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# The effect of leaf-on and leaf-off forest canopy conditions on LiDAR derived estimations of forest structural diversity

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ABSTRACT

Forest structural diversity metrics describing diversity in tree size and crown shape within forest stands can be used as indicators of biodiversity. These diversity metrics can be generated using airborne laser scanning (LiDAR) data to provide a rapid and cost effective alternative to ground-based inspection. Measures of tree height derived from LiDAR can be significantly affected by the canopy conditions at the time of data collection, in particular whether the canopy is under leaf-on or leaf-off conditions, but there have been no studies of the effects on structural diversity metrics. The aim of this research is to assess whether leaf-on/leaf-off changes in canopy conditions during LiDAR data collection affect the accuracy of calculated forest structural diversity metrics. We undertook a quantitative analysis of LiDAR ground detection and return height, and return height diversity from two airborne laser scanning surveys collected under leaf-on and leaf-off conditions to assess initial dataset differences. LiDAR data were then regressed against field-derived tree size diversity measurements using diversity metrics from each LiDAR dataset in isolation and, where appropriate, a mixture of the two. Models utilising leaf-off LiDAR diversity variables described DBH diversity, crown length diversity and crown width diversity more successfully than leaf-on (leaf-on models resulted in $R^2$ values of 0.66, 0.38 and 0.16, respectively, and leaf-off models 0.67, 0.37 and 0.23, respectively). When LiDAR datasets were combined into one model to describe tree height diversity and DBH diversity the models described 75% and 69% of the variance ($R^2$ of 0.75 for tree height diversity and 0.69 for DBH diversity). The results suggest that tree height diversity models derived from airborne LiDAR, collected (and where appropriate combined) under any seasonal conditions, can be used to differentiate between simple single and diverse multiple storey forest structure with confidence.

## 1. Introduction

The 168 signatories (and 196 parties) to the UN Convention on Biological Diversity recognise that biological diversity is an asset of global significance. The Convention was first ratified in 1993 and since that time, it has stimulated research on how to assess the threat to species and ecosystems. At the heart of the Convention is a strategic plan that signatories develop national plans for biodiversity that incorporate measurable targets – the Aichi Biodiversity Targets that were agreed at the 10th Conference of Parties in 2010. Specifically, target-7 states that by 2020 areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity. Many countries recognise the contribution of well managed woodland to enhancing biodiversity and use the *area of forestry land certified as sustainably managed* as one key indicator of success for monitoring and reporting purposes (e.g. UK Biodiversity Indicators 2018 (DEFRA, 2019) and EU Biodiversity Strategy (European Commission, 2019). Woodland and forest biodiversity is a valued component of sustainable forests, contributing to the ecological functioning and health of woodland ecosystems, and providing a range of associated financial benefits (or ecosystem services).

There are a wide range of techniques for mapping and monitoring woodland areas but less attention has been given to mapping woodland biodiversity. An exception is the interest and uptake of airborne LiDAR survey as a remote sensing method that provides a rapid and objective way of deriving three-dimensional measurements to characterise forest structural diversity (Vihervaara et al., 2015). Structural diversity is the most straightforward measurement that indicates the potential biodiversity and habitat suitability of a forest stand. Structurally diverse forest stands with vertical foliage layering provide important habitats

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(for example foraging, nesting, hiding and roosting) for different forest-dwelling organisms (Clawges et al., 2008; Hinsley et al., 2009; Wood et al., 2012). Structural indices generated from airborne LiDAR data such as the coefficient of variation of tree size metrics, standard deviation of tree size metrics, Gini Coefficient (or L-CV of tree size metrics), and Shannon Index (a measure of species richness and evenness) (Latham et al., 1998; McElhinny et al., 2005; Barbeito et al., 2009) are straightforward to understand and calculate. In contrast, with the exception of Diameter at Breast Height (DBH), measuring structural variables in the field can be subjective and time consuming.

While the use of airborne LiDAR data represents an attractive alternative to field survey when analysing large forest estates, there is a need to better understand the influence of seasonal conditions on LiDAR derived structural diversity metrics, especially over deciduous and mixed woodland where it has been shown that laser pulse penetration can differ greatly between leaf-on and -off canopy conditions. The aim of this study is to acquire high-quality leaf-on and leaf-off airborne LiDAR datasets for a forest area with a range of forest structures in order to compare LiDAR-derived forest structure diversity with ground-based measurements.

## 2. Material and methods

### 2.1. Study site

Chopwell Woodland Park, in the North East of England (see Fig. 1), was chosen as the field site for this study because the range of tree species, plantation years and silvicultural practices provides a wide variety of structural characteristics and stand types (pure conifer, mixed conifer, pure deciduous, mixed deciduous, mixed deciduous and conifer) all of varying age class and tree spacing (Forestry Commission, 2009). Chopwell is a mixed coniferous and deciduous woodland of 360 ha (3.6 $km^2$) located on the northern slopes of the Derwent Valley. The woodland encompasses stands classified as Ancient Woodland by the UK Forestry Commission (2009), a designation reserved for only 2% of the country's forested area and one of the rarest habitats in the UK. The woodland has a forest design plan based on natural regeneration of species or planting of native species. As a result, the Forestry Commission is currently removing areas of conifer to help the forest return to its original cover of native trees, whilst thinning forest crops (removing, for example, one in every five trees) and occasionally harvesting full areas.

### 2.2. Field data collection

Measurements were collected from 30 individual sample plots throughout the forest. Data from 19 of these were available through research performed by Ozdemir and Donoghue (2013) who investigated the relationships between the plot-level tree size diversity and diversity variables derived from airborne LiDAR. Ozdemir and Donoghue (2013) undertook a purposive sampling strategy when selecting sample plots based on the criteria of age, percentage canopy cover, tree species and species diversity. Though the 2013 study provides measurements from 27 sample plots within Chopwell Woodland Park, only 19 of these were fully covered by both the leaf-on and the leaf-off LiDAR datasets analysed in this research. As the number of sample plots available from the 2013 amounted to a subset of the full dataset, a simple assessment of the existing structural diversity in the dataset was undertaken. The coefficient of L Variation (L-CV) of tree height, DBH, crown length and crown width were chosen as representations of structural diversity. Coefficient of Variation (CV), analogous to the L-CV has been shown to be a good indicator of structural complexity (Bolton et al., 2013). L-CV, identical to the Gini Coefficient utilised in many studies to convey forest structure diversity (Peck et al., 2014; Lei et al., 2009) is more robust to outliers and reasonably unbiased in small samples. The L-CV is a dimensionless index scaled from zero to one. A theoretical L-CV of 1 describes complete heterogeneity in the chosen measurement of the population in question and an L-CV of 0 describes complete homogeneity. In practice, in the field data available L-CV values of 0 described an even height plantation forest and an L-CV of $> 0.3$ described an age and species diverse, multi-layered stand with uneven tree spacing (see Fig. 2).

The range of L-CV of tree height (THdiv), in the existing sample plots was relatively small ($0.022 - 0.276$) with only a small number of plots at the higher, or more diverse, end. Therefore choosing additional field sample plots aimed to increase this range and therefore the structural diversity available to study.

As diversity of tree species in each plot was found to be correlated with the L-CV of tree height (95% CI) additional plots were sought that displayed high species diversity. In addition, currently under-represented species in the field sites, such as Oak, Birch and coniferous species were sought to ensure the dataset was as diverse and representative as possible.

Sample plots were of a circular shape, the centre of which was referenced using GPS. In European forest management, plot sizes of 0.01 to 0.05 ha (100–500 $m^2$) normally provide a representative sample of trees within a stand depending on tree spacing (Mackie and Matthews, 2008). In this study, three different plot sizes (100, 400, and 1256 $m^2$) were adopted, to ensure a very detailed description of each stand. Smaller plot sizes were chosen in high tree density and age and species homogeneity, and larger plot sizes were chosen in areas with high age and species diversity and greater spacing. These larger plot sizes ensure there is greater spatial overlap between ground-reference and LiDAR datasets for any given GPS error.

The field data collection process follows that used by Ozdemir and Donoghue (2013) to ensure conformity with existing data: At each survey plot, four biophysical tree characteristics were obtained for each tree (DBH $\geq$ 8): DBH, tree height, crown length, and crown width (Davison, 2017). The DBH of each tree was measured using a diameter tape at 1.3 m above the ground surface. When the tree resided on a slope DBH was measured from the uphill side looking downhill to ensure conformity throughout the data, although slopes were uncommon and usually very gentle.

The height of each tree was ascertained through the use of a Vertex-III ultrasonic hypsometer to estimate tree height to the nearest 10 cm (Božić et al., 2005). The Vertex was also used to collect crown length and crown width data. Crown length describes the height from the top of the tree to the lowest live branch forming part of the canopy and crown. The crown width was calculated by measuring the length of two orthogonal axes of the tree crown (the diameter of the maximum axis and the axis at 90°) and taking an average.

### 2.3. LiDAR data collection and pre-processing

As shown in Table 1 the 2009 dataset was collected by Network Mapping Ltd. Trees were under full leaf at the time with understorey vegetation close to its maximum growth. The 2011 dataset was collected by the National Environmental Research Council (NERC) Airborne Research Facility (ARSF) during conditions where the understorey was advanced but leaves had not begun bud burst.

### 2.4. LiDAR pre-processing

The 2009 airborne LiDAR data were pre-processed using information from two ground base stations to establish a precise fit to the OSGB 36 datum. This was a wide area survey where coverage of the whole of Chopwell Woodland Park and past its boundaries was obtained. The 2011 airborne LiDAR data were pre-processed using data from one ground base station to the OSGB 36 datum. The 2011 survey consisted of multiple passes over transmission line corridors resulting in two survey corridors, each approximately 300 m in width.

For each survey dataset, all points were loaded filtered and

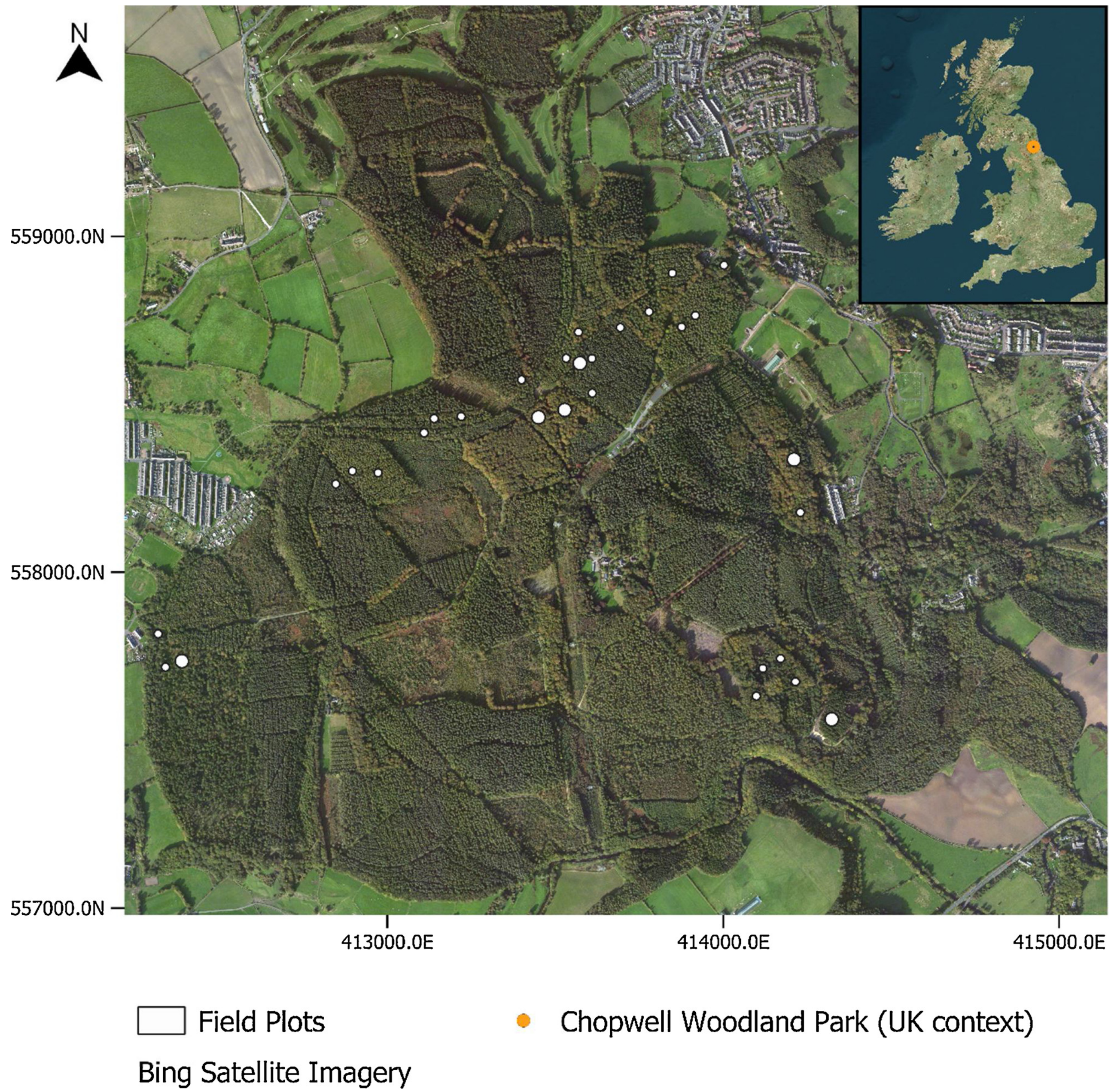



**Fig. 1.** Chopwell Woodland Park. Coordinates in British National Grid.

classified using TerraScan to remove outliers and to generate a ground surface using the progressive densification method (Axelsson, 2000, 1999). Returns not classified as ground or outliers were assigned to vegetation classes as per the ASPRS specification (ASPRS, 2013).

### 2.5. LiDAR post-processing

For each of the 30 field plots the corresponding area of the laser point cloud was extracted as a separate las file. The LiDAR points in each of these files held an elevation with reference to the OSGB36 Newlyn datum. In order to compare the structural diversity metrics between datasets collected at different dates, the standardisation of point heights is obligatory (Vepakomma et al., 2008). This standardisation was undertaken by creating normalised canopy heights from the original sample plots from each survey by subtracting the underlying terrain model generated from ground points for each plot. This resulted in 30 las files over the 30 field plots.

The LiDAR return height distribution statistics calculated (mean and percentiles of return height (P25, P50,…,P99)) were chosen to provide insightful summaries of the datasets which could be compared between leaf-on and leaf-off conditions and within plot types to better understand the pulse penetration differences between datasets. The diversity statistics coefficient of variation (CV), skewness (skew), kurtosis (kurt), standard deviation (SD) and variance (var) were chosen as metrics well suited to model canopy structure in the field plots based on the shape and dispersion of the distribution of tree size measurements (Donoghue et al., 2007). Additionally, L-CV of canopy return heights was chosen to provide a diversity statistic less sensitive to skewness and small sample sizes. Finally, laser-based height percentile ratios (P99/25, P99/50,…, P99/90), utilised by Ozdemir and Donoghue (2013), provide information about the diversity of vertical canopy layers and was shown to be a good estimator of stand based tree size diversity.

The LiDAR statistics were derived from the clipped LAS files which had been normalised to height above ground. Returns with a height less

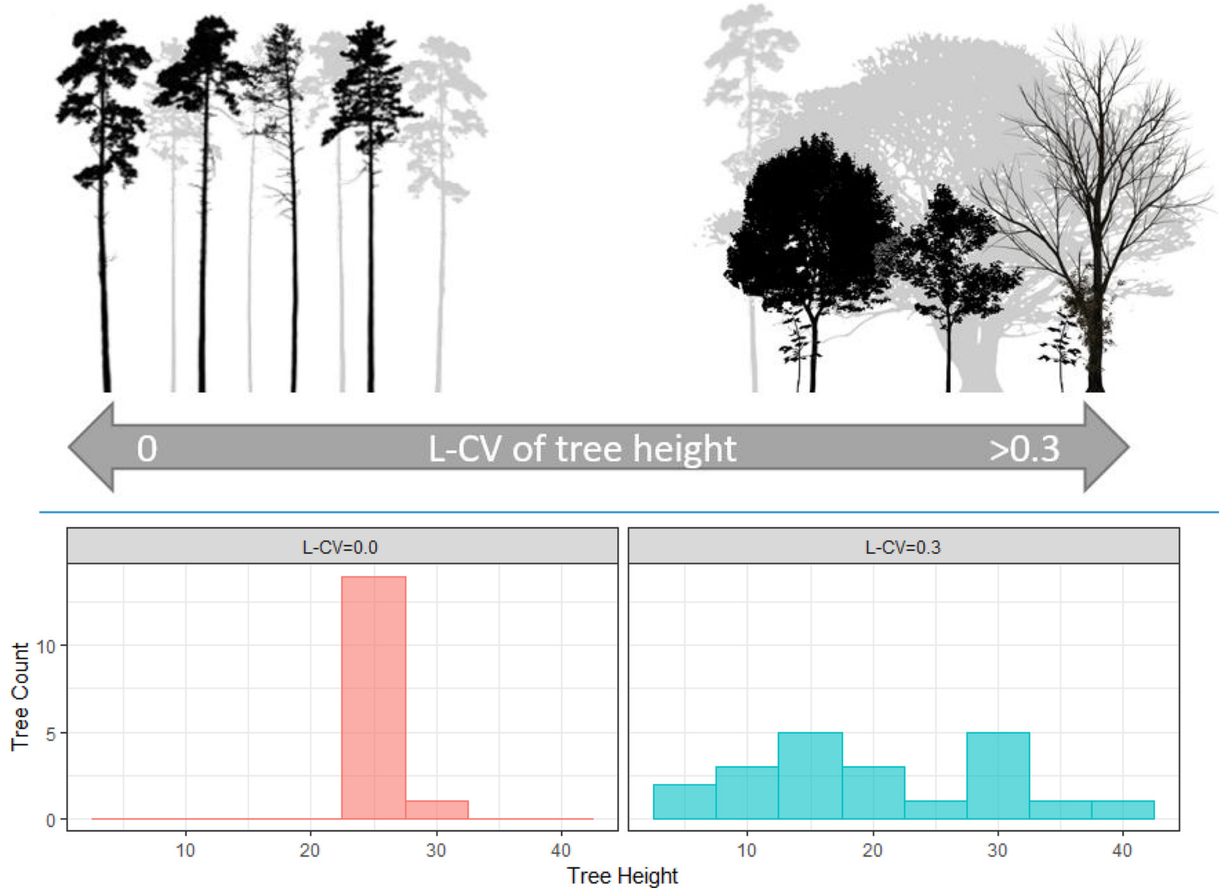



**Fig. 2.** Visual representation of tree height (in metres) diversity measured in the field.

**Table 1**
A summary of the two LiDAR surveys analysed in this research.

| | Leaf-on LiDAR survey | Leaf-off LiDAR survey |
|---|---|---|
| Acquisition date | 18th–19th July 2009 | 23rd March 2011 |
| System | Optech ALTM 3100EA | Leica ALS50-II |
| Platform | Helicopter | Fixed wing plane |
| Laser type | Discrete pulse | Discrete pulse |
| Beam deflection | Oscillating mirror | Oscillating mirror |
| Wavelength | 1064 nm | 1064 nm |
| Flying height | 300 m a.g.l.* | 800 m a.g.l.* |
| Pulse rate (kHz) | 100 | 87 |
| Average point density | 25 ppm$^2$** | 23 ppm$^2$** |
| Returns | Up to four | First and last |
| Survey characteristics | Wide area | Two multiple pass corridors |
| Pulse discrimination distance | 2.14 m | 2.8 m |
| Pulse discrimination method | Constant fraction discriminator | Constant fraction discriminator |

* Above ground level.
** Points per square metre.

than 2 m above the ground were excluded to eliminate the effects of understorey and terrain and heights above 45 m in the survey plots were excluded as these were unlikely to be hits from vegetation, being significantly higher than the tallest trees recorded in the field data. The relationships between field and LiDAR derived diversity estimates were analysed using Ordinary Least Square regression. In total, fourteen models were constructed using independent variables from one LiDAR dataset at a time and a combination of the two where appropriate.

**Table 2**
Summary of diversity metrics (L-CV) generated from field measurements in the 30 field sites.

| Plot type | Mean trees per hectare | Mean tree height (m) | Mean THdiv | Mean DBHdiv | Mean CLdiv | Mean CWdiv |
|---|---|---|---|---|---|---|
| Deciduous | 615.0 | 19.246 | 0.151 | 0.205 | 0.205 | 0.187 |
| Mixed | 660.9 | 18.974 | 0.203 | 0.287 | 0.258 | 0.219 |
| Coniferous | 1148.0 | 19.900 | 0.082 | 0.142 | 0.172 | 0.148 |

## 3. Results

Table 2 describes tree density, height and the mean L-CV or diversity calculated from tree height (THdiv), DBH (DBHdiv), crown length (CLdiv) and crown width (CWdiv) for each plot type. Coniferous plots had, on average, almost twice the density of trees compared to deciduous and mixed plots (1148 versus 615 and 660.9, respectively) likely due to the commercial nature of these stands. All plot types had a similar average tree height but complexity of structural diversity was highest in mixed plots and lowest in coniferous across all metrics (THdiv, DBHdiv, CLdiv and CWdiv).

Table 3 shows the correlations among all field variables; Variables such as DBH diversity (DBHdiv), Tree Height diversity (THdiv), Crown Length diversity (CLdiv) and Crown Width diversity (CWdiv) are highly correlated. On the other hand, the secondary variables such as Plot Age (age) and Trees per Hectare (n), are generally less well correlated.

Models describing field measured tree size diversity metrics are summarised in Table 4 and further summary statistics are shown in Table 5. There are fourteen models in total: six models constructed of leaf-on variables describing tree size diversity field metrics, six models constructed of leaf-off variables describing tree size diversity field

**Table 3**
The Pearson's product-moment correlation of all field variables.

| | | *n* | *nsp* | *%D* | *age* | *THdiv* | *DBHdiv* | *CLdiv* |
|---|---|---|---|---|---|---|---|---|
| Trees per hectare | *n* | 1 | | | | | | |
| Tree species number | *nsp* | −0.15 | 1 | | | | | |
| % Deciduous | *%D* | 0.00 | 0.06 | 1 | | | | |
| Plot age | *age* | −0.23 | −0.05 | −0.09 | 1 | | | |
| Tree height diversity | *THdiv* | −0.09 | 0.38* | 0.21 | 0.28 | 1 | | |
| DBH diversity | *DBHdiv* | −0.07 | 0.38* | 0.14 | 0.33 | **0.93**** | 1 | |
| Crown length diversity | *CLdiv* | 0.09 | 0.09 | 0.08 | 0.30 | **0.78**** | **0.80**** | 1 |
| Crown width diversity | *CWdiv* | 0.11 | 0.07 | 0.08 | 0.32 | **0.60**** | **0.73**** | **0.75**** |

* Statistically significant at the 95% CI.
** Statistically significant at the 99% CI.

**Table 4**
Models constructed for tree size diversity variables.

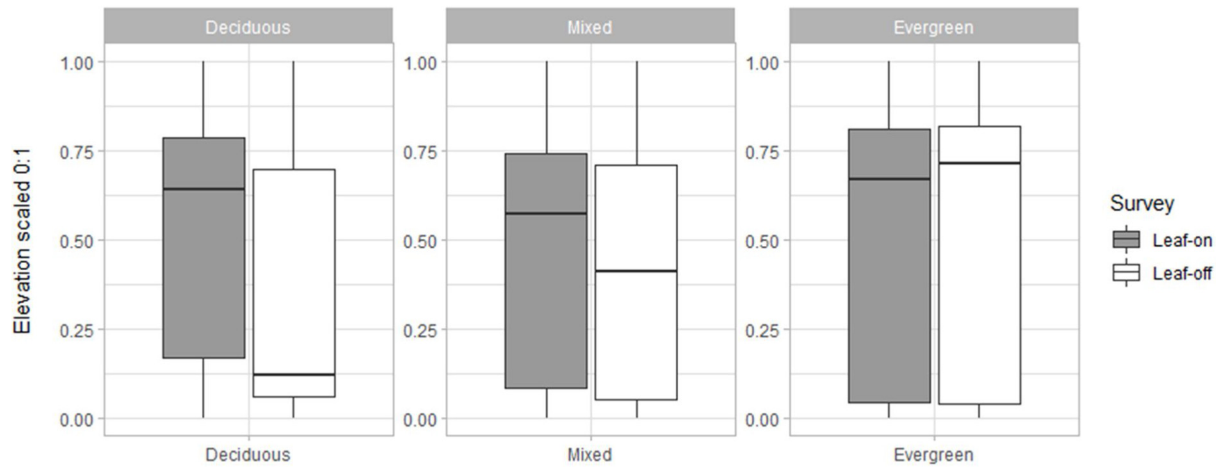
| Model | Equation |
|---|---|
| 1 | $THdiv = 0.234 - 0.091\log(Kurt_{lon}) + 0.003Var_{lon}$ |
| 2 | $THdiv = 0.233 - 0.092\log(Kurt_{loff}) + 0.003Var_{loff}$ |
| 3 | $THdiv = 0.244 - 0.104\log(Kurt_{loff}) + 0.004Var_{lon}$ |
| 4 | $DBHdiv = 0.138 + 0.087Skew_{lon} + 0.0445SD_{lon}$ |
| 5 | $DBHdiv = 0.124 + 0.077Skew_{loff} + 0.046SD_{loff}$ |
| 6 | $DBHdiv = 0.545 + 0.103Skew_{lon} + 0.042SD_{lon} - 0.343P99/90_{lon}$ |
| 7 | $DBHdiv = 1.032 + 0.11Skew_{loff} + 0.048SD_{loff} - 0.789P99/90_{loff}$ |
| 8 | $DBHdiv = 0.149 + 0.093Skew_{loff} + 0.047SD_{lon}$ |
| 9 | $CLdiv = 0.285 + 0.065Skew_{lon}$ |
| 10 | $CLdiv = 0.297 + 0.066Skew_{loff}$ |
| 11 | $CLdiv = 0.397 + 0.444\frac{1}{P99/75_{lon}{}^3} - 0.801\frac{1}{P99/50_{lon}{}^2} + Var_{lon}$ |
| 12 | $CLdiv = 0.35 + 0.568\frac{1}{P99/75_{loff}{}^3} - 0.892\frac{1}{P99/50_{loff}{}^2} + 0.002Var_{loff}$ |
| 13 | $CWdiv = 0.267 - 0.051\log(Kurt_{lon})$ |
| 14 | $CWdiv = 0.287 - 0.061\log(Kurt_{loff})$ |

metrics, and two models where both leaf-on and leaf-off diversity metrics were combined to describe THdiv and DBHdiv. When constructing models for CLdiv and CWdiv no suitable combination of variables would produce a model describing field diversity with any statistical significance and so these are omitted. Additionally, there are multiple single survey models presented describing DBHdiv and CLdiv as we present the best model constructed from leaf-on LiDAR survey variables and a leaf-off model with corresponding variables and vice-versa for leaf-off.

From Table 5 it is apparent that single survey models 4–7 (average $R^2$ of 0.65) describing DBHdiv perform better than models 1 and 2 describing THdiv ($R^2$ of 0.62). Additionally, when combining leaf-on and -off survey variables to produce models of DBHdiv and THdiv (models 3 and 8) the $R^2$ of these models increases between $0.02 - 0.13$ over the single survey models. Model 3 in particular describes up to 75% of THdiv utilising only leaf-off kurtosis and leaf-on variance. It is likely that the combination of metrics from the two separate datasets was able to offer some form of advantage. This was evidenced by the high value of the Link test (Link test value of 1.68, the largest among all of the models), suggesting that these variables could describe the variability in the field data very well. No valid models could be created

**Table 5**
Summary of constructed diversity models where each field diversity measurement has a corresponding model created from leaf-off and leaf-on LiDAR derived diversity metrics. THdiv and DBHdiv also have a corresponding model created from a combination leaf-on and leaf-off LiDAR derived diversity metrics where this improved the adjusted $R^2$ of the regression.

| Model | Dependant variable | Dataset | Independent variables | *t* | P > \|t\| | RMSE | *Adj-R²* | F | *p* |
|---|---|---|---|---|---|---|---|---|---|
| 1 | THdiv | Leaf-on | Kurtosis | −3.74 | 0.000 | 0.05 | **0.62** | 24.61 | < 0.0000 |
| | | | Variance | 2.86 | 0.001 | | | | |
| 2 | | Leaf-off | Kurtosis | −3.88 | 0.001 | 0.05 | **0.62** | 24.68 | < 0.0000 |
| | | | Variance | 3.12 | 0.007 | | | | |
| 3 | | Leaf-on & Leaf-off | Kurtosis (leaf-off) | −6.04 | 0.000 | 0.04 | **0.75** | 44.98 | < 0.0000 |
| | | | Variance (leaf-on) | 5.41 | 0.000 | | | | |
| 4 | DBHdiv | Leaf-on | Skewness | 5.11 | 0.000 | 0.06 | **0.65** | 28.26 | < 0.0000 |
| | | | SD | 5.58 | 0.000 | | | | |
| 5 | | Leaf-off | Skewness | 3.98 | 0.001 | 0.07 | **0.62** | 24.44 | < 0.0000 |
| | | | SD | 4.17 | 0.000 | | | | |
| 6 | | Leaf-on | Skewness | 4.82 | 0.000 | 0.07 | **0.66** | 19.72 | < 0.0000 |
| | | | SD | 4.42 | 0.000 | | | | |
| | | | P99/90 | −1.240 | 0.226 | | | | |
| 7 | | Leaf-off | Skewness | 4.82 | 0.000 | 0.06 | **0.67** | 20.82 | < 0.0000 |
| | | | SD | 4.69 | 0.000 | | | | |
| | | | P99/90 | −2.34 | 0.027 | | | | |
| 8 | | Leaf-on & Leaf-off | Skewness (leaf-off) | 5.65 | 0.000 | 0.06 | **0.69** | 32.88 | < 0.0000 |
| | | | SD (leaf-on) | 5.22 | 0.000 | | | | |
| 9 | CLdiv | Leaf-on | Skewness | 4.36 | 0.000 | 0.06 | **0.38** | 19.02 | 0.0002 |
| 10 | | Leaf-off | Skewness | 4.25 | 0.000 | 0.06 | **0.37** | 18.04 | 0.0002 |
| 11 | | Leaf-on | P99/75 | 1.74 | 0.09 | 0.06 | **0.29** | 4.9 | 0.0079 |
| | | | P99/50 | −2.63 | 0.01 | | | | |
| | | | Variance | 0.51 | 0.62 | | | | |
| 12 | | Leaf off | P99/75 | 2.57 | 0.016 | 0.05 | **0.57** | 13.94 | < 0.0000 |
| | | | P99/50 | −3.63 | 0.001 | | | | |
| | | | Variance | 2.06 | 0.05 | | | | |
| 13 | CWdiv | Leaf-on | Kurtosis | −2.54 | 0.017 | 0.05 | **0.16** | 6.45 | 0.017 |
| 14 | | Leaf-off | Kurtosis | −3.94 | 0.004 | 0.05 | **0.23** | 9.57 | 0.0044 |




| | Leaf-on | Leaf-off | Δ | | Leaf-on | Leaf-off | Δ | | Leaf-on | Leaf-off | Δ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 0.52 | 0.34 | 0.18 | | 0.48 | 0.39 | 0.09 | | 0.47 | 0.50 | -0.03 |
| Median | 0.64 | 0.12 | 0.52 | | 0.57 | 0.41 | 0.16 | | 0.67 | 0.71 | -0.04 |
| IQR | 0.62 | 0.64 | -0.02 | | 0.66 | 0.66 | 0.00 | | 0.77 | 0.78 | -0.01 |

**Fig. 3.** Top) Box plots of LiDAR return heights scaled from 0:1. For the evergreen plots this does not represent a period of leaf-loss only of partial winter needle thinning. Bottom) accompanying statistics.

that combined leaf-on and -off variables to describe CLdiv or CWdiv. Models generated using variables from a single survey describing CLdiv and CWdiv (maximum $R^2$ of 0.57 and 0.23, respectively) did not perform as well as single survey models for THdiv and DBHdiv (maximum $R^2$ of 0.62 and 0.67, respectively).

When comparing between leaf-on and leaf-off single survey models (so excluding models 3 and 8) tree size diversity models (THdiv and DBHdiv) perform similarly (maximum $\Delta R^2$ between best performing models of 0.03). Alternatively, assessing crown shape diversity models (CLdiv and CWdiv), leaf-off models outperform leaf-on models (maximum $\Delta R^2$ of 0.19).

With reference to Fig. 3, the difference in distribution of LiDAR returns through the forest canopy between leaf-on and -off conditions depends on the type of forest stand. Distribution differences, leaf-on to leaf-off, look to be related to the relative presence of deciduous trees. Conversely to deciduous and mixed plot types, LiDAR return penetration through the evergreen coniferous canopy seems to be slightly more impeded during leaf-off conditions than leaf-on. Though pulse penetration is markedly different between surveys in mixed and deciduous plot types, the interquartile range (IQR) of return heights is almost identical between surveys in all plot types (0 to $-0.02$).

Diversity metrics, variance, and several other variables show very little difference between surveys. This pattern is similar to the small difference in the IQRs between the two surveys seen in Fig. 3. Skewness and kurtosis, used several times in the models shown in Table 5, are the only two variables that are significantly different at the 95th% CI in deciduous plots. P99/90 is statistically different over mixed plots but there are no statistically significant differences between diversity variables calculated from different survey conditions over evergreen plots.

Fig. 5 shows raster representations of the three DBHdiv regression models detailed in Table 5 and we can see that for the majority of models the highest structural diversity is concentrated around the transitions between forest stands and in areas of broadleaf forest. With reference to Fig. 6, the areas of high DBHdiv do not seem to differ significantly between leaf-on and -off conditions though we can see in 6c that leaf-on models generally estimate diversity to be higher than leaf-off models. When leaf-off and leaf-on models are combined to estimate DBH diversity (see Fig. 5e) we see several areas with higher structural diversity values reaching up to 0.85 compared to up to 0.64 for leaf-off modelled DBHdiv alone.

Although Fig. 3 shows greater penetration to lower canopy levels in mixed and deciduous plots, the differences between the leaf-on and -off modelled DBHdiv is poorly correlated with forest type. Instead, Fig. 6c shows that differences between DBH diversity calculated from leaf-on and -off models do not differ significantly between forest types; all forest types share very small differences in DBHdiv around of $+/-0.2$. The largest differences between modelled DBHdiv are observed in transition areas between coups of different species where there are more gaps, and in open, broadleaved woodland.

## 4. Discussion

### 4.1. *Combined versus leaf-off versus leaf-on modelled forest structural diversity*

Using airborne LiDAR data collected under leaf-on and leaf-off conditions to measure forest structure, White et al. (2015) and Froidevaux et al. (2013) found that pooled models containing combinations of leaf-on and -off metrics yielded the best estimates of forest structure. This suggests that each dataset alone may capture different aspects of the structure of the forest and that together they summarise the vertical forest structure better. This is particularly evident in deciduous and mixed stands in this study (see Fig. 3) where the distribution of returns through the canopy differs greatly between leaf-on and -off conditions. The LiDAR return distributions suggest that more returns are gathered from the upper canopy layers under leaf-on conditions and during leaf-off conditions LiDAR is able to penetrate to the lower branches and suppressed canopy layers. Hill and Broughton (2009) found that leaf-off data were able to penetrate through the upper canopy enough to characterise the understorey in detail. When looking at what areas of the forest combined DBHdiv models and leaf-off DBHdiv models differed over (see Fig. 6d) there are greater levels of DBHdiv detected in the border areas between coups and in open deciduous woodland in the combined models. This supports the hypothesis that combined models are able to capture more of the variability

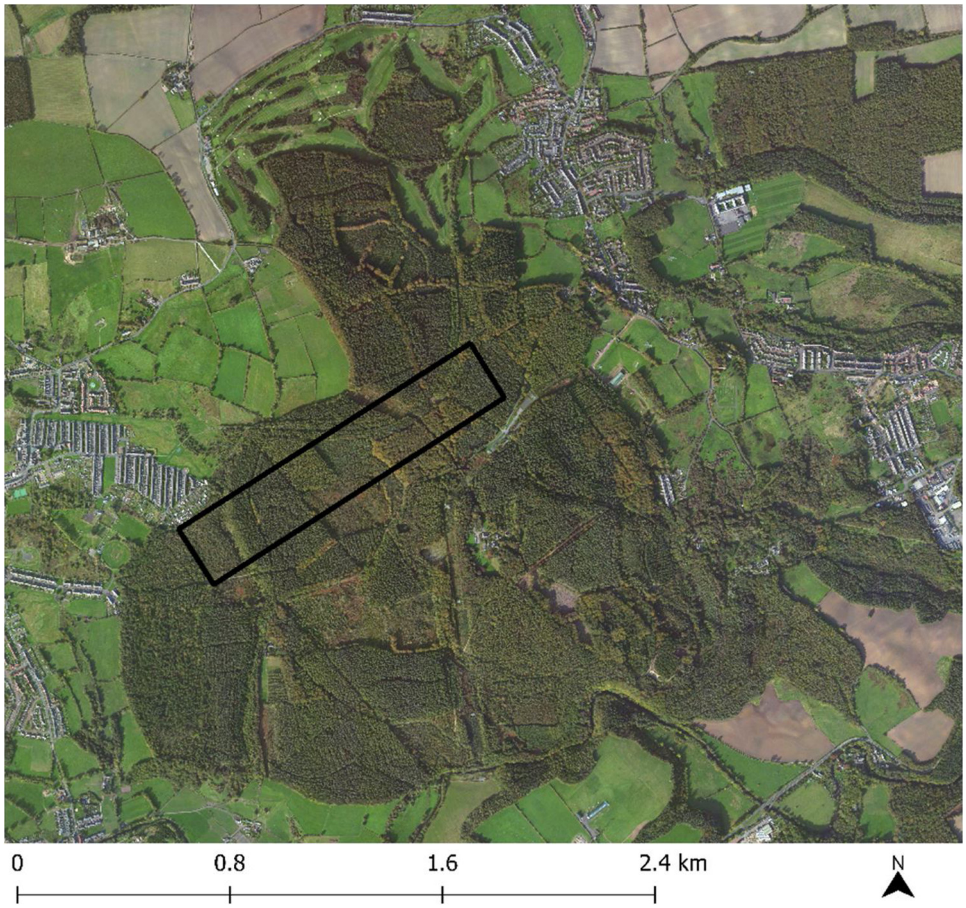



**Fig. 4.** AOI depicted in Figs. 5 and 6.

due to the contrasts between leaf-on and -off characterisation and LiDAR penetration in mixed and deciduous stands.

In our study, leaf-on and -off models perform similarly for describing tree size diversity (THdiv and DBHdiv) but leaf-off models describe crown shape diversity (CLdiv and CWdiv) better. Again, White et al. (2015) and Froidevaux et al. (2013) found that though combined models performed best, leaf-off models were the next best alternative. Additionally, many studies that compare leaf-on and -off models to describe forest volume and biomass (Anderson and Bolstad (2013); Bouvier et al. (2015); Brubaker et al. (2018); Hawbaker et al. (2010); Villikka et al. (2012)), species (Hernández-Stefanoni et al. (2015); Laslier et al. (2017); Ørka et al. (2010)) and further biophysical stand properties (Næsset (2005)) have all found that leaf-on and -off models performed similarly but often leaf-off models performed slightly better. Wasser et al. (2013) and Næsset (2005) note that point distributions, though different, are not significantly affected in the upper canopy layers under leaf-off conditions. However, last and single returns have increased penetration to lower canopy layers, enough so that a more detailed understanding of these forest areas can be generated than from the leaf-on data. This resulted in LiDAR derived canopy height measures of the lower and intermediate parts of the canopy varying greatly between leaf-on and -off survey conditions whilst, in general, direct measurements of canopy maximum height showed little difference between surveys. Similar results have been reported in coniferous stands, where despite most leaves remaining on the trees during this time, penetration through a decreased understorey to the ground can be facilitated. In a study in Norwegian Boreal forests, Ørka et al., 2010 found that last return height distributions were shifted towards the ground under leaf-off conditions. In this study, there are differences in return height distributions in evergreen plots between surveys, however, there are no significant effects seen in the diversity metrics. Evergreen plots generally show small and non-significant differences in diversity metrics calculated between surveys. Mixed and deciduous plots are more variable, showing some larger and statistically significant differences between surveys, indicating the influence of changing canopy conditions on the derived diversity metrics.

This increased penetration to lower canopy layers and decreased characterisation of upper canopy layers aligns well with our findings related to THdiv and DBHdiv but is somewhat at odds with the results indicating leaf-off datasets are better at describing the variability in crown shape diversity (CLdiv and CWdiv). It may be that vertical point height distribution metrics are generally poor at describing lateral features in a stand and it is just an artefact of the correlation between THdiv and CWdiv (see Table 3) that a valid model can be generated.

By comparison, Wasser et al. (2013) found that LiDAR percentile estimates of canopy height are underestimated under leaf-off conditions, and LiDAR estimates of fractional canopy cover are underestimated during leaf-off conditions except in plots with a high proportion of coniferous trees. In this study, leaf-on maximum return heights were higher than the leaf-off (by an average of 42 cm in deciduous plots) and with comparable ground classifications between surveys indications are that leaf-on LiDAR datasets could provide better estimations of canopy height. However, in terms of measuring structural diversity it may be that the increased penetrability into the canopy under leaf-off conditions counteracts the decreased upper canopy characterisation and leads to little effect on measures of forest structure diversity.

Models describing CLdiv under leaf-on conditions and CWdiv under both survey conditions (9, 11, 13 and 14) perform considerably worse than models describing THdiv and DBHdiv. The wide species diversity

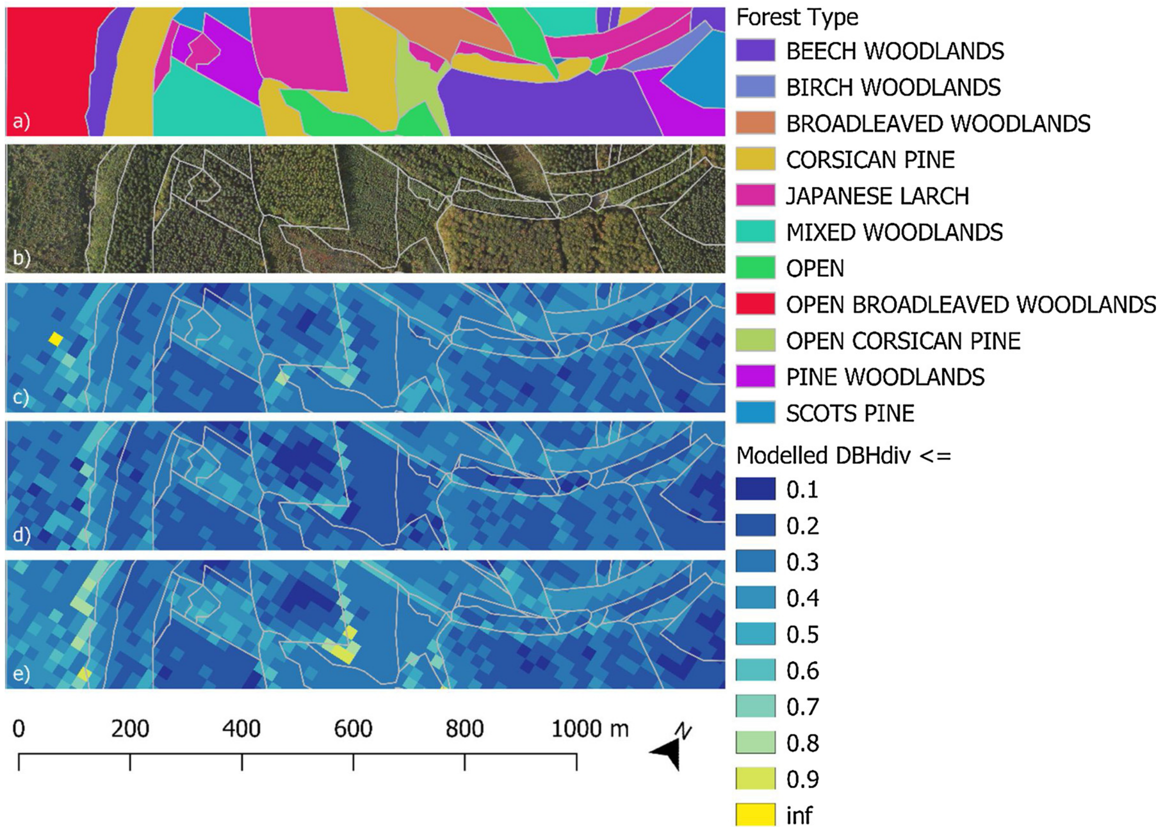



**Fig. 5.** (a) UK Forestry Commission Sub compartmental Database of AOI (Forestry Commission, 2013). (b) Google Satellite image of same area. (c) Leaf-on DBHdiv produced from model 4. (d) Leaf-off DBHdiv produced from model 7. (e) Combined leaf-on and -off DBHdiv produced from model 8. See Fig. 4 for AOI location in the context of the forest.

in the field dataset and the inability of crown width measurements in the field to accurately constrain the whole crown footprint may have contributed to this. Crown width and length can be highly related to variables such as tree spacing (Smith and Reukema, 1986; Khan and Chaudhry, 2007) which were not utilised as dependant variables in the models in this study.

### 4.2. Survey planning for biodiversity

For modelling tree size diversity at the stand level, leaf-off LiDAR data appear to have an equal or better capacity to describe tree size diversity in general. However, where both leaf-on and leaf-off LiDAR data are available the combination of the two can improve estimates of THdiv and DBHdiv (significantly with regards to DBHdiv).

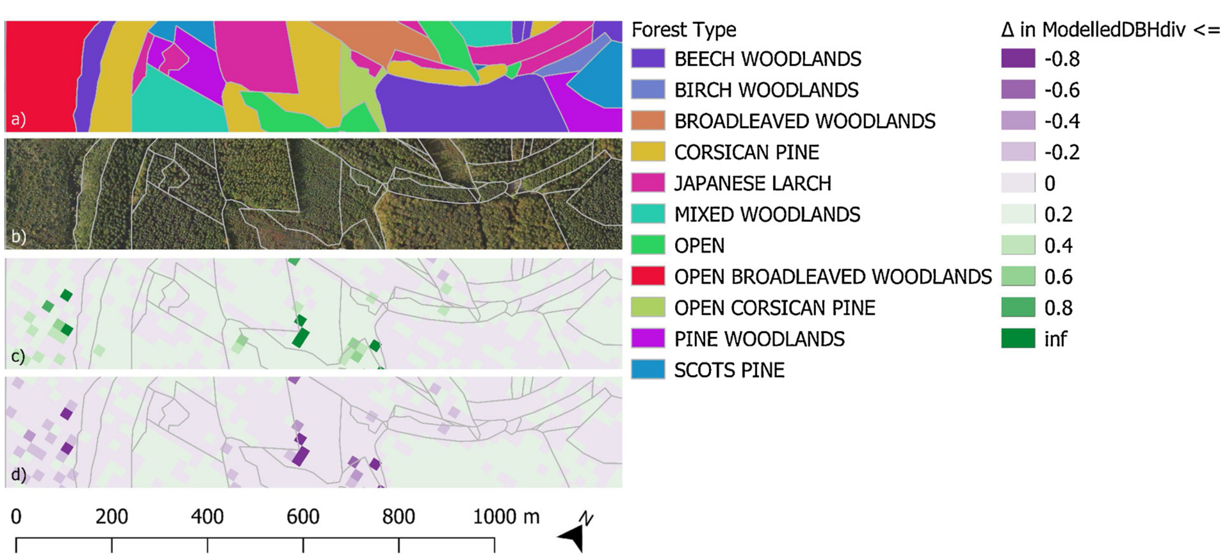



**Fig. 6.** a) UK Forestry Commission Sub compartmental Database of AOI (Forestry Commission, 2013) b) Google Satellite image of AOI. c) Difference between leaf-on DBHdiv (see Fig. 5c) and leaf-off DBHdiv (see Fig. 5d). d) Difference between leaf-off DBHdiv (see Fig. 5d) and combined leaf-on and -off DBHdiv (see Fig. 5e). See Fig. 4 for AOI location in the context of the forest.

Furthermore, leaf-off LiDAR data alone were capable of modelling crown shape diversity indices. This result has important implications for the practical use of such models for biodiversity mapping; vertical forest structure can in itself be used as a conceptual framework for habitat structure (McCoy and Bell, 1991) and so accurate LiDAR representations of this are important. Clawges et al. (2008) and Goetz et al. (2010) found that LiDAR derived vegetation structure diversity data were positively correlated with indices of bird species diversity and greater tree height variability indicates trees of different ages and species that are more suitable to host multiple species of animals (Sullivan et al., 2001; Svensson and Jeglum, 2001; Zenner and Hibbs, 2000). Similarly, DBH diversity is a measure of the variability in tree size, and is considered indicative for the presence and for the diversity of micro-habitats within a forest (Acker et al., 1998; Van Den Meersschaut and Vandekerkhove, 2000). Froidevaux et al. (2013) were able to demonstrate that though combined leaf-on and leaf-off data holds more ecologically relevant structural information than the two individual datasets when mapping bat activity, leaf-off data would be preferable if one had to choose between capture during leaf-on or leaf-off conditions.

## 5. Conclusion

The major conclusion to be drawn from this study is that leaf-off and leaf-on LiDAR variables describe plot-level forest structural diversity to very similar levels of precision. DBH diversity is modelled better than tree height (TH) diversity and combined the leaf-on and leaf-off regression models are able to account for over 10% more of the variance in leaf-on or -off datasets alone. Canopy crown shape diversity indices such as CLdiv and CWdiv are not well described by LiDAR datasets although models built with leaf-off data do perform better.

The results show that both leaf-on and leaf-off airborne LiDAR datasets provide the capacity to describe the structural diversity in a range of woodland types and ages. If diversity in tree height or DBH across a stand is used to facilitate mapping of habitat suitability (Sullivan et al., 2001; Svensson and Jeglum, 2001; Zenner and Hibbs, 2000), then it is unlikely that any significant improvements in LiDAR diversity estimates would be gained by undertaking a LiDAR survey at a particular time of year. However, some advantages may be gained in such a scenario when combining multi-seasonal LiDAR datasets as demonstrated by the greater ability of models to describe height and DBH diversity where leaf-on and -off diversity variables are combined. This would only be appropriate after careful co-registration of the multiple LiDAR datasets to avoid incorporating bias. Additionally, the advantages provided by combining datasets should be weighed up against the increased costs of additional surveys and the time and effort needed to process additional datasets. This is not the case for crown shape diversity indices where better estimates of crown shape diversity (CLdiv and CWdiv) are obtained from LiDAR data collected over deciduous and mixed deciduous/evergreen coniferous plots during leaf-off periods. Combining crown shape diversity metrics obtained from multi-season LiDAR datasets in models does not provide an advantage.

## Declaration of competing interest

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

## CRediT authorship contribution statement

**Sophie Davison:** Conceptualization, Formal analysis, Visualisation, Writing - original draft. **Daniel N.M. Donoghue:** Conceptualization, Writing - review & editing, Supervision. **Nikolaos Galiatsatos:** Supervision, Writing - review & editing.

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