

Heathland above-ground biomass estimation using UAV and LiDAR

Zeren Yang^{1,*}, Jill Kowal¹, Elena Arrigoni¹, Tim Wilkinson¹, Elloise Budd¹, Justin Moat¹,
and Amanda Cooper¹

¹Ecosystems and Conservation Science, Royal Botanic Gardens, Kew, London, UK

* Corresponding author: Z.Yang@kew.org

Abstract

1. Heathland is an important carbon sink and habitat for biodiversity. It is heavily managed Heathland is an important carbon sink and habitat for biodiversity. It is heavily managed through grazing and prescribed fire and faces increasing threats from wildfire and forest encroachment. Because the proportion of overall heathland carbon stock is predominately below-ground, above-ground biomass (AGB) is often neglected. Quantifying both AGB and soil organic carbon (SOC) is therefore important for understanding total heathland carbon storage.
2. This study was conducted at Thursley National Nature Reserve, UK. We evaluated the effectiveness of hand-held Light Detection and Ranging (LiDAR) and unmanned aerial vehicle (UAV) Structure-from-Motion (SfM) for estimating above-ground biomass (AGB) and associated carbon stocks across dry (*Calluna vulgaris*) and wet (*Erica tetralix*) heathlands with different stand ages and fire histories. Vegetation was

scanned before destructive biomass sampling, and the resulting three-dimensional (3D) point clouds were processed to derive structural metrics using canopy height models (CHMs) and voxelization. These metrics were then used to develop and evaluate regression models for AGB estimation, calibrated against the destructively sampled AGB.

3. In dry heathland, *C. vulgaris* stands aged 5, 19 and over 25 years had 95th-percentile canopy heights (H95) of 0.27 ± 0.01 , 0.46 ± 0.04 and 0.76 ± 0.05 m, respectively, and AGB of 5.01 ± 0.55 , 14.31 ± 2.19 and 31.92 ± 2.20 t ha⁻¹, respectively. Volumetric metrics provided better model fits than canopy height alone, with optimal resolutions of 20 mm for LiDAR voxel-derived and SfM CHM-derived volume, and 5 mm for LiDAR CHM-derived volume. LiDAR-derived models showed little evidence that biomass–structure relationships differed between *C. vulgaris*-dominated dry and *E. tetralix*-dominated wet heath, whereas the height-based model showed marginal evidence of heath-type-dependent relationships.

4. SOC were significantly greater in older dry (81.52 ± 9.99 t ha⁻¹) than younger dry heath (56.08 ± 6.27 t ha⁻¹) and were highest in wet heath (181.97 ± 28.08 t ha⁻¹).

Synthesis and applications: Three-dimensional structural metrics provide a non-destructive approach for monitoring AGB and associated carbon stocks in lowland heathlands. This method could enable repeated assessments of vegetation structure and biomass in response to management, while soil carbon measurements highlight the importance of considering below-ground carbon storage when evaluating heathland management strategies.

43 Key words: heathland, biomass, UAV, LiDAR, soil organic carbon, vegetation change

44

45 Introduction

46 European lowland heathlands support exceptionally rich biodiversity and provide vital
47 ecosystem services, including carbon sequestration, climate regulation, and flood
48 mitigation (Friggens et al., 2020; Gregg et al., 2021; Kowal et al., 2024). Lowland
49 heathland has undergone substantial decline across both the UK and Europe since the
50 nineteenth century, primarily due to agricultural intensification and land use change.
51 The remaining ~58,000 ha of lowland heathland in the UK represents approximately 20%
52 of the global extent of this habitat (Duddigan et al., 2024). Despite recognition that UK
53 heathlands have accumulated substantial soil carbon over centuries, current data on
54 carbon storage remain extremely limited (Gregg et al., 2021). When heathland
55 vegetation is undisturbed from intensive grazing, burning, or cutting, biomass
56 accumulation and carbon sequestration increase, supporting ecosystem resilience and
57 service delivery (Mitchell et al., 2000). *Calluna vulgaris*, the dominant species, matures
58 around 18 years of growth before senescence or successional transition (Gimingham,
59 1988; Kopittke et al., 2013). Alday et al., (2015) found that *C. vulgaris* above-ground
60 biomass (AGB) accumulation generally peaked at around 20-25 years, before
61 stabilizing. Within heathlands, below-ground soil organic carbon and integral
62 mycorrhizal fungi dominates total ecosystem storage (Friggens et al., 2020), but the
63 slow-growing, woody biomass of heather represents a significant contribution to total
64 carbon stocks (Kopittke et al., 2013). While management interventions, such as cutting
65 or burning are necessary to maintain heathland structure and biodiversity, they
66 temporarily reduce above-ground biomass carbon storage (Pakeman and Marrs, 1992;
67 Ward et al., 2007). Understanding how these management influences carbon storage is
68 therefore essential, depend on active management to maintain their characteristic

69 vegetation and ecological function, while their contribution to carbon budgets remains
70 under-quantified (Olmeda et al., 2020).

71 Studies show that AGB and carbon stocks in European dry heathlands vary strongly with
72 *C. vulgaris* dominance, stand age, and management. Classic plot studies in Dutch and
73 British heathlands quantified AGB and nutrient/carbon dynamics of *C. vulgaris* and co-
74 dominants (e.g., *Molinia caerulea*), establishing baselines for productivity in dry
75 heathland (Aerts, 1989). Age-structured studies demonstrated that *C. vulgaris* AGB and
76 carbon stocks increase with stand development from pioneer to mature phases
77 (Kopittke et al., 2013). Landscape-scale restoration from graminoid- to *C. vulgaris*-
78 dominated heath increased total carbon and recalcitrant carbon stocks (Quin et al.,
79 2014). More recently, evidence reviews from Scotland have highlighted that upland
80 heathland soils store substantial amounts of carbon—typically less than peatlands but
81 comparable to many mineral soils—and that these stocks remain relatively stable over
82 time unless management regimes are altered (Baggaley et al., 2021).

83 Traditional methods for quantifying vegetation biomass rely on destructive sampling,
84 where vegetation is harvested, dried, and weighed to estimate AGB (Rautiainen et al.,
85 2005). Although this method provides accurate local measurements, they are labour-
86 intensive, time-consuming, and often unsuitable for measuring protected or sensitive
87 habitats such as heathlands (Catchpole and Wheeler, 1992). Moreover, destructive
88 sampling negatively impacts biomass storage and disturb soil, is not possible to follow
89 temporally, limiting long term monitoring (Jonckheere et al., 2004). These constraints
90 highlight the need for replicable, non-destructive approaches that can measure AGB

with accuracy and precision without damaging vegetation or altering ecosystem processes.

Non-destructive biomass estimation using remote sensing (RS) offers a scalable and efficient alternative for monitoring vegetation productivity and carbon stocks (Eitel et al., 2016; Lu, 2006; Lu et al., 2016). By integrating multi-temporal observations, RS-based approaches can capture changes in vegetation growth, canopy height, and structural complexity, providing essential data for understanding AGB dynamics in response to habitat management and environmental change. Recent studies have demonstrated the potential of unmanned aerial vehicle (UAV) and Light Detection and Ranging (LiDAR) to quantify heathland biomass and fuel structure, including estimating biomass consumption from pre- and post-burn height changes (Hout et al., 2025), as well as mapping habitat condition and vegetation structure, monitoring management outcomes, and assessing habitat quality, vegetation composition, and conservation status through multispectral and hyperspectral imagery (Delalieux et al., 2012; Mùcher et al., 2013; Haest et al., 2017; Schmidt et al., 2017, 2018). These studies show that spectral unmixing and imaging spectroscopy can detect community composition, flowering phases, and encroachment processes relevant to Natura 2000 habitat monitoring. At finer spatial scales, UAV imagery has quantified *C. vulgaris* phenology (Neumann et al., 2020) and predicted post-management recovery and grass invasion using combined optical and structural metrics (Neumann et al., 2021). More recently, UAV LiDAR has provided detailed three-dimensional (3D) metrics of heathland canopy height and biomass, including assessments of fuel load and consumption after prescribed burning (Hout et al., 2025). These examples demonstrate the power of RS as

114 a non-destructive and repeatable approach for assessing heathland structure, function,
115 and management.

116 3D RS extends these applications by using active systems, such as LiDAR, directly
117 measure distances between emitted light pulses and their returns to derive precise 3D
118 point clouds that are used to derive models of observed objects (Heritage and Large,
119 2009). Passive systems use techniques like Structure from Motion (SfM) to generate
120 dense 3D point clouds from sequential overlapping 2D images (Snavely et al., 2006;
121 Bendig et al., 2014). LiDAR-based measurements have been applied to estimate canopy
122 height and volume for biomass assessments in shrublands (Greaves et al., 2015; Li et
123 al., 2015), crops (Bendig et al., 2014; Eitel et al., 2016), and grasslands (Cooper et al.,
124 2017; Wallace et al., 2017), highlighting the versatility of 3D RS for ecological
125 monitoring. UAV-based SfM combines flexible image acquisition with automated 3D
126 reconstruction to produce high-resolution digital surface models at relatively low cost.
127 Such workflows have been successfully applied to estimate crop height and biomass
128 (Lu et al., 2019; Zhu et al., 2019) and to capture vegetation structural variability in
129 natural ecosystems (Forsmoo et al., 2018; Cunliffe et al., 2022). Its scalability,
130 repeatability, and centimetre-scale resolution make it particularly well suited to
131 dynamic habitats such as heathlands, where vegetation height, phenology, and
132 recovery after management vary across short distances.

133 Recent research has begun to explore this frontier demonstrating that both LiDAR and
134 UAV SfM can reliably estimate biomass in grasslands (Wijesingha et al., 2019). However,
135 to our knowledge, no study has yet predicted heathland biomass using both SfM- and
136 LiDAR-derived metrics. This study aims to assess the performance of SfM and LiDAR

137 approaches for developing empirical biomass prediction models across heathlands of
138 contrasting hydrology i.e. wet and dry heathland and *C. vulgaris*-dominated stand ages,
139 representing structural variation arising from contrasting management and
140 successional stages of fire recovery and growth. We hypothesize that heathland AGB
141 could be estimated using structural metrics derived from both UAV-SfM and LiDAR point
142 clouds. Additionally, we expected carbon storage (both above- and below-ground) to
143 increase with heathland age and time since disturbance. In summary, the objectives of
144 this study were to:

- 145 • develop empirical models for estimating heathland AGB and associated carbon
146 stocks using structural metrics derived from SfM and LiDAR point clouds;
- 147 • evaluate the performance of biomass prediction models derived from SfM- and
148 LiDAR-based structural metrics across heathland types; and,
- 149 • quantify above- and below-ground carbon stocks across different heathland age
150 and fire histories.

151

152 Materials and Methods

153 Study area

154 The study was carried out in March 2025 at Thursley National Nature Reserve (NNR) in
155 southern England (51°09'25"N 0°42'04"W). The site comprises *C. vulgaris* – *Ulex minor*
156 dry heathland (H2, National Vegetation Classification [NVC] scheme, Rodwell 2006) and
157 *Erica tetralix* - *Sphagnum compactum* wet heathland (M16). It is a Special Area of
158 Conservation (European Union's Habitats Directive, 92/43/EEC).

159 To understand the relationship between age and biomass, and test the methods across
160 developmental stages, we chose three distinct sites within the dry heathland
161 representing a chrono-sequence of heather growth (Figure 1). Two sites were associated
162 with known wildfire events: Site 1 burned in 2020, and Site 2 burned in 2006. These fire
163 histories provided objective estimates of heather stand age: Site 1, 5 years old, and Site
164 2, 19 years old at time of survey. A third dry heathland site was in an area known not to
165 have burned for at least 25 years, representing older and mature heather stands. In
166 addition, a wet heathland site was included to test whether structural–biomass
167 relationships derived from dry heath RS metrics were transferable across different
168 heath types and hydraulic gradients.

169 Both 2020- and 2006-burn dry heath sites were dominated by two types of heather, *C.*
170 *vulgaris* and *Erica cinerea*, with some *Ulex minor* and *Ulex europaeus* (gorse), and a few
171 spotty areas or individuals of *Pinus sylvestris* (Scots Pine) and *Betula pendula* (silver
172 birch). The more recently burned Site 1 had visibly greater bare ground than Site 2. At
173 Site 2, *C. vulgaris* reached maximum heights of up to 130 cm and formed large bush-like
174 structures, while *E. cinerea* grows shorter and often co-located underneath the *C.*

vulgaris. The 2006 fire removed nearly 80% of the heather at Thursley NNR, leaving small areas of heather aged more than 25 years; Site 3 was in one such patch in the south-western corner of the reserve. The wet heathland site differed from the dry heathland sites in species composition and water-table conditions, and was dominated by *Erica tetralix* and *C. vulgaris*, with some *U. europaeus*.

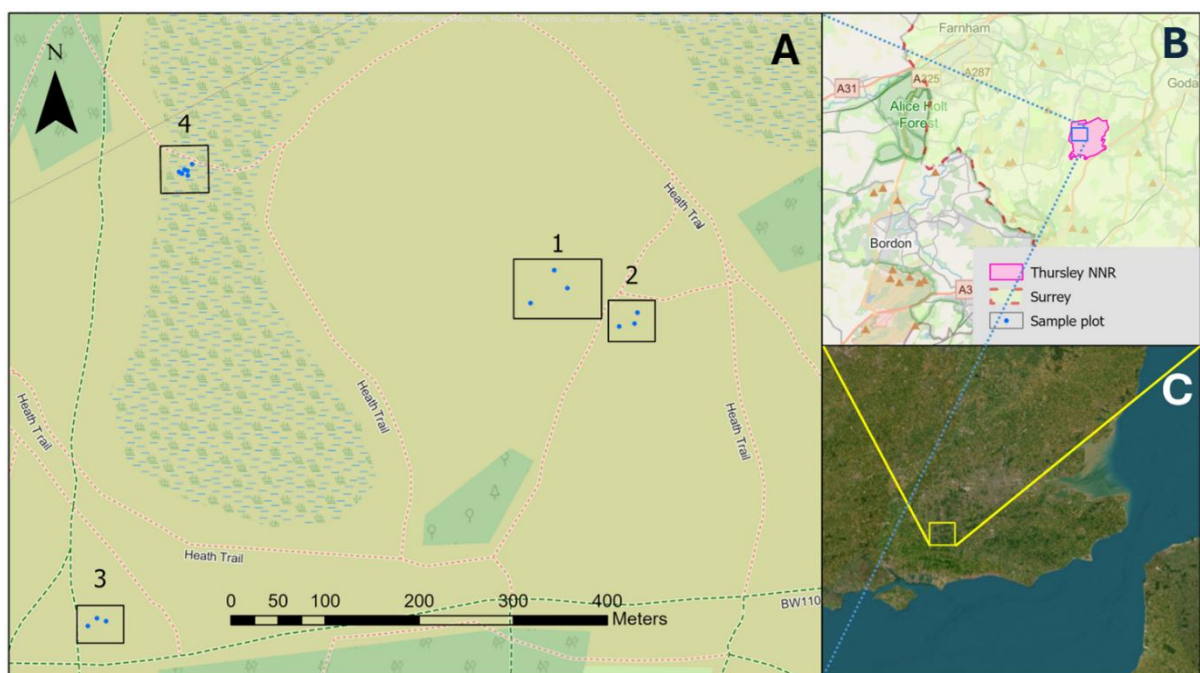


Figure 1 Location of Thursley Nature Reserve and sampling sites. A. Dry heathland: Site1: wildfire in 2020; Site 2: wildfire in 2006; Site 3: no wildfire; Wet heathland: Site 4. B. Thursley Nature Reserve in Surrey County. C. Thursley Nature Reserve in South England.

Data collection

For Sites 1–3, three sample plots were randomly selected within each site; for Site 4, six sample plots were randomly selected. Each sample plot has a size of 0.5 m by 0.5 m.

Reflective poles were placed at the four corners of each sample plot. Before harvesting, the excess vegetation on the edge, extending 5 cm beyond the plot boundary, was cleared to remove the obstruction for scanning the object inside the plot.

UAV-borne images and LiDAR data were collected in each study plot. Data collection followed a process of before and after harvest observation (UAV-LiDAR-Harvest-LiDAR-UAV sequence), as previously implements (Cooper et al., 2026). This method determines the volume of vegetation removed.

UAV data

UAV surveys for each area were conducted using a DJI Mavic 3 Multispectral (DJI). Each flight covered the entire area with a minimum 50m buffer. The UAV followed a predesigned flight plan consisting of two intersecting 90° flight grids. The UAV flight grids were designed using DJI's built-in flight path planner. UAV data were collected with clear sky, no wind, during periods of high solar angle (near midday). These weather conditions help reduce image blur and minimize shadows (Dandois et al., 2015). Each UAV flight was planned with a ground sample distance (GSD) of 0.55 cm and a constant flight speed of 1 m/s to keep motion blur below one GSD (O'Connor et al., 2017; Roth et al., 2018; Hartley et al., 2022). The flight altitude was maintained at a constant height of 12 meters. To obtain a high-resolution point cloud and minimize potential artifacts caused by the complex vegetation structure (Frey et al., 2018), we set the image overlap to 70% side overlap and 80% frontal overlap. Each UAV image was georeferenced using the onboard real-time kinematic (RTK) global navigation satellite system (GNSS), with an accuracy of approximately 1–3 cm. Ground control points (GCPs) were established using markers placed at the four corners and the centre of each site before the flight. Following the UAV flight, the precise positions of the GCPs were recorded using a Leica

213 Zeno GG04 Plus Smart Antenna RTK GNSS device, with an absolute accuracy of
214 approximately 1–3 cm.

215 Handheld LiDAR data

216 Handheld LiDAR scans of each sample plot were conducted using a FARO GeoSLAM
217 ZEB Horizon RT Mobile Scanner (Faro, Lake Mary, FL, USA). The ZEB Horizon RT Mobile
218 Scanner can collect 300,000 scan points per second, with a field of view of 360° x 270°,
219 up to 6mm relative accuracy and a maximum range of 100 m (Table S1). The GeoSLAM
220 relies on a Simultaneous Localization and Mapping (SLAM) algorithm that pulls together
221 the relative position of interception points so that post-processing registration targets
222 are not required.

223 LiDAR data collection was conducted with the same procedure in all plots. LiDAR
224 collection path followed a loop-inside-loop method to form closed circles around each
225 sample plot, with larger loops around the plot to increase the laser's viewing angles.
226 During scanning, the LiDAR height was varied from approximately 0.3 m to 1.37 m with
227 the sensor orientated towards the sample plots. Three reflective disc markers were
228 placed within each scan site and were georeferenced to allow alignment between the
229 LiDAR and the UAV point clouds, also to facilitate the Digital Terrian Model (DTM)
230 generation of each site (Chuang and Jaw, 2017; Petrov et al., 2024). The markers were
231 placed to form an acute triangle to maximise coverage (Horn, 1987). Post harvest, an
232 extra LiDAR scan was conducted for each plot to generate the ground elevation (DTM).
233 The markers remained at the same positions during the two LiDAR scans to reduce
234 errors when georeferencing the two point clouds before and after the harvesting.

AGB data

After the pre-harvesting UAV flight and LiDAR scanning, all above ground plant matter was harvested within each plot. The wet weight was measured using a hand scale in the field immediately after harvesting and a 200 g of collected sub-sample were taken for analysis. These samples were randomly subset to three 30g of subsamples, in a paper bag, and dried in the oven at 70°C for at least 48h, until the weight was constant. The constant weight of each subsample is recorded as the dry biomass weight (Pérez-Harguindeguy et al., 2013). A wet-to-dry ratio was calculated and extrapolated to the whole sample (wet) to get the total dry biomass weight of each sample plot.

Soil data

To estimate below-ground carbon stocks, soil samples containing organic and mineral layers were collected to a depth of up to 15 cm in keeping with previous heathland studies (Gregg et al., 2021). Individual samples weighed at least 500 g and were collected at four time points across 2023 and 2025 in dry heath, and at one time point in 2024 in wet heath, for soil organic carbon (SOC) analysis (Arrigoni et al. 2026). Fresh samples were transferred the next day to NRM laboratories for processing following industry standards (Cawood Scientific, Bracknell, UK). The mean soil carbon stock (t C ha^{-1}) was calculated for each area and time period ($n = 15$).

Data processing

AGB carbon conversion

We converted dry biomass in each $0.5\text{m} \times 0.5\text{m}$ plot (g plot^{-1}) (DM: Dry Matter) to carbon stock (t C ha^{-1}) (C_{mass} : Carbon stock of above-ground carbon (AGC) per hectare) by adopting a carbon fraction (CF) = 0.483 specific to *C. vulgaris* (Allen et al., 2013). The CF

choice is consistent with other measurements of ~48–51% C for heather leaves and wood (Grace and Woolhouse, 1973).

$$C_{mass} = DM \times 0.04 \times CF \quad (1)$$

where:

C_{mass} = AGC stock (t C ha⁻¹)

DM = Dry biomass in each plot (g plot⁻¹)

0.04 = conversion from g plot⁻¹ to t ha⁻¹

and CF = carbon fraction

Point Cloud Processing

Three individual point clouds were generated for each plot: UAV SfM point clouds, LiDAR pre-harvest point clouds, and LiDAR post-harvest point clouds. The UAV SfM point clouds were georeferenced to the British National Grid / OSGB 1936 coordinate reference system (CRS), consistent with the GCPs collected using RTK GNSS.

3D point clouds were generated from UAV imagery using Agisoft Metashape Professional version 2.2.0 (64 bit) software (Agisoft LLC, Russia) using the following SfM workflow. Geo-tagged images from a single UAV flight were first aligned using automated feature matching across overlapping photographs to identify key and tie points. This alignment produced a sparse point cloud representing shared features across the image set and enabled initial georeferencing using the UAV's onboard RTK GNSS data.

To improve spatial accuracy, the ground markers were used as high-precision GCPs. Each GCP was manually marked in at least 20 images prior to camera alignment

optimization. The camera model and alignment were re-optimized using adaptive fitting and tie point covariance adjustment. Following sparse cloud generation, low-quality tie points were removed using Metashape’s “gradual selection” tool, after which the point clouds were “optimized” to minimize spatial error. These steps significantly reduced positional errors.

A dense point cloud was subsequently generated from the optimized sparse model using high-quality settings and mild filtering to preserve detail and limit data loss. The resulting point cloud offered high-resolution 3D structural information of the surveyed area, forming the basis for further products such as a Digital Surface Model (DSM), DTM and orthomosaic imagery.

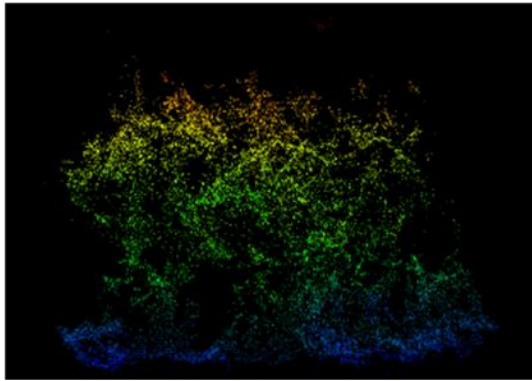
LiDAR data were processed using FARO Connect 2021 (v5.0) to register individual scans into plot-level point clouds, which were then imported into the open-source software CloudCompare (v 2.13.2) (<http://www.cloudcompare.org>) for further processing.

Because the raw LiDAR point clouds were not georeferenced, alignment with the GCPs was required. The reflective disc markers were identified manually in the software when the *Intensity* parameter was selected as the *Scalar Field*, which allowed manual registration of the scan targets with their corresponding GPS-measured coordinates. To align point clouds within each plot, the registration process followed a combination of GCP-based alignment and the Iterative Closest Point (ICP) algorithm. First, GCPs were identified on each of the two point clouds and used as initial references for coarse alignment. The ICP method was then applied within CloudCompare to iteratively compute the rigid transformation—comprising rotation, translation, and scaling

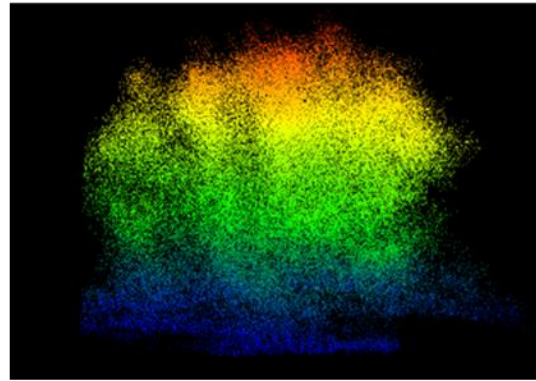
302 factors—that minimized the distance between matching points in the two clouds (Besl
303 and McKay, 1992; Westoby et al., 2012).

304 To improve the delineation of individual plant units and enhance the interpretability of
305 the point clouds, we removed non-vegetative structures (i.e. stones) and cropped to the
306 plots (Figure 2 A and B). This protocol enabled the generation of high-resolution 3D
307 representations of vegetation structure at plot level, supporting accurate downstream
308 analysis of biomass and spatial distribution.

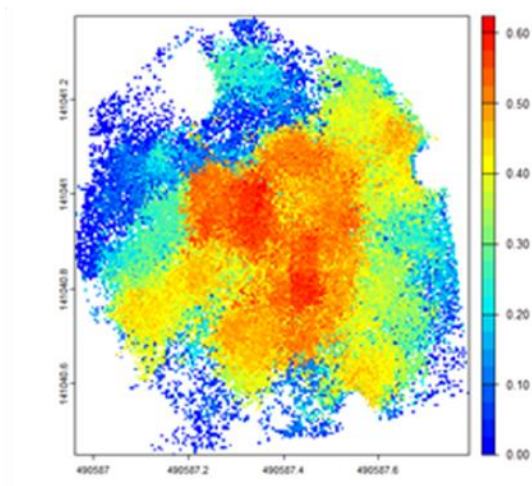
A



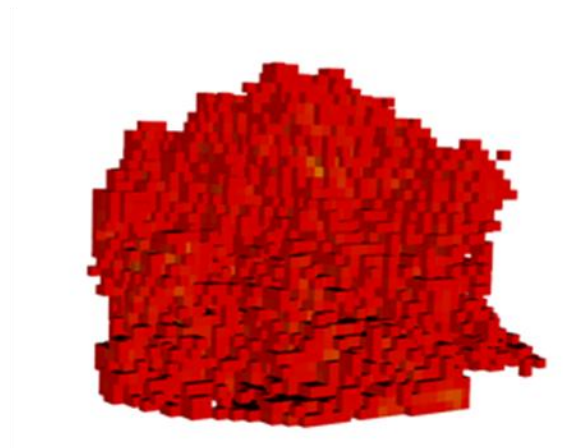
B



C



D



309

310 Figure 2 Individual heather was extracted from A) Unmanned Aerial Vehicle (UAV)

311 Structure-from-Motion (SfM) point clouds; B) Light Detection and Ranging (LiDAR) point

312 clouds, illustrated in CloudCompare. The volumetric measurements using C)

313 voxelization (LiDAR only) and D) Canopy Height Modelling (LiDAR and UAV-SfM),

314 illustrated using lidR package in R.

315 **AGB prediction**

316 To predict AGB we derived structural metrics from point clouds using two approaches:

317 canopy height modelling (CHM) and 3D voxelization. CHM-derived canopy volume was

calculated from both LiDAR and SfM point clouds, whereas voxel-based volume estimation was applied only to LiDAR data. SfM photogrammetry primarily reconstructs canopy surfaces and rarely captures the internal vegetation structure in low-stature shrubs. As a result, voxelization of SfM-derived data is unlikely to reliably represent true vegetation occupancy.

CHM was generated by subtracting the ground elevation from the vegetation elevation, for both LiDAR and UAV point clouds, using the *lidR* package (Version 4.1.2) (Roussel et al., 2026). To derive ground elevation, the post-harvest point cloud was converted into a raster grid following the method of Roussel et al (2020) (Figure 2 C). Canopy volume was calculated as the sum of pixel height multiplied by pixel area across vegetated cells.

In this study, LiDAR-derived point clouds were organized into a regular 3D grid. As defined by Hosoi et al (2013), a voxel—or volumetric pixel—is the smallest unit of discrete volume used to represent a 3D object. To approximate vegetation structure (internal and external), we classified each voxel as either occupied or empty, defining a voxel as occupied if it contained at least one LiDAR return (Figure 2 D). The total vegetation volume was then estimated by multiplying the number of occupied voxels by the volume of a single voxel.

In addition to volumetric metrics, canopy height was evaluated as a simpler structural predictor of biomass. Plot-level canopy height was derived from normalized point clouds using the 95th percentile of vegetation return heights (H95), a robust measure of canopy-top height widely used in LiDAR-based vegetation studies (Chan et al., 2021). This metric effectively captures variation in vegetation structure and canopy development (Cao et al., 2019). Height–biomass relationships were modelled using

linear regression with heath type as a factor. This metric allowed comparison between traditional height-based approaches and volumetric structural representations.

Model Analysis

Linear models (LMs) were used to evaluate relationships between remotely sensed structural metrics and destructively measured dry biomass. Structural predictors included canopy volume derived from LiDAR voxelization, LiDAR CHM, and SfM CHM, as well as canopy height (H95). Heath type (dry and wet) was included as a categorical factor, and interaction terms were tested to assess differences in biomass–structure relationships between vegetation types.

To assess resolution sensitivity and to evaluate how resolution affects volumetric estimation, models were tested using the lidR package (Roussel et al., 2026) at pixel sizes of 0.5 cm, 1 cm, 2 cm, and 4 cm for CHM-derived volume. And for LiDAR voxel-derived volume, voxel edge lengths of 1 cm, 2 cm, 4 cm, and 8 cm were evaluated. Height-based models used the 95th percentile canopy height (H95) as predictor.

Model performance was assessed using the coefficient of determination (R^2), adjusted R^2 , root mean square error (RMSE), and normalized RMSE (NRMSE). NRMSE was calculated by dividing RMSE by the mean observed biomass, allowing comparison of model performance across structural metrics and spatial resolutions. The operational pixel or voxel resolution for each structural method was defined as the resolution yielding the lowest prediction error while showing stability across adjacent scales.

All statistical analyses were conducted in R (version 4.3.0) using the base stats package for linear modelling and ggplot2 for visualization (R Core Team, 2025).

Results

Biomass and carbon

The biomass reference data from all sites showing the basic characteristics of sampled heaths (biomass and height) are in Table S2. Table 1 listed average above-ground dry biomass and corresponding AGC stock calculated using Equation (1), as well as 95th percentile height. Estimates of SOC data are included for sites 1, 2 and 4.

Table 1 Summary statistics of wet and dry heathland in all sampling sites: 95th percentile height, AGB and corresponding carbon stocks and soil organic carbon (SOC). (mean±SE). Soil data were not collected in the mature heathland in Site 3.

Heath type	Site	Stand age (yr)	Height (m)	ABG Biomass (t ha ⁻¹)	ABG Carbon (t ha ⁻¹)	SOC (t ha ⁻¹)
Dry	1	5	0.27±0.01	5.01±0.55	2.42±0.27	56.08±6.27
Dry	2	19	0.46±0.04	14.31±2.19	6.91±1.06	81.52±9.99
Dry	3	25	0.76±0.05	31.92±2.2	15.42±1.06	NA
Wet	4	5	0.32±0.05	7.88±1.6	3.8±0.78	181.97±28.08

AGC stock predictions

Pixel and model selection

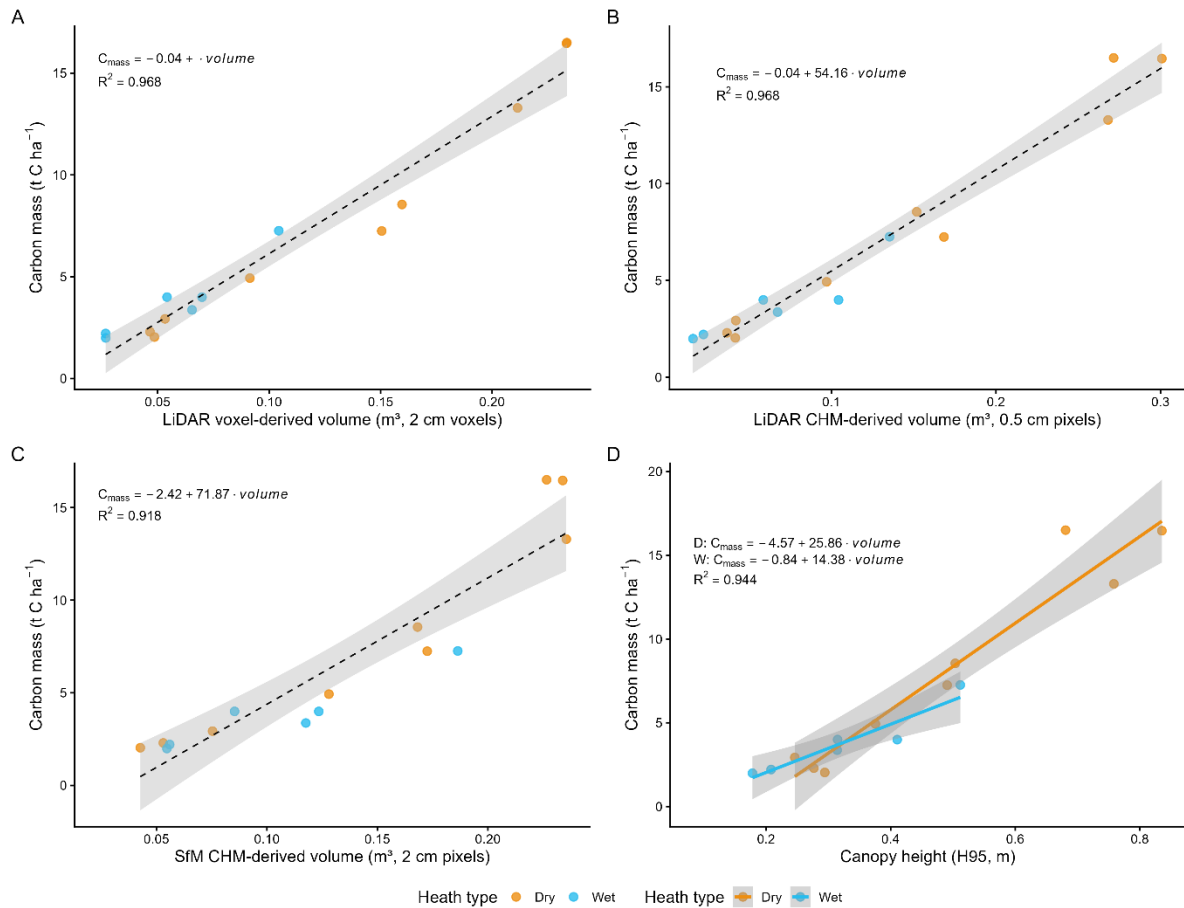
Model performance varied with voxel size (Table 2), with the lowest prediction error at 20 mm for LiDAR voxel-derived and SfM CHM-derived volume, and 5 mm for LiDAR CHM-derived volume.

378 Table 2 Model selection statistics for different biomass prediction methods across
 379 spatial resolutions. Resolution = voxel or canopy height model (CHM) pixel size. R^2 = the
 380 proportion of variance explained. RMSE = normalised root mean square error. p_volume
 381 indicates significance of the relationship between biomass and chosen metrics.
 382 p_interaction indicates significance of the interaction between metrics and heath type.
 383 Metrics includes LiDAR Voxels (terrestrial laser scanning voxel-derived volume), LiDAR
 384 CHM (terrestrial laser scanning canopy height model-derived volume), SfM CHM
 385 (Structure-from-Motion canopy height model-derived volume), and Height (height-
 386 based model using H95):

Resolution (mm)	R^2	NRMSE	p_volume	p_interaction	Metrics
10	0.956	0.160	3.57E-08	0.888	LiDAR Voxels
20	0.968	0.136	6.31E-09	0.493	LiDAR Voxels
40	0.963	0.147	1.51E-08	0.190	LiDAR Voxels
80	0.947	0.175	1.01E-07	0.089	LiDAR Voxels
5	0.968	0.137	6.72E-09	0.148	LiDAR CHM
10	0.966	0.141	8.97E-09	0.049	LiDAR CHM
20	0.963	0.147	1.42E-08	0.034	LiDAR CHM
40	0.957	0.157	3.07E-08	0.032	LiDAR CHM
5	0.917	0.219	1.23E-06	0.034	SfM CHM
10	0.917	0.219	1.22E-06	0.038	SfM CHM
20	0.918	0.218	1.14E-06	0.052	SfM CHM
40	0.908	0.231	2.22E-06	0.095	SfM CHM
NA	0.944	0.181	1.46E-07	0.056	Height

387 Overall, the four structural metrics derived from point clouds showed significant
388 positive relationships with AGB-carbon density (Figure 3). Among the tested
389 approaches, volume-based metrics derived from LiDAR and SfM point clouds generally
390 outperformed height-only measures (H95), indicating that volumetric representations of
391 vegetation structure better captured variation in heathland biomass. LiDAR-derived
392 metrics consistently produced the strongest relationships, particularly voxel-derived
393 volume, suggesting that characterization of 3D vegetation occupancy provides a more
394 robust proxy for biomass-carbon stocks. Model performance also varied between dry
395 and wet heath habitats and across spatial resolutions, highlighting the influence of
396 vegetation structure and density on predictive accuracy.

397



398

399 Figure 3 Correlation between differing structural metrics of *Calluna vulgaris* (Sites 1 – 3)

400 and *Erica tetralix* (Site 4) (A) Light Detection and Ranging (LiDAR) voxel-derived volume;

401 (B) LiDAR Canopy Height Model (CHM)-derived volume; (C) Structure-from-Motion

402 Canopy Height Model-derived volume; (D) Height (H95, m)) and carbon stock (t C ha⁻¹).

403 Each point represents carbon stock derived from observed biomass values collected for

404 dry and wet heath sites. Dash lines indicate linear regression fits for both heath types,

405 and shaded areas represent 95% confidence intervals. The coefficient of determination

406 (R^2) indicates the proportion of variance in biomass explained by the model.

Height

Linear models relating H95 to measured AGC showed a strong positive relationship ($R^2 = 0.94$), indicating that taller heath vegetation was associated with greater biomass and carbon storage.

However, the height-based model exhibited higher prediction error compared with volumetric models and showed evidence of habitat-dependent slopes. Specifically, carbon stock increased more slowly with height in wet heath than in dry heath, suggesting structural differences in canopy architecture between habitat types. Height alone therefore did not fully capture variation in vegetation density or internal structure.

Compared with LiDAR voxel-derived and CHM-derived volume metrics, which explained a greater proportion of carbon stock variance and showed more consistent relationships across heath types, H95 represents a simpler but less complete structural descriptor. While canopy height remains useful for rapid structural characterization, these results demonstrate that 3D volume metrics provide more robust carbon stock predictions in low-stature, structurally heterogeneous heathland vegetation.

Below-ground soil carbon

Soil carbon stock showed statistically significant differences among heathland age classes and heath types (Figure 4). Within dry heath, older stands (2006 burn) contained significantly greater soil carbon stocks ($81.52 \pm 9.99 \text{ t ha}^{-1}$) than younger stands stocks ($56.08 \pm 6.27 \text{ t ha}^{-1}$) which regenerated from a more recent fire disturbance (2020 burn). Soil carbon stocks also differed between dry and wet heath, reflecting contrasts in vegetation composition and hydrological conditions between heathland types.

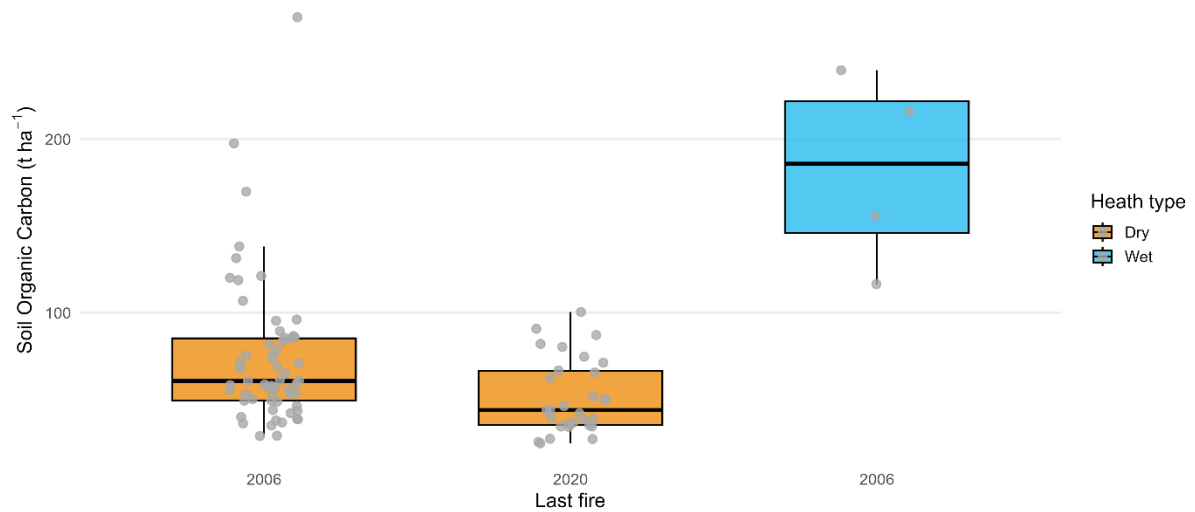


Figure 4. Box plots of soil organic carbon (SOC) (t ha⁻¹) (0–15 cm depth) across heathland types and stand ages. (A) SOC for dry heath (2006 and 2020 burn) and wet heath (2020 burn). (B) Corresponding summary statistics showing heath type, stand age, sample size (n), mean SOC, and Standard Error (SE).

435 Discussion

436 This study examined variation in AGB and carbon stocks across dry and wet heathlands
437 spanning a gradient of time since disturbance. We found that longer time since
438 disturbance was associated with greater AGB and carbon stocks. Across both
439 heathland types, 3D volumetric metrics derived from LiDAR and UAV-based SfM data
440 show strong relationships with AGB.

441 The first objective of this study was to develop empirical models for estimating
442 heathland AGB and associated carbon stocks from structural metrics derived from
443 LiDAR and SfM point clouds. Across both dry and wet heathland, volumetric structural
444 metrics derived from point clouds explained a greater proportion of biomass variation
445 and exhibited higher prediction accuracy than the height-based model, indicating their
446 strong potential for predicting AGB. This demonstrates the potential of 3D RS for non-
447 destructive biomass estimation in heathland ecosystems and suggests that
448 incorporating 3D vegetation structure can improve biomass estimation beyond canopy
449 height alone. Nevertheless, height (H95) remained a strong predictor of biomass ($R^2 =$
450 0.94).

451 The inclusion of wet heathland enabled evaluation of whether biomass–structure
452 relationships developed in dry heath were transferable across contrasting heathland
453 types. Although wet heath differed from dry heath in species composition and
454 hydrological conditions, the LiDAR-derived volumetric models showed little evidence of
455 differing biomass–structure relationships between heath types. In contrast, the height-
456 based model showed evidence of differing biomass–height relationships ($p = 0.056$),
457 suggesting that biomass estimates based on canopy height alone may be more

sensitive to variation in vegetation composition and structure. These results indicate that biomass in heathland vegetation is more closely related to total occupied structural volume than to canopy height alone. Height captures maximum canopy but does not represent the vegetation density or internal structural complexity (Dubayah and Drake, 2000; Zolkos et al., 2013). In contrast, volume-based metrics integrate vertical and horizontal extent, as well as vegetation density, providing a more direct representation of the space occupied by biomass (Ni-Meister et al., 2010; Enterkine et al., 2025). The consistent performance of the LiDAR volumetric models across dry and wet heath suggests that 3D structural metrics may provide a more generalisable basis for biomass estimation across heterogeneous heathland systems.

Structural metrics were also scale dependent. This study included a comprehensive evaluation of variation in volume measures depending on selected voxel size which enabled us to identify that optimal model performance occurred at intermediate voxel sizes (0.02 m), whereas finer voxels likely exaggerated small gaps within the vegetation structure. However, this optimal voxel size is likely to be sensor dependent. CHM-derived volumes were less sensitive to pixel size but represent the external canopy envelope rather than internal vegetation structure. These findings highlight the importance of selecting a spatial resolution that appropriately captures vegetation structure when applying 3D RS methods in low-stature shrub systems.

The stronger performance of the LiDAR-derived metrics is likely because of their ability to capture sub-canopy observation at a fine-scale that allows for detailed measures of vegetation structure and vertical complexity while maintaining high mobility in the field. Handheld LiDAR enables vegetation to be scanned from multiple lateral perspectives

481 throughout the canopy profile, reducing occlusion and improving representation of
482 lower vegetation layers that UAV-SfM may underrepresent. Nonetheless, SfM
483 performance remained strong, demonstrating its suitability for non-destructive biomass
484 estimation where LiDAR acquisition is impractical. While traditional height
485 measurements are inexpensive, they are labour-intensive at larger spatial scales and do
486 not capture 3D vegetation structure. SfM offers a more efficient approach for
487 quantifying vegetation volume and structural complexity.

488 While AGC represents only a small component of total heathland carbon stocks, which
489 are typically dominated by soil pools (Duddigan et al., 2024), our focus on the above-
490 ground component enables us to infer how recent vegetative inputs and fire
491 management cycles may influence the whole-ecosystem carbon trajectories. Our
492 results showed an increase in AGB with dry heathland age, reflecting the accumulation
493 of woody biomass over time, consistent with previous observations that biomass
494 increases with successional stage in heathland systems (Hobbs and Gimingham,
495 1984). Soil carbon storage showed a similar pattern, with greater carbon accumulation
496 beneath older heather stands, here indirectly associated with longer periods since fire
497 disturbance.

498 When compared to other heathland ecosystems, the AGC observed in this study fall
499 within a comparable range. For example, Moor House National Nature Reserve, Alday et
500 al., (2015) reported biomass ranging between $6.72 \pm 0.39 \text{ t ha}^{-1}$ and $8.08 \pm 0.80 \text{ t ha}^{-1}$ for
501 stands aged between 16 and 90 years. These values resemble those of the younger
502 stands in the present study ($5.01 \pm 0.55 \text{ t ha}^{-1}$). Surprisingly, biomass of 5-year-old stands
503 was only $0.60 \pm 0.16 \text{ t ha}^{-1}$ in Alday et al., (2015). This pattern was also reflected in the

504 relatively low vegetation, ranging between 35.0 ± 1.3 cm and 37.4 ± 1.2 cm for stands
505 aged between 16 and 90 years. This likely reflects a combination of long-term sheep
506 grazing management and the high elevation of the sites (600–650 m), associated with
507 colder, wetter, and less polluted environmental conditions than other lowland
508 heathlands. Biomass values reported here were generally lower than those recorded in
509 some lowland systems. For example, in the Peak District, 40- to 50-year-old stands
510 reached biomass ranging from 52.40 to 100 t ha^{-1} , whereas stands aged 16 years or
511 younger ranged between 1.32 and 5.17 t ha^{-1} (Harris et al., 2011). Similarly, in Dorset, at
512 an elevation of approximately 60 m, biomass of 14.28 and 18.15 t ha^{-1} was reported for
513 12- and 18-year-old dry heath stands, respectively (Chapman, 1967). Studies in
514 Dartmoor also reported increasing biomass with stand age, ranging from $3.26 \pm 0.45 \text{ t}$
515 ha^{-1} in 2-year-old stands to $22.18 \pm 3.20 \text{ t ha}^{-1}$ in 18-year-old stands, with 6.32 ± 0.85 and
516 $11.15 \pm 2.37 \text{ t ha}^{-1}$ for 6- and 11-year-old stands, respectively.

517 Both Thursley heathland types store significant SOC — dry heath $81.52 \pm 9.99 \text{ t ha}^{-1}$ and
518 wet heath $181.97 \pm 28.08 \text{ t ha}^{-1}$. Compared to Gregg et al., (2021), which reported SOC
519 being 88 t ha^{-1} , 103 t ha^{-1} , 94 t ha^{-1} on different heathland sites, our results showed
520 similar SOC in dry heath and more SOC in wet heath. It's worth noting that we only
521 sampled wet heath to a depth of 15cm. However, wet heath contains large amounts of
522 peaty soils, with depths of over 200cm in the north of the site. With average depths for
523 the wet heath of 49.55 cm (derived from [https://england-peat-map-portal-](https://england-peat-map-portal-ncea.hub.arcgis.com/)
524 [ncea.hub.arcgis.com/](https://england-peat-map-portal-ncea.hub.arcgis.com/)) this extrapolates to $281.85 \text{ t C ha}^{-1}$, based on data extracted
525 from (Vanguelova et al., 2013). Although heathlands have relatively modest vegetation
526 height and biomass compared to forests, these findings demonstrate that undisturbed
527 or longer intervals. However, increasing disturbance intervals must be balanced against

528 the need to prevent scrub and tree encroachment, maintain habitat for specialist
529 species, and reduce the risk of high-severity wildfires. Unlike uncontrolled wildfires,
530 well-managed prescribed burning is carbon neutral, aiming to minimise damage to the
531 organic soil layer, therefore reduce the loss of below-ground carbon. Together, these
532 findings highlight the importance of balancing AGC accumulation with broader
533 ecosystem management objectives when developing heathland management
534 strategies.

535 Conclusion

536 This study provides the first quantitative assessment of AGC in lowland heathlands
537 using non-destructive, high-resolution RS approaches. Handheld SLAM LiDAR
538 demonstrated the strongest predictive performance for estimating carbon stock, while
539 UAV-SfM also produced reliable estimates in structurally simpler vegetation.

540 These findings confirm that lowland heathlands are important in regional carbon
541 storage and climate regulation. The ability to accurately and efficiently measure their
542 carbon stocks using mobile LiDAR offers significant potential for habitat condition
543 monitoring, evaluating management impacts, and integrating carbon accounting into
544 conservation strategies.

545 From a management perspective, the results highlight the trade-offs between
546 biodiversity conservation and carbon storage: traditional interventions such as burning
547 or cutting can temporarily reduce AGC pools but remain vital for maintaining the open
548 structure, species diversity, and long-term ecological resilience of heathlands.
549 Balancing these ecological and climate-related objectives will require adaptive
550 management approaches that safeguard both carbon and biodiversity outcomes.

551 Future work should extend this framework across broader environmental gradients,
552 incorporate below-ground root architecture and soil carbon, and explore temporal
553 monitoring to assess post-management recovery. Integrating handheld LiDAR and UAV-
554 based photogrammetry offers a scalable and repeatable pathway for quantifying carbon
555 stocks in heathlands and other shrub-dominated ecosystems, contributing valuable
556 data to landscape-scale carbon assessments and nature-based climate solutions.

557 Acknowledgements

558 Funding for this study came from Natural England in association with Joint Nature
559 Conservation Committee Air Pollution Recovery Indices. We are ever grateful to J. Giles,
560 the Thursley National Nature Reserve site warden and Natural England who continue to
561 support our science investigations by providing access to the site.

562

563 **Reference**

- 564 Aerts, R., 1989. Aboveground Biomass and Nutrient Dynamics of *Calluna vulgaris* and
565 *Molinia caerulea* in a Dry Heathland. *Oikos* 56, 31–38. <https://doi.org/10.2307/3566084>
- 566 Alday, J.G., Santana, V.M., Lee, H., Allen, K.A., Marrs, R.H., 2015. Above-ground biomass
567 accumulation patterns in moorlands after prescribed burning and low-intensity grazing.
568 *Perspectives in Plant Ecology, Evolution and Systematics* 17, 388–396.
569 <https://doi.org/10.1016/j.ppees.2015.06.007>
- 570 Allen, K.A., Harris, M.P.K., Marrs, R.H., 2013. Matrix modelling of prescribed burning in
571 *Calluna vulgaris*-dominated moorland: short burning rotations minimize carbon loss at
572 increased wildfire frequencies. *Journal of Applied Ecology* 50, 614–624.
573 <https://doi.org/10.1111/1365-2664.12075>
- 574 Arrigoni, E., Hafferty, R.H., Brekke, T., Gebauer, G., Bradshaw, K., Duckett, J.G., Pressel,
575 S., Andrew, C., Bidartondo, M.I., Suz, L.M., Kowal, J., 2026. *Ericoid mycorrhizal fungi*
576 *recover from nitrogen additions in a lowland dry heathland experiment in southern England*
577 *(In preparation)*
- 578 Baggaley, N., Britton, A., Barnes, A., Buckingham, S., Holland, J., Lilly, A., Pakeman, R.,
579 Rees, R., Taylor, A., Yeluripati, J., 2021. Understanding carbon sequestration in upland
580 habitats (Technical Report). The James Hutton Institute. <https://doi.org/10.7488/era/1021>
- 581 Bendig, J., Bolten, A., Bennertz, S., Broscheit, J., Eichfuss, S., Bareth, G., 2014. Estimating
582 Biomass of Barley Using Crop Surface Models (CSMs) Derived from UAV-Based RGB
583 Imaging. *Remote Sensing* 6, 10395–10412. <https://doi.org/10.3390/rs61110395>
- 584 Besl, P.J., McKay, N.D., 1992. A method for registration of 3-D shapes. *IEEE Transactions*
585 *on Pattern Analysis and Machine Intelligence* 14, 239–256.
586 <https://doi.org/10.1109/34.121791>
- 587 Cao, L., Liu, H., Fu, X., Zhang, Z., Shen, X., Ruan, H., 2019. Comparison of UAV LiDAR
588 and Digital Aerial Photogrammetry Point Clouds for Estimating Forest Structural Attributes
589 in Subtropical Planted Forests. *Forests* 10. <https://doi.org/10.3390/f10020145>
- 590 Catchpole, W.R., Wheeler, C.J., 1992. Estimating plant biomass: A review of techniques.
591 *Australian Journal of Ecology* 17, 121–131. [https://doi.org/10.1111/j.1442-](https://doi.org/10.1111/j.1442-9993.1992.tb00790.x)
592 [9993.1992.tb00790.x](https://doi.org/10.1111/j.1442-9993.1992.tb00790.x)
- 593 Chan, E.P.Y., Fung, T., Wong, F.K.K., 2021. Estimating above-ground biomass of
594 subtropical forest using airborne LiDAR in Hong Kong. *Sci Rep* 11, 1751.
595 <https://doi.org/10.1038/s41598-021-81267-8>
- 596 Chapman, S.B., 1967. Nutrient Budgets for a Dry Heath Ecosystem in the South of England.
597 *Journal of Ecology* 55, 677–689. <https://doi.org/10.2307/2258418>
- 598 Chuang, T.-Y., Jaw, J.-J., 2017. Multi-Feature Registration of Point Clouds. *Remote Sensing*
599 9, 281. <https://doi.org/10.3390/rs9030281>

600 Cooper, A., Davess, R., Lockwood, T., Stone, M., Wilkinson, T., Openshaw, I., Morecroft,
601 M., and Moat, J., *Use of Mobile Laser Scanning for Non-destructive Estimation of Hedgerow*
602 *Biomass Carbon Stocks (Under Review)*

603 Cooper, S.D., Roy, D.P., Schaaf, C.B., Paynter, I., 2017. Examination of the Potential of
604 Terrestrial Laser Scanning and Structure-from-Motion Photogrammetry for Rapid
605 Nondestructive Field Measurement of Grass Biomass. *Remote Sensing* 9.
606 <https://doi.org/10.3390/rs9060531>

607 Cunliffe, A.M., Anderson, K., Boschetti, F., Brazier, R.E., Graham, H.A., Myers-Smith, I.H.,
608 Astor, T., Boer, M.M., Calvo, L.G., Clark, P.E., Cramer, M.D., Encinas-Lara, M.S.,
609 Escarzaga, S.M., Fernández-Guisuraga, J.M., Fisher, A.G., Gdulová, K., Gillespie, B.M.,
610 Griebel, A., Hanan, N.P., Hanggito, M.S., Haselberger, S., Havrilla, C.A., Heilman, P., Ji,
611 W., Karl, J.W., Kirchhoff, M., Kraushaar, S., Lyons, M.B., Marzloff, I., Mauritz, M.E.,
612 McIntire, C.D., Metzen, D., Méndez-Barroso, L.A., Power, S.C., Prošek, J., Sanz-Ablanedo,
613 E., Sauer, K.J., Schulze-Brüninghoff, D., Šimová, P., Sitch, S., Smit, J.L., Steele, C.M.,
614 Suárez-Seoane, S., Vargas, S.A., Villarreal, M., Visser, F., Wachendorf, M., Wirnsberger, H.,
615 Wojcikiewicz, R., 2022. Global application of an unoccupied aerial vehicle photogrammetry
616 protocol for predicting aboveground biomass in non-forest ecosystems. *Remote Sensing in*
617 *Ecology and Conservation* 8, 57–71. <https://doi.org/10.1002/rse2.228>

618 Dandois, J.P., Olano, M., Ellis, E.C., 2015. Optimal Altitude, Overlap, and Weather
619 Conditions for Computer Vision UAV Estimates of Forest Structure. *Remote Sensing* 7,
620 13895–13920. <https://doi.org/10.3390/rs71013895>

621 Delalieux, S., Somers, B., Haest, B., Spanhove, T., Vanden Borre, J., Múcher, C.A., 2012.
622 Heathland conservation status mapping through integration of hyperspectral mixture analysis
623 and decision tree classifiers. *Remote Sensing of Environment* 126, 222–231.
624 <https://doi.org/10.1016/j.rse.2012.08.029>

625 Dubayah, R.O., Drake, J.B., 2000. Lidar Remote Sensing for Forestry. *J of* 98, 44–46.
626 <https://doi.org/10.1093/jof/98.6.44>

627 Duddigan, S., Hales-Henao, A., Bruce, M., Diaz, A., Tibbett, M., 2024. Restored lowland
628 heathlands store substantially less carbon than undisturbed lowland heath. *Commun Earth*
629 *Environ* 5, 15. <https://doi.org/10.1038/s43247-023-01176-8>

630 Eitel, J.U.H., Magney, T.S., Vierling, L.A., Greaves, H.E., Zheng, G., 2016. An automated
631 method to quantify crop height and calibrate satellite-derived biomass using hypertemporal
632 lidar. *Remote Sensing of Environment* 187, 414–422.
633 <https://doi.org/10.1016/j.rse.2016.10.044>

634 Enterkine, J., Hojatimalekshah, A., Vermillion, M., Van Der Weide, T., Arispe, S.A., Price,
635 W.J., Hulet, A., Glenn, N.F., 2025. Voxel Volumes and Biomass: Estimating Vegetation
636 Volume and Litter Accumulation of Exotic Annual Grasses Using Automated Ultra-High-
637 Resolution SfM and Advanced Classification Techniques. *Ecol Evol* 15, e70883.
638 <https://doi.org/10.1002/ece3.70883>

639 Forsmoo, J., Anderson, K., Macleod, C.J.A., Wilkinson, M.E., Brazier, R., 2018. Drone-
640 based structure-from-motion photogrammetry captures grassland sward height variability.
641 *Journal of Applied Ecology* 55, 2587–2599. <https://doi.org/10.1111/1365-2664.13148>

642 Frey, J., Kovach, K., Stemmler, S., Koch, B., 2018. UAV Photogrammetry of Forests as a
643 Vulnerable Process. A Sensitivity Analysis for a Structure from Motion RGB-Image Pipeline.
644 *Remote Sensing* 10, 912. <https://doi.org/10.3390/rs10060912>

645 Friggens, N.L., Hester, A.J., Mitchell, R.J., Parker, T.C., Subke, J.-A., Wookey, P.A., 2020.
646 Tree planting in organic soils does not result in net carbon sequestration on decadal
647 timescales. *Global Change Biology* 26, 5178–5188. <https://doi.org/10.1111/gcb.15229>

648 Gimingham, C.H., 1988. A Reappraisal of Cyclical Processes in Calluna Heath. *Vegetatio* 77,
649 61–64.

650 Grace, J., Woolhouse, H.W., 1973. A Physiological and Mathematical Study of the Growth
651 and Productivity of a Calluna-sphagnum Community. III. Distribution of Photosynthate in
652 *Calluna vulgaris* L. Hull. *Journal of Applied Ecology* 10, 77–91.
653 <https://doi.org/10.2307/2404717>

654 Greaves, H.E., Vierling, L.A., Eitel, J.U.H., Boelman, N.T., Magney, T.S., Prager, C.M.,
655 Griffin, K.L., 2015. Estimating aboveground biomass and leaf area of low-stature Arctic
656 shrubs with terrestrial LiDAR. *Remote Sensing of Environment* 164, 26–35.
657 <https://doi.org/10.1016/j.rse.2015.02.023>

658 Gregg, R., Elias, J., Alonso, I., Muto, P., Morecroft, M., 2021. Carbon storage and
659 sequestration by habitat: a review of the evidence (second edition) (No. NERR094), Natural
660 England Research Report. Natural England, York.

661 Haest, B., Borre, J.V., Spanhove, T., Thoonen, G., Delalieux, S., Kooistra, L., Mûcher, C.A.,
662 Paelinckx, D., Scheunders, P., Kempeneers, P., 2017. Habitat Mapping and Quality
663 Assessment of NATURA 2000 Heathland Using Airborne Imaging Spectroscopy. *Remote*
664 *Sensing* 9. <https://doi.org/10.3390/rs9030266>

665 Harris, M.P.K., Allen, K.A., McAllister, H.A., Eyre, G., Le Duc, M.G., Marrs, R.H., 2011.
666 Factors affecting moorland plant communities and component species in relation to
667 prescribed burning. *Journal of Applied Ecology* 48, 1411–1421.
668 <https://doi.org/10.1111/j.1365-2664.2011.02052.x>

669 Hartley, R.J.L., Davidson, S.J., Watt, M.S., Massam, P.D., Aguilar-Arguello, S., Melnik,
670 K.O., Pearce, H.G., Clifford, V.R., 2022. A Mixed Methods Approach for Fuel
671 Characterisation in Gorse (*Ulex europaeus* L.) Scrub from High-Density UAV Laser
672 Scanning Point Clouds and Semantic Segmentation of UAV Imagery. *Remote Sensing* 14,
673 4775. <https://doi.org/10.3390/rs14194775>

674 Heritage, G.L., Large, A.R.G., 2009. Principles of 3D Laser Scanning, in: *Laser Scanning for*
675 *the Environmental Sciences*. John Wiley & Sons, Ltd, pp. 21–34.
676 <https://doi.org/10.1002/9781444311952.ch2>

677 Hobbs, R.J., Gimingham, C.H., 1984. Studies on Fire in Scottish Heathland Communities II.
678 Post-Fire Vegetation Development. *Journal of Ecology* 72, 585–610.
679 <https://doi.org/10.2307/2260069>

680 Horn, B.K.P., 1987. Closed-form solution of absolute orientation using unit quaternions. *J.*
681 *Opt. Soc. Am. A, JOSAA* 4, 629–642. <https://doi.org/10.1364/JOSAA.4.000629>

682 Hosoi, F., Nakai, Y., Omasa, K., 2013. 3-D voxel-based solid modeling of a broad-leaved
683 tree for accurate volume estimation using portable scanning lidar. *ISPRS Journal of*
684 *Photogrammetry and Remote Sensing* 82, 41–48.
685 <https://doi.org/10.1016/j.isprsjprs.2013.04.011>

686 Hout, A.W.V., Choopani, A., Stavrakoudis, D., Witte, W.D., Gitas, I., Meerbeek, K.V.,
687 Ottoy, S., 2025. Estimation of Burned Fuel Volumes in Heathland Ecosystems Using
688 Multitemporal UAV LiDAR and Superpixel Classification. *Drones* 9.
689 <https://doi.org/10.3390/drones9090615>

690 Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004.
691 Review of methods for in situ leaf area index determination: Part I. Theories, sensors and
692 hemispherical photography. *Agricultural and Forest Meteorology* 121, 19–35.
693 <https://doi.org/10.1016/j.agrformet.2003.08.027>

694 Kopittke, G.R., Tietema, A., van Loon, E.E., Kalbitz, K., 2013. The age of managed
695 heathland communities: implications for carbon storage? *Plant Soil* 369, 219–230.
696 <https://doi.org/10.1007/s11104-012-1558-z>

697 Kowal, J., Pino-Bodas, R., Arrigoni, E., Delhay, G., Suz, L.M., Duckett, J.G., Bidartondo,
698 M.I., Pressel, S., 2024. Assessing above and belowground recovery from ammonium sulfate
699 addition and wildfire in a lowland heath: mycorrhizal fungi as potential indicators.
700 *Restoration Ecology* 32, e14096. <https://doi.org/10.1111/rec.14096>

701 Li, A., Glenn, N.F., Olsoy, P.J., Mitchell, J.J., Shrestha, R., 2015. Aboveground biomass
702 estimates of sagebrush using terrestrial and airborne LiDAR data in a dryland ecosystem.
703 *Agricultural and Forest Meteorology* 213, 138–147.
704 <https://doi.org/10.1016/j.agrformet.2015.06.005>

705 Lu, D., 2006. The potential and challenge of remote sensing-based biomass estimation.
706 *International Journal of Remote Sensing* 27, 1297–1328.
707 <https://doi.org/10.1080/01431160500486732>

708 Lu, D., Chen, Q., Wang, G., Liu, L., Li, G., Moran, E., 2016. A survey of remote sensing-
709 based aboveground biomass estimation methods in forest ecosystems. *International Journal of*
710 *Digital Earth* 9, 63–105. <https://doi.org/10.1080/17538947.2014.990526>

711 Lu, N., Zhou, J., Han, Z., Li, D., Cao, Q., Yao, X., Tian, Y., Zhu, Y., Cao, W., Cheng, T.,
712 2019. Improved estimation of aboveground biomass in wheat from RGB imagery and point
713 cloud data acquired with a low-cost unmanned aerial vehicle system. *Plant Methods* 15, 17.
714 <https://doi.org/10.1186/s13007-019-0402-3>

715 Mitchell, R.J., Auld, M.H.D., Le Duc, M.G., Robert, M.H., 2000. Ecosystem stability and
 716 resilience: a review of their relevance for the conservation management of lowland heaths.
 717 *Perspectives in Plant Ecology, Evolution and Systematics* 3, 142–160.
 718 <https://doi.org/10.1078/1433-8319-00009>

719 Mücher, C.A., Kooistra, L., Vermeulen, M., Borre, J.V., Haest, B., Haveman, R., 2013.
 720 Quantifying structure of Natura 2000 heathland habitats using spectral mixture analysis and
 721 segmentation techniques on hyperspectral imagery. *Ecological Indicators, Biodiversity*
 722 *Monitoring* 33, 71–81. <https://doi.org/10.1016/j.ecolind.2012.09.013>

723 Neumann, C., Behling, R., Schindhelm, A., Itzerott, S., Weiss, G., Wichmann, M., Müller, J.,
 724 2020. The colors of heath flowering – quantifying spatial patterns of phenology in *Calluna*
 725 life-cycle phases using high-resolution drone imagery. *Remote Sensing in Ecology and*
 726 *Conservation* 6, 35–51. <https://doi.org/10.1002/rse2.121>

727 Neumann, C., Schindhelm, A., Müller, J., Weiss, G., Liu, A., Itzerott, S., 2021. The
 728 Regenerative Potential of Managed *Calluna* Heathlands—Revealing Optical and Structural
 729 Traits for Predicting Recovery Dynamics. *Remote Sensing* 13.
 730 <https://doi.org/10.3390/rs13040625>

731 Ni-Meister, W., Lee, S., Strahler, A.H., Woodcock, C.E., Schaaf, C., Yao, T., Ranson, K.J.,
 732 Sun, G., Blair, J.B., 2010. Assessing general relationships between aboveground biomass and
 733 vegetation structure parameters for improved carbon estimate from lidar remote sensing.
 734 *Journal of Geophysical Research: Biogeosciences* 115.
 735 <https://doi.org/10.1029/2009JG000936>

736 O'Connor, J., Smith, M.J., James, M.R., 2017. Cameras and settings for aerial surveys in the
 737 geosciences: Optimising image data. *Progress in Physical Geography: Earth and Environment*
 738 41, 325–344. <https://doi.org/10.1177/0309133317703092>

739 Olmeda, C., Šefferová, V., Underwood, E., Millan, L., Gill, T., Naumann, S., 2020. Action
 740 Plan to Maintain and Restore to Favourable Conservation Status the Habitat Type 4030
 741 European Dry Heaths (Report). European Commission, Directorate-General Environment.

742 Pakeman, R.J., Marrs, R.H., 1992. Vegetation development on moorland after control of
 743 *Pteridium aquilinum* with asulam. *Journal of Vegetation Science* 3, 707–710.
 744 <https://doi.org/10.2307/3235839>

745 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P.,
 746 Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J.,
 747 Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C.,
 748 Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter
 749 Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V.,
 750 Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for
 751 standardised measurement of plant functional traits worldwide. *Aust J Bot* 61, 167–234.
 752 <https://doi.org/10.1071/BT12225>

753 Petrov, S., Dimitrov, S., Ihtimanski, I., 2024. Integrated application of geospatial
754 technologies for digital twining of urbanized territories for microscale urban planning, in:
755 Tenth International Conference on Remote Sensing and Geoinformation of the Environment
756 (RSCy2024). Presented at the Tenth International Conference on Remote Sensing and
757 Geoinformation of the Environment (RSCy2024), SPIE, pp. 48–62.
758 <https://doi.org/10.1117/12.3034288>

759 Quin, S.L.O., Artz, R.R.E., Coupar, A.M., Littlewood, N.A., Woodin, S.J., 2014. Restoration
760 of upland heath from a graminoid- to a *Calluna vulgaris*-dominated community provides a
761 carbon benefit. *Agriculture, Ecosystems & Environment* 185, 133–143.
762 <https://doi.org/10.1016/j.agee.2013.12.022>

763 Rautiainen, M., Stenberg, P., Nilson, T., 2005. Estimating canopy cover in scots pine stands.
764 *Silva Fenn.* 39, 137–142. <https://doi.org/10.14214/sf.402>

765 Roth, L., Hund, A., Aasen, H., 2018. PhenoFly Planning Tool: flight planning for high-
766 resolution optical remote sensing with unmanned areal systems. *Plant Methods* 14, 116.
767 <https://doi.org/10.1186/s13007-018-0376-6>

768 Roussel, J.-R. *et al.* (2020) ‘lidR: An R package for analysis of Airborne Laser Scanning
769 (ALS) data’, *Remote Sensing of Environment*, 251, p. 112061. Available at:
770 <https://doi.org/10.1016/j.rse.2020.112061>

771 Schmidt, J., Fassnacht, F.E., Förster, M., Schmidtlein, S., 2018. Synergetic use of Sentinel-1
772 and Sentinel-2 for assessments of heathland conservation status. *Remote Sensing in Ecology*
773 *and Conservation* 4, 225–239. <https://doi.org/10.1002/rse2.68>

774 Schmidt, J., Fassnacht, F.E., Lausch, A., Schmidtlein, S., 2017. Assessing the functional
775 signature of heathland landscapes via hyperspectral remote sensing. *Ecological Indicators* 73,
776 505–512. <https://doi.org/10.1016/j.ecolind.2016.10.017>

777 Snavely, N., Seitz, S.M., Szeliski, R., 2006. Photo tourism: exploring photo collections in 3D.
778 *ACM Trans. Graph.* 25, 835–846. <https://doi.org/10.1145/1141911.1141964>

779 Vanguelova, E.I., Nisbet, T.R., Moffat, A.J., Broadmeadow, S., Sanders, T.G.M., Morison,
780 J.I.L., 2013. A new evaluation of carbon stocks in British forest soils. *Soil Use and*
781 *Management* 29, 169–181. <https://doi.org/10.1111/sum.12025>

782 Wallace, L., Hillman, S., Reinke, K., Hally, B., 2017. Non-destructive estimation of above-
783 ground surface and near-surface biomass using 3D terrestrial remote sensing techniques.
784 *Methods in Ecology and Evolution* 8, 1607–1616. <https://doi.org/10.1111/2041-210X.12759>

785 Ward, S.E., Bardgett, R.D., McNamara, N.P., Adamson, J.K., Ostle, N.J., 2007. Long-Term
786 Consequences of Grazing and Burning on Northern Peatland Carbon Dynamics. *Ecosystems*
787 10, 1069–1083. <https://doi.org/10.1007/s10021-007-9080-5>

788 Westoby, M.J., Brasington, J., Glasser, N.F., Hambrey, M.J., Reynolds, J.M., 2012.
789 ‘Structure-from-Motion’ photogrammetry: A low-cost, effective tool for geoscience
790 applications. *Geomorphology* 179, 300–314. <https://doi.org/10.1016/j.geomorph.2012.08.021>

791 Wijesingha, J., Moeckel, T., Hensgen, F., Wachendorf, M., 2019. Evaluation of 3D point
792 cloud-based models for the prediction of grassland biomass. *International Journal of Applied*
793 *Earth Observation and Geoinformation* 78, 352–359.
794 <https://doi.org/10.1016/j.jag.2018.10.006>

795 Zhu, W., Sun, Z., Peng, J., Huang, Y., Li, J., Zhang, J., Yang, B., Liao, X., 2019. Estimating
796 Maize Above-Ground Biomass Using 3D Point Clouds of Multi-Source Unmanned Aerial
797 Vehicle Data at Multi-Spatial Scales. *Remote Sensing* 11. <https://doi.org/10.3390/rs11222678>

798 Zolkos, S.G., Goetz, S.J., Dubayah, R., 2013. A meta-analysis of terrestrial aboveground
799 biomass estimation using lidar remote sensing. *Remote Sensing of Environment* 128, 289–
800 298. <https://doi.org/10.1016/j.rse.2012.10.017>

801