



Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America

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Abstract

Questions: How has plant species richness changed over two decades in one of the most species-rich savannas in North America? Is an altered disturbance regime, environmental stress, or both, driving these changes? In what ways can observations in this savanna inform management of other species-rich plant communities?

Location: Longleaf pine savannas in southeast North Carolina, USA.

Methods: In 2011–2013, we re-surveyed permanent plots established in the 1980s and 1990s in a longleaf pine (*Pinus palustris*) savanna in North Carolina to quantify changes in species richness at multiple spatial scales following 15 yr of reduced fire frequency plus periodic drought. For comparison, we re-sampled other longleaf pine savannas in the region that had not experienced reduced fire frequency, but had experienced similar drought. In addition, we identified which types of species were lost and gained, and summarized changes in species frequency by growth form, plant height, and habitat affinity.

Results: We detected substantial declines in small-scale species richness and species frequency from the 1980s to 2011, representing a loss of 33% to 41% of the flora, depending on the spatial scale. Small herbaceous species had become particularly scarce. Additional re-sampling in the wetter years of 2012 and 2013 after consecutive years of fire revealed that species richness had increased slightly from 2011, but was still considerably lower than that in the 1980s. Other savannas did not exhibit such dramatic declines in species richness, suggesting reduced fire frequency in addition to drought contributed to species loss in Big Island Savanna over time.

Conclusions: Our work suggests that nearly annual fire is necessary for the maintenance of high plant species richness in mesic longleaf pine savannas, and even a modest reduction in fire frequency can have dramatic negative impacts. This study also suggests that drought is an important factor structuring grassland ecosystems in the southeastern US, despite relatively high regional precipitation. We believe these findings can be generalized to other species-rich grasslands that are sensitive to changes in disturbance regimes and may require frequent disturbance to maintain plant species richness.

Introduction

In species-rich grassland ecosystems, natural disturbance (e.g. fire, grazing) or processes that mimic natural disturbance through the removal of above-ground biomass (e.g. mowing) are essential for the maintenance of species richness, community structure, and rare species (Collins et al.

1998; Glitzenstein et al. 2003; Fidelis 2010; Peet et al. 2014). Frequent disturbance generally increases species richness by reducing the abundance of dominant species, increasing resource availability in the form of light, space and nutrients (Kirkman et al. 2004), resulting in a shift from asymmetric competition for light to more symmetric below-ground competition (Peet & Christensen 1988; Wil-

son et al. 2012; Peet et al. 2014). In addition to disturbance, grassland community structure is influenced by seasonal, periodic, and multi-year drought events (Gibson & Hulbert 1987), which can have prolonged consequences (Haddad et al. 2002). At local scales, drought can result in declines in plant biomass and species richness, as well as shifts in community composition (Tilman & Haddi 1992; O'Connor 1995; Haddad et al. 2002; Cheng et al. 2011).

Many species-rich grassland ecosystems are experiencing anthropogenic alteration of disturbance regimes (changes in frequency, timing, intensity or severity of disturbance) that have long-term impacts on ecosystem structure and function. These impacts vary depending on the magnitude and direction of alteration, but may result in the loss of species richness and changes in community composition and stand structure (Heyward 1939; Belsky 1992; Glitzenstein et al. 2003). In addition, changes in disturbance regimes are often compounded with habitat destruction, fragmentation or altered environmental conditions (e.g. nitrogen deposition, climate change), resulting in additional pressure on grassland plant communities (Leach & Givnish 1996; Stevens et al. 2011; Potts et al. 2012).

Longleaf pine (*Pinus palustris*) savannas are fire-dependent, species-rich grasslands located in the southeastern US, currently influenced by multiple stressors (e.g. fire suppression, drought, habitat destruction, and habitat fragmentation). Habitat conversion and long-term fire suppression have collectively reduced the longleaf pine ecosystem to only 2–3% of its acreage at the time of European settlement (Outcalt & Sheffield 1996; Frost 2006). Plant species richness within the herbaceous layer can be exceptionally high, and at small scales represents the highest values ever recorded in North America (52 species in

1 m²; Walker & Peet 1983; Peet et al. 2012, 2014) and approaches world-record levels (Wilson et al. 2012). Fire is an important factor responsible for the maintenance of species richness within longleaf pine savannas, and is essential for the survival of small-statured species within the dense grass matrix (Walker & Peet 1983; Glitzenstein et al. 2003; Kirkman et al. 2004). Drought events occur periodically in longleaf pine savannas, most often in early spring (March–May; Noss 2013), although little research has investigated how drought influences species richness in these systems (but see Myers & Harms 2011), despite recognition of the importance of drought in other grassland ecosystems (Cleland et al. 2013). In addition to periodic water stress, the southeastern Coastal Plain of the US in which these systems are embedded has been experiencing ongoing, long-term drought over the last 25 yr (Fig. 1). We believe that both periodic and multi-year drought events may be under-appreciated, yet important drivers of community structure in longleaf pine savannas.

We used a unique, long-term, multi-scale data set from Big Island Savanna of the Green Swamp Preserve, NC, to explore how drought and fire regime have shaped plant species richness over time. Big Island Savanna has been considered one of the most species-rich and high-quality longleaf pine savannas on the Coastal Plain of the southeastern US (McIver 1981; Frost et al. 1986). This site is the source of the North American records of 42 species in 0.25 m² and 52 species in 1 m² (see Peet et al. 2012, 2014), values which rival those reported for other species-rich grasslands throughout the world (Kull & Zobel 1991; Cantero et al. 1999; Klimeš et al. 2001; Dengler et al. 2009, 2012; Wilson et al. 2012). The existence of long-term plot records that span multiple spatial scales presents

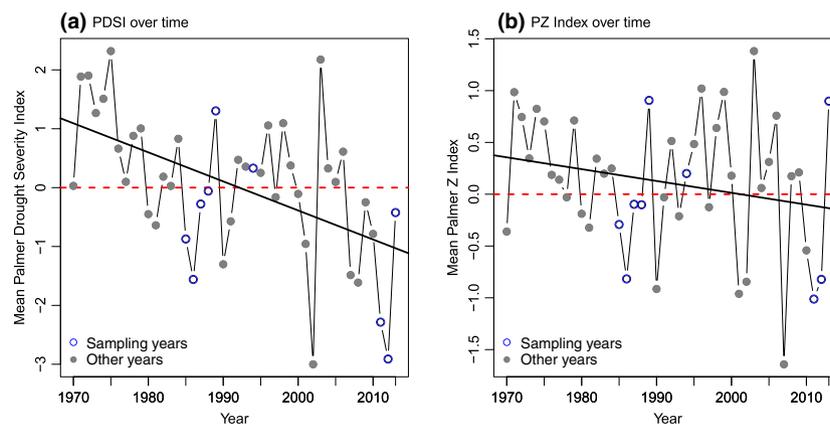


Fig. 1. (a) Mean annual Palmer Drought Severity Index (PDSI) and (b) mean annual Palmer Z Index (PZI) from 1970–2013 for the southeastern Coastal Plain of North Carolina. PDSI and PZI values below 0 indicate drought years, whereas values above zero indicate non-drought years. PDSI quantifies long-term drought conditions, while PZI reflects short-term changes in water availability. The number of drought events has increased since 1980, as indicated by the black linear best-fit lines and a larger proportion of years below the dotted line.

a unique opportunity to document changes in richness and composition. Big Island Savanna experienced a planned shift in its fire management regime from nearly annual fire from at least 1940 to 1997 (Kologiski 1977; Rome 1988) to a fire-return interval of 2–3 yr during 1997–2011. Although fire frequency has changed only modestly, this shift may have had significant impacts on species richness as Big Island Savanna had for decades before experienced a constant fire management regime.

To explore the impact of reduced fire frequency and drought on plant species richness in Big Island Savanna, we re-sampled two sets of permanent vegetation plots established over 25 and 20 yr ago. For comparative purposes and to explore the impact of drought on other longleaf pine savannas, we also re-sampled plots on other species-rich longleaf pine savannas in the region that had not experienced reduced fire frequency. Specifically, we asked:

1. Have species richness and species frequency in Big Island Savanna changed in response to reduced fire frequency and drought?
2. What is the relative importance of reduced fire frequency vs drought in driving changes in species richness and frequency in Big Island Savanna?
3. In what ways can the changes observed in this savanna inform management of other species-rich grasslands?

It is critical that we assess how changes in long-standing fire regimes, compounded with additional stress from drought have influenced plant species richness in this savanna, which, unlike most other longleaf pine sites, did not experience post-colonial fire suppression. From a conservation perspective, Big Island Savanna is irreplaceable within the greater landscape. Moreover, this work has implications not only for fire managers in the longleaf pine ecosystem, but for managers and researchers who study other chronically disturbed, species-rich grassland ecosystems.

Methods

Study area

The Green Swamp Preserve is located in Brunswick County, in the southeastern corner of the North Carolina Coastal Plain (34°5' N, 78°18' W) and covers ca. 6700 ha. The majority of the site consists of shrub-dominated ombrotrophic peatland (pocosin), within which occur scattered islands of savanna on mineral soil (Kologiski 1977). Elevation ranges from 12 to 25 m a.s.l., with very little topographic relief. However, small differences in elevation (>0.2 m) have major consequences for hydrology, soil properties, and hence vegetation (Rome 1988; Christensen 2000). The climate is humid subtropical, with an average mean annual temperature of

15.5 °C and an average annual precipitation of 160 cm, most of which occurs during the growing season (Ruffner 1985; State Climate Office of North Carolina). Droughts occur periodically in the region (mostly during the months of March–May) and result in at least temporary loss or dormancy of species dependent on moist soils (Kologiski 1977; Christensen 1981). Savanna soils in the Green Swamp are typically Leon series, which are derived from acidic, fine-textured, nutrient-poor, marine sediments. They are generally poorly drained, with the water table within 25 cm of the soil surface for 1–4 mo of the year (Kologiski 1977).

This study focused primarily on a single, 30-ha savanna in the Green Swamp: Big Island Savanna. During the 18th–19th centuries, Big Island Savanna likely burned almost annually due to the flatness of the landscape, the large size of the fire compartment, and the flammability of the vegetation (Frost 2006). Written records indicate annual, late-winter fire was implemented in Big Island Savanna for much of the 20th century, from at least and likely prior to 1940 through 1997 (Kologiski 1977; Rome 1988). Thereafter, the fire management regime shifted to a mix of growing-season and dormant-season fires with a return interval of 2–3 yr. Thus, over the 15 yr prior to this study, fire frequency was lower than had been the case with the traditional management strategy. This shift reflected an effort by managers to return to what has recently been perceived as a more 'natural' fire regime with somewhat less frequent fires timed later in the growing season when natural ignition is more likely (Frost et al. 1986; Huffman 2006).

We also examined long-term changes in species richness and composition on other sites besides Big Island Savanna, including other savannas in the Green Swamp Preserve, Holly Shelter Game Lands, Croatan National Forest and Camp Lejeune Marine Corp Base, to determine how long-term drought has impacted savanna vegetation on similar sites in the region (Fig. S1.1, in Appendix S1). All of these sites have experienced long-term drought, but not reduced fire frequency. However, some sites have likely experienced somewhat more frequent fire over the last 20 yr relative to the original fire management regime (e.g. Camp Lejeune, Croatan National Forest), although long-term fire history data for these sites are lacking. In contrast, fire frequency has remained relatively constant over time on other sites (other savannas in the Green Swamp Preserve, Holly Shelter Game Lands). Here, we focus on comparing changes in species richness and frequency patterns in Big Island Savanna to other environmentally similar sites that have experienced drought but not changes in fire frequency (other savannas in the Green Swamp and Holly Shelter Game Lands). We more thoroughly explore patterns of species richness and composition over time in rela-

tion to fire frequency and environmental context on these comparison sites in another study (Palmquist 2014).

Sampling design

Two different sampling protocols were used to examine changes in species richness and composition over time in Big Island Savanna, which reflect the designs of the two separate studies that we re-sampled. The first study (study 1; see Sykes et al. 1994) was based on plots established and surveyed annually during June of 1985–1989, with a sixth sample in 1994. In June 2011, we re-sampled six of the original 2.5-m² plots (see Sykes et al. 1994 for details of plot configuration), each of which contained 10 0.25 m² subplots. Three of the six plots were control plots and three had received sugar additions twice a year to reduce nutrient availability during 1985–1989. The sugar additions had no noticeable impact. Each plot was permanently marked in 1985 with steel conduit and each 0.25 m² subplot was delineated with steel nails, which ensured we sampled the same physical location over time. Within each subplot, vascular plant species presence was recorded in five permanent 0.01 m² and five permanent 0.001 m² plots. This resulted in 300 observations of 0.001 m², 300 observations of 0.01 m², 60 observations of 0.25 m², 12 observations of 1 m² and six observations of 2.5 m². For consistency, plots were re-sampled in June, 4–5 mo after fire during all sampling years.

The second study (study 2) was conducted in Big Island Savanna in June of 1993 by the Carolina Vegetation Survey (CVS) using the protocol described in Peet et al. (1998, 2012). In June 2011, four CVS plots were re-located and re-sampled. CVS plots are 1000 m² (20 × 50 m) with smaller sub plots nested within. Similar to study 1, each CVS plot was permanently marked with ten pieces of steel conduit. Once the plot was re-located, presence of all vascular plant species was recorded at seven spatial scales in permanent subplots (0.01, 0.1, 1, 10, 100, 400 and 1000 m²; see Peet et al. 1998, 2012 for details of plot layout). All plots in Big Island Savanna were located ca. 50–300 m from one another. In addition, twenty-two 1000 m² CVS plots established during 1991–1993 on other sites with similar soils and species composition were re-sampled in 2009–2010 (study 3). All 26 CVS plots are archived in VegBank (<http://vegbank.org/cite/VB.ds.199852.Palmquist2014GreenSwamp>).

Statistical analysis

Prior to analysis, all taxonomic names were standardized across the sampling years to ensure that changes in nomenclature, taxonomic resolution and taxonomic understanding of the flora across time were not affecting

the number or identity of species detected. Species richness was calculated at each spatial scale for all three data sets (study 1: 0.001, 0.01, 0.25, 1 and 2.5 m²; study 2 and study 3: 0.01, 0.1, 1, 10, 100, 400 and 1000 m²). We used the same analytical methods for all three data sets, but analysed them separately. Linear models and linear mixed effects models were used to detect significant changes in species richness at each spatial scale in 2011 relative to richness at each spatial scale during 1985–1994. Random intercepts models, a type of mixed effects model, were used to examine richness at all spatial scales, except the full plot size, as multiple estimates of richness for these scales were drawn from the same plot. This modelling approach accounted for spatial auto-correlation caused by the nested nature of the data (Zuur et al. 2009). In each random intercept model, species richness in the 1980s was regressed against species richness in 2011–2013 using an offset function. The unique plot identifier for each subplot was set as a random effect, to account for spatial autocorrelation between subplots in the same plot. Linear models were used to examine changes in richness over time for the full plot (2.5 and 1000 m², respectively, for study 1 and studies 2 and 3). All statistical analyses were performed in R v 2.15.2 using the nlme package (R Foundation for Statistical Computing, Vienna, AT). Results reported for Big Island Savanna at 2.5 m² and below were calculated from study 1, whereas results reported at scales >2.5 m² were from study 2.

To quantify drought over the long term and to identify individual drought years, we obtained monthly Palmer Drought Severity Index (PDSI) and monthly Palmer Z Index (PZI) data for 1970–2013 from the Southeastern Coastal Plain of North Carolina (National Climatic Data Center 2013). PDSI quantifies the duration and strength of long-term drought, whereas PZI is more sensitive to short-term pulses of water and reflects whether moisture conditions deviate from normal (short-term drought). We identified the sampling years of 1985, 1986, and 2011 as significant drought years (Fig. 1). To determine if changes in richness across time were due to individual drought years, we examined whether there were significant differences between richness values in drought and non-drought years. We also explored whether species richness values from 2011 were lower than richness in early drought years, which would suggest that other factors (e.g. reduced fire frequency) had influenced species richness over time.

In addition to examining changes in species richness, we investigated which species were lost and gained over time by tabulating the total number of times a species occurred at each spatial scale in every year. We summarized this information as both the mean number of species and as the percentage of subplots occupied by

each species in each year. We compared the identity and frequency of species lost in earlier drought years to those lost in 2011. We expected insectivores in particular to decrease over time in response to drought, as they have been shown to be particularly sensitive to drought in other longleaf pine studies (e.g. Folkerts 1982) and became substantially less abundant during the drought years of 1985 and 1986 in our data set. We also expected 'wet' and 'mesic' species to be lost to a greater extent if drought alone was responsible for changes in species richness and identity, as 'dry' species could likely tolerate and survive drought (see Debinski et al. 2013). In addition, we expected shrubs, trees and vines to increase over time in abundance and frequency in response to reduced fire frequency, and rosette herbs, geophytes and other small herbaceous species to decrease, as these groups have previously been shown to be sensitive to fire suppression (Glitzenstein et al. 2003, 2012). To identify which types of species became more or less frequent over time and whether those changes were related to drought or reduced fire frequency, we classified species in three ways. First, we assigned species to one of 12 mutually exclusive growth form categories (caulescent herb, matrix graminoid, fern, geophyte, hemiparasite, insectivore, legume, rosette herb, shrub, single-culm graminoid, subshrub, tree and vine; see Table S2.1 in Appendix S2 for growth form definitions) and then examined how the frequency of each growth form changed over time. Second, we categorized species according to their maximum height (short = most plant growth below 4 dm; tall = most plant growth above 4 dm) to examine whether short-statured species were preferentially lost over time, suggestive of competitive exclusion caused by reduced fire frequency. Third, to determine whether species with environmental optima in mesic or wet environments were preferentially lost relative to species with optima in dry environments, we assigned species to a categorical habitat optimum (dry, mesic, wet) based on Weakley (2012) and our own knowledge of the 96 species in the data set.

To further disentangle the impacts of drought and reduced fire frequency on changes in species richness and frequency over time, we used two approaches. First, we quantified changes in richness over time at other sites on the Southeastern Coastal Plain in North Carolina that have also recently experienced long-term drought. These sites are similar to Big Island Savanna in that they occur on Ultisol soils and have similar hydrologic and soil properties, but differ in that they have not experienced reduced fire frequency in the last 20 yr. In contrast to Big Island Savanna, they have generally been burned consistently or somewhat more frequently (every 2–4 yr) over the last

20 yr relative to the previous fire management regime. If changes in species richness over time in other sites were similar to those in Big Island Savanna, that would suggest long-term drought had strong effects on species richness in the region. Second, we re-sampled all plots in Big Island Savanna again in 2012 and 2013, which were wetter years than 2011 (Fig. 1). In addition, annual fire was returned to Big Island Savanna in 2011–2013, specifically to facilitate this study. Thus, the re-sampling events in 2012 and 2013 allowed us to assess the extent of species richness recovery, if any, after consecutive years of fire and increased water availability.

Results

Species richness and frequency patterns over time

At all spatial scales, species richness in Big Island Savanna was lower in 2011 compared to all other sampling years, and significantly lower for small spatial scales (≤ 2.5 m²; Fig. 2, Table 1). These declines at small scales are exceptional and represent a loss of between 32.7% and 40.8% of the flora, depending on the spatial scale in question (Table 1). In contrast to small scales, richness at larger spatial scales (≥ 10 m²) declined less substantially over time, representing losses of 1.2–14.7% of plant species (Table 1).

In 2011, most species had become less frequent in subplots in Big Island Savanna, although these declines were most extreme at ≤ 1 m² (Tables S2.1, S2.2, S2.3 in Appendix S2). In particular, small-statured, herbaceous

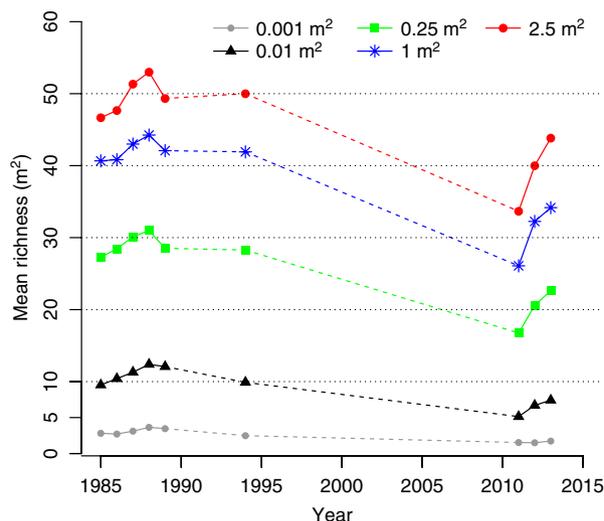


Fig. 2. Mean species richness at each spatial scale in Big Island Savanna during 1985–1989, 1994, and 2011–2013. Richness has decreased significantly from 1994 to 2011 at all scales below 10 m². Although, we plot the linear trajectory between 1989–1994 and 1994–2011 (denoted with a dashed line), the variation in species richness within these intervals is unknown.

Table 1. Average number of species lost and gained over time at each spatial scale in Big Island Savanna from 1985 to 2013.

Area (m ²)	Δ Richness		% Change		Δ Richness		% Change	
	1985–1994	1985–1994	1994–2011	1994–2011	2011–2012	2011–2012	2012–2013	2012–2013
1000	–	–	–1	–1.2	5.8	6.7	1.5	1.7
400	–	–	–4.3	–5.6	7.5*	9.4	0.5	0.6
100	–	–	–2.2	–3.9	7.4**	12.1	0.9	1.4
10	–	–	–5.3*	–14.7	7.6**	19.8	–0.01	0.2
2.5	3.33	6.7	–16.3**	–32.7	6.3*	15.8	3.8*	8.7
1	1.25	3.0	–15.5**	–37	5.7**	17.6	2.2	6.3
0.25	1.02	3.5	–11.5**	–40.8	3.8**	18.6	2.1**	9.1
0.1	–	–	–5*	–40.5	2.5**	25.5	0.4	3.9
0.01	0.36	3.3	–4.8**	–48.1	1.6**	23.3	0.71**	9.6
0.001	–0.33	–10.7	–1**	–38.3	–0.03	0	0.24*	13.6

Δ Richness 1985–1994 represents the mean change in species richness across scales between sequential observations in the original sampling. Δ Richness 1994–2011 is the change in species richness from 1994 to 2011, while Δ Richness 2011–2012 and Δ Richness 2012–2013 are the change in species richness from 2011 to 2012 and from 2012 to 2013, respectively. Double asterisks indicate $P < 0.0001$, single asterisks indicate $P < 0.05$ and single dots indicate $P < 0.10$. % Change is the percentage of species lost or gained over time relative to mean species richness.

species exhibited the largest decrease: insectivores (1.2 of 11.5 species lost on average at 0.25 m²), single-culm graminoids (2.3 of 11.5 species lost on average), rosette herbs (4.3 of 11.5 species lost on average), and caulescent herbs (1.8 of 11.5 species lost on average; Tables 2, S2.2 in Appendix S2). Geophytes, matrix graminoids and hemiparasites also decreased in frequency in 2011 relative to earlier years, but less substantially (0.6, 0.8 and 0.2 species lost on average, respectively; Tables 2, S2.2 in Appendix S2). Legumes and shrubs increased slightly in 2011, while tree species remained constant in frequency (Tables 2, S2.1, S2.2, S2.3 in Appendix S2). However, *P. palustris* seedlings shifted from occupying 21.7% of 0.25-m² subplots in 1985 to 3.3% of subplots in 2011 (Table S2.2 in Appendix S2). Both short (<4 dm) and tall (>4 dm) plant species became less frequent in 2011, but short plants became particularly scarce (8.6 short species lost on average vs 3.5 tall species lost on average; Table 2). In contrast to expectation, species with their habitat optimum in wet environments decreased very little over time, whereas species with their habitat optimum in mesic and dry habitats became substantially less frequent (9.3 and 1.6 species lost, respectively; Table 2).

Species richness and frequency in drought vs non-drought years

To determine whether the loss of species across time was due to the 2011 drought, we compared patterns of species richness and frequency from 2011 to the earlier drought years of 1985 and 1986. Mean species richness was substantially lower in 2011 than in either 1985 or 1986 at small scales, 0.01 m² (5.1 vs 10.0), 1 m² (26.4 vs 40.8) and 2.5 m² (33.6 vs 47.2; Figs 2 and 3). In fact, mean richness at small scales during 1985 and 1986 was more similar to

richness in non-drought years (1987, 1988, 1989, 1994) than richness in 2011 (Figs 2 and 3). The percentage of subplots occupied by most species in 2011 was considerably lower than earlier drought years, especially for rosette herbs and single-culm graminoids (Tables 2, S2.1, S2.2, S2.3 in Appendix S2). Species lost during the droughts of 1985 and 1986 spanned several growth form categories and included both tall shrub species (e.g. *Ilex glabra*, *Morella carolinensis*) and smaller-statured herbaceous species (e.g. *Viola primulifolia*, *Polygala lutea*). Insectivores decreased dramatically during both the 2011 and 1985–1986 droughts, suggesting these species are more sensitive to short-term changes in moisture availability than other species in longleaf pine savannas.

Disentangling the effects of long-term drought and reduced fire frequency

To parse the relative effects of long-term drought and reduced fire frequency, we compared changes in species richness over time at other sites in the Southeastern Coastal Plain of North Carolina to the patterns we observed in Big Island Savanna. Species richness did not decrease at most spatial scales in environmentally similar sites that also experienced long-term drought (Table 3); in fact many sites gained species. Increases in species richness were generally larger on sites that had experienced slightly more frequent fire over the last 20 yr relative to the original fire management regime (Camp Lejeune Marine Corp Base, Croatan National Forest; Table 3). However, species richness also increased or remained constant at most spatial scales on sites with consistent fire frequency (other savannas in the Green Swamp Preserve, Holly Shelter Game Lands; Table 3). When species loss was detected on other sites, the magnitude of loss was substantially less than that

Table 2. Mean number of species of different growth form, plant height (short <4 dm, tall >4 dm), and habitat affinity in 0.25-m² subplots in Big Island Savanna.

	Mean	Drought Year	Non-Drought Year	Mean	Mean	Mean
	1985–1994	1985–1994	1985–1994	2011	2012	2013
Growth form						
Matrix graminoid	4.9	4.9	4.9	4.1	4.4	4.3
Insectivore	2.3	2.0	2.4	1.1	1.4	2.2
Single culm graminoid	5.7	5.5	5.8	3.4	4.8	5.7
Rosette herb	8.9	8.5	9.1	4.6	5.1	5.5
Hemiparasite	1.4	1.3	1.4	1.2	1.4	1.4
Clubmoss	1.0	1.0	1.0	1.0	1.0	1.0
Subshrub	1.4	1.4	1.4	1.3	1.4	1.3
Caulescent herb	3.5	3.4	3.5	1.7	1.9	2.3
Geophyte	1.6	1.6	1.6	1.0	1.2	1.3
Shrub	1.1	1.1	1.0	1.6	1.4	1.4
Tree	1.0	1.0	1.0	1.0	1.0	1.1
Legume	1.0	0.0	1.0	1.3	1.2	1.3
Vine	0.0	0.0	0.0	0.0	1.0	1.0
Plant height						
Short	15.5	15.0	15.7	6.9	9.7	12.0
Tall	13.4	12.9	13.7	9.9	10.9	10.7
Habitat optimum						
Mesic	17.9	17.3	18.2	8.6	11.0	12.9
Dry	8.4	8.1	8.6	6.0	6.7	6.3
Wet	2.6	2.4	2.7	2.5	3.0	3.4

Mean number of species in subplots is summarized for 1985–1994, for the drought years in the 1985–1994 interval (1985, 1986), non-drought years during 1985–1994, and 2011–2013. Small-statured herbaceous species (e.g. rosette herbs, geophytes, caulescent herbs) have decreased in frequency from 1985–1994 to 2011–2013, while shrubs and vines have increased, suggestive of competitive exclusion caused by fire suppression.

detected at Big Island (−4.76 species lost at 0.01 m² in Big Island Savanna, vs −1.08 in Holly Shelter; Table 3).

We re-sampled subplots in Big Island Savanna in 2012 to determine whether species richness had recovered with two consecutive years of fire and somewhat wetter conditions (Fig. 1). Richness in 2012 increased significantly relative to 2011 at all spatial scales except the smallest, which remained stable (Table 1). In addition, most species became more frequent in subplots in 2012, especially insectivores and single-culm graminoids, which increased by 15.4% and 8.8%, respectively, at 0.25 m² (Tables 2, S2.2 in Appendix S2). Very few species decreased in frequency between 2011 and 2012, except one species of club moss (*Lycopodiella appressa*, 18.3% decrease at 0.25 m²), one single-culm graminoid (*Scleria minor*, 8.3% decrease at 0.25 m²) and one rosette herb (*Aletris farinosa*, 6.7% decrease at 0.25 m²; Table S2.2 in Appendix S2). Although species richness rebounded somewhat in 2012, the increase at small spatial scales (2.5 m² and below) was not nearly large enough for recovery to 1985–1994 levels (i.e. species loss from 1994 to 2011 substantially exceeded species gain from 2011 to 2012; Table 2).

We observed that 2013 was a significantly wetter year than either 2011 or 2012 (Fig. 1). In response to higher water availability and continued annual fire, species rich-

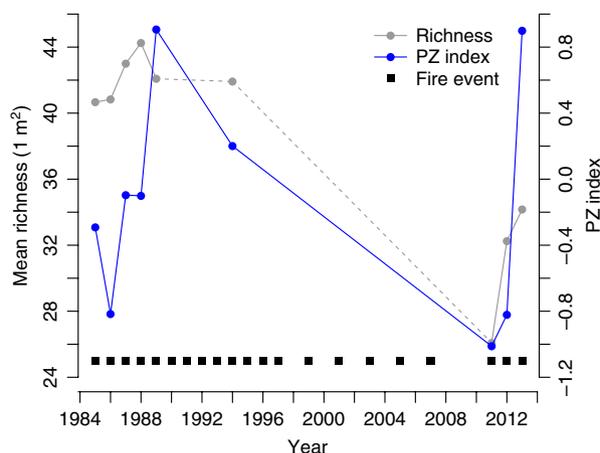


Fig. 3. Comparison of the variation in mean species richness at 1 m² and mean annual Palmer Z Index (PZI) between 1985 and 2013. Prescribed fire events are denoted with black boxes. The trajectory of richness in the intervals 1989–1994 and 1994–2011 is indicated with a dashed line as within-interval variation in richness is unknown.

ness increased from 2012 to 2013 at most spatial scales, although only slightly and often not significantly (Table 1). At the smallest spatial scale (0.001 m²), more species were gained from 2012–2013 than from 2011–2012, however at all other spatial scales the increase

Table 3. Mean change in richness (Δ richness) at three spatial scales from 1993 to 2009 for Ultisol savannas in the southeastern Coastal Plain of NC.

Site	Δ Richness 0.01 m ²	Δ Richness 1 m ²	Δ Richness 10 m ²
Green Swamp – Big Island	–4.8	–15.8	–5.1
Green Swamp – Other	–0.8	0.3	3.1
Camp LeJeune	–0.2	3.5	5.8
Croatan National Forest	1.3	6.3	9.1
Holly Shelter Game Lands	–1.1	1.0	3.4

Negative values indicate sites that have lost species over time, while positive values indicate sites that have gained species. Species richness has increased on Croatan National Forest and Camp LeJeune Marine Corp Base, perhaps owing to somewhat more frequent fire in the last 20 yr relative to the original fire management regime. Species richness has remained constant or increased at all but the smallest spatial scale on other savannas in the Green Swamp Preserve and on Holly Shelter Game Lands, which have experienced constant fire frequency over the last several decades. These environmentally similar sites experiencing long-term drought have not lost as many species as Big Island Savanna, suggesting long-term drought is not the primary driver of species loss in Big Island Savanna.

in species richness from 2012–2013 was substantially less than from 2011–2012 (Table 1, Figs 2 and 3), which is surprising considering how much wetter 2013 was than 2012. Figure 3 shows that species richness patterns across years do not perfectly mirror changes in PZI over time. This is particularly noticeable for 2012–2013 when PZI increased dramatically, but richness did not. In contrast, richness increased substantially from 2011–2012 despite only small increases in PZI, suggesting that species richness patterns are not solely being shaped by soil water availability and that species recovery is likely to be a slow process. Alternatively, it is possible that there is a time lag and species richness has yet to recover due to the wetter years of 2012 and 2013. A time lag may become apparent with continued monitoring of these permanent plots, if increased fire frequency is maintained. Most species increased slightly in frequency or remained constant from 2012 to 2013. However, insectivores and single-culm graminoids both increased dramatically (Tables 2, S2.1, S2.2, S2.3 in Appendix S2). Despite some recovery of species richness in 2012 and 2013, species richness at small spatial scales is still far below the levels documented in the 1980s.

Discussion

The 2011 sampling event revealed large declines in species richness and species frequency in Big Island Savanna at small spatial scales (≤ 2.5 m²; formerly 53 species in 2.5 m² and now 34 species, and formerly 42 in 1 m² and now 26; see Fig. 2). Species loss was ubiquitous across most groups and extremely high for the small-statured, herbaceous species that constitute the bulk of plant species richness at

this site. Despite modest recovery in 2012 and 2013, small-scale species richness remains far below the levels documented in 1985–1994.

Our data suggest that both reduced fire frequency and drought have contributed to species loss in Big Island Savanna, perhaps in a complex and interactive manner. Determination of the degree to which reduced fire frequency vs long-term drought is responsible for this loss will only be fully clarified with continued monitoring of these plots and future experiments manipulating fire frequency. However, several lines of evidence suggest reduced fire frequency during the last 15 yr is the primary factor driving species richness declines in Big Island Savanna. First, the declines in species richness and frequency in response to drought in 1985–1986 were substantially smaller than during the drought year of 2011, which suggests an additional factor, such as reduced fire frequency, is responsible. Although individual drought events may result in small reductions in species abundance, short-term drought is unlikely to result in local extinction of species or large shifts in community composition (Grime et al. 2008). Second, the frequency of species that have a habitat optimum in wet environments has remained constant over time, which is contrary to our expectation that ‘wet’ species would be most sensitive to drought and would be lost preferentially if drought were the major factor influencing species richness patterns. This pattern is most likely a consequence of the ‘wet’ species being almost exclusively in the ‘tall’ group, reflecting the taller and lush growth on wet sites. Third, reduced fire frequency in longleaf pine savannas and other fire-dependent grasslands results in the loss of small-statured species, which are competitively excluded as the abundance of woody species, ferns and large grasses increases post-fire (Leach & Givnish 1996; Glitzenstein et al. 2003; Overbeck et al. 2005). The documented loss in 2011 of mostly small herbaceous species with dry to mesic habitat affinity is indicative of fire suppression. Finally, several species that are known to be weak competitors, and/or highly dependent on fire (i.e. ‘fire-followers’; Lemon 1949) decreased over time in Big Island Savanna (e.g. *Agalinis aphylla*, *Aletris farinosa*, *Aristida virgata*, *Calopogon* spp., *Cleistesopsis divaricata*, *Dichanthelium strigosum*, *Drosera capillaris*, *Lycopodiella appressa*, *Pinguicula* spp., *Xyris ambigua*; Lemon 1949; Wilson & Keddy 1986; Gaudet & Keddy 1995; Brewer 1999a,b; Keddy et al. 2006).

Further evidence suggests reduced fire frequency rather than drought is the primary cause of species loss. For example, other, environmentally similar sites within the region have experienced little if any species loss, despite having also been subjected to long-term drought. In fact, species richness at these sites has, on average, increased at most spatial scales, both on sites with somewhat increased

fire frequency and those with consistent fire frequency (Table 3). Additionally, two consecutive years of fire at Big Island Savanna resulted in some recovery of species richness in 2012. Since 2012 was only slightly wetter than 2011, we attribute the increase in species richness in 2012 largely to two consecutive years of fire. However, long-term drought has likely contributed to species loss in Big Island Savanna and may explain why a few other sites in southeastern North Carolina have lost species at small spatial scales, albeit much less so than has been the case for Big Island Savanna (Table 3).

Species losses of the magnitude we observed at Big Island Savanna in response to alteration of disturbance regimes, compounded with additional stressors (e.g. drought, habitat fragmentation), have been reported in other species-rich grassland systems (Leach & Givnish 1996; Glitzenstein et al. 2012). Some work suggests that species richness may be slow to recover after stressful events, such as drought or fire suppression, due to a loss of local propagule sources, changes in the local environment or shifts in vegetation structure in which often woody, competitively superior species prevent the re-colonization of herbaceous species (Tilman & Haddi 1992). Recovery following stressful events may be especially challenging in fragmented grasslands, such as Big Island Savanna, which is embedded within a matrix of ombrotrophic peatland, dominated by evergreen woody plants. For these reasons, species richness at small spatial scales in Big Island Savanna may take a significant amount of time to recover, especially in the presence of ongoing drought, and likely will not recover with continued reduced fire frequency.

The temporal and spatial breadth of our study was crucial for detecting changes in species richness in Big Island Savanna. Grasslands are structured by multiple processes that vary over space and time (e.g. fire, grazing, drought; see Collins & Smith 2006), and for this reason it is essential to quantify plant species richness patterns across multiple spatial and temporal scales. For example, previous work has suggested that fire frequency has the largest impact on species richness at small spatial scales (Glitzenstein et al. 2003; Collins & Smith 2006; Bowles & Jones 2013). Here, we document a scale-dependent response to changes in fire frequency and drought over time. Some combination of drought and reduced fire frequency have reduced the population sizes of most species in Big Island Savanna, resulting in reduced species packing at small spatial scales, as there are now fewer individuals of each species present. If a nearly annual fire regime is not reinstated in Big Island Savanna, population sizes are likely to continue to decline, which may result in local extinction and declines in species richness at larger spatial scales, especially for already infrequent and rare species. This hypothesis of species loss trickling upward to larger spatial scales with continued fire

suppression has been suggested previously in another longleaf pine study examining species richness patterns over time in relation to fire frequency (Glitzenstein et al. 2012). Had we examined species richness patterns only at 1000 m² in Big Island Savanna, we would have concluded that species richness had remained relatively stable over time and that changes in the fire management regime and/or long-term drought had not affected vegetation patterns in this savanna (Table 1). Hence, monitoring at multiple spatial and temporal scales is critical for understanding patterns, identifying processes that drive those patterns, and informing conservation and land management agencies about best management practices.

One important finding from this study is that small changes in fire management regimes can have large and long-lasting consequences for plant species richness in longleaf pine savannas. Our work suggests that very frequent to annual fire is probably necessary to maintain small-scale biodiversity and species packing in the most species-rich, moist savannas, especially in the face of additional environmental stress. We believe this work can be generalized to other species-rich grasslands that experience chronic or continuous disturbance (e.g. alvar grasslands in Northern Europe, oligotrophic mowed meadows of Eastern Europe, cerrado in Brazil, *Themeda triandra* grasslands in Australia, and mountain grasslands of central Argentina; Wilson et al. 2012). Some evidence from other species-rich systems also suggests that slight changes in disturbance regimes can have large impacts on plant biodiversity (Morgan 1999; Overbeck et al. 2005). In addition, our research indicates that land managers should proceed cautiously when making changes to long-standing management regimes, despite how well intentioned such changes might be, and assess impacts immediately after their implementation. Future work in other species-rich grasslands should both explore whether chronic and nearly continuous disturbance is necessary to maintain species richness and how slight alteration of disturbance regimes can affect plant species richness over time.

Both periodic and multi-year drought events are important factors that shape species richness and community composition patterns in the longleaf pine ecosystem and potentially increase the risk of biodiversity loss with altered disturbance regime. Drought events have been recognized as important processes in many other grassland ecosystems (e.g. Tilman & Haddi 1992; Knapp et al. 2002, 2006; Anderson 2008; Evans et al. 2011; Cherwin & Knapp 2012). The severity and intensity of drought events in the southeastern US have increased in the last 25 yr and are predicted to continue increasing with ongoing climate change (Klos et al. 2009). Thus, future research should explore further the relative and interactive contributions of drought and fire to changes in community structure and

composition in the longleaf pine ecosystem as such knowledge will be critical for protecting these species-rich and threatened communities.

Although longleaf pine savannas, among many other grassland ecosystems, are dominated by long-lived perennial species, species richness and frequency in these ecosystems are surprisingly sensitive, both spatially and temporally, to environmental changes, alteration of disturbance regimes, and stochastic events (Sykes et al. 1994; Collins & Smith 2006). An unusually long history of detailed vegetation sampling at multiple scales in Big Island Savanna has enabled us to document complex changes in species richness in response to drought and reduced fire frequency. Additional studies in the longleaf pine ecosystem and other grass-dominated ecosystems are needed to more fully disentangle the complex and interactive effects of environmental change and altered disturbance regimes on spatial and temporal patterns of species richness. Moreover, understanding these complex relationships will be necessary to provide critical guidance to land managers responsible for conserving important biodiversity sites.

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References

- Anderson, T.M. 2008. Plant compositional change over time increases with rainfall in Serengeti grasslands. *Oikos* 117: 675–682.
- Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* 3: 187–200.
- Bowles, M.L. & Jones, M.D. 2013. Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. *Ecological Applications* 23: 464–478.
- Brewer, J.S. 1999a. Effects of fire, competition and soil disturbances on regeneration of a carnivorous plant (*Drosera capillaris*). *American Midland Naturalist* 141: 28–42.
- Brewer, J.S. 1999b. Short term effects of fire and competition on growth and plasticity of the yellow pitcher plant, *Sarracenia alata* (Sarraceniaceae). *American Journal of Botany* 86: 1264–1271.
- Cantero, J.J., Pärtel, M. & Zobel, M. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns in mountain grasslands of central Argentina. *Oikos* 87: 346–354.
- Cheng, Y., Tsubo, M., Ito, T.Y., Nishihara, E. & Shinoda, M. 2011. Impact of rainfall variability and grazing pressure on plant diversity in Mongolian grasslands. *Journal of Arid Environments* 75: 471–476.
- Cherwin, K. & Knapp, A. 2012. Unexpected patterns of sensitivity to drought in three semi-arid grasslands. *Oecologia* 169: 845–852.
- Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E. & Reiners, W.A. (eds.) *Fire regimes and ecosystem properties: proceedings of the conference*, pp. 112–136. USDA Forest Service, Washington, DC, US.
- Christensen, N.L. 2000. Vegetation of the southeastern Coastal Plain. In: Barbour, M.G. & Billings, W.D. (eds.) *North American terrestrial vegetation*, pp. 397–448. Cambridge University Press, Cambridge, UK.
- Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gross, K.L., Gherardi, L.A., Hallett, L.M., Hobbs, R.J., Hsu, J.S., Turnbull, L. & Suding, K.N. 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* 94: 1687–1696.
- Collins, S.L. & Smith, M.D. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87: 2058–2067.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745–747.
- Debinski, D.M., Caruthers, J.C., Cook, D., Crowley, J. & Wickham, H. 2013. Gradient-based habitat affinities predict species vulnerability to drought. *Ecology* 94: 1036–1045.
- Dengler, J., Ruprecht, E., Szabó, A., Turtureanu, P.D., Beldean, M., Uğurlu, E., Pedashenko, H., Dolnik, C. & Jones, A. 2009. EDGG cooperation on syntaxonomy and biodiversity of *Festuco brometea* communities in Transylvania (Romania): report and preliminary results. *Bulletin of the European Dry Grassland Group* 4: 13–19.
- Dengler, J., Becker, T., Ruprecht, E., Szabó, A., Becker, U., Beldean, M., Pedashenko, H., Biota-Nicolae, C., Dolnik, C., (...) & Uğurlu, E. 2012. *Festuco-Brometea* communities of the Transylvanian Plateau (Romania) – a preliminary overview on syntaxonomy, ecology, and biodiversity. *Tuexenia* 32: 319–359.
- Evans, S.E., Byrne, K.M., Lauenroth, W.K. & Burke, I.C. 2011. Defining the limit to resistance in a drought-tolerant

- grassland: long-term severe drought significantly reduces the dominant species and increases ruderals. *Journal of Ecology* 99: 1500–1507.
- Fidelis, A. 2010. South Brazilian Campos grasslands: biodiversity, conservation and the role of disturbance. In: Runas, J. & Dahlgren, T. (eds.) *Grassland biodiversity: habitat types, ecological processes and environmental impacts*, pp. 223–239. Nova Science, New York, NY, US.
- Folkerts, G.W. 1982. The Gulf Coast Pitcher Plant Bogs: one of the continent's most unusual assemblages of organisms depends on an increasingly rare combination of saturated soil and frequent fires. *American Scientist* 70: 260–267.
- Frost, C. 2006. History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E. & Miller, D. (eds.) *The longleaf pine ecosystem: ecology, silviculture, and restoration*, pp. 9–48. Springer, New York, NY, US.
- Frost, C.C., Walker, J. & Peet, R.K. 1986. Fire-dependent savannas and prairies of the southeast: original extent, preservation status and management problems. In: Kulhavy, D.L. & Conner, R.N. (eds.) *Wilderness and natural areas in the eastern United States*, pp. 348–357. Center for Applied Studies, School of Forestry, Stephen F. Austin University, Nacogdoches, TX, US.
- Gaudet, C.L. & Keddy, P.A. 1995. Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology* 76: 280–291.
- Gibson, D.J. & Hulbert, L.C. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72: 175–185.
- Glitzenstein, J.S., Streng, D.R. & Wade, D.D. 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.
- Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M. & Hermann, S.M. 2012. Fire frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. *Forest Ecology and Management* 264: 197–209.
- Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. & Bennett, C.R. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America* 105: 10028–10032.
- Haddad, N.M., Tilman, D. & Knops, J.M.H. 2002. Long-term oscillations in grassland productivity induced by drought. *Ecology Letters* 5: 110–120.
- Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. *Ecology* 20: 287–304.
- Huffman, J.M. 2006. *Historical fire regimes in southeastern pine savannas*. PhD Thesis, Louisiana State University, Baton Rouge, LA, US.
- Keddy, P.A., Smith, L., Campbell, D.R., Clark, M. & Montz, G. 2006. Patterns of herbaceous plant diversity in southeastern Louisiana pine savannas. *Applied Vegetation Science* 9: 17–26.
- Kirkman, L.K., Goebel, P.C. & Palik, B.J. 2004. Predicting plant species diversity in a longleaf pine landscape. *Ecoscience* 11: 80–93.
- Klimeš, L., Dančák, M., Hájek, M., Jongepierová, I. & Kučera, T. 2001. Scale-dependent biases in species counts in a grassland. *Journal of Vegetation Science* 12: 669–704.
- Klos, R.J., Wang, G.G., Bauerle, W.L. & Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using forest health and monitoring data. *Ecological Applications* 19: 699–708.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & McCarron, J.K. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298: 2202–2205.
- Knapp, A.K., Burns, C.E., Fynn, R.W.S., Kirkman, K.P., Morris, C.D. & Smith, M.D. 2006. Convergence and contingency in production–precipitation relationships in North American and South American C4 grasslands. *Oecologia* 149: 456–464.
- Kologiski, R.L. 1977. *The phytosociology of the Green Swamp, North Carolina*. [North Carolina Agricultural Experiment Station Technical Bulletin 250]. North Carolina Agricultural Experiment Station, Raleigh, NC, US.
- Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. *Journal of Vegetation Science* 2: 715–718.
- Leach, M.K. & Givnish, T.J. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273: 1555–1558.
- Lemon, P.C. 1949. Successional responses of herbs in longleaf-slash pine forest after fire. *Ecology* 30: 135–145.
- McIver, H. 1981. *Green swamp nature preserve*. The Nature Conservancy, Chapel Hill, NC, US.
- Morgan, J.W. 1999. Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. *Plant Ecology* 144: 127–144.
- Myers, J.A. & Harms, K.E. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92: 676–686.
- National Climatic Data Center. 2013. Available at <http://www.ncdc.noaa.gov/> Accessed July, 2013.
- Noss, R.F. 2013. *Forgotten grasslands of the south: natural history and conservation*. Island Press, Washington DC, US.
- O'Connor, T.G. 1995. Transformation of a savanna grassland by drought and grazing. *African Journal of Range & Forage Science* 12: 53–60.
- Outcalt, K.W. & Sheffield, R.M. 1996. *The longleaf pine forest: trends and current conditions*. [USDA Forest Service Southern Research Station resource bulletin 9]. United States Department of Agriculture, Washington, DC, US.
- Overbeck, G.E., Müller, S.C., Pillar, V.D. & Pfadenhauer, J. 2005. Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science* 16: 655–664.
- Palmquist, K.A. 2014. *Vegetation dynamics and plant diversity patterns across space and time in the longleaf pine ecosystem*. Ph.D dis-

- sertation, University of North Carolina at Chapel Hill, Chapel Hill, NC, US.
- Peet, R.K. & Christensen, N.L. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. In: Doring, H.J., Werger, M.J.A. & Willems, J.H. (eds.) *Diversity and pattern in plant communities*, pp. 233–245. SPB Academic Publishing, The Hague, NL.
- Peet, R.K., Wentworth, T.R. & White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63: 262–274.
- Peet, R.K., Lee, M.T., Boyle, M.F., Wentworth, T.R., Schafale, M.P. & Weakley, A.S. 2012. Vegetation plot database of the Carolina Vegetation Survey database. *Biodiversity and Ecology* 4: 243–253.
- Peet, R.K., Palmquist, K.A. & Tessel, S.M. 2014. Herbaceous layer species richness of southeastern forests and woodlands: patterns and causes. In: Gilliam, F.S. & Roberts, M.R., (eds.) *The herbaceous layer in forests of eastern North America*, 2nd ed, pp. 255–276. Oxford University Press, Oxford, UK.
- Potts, D.L., Suding, K.N., Winston, G.C., Rocha, A.V. & Goulden, M.L. 2012. Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland. *Journal of Arid Environments* 81: 59–66.
- Rome, A. 1988. Vegetation variation in a pine–wiregrass savanna in the Green Swamp, North Carolina. *Castanea* 1988: 122–131.
- Ruffner, J.A. 1985. *Climates of the states: National Oceanic and Atmospheric Administration narrative summaries, tables, and maps for each state, with overview of state climatologist programs*, 3rd ed. Gale Research Co., Detroit, MI, US.
- State Climate Office of North Carolina, NC State University. CRONOS [internet database] available at <http://www.nc-climate.ncsu.edu/cronos/> Accessed July 26, 2011.
- Stevens, C., Duprè, C., Gaudnik, C., Dorland, E., Dise, N., Gowing, D., Bleeker, A., Alard, D., Bobbink, R., (...) & Diekmann, M. 2011. Changes in species composition of European acid grasslands observed along a gradient of nitrogen deposition. *Journal of Vegetation Science* 22: 207–215.
- Sykes, M.T., van der Maarel, E., Peet, R.K. & Willems, J.H. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobotanica et Phytotaxonomica* 29: 439–448.
- Tilman, D. & Haddi, A.E. 1992. Drought and biodiversity in grasslands. *Oecologia* 89: 257–264.
- Walker, J. & Peet, R.K. 1983. Composition and species diversity of pine–wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55: 163–179.
- Weakley, A.S. 2012. *Flora of the southern and mid-Atlantic States*. University of North Carolina Herbarium, Chapel Hill, NC.
- Wilson, S.D. & Keddy, P.A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67: 1236–1242.
- Wilson, J.B., Peet, R.K., Dengler, J. & Pärtel, M. 2012. Plant species richness: the world records. *Journal of Vegetation Science* 23: 796–802.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A. & Smith, G.M. 2009. *Mixed effect models and extensions in ecology with R*. Springer, New York, NY.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Map of plot locations in southeastern North Carolina, USA.

Appendix S2. Species frequency and percentage of subplots occupied for all species at 0.01, 0.25 and 1 m².