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Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas

Jonathan A. Myers[1,3] and Kyle E. Harms[1,2]

[1]*Department of Biological Sciences, Division of Systematics, Ecology, and Evolution, Louisiana State University, Baton Rouge, Louisiana 70803 USA*
[2]*Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama*

Abstract. In high-diversity communities, rare species encounter one another infrequently and therefore may compete more intensely with common species or guilds for limiting space and resources. In addition, rare species may be strongly recruitment limited because of their low abundances. Under these conditions, stochastic dispersal and immigration history can have an important influence on community structure. We tested the hypothesis that local immigration and competition from common, large-stature guilds interact to structure local biodiversity in high-diversity longleaf pine savanna groundcover assemblages (>30 species/m^2). In two factorial field experiments, we increased local immigration by adding seeds of 38 mostly rare, small-stature forbs and sedges to plots physically dominated by either a common, large-stature bunchgrass or shrub species and to plots in which competition from these dominant guilds was reduced. We measured species richness and abundance at two spatial scales (0.01 and 0.25 m^2) over two years. Immigration increased total species richness and richness of focal seed addition species regardless of levels of competition with bunchgrasses and shrubs, indicating that many rare, small-stature species can recruit in the face of potential competition from dominant guilds. Removal of dominant guilds increased total and focal species richness in shrub-dominated but not bunchgrass-dominated plots. In addition, competition from both dominant guilds had no clear effect on rank–abundance distributions of focal species. Our results suggest a key role for dispersal assembly in structuring local biodiversity in this high-diversity plant community, but the importance of this mechanism depends on the strength of local niche assembly involving competition from some, but not all, dominant guilds.

Key words: biodiversity; bunchgrass; community assembly; dispersal assembly; dominant guild; local immigration; longleaf pine savanna; niche assembly; recruitment limitation; shrub; species coexistence; species-rich community.

Introduction

The mechanisms maintaining biodiversity in ecological communities can be envisaged as falling along a dynamic continuum bounded by two general models (Hubbell 2001, Gravel et al. 2006). At one extreme are niche-assembly models that view communities as deterministic, limited-membership assemblages in which interspecific competition for limiting resources and space and other biotic interactions determine species' presence and abundance (Hutchinson 1957, MacArthur and Levins 1967, Tilman 1982, Chesson 2000, Chase and Leibold 2003). On the other extreme are dispersal–assembly models that view communities as stochastic, open-membership assemblages in which immigration history, chance dispersal events, and demographic stochasticity primarily influence community structure (MacArthur and Wilson 1967, Sale 1977, van der Maarel and Sykes 1993, Bell 2000, Hubbell 2001). Synthesis of these concepts into a unified model of biodiversity and species coexistence remains a major goal of ecology (Agrawal et al. 2007), and recent theory incorporating deterministic and stochastic processes has gone a long way in moving this synthesis forward (Chase 2003, Tilman 2004, Gravel et al. 2006). A fundamental gap remains, however, in our empirical understanding of where many natural communities fall along this continuum. Here we explore how one key component of niche assembly (competition from dominant guilds) and dispersal assembly (local immigration) interact to structure local biodiversity in a high-diversity plant community.

In high-diversity communities, most species are rare and coexist with few common species. This high degree of rarity has at least three important implications for community assembly. First, rarity increases the importance of demographic stochasticity in community dynamics (Barot 2004). Local extinctions of rare species owing to demographic stochasticity reduce the importance of deterministic processes in community assembly.

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[3] E-mail: jmyer19@lsu.edu

Second, populations of many species in high-diversity communities may be recruitment limited (Hubbell et al. 1999), which can slow rates of local extinction owing to competitive exclusion (Hurtt and Pacala 1995). Under these first two conditions, stochastic dispersal and immigration history can exert a strong influence on community structure, especially in high-diversity communities assembled from large local and regional species pools (Eriksson 1993). Third, rarity limits the degree to which species interact. Consequently, pairwise interactions between rare species occur infrequently, further limiting the degree to which deterministic interactions contribute to community assembly (Grubb 1986, Hubbell and Foster 1986). However, this does not necessarily mean that all species interactions in high-diversity communities are diffuse; interactions between rare and common species can be relatively more predictable in space and time. The strength of these interactions is expected to increase when common species are also of large stature, i.e., when size asymmetries among competing species are large (Keddy and Shipley 1989). Here we test the general hypothesis that local biodiversity reflects the interplay of competition from common, large-stature guilds and local immigration by rare, small-stature species.

Theoretical models predict that high rates of immigration from local and regional species pools increase local species diversity (MacArthur and Wilson 1967, Hubbell 2001, Mouquet and Loreau 2003). What remains controversial, however, is the extent to which the immigration–diversity relationship is influenced by local species interactions (Mouquet and Loreau 2003). Recruitment limitation owing to increased competition or predation has been hypothesized to reduce positive effects of dispersal on diversity (Kneitel and Miller 2003), and this mechanism of community assembly is thought to increase in importance as productivity increases (Grime 1973). We refer to this mechanism as "biotic recruitment limitation" to distinguish it from recruitment limitation owing to seed limitation or establishment limitation due to abiotic conditions (Nathan and Muller-Landau 2000). Experimental studies in plant communities have revealed that positive effects of immigration on diversity are often greater in disturbed relative to undisturbed sites (e.g., Zobel et al. 2000, Foster 2001, Gross et al. 2005). Although these studies suggest an important role for competition at the community level in limiting species membership from local and regional species pools, they provide limited insight into how patterns of seed arrival contribute to local biodiversity in the face of competition from dominant species or guilds. This mechanism of biotic recruitment limitation may play a key role in limiting the extent to which dispersal assembly influences local biodiversity.

We examined how competition from dominant guilds and local immigration interact to structure biodiversity in high-diversity longleaf pine (*Pinus palustris*) savanna groundcover assemblages. From a global perspective, longleaf pine savannas constitute one of the most species-rich plant communities at small spatial scales (40 species/1 m^2, 140 species/1000 m^2), often containing two to three times more species in a square meter than other North American grasslands and similar or higher numbers than other high-diversity grasslands in Europe and Africa (Walker and Peet 1983, Cowling et al. 1994, Fridley et al. 2006, Keddy et al. 2006). We experimentally tested three general hypotheses concerning the maintenance of local biodiversity: (1) competition from common, large-stature guilds reduces diversity; (2) immigration of rare, small-stature species enhances diversity; and (3) positive effects of immigration are dampened in the presence of large-stature guilds owing to biotic recruitment limitation. We tested these hypotheses using two factorial experiments in which we manipulated immigration of 38 small-stature species and competition from two dominant guilds (large-stature bunchgrasses and shrubs).

Methods

The longleaf pine savanna ecosystem formerly covered >370 000 km^2 of the southeastern United States (Earley 2004). Historically, natural lightning-season fires burned these savannas one or more times per decade (Platt 1999). Presently, <2% of the original ecosystem remains, owing to widespread logging, land clearance, and fire suppression (Earley 2004). Most remnant pine savannas exist in a fragmented network of sites, many of which are being restored or maintained with prescribed fires (e.g., Keddy et al. 2006).

We conducted our study at a remnant and restored >100-ha longleaf pine savanna at Camp Whispering Pines, Tangipahoa Parish, Louisiana, USA (30°41′ N, 90°29′ W; mean annual temperature = 19°C, mean annual rainfall = 1626 mm, 25–50 m above mean sea level). Camp Whispering Pines has a large species pool (>300 vascular plant species) and a diverse assemblage of groundcover forbs, grasses, and shrubs at small scales (15 species/0.25 m^2, 22 species/0.5 m^2 [J. A. Myers and K. E. Harms, *unpublished data*], 30 species/1 m^2 [K. E. Harms et al., *unpublished data*], and 103 species/100 m^2 [Platt et al. 2006]). The fertile soils consist of well-drained Pleistocene-aged sands mixed with and capped by windblown loess (Platt et al. 2006). The site has been managed with biennial growing-season prescribed fires (April–May) since 1994 and has never been plowed. Our study was conducted from June 2006 to June 2008 in a site burned in May 2005 and 2007. Platt et al. (2006) provide additional details on the study site.

Experimental design

Our study consisted of two factorial randomized block experiments, one for bunchgrasses and one for shrubs, involving two main treatments: competition and local immigration. Immigration treatments were identical for the two experiments, whereas competition treatments differed according to the biology of each dominant guild. We used one common species within each guild for the experiments: the bunchgrass *Schizachyrium tenerum* (Poaceae) and the shrub *Ilex glabra* (Aquifoliaceae). These species are among the most abundant of their respective dominant guilds, i.e., bunchgrasses and shrubs, at the site (Thaxton and Platt 2006; P. R. Gagnon et al., *unpublished data*). *Schizachyrium* is a perennial, C_4 bunchgrass that attains heights up to 1 m, with spreading foliage often lying flat on the ground. *Ilex* is an evergreen, rhizomatous shrub that reaches heights of 1.5–2 m. At the landscape scale, *Ilex* tends to be patchily distributed and occurs as large clonal thickets in the otherwise bunchgrass-dominated groundcover layer and is considered an invasive native species in wetter pine savannas (Hinman et al. 2008). When present at local scales, reproductive adults of both species can account for >90% of total aboveground community biomass (mean dominance/0.25 m^2: 92% and 98% for *Schizachyrium* and *Ilex*, respectively; $n = 10$ plots sampled in fall 2006). We will henceforth refer to the two species generally as bunchgrasses and shrubs.

The two experiments consisted of a 3 × 2 design (competition × immigration) for bunchgrasses and a 2 × 2 design for shrubs. In each experiment, we established 10 replicate blocks with a minimum distance of 5 m between neighboring blocks. We chose block locations on the basis of having sufficient abundances of bunchgrasses or shrubs; for shrubs, a block usually consisted of a single large clone. We randomly applied treatments to 0.5 × 0.5 m plots within blocks ($n = 4$ or 6 plots/block for shrubs and bunchgrasses, respectively). Plots were oriented in the same cardinal direction (north–south), separated by at least 0.5 m, and located at least 2 m from pine trees. We selected plots on the basis of having similar cover of bunchgrasses or shrubs; *Ilex* shrubs were absent from all bunchgrass plots and *Schizachyrium* bunchgrasses were absent from all shrub plots. We reduced edge effects in two ways: (1) by positioning shrub plots at least 0.5 m inside each clone; and (2) applying competition treatments inside each plot and in a 0.25 m wide buffer strip around plots in both experiments. In order to facilitate data collection at multiple scales, we divided each plot into 25 grid cells with aluminum nails marking the corners of each 10 × 10 cm cell.

Competition treatments

Our competition treatment had three levels: (1) control; (2) cover reduction (bunchgrass experiment only); and (3) removal. To reduce effective bunchgrass cover, without disturbing soil or removing ramets, we gathered bunchgrass foliage together into uncut vertical sheaves and bound them using plastic ties. These ties were removed prior to a prescribed fire at the study site in May 2007; bunchgrasses were retied 4.5 weeks later after attaining sufficient size. To remove bunchgrasses, we carefully applied herbicide (Roundup, Scotts, Marysville, Ohio, USA) to bunchgrass foliage with a paintbrush, removing dead litter <1 week later. The removal treatment mimicked complete bunchgrass mortality (e.g., from a locally intense fire), whereas the cover reduction treatment allowed us to explicitly examine effects of belowground competition when aboveground competition was reduced. We removed shrubs by repeatedly clipping individual stems at ground level. To avoid killing entire clones, we did not apply herbicide to shrubs.

Immigration treatment

Our immigration treatment had two levels: control and increased seed rain. To increase immigration into plots, we added seeds of 38 small-stature, mostly rare forbs and sedges spanning 31 genera and 12 families (Appendix A); we will henceforth refer to these as "focal species." Most of the species are gravity- or wind-dispersed nonlegume forbs, representing the most species-rich functional group in the local species pool at the study site (Platt et al. 2006). All but one of the 38 species (*Plantago virginica*) are perennial. We hand-collected seeds in the field from multiple, spatially separated plants to ensure a variety of genotypes. Because our focus was on patterns of community diversity and not effects of treatments on individual species per se, we did not add the same number or mass of seeds for each species. Accordingly, interspecific differences in seed numbers in part reflected seed availability and thus species relative abundance in the local species pool. In contrast to most previous seed addition experiments (e.g., Tilman 1997, Zobel et al. 2000, Foster 2001, Gross et al. 2005), we added species to plots as seeds became available, rather than as a single seed dispersal event. This method better matches temporal patterns of natural seed rain. Our seed additions spanned two time periods: August–September 2006 and July–November 2007, following a prescribed fire in May 2007.

The goal of our seed addition experiment was to increase immigration into plots at levels that fall within natural levels of potential local seed rain. In a two-year study of local seed densities in 1-m^2 plots across four longleaf pine savanna sites in southeastern Louisiana, E. I. Johnson (2006 and *unpublished data*) recorded mean total seed densities ranging from 600 to 11 666 seeds/m^2 across sites, with the highest mean densities recorded at our study site (Camp Whispering Pines). Wind-dispersed forbs in the family Asteraceae accounted for approximately half of the total density (mean = 5266 seeds/m^2; E. I. Johnson, *unpublished data*). In 2006, we added 15 total species at a median rate of 30 seeds·species^{-1}·plot^{-1} (120 seeds·species^{-1}·m^{-2}, 4840 total seeds/m^2; Appendix A). In 2007, we added 30 species (23 of which were not added in 2006) at a median rate of 50 seeds·species^{-1}·plot^{-1} (200 seeds·species^{-1}·m^{-2}, 11 980 total seeds/m^2). The higher numbers of seeds added in 2007 reflected higher fecundity after the 2007 fire. The most common functional group in our pool of seed addition species was wind-dispersed Asteraceae, accounting for 38% of the total seed density and 36% of the total species richness. Overall, these levels of immigration fall within the range of natural levels of potential local seed rain at the site, both at the level of the entire pool of seed addition species and for the most-common functional group within the pool. In addition, our seed addition treatment generated plant densities that fall within the natural range of focal species' densities observed at the study site (Appendix C).

In 2007, we tested seed viability (Appendix A) in a climate-controlled growth chamber. Light (16-h day length), temperature (32°C day, 22°C night), and relative humidity (90% day, 50% night) were set to approximate growing-season conditions. For each species, we placed 50 seeds on moist filter paper in a petri dish wrapped in parafilm, remoistened and rotated dishes regularly, and recorded germination for six months. After six months, we cold-stratified dishes at 5°C for one month and recorded germination for another two months. Seeds of all 30 species added in 2007 were viable, with a median germination rate of 56% (range = 4–98%; Appendix A); seed viability was not tested in 2006. To aid with field identification, we raised seedlings of all focal species from seeds in small pots and photographed them at various ontogenetic stages.

Data collection and analysis

We measured total species richness, richness of focal species (species added in the immigration treatment), and abundances of focal species in September 2007 and June 2008. The majority of focal species were not present in plots before the start of the experiment. Thus, we used focal species richness and abundances to assess the extent to which recruitment limitation influences community assembly during the juvenile stage and beyond. We measured total species richness at two spatial scales: plot (0.25 m^2) and neighborhood (0.01 m^2). We measured focal species abundance using stem or rosette densities (depending on the morphology of the species).

We examined treatment effects on total and focal species richness using mixed-model ANOVA. Competition and immigration treatments were modeled as fixed effects and blocks as random effects. For the neighborhood-scale analysis, we used the mean species richness calculated from all 25 10×10 cm grid cells in each plot (individual grid cells were not modeled as replicate subplots), yielding identical sample sizes for the neighborhood- and plot-scale analyses ($n = 10$ per treatment combination). When necessary, response variables were $\log_{10}$- or square-root transformed to meet assumptions of homogeneous variances and normally distributed errors. When transformation did not improve homogeneity of variance, we reran the analysis using a heterogeneous variance model (*varIdent* function in the R *nlme* library) and selected the model with the lowest Akaike Information Criterion (AIC).

We also tested for treatment effects on overall patterns of focal species diversity and evenness by comparing 95% confidence intervals of slopes from rank–abundance curves using linear regression (Magurran 2004). For each treatment, we calculated the mean relative abundance of all focal species present in $\geq$1 plot. For the immigration treatments, we used the pooled data from the competition treatments ($n = 30$ or 20 for the bunchgrass and shrub experiments, respectively). For the competition treatment, we only used data from the seed addition plots ($n = 10$ in both experiments). This allowed us to explicitly examine effects of competition on focal species that recruited mostly from seed, as seed control plots contained relatively few focal species. For one analysis (shrub competition), we $\log_{10}$-transformed species ranks to normalize residuals, although we obtained the same qualitative results using untransformed data. Residuals were normally distributed in all other analyses (Shapiro-Wilk tests, $P > 0.07$). We performed all statistical analyses in R (R Development Core Team 2008).

Results

Immigration increased total species richness in both bunchgrass- and shrub-dominated plots, but the effects of competition varied between the two dominant guilds (Figs. 1 and 2; Appendix B). In bunchgrass-dominated plots, immigration increased species richness in both years at both the plot (Fig. 1A, B) and neighborhood (Fig. 1C, D) scales. Contrary to our predictions, however, there were no significant effects of reduced cover or removal of bunchgrasses on species richness at the plot scale (Fig. 1B), despite a positive effect of bunchgrass removal at the neighborhood scale in the second year (mean increase of 0.7 species/0.01 m^2; Fig. 1D). There were also no significant interactive effects of immigration and bunchgrass competition on total species richness. In the second year, immigration increased total richness by 40–60% at the neighborhood and plot scales, respectively (Fig. 1B, D). Competition had a smaller overall effect on total richness (9–28% in the removal treatment in the second year).

Total species richness of shrub-dominated plots, in contrast, increased in response to both immigration and competitor removals at both spatial scales (Fig. 2; Appendix B). The only exception to this general pattern was at the neighborhood scale in the first year, in which immigration, but not competition, influenced species richness (Fig. 2C). As with the bunchgrass-dominated plots, there were no significant interactions between the two treatments on total species richness. In the second year, overall effects of immigration on species richness ranged from 70% to 87% at the neighborhood and plot scales, respectively. Overall positive effects of competitor removals ranged from 45% to 100% at the two spatial scales. In summary, local immigration enhanced total

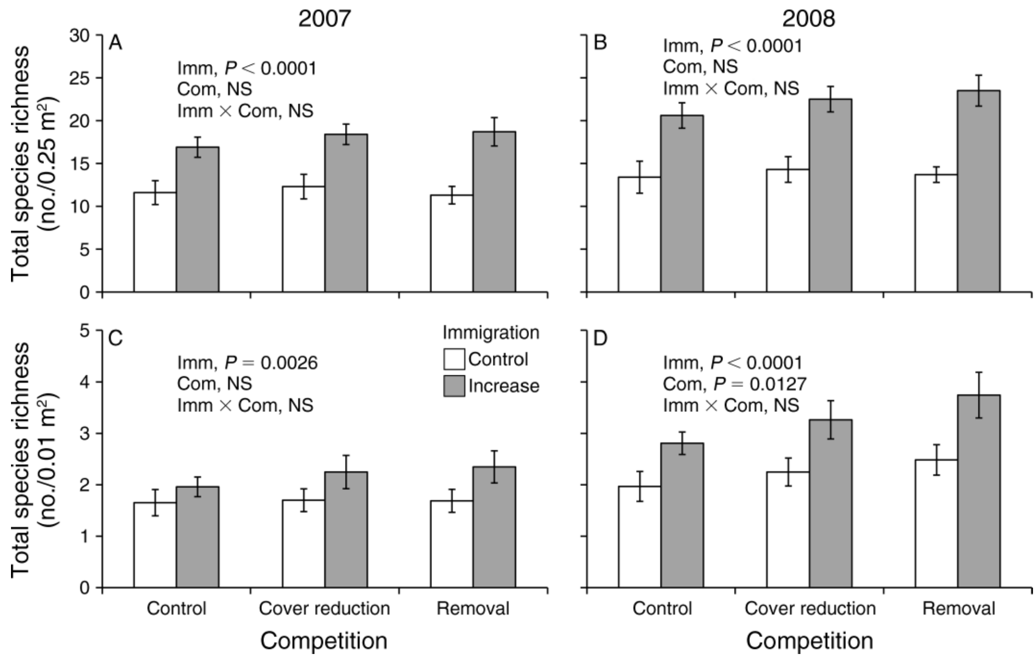

FIG. 1. Total species richness in the immigration and competition treatments in bunchgrass-dominated plots over two years in a high-diversity longleaf pine savanna at the (A, B) plot scale (0.25 m^2) and (C, D) neighborhood scale (0.01 m^2). Bars are means ± SE; $n = 10$ plots/treatment. P values are from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm × Com) and are listed in each panel (NS indicates $P > 0.05$).

species richness in both bunchgrass- and shrub-dominated sites, but competition generally reduced richness only in sites dominated by large-stature shrubs.

Focal species richness (species added in the immigration treatment) paralleled patterns of total species richness: immigration increased focal richness in plots dominated by both large-stature guilds, but competition reduced focal richness only in shrub-dominated plots (Fig. 3; Appendix B). Immigration increased focal richness in both years, whereas competition from shrubs

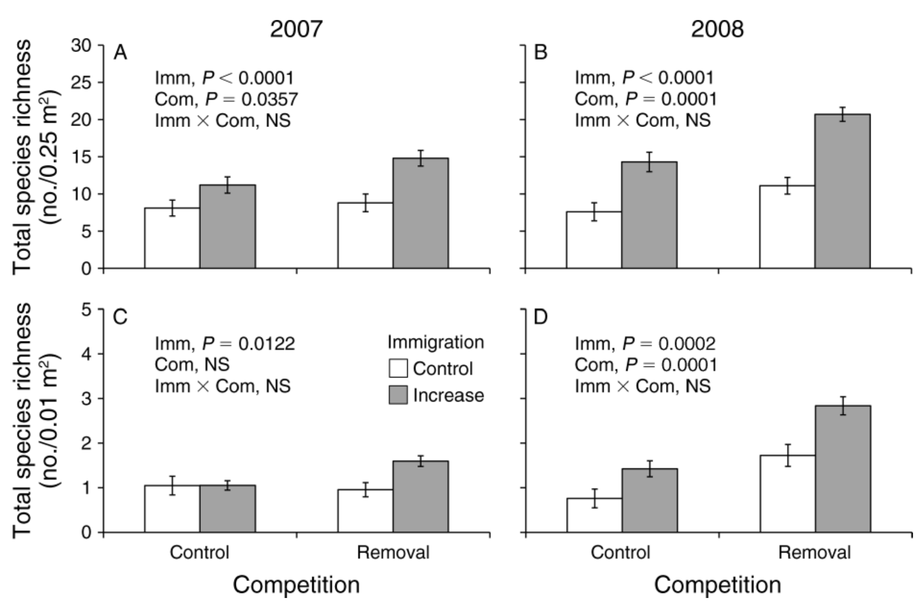

FIG. 2. Total species richness in the immigration and competition treatments in shrub-dominated plots over two years at the (A, B) plot scale (0.25 m^2) and (C, D) neighborhood scale (0.01 m^2). Bars are means ± SE; $n = 10$ plots/treatment. P values are from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm × Com) and are listed in each panel (NS indicates $P > 0.05$). Data in panel (C) were $\log_{10}$-transformed before analysis (untransformed data shown).

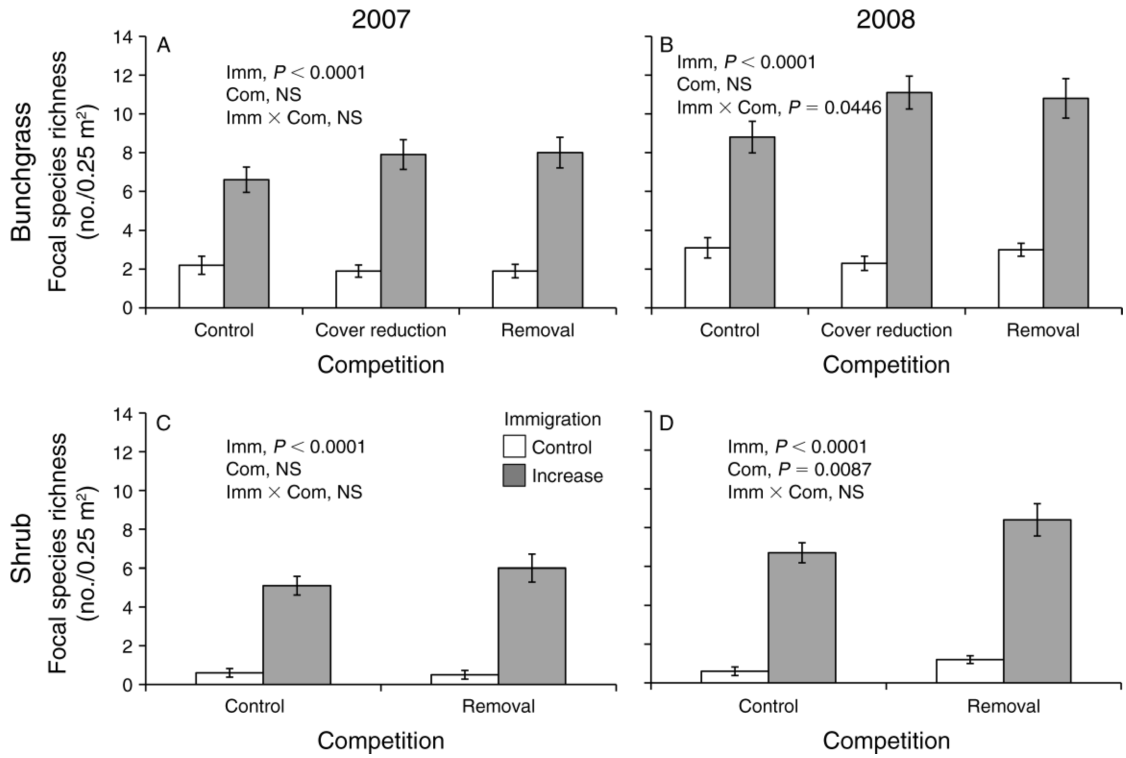

FIG. 3. Richness of seed addition (focal) species in the immigration and competition treatments in (A, B) bunchgrass-dominated and (C, D) shrub-dominated plots over two years. Bars are means $\pm$ SE; $n = 10$ plots/treatment. P values are from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm $\times$ Com) and are listed in each panel (NS, $P > 0.05$). Data in (B) were square-root transformed and data in (D) were $\log_{10}$-transformed before analysis (untransformed data are shown).

decreased richness only in the second year. In bunchgrass-dominated plots, there was a marginally significant interaction between treatments on focal species richness, potentially reflecting a stronger positive effect of immigration in the competition reduction and removal treatments relative to the control (Fig. 3B). Overall, immigration increased focal richness by a factor of 2.7 (bunchgrass) and 3.4 (shrub), whereas removal of shrub competitors increased richness by a factor of 0.6.

Immigration significantly influenced rank–abundance distributions of focal species, whereas competition had no clear effect (Fig. 4). Immigration increased diversity and evenness of focal species in plots dominated by both guilds, indicated by the steeper slopes of the rank–abundance curves in the seed control relative to seed addition plots (Fig. 4A, C). In contrast, slopes were similar among competition treatments for both dominant guilds (Fig. 4B, D). Of the 38 focal species, 29 (76%) and 24 (63%) were present in at least one of the seed addition plots in the bunchgrass and shrub experiments, respectively (Fig. 4A, C; Appendix C). In contrast, only 15–31% were present in seed control plots (Fig. 4A, C; Appendix C). Collectively, these results indicate a strong role for local immigration in maintaining high diversity, a limited effect of competition on diversity in bunchgrass-dominated plots, and that many species can recruit in shrub-dominated plots despite negative effects of shrub competition on overall patterns of species richness.

DISCUSSION

Our results demonstrate key roles for both local immigration and competition from dominant guilds in the assembly of an exceptionally high-diversity plant community. In support of our general hypothesis, we found that immigration enhanced local species richness and diversity in sites dominated by two common, large-stature guilds, at both neighborhood and plot scales. In contrast, we generally found less significant effects of competition from dominant guilds on local biodiversity, owing to: (1) limited evidence that competition from bunchgrasses, one of the most common large-stature functional guilds in this community, reduces species richness; and (2) similarities in species rank–abundance distributions among competition treatments. These patterns suggest a key role for dispersal assembly in structuring local biodiversity in this high-diversity plant community, but that the importance of this mechanism depends on the strength of local niche assembly involving competition from some, but not all, dominant guilds.

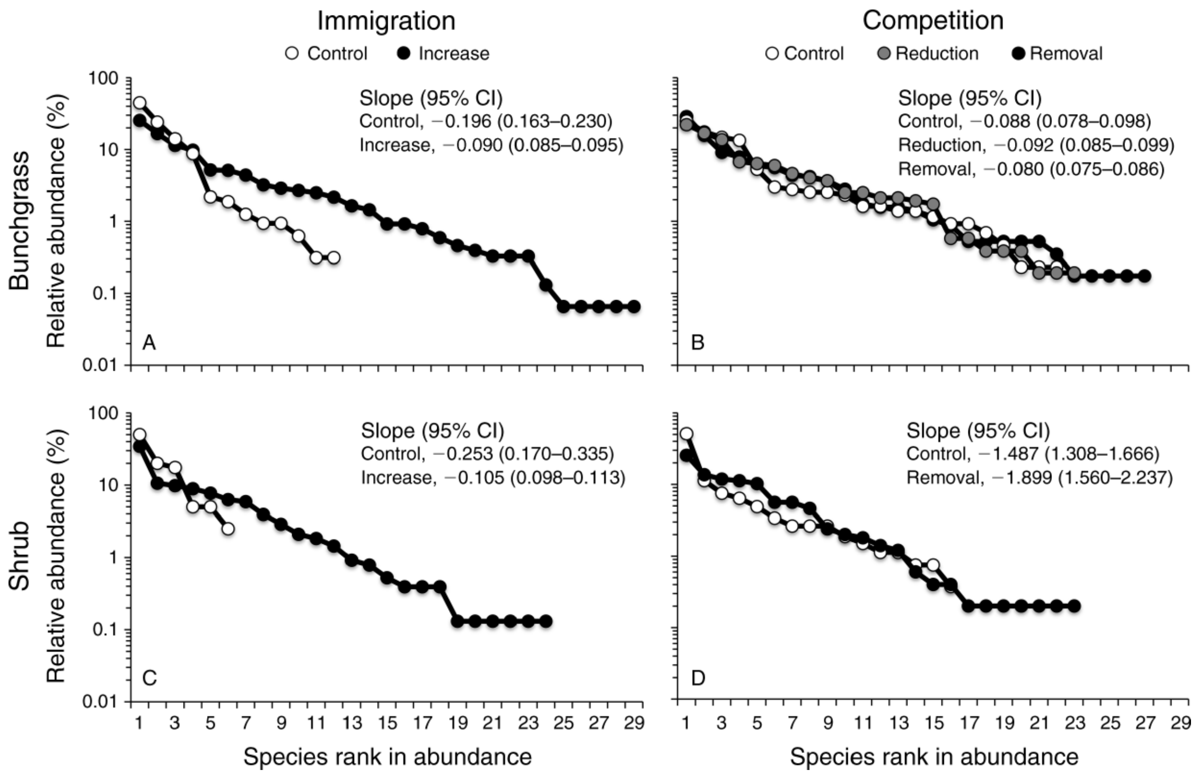

FIG. 4. Rank–abundance curves for seed addition (focal) species in the immigration and competition treatments in (A, B) bunchgrass-dominated and (C, D) shrub-dominated plots in 2008. *Plantago virginica*, an annual species that established and reproduced in 2007, is included in the figure. Estimated slopes (and 95% confidence intervals) from linear regression are shown for each treatment. Slopes and confidence intervals in panel (D) were calculated using $\log_{10}$-transformed species ranks (to normalize residuals). Each point represents the abundance of each established focal species averaged across all plots in a treatment (Appendix C); (A) $n = 30$, (C) $n = 20$, and (B, D) $n = 10$ plots/treatment.

Local immigration and competition from dominant guilds

We hypothesized that positive immigration–diversity relationships would be dampened in sites dominated by common, large-stature species (Kneitel and Miller 2003, Mouquet and Loureau 2003). However, we generally found positive effects of local immigration regardless of levels of competition from bunchgrasses and shrubs (i.e., no strong interactive effects of local immigration and competition on species richness), indicating that rare species can recruit in the face of potential competition from dominant guilds. Under favorable abiotic conditions in the field, at least eight of these focal species can recruit from seed and become reproductive adults by the end of their first two growing seasons (J. A. Myers and K. E. Harms, *unpublished data*).

The positive immigration–diversity patterns observed in our study may be influenced by several mechanisms. First, these effects can be transient or reduced as competition intensifies over longer time scales, e.g., when time between disturbance increases or as individuals and populations increase in size. Under these conditions, the importance of deterministic species interactions may increase through time, even in communities initially assembled by stochastic dispersal (e.g., "noninteractive" vs. "interactive" phases of community assembly; Emerson and Gillespie 2008). Second, positive immigration–diversity patterns may persist when frequent disturbances reduce or remove dominant competitors and litter (Grime 1973) or via local mass effects (Shmida and Ellner 1984, Leibold et al. 2004). In longleaf pine savannas, frequent, locally intense fires increase mortality of shrubs (Thaxton and Platt 2006) and bunchgrasses (P. R. Gagnon et al., *unpublished data*) and therefore may contribute to longer-term coexistence of dominant and rare guilds. Third, recruitment limitation owing to limited fecundity and dispersal prevents rare species from reaching many sites that they would otherwise occupy (Hubbell et al. 1999, Nathan and Muller-Landau 2000). Although dispersal limitation is often viewed as a key mechanism contributing to stochastic community assembly (Hubbell 2001), dispersal limitation can differ among species in important ways that influence niche assembly (Clark 2009) and generate similar results in models built from niche and neutral mechanisms (Adler et al. 2007). Interestingly, the effects of dispersal on biodiversity may therefore include both deterministic (dispersal traits linked to species' niches) and stochastic (e.g., priority effects and stochastic seed arrivals) components.

Given the importance of size asymmetries in determining the position of species along competitive hierarchies (Keddy and Shipley 1989), we expected smaller competitive effects of bunchgrasses relative to shrubs. Nevertheless, we predicted competition from bunchgrasses to leave a strong signature on patterns of species diversity. However, we found limited effects of bunchgrass competition on diversity, a pattern not consistent with the hypothesis that local diversity reflects escape of rare, small-stature species from dominant, large-stature species in space or time ("fugitive" or "peripheral species" concepts; Horn and MacArthur 1972, Keddy et al. 2006). Although bunchgrasses undoubtedly exclude individuals of small-stature species from many microsites that they could otherwise occupy, through mechanisms related to space occupancy (positive effect of bunchgrass removal on species richness at the 0.01-m^2 neighborhood scale; Fig. 1D) or resource-based competition (Tilman 1989), our results suggest that overall effects of bunchgrasses on recruitment limitation are not manifest on larger-scale patterns of diversity. These results are supported by studies of two additional bunchgrass genera in high-diversity pine savannas: Kirkman et al. (2001) found no correlation between dominance of *Aristida* bunchgrasses and species diversity across a productivity gradient; and Roth et al. (2008) found no effect of experimental removal of a dominant *Andropogon* bunchgrass on local species diversity.

The limited effects of bunchgrasses on local biodiversity observed in these studies do not exclude the possibility that dominant guilds negatively affect performance (e.g., fecundity) of smaller-stature species (e.g., Brewer 1998) or other large-stature species (Fargione et al. 2003). Intra-guild competition is a likely mechanism explaining coexistence patterns among large-stature grasses (Fargione et al. 2003), but is a less plausible mechanism to explain the coexistence of rare species that encounter one another infrequently in high-diversity communities. As Grubb (1986:222) pointed out: "It is not that they [rare species] will never have any impact on each other ... The point is that the impact will occur so rarely that even species with extremely similar niches may coexist for a long time." Future studies examining the importance of intra- vs. interguild interactions and their consequences on population performance will deepen our understanding of these additional aspects of niche assembly in high-diversity communities.

Species coexistence (or lack thereof) in the face of competition from dominant guilds may be explained by several key functional traits. Rosette-forming forbs can maintain photosynthetic rates and positive carbon balance under the dense canopy of grasses (Walker and Peet 1983). In addition, recruitment from the soil seed bank may allow some species to germinate and increase in biomass before dominant species mature. For example, many of the small-stature species that were abundant under the shrub canopies in our study were seed-banking annuals that reproduce quickly after fire and before shrubs attain maximum size. Spatially extensive, large-stature shrubs, in contrast, may lower diversity by creating a barrier that limits seed dispersal into the interior of shrub patches, killing competitors via increased flammability during fire (Zedler 1995) and via a suite of other competitive traits (e.g., densely branched rhizomes, tall-stature stems that reduce light availability in the groundcover, and high litter production; Grime 1973). The size-asymmetric effects of shrubs on groundcover forbs and other small-stature species observed in our study parallel patterns observed in other savannas worldwide, where species coexistence reflects niche partitioning between large-stature trees and "smaller-stature" grasses (Sankaran et al. 2004). Similarly, in closed-canopy forests, dense understories of large-stature shrubs limit recruitment opportunities for seedlings that may reduce tree species diversity (e.g., Beckage et al. 2005).

Conclusions

The importance of niche and dispersal assembly mechanisms in ecological communities remains a central question in community ecology (e.g., Chase 2003, Leibold et al. 2004, Holyoak et al. 2006). Here, we develop and test key predictions on how two components of these processes influence the assembly of high-diversity communities, using parallel immigration experiments involving two dominant guilds in exceptionally species-rich pine savannas. We show that immigration by rare, small-stature species enhances local biodiversity, but that the importance of this mechanism depends on the strength of local niche assembly involving competition from some, but not all, dominant guilds. Our study contributes to a broader understanding of how niche- and dispersal-based mechanisms of community assembly vary in their importance in communities of contrasting diversity and suggests that stochastic models of community assembly require some degree of partial determinism to adequately explain biodiversity in species-rich communities.

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APPENDIX A

Thirty-eight focal species added in the immigration treatments in 2006 and 2007, showing their dispersal type based on seed morphology, number of seeds added per plot in each year, and percentage of seed germination on petri dishes for 2007 seeds (*Ecological Archives* E090-194-A1).

APPENDIX B

Results from ANOVA testing fixed effects of immigration, competition, and their interaction on total species richness and focal species richness in the bunchgrass and shrub experiments in 2007 and 2008 (*Ecological Archives* E090-194-A2).

APPENDIX C

Plot occupancy and mean plant density of the 38 focal seed addition species in the immigration treatment in the bunchgrass and shrub experiments in 2008 (*Ecological Archives* E090-194-A3).

Ecological Archives E090-194-A1

Jonathan A. Myers, and Kyle E. Harms. 2009. Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. *Ecology* 90:2745–2754.

Appendix A. Thirty-eight focal species added in the immigration treatments in 2006 and 2007, showing their dispersal type based on seed morphology, number of seeds added per plot in each year, and percentage of seed germination on petri dishes for 2007 seeds (n = 50 seeds/species).

Species	Family	Life form[1]	Disp type[2]	*N* seeds added/plot		Germ (%)
				2006	2007	
Ageratina aromatica	Asteraceae	PF	W	–	150	94
Asclepias sp.	Asclepiadaceae	PF	W	10	–	–
Carex glaucescens	Cyperaceae	PS	G	20	–	–
C. tenax	Cyperaceae	PS	G	–	30	94
Chromolaena ivifolia	Asteraceae	PF	W	–	150	68
Chrysopsis mariana	Asteraceae	PF	W	–	30	26
Cirsium horridulum	Asteraceae	BF	W	–	40	88
Conoclinium coelestinum	Asteraceae	PF	W	–	200	96
Crotalaria purshii	Fabaceae	PL	G	–	50	14
Elephantopus tomentosus	Asteraceae	PF	W	200	300	88
Eryngium yuccifolium	Apiaceae	PF	G	–	50	30
Eupatorium rotundifolium	Asteraceae	PF	W	300	100	40
Eurybia paludosa	Asteraceae	PF	W	–	30	26
Helenium flexuosum	Asteraceae	PF	G	25	50	88
Helianthus angustifolius	Asteraceae	PF	G	–	100	78
H. hirsutus	Asteraceae	PF	G	5	–	–
H. radula	Asteraceae	PF	G	–	100	76
Hibiscus aculeatus	Malvaceae	PF	G	35	–	–
Hieracium gronovii	Asteraceae	PF	W	40	–	–
Hypericum crux-andreae	Clusiaceae	PW	G	–	50	46
H. setosum	Clusiaceae	PF	G	–	200	88
Hyptis alata	Lamiaceae	PF	G	50	200	54
Lespedeza capitata	Fabaceae	PL	C	–	30	4
Liatris pycnostachya	Asteraceae	PF	W	–	30	28
L. squarrulosa	Asteraceae	PF	W	–	30	66
Ludwigia hirtella	Onagraceae	PF	G	150	100	82
Nothoscordum bivalve	Liliaceae	PF	G	15	–	–
Orbexilum pedunculatum	Fabaceae	PL	G	10	–	–
Pityopsis graminifolia	Asteraceae	PF	W	–	30	30
Plantago virginica	Plantaginaceae	AF	G	–	30	98

Pycnanthemum albescens	Lamiaceae	PF	G	–	300	16
P. tenuifolium	Lamiaceae	PF	G	20	–	–
Rhexia alifanus	Melastomataceae	PF	G	30	30	14
Rhynchosia reniformis	Fabaceae	PL	B	–	5	48
Rudbeckia hirta	Asteraceae	PF	G	300	50	30
Salvia lyrata	Lamiaceae	PF	G	–	30	62
Solidago odora	Asteraceae	PF	W	–	100	84
S. rugosa	Asteraceae	PF	W	–	400	36

[1]A = annual, B = biennial, F = non-legume forb, L = legume forb, S = sedge, W = woody

[2]B = ballistic, C = carried, G = gravity, W = wind

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Jonathan A. Myers, and Kyle E. Harms. 2009. Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. *Ecology* 90:2745–2754.

Appendix B. Results from ANOVA testing fixed effects of immigration, competition, and their interaction (Imm × Com) on total species richness (0.01 and 0.25 m^2) and focal species richness (0.25 m^2) in the bunchgrass and shrub experiments in 2007 and 2008.

Variable	Bunchgrass experiment					Shrub experiment				
		2007		2008			2007		2008	
	df	*F*	*P*	*F*	*P*	df	*F*	*P*	*F*	*P*
Total richness (0.25 m^2)										
Immigration	1	51.82	<0.0001	86.23	<0.0001	1	21.62	0.0001	58.04	<0.0001
Competition	2	0.50	<0.6049	1.23	0.2995	1	4.71	0.0390	21.41	0.0001
Imm × Com	2	0.36	0.6955	0.70	0.5016	1	2.09	0.1595	1.83	0.1865
	59					39				
Total richness (0.01 m^2)										
Immigration	1	10.18	0.0026	29.58	<0.0001	1	2.64	0.0112	18.12	0.0002
Competition	2	0.66	0.5189	4.81	0.0127	1	7.41	0.1155	31.93	<0.0001
Imm × Com	2	0.42	0.6532	0.40	0.6683	1	3.52	0.0711	1.18	0.2861
	59					39				
Focal richness (0.25 m^2)										
Immigration	1	140.17	<0.0001	252.45	<0.0001	1	121.60	<0.0001	260.01	<0.0001
Competition	2	0.01	0.9851	0.90	0.4131	1	0.04	0.8360	7.99	<0.0087
Imm × Com	2	1.35	0.2680	3.33	0.0446	1	2.29	0.1418	0.82	0.3728
	59					39				

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Ecological Archives E090-194-A3

Jonathan A. Myers, and Kyle E. Harms. 2009. Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. *Ecology* 90:2745–2754.

Appendix C. Plot occupancy (%) and mean plant density/m^2 of the 38 focal seed addition species in the immigration treatment (Con = control, Inc = increase) in the bunchgrass and shrub experiments in 2008. Plot occupancy indicates the percentage of all plots in which a species was present (n = 30 and 20 plots/treatment for the bunchgrass and shrub experiment, respectively).Observed maximum natural densities of focal species present in 60 0.5-m^2 plots sampled in 2007 and 2008 in a separate, concurrent study at the field site (J. A. Myers and K. E. Harms, *unpublished data*) is shown for comparison against densities observed in the experimental seed addition plots in the current study.

Species	**Plot occupancy (%)**				**Plant density/m^2**				**Max. obs. density/m^2**
	Bunchgrass		**Shrub**		**Bunchgrass**		**Shrub**		
	Con	**Inc**	**Con**	**Inc**	**Con**	**Inc**	**Con**	**Inc**	
Ageratina aromatica	00	003	00	00	00	00.1	0	00	38
Asclepias sp.	00	027	00	40	00	01.2	0	00.2	–
Carex glaucescens	00	000	00	00	00	00	0	00	–
C. tenax	00	000	00	00	00	00	0	00	–
Chromolaena ivifolia	00	000	00	00	00	00	0	00	–
Chrysopsis mariana	03	010	00	00	00.1	00.9	0	00	4*
Cirsium horridulum	03	077	30	85	00.1	08.9	0	09.0	6
Conoclinium coelestinum	00	000	00	00	00	00	0	00	–
Crotalaria purshii	00	027	00	40	00	01.6	0	00.2	–
Elephantopus tomentosus	07	100	00	90	00.4	51.6	0	52.6	66
Eryngium yuccifolium	07	013	05	40	00.4	00.7	0	00	–
Eupatorium rotundifolium	33	060	10	55	03.7	05.1	1.6	03.2	64
Eurybia paludosa	13	017	10	35	00.9	01.9	0	00.6	4
Helenium flexuosum	00	010	00	00	00	00.7	0	00	–
Helianthus angustifolius	07	040	00	20	00.5	03.3	0.4	02.2	38*
H. hirsutus	00	000	00	15	00	00	0	00.2	–
H. radula	27	090	00	40	06.0	33.9	0	15.0	214
Hibiscus aculeatus	00	057	05	55	00	04.4	0	02.8	34*
Hieracium gronovii	00	003	00	00	00	00.3	0	00	4
Hypericum crux-andreae	07	017	00	00	00.2	01.9	0	00.6	8*
H. setosum	10	003	00	05	00.8	00.1	0	00.2	–
Hyptis alata	00	047	05	30	00	05.9	0.4	11.8	–
Lespedeza capitata	00	000	00	00	00	00	0	00	–
Liatris pycnostachya	00	000	00	00	00	00	0	00	–
L. squarrulosa	00	003	00	00	00	00.1	0	00	4
Ludwigia hirtella	00	030	00	10	00	02.9	0	01.2	2
Nothoscordum bivalve	00	000	00	00	00	00	0	00	–

Orbexilum pedunculatum	00	000	00	00	00	00	0	00	–
Pityopsis graminifolia	73	057	10	10	10.0	10.4	1.4	01.4	38*
Plantago virginica	00	083	00	25	00	10.5	0	13.6	–
Pycnanthemum albescens	00	020	00	15	00	00.8	0	00.6	4
P. tenuifolium	00	000	00	00	00	00	0	00	–
Rhexia alifanus	00	013	00	05	00	00.7	0	00.2	–
Rhynchosia reniformis	00	003	00	00	00	00.1	0	00	–
Rudbeckia hirta	00	063	00	30	00	06.5	0.2	06.0	8
Salvia lyrata	00	050	00	30	00	05.5	0	04.4	–
Solidago odora	90	093	15	45	18.8	023.2	4.0	16.2	360
S. rugosa	00	087	00	45	00	019.9	0	09.6	18

*Max. observed density estimated conservatively using presence/absence of species in 0.01-m^2 grid cells.

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