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Community invasibility: from pattern to process across multiple spatial scales in an old-field ecosystem

A Dissertation
Presented for the
Doctor of Philosophy
Degree
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Lara Amaral Goncalves Souza
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Dedication

To my husband:
For his support, love and his patience.

To my family and friends:
For field and editorial work, but most importantly great conversations.

To my co-advisors:
For believing in me, for challenging me and for inspiring me.

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Abstract

Biological invasions threaten biodiversity, and understanding the factors that influence a community's susceptibility to invasion informs both management of invasive species and conservation of biodiversity. The biotic resistance hypothesis postulates that communities with greater number of competitors, predators and/or pathogens will resist biological invasions. The underlying mechanism of biotic resistance, in the realm of competition, is that in species-rich communities harbor fewer open niches for introduced species to colonize therefore decreasing the probability of invasion. My dissertation research evaluated the role of native species diversity, as well as other biotic, abiotic and landscape factors shaping exotic species richness at multiple spatial scales in an old-field ecosystem. I found that old-field communities with greater native diversity are more invasible, having greater exotic richness, at multiple spatial scales. Additionally, I investigated the role of native species diversity, biotic and abiotic factors shaping patterns of abundance by an invasive species, *Lespedeza cuneata*, at multiple spatial scales. *Lespedeza* is a rank one invasive species in several U.S. states including Tennessee due to its potential ecological impacts. I found *Lespedeza* abundance to be negatively associated with the abundance of dominant species, as well as with the abundance of other N-fixing species (mostly native to North America). I then conducted two field experiments which addressed the role of dominant taxa identity, in particular, the genera *Solidago* and *Verbesina* affecting old-field community structure and invasibility by *Lespedeza* (i.e. establishment). The second experiment investigated the role of resource availability structuring an old-field community and early establishment by *Lespedeza*. Overall, my

findings suggest that native species diversity, abiotic and landscape factors influence multiple spatial scales.

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CHAPTER 1

An introduction: community invasibility across space in old fields

Diversity-invasibility across spatial scales

Biological invasions alter community structure and subsequently affect ecosystem processes (Mack et al. 2000, Levine et al. 2003). Thus understanding the role of biotic and abiotic factors associated with community invasibility will provide ecologists and land managers with more effective management tools to combat the successful establishment by exotic species. My dissertation addresses how dominant species and resource availability interact to shape the structure and invasibility of old-field communities through time. In addition, I investigate how resources and native species predict exotic richness across spatial scales.

At small spatial scales (1-m^2), many studies in invasion ecology have documented a negative relationship between native species diversity and the establishment or abundance (estimated as foliar cover) of exotic species (Fridley et al. 2007). Such findings have provided support for the biotic resistance hypothesis posed by Elton (1958) which stated that species-rich communities are more resistant to invasions than species-poor ones. At larger spatial scales (e.g., Stohlgren et al. 1999, Brown and Peet 2003, Fridley et al. 2007), several studies have recorded positive relationships between native diversity and exotic diversity, generating a "invasion paradox". In chapter 2, I investigate the relationship between native and exotic richness across 1-m^2 plots, 50-m^2 transects, and entire old fields testing whether favorable environments or spatial heterogeneity shape native and exotic richness in local old-field communities. I find that native and exotic species richness relationships (NERR) are positively related across spatial scales and that within old fields, total foliar cover is associated with positive NERR. I conclude that certain productive communities promote positive associations between native and exotic species at local 1-m^2 plot scales.

Community invasibility can be also determined by the presence and identity of dominant species which can use a greater proportion of available resources in natural communities (Gurevitch and Unmasch 1989, Wardle and Barker 1997, Wardle et al. 1999, Diaz et al. 2003). As a result, dominant species can reduce resources otherwise available for the successful colonization of introduced species. In fact, in some studies dominant species have been shown to hinder invasions, whereas others show that dominant species might facilitate invasions (Crawley et al. 1999, Smith and Knapp 1999, Dukes 2002, Smith et al. 2004, Wilsey and Polley 2002, Emery and Gross 2006). In chapter 3, I address the role of two co-dominant forb species (*Solidago altissima* and *Verbesina* spp.) on the structure of old-field communities and on the early establishment by an invasive species (*Lespedeza cuneata*). *Solidago* and *Verbesina* together comprise 40 % of the total aboveground biomass in old-field communities in the area (Souza, In review) and therefore can affect both the structure and invasibility of such communities. I find that both *Solidago* and *Verbesina* reduce subdominant evenness, diversity and biomass, facilitating the early establishment by *Lespedeza*. I conclude that the loss of the two co-dominant forbs, *Solidago* and *Verbesina*, may alter community and ecosystem dynamics in old fields, subsequently altering susceptibility of old fields to invasions.

Early establishment by invasive species may also be mediated by resource availability. Recent studies have shown increases in soil nutrients to deter population growth of *Lespedeza* in old-field communities (Ritchie and Tilman 1996, Brandon et al. 2004, Sanders et al. 2007), but little is known on how resources may shape seedling dynamics. In chapter 4, I investigate the role of resource availability on community invasibility asking how increases in soil nitrogen (N) availability may affect the initial establishment *Lespedeza* of and whether similar factors shape patterns of *Lespedeza* abundance across spatial scales in old-field communities. I find that in N-

added plots, *Lespedeza* seedling establishment and persistence are greatly reduced compared to control and N-reduced plots. Additionally, I show that N-added plots stimulate aboveground biomass, reducing light availability in the canopy of old-field communities and thereby likely affecting emerging *Lespedeza* seedlings. Surprisingly, *Lespedeza* abundance, across spatial scales, is not associated with resource availability. Biotic factors, such as aboveground biomass, biomass of N-fixers and biomass of dominant species affect *Lespedeza* abundance at different spatial scales. I conclude that community invasibility by *Lespedeza* in old fields is associated with both biotic and abiotic factors during early establishment, but population growth is mostly shaped by biotic factors across spatial scales.

Taken together, my dissertation research provides additional support to the notion that both biotic and abiotic factors strongly influence the structure of natural communities and affect their susceptibility to biological invasions. Moreover, the relative importance of biotic and abiotic factors affecting community invasibility will likely change with spatial scale, as well as with stage of invasion.

List of References

List of References

Brown, R.L., and Peet, R.K. 2003. Diversity and invasibility of southern Appalachian plant communities. *Ecology* 84:32-39

Brandon, A.L., Gibson, D.J., and Middleton, B.A. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native Lespedeza cuneata (Dum. Cours.) G. Don. *Biological Invasions* 6:483-493.

Crawley, M.J., Brown, S.L., Heard, M.S., and Edwards, G.R. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2:140-148

Diaz, S., Symstad, A.J., Chapin, F.S., Wardle, D.A., and Huenneke, L.F. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution 18:140-146*

Dukes, J.S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* 12:602-617

Elton, C.S. 1958. The ecology of invasions. Methuen, London, UK.

Emery, S.M., and Gross, K.L. 2006. Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115:549-558

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., and Von Holle, B. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88:3-17

Gurevitch, J., and Unnasch, R.S. 1989. Experimental removal of a dominant species at 2 levels of soil fertility. *Canadian Journal of Botany-Revue Canadienne De Botanique* 67:3470-3477

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., and Lavorel, S. 2003.

Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:775-781

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz,F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710

Ritchie, M.E. and Tilman, D. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* 76:2648-2655

Sanders, N.J., Weltzin, J.F., Crutsinger, G.M., Fitzpatrick, M.C., Nunez, M.A., Oswalt, C.M., and Lane, K.E. 2007. Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88:2383-2391

Smith, M.D., and Knapp, A.K. 1999. Exotic plant species in a C-4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* 120:605-612

Smith, M.D., Wilcox, J.C., Kelly, T., and Knapp, A.K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106:253-262

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25-46

Wardle, D.A., Barker, G.M. 1997. Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. *Oikos* 80:470-480

Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N., Ghani, A. 1999. Plant removals in perennial grassland: Vegetation

dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* 69:535-568

Wilsey, B.J., Polley, H.W. 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5:676-684

CHAPTER 2

Exotic richness across spatial scales: some communities with high native richness are highly invasible

Abstract

Biological invasions threaten biodiversity, and understanding the factors that influence a community's susceptibility to invasion informs both management of invasive species and conservation of biodiversity. In this study, we examined the relationship between native and exotic richness across spatial scales and asked what factors alter their relationship, and identified biotic, abiotic and landscape factors that accounted for patterns of exotic species richness across spatial scales, from 1-m^2 plots to entire old fields. We found that native and exotic richness were positively related across all spatial scales, with the strength of their relationship increasing at larger spatial scales. A gradient in foliar cover, not productivity, across communities altered the relationship between native and exotic plant species at the 1-m^2 plot scale. In fields with lower foliar cover, native and exotic richness were negatively related whereas in fields with higher foliar cover native and exotic richness were positively related. Moreover, 1-m^2 plots appear to be unsaturated, with weak effects by native species across a foliar cover gradient. Overall, predictors of exotic species richness depended on spatial scale: at the smallest spatial scale, abiotic factors accounted for most of the variation, but biotic factors accounted for most of the variation at the largest spatial scale. Our findings suggest that fields favorable for native species are also suitable for exotic species and management efforts towards exotic richness should be tailored to spatial scale.

Keywords: *exotic richness, invasibility, spatial scale, favorable, heterogeneity*

Introduction

Invasion ecologists have long sought to understand the roles of biotic and abiotic factors in rendering some communities more resistant than others to invasion (Lonsdale 1999). At small spatial scales ($<10m^2$), the number of exotic species is often negatively correlated with native richness, but at larger spatial scales, this relationship is often positive (Fridley et al. 2007). Fridley et al. (2007) introduced the phrase "invasion paradox" to describe the situation in which the diversity-resistance relationship can change with spatial scale. But why might the relationship between native and exotic species richness vary with spatial scale?

At small spatial scales, Elton (1958) argued that in communities with higher numbers of native species, the probability of successful colonization by exotic species should be lower because the amount of available resources for "invaders" would be lower. Elton's "biotic resistance" hypothesis has generally been supported at small spatial scales (reviewed in Fridley et al. 2007). But at large spatial scales, the relationship between native and exotic species tends to be positive (Stohlgren et al. 1999, Stohlgren et al. 2006, Fridley et al. 2007). Two hypotheses have been proposed to explain the positive relationship between native and exotic richness at larger spatial scales, the favorable environment hypothesis and the spatial heterogeneity hypothesis. The favorable environment hypothesis suggests coexistence of native and exotic species is promoted in sites where favorable conditions (high nutrients, etc.) generate high species richness of both natives and exotics (Stohlgren et al. 1999). One criticism of the favorable environment hypothesis is that it accounts for differences in mean conditions between sites only and disregards the potential importance of variation within sites (Davies et al. 2005, 2007). The spatial heterogeneity hypothesis, by contrast, states that coexistence of native and exotic species richness is promoted because of habitat heterogeneity or spatial variability in

resources or conditions. Therefore, as variability in biotic or abiotic factors increases, so do the numbers of both native and exotic species, thus generating strong positive relationships between native and exotic richness.

In this study, we take a multi-scale approach to investigate the relationship between native and exotic richness and to test the favorable environment and spatial heterogeneity hypotheses about landscape-scale relationships between native and exotic richness. Additionally, we examine the role of other biotic, abiotic and landscape-scale factors in regulating exotic richness at three spatial scales and discuss how the predictors of exotic richness differ among scales. Specifically, we used old-field plant communities to ask the following questions: (1) What is the relationship between native and exotic species richness, and does it vary across spatial scales? (2) Do favorable environments or spatial heterogeneity, or both, drive the relationship between native and exotic species? (3) What biotic and abiotic factors predict exotic richness across spatial scales in old-field communities?

Methods

Study site and field sampling

The Three Bend Scenic and Wildlife Management Refuge Area is part of Oak National Laboratory National Environmental Research Park near Oak Ridge, TN (35-58' N, 84-17' W). The Three Bend Area consists of a mix of hardwood forests and old fields. Soils at the sites are characterized as Typic Hapludult with a silty clay loam texture. Mean monthly temperatures range from approximately 3 ºC in the winter to 31 ºC in the summer and mean rainfall is 1,322 mm.

Sampling biotic variables at local scales

In the summer of 2006, we sampled seventeen old fields ranging from 0.5 - 7 ha. We chose these fields based on the presence of well-defined boundaries such as forests or road cuts. We randomly placed 50-m transects in each field (two to six transects depending on field area). Along each transect, we placed five 1-m^2 plots 10 meters apart.

In each 1-m^2 plot, we identified all plant species, tallied exotic and native species richness, and percent foliar cover of all vascular plant species during the peak of the growing season. We also estimated aboveground biomass in a randomly placed 0.5 m × 1 m subplot within each 1-m^2 plot by clipping all individuals rooted inside to approximately 1cm from the soil surface. We sorted the biomass into total aboveground biomass (i.e. live plant material) and litter mass (i.e. dead plant material) and then oven-dried the biomass samples for 48 hours at 65° C and weighed them. We also estimated light availability in the canopy, percent volumetric water content, and soil properties in each of the 1-m^2 plots (Table 2.1). Then, for each of the 17 old fields, we calculated field area and perimeter, as well as density of roads and vegetation land

cover within a 250 m buffer from the edge of each field and calculated heat load, an integrative measure of the field exposure to incident sunlight.

Statistical analyses

To examine the native and exotic richness relationship (NERR) at different spatial scales, we performed linear regressions using cumulative native richness to predict total exotic richness across the 1-m^2 plots (n = 250), 50-m^2 transects (n = 50), and old fields (n = 17) (Table 2.1). In addition, we assessed variation in the NERR among old fields by regressing exotic richness against native richness for the 1-m^2 plots within each of the 17 old fields. We also examined the support for the favorable environments or spatial heterogeneity mechanisms as influences on the NERR. In order to test the favorable environment and spatial heterogeneity hypotheses, we used a stepwise linear regression with the slope of NERR as a continuous response variable and the mean and variation (estimated as the coefficient of variation) in biotic and abiotic variables at the old-field scale as potential predictor variables. Prior to regression analyses, we created a correlation matrix among mean and variation in biotic and abiotic factors to assess potential covariation among factors. We tested for significant correlations between all predictor variables using Pearson's correlation coefficients. Predictor variables with significant correlation coefficients ($-0.75 > r > 0.75$) were not used in the same model (Kumar et al. 2006). We generated NERR slopes, the correlation matrix and the multiple linear regressions with JMP 6.0 (SAS Institute, Inc., Cary, NC).

To elucidate which factors might influence exotic species richness and assess whether those factors varied among spatial scales, we conducted a series of multiple regressions at each spatial scale. At the 1-m^2 plot, 50-m^2 transect, and old-field scales we included the measured biotic (native richness, total aboveground biomass, exotic cover) and abiotic variables (light

availability, soil moisture, soil N, soil bulk density, soil texture, litter mass, heat load) as well as landscape variables (field density, forest density, road density, field edge, mowing regime) listed in Appendix A in our model selection procedure. Because biotic and abiotic predictors were measured at the 1-m^2 plot scale, we scaled up from 1-m^2 plots to transects by summing values for biotic variables across the five nested1-m^2 plots in each transect. On the other hand, we averaged values for abiotic variables across the five nested 1-m^2 plots in each transect. Similarly, to move from transect to old-field scales, we summed biotic variables and averaged abiotic variables from transects nested within old fields.

We used the Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) to evaluate multiple regression models predicting exotic species richness at the 1-m^2 plot, 50-m^2 transect, and old-field scales. We tested for collinearity among biotc, abiotic, and landscape predictors using the same procedure used during NERR analyses. All regression analyses were performed using SAS 9.1.3 (SAS Institute, Inc., Cary, NC).

We used Moran's I_{std} correlograms to test for spatial autocorrelation in the residuals of the best models (based on biotic and abiotic predictors) for exotic and native species richness at the 1-m^2 plot, 50-m^2 transect, and field scales (Figure 2.1). When we found significant autocorrelation in the environmental model residuals, we constructed spatial models and environment + spatial models to account for this autocorrelation (Borcard and Legendre 2002, Borcard et al. 2004) (Table 2.2).

Results

We encountered 157 plant species in the old-field communities. Of these, 106 species were native, 36 were exotic and 15 could not be identified to species. At the 1-m^2 plot scale, the number of native species ranged from 4 to 9 (4.3 ± 0.12) and the number of exotic species from 3 to 20 (9 ± 0.19). At the 50-m^2 transect scale, the number of native species ranged from 12 to 33 (19.7 ± 0.67) and the number of exotic species from 3 to 15 (8.5 ± 0.37). At the old-field scale, the number of native species ranged from 17 to 46 (30.9 ± 1.86) and the number of exotic species from 7 to 20 (11.7 ± 0.82).

Native and exotic species richness relationship across spatial scales

Native and exotic species richness were significantly positively correlated at all spatial scales (1-m^2 plots: $R^2 = 0.03$, $n = 250$ $P = 0.012$; 50-m^2 transect: $R^2 = 0.13$, $n = 50$ $P = 0.012$; old field: $R^2 = 0.42$, $n = 17$, $P = 0.004$; Fig 2.2). Though the overall NERR at the plot scale was positive across old fields ($n = 250$), it varied within fields: positive in two fields, negative in two fields, and not statistically related in 13 fields (note NERR slope values in Fig. 2.3).

Favorable environment hypothesis vs. spatial heterogeneity hypothesis

Our data support the favorable environment hypothesis but not the environmental heterogeneity hypothesis. Mean foliar cover at the old-field scale was positively correlated with the slope of the NERR ($R^2 = 0.29$, $P = 0.03$; Fig. 2.3 c), but heterogeneity in foliar cover was not related to the NERR slope (Fig. 2.3 d). In addition, neither mean productivity nor heterogeneity in productivity (measured as CV in aboveground biomass) affected the relationship between native and exotic richness (Fig. 2.3 a and 2.3 c) across old fields. Furthermore, the slope of the

NERR was not correlated with either the mean or heterogeneity of any of the measured abiotic resources or conditions across fields.

Biotic, abiotic and landscape predictors of exotic species richness

Abiotic factors accounted for most of the variation in exotic richness at the 1-m^2 plot scale. At this small scale, exotic richness decreased as heat load and litter mass increased, but exotic richness increased with both sand content in soils and the size of the old field (Table 2.3). Soil sand content explained 9 % of the variation of exotic richness, while heat load accounted for 6% of the variation in exotic richness, and litter mass accounted for an additional 5% of the variation. A suite of landscape variables, such as old-field edge, area, and density of forests and fields were significant predictors in the multiple regression model, but each accounted for less than 1% of the variation in exotic richness. Exotic species richness across 1-m^2 plots decreased as length of field edge and amount of nearby forested areas and fields increased. Native species richness, light availability and road density were important predictors of exotic richness in multiple regression models at both the 50-m^2 transect and old-field scales. Together, these variables accounted for 45% and 85% of the variation in exotic species richness at the 50-m^2 transect and old-field scales, respectively.

At the 50-m^2 transect scale, biotic, abiotic and landscape factors accounted for similar amounts of variation in exotic richness. For example, as native richness (partial $R^2 = 0.13$) and light availability (partial $R^2 = 0.17$) increased, so did exotic richness. On the other hand, road density (partial $R^2 = 0.15$) surrounding old fields was negatively correlated with exotic richness. As the density of surrounding fields increased, exotic richness in 50-m^2 transects decreased.

Biotic rather than abiotic predictors accounted for most of the variation in exotic richness at the old-field scale. Exotic richness was positively associated with native richness accounting

for 70% of the total variation, and road density and soil moisture were negatively related to exotic richness, accounting for 13% and 8% of the variation in exotic richness. Finally, exotic richness was positively related to light availability but the latter was a poor predictor, accounting for less than 1% of the variation in exotic richness.

Discussion

Native richness and exotic richness are positively associated across spatial scales

In this study, native and exotic plant species richness were positively correlated across spatial scales, and the strength of the relationship increased as spatial scale increased from 1-m^2 plots to entire old fields. It is not surprising that at larger spatial scales native and exotic richness are positively associated, but encountering such a relationship at smaller spatial scales (1-m^2 plots) across old fields is not as common (Fridley et al. 2007, Belote et al. 2008). In fact, at local scales (1 m^2-plots) where species interact, a negative relationship tends to be more common (but see Cleland et al. 2004). This fact suggests the mechanisms shaping the NERR might vary among systems and depend on context.

Favorable environments shape the NERR

We found support for the favorable environments hypothesis shaping NERR across a foliar cover gradient. Mean foliar cover at the field scale was the most important factor mediating the slope of the NERR within old-fields, and in no case did heterogeneity account for any variation in the NERR, as the spatial heterogeneity hypothesis would predict. Contrary to Shea and Chesson (2002), we documented that the slope of NERR is not scale-dependent, but affected by the favorability of an environment. Davies et al. (2007) also found that a gradient in foliar cover shaped the NERR in a serpentine grassland system. However, Davies et al. (2007) reported positive NERR in communities with low cover and negative NERR in communities with greater foliar cover in serpentine systems in the western US, which contrasts with our result. In that serpentine system, Davies et al. (2007) used foliar cover as a proxy for productivity and attributed differences in NERR to the notion that productive sites have negative NERR because

they are homogeneous, but low productivity sites have positive NERR because they are heterogeneous. There are at least two reasons why our results are not congruent with theirs. First, cover might not be a good proxy for productivity in our system, and in fact mean foliar cover and mean aboveground biomass (i.e. productivity) are uncorrelated ($P = 0.14$). Moreover, fields with greater cover need not be more homogeneous in terms of biotic and abiotic factors as suggested by Davies et al. (2007). In fact, we did not find that fields with greater foliar cover to be more homogeneous in terms of biotic or abiotic factors (data not shown). Second, it could be that in productive systems, such as ours, heterogeneity is not a prerequisite for coexistence among native and exotic species. Unlike the serpentine communities of Davies et al. (2007), local old-field plant communities (i.e.1-m^2 plots) are not saturated across a foliar cover gradient. As a result, native species may exert weak effects on the establishment of exotic species. For instance, most NERRs (negative or positive) within fields were weak and non-significant, indicating that local communities can still accommodate more species.

Landscape and abiotic factors influence exotic richness at the1-m^2 plot scale

Abiotic and landscape variables were important predictors of exotic richness in 1-m^2 plots across old fields. For example, Rasran et al. (2007) found litter accumulation directly hindered seedling establishment by creating a physical barrier or indirectly by reducing light availability. Surprisingly, we found that soil sand content promoted exotic richness across 1-m^2 plots. Soils with greater sand content have lower water holding capacity and are often poor in available nutrients due to lower cation exchange capacity (CEC) (Chapin et al. 2002). Contrary to our studies, Stohlgren et al. (1999) found that most invaded plots had lower sand content (i.e. greater soil clay content) and greater soil nutrient availability. Perhaps, lower water holding

capacity, as well as lower CEC characteristic of high soil sand negatively impact the abundance of exotic species more so than their establishment.

Although landscape factors accounted for less than 1% of the variation in exotic richness, the nature of the relationship between landscape factors and exotic richness produced some interesting patterns. For example, 1-m^2 plots nested within small old fields tended to have fewer exotic species compared to 1-m^2 plots found within larger old fields. Recent studies have demonstrated that regional richness can be the strongest predictor of local (1-m^2 scale) richness after accounting for environmental variation (Harrison 1999, Freestone and Harrison 2006). In fact, species richness in a variety of local communities is linearly related to regional richness when immigration effects override species interactions (Witman et al. 2004, He et al. 2005, Fox and Srivastava 2006). We found that regional exotic richness (i.e. old-field) is positively related to local exotic richness (i.e. plot, $P < 0.0001$, $R^2 = 0.77$) (Figure 2.4). Likewise, exotic richness in the 1-m^2 plots is positively related to exotic richness at the 50-m^2 transect scale ($P < 0.0001$, $R^2 = 0.74$), which is also positively related to exotic richness at a regional scale ($P = 0.008$, $R^2 = 0.54$) (Figure 2.4). Consequently, the total number of exotic species in a field strongly predicts exotic richness at local scales across old-field communities, demonstrating the importance of regional processes at neighborhood scales.

Local exotic richness tended to be lower in old fields surrounded by several other fields and greater in old fields where density of other fields was lower (greater forest matrix). This finding is surprising given that other fields can be sources of propagules for exotic species. However, the density of other fields alone accounted for less than 1% of the variation in exotic richness ($P < 0.05$ in a multiple regression model), whereas regional richness (i.e. at the old-field

scale) immediately surrounding local communities (1-m^2 plots) explained more than 70% of the variation in exotic richness (in a linear regression).

In addition, 1-m^2 plots nested in old fields with greater edge tended to have fewer exotic species than 1-m^2 plots found in fields with less edge. It might be expected that greater edge could promote greater exotic richness as a result of increased habitat diversity, as the microclimate of field margins differs greatly from that of in the center of an old field. However, in many of the old fields in our system, exotic species that are common at field edges, such as *Lespedeza cuneata*, are also common in the center of the fields. Therefore, predictions of increased edge and exotic richness may not apply to our system.

At the 50-m^2 transect scale, abiotic, biotic, and landscape variables accounted for similar amounts of variation in exotic richness. Transects with greater light availability had more exotic species than did transects with lower light availability. Light availability in transects is negatively correlated with litter mass accumulation, which has been shown to impede successful colonization of exotic species by affecting seedling establishment (Rasran et al. 2007). Also, transects within old fields that had higher densities of other fields and roads in their vicinity harbored fewer exotic species than transects nested within fields surrounding by fewer roads or other fields. Again, exotic richness at the old-field scale is a better predictor of exotic richness in the 50-m^2 transects, suggesting that exotic immigration within transects exceeds immigration from other fields or via roads. At the largest spatial scale, old-field scale, native richness was the best predictor of exotic richness. This result is similar to those of other studies (Stohlgren et al 1999, Fridley et al. 2007, Belote et al. 2008) that find native and exotic richness strongly positively correlated at larger spatial scales. At larger spatial scales, both favorable environment or spatial heterogeneity are thought to contribute to higher native and exotic richness. We find

support that favorable environments promote positive NERR in our system, not spatial heterogeneity.

Conclusions

Our findings demonstrate that old-field communities with more native species are likely to have more exotic species than are communities with fewer native species. In fact, native richness was the best predictor of exotic richness at the scale of the old fields. The mechanism driving the relationship between native and exotic species richness at the local plot scale in our system is not productivity or variation in productivity, as has been claimed in other studies (Davies et al. 2007). Instead, variation in mean foliar cover seems to drive the NERR; in particular, fields with greater foliar cover were more likely to generate positive NERR slopes than fields with lower foliar cover. Together, our results suggest that favorable environments drive the relationship between native and exotic species richness, across spatial scales. Furthermore, exotic richness at the local scale was predicted better by abiotic variables than by biotic ones. Finally, management efforts to control colonization by exotic plant species will likely have to focus on different biotic and abiotic factors depending on the spatial scale of interest.

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List of References

List of References

Belote, R.T., Jones, R.H., Hood, S.M., and Wender, B.W. 2008. Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. *Ecology* 89:183-192

Bivand, R., Anselin, L., Bernat, A., Carvalho, M., Dray, S., Halbersma, R., Lewin-Koh, N., Ono, H., Tiefelsdorf, M., and Yu, D. 2005. SPDEP: Spatial dependence: weighting schemes, statistics and models. R package v. 0.3-10. *R Foundation for Statistical Computing*, Vienna, Austria

Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153:51-68

Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826-1832

Cleland, E.E., Smith, M.D., Andelman, S. J., Bowles, C., Carney, K.M., Horner-Devine, M.C., Drake, J.M., Emery, S.M., Gramling, J.M., and Vandermast, D.B. 2004. Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters* 7:947-957

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A., and Rice, K.J. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86:1602-1610

Davies, K.F., Harrison, S., Safford, H.D., and Viers, J.H. 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology* 88:1940-1947

Dray, S., Legendre, P., and Peres-Neto, P.R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196:483-493

Elton, C.S. 1958. The ecology of invasions. Methuen, London, UK.

Fox, J.W., and Srivastava, D.S. 2006. Predicting local-regional richness relationships using island biogeography models. *Oikos* 113:376-382

Freestone, A.L., and Harrison, S. 2006. Regional enrichment of local assemblages is robust to variation in local productivity, abiotic gradients, and heterogeneity. *Ecology* 9:95-102

Fridley, J. D., Stachowicz, J.J., Naeem, S. Sax, D.F. Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., and Von Holle, B. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88:3-17

Harrison, S. 1999. Local and regional diversity in a patchy landscape: Native, alien, and endemic herbs on serpentine. *Ecology* 80:70-80

He, F., Gaston, K.J., Connor, E.F., and Srivastava, D.S. 2005. The local-regional relationship: immigration, extinction, and scale. *Ecology* 86:360-365

Kumar, S., Stohlgren, T.J., and Chong, G.W. 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87: 3186-3199

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710

McCune, B., and Keeon, D. 2002. Equations for potential annual direct incident radiation and heatload. *Journal of Vegetation Science* 13: 603-606

Patton, D.R. 1975. A diversity index for quantifying habitat edge. *Wildlife Society Bulletin* 3, pp. 171–173.

Rasran, L., Vogt, K., and Jensen, K. 2007. Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient. *Folia Geobotanica* 42:271-288

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. and So, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25-46

Stohlgren, T.J., Jarnevich, C., Chong, G.W., and Evangelista, P.H. 2006. Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78:405-426

Witman, J.D., Etter, R.J., and Smith, F. 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proceedings of the National Academy of Sciences U.S.A.* 101:15664-15669

Appendix

Table 2.1. Biotic, abiotic and landscape variables used during variable selection to predict exotic richness across spatial scales. Biotic and abiotic variables were obtained across 1-m^2 plots, whereas landscape variables were calculated based on GPS measurements of field perimeter.

Variable	Description
Biotic variables	
Exotic richness	cumulative number of exotic species within a 1-m^2 plot, 50-m^2 transect, or old field
Native richness	cumulative number of native species within a 1-m^2 plot, 50-m^2 transect, or old field
Native and exotic foliar cover	percent cover of exotic and native species within a 1-m^2 plot, 50-m^2 transect, or old field
Litter mass	mass of litter (g)
Total aboveground biomass	biomass of all live plant species (g)
Abiotic variables	
Light availability	photosynthetic photon flux density (% reaching ground level) using a Li-COR AccuPar
Soil bulk density	soil bulk density
Soil moisture	% volumetric water content using a hand-held hydrosenser with a 12-cm metal probe
Soil pH	2 samples per transect
Soil nitrogen	potential net nitrogen mineralization (g/m2)
Soil texture	subsampled from multiple plots; 1=loam, 2=sandy loam, 3=silt loam, 4=clay loam
Landscape variables	
Field area	field area (acres)
Field perimeter	field perimeter (miles)
Mowing frequency	(1) monthly, (2) split mowing (half of field mowed in fall and half mowed in spring), (3) whole field mowed <1 yr, (4) whole field mowed > 1 yr
Road density	meters of road within 250 m field perimeter
Land cover	hectares of land cover (field and forest) within 250 m of field perimeter
Heat load	McCune and Keon (2002) Eqn. 3
Field edge	Patton (1975) Shape Index [P/(200*((pi*A)^0.5))]

Table 2.2 Summary of the three model types considered for predicting exotic species richness at the 1-m^2 plot scale. Models were compared using the Akaike Information Criterion corrected for small sample size (AIC_c). The environment-only models included biotic, abiotic and landscape predictor variables, the space-only models included significant PCNM vectors, and the environment + space models included a combination of biotic, abiotic, landscape and spatial predictors.

Model	AICc	R^2	*P*
Plot Scale (n=245)			
Exotic richness[1]=environment	202.27	0.39	<0.0001
Exotic richness[1]=space	162.96	0.48	<0.0001
Exotic richness[1]=environment + space	76.73	0.49	<0.0001

[1]Detrended exotic richness was used at the plot scale.

Table 2.3 Comparison of the best models for predicting exotic species richness at the 1-m^2 plot, 50-m^2 transect, and old-field scales. The plot, transect and field scale models included a combination of biotic, abiotic, landscape, and spatial predictors.

Variable	DF	Parameter	Variable P	Partial R^2	Model R^2	Model P
Field scale						
Intercept	1	5.647	0.0979	--	0.93	0.0402
Native Richness	1	0.318	0.0219	0.7254		
Road Density	1	-0.004	0.0956	0.1261		
Soil Moisture	1	-0.288	0.1784	0.0830		
Light Availability	1	5.510	0.3327	<0.0001		
Transect scale						
Intercept	1	8.942	0.0004	--	0.58	<0.0001
Light Availability	1	6.420	0.0004	0.1672		
Road Density	1	-0.003	0.0003	0.1465		
Native Richness	1	0.168	0.0127	0.1253		
Field Density	1	-0.078	0.0698	0.0953		
Soil clay	1	-0.122	0.0354	0.0408		
Plot scale						
Intercept	1	11.398	<.0001	--	0.49	<0.0001
Soil sand	1	0.129	<.0001	0.0855		
Heat load	1	-8.968	<.0001	0.0553		
Litter mass	1	-0.001	0.1265	0.0461		
Field Edge	1	-1.528	0.0015	0.0287		
Forest Density	1	-0.275	<.0001	0.0088		
Soil nitrogen	1	-24.863	0.1479	0.0065		
Field Density	1	-0.392	<.0001	0.0006		
Field Area	1	0.866	<.0001	0.0001		
Space	1	--	--	0.2609		

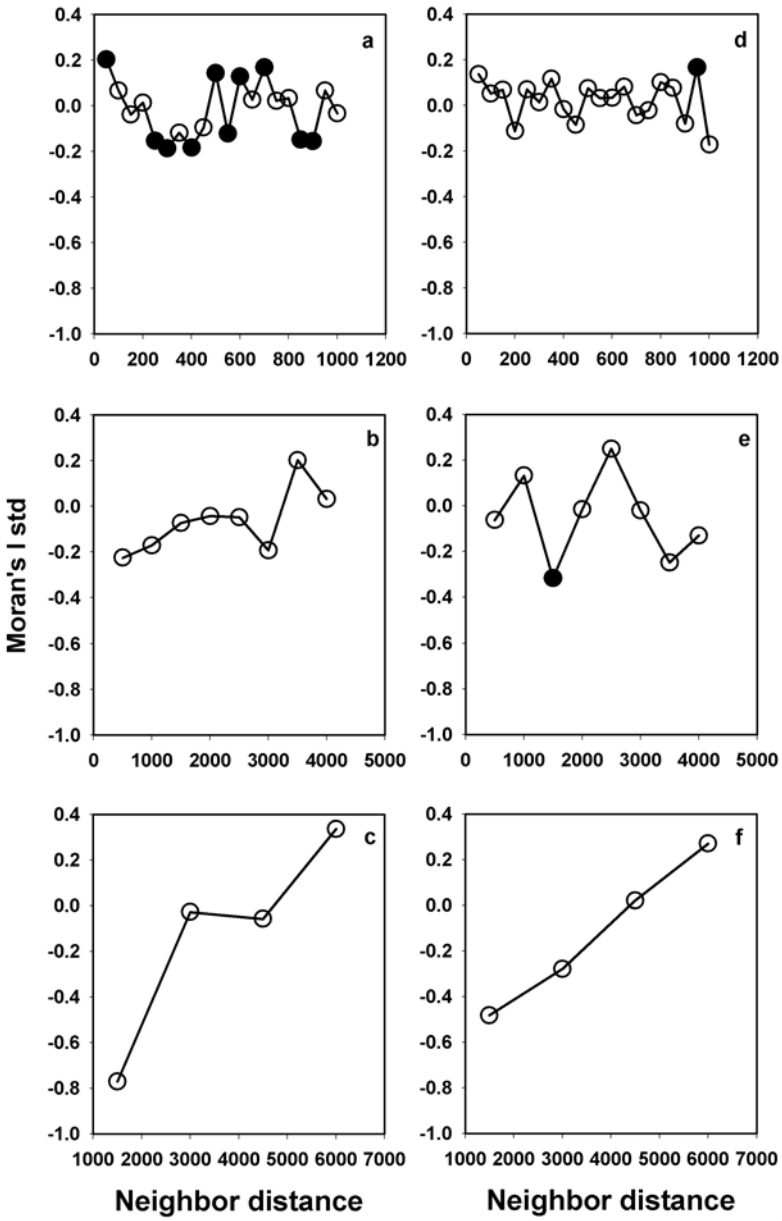


Figure 2.1 Moran's I_{std} correlograms of spatial autocorrelation for exotic (a, b and c) and native (d, e and f) richness at 1-m^2 plot (top panels), 50-m^2 transect (mid panels), and old-field (bottom panels) scales. Black circles indicate significant ($P \leq 0.05$) autocorrelation and white circles represent non-significant autocorrelation. Lag distance is 50 m for 1-m^2 plots, 500 m for 50-m^2 transects and 1500 m for old fields.

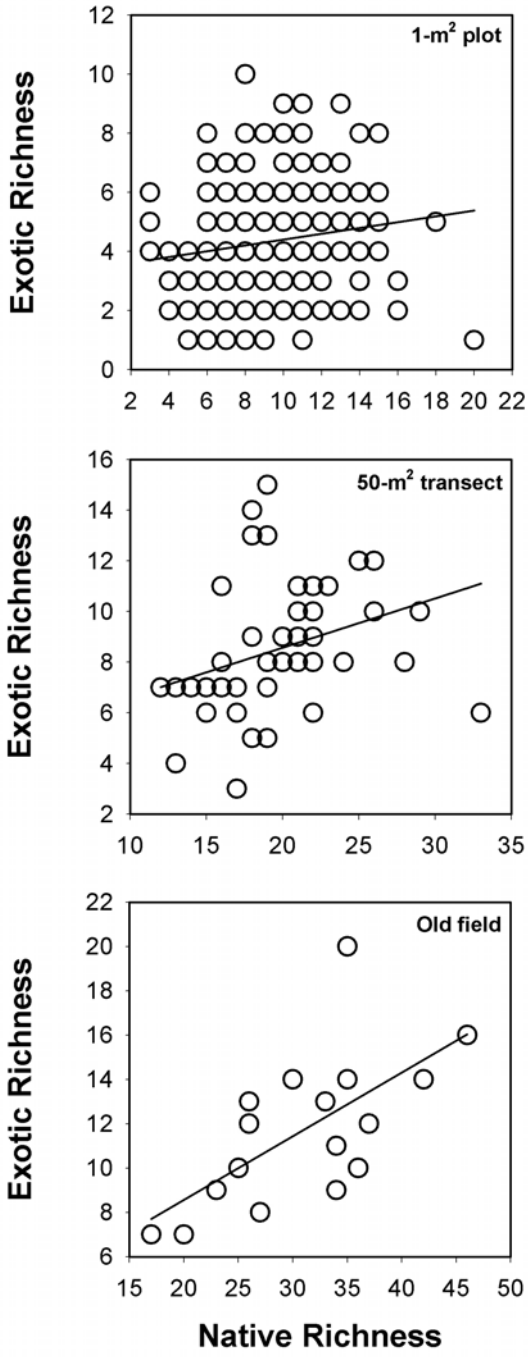


Figure 2.2 The relationship between exotic species richness and native species richness across spatial scales. Cumulative exotic richness is positively related to cumulative native species richness at 1-m^2 plot (top panel), 50-m^2 transect (middle panel), and old-field (bottom panel) scales. Significant ($P < 0.05$) relationships are shown with a regression line.

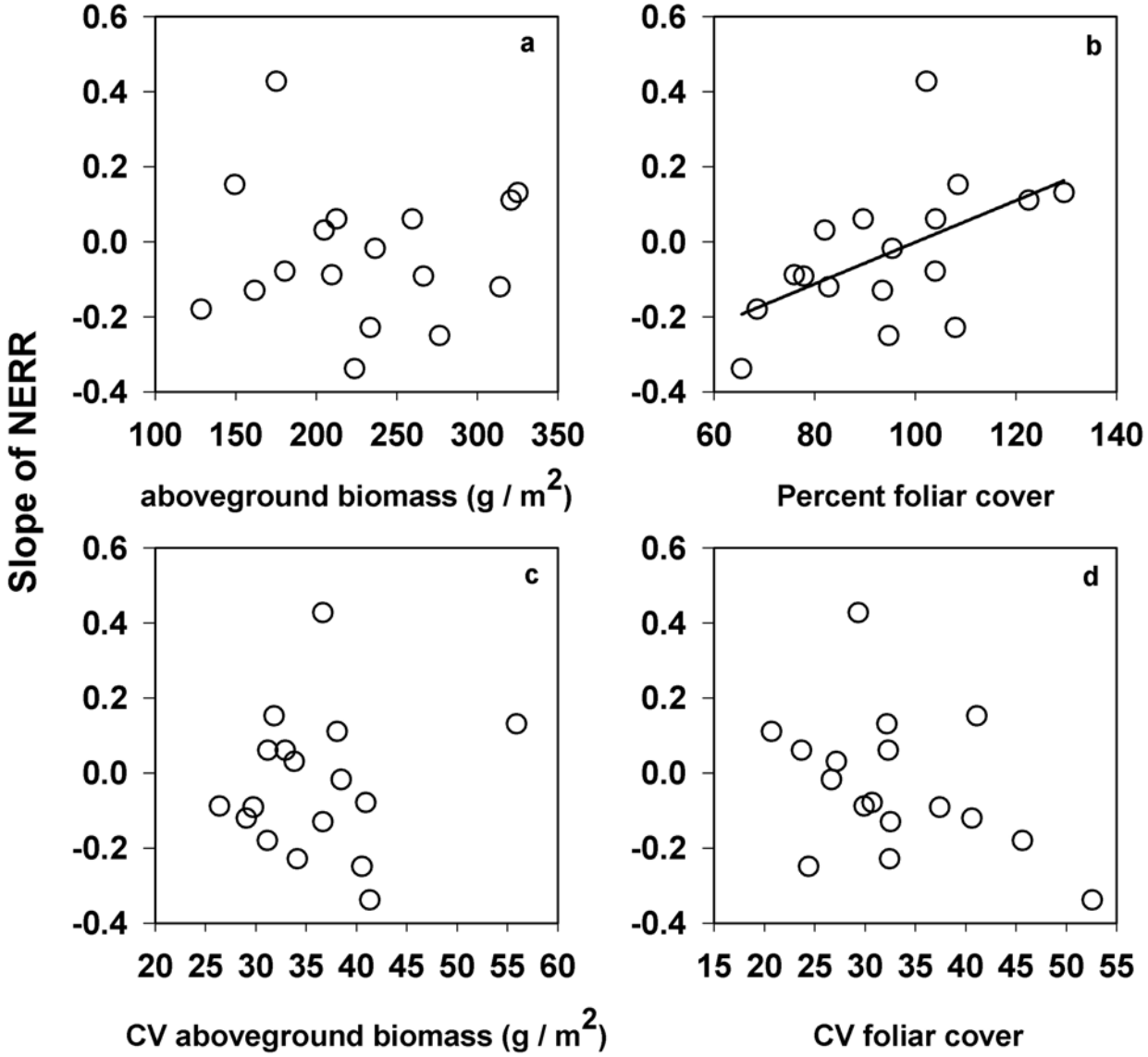


Figure 2.3 The relationship between the slope of the native-exotic richness relationship (NERR) in individual old-fields and (a) mean field aboveground biomass, (b) mean field foliar cover, (c) heterogeneity (CV) in aboveground biomass, and (d) heterogeneity (CV) in foliar cover. Significant ($P < 0.05$) correlations are shown with a regression line.

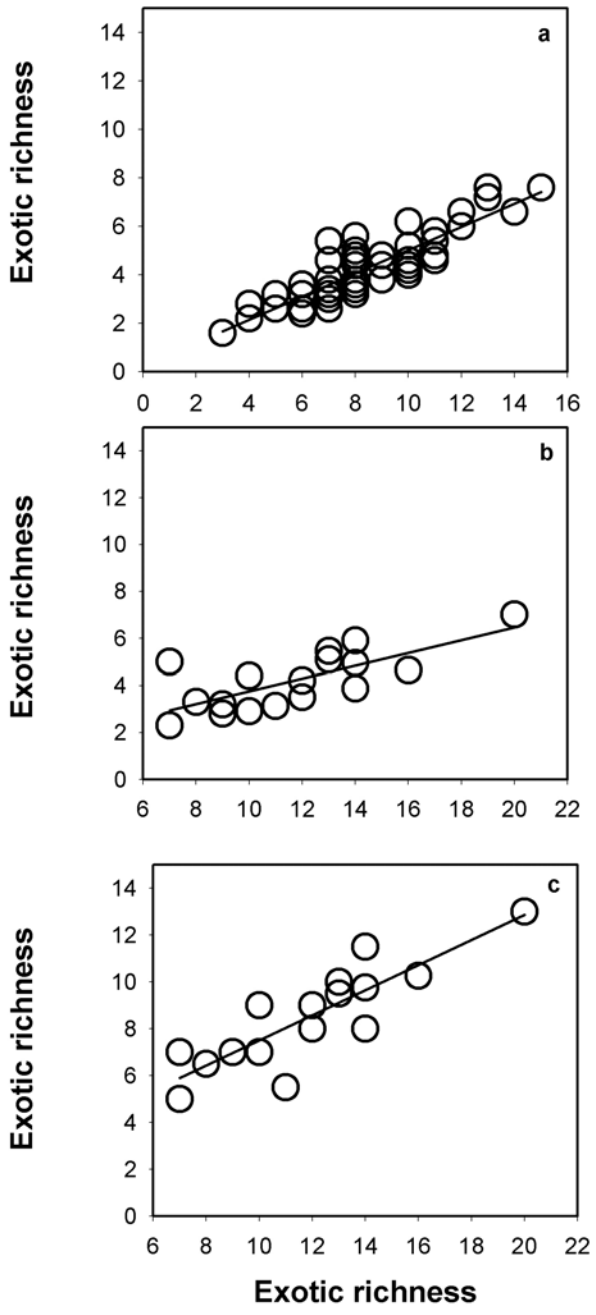


Figure 2.4. Linear regression of exotic richness at 1-m^2 plots vs. exotic richness at the old-field scale (a), exotic richness at 1-m^2 plots vs. exotic richness at 50-m^2 plots (b), and exotic richness at 50-m^2 plots vs. exotic richness at the old-field scale (c). Significant ($P < 0.05$) relationships are shown with a regression line.

Chapter 3

Do dominant species differentially affect community structure, ecosystem processes, and invasibility in an old-field?

Abstract

In this study, we examined the effects of *Solidago altissima* (hereafter *Solidago*) and two species in the genus *Verbesina, V. virginica* and *V. occidentalis* (hereafter *Verbesina*) on the structure of an old-field plant community and establishment of an invasive plant species, *Lespedeza cuneata* (hereafter *Lespedeza*). We removed *Solidago, Verbesina,* and both *Solidago* and *Verbesina* from 4-m^2 plots in an intact old-field community during two growing seasons. To assess how these species affected establishment by *Lespedeza*, we planted 20 seeds in each plot. We found that subdominant community evenness and diversity were greater in plots from which *Solidago* and *Verbesina* were removed relative to control or single species removal plots. However, there were no effects of species removal on species richness or composition of the subdominant community. Total aboveground biomass was not affected by dominant species removal, suggesting that the community of subdominant species exhibited compensation. Light availability was also greater in plots where both *Solidago* and *Verbesina* were removed compared to control plots throughout the growing season. Only *Solidago* removal affected soil moisture compared to other removal treatments and control during peak growing season (July). In addition, dominant species removal indirectly reduced the establishment of *Lespedeza* seedlings by directly increasing subdominant community biomass. Taken together, our results highlight the direct effects of dominant species on the structure and function of plant communities and their potential indirect effects on invasibility in an old-field ecosystem.

Keywords: *Lespedeza cuneata*, *Solidago, Verbesina,* compensation, establishment, invasive.

Introduction

The loss of species from communities can affect ecosystem processes. Most studies to date have examined how changes in some composite community-level measure, such as the number of species, results in changing ecosystem processes, such as productivity, nutrient cycling, or susceptibility to invasion (Chapin et al. 2000, Hooper et al. 2005, Fridley et al. 2007). But the identities of the species that are lost may be more important than diversity *per se*. Dominant species, which may make up a substantial portion of the community biomass, can have important effects on community dynamics and ecosystem processes (McNaughton and Wolf 1970, Wardle et al. 1999; Crawley et al. 1999, Grime 2001), so the loss of dominant species may lead to dramatic shifts in community structure and ecosystem function.

The loss of dominant plant species can affect communities and ecosystems in two general ways. First, dominant species may prevent establishment of other species and affect the structure of the subdominant community (Gurevitch and Unmasch 1989, Wardle and Barker 1997, Wardle et al. 1999, Diaz et al. 2003). In particular, dominant species can also affect the establishment or success of invasive species, with some studies showing that dominant species hinder invasions, whereas others show that dominant species might facilitate invasions (Crawley et al. 1999, Smith and Knapp 1999, Dukes 2002, Smith et al. 2004, Wilsey and Polley 2002, Emery and Gross 2006). Second, dominant species may play key roles in regulating ecosystem processes, such that the loss of dominant species can lead to negative effects on community biomass and productivity (Hooper and Vitousek 1997, Hooper 1998, Hector et al. 1999, Wardle et al. 1999, Spehn et al. 2005).

One complicating factor in understanding how dominant species might influence community structure or regulate ecosystem processes is that different dominant species can affect community structure and ecosystem processes in different ways. For example, Emery and Gross (2006) found that the effect of plant species on invasibility varied among dominant species, with some dominant species having no effect and others having negative effects. In their study, communities that were dominated by exotic species, such as *Bromus inermis* and *Centaurea maculosa,* exhibited high susceptibility to invasion by native and non-native seedlings, whereas communities dominated by the native species *Andropogon gerardii* had high resistance to invasion. Similarly, Suding et al. (2006) found that removal of *Acomastylis rossii* from alpine plant communities led to few changes in the structure of the remaining community, but removal of *Deschampsia caespitosa* altered community structure and affected nitrogen cycling.

Whether the loss of dominant species affects communities and ecosystems depends at least in part on the extent to which the rest of the community compensates for the loss of the species (Ruesink and Srivastava 2001, Larsen et al. 2005, Suding et al. 2006). Some of the remaining species may respond positively to the loss of the dominant species, while others show no response or a negative response to the loss of species. Thus, it could be that it is not the loss of a particular species from a community that affects ecosystem processes, but rather it is the structure of the remaining community (Wardle et al. 1999, Bret-Harte et al. 2004, Buonopane et al. 2005, Suding et al. 2006). If the dominant species reduces the pool of available resources for other community members or for invading species, it negatively affects other community members and limits invasion because of its competitive effects. Alternatively, a species might be dominant because other species in the community under-utilize the pool of available resources,

which might indicate that there are available resources for invading species (Whittaker 1965, Tilman 1987). Under this scenario, removing such a species will have no effect on invasions or the structure of the rest of the community.

In this study, we examined whether the removal of dominant plant species in an old-field community affects community structure, ecosystem processes, and invasibility. We removed the dominant forb species *Solidago* and two species in the genus *Verbesina* which comprise of half of the aboveground biomass in our system. We did not differentiate between *Verbesina* species in the field as they have similar life history traits. In fact, both *Verbesina* species are perennial and have similar phenologies and occur at similar abundances across local old-field communities (Souza and Bunn, unpublished). We then assessed whether these removals affected ecosystem- and community-level attributes and the emergence and survival of seedlings of *Lespedeza*, a rank one invasive legume that displaces native flora in old-field communities (Eddy and Moore 1998). *Solidago* is an abundant and widespread species in old fields in the US (Semple and Cook 2006). *Solidago* makes up, on average, 20% (range = 5 – 47%) of the aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data). Additionally, previous work near our site has shown that *Solidago* can influence ecosystem processes such as productivity (Crutsinger et al. 2006) and invasibility (Crutsinger et al. 2008a), and the structure of associated arthropod communities (Crutsinger et al. 2006, Crawford et al. 2007, Crutsinger et al. 2008b). In other systems, *Solidago* species also exert strong influences on plant community structure and ecosystem processes (Schmitz et al. 2003). Little is known about the effects of *Verbesina*, though it is a common genus in the eastern US (Chappelka et al. 2003, USDA Plant Database 2006). In fact, *Verbesina* makes up on average 18% (range = 0 –73%) of the

aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data).

Specifically, we predicted that (1) the removal of dominant plant species would increase evenness and richness, and alter the composition of the community of subdominant species, (2) the removal of dominant plant species would lead to compensatory responses in biomass production of the subdominant species and alter light, nutrient, and water availability, and consequently (3) the removal of dominant species would increase the emergence and survivorship of *Lespedeza*, and (4) these effects of species removal would depend on the identity of the dominant species

Methods

Study site

In spring 2005, we initiated an experiment in an old field at Oak Ridge National Environmental Research Park, near Oak Ridge, Tennessee (35° 58′ N 84° 17′ W). The old-field site was used for agriculture until 1943 and is mowed each spring. The soil has a silty clay loam texture and is classified as Typic Hapludult. Mean annual rainfall is 1322 mm, mean air temperature ranges from 31.2 °C (July) to 2.7 °C (January). Dominant plant species, by biomass, at this site, and also across old fields in the area, include *Solidago* and *Verbesina*, which together comprise approximately 40% of total aboveground biomass in this system. In addition, approximately 60 subordinate herbaceous and woody native and introduced plant species, including *Lespedeza*, occur at the study site and make up the remainder of the total aboveground biomass (Souza and Bunn, unpublished data).

Experimental manipulation

Beginning in spring 2005, we manipulated the presence of *Solidago* and *Verbesina* in 24 2 m × 2 m plots in existing old-field vegetation. Our plots were spaced one meter from each other in a completely randomized design. The experiment was a single-factor ANOVA design with six replicates each of the following four treatments: control (no species removed), *Solidago* removed, *Verbesina* removed, and both *Solidago* and *Verbesina* removed. During the peak growing season (July and August), target species were clipped as necessary at least every week. Both *Solidago* and *Verbesina* resprouted at a greater rate during the 2005 growing season, whereas in 2006, resprouting was greatly reduced (data not shown) Throughout the experiment, treatments were maintained by selectively clipping the base of the stems of target species (1 cm

from the ground) weekly in 2005 and every two weeks in 2006 growing season, roots were left in place.

On average, control plots (those from which neither *Solidago* nor *Verbesina* were removed) contained 170 g m^{-2} of *Solidago* and 110 g m^{-2} of *Verbesina*. *Solidago* made up, on average, 30% of the total biomass of control plots and *Verbesina* made up, on average, 20% of the total biomass of control plots. The removal of one co-dominant species did not affect the biomass or cover of the other ($P \geq 0.17$ in all cases).

One concern may be that we cannot separate the effects of dominant species identity from the effects of pure biomass removal because we did not remove an equivalent amount of sub-dominant (i.e. random removal) biomass from the control plots. Such an experiment would have been appropriate if our goal was to understand the relative effects of biomass removal and species identity on community structure, ecosystem processes, and invasibility. However, our goal was to elucidate the potential differential effects of two co-dominant species in this system (which together made up 40-50% of the aboveground biomass in this system). Our experimental approach is frequently used (D'Antonio et al. 1998, Wardle et al. 1999, Bret-Harte et al. 2000, Gurvich et al. 2001, Bret-Harte et al. 2004, Smith et al. 2004, Buonopane et al. 2005), so we are confident that the experimental design employed here adequately addresses our central questions.

Community- and ecosystem-level responses

In each of the plots, we tallied plant species richness (S) and foliar cover of each plant species present at the peak of the growing season in August 2006, one year after the initiation of the experiment. We estimated species-specific foliar cover using a modified Braun-Blanquet

cover class scale (Braun-Blanquet 1932). The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-100%. We calculated the Shannon diversity index (H′) from foliar cover data by using the median of each cover class category as our values of abundance. We calculated evenness (J′) as H′/ln(S).

In August 2006, we estimated aboveground biomass by clipping to 1 cm above ground level all plants within a randomly placed 0.5 m × 1 m quadrat within each experimental plot. We categorized each clipped stem into one of the following groups: *Solidago, Verbesina, Lespedeza,* or subdominant species. Clipped biomass was oven-dried at 60 °C for 48 hours and then weighed.

Emergence and survivorship of Lespedeza seedlings

In March 2006, we added 20 *Lespedeza* seeds (Ernst Conservation Seeds, Meadville, PA) to each of the 24 plots. Ten seeds were buried 1 mm deep at 7-cm spacing within each of two grids, within each plot, where each grid was located 0.5 m from the northern and southern edges of the plot. The location of each seed was marked with a painted nail so that we could track emergence and survivorship of seedlings over the course of the growing season. We censused emerged seedlings every two weeks between May and August 2006 and recorded both the number of seedlings that emerged and of the seedlings that emerged, the number of seedlings that survived until August. Although seedling emergence and survival are only the first steps in invasion success, several studies support their importance in driving the distribution of species and invasions in grassland systems (Gross and Werner 1982, Foster et al. 2002).

Environmental variables

To examine how dominant species might indirectly affect community structure and invasibility, we measured photosynthetic photon flux density (PPFD, hereafter light availability) and percent volumetric water content (% VWC) monthly from April to August in 2006 in each of the 24 experimental plots. To estimate light availability, we used a line-integrating ceptometer (Decagon Accupar, Decagon Devices, Pullman, WA) positioned horizontally about 2 cm above the ground. All estimates of PPFD were made on clear days between 11 am and 2 pm. To measure % VWC, we used a hand-held time domain reflectometer with 12-cm probes (Hydrosense, Decagon Devices, Pullman, WA). To assess the availability of NO_3-N and NH_4-N in the soil solution, we placed mixed-bed ion-exchange resin bags in nylon stockings (H-OH form, #R231- 500, Fisher Scientific International Inc., Pittsburgh, PA) at 5-cm soil depth at two locations in each of the 24 experimental plots (Hart et al. 1994). Resin bags were placed into the plots in June 2005 and removed in October 2005. Upon removal from the field, resins were air dried, resins from each plot were combined, and 2 g of resins from each plot were extracted with 2 M KCl. The extracts were then filtered on Whatman no. 1 filter paper after rinsing with dionized water and frozen prior to analysis for concentration of NO_3^- and NH_4^+. Pool sizes of NO_3^- and NH_4^+ were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000, Hach Corporation, Loveland, OH), using the indophenol-blue (Lachat Instruments, Inc. 1990) and cadmium reduction-diazotization (Lachat Instruments, Inc. 1992) methods, respectively. All values expressed in the manuscript are based on air-dried resins.

Statistical analyses

To examine the effects of the removal of co-dominant species on plant community structure and on establishment by *Lespedeza,* and to investigate the potential mechanisms underlying those effects, we used a MANOVA model followed by a series of single-factor ANOVA and ANCOVA models. The MANOVA allowed us to test whether there was an overall effect of the treatments on the linear combination of response variables as a whole. In the MANOVA, the treatment effects were *Solidago* removal, *Verbesina* removal, both *Solidago* and *Verbesina* removal, and control (neither *Solidago* nor *Verbesina* removed). The combined response variables were subdominant species richness, subdominant species evenness, subdominant species diversity, subdominant biomass, total biomass and *Lespedeza* seedling emergence and survival.

The subsequent ANOVAs allowed us to ask more specifically whether the treatments affected particular response variables. In the single-factor ANOVAs, the four treatments were *Solidago* removal, *Verbesina* removal, both *Solidago* and *Verbesina* removal, and control (neither *Solidago* nor *Verbesina* removed). The response variables were subdominant species richness, subdominant diversity, subdominant evenness, subdominant community biomass (excluding *Solidago* and *Verbesina*), total community biomass (including *Solidago* and *Verbesina*), light availability, % VWC, and soil NO^-_3 and NH^+_4. We used Tukey's HSD means separation test ($\alpha = 0.05$) to identify which treatment means differed from one another.

We used an ANCOVA model to examine the main effects of dominant species removal on emergence and survival of *Lespedeza*. For the ANCOVA model we used the following covariates: biomass of the subdominant community, species richness, evenness (excluding

Lespedeza, *Verbesina*, and *Solidago*), light availability, and the foliar cover of mature *Lespedeza*. We built a correlation matrix including covariates to test for significant pairwise correlations ($p<0.05$). If covariates were correlated to each other, they were removed from model prior to performing ANCOVA. Proportional data were arcsine transformed, and cover and biomass data were log transformed to meet the assumptions of ANOVA and ANCOVA.

We used PRIMER (Plymouth Marine Laboratory, UK) to conduct an analysis of similarity (ANOSIM) to examine the effects of dominant species on composition of the subdominant community. In the analysis, we created four main grouping factors: *Solidago* removed, *Verbesina* removed, both *Solidago* and *Verbesina* removed, and neither removed. Based on species-specific foliar cover of each subdominant species, we constructed a non-metric multidimensional scaling (NMDS) plot using Bray-Curtis similarity coefficients from a triangular matrix (Bray and Curtis 1957). We excluded one of the plots from all analyses because it contained a fast-growing autumn olive shrub (*Elaeagnus umbellata)* that was unique to that plot and substantially altered overall biomass and structure of that plot.

Results

Community- and ecosystem-level responses

The MANOVA indicated that the removal treatments differed in their effects on community- and ecosystem-level processes (Wilks' $\lambda = 0.062$, df = 21,38, $P = 0.002$). Because the MANOVA indicated an overall effect of the treatments, we followed the MANOVA with subsequent single-factor ANOVAs.

The removal of dominant species affected some aspects of the structure of the subdominant community. Evenness and diversity of the subdominant community were both on average 30% greater in plots from which both *Solidago* and *Verbesina* were removed relative to control plots and plots from which only one of the species was removed (Table 3.1, Figure 3.1). However, the removal of dominant species did not affect species richness of the subdominant community (Table 3.1). In addition, the NMDS indicated that composition of the subdominant community was not affected by the removal treatments (Global R = -0.019, $P = 0.60$).

Dominant species removal increased the aboveground biomass partitioning in the community of subdominant species. Biomass of the subdominant community was 37% greater in plots from which *Verbesina* was removed, 67% greater in plots where *Solidago* was removed and 55% greater when both *Verbesina* and *Solidago* were removed relative to control plots only (Table 3.1, Figure 3.2a). However, there was no effect of dominant species removals on total community biomass (Table 3.1, Figure 3.2b), suggesting that subdominant species compensated for the removal of both dominant species. For instance, when both dominant species were present total community biomass was, on average, 544 g m^{-2}. When both dominant species were removed, the biomass of the subdominant community was 586 g m^{-2} ($t = 0.20$, $P = 0.85$).

Emergence and survivorship of Lespedeza seedlings

Dominant species removal did not directly affect emergence or survival of *Lespedeza* seedlings. However, subdominant biomass was an important covariate for both seedling emergence and survival, while mature *Lespedeza* cover was an important covariate for seedling emergence only (Table 3.2). Subdominant community biomass was negatively related to both emergence (Figure 3.3) and survival (Figure 3.4) of *Lespedeza* seedlings, while mature *Lespedeza* cover was positively related to seedling emergence.

Environmental responses

The removal of dominant species affected light availability, soil moisture, and soil nitrogen availability. We found that light availability varied throughout the growing season (Wilks' $\lambda = 0.21$, df = 3,18, $P < 0.0001$), but light availability was not affected by the interactive effects of time by removal treatments (Wilks' $\lambda = 0.64$, df = 9,44, $P = 0.496$). Light availability (PPFD) was consistently greater in plots from which both *Solidago* and *Verbesina* were removed relative to control plots throughout the growing season (Table 3.3). Moreover, early in the growing season (June) light availability was greater when both species were removed compared to the removal of *Verbesina*. *Verbesina* comprised a smaller proportion of the total community biomass (20%) than did *Solidago* (30%). As a result, *Verbesina* removal did not affect light availability relative to control plots (because only 20% of the aboveground biomass was removed), but plots from which *Verbesina* was removed had significantly lower light availability than plots from which either *Solidago* or both species were removed (where approximately 30% and 50 % of the aboveground biomass was removed, respectively). By the

peak of the growing season, June and July, light availability was greater only in plots where both dominant species were removed than in plots where either *Solidago* or *Verbesina* were removed.

Soil moisture availability varied significantly throughout the course of the growing season (Wilks' $\lambda = 0.07$, df = 2,19, $P < 0.0001$). In addition, dominant species removal interacted with time, in the effect on soil moisture availability (Wilks' $\lambda = 0.33$, df = 6,38, $P = 0.001$). In fact, soil moisture availability was greater in plots were *Solidago* was removed compared to other removals and control plots only in July (Table 3.3). Finally, soil nitrogen availability in the form of nitrate ($P = 0.13$) was not affected by the removals, while nitrogen availability in the form of soil ammonium ($P = 0.07$) was marginally increased by removal of dominant species. Soil ammonium availability was greater in plots where both species were removed (1.4 ppm ± 0.34) than in plots where only *Solidago* (0.76 ppm ± 0.12) or only *Verbesina* (1.1 ppm ± 0.14) were removed or control plots (0.88 ppm ± 0.15).

Discussion

Dominant species affect subdominant community structure

Our main results are that dominant plant species in this old-field ecosystem alter evenness and diversity in the community of subdominant species, affect biomass partitioning, and potentially indirectly regulate invasion by an exotic species, *Lespedeza*.

Both *Solidago* and *Verbesina* affected the structure of subdominant plant communities in this old-field ecosystem. In particular, the diversity and evenness of the community of subdominant species increased, relative to control or single species removal plots, when both *Solidago* and *Verbesina* were removed. Together, the two dominant species comprise ca. half of total aboveground biomass; subsequently their removal led to an increase in equitability of the remaining subdominant species, at least over the course of this experiment. Though the average percent cover of most species responded to the removals of the co-dominant species, several taxa were especially noteworthy: cover of *Solanum caroliniense* was 9 × greater in removal plots (5.9%) than in control plots (0.6%); cover of *Festuca* sp was 33 × greater in removal plots (3.3%) than in control plots (0.1%); cover of *Sorghum halepense* was 11 × greater in removal plots (5.4%) than in control plots (0.5%); *Lonicera japonica* was 31× greater in removal plots (15.4%) than in control plots (0.5%); and *Elephantopus carolinianus* (5.9% in removal plots), *Rubus flavinanus* (17.1% in removal plots), and *Solidago gigantia* (10.4% in removal plots) were all absent in control plots, but attained high cover values when the co-dominant taxa were removed. *L. japonica*, *R. flavinanus, and Sorghum halepense* are exotic invasive species in eastern Tennessee suggesting that *Solidago* and *Verbesina* might limit the invasion dynamics of other exotic species in addition to their effects on *Lespedeza*.

In contrast to diversity and evenness, subdominant community richness and composition were not affected by the removal treatments. These two community metrics are more likely to be altered over a longer removal period than in a one-year long experiment such as ours. If our experiment continued for several years, recruitment by new species may have been higher in the removal plots than in the control plots. However, in a 3-yr experiment, Schmitz (2003) found that removal of *S. rugosa* did not affect species richness.

Though the removal of *Solidago* and *Verbesina* did not affect richness or composition, biomass of the subdominant community was higher in the removal plots than in the control plots. Competition theory predicts that when a species is removed from a community, the biomass of the rest of the community should increase. In our system, the compensatory responses of the subdominant community were consistent with such a competition hypothesis. Biomass of the subdominant species increased in all removal treatments compared to controls. In fact, total community biomass did not differ between removal treatments and controls, further supporting compensatory responses by subdominant community biomass. Other studies have documented similar compensatory responses. For instance, Polley et al. (2007) found that removing annual species led to compensatory responses of the subdominant species and consequently total community biomass did not differ between removal plots and controls.

More generally, the results from our study are also similar in some ways to a removal experiment conducted in an alpine moist meadow community by Suding et al. (2006). The removal of one co-dominant alpine species, *Deschampsia caespitosa*, altered the structure of the subdominant community (removal increased evenness) and subdominant biomass partitioning. This suggests that the communities of plants in the alpine meadow systems and old fields are

able to compensate for species loss. Other studies, though, have found that subdominant species might not compensate for species loss. For instance, the subdominant species in a Serengeti grassland community did not respond to the removal of dominant species (McNaughton 1983). Understanding why some communities compensate for species loss and others do not should be an avenue of fruitful research (Wardle et al. 1999).

One mechanism by which *Solidago* and *Verbesina* could affect the community of subdominant species is by limiting light. In particular, we found that more light was available when both *Solidago* and *Verbesina* were removed than when they were both present (in the control plots) or when either *Solidago* and *Verbesina* were removed. This suggests that there are cumulative effects of dominant species removal on light availability. However, only the removal of *Solidago* affected soil moisture during the peak of the growing season compared to other removal treatments and control plots. *Solidago* removal led to an increase in soil moisture, but removal of both *Solidago* and *Verbesina* did not. This seems puzzling, as the removal of both species accounted for a greater amount of biomass removed than the removal of *Solidago* alone. Nonetheless, removing both dominant species increased light availability relative to plots where dominant species were present. Such increases in light availability could have led to increases in soil moisture uptake by compensating subdominant community (i.e. increases in evapotranspiration) counteracting the effects of decrease in soil moisture uptake by removal of dominant species. As a result, communities from which both *Verbesina* and *Solidago* were removed did not differ in soil moisture compared to communities in which both were present. Similarly to the results of our study, Smith et al. (2004) found light penetration to increase with the removal of a dominant C_4 grass species in a tallgrass prairie system. They suggested that increased light levels as a result of dominant C_4 grass removal could have increased canopy

temperatures, increased evapotranspiration and decreased soil moisture in local tallgrass prairie communities. Finally, the removal of both dominant species marginally promoted soil nitrogen availability in the form of soil ammonium, but not soil nitrate. We know from an ongoing experiment at the site that these old-field plant communities do not seem to be N-limited (Sanders et al. 2007). Taken together, our results to date suggest that competition for light plays a prominent role in structuring these communities, and availability of light is likely mediated by dominant species such as *Solidago* and *Verbesina* collectively.

Solidago and Verbesina indirectly limit Lespedeza establishment

We found that removing co-dominant species did not directly reduce the emergence or survivorship of the invasive species *Lespedeza.* Though the removal treatments increased evenness, diversity and aboveground biomass of the subdominant community, neither community evenness nor richness were important covariates of *Lespedeza* seedling emergence or survival.

Both experimental and observational studies to date have found mixed support for the idea that evenness of the resident community reduces invasibility. For example, recent experiments by Emery and Gross (2007) and Wilsey and Polley (2002) found little effects of evenness on community invasibility during the first year of each study. In fact, seedling survival in both studies was affected by evenness only in the second year of their experiments. Observational studies addressing the role of species evenness on community invasibility have also shown mixed results. Some studies have found negative effects of species evenness on invasibility (Foster et al. 2002, Tracy et al. 2004), while others have found positive effects (Robinson et al. 1995). However, observational studies are susceptible to a variety of potentially

confounding factors, such as resource heterogeneity and propagule supply. Additionally, both experimental and observational studies often do not account for the role of temporal resource complementarity (i.e. phenological niches) in evenness and invasibility studies. For instance, Losure et al. (2007) found that evenness affected invasibility only when species that were becoming rare had phenological traits similar to those of the invader. More experimental tests are needed to understand when, and under what circumstances, evenness of resident communities can limit invasibility.

Dominant species removal led to compensatory responses of the subdominant community, which in turn negatively affected both *Lespedeza* seedling emergence and survival. Biomass of the subdominant community was higher in species removal plots than in plots where dominant species were present. In turn, total community biomass was not affected by the removal of dominant plant species as the subdominant community compensated for dominant species loss. Furthermore, greater aboveground biomass reduced *Lespedeza* seedling emergence and survival. Previous studies have suggested that high productivity communities have greater resource use complementarity than low productivity communities (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999) and are less likely to be invaded than are low productivity communities. Contrary to that, we found total aboveground production was not related to invasibility in this old-field system. Instead, we found that biomass of the community of subdominant species, rather than the entire community, was negatively associated with invasibility. This suggests that the suite of subdominant species in this system directly compete, most likely for space, with potential colonizing species, rather than for light availability. When we removed dominant species, the subdominant species were able to outcompete the *Lespedeza*

seedlings for available space given that light availability was not an important covariate in our model. But when the dominant species were present, there was no such effect.

Mature *Lespedeza* cover was positively associated with *Lespedeza* seedling emergence, but not survival. *Rhizobium* inoculum can certainly be beneficial for seedling emergence, and plots with greater mature *Lespedeza* foliar cover potentially had higher densities of soil rhizobia than did plots with few mature *Lespedeza* individuals (Acharya et al. 2006). Since *Lespedeza* is a common species in this system, the potential for facilitative effects of adults on seedlings is likely.

Of course, *Lespedeza cuneata* is only one species among many non-native invasive species in this system. However, given that it (1) is a rank 1 invasive species across many U.S. states (Eddy and Moore 1998, Hoveland and Donnelly 1985, Sheley et al. 1999) (2) has been shown to alter native communities (Brandon et al. 2004, Price and Weltzin 2003, Garten et al. 2008), (3) *Lespedeza* is the most common invasive species in this system (Souza et al. In review), and (4) previous and ongoing work in this system has focused on *Lespedeza* (Sanders et al. 2007, Souza et al. in review), we feel justified in focusing on it. Nevertheless, we agree that experiments similar to ours, focusing on the effects of dominant species on other invasive species, would be enlightening. Additionally, experiments addressing the role of dominant species on community structure, ecosystem processes and invasibility should be conducted over longer temporal scales.

Conclusions

Our study, combined with other recent species removal studies, suggests that the consequences of species loss from plant communities may be contingent on the ecosystem type (Wardle et al. 1999, Suding et al. 2006, Bret-Harte et al. 2004, Emery and Gross 2006). Together, these studies clearly show that species loss can directly affect community structure, ecosystem processes, and indirectly affect invasion dynamics. But the effects of species loss on community structure, ecosystem processes, and invasion dynamics may be contingent on the compensatory response of the remaining species in the community and may depend on which species are lost Understanding the links among species loss, compensatory responses, and ecosystem functions should be a critical and fruitful avenue of future research in plant ecology.

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List of References

List of References

Acharya, S.N., Kastelic, J.P., Beauchemin, K.A., and Messenger, D.F. 2006. A review research progress of cicer milkvetch (Astragalus cicer L.) *Canadian Journal of Plant Science* 86: 49-62

Brandon, A.L., Gibson, D.J., and Middleton, B.A. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native Lespedeza cuneata (Dum. Cours.) G. Don. *Biological Invasions* 6:483-493

Braun-Blanquet, J. 1932. Plant sociology. Transl. G. D. Fuller and H. S. Conrad. McGraw-Hill, New York. 539

Bray, J.R., and Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27:326-349

Bret-Harte, M.S., Chapin III, F.S., Whorley, J.R., Garcia, E.A., and Sacre, V.S. 2000. Species and functional types affect ecosystem response to fertilization in artic tundra. *Bulletin of Ecological Society of America* 81:S61

Bret-Harte, M.S., Garcia, E.A., Sacre, V.M., Whorley, J.R., Wagner, J.L., Lippert, S.C., and Chapin III, F.S. 2004. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* 92:635-647

Buonopane, M., Huenneke, L.F., and Remmenga, M. 2005. Community response to removals of plant functional groups and species from a Chihuahuan desert shrubland. *Oikos* 110:67-80

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., and Diaz, S. 2000. Consequences of changing biodiversity. *Nature* 405:234-242

Chappelka, A.H., Neufeld, H.S., Davison, A.W., Somers, G.L., and Renfro, J.R. 200. Ozone injury on cutleaf coneflower (*Rudbeckia laciniata*) and crown-beard (*Verbesina occidentalis*) in Great Smoky Mountains National Park. *Environmental Pollution* 125:53-59

Crawford, K.M., Crutsinger, G.M., and Sanders, N.J. 2007. Host-plant genotypic diversity mediates the distribution of an ecosystem engineer. *Ecology* 88:2114-2120

Crawley, M.J., Brown, S.L., Heard, M.S., and Edwards, G.R. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2:140-148

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., and Sanders, N.J. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966-968

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., and Sanders, N.J. 2008b. Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. *Oikos* 117:255-264

Crutsinger, G.M., Souza, L., and Sanders, N.J. 2008a. Intraspecific diversity and dominant genotypes resist plant invasions. *Ecology Letters* 11:16-23

D'Antonio, C.M., Hughes, R.F., Mack, M., Hitchcock, D., and Vitousek. P.M. 1998 The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *Journal of Vegetation Science* 9:699-712

Diaz, S., Symstad, A.J., Chapin, F.S., Wardle, D.A, and Huenneke, L.F. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* 18:140-146

Dukes, J.S. 2002. Species composition and diversity affect grassland susceptibility and response

to invasion. *Ecological Applications* 12:602-617

Eddy, T.A., and Moore C.M. 1998. Effects of sericea lespedeza (Lespedeza cuneata (Dumont) G. Don) invasion on oak savannas in Kansas. *Transactions of the Wisconsin Academy of sciences, Arts, and Letters* 86: 57-62.

Emery, S.M., and Gross, K.L. 2006. Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115:549-558

Emery, S.M., and Gross, K.L. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology* 88:954-964

Foster, B.L., Smith, V.H., Dickson, T.L., and Hildebrand, T. 2002. Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* 99:300-307

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., and Von Holle, B. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88:3-17

Garten, C.T., Classen, A.T., Norby, R.J., Brice, D. J., Weltzin, J.F., and Souza, L. 2008. Role of N-2-fixation in constructed old-field communities under different regimes of [CO2], temperature, and water availability. *Ecosystems* 11:125-137

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902-910

Gross, K.L., and Werner, P.A. 1982. Colonizing abilities of biennial plant-species in relation to ground cover – implications for their distributions in a successional sere. *Ecology* 63:921-93

Gurevitch, J., and Unnasch, R.S. 1989. Experimental removal of a dominant species at 2 levels

of soil fertility. *Canadian Journal of Botany-Revue Canadienne De Botanique* 67:3470-3477

Hart, S.C., Nason, G.E., Myrold, D.D., and Perry, D.A. 1994. Dynamics of gross nitrogen transformations in an old-growth forest – the carbon connection. *Ecology* 75:880-891

Hector, A., Schmid, B.B., Beirkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, J.D., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., and Lawton, J.H. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123-1127

Hooper, D.U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* 79:704-719

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35

Hooper, D.U., and Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302-1305

Hoveland, S.C., and Donnelly, E.D. 1985. The Lespedezas. Pages 128-135 in M.E. Heath, editor. Forages: the science of grass agriculture. Iowa Sate University Press, Ames, Iowa, USA.

Larsen, T.H., Williams, N.M., and Kremen, C. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8:538-547

Lawton, J.H., Naeem, S., Thompson, L.J., Hector, A., and Crawley, M.J. 1998. Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. *Functional Ecology* 12:848-852

Losure, D.A., Wilsey, B.J., and Moloney, K.A. 2007. Evenness-invasibility relationships differ between two extinction scenarios in tallgrass prairie. *Oikos* 116:87-98

McNaughton, S.J., and Wolf, L.L. 1970. Community ordering and niche width. *Science* 170:1335

McNaughton, S.J. 1983. Serengeti grassland ecology – the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53:291-320

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734-737

Polley, H.W., Wilsey, B.J., and Derner, J.D. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* 116:2044-2052.

Price, C.A., and Weltzin, J.F. 2003. Managing non-native plant populations through intensive community restoration in Cades Cove, Great Smoky Mountains National Park, USA. Restoration. *Ecology* 11:351-358

Robinson, G.R., Quinn, J.F., and Stanton, M.L. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76:786-794

Ruesink, J.L., and Srivastava, D.S. 2001. Numerical and per capita responses to species loss: Mechanisms maintaining ecosystem function in a community of stream insect detritivores. *Oikos* 93:221-234

Sanders, N.J., Weltzin, J.F., Crutsinger, G.M., Fitzpatrick, M.C., Nunez, M.A., Oswalt, C.M. and

Lane, K.E. 2007. Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88:2383-2391

Schmitz, O.J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters* 6:156-163

Semple, J.C., and Cook, R.E. 2006. Flora of North America. Oxford University Press, Oxford.

Sheley, R.J., Petroff, J., and Borman, M. 1999. Introduction to biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis, Oregon, USA.

Smith, M.D. and Knapp, A.K. 1999. Exotic plant species in a C-4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* 120:605-612

Smith, M.D., Wilcox, J.C., Kelly, T., and Knapp, A.K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106:253-262

Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmborg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.D., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., and Lawton, J.H. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* 75:37-63

Suding KN., Miller, A.E., Bechtold, H., and Bowman, W.D. 2006. The consequence of species loss on ecosystem nitrogen cycling depends on community compensation. *Oecologia* 149:141-149

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental

nitrogen gradients. *Ecological Monographs* 57:189-214

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718-720

Tracy, B.F., Renne, I.J., Gerrish, J., and Sanderson, MA. 2004. Effects of plant diversity on invasion of weed species in experimental pasture communities. *Basic and Applied Ecology* 5:543-550

Wardle, D.A., and Barker, G.M. 1997. Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. *Oikos* 80:470-480

Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N., and Ghani, A. 1999. Plant removals in perennial grassland: Vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* 69:535-568

Whittaker, R.H. 1965. Dominance and diversity in land plant communities – numerical relations of species express importance of competition in community function and evolution. *Science* 147:250

Wilsey, B.J., and Polley H.W. 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5:676-684

Appendix

Table 3.1 Results for ANOVA of effects of dominant species removal on total community biomass, subdominant biomass, subdominant richness, subdominant evenness and subdominant diversity. Significant variables ($P < 0.05$) are in bold.

	DF	MS	F	P
Total community biomass	1, 21	7150.80	0.04	0.840
Subdominant community biomass	1, 21	0.18	24.80	**<0.001**
Subdominant community richness	1, 21	22.92	3.19	0.089
Subdominant community evenness	1, 21	0.03	26.65	**<0.001**
Subdominant community diversity	1, 21	0.18	24.80	**<0.001**

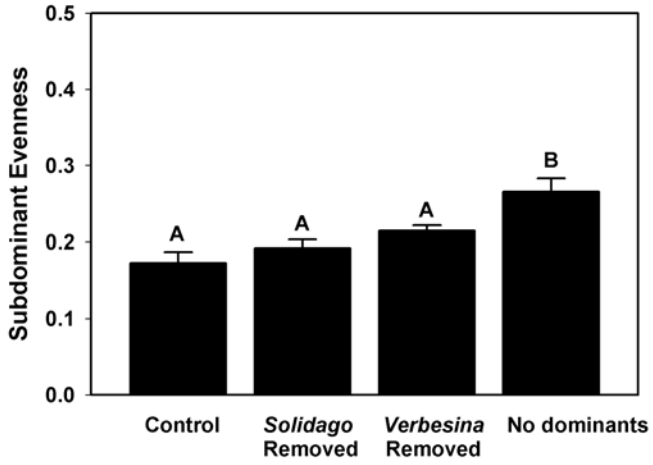
Table 3.2 ANCOVA summary for effects of dominant species removal and covariates on emergence and survival of *Lespedeza* seedlings. P-values ≤ 0.05 are in bold.

			Seedling Emergence		
	DF	Estimate	P	Model P	Model R^2
Removal	6, 22	-0.392	0.668	0.0068	0.63
Subdominant Evenness	6, 22	15.043	0.4629		
Subdominant Richness	6, 22	0.392	0.116		
Subdominant Biomass	6, 22	-4.274	**0.041**		
Light Availability	6, 22	-0.002	0.699		
Lespedeza Foliar Cover	6, 22	1.829	**0.003**		
			Seedling Survival		
	DF	Estimate	P	Model P	Model R^2
Removal	6, 22	-0.106	0.349	0.1249	0.43
Subdominant Evenness	6, 22	2.631	0.294		
Subdominant Richness	6, 22	0.015	0.596		
Subdominant Biomass	6, 22	-0.541	**0.033**		
Light Availability	6, 22	<0.0001	0.869		
Lespedeza Foliar Cover	6, 22	0.089	0.168		

Table 3.3 ANOVA summary for effects of dominant species removal by date on light availability and soil volumetric water content in 2006. P-values ≤ 0.05 are in bold.

		Light Availability (μmol photons m^2 sec^1)			
		Mean	SE	F	P
June	Control	201.6[a]	27.4	5.15	**0.008**
	No *Solidago*	396.9[ab]	31.2		
	No *Verbesina*	319.8[a]	59.4		
	No Dominants	471.7[b]	71.4		
July	Control	135.7[a]	72.0	6.73	**0.003**
	No *Solidago*	344.2[a]	52.0		
	No *Verbesina*	339.1[a]	97.6		
	No Dominants	588.5[b]	54.7		
August	Control	120.3[a]	29.8	6.27	**0.004**
	No *Solidago*	329.2[a]	59.8		
	No *Verbesina*	277.0[a]	67.7		
	No Dominants	545.8[b]	103.4		
		Soil Volumetric Water Content (%)			
		Mean	SE	F	P
April	Control	23.2	0.6	1.97	0.150
	No *Solidago*	21.2	0.6		
	No *Verbesina*	21.1	0.8		
	No Dominants	20.7	0.9		
May	Control	31.7	0.8	0.04	0.988
	No *Solidago*	32.0	0.7		
	No *Verbesina*	31.8	0.4		
	No Dominants	31.5	0.8		
July	Control	12.0[a]	0.5		
	No *Solidago*	14.8[b]	0.7	5.59	**0.006**
	No *Verbesina*	11.7[a]	0.8		
	No Dominants	12.7[a]	0.8		

a.



b.

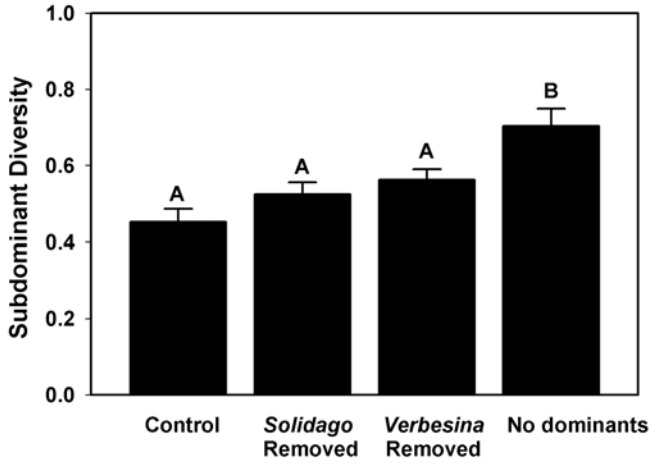
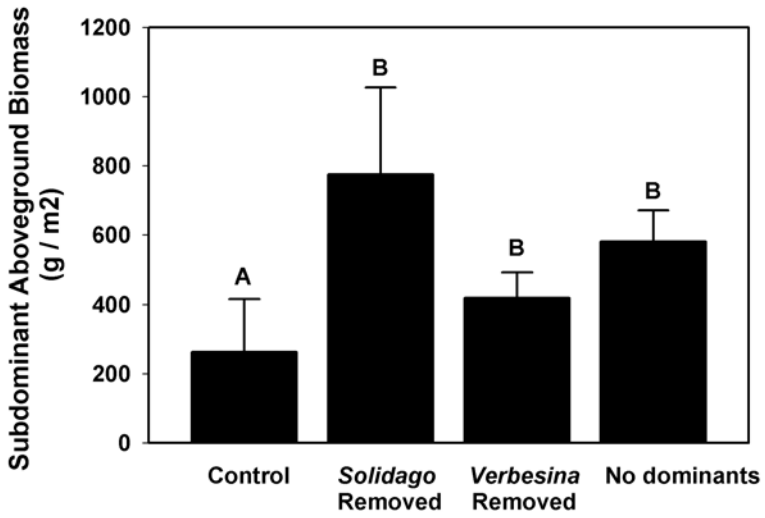


Figure 3.1 Effect of dominant species removal on mean (± SE; n=6) a) subdominant evenness, and b) subdominant diversity. Treatments: Control=no removal, No Solidago = *Solidago* removal, No Verbesina = *Verbesina* removal, No dominants= *Solidago* and *Verbesina* removal respectively. Different letters represent statistical difference at alpha=0.05 using Tukey's HSD means separation test.

a.



b.

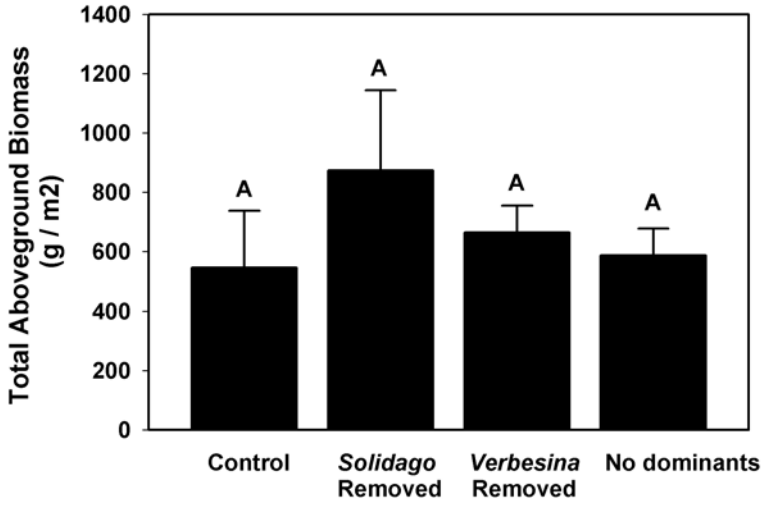


Figure 3.2 Effect of dominant species removal on a) subdominant community biomass and b) total community biomass. Values are mean (± SE; n=6). Treatments: Control=no removal, No Solidago = *Solidago* removal, No Verbesina = *Verbesina* removal, No dominants= *Solidago* and *Verbesina* removal respectively. Different letters represent statistical difference at alpha=0.05 using Tukey's HSD means separation test.

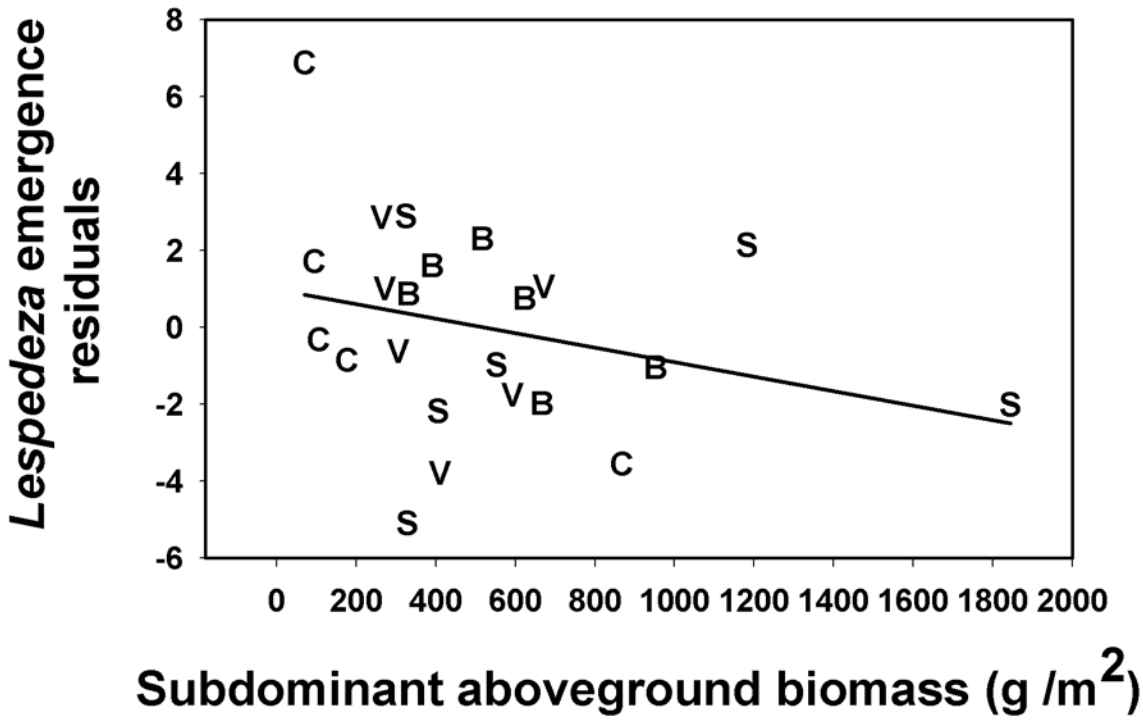


Figure 3.3 A plot of the residuals of *Lespedeza* emergence from an ANCOVA including the main effects (Control, *Solidago* removal, *Verbesina* removal, *Solidago* and *Verbesina* removal) and the covariates (subdominant richness and evenness and foliar cover of *Lespedeza*) against biomass of the subdominant community. The line is the best fit linear regression. Symbols: C=control, V=*Verbesina* removed, S=*Solidago* removed, B=*Solidago* and *Verbesina* removed.

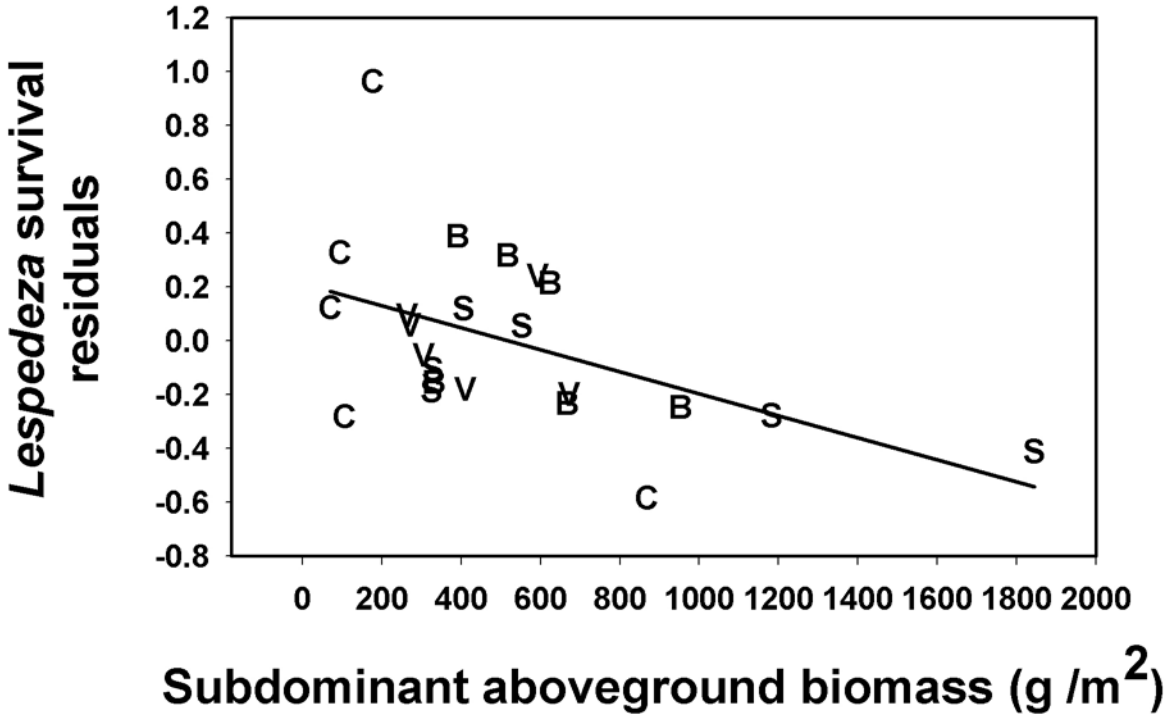


Figure 3.4 A plot of the residuals of *Lespedeza* survival from an ANCOVA including the main effects (Control, *Solidago* removal, *Verbesina* removal, *Solidago* and *Verbesina* removal) and the covariates (subdominant richness and evenness and foliar cover of *Lespedeza*) against biomass of the subdominant community. The line is the best fit linear regression. Symbols: C=control, V=*Verbesina* removed, S=*Solidago* removed, B=*Solidago* and *Verbesina* removed.

CHAPTER 4

Community invasibility across space: Does resource availability matter?

Abstract

Because biological invasions threaten the integrity of natural ecosystems, much research on community invasibility has focused on the controls on establishment and whether those controls vary with spatial scale. Our study investigated the role of both biotic and abiotic factors associated with the initial establishment of *Lespedeza cuneata* (hereafter *Lespedeza*) and its abundance at several spatial scales. In particular, we asked: (1) Does resource availability affect community structure and the establishment of *Lespedeza* in local old-field communities? and (2) Are resource availability and community structure associated with *Lespedeza* abundance across spatial scales, from 1-m^2 quadrats, 50-m^2 transects and entire old-fields? To answer the first question, we manipulated soil nitrogen (N) availability at three levels in existing old-field communities and tracked emergence and survivorship of two *Lespedeza* seedling cohorts over two years. To address the second question, we performed surveys of *Lespedeza* cover across 17 old fields at three spatial scales: 1-m^2 quadrats, 50-m^2 transects and entire old-fields.

Lespedeza seedling density was reduced in nitrogen added plots when compared to ambient and nitrogen-reduced plots. Total biomass was greater in N-elevated plots when compared to N-reduced plots (P <0.05), while mature *Lespedeza* cover was lower. Both light availability and soil moisture were reduced in soils with elevated N compared to N-reduced plots only early in the growing season (date × nutrients: $P < 0.001$). Finally, N-added plots negatively affected *Lespedeza* establishment via direct positive effects on the resident community. In particular, total aboveground biomass in N-added plots was on average 30 % and 40 % greater than ambient and N-reduced plots respectively. The broad-scale surveys indicated that similar biotic factors predicted *Lespedeza* foliar cover

across multiple spatial scales. In fact, dominant species biomass (*Solidago altissima, Verbesina virginica* and V. *occidentalis*), as well as the biomass of other N-fixing species, was negatively associated with *Lespedeza* cover at local and landscape scales. However, soil nutrient availability was not related to *Lespedeza* abundance at any spatial scale. In sum, these results suggest that biotic and abiotic factors associated with establishment of an invasive plant species at local scales are not necessarily related to its distribution at landscape scales.

Keywords: *resource availability, invasibility, spatial scale, establishment, Lespedeza cuneata.*

Introduction

Biological invasions can alter the structure and function of native communities (Mack et al. 2000, Levine et al. 2003, Mack and D'Antonio 2003). Thus, understanding the factors that limit invasions at different stages of invasion is critical, because studies have shown that the factors associated with exotic species establishment might not predict the ultimate spread of exotic species (Kolar and Lodge, 2002) and that they vary with spatial scale.

The availability of resources might influence the success of exotic species across stages of invasion (Davis et al. 2000). Recent studies have documented positive effects of increases in resource availability on the establishment (Hobbs and Atkins 1988) and population growth of exotic species (Hobbs and Atkins 1988, Huenneke et al. 1990, Wedin and Tilman 1996). The proposed mechanism for the positive effects of resources on the growth of exotic populations is that increases in nutrient availability relieve exotic species from competitive effects imposed by native species (Davis et al. 2000). But other studies demonstrate negative effects of resource additions on the establishment by exotic species (Burke and Grime 1996). The negative effects might arise when native species respond to increases in resource availability and reduce the availability of other limiting resources (i.e. light, soil moisture) otherwise available or create a barrier for successful colonization by exotics. This discrepancy among studies suggests that more experimental studies, coupled with observational studies across landscapes, are necessary to understand whether and how resource availability limits invasions (i.e. establishment and population growth). Here I focus on how resources, in particular soil nitrogen, influence the

establishment and distribution *Lespedeza cuneata* (hereafter *Lespedeza*) in old fields in east Tennessee, USA.

Lespedeza, a perennial nitrogen-fixer, was introduced from Japan into US old fields, oak savannas and prairie communities (Guernsey 1970) and is considered a rank one invasive species in several US states owing to its negative effects on community structure and ecosystem function (Price and Weltzin 2003, Brandon et al. 2004, Garten et al. 2008). Dominance by *Lespedeza* has been associated with reductions in native plant species evenness and diversity, along with decreases in total aboveground biomass production (Price and Weltzin 2003). Moreover, *Lespedeza* has been shown to contribute to ca. half of the nitrogen pools in old-field communities, altering species composition and nitrogen cycling (Garten et al. 2008).

Recent studies have shown that resource availability can control the population growth of *Lespedeza* species at small spatial scales (Ritchie and Tilman 1995, Brandon et al. 2004, Sanders et al. 2007). For example, in this system Sanders et al. (2007) found both *Lespedeza* percent foliar cover and density of individuals to be lower in N-added plots when insects were reduced and propagules were added. Similarly, Ritchie and Tilman (1995) found that soil macronutrient amendments reduced the cover of *Lespedeza capitata* in old-field communities. Nonetheless, no studies have addressed the role of resource availability on the seedling establishment of *Lespedeza*.

This study aimed to understand the role of biotic and abiotic factors associated with early establishment and persistence of *Lespedeza* in old-field plant community across spatial scales. First, we experimentally manipulated soil N availability at three levels to examine the effects of soil N availability on establishment and persistence of

Lespedeza over two growing seasons. Second, we conducted a survey of 250 1-m^2 plots in 17 old-field plant communities to ask whether the patterns we documented in the small-scale experimental manipulations were supported in intact old-field communities across spatial scales.

Methods

Experimental Study

We conducted this experiment in an old field at Oak Ridge National Environmental Research Park, near Oak Ridge, Tennessee (35° 58′ N 84° 17′ W). The old field was used for agriculture until 1943 and has been managed with annual mowing each spring since 2001 to reduce woody plant encroachment. The soil has a silty clay loam texture and is classified as Typic Hapludult. Mean annual rainfall is 1322 mm and air temperature ranges from 2.7 °C (January) to 31.2 °C (July). Dominant plant species at this site, and also across old fields in the area, include *Solidago altissima*, *Verbesina occidentalis* and *Verbesina virginica*, which comprise approximately 40% of total aboveground biomass in this system (Souza et al. In review). In addition, approximately 60 subordinate herbaceous and woody native and introduced plant species, including *Lespedeza*, occur at the study site and make up the remainder of the total aboveground biomass. We chose *Lespedeza* as it is the most common exotic species in old fields near our site (Souza et al. In review) and the fourth most abundant species in local old-field communities (Souza et al. In review).

Experimental Design

In a completely randomized design, we set up 72 3 m × 3 m plots spaced with 2-m walkways among the plots in an existing old-field community. The entire field was surrounded by a 3-m tall fence to exclude deer. Each spring since 2004, we have manipulated soil nitrogen (N) availability at three levels: control (no manipulation), soil N-addition (application of urea fertilizer at a rate of 10 g N per m^2 yr^{-1}), and soil N-

reduction (application of carbon in the form of sucrose at a rate of 1,000 g C per m^2). Application of sucrose, which is 46% C in a molecular form readily available to microbes, results in immobilization of plant-available N in the soil solution. These rates are consistent with other studies investigating controls of N and C on grassland and old-field ecosystems (e.g., McLendon and Redente 1992, Siemann 1998). We were able to significantly ($P < 0.0001$) increase soil nitrogen availability in N-added plots by 5-fold relative to control plots and 20-fold relative to N-reduced plots in 2004. In 2005, soil nitrogen availability was greater ($P < 0.0001$) in N-added plots by 2-fold relative to control and 18-fold relative to N-reduced plots (Sanders et al. 2007).

In order to control for dispersal limitation, this study initially focused on only the 36 plots to which propagules of *Lespedeza* were added. For these 36 plots, we broadcast approximately 1,700 *Lespedeza cuneata* seeds m^{-2} (obtained from Ernst Conservation Seeds, Meadville, PA) to each plot in February of 2005 and 2006.

Establishment of Lespedeza

We censused emerging *Lespedeza* seedlings monthly from May - October in 2005 and March - June in 2006 in order to quantify seedling establishment. We established two permanent 0.4 m × 0.4 m quadrats in each of the 36 plots, approximately 0.5 m from the edge of the plot. We recorded the number of seedlings that emerged and died within each permanent 0.16 m^2 quadrat and quantified the persistence of seedlings of the 2005 cohort by calculating the proportion of seedlings that resprouted the following year. For the 2006 cohort, we recorded the emerged and dead seedlings within 18 of the 36 3 m × 3 m plots excluding 18 plots where insects had been reduced. While seedling dynamics constitute only the initial steps in invasion success, their importance in affecting the

distribution of species in grassland systems has been supported by several studies (Gross and Werner 1982, Foster 2002).

Mature *Lespedeza* individuals can be an additional source of propagule rain, and their response to soil nutrients can be important when considering *Lespedeza* seedling establishment. We therefore estimated the foliar cover of mature *Lespedeza* individuals using a modified Braun-Blanquet cover class scale (Braun-Blanquet 1932) in September of both 2004 and 2005. The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-100%. We asked whether the abundance of *Lespedeza* adults is related to seedling establishment.

Community-level responses

To understand whether the intact plant community (all species except *Lespedeza*) responded to the nutrient amendments and in turn influenced *Lespedeza* establishment, we also quantified plant community richness in July of 2005 and total aboveground biomass in September of 2005 and 2006. We obtained total aboveground biomass by clipping to ground level all plants within a randomly placed 0.5 m × 1 m quadrat within each 9-m^2 plot. We categorized each clipped stem into one of the following groups: *Solidago, Verbesina, Lespedeza* and other biomass (subdominant community). Clipped biomass was oven-dried at 60 °C for 48 hours, then weighed.

Environmental variables

We estimated light availability, percent soil volumetric water content (VWC), and soil N availability throughout the 2005 and 2006 growing seasons. We used a line-integrating ceptometer (Decagon Accupar, Decagon Devices, Pullman, WA) to measure light availability below the canopy 2 cm from the soil surface at four locations within the 3 m

× 3 m plots monthly in 2005 and 2006. To measure soil VWC, we installed 2 time domain reflectometers (TDR 100, Campbell Scientific, UK) in each 3 m × 3 m plot recording percent VWC monthly in both 2005 and 2006. To assess the availability of NO_3-N and NH_4-N in the soil solution, we placed mixed-bed ion-exchange resin bags in nylon stockings (H-OH form, #R231- 500, Fisher Scientific International Inc., Pittsburgh, PA) at 5-cm soil depth at two locations in each of the 24 experimental plots (Hart et al. 1994). Resin bags were placed into the plots in June 2005 and removed in October 2005. Upon removal from the field, resins were air-dried in paper bags, resins from each plot were combined, and 2 g of resins from each plot were extracted with 2 M KCl. The extracts were then filtered on Whatman no. 1 filter paper after rinsing with dionized water and frozen prior to analysis for concentration of NO_3^- and NH_4^+. Pool sizes of NO_3^- and NH_4^+ were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000, Hach Corporation, Loveland, OH), using the indophenol-blue (Lachat Instruments, Inc. 1990) and cadmium reduction-diazotization (Lachat Instruments, Inc. 1992) methods, respectively. All values of soil ammonium and nitrate expressed in the manuscript are based on air-dried resins.

Statistical Analysis

We tested for the effects of soil nitrogen availability on *Lespedeza* seedling establishment and persistence of *Lespedeza* using an ANOVA design, with N-treatment (3 levels) as the main factor in the model. Also, we used date as the repeated factor in a repeated measures ANOVA design testing for the effects of the soil nitrogen amendments, time and their interaction on *Lespedeza* seedling establishment in 2005 and 2006.

We also built ANCOVA models with soil nitrogen amendment (3 levels) as the main factor along with several biotic and abiotic covariates that might account for *Lespedeza* seedling establishment. In order to select relevant biotic and abiotic covariates for our model, we generated a correlation matrix among biotic and abiotic covariates and *Lespedeza* seedling establishment across all months. We included biotic (*Verbesina* biomass, *Solidago* biomass, total biomass, mature *Lespedeza* cover) and abiotic (light, soil moisture, soil nitrogen) factors in our correlation matrix.

We tested for the effects of soil nitrogen availability on both biotic (species richness, total community biomass) and abiotic (light and soil moisture availability) community response variables. We used mature *Lespedeza* cover and total aboveground biomass, as well as light and soil moisture availability, as response variables, with N-treatment as the main factor in the model and used a Shapiro-Wilk W Test to determine whether distributions met normality assumptions. We applied the transformations to variables that did not meet normality assumptions. We log-transformed seedling density (log(x)) only in 2005 but applied natural log transformation to mature *Lespedeza* foliar cover (ln(x+1)) during both 2005 and 2006.

Observational Study

We randomly chose 17 old fields ranging in size from 0.5 – 7.0 ha based on the presence of well-defined boundaries such as forests or roadcuts. We randomly placed two to six (depending on field area) 50-m^2 transects in each field. Along each transect, we placed five 1-m^2 plots spaced 10 meters apart.

In each 1-m^2 plot, we estimated the foliar cover of *Lespedeza* using a modified

Braun-Blanquet (Braun-Blanquet 1932) and total richness (minus *Lespedeza*) in July 2006. We also estimated aboveground biomass in a randomly placed 0.5 m × 1 m subplot within each 1-m^2 plot. To estimate aboveground biomass, we clipped all individuals rooted inside the sampling quadrats to approximately 1 cm from the soil surface and sorted the biomass into *Solidago* biomass, *Verbesina* biomass, other N-fixer biomass, and total aboveground biomass. We then oven-dried the samples for 48 hours at 65° C and weighed them.

Environmental variables

We estimated light availability and percent volumetric water content in each of the 1-m^2 plots using the same methods as mentioned in the previous section describing the experimental study. We also collected a 10 cm soil core from the center of each 1-m^2 quadrat to quantify soil texture (percent sand and clay), bulk density, gravimetric water content, pH, and potential net nitrogen ($NO3^-$, $NH4^+$ and total N) mineralization. To estimate potential net nitrogen mineralization, we incubated soil sub-samples from each quadrat for 33 days and compared nitrogen availability of the incubated sub-samples with that of sub-samples extracted prior to incubation. Soil nitrate (NO_3^-) and ammonium (NH_4^+) in samples were extracted by the procedures described in the experimental study section.

Statistical analyses

To elucidate the biotic and abiotic factors associated with *Lespedeza* abundance in the observational study, we built multiple regression models at each spatial scale using all possible regressions for variable selection. We used the Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) to evaluate multiple

regression models accounting for variation in *Lespedeza* abundance. Prior to regression analysis, we tested for significant correlations between all predictor variables using Pearson's correlation coefficient. Predictor variables with significant pairwise correlation coefficients ($P \leq 0.05$) were not used in the same model. All regression analyses were performed using SAS 9.1.3 (SAS Institute, Inc., Cary, NC).

At the 1-m^2 plot, 50-m^2 transect, and old-field scales we included the measured biotic (*Solidago* biomass, *Verbesina* biomass, N-fixer biomass, total biomass) and abiotic variables (light availability, soil moisture, and potential soil nitrogen availability) in our model selection procedures. For 50-m^2 transects, biotic variables were calculated as the sum of 1-m^2 plots in each transect. Likewise, at the old-field scale, biotic variables were calculated by obtaining the sum of 50-m^2 transects within each field.

Results

Lespedeza seedling establishment was 15 × lower in N-added plots than N-reduced and control plots during two growing seasons. In 2005, time (Wilks' λ =0.63, df = 2,33, P = 0.002) and time × nutrient interaction (Wilks' λ =0.68, df = 2,33, P = 0.057) affected *Lespedeza* seedling establishment. N-added plots had on average 5 seedlings m^{-2} compared to 84 and 77 seedlings m^{-2} in N-reduced and control plots, respectively (Figure 1). In 2006, neither time (Wilks' λ =0.75, df = 2,15, P = 0.133) nor the time × nutrient interaction (Wilks' λ =0.80, df = 2,15, P = 0.534) affected seedling establishment. But the effects of the treatment alone in 2006 were strong: N-reduced plots had 90 *Lespedeza* seedlings m^{-2} relative to 1 seedling m^{-2} in N-added plots (Figure 4.1). However, the establishment of *Lespedeza* seedlings in N-added plots did not differ from control plots across seasons in either year ($P > 0.05$). Furthermore, the negative impact of elevated soil N increased as the growing season progresses (Figure 4.1) in both 2005 and 2006.

Lespedeza seedling persistence was 2 × and 5 × lower in N-added plots than in ambient and N-reduced plots respectively in a local old-field community. For example, *Lespedeza* seedling persistence was 76 % lower in N-added plots compared to N-reduced plots (F = 4.42, P = 0.03). On the other hand, neither the reduction of (P = 0.98) nor the addition of soil nitrogen (P = 0.23) affected *Lespedeza* seedling persistence relative to control plots (Figure 4.2).

Mature *Lespedeza* cover was 30% lower in N-added plots compared to control and N-added plots across two growing seasons. In 2005, foliar cover of *Lespedeza* individuals was 8 × lower in N-added plots than in control plots and 4× lower in N-added

plots than in N-reduced plots (Figure 4.3). By 2006, soil nitrogen had no effect ($P = 0.22$) on *Lespedeza* foliar cover (Figure 4.3).

N-added plots had on average 30 % lower light availability than control and N-reduced plots in both 2005 and 2006. In 2005, time (Wilks' $\lambda = 0.26$, df = 2,33, $P < 0.0001$) and the time × nutrient interaction (Wilks' $\lambda = 0.29$, df = 2,33, $P < 0.0001$) affected light availability in this old-field community. In fact, N-added plots had on average 14 % lower light than controls and 47% lower light than N-reduced plots. By 2006, only time (Wilks' $\lambda = 0.05$, df = 2,15, $P < 0.0001$) affected light availability, whereas time x nutrient interaction (Wilks' $\lambda = 0.53$, df = 2,15, $P = 0.20$) no longer affected light. N-added plots had on average 35 % less light than controls and 40 % less light than N-reduced plots.

Soil moisture availability was 15 % lower in N-added plots than for two growing seasons. In 2005, time (Wilks' $\lambda = 0.01$, df = 2,33, $P < 0.0001$) and the time × nutrient interaction (Wilks' $\lambda = 0.59$, df = 2,33, $P = 0.02$) affected soil moisture in this old-field community. In fact, volumetric water contact was 5% lower in N-added plots than in control plots and light availability was 15 % lower in N-reduced plots than in control plots. By 2006, both time (Wilks' $\lambda = 0.04$, df = 2,15, $P < 0.0001$) and the time x nutrient interaction (Wilks' $\lambda = 0.43$, df = 2,15, $P = 0.06$) affected soil moisture availability. N-added plots had on average 10 % lower light availability than did controls and 24% lower light than N-reduced plots.

Light availability and mature *Lespedeza* cover were positively associated with *Lespedeza* seedling establishment (Table 4.1). In fact, higher light availability only early in the growing season ($0.49 > r < 0.60$, $P < 0.01$) along with greater cover of mature

Lespedeza individuals (Table 4.1, Figure 4.3) promoted *Lespedeza* seedling establishment across time in both 2005 and 2006.

Mature established *Lespedeza* became the only important biotic covariate in predicting *Lespedeza* seedling establishment in 2005 and 2006 (Table 4.2). In fact, mature *Lespedeza* was consistently related to increased seedling establishment during the growing season (May-October) in 2005 but was important for establishment only early in the season (March) in 2006.

Although soil nitrogen did not affect species richness (F = 0.86, P = 0.43), it stimulated total aboveground biomass, reducing light and soil moisture availability in both 2005 and 2006. While soil nitrogen had marginal (P = 0.09) effects on total aboveground biomass in 2005, by 2006, N-added plots had 30 % greater (F = 5.2, df = P = 0.02) total aboveground biomass compared to controls and 40 % greater biomass than N-reduced plots (Figure 4.5). Consequently, increases in biomass negatively affected light availability (R^2 = 0.30, P = 0.02) in 2006 but not in 2005 (P > 0.05)(Figure 4.6).

Observational study

Biotic rather than abiotic factors, accounted for the variation in *Lespedeza* cover across spatial scales in old-field communities. Across 1-m^2 plots, aboveground biomass was positively associated with *Lespedeza* cover, whereas the biomass of N-fixers and dominant species was negatively associated with abundance of *Lespedeza* (Table 4.3, Figure 4.4). At the old-field scale, fields with greater N-fixer biomass and total aboveground biomass had lower *Lespedeza* cover compared to fields with lower N-fixer and total aboveground biomass (Table 4.3, Figure 4.4). While total aboveground biomass accounted for ~50% of the variation in *Lespedeza* cover, nitrogen-fixer biomass

accounted for between 30 % to 100 % of the variation in *Lespedeza* cover in multiple regression models at spatial scales (Table 4.3). *Solidago* biomass accounted for only 10 % of the variation in *Lespedeza* cover across two spatial scales.

The relationship between *Lespedeza* abundance and total aboveground biomass changed with spatial scale. At the 1-m^2 plot scale, *Lespedeza* cover was greater in plots where aboveground biomass was higher than in 1-m^2 plots where aboveground biomass was lower (Table 4). In fact, aboveground biomass accounted for half of the variation of *Lespedeza* cover in 1-m^2 plots. But, at the scale of entire old fields, total aboveground biomass was negatively associated with *Lespedeza* cover; old fields with greater community biomass were less invaded than fields with lower biomass (Table 4).

Overall, multiple regression models predicting *Lespedeza* cover at the old-field scale accounted for a greater amount of variation (68%) in *Lespedeza* abundance than multiple regression models at the transect (13%) or plot-scales (10%). Surprisingly, only biotic variables were important predicting *Lespedeza* abundance across spatial scales, meaning that resource availability was not associated with the successful establishment of *Lespedeza*.

Discussion

Increases in resource availability deter seedling establishment by Lespedeza

Lespedeza seedling establishment and persistence were lowered in plots where soil N was added than in plots where soil N was reduced. Similarly, Sanders et al. (2007) and Ritchie and Tilman (1995) found that increasing soil nitrogen or increasing soil macronutrients (i.e., non-nitrogen), respectively, decreased *Lespedeza* establishment (i.e. cover and stem density). One proposed mechanism is that increases in soil N availability directly stimulate the production of resident plant species, consequently altering the abiotic environment (i.e. soil moisture, light or macronutrient limitation). Such alteration of microhabitat can decrease community invasibility if change in conditions or reduction in resources is limiting for invaders. For example, increases in aboveground biomass can affect *Lespedeza* establishment in two ways. First, greater aboveground biomass can result in greater litter accumulation, which serves as a physical barrier to the establishment and/ or persistence of *Lespedeza* seedlings (Rasran et al. 2007). Secondly, greater biomass production can result in lower soil moisture and/or light availability limiting seedling survival and subsequent persistence (Davis and Pelsor 2001).

N availability stimulates production of the resident community and alters the abiotic environment

Old-field community aboveground biomass increased in N-added plots compared to N-reduced plots. Other studies (Tilman 1984, 1987) have also found old-field ecosystems to be N-limited, with the abundance of resident plant species increasing under soil N-enrichment. In turn, both soil moisture and light availability decreased in N-added plots than in N-reduced plots. Davis and Pelsor (2001) increased soil moisture availability in an old-field community in

Minnesota. They found that light availability was lower in wet plots than in dry plots as a result of increases in aboveground biomass of three non-native grass species in wet plots. As a result, community invasibility in their system, by native forbs, was dependent on both disturbance (removing resident species) and resource availability (manipulating soil moisture). Plots where resident non-native species were absent and soil moisture increased had greater establishment by native forb species.

Although both light availability and mature *Lespedeza* cover promoted seedling establishment in both growing seasons, only mature *Lespedeza* cover became an important covariate in our ANCOVA model. Mature *Lespedeza* cover promoted the establishment of *Lespedeza* seedlings in two ways. An additional propagule rain by greater mature *Lespedeza* cover likely took place. Mature *Lespedeza* individuals can produce hundreds of seeds (Schutzenhofer and Knight 2007); greater numbers of individuals can contribute to greater establishment. Secondly, greater soil rhizobia surrounding mature *Lespedeza's* rhizosphere (Acharya et al. 2006) can promote seedling survival by stimulating seedling growth rates.

Lespedeza establishment across spatial scales is determined by biotic predictors

Unlike the experimental findings, soil nitrogen mineralization was not related to the abundance of *Lespedeza* across spatial scales in old-field communities. Instead, biotic predictors were strongly associated with the variation in *Lespedeza* abundance across spatial scales. For example, the abundance of other N-fixing species was consistently negatively associated with *Lespedeza* abundance across all spatial scales. It is likely that across 1-m^2 plots, as well as 50-m^2 transects and old fields, greater N-fixer abundance deter invasion by *Lespedeza* because established N-fixers are as well-adapted to low N environments as *Lespedeza* is and are potentially competitively superior. Alternatively, *Lespedeza*, especially at greater abundance, can

lower light availability limiting the abundance and distribution of shade-intolerant species, such as other N-fixing species (Tilman 1987). One may ask *Why won't Lespedeza limit itself?* Likely, *Lespedeza* individuals share bacteria in the same species in the genus *Rhizobia* and facilitation, rather than competition takes place within N-fixing species (i.e. within *Lespedeza cuneata*)

The 1-m^2 plots with greater biomass had greater *Lespedeza* cover than did 1-m^2 plots with lower biomass. However, old fields with greater total aboveground biomass exhibited lower abundance by *Lespedeza* compared to old-fields with lower total aboveground biomass. Although these are contrasting results, total aboveground biomass was a weak predictor accounting for only 5 % of *Lespedeza* cover at the 1-m^2 plot level, whereas it accounted for 40 % of the *Lespedeza* cover at the old-field scale. Greater aboveground biomass can contribute to greater litter accumulation and lower light availability which lowers both the establishment and growth of species in natural communities (Rasran et al. 2007).

Overall, we found that increasing soil N availability lowers initial invasion by *Lespedeza* in old-field communities. Likely, decreases in light availability, as well as lower cover of mature *Lespedeza* and increases in community biomass in N-added plots, reduced seedling establishment relative to N-reduced plots. In old-field communities, biotic factors accounted for *Lespedeza* abundance at three different spatial scales. In 1-m^2 plots, *Lespedeza* cover was promoted under greater aboveground biomass, but reduced with increases in N-fixer species. Old-field communities with either greater aboveground biomass or greater N-fixer biomass had the lowest abundance of *Lespedeza* than communities with lower total biomass or N-fixer biomass. The management of *Lespedeza* will depend on both stage of invasion and spatial scales

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List of References

List of References

Acharya, S.N., Kastelic, J.P., Beauchemin, K.A., and Messenger, D.F. 2006. A review research progress of cicer milkvetch (Astragalus cicer L.). *Canadian Journal of Plant Science* 86: 49-62

Brandon, A.L., Gibson, D.J., and Middleton, B.A. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native Lespedeza cuneata (Dum. Cours.) G. Don. *Biological Invasions* 6:483-493

Braun-Blanquet, J. 1932. Plant sociology. Transl. G. D. Fuller and H. S. Conrad. McGraw-Hill, New York. 539

Burke, M.J.W., and Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77:776-790

Davis, M.A., Grime, J.P., and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528-534

Davis, M. A., and Pelsor, M. 2001. Experimental support for a resource-based mechanistic model of invasiblity. *Ecology Letters* 4:421-428

Foster, B.L., Smith, V.H., Dickson, T. L., and Hildebrand, T. 2002. Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* 99:300-307

Garten, C.T., Classen, A.T., Norby, R. J., Brice, D.J., Weltzin, J.F., and Souza, L. 2008. Role of N-2-fixation in constructed old-field communities under different regimes of [CO2], temperature, and water availability. *Ecosystems* 11:125-137

Gross, K.L., and Werner, P.A. 1982. Colonizing abilities of biennial plant species in

relation to ground cover- implications for their distributions in a successional sere. *Ecology* 63:921-931

Hobbs, R.J., and Atkins, L. 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheat-belt *Australian Journal of Ecology* 13:171-179

Huenneke, L.F., Hamburg, S.P., Koide, R. , Mooney, H.A., and Vitousek, P.M. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology* 71:478-491

Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16:199-204

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., and Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:775-781

Mack, M.C., and D'Antonio, C.M. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecological Applications* 13:154-166

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710

McLendon, T., and Redente, E.F. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semi-arid sagebrush site. *Oecologia* 91:312-317

Price, C.A., and Weltzin, J.F. 2003. Managing non-native plant populations through

intensive community restoration in Cades Cove, Great Smoky Mountains National Park, USA. *Restoration Ecology* 11:351-358

Rasran, L., Vogt, K., and Jensen, K. 2007. Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient. *Folia Geobotanica* 42:271-288

Ritchie, M.E., and Tilman, D. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* 76:2648-2655

Sanders, N.J., Weltzin, J.F., Crutsinger, G.M. Fitzpatrick, M.C. Nunez, M.A., Oswalt, C.M., and Lane, K.E. 2007. Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88:2383-2391

Schutzenhofer, M.R., and Knight, T.M. 2007. Population-level effects of augmented herbivory on Lespedeza cuneata: Implications for biological control. *Ecological Applications* 17: 965-971

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057-2070

Smith, M.D., Wilcox, J.C., Kelly, T., and Knapp, A.K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106:253-262

Tilman, D. 1984. Plant dominance along and experimental gradient. *Ecology* 65:1445-1453

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57: 189-214.

Wedin, D.A., and Tilman, D. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274:1720-1723.

Appendix

Table 4.1 Correlation matrix of biotic (*Solidago biomass*, *Verbesina* biomass, Total biomass, Mature *Lespedeza* cover) and abiotic (light and soil moisture availability) variables against *Lespedeza* seedling establishment through time (March – October) in 2005 and 2006. Values in bold are statistically significant ($p < 0.05$).

2005	May		June		August		October	
Variable								
Light May	**0.4914**	**0.0023**	**0.5**	**0.002**	**0.492**	**0.002**	**0.6**	**0.001**
Light June	-0.1653	0.3353	-0.154	0.371	-0.137	0.425	-0.07	0.669
Light July	-0.0025	0.9884	-0.014	0.936	0.011	0.95	-0.03	0.839
Light August	0.056	0.7457	0.047	0.785	0.107	0.535	0.214	0.21
Soil Moisture May	0.2497	0.1481	0.194	0.264	0.205	0.237	0.167	0.339
Soil Moisture June	0.2038	0.2331	0.216	0.205	0.188	0.272	0.251	0.139
Soil Moisture July	0.265	0.1183	0.344	0.04	0.309	0.067	0.401	0.015
Soil Moisture September	0.139	0.4187	0.225	0.186	0.206	0.228	0.298	0.078
***Lespedeza* Cover**	**0.6286**	**<0.001**	**0.62**	**<0.001**	**0.566**	**<0.001**	**0.521**	**0.001**
***Solidago* Biomass**	-0.1907	0.2652	-0.233	0.171	-0.248	0.144	-0.274	0.106
***Verbesina* Biomass**	0.0397	0.8183	0.044	0.799	0.035	0.839	0.006	0.971
Total Biomass	-0.173	0.313	-0.237	0.163	-0.248	0.144	-0.299	0.077

Table 4.1 Continued

2006	March		May		June			
Variable								
Light April	0.4226	0.0806	0.2963	0.2325	**0.481**	**0.0433**	--	--
Light May	**0.7443**	**0.0004**	0.4668	0.0508	**0.589**	**0.0101**	--	--
Light June	**0.543**	**0.0199**	**0.6556**	**0.0031**	**0.6441**	**0.0039**	--	--
Soil Moisture April	0.1696	0.5012	0.1947	0.4388	-0.1238	0.6245	--	--
Soil Moisture May	0.4647	0.052	0.3742	0.1261	0.3289	0.1827	--	--
Soil Moisture June	0.4134	0.0882	**0.4949**	**0.0368**	0.3611	0.1409	--	--
***Lespedeza* Cover**	**0.5653**	**0.0145**	0.3746	0.1256	0.4473	0.0627	--	--
***Solidago* Biomass**	-0.3842	0.1155	-0.3344	0.1749	**-0.4885**	**0.0397**	--	--
***Verbesina* Biomass**	0.0434	0.8643	-0.2768	0.2661	-0.1728	0.4928	--	--
Total Biomass	-0.1574	0.5327	-0.0358	0.8879	-0.2879	0.2467	--	--

Table 4.2 ANCOVA table of the effects of soil nitrogen availability in the context of biotic (Mature *Lespedeza*) and abiotic (light availability) covariates. Values in bold are statistically significant ($p < 0.05$).

		***Lespedeza* May**		***Lespedeza* June**		***Lespedeza* August**		***Lespedeza* October**	
2005									
Variables	DF	F	P	F	P	F	P	F	P
Soil Nitrogen	2	0.34	0.713	2.01	0.151	3.01	0.061	0.69	0.510
Mature *Lespedeza*	1	21.48	**<0.001**	25.79	**<0.001**	21.64	**<0.001**	14.98	**<0.001**
Light Availability	1	1.41	0.243	0.04	0.848	0.14	0.715	1.53	0.225
		***Lespedeza* March**		***Lespedeza* May**		***Lespedeza* June**			
2006									
Variables	DF	F	P	F	P	F	P		
Soil Nitrogen	2	1.27	0.314	1.49	0.263	1.48	0.264		
Mature *Lespedeza*	1	7.74	**0.015**	0.19	0.664	2.33	0.150		
Light Availability	1	1.22	0.289	2.44	0.142	2.98	0.108		

Table 4.3 Best multiple regression models explaining the variation of *Lespedeza* abundance at three spatial scales: plots, transects, and fields.

Variable	DF	Parameter	P	Partial R2	Model R2	P
Old field						
Intercept	1	0.4085	0.1242		0.69	0.001
Total aboveground biomass	1	0.0007	0.0014	0.39		
N-fixer aboveground biomass	1	-0.0021	0.0156	0.221		
Solidago aboveground biomass	1	0.0009	0.0249	0.075		
50-m^2 transect						
Intercept	1	0.5613	<.0001	.	0.13	<.0001
N-fixer aboveround biomass	1	-0.0018	0.0102	0.13241		
1-m^2 plot						
Intercept	1	0.0629	0.0047	.	0.11	<.0001
Total aboveground biomass	1	0.0004	0.0001	0.05727		
N-fixer aboveground biomass	1	-0.0017	<.0001	0.03363		
Verbesina aboveground biomass	1	0.0005	0.0021	0.01499		
Solidago aboveground biomass	1	0.0005	0.0005	0.00317		

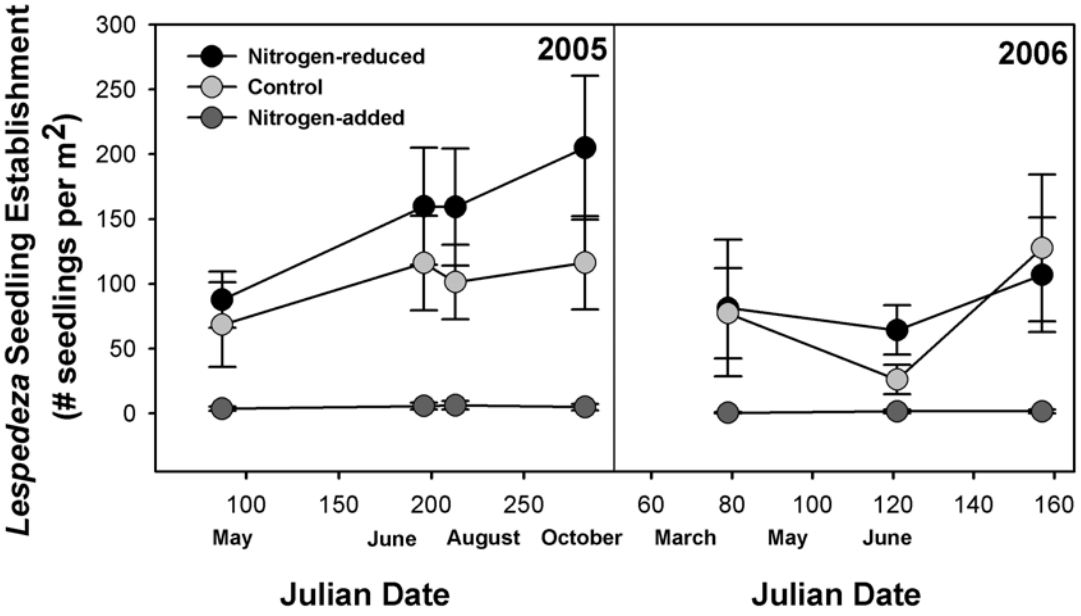


Figure 4.1 *Lespedeza* seedling establishment (seedlings per m^2) at each level of soil nitrogen availability in 2005 and 2006. Values are means and ± SE. Different letters represent statistical difference at alpha=0.05 using Tukey's HSD means separation test.

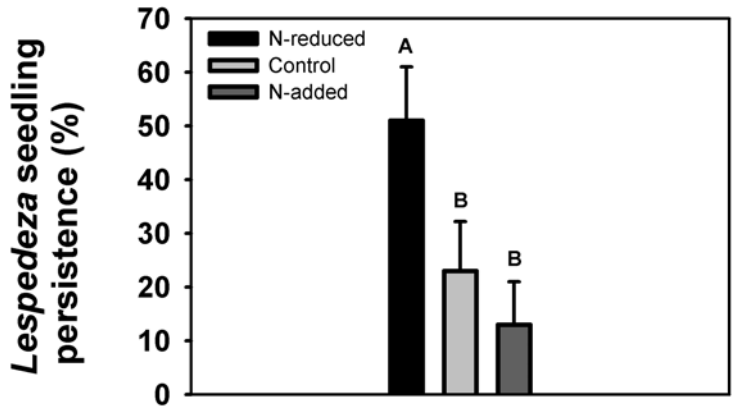


Figure 4.2 *Lespedeza* seedling persistence (seedlings per m^2) at each level of soil nitrogen availability in 2006. Values are means and ± SE. Different letters represent statistical difference at alpha=0.05 using Tukey's HSD means separation test.

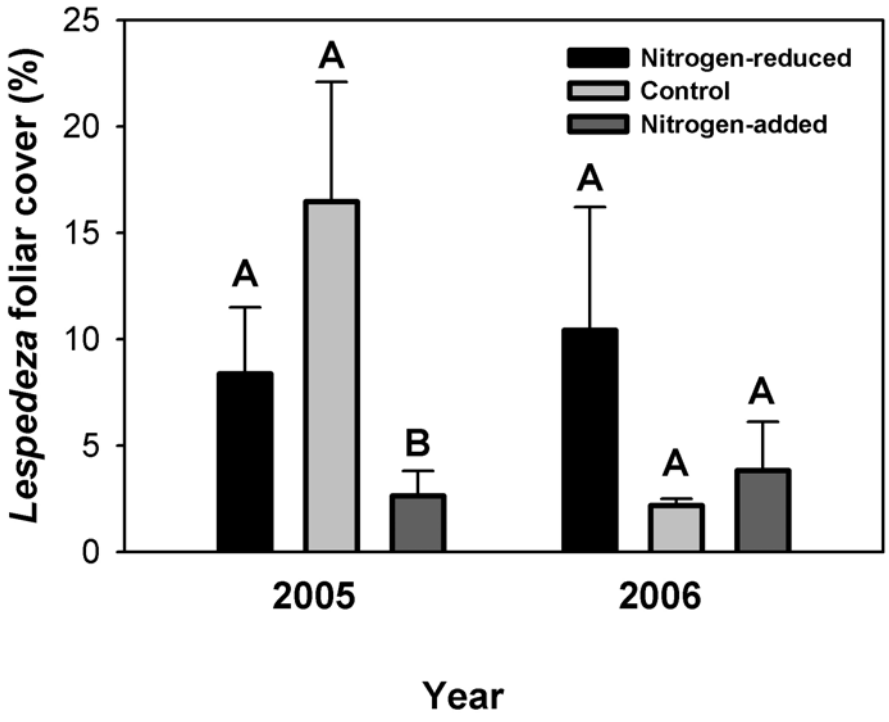


Figure 4.3 *Lespedeza* foliar cover (%) at each level of soil nitrogen availability in 2005 and 2006. Values are means and ± SE. Asterisks represent statistical difference among the treatment levels at alpha=0.05 using Tukey's HSD means separation test.

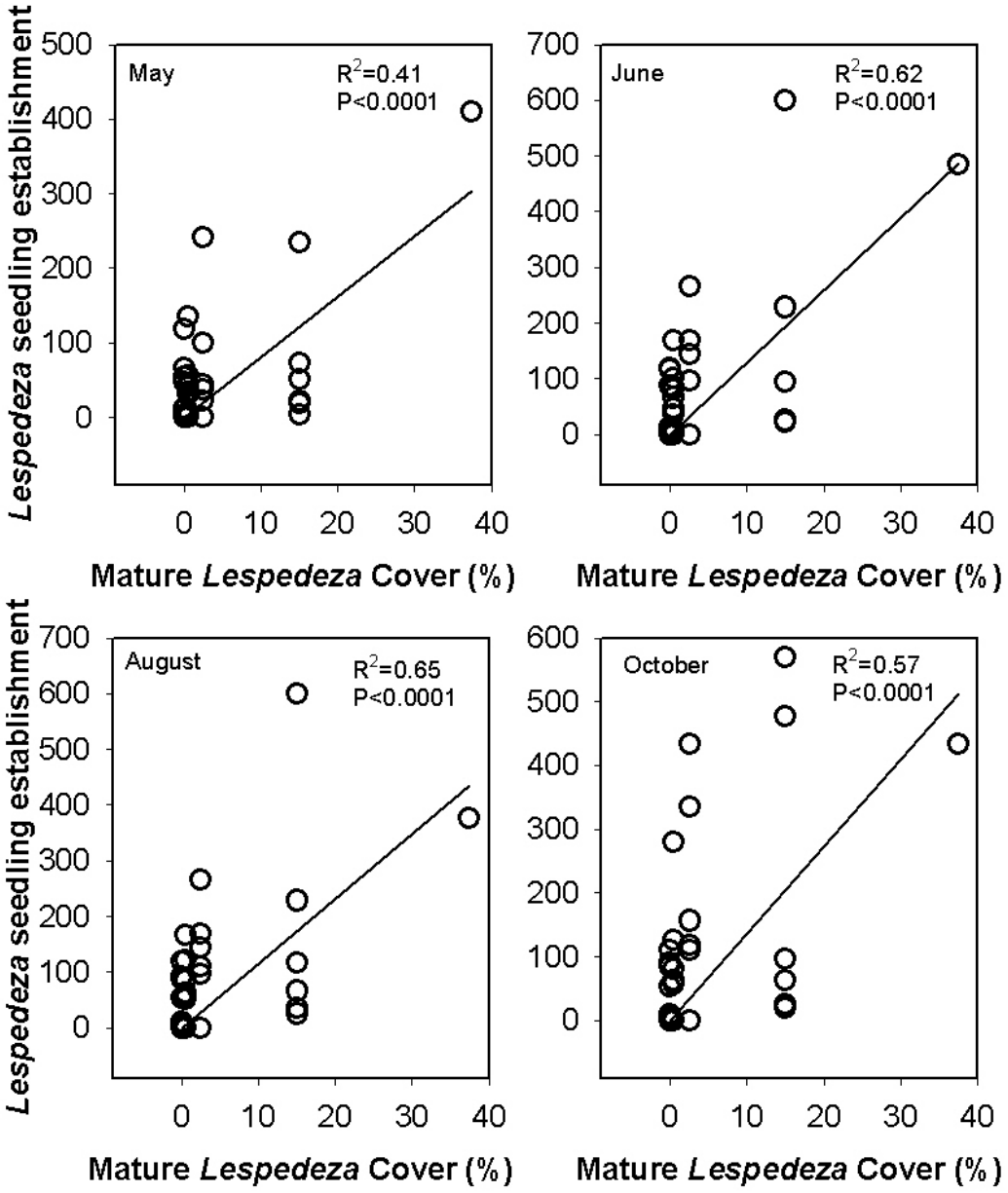


Figure 4.4 Linear relationship between established adult *Lespedeza* and *Lespedeza* seedling establishment through time in 2005 and 2006

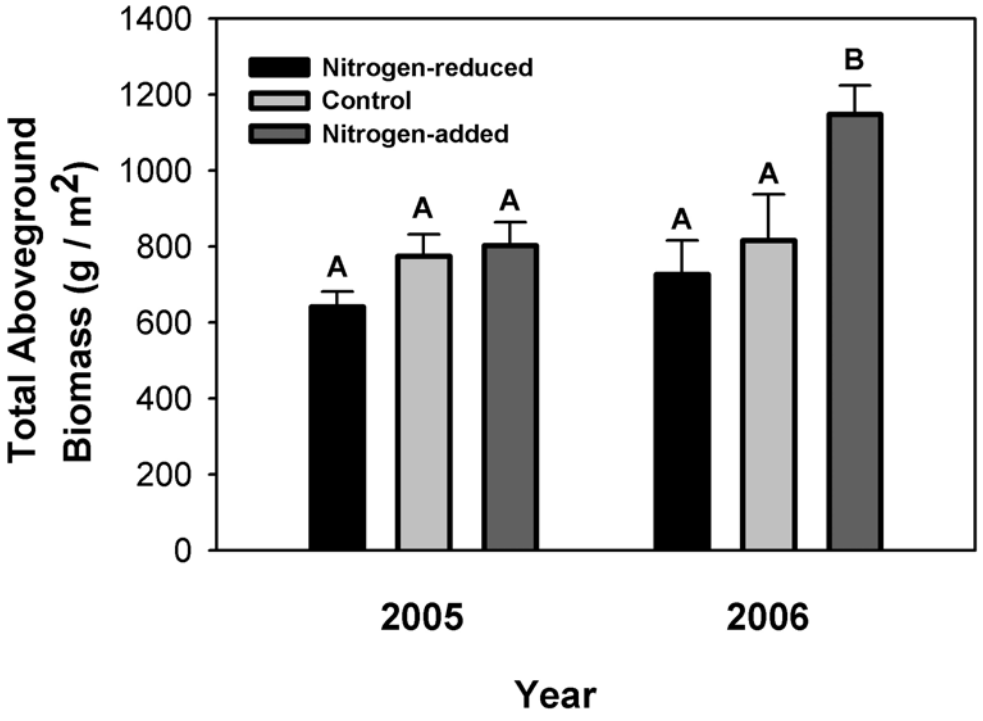


Figure 4.5 Total aboveground biomass at each level of soil nitrogen availability in 2005 and 2006. Values are means and ± SE . Asterisks represent statistical difference amongst treatment levels at alpha=0.05 using Tukey's HSD means separation test

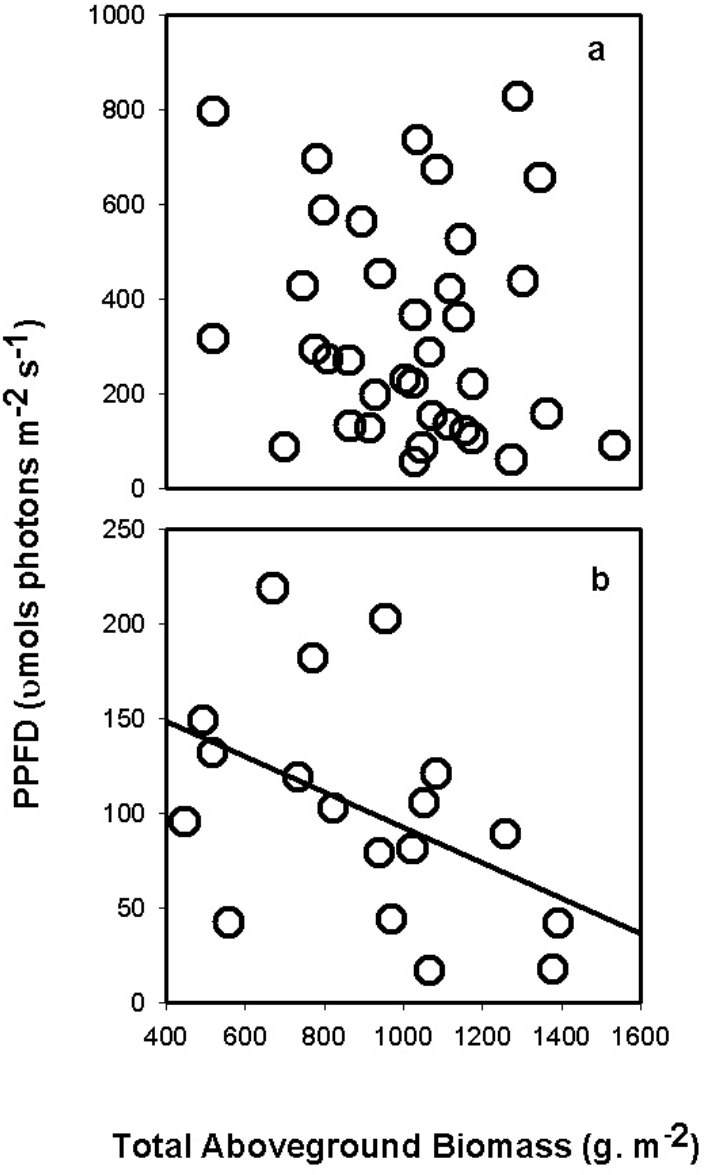


Figure 4.6 Linear relationship between total aboveground biomass and light availability in 2005 and 2006.

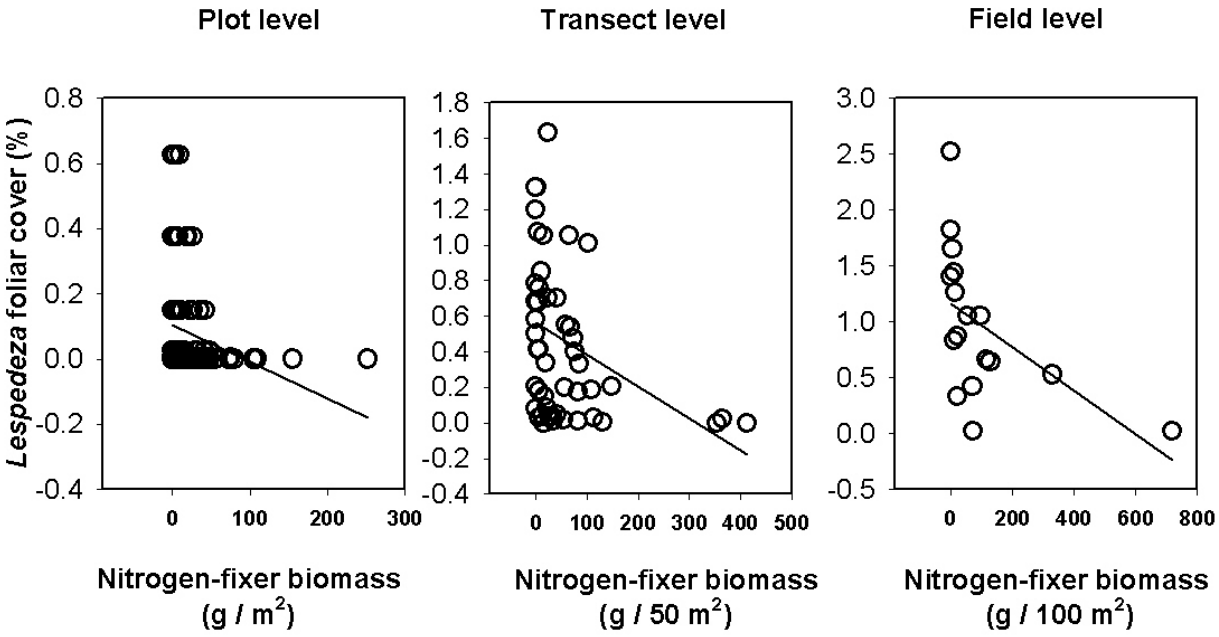


Figure 7. Linear relationship between *Lespedeza* foliar cover (%) and N-fixer aboveground biomass across 1-m^2 plots (a), 50-m^2 transects (b), and old fields (c) in 2005 and 2006

CHAPTER 5

Future Directions: Community invasibility across space beyond old fields

My dissertation work has demonstrated the important role of dominant species and resources in structuring plant communities and affecting their susceptibility to invasions across spatial scales in an old-field ecosystem. Although I have addressed age-old questions in both community and invasion ecology, my work has left many questions unanswered. I am sure that either a highly motivated undergraduate or graduate student will be able to take advantage of the following research opportunities.

- I chose *Lespedeza* as the focal invasive plant species in both my observational and experimental studies. But, there are several other invaders across old-field communities where establishment data is lacking. I think someone should address how resource availability and dominant species affect different stages of invasion by a variety of exotic species.
- In addition, studies addressing early establishment by exotics generally take place within single communities. Understanding how dominant species and resources affect community structure and invasibility (in particular early establishment by exotics) across several communities will be key to improve our inference on controls on invasions at landscape scales.
- The role of dominant species on community structure is often addressed by carrying out removal experiments. Species additions can also be a great way to answer the same questions. In fact, addressing how the addition of dominant species, such as *Solidago* and *Verbesina* affect community structure and consequently community invasibility will provided additional insights into the role of dominant species in old-field ecosystems.

- In chapter 4, I manipulated resource availability, in particular soil N, at only three levels. Likely, variation in soil N across old-field communities occurs in a gradient and it would be important to design an experiment to address community invasibility to several levels of soil N.
- Finally, understanding processes influencing the trajectories of communities over time is an important challenge posed to ecologists. Introduced species provide us with a natural experiment to address how biotic interactions affect community composition and function across space and time. I find that certain old-field communities are more invaded than others and tracking compositional changes of such communities through time will allow one to address how invaded communities change compared to less invaded communities.

Vita

Lara Souza was born in Sao Paulo, Brazil, where she grew up until the age of 17. At age 17, Lara participated in an exchange program where she attended Camden High School in Camden, South Carolina, for one year. She then attended Appalachian State University where she received her Bachelor of Science degree in Journalism with a minor in Biology in 1999. In Spring 2003, Lara received her Master of Science degree in Biology from Appalachian State University where she studied the patterns and processes of ozone-induced foliar injury in native plant species in Great Smoky Mountains National Park. In Fall 2003, Lara began a Ph.D. program at University of Tennessee where she investigated patterns and processes of community invasibility in an old-field ecosystem. She completed her dissertation in Summer of 2008. Lara's future research program will be to address community invasibility in the tropics and temperate grasslands at multiple spatial scales.