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

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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 quadrate 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, Klimes, 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 (Gómez-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 objec-
tive, 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 ef-
iciency 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. Ad-
vancements in the technology have also allowed for more portable de-
vices 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 applica-
tions 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 elliottii 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 navig-
gated 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 (approximate 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 esti-
mating basal area, percent cover of canopy, shrubs, palmetto, titi (Cyprilla
racemiflora L. and Cliftonia monophylla (Lam.)Sarg.), herbs, graminoids,
pyrogenic graminoids, wiregrass, litter, and bare ground. Basal area was
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%,
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 commu-
nity 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
(about $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 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
plot since returns do not penetrate vegetation. Therefore, stands with a
within each stratum to ensure appropriate scaling for regression and
– 15 returns in meters.

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.

2.4. Analysis

After exporting the files from the LiDAR scanner, we used Cloud-
Compare (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 vari-
ability 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 hetero-
geneous, 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 distribu-
tion’ 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, tiki, herb, graminoid, wiregrass, pyrogenic
graminoid, litter, and bare ground cover, and shrub, palmetto, and tiki
height. The TLS data model was composed of variables derived from
metrics provided by the scanner (maximum value of x, mean and stan-
dard 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:
one 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 su-
perior 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 pa-
rameters 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 ‘Per-
formance’ package by multiple indices of model fit (AIC, Bayesian in-
f ormation 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 rich-
ness, 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 spe-
cies richness. The models made using the 2.5-m radius TLS clips, which
identically matched the vegetation plot size, were consistently out-
performed 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 measure-
ments, 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
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 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 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
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 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.

Table 4  
The best model to predict shrub species was the stepwise reduced full model.

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

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).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>BIC</th>
<th>RMSE</th>
<th>BF</th>
<th>Performance Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full step</td>
<td>379.00</td>
<td>411.63</td>
<td>2.44</td>
<td>1.63×10^15</td>
<td>98.22%</td>
</tr>
<tr>
<td>Combination</td>
<td>393.95</td>
<td>417.26</td>
<td>2.83</td>
<td>9.77×10^14</td>
<td>66.28%</td>
</tr>
<tr>
<td>Combination</td>
<td>399.68</td>
<td>432.31</td>
<td>2.79</td>
<td>5.25×10^11</td>
<td>56.65%</td>
</tr>
<tr>
<td>Traditional</td>
<td>403.15</td>
<td>426.45</td>
<td>3.01</td>
<td>9.84×10^12</td>
<td>56.18%</td>
</tr>
<tr>
<td>Full</td>
<td>401.01</td>
<td>477.92</td>
<td>2.19</td>
<td>65.57</td>
<td>47.44%</td>
</tr>
<tr>
<td>Traditional</td>
<td>415.32</td>
<td>457.27</td>
<td>2.94</td>
<td>2.00×10^6</td>
<td>45.43%</td>
</tr>
<tr>
<td>Lidar step</td>
<td>432.02</td>
<td>441.35</td>
<td>3.94</td>
<td>5.75×10^9</td>
<td>39.34%</td>
</tr>
<tr>
<td>Lidar</td>
<td>434.95</td>
<td>460.59</td>
<td>3.66</td>
<td>3.81×10^9</td>
<td>34.21%</td>
</tr>
<tr>
<td>Strata step</td>
<td>451.83</td>
<td>461.15</td>
<td>4.49</td>
<td>2.87×10^5</td>
<td>23.86%</td>
</tr>
<tr>
<td>Strata</td>
<td>456.20</td>
<td>479.51</td>
<td>4.27</td>
<td>29.65</td>
<td>18.26%</td>
</tr>
<tr>
<td>Null</td>
<td>481.63</td>
<td>486.29</td>
<td>5.60</td>
<td>1.00</td>
<td>0.00%</td>
</tr>
</tbody>
</table>

Table 6  
The best model to predict herb species was the stepwise reduced full model.

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

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.

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., 2015). 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., 2016; 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 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 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.

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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.

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