Productivity and Species Richness in Longleaf Pine Woodlands:
Resource-Disturbance Influences across an Edaphic Gradient

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Productivity and species richness in longleaf pine woodlands: resource-disturbance influences across an edaphic gradient

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Abstract. This study examines the complex feedback mechanisms that regulate a positive relationship between species richness and productivity in a longleaf pine-wiregrass woodland. Across a natural soil moisture gradient spanning wet-mesic to xeric conditions, two large scale manipulations over a 10-yr period were used to determine how limiting resources and fire regulate plant species diversity and productivity at multiple scales. A fully factorial experiment was used to examine productivity and species richness responses to N and water additions. A separate experiment examined standing crop and richness responses to N addition in the presence and absence of fire. Specifically, these manipulations addressed the following questions: (1) How do N and water addition influence annual aboveground net primary productivity of the midstory/overstory and ground cover? (2) How do species richness responses to resource manipulations vary with scale and among functional groups of ground cover species? (3) How does standing crop (including overstory, understory/midstory, and ground cover components) differ between frequently burned and fire excluded plots after a decade without fire? (4) What is the role of fire in regulating species richness responses to N addition? This long-term study across a soil moisture gradient provides empirical evidence that species richness and productivity in longleaf pine woodlands are strongly regulated by soil moisture. After a decade of treatment, there was an overall species richness decline with N addition, an increase in richness of some functional groups with irrigation, and a substantial decline in species richness with fire exclusion. Changes in species richness in response to treatments were scale-dependent, occurring primarily at small scales (≤10 m²). Further, with fire exclusion, standing crop of ground cover decreased with N addition and non-pine understory/midstory increased in wet-mesic sites. Non-pine understory/midstory standing crop increased in xeric sites with fire exclusion, but there was no influence of N addition. This study highlights the complexity of interactions among multiple limiting resources, frequent fire, and characteristics of dominant functional groups that link species richness and productivity.

Key words: aboveground annual net primary productivity; fire disturbance; fire exclusion; ground cover species; legumes; limiting resources; longleaf pine woodland; nitrogen fertilization; productivity-species richness relationship; resource manipulations; scales of species richness; soil moisture gradient; species assemblage processes.

Introduction

The relationship between productivity and plant species richness (biodiversity) has been a central issue of research and debate in ecology for many decades. Several reviews conclude that patterns of diversity and productivity are heterogeneous, and include unimodal, positive, negative, or no relationship at all, and the mechanisms that structure the relationship are varied and complex (Grace 1999, Waide et al. 1999, Gough et al. 2000, Foster 2001, Mittelbach et al. 2001, Pausas and Austin 2001, Adler et al. 2011). Various conceptual models have attributed patterns of productivity-species richness to interacting gradients of disturbance, environmental condition, propagule availability, interspecific competition and facilitation, litter accumulation, temporal and spatial resource heterogeneity, the spatial scale relative to species turnover, and characteristics of the species pool (Grime 1973, Huston 1979, Keddy 1992, Grace 1999, Huston 2014, and many others).

Attempts to gain a mechanistic understanding of the factors structuring productivity and richness in terrestrial vegetation often include experimental manipulations of productivity through additions of the limiting resource(s) (e.g., nutrients, water), or focus on a dominant disturbance agent. Although numerous studies spanning a wide range of ecosystems have been conducted, critical reviews of such studies have identified limitations including the small scale (several square meters) at which most experiments are performed, the use of natural or artificial ecosystems of low species richness, the short-term duration of experimental

observation (generally fewer than 4 yr), the common manipulation of single variables, and the tendency to overwhelm the soil chemistry with excessive nutrient loading (Grace 1999, Waide et al. 1999, Gough et al. 2000, Mittelbach et al. 2001, Pausas and Austin 2001, Clark et al. 2007). Gough et al. (2000) further caution that experimentally increasing fertility at one small area over a relatively short time does not adequately incorporate the long-term processes that ultimately shape productivity and richness patterns across a natural gradient. More useful approaches for examining complex relationships between disturbance, resources, and richness have been advocated, such as experimentation in high-diversity ecosystems (Waide et al. 1999), using temporal and spatial scales of observation that match the ecological forces that contribute to species assemblages (Gough et al. 2000, Mittelbach et al. 2001, Zobel and Partel 2008), and examining multiple factors and their interactions across natural productivity gradients (Mittelbach et al. 2001, Pausas and Austin 2001).

Longleaf pine-wiregrass woodlands provide an archetypal setting to examine the relationships among productivity, species richness, limiting resources, and disturbance in a natural environment because of the extremely high number of species at small and large scales (0.1 m^2 to thousands of hectares), the wide ecological range of this ecosystem (hydric to xeric), and their requirement of frequent prescribed fire (2–3 yr return interval; Walker and Peet 1984, Kirkman et al. 2001, Peet 2006, Iacona et al. 2010, Myers and Harms 2011, Palmquist et al. 2014, 2015). In the absence of fire, rapid encroachment by fire-intolerant woody species occurs, eventually leading to degradation of the ecosystem and changes in species richness and dominance (Garren 1943, Monk 1968, Veno 1976, Myers 1990, and many others).

Productivity of this ecosystem appears to be limited by multiple resources, and the availability of some nutrients is complexly linked to fire regime across a soil moisture gradient (Mitchell et al. 1999, Wilson et al. 2002). Previous studies suggest that soil moisture availability is a strong regulator of productivity. For example, annual aboveground net primary productivity (ANPP) measured in longleaf pine-wiregrass woodlands varied nearly twofold across a soil moisture/texture gradient and was positively correlated with soil moisture (Mitchell et al. 1999). ANPP, however, was negatively correlated with net soil N mineralization rates, which are among the lowest reported for North American forests (Mitchell et al. 1999, Wilson et al. 1999). A potential explanation for the site variation across complex ecological gradients is that xeric sites have more hardwood litter inputs than wet-mesic sites due to a larger presence of fire-tolerant oaks that have greater nutrient demands than other species (Jacqmain et al. 1999). Thus, the greater abundance of higher quality litter, coupled with higher soil temperature of the xeric site, results in increased rates of N mineralization (Wilson et al. 1999).

Nitrogen availability is also directly linked to fire. For example, frequent fire limits the accumulation of a litter layer (Hiers et al. 2007), volatilizing up to 80–90% of the N in litter and ground cover (Boring et al. 2004). More indirectly, frequent fire favors species that promote substantial N mineralization from fine root turnover at deeper soil depths (Wilson et al. 2002, Guo et al. 2008). Also, the grass-dominated and species-rich ground cover is characterized by a high abundance and richness of nitrogen-fixing legumes (Hainds et al. 1999, Hiers and Mitchell 2007, Cathey et al. 2010), which is consistent with predictions for sites with low soil nitrogen availability (Leach and Givnish 1998). In contrast to the high degree of volatilization of N with fire, all P present in litter is thermally mineralized and returned to the soil. Hainds et al. (1999) reported that extractable P was highest in xeric sites and decreased as moisture increased, similar to that of N; however, microbial P increased with soil moisture.

Contrasting theoretical models have been suggested to explain patterns and dynamics of biodiversity in species-rich ecosystems, including niche differentiation (Grubb 1977, Keddy 1992, Silvertown 2004), lottery-based seed supply (Sale 1977, Hurtt and Pacala 1995), disturbances that limit competition (Huston 1979, 1999), and ecological drift (Hubbell 2001). One model that explains a positive productivity-species richness relationship is based on the interactive effects of frequent disturbance and increasing productivity that discourages competitively superior species and increases colonization, thereby resulting in coexistence of more species (Kondoh 2001).

In the species-rich longleaf pine ecosystem, there are most likely elements of all of these processes regulating patterns of community assemblage, similar to the continuum hypothesis suggested by Gravel et al. (2006). Due to frequent fire, competitive exclusion does not appear to be a significant filter of species distribution (Roth et al. 2008, Myers and Harms 2009), whereas stress tolerance, dispersal traits, species pool, and perhaps facilitation most likely drive patterns in plant species composition (Iacona et al. 2012). Because of the severity of water limitation in significant portions of upland longleaf pine-wiregrass environments, even periodically in the mesic end of the gradient (Mitchell et al. 1999), species establishment may be limiting. However, many species in this system appear to be tolerant to drought stress, once established. Although turnover rates of individuals in these communities are unknown (but see Gagnon et al. 2012), observations suggest that many of these predominantly perennial species are long-lived (Clewell 1989, Kirkman et al. 2004, Glitzenstein et al. 2012, Palmquist et al. 2014, 2015).

Understanding the ecosystem processes that regulate and sustain species richness and productivity of longleaf pine communities at multiple scales is foundational to guiding conservation management strategies with the goal of promoting biodiversity, particularly in regard to

reassembly and recovery processes associated with restoration of such a species-rich ecosystem. In this study, we use large scale manipulations over a 10-yr period to determine how complex feedback mechanisms among site resources and fire influence patterns of productivity and richness in longleaf pine-wiregrass woodlands at multiple scales across a soil moisture gradient spanning wet-mesic to xeric conditions. We ask the following questions: (1) How do N and water addition influence annual aboveground net primary productivity of the midstory/overstory and ground cover? (2) How do species richness responses to resource manipulations vary with scale and among functional groups of ground cover species? (3) How does standing crop (including overstory, understory/midstory, and ground cover components) differ between frequently burned and fire excluded plots after a decade without fire? (4) What is the role of fire in regulating species richness responses to N addition?

Methods

Study site

We conducted the experiment in naturally regenerated second growth longleaf pine-wiregrass (*Pinus palustris* Mill.-*Aristida stricta* Michx. var. *beyrichiana* [Trin. & Rupr.] D. B. Ward) woodlands at Ichauway, a privately owned property of the J. W. Jones Ecological Research Center, located in Baker County, Georgia, USA (31° 13′ N, 84° 28′ W, elevation 48.1 m above sea level). These longleaf pine woodlands have been managed for more than eight decades with frequent prescribed fire. Annual precipitation at the site is 140 cm. Mean annual temperature is 18.6°C, with mean annual maximum temperature of 25.2°C and mean annual minimum of 11.9°C (NOAA 2011).

The study is part of a long-term landscape-scale experiment designed to examine the ecological structure and process responses to resource manipulations and burn exclusion. Consequently, considerable baseline data on ecosystem processes, particularly nutrient cycling and productivity, have been collected at these sites (Mitchell et al. 1999, Wilson et al. 1999, 2002, Kirkman et al. 2001, Hendricks et al. 2002, Guo et al. 2008, Cathey et al. 2010, Whelan et al. 2013).

The study sites were established at the wet-mesic and xeric extremes of a natural soil moisture gradient that longleaf pine occupies at Ichauway. Soils at the wet-mesic extreme are classified as Aquic Arenic and Typic Paleudults and are characterized as sandy loam over sandy clay and sandy clay loam. These soils are poorly drained because of the presence of a clay-textured lens that decreases water infiltration into deeper soil layers. Evidence of poor drainage (mottling) occurs within 0–30 cm, and standing water occasionally ponds on the surface after significant rainfall events in the winter months. Soils of the xeric sites, which occur on upland sand ridges, are classified as Typic Quartzipsamments, with inclusions of Arenic or Grossarenic Kandiudults.

These soils are characterized by coarse sand that exceeds 2.5 m in depth, weak development of soil horizons due to mixing by soil fauna, low organic matter content, and lack of silt and clay. These soils are well-drained, with a water holding capacity of 18 cm per m of soil.

The widely spaced canopy trees are 80–100+ yr old and the basal area of pine trees at the wet-mesic site ranged from 8 to 17 m^2/ha, while pine basal area of the xeric site ranged from 4 to 14 m^2/ha. The diverse ground cover is dominated by wiregrass; the presence of this dominant perennial bunchgrass is indicative of sites with a land-use history of nominal soil disturbance and a frequent fire history because of its characteristic decline with agricultural practices or fire exclusion (Clewell 1989). The ground cover also consists of numerous other perennial warm-season (C4) grasses, forbs, and shrubs as interstitial species. All plots were burned in January 2001, prior to initiation of treatments.

Experimental approach

Resource manipulation plots.—In 2000, we established a 2 × 2 factorial design in which we manipulated the main factors of soil moisture (with and without irrigation) and nitrogen availability (with and without N addition) in a wet-mesic and a xeric site. In both sites, we established sixteen 50 × 50 m treatment plots and randomly assigned four replicate plots to each of four treatments (fertilized only, irrigated only, fertilized plus irrigated, and control). At a central location at each site, we drilled a well (37 m deep, 10 cm diameter) to provide irrigation. Irrigation water was treated with reverse osmosis (ANCOSOFT 2 ATM Dual Softener and Delta 15 Reverse Osmosis System; Anderson Chemical Company, Macon, Georgia, USA) due to the high concentration of Ca^{2+}. Water was delivered to the irrigated plots via 8-cm pipes fitted with 10 sprinkler heads per plot with a maximum capacity of delivering 9.5 L/min. Irrigation treatment plots were irrigated at a rate of 18 mm every 8 d, which was the length of time needed to complete the four replications in both irrigation treatments given the capacity for delivering 18 mm of water in 24 h. The irrigation regime was initiated in 2003 and increased water input by more than 50% compared to average rainfall. In the xeric site prior to irrigation, mean annual volumetric soil moisture (VSM) marginally differed at 30 cm ($P = 0.048$) and 90 cm ($P = 0.053$; Appendix S1: Tables S1–S2). However, the difference between irrigated and non-irrigated plots was significant in each year following treatment initiation at both depths. This was also the case for the post-treatment VSM at the wet-mesic site at 30 cm depth in most years. Although the 90 cm VSM tended to be greater in irrigated relative to non-irrigated treatments, the difference between them was not significant in any year at α < 0.05, even in dry years. Thus, given the high maintenance cost of this treatment, irrigation in the wet-mesic site ceased at the end of 2008; however, it was continued at the xeric site through the end of the

experiment. The N addition treatment was achieved via application of ammonium nitrate (34-0-0) at a rate of $50\ kg\ ha^{-1}\ yr^{-1}$, which is about six times the rate of natural atmospheric deposition at this site (Allen and Gholz 1996, Boring et al. 2004), using a cyclone spreader (EarthWayEV-N-SPRED, Earthway Products, Inc., Bristol, Inidiana, USA). Nitrogen addition treatments were conducted three times in each year to mimic seasonality of natural mineralization rates (Wilson et al. 1999), with 23% (11.5 kg/ha) applied in January, 60% (30 kg/ha) in May and 17% (8.5 kg/ha) in September. Resource manipulation plots were burned every other year, during the dormant season (January–April).

Fire exclusion plots.—In an additional 16 plots (eight plots per site), in the same locale and the same size as resource manipulation plots, we implemented a 2 × 2 factorial design using fire exclusion and nutrient addition. Non-irrigated (fertilized only and control) plots from the resource manipulation experiment were paired with fertilized and unfertilized plots where fire was excluded after the January 2001 prescribed fire, with the exception of one plot that was burned by a wildfire caused by a broken power line in October 2003. Fertilizer addition in unburned plots was as described earlier for resource manipulation plots.

Vegetation sampling

Prior to treatment applications (in 2000 for resource manipulation plots, and 2001 for fire exclusion plots), we sampled vegetation composition (species richness) within each treatment plot in 20 × 20 m species–area plots using a nested quadrat sampling design adapted from Peet et al. (1998). Each vegetation whole plot ($400\ m^2$) was divided into four 10 × 10 m modules. Within each module, we sampled vegetation in nested square quadrats of 0.1, 1, and $10\ m^2$ from each of two corners. Thus, for each whole plot, we had eight species counts at scales of 0.1, 1, and $10\ m^2$, four counts at $100\ m^2$, and one count at $400\ m^2$. We recorded all species present in each module; nomenclature followed Wunderlin and Hansen (2003). We resampled vegetation in 2005 (32 resource manipulation plots), 2008 (16 fire exclusion plots), and 2011 (all plots) during July–October. For resource manipulation plots, we conducted vegetation sampling approximately 6 months after late winter/early spring fire. All five sampling scales in each whole plot were sampled in fire excluded plots in 2001, but only the $1\ m^2$ level was sampled in 2008 and the 0.1 and $1\ m^2$ levels in 2011, because of difficulty sampling at larger scales in the thick duff layer that accumulated in the absence of fire.

Productivity measurements

In resource manipulation plots, we measured aboveground ANPP for overstory and midstory tree species and dominant ground cover functional groups: woody species, wiregrass, other grasses (excluding wiregrass), forbs (excluding legumes), and legumes. These groups were selected based on their major functional roles, dominance, and growth form. Overstory trees (those with a diameter at breast height [DBH] ≥ 10 cm) and midstory trees (5 cm ≥ DBH < 10 cm) were tagged and their DBH was recorded annually. Overstory and midstory standing crop was calculated using DBH measurements and species-specific allometric equations (Mitchell et al. 1999). Annual ANPP was estimated by subtracting stem/branch standing crop biomass of the previous year from stem/branch biomass of the current year and adding current year foliage using the same allometric equations. We determined ground cover standing crop (equivalent to annual ANPP in burn years) by destructively subsampling 5–7 circular plots (1 m diameter) per main plot in November before the first killing frost, sorting by functional group, drying to a constant weight, and weighing.

In fire excluded plots, we collected overstory, midstory, and ground cover data as described above for resource manipulation plots. Additionally, due to the development of a conspicuous hardwood (i.e., non-pine) understory in fire excluded plots, we also collected understory standing crop at the end of the project. Understory trees (those that were >1 m tall, but with a DBH < 5 cm) were measured within four 25 × 2 m transects in each 50 × 50 m treatment plot by averaging two perpendicular stem diameters and applying site-specific allometric equations for the relationship between ground-level diameter and biomass (R. Mitchell, *unpublished data*). We also collected understory standing crop data as described earlier from the control and fertilized only plots of the resource manipulation project to compare standing crop that developed after a decade of fire exclusion with that of frequently burned plots.

Data analyses

To examine the relationship between species richness and ANPP prior to initiation of the experiment, we developed a linear regression model using ANPP data from 2001 as the predictor value and species richness data at the $1\ m^2$ level from 2000 (resource manipulation plots) or 2001 (burn excluded fire manipulation plots) as the response variable.

We analyzed total species richness at subplot scales of 0.1, 1, 10, and $100\ m^2$ and at the whole plot level ($400\ m^2$) using a repeated measures general linear mixed model approach via the SAS procedure PROC MIXED (Version 9.3; SAS Institute, Cary, North Carolina, USA). Given the VSM trend and potential for an irrigation effect on species richness over the long term, we retained irrigation in the models for the wet-mesic site. Thus, fixed effects included in the models for the resource manipulation project included fertilizer, irrigation, and year, and their interactions, while fixed effects for the fire manipulation project included fertilizer, burn regime, and year, and their interactions. We developed separate models for each site (i.e., wet-mesic and xeric) due to the presence of significant

($P < 0.05$) four-way interactions among all fixed effects when site was included in the model. Given that data at the subplot scales were collected in a nested plot scheme, these models included random effects for plot for all sampling scales, module nested within plot for scales ≤ 100 m^2, and corner nested within module for scales ≤ 10 m^2. Because plots were measured repeatedly over time, random effects were also included to account for temporal correlation among measurements taken on the same experimental unit at all subplot scales as well as the whole plot.

We developed a series of candidate models for each scale of analysis. The first model in each series was a full model that included all possible random and fixed effects. In cases where inclusion of all random effects resulted in non-convergence, we eliminated the lowest order random effect until model convergence was achieved. We initially used restricted maximum likelihood and an unstructured covariance structure to describe the pattern of correlation among measurements over time in each model. We then compared these results to those of models with autoregressive order 1 (adjusted for unevenly spaced sample intervals) or antedependence structures to determine the most appropriate variance-covariance structure for the given model. Finally, we used maximum likelihood to determine whether to include the higher-level interaction among all fixed effects. Akaike Information Criterion (AIC) was used to select the best-fitting, most parsimonious model at each step; the higher-order interaction was eliminated when its removal resulted in a ΔAIC ≥ 2 compared with retaining the interaction (Burnham and Anderson 2002). A Kenward-Rogers adjustment to the degrees of freedom was employed to account for complex spatial and temporal correlation of the data. Functional group species richness was analyzed using the same procedure. Where simple effects were found, marginal means were calculated to isolate the effect, holding all other model effects constant. Where significant interactions were found, comparisons of each underlying effect were made via simple effects tests (Winer 1971) while holding the other effect constant. An interaction between a treatment (i.e., fertilizer addition, irrigation, or fire) and year indicates a significant change over time due to treatment. A main effect of treatment indicates that the treatment effect was present in all years, including prior to treatment, and hence, the effect may not be due to experimental manipulations. In such cases, we examined the magnitude of the difference over time to further evaluate the role of treatment. In the interest of brevity, we report only significant treatment × year interactions, as well as significant main effects in which the magnitude of the difference between treatment levels increased over time.

Rather than examining the effect of treatments on ANPP in a single year (on which climatic conditions could have a strong influence), we examined the effect of resource manipulations on mean annual ANPP over the duration of experimental treatments. We calculated mean values for ground cover, midstory/overstory, and total ANPP per plot using ANPP data collected annually throughout the duration of irrigation (i.e., through 2008 or 2011, wet-mesic and xeric sites, respectively). Midstory and overstory were combined for this analysis given the sparseness of trees in the midstory due to frequent fire. Additionally, for the ground cover, we used standing crop data from burned years only, as standing crop in an unburned year is not equivalent to annual ANPP. We examined the effect of resource manipulations on mean ANPP using two-way analysis of covariance with pre-treatment ANPP as a covariate.

We examined the effect of fire manipulation and N addition on final year standing crop of ground cover (including functional groups), understory/midstory, overstory (including pine and non-pine components), and total standing crop using two-way analysis of covariance with pre-treatment standing crop as a covariate. Understory and midstory trees were combined for this analysis due to the conspicuous development of subcanopy trees in the absence of fire.

Results

Productivity and richness responses to resource additions

Prior to treatment applications, total aboveground ANPP for the wet-mesic sites ranged from 7.6 to 12.8 Mg/ha and total ANPP in the xeric site ranged from 3.3 to 11.5 Mg/ha. Prior to treatments, mean species richness at the wet-mesic site was 18.5 species/m^2 with a total of 218 species in all plots sampled, whereas at the xeric site initial mean richness was 12.9 species/m^2 with a total of 214 species in all plots. Species richness was positively correlated with ANPP across the soil moisture gradient ($r = 0.46$, $P = 0.01$; Fig. 1).
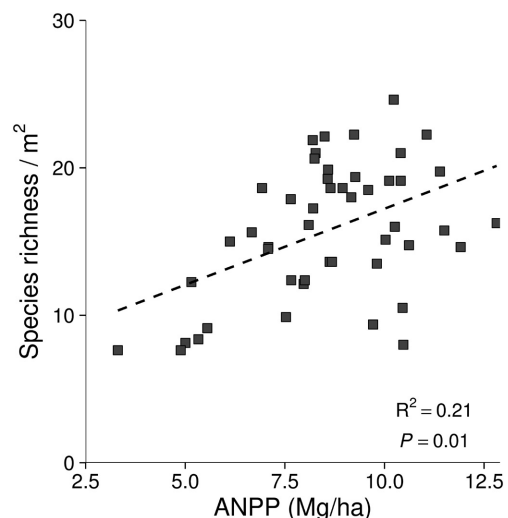

Fig. 1. Relationship between initial (2000/2001) aboveground net primary productivity (ANPP) and initial (2000/2001) mean species richness (m/plot).
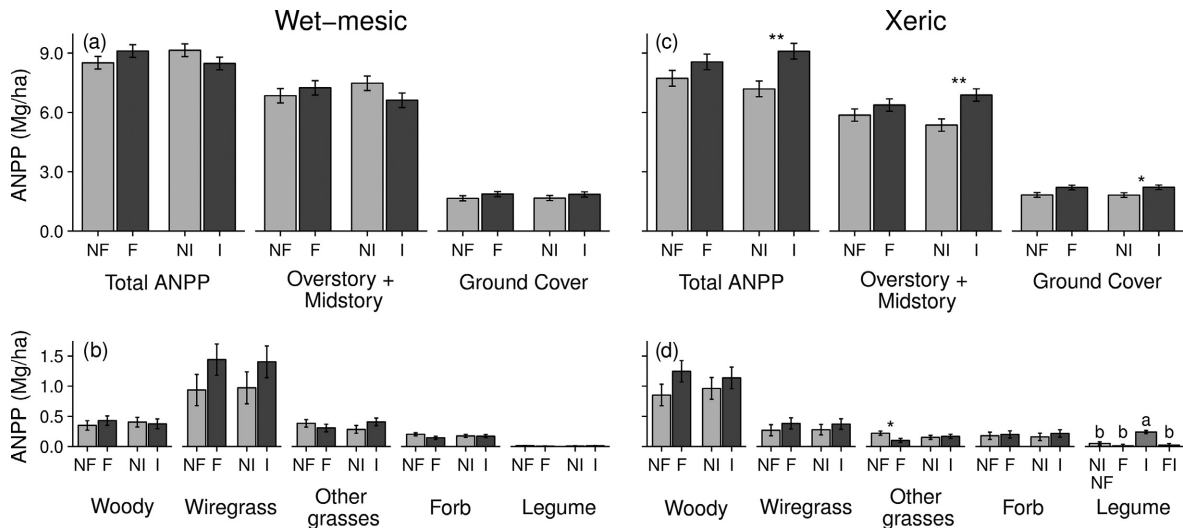
FIG. 2. Marginal mean annual aboveground net primary productivity (ANPP) of resource manipulation plots (significant effects shown, with all other variables in the model at their average values) for total, overstory + midstory, and total ground cover ANPP for (a) wet-mesic and (c) xeric site and ground cover functional groups for (b) wet-mesic and (d) xeric sites. Error bars represent one standard error. *$P < 0.05$, **$P < 0.01$ for differences between factor levels; different letters represent significant differences among treatment levels. Simple (one-way) effect factors: NF = not fertilized, F = fertilized, NI = not irrigated, I = irrigated. Interactive (two-way) effect factors (panel d) ground cover): NINF = conrol, F = fertilized only, I = irrigated only, FI = fertilized and irrigated.

ANPP: wet-mesic site.—For the resource manipulation plots in the wet-mesic site, no differences in mean total, midstory/overstory, or ground cover ANPP were attributable to irrigation or fertilizer addition (Fig. 2a; Appendix S2: Table S1). Similarly, mean ANPP of ground cover functional groups did not differ due to resource manipulations (Fig. 2b; Appendix S2: Table S2).

ANPP: xeric site.—In contrast to wet-mesic sites, irrigation at the xeric site resulted in greater mean total, midstory/overstory, and ground cover ANPP compared to non-irrigated plots (Fig. 2c; Appendix S2: Table S1). A marginal increase in mean ground cover ANPP occurred with N addition (Appendix S2: Table S1). Mean ANPP of grasses (excluding wiregrass) decreased due to N addition, and there was a significant irrigation × N addition interaction such that mean legume biomass was higher in irrigated only plots compared with all other treatment combinations (Fig. 2d; Appendix S2: Table S2).

Species richness: wet-mesic site.—At the wet-mesic site, N addition resulted in lower total species richness at the 0.1 m² scale and lower legume richness at the 1 m² scale (Figs. 3a, b; Appendix S2: Tables S3 and S4). There was a negative main effect of fertilizer on forb richness at the 0.1 m² scale, the magnitude of which increased greatly from 2000 to 2005, and to 2011 (Fig. 3c; Appendix S2: Table S5). Irrigation at the wet-mesic site had an effect on woody species richness. Although woody species richness did not differ between irrigated and non-irrigated plots in any year or at any scale, richness increased over time for irrigated plots at small scales

(≤ 1 m²) and decreased over time at a larger scale (100 m²) (Appendix S4: Fig. S1a, Appendix S2: Table S6). For grass richness, there was an interaction between N addition, irrigation, and year, such that richness decreased over time at the 10 m² scale in plots that were both fertilized and irrigated, while there was no change in richness for the other treatment combinations (Appendix S2: Table S7).

Species richness: xeric site.— Both fertilizer addition and irrigation resulted in several significant responses in species richness at the xeric site. Fertilizer addition had a negative effect on total species richness (scales ≤ 10 m²), with reduced richness of legumes (scales ≤ 10 m²), forbs (1 and 10 m² scales), and grasses (scales ≤ 1 m²; Figs. 3d–f and Appendix S4: Fig. S1d, Appendix S2: Tables S3–S5, S7). There was also a negative main effect of fertilizer addition on forb richness (0.1 m²; Fig. 3f; Appendix S2: Table S5). Irrigation resulted in higher forb species richness (0.1 m² scale) and woody species richness (1 and 10 m² scales; Figs. 3f and Appendix S4: Fig. S1c; Appendix S2: Tables S5–S6). Irrigation also had a positive main effect on total species richness (0.1 and 1 m² scales), legume richness (100 and 400 m² scales) and forb richness (1 and 10 m² scales), with the magnitude of the differences increasing over time (Figs. 3d–f; Appendix S2: Tables S3–S5).

Standing crop and richness responses to burn manipulation and fertilizer addition

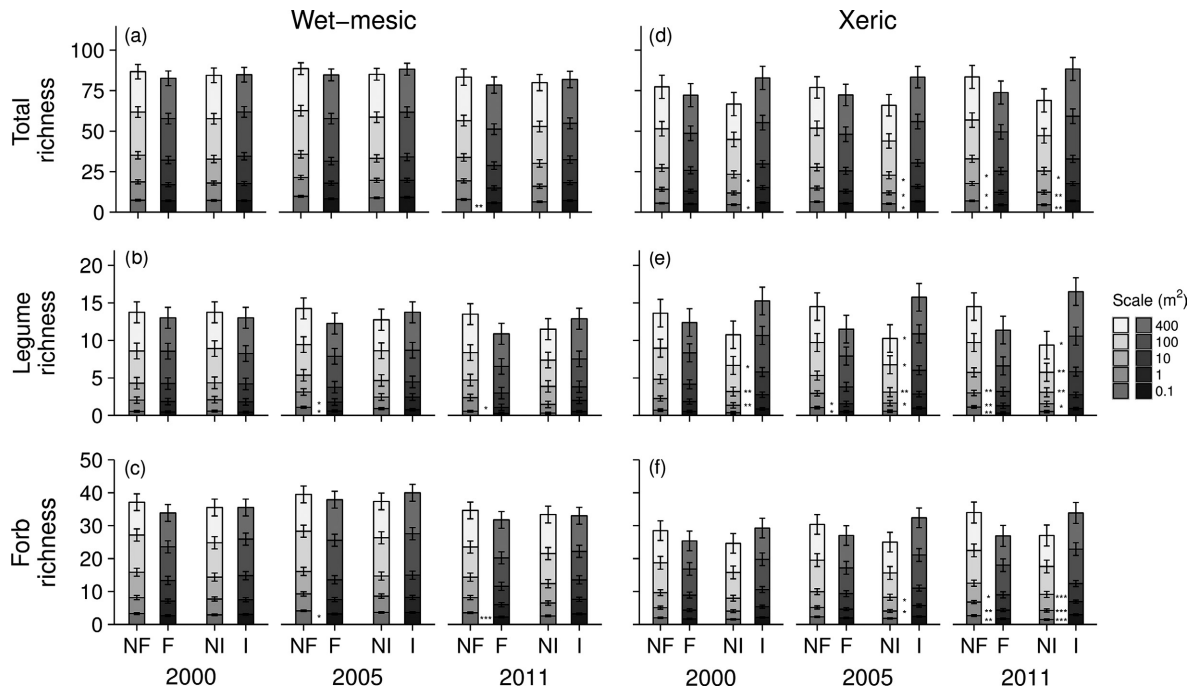*Standing crop: wet-mesic site.*—No differences in standing crop biomass of the overstory were attributable

FIG. 3. Marginal mean species richness of resource manipulation plots at each scale (0.1, 1, 10, 100, and 400 m²) (significant effects shown, with all other variables in the model at their average values) for total species richness at (a) wet-mesic and (d) xeric sites, legume richness at (b) wet-mesic and (e) xeric sites, and forb richness at (c) wet-mesic and (f) xeric sites. Error bars represent one standard error. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ for differences between factor levels. Simple (one-way) effect factors: NF = not fertilized, F = fertilized, NI = not irrigated, I = irrigated.

to N addition or fire manipulation in the mesic site (Fig. 4a; Appendix S3: Table S1). However, for the understory/midstory standing crop an interaction occurred between N addition and fire manipulation that resulted in higher biomass of the non-pine component in fire excluded plus N addition plots compared with all other treatment combinations (Fig. 4b; Appendix S3: Table S1). Total ground cover standing crop decreased with N addition in fire excluded sites relative to burned plus fertilized sites, and standing crop biomass of forbs and grasses (excluding wiregrass) decreased with fire exclusion (Fig. 4c; Appendix S3: Table S2).

Standing crop: xeric site.—No differences in standing crop biomass of the overstory were attributable to N addition or fire manipulation in the xeric site (Fig. 4d; Appendix S3: Table S1). Although total standing crop and non-pine standing crop of the understory/midstory increased with burn exclusion, there was no effect of fertilizer treatment (Fig. 4e; Appendix S3: Table S1). Total ground cover biomass decreased with fire exclusion due to decreased standing crop of woody species, wiregrass, and legumes (Fig. 4f; Appendix S3: Table S2).

Species richness: wet-mesic site.—At the wet-mesic site, fire exclusion resulted in a significant reduction in total species richness and forb richness at both spatial scales and grass richness at the 1 m² scale (Figs. 5a, c; and Appendix S4: Fig. S2b, Appendix S3: Tables S3, S5,

and S7). A significant fire × year interaction occurred at both scales for legume species richness due to significantly greater richness at unburned plots relative to burned plots prior to treatment; following treatment application, legume richness did not differ between burned and unburned treatments (Fig. 5b; Appendix S3: Table S4). Fertilizer addition did not impact total or functional group species richness at any scale in fire manipulation plots.

Species richness: xeric site.—In fire manipulation plots at the xeric site, both fire exclusion and fertilizer addition resulted in significant richness responses. Fire exclusion led to a reduction in total species richness and forb richness at both scales (Figs. 5d, f; Appendix S3: Tables S3 and S5). Although legume richness did not differ between burned and unburned plots, legumes declined in fire excluded plots at both scales, while richness of burned plots did not change over time (Fig. 5e; Appendix S3: Table S4). A decrease in total species richness and forb richness occurred in response to fertilizer addition at the 1 m² scale (Figs. 5d, f; Appendix S3: Tables S3 and S5). Legumes responded similarly to fertilizer addition as to fire exclusion in these plots: legume richness did not differ between fertilized and non-fertilized plots in any year, but richness declined in fertilized plots at the 1 m² scale and remained unchanged in non-fertilized plots (Fig. 5e; Appendix S3: Table S4). Additionally, for total richness and for forbs and grass functional groups, there was a negative main effect of fertilizer addition at the 0.1 m² scale with the magnitude of
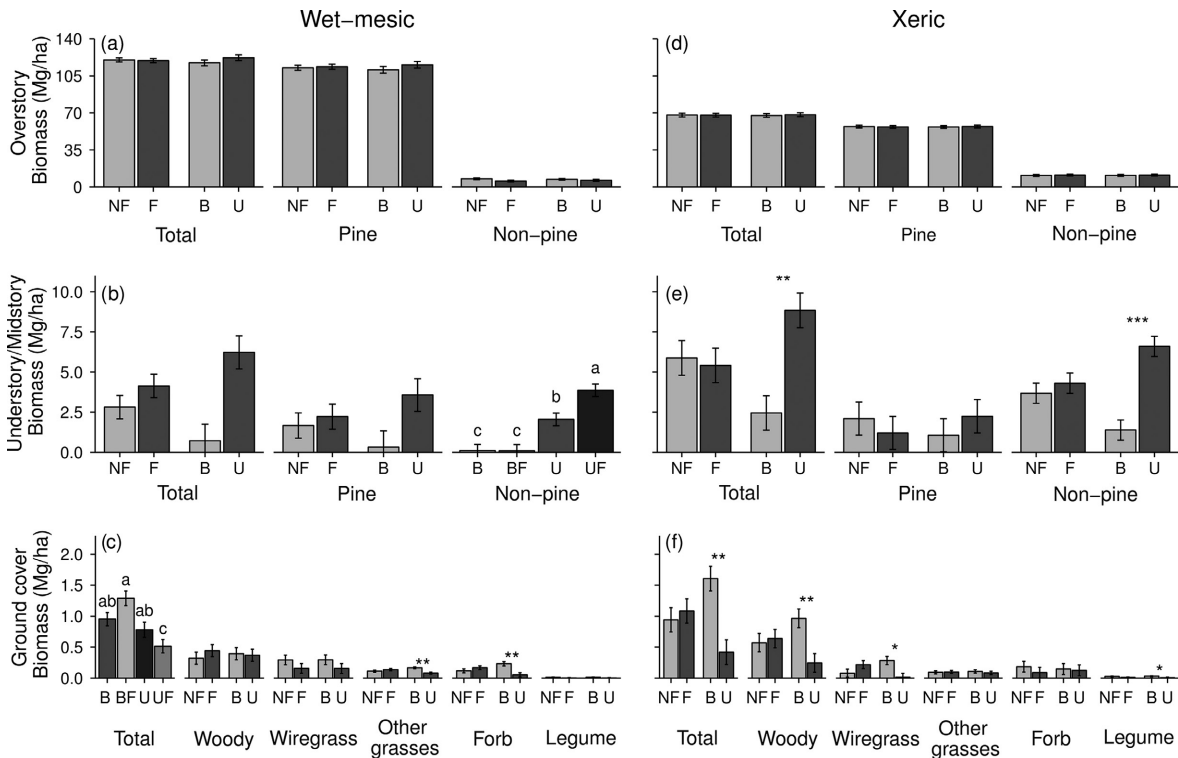
Fɪɢ. 4. Marginal mean standing crop biomass of fire manipulation plots (significant effects shown, with all other variables in the model at their average values) for total, pine, and non-pine components for overstory trees at (a) wet-mesic and (d) xeric sites, understory/midstory trees at (b) wet-mesic and (e) xeric sites, and ground cover functional groups (total ground cover, woody species, wiregrass, other grasses, forb, and legume) for (c) wet-mesic and (f) xeric sites. Error bars represent one standard error. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ for differences between factor levels; different letters represent significant differences among treatment levels. Simple (one-way) effect factors: NF = not fertilized, F = fertilized, B = burned, U = unburned. Interactive (two-way) effect factors (panels c) mesic understory/midstory and (e) mesic ground cover): B = burned only, BF = burned and fertilized, U = unburned only, UF = unburned and fertilized.

the difference between fertilized and non-fertilized treatments increasing over time (Figs. 5d, f; and Appendix S4: Fig. S2d, Appendix S3: Tables S3, S5, and S7).

DISCUSSION

This study is the first long-term manipulative study in a high diversity forested ecosystem to empirically examine the role of resource availability and disturbance in regulating a positive productivity and species richness relationship across a natural soil moisture gradient. In summary, we found that irrigation increased both species richness and ANPP at the xeric end of the gradient, whereas no changes in ANPP and minor changes in woody richness occurred for wet-mesic conditions. Nitrogen addition had a negative effect on total species richness, and notably, legume richness at both ends of the gradient. Changes in species richness occurred primarily at smaller scales (≤10 m²). In the absence of fire, N addition resulted in increased standing crop of understory/midstory hardwoods and decreased ground cover standing crop in the mesic site. At the xeric site, understory/midstory hardwoods increased in the absence of fire alone, and ground

cover standing crop correspondingly decreased; N addition had no effect on standing crop at this site.

Across the edaphic conditions of our study, our evidence confirms that the combination of fire and soil moisture strongly influences species richness and that ANPP is not a primary causative agent structuring patterns of species richness. As expected, in the extended absence of fire (a decade), hardwoods became dominant in both stature and biomass in the understory and midstory, competition for light by forbs and grasses increased as a result of increased leaf area and/or increased litter accumulation (Hiers et al. 2007, Addington et al. 2012), and in turn, species richness declined. Because fire reduces aboveground competition for light by ground cover species, and species richness is not reduced with increasing standing crop except as a result of fire exclusion, fire is clearly shown to be the filter eliminating competitive exclusion as a strong structuring influence on patterns of species richness. Further, two studies of removal of bunchgrasses in longleaf pine sites have demonstrated that these dominant guilds do not competitively exclude other species (Roth et al. 2008, Myers and Harms 2009) and
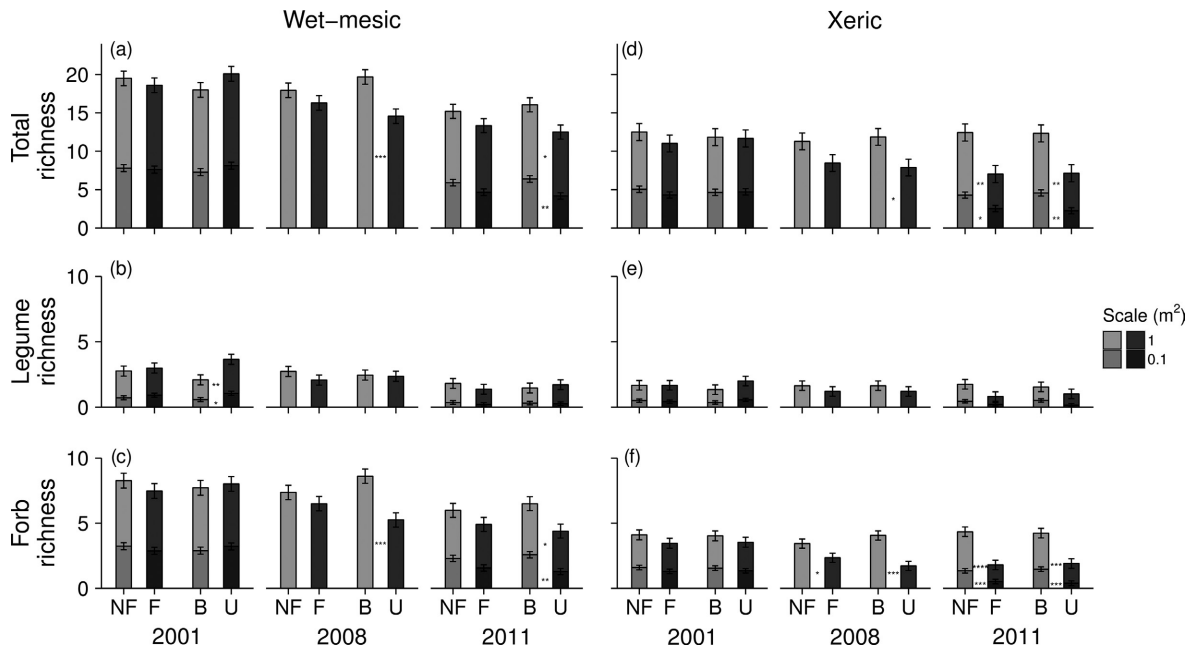
FIG. 5. Marginal mean species richness of fire manipulation plots at both scales (0.1 and 1 m²) (significant effects shown, with all other variables in the model at their average values) for total species richness at (a) wet-mesic and (d) xeric sites, legume richness at (b) wet-mesic and (e) xeric sites, and forb richness at (c) wet-mesic and (f) xeric sites. Error bars represent one standard error. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$ for differences between factor levels. Simple (one-way) effect factors: NF = not fertilized, F = fertilized, B = burned, U = unburned.

substantiated our previous observations that species richness and standing crop of ground cover dominated by wiregrass were positively correlated across a natural wet-mesic to xeric gradient (Kirkman et al. 2001). The distinctive absence of increased competitiveness of dominant grasses with increasing soil fertility as well as with frequent fire (Glitzenstein et al. 2012), and a large species pool of fire-tolerant perennial species, are traits that uniquely contribute to species co-existence of this ecosystem relative to community assemblages of other grasslands (Gurevitch and Unnasch 1989, Shipley and Keddy 1994, Roth et al. 2008).

The implications of scale.—The scale-dependent response of species richness to resource amendments and fire in this study corroborates previous observations in which differences in richness in longleaf pine sites were most evident at the smallest spatial scales (Kelly et al. 2002, Glitzenstein et al. 2003, 2012, Palmquist et al. 2014, 2015). This phenomenon is likely explained by the characteristically high number of species in frequently burned natural longleaf pine woodlands at all scales, as well as by the infrequent occurrence of most species (Kirkman et al. 2001, Clark et al. 2008), such that patterns of recruitment and extinction of individuals result in more pronounced changes in species number at finer scales. Our empirical findings also concur with growing evidence that a complex balance of fine-scale processes, such as temporal and spatial variability in soil moisture and fire effects, influences recruitment, microsite supply, survival,

and coexistence of species (Iacona et al. 2010, Myers and Harms 2011, Gagnon et al. 2012, Wiggers et al. 2013). Collectively, such evidence confirms the importance of measurement of species richness at multiple scales to adequately capture patterns of community assemblage over time.

Variation of responses in wet-mesic and xeric conditions.—Decreased species richness with N addition in the xeric site and the trend of increased richness with irrigation, which was coupled with an increase in ANPP, supports our assertion that the relationship of N amendments and species richness is strongly regulated by soil moisture across the gradient. The absence of an increase in ANPP in response to resource manipulations at the wet-mesic site may reflect the fact that water is not usually limiting at this end of the gradient. The response in midstory growth to N addition with fire exclusion in the mesic but not the xeric sites also suggests that water availability may have been more limiting to growth of the encroaching hardwoods at the drier end of the gradient than N availability. The contrasting lack of ANPP response to N addition with fire in the mesic site may be related to the compositional change associated with fire exclusion and the greater N demand of encroaching hardwoods relative to that of the dominant C4 grasses that are adapted to grow under low available N regimes created by frequent fire (Seastedt et al. 1991).

The decrease in legume species richness with N addition in both sites is similar to results reported in tallgrass

prairies (Suding et al. 2005) and other ecosystems (Oksanen 1996, Aerts and Chapin 2000, Craine et al. 2002, Suding et al. 2005, Clark et al. 2007). The mechanistic explanation generally invoked is a shift from belowground competition for nutrients to aboveground competition for light as N resources are enhanced. Plausibly, another explanation could be related to the response of legumes to the altered N:P ratio in the soil. The high P demand of nitrogen-fixing legumes relative to non-fixers (Dixon and Wheeler 1983) means that nitrogen fixers cannot compete effectively for very low levels of phosphorus when N ceases to be the most limiting resource (Vitousek and Howarth 1991).

Even though productivity did not vary with resource manipulations in the wet-mesic site as occurred in the xeric site, the increased small-scale richness of woody species in the ground cover with irrigation at both sites, and legumes and forbs at the xeric site, suggests that microsites for establishment and growth were increased for these functional groups of species in response to increased soil moisture. Although N addition marginally increased mean ANPP of ground cover in the xeric site, the decline in grass richness is more plausibly attributable to increased susceptibility of seedlings of some species to drought with additional N (Bobbink et al. 2010) than due to competitive interactions in response to the minor increase in productivity.

Provided that potential species pools are equivalent, differences in rates of colonization and extinction of species across a resource gradient should directly influence patterns of species richness (Huston and DeAngelis 1994). While evidence from seed addition studies indicate that species richness in longleaf pine woodlands depends on seed supply (Iacona et al. 2010, Myers and Harms 2011), these studies also suggest that episodic availability of microsites for recruitment is undoubtedly a significant influence. Stochastic seed and seedling mortality associated with soil moisture stress and frequent fire also appear to be ecological filters on local species richness (Iacona et al. 2010, Myers and Harms 2011, Wiggers et al. 2013, Gagnon et al. 2015). Other potential sources of variation that may influence patterns of establishment include propagule abundance relative to soil fertility and variable seed predation, as well as local-scale neighborhood interactions among individual plants associated with the availability of recruitment sites. Thus, in fire-dependent longleaf pine communities, nuanced patterns in species assemblages are likely to develop over time due to multiple fire events and varying climatic conditions, and across landscape-scale gradients of soil moisture and fertility (Peet 2006, Carr et al. 2009, Peet et al. 2014).

Temporal variability.—Potential factors accounting for the temporal variation in species richness (significant main effect of year) are unclear. It is possible that differences in seasonality of precipitation among years or timing of precipitation relative to prescribed fire and subsequent effects on fuels may have had an influence on species establishment or recruitment. Annual measurements of species richness would be necessary to determine this relationship.

Comparison with other studies.—An experiment with seed addition and increased water was conducted in a wet longleaf pine site in Louisiana (Myers and Harms 2011) in which little to no increases in species richness occurred with these amendments. They speculated that in this situation, high rainfall conditions likely functioned as a niche-based filter of seedling establishment based on their tolerance to elevated soil moisture. This difference does not necessarily contradict our conclusions, but instead suggests that different filters may operate in longleaf pine sites with soils having greater water holding capacity than that of our xeric to wet-mesic sites, or perhaps in locations outside of the range of wiregrass in which ground cover is dominated by other species or functional groups. In addition, different abiotic filters may also operate at different life-history stages and could, in part, explain some of the variation observed across experiments.

Our results are especially consistent with numerous other studies in North American grassland communities (including shortgrass and tallgrass prairies) that have demonstrated species reduction with N addition (see review in Gough et al. 2000). However, comparisons of the relationship between productivity and species richness of these communities revealed no consistent patterns and Gough et al. (2000) concluded that local, community-specific mechanisms govern community changes as a result of N addition. Further review of productivity-species richness relationships of other ecosystems (including grasslands and forests) at local, regional, and global extents have similarly concluded that complex multivariate processes both regulate and link productivity and richness (Grace 1999, Waide et al. 1999, Cornwell and Grubb 2003, Adler et al. 2011, Kirkman et al. 2014). We demonstrate that while soil moisture is a strong driver of both species recruitment and productivity of longleaf pine-wiregrass woodlands under frequent fire regimes and soil conditions representative of this study, complex interactions among multiple limiting resources, frequent fire, and unique characteristics of dominant functional groups clearly link species richness and productivity.

Conclusions

Our long-term experiment examines some of the complex relationships between fire, resource availability, productivity, and species richness in an exceptionally diverse ecosystem across a natural soil moisture gradient. Certainly the coexistence of numerous species in the longleaf pine ecosystem is due to the high frequency of prescribed fire that removes competing understory/midstory hardwood vegetation and litter. However, our data further suggest that processes influencing species establishment and survival occur at fine scales that appear to be linked to spatial and temporal variability

of soil moisture and are likely coupled with environmental filtering associated with variable fire behavior, as well as other local-scale processes. Further, this study helps to identify how process-based restoration may be an important step in reassembly of the diverse native ground cover of the longleaf pine ecosystem that differs from restoration strategies in more fertile grassland ecosystems. In addition to reestablishment of the longleaf pine canopy, promoting elements of the longleaf pine ecosystem that uniquely accelerate key system attributes, such as introduction of N-fixing legume species; encouraging dominance of noncompetitive, perennial grasses for fine fuel (e.g., wiregrass); reintroduction of dispersal-limited species; and maintaining or restoring a frequent fire regime, is most likely to establish a baseline trajectory for successful restoration of this ecosystem. Finally, the apparent stochasticity involved in community reassembly processes suggests that the development of fine-scale diversity will require considerable time, coupled with persistent and frequent application of prescribed fire.

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