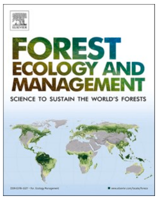
Forest Ecology and Management 605 (2026) 123490

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Structural complexity across a continuum of woodland establishment methods from planting to natural colonisation

Samuel Hughes [a], Thiago S.F. Silva [b,*], Laura Braunholtz [b], Kevin Watts [a,b], Matt Guy [a], Kirsty J. Park [b], Vanessa Burton [c], Marc J. Metzger [d], Julia Koricheva [e], Elisa Fuentes-Montemayor [b]

[a] *Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK*
[b] *Biological and Environmental Sciences, University of Stirling, Scotland FK9 4LA, UK*
[c] *The Woodland Trust, Kempton Way, Grantham, Lincolnshire NG31 6LL, UK*
[d] *School of Geosciences, University of Edinburgh, Edinburgh EH8 9XP, UK*
[e] *Department of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK*

ARTICLE INFO

Keywords:
Woodland creation
Natural colonisation
Tree planting
LiDAR
Structural complexity
Restoration
Forest management

ABSTRACT

Expanding forest and woodland cover is a global strategy to mitigate and adapt to the climate crisis and reverse biodiversity decline. While most woodland in temperate regions is created through tree planting, natural colonisation has been advocated for as an alternative or complementary approach. However, there is limited understanding on how the structural attributes of woodlands created through these different approaches develop through time. To address this knowledge gap, we assessed a suite of structural metrics for 28 woodland sites (aged 13–43 years) that were established along a planted to natural colonisation continuum in England. We used an Uncrewed Aerial System to collect LiDAR data alongside field surveys and calculated metrics relating to above-ground biomass accumulation (canopy height and basal area) and metrics relating to structural complexity (the horizontal and vertical arrangement of canopy) as a proxy for biodiversity potential. Canopy height and basal area were higher in woodlands with larger proportions of planting. Additionally, woodlands with higher proportions of planting displayed greater vertical complexity (canopy stratification) whereas there was weak evidence that woodlands with higher proportions of natural colonisation develop greater horizontal complexity (gap fraction). This suggests that tree planting is the better option when biomass accumulation is the primary goal, whereas natural colonisation or hybrid approaches are likely to be beneficial when the focus is biodiversity or a mix of outcomes. Woodlands created through hybrid approaches that combine planting and natural colonisation offered intermediate values of biomass accumulation and structural complexity.

1. Introduction

There is a global drive to increase forest and woodland cover to reverse centuries of loss and degradation and to respond to the climate and biodiversity crises. This is exemplified by international commitments, such as the 2011 Bonn Challenge to restore 350 million hectares of degraded and deforested lands by 2030 (IUCN, 2020), and the UN Decade on Ecosystem Restoration (2021–2030) (United Nations Environment Agency, 2019). However, the suitability of forest and woodland creation is highly context-dependent (Holl and Brancalion, 2020), and decisions on where, and how, to create forest and woodland will significantly impact development outcomes. For example, forest and woodland can be created through conventional tree planting, allowing trees to establish through natural processes, or using hybrid approaches which combine the two. Woodland is a standard term for forest in Britain and will be used hereafter.

Woodland creation through planting has many benefits, for example, it is a reliable process (Fox et al., 2007; Fuentes-Montemayor, Park, et al., 2022) that can increase biodiversity when targeted and managed effectively (Fuentes-Montemayor et al., 2020; Hughes et al., 2023; Lima and Vieira, 2013). However, natural colonisation, where trees colonise and establish through natural processes, is receiving increasing attention as a large-scale woodland creation strategy in temperate regions (Acuña-Míguez et al., 2024; Bauld et al., 2023; Porton et al., 2024).

---

* Corresponding author.
E-mail address: thiago.sf.silva@stir.ac.uk (T.S.F. Silva).

https://doi.org/10.1016/j.foreco.2025.123490

There are many potential benefits to using natural colonisation to create woodlands: (1) the strategy is cost- and resource-effective (Campanhã Bechara et al., 2021); (2) local trees are well suited to their environment which promotes resilience (Chazdon and Guariguata, 2016); and (3) there is no risk of disease spreading through imported planting materials (Di Sacco et al., 2021). Earlier research suggests that naturally colonised woodlands are expected to be more biodiverse and resilient than planted woodlands due to their higher structural complexity (Chazdon and Guariguata, 2016; Siminski et al., 2021) whereas planted woodlands often comprise even-aged trees with minimal variation across their canopies during early stages (Fuentes-Montemayor, Park, et al., 2022).

However, there are challenges in using natural colonisation as a woodland creation approach. A study by Bauld et al. (2023) identified 90 naturally colonised woodlands across the UK, all aged ~20 years and created on a variety of former land-use types. Results showed that in areas located more than 100 m away from existing seed sources the resulting woodlands rarely exceeded 100 trees ha^{-1}. The authors also found that the outcomes of natural colonisation were hugely variable, with some sites completely failing to establish while others were successful.

Hybrid approaches, which combine tree planting (e.g. in spatially-discrete blocks, spatially-mixed in small clusters, or low-density planting) with natural colonisation, have been proposed to overcome the challenges of utilising natural processes while maintaining many of the benefits (Corbin and Holl, 2012; Kikuchi et al., 2024). Work in the tropics has shown hybrid approaches to be much cheaper than tree planting while achieving similar results (Campanhã Bechara et al., 2021; Corbin and Holl, 2012). However, no work has explored the development of hybrid woodlands at appropriate scales in temperate regions, where much of global woodland creation is taking place. Furthermore, there have been no efforts to compare the structural attributes of woodlands created through planting, natural colonisation or hybrid approaches.

One reason for this lack of evidence is that quantitatively describing the structure of woodland creation sites across appropriate spatial scales is costly and time intensive when employing traditional inventory techniques. However, in recent years Uncrewed Aerial Systems (UAS; 'drones') have been deployed to collect Light Detection and Ranging (LiDAR) data through laser scanning technologies (de Almeida et al., 2020). Entire woodland stands can be scanned in single flight missions to produce whole-site, high density point clouds, while field surveys rely on smaller scale plot-level sampled measurements to represent sites. In fact, LiDAR-derived structural metrics have the potential to relate more accurately to ecological processes than field-based measurements (McNeil et al., 2023).

In the first instance LiDAR-derived point clouds can be used to obtain canopy height measurements by subtracting the ground height (interpolated from ground returns) from each point (Mielcarek et al., 2018). LiDAR can further be used to derive a suite of metrics relating to different aspects of structural diversity - the volumetric capacity, physical arrangement, and identity of biotic components (LaRue, Fahey, et al., 2023). For example, LiDAR can effectively measure canopy gaps, a measure of horizontal structural complexity (Dalagnol et al., 2021) and Foliage Height Diversity (FHD), an entropy-based index of vertical structural complexity (Clawges et al., 2008).

Our study combines high density UAS-based LiDAR scanning (ULS) data with in-situ inventory data to quantify structural differences between woodlands created through planting, natural processes and hybrid approaches in England, UK. Specifically, we quantify metrics relating to canopy height, basal area, canopy openness, and structural complexity, to test two main hypotheses: 1) Planted woodlands will be taller, have higher basal area, and lower canopy openness than hybrid and naturally colonised woodlands. This is because planted woodlands are not limited by dispersal and establishment, since they are given a 'head start'; 2) Sites with a higher proportion of natural colonisation will be more structurally complex in both vertical and horizontal dimensions, due to the gradual and patchy colonisation and establishment of trees across the site from nearby seed sources.

2. Material and methods

2.1. Study design

Twenty-eight broadleaf woodland creation sites across England were selected (Fig. 1). Potential sites were located using the Woodland Grant Scheme database (Forestry Commission, 2025) with woodlands that had "New Natural Regeneration" contracts shortlisted as potential hybrid and natural colonisation sites and woodlands that had "New Planting" contracts as potential planted sites. Permission to carry out research was granted by all landowners prior to the start of surveys.

Sites that met the selection criteria (10 + years since woodland establishment; ≥1 ha in area; ≥1 km distance from other selected sites; in close proximity to established woodland) were identified using historical aerial imagery in Google Earth Pro and the 1990 Land Cover Map (Rowland et al., 2020) and finally chosen to achieve greatest spatial coverage of England while ensuring logistical feasibility. The selected 28 woodlands covered a range of ages (13–43 years since establishment) and sizes (1–18.2 ha). All were located on low elevation sites (10–170 m.a.s.l.) that were previously improved grassland or arable land and adjacent to established woodlands. For all woodland sites, the proportion of the site left to natural colonisation was estimated using historical satellite imagery from around the point of woodland establishment, based on the presence of rows of saplings. Polygons were drawn around areas of natural colonisation and the area of these polygons was taken as a proportion of the total site area. Sites with no natural colonisation were categorised as planted sites, sites with complete

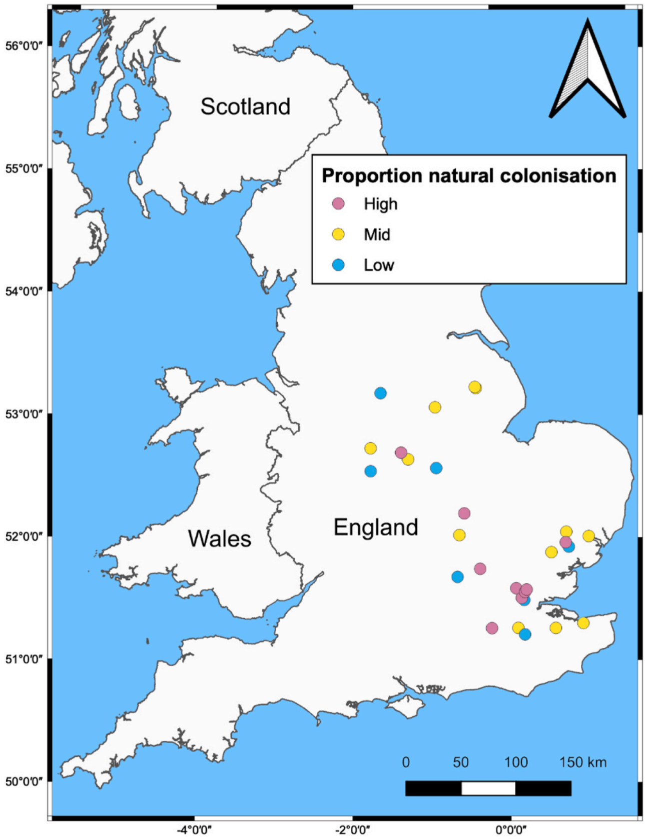


Fig. 1. A map showing the locations of nine woodlands created through natural colonisation (pink circles), seven planted woodlands (blue circles) and twelve woodlands created through hybrid approaches (yellow circles). All woodlands were located in England.

natural colonisation as natural colonisation sites, and sites with a mix of natural colonisation and planting (anywhere between a 1 and 0 proportion of natural colonisation) as hybrid sites. The proportion of natural colonisation in hybrid sites ranged from 0.1 to 0.98. Our final sample comprised seven planted sites, nine naturally colonised sites, and 12 hybrid sites (SI table 1).

2.2. Field data collection

Field surveys took place in summer of 2023. At each site, between three and five circular plots with 10 m radius were established (Fig. 2). Plot centres, a minimum of 30 m apart, were generated prior to fieldwork using random point generators within the site polygons (QGIS v3.10.4). A 10 m buffer around the site perimeter was used to ensure plots did not capture woodland edges. Within each 10 m radius plot, all tree stems with diameter at breast height (DBH; 1.3 m above ground) $\geq$ 7 cm were identified and their DBH was measured. This was used to calculate basal area (BA), with BA = (DBH)ˆ2 * 0.00007854 (Edwards, 1998).

2.3. LiDAR data processing

We used a UAS to generate 3D point cloud models of woodland structure across the whole site. Our system comprised of a DJI Matrice 300 RTK drone equipped with a DJI Zenmuse L1 airborne laser scanner (https://www.dji.com/support/product/zenmuse-l1). Each site was surveyed from a height of 80 m above the ground, at an average speed of 5 m/s and using 50 % track overlap, during August of 2023. We set the LiDAR sensor to recording dual LiDAR returns, at a frequency of 240khz. This combination of flight and sensor parameters yielded an average point density of 700–1000 returns/m^2. Each flight was supported by a ground GNSS station (DJI D-RTK2) operating in Real Time Kinematic (RTK) mode to ensure consistency in the flight trajectory.

The raw GNSS data acquired by the ground base station was processed using Emlid Studio (https://emlid.com/emlid-studio/) to determine the accurate geographic location of the base. For that, the base station logs were processed in Post-Processed Kinematic (PPK) mode, using as reference data the nearest OS Net ground station (Ordnance Survey of the UK, https://osdatahub.os.uk/downloads/osnet). This ensured positional accuracies of + - 5 cm.

Once the absolute position of each ground base station was determined, the raw LiDAR data was reconstructed using the DJI Terra V3.6 software (DJI, 2025), using the point-cloud optimization option of the DJI software. The reconstructed point clouds were exported in LAS format, using the Ordnance Survey National Grid (OSGB) horizontal coordinate system (EPSG 27700) and the European Vertical Reference System (EVRS) 2019 as height reference.

Fig. 2. An example of 10 m radius sampling plots laid out in one of the woodland study sites.

After reconstruction all point cloud processing was done using the R package *LidR* version 4.1.0 (Roussel et al., 2020) in R version 4.3.1. First, all point clouds were normalised so that the height of all points was relative to the ground below them. To do this, ground returns were classified using a progressive morphological filter (window size = 20, threshold = 0.2) and then Digital Terrain Models (DTMs) were created using a kriging algorithm (k = 50). Finally, DTM values were subtracted from each point to normalize the point cloud.

2.4. Structural metrics

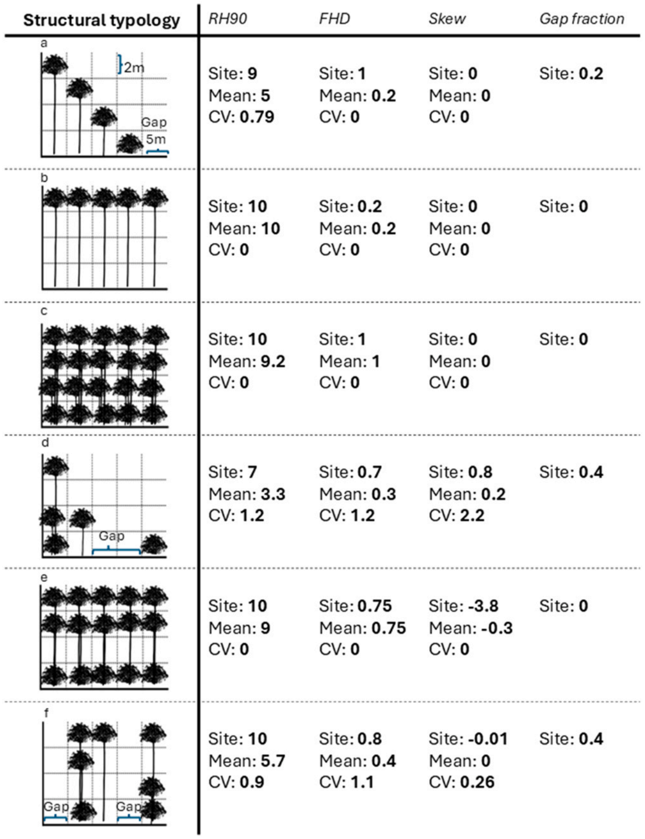
There are myriad metrics which can be extracted from point cloud data (LaRue et al., 2022). However, because our study focuses on comparing woodland creation approaches primarily aimed at accumulating biomass and/or enhancing biodiversity, we chose metrics to reflect this. This included canopy height, which alongside field derived basal area is a proxy of above-ground biomass (Lang et al., 2016), and Foliage Height Diversity (FHD), skewness of the height distribution, and gap fraction as proxies of structural diversity – a known driver of biodiversity (Fuentes-Montemayor, Watts, et al., 2022; LaRue, Downing, et al., 2023; LaRue, Fahey, et al., 2023). Except for basal area, which was derived from field plot measurements, all variables were derived from the LiDAR scans.

Canopy height was calculated as the height of the 90th percentile of the maximum height of point returns (rh90) and basal area was aggregated to site level as the mean and coefficient of variation (cv) of basal area m^2 ha^{-1} across all field plots. FHD was calculated as a modified Shannon's evenness index using the leaf area density (LAD) of 2 m height bins (stratified canopy layers). High FHD values mean that points are evenly distributed across all available height bins (available height bins include any below the maximum canopy height). A highly positive skew represents most foliage occurring in the shrub layer with a few very tall trees skewing the distribution upwards, while a highly negative skew indicates most foliage occurring in a tall canopy layer with a few shrubs in the understory layer. Finally, canopy gap fraction was calculated using the *gap_detection* function from the *LidaRtRee* (Monnet, 2025) package. Here we defined a gap as any 5 m^2 contiguous area lower than 1 m in height. This strict definition reflects the age of our woodlands and the fact that we aimed to detect areas where trees have failed to establish and not areas where trees are slow to develop.

For metrics which aggregate information from sub canopy layers, FHD and Skew, we used Leaf Area Density (LAD) profiles instead of raw point clouds. This is to correct for dense top canopies occluding subcanopy foliage. The LAD for each height bin is calculated by taking the number of returns as a proportion of the number of returns to reach the respective height bin or lower. It is then corrected for using an extinction coefficient of 1 to account for how light is absorbed as it moves through the canopy (Bouvier et al., 2015).

All LiDAR metrics were first calculated at the site level using the entire point cloud, and from hereon are referred to as 'Site <Metric> '. Additionally, rh90, FHD, and Skewness were also gridded at a 5 m pixel resolution to better understand horizontal variability within sites. These variables are referred to as 'Gridded <Metric> '. From the gridded values both the mean and cv were extracted to help us gain a fuller understanding of how structure varied horizontally within sites. Structural typologies are displayed in Fig. 3 alongside how they may alter structural metrics.

We chose to calculate both site-level metrics and gridded metrics as focusing only on site-level metrics can disguise meaningful variation within sites. For example, Fig. 3a shows how a high site rh90 may disguise gridded variation in height – its site level rh90 value is large even though many columns have short canopies. Furthermore, site FHD can be driven by either canopy stratification (high mean FHD, e.g.



Structural typology	RH90	FHD	Skew	Gap fraction
a	Site: **9** Mean: **5** CV: **0.79**	Site: **1** Mean: **0.2** CV: **0**	Site: **0** Mean: **0** CV: **0**	Site: **0.2**
b	Site: **10** Mean: **10** CV: **0**	Site: **0.2** Mean: **0.2** CV: **0**	Site: **0** Mean: **0** CV: **0**	Site: **0**
c	Site: **10** Mean: **9.2** CV: **0**	Site: **1** Mean: **1** CV: **0**	Site: **0** Mean: **0** CV: **0**	Site: **0**
d	Site: **7** Mean: **3.3** CV: **1.2**	Site: **0.7** Mean: **0.3** CV: **1.2**	Site: **0.8** Mean: **0.2** CV: **2.2**	Site: **0.4**
e	Site: **10** Mean: **9** CV: **0**	Site: **0.75** Mean: **0.75** CV: **0**	Site: **-3.8** Mean: **-0.3** CV: **0**	Site: **0**
f	Site: **10** Mean: **5.7** CV: **0.9**	Site: **0.8** Mean: **0.4** CV: **1.1**	Site: **-0.01** Mean: **0** CV: **0.26**	Site: **0.4**

Fig. 3. A graphical representation of six structural typologies alongside how they may impact the relevant metrics. Metrics (excluding gap fraction) are calculated at the site level, as a mean of gridded values (5 m resolution), and as the coefficient of variation (cv) of gridded values.

Fig. 3c), or variation in canopy top height (low mean FHD, e.g. Fig. 3a). Finally, site skewness can equal 0, even when there is heavy localised skewness within the site (e.g. Fig. 3f). By calculating gridded metrics, we can understand both site level and within site structural variation.

2.5. Data analysis

We tested for structural differences between woodland creation approaches using generalised linear models assuming either normal or beta-distributed errors depending on the response variable. We used the R package *GLMMTMB* (Brooks et al., 2017). All models included two continuous predictors, the proportion of each site left to natural colonisation (proportion NC) and site age. Proportion NC was always 0 for planted sites and 1 for naturally colonised sites but varied along a continuum for hybrid sites. An interaction term between site age and proportion NC was also included to account for differing rates of structural development along the proportion NC continuum. If this interaction term was not statistically significant it was removed from the model. Total rh90 and skewness alongside their respective means, and basal area were tested assuming normally distributed errors. Total FHD and its mean, alongside Gap fraction were tested assuming beta distributed errors as these are proportional responses. Gap fraction was transformed using the following Eq. (1) to deal with 0 s and 1 s, which the beta regression is unable to handle. Here, x is the gap fraction value and N is the studies sample size (28).

$$\frac{x(N-1)+0.5}{N-1} \tag{1}$$

All cv metrics were logged to ensure model predictions and standard errors did not stray below 0. All data analysis was done using R version 4.4.1.

Finally, our results are interpreted following the framework of the language of evidence suggested by Muff et al. (2022).

3. Results

Our results provide strong evidence that woodlands with a lower proportion of natural colonisation accumulate biomass more quickly than fully naturally colonised woodlands, indicated here by site canopy height (rh90), mean gridded canopy height (mean rh90), and mean basal area $m^2\ ha^{-1}$(Table 1; Fig. 4). Furthermore, there is strong evidence that site FHD is higher in sites with lower proportions of natural colonisation than in sites with higher proportions of natural colonisation (Table 1; Fig. 4). There was no evidence that gridded mean FHD cv FHD, or cv RH90 varied with the proportion of natural colonisation.

There is weak evidence that site skewness is more positive in sites with a higher proportion of natural colonisation (Table 1; Fig. 4; Fig. 5 for visualisation) which suggests these sites have fewer tall trees and a higher proportion of foliage in the subcanopy layer (e.g. Fig. 3d). This is considered weak evidence as the global model predicting site level skewness had a p value of 0.15 (Table 1). There is no evidence that mean skew or cv skew varies with the proportion of natural colonisation.

Gap fraction decreased with age regardless of woodland creation method. There is also weak evidence showing that gap fraction is higher in sites with higher proportions of natural colonisation (Table 1; Fig. 4). Examples of high gap fraction can be seen in Figs. 3d and 3f, where trees have not yet established across the entire site. An example of low gap fraction can be seen in Fig. 3c where trees have established across the whole site.

4. Discussion

4.1. Structural differences between woodland creation strategies

Using laser scanning technology, we have revealed differences in structure between woodlands created through different establishment methods. Metrics relating to above-ground biomass increased with age at higher rates in planted sites and in hybrid sites with lower percentages of natural colonisation. In fact, basal area and canopy height increased extremely slowly in naturally colonised sites, which concurs with results from other temperate studies which show naturally colonised woodlands to take decades to develop (Bauld et al., 2023; Pedersen et al., 2023). However, this contrasts with studies from the tropics, which show significant short-term above ground biomass gains in naturally colonised sites (Siminski et al., 2021), although these still lag behind planted sites in the same region (Holl et al., 2020). These differences exemplify the context dependency of woodland creation through natural processes.

We found weak evidence that woodlands with higher proportions of natural colonisation display greater horizontal variability and strong evidence that woodlands with higher proportions of planting have higher vertical complexity but are more uniform horizontally. These results concur with previous research showing how the natural colonisation process varies broadly with distance to seed source (Bauld et al., 2023). Even after dispersal limitations are overcome, a range of factors, such as low microsite quality or herbivory, can further constrain the successful establishment of naturally colonising trees (Hulme, 1996; Porton et al., 2024). These factors cause significant spatial autocorrelation in the successful establishment of trees across natural colonisation sites (You-zhi and Zheng-quan, 2000) leading to the observed horizontal variation in the present study.

This variability has been shown to manifest both within and among natural colonisation sites as trees readily colonise certain sites and not others (Bauld et al., 2023). Work in the tropics has shown how hybrid approaches can help to overcome this variability while still maintaining the cost effectiveness of natural processes (Campanhã Bechara et al.,

Table 1
Results reported from models testing how structural metrics differ by woodland creation strategy (Prop NC), woodland age, and the interaction between these two. Where interaction terms were $p < 0.05$ they were removed. Models with proportional responses assumed beta distributed errors. P values are highlighted as *** for $p < = 0.001$, ** for $p < = 0.01$, and * for $p < = 0.05$. if a response was estimated on a log scale it is denoted by superscript. Ferrari's pseudo R squared was used for beta distributed generalized linear models. Variable abbreviations are explained in Section 2.5 of the main text.

Response	Model P	Residual DF	R^2 (Ferarri's)	Predictor	Estimate (SE)	P
Gap fraction	*	23	0.29	Age	-0.05 (0.02)	**0.026***
				Prop NC	0.5 (0.3)	0.094
cvBA^{log}	.	24	0.03	Age	0 (0)	0.941
				Prop NC	0.06 (0.07)	0.427
cvFHD^{log}	.	24	0.04	Age	0 (0)	0.379
				Prop NC	0 (0.01)	0.689
cvRH90^{log}	.	24	0.12	Age	0 (0)	0.253
				Prop NC	0.06 (0.04)	0.134
cvSkew^{log}	.	24	0.05	Age	0 (0)	0.399
				Prop NC	-0.02 (0.03)	0.448
meanBA	**	23	0.39	Age	1.45 (0.47)	**0.005****
				Prop NC	23.07 (12.61)	0.08
				Age:Prop NC	-1.26 (0.56)	**0.032***
meanFHD	.	23	0.13	Age	0.02 (0.01)	0.097
				Prop NC	-0.25 (0.17)	0.155
meanRH90	**	23	0.43	Age	0.67 (0.17)	**< 0.001*****
				Prop NC	12.84 (4.65)	**0.011***
				Age:Prop NC	-0.64 (0.2)	**0.005****
meanSkew	.	24	0.18	Age	-0.01 (0.01)	0.072
				Prop NC	0.13 (0.09)	0.135
SiteFHD	*	23	0.21	Age	0.03 (0.01)	0.072
				Prop NC	-0.44 (0.22)	0.047
SiteRH90	***	23	0.51	Age	0.8 (0.2)	**< 0.001*****
				Prop NC	13.29 (5.27)	**0.019***
				Age:Prop NC	-0.71 (0.23)	**0.006****
SiteSkew	.	24	0.15	Age	0 (0.02)	0.952
				Prop NC	0.49 (0.24)	**0.049***

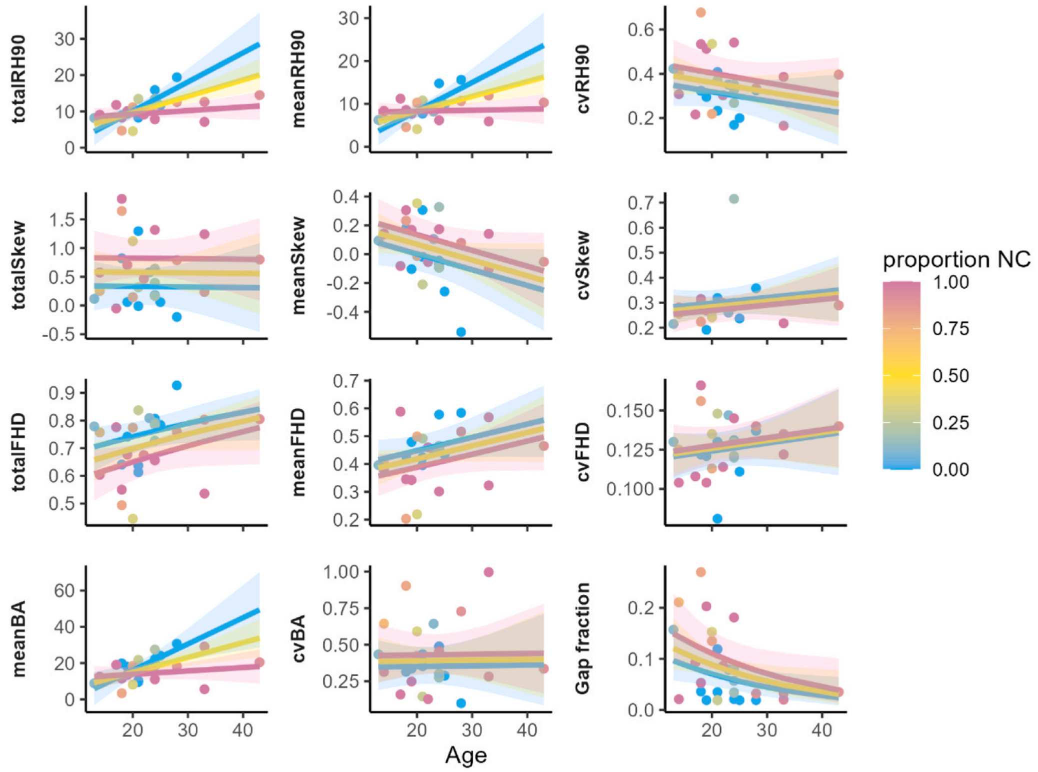


Fig. 4. Conditional effect scatter plots and model predictions with 95 % confidence intervals showing how a range of structural metrics (canopy height (RH90), Foliage Height Diversity (FHD), skewness, gap fraction, and basal area) vary with site age and the proportion of natural colonisation within a site. Predictions were chosen at 0, 0.5, and 1 proportion natural colonisation to illustrate conditional model effects, however in the model this was a continuous predictor ranging between 0 and 1.

2021; Corbin and Holl, 2012). Our results support these findings and suggest that hybrid approaches can be used to reduce uncertainty if land managers desire more predictable outcomes from their woodland creation endeavours.

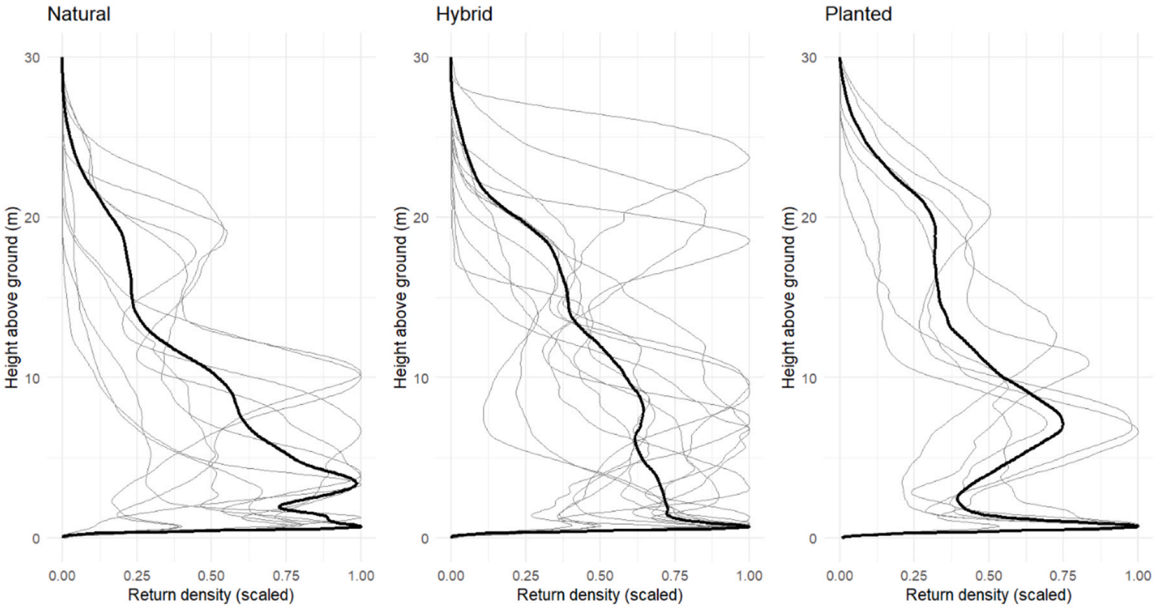


Fig. 5. Vertical return density plots (filtered for heights > 0.5 m) for naturally colonised, hybrid and planted woodland sites. Thin grey lines represent individual sites, and thick black lines show the average density for all woodlands of the same woodland establishment type. Natural colonisation sites all had 100 % natural colonisation, planted sites all had 0 % natural colonisation, hybrid sites ranged between 10 % and 98 % natural colonisation.

Differences in structure can also be caused by differences in tree species composition (Pretzsch and Schütze, 2016). The tree communities in planted woodlands are more controlled by land managers whereas the tree communities of naturally colonised woodlands are driven by the local species pool and dispersal capabilities (Butaye et al., 2002). Therefore, this is another likely mechanism for differences in structural outcomes between woodland creation strategies. Tree species communities from our study sites are being analysed as part of broader biodiversity assessments (ongoing work by the authors).

4.2. The benefits of UAS LiDAR for woodland restoration monitoring

There have been recent calls to utilise UAS laser scanning in woodland restoration monitoring to collect highly detailed structural data across large areas (de Almeida et al., 2020; Shokirov et al., 2022). Studies from Brazil have shown that these data can distinguish between management practices and track structural development in recently restored tropical stands (Almeida et al., 2019). Our study further demonstrates the utility of UAS laser scanning for monitoring the restoration of native broad-leaved woodlands in temperate regions. While field-based measurements (e.g. basal area in our case) could only characterize a small portion of each site, using data derived from UAS laser scanning we were able to quantitatively describe entire sites in less than an hour (with additional processing time of around 30 min per site) yielding high density 3D point clouds from which a range of ecologically meaningful metrics can be calculated.

4.3. Limitations

Our study focused on young woodlands of a relatively small age range (13–43 years since establishment), which to an extent limits our view of how structural development may vary among woodland creation approaches over longer periods. Research which looked at the structural development of planted broadleaf woodlands in temperate regions, showed that it can take in excess of 80 years for woodland creation sites to develop structural attributes similar to those of mature ancient woodlands (Fuentes-Montemayor, Park, et al., 2022). This previous research found that woodland creation sites displayed similar vegetation development patterns to those described for other woodland systems. It may be that woodlands established through different approaches vary across all stages of development in different ways. It would be particularly interesting to know how the structure of these sites develops as they reach maturity (Broughton et al., 2021), and the ease and low cost of UAS laser scanning opens up the possibility for continued monitoring of woodland development over time.

4.4. Implications

The results presented here are of great relevance to woodland creation practitioners and policymakers (Ambrose-Oji et al., 2025). We show that different woodland creation approaches along the planting to natural colonisation continuum have different structural outcomes, each of which may be better suited to specific objectives. For example, if the intention is to create a productive woodland, or to accumulate above ground biomass quickly, then tree planting may be the preferred approach, as this results in taller canopies and higher basal area. If a woodland is being created to increase biodiversity, then the vertical complexity provided by planted woodlands may provide more niches for woodland specific species (Lindenmayer et al., 2003); however, we provide some evidence that horizontal variation is greater in naturally colonised sites which would likely provide a mosaic of open and closed habitats allowing the coexistence of woodland species and open habitat species, thus further enhancing biodiversity (Smith et al., 2007). Hybrid approaches appear to offer an intermediate alternative between natural colonisation and conventional tree planting, and by controlling how much of a site is left to natural colonisation practitioners can direct the woodland creation process to the balance between biomass accumulation and heterogeneity that best suits their intended outcomes. Understanding this variability of outcomes also has implications for woodland creation grants, which should provide flexibility for using a range of approaches for a range of objectives.

CRediT authorship contribution statement

Elisa Fuentes-Montemayor: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Samuel Hughes:** Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Vanessa Burton:**

Writing – review & editing, Project administration. **Kirsty J Park:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Julia Koricheva:** Writing – review & editing, Funding acquisition. **Marc J Metzger:** Writing – review & editing, Funding acquisition. **Laura Braunholtz:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation. **Thiago SF Silva:** Writing – review & editing, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Matt Guy:** Writing – review & editing, Methodology, Conceptualization. **Kevin Watts:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Elisa Fuentes-Montemayor reports financial support was provided by UK Research and Innovation. Thiago Sanna Freire Silva reports administrative support and article publishing charges were provided by University of Stirling. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Megan Layton and Billy Dykes for assistance with field surveys, Heather Gilbert, Bianca Ambrose-Oji, Rachel Orchard and Susannah Fleiss for their contributions to the Treescape Expansion through Planting and Natural Colonisation (TreE_PlaNat) project, National Forest Company, Woodland Trust and other land owners for granting us permission to conduct surveys on their land, and UKRI's Future of UK Treescapes Programme for their financial support (grant number NE/X004619/1).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123490.

Data availability

Data will be made available on request.

References

Acuña-Míguez, B., Rincón, A., Valladares, F., Cordero, I., Bravo-Oviedo, A., 2024. Natural forest colonisation as a management strategy to restore soil functioning of abandoned agricultural lands. J. Appl. Ecol. 61, 2690–2700. https://doi.org/10.1111/1365-2664.14780.

Almeida, D.R.A., Stark, S.C., Chazdon, R., Nelson, B.W., Cesar, R.G., Meli, P., Gorgens, E. B., Duarte, M.M., Valbuena, R., Moreno, V.S., Mendes, A.F., Amazonas, N., Gonçalves, N.B., Silva, C.A., Schietti, J., Brancalion, P.H.S., 2019. The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. For. Ecol. Manag. 438, 34–43. https://doi.org/10.1016/j.foreco.2019.02.002.

de Almeida, D.R.A., Stark, S.C., Valbuena, R., Broadbent, E.N., Silva, T.S.F., de Resende, A.F., Ferreira, M.P., Cardil, A., Silva, C.A., Amazonas, N., Zambrano, A.M. A., Brancalion, P.H.S., 2020. A new era in forest restoration monitoring. Restor. Ecol. 28 (1), 8–11. https://doi.org/10.1111/rec.13067.

Ambrose-Oji, B., Pearson, M., Spencer, K., Colley, E., Guy, M., Watts, K., 2025. Tree planting, natural colonisation, hybrid approaches: land manager decisions explored. People Nat. https://doi.org/10.1002/pan3.70071.

Bauld, J., Guy, M., Hughes, S., Forster, J., Watts, K., 2023. Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. Restor. Ecol. 31 (8), e14004. https://doi.org/10.1111/rec.14004.

Bouvier, M., Durrieu, S., Fournier, R.A., Renaud, J.-P., 2015. Generalizing predictive models of forest inventory attributes using an area-based approach with airborne LiDAR data. Remote Sens. Environ. 156, 322–334. https://doi.org/10.1016/j.rse.2014.10.004.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9 (2). https://doi.org/10.32614/RJ-2017-066.

Broughton, R.K., Bullock, J.M., George, C., Hill, R.A., Hinsley, S.A., Maziarz, M., Melin, M., Mountford, J.O., Sparks, T.H., Pywell, R.F., 2021. Long-term woodland restoration on lowland farmland through passive rewilding. PloS One 16 (6), e0252466.

Butaye, J., Jacquemyn, H., Honnay, O., Hermy, M., 2002. The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. J. Veg. Sci. 13 (1), 27–34. https://doi.org/10.1111/j.1654-1103.2002.tb02020.x.

Campanhã Bechara, F., Trentin, B.E., Lex Engel, V., Estevan, D.A., Ticktin, T., 2021. Performance and cost of applied nucleation versus high-diversity plantations for tropical forest restoration. For. Ecol. Manag. 491. https://doi.org/10.1016/j.foreco.2021.119088.

Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48 (6), 716–730. https://doi.org/10.1111/btp.12381.

Clawges, R., Vierling, K., Vierling, L., Rowell, E., 2008. The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. Remote Sens. Environ. 112 (5), 2064–2073. https://doi.org/10.1016/j.rse.2007.08.023.

Corbin, J.D., Holl, K.D., 2012. Applied nucleation as a forest restoration strategy. For. Ecol. Manag. 265, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013.

Dalagnol, R., Wagner, F.H., Galvão, L.S., Streher, A.S., Phillips, O.L., Gloor, E., Pugh, T.A. M., Ometto, J.P.H.B., Aragão, L.E.O.C., 2021. Large-scale variations in the dynamics of Amazon forest canopy gaps from airborne lidar data and opportunities for tree mortality estimates. Sci. Rep. 11 (1), 1388. https://doi.org/10.1038/s41598-020-80809-w.

Di Sacco, A., Hardwick, K.A., Blakesley, D., Brancalion, P.H.S., Breman, E., Cecilio Rebola, L., Chomba, S., Dixon, K., Elliott, S., Ruyonga, G., Shaw, K., Smith, P., Smith, R.J., Antonelli, A., 2021. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. Glob. Change Biol. 27 (7), 1328–1348. https://doi.org/10.1111/gcb.15498.

DJI, 2025. DJI TERRA. 〈https://enterprise.dji.com/dji-terra〉.

Edwards, P.N., 1998. Timber Measurement: A Field Guide. Forestry Commission.

Forestry Commission, 2025. Woodl. Gd. Scheme 3 Engl. 〈https://www.data.gov.uk/dataset/e59087ff-8a1c-46da-abae-324cec3f7852/woodland-grant-scheme-3-england〉.

Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. J. For. 105 (7), 337–347. https://doi.org/10.1093/jof/105.7.337.

Fuentes-Montemayor, E., Ferryman, M., Watts, K., Macgregor, N.A., Hambly, N., Brennan, S., Coxon, R., Langridge, H., Park, K.J., 2020. Small mammal responses to long-term large-scale woodland creation: the influence of local and landscape-level attributes. Ecol. Appl. 30 (2), e02028. https://doi.org/10.1002/eap.2028.

Fuentes-Montemayor, E., Park, K.J., Cordts, K., Watts, K., 2022. The long-term development of temperate woodland creation sites: from tree saplings to mature woodlands. Forestry 95 (1), 28–37. https://doi.org/10.1093/forestry/cpab027.

Fuentes-Montemayor, E., Watts, K., Sansum, P., Scott, W., Park, K.J., 2022. Moth community responses to woodland creation: the influence of woodland age, patch characteristics and landscape attributes. Divers. Distrib. 28 (9), 1993–2007. https://doi.org/10.1111/ddi.13599.

Holl, K.D., Brancalion, P.H.S., 2020. Tree planting is not a simple solution. Science 368 (6491), 580–581. https://doi.org/10.1126/science.aba8232.

Holl, K.D., Reid, J.L., Cole, R.J., Oviedo-Brenes, F., Rosales, J.A., Zahawi, R.A., 2020. Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. J. Appl. Ecol. 57 (12), 2316–2328. https://doi.org/10.1111/1365-2664.13684.

Hughes, S., Kunin, W., Ziv, G., Watts, K., 2023. Spatial targeting of woodland creation can reduce the colonisation credit of woodland plants. Ecol. Solut. Evid. 4 (3). https://doi.org/10.1002/2688-8319.12263.

Hulme, P.E., 1996. Natural Regeneration of Yew (Taxus baccata L.): microsite, Seed or Herbivore Limitation? J. Ecol. 84 (6), 853–861. https://doi.org/10.2307/2960557.

IUCN, 2020. BONN Chall. 〈https://www.bonnchallenge.org/〉.

Kikuchi, T., Seidel, D., Ehbrecht, M., Zemp, D.C., Brambach, F., Irawan, B., Sundawati, L., Hölscher, D., Kreft, H., Paterno, G.B., 2024. Combining planting trees and natural regeneration promotes long-term structural complexity in oil palm landscapes. For. Ecol. Manag. 569. https://doi.org/10.1016/j.foreco.2024.122182.

Lang, M., Lilleleht, A., Neumann, M., Bronisz, K., Rolim, S.G., Seedre, M., Uri, V., Kiviste, A., 2016. Estimation of above-ground biomass in forest stands from regression on their basal area and height. For. Stud. 64, 70–92. https://doi.org/10.1515/fsmu-2016-0005.

LaRue, E.A., Downing, A.G., Saucedo, S., Rocha, A., Zesati, S.A.V., Mata-Silva, V., Harvey, M.G., 2023. Diversity – volume relationships: adding structural arrangement and volume to species – area relationships across forest macrosystems. Ecography 2023 (10). https://doi.org/10.1111/ecog.06723.

LaRue, E.A., Fahey, R.T., Alveshere, B.C., Atkins, J.W., Bhatt, P., Buma, B., Chen, A., Cousins, S., Elliott, J.M., Elmore, A.J., Hakkenberg, C.R., Hardiman, B.S., Johnson, J. S., Kashian, D.M., Koirala, A., Papeş, M., St Hilaire, J.B., Surasinghe, T.D., Zambrano, J., Fei, S., 2023. A theoretical framework for the ecological role of three-dimensional structural diversity. Front. Ecol. Environ. 21 (1), 4–13. https://doi.org/10.1002/fee.2587.

LaRue, E.A., Fahey, R., Fuson, T.L., Foster, J.R., Matthes, J.H., Krause, K., Hardiman, B. S., 2022. Evaluating the sensitivity of forest structural diversity characterization to LiDAR point density. Ecosphere 13 (9). https://doi.org/10.1002/ecs2.4209.

Lima, T.A., Vieira, G., 2013. High plant species richness in monospecific tree plantations in the Central Amazon. For. Ecol. Manag. 295, 77–86. https://doi.org/10.1016/j.foreco.2013.01.006.

Lindenmayer, D.B., R. J, H., Salt, D., 2003. Plantation forests and biodiversity conservation. Aust. For. 66 (1), 62–66. https://doi.org/10.1080/00049158.2003.10674891.

McNeil, D.J., Fisher, G., Fiss, C.J., Elmore, A.J., Fitzpatrick, M.C., Atkins, J.W., Cohen, J., Larkin, J.L., 2023. Using aerial LiDAR to assess regional availability of potential habitat for a conservation dependent forest bird. For. Ecol. Manag. 540, 121002. https://doi.org/10.1016/j.foreco.2023.121002.

Mielcarek, M., Stereńczak, K., Khosravipour, A., 2018. Testing and evaluating different LiDAR-derived canopy height model generation methods for tree height estimation. Int. J. Appl. Earth Obs. Geoinf. 71, 132–143. https://doi.org/10.1016/j.jag.2018.05.002.

Monnet, J.-M., 2025. lidaRtRee: forest analysis with airborne laser scanning LiDAR data. Rech. Data Gouv. https://doi.org/10.57745/JV66MZ.

Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. Trends Ecol. Evol. 37 (3), 203–210. https://doi.org/10.1016/j.tree.2021.10.009.

Pedersen, N.K., Schmidt, I.K., Kepfer-Rojas, S., 2023. Drivers of tree colonization, species richness, and structural variation during the initial three decades of natural forest colonization in abandoned agricultural soils. For. Ecol. Manag. 543, 121138. https://doi.org/10.1016/j.foreco.2023.121138.

Porton, G., Wrigley, R., Scott, C.E., Spracklen, D.V., 2024. Natural colonisation rates in a UK upland landscape under different conservation management approaches following sheep removal. Ecol. Solut. Evid. 5 (2). https://doi.org/10.1002/2688-8319.12338.

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. Issue 1. In: In European Journal of Forest Research, 135. Springer Verlag, pp. 1–22. https://doi.org/10.1007/s10342-015-0913-z. Issue 1.

Roussel, J.-R., Auty, D., Coops, N.C., Tompalski, P., Goodbody, T.R.H., Meador, A.S., Bourdon, J.-F., de Boissieu, F., Achim, A., 2020. lidR: an R package for analysis of Airborne Laser Scanning (ALS) data. Remote Sens. Environ. 251, 112061. https://doi.org/10.1016/j.rse.2020.112061.

Rowland, C.S., Marston, C.G., Morton, R.D., 2020. Land cover map 1990 (25 m raster, GB), version 2. Natural Environment Research Council, Swindon, UK. https://doi.org/10.5285/1be1912a-916e-42c0-98cc-16460fac00e8.

Shokirov, S., Jucker, T., Levick, S.R., Manning, A.D., Bonnet, T., Yebra, M., Youngentob, K.N., 2022. Habitat highs and lows: using terrestrial and UAV LiDAR for modelling avian species richness and abundance in a restored woodland. Remote Sens. Environ. 285 (10). https://doi.org/10.1016/j.rse.2022.113326ï.

Siminski, A., Zambiazi, D.C., dos Santos, K.L., Fantini, A.C., 2021. Dynamics of natural regeneration: implications for landscape restoration in the Atlantic Forest, Brazil. Front. For. Glob. Change 4. https://doi.org/10.3389/ffgc.2021.576908.

Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S., Mitchell, F.J.G., 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. Biol. Conserv. 136 (2), 283–294. https://doi.org/10.1016/j.biocon.2006.12.001.

United Nations Environment Agency, 2019. Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021-2030). ⟨Https://Undocs.Org/A/RES/73/284⟩.

You-zhi, H., Zheng-quan, W., 2000. Effect of spatial heterogeneity on natural regeneration of Manchurian ash. J. For. Res. 11 (2), 89–94. https://doi.org/10.1007/BF02856680.