	-687.6
BM + total herb + nitrate + ammonium	18834.46	-716.2
BM + total herb + nitrate + moisture	18827.17	-723.2
BM + total herb + ammonium + moisture	18832.36	-678.3
BM + BGB + light + nitrate	18833.95	-719.2
BM + BGB + light + ammonium	18834.36	-687.1
BM + BGB + light + moisture	18827.85	-692.4
BM + BGB + nitrate + ammonium	18831.41	-718.2

BM + BGB + nitrate + moisture	18823.66	-725.3
BM + BGB + ammonium + moisture	18829.83	-688.2
BM + AGB + light + nitrate	18838.28	-726.4
BM + AGB + light + ammonium	18834.75	-673
BM + AGB + light + moisture	18827.39	-677.2
BM + AGB + nitrate + ammonium	18836.92	-721.9
BM + AGB + nitrate + moisture	18829.48	-729.2
BM + AGB + ammonium + moisture	18831.63	-678
BM + light + nitrate + ammonium	18833.77	-730.3
BM + light + nitrate + moisture	18825.8	-737.5
BM + light + ammonium + moisture	18826.49	-686.5
BM + nitrate + ammonium + moisture	18821.84	-736.6
BM + total herb + light + nitrate + ammonium	18871.66	-711.3
BM + total herb + light + nitrate + moisture	18863.15	-718.6
BM + total herb + light + ammonium + moisture	18866.45	-682.3
BM + total herb + nitrate + ammonium + moisture	18861.5	-717.1
BM + BGB + light + nitrate + ammonium	18870.36	-713
BM + BGB + light + nitrate + moisture	18861.75	-720.3
BM + BGB + light + ammonium + moisture	18866.5	-686.9
BM + BGB + nitrate + ammonium + moisture	18858.16	-719.1
BM + AGB + light + nitrate + ammonium	18875.03	-720.4
BM + AGB + light + nitrate + moisture	18866.56	-727
BM + AGB + light + ammonium + moisture	18867.76	-673.7
BM + AGB + nitrate + ammonium + moisture	18864.38	-723
BM + light + nitrate + ammonium + moisture	18862.35	-731.4
BM + total + light + nitrate + ammonium + moisture	18900.11	-712.5
BM + BGB + light + nitrate + ammonium + moisture	18898.56	-714.1
BM + AGB + light + nitrate + ammonium + moisture	18903.86	-720.9

Appendix B. The effects of herbaceous species richness and seedling size class on pine seedling survival, when individual year measurements were taken into account. Survival was measured separately for year one and year two, where those that died in the first year were not included in analyses from the second year; year was then included as a random effect in the statistical model to account for correlations among measurements on the same plot at different points in time. Seedlings survived less in higher diversity plots and small seedling survival was lower than large seedling survival.

Fixed Effect	d.f.†	F	P
Species Richness	1, 156.1	12.87	**0.0004***
Size Class	2, 284.1	30.28	**<0.0001***
Sp Richness x Size Class	2, 282.2	0.07	0.93

† This analysis took into account spatial variation associated with the blocked design ("Ring" in the BioCON framework) as well as variation associated with taking measurements on the same individuals in a single plot over time. In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom are different depending on the metric described in this table.

Appendix C. The effects of herbaceous species richness and seedling size class on seedling survival for each individual 2-week census interval. In order to avoid pseudo-replication of measurements taken on the same individuals over time, seedling ID was included as a random effect in the statistical model. There was 76% overall mortality by the final census interval; thus, sample size was too small by the end of the study to do a full analysis with the three-way interaction including census. This is the generalized linear mixed effects model equivalent of a repeated measures model. Species richness had no overall effect on seedling survival, but changed across two-week intervals, and the effect of species richness on pine survival varied from neutral to strongly competitive depending on time interval. Pine mortality was estimated based on greenness of tissue and growth in the subsequent measurements. We don't think that mortality can be reliability attributed to a particular date and therefore take little from this time-structured analysis.

Fixed Effect	d.f.†	Chi-Sq	P
Species Richness	1	1.11	0.29
Size Class	2	188.83	**<<0.0001***
Census Interval	18	957.71	**<<0.0001***
Sp Richness x Size Class	2	2.16	0.34
Sp Richness x Census Interval	18	58.84	**<0.0001***
Size Class x Census Interval	36	245.75	**<<0.0001***

† This analysis took into account spatial variation associated with the blocked design ("Ring" in the BioCON framework) as well as variation associated with taking measurements on the same individuals over time. In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of spatial variation attributed to random effects (year and ring), this is why denominator degrees of freedom are different depending on the metric described in this table. Analyses reflect likelihood ratio tests (https://stat.ethz.ch/pipermail/r-help/2011-January/265876.html)

Appendix C. Daily average relative humidity drives less negative midday and daily difference in plant water status (ψmd- ψpd).

	Predawn (r^2=0.19)			Midday (r^2=0.24)			Diff (r^2=0.13)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 19.8	7.95	**0.01***	1, 36.6	0.12	0.73	1, 33.5	2.62	0.12
RH	1, 188	7.15	**0.008***	1, 186.7	29.01	**<0.0001***	1, 189.7	17.2	**<0.0001***
Sp Rich x RH	1, 185	2.12	0.15	1, 184.9	0.0003	0.99	1, 187.9	0.35	0.56

Appendix D. Effects of all daily RH differences with aboveground biomass production included.

	Predawn (r^2=0.21)			Midday (r^2=0.25)			Diff (r^2=0.14)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 19	6.79	**0.02***	1, 30	0.32	0.58	1, 25	3.58	0.07
RH	1, 187	7.25	**0.008***	1, 187	28.1	**<0.0001***	1, 189	16.6	**<0.0001***
Sp Rich x RH	1, 184	2.18	0.14	1, 185	0.007	0.93	1, 188	0.28	0.60
Herbaceous AGB	1, 15	0.56	0.47	1, 24	2.43	0.13	1, 19	2.76	0.11

† These analyses took into account spatial variation associated with the blocked design (“Block” in the BioCON framework). In the linear mixed effects model framework, denominator degrees of freedom “float” based on the degree of variation attributed to block differences, this is why denominator degrees of freedom are different depending on the metric described in this table.

Appendix E. Daily average vapor pressure deficit, species richness, and interactions drive predawn leaf water potential. Midday and diff in plant water status (ψmd- ψpd) become more negative with increasing VPD.

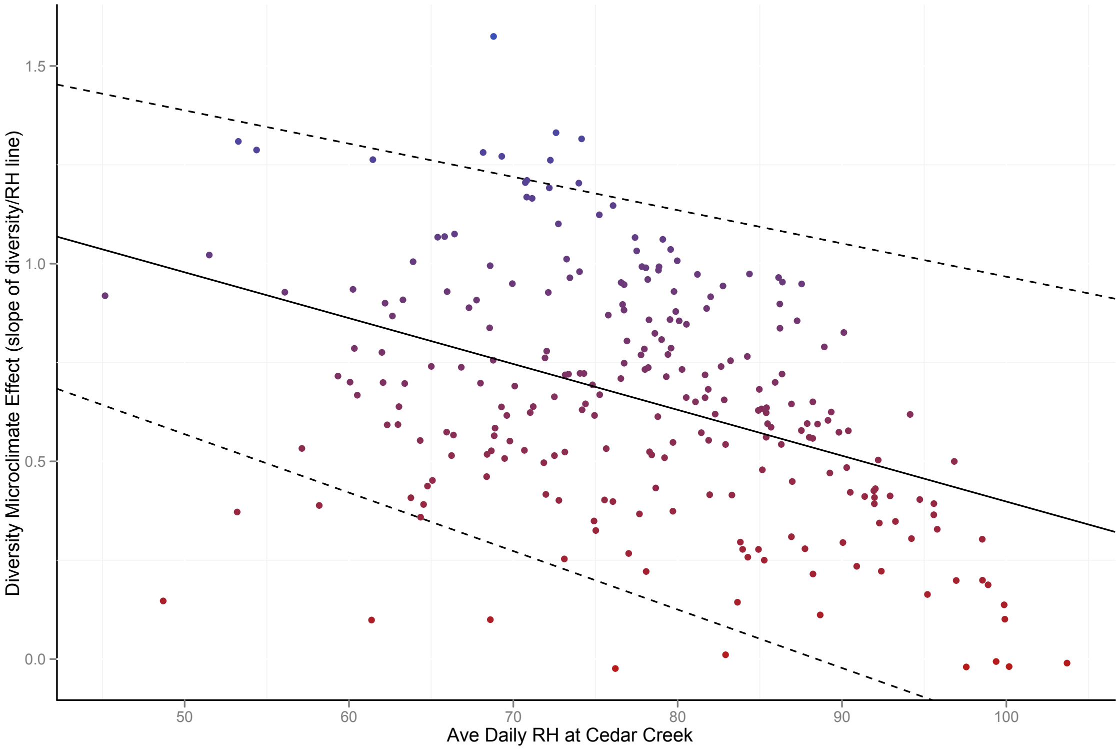
	Predawn (r^2=0.23)			Midday (r^2=0.23)			Diff (r^2=0.12)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 22.5	8.85	**0.007***	1, 35.9	0.05	0.81	1, 32.3	2.32	0.14
VPD	1, 190.1	11.1	**0.001***	1, 188.2	27.8	**<0.0001***	1, 189.9	14.53	**0.0002***
Sp Rich x VPD	1, 189.3	10.3	**0.002***	1, 184.9	0.14	0.71	1, 189	2.97	0.09

Appendix F. Effects of all daily VPD differences with aboveground biomass production included.

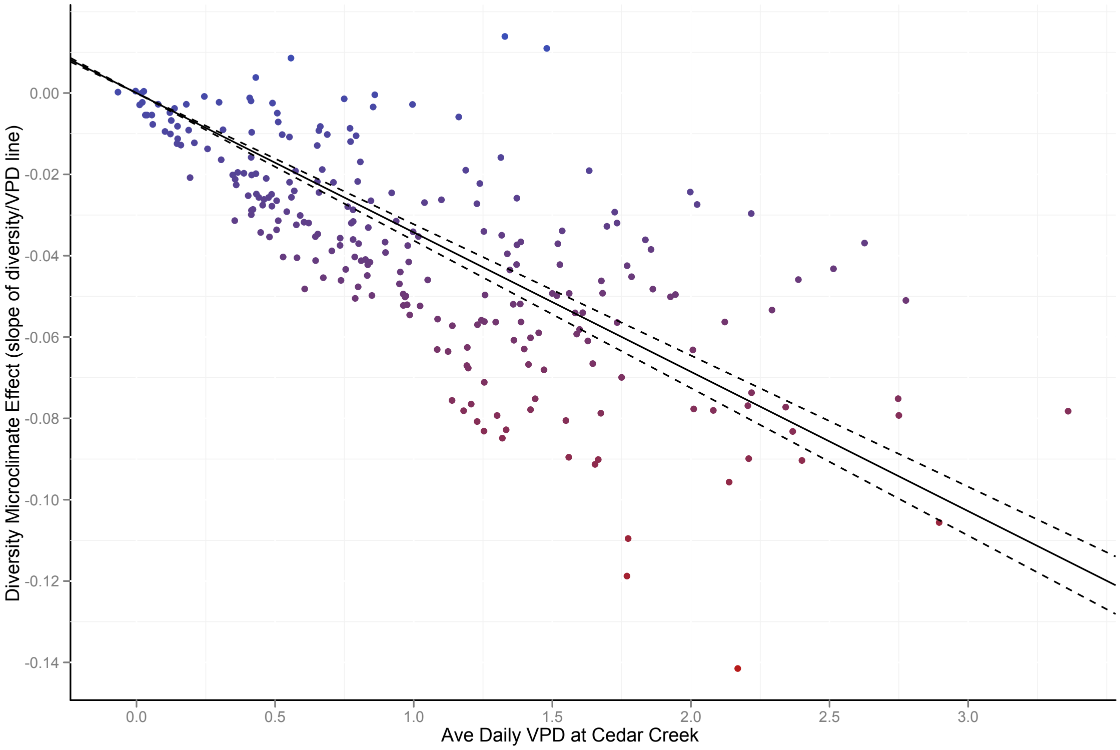
	Predawn (r^2=0.25)			Midday (r^2=0.24)			Diff (r^2=0.13)		
Fixed Effect	d.f.†	F	P	d.f.†	F	P	d.f.†	F	P
Species Richness	1, 21	7.63	**0.01***	1, 30	0.20	0.66	1, 24	3.15	0.09
VPD	1, 189	11.0	**0.001***	1, 188	26.9	**<0.0001***	1, 188	13.87	**0.0003***
Sp Rich x VPD	1, 188	10.7	**0.001***	1, 188	0.09	0.77	1, 188	2.81	0.10
Herbaceous AGB	1, 17.3	0.86	0.37	1, 23.5	2.37	0.14	1, 17	2.58	0.13

† These analyses took into account spatial variation associated with the blocked design ("Block" in the BioCON framework). In the linear mixed effects model framework, denominator degrees of freedom "float" based on the degree of variation attributed to block differences, this is why denominator degrees of freedom are different depending on the metric described in this table.

Appendix G. Daily effects of species richness and site-level RH on plot-level RH.



Appendix H. Daily effects of species richness and site-level VPD on plot-level VPD.



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Cowles, JM, Clark, AT, Kosmala, M., Whittington, HR, Wragg, PD, **Wright,** AJ, Powers, JS, and Tilman, D. *In process*. Interactive effects of warming and diversity on grassland community composition and ecosystem productivity.

Strini, J, Barry, K, Kruse, H, Lauko, I, Pinter, G, Reich, PB, Schnitzer, SA, Tilman, D, Yang, K, **Wright, A**. *In process.* The importance of spatial scale in the study of biodiversity.

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Other Publications:

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Conference Abstracts:

Cowles, JM, Clark, AT, Kosmala, M., Whittington, HR, Wragg, PD, **Wright,** AJ, Powers, JS, and Tilman, D. Interactive effects of warming and diversity on grassland community composition and ecosystem productivity. 2012 Annual Meeting for the Ecological Society of America. Portland, OR.

Miller J, A Atkinson, R Waara, M Patterson, A **Wright**, B Witcher, K Whelan. 2006. Trends, Power and Sample Design: Lessons Learned During 7 Years of Coral Reef Monitoring. Protocol development to monitoring implementation: Lessons learned from the National Park Service's South Florida/ Caribbean Inventory & Monitoring Network coral reef monitoring program, Eos Trans. AGU, 87(36), Ocean Sci. Meet. Suppl., Abstract OS46I-02.

Strini, J., Yang, K., Kruse, H., **Wright**, A.J. The importance of spatial scale in the study of biodiversity. 2012. Oral Presentation. National Institute for Mathematical and Biological Synthesis, Undergraduate Research Conference. Knoxville, TN.

Tobin, M., **Wright,** A., Mangan, S., and Schnitzer, S. 2008. The effects of liana infestation on water relations and sap flow in a tropical forest. Annual Meeting for the Ecological Society of America. Milwaukee, WI.

Wright, A. 2006. Virgin Islands National Park. 3D Visualizations for Resource Management. 2006 ESRI International User Conference Map Gallery. ESRI International User Conference

Wright, A., Schnitzer, S.A., Dickie, I., Gunderson, A., Mangan, S., and P.B. Reich. 2009. Diversity facilitates woody seedling establishment. Annual Meeting for the Ecological Society of America. Albuquerque, NM.

Wright, A., Tobin, M., Mangan, S., and Schnitzer, S. 2010. Lianas and saplings have similar effects on seedling performance in a tropical forest understory. Annual Meeting for the Ecological Society of America. Pittsburgh, PA.

Wright, A., Reich, P.B., and S. Schnitzer. 2012. Plant facilitation: the importance of diversity and seedling ontogeny. 2012 Annual Meeting for the Ecological Society of America. Portland, OR.

Research Presentations:

April 1, 2011, University of Minnesota Forest Ecology seminar series, *"Plant facilitation: models, experiments, and observations."*

May 6, 2011, University of Minnesota Forest Ecology seminar series, *"Competition and facilitation in Minnesota grasslands."*

October 27, 2011, UMN Forest Ecology seminar series, *"Bayesian Statistics and probability distributions."*

February 2012, UMN Dave Tilman lab group, *"Facilitation in the biodiversity and climate experiment."*

February 21, 2012, Museo Nacional de Ciencias Naturales, Madrid, Spain, *"Plant facilitation: models, experiments, and observations."*

March 2, 2012, Wageningen University, Netherlands, *"Plant facilitation: models, experiments, and observations."*

November 2012, UW- Eau Claire Invited Speaker for departmental seminar series

Professional Societies:

Ecological Society of America	**2007- Present**
Sigma Xi, the Scientific Research Society	**2010- Present**
Phi Kappa Phi Honor Society	**2010- Present**
Golden Key International Honor Society	**2010- Present**
American Geophysical Union, Spilhaus Award Committee	**2013- Present**