

Estimation of woodland canopy complexity with terrestrial LiDAR: extended methods

John L. Godlee

30th August 2021

1 1 Introduction

This chapter provides expanded field and analytical methods for the study of tree canopy structure in southern African woodlands, presented in brief in Chapter 5. The study aimed to understand the effects of tree species diversity and stand structure on tree canopy structural complexity, using terrestrial LiDAR. Firstly, I provide technical details on the field setup for the terrestrial LiDAR and the hemispherical photography used to validate terrestrial LiDAR canopy closure estimates. Secondly, I describe the processing chain used to extract canopy complexity metrics from the terrestrial LiDAR point clouds. Thirdly, I describe in further detail the behaviour and suitability of the different canopy complexity and stand structural metrics used in the study.

11 2 Terrestrial LIDAR field setup

Within each 1 ha (100×100 m) square plot, nine 10 m diameter circular subplots were laid out in a grid, with 35 m between subplot centre points (Figure 1). These subplots constitute the basic sampling unit of the study. Within each subplot, a Leica HDS6100 phase-shift Terrestrial Laser Scanner (TLS) was used to capture woodland canopy structure. The number and position of scan locations within a subplot was determined by the arrangement and density of canopy material in the subplot, with the aim to minimise shadows within the canopy, and to maximise canopy penetration (Béland & Kobayashi, 2021). Between one and five scans were recorded per subplot, across all plots. Further information on the field setup of the TLS is presented in Table 1.

Five Leica 6" (15.24 cm) diameter planar tilt-and-turn cross-pattern reflective targets were located in each subplot to facilitate alignment of scans (Figure 2). The five targets were located roughly in a quincunx pattern, with one target at the subplot centre and the remaining four targets arranged in a cross pattern around the edges of the subplot, ensuring that all scans could see all five targets. To facilitate alignment of scans among subplots, the location of each target in real space was recorded using a Leica VIVA GS10 GNSS (Global Navigation Satellite Systems) unit (Figure 3). The GNSS was set up in a Post-Processing Kinematic (PPK) configuration with a base-station located ~100 m from the edge of each 1 ha plot with an unobstructed view of the sky hemisphere where possible. The location of each target was measured for at least four minutes to minimise measurement error (Figure 4).

31 3 Hemispherical photography field setup

To validate TLS canopy closure estimates, at the centre of each subplot a single photograph was taken with a full-frame DSLR camera, equipped with a circular fisheye lens. Further information on the hemispherical photography setup is presented in Table 2.

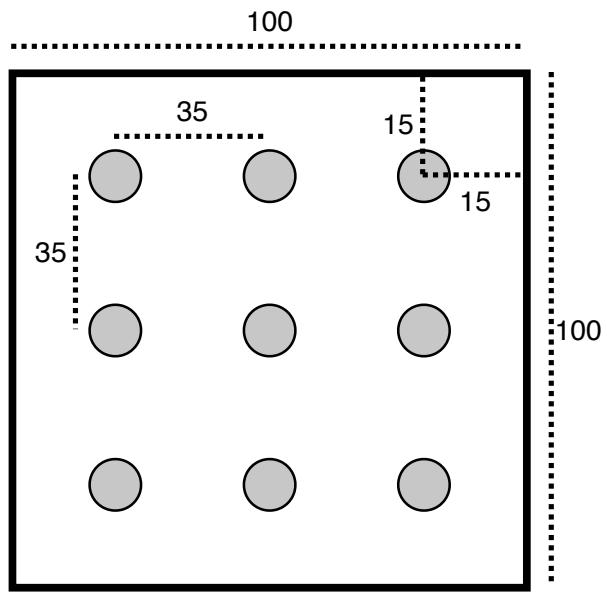


Figure 1: The layout of 10 m diameter subplots within each 1 ha plot. Each subplot is situated inside a 15 m buffer from the plot edge, with 35 m between subplot centres. Subplots are arranged in a 3×3 grid. All distances are in metres.



(a)



(b)

Figure 2: Example of a Leica 6" diameter reflective target, (a) in situ mounted on a length of threaded bar, and (b) showing the cross pattern face of the target.



Figure 3: A Leica VIVA GS10 GNSS unit in the field, showing the antenna atop an aluminium pole, attached to the base station on the ground, and the rover terminal in the hand of a research assistant.

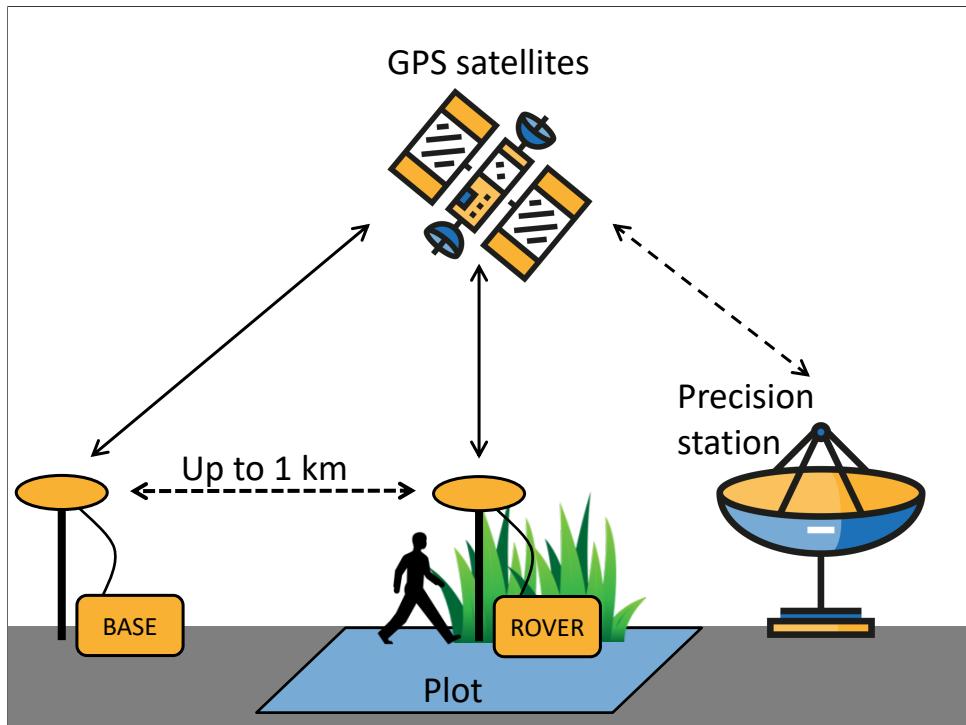


Figure 4: Schematic diagram of the GNSS PPK configuration used to precisely locate targets in real space. The base station is located in an area with a full unobstructed view of the sky hemisphere, up to ~1 km from the plot, and is left in the same location for the duration of the data collection, recording its location once per second. The rover is moved around inside the plot to record the location of each target, for >4 minutes at each target. The rover and the base station both utilise GPS and GLONASS satellites to record their position. After data collection, a two stage validation technique is used to improve the precision of the recorded positions, firstly using the base station, and secondly using the TrimbleRTX service which utilises highly precise distributed regional stations.

Table 1: Description of scan settings used for each scan.

Setting	Value
TLS model	Leica HDS6100
Wavelength	650-690 nm
Spot size at exit	3 mm
Beam divergence	0.22 mrad
Range	79 m @90%; 50 m @18% albedo
Azimuth range	0-360°
Zenith range	0-155°
Increment	0.018°
Point spacing over 25 m	7.9 mm
Pixels per line	20,000
Lines	10,000
Compressed file size	~800 MB
Duration of scan	6 minutes 44 seconds

35 The fisheye lens had an equisolid (equal area) projection, with a projection function given by:

$$R = 2f \sin\left(\frac{\theta}{2}\right) \quad (1)$$

36 Where R is the radial position of a point on the image, f is the focal length of the lens, and θ is
37 the angle in radians of incident light on the lens. Equisolid lenses are preferred for hemispherical
38 photography because they maintain an equal area for each pixel, i.e. a pixel projected through
39 the lens has the same solid angle irrespective of the incident light angle, meaning that canopy
40 closure estimations are not biased towards any part of the sky hemisphere (Herbert, 1987).

41 Photographs were taken facing directly to zenith using a camera-mounted spirit level, with
42 the top of the camera body facing magnetic north, at a height of 1.3 m or above understorey
43 vegetation, whichever was higher. Photographs were captured under uniform light conditions as
44 much as possible, either under overcast skies or early in the day before direct sunlight could
45 be seen on the photograph, to minimise lens flare, which can preclude accurate differentiation
46 of plant material and sky, and to minimise ‘blooming’, a phenomenon where light ‘bleeds’ into
47 dark areas of the image in highly contrasting light conditions (Frazer et al., 2001).

48 ImageJ (Fiji version 2.1.0/1.53c) was used to binarise hemispherical photographs, to separate
49 plant material from sky (Schneider et al., 2012). Images were binarised using the Huang algorithm
50 (Huang & Wang, 1995) using only the blue channel of the image, under the assumption that
51 plant material reflects little blue light, while the sky reflects much more (Brusa & Bunker,
52 2014). Images were saved as PNG files at the original pixel resolution, with a circular image of
53 4016×4016 pixels.

54 4 Terrestrial LiDAR processing

55 4.1 Scan alignment and registration

56 Point clouds within a subplot were aligned using the reflective targets as anchor points. Point
57 cloud alignment was conducted in Leica Cyclone (version 9.1) (Leica Camera AG, 2009).
58 Reflective targets were manually located within each point cloud, then the precise centre of
59 each target was identified automatically by Cyclone. Anchor points were discarded if they had

Table 2: Description of camera settings used for hemispherical photographs. Note that shutter speed and ISO are deliberately variable within sensible thresholds to allow adjustments for ambient light conditions.

Setting	Value
Camera model	Nikon D750
Lens model	Sigma 8 mm f/3.5 EX DG Circular Fisheye
Pixel pitch	5.95 μm
Sensor resolution	24.3 MP
Shutter speed	>1/60s
Aperture	5-7
ISO	100-200
Exposure compensation	-0.7 (Brusa & Bunker, 2014)
Focus	∞ (Frazer et al., 2001; Hu & Zhu, 2009)
Image size	Large Fine JPEG - circular image 4016×4016 px
Orientation	Landscape

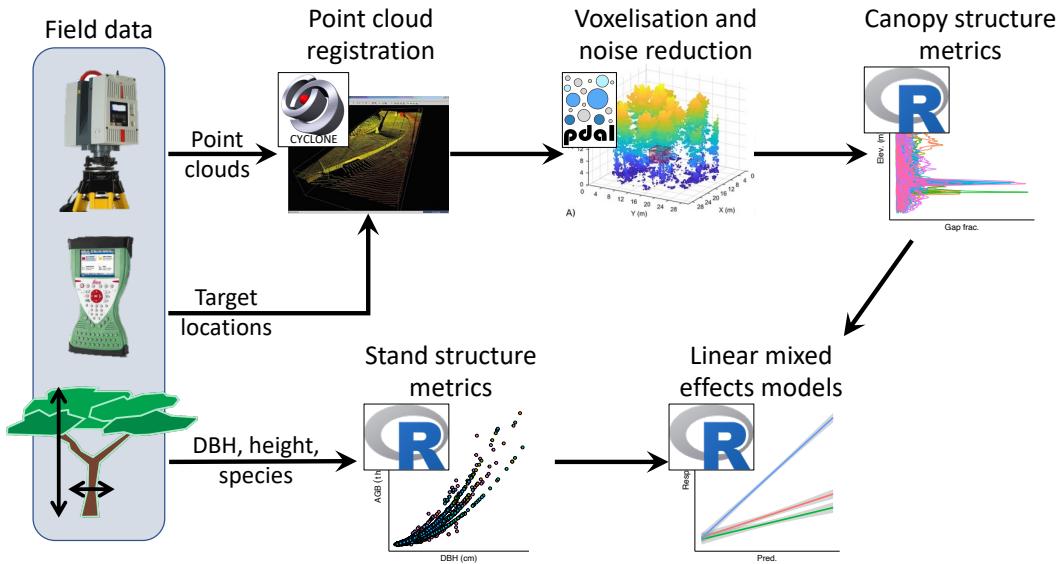


Figure 5: Schematic diagram summarising the data processing and analysis workflow for the TLS data. Processing steps are labelled according to the principal software used during that step.

Table 3: The five closes regional base stations to each site, used by TrimbleRTX to refine GNSS measurements

Site	Receiver	Distance (km)
Bicuar	JAVAD TRE 3	863
	JAVAD TRE 3 DELTA	1448
	TRIMBLE NETRS	1630
	TRIMBLE NETRS	1648
	JAVAD TRE G3TH DELTA	1796
Mtarure	SEPT POLARX5	686
	TRIMBLE ALLOY	795
	LEICA GRX1200GGPRO	903
	JAVAD TRE 3 DELTA	1119
	JAVAD TRE 3 DELTA	1315

- 60 a location uncertainty of >3 cm. After alignment, subplot point clouds were exported from
 61 Cyclone as PTX files for further processing.
- 62 GNSS measurements of target locations were used to register point clouds in real space. The
 63 TrimbleRTX GNSS post-processing service was used to improve the precision of target locations
 64 recorded with GNSS, using distributed regional stations to validate the rover and base station
 65 GNSS measurements (Table 3) (Chen et al., 2011). Following point cloud registration, subplot
 66 point clouds were combined to a plot level point cloud.
- 67 PTX files were converted to compressed LAZ files using PDAL (PDAL Contributors, 2018), to
 68 reduce file size and speed up further processing. Code 1 contains the code used to transform
 69 PTX to LAZ.

```

1 # Get file name without extension
2 noext=${1%.ptx}
3
4 # Find the PTX scan array dimension header material
5 lines=$(grep -E -n '^.{1,10}$' $1 |
6   cut -f1 -d: |
7   awk 'NR%2!=0' |
8   tr '\n' ' ' |
9   sed 's/^([0-9])\s//g')
10
11 # Split PTX file into individual scans
12 csplit -f "$noext" -b "%d.ptx" $1 $lines
13
14 $ Find split files
15 ptxsplit=$(find . -type f -regex ".*/${noext}_[0-9].ptx")
16
17 # For each file:
18 for j in ${ptxsplit}; do
19   jnoext="${j%.ptx}"
20   matrix=$(head -n 10 $j | tail -4 | sed -r 's/0\s+?$/0.0/g' | dos2unix)
21   pdal pipeline ptx_laz.json --readers.text.filename=$j \
22     --filters.transformation.matrix="${matrix}" \
23     --writers.las.filename=${jnoext}.laz
24 done
25
26 # List LAZ files
27 lazsplit=$(find . -type f -regex ".*/${noext}_[0-9].laz")
28
29 # Merge LAZ files
30 pdal merge ${lazsplit} ${noext}.laz

```

Code 1: The processing chain used to convert Leica Cyclone PTX files to LAZ files, using PDAL, POSIX shell scripting, and common UNIX utilities. The `ptx_laz.json` JSON pipeline is shown in Code 2.

```

1 [
2   {
3     "type" : "readers.text",
4     "filename" : "input.txt",
5     "header" : "X Y Z I",
6     "skip" : 10
7   },
8   {
9     "type" : "filters.transformation",
10    "matrix" : "0 -1 0 1 1 0 0 2 0 0 1 3 0 0 0 1"
11  },
12  {
13    "type" : "writers.las",
14    "compression" : "true",
15    "minor_version" : "2",
16    "dataformat_id" : "0",
17    "forward" : "all",
18    "filename" : "output.laz"
19  }
20 ]

```

Code 2: The JSON pipeline used in Code 1 to convert PTX files to LAZ files, and applying a rotation matrix.

72 4.2 Voxelisation

73 Point clouds were voxelised to different voxel sizes depending on the application of the data. 5
74 cm^3 cubic voxels were used for subplot height profile estimation, while 50 cm^3 voxels were used
75 for whole plot canopy rugosity. Variation in voxel size reflects the spatial scale of each analysis,
76 and is bounded by the beam divergence of the TLS over longer distances (Grau et al., 2017).
77 Choosing voxels that are too small can result in pock-marked representations of surfaces that
78 are especially problematic when calculating larger scale canopy structure metrics such as canopy
79 top roughness, while voxels that are too large can result in an over-estimation of plant volume
80 when estimating canopy foliage density at the subplot scale, especially when foliage is clumped
81 (Cifuentes et al., 2014; Seidel et al., 2012). Voxels were classified as ‘filled’ if they intersected
82 one or more points.

83 4.3 Noise reduction

84 Outlier detection and noise reduction of point clouds was conducted in PDAL, using the
85 “statistical method” of `filters.outlier` (Rusu et al., 2008), with $k = 8$ (mean number of
86 neighbours), and $m = 1.96$ (outlier distance threshold multiplier, here approximating a 95%
87 confidence interval):

$$\begin{aligned}\bar{\mu} &= \frac{1}{N} \sum_{i=1}^N \mu_i \\ \sigma &= \sqrt{\frac{1}{N-1} \sum_{i=1}^N (\mu_i - \bar{\mu})^2} \\ t &= \mu + m\sigma \\ \text{with } outlier_i &= \begin{cases} \text{true,} & \text{if } \mu_i \geq t \\ \text{false,} & \text{otherwise} \end{cases}\end{aligned}\tag{2}$$

88 Where μ_i is the mean distance from point i to all k nearest neighbour points, N is the number
89 of points in the scene, $\bar{\mu}$ is the mean distance to nearest neighbour points, σ is the standard
90 deviation of these mean distances, t is the threshold distance used to define an outlier and
91 $outlier_i$ is the condition of a point in the scene being identified as an outlier.

92 4.4 Foliage density profiles

93 To calculate subplot foliage density profiles, the 5 cm^3 voxelised point cloud was first cropped to
94 a 10 m diameter cylinder of infinite height. Ground points were identified using `filters.pmf`
95 (Progressive Morphological Filter - PMF) in PDAL (Zhang et al., 2003), and the height above
96 ground of all points was calculated using `filters.hag_nn` (Nearest Neighbour) in PDAL. Points
97 below ground level and above the 99th percentile of height were excluded from further analyses.
98 Height profile points were exported to XYZ coordinates then imported into R for further
99 processing.
100 In R, foliage density was calculated in 5 cm layers as the proportion of filled 5 cm^3 voxels. A
101 loess model with a span of 0.1 was fitted to the foliage density values in each layer to estimate
102 the foliage density profile (Figure 7). The foliage density profile was further filtered to only tree
103 canopy material, by discarding all points below 1.3 m.

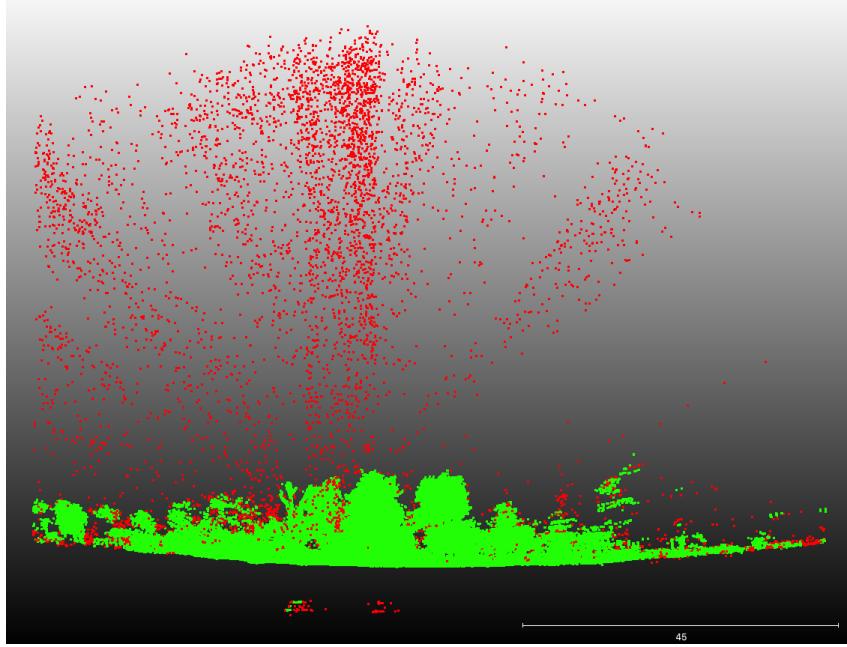


Figure 6: A 2 m deep cross section of a subplot point cloud showing the efficacy of the noise reduction and voxelisation process. Red points are excluded by the process, while green points are preserved for further analysis.

¹⁰⁴ 5 Subplot canopy complexity metrics

¹⁰⁵ 5.1 Effective Number of Layers

¹⁰⁶ The Effective Number of Layers (ENL) in the foliage density profile was used to estimate canopy
¹⁰⁷ structural complexity, using the true-numbers equivalent Shannon entropy of foliage density
¹⁰⁸ among 50 cm vertical layers (Ehbrecht et al., 2016):

$$\text{ENL} = \exp \left(- \sum_{i=1}^N p_i \times \ln p_i \right) \quad (3)$$

¹⁰⁹ Where N is the number of 50 cm bins in the height profile, and p_i is the proportion of filled
¹¹⁰ voxels in layer i (foliage density). While Ehbrecht et al. (2016) used 1 m layers, their study
¹¹¹ was conducted in temperate deciduous forest where the maximum height of the sampled forest
¹¹² stands was 40 m, whereas the maximum canopy height in this study was only 22 m. Both
¹¹³ Ehbrecht et al. (2016) and Montes et al. (2004) assert that the choice of layer thickness is largely
¹¹⁴ arbitrary, but should be determined with respect to the variability within the canopy, thus in the
¹¹⁵ sparse and highly variable savanna tree canopies measured in this study, narrower layers were
¹¹⁶ chosen. As with the conventional Shannon-Wiener diversity index, ENL increases with number
¹¹⁷ of layers and so increases with canopy height, and also increases with increasing variation in the
¹¹⁸ proportion of filled voxels per layer (Jost, 2006), but not with increasing total foliage density.

¹¹⁹ 5.2 Foliage density profiles and foliage uniformity

¹²⁰ Subplot canopy foliage density was calculated as the area under the curve of the canopy foliage
¹²¹ density profile, using trapezoid estimation. Foliage density correlates with Gross Primary
¹²² Productivity (GPP), as a greater foliage surface area allows more complete usage of the available
¹²³ light in the canopy (Kotchenova et al., 2004). To describe the uniformity of the foliage density

¹²⁴ distribution through the canopy, a linear model of cumulative foliage volume vs. height was
¹²⁵ fitted (Figure 7). Under a completely even distribution of foliage material through the canopy,
¹²⁶ the residuals of the linear model tend to zero, while clumping causes deviations from this uniform
¹²⁷ distribution and increases the sum of squared residuals. Vertical distribution of foliage is a
¹²⁸ key measure of canopy complexity. Increased foliage clumping has been linked to increased
¹²⁹ biodiversity within the canopy (Ishii et al., 2004), deeper light penetration in the canopy (Béland
¹³⁰ & Baldocchi, 2021), and overall greater canopy photosynthesis (Baldocchi & Hutchison, 1986;
¹³¹ Béland & Baldocchi, 2021).

¹³² Maximum canopy height has been used in other studies to describe canopy structural complexity
¹³³ (Scheuermann et al., 2018). At the small spatial scale of the subplots used in this study however,
¹³⁴ there proved to be too much stochastic variation in canopy height among subplots due to
¹³⁵ the distribution of individual trees to make this statistic informative as a measure of canopy
¹³⁶ complexity. Canopy height was instead calculated later at the plot level.

¹³⁷ 5.3 Canopy closure

¹³⁸ Subplot canopy closure, i.e. the proportion of the sky hemisphere occluded by plant material,
¹³⁹ a.k.a. gap fraction or site factor (Jennings, 1999), was measured by simulating a hemispherical
¹⁴⁰ image at the centre of the subplot using the point cloud data from all scans per subplot. The
¹⁴¹ point cloud was first cropped to a 20 m diameter cylinder around the subplot centre using
¹⁴² PDAL. Points below 1.3 m and within a 50 cm sphere around the subplot centre at 1.3 m height
¹⁴³ were discarded, to prevent the simulated hemispherical image being occluded by understorey
¹⁴⁴ vegetation. POV-Ray was used to simulate the hemispherical image using ray-tracing (Persistence
¹⁴⁵ of Vision Pty. Ltd., 2004). Filled voxels were represented in POV-Ray as non-reflective black
¹⁴⁶ cubes filling the 5 cm^3 voxel volume, with a white uniform sky box and no light source. POV-Ray
¹⁴⁷ produced an image with identical qualities to that of the real hemispherical photograph, using a
¹⁴⁸ fisheye lens with an equisolid projection and a view angle of 180° , located at the subplot centre
¹⁴⁹ at 1.3 m above the ground, with the top of the camera facing magnetic north and the camera
¹⁵⁰ facing directly to zenith, producing a circular image of 4016×4016 pixels.

¹⁵¹ Hemiphot (ter Steege, 2018) was used to estimate closure from both the hemispherical photo-
¹⁵² graphs and the TLS POV-Ray simulation. Images were cropped to a circle of 60° zenith angle.
¹⁵³ It can be supposed that below 60° , under most woodland canopies, variation in tree canopy
¹⁵⁴ density does little to affect sunlight penetration, due to the greater depth of canopy at these
¹⁵⁵ angles (Jupp et al., 2008). To obtain the total closure (C_α) of a circular image:

$$C_\alpha = 1 - G_{\text{tot}} = \sum_{\alpha=0.5}^{\alpha=60.0} (G_\alpha A_\alpha / A_{\text{tot}}) \quad (4)$$

¹⁵⁶ Where G_α is the fraction of unfilled pixels in ring α , A_α is the sky area of the ring segment, and
¹⁵⁷ A_{tot} is the total sky area of the hemisphere.

¹⁵⁸ Canopy closure estimates from the TLS were validated using estimates from hemispherical
¹⁵⁹ photography. A Pearson's correlation analysis showed that both methods were highly correlated
¹⁶⁰ ($r(195)=0.87$, $p<0.001$). TLS estimates of closure were almost exclusively higher than hemispherical
¹⁶¹ photography estimates, except in a few subplots with particularly low canopy closure. At
¹⁶² higher canopy closure the over-estimation of canopy closure by TLS was larger (Figure 8). This
¹⁶³ finding is in agreement with previous studies which have found that the magnitude of TLS
¹⁶⁴ canopy closure over-estimation depends on gap size distribution, where a site with greater canopy
¹⁶⁵ cover and a gap fraction dominated by small within crown gaps will have a larger over-estimate
¹⁶⁶ than a more open site with a gap fraction dominated by large between crown gaps (Seidel et al.,
¹⁶⁷ 2012). A linear mixed model which included nested random intercept effects for subplots within

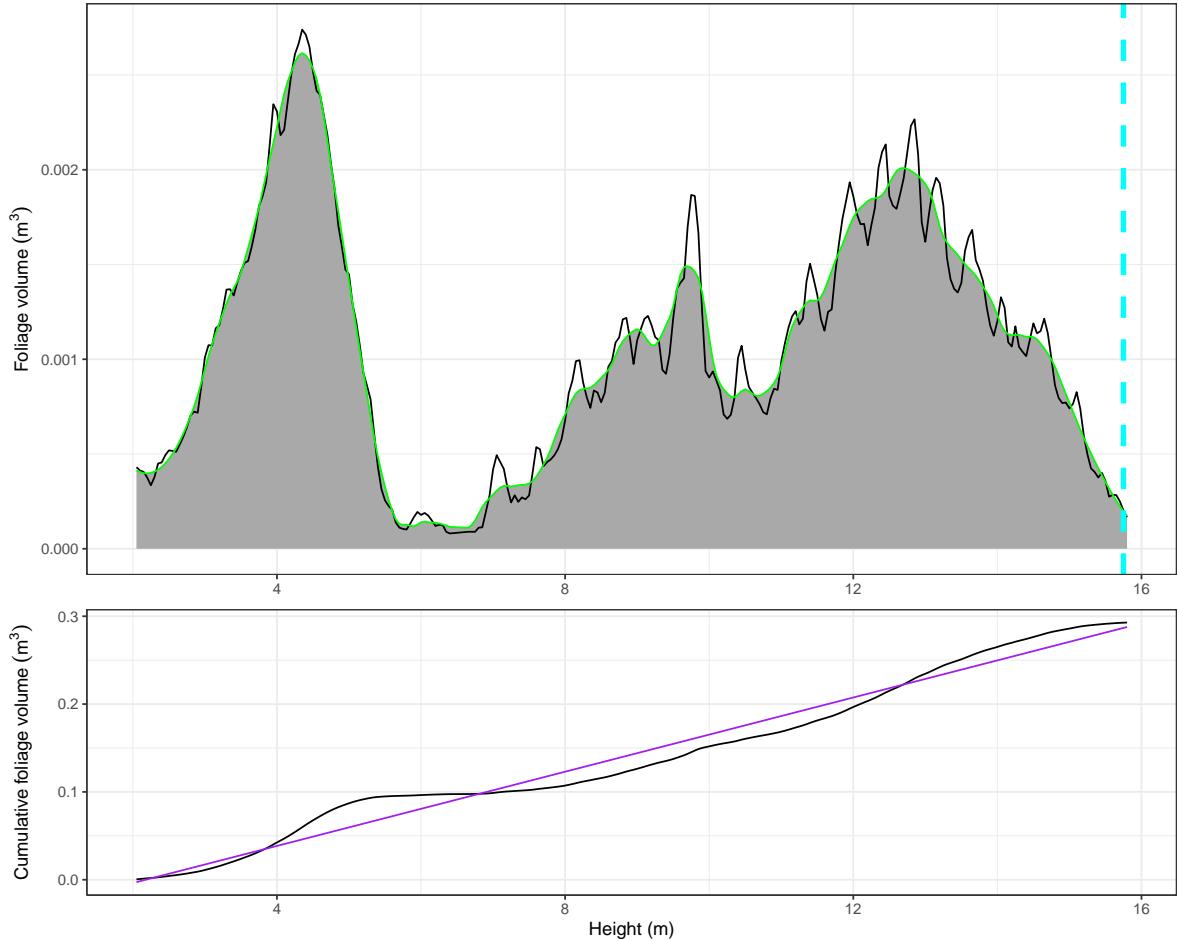


Figure 7: Subplot foliage volume height profile (top) and cumulative foliage volume profile (bottom) for a subplot in Bicuar National Park, Angola, to illustrate some of the canopy structure metrics extracted from each height profile. In the top panel: the dashed cyan line shows the 99th percentile of canopy height, used here as a measure of canopy top height in plot level canopy surface modelling. The black trace shows the foliage density height profile, and the green trace shows the loess model fitted to the data, with the area under the canopy shaded grey. The bottom panel: the black trace shows the cumulative foliage volume through the canopy, taken from the loess fit in the top panel. The purple line shows the line of best fit of a linear model through this data. Not illustrated is the Effective Number of Layers (ENL) metric.

168 plots was used to identify if sites differed significantly in their relationship between hemispherical
169 photography and TLS estimates of canopy closure. There was no significant difference in model
170 fixed effect slope between plots in Bicuar National Park, Angola, and those in Mtarure, Tanzania
171 ($\beta(173)=0.13\pm 0.011$, $p=0.21$).

172 Measurements of canopy closure are expected to positively correlate with foliage density, as
173 increased foliage density will reduce the number and size of canopy gaps. However, canopy
174 closure and foliage density do access subtly different aspects of canopy complexity. Clumping
175 of foliage affects the relationship between canopy closure and foliage density. As clumping
176 increases, all else being equal the value of foliage density will remain constant, while the value
177 of canopy closure may decrease as between canopy gaps increase in size (Béland & Baldocchi,
178 2021). Foliage density is more often related to productivity as it is a more direct measure of leaf
179 area (Seidel et al., 2013), while canopy closure is more often related to understorey processes
180 and light penetration, as it is only a 2D measurement of canopy structure.

181 6 Whole plot canopy complexity metrics

182 6.1 Canopy height

183 The canopy height of each 1 ha plot was estimated using unified point clouds from all subplots.
184 The unified point cloud was voxelised to 10 cm^3 , and the 99th percentile of height was recorded
185 as the canopy height of each 10 cm^2 column. Maximum height was not used as this occasionally
186 constituted a severe outlier which skewed further canopy surface model smoothing. The point
187 cloud was then cropped to the plot boundaries, located using PPK GNSS similar to the TLS
188 targets. A pit-filling algorithm described in Khosravipour et al. (2014) was used to smooth the
189 canopy surface model, at a resolution of 50 cm, removing gaps within trees caused by incomplete
190 penetration of the LiDAR beam (Figure 10).

191 Mean canopy height across the plot and the coefficient of variation (CV) of canopy height
192 were extracted from the canopy surface model for use in statistical analyses. Canopy height
193 CV describes canopy structural diversity measured by the heterogeneity of the canopy surface
194 (Parker & Russ, 2004). Other studies in closed canopy temperate and boreal forests have used
195 metrics similar to the Topographic Roughness Index to measure canopy surface heterogeneity,
196 by comparing canopy height to that of neighbouring pixels in the canopy height model (Herrero-
197 Huerta et al., 2020; Weligepolage et al., 2012). In this study however, the sparse nature of the
198 tree canopies meant that these metrics were overly influenced by canopy density and the edges
199 of individual tree canopies.

200 6.2 Canopy rugosity and foliage density

201 Canopy rugosity (R_c) was calculated to describe structural complexity across the entire canopy
202 profile of each plot, rather than just the canopy surface (Hardiman et al., 2011). R_c first
203 calculates the standard deviation of foliage density in 50 cm^2 columns across the plot (σG_z),
204 then calculates the standard deviation of those standard deviations:

$$R_c = \sigma(\sigma G_z)_x \quad (5)$$

205 Where G_z is the vertical height axis z , x is the horizontal axis, and σ is the standard deviation.
206 Additionally, foliage density was calculated at the plot level as the sum of filled 50 cm^3 voxels
207 across the plot, and plot canopy closure was calculated as the mean of all subplot canopy closure
208 estimates.

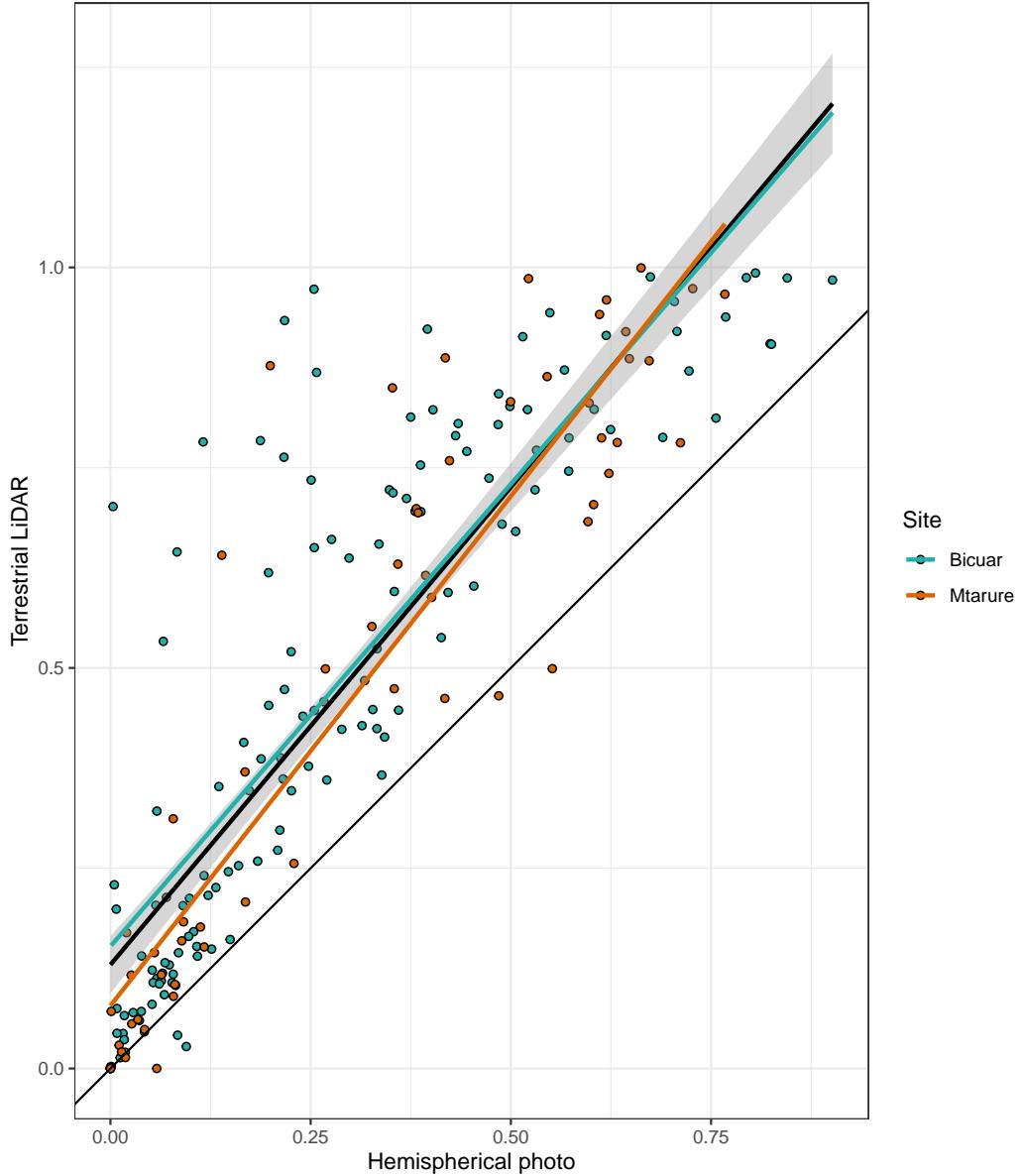
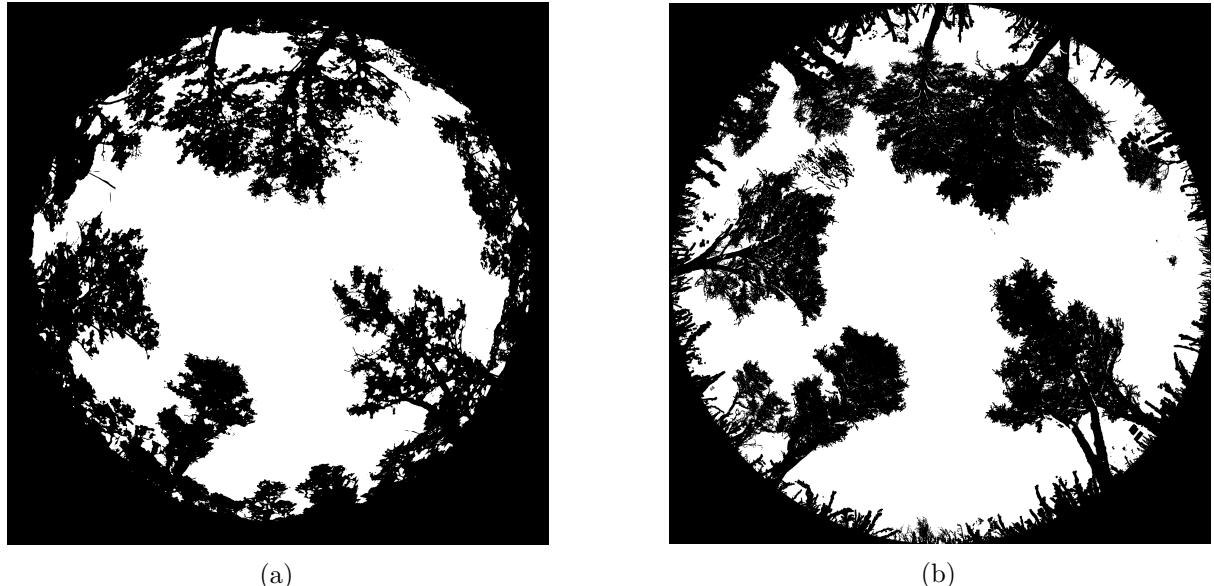


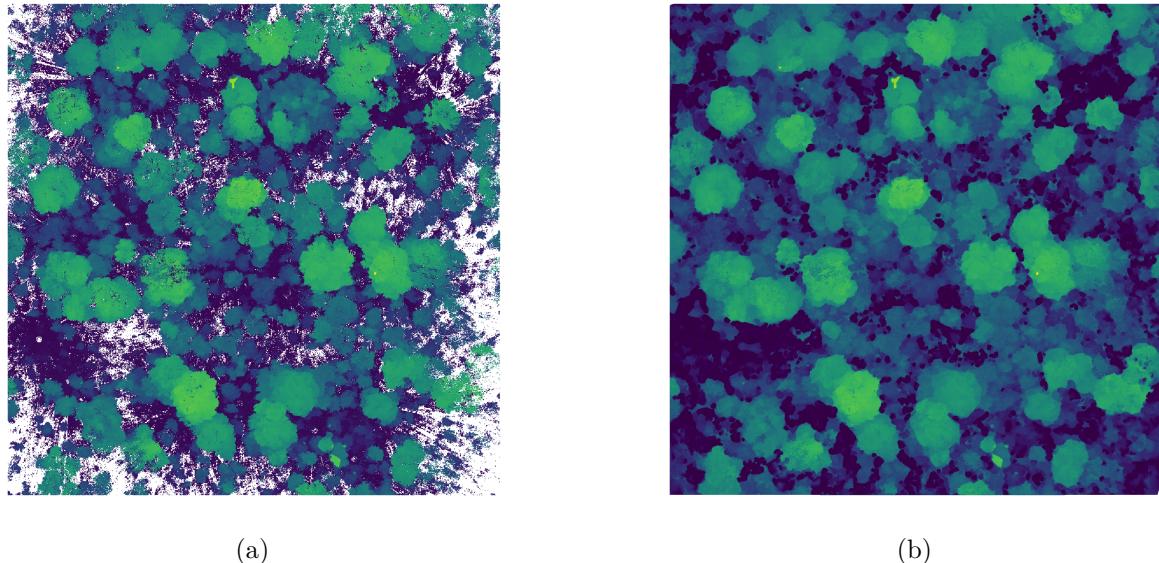
Figure 8: Comparison of canopy closure estimation from TLS and hemispherical photography. The thick black line of best fit is a linear model of all points ± 1 standard error, while the coloured lines are site specific linear models. The thin black line shows the 1:1 fit.



(a)

(b)

Figure 9: Comparison of hemispherical images for a subplot in Bicuar National Park, Angola. (a) A hemispherical photograph, and (b) a multi-scan point cloud modelled as cubic voxels with POV-Ray. The hemispherical photograph (left) shows some blooming, especially in the tree on the bottom right of the image, where light is seen ‘bleeding’ through the darker canopy material, causing an under-estimation in canopy closure. Note also that while there are minor variations in image height between TLS and hemispherical photos, this does not affect canopy closure estimates, as images were first cropped to a 60° angle of view.



(a)

(b)

Figure 10: Top-down view of a 1 ha plot in Bicuar National Park. (a) The point cloud after voxelisation, noise reduction, and taking the 99th percentile of stem height in each 5 cm vertical bin. (b) The same point cloud after pit filling to generate a smooth canopy height profile. Points are coloured according to point height from the ground.

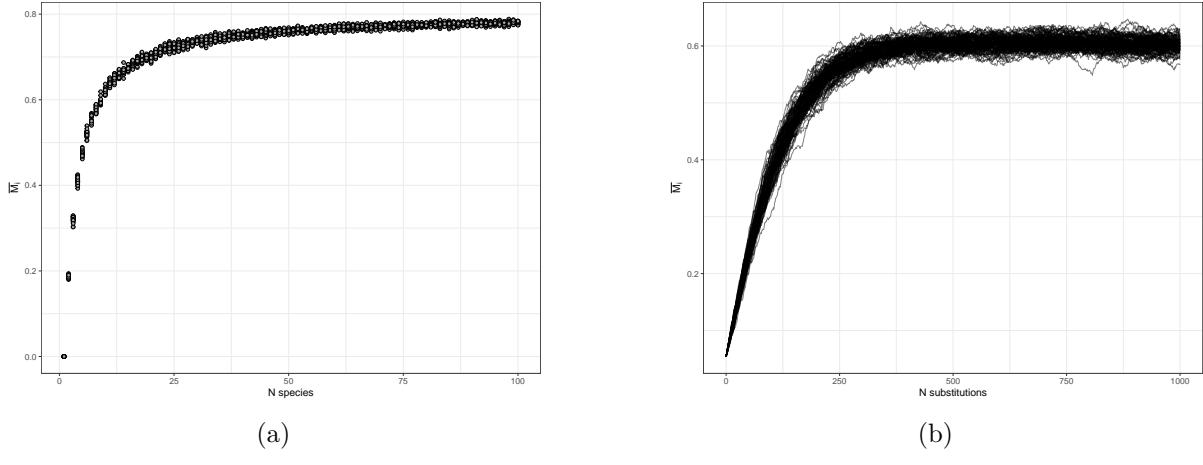


Figure 11: The behaviour of the spatial mingling index (M_i) with increasing number of species (a), and increasing spatial mixing of species (b). The left panel was generated by randomly assigning different numbers of species, in equal proportions, to an evenly spaced grid of individuals. 20 replicates were conducted for each number of species. The right panel was generated by randomly swapping pairs of individuals in a plot with 9 species arranged in mono-specific square blocks in an evenly spaced grid. Each line shows a single replicate, where individuals were swapped in an additive fashion, with 100 total.

209 7 Stand structure metrics

210 7.1 Spatial mingling of species

211 The spatial mingling index (M_i) is a spatially explicit estimate of the degree to which species are
 212 spatially mixed within a plot. Here, M was calculated at the plot level as the mean of M_i (von
 213 Gadow & Hui, 2002), with the adjustment for potential neighbourhood species pool suggested
 214 by Hui et al. (2011):

$$M = \bar{M}_i$$

$$M_i = \frac{S_i}{n_{\max}} \frac{1}{k} \sum_{j=1}^k v_j \quad (6)$$

with $v_j = \begin{cases} 0, & \text{neighbour } j \text{ same species as reference } i \\ 1, & \text{otherwise} \end{cases}$

215 Where k is the number of nearest neighbours considered for each reference tree, S_i is the number
 216 of species found among the k nearest neighbours of tree i , n_{\max} is the potential number of
 217 species in the neighbourhood, i.e. $k + 1$, and N is the total number of trees in the plot. The
 218 conventional value of $k = 4$ was used here (Hui & Albert, 2004; Hui et al., 2007; von Gadow &
 219 Hui, 2002). The value of M_i increases with greater mixing of species, and all else being equal
 220 will increase with number of species within the plot (Figure 11).

221 7.2 Uniform angle index

222 The uniform angle index (winkelmass, W) was calculated to estimate the degree of spatial
 223 regularity in stem spatial distribution. Here, W was calculated at the plot level as the mean of
 224 W_i (von Gadow & Hui, 2002):

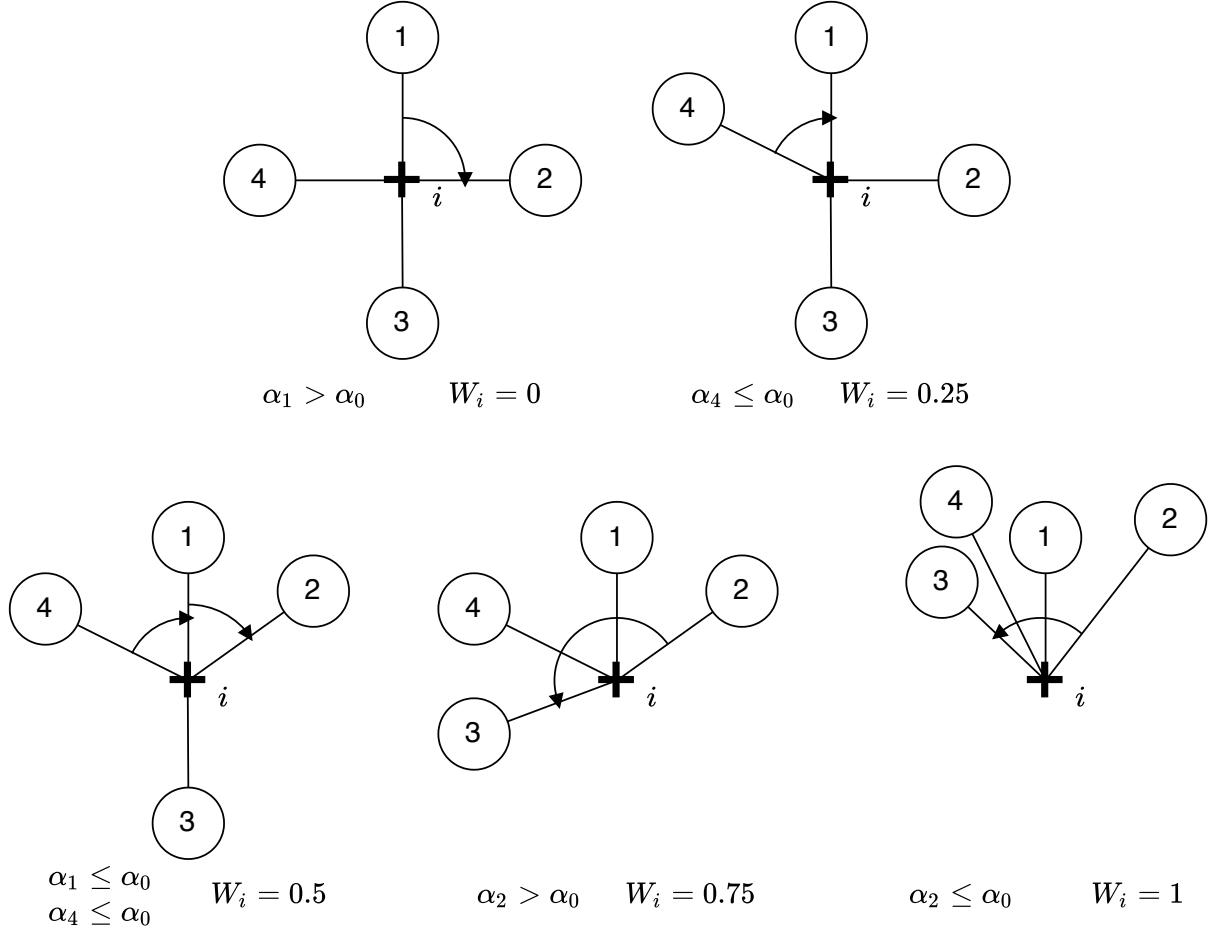


Figure 12: Possible values of W_i at a sample point i , denoted by a cross. Neighbours are represented as circles numbered sequentially from 1 to 4, where $k = 4$. The angles of arrows in each example are given below, along with the uniform angle index for that example.

$$\begin{aligned}
 W &= \overline{W}_i \\
 W_i &= \frac{1}{k} \sum_{j=1}^k v_j \\
 \text{with } v_j &= \begin{cases} 0, & \alpha_j \leq \alpha_0 \\ 1, & \text{otherwise} \end{cases}
 \end{aligned} \tag{7}$$

225 Where k is the number of neighbours considered, α_j is the angle between consecutive neighbours
 226 and α_0 is the critical angle, where $\alpha_0 = 72^\circ$ (Hui & Gadow, 2002). Figure 12 demonstrates
 227 how the value of W_i varies according to spatial distribution of neighbours. The value of the
 228 uniform angle index increases with increasing spatial clumping (decreasing spatial regularity)
 229 of individuals (Figure 13), and in a plot with random tree distribution will increase as more
 230 neighbours are considered (Figure 14).

231 7.3 Voronoi tessellation

232 In addition to spatial regularity, the spatial uniformity of stems is another important aspect
 233 of tree spatial distribution. While the uniform angle index effectively measures similarity to a

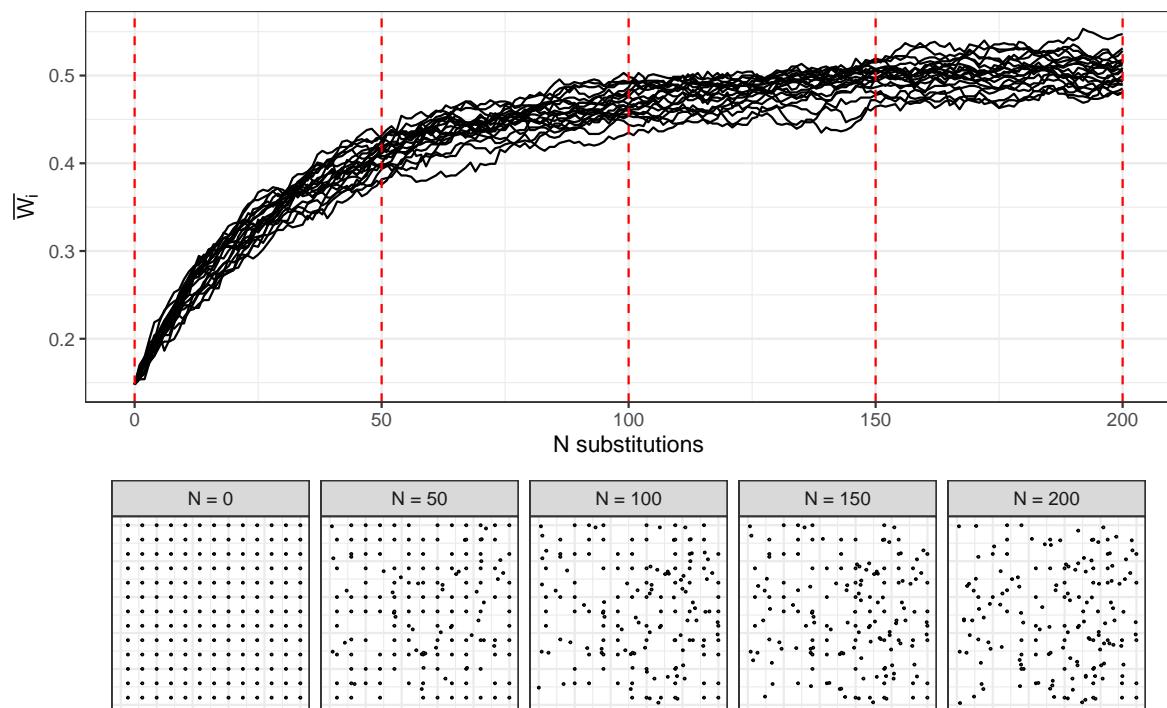


Figure 13: Variation in uniform angle index with increasing spatial irregularity of individuals. The top panel shows variation of uniform angle index in 20 plots as individuals are sequentially moved to a random location within the plot. Red dotted lines correspond to the panels below which show the spatial distribution of individuals after a given number of random individual movements.

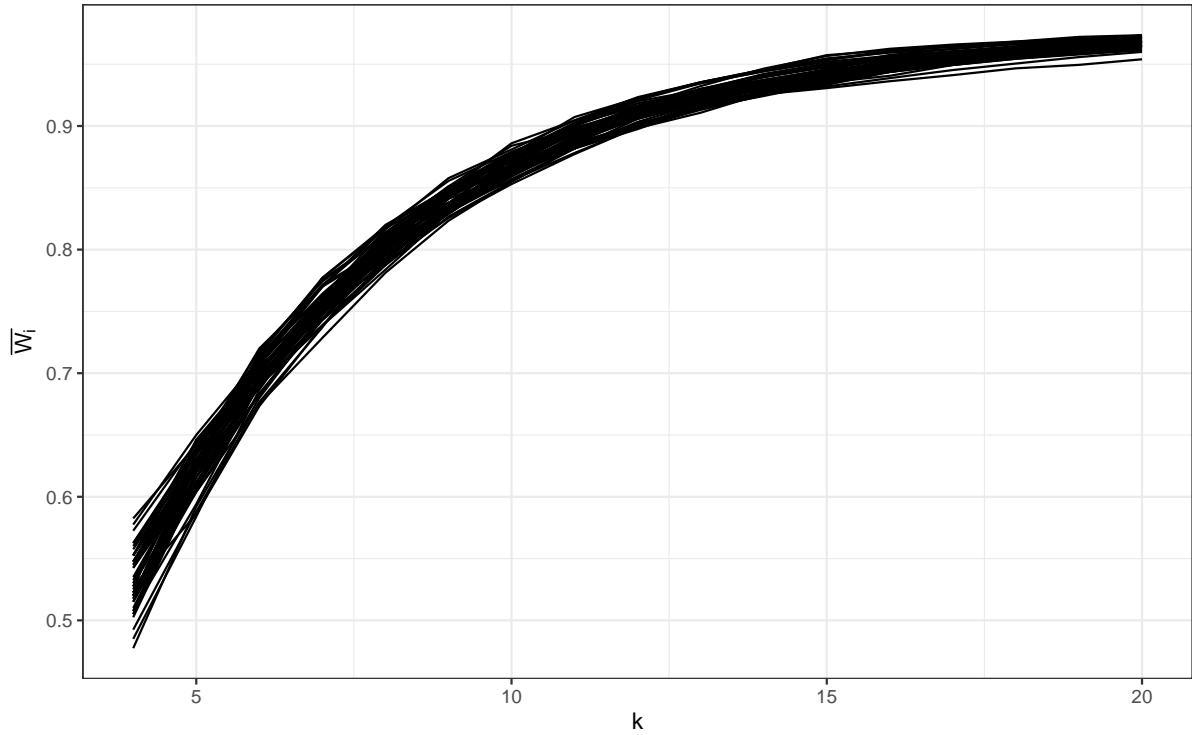


Figure 14: Variation in uniform angle index with increasing number of neighbours k considered in the calculation. 50 replicate plots were used, each with 100 individuals randomly distributed in space.

grid-like distribution of individuals, it does not account for variation in the relative distance of stems from their neighbours over the plot area. Spatial uniformity is defined here by two criteria: equality of spacing among individuals within the plot, and even coverage of individuals across the plot (Ong et al., 2012). Departures from spatial uniformity indicate clustering of individuals. Voronoi tessellation is a method of partitioning an n-dimensional space into regions according to the closest individual (Figure 15). Voronoi tessellation was conducted using stem location within each plot. The CV of the area of Voronoi cells was then used as a measure of spatial clustering which is sensitive to both the criteria defining spatial uniformity, and is independent of tree density (Figure 16). As clustering increases, individuals within clusters will exhibit progressively smaller Voronoi cells, while individuals at the edges of clusters will exhibit progressively larger Voronoi cells, thus increasing the cell area CV.

7.4 Subplot canopy crowding

An adapted version of the Iterative Hegyi Index (H_i) was used to estimate tree spatial structure in subplots (Hegyi, 1974). The adapted formula used here allows the index to be based on a point rather than a focal tree, transforming it from a tree-centric competition index to a point-centric crowding index:

$$H_i = \log \sum_{j=1}^n \left(\frac{1}{L_{ij}} D_j \right) \quad (8)$$

Where n is the number of stems with canopy material within the subplot, D_j is the stem diameter of stem j and L_{ij} is the distance of stem j from the subplot centre i . H_i uses an iterative method for choosing active canopy occupants at the subplot centre, where the nearest individual to the

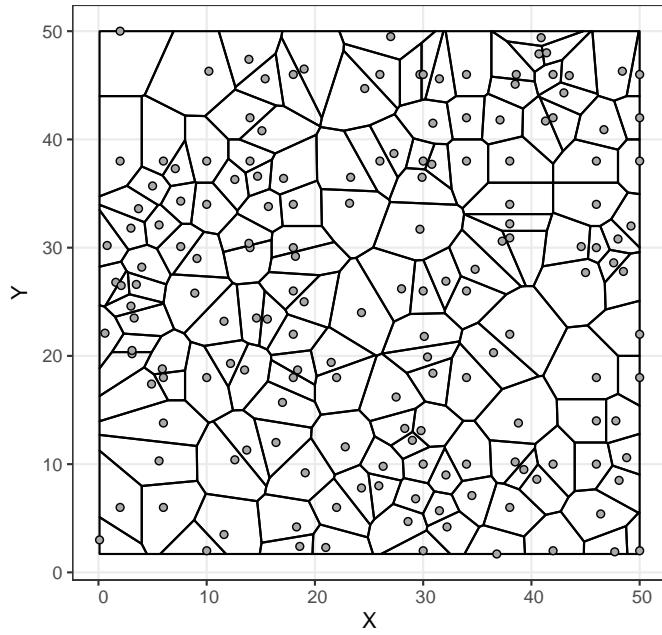


Figure 15: An example of a square plot with 100 randomly located individuals, with polygons constructed by Voronoi tessellation.

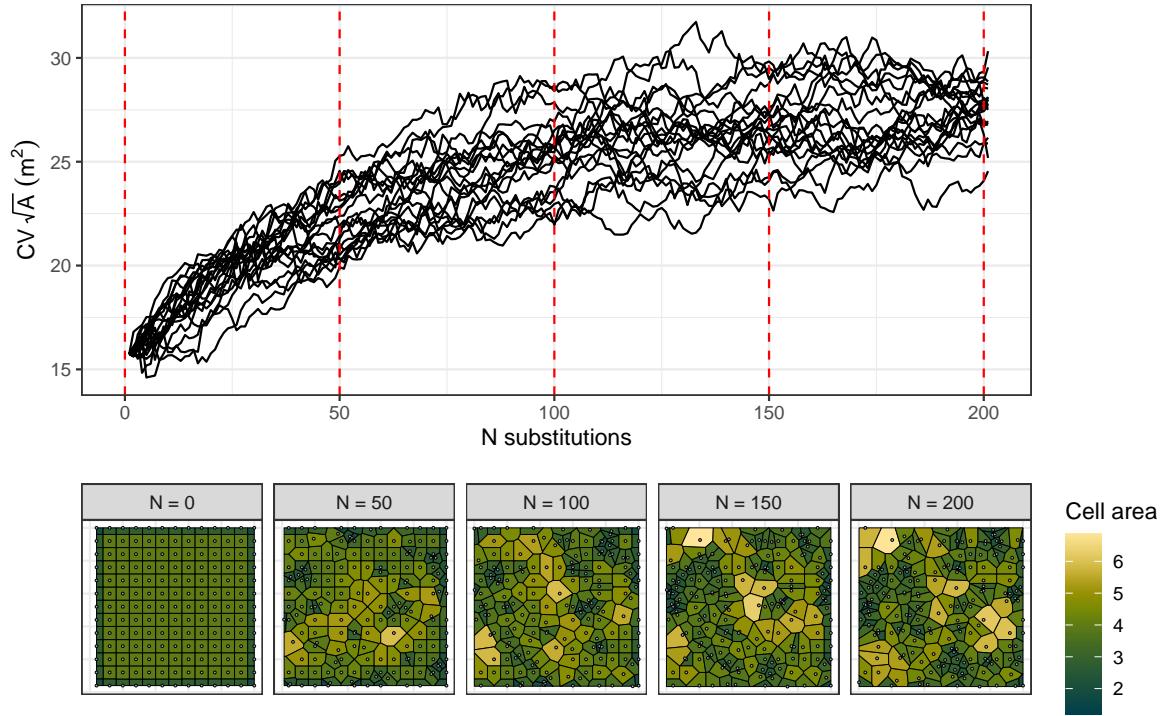


Figure 16: Voronoi cell area CV with increasing spatial irregularity of individuals. The top panel shows variation in Voronoi cell area CV in 20 plots as individuals are sequentially moved to a random location within the plot. Red dotted lines correspond to the panels below which show the spatial distribution of individuals after a given number of random individual movements. Voronoi cells in the bottom panels are shaded according to their area.

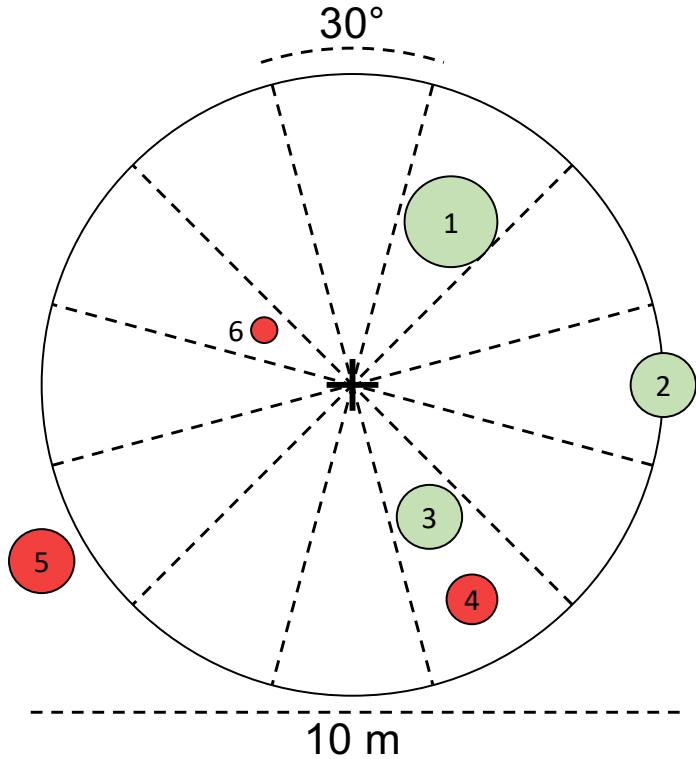


Figure 17: Schematic diagram demonstrating use of the Iterative Hegyi Index to assess crowding within each subplot. The 10 metre diameter subplot is divided into 12 equally sized sectors. Within each sector, the nearest stem of sufficient size (>5 cm diameter) to the subplot centre is recorded (e.g. 1). All stems with any canopy material inside the subplot are valid (e.g. 2). Stem 4 is not valid as it is behind stem 3. Stem 5 is invalid as all its canopy is outside the subplot. Stem 6 is too small to be recorded.

253 subplot centre from each of 12 equally sized sectors is classified as the active stem (Figure 17).
 254 H_i was preferred over stem density to describe stem crowding in subplots because it is sensitive
 255 to how close a stem is to the subplot centre, which will affect canopy closure even if the number
 256 of stems in the subplot remains the same.

257 References

- 258 Baldocchi, D. D. & B. A. Hutchison (1986). ‘On estimating canopy photosynthesis and stomatal
 259 conductance in a deciduous forest with clumped foliage’. In: *Tree Physiology* 2.1-2-3, pp. 155–
 260 168. DOI: [10.1093/treephys/2.1-2-3.155](https://doi.org/10.1093/treephys/2.1-2-3.155).
- 261 Béland, M. & D. D. Baldocchi (2021). ‘Vertical structure heterogeneity in broadleaf forests: Effects
 262 on light interception and canopy photosynthesis’. In: *Agricultural and Forest Meteorology* 307,
 263 p. 108525. DOI: [10.1016/j.agrformet.2021.108525](https://doi.org/10.1016/j.agrformet.2021.108525).
- 264 Béland, M. & H. Kobayashi (2021). ‘Mapping forest leaf area density from multiview terrestrial
 265 lidar’. In: *Methods in Ecology and Evolution* 12.4, pp. 619–633. DOI: [10.1111/2041-210x.13550](https://doi.org/10.1111/2041-210x.13550).
- 266 Brusa, A. & D. E. Bunker (2014). ‘Increasing the precision of canopy closure estimates from
 267 hemispherical photography: Blue channel analysis and under-exposure’. In: *Agricultural and
 268 Forest Meteorology* 195–196, pp. 102–107. DOI: [10.1016/j.agrformet.2014.05.001](https://doi.org/10.1016/j.agrformet.2014.05.001).
- 269 Chen, X., T. Allison, W. Cao, K. Ferguson, S. Grunig, V. Gomez, A. Kipka, J. Kohler, H.
 270 Landau, R. Leandro et al. (2011). *Trimble RTX, an innovative new approach for network*

- 272 RTK. Tech. rep. Portland OR, USA: International Technical Meeting of the Satellite Division
273 of the Institute of Navigation, ION GNSS, pp. 2214–2219.
- 274 Cifuentes, R., D. V. der Zande, J. Farifteh, C. Salas & P. Coppin (2014). ‘Effects of voxel size
275 and sampling setup on the estimation of forest canopy gap fraction from terrestrial laser
276 scanning data’. In: *Agricultural and Forest Meteorology* 194, pp. 230–240. DOI: 10.1016/j.
277 agrformet.2014.04.013.
- 278 Ehbrecht, M., P. Schall, J. Juchheim, C. Ammer & D. Seidel (2016). ‘Effective number of layers:
279 A new measure for quantifying three-dimensional stand structure based on sampling with
280 terrestrial LiDAR’. In: *Forest Ecology and Management* 380, pp. 212–223. DOI: 10.1016/j.
281 foreco.2016.09.003.
- 282 Frazer, G. W., R. A. Fournier, J. Trofymow & R. J. Hall (2001). ‘A comparison of digital and
283 film fisheye photography for analysis of forest canopy structure and gap light transmission’. In:
284 *Agricultural and Forest Meteorology* 109.4, pp. 249–263. DOI: 10.1016/s0168-1923(01)00274-
285 x.
- 286 Grau, E., S. Durrieu, R. Fournier, J.-P. Gastellu-Etchegorry & T. Yin (2017). ‘Estimation
287 of 3D vegetation density with Terrestrial Laser Scanning data using voxels. A sensitivity
288 analysis of influencing parameters’. In: *Remote Sensing of Environment* 191, pp. 373–388. DOI:
289 10.1016/j.rse.2017.01.032.
- 290 Hardiman, B. S., G. Bohrer, C. M. Gough, C. S. Vogel & P. S. Curtis (2011). ‘The role of canopy
291 structural complexity in wood net primary production of a maturing northern deciduous
292 forest’. In: *Ecology* 92.9, pp. 1818–1827. DOI: 10.1890/10-2192.1.
- 293 Hegyi, F. (1974). ‘A simulation model for managing jack-pine stands’. In: *Royal College of
294 Forestry, editor*. Stockholm, Sweden: Royal College of Forestry, pp. 74–90.
- 295 Herbert, T. J. (1987). ‘Area projections of fisheye photographic lenses’. In: *Agricultural and
296 Forest Meteorology* 39.2-3, pp. 215–223. DOI: 10.1016/0168-1923(87)90039-6.
- 297 Herrero-Huerta, M., A. Bucksch, E. Puttonen & K. M. Rainey (2020). ‘Canopy Roughness: A
298 New Phenotypic Trait to Estimate Aboveground Biomass from Unmanned Aerial System’. In:
299 *Plant Phenomics* 2020, pp. 1–10. DOI: 10.34133/2020/6735967. URL: <https://doi.org/10.34133%2F2020%2F6735967>.
- 300 Hu, L. & J. Zhu (2009). ‘Determination of the tridimensional shape of canopy gaps using two
301 hemispherical photographs’. In: *Agricultural and Forest Meteorology* 149.5, pp. 862–872. DOI:
302 10.1016/j.agrformet.2008.11.008.
- 303 Huang, L. & M. J. Wang (1995). ‘Image thresholding by minimizing the measures of fuzziness’.
304 In: *Pattern Recognition* 28.1, pp. 41–51. DOI: 0031-3203/95.
- 305 Hui, G. & M. Albert (2004). ‘Stichprobensimulationen zur Schätzung nachbarschaftsbezogener
306 Strukturparameter in Waldbeständen [Simulation studies for estimating neighborhood-based
307 structural parameters in forest stands]’. In: *Allgemeine Forst und Jagdzeitung* 175, pp. 10–11.
- 308 Hui, G., K. von Gadow, Y. Hu & H. Xu (2007). *Structure-based forest management*. Beijing,
309 China: China Forestry Publishing House.
- 310 Hui, G., X. Zhao, Z. Zhao & K. von Gadow (2011). ‘Evaluating tree species spatial diversity
311 based on neighbourhood relationships’. In: *Forest Science* 57.4, pp. 292–300. DOI: 10.1093/
312 forestscience/57.4.292.
- 313 Hui, G. & K. Gadow (2002). ‘Das Winkelmaß-Theoretische Überlegungen zum optimalen
314 Standardwinkel’. In: *Allgemeine Forst U. Jagdzeitung* 173 (9), pp. 173–177.
- 315 Ishii, H. T., S.-i. Tanabe & T. Hiura (2004). ‘Exploring the relationships among canopy structure,
316 stand productivity, and biodiversity of temperate forest ecosystems’. In: *Forest Science* 50.3,
317 pp. 342–355. DOI: 10.1093/forestscience/50.3.342.
- 318 Jennings, S. (1999). ‘Assessing forest canopies and understorey illumination: canopy closure,
319 canopy cover and other measures’. In: *Forestry* 72.1, pp. 59–74. DOI: 10.1093/forestry/72.
320 1.59.

- 322 Jost, L. (2006). ‘Entropy and diversity’. In: *Oikos* 113.2, pp. 363–375. DOI: 10.1111/j.2006.0030-1299.14714.x.
- 323
- 324 Jupp, D. L. B., D. S. Culvenor, J. L. Lovell, G. J. Newnham, A. H. Strahler & C. E. Woodcock
325 (2008). ‘Estimating forest LAI profiles and structural parameters using a ground-based laser
326 called ‘Echidna’’. In: *Tree Physiology* 29, pp. 171–181. DOI: 10.1093/treephys/tpn022.
- 327 Khosravipour, A., A. K. Skidmore, M. Isenburg, T. Wang & Y. A. Hussin (2014). ‘Generating
328 Pit-free Canopy Height Models from Airborne LiDAR’. In: *Photogrammetric Engineering &*
329 *Remote Sensing* 80.9, pp. 863–872. DOI: 10.14358/pers.80.9.863.
- 330 Kotchenova, S. Y., X. Song, N. V. Shabanov, C. S. Potter, Y. Knyazikhin & R. B. Myneni
331 (2004). ‘Lidar remote sensing for modeling gross primary production of deciduous forests’. In:
332 *Remote Sensing of Environment* 92.2, pp. 158–172. DOI: 10.1016/j.rse.2004.05.010.
- 333 Leica Camera AG (2009). *Leica Cyclone*. Version 9.1.
- 334 Montes, F., I. Cañellas, M. del Río, R. Calama & G. Montero (2004). ‘The effects of thinning
335 on the structural diversity of coppice forests’. In: *Annals of Forest Science* 61.8, pp. 771–779.
336 DOI: 10.1051/forest:2004074.
- 337 Ong, M. S., Y. C. Kuang & M. P.-L. Ooi (2012). ‘Statistical measures of two dimensional
338 point set uniformity’. In: *Computational Statistics & Data Analysis* 56.6, pp. 2159–2181. DOI:
339 10.1016/j.csda.2011.12.005.
- 340 Parker, G. G. & M. E. Russ (2004). ‘The canopy surface and stand development: assessing
341 forest canopy structure and complexity with near-surface altimetry’. In: *Forest Ecology and
342 Management* 189.1-3, pp. 307–315. DOI: 10.1016/j.foreco.2003.09.001.
- 343 PDAL Contributors (2018). *PDAL Point Data Abstraction Library*. DOI: 10.5281/zenodo.
344 2556738.
- 345 Persistence of Vision Pty. Ltd. (2004). *Persistence of Vision Raytracer (Version 3.7)*. [Computer
346 software].
- 347 Rusu, R. B., Z. C. Marton, N. Blodow, M. Dolha & M. Beetz (2008). ‘Towards 3D Point cloud
348 based object maps for household environments’. In: *Robotics and Autonomous Systems* 56.11,
349 pp. 927–941. DOI: 10.1016/j.robot.2008.08.005.
- 350 Scheuermann, C. M., L. E. Nave, R. T. Fahey, K. J. Nadelhoffer & C. M. Gough (2018).
351 ‘Effects of canopy structure and species diversity on primary production in upper Great
352 Lakes forests’. In: *Oecologia* 188.2, pp. 405–415. DOI: 10.1007/s00442-018-4236-x. URL:
353 <https://doi.org/10.1007%2Fs00442-018-4236-x>.
- 354 Schneider, C. A., W. S. Rasband & K. W. Eliceiri (2012). ‘NIH Image to ImageJ: 25 years of
355 image analysis’. In: *Nature Methods* 9.7, pp. 671–675. DOI: 10.1038/nmeth.2089.
- 356 Seidel, D., S. Fleck & C. Leuschner (2012). ‘Analyzing forest canopies with ground-based
357 laser scanning: A comparison with hemispherical photography’. In: *Agricultural and Forest
358 Meteorology* 154-155, pp. 1–8. DOI: 10.1016/j.agrformet.2011.10.006.
- 359 Seidel, D., C. Leuschner, C. Scherber, F. Beyer, T. Wommelsdorf, M. J. Cashman & L. Fehr-
360 mann (2013). ‘The relationship between tree species richness, canopy space exploration and
361 productivity in a temperate broad-leaf mixed forest’. In: *Forest Ecology and Management* 310,
362 pp. 366–374. DOI: 10.1016/j.foreco.2013.08.058.
- 363 ter Steege, H. (2018). *Hemiphot.R: Free R scripts to analyse hemispherical photographs for
364 canopy openness, leaf area index and photosynthetic active radiation under forest canopies*.
365 Unpublished report. Leiden, The Netherlands: Naturalis Biodiversity Center. URL: <https://github.com/Naturalis/Hemiphot>.
- 366
- 367 von Gadow, K. & G. Hui (2002). ‘Characterising forest spatial structure and diversity’. In:
368 *Proceedings of the IUFRO International workshop ‘Sustainable forestry in temperate regions’*.
369 Ed. by L. Bjoerk. Lund, Sweden, pp. 20–30.
- 370 Weligepolage, K., A. Gieske & Z. Su (2012). ‘Surface roughness analysis of a conifer forest canopy
371 with airborne and terrestrial laser scanning techniques’. In: *International Journal of Applied*

- ³⁷² *Earth Observation and Geoinformation* 14.1, pp. 192–203. DOI: 10.1016/j.jag.2011.08.014.
³⁷³ URL: <https://doi.org/10.1016%2Fj.jag.2011.08.014>.
- ³⁷⁴ Zhang, K., S.-C. Chen, D. Whitman, M.-L. Shyu, J. Yan & C. Zhang (2003). ‘A progressive
³⁷⁵ morphological filter for removing nonground measurements from airborne LiDAR data’. In:
³⁷⁶ *IEEE Transactions on Geoscience and Remote Sensing* 41.4, pp. 872–882. DOI: 10.1109/tgrs.
³⁷⁷ 2003.810682.