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1 **Habitat highs and lows: Using terrestrial and UAV LiDAR for**
2 **modelling avian species richness and abundance in a restored**
3 **woodland**

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16
17 **1. Abstract**

18 Vegetation structure influences landscape use and habitat quality for many bird
19 species. Owing to the difficulties associated with collecting structural data from
20 traditional field measurements, numerous studies have investigated the utility of
21 Light detection and ranging (LiDAR) for providing landscape-scale structural
22 information that may be useful for exploring animal-habitat associations. Notably,
23 almost all of these studies have involved the use of LiDAR from airborne rather than
24 terrestrial platforms. However, vegetation metrics that might be important for
25 explaining bird species occurrence and diversity, such as understory vegetation
26 complexity and overall vegetation volume, may be partially obscured from airborne
27 sensors by tree canopy cover. These challenges might be overcome by terrestrial
28 and UAV LiDAR sensors that can provide detailed information of understory forest
29 strata. For the first time, we collected terrestrial LiDAR (TLS) and unoccupied aerial
30 vehicle LiDAR (ULS) data in a woodland landscape to compare the ability of both
31 sensors to identify relationships among vegetation structural metrics and bird
32 species richness and abundance. Overall, TLS and ULS models provided similar
33 results based on the sampling methodology we used for LiDAR data collection in an
34 open woodland landscape. Canopy roughness, ground vegetation vertical
35 complexity, total vegetation volume and canopy height derived from these sensors
36 were among the most common significant variables in explaining avian diversity and

37 individual species abundance. Individual species abundance models provided better
38 prediction power (up to $R^2 = 0.82$ (TLS) and $R^2 = 0.83$ (ULS)) than bird community
39 abundance by functional guilds (up to $R^2 = 0.40$ (TLS), $R^2 = 0.41$ (ULS)) and overall
40 bird abundance ($R^2 = 0.10$ (TLS), $R^2 = 0.16$ (ULS)), species richness ($R^2 = 0.14$ (TLS),
41 $R^2 = 0.14$ (ULS)) and diversity ($R^2 = 0.17$ (TLS), $R^2 = 0.16$ (ULS)). Additionally, we
42 found that several vulnerable bird species are strongly associated with LiDAR
43 structural variables, which may assist with habitat assessment and conservation
44 management.

45 **Keywords:** TLS, laser scanning, birds, remote sensing, habitat modelling, Australia,
46 vegetation structure

47 **2. Introduction**

48 Vegetation structure is the horizontal and vertical arrangement of plants across the
49 landscape (Davies and Asner 2014; Verschuyt et al., 2008). Vegetation structural
50 complexity and heterogeneity have been shown to have a positive relationship to
51 biodiversity because they create a greater variety of microclimate and microhabitats
52 that produce more food and cover for a range of species (Verschuyt et al., 2008).
53 Previously, a number of studies have identified strong relationships between bird
54 diversity and abundance and vegetation structure across different layers of
55 vegetation (Kikkawa 1982; MacArthur 1961; Sekercioglu 2002; Stanley and Herman
56 1974). However, traditional methods to measure vegetation structure can be very
57 time consuming and are often limited to point sampling a subset of the landscape
58 (David et al., 2010; James and Shugart Jr 1970; Zehm et al., 2003).

59 Light Detection and Ranging (LiDAR) remote sensing technology can provide high-
60 resolution topographic maps and information on vegetation height, cover, volume
61 and complexity with a high level of detail and accuracy across landscapes (Bergen et
62 al., 2009; Lefsky et al., 2002; Levick et al., 2019). Unlike passive sensors that
63 depend on sun light reflected from objects, LiDAR uses a laser pulse emitted from
64 the sensor. The reflected light is detected and digitized by the sensor creating a
65 record of returns that are a function of the distance between the sensor and the
66 reflected object (Anderson et al., 2016; Goetz et al., 2007; Lefsky et al., 2002).
67 LiDAR sensor platforms can be terrestrial (Terrestrial Laser Scanner - TLS), mobile,

68 UAV (Unoccupied Aerial Vehicle) laser scanner (ULS), airborne (Airborne Laser
69 Scanner - ALS) or satellite based (Sumnall et al., 2016; Vierling et al., 2008).

70 Vegetation structural metrics derived from LiDAR data have been widely used to
71 investigate animal-habitat relationships, with a particular focus on birds (Bradbury et
72 al., 2005; Eldegard et al., 2014; Goetz et al., 2007; Müller et al., 2010). Goetz et al.
73 (2007) found that LiDAR derived canopy height distribution variables were a stronger
74 predictor of bird species richness in temperate forest ecosystems than a commonly
75 used vegetation index, Normalized Difference Vegetation Index (NDVI) derived from
76 Landsat imagery. Various LiDAR-derived vegetation height, complexity and volume
77 metrics are significantly correlated to bird species presence, diversity and
78 abundance in many different forest environments (Clawges et al., 2008). Forest
79 songbird species richness by different functional guilds also has been predicted from
80 LiDAR-derived canopy and mid-story height and mid-story density in mixed
81 hardwood forest (Clawges et al. 2011). A review by Davies and Asner (Davies and
82 Asner 2014) revealed that 23 avian studies found a positive relationship between
83 species richness and abundance and canopy structural diversity and vertical
84 distribution of vegetation. In particular, vegetation structural heterogeneity appeared
85 to have a stronger relationship to bird observations than canopy cover alone (Davies
86 and Asner 2014).

87 Notably, most of the studies that used LiDAR to investigate relationships between
88 vegetation structure and habitat quality for birds have used airborne LiDAR
89 (Carrasco et al., 2019; Eldegard et al., 2014; Sasaki et al., 2016). While airborne
90 LiDAR sensors provide accurate information on canopy structure, they have limited
91 penetration to the ground and mid layer vegetation because of occlusion from the
92 upper canopy (Bakx et al., 2019; Crespo-Peremarch et al., 2020; LaRue et al.,
93 2020). A recent review analyzed 50 papers on bird species distributions and species
94 richness in relation to LiDAR-based vegetation variables (Bakx et al., 2019). It was
95 found that most of the studies used low density ALS data, usually 10 points/m²,
96 which have limited penetration below the canopy, especially to ground layer
97 vegetation. The authors recommended that future studies should focus on higher
98 density point clouds that can capture more details below the canopy, as the lower
99 strata of vegetation is also important for many bird species (Bakx et al., 2019). They
100 also suggested that, in addition to the widely used horizontal and height diversity

101 vegetation metrics, future research should also consider vegetation volume in
102 different strata, which can be calculated from voxelized point cloud. Voxelized point
103 cloud are three-dimensional grids or “voxels” that are created from one or more
104 LiDAR points (Sasaki et al., 2016).

105 ULS may be able to overcome some of the limitations of airborne LiDAR sensors,
106 since it can provide higher point density and still collects data relatively quickly. Fritz
107 et al. (2018) demonstrated the potential of this technology for identifying important
108 structural characteristics that help explain landscape use by an alpine bird
109 community; however, the use of ULS for modelling bird-habitat associations has not
110 been widely explored (Acebes et al. 2021). Ground-based TLS is an alternative
111 platform that can provide more detailed information on vegetation below the canopy
112 of forests because it measures the vegetation from the ground level and typically
113 with higher resolution than airborne sensors (LaRue et al., 2020). Depending on the
114 vegetation height and density, TLS can still be limited by occlusions though, where
115 vegetation or other landscape structural features block the field of view (Crespo-
116 Peremarch et al., 2020; LaRue et al., 2020). TLS data is typically only applied to
117 smaller areas (< 1 ha) because collection time is slower than ULS and airborne
118 LiDAR data (Liang et al., 2016). However, where logistically feasible, TLS may offer
119 some advantages for measuring some understory vegetation structural metrics that
120 are known to be important predictors of bird habitat quality and the occurrence and
121 diversity of bird species (Michel et al., 2008).

122 For the first time, we utilized high-density TLS and ULS LiDAR derived vegetation
123 structural variables for modelling vegetation structural classes and avian abundance
124 and diversity in an Australian woodland. Incorporating the suggestions of earlier
125 studies to investigate high-density point clouds and to incorporate vegetation volume
126 metrics from voxelized point-clouds (Bakx et al., 2019; Sasaki et al., 2016), we used
127 the data from both sensors to test the following hypotheses:

128 (1) the high-density TLS point clouds will perform better for modelling overall bird
129 abundance, species richness and diversity than lower density ULS point clouds;

130 (2) the relationship between vegetation structural data and particular bird species
131 and groups will be modelled more accurately from the TLS platform for bird species

132 and guilds that are most associated with ground and mid-story vegetation layers and
133 ULS for those that primarily use the canopy strata.

134 We anticipate that the outcomes of this study will be useful for conservation and
135 management projects focused on identifying animal-habitat associations and
136 establishing appropriate habitat structure for wildlife management.

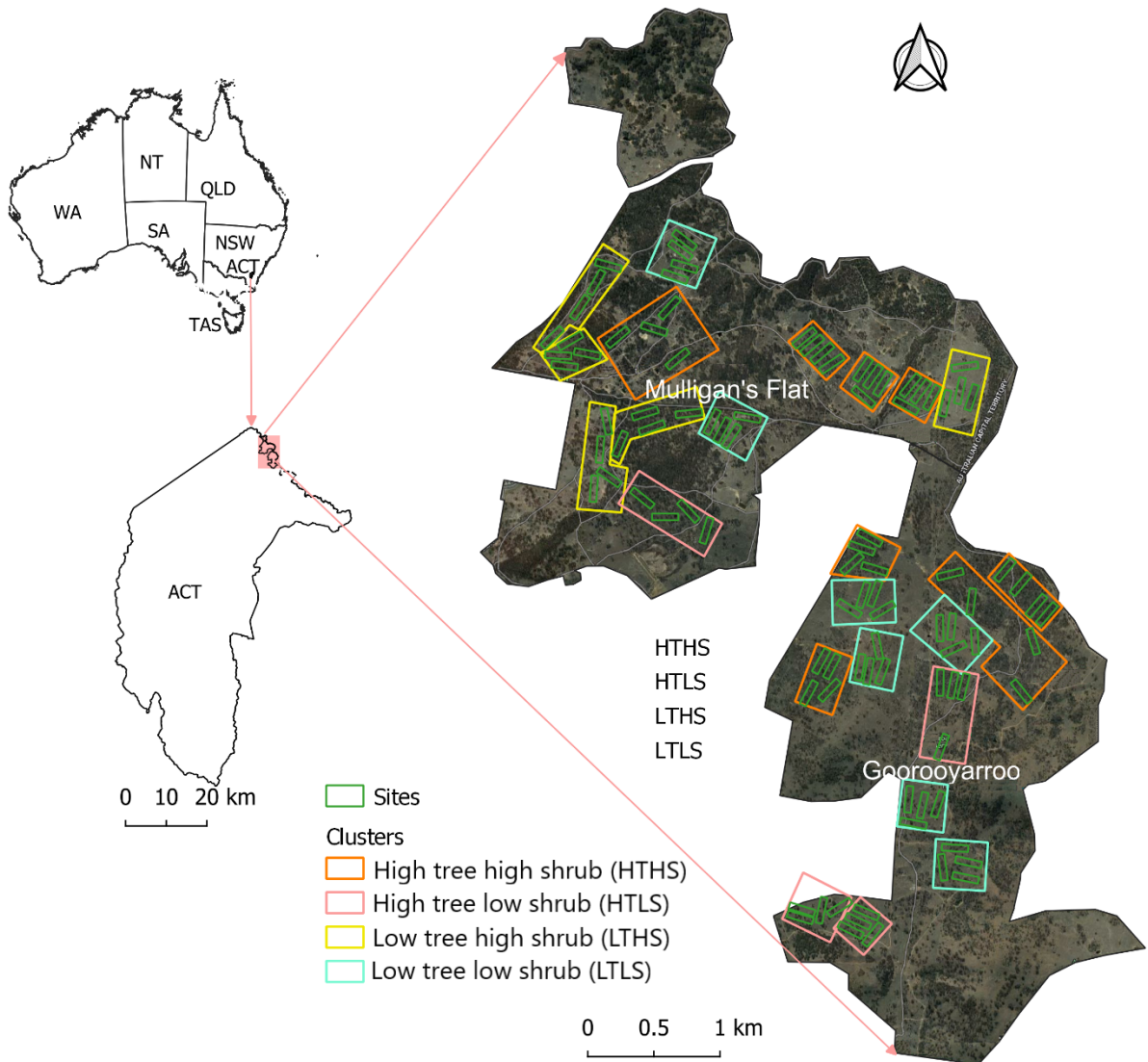
137 **3. Methods**

138 Study area

139 The study area is in Mulligan's Flat (683 ha) and Goorooyarroo (702 ha) nature
140 reserves (MFGO) in the north-eastern corner of the Australian Capital Territory
141 (ACT), Australia (35°09' S - 149°09' E; Fig. 1). These two adjacent reserves were
142 established in 1994 and 2006 respectively to conserve and restore a critically
143 endangered grassy woodland ecosystem (Manning et al., 2011). The dominant
144 overstory tree species include Blakely's Red Gum (*Eucalyptus blakelyi*), Yellow Box
145 (*E. melliodora*), Red Stringy Bark (*E. machrorhyncha*), and Scribbly gum (*E. rossii*)
146 with a relatively open midstory of primarily *acacia spp.* The grassy ground-layer
147 vegetation is dominated by *Joycea pallida*, *Austrodanthonia spp.*, *Themeda australis*
148 and *Aristida ramosa* (McIntyre et al., 2014; McIntyre et al., 2010; Shorthouse et al.,
149 2012). Prior to becoming reserves, MFGO was leasehold grazing land with some
150 areas of past cropping and pasture improvement (Manning et al., 2011; Shorthouse
151 et al., 2012). The topography is gently undulating with a few hills and the elevation
152 ranges from 650 m to 700 m. Average daily temperature in 2018 ranged from a
153 minimum of 6.9°C to a maximum of 22.0 °C, and mean annual rainfall was 472.0 mm
154 (Bureau of Meteorology 2019).

155 The reserves are the location of a long-term ecological experiment the "Mulligans
156 Flat – Goorooyarroo Woodland Experiment" (Manning et al., 2011) As part of this
157 experiment, restoration treatments have been undertaken in an attempt to restore
158 the function and biodiversity of the area, and feral predators and grazers have been
159 excluded with fencing around the reserves (Manning et al., 2013). To monitor
160 ecosystem recovery over time, animal and vegetation surveys are periodically
161 conducted across 96, 1 ha permanent sites (200 m x 50 m). These sites are stratified
162 across the reserves in 24 clusters that each include one of the four different
163 vegetation structural classes: 1) high tree cover, high shrub cover (HTHS), 2) high

164 tree cover, low shrub cover (HTLS), 3) low tree cover, low shrub cover (LTLS), and
 165 4) low tree cover, high shrub cover (LTHS) (Fig 1). The clusters are the key
 166 stratifying unit of this experiment and are defined as homogenous areas of
 167 vegetation structure and type (Manning et al., 2011). Each site is marked in the field
 168 along the long axis by plastic pegs at the 0 m and 200 m points, and with star pickets
 169 (A and B) at the 50 m and 150 m points (Manning et al., 2011).



170
 171 Figure 1. Map of study area in Mulligan's Flat-Goorooyarro Woodland Sanctuaries
 172 (right panel), which is located in the north-east corner of the Australian Capital
 173 Territory (ACT), Australia. The green rectangles are 1 ha sites (n = 96) that are
 174 grouped by vegetation classes (clusters), which are outlined by the multi-color
 175 polygons. HTHS is high tree cover, high shrub cover, HTLS is high tree cover, low

176 shrub cover, LTHS is low tree cover, high shrub cover, and LTLS is low tree cover,
177 low shrub cover.

178

179 **3.1. Bird data collection**

180 As part of long-term monitoring at MFGO, annual bird surveys have been conducted
181 since 2005 at each site during two separate visits in October by different
182 experienced bird observers using an acoustic and visual point count method
183 (Manning et al., 2011). During the surveys, observers stand at the A and B star
184 picket at the 50 m and 150 m position along the long axes of each site. The
185 presence and abundance of birds in concentric bands (0 – 25 m, 25 – 50 m, 50 –
186 100 m and over 100 m and overhead) are recorded for ten minutes. Detailed
187 information about bird survey methods are provided in (Manning et al., 2011). For
188 this study, we used bird data collected from 2017, 2018, and 2019 because it is
189 unlikely that the vegetation structure would have changed substantially in the period
190 between LiDAR data acquisition in October-November 2018 and the bird counts from
191 those adjacent years.

192

193 **3.2. TLS data collection and post-processing**

194 TLS data was collected in fine weather from 1 to 31 October 2018 with a Topcon
195 GLS2000 (Topcon Corporation, Japan). The Topcon GLS2000 is a high-density
196 laser scanner that emits near-infrared light (1064 nm) laser pulses at up to 120,000
197 laser pulses per second. The field-of-view of the scanner is 360° and 270°
198 (horizontal and vertical direction, respectively). The beam diameter of the single
199 pulse is 4 mm at 20 m. Information on a pilot study conducted to determine the
200 number of TLS scans to be used for each site is provided in Appendix 1. We
201 collected seven individual scans without co-registration in all 96, 1 ha sites for a total
202 of 672 scans with 6 mm point spacing at 10 m from the scanner. The position of
203 each scan was measured with a differential GPS (Trimble Geoexplorer 6000 series)
204 and post-processing was performed using local base station data to improve the
205 point location accuracy to approximately 50 cm (Shokirov 2021; Shokirov et al.,
206 2020).

207 Point clouds from seven individual scan stations were then co-registered during post-
208 processing using Multi-station Adjustment (MSA) plugin in RiScan Pro software
209 (RIEGL Laser Measurement Systems GmbH). The MSA uses the iterative closest
210 points (ICP) algorithm that minimizes the 3D distance between the identical points by
211 translating and rotating the entire point cloud along X, Y, Z axes until the least
212 minimum distance between the identical points from two datasets is achieved (Šašak
213 et al., 2019). The exact procedure we followed is described in detail in Shokirov et al.
214 (2021). Next, the point cloud from each site was georeferenced using DGPS
215 locations of each scan position measured in the field and clipped to the spatial extent
216 of each of the 96 sites. Point clouds were then subsampled into 1 cm spacing to
217 homogenize the point distributions and duplicate points were removed using Cloud
218 Compare (CloudCompare 2020).

219

220 **3.3. ULS data collection and post-processing**

221 We collected ULS LiDAR data across all of the 96, 1 ha sites in fine weather
222 conditions from 7 to 14 November, 2018. The ULS LiDAR platform consisted of a
223 quadcopter integrated with RIEGL miniVUX-1UAV LiDAR sensor (RIEGL Laser
224 Measurement Systems GmbH, Austria) and APX INS/GNSS system (Trimble, USA).
225 The flights were performed at approximately 80 m above the take off point with
226 approximately 25.2 km/h speed, up to 5 returns per pulse, 100 kHz pulse repetition
227 rate, and up to 100,000 measurements/second (Shokirov 2021; Shokirov et al.,
228 2020). Maximum scan angle of the LiDAR sensor was approximately $\pm 60^\circ$ with swath
229 width about 100 m. We used DJI ground station pro V2 to plan the flight missions
230 (SZ DJI TECHNOLOGY CO. 2018). The ULS LiDAR sensor failed to collect data on
231 two sites, which were excluded from further analysis of ULS and TLS data.

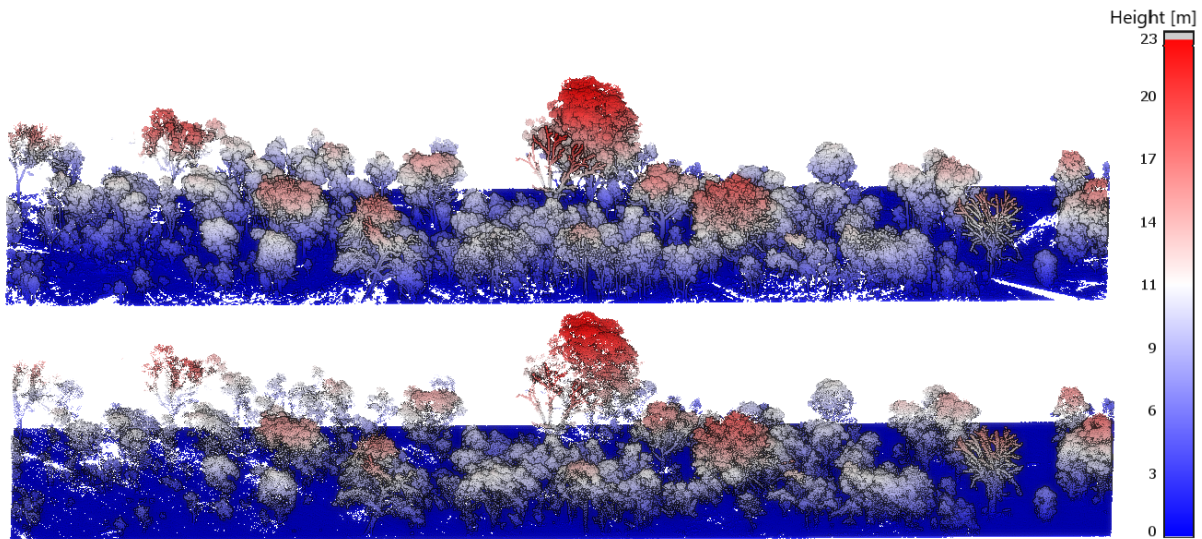
232 Data processing was done in RiPROCESS software suite by RIEGL which allowed
233 us to bring in the trajectory data of the drone flight, align the flight paths,
234 georeference the point cloud and then export it in LAS format. The trajectory data of
235 the UAV LiDAR that was fed into RiPROCESS was generated using POSPAC UAV
236 (Applanix) using the IMU/GNSS data from the drone and RINEX data from the base
237 station which was obtained from the Gungahlin location of Smartnet global
238 network. The ULS LiDAR data collected over the 94 sites were clipped by

239 corresponding polygons to create a separate point cloud for each site. Point spacing
240 in ULS data across 94 sites ranged from 5 cm to 17 cm with an average of 10 cm.
241 For this reason, we homogenized the point cloud with 10 cm spacing and removed
242 duplicate points using Cloud Compare 2.10.2 (CloudCompare 2020).

243

244 **3.4. Canopy height model**

245 Point clouds were cleaned from noise points and classified into ground and non-
246 ground points using *LAStools* (Isenburg 2012). We normalized point clouds by
247 converting elevation values to height above ground values with *LAStools* (Isenburg
248 2012) (Fig. 2).



249

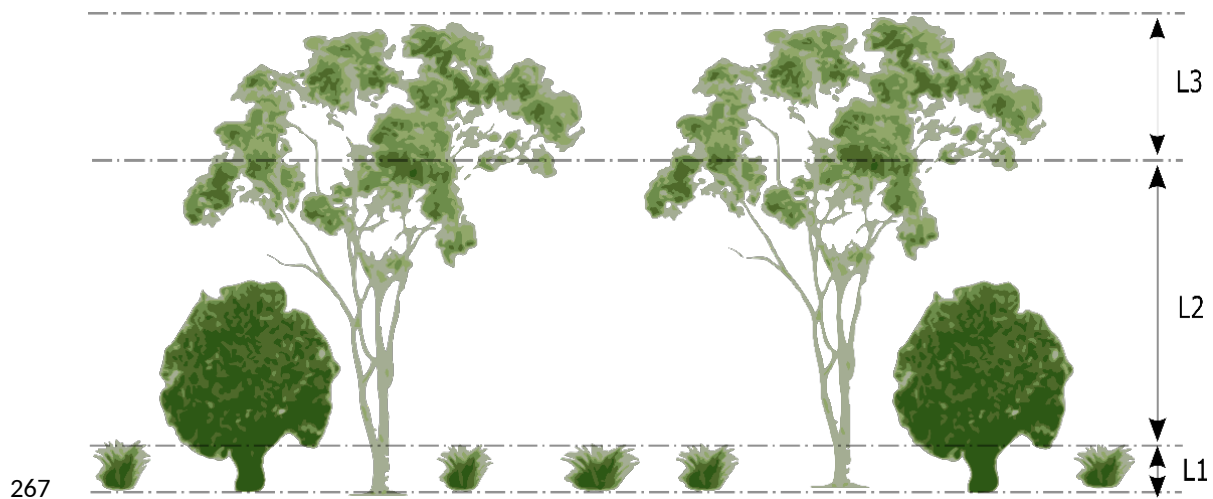
250 Figure 2. Normalized TLS (a) and ULS (b) point clouds of site GO72A-3 colored by
251 height.

253

254 **3.5. Calculating vegetation variables from the LiDAR datasets**

255 Canopy metrics were calculated from points above 1.3 m (Table 1). Based on
256 existing vegetation layer descriptions for eucalypt grassy woodlands (Department of
257 Environment 2013), we divided the point cloud into three layers representing the
258 ground layer (L1, points $\leq 1\text{m}$), the mid-story (L2, $1\text{m} < \text{points} \leq 10\text{m}$) and the upper
259 story (L3, points $> 10\text{m}$) (Fig. 3) and calculated additional vegetation metrics for each
260 layer (Table 1). Vegetation volume was estimated by excluding ground points and

261 constructing 0.5 m voxels (volumetric pixels) from point clouds, with each voxel
 262 made of one or more points. A fraction of woody canopy cover for each site was
 263 calculated by creating 0.25 m grids from points above 1.3 m and dividing the sum of
 264 the areas of all pixels by the size of the total area of the site (200m×50m). A total of
 265 37 metrics were computed with lidR package (Roussel, 2017). List of LiDAR-derived
 266 vegetation variables and descriptions are provided in Table 1.



267
 268 Figure 3. Vegetation layers: L1 - ground layer (points $\leq 1\text{m}$), L2 - mid-story layer (1m
 269 $< \text{points} \leq 10\text{m}$), L3 - upper story layer (points $> 10\text{m}$).

270 Table 1. Description of calculated vegetation structural variables from LiDAR dataset

Name of variable	Description
maxH	Maximum height of canopy (points $> 1.3\text{m}$).
meanH	Mean height of canopy (points $> 1.3\text{m}$).
stdH	Standard deviation of canopy height (points $> 1.3\text{m}$), which describes the variation in the canopy height.
skewH	Skewness of canopy height (points $> 1.3\text{m}$). Negative skewness means that the distribution is dominated by higher points (upper canopy is dominant) but a few extreme lower points. Positive skewness means that the distribution dominated by lower points (lower canopy is dominant) but a few extreme higher points.
kurH	Kurtosis of canopy height (points $> 1.3\text{m}$). Negative kurtosis means the distribution of points centered around the mean (mid-canopy is dominant). Positive kurtosis means the point

	distribution is heavy on tails and less around the mean (lower and upper canopy is dominant).
p_05, p_10, p_25, p_50, p_75, p_90, p_95, p_99	Canopy height percentiles (points > 1.3m). Canopy height percentiles are the height below which a specified percentage of total point clouds were located. For example, p_05 = 2 m means that 5% of vegetation points are found below 2 m.
vci_2m, vci_5m, vci_10m, vci_15m, vci_20m	<p>Vertical complexity indexes (VCI) at 2m, 5m, 10m, 15m, 20m height bins, (points > 1.3m).</p> <p>Vertical complexity indexes (VCI) at 2m, 5m, 10m, 15m, 20m height bins, (points > 1.3m).</p> $VCI = (-\sum_{i=1}^{HB} [(p_i \ln(p_i))]) / \ln(HB)$ <p>Where <i>VCI</i> is a vertical complexity index, <i>HB</i> is the total number of height bins, and p_i is the proportional abundance of LiDAR returns in height bin <i>i</i>.</p> <p>A VCI value close to one indicates that most height bins have an equal amount of vegetation. VCI value decreases if the distribution of canopy in the height bin becomes more uneven (van Ewijk et al., 2011).</p>
Cov	Fraction of canopy cover, (points > 1.3m).
height_cv	Coefficient of variation of height, (points > 1.3m). Indicates the canopy height variation.
canopy_roughness	Canopy roughness describes complexity/variability of canopy height (Herrero-Huerta et al., 2020) (points > 1.3 m). Higher variability in the canopy height provides higher roughness index and vice versa.
canopy_shannon	Normalized Shannon diversity index of canopy (Pretzsch 2009), (points > 1.3m). Indicates canopy height diversity.
Tvolume	Total vegetation volume (m ³) – number of 0.5 m ³ voxels divided by 8 (ground points excluded).
vlayer_L1	Vegetation volume (m ³) in 1 st layer (points 0-1m, ground points excluded).

vlayer_L2	Vegetation volume (m ³) in 2 st layer (points 1m-10m).
vlayer_L3	Vegetation volume (m ³) in 3 st layer (points 10m and above).
meanH_L1, meanH_L2, meanH_L3	Mean height of 1 st , 2 nd , 3 rd layer.
sdH_L1, sdH_L2, sdH_L3	Standard deviation of vegetation height in 1 st , 2 nd , 3 rd layer.
roughness_L1, roughness_L2, roughness_L3	Roughness indexes of 1 st , 2 nd , 3 rd layer (Jenness, 2004). Horizontal distribution of vegetation across different layers.
vci_L1, vci_L2, vci_L3	Vertical complexity indexes of 1 st , 2 nd , 3 rd layer (van Ewijk et al., 2011). Vertical distribution of vegetation across different layers.

271

272 **3.6. Statistical analysis**

273 **3.6.1. Bird data**

274 We calculated bird abundance (maximum number of individual birds counted),
275 species richness (cumulative total number of species), Shannon diversity index using
276 “vegan” R package (Jari Oksanen 2019) and functional diversity indices including
277 functional richness, functional evenness, functional divergence, functional dispersion
278 and Rao's quadratic entropy for each site using “FD” package (Laliberté and
279 Legendre 2010) in R language (R Core Team 2020). Shannon diversity index is used
280 to characterize species diversity in a community (Morris et al., 2014). Functional
281 richness is defined as the amount of niche space occupied by the species within a
282 community. Functional evenness measures the regularity of the distribution of
283 species abundances and dissimilarities in a functional space. Functional divergence
284 is the degree to which abundance distribution in niche space maximizes divergence
285 in functional characters within the community (Mason et al., 2005). Functional
286 diversity indices quantify the trait diversity and act as a surrogate for the diverse
287 ecological functions performed in the community. Rao's quadratic entropy measures
288 the diversity of ecological communities and is based on the proportion of the
289 abundance of species in a community and a measure of dissimilarity between the

290 species (Ricotta and Szeidl, 2009). The diversity of trait values within a community is
291 therefore referred as either trait diversity or functional diversity (FD) (Karadimou et
292 al., 2016). Bird guilds were assigned based on different functional traits (i.e.,
293 grassland specialist, water bird, woodland generalist, woodland specialist), nesting
294 substrate (i.e., arboreal, ground, hollow, opportunistic, understory), foraging
295 substrate (i.e., air, aquatic, arboreal, ground, opportunistic), and dispersion (low,
296 partial, high) (Le Roux et al., 2018, Ikin et al., 2012).

297

298 **3.6.2. Model selection process**

299 A key stratifying unit of the sites established in our study area were the clusters,
300 which were comprised of one of four vegetation types (HTHS, HTLS, LTLS, LTHS)
301 (Manning et al., 2011). Although it was not the primary goal of the study, we first
302 explored the ability of ULS and TLS data to correctly classify sites according to these
303 vegetation categories. The outcomes from this classification exercise were used to
304 select a modelling approach for relating the LiDAR structural data to the animal data.
305 We used a multinomial regression model by means of “multinom” function in “nnet” R
306 package (Venables and Ripley 2003) for this analysis. We tested two models, one
307 based on the first four principle components from the PCA calculated from all TLS
308 and ULS LiDAR variables (Appendix 2) and a model based on selected TLS and
309 ULS LiDAR variables (3.6.3) to classify vegetation types. We also tested the
310 performance of the four PCA components model and the selected variable model to
311 predict overall bird abundance, species richness and diversity. However, we used
312 the model type that most accurately classified the sites into their appropriate
313 vegetation class for the full analysis of the bird data.

314

315 **3.6.3. Variable selection process**

316 For the selected variable model, we chose variables that were not highly correlated
317 (0.7 maximum threshold), and this is in keeping with other studies (Dormann et al.,
318 2013; Sasaki et al., 2016){Sasaki, 2016 #190}{Sasaki, 2016 #190}. Pearson
319 correlation matrices of TLS and ULS variables are provided in Appendix 3 and
320 Appendix 4, respectively. When selecting between two highly correlated variables,
321 we attempted to select for the most ecologically meaningful variable (e.g. average
322 height (*meanH*) and 75th percentile height (*p_75*) resulted in us selecting average

323 height). We also selected at least one variable from each strata of vegetation and
324 several canopy metrics to cover all layers of vegetation in the landscape. The
325 variable selection was conducted for each sensor, respectively. However, we gave
326 preference to variables that were the same across sensors when the above criteria
327 had been met. Although it was not our intention, our final variables consisted of the
328 same 12 for each sensor. This was probably due to a combination of our selection
329 method and the fact that the variables from the two sensors were highly correlated
330 (Fig. 4), despite these sensors having different viewing geometry and point densities.
331 All explanatory variables were standardized so that they have a mean of zero
332 (“centering”) and standard deviation of one (“scaling”) (Becker et al., 1988).
333 Additionally, a cross correlation matrix was calculated to examine the relationship
334 between TLS and ULS variables.

335

336 **3.6.4. Modelling bird diversity and abundance by guilds and individual** 337 **species.**

338 To evaluate which selected LiDAR based variables had the strongest relationship to
339 bird abundance, species richness, species diversity, and functional diversity of birds
340 across sites, we fitted linear mixed effects models. Correlations between individual
341 bird abundance and bird abundance within functional guilds and vegetation structural
342 metrics were evaluated using Poisson distribution generalized linear mixed effects
343 models (GLMM) with glmer function in lme4 R package (Bates et al., 2015). Mixed
344 models extend the basic linear model such that they recognize grouped or nested
345 structures in data by random effects (Melin et al., 2018). In these models, predictor
346 variables were the selected vegetation structural metrics (fixed effects) and twenty-
347 four polygons (random effects), with each polygon containing four transects
348 representing one of the four vegetation classes (see Fig. 1). Response variables
349 were overall bird metrics, guilds and individual species abundance.

350

351 **3.6.5. Examination of model fit**

352 We used Residual Diagnostics for HierARchical Models (DHARMA) package (Hartig
353 2017) for examining the model fit, dispersion and zero-inflation. Marginal and

354 conditional R^2 were calculated to evaluate the proportion of variance explained by
 355 fixed and mixed effects for models by species and guilds (Nakagawa et al., 2013).

356 To avoid model convergence issue, we retained the species or guilds that had at
 357 least 10% count data across the sites. If the model convergence issue persisted, we
 358 were able to resolve this by decreasing the number of fixed effects by removing
 359 those with the lowest explanatory values. We considered a predictor to be significant
 360 if the absolute value of its z-score was greater than 1.96, corresponding to a p-value
 361 smaller than 0.05.

362 4. Results

363 4.1. Bird data

364 A total of 12117 bird observations ($n = 5540$ in Mulligan’s Flat and $n = 6577$ in
 365 Goorooyarroo) from 84 bird species were observed from the double surveys each
 366 year across the three-year period from 2017 to 2019. A maximum of 238 birds and
 367 36 species and a minimum of 42 birds and 10 species were counted in any one site
 368 (Table 2). Most of the surveyed birds belong to the woodland specialist habitat class
 369 (WS.HC, $n = 8725$), nested in hollows (Hol.Nest, $n = 4668$), foraged in the trees
 370 (Arb.Forage, $n = 6649$) and displayed low dispersal (Low.Disp, $n = 8187$) (Table 3).

371

372 Table 2. Basic statistics from bird data across sites. The table column headings are:
 373 Abundance = bird abundance, SR = species richness, Bird_shannon = shannon
 374 diversity, FRic = functional richness, FEve = functional evenness, FDiv = functional
 375 diversity, FDis = functional dispersion, and RaoQ = Rao’s quadratic entropy.

Statistics	Abundance	SR	Bird_shannon	FRic	FEve	FDiv	FDis	RaoQ
Maximum	238.00	36.00	3.22	0.09	0.82	0.96	0.29	0.09
Mean	126.22	21.97	2.63	0.01	0.67	0.87	0.24	0.07
Stdev	42.60	5.91	0.35	0.02	0.07	0.04	0.02	0.01
Median	121.50	22.00	2.69	0.01	0.67	0.87	0.24	0.07
Minimum	42.00	10.00	1.68	0.00	0.50	0.78	0.17	0.04

377 Table 3. Basic statistics about bird abundance within functional traits across sites.
 378 Habitat classes (GS.HC = grassland specialist habitat class, WB.HC = water bird
 379 habitat class, WG.HC = woodland generalist habitat class, WS.HC = woodland
 380 specialist habitat class), nesting substrate (Arb.Nest = arboreal nesting, Hol.Nest =
 381 hollow nesting, Usty.Nest = understory nesting, Opp.Nest = opportunistic nesting),
 382 foraging substrate (Air.Forage = aerial foraging, Aqu.Forage = aquatic foraging,
 383 Arb.Forage = arboreal foraging, Grnd.Forage = ground foraging, Opp.Forage =
 384 opportunistic foraging), dispersion (Low.Disp – low dispersion, Partial.Disp – partial
 385 dispersion) groups.

Stats.	GS. HC	WB. HC	WG. HC	WS. HC	Arb. Nest	Grnd. Nest	Hol. Nest	Opp Nest	Usty. Nest	Air. Forage	Aqu. Forage	Arb. Forage	Grnd. Forage	Opp. Forage	Low. Disp	Partial. Disp
Sum	238	83	2868	8725	6174	44	4668	749	279	165	83	6649	2879	2138	8187	3722
Max	17	14	106	200	148	11	159	31	24	28	14	141	98	71	210	118
Mean	2.53	0.88	30.51	92.82	65.68	0.47	49.66	7.97	2.97	1.76	0.88	70.73	30.63	22.75	87.10	39.60
Stdev	3.14	2.35	20.33	34.72	28.19	1.59	32.00	7.93	4.81	4.08	2.35	27.53	18.98	13.64	34.44	23.14
Median	1.50	0.00	26.50	86.00	62.50	0.00	40.00	6.00	1.00	0.00	0.00	65.00	25.00	19.50	84.50	37.50
Min	0	0	2	28	11	0	5	0	0	0	0	19	5	1	29	3

386

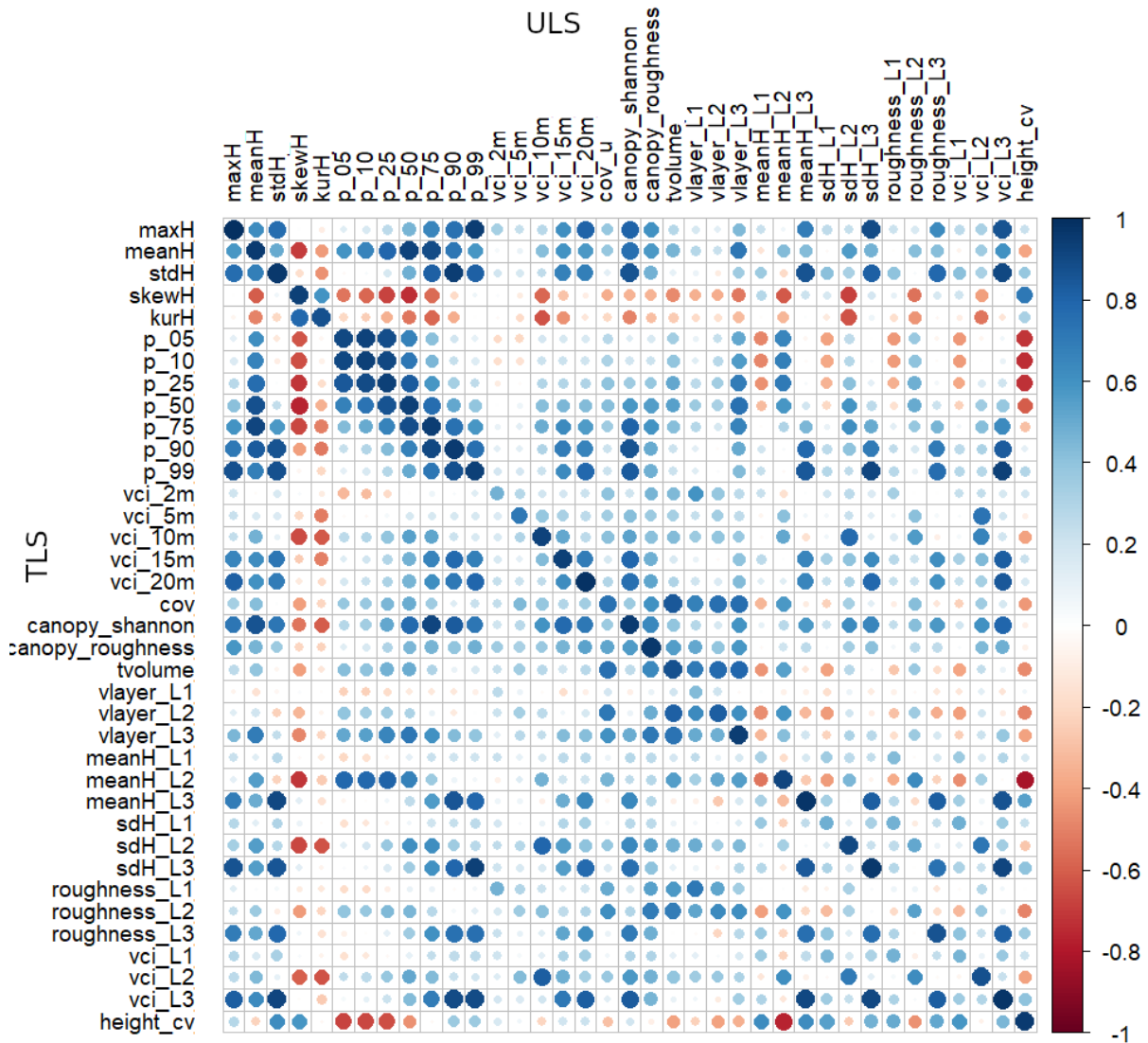
387 **4.2. Predicting vegetation classes from the LiDAR dataset**

388 Multinomial regression models showed that selected LiDAR variables provided better
 389 accuracy in predicting vegetation classes than the first four PCA variables for both
 390 TLS and ULS data (Appendix 5. Table A5.1 and Table A5.2). Therefore, we decided
 391 to use selected variables over PCA variables as predictors in our models. For both
 392 TLS and ULS datasets, models were better at classifying HTHS and LTLS
 393 vegetation classes than HTLS and LTHS vegetation classes.

394

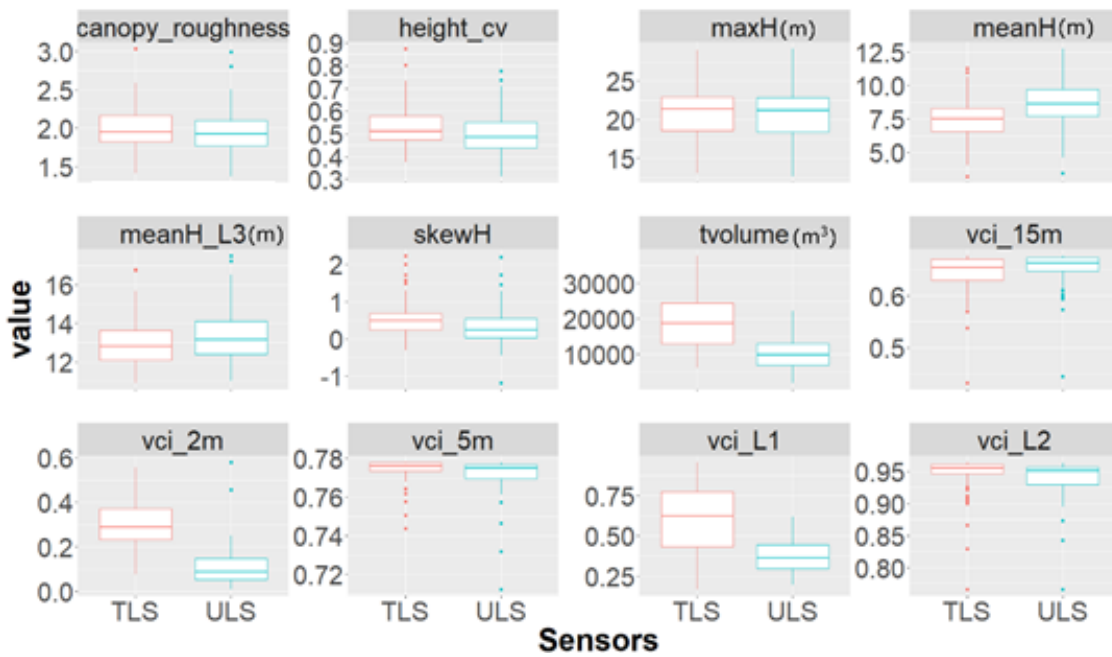
395 **4.3. Selected variables**

396 Our variable selection method resulted in 12 out of 37 LiDAR metrics being selected
 397 for the models. The Pearson correlation matrix showed that most of the TLS and
 398 ULS variables are strongly correlated to each other ($r > 0.7$) (Fig. 4). Only the L1
 399 metrics and lower strata canopy metrics showed a weak correlation ($r < 0.3$) to each
 400 other. Basic statistics for these TLS and ULS variables are provided in Figure 5.



401
 402 Figure 4. Correlation matrix of Terrestrial Laser Scanner (TLS) and Unoccupied
 403 Aerial Vehicle Laser Scanner (ULS) variables

404



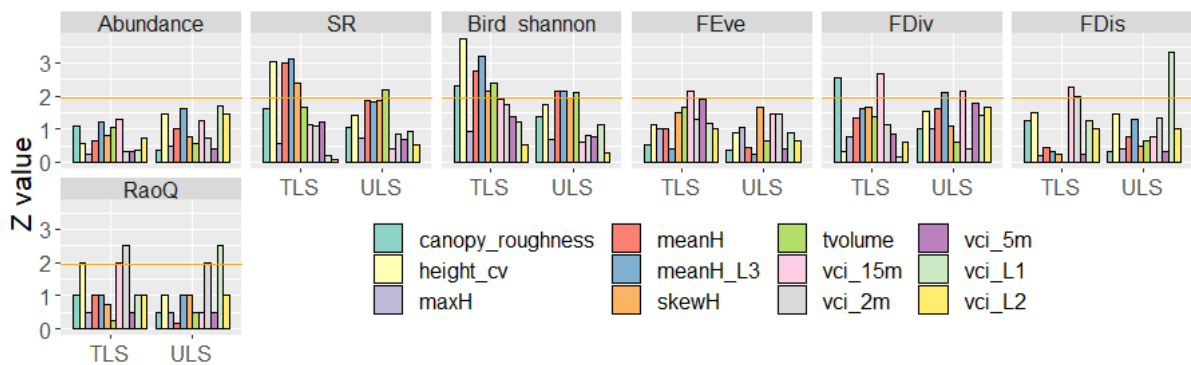
405

406 Figure 5. Boxplots represent the distribution of selected terrestrial laser scanner
 407 (TLS) and unoccupied aerial vehicle laser scanner (ULS) variables. Upper, mid, and
 408 lower horizontal lines of the box indicate 1th, median, and 3rd quartiles. Whiskers
 409 extend to the highest and lowest extreme of observations, and the dots on the
 410 whiskers are outliers

411

412 **4.4. Overall bird abundance, species richness and diversity**

413 The GLMM for the overall bird abundance did not show a significant relationship with
 414 any of the 12 selected variables from the ULS or TLS data (Appendix 6,
 415 “Abundance”, Fig. 6). Bird species richness (SR) was positively related to several
 416 TLS-derived variables including *meanH*, and *skewH* and *height_cv* and negatively
 417 correlated to *meanH_L3*. However, *tvolume* was the only significant predictor among
 418 the ULS selected variables for predicting bird species richness (SR). Bird diversity
 419 (*Bird_shannon*) was positively influenced by TLS and ULS *meanH* and *tvolume*, and
 420 negatively influenced by *meanH_L3* (Appendix 6, “Bird_shannon, Fig. 6). Among the
 421 functional diversity indexes, functional evenness (*FEve*) was negatively correlated to
 422 only TLS-based *vci_15m*. However, *vci_15m* derived from TLS and ULS data was
 423 negatively related to functional divergence. Functional dispersion (*FDis*) and Rao's
 424 quadratic entropy (*RaoQ*) were negatively influenced by TLS and UAV – derived
 425 *vci_2m* and *vci_15m*, and positively related to ULS – based *vci_L1* (Appendix 6, Fig.
 426 6). However, all these models showed relatively poor performance with explained
 427 variance between 10.0% and 20.0% (Appendix 6).



428

429 Figure 6. Plots illustrate the significance of predictor variables (by z value) for
 430 predicting overall bird abundance, species richness and diversity. Bars represent
 431 predictor variables. The horizontal orange line shows the significance threshold (z =
 432 1.96, or p < 0.05) of predictors. The abbreviations are: FDis = Functional dispersion,
 433 FDiv = functional divergence, FEve = functional evenness, RaoQ = Rao’s quadratic
 434 entropy, SR = species richness, TLS = terrestrial laser scanner, and ULS is
 435 unoccupied aerial vehicle laser scanner.

436

437 **4.5. Bird abundance within functional guilds**

438 All of the 16 functional guilds (Table 3) were significantly correlated to one or more
439 LiDAR variables, and some guilds showed a stronger response to vegetation
440 structure than others (Appendix 7, Fig. 7). Models from TLS data explained between
441 8.5% and 39.9% (average of 22.6%) variability, and ULS models explained between
442 6.8% and 40.8% (average of 23.5%) variability in abundance of birds across
443 functional guilds.

444 The most robust TLS-based explanatory models were the water bird habitat class
445 ($R^2=0.40$) and aquatic foragers abundance ($R^2=0.40$), which were positively
446 correlated to *meanH*, *skewH* and *vci_5m*, and negatively correlated to *maxH* and
447 *meanH_L3*. The ground nesting guild model from TLS data explained substantial
448 variance ($R^2 = 0.34$), and was negatively influenced by *maxH* and positively
449 influenced by *skewH*, *tvolume* and *vci_L2*. The TLS-based opportunistic foraging
450 model was the third best at explaining variance in the data ($R^2 = 0.31$). That model
451 was negatively correlated to *maxH*, *meanH*, *skewH* and *height_cv* and strongly
452 positively correlated to *canopy_roughness* and *meanH_L3* (Appendix 7, Fig. 7).

453 The ULS-based models also performed best for aquatic foraging and water bird
454 habitat guilds ($R^2 = 0.41$), which were positively related to *vci_5m*, *vci_15m* and
455 *vci_L1*. The next best performing ULS guild model was for woodland generalist
456 abundance ($R^2 = 0.37$) and was positively associated with *maxH* and *vci_L1*. The
457 ULS model also explained substantial variance in abundance of ground nesting birds
458 ($R^2=0.35$), which were positively influenced by *meanH* and *skewH*, but negatively
459 related to *maxH* (Appendix 7, Fig. 7).

460 Canopy roughness (*canopy_roughness*) was the best predictor variable for the TLS-
461 based models with a significant correlation to 10 functional guilds followed by *skewH*,
462 *maxH* and *meanH* height of canopy and *meanH_L3* (Fig. 7). The best predictor
463 variables for ULS-based models were *vci_5m*, which was significantly correlated to 9
464 guilds, *maxH*, *canopy_roughness* and *vci_L1* (Fig. 7).

465



466

467 Figure 7. Plots illustrate the significance of predictor variables (by z value) from
 468 terrestrial laser scanner (TLS) and unoccupied aerial vehicle laser scanner (ULS) for
 469 predicting bird abundance by functional guilds. Bars represent predictor variables.
 470 Horizontal orange line shows the significance threshold ($z = 1.96$, or $p < 0.05$) of
 471 predictors. The abbreviations are: habitat classes (GS.HC = grassland specialist,
 472 WB.HC = water bird, WG.HC = woodland generalist, and WS.HC = woodland
 473 specialist), dispersal (Low.Disp = low, and Partial.Disp = partial), nesting substrate
 474 (Arb.Nest = arboreal, Hol.Nest = hollow, Usty.Nest = understory, and Opp.Nest =
 475 opportunistic), foraging substrate (Air.Forage = air, Aqu.Forage = aquatic,
 476 Arb.Forage = arboreal, Grnd.Forage = ground, and Opp.Forage = opportunistic).

477

478 4.5.1. Individual bird species abundance

479 Abundance of forty-nine out of fifty-one bird species responded to TLS and ULS –
 480 derived vegetation structural variables (Appendix 8). Only Grey Shrike Thrush and
 481 Pallid Cuckoo abundance showed no relationship to any TLS or ULS LiDAR
 482 structural variables. For the TLS-based models, *canopy_roughness* was significantly
 483 related to the abundance of 16 bird species, followed by *tvolume*, which was related
 484 to the abundance of 15 bird species (Fig. 8). In the ULS models, *vci_L1* related to
 485 bird species abundance more than any other variable (22 bird species), followed by

486 *canopy_roughness* (17 bird species) (Fig. 8). Explained variance of TLS models
 487 ranged from 4.2% to 81.7% (average of 31.1%). Similarly, ULS-models explained
 488 4.9% to 83.4% (average of 30.5%) of variation in bird species abundance.



489

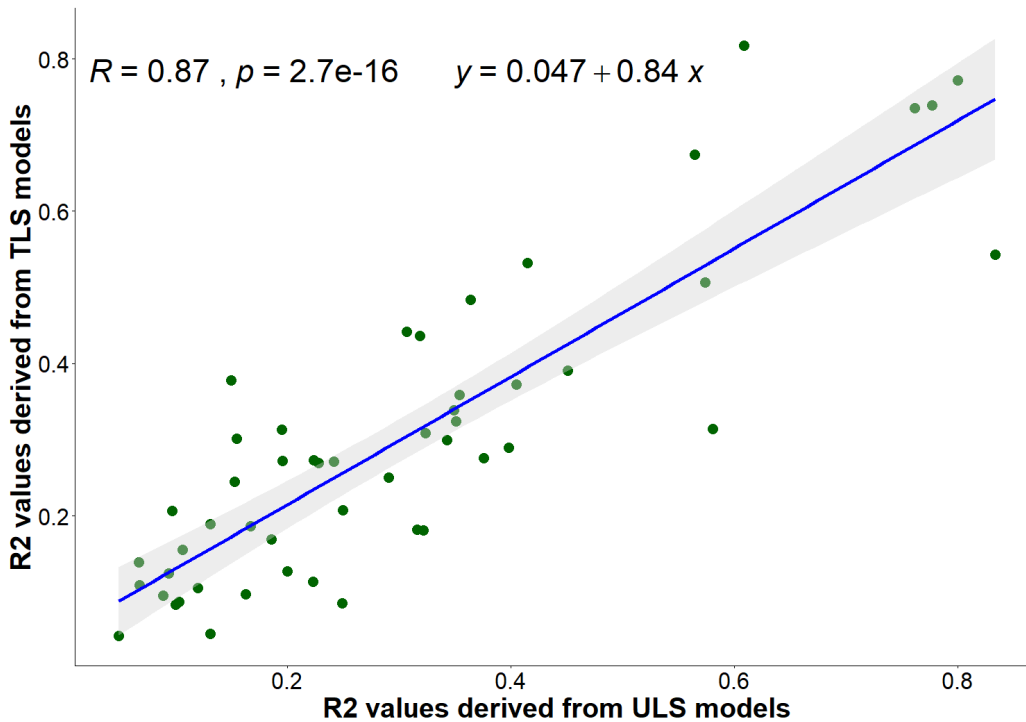
490 Figure 8. Plot illustrates the significance of predictor variables (by z value) from
491 terrestrial laser scanner (TLS) and unoccupied aerial vehicle laser scanner (ULS) for
492 predicting individual bird species abundance. Bars represent predictor variables.
493 Horizontal orange line shows the significance threshold ($z = 1.96$, or $p < 0.05$) of
494 predictors.

495

496 The model for Nankeen Kestrel abundance was the best performing TLS model (R^2
497 = 0.82), and was strongly correlated to *vci_15m*, *canopy_roughness*, *meanH_L3* and
498 *vci_L2* and negatively related to *meanH* and *tvolume* (Appendix 8, Fig 8). The
499 second best TLS model was Spotted Pardalote abundance ($R^2 = 0.77$), which was
500 correlated to *maxH*, *meanH*, *skewH* and *tvolume*. White Throated Treecreeper
501 abundance was also strongly related to TLS LiDAR-derived vegetation structure (R^2
502 = 0.74) and had a positive relationship to *skewH*, *vci_15m*, *tvolume* and *vci_L2*, and
503 a negative relationship with *maxH* and *vci_5m* (Appendix 8, Fig 8).

504 The best performing ULS model was for Varied Sittela abundance ($R^2 = 0.83$), which
505 was explained by *maxH*, *meanH*, *skewH* and *meanH_L3*. The White Throated
506 Treecreeper abundance model ($R^2 = 0.78$) showed significant correlation with
507 *meanH*, *skewH*, *canopy_roughness*, *meanH_L3* and *vci_L1*. Likewise, the Sacred
508 Kingfisher abundance model explained 76.2% variance and was related to *maxH*,
509 *meanH*, *skewH*, *meanH_L3*, *vci_L1* and *height_cv* (Appendix 8, Fig. 8).

510 Overall, TLS and ULS data produced very similar results in predicting individual bird
511 species abundance, and this was demonstrated by the linear relationship between
512 the explained variances of TLS and ULS models (Fig. 9).



513

514 Figure 9. The relationship between explained variance (R2) calculated from TLS and
 515 ULS based Poisson distribution mixed model for predicting individual bird species
 516 abundance.

517 **5. Discussion**

518 This is the first study that uses both ULS and TLS data for investigating relationships
 519 between a wide range of bird population data and vegetation structure in a woodland
 520 landscape. It is also the first study in Australia to model avian abundance and
 521 species richness using LiDAR data. Overall (combined species) bird abundance was
 522 not significantly related to any TLS or ULS LiDAR-derived variables, and this may be
 523 due to the number of different bird species that occupied a wide variety of structural
 524 niches in the landscape (Lesak et al., 2011). Models for predicting bird species
 525 richness, diversity and abundance within functional guilds performed better than
 526 overall bird abundance.

527 Some individual bird species abundance models were able to explain a very large
 528 amount of variability in abundance of particular species, which is promising for using
 529 this data for habitat assessments and improving our understanding of habitat
 530 requirements for threatened species in particular. Canopy roughness, vertical
 531 complexity of the first layer, total vegetation volume and canopy height were the

532 variables that were most strongly associated with bird community and individual
533 species abundance. Our assumption that higher density LiDAR point clouds from the
534 TLS platform would create better models than the lower density, airborne ULS data
535 was not supported by our data. This was likely influenced by low-lying occlusions in
536 the data that were more substantial for the TLS than the ULS owing to the
537 positioning of the sensors and the characteristics of the woodland landscape
538 (Olschofsky et al., 2016). As a result, the ULS generally provided better results for
539 predicting the abundance of individual bird species and guilds that forage on the
540 ground than the TLS based on our methodology. We discuss the overall finding in
541 more detail below and provide recommendations for future research.

542

543 **5.1. Overall bird abundance, species richness and diversity**

544 The lack of significant relationships between TLS and ULS structural metrics and
545 overall bird abundance may be due to contrasting habitat requirement across the
546 large suite of different species included in the total abundance tally (Wiens and
547 Rotenberry, 1981). Models for predicting overall bird species richness did find
548 significant relationships to some variables but these were dependent on the data
549 source (TLS or ULS). Species richness was positively related to TLS canopy height
550 diversity and upper canopy height. The only ULS predictor that was significantly
551 related to bird species richness was the total volume of vegetation. The TLS sensor
552 may be able to capture more meaningful structural variation below the canopy for
553 birds than the ULS data owing to the positioning of the sensor under the canopy.
554 Overall species diversity models from TLS and ULS data provided similar results
555 with canopy height and total volume being strongly related to the bird diversity
556 indices, but *height_cv* was only significant in TLS-based metrics (Appendix 6). This
557 further supports the idea that the TLS sensor was able to capture canopy height
558 variation in a more meaningful way for bird habitat quality, probably owing to the
559 positioning of the sensor (Ashcroft et al., 2014; Blakey et al., 2017). Nonetheless, the
560 higher density TLS data did not perform better than the ULS data in terms of overall
561 ability to explain variance in this data. Therefore, our first hypothesis that high
562 density TLS LiDAR point clouds will perform better for modelling overall bird
563 abundance, species richness and diversity than lower density ULS point clouds was
564 not supported with the number of TLS scans per site that we collected.

565 Generally, our results from species richness and diversity models agree with
566 relationships identified in previous studies (Clawges et al., 2008; Lesak et al., 2011;
567 Sasaki et al., 2016). Clawges et al. (2008) found a significant correlation between
568 ALS LiDAR-derived canopy height diversity and bird species diversity. Similarly, ALS
569 LiDAR – derived canopy height and mid-story density and height has been
570 associated with song bird species richness (Lesak et al., 2011). Notably, these
571 studies reported relatively low overall explained variance ($R^2 \leq 0.2$), which is also in
572 keeping with our findings. The typically low explained variance for community level
573 data (e.g., bird species richness and diversity) in these models may be due to a
574 mismatch in scale, since some of the bird species frequently use landscape areas
575 beyond the site level that have different overall structural characteristics. Bird
576 occurrence and habitat relationships can be scale-dependent (Seavy et al., 2009;
577 Weisberg et al., 2014). Weisberg et al. (2014) investigated multiscale habitat
578 heterogeneity and bird occurrence using LiDAR data, and they found the strongest
579 associations at a 200 m (4 ha) scale and the weakest associations at a 50 m (0.25
580 ha) scale. A similar study on multiscale analysis using LiDAR derived canopy height
581 measurements (Seavy et al., 2009) found that specific bird species responded
582 differently to vegetation structure at different spatial scales. Future studies should
583 revisit this dataset at a variety of scales.

584 **5.2. Modelling bird abundance within functional guilds**

585 All of the functional guilds that we analyzed were significantly related to LiDAR
586 derived vegetation structural metrics. Generally, TLS and ULS data achieved similar
587 results in predicting functional guild abundance (average $R^2 = 0.23$). A few earlier
588 studies have also used remote sensing to investigate relationships between bird
589 functional guilds and vegetation structure, but they used species richness within
590 guilds, rather than species abundance within guilds (Lee et al., 2017; Lesak et al.,
591 2011). For example, ALS-derived vegetation measures have been used for
592 estimating songbird species richness by nesting, foraging and edge preferring guilds
593 (Lesak et al., 2011). In that study, models using structural metrics from ALS data
594 explained between 7.0% and 16.1% of the variance in species richness in nesting
595 guilds, whereas our study explained between 8.5% and 33.7% (TLS) and 6.8% and
596 35.5% (ULS) variance in the abundance of birds from various nesting guilds. Another
597 study also found significant relationships between canopy height and density

598 variables and foraging guilds (Lesak et al., 2011). Our models showed that bird
599 abundance by functional guilds is often influenced by canopy height variables,
600 canopy roughness and vertical complexity of vegetation in the ground layer. Notably,
601 the ULS models found strong correlations between ground foraging guilds and
602 ground-layer vegetation structure, but the TLS models did not show this relationship.
603 This indicates that the ULS may capture more structural heterogeneity due to less
604 occlusion in the ground-layer in an open woodland than the TLS. As a result, a
605 portion of our second hypothesis that overall, TLS data from the seven scan stations
606 per site will perform better than ULS data in predicting avian functional guild
607 abundance for ground foraging or low nesting species is rejected.

608 **5.3. Modelling individual bird species abundance**

609 The relationship between specific vegetation structural metrics and the abundance of
610 certain bird species may be useful for future management and conservation efforts,
611 particularly for vulnerable species. In many cases, the link between the structural
612 metrics and specific bird species can be easily explained by their habitat preference,
613 lending more weight to this relationship. For example, we found that the abundance
614 of the vulnerable Superb Parrot (*Polytelis swainsonii*, Nature Conservation Act 2014)
615 is positively influenced by TLS-derived maximum height of trees and ULS-derived
616 maximum height of trees and the complexity of the first layer vegetation and
617 negatively influenced by horizontal distribution of canopy (*canopy roughness*).
618 Separate studies have found that Superb Parrots use large trees for nesting and
619 breeding and ground vegetation for foraging (Manning et al., 2004a). In addition to
620 the Superb Parrot, our LiDAR-derived structural models also performed very well in
621 predicting the abundance of two other threatened species, the White-winged Triller
622 (*Lalage tricolor*, Nature Conservation Act 2014), and the Varied Sittella
623 (*Daphoenositta chrysoptera*, Nature Conservation Act 2014).

624 Some woodland sensitive birds also responded to the LiDAR derived vegetation
625 structural metrics. For example, the Brown Thornbill (*Acanthiza pusilla*) is a species
626 found in sparse eucalypt woodlands (Stagoll et al., 2010) and its abundance was
627 negatively correlated to canopy roughness and mean height of canopy (Appendix 8,
628 Fig 8). Prior studies found that Noisy Miners (*Manorina melanocephala*) are less
629 likely to occur in areas with high shrub cover (Crates et al., 2018; Montague-Drake et
630 al., 2011; Val et al., 2018), and our noisy miner model also found a significant

631 negative relationship to shrub layer vegetation (Appendix 8). This finding suggests
632 that managing landscapes to increase shrub cover should reduce the negative
633 impact of this aggressive species, which is native, but often overabundant in human
634 modified landscapes (Debus 2008).

635 On the other end of the extreme, we found no relationship between our site-level
636 structural variables and the abundance of the Grey Shrike-thrush (*Colluricincla*
637 *harmonica*) or Pallid Cuckoo (*Cacomantis pallidus*). These common species are
638 widely distributed across Australia and use habitat at large spatial scales and across
639 a wide range of landscape types (BirdLife 2020). If relationships between these
640 species and specific structural variables are to be found, then it is more likely to be at
641 larger spatial scales than our 1 ha site-level metrics. Overall though, the individual
642 bird species models from both TLS and ULS performed better than the community-
643 based models, and that's notable because habitat is a species specific concept
644 (Betts et al., 2014; Manning et al., 2004b). In trying to understand the structural
645 requirements of wildlife using LiDAR data, it may be best to focus on individual
646 species rather than overall abundance or diversity (Manning et al., 2004b).
647 Contrasting requirements from multiple species may frustrate attempts to model
648 relationships to structural vegetation data (Halstead et al., 2019).

649 Out of 51 bird species, ULS ground-layer vegetation structure was important for 22
650 species, compared to 13 species for the TLS models (Appendix 8, Fig. 8). The
651 abundance of ground foraging birds such as Yellow-rumped Thornbill (*Acanthiza*
652 *chrysorrhoa*), Yellow-faced Honeyeater (*Lichenostomus chrysops*), Sulphur-crested
653 Cockatoo (*Cacatua galerita*), Superb Parrot (*Polytelis swainsonii*), Red-rumped
654 Parrot (*Psephotus haematonotus*), Little Corella (*Cacatua sanguinea*) were
655 significantly influenced by ground layer vegetation complexity for ULS but not TLS
656 data (Appendix 8, Fig 8). This might be related to the occlusion of TLS laser pulses
657 by ground vegetation (LaRue et al., 2020) and the ability of ULS to capture ground
658 vegetation structure in an open woodland due to the open canopy architecture of this
659 landscape (Yebra et al., 2015). As expected though, we did find that some species
660 that depend on canopy strata such as Buff-rumped Thornbill (*Acanthiza reguloides*),
661 Eastern Rosella (*Platycercus eximius*), Red-rumped Parrot (*Psephotus*
662 *haematonotus*) and Red Wattlebird (*Anthochaera carunculata*) were significantly
663 associated with more ULS canopy variables than TLS. For these reasons, our

664 second hypothesis is partially supported because the relationship between
665 vegetation structural data and particular bird species was modelled more accurately
666 from the ULS data for species that primarily use the canopy strata.

667 **5.4. TLS and ULS datasets**

668 Although we compared the performance of TLS and ULS data in modelling bird-
669 habitat associations, it is important to recognize that we collected 7 scans of TLS
670 data in each 1 ha site, and this is a relatively low number of scans compared to
671 recent studies that acquired more than 16 scans in 1 ha sites (Levick et al., 2021;
672 Wilkes et al., 2017). However, most of those studies collected data over only a few
673 hectares in total, which makes more scans per ha and associated post-processing
674 feasible. Increasing the number of TLS scans across our 96, 1 ha sites would
675 increase the time required for data collection, making it less comparable in effort to
676 the ULS data. However, more TLS scans would decrease incident angle (i.e., the
677 angle between the incoming laser pulse and surface), which would capture dense
678 vegetation and ground more completely, substantially reducing occlusions
679 (Soudarissanane et al., 2009).

680 Topcon GLS2000 is a single return LiDAR sensor, and a multiple return TLS sensor
681 would have been able to penetrated farther into vegetation (Wilkes et al., 2017). The
682 ability of the ULS sensor to record multiple returns, as well as its smaller incident
683 angle, provided advantages over the TLS. Higher point density TLS LiDAR data in
684 itself does not offer an advantage over lower point density ULS data if the coverage
685 is less complete and the landscape type allows a ULS sensor to view lower strata
686 vegetation to successfully model structural associations between plants and animals.

687 **5.5. Conclusions**

688 Mixed models showed strong relationships between vegetation structural metrics
689 derived from TLS and ULS sensors and the abundance of many individual bird
690 species and their functional guilds. This type of data can be useful for identifying
691 habitat requirements for a variety of bird species (Graf et al., 2009). The
692 performance of ULS models and the speed at which ULS data can be collected
693 relative to TLS sensors is particularly promising for this application. Understanding
694 the landscape-scale that species use and matching this to the scale of LiDAR

695 structural metrics may improve our ability to identify relationships between remotely
696 sensed vegetation structure and wildlife (Seavy et al., 2009).

697

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716 project licenses LT2005201, LT2007279, LT2009347, LT2010417, LT2014769,
717 LT2015834, LT2016905 and LT2017959.

718

719

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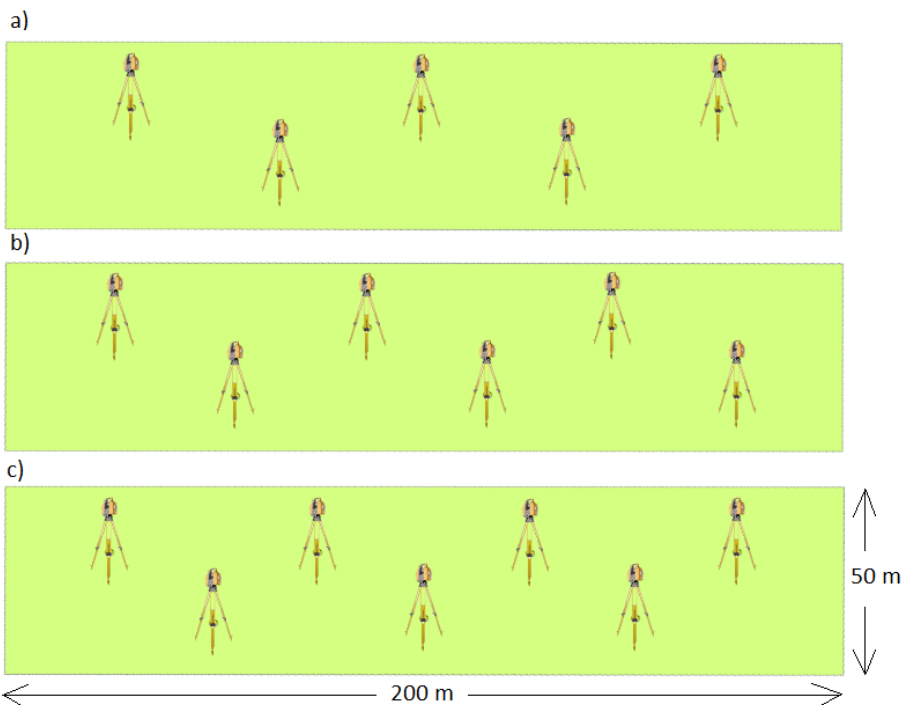
977

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979

980 **Appendix 1.**

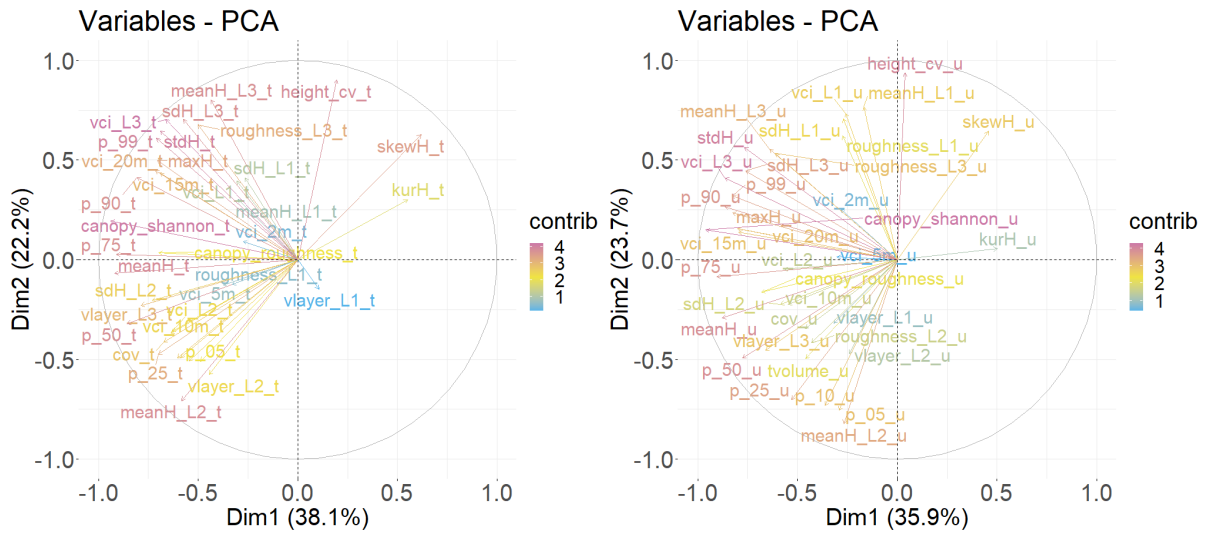
981 We conducted a pilot study in March 2018 to determine the best method to
982 characterize the 96 X 1 ha (50 m X 200 m) experimental sites with TLS data to
983 achieve the most complete coverage within a timeframe that would allow us to scan
984 all of the sites within a month. We collected TLS data at 1.7m scanner height with 6
985 mm point spacing at 10 m distance from the scanner. Data were collected from 5, 6
986 and 7 scanning stations in a test site (Fig A1). These stations were established in a
987 zigzag formation with approximately equal spacing between the stations to cover the
988 200 m x 50 m site. Data collection was performed with and without co-registering the
989 scanning stations to determine whether co-registration during collection was more
990 efficient than later co-registration during post-processing. Co-registration allows a
991 surveyor to tie multiple scans in the same site together using targets directly in the
992 field. However, this method requires more time to place and scan targets and could
993 reduce the number of scan points within a site in a given timeframe (Liang et al.,
994 2016b, Blakey et al., 2017). We found that data could be co-registered effectively
995 during post-processing, and that allowed us to maximize the number of scans
996 collected in the field.



997 Figure A1. Test scan positions: a) 5 scans, b) 6 scans and c) 7 scans for 200 m by
 998 50 m size sites.

999

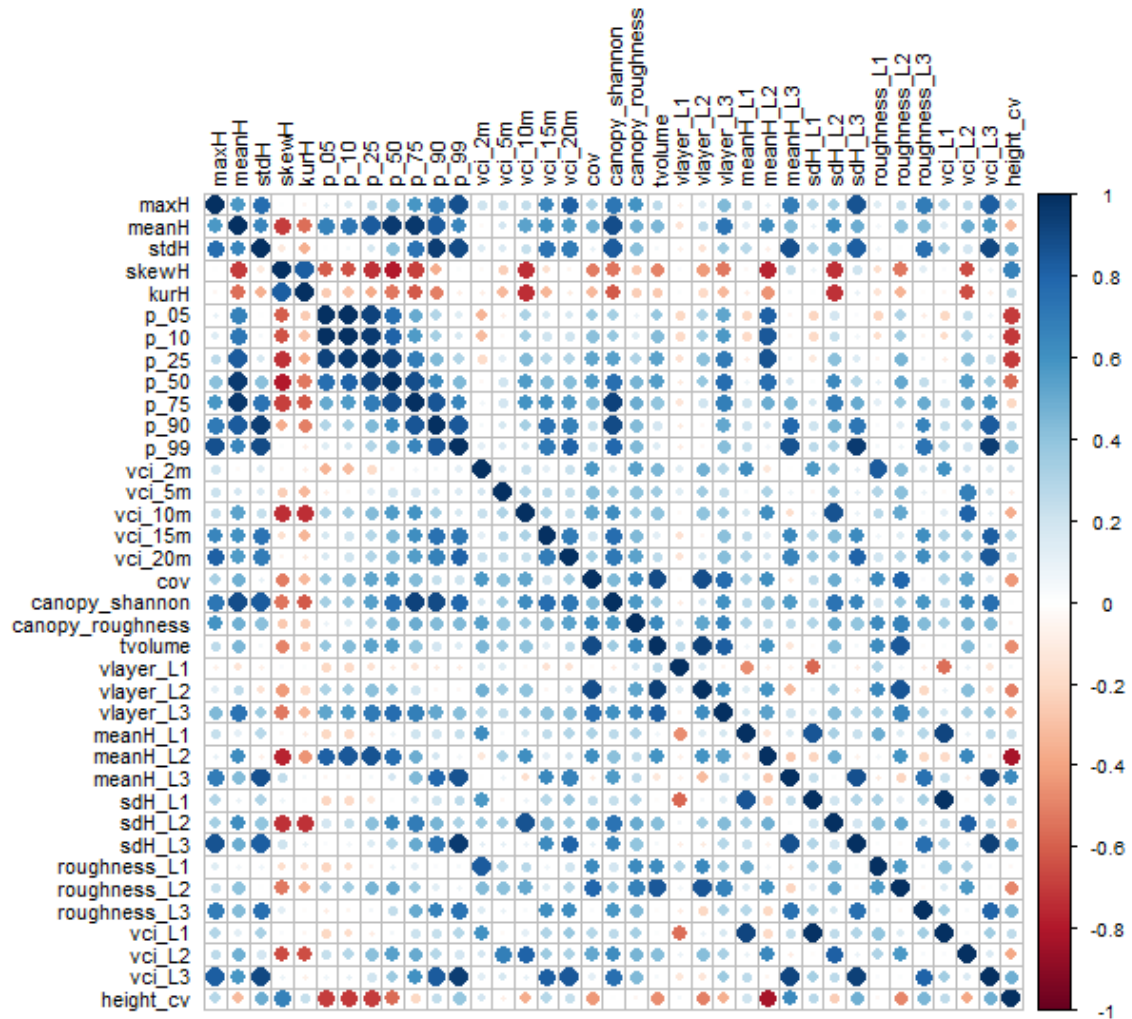
1000 **Appendix 2. Contribution of TLS (left) and ULS (right) LiDAR variables for the**
 1001 **first and the second PCA axis**



1002

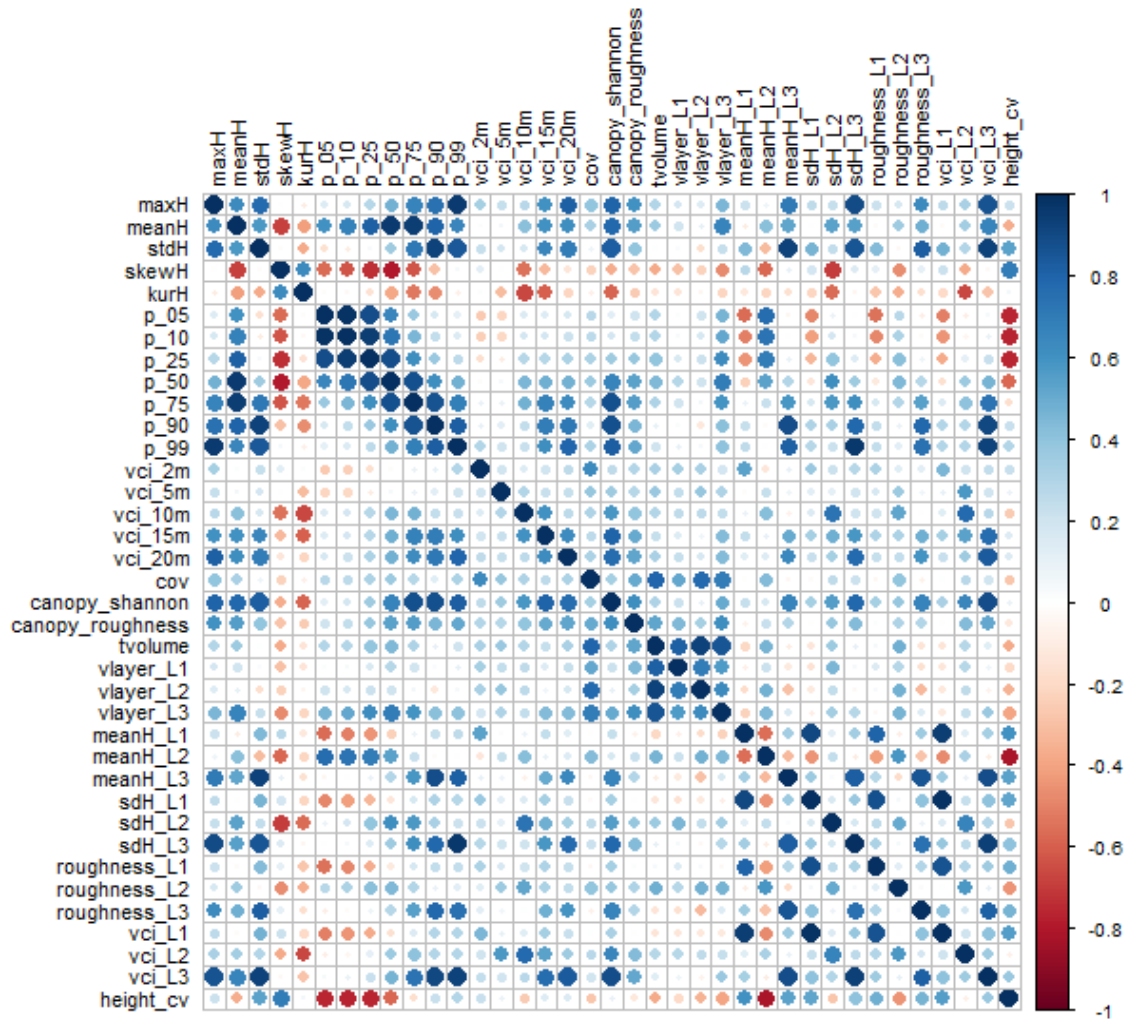
1003

1004 **Appendix 3. Pearson correlation matrix of TLS variables**



1005

1006 **Appendix 4. Pearson correlation matrix of ULS variables**



1007

1008

1009 **Appendix 5.**

1010 Table A5.1. Confusion matrix for vegetation classes predicted using terrestrial laser
 1011 scanner (TLS) LiDAR variables. Vegetation classes are high tree high shrub (HTHS),
 1012 high tree low shrub (HTLS), low tree high shrub (LTHS), and low tree low shrub
 1013 (LTLS).

Vegetation classes were predicted from the first four PCA variables calculated from all TLS LiDAR variables	User's accuracy (%)				Vegetation classes were predicted from 12 selected TLS LiDAR variables				User's accuracy (%)	
	HTHS	HTLS	LTHS	LTLS	HTHS	HTLS	LTHS	LTLS		
HTHS	21	5	6	4	58.3	26	5	6	3	65.0
HTLS	3	3	1	0	42.9	2	6	0	0	75.0
LTHS	6	5	9	0	45.0	1	3	9	3	56.3
LTLS	0	3	4	24	77.4	1	2	5	22	73.3
Producer's accuracy (%)	70.0	18.8	45.0	85.7		86.7	37.5	45.0	78.6	
Classification accuracy (%)	60.6					67.0				

1014

1015 Table A5.2. Confusion matrix of vegetation classes predicted using UAV laser
1016 scanner (ULS) LiDAR variables. Vegetation classes are high tree high shrub
1017 (HTHS), high tree low shrub (HTLS), low tree high shrub (LTHS), and low tree low
1018 shrub (LTLS).

Vegetation classes were predicted from the first four PCA variables calculated from ULS LiDAR variables					User's accuracy (%)	Vegetation classes were predicted from 12 selected ULS LiDAR variables				User's accuracy (%)
	HTHS	HTLS	LTHS	LTLS		HTHS	HTLS	LTHS	LTLS	
HTHS	24	4	13	3	54.5	25	3	4	1	75.8
HTLS	3	5	1	2	45.5	3	8	2	1	57.1
LTHS	3	3	1	0	14.3	1	4	11	3	57.9
LTLS	0	4	5	23	71.9	1	1	3	23	82.1
Producer's accuracy (%)	80.0	31.3	5.0	82.1		83.3	50.0	55.0	82.1	
Classification accuracy (%)	56.4					71.3				

1019