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Lidar-derived estimates of forest structure in response to fire frequency

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Abstract

Background Longleaf pine (*Pinus palustris*) ecosystems are recognized as biodiversity hotspots, and their sustainability is tightly coupled to a complex nexus of feedbacks between fire, composition, and structure. While previous research has demonstrated that frequent fire is often associated with higher levels of biodiversity, relationships between fire frequency and forest structure are more nuanced because structure can be difficult to measure and characterize. We expanded on this body of research by using lidar to characterize vegetation structure in response to fire frequency at a long-term prescribed-fire experiment. We asked (1) how does prescribed fire frequency affect structure and (2) how do structural metrics vary in the strength of their relationships with fire frequency.

Results Our results indicated that forest structure varied significantly in response to fire frequency, with more frequent fire reducing vegetation structural complexity. Metrics that characterized the central tendency of vegetation and/or the variance of canopy-related properties were weakly to moderately correlated with prescribed fire frequency, while metrics that captured the vertical dispersion or variability of vegetation throughout the forest strata were moderately to strongly correlated with fire frequency. Of all the metrics evaluated, the understory complexity index had the strongest correlation with fire frequency and explained 88% of the structural variation in response to prescribed fire treatments.

Conclusions The findings presented in this study highlight the usefulness of lidar technology for characterizing forest structure and that structural complexity cannot be fully characterized by a single metric. Instead, a range of diverse metrics is required to refine scientific understanding of the feedbacks between fire, composition, and structure in support of longleaf pine sustainability. Furthermore, there is a need for further research to broaden structural assessments beyond the overstory and incorporate more understory components, particularly within the realm of prescribed fire science and land management.

Keywords Controlled burns, Fire frequency, Laser scanning, Longleaf pine, Prescribed fire, Structural complexity, UAS, UAV, Understory complexity index, Wildland fire

Resumen

Antecedentes Los ecosistemas de pino de hoja larga (Pinus palustris) son reconocidos como focos de biodiversidad y su sustentabilidad está fuertemente ligada a un complejo nexo de retroalimentaciones entre fuegos, composición, y estructura. Aunque investigaciones previas han demostrado que fuegos frecuentes se asocian usualmente con altos niveles de biodiversidad, las relaciones entre la frecuencia de fuegos y la estructura forestal son variadas, dado que la

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estructura puede ser difícil de medir y caracterizar. Nos expandimos en este cuerpo de investigación mediante el uso del LIDAR para caracterizar la estructura de la vegetación en respuesta a la frecuencia del fuego, en un experimento de quemas prescriptas a largo plazo. Nos preguntamos (1) ¿cómo la frecuencia de las quemas prescriptas afecta la estructura? y (2) ¿cómo las medidas estructurales varían en la fortaleza de sus relaciones con la frecuencia del fuego?

Resultados Nuestros resultados indicaron que la estructura forestal varió significativamente en respuesta a la frecuencia del fuego, con fuegos más frecuentes reduciendo la complejidad estructural. Las medidas que caracterizaron la tendencia central de la vegetación y/o la variación de las propiedades relacionadas con el dosel fueron de débiles a moderadamente correlacionadas con la frecuencia de las quemas prescriptas, mientras que las medidas que capturaron la dispersión vertical o la variación de la vegetación a través del estrato forestal fueron de moderada a fuertemente correlacionadas con la frecuencia de las quemas. De todas las medidas evaluadas, el índice de complejidad del sotobosque presentó la correlación más fuerte con la frecuencia de las quemas, y explicó el 88% de la variación estructural en respuesta a los tratamientos de quemas prescriptas.

Conclusiones Los resultados presentados en este estudio enfatizan la utilidad de la tecnología LIDAR para caracterizar la estructura forestal, y que la complejidad estructural no puede ser caracterizada por una simple medición. En cambio, un rango de diversas medidas es requerido para refinar el entendimiento científico sobre las retroalimentaciones entre fuego, composición, y estructura, para consolidar la sustentabilidad del pino de hoja larga. Además, es una necesidad para futuras investigaciones, el ampliar las determinaciones de las estructuras más allá del dosel, e incorporar más componentes del sotobosque, particularmente dentro del dominio de la ciencia de las quemas prescriptas y el manejo de tierras.

Background

Decades of fire exclusion has disrupted natural fire regimes and led to dramatic shifts in the structure and function of many forested and non-forested landscapes globally (Loudermilk et al. 2022). These shifts are particularly pronounced in longleaf pine (*Pinus palustris* Mill.) ecosystems, which were historically characterized by frequent fires that maintained a structurally open habitat vital for both pine regeneration and maintaining the biologically rich understory community (O'Brien et al. 2008; Dell et al. 2017; Loudermilk et al. 2019). According to dendrochronology records, fire historically varied from 1 to 10 years with an average return interval of 2.2 years (Stambaugh et al. 2011). Today, less than 20,000 km^2 of longleaf pine remain, representing about 5% of the historical range (Oswalt and Guldin 2021). The remaining intact ecosystems include some of the most diverse plant communities outside of the tropics, with the richest tracts containing 900 types of plants and hundreds animal species, including 29 species federally listed as threatened or endangered (Walker and Silletti 2006). Given the enormous loss of this once dominant ecosystem, conservation and restoration efforts have become a priority, with non-governmental organizations leading the way in close partnership with federal agencies, private landowners, universities, and industry experts (Kirkman and Jack 2017; Bigelow et al. 2018). These collaborations have not only halted, but reversed the decades-long habitat decline and produced a wealth of integrated knowledge (McIntyre et al. 2018).

A key element of the region's success is the reintroduction of periodic fire. Frequent, low-intensity fires have an overall positive effect on longleaf pine during its various life stages due to numerous adaptations that facilitate fire spread in addition to protective traits, such as a grass-stage morphology, thick bark, and insulated buds (Wilson et al. 2022). However, seedlings are vulnerable to high intensity fire as well as competition for resources, making their regeneration and productivity in early developmental stages dependent on lowintensity fires to control competing vegetation and to maintain canopy gaps that facilitate light transmittance to the forest floor, which is vital for the germination and growth of longleaf pine seedlings (Palik et al. 2011). This nexus between fire intensity, resource competition, and canopy gaps plays a crucial role in facilitating seedling growth beyond the grass stage. Due to the region-wide exclusion of fire, conservation and restoration practitioners facilitate longleaf pine sustainability by managing the structure and composition of these forests with prescribed fire.

Previous research has demonstrated that fire return intervals of four years or less are needed to sustain an open canopy structure that is associated with higher levels of biological diversity (Mitchell et al. 2006; Loudermilk et al. 2011; Glitzenstein et al. 2012). However, measures of forest structure, or structural complexity, can vary widely depending on the methods and scale of analysis. Traditional field-based monitoring campaigns, for example, tend to focus on structural attributes (e.g., species, height, diameter, crown spread) that can be readily measured or estimated in the field (Smith 2002).

However, field-based assessments require significant initial setup, are time consuming and costly, vulnerable to data collection and entry errors, and are not fully reproducible because such evaluations often rely on some degree of subjective interpretation by observers. As such, there is substantial interest in developing and applying more efficient, reproducible, and scalable methodologies for vegetation monitoring (Pokswinski et al. 2021).

The utilization of remote sensing technologies for measuring and monitoring vegetation structure to evaluate land management and sustainability goals is advantageous in the sense that the methods can be replicated in a systematic and standardized manner (White et al. 2016). Moreover, remote sensing technologies offer economies of scale, with data often becoming less expensive as the area of interest increases (White et al. 2016). Advances in remote sensing, specifically light detection and ranging, or lidar, have enabled the mapping of forest structure with unprecedented precision. Utilized across a diverse array of landborne, airborne, and spaceborne platforms, lidar has refined scientific understanding of structural attributes across a variety of spatial scales, including fine-scale mapping and monitoring of surface fuels (Hiers et al. 2009; Loudermilk et al. 2012), stand-level mapping of canopy structure and individual tree attributes (Silva et al. 2016; Ross et al. 2022; Traylor et al. 2022; Sánchez-López et al. 2023), and large-scale assessments of structure and aboveground biomass (Karna et al. 2020; Silva et al. 2021; Ross et al. 2021; Ceccherini et al. 2023).

To date, most lidar-derived assessments of forest structure have been conducted with aerial laser scanning systems (ALS) due their ability to rapidly retrieve submeter resolution information across large spatial scales. However, sub-canopy vegetation is difficult to detect and characterize with airborne lidar because of the relatively low-density point clouds in addition to occlusion from the overstory, which can artificially skew the distribution of lidar-detected vegetation towards the overstory (Ross et al. 2022). As such, the accuracy of sub-canopy structural measurements varies across studies. Moreover, indices that characterize the distribution and structure of understory vegetation have received comparatively less attention (Jarron et al. 2020), but are important for evaluations of forest structure in response to prescription burning because fire effects are most prominent in the understory and forest floor.

Unmanned aerial vehicles (UAV) equipped with lidar are increasingly utilized to address such limitations, improving the ability to measure understory vegetation in areas where conventional remote sensing approaches faced limitations (Hämmerle et al. 2017; Kuželka and Surový 2018; Hernandez-Santin et al. 2019). The increased spatial resolution afforded with UAV laser scanning (ULS) is crucial for pushing the boundaries of scientific knowledge at fine scales, surpassing the capabilities of conventional aerial or satellite imagery (Shrestha et al. 2021; Zhou et al. 2022). Moreover, UAV integration in the wildland fire sciences extends beyond remote sensing applications, and is increasingly used to conduct aerial ignitions for both prescribed fire and wildfire operations, highlighting its multifaceted role in advancing forest management practices (Lawrence et al. 2023). However, few studies have utilized randomized and replicated experimental designs to investigate relationships between fire frequency and forest structure, due in part to the complexities and barriers of conducting controlled burns in addition to the challenges associated with measuring forest structure. Collaborative efforts among interdisciplinary teams, including ecologists, wildland fire crews, and remote sensing scientists are needed to refine scientific understanding of these relationships.

The overarching objective of this study was to investigate relationships between fire frequency and forest structure in a frequently burned longleaf pine ecosystem. Specifically, we wanted to answer two questions: (1) how does prescribed fire applied with varying frequency affect structure and (2) how do structural metrics vary in the strength of their relationships with fire frequency.

Methods

Site description

Established by the USDA Forest Service Southern Research Station in 1957, the Osceola fire experiment is one of the longest running of its kind in the world. The study site covers approximately 20-ha within the Olustee Experimental Forest, which is part of the Osceola National Forest located in northeast Florida, USA (Fig. 1). Although the fire history prior to the establishment of the study was not recorded, application of dormant season backfires (i.e., burning against the wind) every 4–6 years was a common component of land management practiced by the local community. The native stand of longleaf pine (*Pinus palustris* Mil.) was clearcut in the early 1900s, coinciding with WWI and an increased demand for naval stores (Snitker et al. 2022a). The forest was restocked primarily in longleaf and some slash pine ca. mid-century. Records indicate that the stand age was 45 years, tree height averaged 20 m, and diameter at breast height (DBH) averaged 28 cm when the experiment was established. With elevational differences less than 1 m, the landscape is flat and referred to as flatwoods and/or pine savannas. The midstory vegetation native to longleaf pine varies depending on landscape position and soil moisture conditions. In the Osceola study, shrubs tend to dominate the understory, being primarily of gallberry

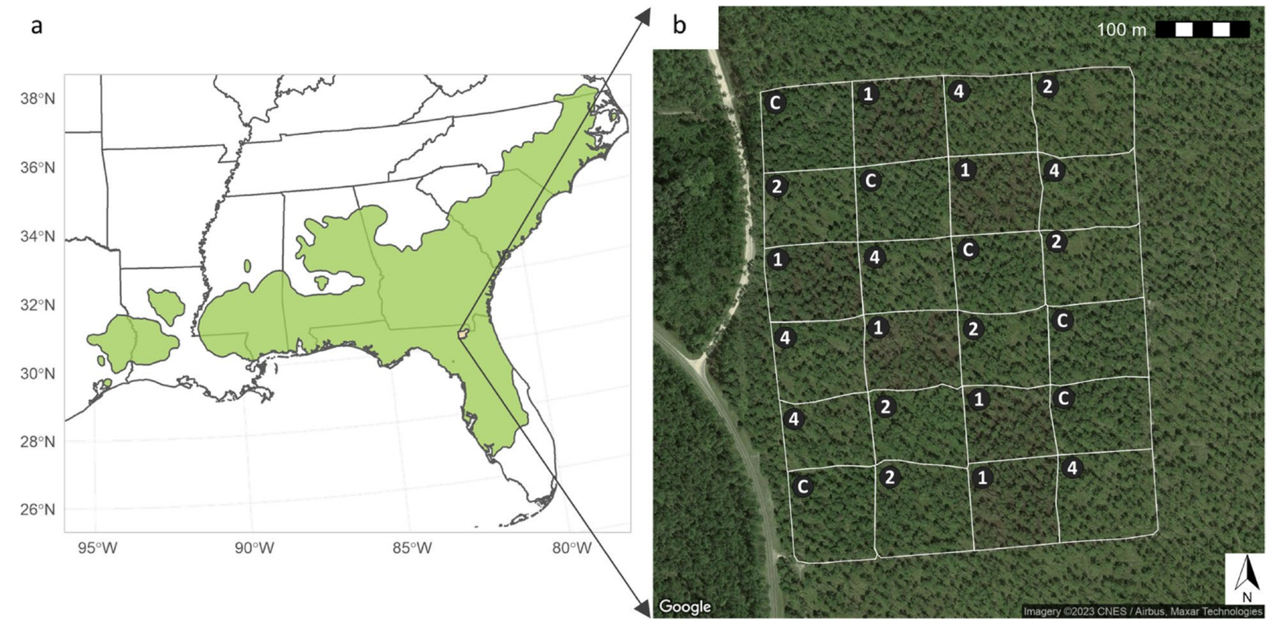

Fig. 1 The Osceola study. **a** Location of the study site within the Osceola National Forest (tan) in North Central Florida, USA. The map also depicts the native range of longleaf pine (green) and **b** the prescribed fire treatment plots—white lines represent fire control lines, 1, 2, and 4 correspond to annual, biennial, and quadrennial burns, C corresponds to the check plots (i.e., fire exclusion)

(*Ilex* spp.), wax myrtle (*Morella cerifera*), and saw palmetto (*Serenoa repens*).

Experimental design

The experimental design consists of a completely randomized design with 6 replications of each fire frequency treatment (unburned, annual, biennial, and quadrennial fire) in a longleaf pine ecosystem, with a mean plot size of 0.85 ha. Strip-head fire is applied to the plots during the dormant season as the treatment and fire is excluded from the check plots. Prior to the studies initialization, a backfire was applied to all plots (including check plots) in the winter of 1958–1959 to establish a baseline for analyzing treatment effects on successional dynamics.

Data collection and preprocessing

Vegetation was measured using discrete-return light detection and ranging (lidar) affixed to an unmanned aerial vehicle (UAV) in February of 2022, 1 day prior to first ignition. The lidar sensor was a Zenmuse L1 affixed to a DJI Matrice 300 RTK. Acquisition height was 100 m using repetitive scanning to capture three returns, operating at a frequency of 160 kHz. Flight speed was 5.4 m per second, using a flight line overlap of 50%. The resulting point cloud had an average density of 1,178 returns per m^2. Using the R lidR package (Roussel et al. 2020), pre-processing steps included removal of point-cloud noise (outliers) using one pass with statistical outliers removal (SOR) algorithm and one pass with the isolated voxels filter (IVF), classification of ground returns using cloth simulation function (csf) with a class threshold of 0.1 m, cloth resolution = 0.1 m, and rigidness of 3 (i.e., flat) with k-nearest neighbors (KNN) inverse-distance weighting (IDW) for height-normalization of the point cloud such that the elevation of ground returns correspond to zero meters. The point cloud was then voxelized using a 0.05 m resolution, resulting in a density of ca. 398 voxels per m^2.

Estimation of structural attributes

With the exception of canopy cover, vegetation structural attributes were characterized from a height-normalized and voxelized point cloud using a voxel resolution of 0.05 m. The lidR pixel metrics function was used with the equations described below to produce gridded maps with a horizontal resolution of 1 m^2. Structural metrics were then calculated for each treatment group. Each raster map was clipped prior to calculating plot-level metrics to avoid "edge effects" and/or gaps at or near fire control lines and roads. This was performed by first determining the centroid of each treatment unit and then adding a 30 m circular buffer around the centroid. Summary statistics for the structural complexity metrics were derived by averaging across each circular plot, grouped by treatment frequency.

Canopy cover

Canopy cover was estimated from the voxelized point cloud in a similar manner as described by Ross and colleagues (2022) using a voxel resolution of 0.25 m. Voxels with height values < 1.4 m were excluded from the calculation of canopy cover (Eq. 1). Briefly, canopy gaps were estimated from the voxelized point-cloud data at each burn unit by extracting the coordinate (X, Y, and Z) information into a data frame. Voxels with spatially coincident X and Y coordinate values were filtered from the data frame using the dplyr "distinct" function. We used 0.25 m voxels for this calculation, as ALS-derived canopy cover estimates at this resolution were shown to have the best agreement with digital hemispherical photography (Ross et al. 2022).

$$Canopy\ cover = Lv^2/\pi * r^2 \tag{1}$$

where Lv is voxel side length (i.e., resolution) in point cloud units (e.g., 0.25 m), and πr^2 is the circular area of the transect with radius r (30 m).

Canopy relief ratio

Canopy relief ratio is used to quantify the vertical variation or roughness of a forest canopy and describes the degree to which canopy surfaces are in the upper (CRR > 0.5) or in the lower (CRR < 0.5) portions of the height Range (Torresan et al. 2016). A higher canopy relief ratio is considered to have a more complex or rugged canopy structure, while a lower ratio reflects a relatively uniform or even canopy. In this study, CRR was calculated from the height normalized point cloud by dividing the difference between the maximum and minimum height values by the average height (Eq. 2).

$$CRR = (Z_{max} - Z_{min}/Z_{mean}) \tag{2}$$

where Z_{max}, Z_{min}, and Z_{mean} is the maximum, minimum, and mean heights of the lidar returns.

Foliar height diversity

Foliar height diversity refers to vegetation variation or diversity in the vertical distribution of a forest canopy. It represents the range or spread of leaf or foliage positions along a vertical profile (Eq. 3).

$$FHD = -\sum p_i log_e p_i \tag{3}$$

where pi = proportion of horizontal vegetation coverage in the ith layer.

Top rugosity

Top rugosity (R_T), or surface rugosity, is the standard deviation of maximum canopy height and is often used to characterize differences in canopy heterogeneity during forest stand development or after disturbance events. Top rugosity was calculated according to Eq. 4.

$$R_T = sd(Z_1) \tag{4}$$

where sd is standard deviation and Z_1 is the lidar first returns.

Vertical distribution ratio

The vertical distribution ratio (VDR) quantifies the proportion of vegetation present in different height strata or layers within the vertical profile of the forest and was first used to associate vegetation structure with bird species diversity (MacArthur and MacArthur 1961). In older forests, for instance, the VDR may indicate a more stratified canopy structure with distinct vertical layers of biomass or foliage. In contrast, VDR may be more evenly distributed across the vertical strata in younger or more even-aged forests. VDR was calculated according to Eq. 5.

$$VDR = (Z_{max} - Z_{med}/Z_{max}) \tag{5}$$

where Z_{max} and Z_{med} are the maximum and median lidar returns.

Vertical complexity index

Vegetation vertical complexity was characterized using the vertical complexity index (VCI) as implemented in the R lidR package, which is a fixed normalization of entropy across user defined height bins (van Ewijk et al. 2011; Roussel et al. 2020). We calculated VCI for the entire vertical profile using 1 m height bins and a horizontal grid resolution of 1 m^{-2} (Eq. 6). Regarding its interpretation, understory complexity approaches 1.0 as vegetation structure becomes more homogeneously distributed throughout the forest strata, and approaches 0.0 as it becomes more heterogeneous, or stratified.

$$VCI = (-\sum_{i=1}^{\text{HB}} [(p_i * \ln(p_i)]))/\ln(\text{HB}) \tag{6}$$

where HB is the total number of height bins, and p_I is the proportional abundance of lidar returns in height bin i.

Understory complexity index

The structural complexity of the understory was calculated in this study by limiting the height in p_I of Eq. 6 to 3 m. Additionally, 0.25 m height bins were utilized, rather than the default of 1 m, to characterize fine scale heterogeneity of understory vegetation.

Statistical testing

The Kruskal-Wallis test, as implemented in R, was used to determine if the frequency of prescribed fire treatments has an effect on vegetation structure (R Core Team 2023). The null hypothesis of the Kruskal-Wallis test assumes that the mean ranks of the groups originate from the same distribution. Kruskal-Wallis is often referred to as a one-way ANOVA on ranks; however, the test is nonparametric and does not assume a normal distribution of the underlying data. Kruskal-Wallis is therefore more suitable for analysis of environmental data, which often do not meet assumptions of normality and may contain outliers. It is more appropriate to use ranks rather than actual values as to avoid the test being affected by the presence of influential outliers and/or by non-normally distributed data. While the Kruskal-Wallis test indicates whether or not significant differences exist between groups (i.e., treatments), it does not indicate which groups are significantly different. Therefore, post hoc multiple comparisons were performed with the pairwise Wilcoxon rank sum test to calculate pairwise comparisons between treatments, indicating which of the groups, if any, were significantly different. Bonferroni correction was used to correct for family-wise errors that can occur with multiple comparisons, which sets the alpha value (α) for the entire number of comparisons (n) equal to alpha by taking the alpha value for each comparison equal to α/n.

Results

Both the vertical and horizontal distribution of lidar-detected vegetation varied considerably within and between treatment groups; however, the majority of this variability occurred within the understory as shown in the point-cloud cross section of Fig. 2a. The vertical distribution of vegetation, characterized from the point cloud using probability density estimation, shows that the distribution of vegetation becomes increasingly bimodal (i.e., more stratified) in response to less frequent fire (Fig. 2b). In the plots subjected to fire treatment, most of the vegetation was distributed within the overstory. Conversely, a substantial amount of vegetation is distributed within the understory of the fire exclusion plots. This phenomenon is further demonstrated by the vertical complexity index (Fig. 2c), illustrating that vegetation structure becomes increasingly complex and dense in response to less frequent burning.

Vegetation height

Dominant tree height averaged 29 ± 0.7 m (± one standard deviation) across the entire study area but showed little variation within or between treatment groups and had no discernible response ($R^2 = 0.04$) to fire frequency (Fig. 2d). Most of the variation regarding dominant tree height occurred in the fire exclusion plots, but significant differences were not detected ($P = 0.96$) between any of the treatment groups. Mean vegetation height (19 ± 3 m, Fig. 2d) had a discernible response and decreased in response to less frequent burning. Mean vegetation height (19 m) in the annual burn plots was significantly higher ($P = 0.013$) than the 2-year, 4-year, and check plots and decreased in response to less frequent burning by 23%, 32%, and 39%, respectively. Post hoc multiple comparisons with the pairwise Wilcoxon rank-sum test indicated that significant differences were detected between the 2-year burns and the fire exclusion plots ($P = 0.01$) but were not detected between the 2-year and 4-year plots ($P = 0.55$) or between the 4-year plots and the fire exclusion plots ($P = 0.99$). Variance was lowest in the annual burns and increased as the distribution of understory vegetation increased in response to less frequent fire.

Canopy cover

Mean canopy cover (61 ± 11%) varied considerably both within- and between-treatment groups (Fig. 2e). Canopy cover was largest in the fire exclusion plots (74 ± 4%), which was significantly greater than the 1-, 2-, and 4-year treatments ($P = 0.01$). While canopy cover was lowest in the 2-year plots (50 ± 9%), significant differences were not detected amongst the fire treated plots. While similar trends were observed when considering just the overstory vegetation (> 12 m), significant differences were not detected between any of the treatment groups. Overstory canopy cover was again lowest in the 2-year burns (50 ± 9%), followed by the 4-year (55 ± 7%), fire exclusion plots (61 ± 7%), and the annual burns (62 ± 5%).

Canopy relief ratio

Canopy relief ratio (CRR) averaged 53 ± 8% across the study area and decreased in response to less frequent burning ($r = -0.56$). CRR was highest in the annual burn plots (65 ± 3%) and decreased to 45 ± 4% in the fire exclusion plots (Fig. 2f). According to the post hoc comparisons, CRR in the annual burns was significantly greater than CRR in the 2-year ($P = 0.002$) and 4-year burns ($P = 0.002$) as well as the fire exclusion plots ($P = 0.002$). CRR in the 2-year plots was significantly greater than the fire exclusion plots ($P = 0.01$) but did not differ significantly from the 4-year plots ($P = 0.13$). The 4-year plots did not differ significantly from the fire exclusion plots ($P = 0.09$).

Foliar height diversity

Foliar height diversity (FHD) averaged 247 ± 19 across the study. In the fire treated plots, FHD exhibited a nearly linear decline as the frequency of fires decreased (Fig. 2g). However, foliar height diversity was greatest in the fire exclusion plots (268 ± 11), which yielded an overall positive correlation ($r = 0.6$) with fire frequency. While foliar height diversity in the annual burns did not differ significantly from the 2-year burns ($P = 0.09$) or the fire exclusion plots

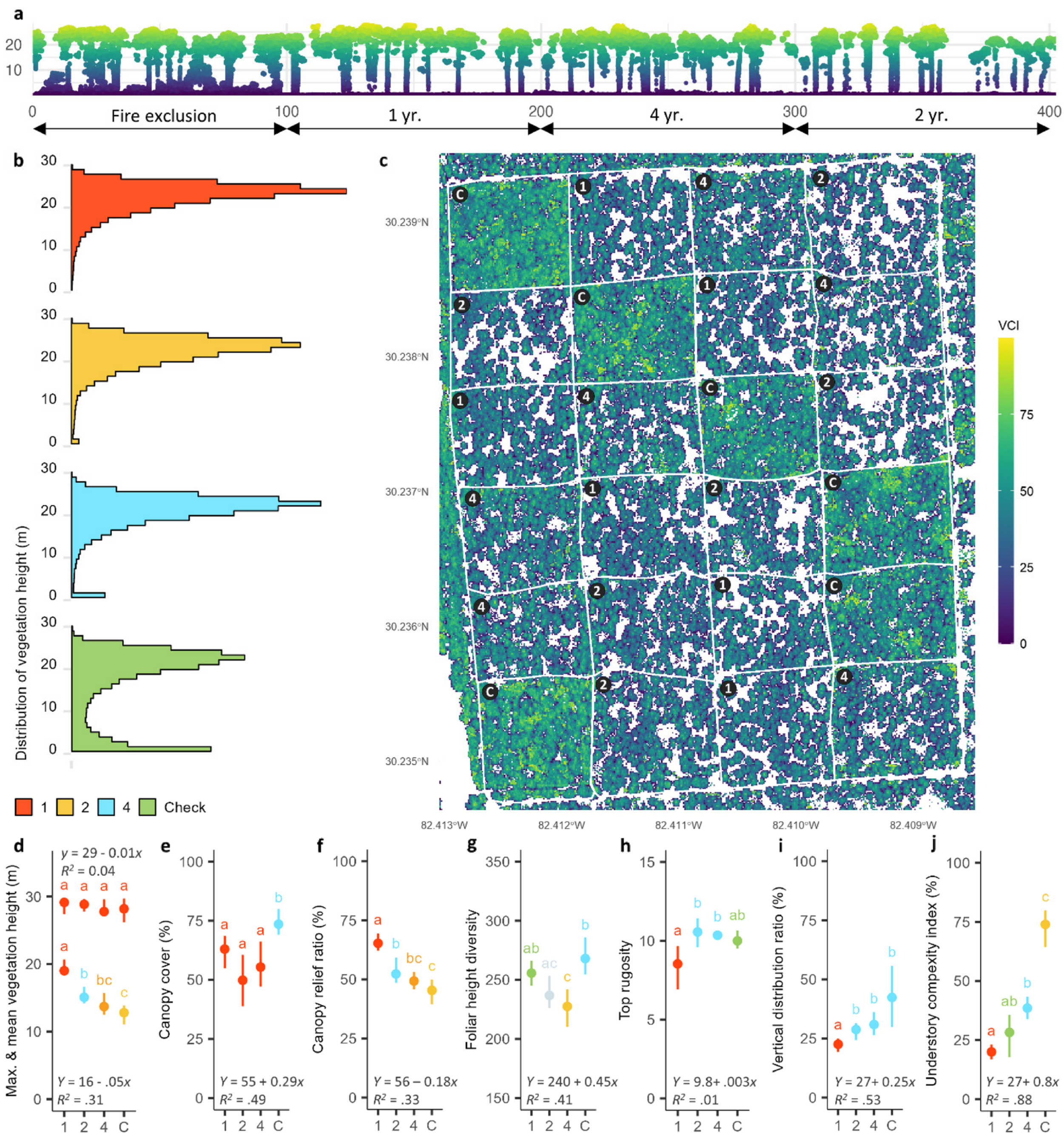

Fig. 2 Lidar-derived vegetation metrics. **a** Cross-section of the height-normalized point cloud depicts the within- and between-treatment heterogeneity of vegetation. **b** Probability density estimates of vegetation vertical distribution. **c** Map of vertical complexity index (VCI) illustrates horizontal and vertical variation of vegetation. **d** Maximum and mean vegetation height. **e** Canopy cover. **f** Canopy relief ratio. **g** Foliar height diversity. **h** Top rugosity. **i** Vertical distribution ratio. **j** Understory complexity index. The colors and letters of the point-range plot (**d** – **j**) signify statistically significant differences among treatment groups, each denoted by distinct groupings

($P=0.25$), it was significantly greater than the 4-year burns ($P=0.01$). In the 2-year burns, foliar height diversity was significantly lower than the fire exclusion plots ($P=0.01$) but not significantly different from the 4-year burns ($P=0.79$). Foliar height diversity in the 4-year burns was significantly lower ($P=0.01$) than in the fire exclusion plots.

Top rugosity

Top rugosity, or surface rugosity, averaged 10 ± 1 across all treatment groups and varied the most in the annual burns (Fig. 2h). No meaningful trends ($r = 0.1$) were detected in response to fire frequency; however, post hoc comparisons indicated that top rugosity in the annual burns (9 ± 1) was significantly lower than the 2-year (11 ± 1) and 4-year burns (10 ± 0.2) but did not differ significantly from the fire exclusion plots (10 ± 0.4). The 2- and 4-year plots did not differ significantly from the fire exclusion plots.

Vertical distribution ratio

The vertical distribution ratio (VDR) and variation around the group means (32 ± 9) showed a discernible response ($r = 0.73$) to the treatments, increasing as fire frequency decreased (Fig. 2i). Post hoc comparisons indicated that VDR in the annual plots (23 ± 2) was significantly lower than VDR in the 2-year (29 ± 3, $P = 0.02$) and 4-year plots (31 ± 4, $P = 0.01$) as well as the fire exclusion plots (42 ± 11, $P = 0.01$). Significant differences between the 2-year, 4-year, and fire exclusion plots were not detected.

Vertical complexity index

The vertical complexity index, or VCI, averaged 77 ± 5% across the study site and showed similar trends as FHD, where it decreased in the fire treated plots but was greatest ($P \leq 0.02$) in the unburnt fire exclusion plots. VCI differed significantly between the 1- and 2-year plots ($P = 0.02$) as well as the 1- and 4-year plots ($P = 0.01$), but significant differences were not detected between the 2- and 4- year plots ($P = 0.9$).

Understory complexity index

The understory complexity index (UCI) had the strongest correlation with fire frequency ($r = 0.94$) and increased as fire frequency decreased (Fig. 2j). Understory complexity was greatest (74 ± 6%) in the fire exclusion plots where it differed significantly from the 1-year (20 ± 2%, $P = 0.01$), 2-year (28 ± 7%, $P = 0.01$), and 4-year plots (39 ± 4%, $P = 0.01$). Significant differences were not detected between the 1- and 2-year plots ($P = 0.39$) or the 2- and 4-year plots ($P = 0.09$). However, significant differences were detected between the 1- and 4-year plots ($P = 0.01$).

Discussion

By leveraging a randomized and replicated experimental design, we systematically quantified structural variation in response to six decades of prescription burning under multiple fire return intervals. Our work contributes to a general understanding of longleaf pine sustainability in the context of prescribed fire effects on forest structure in three ways. First, we demonstrate how decades of prescribed fire has shaped the structural distribution of vegetation. Second, we show that prescribed fire effects differ significantly between treatment groups of fire return interval and that these effects are primarily limited to the understory. Third, lidar-derived metrics vary widely in their ability to detect structural differences in response to prescription burning.

In general, metrics that characterized the central tendency of vegetation and/or variance of canopy-related properties were weakly to moderately correlated with prescribed fire frequency, indicating that such structural characteristics were not strongly influenced by prescribed fire frequency. Conversely, metrics that captured the vertical dispersion or variability of vegetation throughout the forest strata were moderately to strongly correlated with fire frequency, indicating that fire frequency played a significant role in shaping the structural distribution of vegetation, particularly in the understory. Measures of dispersion outperformed those of central tendency because they better characterized the overall distribution of vegetation in response to treatment frequency. These findings support those reported by Atchley et al. (2021), who found that the inclusion of vegetation heterogeneity improved simulations of wildland fire spread by providing a more accurate representation of real-world conditions, allowing for a better understanding of how spatial variability influences wind entrainment and fire behavior.

Of the nine metrics tested in this study, the understory complexity index had the strongest positive correlation with fire frequency, explaining 88% of the structural variation when using ordinary least squares regression. The understory complexity index outperformed the other structural metrics in this analysis by utilizing 25 cm height bins to focus on the fine-scale structural variation within the understory (< 3 m), where prescribed fire effects are most prominent. The vertical distribution ratio, which ranked second in performance, primarily captures the variability within the overstory and midstory strata (Eq. 5). As such, VDR explained just 53% of the structural variation because frequent, low-intensity fires primarily consume herbaceous understory plants close to the ground (O'Brien et al. 2009).

Structure and biodiversity

Because frequent fire limited the establishment of shrubs and other woody vegetation to the understory, the distribution of vegetation in the fire treated plots was skewed towards the overstory, resulting in significantly lower understory complexity when compared with the fire exclusion plots. Moreover, there was a noticeable transition from herbaceous to woody dominated communities as fire frequency decreased (Ross, personal observation), which resulted in the development of an increasingly complex understory attributable to distinct structural differences. The annual plots, for example, are distinguished by a reduced dominance of *Serenoa repens* and a comparatively greater abundance of forbs and grasses but saw palmetto and other woody plants increase in abundance as fire frequency decreases to 2- and 4-year intervals (Glitzenstein et al. 2003). Exclusion of fire in the check plots has resulted in a distinct bimodal distribution, facilitating the development of relatively dense understory strata consisting mainly of shade-tolerant woody vegetation, such as *Quercus*.

While this study did not assess species composition, Glitzenstein and colleagues (2003) reported that species richness at the Osceola study decreased linearly as fire frequency decreased, suggesting that species richness is inversely related to structural complexity in frequently burned longleaf pine ecosystems. These findings contrast with conclusions drawn from previous studies conducted in other ecosystems, where species richness has been shown to increase as canopy structural complexity increases (Atkins et al. 2018; LaRue et al. 2019; Walter et al. 2021). Forests characterized by higher species diversity, for example, are more likely to have different growth forms represented, resulting in higher structural complexity.

In contrast, the Osceola study exhibits a relatively homogenous canopy structure, with most of the diversity concentrated within the understory. This is primarily attributed to an abundance of herbaceous ground cover species that promote the spread of fire (Walker and Silletti 2006). Even minor reductions in fire frequency in hydric flatwoods, such as the Osceola study, allows woody shrubs to increasingly dominate the understory and, given enough time, competitively exclude grasses and forbs. Among the plants most sensitive to decreases in fire frequency, and therefore changes in structure, are various groups of hydric indicator species, including small rosette forbs and sedges, *Orchidaceae*, and insectivorous plants (Glitzenstein et al. 2003). In fact, fire exclusion in longleaf pine ecosystems has led to localized extirpations of keystone species, including the red-cockaded woodpecker (*Picoides borealis*) and the gopher tortoise (*Gopherus polyphemus*), both of which require structurally open habitat (Walters 1991).

Previous studies have also demonstrated that (1) canopy cover typically increases in longleaf pine ecosystems in response to less frequent fire and (2) canopies begin to close (> 90% cover) when fire return intervals increase beyond 2 years (Glitzenstein et al. 2012). Apart from the 1-year treatment group, canopy cover trends from this study generally agree with the aforementioned findings. However, maximum canopy cover did not exceed 80% in any of the plots, while mean canopy cover in the fire-treated plots showed a nonlinear u-shaped response to fire frequency. The study by Glitzenstein et al. relied on a spherical densiometer for ocular estimates of canopy cover in subplots, while this study utilized a voxelized lidar point-cloud to estimate canopy cover at the plot level by considering all vegetation greater than 1.4 m aboveground (Eq. 1).

While it is possible that methodological differences could account for this discrepancy, canopy cover differences between the two studies are likely explained by variation in the spatial arrangement of restocking patterns, as the native stand of longleaf pine (*Pinus palustris* Mil.) was clearcut in the early 1900s, coinciding with WWI and an increased demand for naval stores, such as turpentine, tar, pitch, and rosin (Snitker et al. 2022a). Furthermore, the midstory of the Stoddard Fire Plot study (Glitzenstein et al. 2012) is dominated by broad leaved hardwoods such as turkey oak (*Quercus laevis*), sand live oak (*Quercus geminata*), and running oak (*Quercus pumila*) due to the mesic site conditions comprised primarily of clay soils (e.g., Ultisols). Conversely, gallberry (*Ilex* spp.), saw palmetto (*Serenoa repens*), and other short statured woody shrubs tend to dominate sites with hydric soil conditions, such as the Osceola study. In fact, soil moisture rather than fire frequency has been shown to be the dominant mode of variation for cover within the understory at the Osceola experiment (Glitzenstein et al. 2003).

Implications for monitoring and future research

The results of this study have important implications for our ability to effectively detect and characterize fine-scale structural differences in response to prescription burning as well as forest monitoring programs. Land managers, for example, are often mandated to engage in monitoring activities within the areas under their care. Monitoring data is commonly utilized to evaluate shifts in ecological processes or the impacts of management practices, such as prescribed fire. Although these data are often used to gauge the success of management efforts and identify future needs, establishing and maintaining an effective monitoring program can be challenging, both in terms of implementation and utilization for research, data collection, or management decision-making (Yoccoz et al. 2001; Pokswinski et al. 2021). Substantial effort is often dedicated to establishing and designing a monitoring program; however, it can be difficult to fully identify the evolving data requirements of end users, thus hindering the program's effectiveness in informing management decisions. This oversight often undermines the effectiveness of the monitoring efforts (Legg and Nagy 2006).

Lidar is uniquely poised to resolve some of these limitations by standardizing data collection with a reproducible approach while improving efficiency, reducing error, and creating easily analyzed numerical datasets, where a virtually unlimited number of metrics can be calculated. For instance, lidar has been used with machine learning techniques to efficiently monitor and classify successional stages across structurally diverse, mixed-species forests (Falkowski et al. 2009). Lidar monitoring data coupled with feature engineering holds immense potential for discovery of novel metrics that better characterize diverse aspects of forest ecosystems through both space and time, such as forest health, wildlife populations, fire severity, or various stages of post-fire recovery, particularly when integrated with other remote sensing modalities (Wang and Glenn 2009; Chu and Guo 2014; Linn et al. 2020; Ecke et al. 2022).

Monitoring programs will further benefit from the integration of various laser-scanning platforms (Levick et al. 2021; Fekry et al. 2022; Shao et al. 2022). Terrestrial laser scanning (TLS), for example, offers distinct advantages in capturing sub-canopy structures, as it operates beneath the tree canopy. This technology is increasingly being integrated into structural assessments of forested ecosystems and the study of fine-scale variations in the understory (Atkins et al. 2018; LaRue et al. 2020; Pokswinski et al. 2021; Walter et al. 2021; Gallagher et al. 2021; Ross et al. 2022). Although occlusion issues persist even with TLS, they can be alleviated through the process of registering and merging scans obtained from multiple locations and different platforms, enabling a more comprehensive assessment of vegetation structure by overcoming laser scanning limitations posed by occlusion.

The initial setup costs associated with acquiring lidar equipment for establishing monitoring campaigns is considerable; however, ongoing advancements in lidar technology and data processing techniques have progressively lowered costs, rendering lidar monitoring more accessible and cost-efficient, especially when considering the long-term benefits for ecosystem management and research (White et al. 2016; Almeida et al. 2019). Moreover, lidar monitoring data can be integrated with wildland fire models to provide up-to-date information on forest structural complexity, enhancing the accuracy of real-time fire behavior predictions with tools such as QUIC-Fire (Linn et al. 2020). Indeed, there are a myriad of use cases for lidar data, including infrastructure planning, archaeological studies, and hydrological analyses, all of which increase the return-on-investment (ROI) of monitoring programs (Jones et al. 2008; Buján et al. 2021; Snitker et al. 2022b).

Conclusions

The results presented in this study highlight the effectiveness of ULS for measuring forest structure, with metrics of vertical dispersion outperforming those of central tendency, emphasizing the necessity of a diverse set of metrics for a holistic characterization of structural complexity. The strongest correlation with fire frequency was observed with the understory complexity index, demonstrating the importance of accounting for fine-scale heterogeneity in the understory when assessing fire effects within forests subjected to frequent, low-intensity fire. Further research is needed to develop methodologies and metrics that better characterize both the vertical and horizontal distribution of vegetation. Terrestrial lidar is uniquely positioned to address such needs, particularly when co-registering both ULS- and TLS-derived point clouds. Ultimately, advancing research in the interconnected fields of prescribed fire and forest structure holds immense potential to mitigate the impacts of wildfires, improve wildlife habitat, and ensure the long-term sustainability of our natural resources for the benefit of society and future generations.

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Authors' contributions

C.W.R. conceptualized this analysis and performed the research, data processing, visualizations, and writing. J.M. performed the lidar data collection. T.L. provided the UAS and assisted with flight parameters and point-cloud registration. C.W.R., E.L.L., J.J.O., S.A.F., J.M., D.P.A., T.L., J.K.H., and N.S.S. helped with the writing, review, and revisions.

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Availability of data and materials

Data and material may be made available by contacting the primary author and with consent from the data owners.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare no competing interests.

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