

## Understory dynamics in North Carolina longleaf pine savannas: Biodiversity, dominance, and biomass

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**Location** Fifteen observational study sites in North Carolina spanning from the Sandhills to the Coastal Plain.

**Methods** At each of the 15 sites, 25 sampling plots were established where above-ground herbaceous biomass, species presence and abundance, soil characteristics and light availability were measured along with numerous other environmental variables.

**Results** Considerable variation exists across study plots within and across sites, with plant species richness ranging from 1 to 17 per m<sup>2</sup>. The relative cover of the dominant grass species, *Aristida stricta* (wiregrass), also varied greatly within and across sites, with a median of ca. 30% relative cover per plot. Wiregrass was a significant predictor of biomass and biodiversity at small scales. With increasing wiregrass abundance, richness decreases, with 25% relative wiregrass cover leading to the highest levels of biodiversity. Likewise, because wiregrass abundance is one of the stronger predictors of above-ground biomass, we also found a unimodal richness–biomass relationship.

**Conclusions** Our results indicate that at lower ends of the productivity and richness gradients, land managers can increase all three restoration targets in the understory at the same time; however, at more diverse and productive sites, restoration practitioners may need to prioritize one target or find a balance between all three.

**Keywords:** above-ground biomass | *Aristida stricta* | biodiversity | dominant species | ground layer | productivity | richness | understory restoration | wiregrass

### Article:

\*\*\*Note: Full text of article below

## RESEARCH ARTICLE

# Understory dynamics in North Carolina longleaf pine savannas: Biodiversity, dominance, and biomass

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## KEYWORDS

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## 1 | INTRODUCTION

To fight the climate crisis and enhance biodiversity (among other things), the United Nations has declared 2021–2030 the decade for ecosystem restoration, with the aim to massively upscale restoration efforts of degraded and destroyed ecosystems (UN Environmental Programme, 2019). Although this new goal is encouraging to restoration practitioners globally, restoration of ecosystems is complex, and often has multiple targets that work in concert or may conflict with each other. Commonly, the goal of restorations is to return ecosystems to their historical reference conditions, pre-human disturbance (Buisson et al., 2021; Bullock et al., 2011; Miller et al., 2017; Pollock et al., 2012). However, some argue that historical reference conditions are unattainable and that we should instead focus on restoring ecosystems to a contemporary reference condition, including to a stable and functioning state (Hobbs et al., 2014; Hughes et al., 2017; McNellie et al., 2020; Suding, 2011; Thorpe & Stanley, 2011). The stability and functioning of ecosystems encompasses many aspects of ecosystems, such as biodiversity, productivity, inter- and intraspecific interactions, dominance of a particular species, and resilience to disturbances or climate extremes (Buisson et al., 2021; Thorpe & Stanley, 2011). However, balancing all of these restoration targets can be challenging, because management strategies may promote one target while harming another causing conflict among the various targets. For example, it may be an achievable goal to restore an iconic, dominant species, but in the process, increased competition between that dominant species and other species may lead to a decrease in biodiversity (Howe, 1999). Although finding a harmony between multiple restoration targets may be challenging, understanding the drivers of and relationships between these different targets can better inform restoration practices and help balance restoration goals, maximizing most, if not all restoration outcomes.

Once dominant across the southeastern United States (US), the fire-dependent longleaf pine (LLP) savanna ecosystem is of high conservation concern and is gaining traction as a restoration priority (Noss et al., 2015; Oswalt et al., 2012). Prior to European settlement of North America, the LLP savanna ecosystem was dominant across nine coastal states of the southeast USA and covered an estimated 92 million acres (Frost, 2006). However, owing to overexploitation of the dominant canopy tree, longleaf pine (*Pinus palustris*), as well as other anthropogenic influences, such as fire suppression, fewer than 3% (2 million acres) of natural stands remain across the historical range of the LLP ecosystem (Oswalt et al., 2012). In recent decades, the LLP tree has been the focus of restoration efforts, with overstory LLP tree thinning in overgrown stands and planting of LLP seedlings in open fields helping to maintain the open canopy structure dominated by LLP trees that characterizes these savannas and promotes fire spread and understory biodiversity (Johnson & Gjerstad, 2006). Through these practices, and owing to the vast body of research on restoring the tree in LLP stands, restoration of the overstory has been largely successful (Johnson & Gjerstad, 2006). However, the LLP savanna ecosystem is among the most biodiverse in the world at small spatial scales because of its high density of understory plant

species, consisting mainly of graminoids and forbs (J. Walker & Peet, 1984). Restoration of this rich understory is more complex, and thus its restoration requires further study and cutting-edge tools that will promote successful understory restorations (Oswalt et al., 2012). Successful restoration of the LLP understory generally has three main targets—above-ground biomass, dominant species and plant biodiversity—each of which are critical to the long-term sustainability and ecosystem services provided by LLP savannas (Aschenbach et al., 2010; D. Brockway et al., 2005; Johnson & Gjerstad, 2006; Outcalt et al., 1999; J. L. Walker & Silletti, 2006). Owing to the complex nature of the system feedbacks, these three targets cannot be tackled independently, but must be restored in conjunction.

Restoring ecosystem productivity to degraded ecosystems is a primary goal and basic target of ecological restoration globally, because function frequently yields numerous ecosystem services (Dobson et al., 1997; Falk et al., 2013; C. A. Harrington, 1999). In LLP savannas, frequent fires are essential for maintaining community structure, allowing these areas to remain open grasslands (D. Brockway et al., 2006; Gagnon et al., 2015; J. L. Walker & Silletti, 2006). Fine fuels on the ground (grasses and pine needles) are responsible for fire spread and thus, net primary productivity (NPP) of the understory is a critical component of LLP savanna restoration.  $C_4$  grasses in this system, and other savanna ecosystems, help contribute to the fine fuels for carrying fire, because they are highly flammable once dried out during the dry season (D'Antonio & Vitousek, 1992). The fire, in turn, creates an open environment, enhancing light conditions, and promoting grass growth and the generation of more fine fuels for the next fire (Accatino et al., 2010; Beckage et al., 2011; Bond, 2008; Platt et al., 2006). In the absence of fire, woody species quickly take over, and these LLP savannas can become deciduous forest, losing the diverse understory in the process (Beckage et al., 2009; D. G. Brockway & Lewis, 1997; Olson & Platt, 1995; Peet et al., 2018). This vegetation–fire feedback is critical for the long-term sustainability of the LLP savanna ecosystem. In addition to promoting the vegetation–fire feedback, NPP provides wildlife habitat for many species, such as the threatened northern bobwhite quail (*Colinus virginianus*) in the LLP savanna ecosystem (Van Lear et al., 2005), yielding economic incentives through hunting revenue. Further, terrestrial productivity acts as a carbon sink, capturing carbon from the atmosphere and sequestering it both above- and below-ground (Knapp et al., 2014). Grass-dominated systems, in particular, store much of their carbon below ground, especially those that experience frequent fire (Johnson & Matchett, 2001; Kitchen et al., 2009), making LLP savannas and grasslands worldwide important for global carbon sequestration (Scurlock & Hall, 1998). Restoring NPP therefore contributes to long-term sustainability, conservation and economic restoration goals.

Wiregrass (*Aristida stricta*) is the dominant bunchgrass species in LLP savannas of North Carolina and northern South Carolina, and is thus a major contributor to NPP in this ecosystem (L. K. Kirkman et al., 2016; Mitchell et al., 1999; Outcalt et al., 1999). The long, thin, wire-like leaves of wiregrass spread outward from the center of the bunch and overlap with adjacent wiregrass bunches, creating



a relatively continuous cover on the ground (Parrott, 1967). This continuous wiregrass cover also functions to catch the falling, resinous and flammable LLP needles, which together, provide the fuel for frequent, low-intensity fires that move rapidly across the surface of the landscape (L. K. Kirkman, et al., 2004). Therefore, wiregrass has an essential role in structuring the understory through its effect on fire behavior (Outcalt et al., 1999). Although other grasses also contribute to NPP and fuel load, the wiry nature and high flammability of wiregrass make it critical for the even spread of fire in the understory (Fill et al., 2016). In addition, wiregrass recovers quickly after fire (Fill et al., 2012) and is therefore a critical component of the vegetation–fire feedback. As such, wiregrass is a keystone species, integral to the maintenance of ecosystem function and biodiversity in LLP savannas (Landers et al., 1995; Noss, 1989).

The dominant grass species contribute substantially to productivity in LLP savannas (D. G. Brockway & Lewis, 1997; Landers et al., 1995), whereas forb species drive biodiversity (J. L. Walker & Silletti, 2006), as in most grasslands and savannas (Bräthen et al., 2021). This biodiverse group provides numerous ecosystem functions and services. For example, LLP savannas are rich in herbaceous legume (Fabaceae) species that fix atmospheric nitrogen through symbioses with rhizobia. Nitrogen fixation can replenish the plant available nitrogen that is lost to the atmosphere during fires, conferring the nitrogen benefit to the surrounding plant community (Høgh-Jensen, 2006; Temperton et al., 2007). Understory plant diversity also functions to support pollinator populations (Ulyshen et al., 2020), generating a positive feedback loop because nearly 75% of the endemic forb species in LLP savannas rely on insect pollinators for reproduction (Folkerts & Deyrup, 1993). Because global biodiversity loss is at an all-time high (Díaz et al., 2019), understanding the drivers and dynamics of biodiversity is particularly important.

Many studies across different ecosystems suggest that productivity is influenced by biodiversity and dominance. Highly abundant or dominant species within communities should have large effects on many biological processes such as productivity (i.e., mass ratio hypothesis; Avolio et al., 2019; Grime, 1998; Smith et al., 2020). A recent meta-analysis of 57 plant species removal experiments found that dominant species removal decreased all measures of ecosystem function (Avolio et al., 2019). In addition, biodiversity is also frequently linked to both productivity (Grace et al., 2016; Yachi & Loreau, 1999) and stability of productivity (Tilman, 1996; Tilman et al., 2006), yet the directionality of these relationships is debated. It is generally thought that richness promotes productivity, but in some cases, as resources increase, coexistence of species at high productivity reaches a limit, and diversity declines (Chalcraft et al., 2009; Gough et al., 2000; Rosenzweig, 1995; Waide et al., 1999). Further, the dominance–diversity relationship is also well-studied and debated (Gilbert et al., 2015; Myers & Harms, 2009; Polley et al., 2007). Typically, when dominance of one species is high, the remaining species may exist at such low abundances that populations cannot persist, and so diversity declines (Howe, 1999). These relationships are intertwined, and productivity, dominant species and diversity all interact to influence each other. Therefore, all three

restoration targets need to be considered together in restoration of the understory to bring back these complex and tightly coupled ecosystem components.

In this study, we have three major objectives. First, we describe the (1) biomass (2) dominance, and (3) diversity seen in the herbaceous understory layer, providing a current understanding of the state of LLP savanna understory health across 15 xeric, North Carolina LLP savanna sites. Although the LLP ecosystem spans large gradients in moisture, and therefore productivity, this study focuses on the dry end of this gradient. Although not representative of the ecosystem as a whole, this work highlights the xeric LLP sites where successful restoration of understory productivity and richness may be more challenging because water is limited. Second, we explore the predictors of those three ecosystem components. By combining both biotic (wiregrass cover, litter biomass, richness, LLP tree number and shrub stem number) and abiotic (soil characteristics, understory and soil-surface light availability, time in years since fire and precipitation) variables, we determine how each predictor alone and in combination correlates with each of the three restoration targets. Lastly, we explore the much-studied relationships between these three critical restoration targets (Aarssen, 2001; Guo, 2007; Huston, 1997; Loreau et al., 2002), using this unique, endangered and anthropogenically altered ecosystem. Once the inherent range that exists in these three restoration targets and the factors that influence them are understood, the restoration, management and health of LLP savannas can improve.

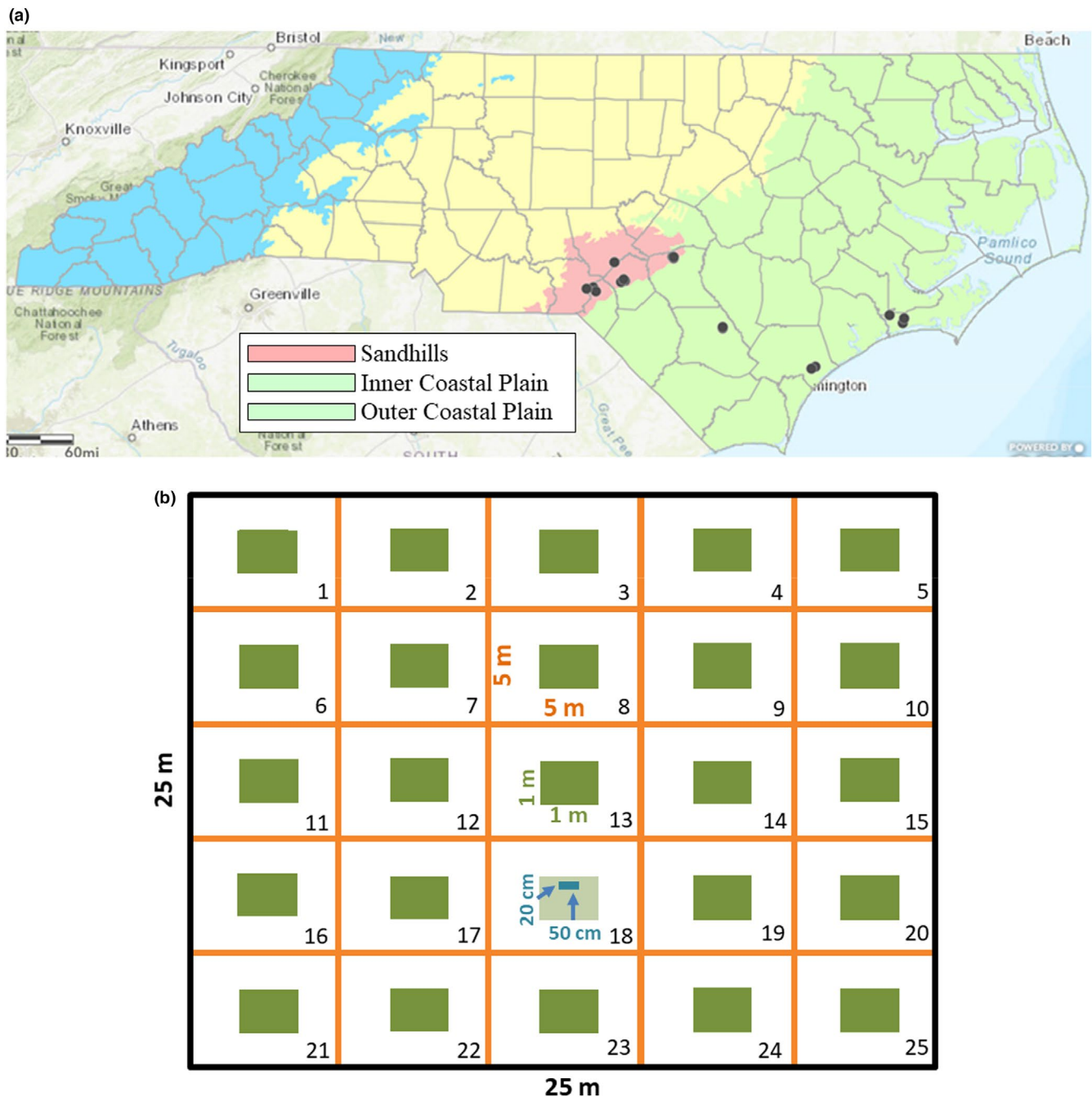
## 2 | METHODS

### 2.1 | Study area

We selected 15 sites across North Carolina LLP savannas (Appendix S1). The study area is located within three ecoregions (Sandhills, Inner Coastal Plain and Outer Coastal Plain) of North Carolina (34°44'–35°11'N, 76°58'–79°35'E, 9–130 m a.s.l.; Figure 1a). The mean annual temperature across this range is 21°C and the mean annual precipitation (MAP) ranges from 1,170 to 1,351 mm. Owing to geographical and environmental variation across the LLP range, the composition of vegetation changes. Although there are many ecological classifications of LLP vegetation across the nine coastal states in the southeast, with each community type being associated with different levels of biodiversity (Peet, 2006), study sites here were all xeric with soils that were Ultisols and Spodosols (Appendix S1), and that had a canopy dominated by *Pinus palustris*, an herbaceous understory, and a history of relatively frequent fire (every 2–6 years; Appendix S1).

### 2.2 | Sampling design and methods

With guidance and approval from land managers, at each site, a 25 m × 25 m sampling area was selected in LLP stands that had a



**FIGURE 1** Location of the 15 study sites within the Sandhills (pink) and Inner Coastal Plain and Outer Coastal Plain (both in green) in North Carolina (a) and the experimental layout at each of the study sites (b). Within each 25 m × 25 m study site (outlined in black), 25 plots (each 5 m × 5 m, outlined in orange) were arranged in a grid. Within each plot, there was a 1 m × 1 m quadrat (filled in green) in which species composition was recorded. Within each quadrat, there was a nested 20 cm × 50 cm quadrat (filled in blue) used for destructive sampling of above-ground biomass. See Appendix S1 for latitude and longitude of each site

continuous understory grass layer and where LLP was the only overstory tree. The sampling area was divided into 25 plots (each 5 m × 5 m) arranged in a grid (Figure 1b). Within each plot ( $n = 25$ ), a 1 m × 1 m species composition quadrat was established and permanently marked with flags. In each quadrat, all plants were identified to species, and percent cover of each species was visually estimated in both the early and late growing season (in April and September, respectively). The maximum cover obtained from the two time

points for each species was used in all analyses. Late in the growing season, above-ground biomass ( $\text{g}/\text{m}^2$ ) was measured by clipping all above-ground herbaceous biomass in one 0.1- $\text{m}^2$  quadrat nested within each 1- $\text{m}^2$  quadrat ( $n = 25$ ); above-ground biomass is a proxy for above-ground NPP in these systems. All plants at ground level were harvested with scissors and sorted by growth form and live versus dead tissue (graminoid, woody, forb, past year's dead and litter, including LLP needle litter). Above-ground biomass clippings





were put into paper bags and placed in a forced air oven at 60°C for a minimum of 48 hr until dry weights were measured and recorded. In each 5 m × 5 m plot, tree and shrub species of the over- and mid-story were documented via several measurements because their presence and associated canopy cover and litter-fall flammability are known to influence plant species richness and understory community composition (Baldwin et al., 1996; Beckage & Stout, 2000; Drewa et al., 2002a; T. B. Harrington, 2006; Platt et al., 2006, 2016; Veldman et al., 2013). First, the only canopy trees present (LLP trees) with a diameter at breast height (DBH) greater than 10 cm were recorded as alive or dead, as well as their DBH. Second, if LLP trees were shorter than 1.37 m and/or had a DBH less than 10 cm, only presence was recorded. Third, shrub species were recorded as the number of stems coming out of the ground to accurately describe mid-story cover; recording only the occurrence of shrubs would not account for the varying cover of each, which is critical to understanding their influence on the understory.

Photosynthetically active radiation (PAR) was measured with a ceptometer in each plot above the understory canopy and below the understory and litter layer. To calculate percent light availability, light measurements were taken under open sky (i.e., no trees overhead), at the top of the understory layer and at the soil surface. Understory light availability was then calculated as the percent transmittance of light that made it through the overstory canopy (above understory layer PAR/open sky PAR) and was represented as a percentage. Soil-surface light availability was then calculated as the percent of light that was transmitted through the over and understory canopies (soil-surface PAR/open sky PAR) and was used as a percentage. To address soil characteristics, three soil samples (10 cm deep) were collected within each plot using a soil core, and samples were placed in a forced air oven at 35°C until being sent to the North Carolina Department of Agriculture where samples were analyzed for cation-exchange capacity, base saturation (percent of cation-exchange capacity occupied by base cations), pH, phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn), copper (Cu), sulfur (S) and sodium (Na). Soil characteristics of each plot were combined into principal components using principal component analysis (PCA). The first two principal components together accounted for 55.66% of the total variance in the data (Appendix S2). PCA axis 1 (PC1) accounted for 32.50% of the cumulative variance among the data, with the contributions of base saturation, Ca, Mg and Na decreasing, and P increasing as PC1 increases. For PC1, base saturation and Ca were the most important factors in explaining the variability in the data (23.99% and 23.38% contribution to PC1, respectively; Appendix S3). PCA axis 2 (PC2) accounted for 23.16% of the cumulative variance among the data, with the contributions of K, Zn, CEC, Mn, Cu and S increasing, and pH decreasing as PC2 increases. For PC2, K was the most important nutrient in explaining the variability in the data (23.34% contribution to PC2; Appendix S3). Because PC1 explained the most variance, PC1 was used as a reduced soil characteristic metric in all analyses, and represents an axis of soil fertility, where more negative numbers are more fertile soils (higher base cations). In addition, we collected

burn data from site managers, specifically the number of years since the last burn (Appendix S1). Although the numbers of fires in the recent past or the fire-return interval would be more informative metrics to use as a potential predictor of understory dynamics (Veldman et al., 2014), longer-term fire data were unavailable across all study sites, and therefore the time since the last fire was used instead. To account for natural variation in vegetation across landscapes, each plot was grouped by ecoregion of North Carolina (Sandhills, Inner Coastal Plain or Outer Coastal Plain) and then MAP (mm) and average high and low temperature (°C) data per region was extracted from US Climate Data (<https://www.usclimatedata.com>).

### 2.3 | Vegetation metrics

Multiple vegetation metrics were calculated on two spatial scales. Dell et al. (2019) found that  $\beta$ -diversity (change in diversity between sampling units in an area), was maximized when sampling occurred at small spatial scales, and thus suggests that vegetation sampling should be done at 1-m<sup>2</sup> scales in LLP savannas to enhance sampling efficiency; however, larger spatial scales are likely to be extremely informative to public land restoration practitioners. Here, we focus on small spatial scales (1 m<sup>2</sup>) to accurately depict differences between communities within sites, as well as local spatial scales (25 m<sup>2</sup>) to better inform management. The measure of biodiversity in this study was plant species richness (S) and the measure of dominance is represented as the relative abundance (relative percent cover) of the dominant species, wiregrass (percent cover of wiregrass/total plant percent cover). Relative percent cover was used here as opposed to absolute cover to standardize the cover of wiregrass by the total cover in the plot, to accurately describe its dominance. These were calculated at both plot (1 m<sup>2</sup>) and site (25 m<sup>2</sup>) levels. For site-level calculations, we combined all plot species composition data into a single plot and then calculated the metrics (Appendix S1). Total above-ground biomass (g/m<sup>2</sup>) was calculated at the plot level by summing the weights of graminoid, forb and woody species. Site-level estimates were also created by taking the mean of all 25 plots within a site. To visualize the variability in these metrics across the two scales, histograms were created (Figure 2).

### 2.4 | Statistical analysis

Through preliminary analyses, we were able to narrow down our list of predictor variables to include relative wiregrass cover, litter biomass, species richness, LLP tree number, shrub stem number, PC1 for soil characteristics, understory light availability, soil-surface light availability, time (years) since fire and precipitation (mm). We focused on a small subset of the potential predictor variables that we collected to meet power requirements, because many of the variables covaried. To explore the importance of these potential predictors (see green boxes in Figure 3) of understory dynamics at small spatial scales (1 m<sup>2</sup>), we used path analysis conducted in IBM SPSS

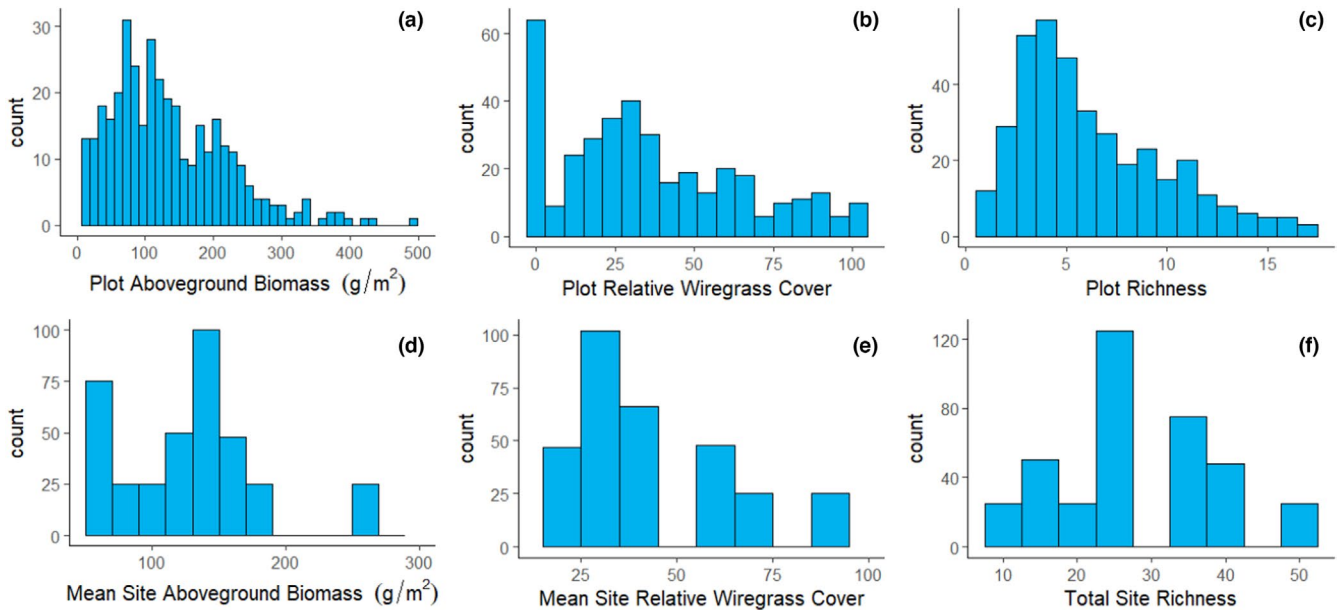


FIGURE 2 Variability in above-ground biomass ( $\text{g}/\text{m}^2$ ), relative wiregrass cover and species richness at small scales ( $1 \text{ m}^2$ ; a, b and c, respectively) and at local scales ( $25 \text{ m}^2$ ; d, e and f, respectively)

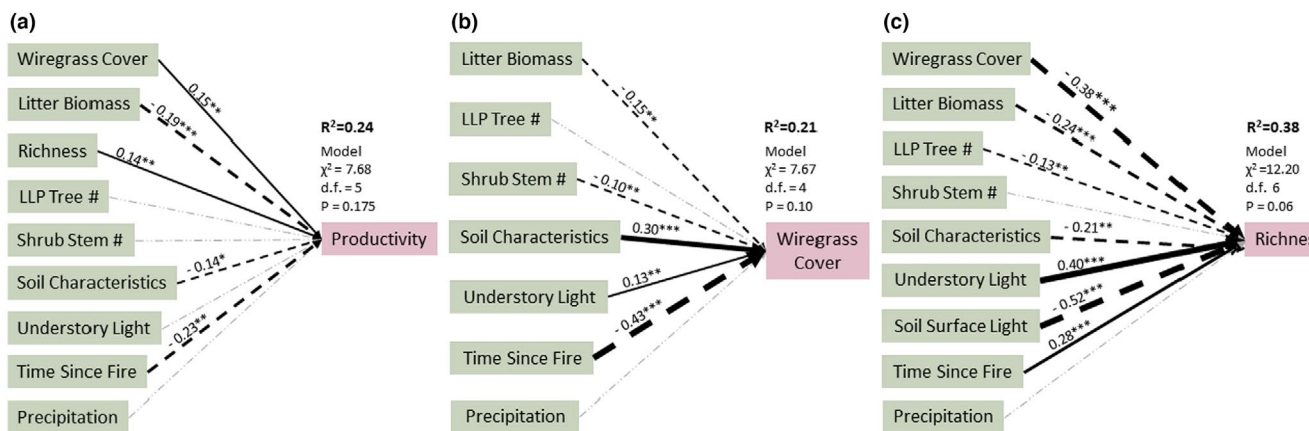


FIGURE 3 Path analyses testing the importance of potential predictors of (a) biomass, (b) dominant species (wiregrass) relative cover and (c) biodiversity (richness). \*\*\* $p < 0.001$ , \*\* $p < 0.05$ , \* $p < 0.10$ . Solid black arrows represent positive relationships, and dashed black arrows represent negative relationships. Standardized effect sizes are shown, with arrow thickness proportional to the strength of relationship. Non-significant relationships are shown using gray dashed arrows. Correlations between exogenous variables were included when necessary (Appendices S4–S6). All models were a good fit to the data based on the chi-squared statistic ( $p > 0.05$ ) as well as other measures of goodness-of-fit (Appendix S7)

AMOS version 28. All models also included hypothesized influential covariates, such as the characteristics of the plant community, the environment, and land management. Data were screened for distributional properties and nonlinear relations. Model 1 examined the relationship between potential predictor variables and above-ground biomass (Figure 3a). Model 2 examined the relationship between potential predictor variables and relative wiregrass cover (Figure 3b) and used the same data as Model 1 but without measures of richness. Model 3 examined the relationship between potential predictor variables and richness and was the same as Model 2 but included soil-surface light availability (Figure 3c). Several input

variables were correlated (based on AMOS recommendations for correlated variables that improve model fit), and therefore, were included in the models (Appendices S4–S6). All models were a good fit to the data, according to the chi-squared statistic with  $p > 0.05$  as well as other measures of goodness-of-fit (Appendix S7).

To further explore the inter-relatedness of above-ground biomass, relative wiregrass cover, and richness at the plot and site-level spatial scale, polynomial mixed effect regressions were used. For analyses at the site level, site was included as a random effect in the regression models to account for the inherent variation among the sampling sites across North Carolina. For these analyses, the

richness of woody species was excluded and only graminoid and forb species were used to calculate understory richness, as these are the species that contribute to the diversity of the ecosystem. The polynomial models were richness as predicted by above-ground biomass (Figure 4a), richness as predicted by relative wiregrass cover (Figure 4b) and above-ground biomass as predicted by relative wiregrass cover (Figure 4c).

IBM SPSS AMOS version 28 and R version 3.5.1 (R Core Team, Foundation for Statistical Computing, Vienna, AT) were utilized for all statistical analyses. Vegetation metrics were calculated using the 'community\_structure' and 'diversity' functions in the *codyn* (Hallett et al., 2016) and *vegan* (version 2.5-7, R Core Team, Foundation for Statistical Computing, Vienna, AT) packages, respectively. Mixed effect regressions were performed using the 'lmer' function in the package *lme4* (Bates et al., 2015), and polynomial regressions were performed using the 'lm' function in the *stats* package (R Core Team, Foundation for Statistical Computing, Vienna, AT).

### 3 | RESULTS

#### 3.1 | Variability in above-ground biomass, wiregrass cover and plant biodiversity

All three of the target metrics varied substantially at both the plot and site level, demonstrating that a large range of typical values can be found in North Carolina LLP savannas. Above-ground biomass varied from 0.0 to 493.8 g/m<sup>2</sup> across plots (Figure 2a) and from 63.76 to 258.03 g/m<sup>2</sup> across sites (Figure 2d). The relative cover of the dominant grass species, wiregrass, ranged from 0% to 100% at the plot level and from 0% to 85.46% at the site level (Figure 2b,e,

respectively), with most plots that contained wiregrass having ca. 30% relative cover (Figure 2b). Richness was also variable, ranging from 1 to 17 species per plot (Figure 2c), and from 10 to 49 total species per site (Figure 2f). In addition, the total plant species found at a regional scale (across all 15 study sites) was 143 (data not shown).

#### 3.2 | Predictors of above-ground biomass, wiregrass cover and plant biodiversity at the plot level

Approximately 24% of the variability seen in above-ground biomass was described by the measured variables (Figure 3a) with numerous abiotic and biotic variables showing significant relationships. Above-ground biomass is influenced predominantly by the time since last burn ( $r = -0.23$ ) and litter biomass ( $r = -0.19$ ), with both factors having a significant negative effect on productivity. Relative wiregrass cover ( $r = 0.15$ ) and richness ( $r = 0.14$ ) had significant positive effects on productivity, showing the importance of both the dominant species and biodiversity in driving above-ground biomass. Surprisingly, precipitation had no relationship with above-ground biomass, and soil characteristics ( $r = -0.14$ ) had a significant negative relationship with above-ground biomass.

Approximately 21% the variability seen in cover of wiregrass was described by our measured variables (Figure 3b). The dominant understory grass is influenced predominantly by time since last burn ( $r = -0.43$ ), with soil characteristics ( $r = 0.30$ ) also contributing significantly. Decreases in soil characteristics (e.g., base cations) positively influences wiregrass cover, and as time since fire increases, wiregrass cover decreases. Understory light availability ( $r = 0.13$ ) had a significant positive effect on wiregrass cover, whereas litter biomass ( $r = -0.15$ ) and shrubs ( $r = -0.10$ ) had significant negative

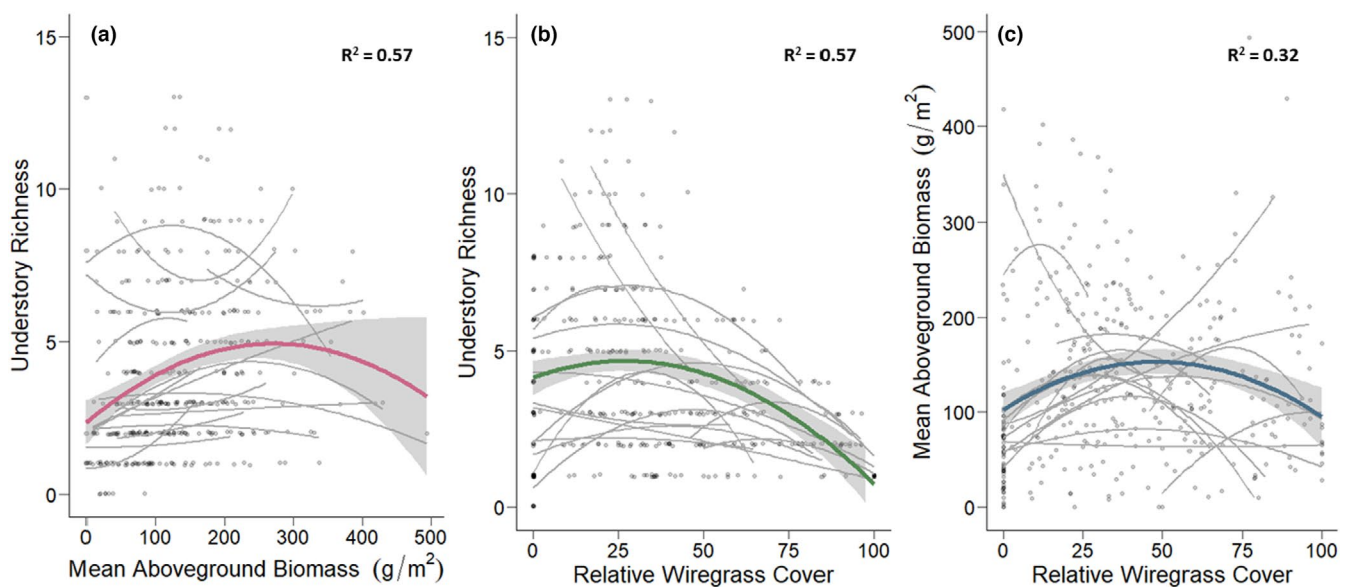


FIGURE 4 Relationship between above-ground biomass and understory richness (a), relative wiregrass cover and understory richness (b), and relative wiregrass cover and above-ground biomass (c) using polynomial regression. Thin gray lines represent the trends for each site ( $n = 15$ ), and the bold, colored lines represent the overall trend across sites. See Appendices S8–S11 for within-site trends



effects on relative wiregrass cover, probably due to their effects on light availability.

Approximately 38% the variability seen in richness was described (Figure 3c) with all of the measured variables except precipitation and shrubs playing a role in determining richness. This suggests that the factors influencing understory richness are quite complex. However, many of the important predictors relate to light availability. The most important factors were soil-surface light availability ( $r = -0.52$ ) and relative wiregrass cover ( $r = -0.38$ ), with both factors having a significant negative effect. Additionally, we found that factors that could affect soil-surface light availability, such as the number of LLP trees ( $r = -0.13$ ) and litter biomass ( $r = -0.24$ ), had significant negative effects on richness as well. Understory light availability ( $r = 0.40$ ) also had a strong significant effect on richness, but as understory light availability increases, so does richness in the understory. Lastly, richness was negatively influenced by soil characteristics ( $r = -0.21$ ).

### 3.3 | Inter-relatedness of above-ground biomass, wiregrass cover and plant biodiversity

Importantly, relationships between all three restoration targets were unimodal. At the site level, understory richness (graminoid + forb) was related to productivity as well as wiregrass cover with a hump-shaped curve most accurately describing the two relationships (Figure 4a and b, respectively). Richness peaked at 5 species per 1 m<sup>2</sup> at ca. 275 g/m<sup>2</sup> of above-ground biomass and ca. 25% relative cover of wiregrass. Of note, the relationship between relative wiregrass cover and understory richness ( $R^2 = 0.57$ ; Table 1) was the same as the relationship between primary production and understory richness ( $R^2 = 0.57$ ; Table 1). Lastly, the relationship between relative wiregrass cover and above-ground biomass was also best described by a hump-shaped curve, where above-ground biomass peaked at ca. 150 g/m<sup>2</sup> and at ca. 50% relative cover of wiregrass ( $R^2 = 0.32$ ; Table 1; Figure 4c). Interestingly, at the plot level within a site, there were very few significant relationships between the three target variables (Appendices S8–S11).

## 4 | DISCUSSION

Overall, we found that above-ground biomass, dominance and diversity varied significantly across study plots and sites within LLP savannas of North Carolina. Further, we identified several key factors (time since fire, light availability and soil characteristics) that strongly influence these restoration targets in a variety of ways, as well as how the targets influence each other. The understory dynamics in LLP savannas are complex, and many aspects of the understory are tightly intertwined, which complicates restoration of understory plant communities in this system. For many sites, especially those with higher levels of productivity, dominance and diversity, trade-offs exist between these three targets, and land managers will have

to prioritize which of the targets is most important for their specific LLP savanna understory.

### 4.1 | Natural variation seen in the three restoration targets across North Carolina

In this study, we found large variability in plant community characteristics and above-ground biomass across the 15 study sites. On average, our plots (1 m<sup>2</sup> average) and sites (25m<sup>2</sup> average) supported ca. 133 g/m<sup>2</sup> of above-ground biomass, which is lower than that found in other LLP sites in North Carolina (e.g., 216 g/m<sup>2</sup>, J. Walker & Peet, 1984; 145 g/m<sup>2</sup>, Mitchell et al., 1999), as well as sites like ours that receive a relatively large amount of precipitation, such as in the tallgrass prairie (e.g., 158–290.1 g/m<sup>2</sup>, Polley et al., 2005; ca. 377 g/m<sup>2</sup>, Nippert et al., 2006; 300–500 g/m<sup>2</sup>, Buis et al., 2009). In addition, maximum richness across plots occurred at ca. 275 g/m<sup>2</sup> above-ground biomass, similar to another North Carolina LLP savanna where understory richness peaked at ca. 280 g/m<sup>2</sup> (J. Walker & Peet, 1984). However, the majority of sites presented here have coarse, sandy soil that is very well-drained, leading to xeric conditions, potentially the reason for low productivity (above-ground biomass) that does not correspond with the MAP. Although above-ground biomass across these sites was lower than that of other studies, at the plot and site level, the average relative wiregrass cover (36%) was ca. 15% greater than what has been documented in the more southern range of wiregrass (Outcalt et al., 1999). Although the range in small scale richness (1–17 species) across plots was large, the study plots averaged six species per 1 m<sup>2</sup>, similar to a study from LLP savannas of North and South Carolina (Brudvig et al., 2013; Peet, 2006, respectively), which support fewer species compared with other studies conducted in southern Georgia (ca. 15 species per 1 m<sup>2</sup>; Hedman et al., 2000), Florida (ca. 22 species per 1 m<sup>2</sup>; Orzell & Bridges, 2006) and North Carolina (ca. 12 and > 40 species per 1 m<sup>2</sup>; Palmquist et al., 2015, J. Walker & Peet, 1984, respectively). At the local scale (25 m<sup>2</sup>), our sites supported an average of ca. 28 species, which is similar to what has been found at other sites in North and South Carolina (Brudvig et al., 2013; Palmquist et al., 2015; Peet, 2006), but at a larger scale (100 m<sup>2</sup>) than was used in this study. However, further down the latitudinal gradient of the LLP ecosystem, in Louisiana, richness at the 100-m<sup>2</sup> scale (100 species per 100 m<sup>2</sup>; Platt et al., 2006) is actually similar to that found at larger scales in other areas. Species area relationships within the LLP ecosystem have been addressed, with patterns of species richness being documented across a broad range of spatial scales, and as spatial scale increases, so does richness (Keddy et al., 2006; L. Kirkman & Myers, 2017; Palmquist et al., 2015; Peet, 2006). Although not studied here, richness at very small scales (0.01 and 0.1 m<sup>2</sup>) averages 2 and 5.6, respectively, and increases to an average of 65 species at larger spatial scales (1,000 m<sup>2</sup>; Peet, 2006; Palmquist et al., 2015). The pattern of increasing richness with spatial scale could be due to there being larger species pools at larger scales (Harms et al., 2017; Pärtel, 2002), unique species sets across edaphic gradients in the

**TABLE 1** Polynomial mixed effect regressions showing inter-relatedness of above-ground biomass, relative wiregrass cover, and biodiversity across all plots and sites. Significant p-values ( $P < 0.05$ ) are bolded

Metric	Predictor variable	Estimate	SE	t	p
Understory richness	Above-ground biomass				
	First order	3.301	2.235	1.477	0.141
	Second order	-4.437	1.937	-2.290	<b>0.023</b>
	Full model	Conditional $R^2$ : 0.571			
Understory richness	Relative wiregrass cover				
	First order	-8.594	2.695	-3.189	<b>0.002</b>
	Second order	-7.788	2.154	-3.656	<b>&lt;0.001</b>
	Full model	Conditional $R^2$ : 0.571			
Above-ground biomass	Relative wiregrass cover				
	First order	54.476	23.503	2.318	<b>0.050</b>
	Second order	-21.687	20.376	-1.064	0.171
	Full model	Conditional $R^2$ : 0.324			

landscape (Carr et al., 2009; Kirkman, et al., 2001, 2004), and peak propagule dispersal occurring across these heterogeneous landscapes (Shmida & Wilson, 1985). In addition, richness at both the 1- and 25-m<sup>2</sup> scales in this study was substantially lower than that documented in tallgrass prairie sites (Collins & Calabrese, 2012; Polley et al., 2005), which have similar precipitation and fire frequency as sites in this study.

## 4.2 | Predictors of the three restoration targets

Fire is an important factor, strongly influencing all three restoration targets, with more recent fire disturbances facilitating an increase in the dominant grass species and overall understory productivity. Shrubs in this system are able to assume dominance in the absence of fire (Beckage et al., 2009; D. G. Brockway & Lewis, 1997; Olson & Platt, 1995; Peet et al., 2018), whereas frequent fire decreases litter and the abundance of shrubs and other woody species, increasing light availability to the understory as well as at the soil surface. Relative cover of the dominant grass varied mainly in response to time since last burn, with sites that had an infrequent history of fire, and therefore a greater abundance of shrubs and pine needle litter in the understory, having less wiregrass abundance. Although many LLP savanna understory species can only establish and grow under frequent fire regimes (D. G. Brockway & Lewis, 1997) such as the dominant species, wiregrass (Streng et al., 1993), we found that understory richness actually benefitted from a longer time since fire disturbance. Longer intervals between fire disturbances may allow sensitive understory species, such as small forbs, to become established. Although an increase in time since fire benefitted richness in our model, the range in time since fire across sites was small, with most sites having <1 or 1 year post fire event. Therefore, it is not surprising that richness would increase over the year following the fire event, especially as pulses of seeds from the species pool could be increasing dispersal following fire disturbances (Harms et al., 2017; L. K. Kirkman et al., 2016; Peet et al., 2014). Alternatively, in sites with longer time since fire, such as 4 or 10 years, we would

expect richness to decrease as woody shrubs begin to dominate, and this trend has been documented in other studies (Beckage et al., 2009; Palmquist et al., 2014; Peet et al., 2018). Light availability to the understory positively impacted richness, but surprisingly, light availability at the soil surface negatively impacted richness. In other mesic grassland systems, light at the soil surface tends to be positively correlated with richness because it allows small understory forbs a chance to compete with larger tall grasses for light (Collins, 1987). In our study sites, light competition among understory species is potentially low, with bare spaces common. As more light reaches the soil surface, it often means there is less plant cover, and thus we hypothesize that is why there was lower richness.

Above-ground biomass was negatively influenced by our integrative soil metric (PC1), increasing with base saturation, Ca, Mg and Na, but decreasing with P. This indicates that above-ground biomass in this system is in part influenced by nutrient availability, which is highly correlated with base saturation (Fenn & Taylor, 1991). Increased richness was also correlated with an increase in base saturation and secondary nutrients (i.e., a decrease in PC1). Commonly, across southeastern North American vegetation types, soils rich in bases and higher in pH are strong predictors of plant species richness (Peet et al., 2003, 2014). Although base saturation has been found to be a weak predictor of richness compared with other environmental variables in Coastal Plain pine woodlands (Peet et al., 2014), here we found that across all soil characteristics measured, base saturation is the strongest predictor of richness. Nutrient additions frequently cause a decrease in species richness (Elser et al., 2007; Hautier et al., 2009), typically attributed to the corresponding increase in productivity and drop in light availability at the soil surface. However, in this case, nutrient levels are low overall, and the understory is sparse enough to allow light to the soil surface even at the more fertile end sampled. Surprisingly, unlike above-ground biomass and richness, wiregrass cover was positively influenced by our integrative soil metric (PC1), benefitting from decreases in base saturation and secondary nutrients (i.e., decreased soil fertility). In addition, increased Ca is associated with increased N as Ca enables ammonium absorption in plants (Fenn & Taylor, 1991), indicating that

because wiregrass benefitted from lower levels of nutrients such as Ca, wiregrass may also respond better to soils depleted in N. A similar response has also been documented in field fertilization studies where wiregrass biomass was not significantly different between control and nutrient enriched plots in either xeric or mesic sites (Ford et al., 2008; L. K. Kirkman et al., 2016). Additionally, in tall-grass prairies, the dominant grass, *Andropogon gerardii*, has also been found to perform very well in degraded, nutrient poor, sites (Scott & Baer, 2018) probably due to reduced competition because low soil nutrient availability limits other species, such as forbs. Potentially, wiregrass is in part dominant because it is able to outcompete individuals in a wider range of nutrient availability. Although wiregrass cover appeared to benefit from lower soil fertility, the contrasting effect on overall above-ground biomass could be that other common, less-dominant C<sub>4</sub> grasses (e.g., *Schizachyrium scoparium*) and small, woody species (e.g., *Vaccinium tenellum*, *Diospyros virginiana*, *Sassafras albidum* and *Quercus* species) fare better in higher pH soils enriched in base cations.

In addition to soil characteristics, water availability also strongly influences plant communities, with soil moisture often limiting plant growth. In LLP savannas, increased soil moisture (often attributed to elevation gradients and soil composition) is associated with increased productivity, wiregrass biomass and richness (Carr et al., 2009; Drewa et al., 2002b; Ford et al., 2008; L. K. Kirkman et al., 2001; Mitchell et al., 1999). Although it is well known that soil moisture availability can vary on the microhabitat scale and is strongly linked to soil texture and topography (Abrahamson et al., 1984; Moeslund et al., 2013; Silvertown et al., 1999), there is also a positive correlation between precipitation and soil moisture (Sehler et al., 2019); therefore, in this study, we used precipitation as a proxy for site-level differences in soil moisture. Although precipitation is a strong driver of productivity and richness across grasslands globally and in LLP savannas (Adler & Levine, 2007; Del Grosso et al., 2008; Knapp & Smith, 2001; Mitchell et al., 1999; O. Sala et al., 2012; O. E. Sala et al., 1988), as well as within sites across years (Huxman et al., 2004), we found no effect of MAP on the three restoration targets across our sites. We hypothesize that this lack of precipitation response is due to the fact that across all sites, there was relatively low variation in MAP (1,170–1,351 mm), and many of the patterns seen in grasslands span larger gradients in precipitation (e.g., 156–841 mm, O. Sala et al., 2012; 321–835 mm: Adler & Levine, 2007). Although factors such as elevation gradients and soil composition, texture and moisture are important edaphic factors influencing plant cover, richness and overall community composition (Carr et al., 2009; Drewa et al., 2002b; L. K. Kirkman et al., 2001; Mitchell et al., 1999; Peet, 2006; Peet et al., 2014), unfortunately, soil texture and moisture were not measured in this study. Within our xeric study sites, the unexplained variation in above-ground biomass, wiregrass cover and species richness (Figure 3) is probably due to differences in soil moisture. Although this is a major limitation of the study, it does allow us to focus on the remaining variation not explained by soil moisture in these characteristically dry sites. In fact, here we show that wiregrass cover, light availability, soil characteristics other than

texture and moisture, and time since fire are also important drivers of our restoration targets; all of which are more in the control of land managers. For example, land managers can manipulate how much wiregrass is planted in restorations, and how much light reaches the understory and soil surface through regular fire, overstory LLP thinning and herbicide treatment of woody shrubs.

### 4.3 | Inter-relatedness of the three restoration targets

In this study, we highlighted the three critical targets of a successful understory LLP restoration and explored their inter-relatedness. All three of our restoration targets were significantly related to each other across sites with a hump-shaped, concave curve. Productivity and diversity are frequently theorized to be related to each other, with some arguing that biodiversity promotes ecosystem function (i.e., increased richness should yield an increased productivity-positive relationship; Tilman et al., 2001; L. K. Kirkman et al., 2001; Adler et al., 2011), and others suggesting the opposite, that increased biomass causes a reduction in richness (negative relationship; Chalcraft et al., 2009; Gough et al., 2000; Rosenzweig, 1995; Waide et al., 1999) because biomass limits light availability and increases competition for resources (Hautier et al., 2009). Across large gradients and grasslands globally, the relationship between productivity and diversity is generally concave down (Fraser et al., 2015), with sites at the least and most productive ends of the gradient declining in diversity. Whereas a previous study looking across sites within the LLP ecosystem found a positive linear relationship (L. K. Kirkman et al., 2001), we found a hump-shaped curve similar to the global trend. Interestingly, however, although this relationship was significant, the strength of the relationship was quite weak, suggesting that across sites, productivity is neither causing decreases in richness nor is richness supporting higher levels of productivity, and in fact, in this system, these two factors may be slightly decoupled.

Richness instead was more strongly related to cover of the dominant species. Dominance is frequently theorized to cause a decrease in richness (Koerner et al., 2018; McNaughton & Wolf, 1970; Olff & Ritchie, 1998). Here we saw a hump-shaped curve. After ca. 25% wiregrass cover, as wiregrass cover continued to increase, we saw a decrease in richness because wiregrass likely utilized more soil resources with increasing abundance, limiting the growth of other understory species. Throughout the range of the LLP ecosystem, C<sub>4</sub> bunchgrasses dominate the groundcover (Peet, 2006). Many of these bunchgrasses, particularly wiregrass, have tussocks that are non-random, or over-dispersed across space (Hovanes et al., 2018). There are two proposed causes of over-dispersion of wiregrass. Either intraspecific competition for resources (e.g., light, water, nutrients) prevents tussocks from growing directly adjacent to each other, or the increased fuel accumulation between tussocks where the leaf blades overlap each other (Parrott, 1967) leads to increased soil heating, causing seedling death during fire in between tussocks (Gagnon et al., 2015; Hovanes et al., 2018). Over-dispersion of

species, in this case wiregrass, reduces the frequency of interactions among individuals of the same species and increases the frequency of interactions between the over-dispersed species (wiregrass) and other ground layer species (Hovanes et al., 2018). This mechanism, along with the direct heat during fires caused by wiregrass tussocks could explain why wiregrass cover has such a strong, negative effect on species richness in our model. Our dominant species also displayed a hump-shaped curve with above-ground biomass. At the low ends of wiregrass cover, we saw as cover increased so did overall above-ground biomass, but after ca. 50% cover, above-ground biomass decreased as wiregrass increased. Dominant species have strong effects on ecosystem productivity, with cascading effects on other ecosystem processes (Grime, 1998). Dominant species frequently contribute largely to ecosystem function (Smith & Knapp, 2003) and this appears to be the case in lower productivity LLP savannas, with an increase in dominance contributing to an increase in productivity, as wiregrass is a photosynthetically efficient,  $C_4$  bunchgrass. Although not tested here, we hypothesize that at the higher end of the productivity gradient, wiregrass competitively excludes other species decreasing niche complementarity of the system and thereby decreasing productivity (Olff & Ritchie, 1998). These hump-shaped relationships between all three restoration targets have large implications for LLP management across its range. Our results indicate that at lower productivity, wiregrass cover and richness, land managers can aim to increase all three restoration targets in the understory at the same time, because they are positively correlated with one another. However, at more diverse and productive sites, the restoration targets negatively impact each other, forcing restoration practitioners to prioritize one target or to find a balance between all three. Here we provide baseline data on LLP savannas in North Carolina so that land managers can put their sites into this broader context, helping them to determine if the focus of their restoration should be on a single restoration target or on enhancing all three.

#### 4.4 | Implications for restoration

The majority of LLP savanna is found on private land, with 62% of LLP-dominated stands range-wide being owned by non-industrial private landowners (Oswalt et al., 2012). Importantly, some of those private landowners restore LLP savanna, but typically this is not done at the landscape scale (Gordon et al., 2020). Smaller-scale restorations on private land occur for many reasons including owners having only a small tract of land or minimal resources to dedicate to restoration. In addition, private landowners may not be aware of cost-share programs for restoration, or they are only interested in restoring a portion of their land back to LLP. Therefore, information at smaller spatial scales—like that provided here—is crucial for private landowners desiring certain biodiversity targets on a small scale. Although this study is not representative of highly biodiverse, mesic LLP sites in North Carolina, such as those studied by J. Walker and Peet (1984), it does represent the most current

condition of LLP sites commonly found across North Carolina and spans three North Carolina ecoregions. Therefore, this study allows landowners to put their site into the broader context of LLP savanna across North Carolina and determine whether their goals for each of the three targets are reasonable and complementary. Managing LLP trees alone is not enough to bring back the biodiversity and complexity of the critical understory, without which LLP savanna cannot be maintained long-term unless heavily managed. Our work here suggests that the dominant understory species is critical and plays a large role in creating a productive understory—necessary for the spread of fire—as well as in understory richness. The dominant species frequently consumes the majority of resources, thereby controlling the resources left for the other species. Other studies in LLP-wiregrass communities have suggested that managers should encourage the dominance of wiregrass, because it is a non-competitive grass species (Myers & Harms, 2009; Roth et al., 2008), and would provide fine fuel for fire, thereby increasing richness and diversity (L. K. Kirkman et al., 2016). However, our study shows that this dominance is only beneficial up to a certain point. Therefore, field experiments and mechanistic studies are needed to determine the abundance of wiregrass at small spatial scales that is ideal for maintaining and enhancing biodiversity and to identify the restoration targets and determine the best strategies for restoration. Overall, this study provides a baseline of understory biodiversity and plant community dynamics for LLP savannas in North Carolina as well as a broad understanding of the factors that may control the variability seen at multiple spatial scales.

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#### AUTHOR CONTRIBUTIONS

ALY and SEK conceived and designed the experiments. ALY collected all data and performed all analyses. ALY and SEK wrote and edited the manuscript.

#### DATA AVAILABILITY STATEMENT

Data and code used for this study are available via GitHub ([https://github.com/alyoung6720/NC\\_LL\\_P\\_Variation\\_RestorationTargets\\_2018](https://github.com/alyoung6720/NC_LL_P_Variation_RestorationTargets_2018)).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**Appendix S1.** Study site locations, characteristics, and mean target metrics.

**Appendix S2.** Principal components analysis (PCA) plot of nutrient data across all 15 study sites.

**Appendix S3.** Percent contributions of soil characteristics to principal component axes.

**Appendix S4.** Correlated variables included in structural equation exploring the predictors of productivity.

**Appendix S5.** Correlated variables included in structural equation exploring the predictors of dominance.

**Appendix S6.** Correlated variables included in structural equation exploring the predictors of richness.

**Appendix S7.** Goodness-of-fit metrics for all structural equation models.

**Appendix S8.** Polynomial regressions showing inter-relatedness of biodiversity, dominance, and biomass.

**Appendix S9.** Plots of polynomial regressions showing the relationship between above-ground biomass and richness across sites.

**Appendix S10.** Plots of polynomial regressions showing the relationship between relative wiregrass cover and richness across sites.

**Appendix S11.** Plots of polynomial regressions showing the relationship between relative wiregrass cover and above-ground biomass across sites.

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