Ecology, 92(3), 2011, pp. 676–686

Seed arrival and ecological filters interact to assemble high-diversity plant communities

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. Two prominent mechanisms proposed to structure biodiversity are niche-based ecological filtering and chance arrival of propagules from the species pool. Seed arrival is hypothesized to play a particularly strong role in high-diversity plant communities with large potential species pools and many rare species, but few studies have explored how seed arrival and local ecological filters interactively assemble species-rich communities in space and time. We experimentally manipulated seed arrival and multiple ecological filters in high-diversity, herbaceous-dominated groundcover communities in longleaf pine savannas, which contain the highest small-scale species richness in North America (up to >40 species/m^2). We tested three hypotheses: (1) local communities constitute relatively open-membership assemblages, in which increased seed arrival from the species pool strongly increases species richness; (2) ecological filters imposed by local fire intensity and soil moisture influence recruitment and richness of immigrating species; and (3) ecological filters increase similarity in the composition of immigrating species. In a two-year factorial field experiment, we manipulated local fire intensity by increasing pre-fire fuel loads, soil moisture using rain shelters and irrigation, and seed arrival by adding seeds from the local species pool. Seed arrival increased species richness regardless of fire intensity and soil moisture but interacted with both ecological filters to influence community assembly. High-intensity fire decreased richness of resident species, suggesting an important abiotic filter. In contrast, high-intensity fire increased recruitment and richness of immigrating species, presumably by decreasing effects of other ecological filters (competition and resource limitation) in postfire environments. Drought decreased recruitment and richness of immigrating species, whereas wet soil conditions increased recruitment but decreased or had little effect on richness. Moreover, some ecological filters (wet soil conditions and, to a lesser extent, high-intensity fire) increased similarity in the composition of immigrating species, illustrating conditions that influence deterministic community assembly in species-rich communities. Our experiment provides insights into how dispersal-assembly mechanisms may interact with niche-assembly mechanisms in space (spatial variation in disturbance) and time (temporal variation in resource availability) to structure high-diversity communities and can help guide conservation of threatened longleaf pine ecosystems in the face of habitat fragmentation and environmental change.

Key words: community assembly; dispersal assembly; environmental filtering; fire disturbance intensity; niche assembly; resource availability; soil moisture; species diversity; species pool; species-rich longleaf pine savanna.

INTRODUCTION

Community ecology is currently in a period of rapid synthesis, with an increased emphasis on integrating local processes (e.g., habitat selection, species interactions) with regional processes (e.g., metacommunity dynamics) to understand patterns and dynamics of biodiversity (Leibold et al. 2004, Ricklefs 2004, Vellend 2010). Fundamental to this synthesis are pluralistic theories of biodiversity that incorporate elements from two general but contrasting conceptual models. The niche-assembly model views local communities as deterministic, "limited-membership" assemblages in which local environmental conditions and biotic interactions influence the assembly, diversity, and composition of communities (Hutchinson 1957, Chesson 2000, Hubbell 2001, Chase and Leibold 2003). In contrast, the dispersal-assembly model views local communities as "open-membership" assemblages in which the size of the species pool, chance colonization and immigration history, and demographic stochasticity primarily influ-

Manuscript received 20 May 2010; revised 6 July 2010; accepted 26 July 2010; final version received 28 August 2010. Corresponding Editor: J. Cavender-Bares.

[3] Present address: Department of Biology and Tyson Research Center, Washington University in St. Louis, Campus Box 1137, One Brookings Drive, St. Louis, Missouri 63130 USA. E-mail: jamyers@wustl.edu

ence community assembly (MacArthur and Wilson 1967, Bell 2001, Hubbell 2001). Although there is an emerging consensus that both deterministic and stochastic processes influence biodiversity and species coexistence (Tilman 2004, Gravel et al. 2006, Adler et al. 2007, Chase 2007), most empirical studies have focused on testing predictions at the extreme ends of this theoretical continuum (e.g., McGill et al. 2006). Consequently, there is a major gap in our understanding of how niche- and dispersal-assembly processes interact in space and time to structure natural communities, a critical gap to bridge in light of current threats to biodiversity owing to global environmental change (Clark 2009).

Ecological theory suggests conditions in which dispersal- and niche-assembly mechanisms may structure biodiversity (e.g., Chase 2003, Tilman 2004, Gravel et al. 2006, Chase 2007), but few empirical studies have examined the interplay between these processes in high-diversity communities. Species-rich communities have played a prominent role in the continued debate over the relative importance of niche and dispersal assembly in community ecology (e.g., Hubbell 2001, Tuomisto et al. 2003, Silvertown 2005, Wills et al. 2006, John et al. 2007, Kraft et al. 2008, Myers and Harms 2009*a*, Paine and Harms 2009, Vergnon et al. 2009). In these communities, arrival of propagules from the species pool is often predicted to have a strong influence on local biodiversity and species composition, for at least three reasons. First, a striking feature of many species-rich communities is that they contain large numbers of rare species (e.g., Volkov et al. 2007). Populations of rare species, in turn, will often be recruitment limited owing to reduced dispersal and fecundity ("recruitment limitation as a rule"; Barot 2004). Under these conditions, competitive exclusion can be delayed (Hurtt and Pacala 1995), allowing species that arrive to communities from the potential species pool (or metacommunity) to persist in those communities, thereby maintaining or increasing local diversity (Hubbell 2001). In the absence of immigration, populations of many rare species will be prone to demographic stochasticity, which increases the importance of ecological drift in community assembly (Hubbell 2001). Second, high-diversity communities are often assembled from large species pools. Consequently, many species can potentially attain membership in a given local community, increasing the likelihood that chance colonization and immigration history influence species composition (Chase 2003). Dispersal-assembled communities with similar environmental conditions are therefore predicted to have dissimilar species composition (Chase 2007). Finally, rare species may interact infrequently in high-diversity communities (Grubb 1986, Hubbell and Foster 1986), which reduces the likelihood that deterministic, pairwise species interactions (e.g., interspecific competition) contribute to community assembly (Myers and Harms 2009*a*).

Although theory suggests an important role for dispersal assembly in high-diversity communities, membership in local communities may also depend on the ability of species to tolerate niche-based "ecological filters" imposed by local abiotic or biotic conditions (e.g., Keddy 1992, Diaz et al. 1998, Myers and Harms 2009*b*). Here, immigration may have a weaker influence on local diversity if ecological conditions prevent species from establishing in local communities (e.g., as in species-sorting metacommunity models; Leibold et al. 2004), resulting in more limited-membership assemblages. Alternatively, high rates of immigration may decrease local diversity if they increase the probability that dominant competitors or predators are introduced into local communities (Mouquet and Loreau 2003). The relationship between immigration and local diversity will also be influenced by the strength of niche-based filters in space and time: In the presence of an exceptionally strong filter, local diversity may be largely decoupled from immigration, resulting in relatively closed-membership assemblages. In contrast to dispersal-assembled communities, niche assembly is predicted to increase similarity in species composition among communities with similar environmental conditions, especially when those conditions include strong ecological filters (Chase 2003, 2007).

Here, we used an experimental approach to investigate how seed arrival from the species pool interacts with multiple ecological filters to assemble high-diversity, herbaceous-dominated groundcover communities in the longleaf pine (*Pinus palustris*) ecosystem. This ecosystem provides an ideal setting for exploring mechanisms of community assembly in species-rich plant communities, in several important ways. First, at small spatial scales, these groundcover communities harbor the highest levels of plant species richness in North America and comparable levels of species richness to other high-diversity, herbaceous-dominated plant communities worldwide (Walker and Peet 1983, Peet and Allard 1993), and are therefore highly amenable to experiments relative to many species-rich, woody-dominated communities (e.g., tropical forests). Second, frequent fire is a key component of this ecosystem (Earley 2004). At the landscape scale, frequent, low-intensity fires maintain high local diversity through a variety of potential mechanisms, such as reduction of biomass and litter, and by reducing dominance of woody species (Walker and Peet 1983, Glitzenstein et al. 2003). At small scales, spatial variation in local fire intensity reduces abundances of dominant groundcover species (shrubs and bunchgrasses; Thaxton and Platt 2006; P. R. Gagnon, K. E. Harms, W. J. Platt, H. A. Passmore, and J. A. Myers, *unpublished data*) and may function as an important niche-based filter influencing local community assembly and species coexistence (e.g., Walker and Peet 1983, Brewer 2006, Platt et al. 2006, Myers and Harms 2009*a*). Third, soil moisture plays an important role in shaping patterns of species richness and composition at multiple scales (Walker and Peet 1983, Peet and Allard 1993, Kirkman et al. 2001), suggesting a second important niche-based filter, especially for seed and seedling recruitment (Iacona et al. 2010). Finally, this ecosystem has experienced some of the highest levels of habitat destruction worldwide (<2% of the original ecosystem remains), underscoring the need to understand ecological processes that can aid in the conservation and restoration of threatened biodiversity (Earley 2004).

We used a factorial field experiment to test three mechanistic hypotheses concerning community assembly and the maintenance of local biodiversity. First, we tested the hypothesis that species-rich groundcover communities constitute relatively open-membership assemblages. For this hypothesis, we used a seed-addition experiment to test the prediction that seed arrival from the species pool increases local diversity. This approach provides insight into the consequences of an expanded species pool on local community assembly (Myers and Harms 2009*b*), but does not disentangle the causes of seed arrival (e.g., dispersal vs. fecundity limitation; Clark et al. 1998) or its stochastic and deterministic components (Turnbull et al. 2008, Clark 2009). Second, we tested the hypothesis that two types of ecological filters influence local diversity and membership from the species pool: local fire intensity and soil moisture. We increased pre-fire fuel loads to test the prediction that locally intense fires decrease local diversity of resident species, but increase recruitment and diversity of immigrating seeds by reducing effects of other ecological filters in postfire environments (e.g., space and biomass). In the soil moisture experiment, we tested the predictions that dry and wet soil conditions decrease and increase local diversity, respectively, especially through their effects on recruitment of immigrating seeds. Third, we tested the hypothesis that ecological filters increase similarity in the species composition of immigrating seeds. This analysis allowed us to assess whether local communities assembled from an experimentally standardized species pool exhibited more deterministic community composition when ecological filters are present relative to when they are absent or weak.

METHODS

We conducted our study in an upland, mesic, >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; see Platt et al. 2006 for a detailed description of the study site). The site has a large potential species pool (>300 vascular plant species) and high species richness at local scales (22 species/0.5 m^2 [our findings]; ~30 species/1 m^2 [K. E. Harms, W. J. Platt, H. A. Passmore, J. A. Myers, and P. R. Gagnon, *unpublished data*]; 103 species/100 m^2 [Platt et al. 2006]), including a diverse groundcover assemblage of forbs, grasses, sedges, and shrubs. The relatively fertile soils consist of well-drained sands mixed with and capped by windblown loess (Platt et al. 2006). The site has been restored and maintained with biennial growing-season prescribed fires (April–May; Fig. 1a) since 1994. Our two-year experiment was conducted from May 2007 to April 2009 in an area burned in May 2007.

Experimental design

Our experiment consisted of a 2 × 3 × 2 factorial, split-plot design with three treatments: local fire intensity (control [natural, low-intensity fire], high), soil moisture (low, control, high), and seed arrival (control, high). We randomly assigned disturbance and soil moisture treatments to 60 2 × 3 m plots located in two sites (blocks) separated by ~400 m ($n = 30$ plots/block). Plots were oriented with the long axis north–south, positioned at least 7 m apart and at least 2 m from pine trees, located in areas with relatively homogeneous cover of large-stature bunchgrasses, and, to maximize light availability, located in or just south of gaps in the pine overstory. In each plot, we randomly assigned seed arrival treatments to 2 0.5-m^2 subplots. To reduce edge effects, we positioned subplots 0.5 m inside plots and separated them by 1 m. In order to record locations and densities of plants, we divided each subplot into 50-grid cells with aluminum nails marking the corners of each 10 × 10 cm cell (Fig. 1d). In total, each treatment combination was replicated 10 times.

We manipulated local fire intensity by increasing fine-fuel loads (pine needles) in plots before an early-growing-season prescribed fire in May 2007 (Fig. 1a). On the morning of the fire, we evenly distributed 12 kg of dry pine needles over half of the plots (high-intensity treatment; 2 kg/m^2), mimicking the upper range of observed fuel loads at our study site (Thaxton and Platt 2006). Fire-logger data collected in a separate, concurrent experiment using similar methods (addition of 2 kg/m^2 of pine needles to nearby 4-m^2 plots burned the same morning) demonstrated significantly higher maximum fire temperatures and total heat release in fuel-addition relative to control plots (H. A. Passmore, P. R. Gagnon, W. J. Platt, K. E. Harms, and J. A. Myers, *unpublished data*). All control and fuel-addition plots burned during the fire. One week postfire, we collected a litter/ash sample from a central 20 × 20 cm area in each plot and monitored the samples for seedling emergence in a growth chamber. There was little to no seedling emergence in either fuel treatment, indicating that any seeds potentially present in the litter and added pine needles were either consumed by, or killed during, the fire. In addition, even though most litter was consumed by fire in both fire intensity treatments, photographs taken in the field prior to collection of the litter/ash samples showed less litter remaining in the fuel-addition plots relative to control plots (Fig. 1e, f).

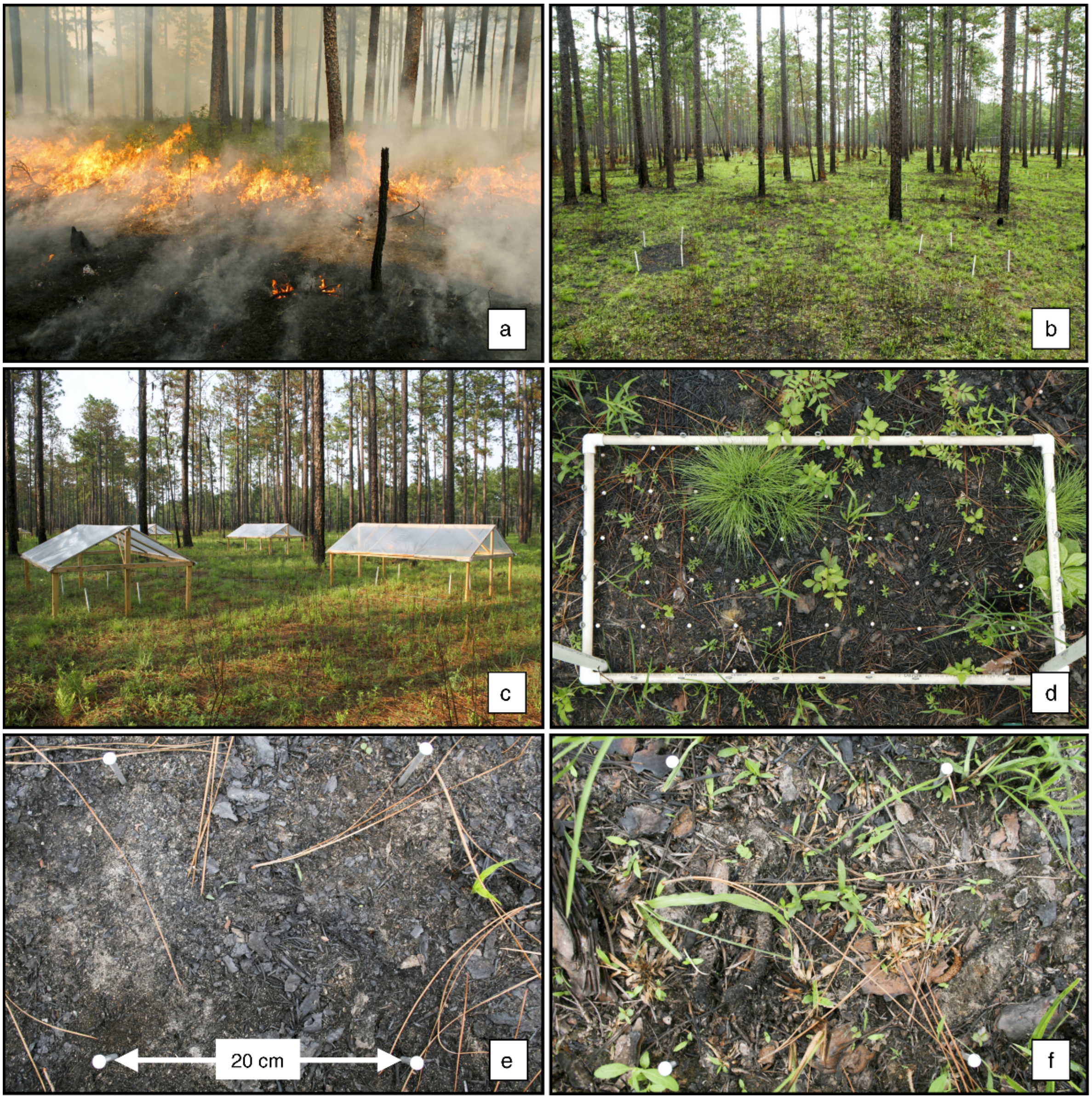

FIG. 1. Field experiment testing effects of seed arrival and ecological filters on community assembly and local biodiversity in a species-rich longleaf pine savanna at Camp Whispering Pines, Louisiana, USA. (a) Prescribed fire. (b) Environmental heterogeneity created by spatial variation in local fire intensity in 6-m^2 plots one month postfire. High-intensity fire (left plot, marked with white stakes) increased space and decreased biomass relative to low-intensity fire (right plot). (c) Rain shelters used to impose drought conditions on local communities. (d) Local community (0.5-m^2 subplot) in the low-intensity fire treatment one month postfire. Postfire litter and plant density in an adjacent pair of (e) high-intensity and (f) low-intensity fire plots photographed <1 week postfire (central 20 × 20 cm area of the plot, marked with nails at the four corners). Note that there was reduced litter and postfire densities of resprouting and seed-bank species following locally intense fires. Photo credits: J. A. Myers.

We manipulated postfire soil moisture using rain shelters and irrigation to decrease and increase soil moisture as would occur under drought and high-rainfall conditions, respectively. In our high soil moisture treatment, we irrigated 20 plots 2–4 days per week during the growing seasons of 2007 and 2008 using an automated sprinkler system connected to the camp's water supply. Plots were generally watered for 30–60 min in the early morning and late afternoon. Natural rainfall at a nearby weather station (Amite, Louisiana; 6 km northwest) averages 1670 mm/year, with a mean monthly maximum in January (170 mm), a monthly minimum in October (100 mm), and additional peaks in March (150 mm) and July (160 mm). Approximately 30% of the total mean annual rainfall occurs during the three warmest summer months (June–August). We added ~1700 mm of water to each irrigated plot over a period of 6 months (June–November) in 2007, and ~800 mm of water over a period of 3 months (June–August) in 2008. Relative to control plots, we estimate that we increased total mean annual rainfall by ~100% in 2007 and by ~50% in 2008.

In our low soil moisture treatment, we covered 20 plots (3 × 2 m) with individual rain shelters (3.5 m length × 2.5 m width × 1.5 m height) constructed out of a wooden frame and transparent polyethylene film roof (Tufflite IV 6-mil [0.15 mm], clear [91% light transmission] four-year poly film; Gothic Arch Greenhouses, Mobile, Alabama, USA) 2 weeks after the fire (Fig. 1c). The rain shelters were sufficiently tall to allow unimpeded growth and reproduction of plants from the tallest functional group in the plots (bunchgrasses). To minimize temperature and light effects, the frames were left uncovered on both ends and up to ~1 m on both sides (Fig. 1c). We measured photosynthetically active radiation (PAR; μmol/m^2/s) at the end of the two-year experiment, after the plastic showed slight signs of degradation, using a quantum sensor (LI-190; LI-COR, Lincoln, Nebraska, USA) positioned ~60 cm above the ground at 4–6 stratified subplot positions in four rain-shelter plots located in large canopy gaps, with and without rain shelters present. PAR transmission averaged 81% (range = 74–84%). In addition, to test for any effects of rain shelters themselves (beyond their effect on soil moisture), we also irrigated 10 additional plots that were also covered with rain shelters. Due to logistical constraints, we could not manipulate fire intensity or seed arrival in these plots, and therefore did not include this treatment in the factorial analyses of species richness. Rather, we primarily used this treatment to test whether the effects of rain shelters on biomass, presumably due to drought conditions, were ameliorated when rain shelters were irrigated. The remaining 20 plots were used as controls and received natural rainfall.

We manipulated seed arrival by adding seeds of 31 species of forbs and sedges from the local species pool to one of the two subplots (Appendix A). The other subplot was used as a control and received natural immigration. We added field-collected seeds over a period of 5 months (July–December) as seeds became available, mimicking the timing of natural seed dispersal for most species. The majority of our seed-addition species are gravity- and wind-dispersed forbs, which constitute the most species-rich functional group at the study site (Platt et al. 2006). We added a total of 4650 seeds/subplot (9300 seeds/m^2), at a median rate of 100 seeds·species^{-1}·subplot^{-1} (200 seeds·species^{-1}·m^{-2}). Approximately half of the added seeds were wind-dispersed forbs (4570 seeds/m^2). Natural total seed densities at our study site average 11 666 seeds/m^2, approximately half of which are wind-dispersed forbs (E. I. Johnson 2006, *unpublished data*). Thus, we estimate that we approximately doubled local seed densities, both at the level of the total pool of seed-addition species and for the most common functional group (wind-dispersed forbs). Seeds of all 30 species tested for germination were viable under growth-chamber conditions, with a median germination probability of 65% (range = 12–98%; Appendix A; see Myers and Harms 2009*a* for germination methods).

Data collection and analysis

We measured species richness, composition, densities of seed-addition species, aboveground biomass, and soil moisture. Species richness, composition, and densities of stems or rosettes (depending on the species) were measured in each of the 120 subplots in three censuses: September–October 2007 (5 months postfire); August–September 2008 (15 months postfire); and April 2009 (23 months postfire). In total, we recorded ~115 species, 80 genera, and 40 families in the subplots over the course of the experiment. We sampled biomass in November 2007 (6 months postfire) by clipping all plants at ground level in two stratified sample areas (0.25 m^2 total) located between the two subplots within each plot. Biomass samples were dried at 75°C for 48 h and then weighed. In June 2008, we measured soil volumetric water content (hereafter "soil moisture") after several rain-free days at two soil depths (7.5 cm and 20 cm) in each plot using a time domain reflectometer (Field Scout TDR 200; Spectrum Technologies, Plainfield, Illinois, USA). In each plot, we measured the mean soil moisture based on four measurements taken 5–10 cm outside of the north and south edges of each subplot.

We analyzed total species richness, richness of seed-addition species, total density of seed-addition species, biomass, and soil moisture using linear mixed-effects models (lme function in the R nlme package; Pinheiro et al. 2009). For species richness and density, we used repeated-measures models to account for correlation among subplot measurements across the three censuses. Our model for total species richness included the three treatments (fire intensity, soil moisture, seed arrival) and census as fixed effects, and blocks and plots as random effects. To analyze richness and density of seed-addition species, we only used data from the seed-addition (high seed arrival) subplots, which allowed us to explicitly examine the effects of ecological filters on seed-addition species that mostly recruited from seed (most seed-addition species were absent or rare in the control subplots). These models included the two filter treatments and census as fixed effects, and blocks as random effects. The same model structure was used for biomass, whereas soil depth was included as an additional fixed effect for soil moisture. When necessary, we log$_{10}$- or square-root-transformed response variables to meet the assumptions of ANOVA. If transformation did not improve homogeneity of variances, we used a heterogeneous variance model (varIdent function) and selected the model with the lowest Akaike Information Criterion (AIC).

There were no significant four-way (total species richness) or three-way (all other response variables)

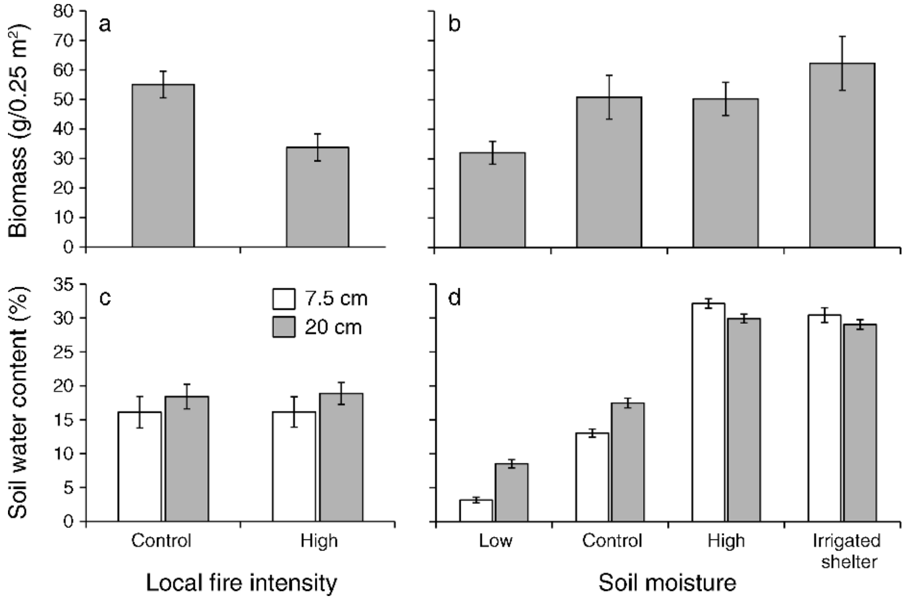

FIG. 2. Total aboveground dry biomass and soil volumetric water content (soil moisture) in the fire intensity treatments (control with natural low-intensity fire vs. high-intensity fire) and soil moisture treatments (low, control, high, and irrigated rain shelter). Biomass was measured six months postfire, and soil moisture was measured during dry summer conditions at two depths (7.5 and 20 cm). Data are means ± SE; $n = 30$ (fire intensity), 20 (soil moisture), and 10 plots (irrigated rain shelter).

interactions, nor were there any significant two-way interactions between fire intensity and soil moisture treatments for any response variable. For simplicity, we therefore focus on and present figures showing interactions between the ecological-filter and seed arrival treatments, and we provide ANOVA results for all two- and three-way interactions in Appendix B.

We analyzed effects of ecological filters on species composition using the R vegan package (Oksanen et al. 2009). For these analyses, we focused on composition of seed-addition species in the high seed arrival treatment 23 months postfire, because this allowed us to test for effects of ecological filters in local communities assembled from a standardized species pool. First, we created a matrix of community similarity using the abundance-based Bray-Curtis index. Second, we used analysis of similarity (ANOSIM) to test for treatment differences in community composition separately for the fire intensity and soil moisture experiments. Third, we used nonmetric multidimensional scaling (NMDS; isoMDS function) to generate a two-dimensional ordination showing differences in community similarity among treatments. We obtained similar results using the incidence-based Jaccard's index, so for simplicity, we only present results based on the Bray-Curtis index.

RESULTS

Effects of ecological-filter treatments on biomass, space, and soil moisture

Local fire intensity influenced aboveground biomass ($P < 0.0001$) but not soil moisture ($P = 0.68$), whereas the soil moisture treatments influenced both variables ($P = 0.001$ for biomass, $P < 0.0001$ for soil moisture; Fig. 2; Appendix B: Table B1). High-intensity fire decreased mean biomass by ~40% relative to low-intensity (control) fire (Fig. 2a), resulting in local communities with decreased plant cover (Fig. 1b). Locally intense fires also increased space in local communities; a median of 50% of microsites ($n = 25$, 10 × 10 cm grid cells/subplot) contained no rooted plants five months postfire in the high-intensity fire treatment, compared to a median of only 3.5% in the low-intensity treatment (Appendix D). Low soil moisture decreased mean biomass by 35% relative to control plots, but high soil moisture had no effect on biomass (Fig. 2b). Moreover, biomass was similar between control and irrigated rain shelter treatments, indicating that the decrease in biomass under rain shelters reflected low soil moisture. Rain shelters reduced soil moisture by 50–75% across the two soil depths (20 cm and 7.5 cm, respectively), whereas irrigation increased soil moisture by 75–145% (Fig. 2d). Soil moisture was lower at shallow depths in rain shelter plots, but was similar between depths in irrigated plots (soil moisture × soil depth interaction, $P < 0.0001$; Fig. 2d). In summary, high-intensity fire decreased biomass and increased space, rain shelters decreased soil moisture and biomass, and irrigation increased soil moisture but had no effect on biomass over the short-term.

Interactive effects of seed arrival and ecological filters on species richness and composition

Seed arrival increased total species richness regardless of local fire intensity and soil moisture ($P < 0.0001$; Fig.

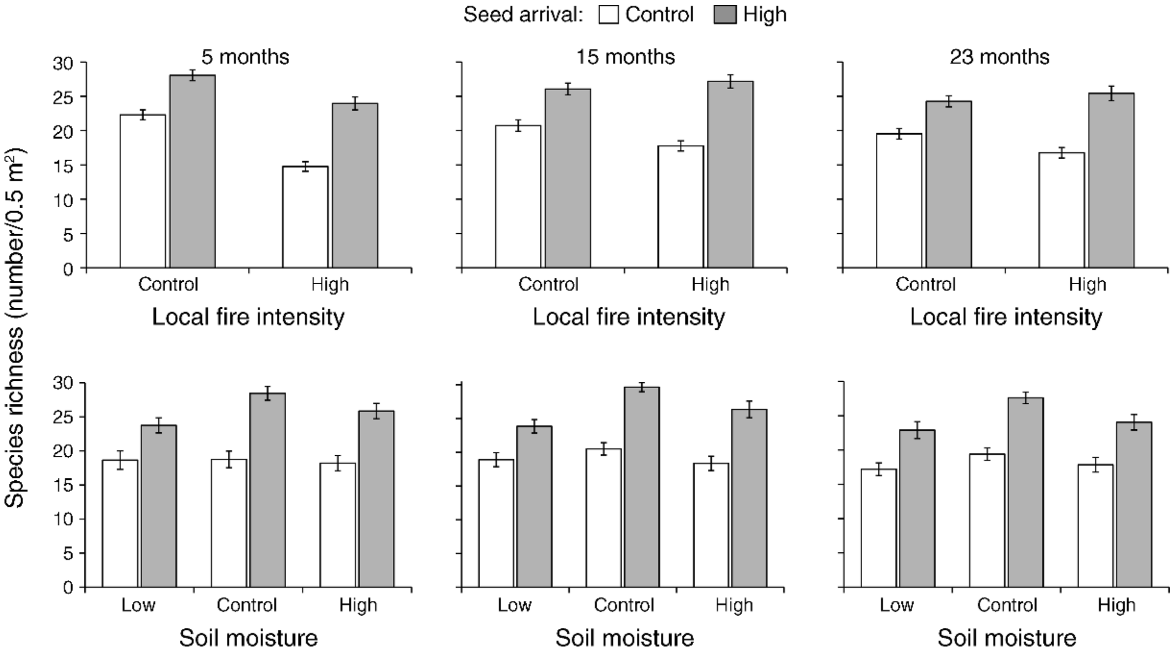

FIG. 3. Total species richness in the seed arrival, fire intensity, and soil moisture treatments 5, 15, and 23 months postfire. Data are means ± SE; $n = 30$ (fire intensity) and 20 (soil moisture) subplots. See Fig. 2 for a description of the treatments.

3; Appendix B: Table B2). At the end of the experiment, seed arrival increased mean total species richness by 25–50% across ecological-filter treatments (Fig. 3). Moreover, seed-addition species constituted 40% of the total mean species richness in high seed arrival communities, but only 15% of the species richness in control communities, indicating that the increase in total species richness reflected recruitment of seed-addition species that were initially absent or rare. Of the 31 seed-addition species, 87% (27 species) were recorded in ≥ 1 of the seed-addition subplots, and of those species, at least 10 reached reproductive maturity from seed. Post hoc analyses indicated that recruitment of seed-addition species (mean plant density in seed-addition subplots at the end of the experiment/estimated number of viable seeds added) was not correlated with seed mass (linear regression, $P = 0.74$) and also did not differ significantly between gravity- and wind-dispersed species (ANOVA, $P = 0.37$).

Seed arrival and ecological filters interactively assembled local communities (Fig. 3; Appendix B: Table B2). High-intensity fire decreased total species richness ($P < 0.001$), primarily in communities with low seed arrival (fire intensity × seed arrival interaction, $P < 0.002$). Under low seed arrival, high-intensity fire decreased total species richness by 33% in the first growing season, but this effect dissipated with time (fire intensity × time interaction, $P < 0.0001$). Under high seed arrival, in contrast, high-intensity fire had little to no influence on total species richness. Moreover, high-intensity fire increased richness of seed-addition species ($P = 0.01$), especially after the first growing season (fire intensity × time interaction, $P = 0.006$; Appendix C: Fig. C1), as well as the total density of seed-addition species only after the first growing season (fire intensity × time interaction, $P = 0.02$; Appendix C: Fig. C2). Thus, high-intensity fire decreased richness of resident species, but increased recruitment and richness of immigrating species.

High and low soil moisture decreased total species richness ($P = 0.01$), primarily in communities with high seed arrival (soil moisture × seed arrival interaction, $P = 0.02$; Fig. 3; Appendix B: Table B2). Soil moisture also influenced the richness and total density of seed-addition species ($P = 0.0002$ for richness; $P < 0.0001$ for density). Low soil moisture decreased richness and density of seed-addition species by 30% and 65%, respectively, whereas high soil moisture had little to no effect on richness of seed-addition species but increased their total density by 25% (Appendix C: Fig. C1, C2). In addition, total density was positively correlated with soil moisture at 7.5 and 20 cm in both the low-intensity fire ($P < 0.001$, $r^2 = 0.30$–0.33, $n = 30$ seed-addition subplots) and high-intensity fire ($P < 0.0001$, $r^2 = 0.42$–0.45, $n = 30$) treatments.

Local fire intensity and soil moisture influenced the composition of seed-addition species (Fig. 4). Communities assembled following high-intensity fire were more similar in species composition than communities assembled following low-intensity fire, but the overall difference was small (ANOSIM, $R = 0.04$, $P = 0.039$; Fig. 4). High soil moisture significantly increased similarity in species composition relative to the low soil moisture and control treatments ($R = 0.33$, $P = 0.001$), but there was no strong difference in similarity between low soil moisture and control treatments (Fig. 4).

Discussion

Our results support the general hypothesis that immigration from the species pool and niche-based ecological filters interactively structure species-rich plant communities. We found that seed arrival increased species richness regardless of local fire intensity and soil moisture, indicating that high-diversity groundcover communities constitute relatively open-membership assemblages. Although there is growing experimental evidence that seed arrival from local and regional species pools strongly limits local diversity in species-rich plant communities (e.g., chalk grasslands [Zobel et al. 2000], longleaf pine communities [Myers and Harms 2009*a*], tropical forests [Paine and Harms 2009]), our study provides insights into how multiple ecological filters limit local species membership in both space (e.g., spatial variation in disturbance) and time (e.g., temporal variation in resource availability). Moreover, we found that communities assembled from a standardized species pool were more similar in species composition in the presence of some ecological filters (wet soil conditions, and to a lesser extent, high-intensity fires), illustrating conditions that may increase deterministic community assembly in extremely species-rich communities.

Locally intense fires may function as an abiotic filter that removes some resident species from local communities, as well as a process that influences the effects of other ecological filters in postfire environments (e.g., competition and resource availability). Locally intense fires decreased richness of resident species and aboveground biomass (Figs. 2 and 3) and increased space (microsite availability) in local communities (Appendix D). To the extent that this biodiversity loss is nonrandom with respect to species and their functional traits, locally intense fires may function as an important niche-based filter influencing community assembly. For example, species with shallow root systems or seed banks may experience higher mortality from increased soil heating than species with deeper root systems or seed banks (e.g., Odion and Davis 2000, Gagnon et al. 2010). In contrast, high-intensity fire may also remove many rare (e.g., low biomass) species irrespective of their functional traits. Although our results cannot distinguish between these alternative mechanisms, other studies in this community demonstrate that populations of some common, large-stature species are negatively affected by locally intense fires (e.g., dominant bunchgrasses [P. R. Gagnon, K. E. Harms, W. J. Platt, H. A. Passmore, and J. A. Myers, *unpublished data*] and shrubs [Thaxton and Platt 2006]). In this way, spatial variation in local fire intensity may play an important role in the coexistence of dominant and rare species (Thaxton and Platt 2006, Myers and Harms 2009*a*), as well as in creating recruitment opportunities for seeds that arrive from the species pool.

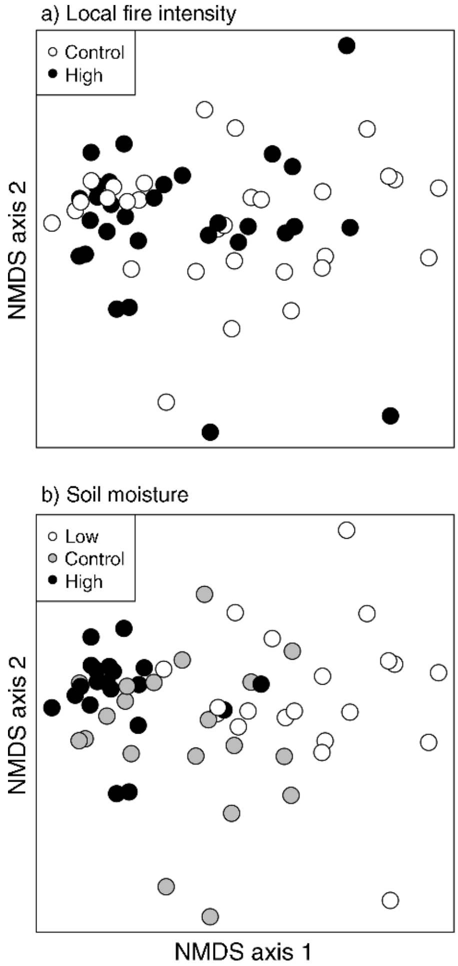

FIG. 4. Ordination of seed-addition species composition (Bray-Curtis similarity) in the fire intensity and soil moisture treatments 23 months postfire derived from nonmetric multidimensional scaling (NMDS; stress = 0.18). Circles represent replicate subplots (local communities) in the seed-addition (high seed arrival) treatment; communities close together in ordination space are more similar in their composition of seed-addition species. See Fig. 2 for a description of the treatments.

We found that high-intensity fire influenced postfire recruitment, richness, and composition of immigrating species. Locally intense fires increased environmental heterogeneity by creating a spatial mosaic of gaps in the landscape (Fig. 1). Over the short term, high-intensity fire can therefore play an important role in the maintenance of species diversity by promoting recruitment from the species pool. Over the longer term, variation in local fire intensity may help maintain diversity by enhancing individual performance (growth, survival, and fecundity) of rare recruits in sites with low densities of competitors (Chesson 2000), as well as by promoting coexistence of species with different postfire regeneration traits. The difference in community composition we observed in the fire intensity treatments is consistent with this hypothesis: Communities assembled following high-intensity fire were more similar in composition of seed-addition species relative to communities assembled following low-intensity fire, but the overall difference among these communities was small. High-intensity fires may increase deterministic community assembly by promoting recruitment of gap-dependent species, e.g., species with traits that enhance relative growth rates in resource-rich environments. Although our experiment primarily focused on recruitment of the most species-rich functional group at our study site (gravity- and wind-dispersed forbs), it is likely that we would have uncovered a stronger, deterministic effect of disturbance if we had expanded our experimental species pool to include greater functional diversity (Questad and Foster 2008, Myers and Harms 2009*a*).

Our results suggest a key role for soil moisture as an abiotic filter influencing community assembly, especially through its effects on recruitment from the species pool. We found that drought conditions reduced recruitment and richness of immigrating species. In contrast, wet soil conditions increased recruitment but decreased or had little influence on species richness. These results support the hypothesis that soil moisture plays an important role in regulating seed and seedling recruitment in this and other herbaceous-dominated communities (Kirkman et al. 2001, Foster and Dickson 2004, Iacona et al. 2010), but also suggest that positive effects of soil moisture on species richness may be reduced under wet soil conditions. Moreover, we found that communities assembled under wet soil conditions were more similar in species composition relative to communities assembled under drought and control conditions. This result suggests that high-rainfall conditions may function as a niche-based filter that contributes to deterministic community assembly in this species-rich community, a process that may parallel effects of drought in aquatic mesocosm communities (Chase 2007). The mechanisms underlying this pattern may include niche-based differences in the tolerance of seeds and seedlings to soil moisture (Silvertown et al. 1999), as well as fast growth rates and competitive dominance of some immigrating species under wet soil conditions. The higher variability in community composition under low soil moisture, in contrast, may have been more influenced by stochastic loss of individuals and species owing to small population sizes imposed by drought conditions, as well as by smaller changes in soil moisture under rain shelters relative to irrigated communities. The interactive effects of seed arrival and soil moisture observed in our experiment support the view that community invasibility depends on the dynamics of local resource availability (e.g., the "fluctuating resources hypothesis"; Davis et al. 2000), even in relatively open-membership assemblages.

Our experiment provides mechanistic insights into the assembly and maintenance of biodiversity in species-rich communities. First, our results underscore the importance of synthetic models in community ecology that integrate effects of dispersal and niche assembly to understand the ecological conditions in which stochastic and deterministic processes are expected to influence community structure (e.g., Tilman 2004, Gravel et al. 2006, Chase 2007). Although dispersal assembly is generally predicted to play an important role in high-diversity communities that contain large numbers of rare species and that are assembled from large species pools (e.g., Hubbell 2001, Chase 2003), our results suggest that niche-based recruitment limitation imposed by multiple ecological filters constrains effects of seed arrival on community assembly in space and time. In contrast, previous studies in species-rich plant communities, predominantly focused on tree-dominated communities in tropical forests, have largely examined components of niche and dispersal assembly in isolation from one another (e.g., Condit et al. 2006, Wills et al. 2006, John et al. 2007), thereby limiting our ability to understand how these processes interact in community assembly (e.g., Tuomisto et al. 2003, Myers and Harms 2009*a*, Paine and Harms 2009). In high-diversity pine savannas, we propose that dispersal assembly generally plays an important role in structuring groundcover biodiversity, but that the importance of dispersal assembly can be tempered by multiple niche-based processes, including spatial variation in local fire intensity, heterogeneous soil moisture conditions, and competition from some dominant guilds (Myers and Harms 2009*a*). Second, frequent fire in this ecosystem, and spatial variation in local fire intensity, play important roles in limiting abundances of common species (Thaxton and Platt 2006; P. R. Gagnon, K. E. Harms, W. J. Platt, H. A. Passmore, and J. A. Myers, *unpublished data*) and promoting recruitment of rare species from the species pool (Fig. 3). In this way, fire may play a similar ecological role as grazers in species-rich chalk grasslands and natural enemies in tropical forests (Silvertown 2005), suggesting some intriguing commonalities in the general mechanisms that maintain extremely diverse plant communities.

Our results also have applied implications for restoration and conservation of threatened longleaf pine ecosystems. Today, most remnant longleaf pine communities exist in a fragmented landscape and are largely isolated from one another (e.g., Keddy et al. 2006). Restoration and biodiversity conservation in these fragments require prescribed fire, and in many cases, reintroduction of plant species from the regional species pool using seed introductions (Walker and Silletti 2006) or corridors to facilitate dispersal among fragments (Damschen et al. 2006). Our results suggest that seed introductions are likely to have the largest effect on recruitment and local biodiversity when seeds are added in years in which sites are burned and rainfall is less likely to limit seed germination and seedling establishment. Moreover, to the extent that the maintenance of diversity is promoted by heterogeneity in local fire intensity, land managers can manipulate pre-fire fuel loads to create a mixture of postfire conditions. Synergistic effects involving fire, rainfall, and immigration from the regional species pool will likely play an increasingly important role in the conservation of biodiversity in the face of climate change (e.g., increased droughts and extreme rainfall), habitat loss (smaller communities and species pools), and fragmentation (reduced dispersal and genetic diversity).

Acknowledgments

We thank Natalia Aristizabal, Adriana Bravo, Jane Carlson, Santiago Claramunt, Rae Crandall, Jim Cronin, Sandra Galeano, Paul Gagnon, Morgan Kerns, Metha Klock, Teresa Kurtz, John Morgan, Tim Paine, Heather Passmore, Bill Platt, Ellen Reid, and Richard Stevens for assistance and helpful suggestions throughout the course of the study; Erik Johnson for sharing unpublished data on seed densities in longleaf pine savannas; the Southeastern Girl Scout Council and Larry Ehrlich for access to the field site and for maintaining prescribed fires; and two anonymous reviewers for constructive comments on the manuscript. Financial support was provided by the Torrey Botanical Society, Sigma Xi, the Louisiana Office of Environmental Education, LSU Biological Sciences Graduate Student Association (BioGrads), and the National Science Foundation.

Literature Cited

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Barot, S. 2004. Mechanisms promoting plant coexistence: Can all the proposed processes be reconciled? Oikos 106:185–192.

Bell, G. 2001. Ecology: neutral macroecology. Science 293:2413–2418.

Brewer, J. S. 2006. Resource competition and fire-regulated nutrient demand in carnivorous plants of wet pine savannas. Applied Vegetation Science 9:11–16.

Chase, J. M. 2003. Community assembly: When should history matter? Oecologia 136:489–498.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences USA 104:17430–17434.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: Linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clark, J. S. 2009. Beyond neutral science. Trends in Ecology and Evolution 24:8–15.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68:213–235.

Condit, R., et al. 2006. The importance of demographic niches to tree diversity. Science 313:98–101.

Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. Science 313:1284–1286.

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

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Earley, L. S. 2004. Looking for longleaf: the fall and rise of an American forest. University of North Carolina Press, Chapel Hill, North Carolina, USA.

Foster, B. L., and T. L. Dickson. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. Ecology 85:1541–1547.

Gagnon, P. R., H. A. Passmore, W. J. Platt, J. A. Myers, C. E. T. Paine, and K. E. Harms. 2010. Does pyrogenicity protect burning plants? Ecology 91:3481–3486.

Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal 23:22–37.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9:399–409.

Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–225 *in* J. Diamond, and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and the structure of tropical rain forest tree communities. Pages 314–329 *in* J. Diamond, and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1–12.

Hutchinson, G. E. 1957. Population studies—animal ecology and demography—concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Iacona, G. D., L. K. Kirkman, and E. M. Bruna. 2010. Effects of resource availability on seedling recruitment in a fire-maintained savanna. Oecologia 163:171–180.

John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo, and R. B. Foster. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences USA 104:864–869.

Johnson, E. I. 2006. Effects of fire on habitat associations, abundance, and survival of wintering henslow's sparrows (*Ammodramus henslowii*) in southeastern Louisiana longleaf pine savannas. Thesis. Louisiana State University, Baton Rouge, Louisiana, USA.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Keddy, P. A., L. Smith, D. R. Campbell, M. Clark, and G. Montz. 2006. Patterns of herbaceous plant diversity in southeastern Louisiana pine savannas. Applied Vegetation Science 9:17–26.

Kirkman, L. K., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. American Journal of Botany 88:2119–2128.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

McGill, B. J., B. A. Maurer, and M. D. Weiser. 2006. Empirical evaluation of neutral theory. Ecology 87:1411–1423.

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist 162:544–557.

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

Myers, J. A., and K. E. Harms. 2009*b*. Seed arrival, ecological filters, and plant species richness: A meta-analysis. Ecology Letters 12:1250–1260.

Odion, D. C., and F. W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. Ecological Monographs 70:149–169.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2009. vegan: community ecology package. R package version 1.15-3. ⟨http://cran.r-project.org/web/packages/vegan/index.html⟩

Paine, C. E. T., and K. E. Harms. 2009. Quantifying the effects of seed arrival and environmental conditions on tropical seedling community structure. Oecologia 160:139–150.

Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern atlantic and eastern gulf coast regions: A preliminary classification. Proceedings of the Tall Timbers Fire Ecology Conference 18:45–81.

Pinheiro, J. D., D. Bates, D. Saikat, D. Sarkar, and the R Core Team. 2009. nlme: linear and nonlinear mixed effects models. R package version 3.1-92. ⟨http://cran.r-project.org/web/packages/nlme/index.html⟩

Platt, W. J., S. M. Carr, M. J. Reilly, and J. Fahr. 2006. Pine savanna overstorey influences on ground-cover biodiversity. Applied Vegetation Science 9:37–50.

Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. Ecology Letters 11:717–726.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1–15.

Silvertown, J. 2005. Demons in eden: the paradox of plant diversity. Chicago University Press, Chicago, Illinois, USA.

Silvertown, J., M. E. Dodd, D. J. G. Gowing, and J. O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Thaxton, J. M., and W. J. Platt. 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87:1331–1337.

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 USA 101:10854–10861.

Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western amazonian forests. Science 299:241–244.

Turnbull, L. A., M. Rees, and D. W. Purves. 2008. Why equalising trade-offs aren't always neutral. Ecology Letters 11:1037–1046.

Vellend, M. 2010. Conceptual synthesis in community ecology. Quarterly Review of Biology 85:183–206.

Vergnon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. Ecology Letters 12:1079–1090.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2007. Patterns of relative species abundance in rainforests and coral reefs. Nature 450:45–49.

Walker, J., and R. K. Peet. 1983. Composition and species-diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55:163–179.

Walker, J. L., and A. M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. Pages 297–333 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York, USA.

Wills, C., et al. 2006. Nonrandom processes maintain diversity in tropical forests. Science 311:527–531.

Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Mols. 2000. Is small-scale species richness limited by seed availability or microsite availability? Ecology 81:3274–3282.

APPENDIX A

Species, densities, and viability of seeds used in the seed arrival treatment (*Ecological Archives* E092-056-A1).

APPENDIX B

ANOVA tables for biomass, soil moisture, species richness, and total density (*Ecological Archives* E092-056-A2).

APPENDIX C

Richness and total density of seed-addition species in the fire intensity and soil moisture treatments (*Ecological Archives* E092-056-A3).

APPENDIX D

Space occupancy in the fire intensity treatments (*Ecological Archives* E092-056-A4).

Ecological Archives E092-056-A1

Jonathan A. Myers and Kyle E. Harms. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92:676–686.

Appendix A (TABLE A1). Species, densities, and viability of seeds used in the seed arrival treatment. Thirty-one species added in the seed arrival treatment in 2007, showing dispersal type based on seed morphology, number of seeds added per 0.5 m^2 subplot, and percent seed germination on petri dishes (*N* = 50 seeds/species; germination was not tested for *H. gronovii*).

Species	Family	Life form[1]	Dispersal� type	*N* seeds added	Germination (%)
Ageratina aromatica	Asteraceae	PF	Wind	300	94
Carex glaucescens	Cyperaceae	PS	Gravity	30	84
C. tenax	Cyperaceae	PS	Gravity	30	94
Chromolaena ivifolia	Asteraceae	PF	Wind	200	68
Chrysopsis mariana	Asteraceae	PF	Wind	30	26
Cirsium horridulum	Asteraceae	BF	Wind	50	88
Conoclinium coelestinum	Asteraceae	PF	Wind	300	96
Crotalaria purshii	Fabaceae	PL	Gravity	25	12
Elephantopus tomentosus	Asteraceae	PF	Wind	350	88
Eryngium yuccifolium	Apiaceae	PF	Gravity	100	28
Eupatorium album	Asteraceae	PF	Wind	50	14
Eupatorium rotundifolium	Asteraceae	PF	Wind	200	40
Eurybia paludosa	Asteraceae	PF	Wind	50	26
Helenium flexuosum	Asteraceae	PF	Gravity	200	86
Helianthus angustifolius	Asteraceae	PF	Gravity	100	68
H. radula	Asteraceae	PF	Gravity	200	68
Hieracium gronovii	Asteraceae	PF	Wind	30	�
Hypericum crux-andreae	Clusiaceae	W	Gravity	100	46
H. setosum	Clusiaceae	PF	Gravity	200	88
Hyptis� alata	Lamiaceae	PF	Gravity	500	54
Liatris pycnostachya	Asteraceae	PF	Wind	50	28
L. squarrulosa	Asteraceae	PF	Wind	75	66
Ludwigia hirtella	Onagraceae	PF	Gravity	100	82
Plantago virginica	Plantaginaceae	AF	Gravity	30	98
Pycnanthemum					

albescens	Lamiaceae	PF	Gravity	400	16
Rhexia alifanus	Melastomataceae	PF	Gravity	50	14
Rhexia mariana	Melastomataceae	PF	Gravity	50	64
Rudbeckia hirta	Asteraceae	PF	Gravity	200	30
Salvia lyrata	Lamiaceae	PF	Gravity	50	62
Solidago odora	Asteraceae	PF	Wind	100	84
S. rugosa	Asteraceae	PF	Wind	500	36

[1] AF = annual non-legume forb, BF = biennial non-legume forb, PF = perennial non-legume forb, PL = perennial legume forb, PS = perennial sedge, W = woody.

[Back to E092-056]

Ecological Archives E092-056-A2

Jonathan A. Myers and Kyle E. Harms. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92:676–686.

Appendix A. ANOVA tables for biomass, soil moisture, species richness, and total density.

Table B1. Results from mixed-effects ANOVA testing for effects of local fire intensity and soil moisture on total aboveground plant biomass in Fall 2007 and soil volumetric water content (soil moisture) in Summer 2008. Soil water was analyzed at two depths (7.5 and 20 cm). *P* values < 0.05 are indicated in bold.

Variable	***df***	**den *df***	***F***	***P***
Total biomass/0.25 m^2	�	�	�	�
Fire intensity	1	53	021.01	< **0.0001**
Soil moisture	2	53	007.70	< **0.0012**
Fire intensity × Soil moisture	2	53	000.54	< 0.5850
Soil moisture	�	�	�	�
Fire intensity	1	53	000.16	< 0.6839
Soil moisture	2	53	586.32	< **0.0001**
Depth	1	54	109.03	< **0.0001**
Fire intensity × Soil moisture	2	53	000.75	< 0.4752
Fire intensity × Depth	1	54	000.77	< 0.3840
Soil moisture × Depth	2	54	097.91	< **0.0001**
Fire intensity × Soil moisture × Depth	2	54	001.25	< 0.2936

Table B2. Results from mixed-effects ANOVA testing for effects of local fire intensity, soil moisture, seed arrival, and time on total species richness, seed-addition species richness, and total density of seed-addition species. Seed-addition species richness and density were analyzed using data only from seed-addition subplots because seed-addition species occurred infrequently in seed-control subplots. Seed-addition species richness was square-root transformed and total density was log$_{10}$-transformed to normalize residuals. *P* values < 0.05 are indicated in bold.

Variable	***df***	**den *df***	***F***	***P***
Total species richness	�	�	�	�
Fire intensity	1	053	013.22	< **0.0006**
Soil moisture	2	053	004.99	< **0.0103**
Seed arrival	1	054	144.74	< **0.0001**
Time	1	220	016.50	< **0.0001**
Fire intensity × Soil moisture	1	053	001.84	< 0.1674
Fire intensity × Seed arrival	2	054	010.65	< **0.0019**
Fire intensity × Time	2	220	045.20	< **0.0001**
Soil moisture × Seed arrival	2	054	004.01	< **0.0238**

Soil moisture × Time	4	220	001.67	< 0.1566
Seed arrival × Time	2	220	0.99	< 0.3721
Fire intensity × Soil moisture × Seed arrival	2	054	000.44	< 0.6442
Fire intensity × Soil moisture × Time	4	220	001.37	< 0.2446
Fire intensity × Seed arrival × Time	2	220	000.18	< 0.8316
Soil moisture × Seed arrival × Time	4	220	001.24	< 0.2914
Seed-addition species richness	�	�	�	�
Fire intensity	1	053	006.75	**< 0.0121**
Soil moisture	2	053	0� 9.75	**< 0.0002**
Time	2	108	0� 3.55	**< 0.0319**
Fire intensity × Soil moisture	2	053	000.62	< 0.5393
Fire intensity × Time	2	108	005.35	**< 0.0060**
Soil moisture × Time	4	108	000.48	< 0.7447
Fire intensity × Soil moisture × Time	4	108	000.25	< 0.9041
Total density of seed-addition species	�	�	�	�
Fire intensity	1	053	003.55	< 0.0650
Soil moisture	2	053	042.91	**< 0.0001**
Time	2	108	0� 9.03	**< 0.0002**
Fire intensity × Soil moisture	2	053	000.15	< 0.8582
Fire intensity × Time	2	108	003.98	**< 0.0214**
Soil moisture × Time	4	108	001.46	< 0.2186
Fire intensity × Soil moisture × Time	4	108	000.18	< 0.9452

[Back to E092-056]

Ecological Archives E092-056-A3

Jonathan A. Myers and Kyle E. Harms. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92:676–686.

Appendix C. Richness and total density of seed-addition species in the fire intensity and soil moisture treatments.

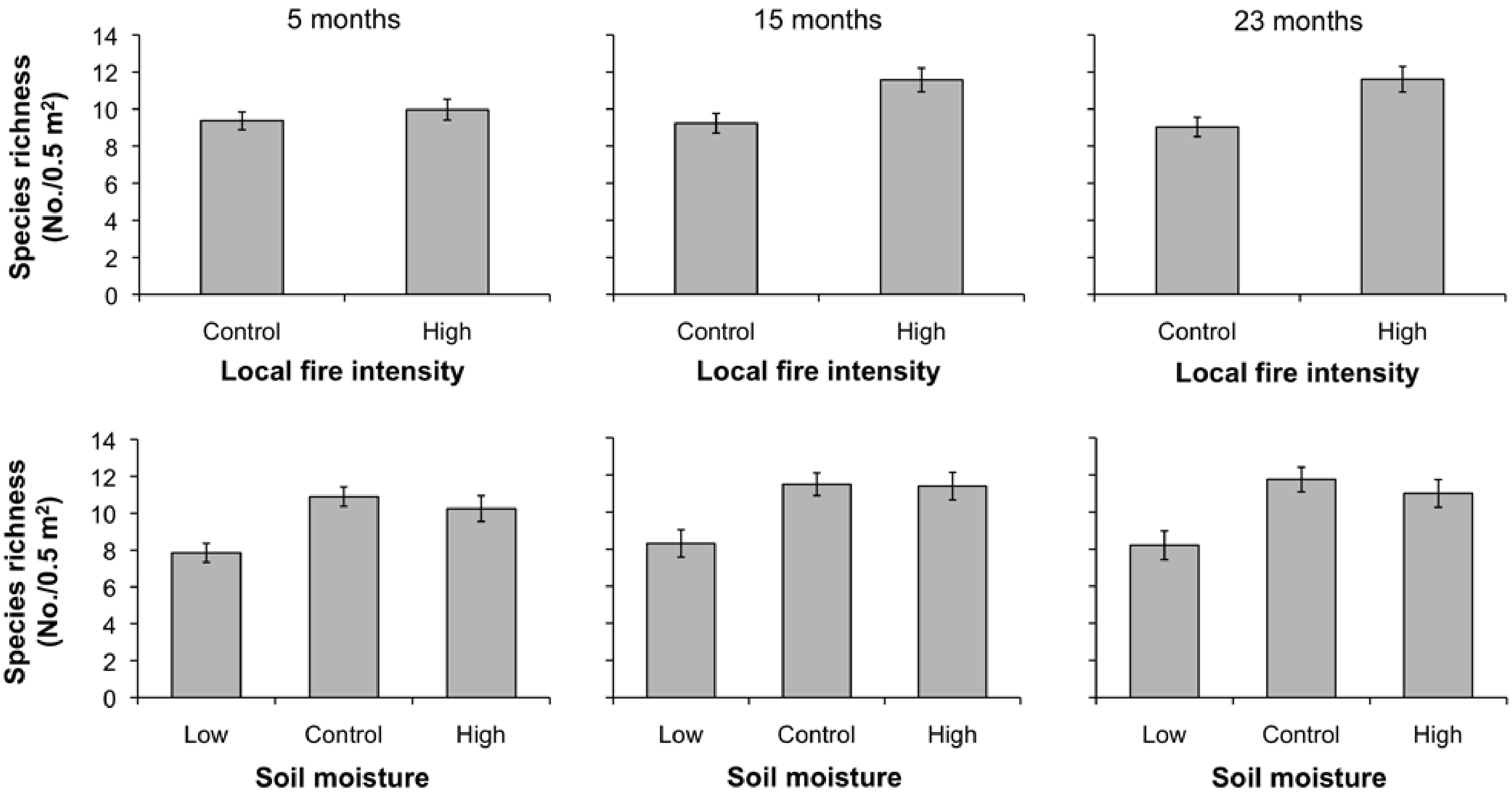

FIG. C1. Richness of seed-addition species in the fire intensity and soil moisture treatments 5, 15, and 23 months post fire. Bars = means � 1 SE; *N* = 30 (fire intensity) and 20 (soil moisture) subplots. Results are shown for the high seed arrival (seed addition) treatment; most species were absent or rare in the low seed arrival (control) treatment.

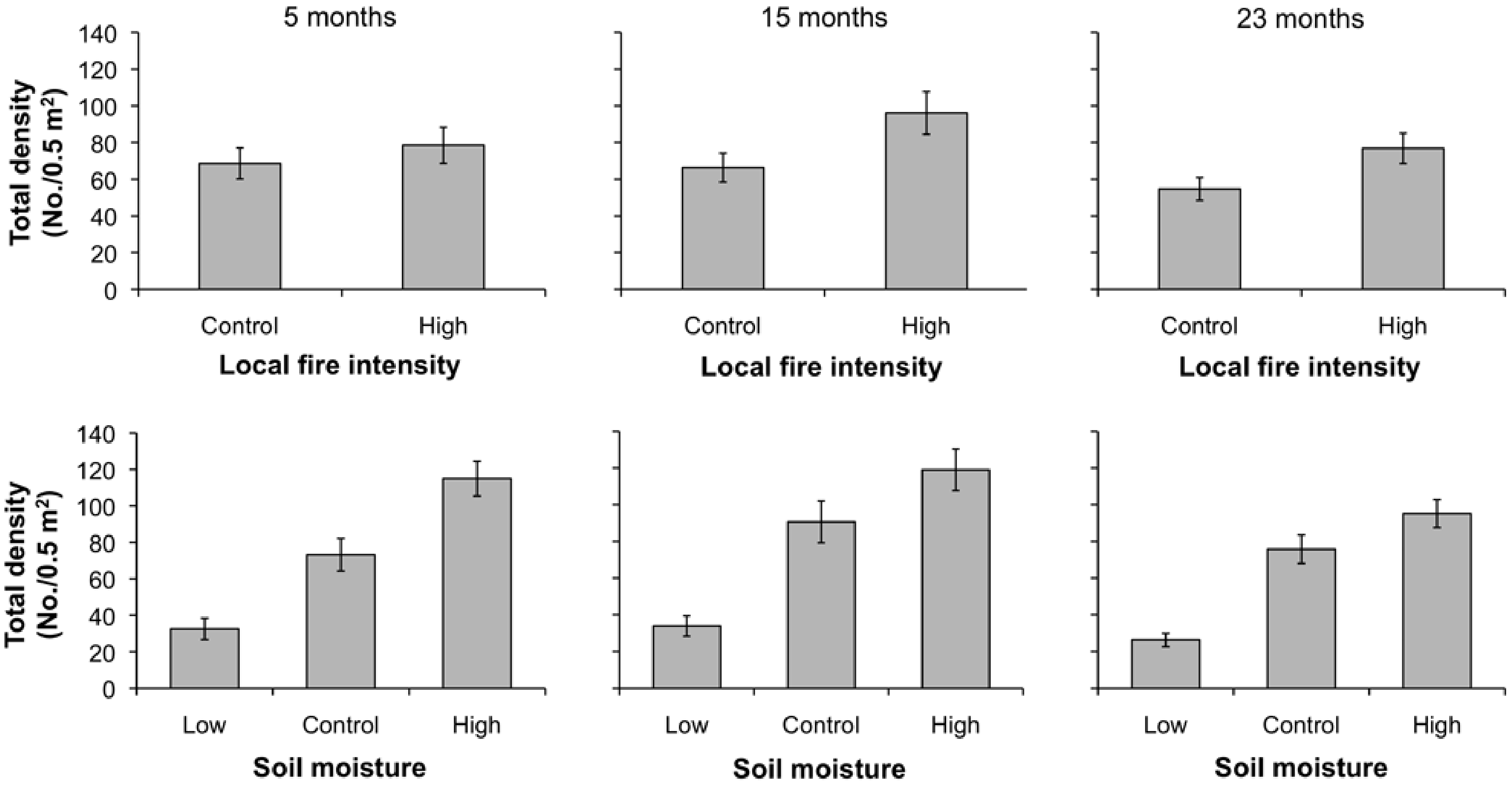

FIG. C2. Total density of seed-addition species in the fire intensity and soil moisture treatments 5, 15, and 23 months post fire. Bars = means � 1 SE; *N* = 30 (fire intensity) and 20 (soil moisture) subplots. Results are shown for the high seed arrival (seed addition) treatment; most species were absent or rare in the low seed arrival (control) treatment.

[Back to E092-056]

Ecological Archives E092-056-A4

Jonathan A. Myers and Kyle E. Harms. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92:676–686.

Appendix D. Space occupancy in the fire intensity treatments.

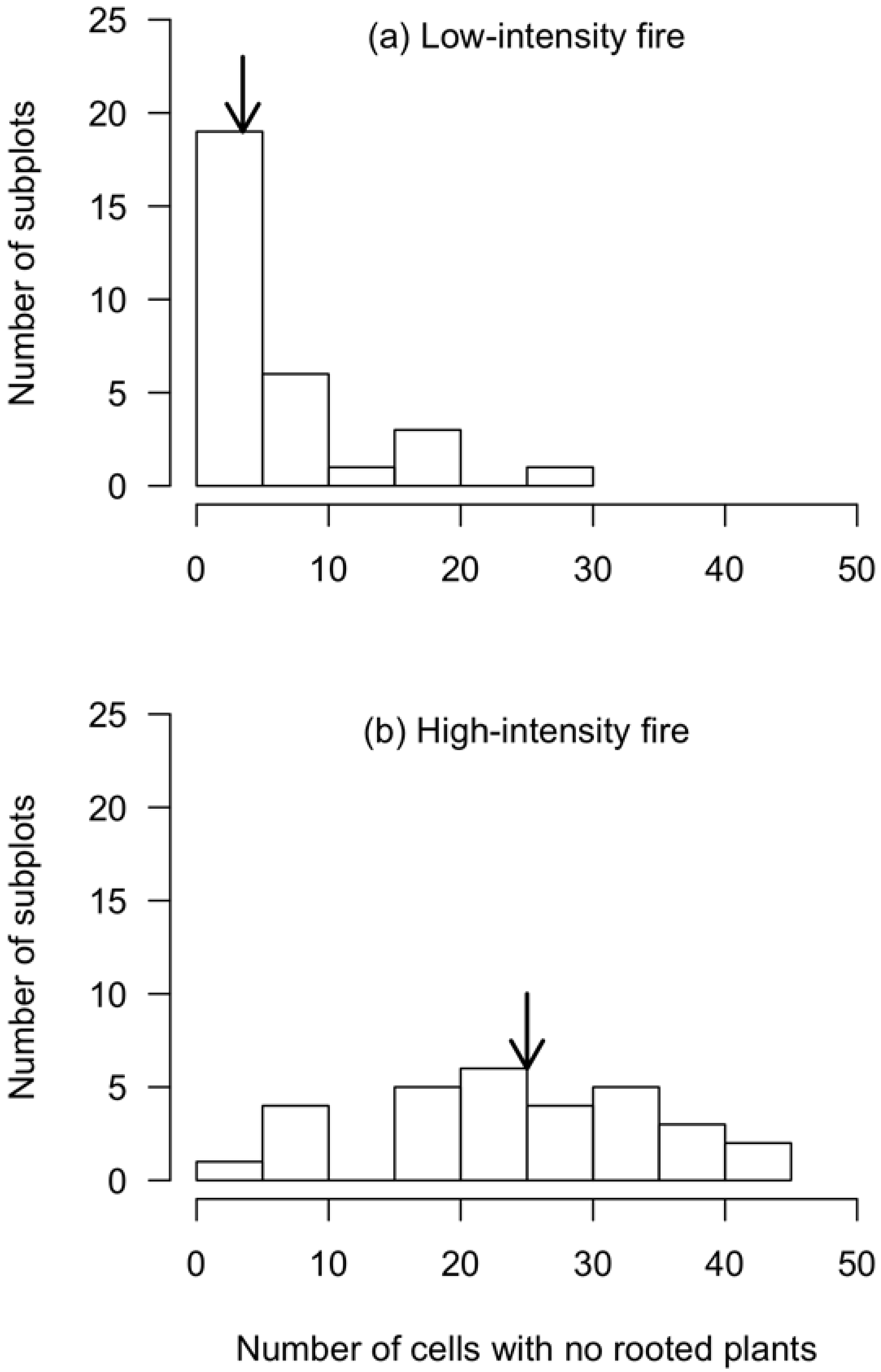

FIG. D1. Space occupancy in the fire intensity treatments 5-months post fire. The histograms show the distribution of microsite availability (number of 10 × 10 cm grid cells that contained no rooted plants) in the (a) low-intensity and (b) high-intensity fire treatments. Results are shown for the 60 subplots in the low seed arrival treatment. The arrow indicates the median value for each treatment. Note that high-intensity fires increased space in local communities.

[Back to E092-056]