



Traditional field metrics and terrestrial LiDAR predict plant richness in southern pine forests

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ARTICLE INFO

Keywords:

Ground-based LiDAR
Terrestrial laser scanning
Biodiversity
Community richness
Daubenmire
Vegetation monitoring
Forest monitoring

ABSTRACT

Terrestrial LiDAR is a promising tool for providing accurate and consistent measurements of forest structure at fine scales and has the potential to address some of the drawbacks associated with traditional vegetation monitoring methods. To compare terrestrial LiDAR to traditional methods, we conducted vegetation surveys using common methods of estimating cover and structure, and scanned surveyed areas using a terrestrial LiDAR device, the Leica BLK360. We developed simple methods for using point cloud data to make approximations of complex forest structure metrics and compared the ability of both data collection types to predict species richness. Hybrid models accurately predicted total, herb, and shrub richness in southern pine forests using combinations of metrics collected from terrestrial LiDAR and traditional field-based sampling methodology. Our findings indicate terrestrial LiDAR data may be used to accurately predict species richness in community types where structure and richness are related. In addition, our results suggest terrestrial LiDAR technology has the potential to address the limitations of traditional methods used to quantify vegetation structure and improve our ability for studying forest structure-richness relationships.

1. Introduction

One topic at the forefront of current ecological and conservation research is the importance of monitoring to protect, promote, and manage biodiversity (Di Marco et al., 2016, Lovejoy, 2020). However, quantifying plant richness, a critical metric of biodiversity, is often limited by the botanical expertise of observers (Dell et al., 2019). To overcome some of these challenges, quantifying vegetation structure, which is often closely related to potential niche space and species richness (Tews et al., 2004), has become the focus of many monitoring and restoration programs. Traditional methods to quantify structure have focused on simplifying complex three-dimensional structures into simple estimations of cover and height. Generally, vegetation is classified by broad functional groups and quantified with ocular estimates (Bonham et al., 2004; Braun-Blanquet, 1964, Daubenmire, 1959, Bonham, 1989) made within small radial or quadrat plots (Kent and Coker, 1992). As a result, the inferences made with these data are likely subject

to bias and lack fine-scale detail, reducing the ability to detect change (Floyd and Anderson, 1987, Kennedy and Addison, 1987, Klimeš, 2003, Milberg et al., 2008; Vittoz et al., 2010).

Despite the development of a number of additional methods to measure vegetation cover, such as point and line intercept methods, it is difficult to conduct repeatable studies with high levels of precision because observations are often erroneous and lack consistency (Godinez-Alvarez et al., 2009, Kent and Coker, 1992, Levy and Madden, 1933). These limitations have consequences for monitoring programs and long-term research studies that require repeatable surveys to quantify changes in vegetation over time in response to treatment or restoration. In more recent years, attempts have been made to address some of the drawbacks of traditional methods. For example, North Carolina Vegetation Survey (NCVS) plots (Peet et al., 1998), offer a highly standardized way of collecting community composition and structure data that allow for long-term monitoring of various ecosystems. However, conducting NCVS plots or other plots rigorously

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designed for repeatability requires a significant time investment and for surveyors to have the botanical expertise needed for comprehensive plant identification. For these reasons, researchers require more objective, repeatable, and practical methods for quantifying vegetation composition and structure.

Terrestrial laser scanning (TLS), also called terrestrial or ground-based LiDAR (Loudermilk et al., 2009, Liang et al., 2016), is an emerging remote sensing technology with the potential to address the challenges associated with traditional forest monitoring techniques (Donager et al., 2018). TLS data create a point cloud that reflects the features of the scanned landscape in three-dimensions and allows extremely fine-scale (mm) measurement of microstructure (Rowell et al., 2020, Maguire et al., 2019). The incorporation of TLS into both research and monitoring programs has the potential to improve the efficiency of data collection of traditional forest attributes. TLS collects vast quantities of fine-scale habitat data in a consistent manner and with fewer resources than are required using traditional field methods. Advancements in the technology have also allowed for more portable devices which are better suited for field studies in forest conditions. However, before TLS can become commonplace in ecological research and monitoring, studies are required to determine the effectiveness of this technology in quantifying vegetation structure and richness. Our study aims to address this need by investigating the potential applications of TLS in forest monitoring programs. We compared the ability of TLS derived structure data and plot-based vegetation data to determine which method, or combination of methods, best predict species richness in pine flatwoods communities.

2. Methods

2.1. Study sites

We conducted plots at Flint Rock Wildlife Management Area (FRWMA) and Tyndall Air Force Base (TAFB) in northwestern Florida (USA). The vegetation communities at FRWMA and TAFB exemplify the typical habitat of many forests along the Gulf Coast of Florida. Both sites are a patchy mosaic of wet flatwoods, mesic flatwoods, and wet prairie plant communities composed of both natural and planted stands of slash pine (*Pinus elliotii* Engelm.) and longleaf pine (*Pinus palustris* Mill.). The understory vegetation is generally characterized by saw palmetto (*Serenoa repens* (W.Bartram)Small), gallberry (*Ilex glabra* (L.)A.Gray), wiregrass (*Aristida stricta* Michx.) and other species typical of coastal southern pine forests. We sampled at FRWMA in August 2019 and TAFB in October 2019. Both visits were made in the late growing season, when more reproductive structures would be visible, to improve our ability to identify species.

2.2. Traditional vegetation metrics

We randomly placed 16 macro plots in flatwoods communities at FRWMA and TAFB. Each macro plot was composed of 9, 2.5-m radius plots arranged in a 3x3 grid (Fig. 1). To set up a macro plot, we navigated to a random point placed in flatwoods communities and used this point as the center of a corner plot. We located the remaining plots using a compass and measuring tape to ensure plots were evenly spaced. The center of each plot was 10 m from the center of the adjacent plots, such that each macro plot encompassed a total area of 625 m². Each plot center was permanently marked with ¼" rebar. A 2.5-m radius plot was chosen because it encompasses an area (approximately 20 m²) in which it is reasonable to estimate the cover of vegetation and not prohibitively time-consuming to identify all plant species present (adapted from Saha et al., 2011). In total, our study included 144 plots (16 macro plots). In each plot, we collected information on vegetation structure by estimating basal area, percent cover of canopy, shrubs, palmetto, titi (*Cyrtia racemiflora* L. and *Cliftonia monophylla* (Lam.)Sarg.), herbs, graminoids, pyrogenic graminoids, wiregrass, litter, and bare ground. Basal area was

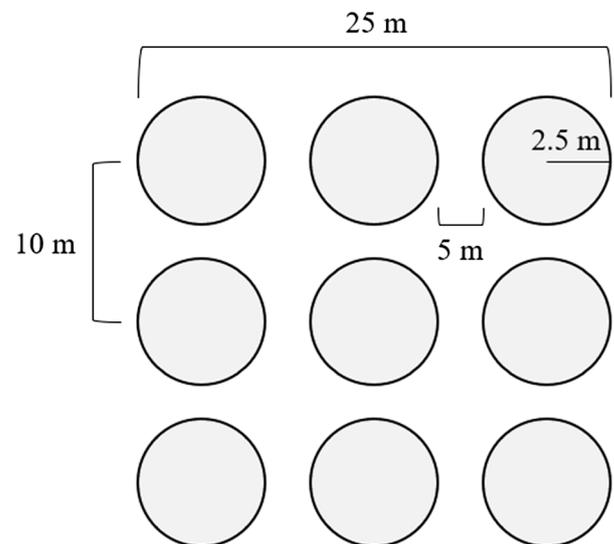


Fig. 1. A schematic of the macro plot design. Each macro plot was composed of 2.5-m radius plots arranged in a grid. The center of each plot was 10 m from the center of the adjacent plots.

estimated from the center of the plot using a 10-factor prism as an index of forest structure surrounding the plot. We made ocular estimates of percent cover using a modified Daubenmire classification (<1%, 1–5%, 6–15%, 16–25%, 26–35%, 36–45%, 46–55%, 56–65%, 66–75%, 76–85%, 86–95%, > 95%) (Daubenmire, 1959). We also made ocular estimates of shrub, palmetto, and titi height by determining which of the following height classes best characterized the target vegetation: <1 ft, 1–3 ft, 3–6 ft, or 6–9 ft. Canopy height was estimated visually using the following height classes: 6–15 ft, 15–30 ft, 30–45 ft, 45–60 ft, 60–100 ft, and > 100 ft. Additional details of how vegetation metrics were collected can be found in the supplemental materials. We identified each plant rooted in the plot to species and determined the natural community type of each macro plot according to FNAI (2010).

2.3. Terrestrial LiDAR using the BLK 360

We used the BLK360 (Leica Geosystems, Heerbrugg, Switzerland) to collect terrestrial LiDAR data. The BLK360 is a compact (height: 165 mm, diameter: 100 mm), lightweight (1 kg), comparatively affordable (~\$20,000), splash resistant terrestrial laser scanning system that can be mounted on a camera tripod. The scanner emits a series of laser pulses, which return to the scanner after bouncing off an object. The position of each object is quantified by the timing and strength of the return. Collectively, the returns create a three-dimensional (i.e. each point has an x, y, and z coordinate) point cloud that represents the topography of the scanned landscape. Scans made using the BLK360 capture 360° horizontally and 300° vertically, are capable of measuring millions of points in less than three minutes (360,000 points per second), and can capture data with up to 4 mm accuracy at 10 m from the scanner. In total, we scanned 77 of the 144 plots in the study. Of the plots scanned, 29 were at FRWMA and 48 were at TAFB. Plots were not scanned if a plot was in standing water or if it was raining during field data collection because water can scatter, weaken, and reflect returns, creating data anomalies (Chust et al., 2008, Milan et al., 2010). We did not scan plots where excessive coarse woody debris was present, such as multiple downed trees, because debris would have obstructed the lidar and resulted in an incomplete scan of the plot. Macro plots with more than one third of the plots under water or blocked by excessive debris were shifted a maximum of 25 m. If a 25-m shift of the microplot did not enable access to at least two thirds of the plots, it was eliminated from our study. We collected TLS data in each plot by placing the scanner on a tripod in the center of a plot. We recorded plot ID, time, and date for

each scan, so that traditionally measured vegetation data could be compared to the corresponding scan data.

2.4. Analysis

After exporting the files from the LiDAR scanner, we used CloudCompare (version 2.11, GPL), to convert the imported scans to an ascii file format. Because the scanner sits above the ground, points in the z-plane horizontal to the scanner receive values of zero, while those below the scanner receive negative z values. To account for potential variability in scanner height between scans, we corrected the z-plane so that the ground is at zero and no points are recorded below zero. To avoid overlapping scans, we clipped the point cloud of each plot by excluding all points with values of x or y that fell beyond five meters from the scanner (Fig. 2). We made a second, more conservative clip, by excluding all points that fell beyond 2.5 m from the scanner to assess whether additional scan data improved predictions of species richness.

We binned the remaining points based on their z-coordinate (height) to delineate important structural breaks in the forest understory, mid-story, and canopy. We delineated points into the following strata based on their z-coordinate: <1 m, 1–3 m, 3–6 m, 6–9 m, 9–12 m, 12–15 m, 15–18 m, 18–21 m, and > 21 m. We calculated percentage of points within each stratum to ensure appropriate scaling for regression and increase the interpretability of the findings. We used the mean and standard deviation of horizontal distance (x and y) values and vertical distance (z) values as an estimate of the openness and variability of the plot since returns do not penetrate vegetation. Therefore, stands with a larger mean can be interpreted as being more open, and those with higher standard deviations can be interpreted as having more heterogeneous, or highly variable, structure. Additionally, we included the maximum values of x and y to represent horizontal openness. We also used mean and standard deviation of the intensity of returns in our analysis. Intensity is a relative value that measures the strength of each return and can be used to detect features in the scan.

We developed generalized linear models (GLM) using traditional

field measurements, TLS data, and TLS derived structure data to predict species richness. For the purposes of this analysis, we treated each plot as independent because our goal was to relate fine scale vegetation structure and richness within the plot rather than extrapolating to a larger area. Using R (R Core Team, 2019), we ran GLM models with a Gaussian distribution and a log link function. We checked our model assumptions using the package ‘Performance’ with the ‘check distribution’ and ‘check model’ commands (Lüdecke et al., 2020). The model of traditional field measurements was composed of all variables collected by field staff using ocular estimates and included the natural community type (mesic flatwoods, wet flatwoods, pine plantation, or wet prairie), basal area, shrub, palmetto, titi, herb, graminoid, wiregrass, pyrogenic graminoid, litter, and bare ground cover, and shrub, palmetto, and titi height. The TLS data model was composed of variables derived from metrics provided by the scanner (maximum value of x, mean and standard deviation of x, z, and intensity values for each point in the cloud). We excluded the y horizontal data in our models as it was correlated to x data in all cases. The TLS derived structure model included the percent of returns in each stratum as described above. We included a full model that was a combination of all three of the above models, for a total of four primary models.

To develop additional hypotheses about factors that predict species richness, we used the R package ‘MASS’ (Venables, 2002) to conduct a stepwise reduction of each primary model using the ‘stepwise’ function. For each primary model the stepwise reduction was performed twice: once using ‘forwards/backwards’ selection and once using ‘backwards/forwards’ selection. We compared the two resulting models and retained the one with the lowest Akaike Information Criterion (AIC) score as the reduced model. We generated a simplified model using this process for each of the four primary models. Finally, we created an additional model by combining the variables from the reduced traditional, LiDAR, and strata models, to see if a combination of the model parameters was superior to any of the reduced or full models. To further simplify the combined model, we used the same stepwise reduction process to develop a reduced model. We evaluated each model for collinear parameters using the ‘Performance’ package’s ‘check collinearity’ tool. If parameters were collinear, we excluded the parameter that explained less variance. In total, we compared eleven candidate models for each TLS clip (2.5- and 5-m radius). Models were compared using the ‘Performance’ package by multiple indices of model fit (AIC, Bayesian information criterion, root mean square error, and Bayes factor) and given a performance score based on how well they explained the data given all the comparison indices. In addition to predicting overall species richness, we repeated this process of creating and comparing models to predict herb richness and shrub richness.

3. Results

3.1. Evaluation of LiDAR plot size to predict richness

We compared models made with TLS data clipped to 2.5 and five meters to determine whether additional data would better predict species richness. The models made using the 2.5-m radius TLS clips, which identically matched the vegetation plot size, were consistently outperformed by the models containing TLS data clipped to a five-meter radius using performance scores. For this reason, we excluded models with TLS data clipped to a 2.5-m radius in the final presentation of the data.

3.2. Total richness

Richness was best predicted by a mix of traditional field measurements, LiDAR derived parameters, and the percentage of points in different vertical strata. Richness averaged 18.2 ± 6.4 species per plot. The best model to predict total richness was the model generated by the stepwise reduction of the full model. The standard deviation of z and z

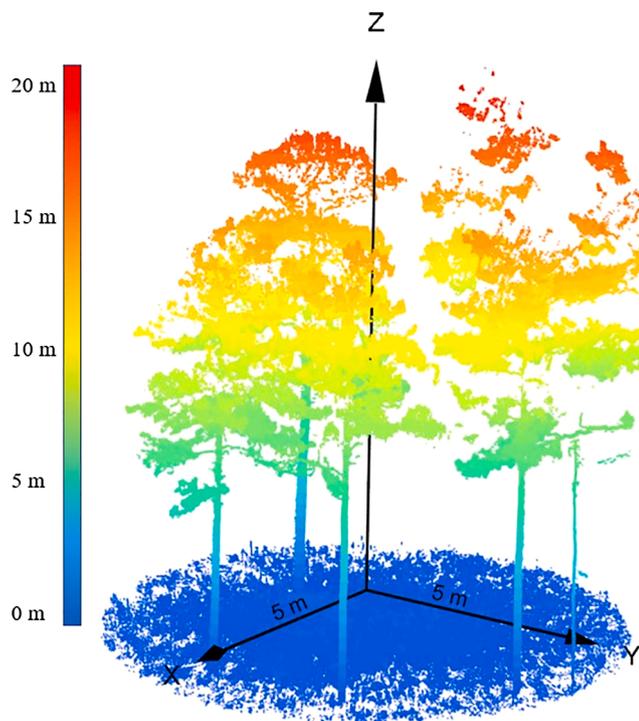


Fig. 2. An example of a clip from a Terrestrial LiDAR scan point cloud taken using the Leica BLK360. The color gradient shown represents the height (Z) of returns in meters.

mean were highly correlated, so we excluded the standard deviation of z from the model because it explained less variance than z mean. The top model received a performance score of 96.70% and had the lowest AIC and BIC, second lowest RMSE, and the highest BF (Table 1, Fig. 3). The model included herb cover, natural community type, palmetto cover, z mean, standard deviation of x, maximum value of z, and the percentage of points at < 1 m (Table 2). The second-best model to predict total richness was the combined and reduced model, which received a performance score of 90.14% and contained herb and palmetto cover, natural community type, z mean, the percentage of points from 1 to 3 m, and the percentage of points from 6 to 9 m (Table 1).

3.3. Shrub richness

On average, shrub richness was 9.8 ± 5.6 species per plot. The top model received a performance score of 96.45% and had the lowest AIC and BIC, second lowest RMSE, and with the highest BF (Table 3, Fig. 4). This model contained the z mean and the standard deviation of z, which were highly correlated, so we excluded the standard deviation of z from the model. The top model included natural community type, the maximum value of x, z mean, the percentage of points from 1 to 3 m, and the percentage of points from 9 to 12 m (Table 4). The second-best model was the combined model, which was less parsimonious than the top model and received a performance score of 69.23% (Table 3).

3.4. Herb richness

Herb richness averaged 6.7 ± 2.3 species per plot. Similar to total richness and shrub richness, the best model to predict herb cover was the reduced full model. The top model received a performance score of 98.22% and had the lowest AIC and BIC, second lowest RMSE, and the highest BF (Table 5, Fig. 5). This model contained herb, palmetto, and canopy cover, natural community type, the maximum value of z, the percentage of points from 6 to 9 m, the percentage of points from 12 to 15 m, and the percentage of points > 21 m (Table 6). The second-best model to predict herb richness only received a performance score of 66.28% (Table 5).

4. Discussion

Richness is a vital biodiversity metric used by managers to evaluate habitat quality and the effectiveness of management and restoration actions. However, quantifying biodiversity remains a challenge for many land managers because of the extensive resources and expertise required to make accurate estimates (Dell et al., 2019). Here, we demonstrate the potential for TLS to improve the data collection of inventory and monitoring programs, and its potential to predict richness, a key component of biodiversity estimates. Our findings indicate that species richness in southern pine communities is well explained using a

Table 1

The performance scores for the models predicting total richness. The best model was the stepwise reduced full model (Full Step). The second-best model was simplified from the combination of the stepwise reduced traditional, LiDAR, and strata models (Combination Step).

Model	AIC	BIC	RMSE	BF	Performance Score
Full step	425.63	451.27	3.44	$3.61e^{11}$	96.70%
Combination Step	428.38	451.69	3.55	$2.94e^{11}$	90.14%
Combination	434.45	469.42	3.46	$4.15e^{07}$	62.52%
Traditional step	441.19	462.17	3.93	$1.56e^{09}$	59.35%
Full	449.03	525.95	3.01	0.00	42.12%
Traditional	457.21	499.17	3.87	14.36	41.84%
LiDAR step	469.05	478.37	5.02	$4.72e^{05}$	36.06%
LiDAR	475.33	500.97	4.78	5.83	28.26%
Strata step	480.00	493.98	5.26	191.84	25.37%
Strata	485.86	509.17	5.19	0.10	18.86%
Null	499.84	504.50	6.32	1.00	7.18%

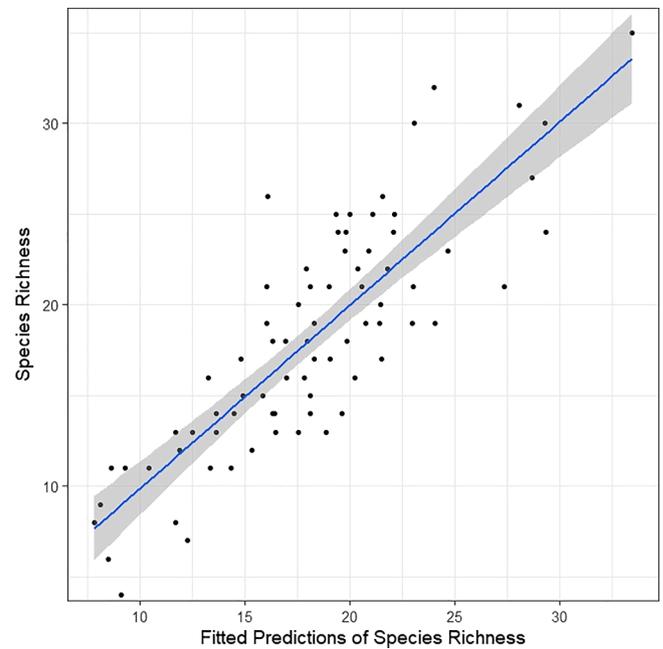


Fig. 3. Fitted predictions of the best model to predict total richness, which was the stepwise reduced full model (Full Step). The grey shaded area represents the 95% confidence interval of the model fit.

Table 2

The best model to predict total species was the stepwise reduced full model.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	2.79	0.04	63.48	<0.001
Pine plantation	-0.13	0.07	-1.80	0.08
Wet flatwoods	0.27	0.06	4.09	<0.001
Wet prairie	0.28	0.09	3.05	0.003
z mean	-0.41	0.09	-4.61	<0.001
z maximum	0.04	0.03	1.56	0.12
x sd	0.12	0.06	1.83	0.07
Herb cover	0.12	0.03	4.11	<0.001
Palmetto cover	-0.11	0.04	-2.51	0.01
Percentage of points < 1 m	-0.18	0.05	-3.61	<0.001

Table 3

The performance scores for the models predicting shrub richness. The best model was the stepwise reduced full model (Full Step). The second-best model was simplified from the combination of the stepwise reduced traditional, LiDAR, and strata models (Combination Step).

Model	AIC	BIC	RMSE	BF	Performance score
Full step	300.59	321.57	1.55	$2.12e^{06}$	96.45%
Combination step	305.09	326.06	1.60	$2.24e^{05}$	69.23%
Combination	313.56	348.52	1.56	2.98	57.54%
Traditional step	317.37	336.02	1.76	1545.43	53.04%
Traditional	333.70	375.65	1.72	0.00	38.96%
LiDAR step	329.56	343.54	1.96	35.85	35.65%
Full	340.06	421.63	1.43	0.00	32.65%
LiDAR	340.22	365.86	1.96	0.00	29.01%
Strata step	338.83	350.48	2.10	1.12	27.96%
Strata	347.60	370.91	2.09	0.00	18.68%
Null	346.04	350.70	2.30	1.00	18.55%

combination of LiDAR derived parameters and a few key traditional field metrics that are easy to collect without significant expertise. Additionally, the TLS derived parameters necessary to predict richness in our study required minimal post-scan processing, allowing technicians that lack both botanical and statistical expertise to make accurate richness assessments. These findings may be especially useful when exact

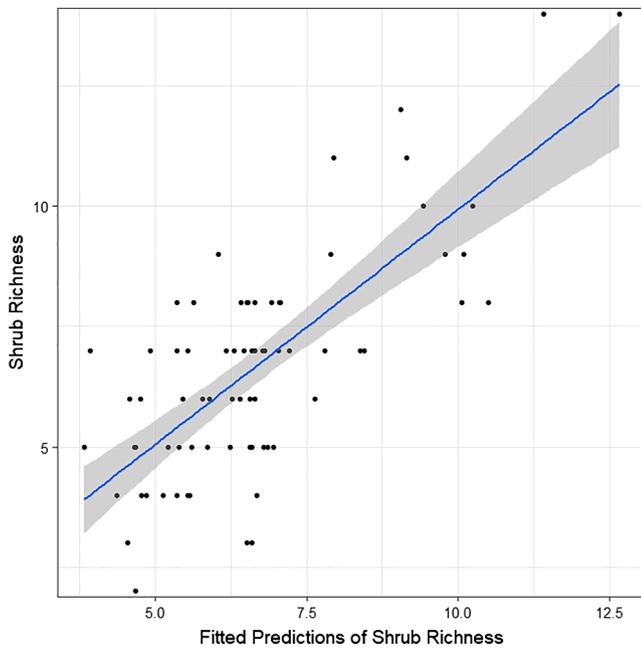


Fig. 4. Fitted predictions of the best model to predict shrub richness, which was the stepwise reduced full model (Full Step). The grey shaded area represents the 95% confidence interval of the model fit.

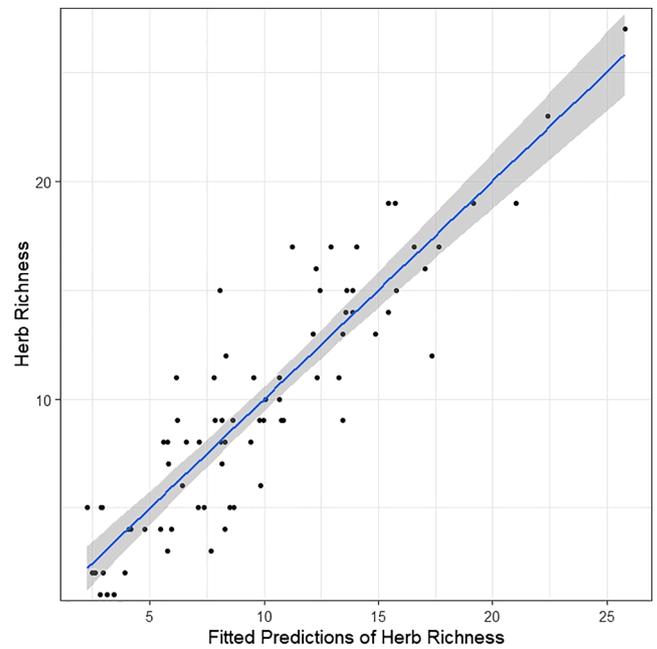


Fig. 5. Fitted predictions of the best model to predict herb richness, which was the stepwise reduced full model (Full Step). The grey shaded area represents the 95% confidence interval of the model fit.

Table 4

The best model to predict shrub species was the stepwise reduced full model.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	0.90	0.56	1.62	0.11
Pine plantation	-0.16	0.09	-1.89	0.06
Wet flatwoods	0.34	0.07	5.13	<0.001
Wet prairie	0.16	0.13	1.20	0.23
z mean	-0.24	0.04	-5.83	<0.001
x maximum	0.02	0.01	1.62	0.11
Percentage of points between 1 and 3 m	0.16	0.03	5.04	<0.001
Percentage of points between 9 and 12 m	0.05	0.04	1.44	0.15

Table 5

The performance scores for the models predicting herb richness. The best model was the stepwise reduced full model (Full Step). The second-best model was simplified from the combination of the stepwise reduced traditional, LiDAR, and strata models (Combination Step).

Model	AIC	BIC	RMSE	BF	Performance Score
Full step	379.00	411.63	2.44	1.63e ¹⁶	98.22%
Combination step	393.95	417.26	2.83	9.77e ¹⁴	66.28%
Combination	399.68	432.31	2.79	5.25e ¹¹	58.65%
Traditional step	403.15	426.45	3.01	9.84e ¹²	58.18%
Full	401.01	477.92	2.19	65.57	47.44%
Traditional	415.32	457.27	2.94	2.00e ⁰⁶	45.43%
Lidar step	432.02	441.35	3.94	5.75e ⁰⁹	39.34%
Lidar	434.95	460.59	3.66	3.81e ⁰⁵	34.21%
Strata step	451.83	461.15	4.49	2.87e ⁰⁵	23.86%
Strata	456.20	479.51	4.27	29.65	18.26%
Null	481.63	486.29	5.60	1.00	0.00%

richness numbers are not needed, but instead classes of richness (e.g., high, medium, low) would be sufficient to monitor the result of management actions, trends overtime, or to conduct rapid assessments. The methods outlined here have great utility for those which seek to rapidly assess the effects of management actions and progress toward desired future conditions in southeastern pine forests, and perhaps all forests

Table 6

The best model to predict herb species was the stepwise reduced full model.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	2.10	0.08	27.27	<0.001
Pine plantation	-0.12	0.09	-1.28	0.21
Wet flatwoods	0.20	0.12	1.69	0.10
Wet prairie	0.44	0.09	4.72	<0.001
Z mean	-0.30	0.10	-3.06	0.003
Z maximum	0.14	0.04	3.68	0.005
Herb cover	0.19	0.04	4.75	<0.001
Canopy cover	-0.16	0.06	-2.61	0.01
Palm cover	-0.25	0.08	-3.17	0.002
Percentage of points between 6 and 9 m	0.13	0.04	3.12	0.003
Percentage of points between 12 and 15 m	0.11	0.04	2.74	0.008
Percentage of points between 15 and 18 m	-0.15	0.08	-1.75	0.084
Percentage of points > 21 m	0.10	0.07	1.50	0.14

where structure and plant richness are strongly related.

Our models predicted herb richness more accurately than shrub richness, which may be a drawback if shrub richness is a primary concern. However, if more accurate estimates of shrub richness are needed, direct field observations to identify shrubs typically require less taxonomic skill than herb or graminoid species. In contrast, herb richness was accurately predicted. Since herb species are generally more taxonomically diverse and more challenging to identify than shrubs, we believe these findings show promise for expanding the capability of many monitoring and research programs to collect biodiversity data.

Natural community type was retained in the best model for all three richness assessments. Site type and history have been shown to be an important predictor of species richness in other studies (Christensen and Emborg, 1996, Kirkman et al., 2013, Török et al., 2014), which is congruent with our finding that natural community type was a significant predictor in all three models. Pine plantations had a negative effect on richness in all three models, further confirming existing knowledge that this type of heavily managed habitat is lower in richness than

natural forests (Iezzi et al., 2018).

The mean value of z was retained and had a negative effect on richness in all three models. Though one value, z mean presumably reflects a measure of vertical complexity as it is influenced by the height and vertical openness of the forest. Given the positive relationship between canopy gaps and understory cover (De Grandpré et al., 2011), and the positive relationship between canopy height and vascular species richness (Gatti et al., 2017), the negative effect of z mean on richness indicates a lower and denser canopy shades out understory species (Moreno et al., 2013). This finding has important implications for monitoring programs because height is a highly repeatable and easy to obtain metric that can be used to assess vertical complexity across multiple forest types.

Multiple studies have linked stand heterogeneity to richness (Brose, 2001, Kumar et al., 2006). Even so, the mechanisms driving this relationship are not well understood (Ortega et al., 2018). Presumably, the relationship arises because of the increase in microclimates and habitat niches available in heterogeneous landscapes (Chessen, 2000). However, effective and efficient methods to monitor this metric can be elusive using traditional methods. In our study, TLS derived parameters representing horizontal complexity were retained in the top total and shrub richness models. The standard deviation of x was included in the total richness model, which reflects the importance of heterogeneity of the shrub layer and forest to species richness. Additionally, the maximum value of x was retained in the shrub richness model, which reflects the maximum distance returns were able to penetrate the shrub layer and forest stand. Though both x metrics were non-significant as individual parameters, their retention improved the shrub and overall richness models, highlighting their value in explaining richness through horizontal structure. Our results not only offer additional support for the link between horizontal complexity and richness but suggest that TLS may be an effective tool for studying the mechanisms of this relationship.

Though investigations of the relationships between richness and structure using TLS data are extremely limited, aerial laser scanning (ALS) data has been used to relate structure to species richness for individual taxa and forest communities (Müller et al., 2010; Carrasco et al., 2019, Moeslund et al., 2019). These studies also rely on a combination of field collected and ALS derived parameters to best predict richness. For example, a study by Thers et al. (2017), used ALS data in conjunction with abiotic and biotic factors to predict fungal richness in a variety of habitat types. While they were able to predict total fungal richness using only ALS derived parameters, the model became a better fit when additional abiotic and biotic parameters were included. A finding by Lopatin et al. (2015) adds further evidence that models are better fit when using a combination of ALS and field collected metrics. In that study, vascular plant richness was predicted solely by ALS data, but the model had a tendency to overestimate richness when diversity was low. The ability to use a combination of ALS and field derived data to predict species richness across a diverse array of taxa strengthens our confidence that TLS data can be similarly applied to assess biodiversity in monitoring and management programs.

Few studies have been conducted to investigate the correlation between TLS derived structure data and species richness. Early studies of the application of TLS in estimating plant species richness used the data to estimate traditional forest structure metrics, such as canopy cover or herb cover, coupled with additional parameters to predict richness (Dormann et al., 2020, Vockenhuber et al., 2011). More recently, Walter et al. (2020) found a positive correlation between richness and a TLS derived structure parameter representative of forest complexity. However, our study is one of the first to compare multiple combinations of field and TLS derived parameters to determine the best predictors of richness.

TLS is a relatively new technology, and there are currently a limited number of studies that explore how to process and apply this data in ecological studies. Our study demonstrates the value of TLS as a flexible and effective method of monitoring forest structure when combined

with basic traditional field metrics. Using TLS devices, a single individual can gather the required vegetation structure and LiDAR data of a given plot in a just a few minutes. As a result, we believe TLS improves the surveying capabilities for many studies, where time and staff expertise limit the amount of data collected and area that can be surveyed. We predict that some study sites will require larger radius sample plots due to the dimensions of the forest structure but may still benefit from incorporating TLS data by making simple adjustments to the methods presented here. However, our approach may not be applicable in prairie systems where there is little variation in vertical structure. Regardless of methodology, a potential challenge of using TLS is the processing necessary to analyze the scan data. However, our method of predicting species richness requires minimal processing and simple R commands, meets a primary need of many monitoring programs, and could be adapted to address other management needs. Despite the potential challenges, we believe TLS has outstanding potential to improve ecological monitoring programs and warrants further investigation to understand its applications.

Funding acknowledgement

This publication was funded by a cooperative agreement between the Florida Natural Areas Inventory and the U.S. Fish and Wildlife Service. We thank The Nature Conservancy for making field work at Flint Rock Wildlife Management Area possible through providing in-kind field work and arranging funding from the Apalachicola Regional Stewardship Alliance via the National Fish and Wildlife Foundation's Longleaf Stewardship Fund.

CRediT authorship contribution statement

C.T. Anderson: Conceptualization, Methodology, Writing - original draft, Formal analysis, Visualization, Investigation, Supervision. **S.L. Dietz:** Data curation, Writing - original draft, Formal analysis, Software, Visualization, Validation. **S.M. Pokswinski:** Writing - review & editing, Visualization, Methodology, Resources. **A.M. Jenkins:** Investigation, Project administration, Methodology, Resources, Writing - review & editing. **M.J. Kaeser:** Funding acquisition, Writing - review & editing, Project administration. **J.K. Hiers:** Conceptualization, Methodology, Funding acquisition, Writing - review & editing. **B.D. Pelc:** Investigation, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119118>.

References

- Bonham, 1989. *Measurements for Terrestrial Vegetation*. John Wiley and Sons, New York, USA, p. 352.
- Bonham, C.D., Mergen, D.E., Montoya, S., 2004. Plant cover estimation: a contiguous daubenmire frame. *Rangelands* 26 (1), 17–22.
- Braun-Blanquet, J., 1964. *Pflanssoziologie*, third ed. Springer, Vienna, Austria.
- Brose, U., 2001. Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in East-German Farmland. *Ecography* 24, 722–730.
- Carrasco, L., Giam, X., Papeş, M., Sheldon, K.S., 2019. Metrics of lidar-derived 3D vegetation structure reveal contrasting effects of horizontal and vertical forest heterogeneity on bird species richness. *Remote Sens.* 11, 43. <https://doi.org/10.3390/rs11070743>.
- Chessen, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Evol. Syst.* 31, 343–366.
- Christensen, M., Emborg, J., 1996. Biodiversity in natural versus managed forest in Denmark. *For. Ecol. Manage.* 85, 47–51.

- Chust, G.I., Galparsoro, Á., Borja, J., Franco, A. Uriarte. Coastal and estuarine habitat mapping, using LIDAR height and intensity and multi-spectral imagery. *Estuarine, Coastal and Shelf Sci.* 78:633-643.
- Daubenmire, R.F., 1959. A canopy-cover method of vegetational analysis. *Northwest Sci.* 33, 43–46.
- Dell, J.E., Pokswinski, S.M., Richards, L.A., Hiers, J.K., Williams, B., O'Brien, J.J., Loudermilk, E.L., Hudak, A.T., Dyer, L.A., 2019. Maximizing the monitoring of diversity for management activities: Additive partitioning of plant species diversity across a frequently burned ecosystem. *For. Ecol. Manage.* 432, 409–414.
- De Grandpré, L., Boucher, D., Bergeron, Y., Gagnon, D., 2011. Effects of small canopy gaps on boreal mixedwood understory and vegetation dynamics. *Community Ecol.* 12 (1), 67–77.
- Di Marco, M., Watson, J.E., Venter, O., Possingham, H.P., 2016. Global biodiversity targets require both sufficiency and efficiency. *Conservation Lett.* 9, 395–397. <https://doi.org/10.1111/conl.12299>.
- Donager, J.J., Sankey, T.T., Sankey, J.B., Sanchez Meador, A.J., Springer, A.E., Bailey, J. D., 2018. Examining forest structure with terrestrial lidar: Suggestions and novel techniques based on comparisons between scanners and forest treatments. *Earth Space Sci.* 5 (11), 753–776.
- Dormann, C.F., Bagnara, M., Bock, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., Hartig, F., 2020. Plant species richness increases with light availability, but not variability, in temperate understorey. *BMC Ecol.* 20, 43.
- Floyd, D.A., Anderson, J.E., 1987. A comparison of 3 methods for estimating plant cover. *J. Ecol.* 75, 221–228.
- Gatti, R.C., Di Paola, A., Bombelli, A., Noce, S., Valentini, R., 2017. Exploring the relationship between canopy height and terrestrial plant diversity. *Plant Ecol.* 218, 899–908.
- Godínez-Alvarez, H., Herrick, J.E., Mattocks, M., Toledo, D., Van Zee, J., 2009. Comparison of three vegetation monitoring methods: Their relative utility for ecological assessment and monitoring. *Ecol. Ind.* 9, 1001–1008.
- Iezzi, M.E., Cruz, P., Varela, D., De Angelo, C., Di Bitetti, M.S., 2018. Tree monocultures in a biodiversity HotSpot: Impact of pine plantations on mammal and bird assemblages in the Atlantic forest. *For. Ecol. Manage.* 216–227.
- Kennedy, K.A., Addison, P.A., 1987. Some considerations for the use of visual estimates of plant cover in biomonitoring. *J. Ecol.* 75, 151–157.
- Kent, M., Coker, P., 1992. *Vegetation description and analysis*. Belhaven, London, UK.
- Klímeš, L., 2003. Scale-dependent variation in visual estimates of grassland plant cover. *J. Veg. Sci.* 14, 815–821.
- Kirkman, L.K., Barnett, A., Williams, B.W., Hiers, J.K., Pokswinski, S.M., Mitchell, R.J., 2013. A dynamic reference model: a framework for assessing biodiversity restoration goals in a fire-dependent ecosystem. *Ecol. Appl.* 23 (7), 1574–1587.
- Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87 (12), 3186–3199.
- Levy, E.B., Madden, E.A., 1933. The point method of pasture analyses. *New Zealand J. Agriculture* 46, 267–279.
- Liang, X., Kankare, V., Hyyppä, J., Wang, Y., Kukko, A., Haggrén, H., Yu, X., Kaartinen, H., Jaakkola, A., Guan, F., Holopainen, M., Vastaranta, M., 2016. Terrestrial laser scanning in forest inventories. *ISPRS J. Photogramm. Remote Sens.* 115, 63–77.
- Lopatin, J., Galleguillos, M., Fassnacht, F.E., Ceballos, A., Hernández, J., 2015. Using a multistructural object-based lidar approach to estimate vascular plant richness in mediterranean forests with complex structure. *IEEE Geosci. Remote Sens. Lett.* 12 (5), 1008–1012.
- Loudermilk, E.L., Hiers, J.K., O'Brien, J.J., Mitchell, R.J., Singhania, A., Fernandez, J.C., Cropper, W.P., Slatton, K.C., 2009. Ground-based LIDAR: a novel approach to quantify fine-scale fuelbed characteristics. *Int. J. Wildland Fire* 18 (6), 676–685.
- Lovejoy, T.E., 2020. Biodiversity conservation targets: how to allocate resources. *One Earth* 2(5):415–416. <https://doi.org/10.1016/j.oneear.2020.05.003>.
- Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., 2020. Performance: Assessment of regression models performance. CRAN. doi:10.5281/zenodo.3952174, R package, <https://easystats.github.io/performance/>.
- Milberg, P., Bergstedt, J., Fridman, J., Odell, G., Westerberg, L., 2008. Observer bias and random variation in vegetation monitoring data. *J. Veget. Sci.* 19 (5), 633–644.
- Maguire, A.J., Eitel, J.U., Vierling, L.A., Johnson, D.M., Griffin, K.L., Boelman, N.T., Jensen, J.E., Greaves, H.E., Meddens, A.J., 2019. Terrestrial lidar scanning reveals fine-scale linkages between microstructure and photosynthetic functioning of small-stature spruce trees at the forest-tundra ecotone. *Agric. Forest Meteorol.* 269, 157–168.
- Milan, D.J., Heritage, G.L., Large, A.R.G., Entwistle, N.S., 2010. Mapping hydraulic biotopes using terrestrial laser scan data of water surface properties. *Earth Surf. Proc. Land.* 35, 918–931.
- Moeslund, J.E., Zlinszky, A., Ejrnæs, R., Brunbjerg, A.K., Bocher, P.K., Svenning, J., Normand, S., 2019. Light detection and ranging explains diversity of plants, fungi, lichens, and bryophytes across multiple habitats and large geographic extent. *Ecol. Appl.* 29 (5), e01907.
- Moreno, G., Bartolome, J.W., Gea-Izquierdo, G., Cañellas, I., 2013. Overstorey–understorey relationships. In: Campos, P., et al., (Ed.) *Mediterranean Oak Woodland Working Landscapes*. Landscape Series, vol. 16. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6707-2_6.
- Müller, J., Stadler, J., Brandl, R., 2010. Composition versus physiognomy of vegetation as predictors of bird assemblages: the role of lidar. *Remote Sens. Environ.* 114, 490–495.
- Ortega, J.C.G., Thomaz, S.M., Bini, L.M., 2018. Experiments reveal that environmental heterogeneity increases species richness but they are rarely designed to detect the underlying mechanisms. *Oecologia* 188, 11–12.
- Peet, R., Wentworth, T., White, P., Flexible, A., 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63 (3), 262–274.
- R Core Team, 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rowell, E.E.L., Loudermilk, C., Hawley, S., Pokswinski, C., Seielstad, L., Queen, J.J., O'Brien, A.T., Hudak, S., Goodrick, J.K., Hiers, 2020. Coupling terrestrial laser scanning with 3D fuel biomass sampling for advancing wildland fuels characterization. *Forest Ecol. Manage.* 462, 117945.
- Saha, S., Bradley, K., Ross, M.S., Hughes, P., Wilmers, T., Ruiz, P.L., Bergh, C., 2011. Hurricane effects on subtropical pine rocklands of the Florida Keys. *Clim. Change* 107 (1), 169–184.
- Vittoz, P., Bayfield, N., Brooker, R., Elston, D.A., Duff, E.I., Theurillat, J.-P., Guisan, A., 2010. Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *J. Veg. Sci.* 21, 1035–1047.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92.
- Thers, H., Brunbjerg, A.K., Læssøe, T., Ejrnæs, R., Bocher, P.K., 2017. Lidar-derived variables as a proxy for fungal species richness and composition in temperate northern Europe. *Remote Sens. Environ.* 200, 102–113.
- Török, P., Valkó, O., Deák, B., Kelemen, A., Tóthmérész, 2014. Traditional cattle grazing in a mosaic alkali landscape: effects on grassland biodiversity along a moisture gradient. *PLoS ONE* 9(5): e97095.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, Fourth edition. Springer, New York. <http://www.stats.ox.ac.uk/pub/MASS4/>.
- Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tschamtk, T., 2011. Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspect. Plant Ecol., Evol. System.* 13, 111–119.
- Walter, J.A., Stovall, A.E.L., Atkins, J.W., 2020. Vegetation structural complexity and biodiversity across elevation gradients in the great smoky mountains. Preprints. <https://doi.org/10.20944/preprints202004.0415.v1>.