



Competitive Responses and Effects of the Invasive Grass *Microstegium vimineum* during Oak Woodland Restoration

Authors: Moyer, Sean A., and Brewer, J. Stephen

Source: Natural Areas Journal, 38(2) : 139-147

Published By: Natural Areas Association

URL: <https://doi.org/10.3375/043.038.0204>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

•

Competitive Responses and Effects of the Invasive Grass *Microstegium vimineum* during Oak Woodland Restoration

Sean A. Moyer^{1,3}

¹Department of Biology
University of Mississippi
University, MS 38677-1848

J. Stephen Brewer^{1,2}

² Corresponding author:
jbrewer@olemiss.edu; (662) 915-1077

³ Current address: Albany Pine Bush Preserve Commission, 195 New Karner Rd, Suite 1, Albany, NY 12205

Natural Areas Journal 38:139–147

ABSTRACT: The relevance of diversity–invasibility studies to the conservation of biodiversity has been questioned on grounds that species-rich assemblages may not deter invasion by competitively superior invaders. Few studies have compared the competitive effects of invaders on native species individually vs. in mixture. Using field experiments, we measured competition between an invasive grass, *Microstegium vimineum*, and six species of large native groundcover plants. We first examined whether planting six native species was more effective than planting an equivalent number of a single species in competitively suppressing *Microstegium*. Using a split-plot design, naturally occurring patches of *Microstegium* were treated with one of the two planting treatments or a control. We monitored *Microstegium* emergence and percent cover through 2015 and into the spring of 2016. We then tested the competitive effect of *Microstegium* on plantings of native species within *Microstegium* patches using a removal experiment in 2016. Although initial transplant survival was high in spring 2015, subsequent mortality during the growing season was also high in both planting treatments and, thus, there was no evidence of competitive suppression of *Microstegium*. In contrast, removal of *Microstegium* benefited the growth (and flowering) of native transplants in 2016, and all native species were more or less equally affected. These results suggest that neither high native diversity nor the presence of certain native species is likely to be effective in constraining the abundance of invaders demonstrated to have strong competitive effects on most or all native species under conditions that favor both native diversity and the invader.

Index terms: biodiversity–invasibility, competitive superiority, endemic, fire restoration, invasion resistance, oak woodland

INTRODUCTION

Nonnative species are a paradox in that ecologists have argued that they can both reduce and be reduced by species diversity. Numerous reviews on the impacts of nonnative invaders have revealed that there are at least a few high-profile species with strong competitive effects that can lead to significant losses of species diversity (Davis 2003; Levine et al. 2003; Gurevitch and Padilla 2004; Huston 2004; Ricciardi and Cohen 2007; Hejda et al. 2009; Powell et al. 2011; Brewer and Bailey 2014). On the other hand, theory and the results of several experiments have revealed that artificially assembled communities that are species-rich or that contain species functionally similar to potential invaders tend to competitively suppress invaders (Levine and D’Antonio 1999; Funk et al. 2008; Cleland et al. 2013; Price and Pärtel 2013). These seemingly contradictory conclusions suggest there is a need to better understand how invaders known to be strong competitors affect and are affected by diverse species assemblages.

Most studies of diversity-mediated resistance to invasion have focused on understanding community stability and assembly, rather than effective control of competitively superior invaders. Existing theory predicts that species-rich communities at competitive equilibrium can reduce

the successful establishment or abundance of invaders (Case 1990; Luh and Pimm 1993; Law and Morton 1996; Tilman 2004). Numerous experimental studies at small spatial scales appear to support theoretical predictions (Knops et al. 1999; Levine 2000; Naeem et al. 2000; Wilsey and Polley 2002; Zavaleta and Hulvey 2004; Maron and Marler 2007). However, with the exception of the empirical study by Maron and Marler (2007), none explicitly investigated whether the invaders had strong competitive effects on the resident species. It thus remains unclear in theory or in practice whether the complementary or multiplicative effects of species in mixture typically allow diverse assemblages to competitively suppress species that could outcompete each resident species in isolation. Invasions by competitively superior species would most likely cause catastrophic reductions in biodiversity and are the greatest cause for concern (Brewer and Bailey 2014). It is, therefore, imperative to assess the combined competitive effects of species-rich communities on invaders known to be competitively superior to most or all of the resident species in an assemblage.

In contrast to theory and artificial experiments on diversity-mediated resistance, a meta-analysis of field studies found very few cases in which competitive resistance was strong enough to completely repel

invasions (Levine et al. 2004). High propagule supplies frequently allow invaders to overcome diversity-mediated resistance to invasion (Levine 2000; Von Holle and Simberloff 2005). Hence, Levine et al. (2004) hypothesized that competition from native species is more likely to constrain the abundance of invaders than to completely block entry by invaders. To our knowledge, however, this hypothesis has rarely been tested for highly competitive invaders. Furthermore, some management actions that increase diversity (e.g., prescribed burning) also have the potential to increase the abundance (Keeley 2006) and perhaps even the competitive ability (Brewer 2011a) of some invaders. For diversity management to be relevant to control of invasive species, there is a greater need to focus on how native species diversity constrains the abundance of invaders that have already entered natural communities.

Upland, oak-dominated forests of the eastern United States are well suited for examining the competitive responses and effects of invasive species. Local native species diversity, the abundance of native habitat specialists and generalists, and the abundance of invasive species are potentially affected by restoration of natural fire regimes (Hutchinson et al. 2005; Brawn 2006; Brewer et al. 2015). Such fire restoration treatments increase diversity and abundance of native groundcover plants in oak-dominated systems (Hutchinson et al. 2005, Brawn 2006, Brewer et al. 2015; Brewer 2016). However, the reestablishment of natural fire regimes may also promote increases in invasive plant species (Crawford et al. 2001; Glasgow and Matlack 2006; Keeley 2006; Brewer et al. 2015). One potential invader of eastern U.S. deciduous forests with increasing notoriety for positive responses to prescribed fire and canopy openings is the exotic C_4 annual grass, *Microstegium vimineum* (Trin.) A. Camus (Glasgow and Matlack 2006; Brewer et al. 2015). Following its establishment in forest understories, *Microstegium* can alter forest succession dynamics, competitively suppress native plant species, and increase the intensity of prescribed fires (Flory and Clay 2010; Aronson and Handel 2011; Brewer 2011b; Emery et al. 2011; Wagner and Fraterrigo

2015). Given that native plant diversity increases in response to fire restoration, simultaneous increases in *Microstegium* to fire restoration must either be occurring in areas where native diversity is not increasing or in areas where native diversity is increasing but is not competitively suppressing *Microstegium*. Examining competition between native species and a competitive invader in response to restoration, thus provides a realistic test of the effect of diversity management on a competitive invader.

We tested the following hypotheses: (1) planting native plant species into patches of *Microstegium* suppresses its growth and ground cover (hereafter, the general suppression hypothesis); (2) raised diversity of native species suppresses the growth and ground cover of *Microstegium* (hereafter, the diversity-mediated suppression hypothesis); (3) suppression of *Microstegium* by the raised diversity is caused by the presence of a few relatively highly competitive species (hereafter, the selective suppression hypothesis); and (4) removal of *Microstegium* enhances the survival and growth of all native species examined, because of its competitive superiority to all of them.

METHODS

Study Site

The study described here took place in upland mesic hardwood forest at Strawberry Plains Audubon Center, an ~1000-ha wildlife sanctuary located in the loess plains of north-central Mississippi. The sites studied here are currently being managed with the primary goal of restoring oak–hickory woodlands with more open canopies (>20% canopy gap fraction), indicative of the early 1800s (before extensive logging and fire exclusion; Brewer and Menzel 2009). In 2004, a pair of treatment and control areas (1-ha each) was established at each of two sites within Strawberry Plains separated by approximately 2 km (Site 1: 34°49'60"N, 89°28'32"W; Site 2: 34°49'52"N, 89°27'7"W). Details of experimental treatments, which involved tree thinning and repeated prescribed burning, are provided in Brewer et al. (2015). By

2014, after multiple rotations of prescribed burning and restoration treatments at both sites, there were significant increases in several native plant species that are indicative of fire-maintained open habitats (e.g., *Helianthus* spp., *Desmodium* spp., native *Lespedeza* spp., and *Coreopsis tripteris* L.). There were also significant increases in generalist native species indicative of early- and mid-successional habitats, most notably, *Saccharum giganteum* (Walter) Pers., *Schizachyrium scoparium* (Michx.) Nash, *Andropogon virginicus* L., and *Solidago canadensis* L. In addition to increases by native species, the nonnative grass, *Microstegium vimineum*, increased in the treated plots of both sites (Brewer et al. 2015).

Experimental Design

Effect of Raised Diversity on *Microstegium*

In November 2014, we established twelve, 3-m² plots (two at Site 1 and ten at Site 2) in all available patches of *Microstegium* in the treated areas (Figure 1). Each plot was split into three 0.75-m² subplots, yielding a total of 36 subplots. To minimize edge effects of the treatments, each subplot was spaced approximately 0.2 m from neighboring subplots. Each subplot received one of the following treatments at random within each plot: (1) planting six native species consisting of one individual per species for high diversity; (2) planting six individuals of a single species for low diversity; or (3) a control treatment simulating the soil disturbance of the planting treatments for no added diversity. These planting densities were comparable to natural densities of these species or species mixtures observed under optimal conditions in burned and thinned plots at these sites (Brewer et al. 2015).

Three of the six species used in this experiment—*Helianthus silphoides* Nutt. (Ozark sunflower), *Desmodium laevigatum* (Nutt.) DC (smooth tick trefoil), and *Coreopsis tripteris* (tall coreopsis)—are best characterized as indicative of fire-maintained open woodlands, whereas the others—*Saccharum giganteum* (sugarcane

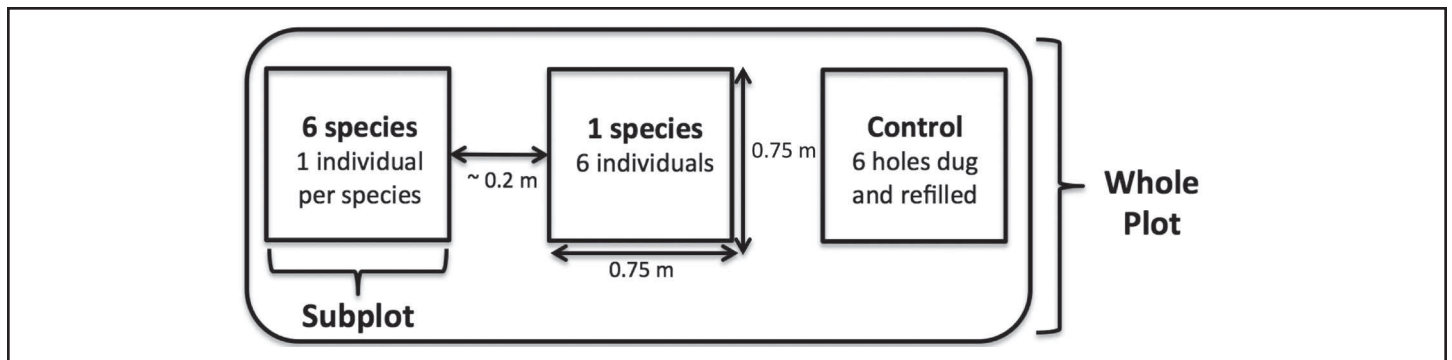


Figure 1. Layout of the split-plot experimental design for examining competitive responses of *Microstegium* to transplanted native species in 2015. Subplots were spaced apart by approximately 0.2 m to avoid edge effects. In total, 12 whole plots were established across Sites 1 and 2. The identity of each whole plot was defined by the randomly assigned species identity of the single-species split-plot treatment.

plumegrass), *Schizachyrium scoparium* (little bluestem), and *Solidago canadensis* (Canada goldenrod)—represent species that typically occur in the habitats of early- and mid-successional stages in our study area. The six species also consisted of three functional groups: two C_4 grasses, three C_3 composites, and one C_3 legume (USDA 2016).

In December 2014, transplants of the native species were collected (144 plants total) near Site 1. Bulk soil was removed from the roots, all aboveground tissues were removed, and the plants were weighed and transplanted as individual ramets or clumps of no more than three tillers. A previously published study with one of the species (*S. scoparium*) and personal experience with transplanting the other species showed that such a method was sufficient to promote high survival in open areas or in forests with sparse canopies (Maynard and Brewer 2013). The transplants were individually marked with a metal wire and tag and received 150 mL of water to stabilize soil surrounding the plant roots. For the six-species treatment, the locations of all six individual transplants were randomized within each plot. Control treatments were applied to simulate a comparable amount of soil disturbance associated with the planting treatments. Six holes corresponding to planting locations in treated plots were dug, refilled with soil, and then given approximately 150 mL of water.

To quantify the performance of *Microstegium*, we measured *Microstegium* percent cover in a 20 × 20-cm sub-subplot centered on each individual transplanted plant or

control disturbance point (six sub-subplots per subplot), during mid-May 2015, early October 2015, and mid-May 2016. These dates coincided with the approximate emergence (mid-May) and peak biomass (early October) of *Microstegium* at 34°49'N. To account for initial cover effects, we used the log-transformed proportional cover in mid-May as a covariate in the analysis of treatment effects on the relative change in log proportion cover from mid-May to early October 2015 (hereafter, rgr_{2015} [i.e., per capita growth rate in 2015]). We used the log-transformed proportional cover in early October as a covariate in the analysis of treatment effects on the relative change in log proportion cover from October 2015 to mid-May 2016 (hereafter, rgr_{2016}). We also followed the emergence and survival of the native transplants through the 2015 growing season, as well as their subsequent emergence in spring 2016.

Effect of *Microstegium* Removal on Native Plants

In late May of 2016, we superimposed a new treatment, *Microstegium* removal, to test the effect of *Microstegium* removal on the growth, survival, and flowering responses of the planted native species. In this experiment, we excluded *S. giganteum* and the two shadiest whole plots because of low transplant survival in 2015. We planted a new mixture of five species and a new monoculture of five individuals of each species into the five-species and one-species subplots (Figure 2). We hereafter refer to the paired five-species and single-species treatment levels as the richness treatment.

The *Microstegium* removal treatment was applied to the subplot pairs in a way that confounded the removal × richness × species interaction with differences between replicate plot pairs per species. The control for *Microstegium* removal was removal of all resident herbs and tree seedlings, including both native and exotic species. Densities (counts of individual stems/clumps) of resident species and cover of *Microstegium* were quantified before removal and again in September 2016. In contrast to the competitive response experiment, we did not remove aboveground parts of the transplants and obtained measurements of initial height of the transplants. We did this (instead of weighing them) to account for the initial size of the transplants. In many cases, these initial stems died. Survival of the rootstock, however, allowed for the replacement of these stems by basal resprouts. We then summed the heights for all five transplants at the initiation of the experiment and again in late September 2016 for each subplot, allowing us to quantify the relative change in summed heights. In addition, we examined treatment and species effects on the number of flowering and browsed native transplants per subplot.

Data Analysis

In the first experiment, differences in *Microstegium* cover among the three treatments (six species, single species, and control) were tested by split-plot analysis of variance (ANOVA) for each of the two sampling periods. A description of the specific statistical analyses associated

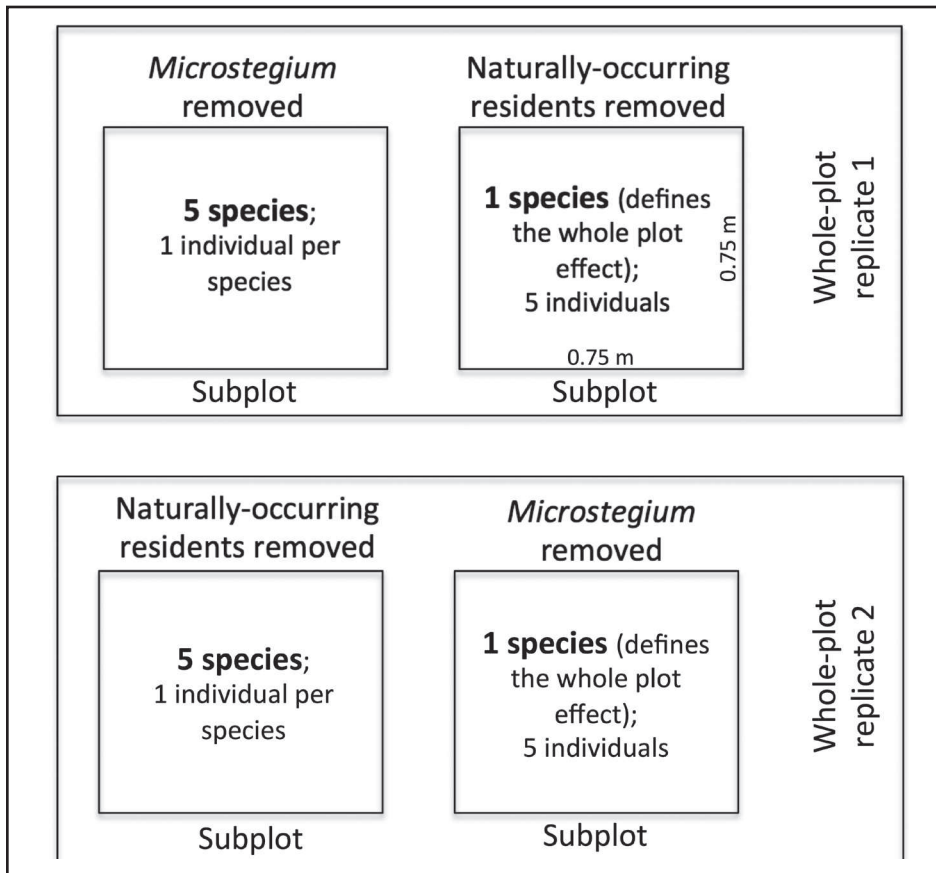


Figure 2. Split-plot experimental design for examining competitive effects of *Microstegium* on transplanted native species in 2016. Ten of the twelve whole plots used in the competitive response experiment were reused (with two eliminated because of excessive shade). New transplants of five of the six species used in the competitive response experiment were used, with one (*Saccharum giganteum*) being eliminated due to anticipated high mortality in 2016 following from low transplant survival in 2015. Two split-plot treatment factors were assigned to the subplots, *Microstegium* removal (2 levels: *Microstegium* removal and a control [removal of naturally occurring residents]) and richness (2 levels: 5 species and 1 species). Split-plot treatments were assigned in a way that confounded the two-way split-plot interaction with the whole-plot replicate error.

with the various hypotheses of competitive suppression of *Microstegium* in 2015 is presented in Table 1. In the second experiment (*Microstegium* removal), split-plot ANOVA

with a confounded three-way interaction term was used to test the whole-plot effect, split-plot effects, and their interaction on relative change in height, flowering, and

herbivory (i.e., evidence of damage to stems, buds, or leaves) of native transplants in 2016. A description of the specific statistical analyses associated with the various hypotheses of competitive suppression of native transplants by *Microstegium* in 2016 is presented in Table 2. The species that comprised the single-species subplot was the whole-plot effect and richness and *Microstegium* removal were considered split-plot effects. We took the log ratio of final and initial summed heights prior to analysis to normalize data and to provide a relativized measure of response (i.e., combined survival and growth) of the native transplants to removal. Likewise, we calculated log-odds ratios of counts of flowering and browsed transplants, adding a constant of 1 to each count to deal with zeroes. Changes in percent cover of *Microstegium* in 2016 in control subplots were regressed against pre-removal densities of resident vegetation. Likewise, changes in resident densities in 2016 in *Microstegium*-removal subplots were regressed against pre-removal cover of *Microstegium*. ANOVA and regression tests were conducted using JMP version 5.

RESULTS

Effect of Raised Diversity on Microstegium

Initial survival of the native transplants in the spring of 2015 was high, with over 85% of all transplants emerging. Nevertheless, we found no support for competitive suppression of *Microstegium* caused by the native transplants, indicated by a lack of

Table 1. Hypotheses of effects of native transplants on *Microstegium* and associated statistical tests.

Hypothesis	ANOVA result	Contrast result
General suppression	Significant split-plot planting treatment effect	Cover in six-species and single-species treatments lower than in no added plants control
Diversity-mediated suppression	Significant split-plot planting treatment	Cover lower in six-species treatment than in single-species treatment
Selective suppression	Significant split-plot planting by whole-plot interaction	Difference in cover between six-species and single-species treatments depends on species comprising the monoculture
No suppression by natives	Lack of a significant split-plot means no suppression of any kind	

Table 2. Hypotheses of effects of *Microstegium* removal and transplant richness on performance of native transplants and associated statistical tests.

Hypothesis	ANOVA result
Suppression of natives by <i>Microstegium</i>	Significant split-plot effect of <i>Microstegium</i> removal
Polycultures grow and survive better (or worse) than monocultures	Significant split-plot of richness
Differential suppression of native transplants by <i>Microstegium</i>	Significant <i>Microstegium</i> removal by whole-plot interaction: difference in transplant performance between <i>Microstegium</i> removal and resident species removal depends on the transplant species comprising the single-species treatment

a significant split-plot effect of planting treatment on either the increase in cover in 2015 (rgr_{2015} ; $F_{2,12} = 0.04$, $P = 0.96$; Figure 3a) or between the fall of 2015 and spring 2016 (rgr_{2016} ; $F_{2,12} = 0.84$, $P = 0.45$; Figure 3b). Because there was no overall effect of the split-plot treatment, we did not pursue the contrast of differences between the six-species and single-species treatments on *Microstegium* cover increases. Hence, we found no support for the diversity-mediated suppression hypothesis in this study (Figures 3a, 3b). We also found no support for the selective suppression hypothesis, as indicated by the lack of split-plot treatment by species interaction for either sampling period (rgr_{2015} ; $F_{2,12} = 0.79$, $P = 0.69$; rgr_{2016} ; $F_{2,12} = 0.37$, $P = 0.94$). Although initial cover was negatively correlated with the relative increase in cover by *Microstegium* in 2015 ($r = -0.35$; $P = 0.03$; Figure 4), suggesting negative density dependence, there was no interaction between initial cover and the split- or whole-plot treatment effects ($P > 0.3$). There was no whole-plot effect of species on the increase in *Microstegium* cover during either sampling period (rgr_{2015} ; $F_{5,6} = 0.98$, $P = 0.84$; rgr_{2016} ; $F_{5,6} = 0.37$, $P = 0.50$).

In contrast to the high initial emergence and survival of the native transplants, survival (i.e., presence of aboveground green tissue) through 2015 was relatively low, with only 38% of all transplants persisting or remaining green until fall senescence and only 13% of all transplants flowering. Only 42% of transplants reemerged in spring 2016.

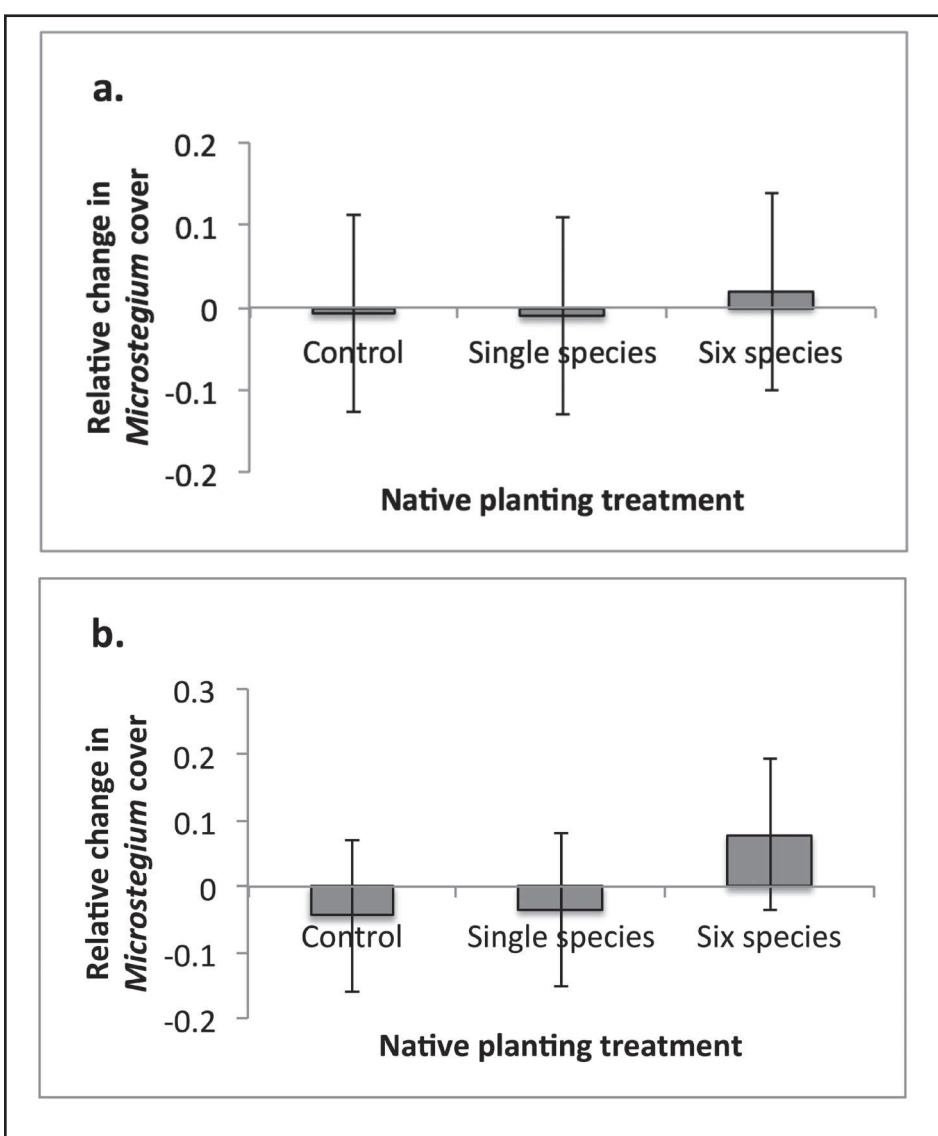


Figure 3. Relative change in *Microstegium* cover in response to the main effect of the split-plot native vegetation planting treatment, between (a) mid-May and October of 2015 and between (b) October 2015 and mid-May 2016. Values are least square means of cover change corrected for initial log proportional cover. Error bars are \pm the mean square error for the analysis.

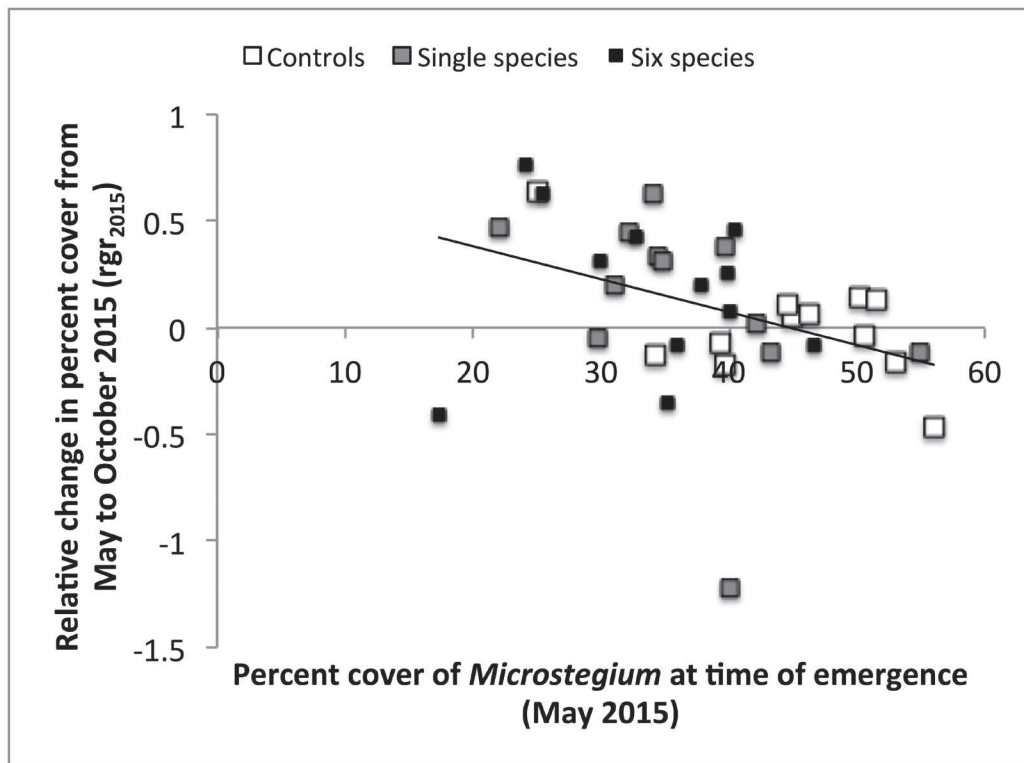


Figure 4. The relative change in percent cover of *Microstegium* from May to October 2015 (rgr_{2015}) as a function of initial percent cover at the time of emergence (mid-May 2015). Regression line shows the negative relationship between rgr_{2015} and initial percent cover for all treatments combined ($r = -0.35$; $P = 0.03$). Slopes were not significantly for different treatments ($P > 0.3$).

Effects of *Microstegium* Removal on Native Plants

The summed heights of native transplants benefited more from the removal of *Microstegium* than from the removal of intact resident vegetation, as indicated by a significant main effect of *Microstegium* removal on the relative change in summed heights during the 2016 growing season ($F_{1,5} = 6.88$, $P = 0.05$; Table 3). The summed heights of transplants did not decrease in the *Microstegium* removal subplots (Figure 5a), but were 76% lower in control plots (as computed from back-transformation of log differences in Figure 5a). The change in *Microstegium* cover was not correlated with initial resident density ($r = 0.05$ for log change in cover versus initial resident cover; $P = 0.89$), suggesting no evidence for competitive suppression of *Microstegium* caused by native transplants. The change in the density of established resident vegetation was not correlated with the pre-removal cover of *Microstegium* ($r = 0.08$ for log change in resident density

versus initial *Microstegium* cover). There was a trend towards lower average growth/survival in monoculture subplots than in polyculture subplots (-1.18 ± 0.4 vs. -0.25 ± 0.40 for single-species and five-species treatments, respectively), but the main effect of richness was not statistically significant ($F_{1,5} = 2.69$, $P = 0.16$). There was no main effect of species on relative change in height, and neither of the testable two-way interactions was significant ($P > 0.36$). The lack of interaction between *Microstegium* removal and the species comprising the single-species subplot ($F_{(S \times M)} = 0.89$, $P = 0.53$; Table 3) supported the hypothesis that *Microstegium* was more or less equally competitively superior to all five native species considered.

The flowering of native transplants benefited more from the removal of *Microstegium* than from the removal of intact resident vegetation, as indicated by a main effect of *Microstegium* removal on flowering during the 2016 growing season that approached statistical significance ($F_{1,5} = 6.21$, $P =$

0.055; Figure 5b). No other effects approached statistical significance ($P > 0.22$). Although herbivory of transplants was observed and showed a slight trend towards greater frequency in some species (e.g., *D. laevigatum* and *S. canadensis*), the main effect of species was not statistically significant ($F_{1,5} = 3.67$, $P = 0.09$). The incidence of herbivory was unrelated to *Microstegium* removal ($P = 0.33$), richness ($P = 0.50$), or to either of the testable two-way interactions ($P > 0.21$).

DISCUSSION

Determining the practical relevance of diversity–invasion theory to management of diversity and invasion requires quantifying the competitive abilities of resident species and nonresident invaders. Large native perennials planted into natural patches of *Microstegium*, either as single-species groups or as a six-species mixture, did not competitively suppress *Microstegium*. These results thus provide no support for the hypothesis that competition from native

Table 3. Summary of split-plot ANOVA for relative change in summed heights of five native transplant species in 2016. Whole-plot effect is Species (S); split-plot effects are the main effects of *Microstegium* removal (M; *Microstegium* removal or native vegetation removal) and richness (R; single-species or five-species treatment) and the species by *Microstegium* removal interaction and the species by richness interaction. The whole-plot replicate error (two replicates per species) is confounded with the split-plot error (the pooled *Microstegium* removal \times richness interaction and the three-way interaction), which in turn is used to test all effects.

Source	df	F	P
Species (S)	4	1.37	0.36
<i>Microstegium</i> removal (M)	1	6.88	0.05
Richness (R)	1	2.69	0.16
S \times M	4	0.89	0.53
S \times R	4	1.31	0.38
Confounded whole-plot and split-plot error term	5		
Total	19		

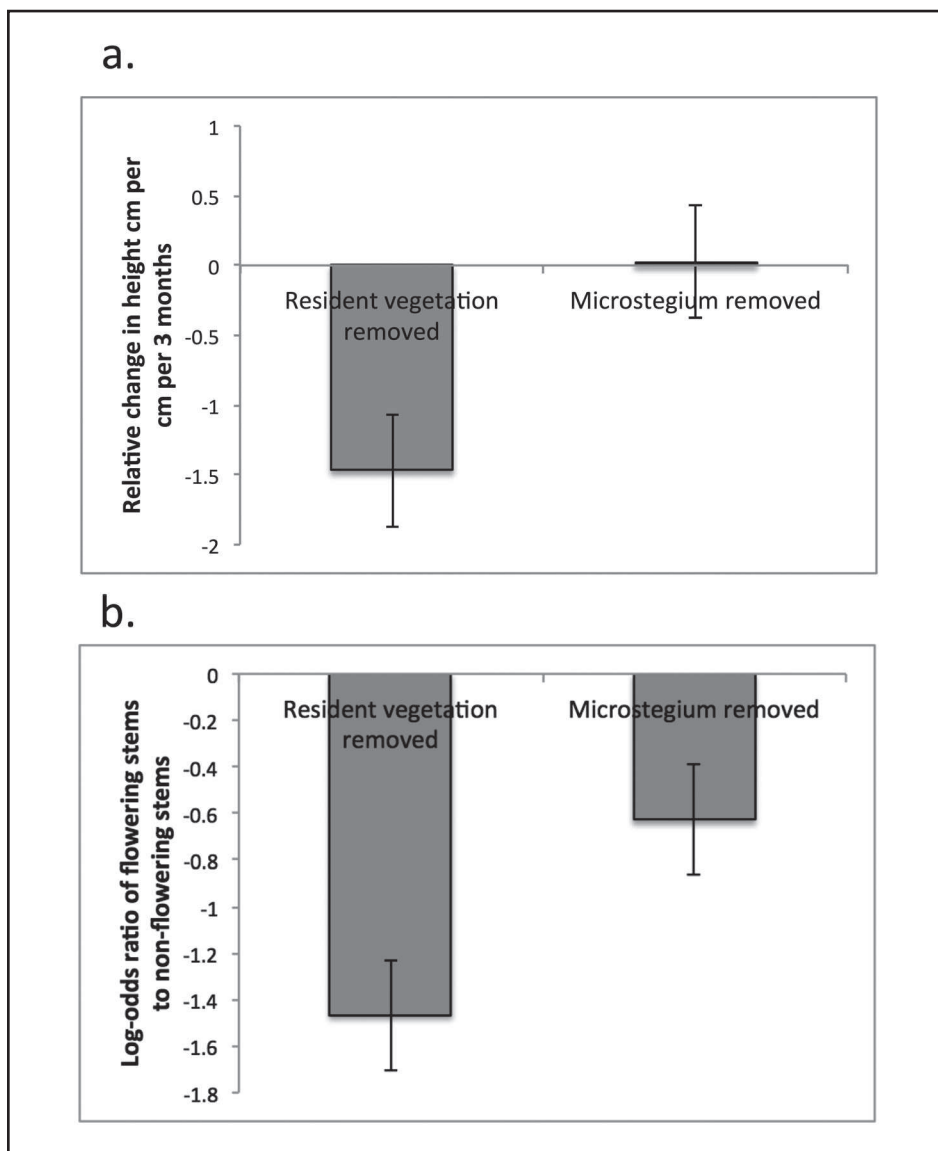


Figure 5. Effects of *Microstegium* removal on (a) the relative change (log response ratio) in the summed heights of five transplants between May and late September 2016 and (b) log-odds ratio of flowering to nonflowering stems of five transplants in 2016. Values are least-squares means correcting for transplant species and richness treatments. Error bars are \pm the mean square error.

species could constrain the abundance of an invader already established within a natural community (Levine et al. 2004). An established competitive equilibrium of native plants was never achieved, and we cannot rule out the possibility that the competitive ability of the native transplants was compromised to some degree by transplant shock. We suggest, however, that competitive superiority of *Microstegium* over all resident species was a more important contributing factor for four reasons. First, previously published and unpublished work involving transplants of these species revealed little or no evidence of transplant shock (Maynard and Brewer 2013). Second, initial transplant survival was high in both 2015 and 2016 and remained high in 2016 in the *Microstegium*-removal plots (but not in the control plots). Third, increases in *Microstegium* density in response to fire restoration at these sites resulted in reduced abundance of naturally established individuals of these native species (Brewer et al. 2015). Hence, their demise could not be attributed to transplant shock. Finally, our results (Figure 5) revealed a beneficial effect of *Microstegium* removal on transplant height growth and flowering by the end of the first growing season. The competitive effect of *Microstegium* on native species did not vary in response to which species dominated the monoculture subplots. This result suggests that *Microstegium* was a superior competitor to all of the native plant species studied here. If these species, which include among the largest native herbaceous plants in this system, cannot compete with *Microstegium*, then it seems unlikely that any desired native

groundcover species in this system could compete with it, either.

Most field studies focused on the competitive effects of problematic invaders have found no direct or indirect evidence of such competitive effects being reduced in diverse communities (Ortega and Pearson 2005; Brewer 2008; Corbin and D'Antonio 2010; Case et al. 2016). Management aimed at increasing native diversity may also improve environmental conditions for potential invaders (Keeley 2006; Brewer et al. 2015) and, thus, increase the competitive ability of the invaders. Restoration of fire and reopening the canopy at Strawberry Plains Audubon Center appears to have increased competitive effects of *Microstegium* on the native vegetation. There is no evidence that *Microstegium* is reducing the abundance or diversity of native species in shady and unburned upland forests at Strawberry Plains Audubon Center (Brewer et al. 2015). Diversity-mediated competitive suppression of invaders will not be an operationally effective and meaningful management strategy if the environmental conditions that increase native species diversity also increase competitive effects of invaders. In the case of *Microstegium*, achieving the restoration goal of maximizing native plant diversity will likely require removing *Microstegium* entirely before attempting to restore natural fire regimes in upland oak-dominated ecosystems.

MANAGEMENT IMPLICATIONS

To date, the primary motivation of most diversity–invasibility studies has been to demonstrate the importance of niche complementarity and/or limiting similarity in the maintenance of species diversity and stability, rather than relevance to management of invasive species (but see Funk et al. 2008; Cleland et al. 2013; Price and Pärtel 2013). This is because most diversity–invasibility studies consider only the competitive responses of invaders to resident species and not the competitive effects of invaders on resident species (Knops et al. 1999; Levine 2000; Naeem et al. 2000; Wilsey and Polley 2002; Zavaleta and Hulvey 2004). While we agree that management that minimizes native species losses and retains important func-

tional groups of native species should be encouraged, we argue that such practices should not be viewed as a sufficient or viable means of managing the most problematic invaders. Rather than managing for biodiversity and hoping for the best, early detection and eradication of such invaders when populations are still small may be the only effective means of control. The presence of native species that are functionally similar to potential invaders may discourage invasion by such invaders (Funk et al. 2008; Cleland et al. 2013; Price and Pärtel 2013). The effectiveness of such limiting similarity in resisting invasion assumes, however, that the potential invader is not vastly competitively superior to functionally similar native species (Corbin and D'Antonio 2010). In those cases in which competition from native species represents a persistent deterrent to invasion by particular species, one must ask whether such potential invaders are capable of outcompeting native species and, thus, whether they represent a serious threat to native plant diversity (Brewer and Bailey 2014).

ACKNOWLEDGMENTS

We would like to thank thesis committee members Jason Hoeksema and Clifford Ochs for their advice in improving this project and the final manuscript. We also thank three anonymous reviewers for their comments on the manuscript. We thank Matt Abbott, Emily McCann, and John Banusiewicz for their assistance with work in the field and Strawberry Plains Audubon Center for providing logistical support and access to the field sites. This project was funded by a grant from the Sigma Xi Grants-In-Aid of Research Program.

Sean Moyer is currently a Restoration Technician at the Albany Pine Bush Preserve Commission in Albany, NY. His research interests include the ecology of invasive plants, effects of fire on plant species diversity, and improvements in the management of invasive plants. He received an MS in Biology from the University of Mississippi.

Steve Brewer is a Professor of Biology at the University of Mississippi. His research

interests include plant competition, effects of fire on plant species diversity, and the ecology of invasive plants. He received a PhD in Botany from Louisiana State University.

LITERATURE CITED

- Aronson, M.F.J., and S.N. Handel. 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. *Natural Areas Journal* 31:400-407.
- Brawn, J.D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460-469.
- Brewer, J.S. 2008. Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. *Biological Invasions* 10:1257-1264.
- Brewer, J.S. 2011a. Disturbance-mediated competition between perennial plants along a resource-supply gradient. *Journal of Ecology* 99:1219-1228.
- Brewer, J.S. 2011b. Per capita community-level effects of an invasive grass, *Microstegium vimineum*, on vegetation in mesic forests in northern Mississippi (USA). *Biological Invasions* 13:701-715.
- Brewer, J.S. 2016. Natural canopy damage and the ecological restoration of fire-indicative groundcover vegetation in an oak-pine forest. *Fire Ecology* 12:205-226.
- Brewer, J.S., M.J. Abbott, and S.A. Moyer. 2015. Effects of oak-hickory woodland restoration treatments on native groundcover vegetation and the invasive grass, *Microstegium vimineum*. *Ecological Restoration* 33:256-265.
- Brewer, J.S., and W.C. Bailey. 2014. Competitive effects of non-native plants are lowest in native plant communities that are most vulnerable to invasion. *Plant Ecology* 215:821-832.
- Brewer, J.S., and T. Menzel. 2009. A method for evaluating outcomes of restoration when no reference sites exist. *Restoration Ecology* 17:4-11.
- Case, E.J., S. Harrison, H.V. Cornell, and E. Allen. 2016. Do high-impact invaders have the strongest negative effects on abundant and functionally similar resident species? *Functional Ecology* 30:1447-1453.
- Case, T.J. 1990. Invasion resistance arises in strongly competitive model communities. *Proceedings of the National Academy of Sciences of the United States of America* 87:9610-9614.
- Cleland, E.E., L. Larios, and K.N. Suding. 2013. Strengthening invasion filters to reassemble native plant communities: Soil resources and

- phenological overlap. *Restoration Ecology* 21:390-398.
- Corbin, J.D., and C.M. D'Antonio. 2010. Not novel, just better: Competition between native and non-native plants in California grasslands that share species traits. *Plant Ecology* 209:71-81.
- Crawford, J.A., C-H.A. Wahren, S. Kyle, and W.H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12:261-268.
- Davis, M.A. 2003. Biotic globalization: Does competition from introduced species threaten biodiversity? *BioScience* 53:481.
- Emery, S.M., J. Uwimbabazi, and S.L. Flory. 2011. Fire intensity effects on seed germination of native and invasive Eastern deciduous forest understory plants. *Forest Ecology and Management* 261:1401-1408.
- Flory, S.L., and K. Clay. 2010. Non-native grass invasion suppresses forest succession. *Oecologia* 164:1029-1038.
- Funk, J.L., E.E. Cleland, K.N. Suding, and E.S. Zavaleta. 2008. Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology and Evolution* 23:695-703.
- Glasgow, L.S., and G.R. Matlack. 2006. The effects of prescribed burning and canopy openness on establishment of two non-native plant species in a deciduous forest, southeast Ohio, USA. *Forest Ecology and Management* 238:319-329.
- Gurevitch, J., and D.K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19:470-474.
- Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97:393-403.
- Huston, M.A. 2004. Management strategies for plant invasions: Manipulating productivity, disturbance, and competition. *Diversity and Distributions* 10:167-178.
- Hutchinson, T.F., R.E.J. Boerner, S. Sutherland, E.K. Sutherland, M. Ortt, and L.R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forestry Research* 35:877-890.
- Keeley, J.E. 2006. Fire management impacts on invasive plants in the western United States. *Conservation Biology* 20:375-384.
- Knops, J.M.H., D. Tilman, N.M. Haddad, S. Naeem, C.E. Mitchell, J. Haarstad, M.E. Ritchie, K.M. Howe, P.B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286-293.
- Law, R., and R.D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762-775.
- Levine, J.M. 2000. Species diversity and biological invasions: Relating local process to community pattern. *Science* 288:852-854.
- Levine, J.M., P.B. Adler, and S.G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975-988.
- Levine, J.M., and C.M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87:15-26.
- Levine, J.M., M. Vilà, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270:775-781.
- Luh, H.-K., and S.L. Pimm. 1993. The assembly of ecological communities: A minimalist approach. *Journal of Animal Ecology* 62:749-765.
- Maron, J., and M. Marler. 2007. Native plant diversity resists invasion at both low and high resource levels. *Ecology* 88:2651-2661.
- Maynard, E.E., and J.S. Brewer. 2013. Restoring perennial warm-season grasses as a means of reversing mesophication of oak woodlands in northern Mississippi. *Restoration Ecology* 21:242-249.
- Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97-108.
- Ortega, Y.K., and D.E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: Assessing invasibility and impact. *Ecological Applications* 15:651-661.
- Powell, K.I., J.M. Chase, and T.M. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany* 98:539-548.
- Price, J.N., and M. Pärtel. 2013. Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos* 122:649-656.
- Ricciardi, A., and J. Cohen. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9:309-315.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 101:10854-10861.
- [USDA] US Department of Agriculture. 2017. The PLANTS Database. Natural Resources Conservation Service, National Plant Data Team, Greensboro, NC. <<http://plants.usda.gov>>
- Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3213-3218.
- Wagner, S.A., and J.M. Fraterrigo. 2015. Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. *Forest Ecology and Management* 354:170-176.
- Wilsey, B.J., and H.W. Polley. 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5:676-684.
- Zavaleta, E.S., and K.B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306:1175-1177.