

1 **Comparison of small-footprint discrete return and full waveform airborne lidar data for**  
2 **estimating multiple forest variables**

3

4 Matthew J. Sumnall<sup>a,b</sup>, Ross A. Hill<sup>b</sup>, Shelley A. Hinsley<sup>c</sup>

5

6 <sup>a</sup> *Virginia Polytechnic Institute and State University, Department of Forest Resources and*  
7 *Environmental Conservation, Blacksburg, VA 24061, USA.*

8 <sup>b</sup> *Department of Life and Environmental Sciences, Bournemouth University, Poole, Dorset, UK.*

9 <sup>c</sup> *Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK.*

10

11 **Abstract:**

12 The quantification of forest ecosystems is important for a variety of purposes, including the  
13 assessment of wildlife habitat, nutrient cycles, timber yield and fire propagation. This research  
14 assesses the estimation of forest structure, composition and deadwood variables from small-  
15 footprint airborne lidar data, both discrete return (DR) and full waveform (FW), acquired  
16 under leaf-on and leaf-off conditions. The field site, in the New Forest, UK, includes managed  
17 plantation and ancient, semi-natural, coniferous and deciduous woodland. Point clouds were  
18 rendered from the FW data through Gaussian decomposition. An area-based regression  
19 approach (using Akaike Information Criterion analysis) was employed, separately for the DR  
20 and FW data, to model 23 field-measured forest variables. A combination of plot-level height,  
21 intensity/amplitude and echo-width variables (the latter for FW lidar only) generated from  
22 both leaf-on and leaf-off point cloud data were utilised, together with individual tree crown  
23 (ITC) metrics from rasterised leaf-on height data. Statistically significant predictive models ( $p$   
24  $< 0.05$ ) were generated for all 23 forest metrics using both the DR and FW lidar datasets, with  
25  $R^2$  values for the best fit models in the range  $R^2 = 0.43 - 0.94$  for the DR data and  $R^2 = 0.28 -$   
26  $0.97$  for the FW data (with normalised RMSE values being 18% - 66% and 16% - 48%

27 respectively). For all but two forest metrics the difference between the NRMSE of the best  
28 performing DR and FW models was  $\leq 7\%$ , and there was an even split (11:12) as to which  
29 lidar dataset (DR or FW) generated the best model per forest metric. Overall, the DR data  
30 performed better at modelling structure variables, whilst the FW data performed better at  
31 modelling composition and deadwood variables. Neither showed a clear advantage at  
32 modelling variables from a particular vegetation layer (canopy, shrub or ground). Height,  
33 intensity/amplitude, and ITC-derived crown variables were shown to be important inputs  
34 across the best performing models (DR or FW), but the additional echo-width variables  
35 available from FW point data were relatively unimportant. Of perhaps greater significance to  
36 the choice between lidar data type (i.e. DR or FW) in determining the predictive power of the  
37 best performing models was the selection of leaf-on and/or leaf-off data. Of the 23 best  
38 models, 10 contained both leaf-on and leaf-off lidar variables, whilst 11 contained only leaf-on  
39 and two only leaf-off data. We therefore conclude that although FW lidar has greater vertical  
40 profile information than DR lidar, the greater complimentary information about the entire  
41 forest canopy profile that is available from both leaf-on and leaf-off data is of more benefit to  
42 forest inventory, in general, than the selection between DR or FW lidar.

43 Keywords: remote sensing; forest inventory, airborne laser scanning; area-based regression

44

## 45 **1. Introduction**

46 A forest ecosystem can be described in terms of its structural, compositional and functional  
47 properties, which can be strongly influenced by any management strategies applied to a site.

48 The quantification of forest structure is important for a range of disciplines, as vegetation  
49 structure is related to a wide variety of ecosystem processes. However, a comprehensive  
50 understanding of the overall spatial patterns of structural variation in large forested landscapes  
51 is still largely incomplete (Anderson et al., 2008).

52  
53 The management of an area is often assisted by landscape-scale monitoring (Newton et al.,  
54 2009), with a requirement of measuring both vertical and horizontal metrics. For example, the  
55 assessment of timber yields requires information on the density of trees, together with their  
56 species and size (Matthews & Mackie, 2006). Such data allow the quantification of timber  
57 yield and its associated economic value, and in addition risk assessment for fire, wind or pest  
58 damage, which are also partially dependent on canopy structure. Vertical structure is of  
59 importance in determining the species composition of ground flora (Ferris et al., 2000), in the  
60 assessment of habitat quality for many forest-dwelling species (Hinsley et al., 2009), and as an  
61 indicator of biodiversity (Ferris & Humphrey, 1999). Traditionally forest inventory data are  
62 collected through manual field observations in sample plots. The benefit of this approach can  
63 be high accuracy, but it is time consuming and expensive (Aplin, 2005).

64  
65 Airborne remote sensing technologies such as lidar can characterise both horizontal and  
66 vertical structures in forested environments. The use of lidar has rapidly come to prominence  
67 in estimating forest biophysical characteristics, such as canopy height and basal area (Evans et  
68 al, 2009). Most commercial airborne lidar systems are small-footprint (i.e. < 1m) and deliver  
69 discrete return (DR) point data. The point data correspond to high intensities in the back-  
70 scattered light of the laser pulse interacting with a surface, allowing some systems to record  
71 multiple returns per laser pulse (typically 1 - 5). Due to limitations in the design of most multi-  
72 return airborne lidar systems, there is a sizable 'blind spot' (or dead zone) following each  
73 detected return (typically 1.2 m to 5.0 m) in which no other surfaces can be detected  
74 (Reitberger et al., 2008). Range resolution is determined by the length of the transmitted pulse  
75 and the maximum number of returns recorded by the sensor. The signal processing algorithms

76 which are used to detect returns are often proprietary and differ between DR lidar sensors  
77 (Disney et al., 2010; Næsset, 2009).

78

79 Recent developments in scanning lidar technology resolve the issue of a blind spot. Small-  
80 footprint, full waveform (FW) lidar systems have become available commercially. FW lidar  
81 sensors digitize the total amount of laser energy returned to the sensor in fixed time intervals  
82 (typically 1 ns to 5 ns), providing a near continuous distribution of back-scattered laser  
83 intensity for each recorded pulse (Wagner et al., 2008). Instead of clouds of individual three-  
84 dimensional points, such as with DR lidar, small-footprint FW lidar devices provide connected  
85 profiles of the three dimensional scene, which contain more detailed information about the  
86 structure of the illuminated surfaces (Alexander et al., 2010). Each waveform consists of a  
87 series of temporal modes (or echoes), where each corresponds to an individual reflection event  
88 from an object or set of close but separated objects. Each laser pulse waveform represents  
89 complex data, which requires sophisticated processing before metrics can be generated  
90 (Chauve et al., 2009). One potential approach to derive information from the waveform is to  
91 identify proximal peaks, or returns, to present the waveform as a series of Gaussian curves;  
92 fitted by a non-linear least squares approach (Miura & Jones, 2010; Wagner et al., 2006). The  
93 replacement of Gaussian functions with stochastic functions based on marked point processes  
94 (Mallet et al., 2010) has also been suggested as a method of processing small-footprint FW  
95 lidar data. Extracting individual returns from FW data can have the effect of removing the  
96 blind spot present in DR data that have been processed by proprietary software.

97

98 Airborne DR lidar systems have been utilised for the estimation and retrieval of various forest  
99 related variables, which are important to management and ecological monitoring. This is due  
100 to an inherent ability to provide both geo-referenced horizontal and vertical information on the

101 structure of forest canopies, with sampling dependent on the type of lidar system used and  
102 flight configuration (Evans et al., 2009; Næsset, 2009). The most obvious vegetation measure  
103 extracted from lidar is that of canopy height. Plot- or stand-level regression analysis or non-  
104 parametric model estimates of canopy density, mean tree height, basal area and volume have  
105 been applied (Bouvier et al. 2015; Hyypä et al., 2008; Næsset, 2007). Other studies have  
106 been able to characterise understorey vegetation cover and detect suppressed trees (Estornell  
107 et al., 2011; Maltamo et al., 2005), assess regeneration patterns and floristic composition  
108 (Bollandsås et al., 2008; Leutner et al., 2012), and estimate deadwood volume (Kim et al.,  
109 2009b; Pesonen et al., 2008). Lidar sensors, typically DR, can collect data at point densities  
110 sufficient to identify individual tree crowns in forest canopies and delineate crown horizontal  
111 extent and vertical depth (Kaartinen et al., 2012). Such individual tree crown (ITC) metrics  
112 have been identified as important inputs into predicative models of forest variables (e.g.  
113 Hyypä et al., 2001; Persson et al., 2002; Popescu et al., 2004).

114  
115 With an increasing accessibility of small-footprint FW lidar, there is a small but growing  
116 number of published studies which evaluate FW and DR lidar for the estimation of forest  
117 structural and compositional parameters. For example, Cao et al. (2014) compared statistical  
118 predictions of total living biomass obtained from DR lidar metrics (i.e. height and height  
119 variance measures, canopy return density measures, and canopy cover measures) and from FW  
120 lidar metrics (i.e. height of median energy, waveform distance, height/median ratio, number of  
121 peaks, roughness of outermost canopy, front slope angle, return waveform energy and vertical  
122 distribution ratio). They extracted the DR data by Gaussian decomposition of the FW data, and  
123 therefore the two datasets shared the same sampling rate characteristics but supplied different  
124 sets of metrics due to the way the full waveform information was processed. They found that  
125 lidar metrics related to canopy height (either DR or FW derived) were the strongest predictors

126 of total biomass, but that there were benefits from the synergistic use of DR and FW lidar  
127 metrics in estimating the different biomass pools in the forest vertical structure. Lindberg et al.  
128 (2012) outlined a method to analyse both DR and FW lidar data for the estimation of canopy  
129 vegetation volume for coniferous and deciduous forest. Estimates of volume from FW lidar  
130 were predicted more accurately than from DR lidar, especially when corrections were applied  
131 for the shielding effects of higher vegetation layers based on the Beer-Lambert Law. Allouis et  
132 al. (2013) reported similar results where the inclusion of FW metrics improved model  
133 estimates for the prediction of above-ground biomass of individual trees, but gave slightly  
134 inferior estimates of stem volume when compared with DR lidar only. Yu et al. (2014)  
135 compared DR and FW lidar for individual tree crown delineation and boreal forest species  
136 classification, reporting that FW lidar was slightly better for detecting trees, whilst DR metrics  
137 combined with FW metrics improved species classifications. Armston et al. (2013) compared  
138 DR and FW lidar data for the estimation of vertical canopy gap probability for savanna  
139 woodland, showing that models produced using FW lidar data were superior.

140  
141 The use of small-footprint DR lidar data for forest inventory using an area-based regression  
142 approach is now well established (Næsset, 2007). As small-footprint FW lidar data become  
143 more readily available, early studies suggest possible benefits and potential drawbacks in  
144 moving towards these data. As yet there has been no systematic study to compare small-  
145 footprint DR and FW data for the estimation of multiple inventory variables from across a  
146 forest profile. This study addresses this research gap, comparing point cloud data and derived  
147 products from DR lidar and from Gaussian decomposition of FW lidar. The work of Cao et al.  
148 (2014) compared standard DR height metrics with newer sets of FW lidar metrics, and  
149 specifically avoided investigating the effects of higher density point clouds provided by FW  
150 lidar decomposition. Here we specifically focus on a comparison between the different

151 information content on forest vertical and horizontal structure and recorded return pulse  
152 characteristics in DR and FW-derived point clouds. We assess 23 common forest inventory  
153 variables covering all forest vegetation layers (canopy, shrub and ground layer) and both  
154 living and dead wood. Airborne DR and FW lidar data were acquired simultaneously under  
155 both leaf-on and leaf-off conditions, and variables from both (including point cloud and ITC-  
156 derived lidar variables) are used in area-based regression modelling of forest inventory  
157 variables. The wider context of this work was forest condition assessment.

158

## 159 **2. Data and Methods**

### 160 *2.1 Study site*

161 The study site is located within the New Forest National Park, between Southampton and  
162 Bournemouth, in southern England (lat: 50° 50' N, long: 1° 30' W). This National Park has  
163 multiple land covers and land uses, with much of the forested area actively managed (see  
164 Tubbs 2001). This study is focused on a ca. 22 km<sup>2</sup> area that sits in a triangle between the  
165 villages of Lyndhurst, Brockenhurst, and Beaulieu. This area is low lying, between 5m and  
166 45m above sea level, with only gently undulating terrain. The forest includes managed  
167 inclosures, in addition to unenclosed areas which are not subject to felling operations and are  
168 permanently open to grazing by large ungulates (mostly ponies, deer and cattle).

169

170 The study area contains several types of semi-natural and plantation coniferous and deciduous  
171 forests in close proximity (Newton et al., 2010). Deciduous species include: oaks (*Quercus*  
172 *robur* and *Quercus petraea*), beech (*Fagus sylvatica*), common alder (*Alnus glutinosa*), silver  
173 birch (*Betula pendula*), sweet chestnut (*Castanea sativa*), and holly (*Ilex aquifolium*).  
174 Coniferous species include: Corsican pine (*Pinus nigra* var. *maritime*), Scots pine (*Pinus*  
175 *sylvestris*), Douglas fir (*Pseudotsuga menziesii*) and Norway spruce (*Picea abies*). This array

176 of forest types within close proximity to each other presents a wide range of available  
177 structural and compositional variables of interest, such as canopy gaps and the presence of  
178 deadwood or understorey.

179

## 180 *2.2 Field data collection*

181 Using pre-existing data, the woodland areas of the study site were split into coniferous,  
182 deciduous and mixed woodland compartments and stratified according to their relative  
183 biomass, as derived from Normalised Difference Vegetation Index (NDVI) data. A total of 41  
184 field plots were then randomly located across this stratification to enumerate a range of forest  
185 types and canopy conditions. An initial 21 plots were visited in the summer of 2010  
186 (subsequently used for establishing relationships), with the remaining 20 plots visited in a  
187 further field campaign in the summer of 2012 (used for validating relationships). The field  
188 plots were only enumerated if they were located a minimum of 10 m away from a stand  
189 boundary in order to limit any potential edge effects.

190

191 Field data were collected from north-oriented 30 m × 30 m plots with a 10 m × 10 m subplot  
192 in the south-west corner. Plot positions were located accurately using a combination of a Leica  
193 GPS 500 (Leica Geosystems) and Sokkia 6F total station (SOKKIA TOPCON Co. Ltd.). Post-  
194 processing of the coordinates was performed in Leica Geo-office software (version 8.2). Total  
195 horizontal positional error was calculated as  $\leq 0.08$  m.

196

197 Plot-level totals and averages were calculated for each field recorded metric. Within each plot,  
198 diameter at breast height (DBH) was recorded at 1.3 m above the ground for every stem, and  
199 for those with DBH > 10 cm, a 3D position (via total station) was recorded to estimate stem  
200 spacing. In addition, canopy top height (m), height to the living crown (HTLC) (m), crown



201 horizontal dimensions in the east-west and north-south directions, and species type were  
202 recorded. Vertical height measurements were calculated via trigonometry, using a measured  
203 horizontal distance from the tree stem and an angular measurement, from a clinometer, to the  
204 required vertical feature. Plot-level basal area was calculated by summing the area of a circle  
205 calculation applied to each tree DBH measurement within the plot extent. The number of  
206 stems of native tree species was recorded. Native tree species within the study site were  
207 considered to include Scots pine, common alder, oak, beech, silver birch, holly and sweet  
208 chestnut.

209  
210 The species compositional indices of the Shannon-Wiener index (SH) (Shannon, 1948) and the  
211 Simpson index (SI) (Simpson, 1949) were utilised in this study. The Shannon-Wiener  
212 diversity index for all tree species was calculated as:

$$SH = \sum_{i=1}^n p_i \log_e p_i \quad [1]$$

213 where  $p_i$  = the proportion of individuals (plot stem number) in the  $i$ th species, and  $n$  is the  
214 number of species. The Simpson index was calculated for tree species in each plot as:

$$SI = 1 - \left( \sum_{i=1}^n (1 - p_i)p_i \right) \quad [2]$$

215 where  $p_i$  = the proportion of individuals (plot stem number) in the  $i$ th species, and  $n$  is the  
216 number of species.

217  
218 Each of the standing deadwood items, or snags, within a field plot was recorded. Snags were  
219 defined as standing deadwood > 10 cm DBH (Spies et al., 1988). Snag volume was calculated  
220 using the formula for determining cylindrical volume using height and girth measurements.  
221 Downed deadwood (DDW) was defined as deadwood logs or branches of at least 10 cm  
222 diameter lying on the ground (Spies et al., 1988). Measurements for DDW were made in the

223 10 m × 10 m sub-plot only. Length and girth around the maximum and minimum diameters of  
224 the log were recorded. Estimates of DDW volume were determined using the equation for a  
225 frustum of a cone. To assess deadwood decay class, snags and DDW were divided into three  
226 decay classes according to the following criteria, as defined in Cantarello & Newton (2008):  
227 (i) logs with a low decay state, no surface breakdown, bark still intact, wood structure firm; (ii)  
228 logs with a moderate decay state, with some surface breakdown, wood structure weaker but  
229 bole mostly sound; and (iii) logs with high decay state, extensive surface breakdown, bark  
230 mostly absent, bole with no sound wood present and colonised with vegetation. A size-  
231 weighted average decay class score was then calculated at the plot level.

232  
233 The number of saplings and their species types (including the number of saplings of a native  
234 species) were recorded within each field plot. Saplings were defined as tree stems > 1.3 m in  
235 height with DBH < 10 cm. The total number of seedlings, their species type, and number of  
236 seedling stems of native species within the sub-plot extent were also recorded. Seedlings were  
237 defined as tree stems < 1.3 m in height. The number of vascular plant species and the  
238 percentage of bare ground within each 30 m × 30 m plot were also recorded.

239  
240 In total, 23 forest variables were recorded in the field and subsequently investigated using  
241 airborne lidar data. Summary information of field data across the 21 plots surveyed in 2010  
242 and 20 plots surveyed in 2012 is given in Table 1.

243  
244 [insert Table 1 here]

245

246 *2.3 Airborne lidar data collection*

247 Small-footprint lidar data were acquired for the study area under leaf-off (April 8) and leaf-on  
248 (July 6) conditions in 2010. The lidar instrument used was the Leica ALS50-II airborne laser  
249 scanner with an upgrade to allow the simultaneous recording of DR and FW data. On both  
250 dates the lidar data were acquired at a flying altitude of ca. 1600 m, with a pulse repetition  
251 frequency (PRF) of 147 kHz, a beam divergence of 0.22 mr, and a scan half angle of 10°. The  
252 geometric accuracy for the scanner is stated by the manufacturer (Leica Geosystems) as a  
253 nominal vertical accuracy of 0.05 m to 0.10 m, and horizontal accuracy of 0.13 m to 0.61 m.  
254 With the chosen flight and sensor configuration, the average sampling rate for the leaf-on and  
255 leaf-off data was 5.0 and 5.2 pulses m<sup>-2</sup> respectively (including areas of flight-line overlap).  
256 The DR and FW data were recorded from the same set of emitted pulses, but the ALS50-II  
257 scanner could only digitise the full waveform of every other pulse at the PRF used for these  
258 acquisitions. In actuality, the sampling rate for the FW lidar data was slightly less than half  
259 that of the DR data quoted above (49% and 48% for the leaf-on and leaf-off data respectively)  
260 due to minor recording errors. The DR data had up to four discrete returns per laser pulse, with  
261 x-, y- and z-coordinates, intensity, and return number supplied for the first, intermediate, and  
262 last significant returns per pulse. For the FW data, 256 return signal amplitude values  
263 (sampled every two nanoseconds for the April data and every one nanosecond for the July  
264 data) were supplied for each laser pulse.

265

#### 266 *2.4 Airborne lidar data processing*

267 The DR lidar data were supplied as LAS 1.0 format files, with a basic classification  
268 identifying noise returns already applied using Terrascan software (<http://www.terrasolid.fi>).  
269 A number of pre-processing steps were required before metrics could be derived from the lidar  
270 data for subsequent analysis. All of these steps were performed using the RSC LAS Tools  
271 software (version 1.9.3) (<http://code.google.com/p/rsclastools>). The DR point cloud data

272 required filtering to separate the ground and vegetation hits so that ground elevation could be  
273 determined and used to normalise vegetation hits to above-ground height. RSC LAS Tools  
274 software employs a progressive morphological filter, as outlined in Zhang et al. (2003), to  
275 filter out ground returns, which were then interpolated into a surface at 1m resolution using the  
276 nearest neighbour method. Ground elevation values were then removed from the DR lidar  
277 dataset to yield vegetation height. All points which intersected within field plot locations were  
278 clipped from the dataset and used to create plot-level lidar variables, as in Falkowski et al.  
279 (2009) and Hudak et al. (2008). These included eight variables (mean, median, maximum,  
280 standard deviation, variance, absolute deviation, skewness and kurtosis) which were calculated  
281 from the height data (separately for all and non-ground returns) and from the intensity data  
282 (separately for all, non-ground and ground returns) for both leaf-on and leaf-off lidar  
283 acquisitions. This totalled 80 variables. In addition, percentiles at 5% intervals between 5%  
284 and 95% were created for both height and intensity data using all returns, separately for both  
285 leaf-on and leaf-off acquisitions. This totalled an additional 72 variables (as the maximum and  
286 median values were already calculated above).

287

288 In addition, canopy cover was calculated as:

$$CC = \left( \frac{h_{ng}}{h_{all}} \right) \quad [3]$$

289 where  $h_{ng}$  and  $h_{all}$  denote the sum total of non-ground returns and the sum of all returns,  
290 respectively. A vertical profile was generated by stratifying the frequency of all returns at the  
291 plot-level vertically for every metre. The number of vertical layers was estimated by  
292 iteratively fitting Weibull functions to the vertical profile (fit to the frequency of return height  
293 bins), where local maxima or ‘peaks’ were taken to represent vertical layers and troughs were  
294 taken to be layer divisions (Coops et al., 2007). The number of local maxima was considered  
295 to identify the number of vertical layers. The largest vertical separation between layers, or

296 between a layer and ground, was then calculated for each plot to derive the largest vertical gap  
297 within the canopy profile. These three metrics (canopy cover, number of canopy layers, and  
298 the size of largest vertical canopy gap) were calculated separately for the leaf-on and leaf-off  
299 DR lidar data. Thus, a total of 158 metrics were derived from the DR point cloud data for each  
300 30 m x 30 m field plot area.

301  
302 The FW lidar data were provided in LAS 1.3 file format, containing GPS, IMU, and laser  
303 pulse return waveform data. The FW lidar pre-processing tasks were performed using the  
304 Sorted Pulse Software Library (SPDlib) (version 1.0.0) (Bunting et al., 2013a, 2013b). In order  
305 to derive 3D point information from the recorded waveforms, it was necessary to apply a  
306 process of Gaussian decomposition to each (as described in Wagner et al., 2006), identifying  
307 peaks in the return signal above a background threshold level representing noise. A  
308 combination of angular measurements, bearing, positional information of the aircraft and first  
309 peak coordinates, trigonometry and the relevant pulse timings (2 ns or 1 ns) allowed the  
310 estimation of the 3D locations for each of the fitted Gaussian peaks, in addition to peak  
311 attributes such as amplitude and width. This yielded between 1 and 11 returns per pulse,  
312 supplying x-, y- and z- coordinates, amplitude and width per return. The majority of pulses  
313 generated at least two returns in the leaf-on data and at least three returns in the leaf-off data,  
314 which compared with the majority of pulses generating only single returns in both the leaf-on  
315 and leaf-off DR lidar data. The sampling rates of the DR and FW point clouds are summarised  
316 in Table 2. Overall, the FW lidar provided more returns for each pulse than the DR lidar (and  
317 more information per return), supplying a higher vertical sampling rate (Figure 1). However,  
318 the total sampling rate was lower in the FW data, and in particular the horizontal sampling rate  
319 at the canopy surface was considerably higher in the DR data. This contrast in sample

320 distribution between DR and FW lidar across the 3D volume of a forest landscape is the focus  
321 of the data comparison being made here.

322

323 [insert Table 2 & Fig 1 here]

324

325 The SPDLib software also provided tools for noise filtering, vegetation classification and  
326 height normalisation on the extracted point data. As with the DR data processing, this used the  
327 progressive morphological filter, as outlined in Zhang et al. (2003), to identify ground returns.

328 The above-ground heights were then calculated by subtracting the ground elevation surface (as  
329 interpolated by a natural neighbour algorithm from the classified ground returns) from all  
330 returns. Subsequently, all returns which intersected within field plot locations were clipped  
331 from the dataset, and eight variables (mean, median, maximum, standard deviation, variance,  
332 absolute deviation, skewness and kurtosis) were calculated from the height data (separately for  
333 all and non-ground returns) and from both the amplitude and echo-width data (separately for  
334 all, non-ground and ground returns), all for both leaf-on and leaf-off lidar acquisitions. This  
335 totalled 128 variables. In addition, percentiles at 5% intervals between 5% and 95% were  
336 created for height, amplitude and echo-width data using all returns, separately for leaf-on and  
337 leaf-off acquisitions. This totalled an additional 108 variables. The metrics derived from  
338 analysis of the canopy horizontal and vertical profile (i.e. canopy cover, largest vertical gap,  
339 and number of vertical layers) were also calculated from leaf-on and leaf-off FW data in the  
340 same way as for the DR metrics. A total of 242 metrics were derived from the FW-derived  
341 point cloud data for each 30 x 30 m field plot area.

342

343 Individual tree crown (ITC) delineation techniques were implemented on the DR and FW lidar  
344 data (leaf-on only) using the Toolbox for Lidar Data Filtering and Forest Studies (TIFFS)

345 software (version 5.0) (<http://www.globalidar.com>). A 1 × 1 m resolution raster Canopy  
346 Height Model (CHM) was created using the maximum above-ground height in each cell. Tree  
347 crowns were isolated using a marker-controlled watershed segmentation method, as used in  
348 Chen et al. (2006), where tree top positions were located and regions ‘grown’ into areas of  
349 decreasing height. The identification of individual tree crowns was performed separately using  
350 leaf-on DR and FW lidar data, resulting in a GIS database of individual tree locations and  
351 crown attributes. Note that ITC objects with a crown horizontal radius < 1.5 m or a height  
352 ≤ 1.3 m were removed from this database as non-tree features. All remaining ITC objects with  
353 a centroid within the field plot extent were extracted and this was used to generate eight plot-  
354 level ITC variables for both the DR and FW data: mean tree height, mean and total crown  
355 area, mean and total canopy volume, mean and standard deviation of distance between trees,  
356 and the number of trees per plot. These were extracted using R software (version 2.15.2)  
357 (<http://www.r-project.org/>).

358

### 359 *2.5 Statistical analysis*

360 A modification to the approach outlined in Langton et al. (2010) was used to conduct a ‘data  
361 mining’ exercise to identify important predictor variables for subsequent regression analyses.  
362 This was necessary due to the high number of lidar predictor variables and their potential high  
363 collinearity with one another, (up to  $r = 0.9$  in many cases). Therefore, the ‘MuMin’ (Multi-  
364 Model Inference) package for R software (version 1.9.5) ([http://CRAN.R-  
365 project.org/package=MuMin](http://CRAN.R-project.org/package=MuMin)) was used to run Akaike Information Criterion (AIC) analysis to  
366 regress the field data from the 21 plots visited in 2010 against the corresponding lidar metrics.  
367 In this case, due to the small number of field plots available, a second order information  
368 criterion (AICc) was implemented. AICc incorporates a greater relative penalty for extra  
369 parameters, therefore decreasing the probability of selecting models that have too many

370 parameters and might over-fit the data (Burnham & Anderson, 2002). Analyses were  
371 performed separately for the DR and FW lidar data. To determine which lidar variables had  
372 the most potential for the prediction of forest attributes, an automatic stepwise AICc selection  
373 was used on the dataset for 500,000 iterations, where each iteration functioned on a subset of  
374 six randomly selected predictor variables. Significant predictors were recorded for each  
375 iteration and the variables with the most counts across all iterations identified. For each of the  
376 23 field metrics assessed, a subset of the lidar predictor variables determined to be the most  
377 significant (i.e. those with the highest counts) were input into a further stepwise AICc process  
378 to derive a final regression equation. Twenty predictor variables determined to be the most  
379 significant for each field metric were entered into the stepwise approach. Note that zero values  
380 in the field plot data were included in the regression analyses.

381  
382 The stepwise procedure thus produced a regression model using a subset of the input lidar  
383 variables for each field metric. Several criteria were used to examine potential models,  
384 including  $R^2$  and adjusted  $R^2$ ; individual covariate significance (Type III error  $t$  tests,  $p \leq$   
385 0.05); absence of multi-collinearity (i.e. variance inflation factor  $\leq 1$ , see Bowerman &  
386 O'Connell, 1990); and residual homoscedasticity. Root Mean Square Error (RMSE) of each  
387 model was assessed using the 20 field plots that were not used in establishing the models. The  
388 final models selected were those which exhibited a combination of the lowest changes of  $R^2$  to  
389 adjusted  $R^2$  and the lowest overall dataset RMSE, whilst still satisfying individual covariate  
390 criteria. Adjusted  $R^2$  is considered more conservative than  $R^2$ , thus models where the two  
391 showed little change were sought when using multiple predictors. The exclusion of redundant  
392 covariates was addressed by the examination of individual standard error and variance  
393 inflation factor values, as model validity in multiple linear regression relies partly on the  
394 number of observations and covariates.



395

### 396 **3. Results**

397 Statistical models were developed for each of the 23 field metrics using the DR and FW lidar  
398 as separate datasets. Input variables for each model could potentially be drawn from ground,  
399 non-ground or all returns, from leaf-on or leaf-off data, for height, intensity/amplitude or echo-  
400 width measures, and could also include ITC-derived metrics. A statistically significant model  
401 (at  $p < 0.05$ ) was created for all field metrics using the two lidar datasets (DR and FW). Across  
402 the 23 field metrics, the  $R^2$  value for the best fit model covered the range  $R^2 = 0.43 - 0.94$  for  
403 the DR data and  $R^2 = 0.28 - 0.97$  for the FW data (Table 3). The normalised RMSE covered  
404 the range 18% - 66% for the DR models and 16% - 48% for the FW models. The difference in  
405 NRMSE between the best fit DR and FW model was low ( $\leq 7\%$ ) for all but two forest metrics  
406 (number of sapling species and number of vascular plant species). It should be noted that for  
407 11 of the 23 forest metrics, the best fit models (i.e. those with the highest  $R^2$ ) did not generate  
408 the best predictions based on independent field validation data, thus demonstrating over-fitting  
409 of some models to the input data. This was particularly notable for mean crown horizontal  
410 area, standing deadwood decay class, number of sapling species and number of seedling  
411 species.

412

413 [insert Table 3 here]

414

415 Across the 23 best performing models (i.e. those with the lowest NRMSE) the number and  
416 composition of input lidar variables differed (Table 4). Thus, all models had between one and  
417 four input variables; with 11 models having two input variables, six models having three input  
418 variables, and three models each with either one variable (number of tree stems of native  
419 species, downed deadwood decay class, and number of vascular plant species) or four

420 variables (number of tree stems, Shannon-Weiner index of diversity, and mean height to the  
421 living crown). In terms of the nature of input variables, six of the best performing models had  
422 input variables of a single type (i.e. intensity/amplitude, height, echo-width, or ITC-derived),  
423 whilst the remaining 17 had input variables of multiple types. In total, 18 of the best  
424 performing models contained intensity/amplitude variables, 14 contained height variables, a  
425 further 11 contained ITC variables, and 2 contained echo-width variables. Focussing on the  
426 timing of lidar input variables; 11 of the best performing models contained only leaf-on data,  
427 10 models contained both leaf-on and leaf-off variables, and 2 models contained only leaf-off  
428 data.

429

430 [Insert Table 4 here]

431

432 Separating the best performing models into those containing DR lidar data (11 models) and  
433 those containing FW lidar data (12 models), there was little difference between the two sets of  
434 models in the proportional composition of intensity/amplitude, height, echo-width, or ITC-  
435 derived input variables (Table 5), and between those point cloud variables derived using all,  
436 ground or non-ground lidar returns (Table 6). However, there was a notable difference  
437 between the proportion of input variables from leaf-on and leaf-off data between the best  
438 performing DR and FW lidar models. Thus, 22 of 26 input variables in the best performing  
439 DR models were leaf-on, compared with 18 of 29 input variables in the best performing FW  
440 models. In terms of the type of forest metric, 6 of 9 structure metrics were best modelled in  
441 DR data, whilst 6 of 10 composition and 3 of 4 deadwood metrics were best modelled in FW  
442 data. There was an even division between the two lidar datasets in relation to generating the  
443 best performing models across the vegetation layers; thus DR lidar data were used in 6 of 13  
444 canopy layer models, 2 of 3 shrub layer models, and 3 of 7 ground layer models.

445

446 [Insert Tables 5 & 6 here]

447

#### 448 **4. Discussion**

449 As outlined in Matthews & Mackie (2006) there is a requirement for knowledge within a  
450 defined area of how many trees exist, what species they are and their relative sizes, in order to  
451 make predictions for management purposes. Both structural and compositional information  
452 from remote sensing sources have been used in a number of studies to estimate forest  
453 inventory metrics, and assess habitat and species presence (Lesak et al., 2011; Martinuzzi et  
454 al., 2009). This study has demonstrated the ability of both DR and FW lidar data to estimate  
455 multiple forest metrics across a study area.

456

457 For the 23 forest metrics investigated here, one was determined with high accuracy (i.e.  
458 NRMSE < 20%), 17 with moderate accuracy (NRMSE 20% - 35%), and two with low  
459 accuracy (NRMSE > 35%) in the best performing models. Some of this error may have been  
460 the result of a 2 year time lag between the collection of both the airborne lidar data and the  
461 field plot data used to establish the models (2010) and the field plot data used to validate these  
462 models (2012). Also, for many forest variables, the range of data from the field plots surveyed  
463 in 2012 was outside that from the field plots surveyed in 2010, which would also have had a  
464 likely impact on the estimated prediction accuracy of models established using the 2010 data.

465

466 There is extensive surrounding literature on the estimation of forest structural and  
467 compositional metrics using airborne lidar data and an area-based regression approach.  
468 However, many only predict a relatively limited number of forest metrics (e.g. Hudak et al.,  
469 2009; Hyyppä et al., 2008; Li et al., 2014; Lim et al., 2003; Næsset 2004; Richardson &

470 Moskal, 2011). Thus, no single study has covered such an extensive range of forest metrics as  
471 that presented here, especially relating to all vegetation layers in a forest. For those metrics for  
472 which direct comparison can be made with other published studies; e.g. number of tree stems  
473 (Lee & Lucas, 2007; Næsset, 2002), mean height to the living crown (Andersen et al., 2005;  
474 Muss et al., 2011), DBH and basal area (Næsset, 2002; 2004), and downed deadwood volume  
475 (Mücke et al., 2013), the prediction accuracy in the current study is of a similar magnitude.  
476 Standing deadwood volume was predicted with the highest NRMSE (16%), with three FW  
477 lidar variables contributing to the best performing model: skewness of amplitude in non-  
478 ground returns (leaf-off), the 25<sup>th</sup> percentile of echo-width in all returns (leaf-on) and the  
479 standard deviation of ITC centroid spacing (leaf on). Thus, standing deadwood is detectable  
480 where the return signal strength is low and skewed in relation to surrounding living biomass,  
481 and where there is variation in tree spacing. By contrast, the percentage of bare ground cover  
482 and number of sapling species were the least well modelled forest measures (with NMRSE of  
483 42% and 48% respectively). Whilst the input lidar variables for the best performing models for  
484 these two forest metrics are readily understandable (relating to low order height percentiles,  
485 canopy vertical structure, and variation in either amplitude or crown size), these are  
486 nonetheless indicators of below canopy conditions in which saplings and ground flora may  
487 exist rather than direct measures of the features themselves. The implication here is that  
488 variance in overstorey canopy structure indicates structural and compositional diversity in the  
489 lower portions of the forest.

490  
491 In general, the DR and FW lidar datasets performed similarly in terms of the predictive power  
492 of the models generated for each forest metric. In total, 12 of the best performing models  
493 included FW lidar data whilst the remaining 11 included DR lidar data. There was a slight bias  
494 in these models of the DR data towards forest structure variables and the FW data towards

495 compositional and deadwood variables. Nonetheless, in all but two cases (the number of  
496 sapling and vascular plant species), the difference in the NRMSE between the best performing  
497 DR and FW model was slight ( $\leq 7\%$ ). A disparity existed between sample densities of DR and  
498 FW lidar data in this study resulting from fewer FW pulses being recorded. However, small-  
499 footprint full waveform lidar data offer a much higher potential for detecting returns beneath  
500 the canopy (Wagner et al., 2006). Thus, with the detection of a greater number of return points  
501 through Gaussian fitting for the FW lidar data, which provided information along the vector of  
502 the laser pulse penetrating the canopy, the distribution of points and total sampled forest  
503 elements were different between the DR and FW lidar data in this study. The DR data had a  
504 higher horizontal sampling rate at the canopy surface, whilst the FW data had a higher  
505 sampling rate through the canopy vertical profile. It was notable that neither DR nor FW data  
506 showed a clear advantage at modelling forest metrics at the canopy, shrub or ground level.  
507 Thus the perceived advantages of a higher canopy surface sampling rate in the DR data and a  
508 higher vertical sampling rate in the FW data for modelling different elements of a forest were  
509 not demonstrated as particularly significant in the results of this study. It should be noted, that  
510 the reduced sampling rate of the FW data (compared with the DR data) in this study was  
511 specific to the lidar system and PRF used for data acquisition. No attempt was made in this  
512 study to thin the DR data to the same horizontal sampling rate as the FW data, as the  
513 difference between the horizontal and vertical sampling rate of the two datasets and the effect  
514 of this when using the data in area-based modelling of forest inventory was the core  
515 comparison being made here. Processing techniques to derive usable metrics from FW lidar  
516 data for input into forest modelling are still in development, and may provide more metrics  
517 beneficial to future analyses, such as the backscatter cross-section or coefficient for each  
518 waveform (Alexander et al., 2010; Wagner et al., 2010).

519

520 The majority of the best performing statistical models for field metric estimation (i.e. 18 out of  
521 23) involved the use of lidar intensity/amplitude variables from either DR or FW lidar. Moffiet  
522 et al. (2005) and Kim et al. (2009a) indicated that the distribution of lidar intensity values in a  
523 forest is related to the presence or absence of foliage and its spatial arrangement within the  
524 vertical profile, which is dependent on stem density, canopy openness and species types.  
525 Hence deadwood biomass volume in a forest context exhibits different lidar intensity values  
526 when compared with living biomass (Kim et al., 2009b). Furthermore, Reitberger et al. (2008)  
527 showed that lidar return intensity can be used to distinguish between tree bark and coniferous  
528 needles, and that the distribution of intensity values could be indicative of broad species types  
529 (e.g. coniferous and deciduous), especially under leaf-off conditions. Lidar intensity from the  
530 mid-canopy has been shown to be indicative of species number (Brandtberg et al., 2003),  
531 whilst intensity metrics from the higher portion of the canopy (in combination with height  
532 data) have been shown to make significant contributions to the prediction of forest biomass (Li  
533 et al., 2014). The usage of intensity information from small-footprint DR lidar systems  
534 remains a somewhat contested issue, however, due to the proprietary methods that commercial  
535 systems use to report return intensity which can change in flight, making it impossible to  
536 directly compare two returns (Disney et al., 2010). Nonetheless, Kaasalainen et al. (2009)  
537 showed the potential to calibrate DR lidar intensity data using reference targets of known  
538 backscatter properties from laboratory testing.

539  
540 FW lidar echo-width metrics were utilised in just two best performing models; standing  
541 deadwood volume, and the number of seedling species. FW return echo-width relates to small  
542 height variations of scattering elements within the footprint of the laser beam, and is  
543 considered a means of inferring surface roughness (Wagner 2010). Mücke et al. (2013)  
544 considered the forest ground-level and fallen stems to have smooth surfaces, whereas other

545 vegetated elements, such as shrub vegetation, were considered to be rougher. It should be  
546 noted that echo-width metrics were the predictor variables with the smallest contribution in the  
547 regression models in this study, and therefore this additional variable only available in FW  
548 data may be considered relatively unimportant for forest inventory purposes.

549  
550 It was notable that almost as many of the best performing models contained ITC-derived  
551 variables (11) as contained point cloud height variables (14). All but one of the field metrics  
552 relating to tree structure and density (i.e. number of tree stems, their mean spacing, mean  
553 DBH, basal area, HTLC, and mean crown horizontal area) utilised plot-level ITC-derived  
554 variables within the predictive model equation. Of these, variables related to the horizontal  
555 areas of ITC delineated crowns and the spacing between ITC objects were most used in the  
556 modelling of tree structural properties. A number of other studies have reported the benefits of  
557 using ITC estimates of crown area in addition to variables related to the distribution of height  
558 values in the prediction of forest structural characteristics, such as mean DBH and basal area  
559 (e.g. Hyyppä et al., 2001; Maltamo et al., 2004). It should be noted that image-based ITC  
560 delineation methods, such as those used in this study, have a number of challenges relating to  
561 how well both the vertical and horizontal components of a forest can be quantified (Kaartinen  
562 et al., 2012), which can constitute a source of error as non-dominant trees are often obscured  
563 or incorrectly identified in structurally complex forests.

564  
565 Almost half of the best performing models (i.e. 10 of 23) utilised a combination of variables  
566 produced from both leaf-on and leaf-off datasets. These datasets will capture different  
567 properties of the forest when acquired at peak and lowest leaf area, due to the different  
568 penetration of the laser pulses through the canopy for both coniferous and deciduous species  
569 (where deciduous leaf-loss is typically more obvious) (Næsset, 2005). Lidar data flown under

570 leaf-off conditions are optimal for surface feature mapping, as features close to the ground are  
571 less likely to be obscured; likewise this has applications for understory mapping when data  
572 acquisition is appropriately timed (Hill & Broughton, 2009). Kim et al. (2009a) reported that a  
573 combination of both leaf-on and leaf-off intensity values gives additional explanatory power  
574 when combined in a single model for species differentiation, which goes some way to  
575 capturing the variability in multiple forest structural types.

576  
577 Only relatively basic lidar metrics were used within the context of this study, of which many  
578 have also been used within the surrounding literature. There exists a number of alternative  
579 methods which could be implemented in future research, such as the detection of vertical  
580 layers by examining the return frequencies at different binned heights (or voxels) above  
581 ground (e.g. Popescu & Zhao 2008; Wang et al., 2008). In addition, the computation of indices  
582 relating to the overall vertical density of vegetative features, e.g. the vertical distribution ratio  
583 or height-scaled crown openness index (Lee & Lucas, 2007) may improve model estimates.  
584 More complex analysis of the FW waveform could also be performed to derive variables  
585 relating to the waveform shape, such as height of median energy, waveform distance, and front  
586 slope angle, as used in Cao et al. (2014). There are also a number of alternative approaches  
587 available for the estimation of plot-level field metrics, for example the random forest  
588 algorithm (Breiman, 2001), whilst more fieldwork samples from the same year as lidar data  
589 acquisition would potentially improve the precision and validity of model estimates (Strunk et  
590 al., 2012).

591  
592 **5. Conclusions**  
593 The approaches used in the current study demonstrate that it is possible to estimate a range of  
594 structural, compositional and deadwood forest metrics from airborne lidar data throughout the



595 vertical profile and across a landscape. For 23 metrics examined, statistically significant  
596 predictive models were generated for each using both DR and FW lidar datasets in an area-  
597 based approach. There was an even division between the best performing models that  
598 incorporated DR and FW data, and in all but two cases the difference between the NRMSE of  
599 the best performing DR and FW models was slight (i.e.  $\leq 7\%$ ). The prediction accuracy for the  
600 best performing models ranged from an NRMSE of 16% for standing deadwood volume to  
601 48% for the number of sapling species.

602  
603 Lidar intensity or amplitude variables (DR or FW respectively) were the most numerous  
604 selected in the best performing models. However, only two of the best performing models  
605 contained the extra intensity-related variable (echo-width) available only from FW lidar data.  
606 Although these intensity variables were not calibrated in this study, they were indicative of the  
607 presence and distribution of foliar and woody features within the vertical profile. ITC-derived  
608 variables were of almost equal importance as plot-level height variables derived from the point  
609 cloud in contributing to the best performing models.

610  
611 Perhaps of greater significance to the choice between lidar data type (i.e. DR or FW) in  
612 determining the predictive power of the best performing models was the selection of both leaf-  
613 on and leaf-off data. Thus, of the 23 best performing area-based regression models, 10  
614 contained both leaf-on and leaf-off data, whilst 11 contained only leaf-on data. We can  
615 therefore conclude that the complimentary information about the entire forest canopy profile  
616 that is available from both leaf-on and leaf-off data is of greater benefit to forest inventory in  
617 general than the selection between DR or FW lidar data (if used as point clouds). However,  
618 this can be forest metric specific.

619

620 The area-based method of developing models for the characterisation of forest composition  
621 and structure of the selected New Forest field site has direct applications in forest management  
622 and for wider objectives (such as forestry and habitat modelling) in other forested regions.  
623 Although the models which incorporate lidar intensity are inherently non-transferable because  
624 of the lack of calibration, the approach is transferable and could be applied in many  
625 environmental contexts and to estimate other forest attributes (e.g. above-ground biomass) or  
626 combined into estimates of forest condition.

627

## 628 **6. Acknowledgements**

629 We would like to acknowledge the Airborne Research and Survey Facility of the National  
630 Environment Research Council for providing the airborne remote sensing datasets, in addition  
631 to the assistance of the Forestry Commission for providing site access and supplementary site  
632 and management information. We also thank the anonymous reviewers for helpful input into  
633 the structuring and content of this manuscript.

634

## 635 **7. References**

636 Alexander, C., Tansey, K., Kaduk, J., Holland, D., & Tate, N.J., 2010. Backscatter coefficient  
637 as an attribute for the classification of full-waveform airborne laser scanning data in urban  
638 areas. *ISPRS Journal of Photogrammetry and Remote Sensing*, 64, 423-432.

639 Allouis, T., Durrieu, S., Vega, C., & Coutron, P., 2013. Stem volume and above-ground  
640 biomass estimation of individual pine trees from LiDAR data: contribution of full-  
641 waveform signals. *IEEE Journal of Selected Topics in Applied Earth Observations and*  
642 *Remote Sensing*, 6, 924-934.

643 Andersen, H.E., Mcgaughey, R.J., & Reutebuch, S.E., 2005. Estimating forest canopy fuel  
644 parameters using lidar data. *Remote Sensing of Environment*, 94, 441-449.

645 Anderson, J.E., Plourde, L.C., Martin, M.E., Braswell, B.H., Smith, M.L., Dubayah, R.O.,  
646 Hofton, M.A., & Blair, J.B., 2008. Integrating waveform lidar with hyperspectral imagery  
647 for inventory of a northern temperate forest. *Remote Sensing of Environment*, 112, 1856-  
648 1870.

649 Aplin, P., 2005. Remote sensing: ecology. *Progress in Physical Geography*, 29, 104-113.

650 Armston, J., Disney, M., Lewis, P., Scarth, P., Phinn, S., Lucas, R., Bunting, P., & Goodwin,  
651 N. 2013. Direct retrieval of canopy gap probability using airborne waveform lidar. *Remote*  
652 *Sensing of Environment*, 134, 24-38.

653 Bollandsåsa, O. M., Hanssen K. H., Marthiniussen, S., & Næsset, E., 2008. Measures of  
654 spatial forest structure derived from airborne laser data are associated with natural  
655 regeneration patterns in an uneven-aged spruce forest. *Forest Ecology and Management*.  
656 255, 953–961.

657 Bouvier, M., Durrieu, S., Fournier, R.A., & Renaud, J.P., 2015. Generalizing predictive  
658 models of forest inventory attributes using an area-based approach with airborne LiDAR  
659 data. *Remote Sensing of Environment*, 156, 322-334.

660 Bowerman, B.L. & O'Connell, R.T., 1990. *Linear Statistical Models: An Applied Approach*  
661 (2nd ed.). Belmont, CA: Duxbury.

662 Brandtberg, T., Warner, T. A., Landenberger, R. E., & McGraw, J. B., 2003. Detection and  
663 analysis of individual leaf-off tree crowns in small footprint, high sampling density lidar  
664 data from the eastern deciduous forest in North America. *Remote Sensing of Environment*,  
665 85, 290-303.

666 Breiman, L., 2001. Random forests. *Machine Learning*, 45, 5-32.

667 Bunting, P., Armston, J., Lucas, R.M., & Clewley, D. 2013a. Sorted pulse data (SPD) library.  
668 Part I: a generic file format for LiDAR data from pulsed laser systems in terrestrial  
669 environments. *Computers and Geosciences*, 56, 197-206.

670 Bunting, P., Armston, J., Clewley, D., & Lucas, R., 2013b. Sorted pulse data (SPD) library  
671 Part II: a processing framework for LiDAR data from pulsed laser systems in terrestrial  
672 environments. *Computers and Geosciences*, 56, 207-215.

673 Burnham, K. P., & Anderson, D. R., 2002. *Model Selection and Multimodel Inference: A*  
674 *Practical Information-Theoretic Approach* (2nd ed.). New York: Springer-Verlag.

675 Cantarello, E., & Newton, A. C., 2008. Identifying cost-effective indicators to assess the  
676 conservation status of forested habitats in Natura 2000 sites. *Forest Ecology and*  
677 *Management*, 256, 815-826.

678 Cao, L., Coops, N.C., Hermosilla, T., Innes, J., Dai, J., & She, G. 2014. Using small-footprint  
679 discrete and full-waveform airborne lidar metrics to estimate total biomass and biomass  
680 components in subtropical forests. *Remote Sensing*, 6, 7110-7135.

681 Chauve, A., Vega, C., Durrieu, S., Bretar, F., Allouis, T., Deseillgny, M.P., & Puech, W.,  
682 2009. Advanced full-waveform lidar data echo detection: assessing quality of derived  
683 terrain and tree height models in an alpine coniferous forest. *International Journal of*  
684 *Remote Sensing*, 30, 5211-5228.

685 Chen, Q., Baldocchi, D., Gong, P., & Kelly, M., 2006. Isolating individual trees in a savanna  
686 woodland using small footprint lidar data. *Photogrammetric Engineering and Remote*  
687 *Sensing*, 72, 923-932.

688 Coops, N., Hilker, T., Wulder, M., St-Onge, B., Newnham, G., Siggins, A., & Troftmow, J.,  
689 2007. Estimating canopy structure of Douglas-fir forest stands from discrete-return LiDAR.  
690 *Trees* 21, 295–310.

691 Disney, M. I., Kalogirou, V., Lewis, P., Prieto-Blanco, A., Hancock, S. & Pfeifer, M., 2010.  
692 Simulating the impact of discrete-return lidar system and survey characteristics over young  
693 conifer and broadleaf forests. *Remote Sensing of Environment*, 114, 1546-1560.

694 Estornell, J., Ruiz, L.A., Velazquez-Marti, B., & Fernandez-Sarria, A., 2011. Estimation of  
695 shrub biomass by airborne lidar data in small forest stands. *Forest Ecology and*  
696 *Management*, 262, 1697-1703.

697 Evans, J.S., Hudak, A.T., Faux, R., & Smith, A.M.S., 2009. Discrete return lidar in natural  
698 resources: Recommendations for project planning, data processing, and deliverables.  
699 *Remote Sensing*, 1, 776-794.

700 Falkowski, M.J., Evans, J.S., Martinuzzi, S., Gessler, P.E., & Hudak, A.T., 2009.  
701 Characterizing forest succession with lidar data: an evaluation for the inland northwest,  
702 USA. *Remote Sensing of Environment*, 113, 946-956.

703 Ferris, R., & Humphrey, J.W., 1999. A review of potential biodiversity indicators for  
704 application in British forests. *Forestry*, 72, 313-328.

705 Ferris, R., Peace, A.J., Humphrey, J.W., & Broome, A., 2000. Relationships between  
706 vegetation, site type and stand structure in coniferous plantations in Britain. *Forest Ecology*  
707 *and Management*, 136, 35-51.

708 Hill, R.A., & Broughton, R.K., 2009. Mapping the understorey of deciduous woodland from  
709 leaf-on and leaf-off airborne lidar data: a case study in lowland Britain. *ISPRS Journal of*  
710 *Photogrammetry and Remote Sensing*, 64, 223-233.

711 Hinsley, S.A., Hill, R.A., Fuller, R.J., Bellamy, P.E., & Rothery, P., 2009. Bird species  
712 distributions across woodland canopy structure gradients. *Community Ecology*, 10, 99-110.

713 Hudak, A.T., Crookston, N.L., Evans, J.S., Hall, D.E., & Falkowski, M.J., 2008. Nearest  
714 neighbor imputation of species-level, plot-scale forest structure attributes from lidar data.  
715 *Remote Sensing of Environment*, 112, 2232-2245.

716 Hudak, A.T., Evans, J.S., & Smith, A.M.S., 2009. Lidar utility for natural resource managers.  
717 *Remote Sensing*, 1, 934-951.

718 Hyypä, J., Hyypä, H., Leckie, D., Gougeon, F., Yu, X., & Maltamo, M., 2008. Review of  
719 methods of small-footprint airborne laser scanning for extracting forest inventory data in  
720 boreal forests. *International Journal of Remote Sensing*, 29, 1339-1366.

721 Hyypä, J., Kelle, O., Lehtikoinen, M., & Inkinen, M., 2001. A segmentation-based method to  
722 retrieve stem volume estimates from 3-D tree height models produced by laser scanners.  
723 *IEEE Transactions on Geoscience and Remote Sensing*, 39, 969-975.

724 Kaartinen, H., Hyypä, J., Yu, X.W., Vastaranta, M., Hyypä, H., Kukko, A., Holopainen, M.,  
725 Heipke, C., Hirschmugl, M., Morsdorf, F., Næsset, E., Pitkanen, J., Popescu, S., Solberg,  
726 S., Wolf, B.M., & Wu, J. C., 2012. An international comparison of individual tree detection  
727 and extraction using airborne laser scanning. *Remote Sensing*, 4, 950-974.

728 Kaasalainen, S., Hyypä, H., Kukko, A., Litkey, P., Ahokas, E., Hyypä, J., Lehner, H.,  
729 Jaakkola, A., Suomalainen, J., Akujarvi, A., Kaasalainen, M., and Pyyalo, U., 2009.  
730 Radiometric calibration of lidar intensity with commercially available reference targets.  
731 *IEEE Transactions on Geoscience and Remote Sensing*, 47, 588-598.

732 Kim, S., Mcgaughey, R.J., Andersen, H.E., & Schreuder, G., 2009a. Tree species  
733 differentiation using intensity data derived from leaf-on and leaf-off airborne laser scanner  
734 data. *Remote Sensing of Environment*, 113, 1575-1586.

735 Kim, Y., Yang, Z.Q., Cohen, W.B., Pflugmacher, D., Lauver, C.L., & Vankat, J.L., 2009b.  
736 Distinguishing between live and dead standing tree biomass on the north rim of Grand  
737 Canyon National Park, USA using small-footprint lidar data. *Remote Sensing of*  
738 *Environment*, 113, 2499-2510.

739 Langton, S.D., Briggs, P.A., & Haysom, K.A., 2010. Daubenton's bat distribution along rivers  
740 - developing and testing a predictive model. *Aquatic Conservation-Marine and Freshwater*  
741 *Ecosystems*, 20, 45-54.

742 Lee, A.C., & Lucas, R.M., 2007. A lidar-derived canopy density model for tree stem and  
743 crown mapping in Australian forests. *Remote Sensing of Environment*, 111, 493-518.

744 Lesak, A.A., Radeloff, V.C., Hawbaker, T.J., Pidgeon, A.M., Gobakken, T., and Contrucci,  
745 K., 2011. Modeling forest songbird species richness using lidar-derived measures of forest  
746 structure. *Remote Sensing of Environment*, 115, 2823-2835.

747 Leutner, B.F., Reineking, B., Mueller, J., Bachmann, M., Beierkuhnlein, C., Dech, S. &  
748 Wegmann, M. 2012. Modelling forest alpha-diversity and floristic composition - on the  
749 added value of lidar plus hyperspectral remote sensing. *Remote Sensing*, 4, 2818-2845.

750 Li, M., Im, J., Quackenbush, L.J., & Liu, T., 2014. Forest biomass and carbon stock  
751 quantification using airborne LiDAR data: a case study over Huntington Wildlife Forest in  
752 the Adirondack Park. *IEEE Journal of Selected Topics in Applied Earth Observations and*  
753 *Remote Sensing*. 7, 3143-3156.

754 Lim, K., Treitz, P., Baldwin, K., Morrison, I., & Green, J., 2003. Lidar remote sensing of  
755 biophysical properties of tolerant northern hardwood forests. *Canadian Journal of Remote*  
756 *Sensing*, 29, 658-678.

757 Lindberg, E., Olofsson, K., Holmgren, J., & Olsson, H., 2012. Estimation of 3D vegetation  
758 structure from waveform and discrete return airborne laser scanning data. *Remote Sensing*  
759 *of Environment*, 118, 151-161.

760 Matthews, R., & Mackie, E., 2006. *Forest Mensuration: A Handbook for Practitioners*.  
761 Edinburgh: HMSO.

762 Mallet, C., Lafarge, F., Roux, M., Soergel, U., Bretar, F., & Heipke, C., 2010. A marked point  
763 process for modelling lidar waveforms. *IEEE Transactions on Image Processing*, 19, 3204-  
764 3221.

765 Maltamo, M., Eerikainen, K., Pitkanen, J., Hyypä, J., & Vehmas, M., 2004. Estimation of  
766 timber volume and stem density based on scanning laser altimetry and expected tree size  
767 distribution functions. *Remote Sensing of Environment*, 90, 319-330.

768 Maltamo, M., Packalen, P., Yu, X., Eerikainen, K., Hyypä, J., & Pitkanen, J., 2005.  
769 Identifying and quantifying structural characteristics of heterogeneous boreal forests using  
770 laser scanner data. *Forest Ecology and Management*, 216, 41-50.

771 Martinuzzi, S., Vierling, L.A., Gould, W.A., Falkowski, M.J., Evans, J.S., Hudak, A.T., &  
772 Vierling, K. T., 2009. Mapping snags and understory shrubs for a lidar-based assessment of  
773 wildlife habitat suitability. *Remote Sensing of Environment*, 113, 2533-2546.

774 Miura, N., & Jones, S.D., 2010. Characterizing forest ecological structure using pulse types  
775 and heights of airborne laser scanning. *Remote Sensing of Environment*, 114, 1069-1076.

776 Moffiet, T., Mengersen, K., Witte, C., King, R., & Denham, R., 2005. Airborne laser  
777 scanning: Exploratory data analysis indicates potential variables for classification of  
778 individual trees or forest stands according to species. *ISPRS Journal of Photogrammetry  
779 and Remote Sensing*, 59, 289-309.

780 Mücke, W., Deak, B., Schroiff, A., Hollaus, M. & Pfeifer, N. 2013. Detection of fallen trees in  
781 forested areas using small footprint airborne laser scanning data. *Canadian Journal of  
782 Remote Sensing*, 39, 32-40.

783 Muss, J. D., Mladenoff, D.J., & Townsend, P. A., 2011. A pseudo-waveform techniques to  
784 assess forest structure using discrete lidar data. *Remote Sensing of Environment*. 115, 824-  
785 835.

786 Næsset, E., 2002. Predicting forest stand characteristics with airborne scanning laser using a  
787 practical two-stage procedure and field data. *Remote Sensing of Environment*, 80, 88-99.

788 Næsset, E., 2004. Practical large-scale forest stand inventory using a small-footprint airborne  
789 scanning laser. *Scandinavian Journal of Forest Research*, 19, 164-179.



790 Næsset, E., 2005. Assessing sensor effects and effects of leaf-off and leaf-on canopy  
791 conditions on biophysical stand properties derived from small-footprint airborne laser data.  
792 *Remote Sensing of Environment*, 98, 356-370.

793 Næsset, E., 2007. Airborne laser scanning as a method in operational forest inventory: Status  
794 of accuracy assessments accomplished in Scandinavia. *Scandinavian Journal of Forest*  
795 *Research*, 22, 433-442.

796 Næsset, E., 2009. Effects of different sensors, flying altitudes, and pulse repetition frequencies  
797 on forest canopy metrics and biophysical stand properties derived from small-footprint  
798 airborne laser data. *Remote Sensing of Environment*, 113, 148-159.

799 Newton, A.C., Cantarello, E., Myers, G., Douglas, S., & Tejedor, N., 2010. The condition and  
800 dynamics of new forest woodlands. In: Newton, A. C. ed. *Biodiversity in the New Forest*.  
801 Newbury, Berkshire: Pisces Publications, pp. 132-147.

802 Newton, A.C., Hill, R.A., Echeverria, C., Golicher, D., Benayas, J.M.R., Cayuela, L., &  
803 Hinsley, S.A., 2009. Remote sensing and the future of landscape ecology. *Progress in*  
804 *Physical Geography*, 33, 528-546.

805 Persson, Å., Holmgren, J., & Soderman, U., 2002. Detecting and measuring individual trees  
806 using an airborne laser scanner. *Photogrammetric Engineering and Remote Sensing*, 68,  
807 925-932.

808 Pesonen, Å., Maltamo, M., Eerikainen, K., & Packalen, P., 2008. Airborne laser scanning-  
809 based prediction of coarse woody debris volumes in a conservation area. *Forest Ecology*  
810 *and Management*, 255, 3288-3296.

811 Popescu, S.C., & Zhao, K., 2008. A voxel-based lidar method for estimating crown base  
812 height for deciduous and pine trees. *Remote Sensing of Environment*, 112, 767-781.

813 Popescu, S.C., Wynne, R.H., & Scrivani, J.A., 2004. Fusion of small-footprint lidar and  
814 multispectral data to estimate plot-level volume and biomass in deciduous and pine forests  
815 in Virginia, USA. *Forest Science*, 50, 551–565

816 Reitberger, J., Krzystek, P., & Stilla, U., 2008. Analysis of full waveform lidar data for the  
817 classification of deciduous and coniferous trees. *International Journal of Remote Sensing*,  
818 29, 1407-1431.

819 Richardson, J.J., & Moskal, L.M., 2011. Strengths and limitations of assessing forest density  
820 and spatial configuration with aerial lidar. *Remote Sensing of Environment*, 115, 2640-  
821 2651.

822 Shannon, C.E., 1948. The mathematical theory of communication. In: Shannon, C. E., and  
823 Weaver, W. eds. *The Mathematical Theory of Communication*. Urbana: University of  
824 Illinois Press, pp. 29-125.

825 Simpson, E. H., 1949. Measurement of diversity. *Nature*, 163, 688.

826 Spies, T., Franklin, J. & Thomas, T., 1988. Coarse woody debris in Douglas-fir forests of  
827 western Oregon and Washington. *Ecology*, 69, 1689-1702.

828 Strunk, J., Temesgen, H., Andersen, H.E., Flewelling, J.P., & Madsen, L., 2012. Effects of  
829 lidar pulse density and sample size on a model-assisted approach to estimate forest  
830 inventory variables. *Canadian Journal of Remote Sensing*, 38, 644-654.

831 Tubbs, C. R., 2001. *The New Forest. History, Ecology, and Conservation*. Lyndhurst,  
832 Hampshire: New Forest Ninth Centenary Trust.

833 Wagner, W., 2010. Radiometric calibration of small-footprint full-waveform airborne laser  
834 scanner measurements. *ISPRS Journal of Photogrammetry and Remote Sensing*, 65, 505-  
835 513.

836 Wagner, W., Hollaus, M., Briese, C., & Ducic, V., 2008. 3D vegetation mapping using small-  
837 footprint full-waveform airborne laser scanners. *International Journal of Remote Sensing*,  
838 29, 1433-1452.

839 Wagner, W., Ullrich, A., Ducic, V., Melzer, T., & Studnicka, N., 2006. Gaussian  
840 decomposition and calibration of a novel small-footprint full-waveform digitising airborne  
841 laser scanner. *ISPRS Journal of Photogrammetry and Remote Sensing*, 60, 100-112.

842 Wang, Y.S., Weinacker, H., & Koch, B., 2008. A lidar point cloud based procedure for  
843 vertical canopy structure analysis and 3d single tree modelling in forest. *Sensors*, 8, 3938-  
844 3951.

845 Yu, X., Litkey, P., Hyypä, J., Holopainen, M., & Vastaranta, M., 2014. Assessment of low  
846 density full-waveform airborne laser scanning for individual tree detection and tree species  
847 classification. *Forests*, 5, 1011-1031.

848 Zhang, K. Q., Chen, S. C., Whitman, D., Shyu, M. L., Yan, J. H., & Zhang, C. C., 2003. A  
849 progressive morphological filter for removing non-ground measurements from airborne  
850 lidar data. *IEEE Transactions on Geoscience and Remote Sensing*, 41, 872-882.

851

## Tables

**Table 1.** Summary of field data enumerated across the 21 plots surveyed in 2010 (used to establish regression-based relationships with airborne lidar data) and the 20 plots surveyed in 2012 (used to validate the regression-based relationships with airborne lidar data).

Field metric name	Forest layer	Metric type	2010 field plots				2012 field plots			
			Min	Max	Mean	St. Dev.	Min	Max	Mean	St. Dev.
Number of tree stems	Canopy	Structure	7	52	24.86	11.12	16	90	32.20	18.86
Mean tree stem spacing (m)	Canopy	Structure	2.65	8.45	4.09	1.33	1.84	5.17	3.20	1.05
Number of tree species	Canopy	Composition	1	7	3.52	1.40	1	5	3.45	1.28
Number of tree stems of native species	Canopy	Composition	2	34	15.67	9.46	0	52	19.85	12.66
Shannon-Wiener index of diversity	Canopy	Composition	0.00	1.47	0.86	0.39	0.00	1.43	0.86	0.41
Simpson index of diversity	Canopy	Composition	0.00	1.00	0.50	0.27	0.00	1.29	0.73	0.36
Mean height to the living crown (m)	Canopy	Structure	3.30	13.94	8.00	3.20	2.83	13.46	7.78	3.10
Mean crown horizontal area (m <sup>2</sup> )	Canopy	Structure	23.61	119.91	57.52	28.96	13.03	100.11	49.67	23.55
Total crown horizontal area (m <sup>2</sup> )	Canopy	Structure	590.17	2198.75	1219.05	402.72	658.59	2102.26	2136.94	382.30
Mean DBH (cm)	Canopy	Structure	27.45	61.84	40.06	9.41	18.72	47.86	33.71	29.14
Plot level basal area (m <sup>2</sup> )	Canopy	Structure	2.10	5.24	3.28	0.83	2.06	5.27	3.26	0.86
Standing deadwood volume (m <sup>3</sup> )	Canopy	Deadwood	0.00	10.12	1.93	3.22	0.00	8.27	0.87	1.97
Standing deadwood decay class (1-3)	Canopy	Deadwood	0.00	2.88	2.19	0.42	0.00	3.00	0.74	0.18
Downed deadwood volume (m <sup>3</sup> )	Ground	Deadwood	0.09	14.62	3.54	4.58	0.22	38.42	4.44	8.29
Downed Deadwood decay class (1-3)	Ground	Deadwood	1.56	2.85	2.34	0.39	0.48	2.85	0.68	0.11
Number of sapling stems	Shrub	Structure	0	42	4.33	9.31	0	108	9.85	24.74
Number of sapling species	Shrub	Composition	0	4	1.00	1.22	0	3	1.00	0.97
Number of sapling stems of native species	Shrub	Composition	0	34	3.86	7.72	0	38	2.90	8.45
Number of seedling stems	Ground	Structure	9	864	145.29	206.44	0	936	339.70	297.62
Number of seedling species	Ground	Composition	1	7	2.05	1.40	0	13	4.40	2.89
Number of seedling stems of native species	Ground	Composition	9	405	109.29	123.94	0	936	230.60	278.95
Number of vascular plant species	Ground	Composition	2	6	3.86	1.35	2	8	4.56	1.82
Percentage bare ground cover (%)	Ground	Composition	0	90	21.69	26.45	0	95	43.50	38.01

**Table 2.** Summary of the sampling rate for DR and FW lidar data under leaf-on and leaf-off conditions, and the number of returns generated from the resulting point clouds. These values include data for overlapping flight-lines and are average values across the entire field site (i.e. including forest and non-forest areas).

Lidar data	Leaf-on			Leaf-off		
	No. of pulses per m <sup>2</sup>	No. of derived points per m <sup>2</sup>	1 <sup>st</sup> returns as a % of the point cloud	No. of pulses per m <sup>2</sup>	No. of derived points per m <sup>2</sup>	1 <sup>st</sup> returns as a % of the point cloud
DR	4.97	6.02	82.5%	5.25	7.57	69.4%
FW	2.43	5.09	47.7%	2.51	6.50	38.6%

**Table 3.** Summary of R<sup>2</sup>, RMSE and NRMSE for the best performing regression model produced from the DR and FW lidar data. All models shown are significant at p < 0.05. The values underlined show the best performing model per field metric.

Field metric	<i>DR lidar</i>			<i>FW lidar</i>		
	R <sup>2</sup>	RMSE	NRMSE	R <sup>2</sup>	RMSE	NRMSE
Number of tree stems	0.67	18.04	24%	<u>0.67</u>	<u>15.97</u>	<u>22%</u>
Mean tree stem spacing (m)	0.91	1.71	40%	<u>0.91</u>	<u>1.32</u>	<u>33%</u>
Number of tree species	<u>0.43</u>	<u>1.50</u>	<u>25%</u>	0.32	1.66	28%
Number of tree stems of native species	0.55	15.05	29%	<u>0.61</u>	<u>13.93</u>	<u>27%</u>
Shannon-Wiener index of diversity	<u>0.57</u>	<u>0.53</u>	<u>37%</u>	0.67	0.58	40%
Simpson index of diversity	0.59	0.31	24%	<u>0.55</u>	<u>0.29</u>	<u>22%</u>
Mean height to the living crown (m)	0.88	2.68	25%	<u>0.88</u>	<u>2.54</u>	<u>24%</u>
Mean crown horizontal area (m <sup>2</sup> )	<u>0.63</u>	<u>23.53</u>	<u>27%</u>	0.86	24.39	28%
Total crown horizontal area (m <sup>2</sup> )	<u>0.75</u>	<u>561.55</u>	<u>39%</u>	0.69	645.64	45%
Mean DBH (cm)	<u>0.80</u>	<u>9.71</u>	<u>33%</u>	0.80	10.11	35%
Plot level basal area (m <sup>2</sup> )	<u>0.66</u>	<u>0.83</u>	<u>26%</u>	0.69	0.91	28%
Standing deadwood volume (m <sup>3</sup> )	0.91	1.50	18%	<u>0.92</u>	<u>1.36</u>	<u>16%</u>
Standing deadwood decay class (1-3)	0.88	0.72	36%	<u>0.59</u>	<u>0.57</u>	<u>29%</u>
Downed deadwood volume (m <sup>3</sup> )	0.51	2.74	30%	<u>0.45</u>	<u>2.49</u>	<u>27%</u>
Downed Deadwood decay class (1-3)	<u>0.79</u>	<u>0.51</u>	<u>36%</u>	0.75	0.60	43%
Number of sapling stems	<u>0.92</u>	<u>24.41</u>	<u>23%</u>	0.97	26.46	25%
Number of sapling species	0.94	1.99	66%	<u>0.70</u>	<u>1.42</u>	<u>48%</u>
Number of sapling stems of native species	<u>0.90</u>	<u>10.40</u>	<u>27%</u>	0.97	11.47	30%
Number of seedling stems	<u>0.82</u>	<u>295.24</u>	<u>32%</u>	0.28	331.96	36%
Number of seedling species	0.74	3.16	24%	<u>0.45</u>	<u>3.10</u>	<u>24%</u>
Number of seedling stems of native species	<u>0.63</u>	<u>239.08</u>	<u>33%</u>	0.68	245.15	34%
Number of vascular plant species	0.75	2.36	39%	<u>0.77</u>	<u>1.70</u>	<u>28%</u>
Percentage bare ground cover (%)	0.76	44.04	46%	<u>0.86</u>	<u>39.82</u>	<u>42%</u>

**Table 4.** The input predictor variables used in the 23 best performing regression models (i.e. those which produced estimates with the smallest RMSE)

Estimated field metric name	Field metric type	Data set used in the model	Model input variables
Number of tree stems	Structure	FW lidar	(1) mean ITC horizontal area (leaf-on); (2) 20th height percentile [all returns] (leaf-on); (3) kurtosis of amplitude [non-ground returns] (leaf-off); (4) skewness of height [non-ground returns] (leaf-off).
Mean tree stem spacing (m)	Structure	FW lidar	(1) mean spacing of ITC centroids (leaf on); (2) 20th amplitude percentile [all returns] (leaf-off).
Number of tree species	Composition	DR lidar	(1) 50th height percentile [all returns] (leaf-off); (2) variance of intensity [non-ground returns] (leaf-on).
Number of tree stems of native species	Composition	FW lidar	(1) kurtosis of height [all returns] (leaf-on).
Shannon-Wiener index of diversity	Composition	DR lidar	(1) median height [non-ground returns] (leaf-off); (2) skewness of intensity [non-ground returns] (leaf-on); (3) total ITC horizontal area (leaf-on); (4) total ITC volume (leaf-on).
Simpson index of diversity	Composition	FW lidar	(1) skewness of amplitude [non-ground returns] (leaf-on); (2) total ITC horizontal area (leaf-on); (3) variance of height [all returns] (leaf-on).
Mean height to the living crown (m)	Structure	FW lidar	(1) maximum vertical gap identified in the vertical height profile (leaf-off); (2) mean spacing of ITC centroids (leaf-on); (3) ITC mean canopy geometric volume (leaf-on), (4) variance of amplitude [non-ground returns] (leaf-on).
Mean crown horizontal area (m <sup>2</sup> )	Structure	DR lidar	(1) kurtosis of intensity [non-ground return] (leaf-off); (2) mean spacing of ITC centroids (leaf-on); (3) total ITC horizontal area (leaf-on).
Total crown horizontal area (m <sup>2</sup> )	Structure	DR lidar	(1) mean height [all returns] (leaf-on); (2) standard deviation of height [all returns] (leaf-on); (3) variance of intensity [all returns] (leaf-on).

Mean DBH (cm)	Structure	DR lidar	(1) mean spacing of the ITC centroids (leaf-on); (2) ITC mean canopy geometric volume (leaf-on).
Plot level basal area (m <sup>2</sup> )	Structure	DR lidar	(1) 55th intensity percentile [all returns] (leaf-on); (2) mean spacing of ITC centroids (leaf-on).
Standing deadwood volume (m <sup>3</sup> )	Deadwood	FW lidar	(1) skewness of amplitude [non-ground returns] (leaf-off); (2) standard deviation of the ITC centroids spacing (leaf-on); (3) 25th percentile echo-width [all returns] (leaf-on).
Standing deadwood decay class (1-3)	Deadwood	FW lidar	(1) 35th amplitude percentile [all returns] (leaf-on); (2) 20th height percentile [all returns] (leaf-on).
Downed deadwood volume (m <sup>3</sup> )	Deadwood	FW lidar	(1) skewness of amplitude [non-ground return] (leaf-off); (2) absolute deviation of heights [all returns] (leaf-off).
Downed Deadwood decay class (1-3)	Deadwood	DR lidar	(1) mean intensity [non-ground returns] (leaf-on).
Number of sapling stems	Structure	DR lidar	(1) 60 <sup>th</sup> percentile for intensity [all returns] (leaf-on), (2) 60 <sup>th</sup> height percentile [all returns] (leaf-on), (3) mean intensity [all returns] (leaf-on).
Number of sapling species	Composition	FW lidar	(1) 35 <sup>th</sup> height percentile [all returns] (leaf-on); (2) variance of amplitude [all returns] (leaf-off).
Number of sapling stems of native species	Composition	DR lidar	(1) 60 <sup>th</sup> intensity percentile [all returns] (leaf-on); (2) median height [non-ground returns] (leaf-on);
Number of seedling stems	Structure	DR lidar	(1) mean absolute deviation of intensity [ground returns] (leaf-off); (2) mean of intensity [ground returns] (leaf-on).
Number of seedling species	Composition	FW lidar	(1) mean amplitude [ground returns] (leaf-off); (2) standard deviation of echo-width [ground returns] (leaf-off).
Number of seedling stems of native species	Composition	DR lidar	(1) standard deviation of ITC spacing (leaf-on); (2) mean ITC canopy geometric volume (leaf-on).
Number of vascular plant species	Composition	FW lidar	(1) variance of heights [non-ground returns] (leaf-on)
Percentage bare ground cover (%)	Composition	FW lidar	(1) 20 <sup>th</sup> height percentile [all returns] (leaf-on); (2) height of largest vertical gap in return height profile (leaf-off); (3) standard deviation of ITC area (leaf-on conditions).



**Table 5.** The number of input variables used in the 23 best performing models by variable category. Percentage contribution is shown in parentheses.

Data set used in the model	ITC variables (from raster)	Height variables (from point cloud)	Intensity/amplitude variables (from point cloud)	Echo-width variables (from point cloud)	Total
DR	9 (35%)	6 (23%)	11 (42%)	-	26
FW	7 (24%)	11 (38%)	9 (31%)	2 (7%)	29

**Table 6.** The number of variables using ground, non-ground and all returns used as inputs to the 23 best performing models. Percentage contribution is shown in parentheses.

Data set used in the model	Ground	Non-ground	All	Total
DR	2 (12%)	6 (35%)	9 (53%)	17
FW	2 (9%)	7 (32%)	13 (59%)	22

**Figure 1**

Sample cross section (100 m x 20 m) of a point cloud from leaf-on DR lidar data (top) and FW lidar data (bottom). Points classified as ground or non-ground are indicated.

