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Effects of deer on woodland structure revealed through terrestrial laser scanning

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Summary

1. Terrestrial laser scanning (TLS) captures the three-dimensional structure of habitats. Compared to traditional methods of forest mensuration, it allows quantification of structure at increased resolution, and the derivation of novel metrics with which to inform ecological studies and habitat management.

2. Lowland woodlands in the UK have altered in structure over the last century due to increased abundance of deer and a decline in management. We compared whole-canopy profiles between woodlands with high (>10 deer km^{-2}) and low deer density (c. 1 deer km^{-2}), and in stands with and without records of management interventions in the last 20 years, providing a test case for the application of TLS in habitat assessment for conservation and management.

3. Forty closed-canopy lowland woodlands (height range 16·5–29·4 m) were surveyed using TLS in two regions of the UK, divided into areas of high- and low-deer abundance, and between plots which had been recently managed or were unmanaged. Three-dimensional reconstructions of the woodlands were created to document the density of foliage and stem material across the entire vertical span of the canopy.

4. There was a 68% lower density of understorey foliage (0·5–2 m above-ground) in high-deer woodlands, consistent in both regions. Despite this, total amounts of foliage detected across the full canopy did not differ between deer density levels. High-deer sites were 5 m taller overall and differed in the distribution of foliage across their vertical profile. Managed woodlands, in contrast, exhibited relatively minor differences from controls, including a lower quantity of stem material at heights from 2 to 5 m, but no difference in foliage density. All main effects were replicated equally in both regions despite notable differences in stand structures between them.

5. *Synthesis and applications*. Terrestrial laser scanning allows ecologists to move beyond two-dimensional measures of vegetation structure and quantify patterns across complex, heterogeneous, three-dimensional habitats. Our findings suggest that reduction of deer populations is likely to have a strong impact on woodland structures and aid in restoring the complex understorey habitats required by many birds, whereas management interventions as currently practiced have limited and inconsistent effects.

Key-words: deer browsing, foliage profile, forest canopy, forest management, forest structure, forest understorey, LiDAR, oak, woodland management

Introduction

Deer densities in north-temperate forests are at extraordinarily high levels (Côté *et al.* 2004; Takatsuki 2009; McShea 2012). This is due to a combination of factors including the absence of large predators, a decline in hunting pressure, concentration of populations in habitat fragments and the widespread invasion of non-native, smaller deer species such as Chinese muntjac *Muntiacus reevesi* Ogilby 1839 (Côté *et al.* 2004; Dolman & Wäber 2008). In Britain, increases in woodland area and autumn

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sowing of crops providing winter forage are likely to be locally influential (Fuller & Gill 2001). The increased density of deer has direct impacts on the structure of forests, most markedly through the creation of browse lines where edible foliage has been removed from the understorey, and the imposition of severe recruitment limitation on trees, whose seedlings are damaged and unable to establish (Côté *et al.* 2004; Gill & Morgan 2010). Damage is also often caused to the bark of standing trees (Gill 1992). The removal of gap-colonising seedlings increases understorey light levels, favouring the growth of herbaceous plants that subsequently impede tree regeneration (Royo & Carson 2006).

Across Europe, increasing deer densities have occurred alongside a decline in woodland management, particularly over the course of the last century (Rackham 2003). Within British woodlands there is concern that their structure may have been systematically altered, with reductions in understorey vegetation driven by an interaction between increased deer browsing and greater shading from fully closed canopies (Fuller *et al.* 2007). Management to modify forest structure has been carried out in Europe for at least 4500 years (Stephenson & Harrison 1992). Traditional objectives were the promotion of favoured species for food, fuel and timber. More recently there has been a growing focus on conservation and the maintenance of traditional landscapes, and much discussion regarding the best means of achieving conservation goals through woodland structural management (Kirby & Watkins 2015).

Changes in deer abundance and management have both direct and indirect effects on forest structure and composition, and thereby for the many species that live on and around trees. Documentation of changes in forest structure has been constrained by a tool set which represents our terrestrial viewpoint (McElhinny *et al.* 2005; Newton 2007). Typical parameters measured include the diameter and spatial distribution of stems, with the vertical dimension captured by coarse metrics such as tree height or canopy openness. Quantitative estimates such as foliage height diversity, while often applied, suffer from a lack of standardisation within the literature (McElhinny *et al.* 2005). The development of airborne remote-sensing technology has provided new perspectives whose scale and resolution continue to increase (Davies & Asner 2014). Nevertheless, given that the majority of woodland species live beneath the canopy and experience habitat heterogeneity at highly localised scales, there is a need to capture and describe forest understorey structure with greater detail.

Terrestrial laser scanning (TLS) provides an opportunity to visualise the three-dimensional properties of forests at high resolution (Dassot, Constant & Fournier 2011). In doing so, it allows not only for measurement of standard parameters with greater accuracy but also for the creation of new metrics which capture additional aspects of forest structure (Newnham *et al.* 2015). These have provided fresh insights into the factors determining the distribution, abundance and diversity of a range of species (Davies & Asner 2014). TLS data can therefore be used to inform site managers as to the impacts of interventions, disturbances or other drivers of forest structure.

In this study, we used TLS to capture the three-dimensional structures of 40 woodland plots in Britain. This formed part of a larger research project investigating the implications of forest structure for the conservation of woodland birds (Fuller *et al.* 2007, 2014), with the aim of developing a tool to inform management decisions both at local (woodland) and landscape scales. In order to assess the impacts of two major forces known to influence forest structure, we sampled plots from regions of high- and low-deer abundance, and with and without records of recent management interventions. Our *a priori* expectation was that high deer density would be associated with a reduction in low-level foliage due to browsing. Due to the relative novelty of our methods, however, we did not formulate explicit predictions for all factors, and instead use our work as an exploratory investigation. The study highlights the potential of TLS to describe and compare forest stands, with broad applications. Accurate quantification of the magnitude and vertical range of differences in forest structures can be used to inform management practices and support biodiversity priorities.

Materials and methods

PLOT SELECTION

This work was undertaken as part of a broader project examining bird communities and vegetation in 300 study plots in two regions of Britain – the Weald and the Welsh Marches (see Fig. S1, Supporting Information; Fuller *et al.* 2014). A subsample of comparable plots were identified as potentially suitable for TLS. Criteria for inclusion were (i) mature, closed-canopy broadleaved forest; (ii) availability of an initial deer density estimate and record of management interventions; (iii) road access to allow transport of survey equipment; and (iv) a minimum 1 km distance among plots to reduce spatial autocorrelation of main effects. Management was characterised based on explicit documentation of interventions (or lack thereof) at the stand level within the last 20 years; in the majority of cases this implied stand thinning, although detailed records of protocols or intensity were seldom available. Deer densities were initially classified as high or low.

From this subsample of plots a selection of 40 plots was made to enable a fully factorial comparison among regions, management type and deer density. In several cases a site was deemed unsafe to access on inspection in the field and was therefore replaced with the nearest suitable plot from a predetermined shortlist. This led to a minor imbalance in the factor groups (see Table S1 for plot details). Although some plots were within the same named wood, the minimum distance of 1 km apart was a more important criterion, as in the Weald there were numerous small woods close together. The majority of plots were in oak-dominated forest (*Quercus* spp.; 35), with the remainder dominated by birch (*Betula* spp.; 2), ash (*Fraxinus excelsior*; 2) or mixed (1).

High- and low-deer sites were confirmed by concurrent deer surveys (see Appendix S1). In four cases, direct deer surveys did not take place in the woods themselves (Ampfield, Ellenden, Haugh Wood, Lea and Pagets Wood); classification was therefore based on proximity to other woods from which data were available. High deer densities (>10 deer km^{-2}) were consistent with those reported in other studies (e.g. Tanentzap *et al.* 2011). Low-deer densities did not exceed 1·2 deer km^{-2}. Fallow deer *Dama dama* Linnaeus 1758 were the dominant species (>85%), although counts included roe *Capreolus capreolus* Linnaeus 1758 and muntjac.

To examine whether underlying edaphic trends might be responsible for any covariance between forest structural attributes and the factors under study, we obtained data on soil nutrient regime and soil moisture regime for the grid reference of each plot from the Soil Survey 1 : 250K map of England and Wales (http://www.landis.org.uk/).

SURVEY PROTOCOL

Woods were surveyed from 4 June to 30 June 2013 by two people. An average of two transects were completed per working day. Within each compartment a randomly situated 10 × 50-m transect was surveyed. Start points were located using a Garmin handheld GPS receiver (accuracy c. 20 m). Unusual topographic features or obstacles (e.g. large boulders) were avoided and a new location selected.

Surveys were conducted using a FARO Focus 3D 125 scanner set to allow data to be collected at a point separation of 7·67 mm at 10 m distance (beam diameter was c. 4 mm at 10 m and c. 6 mm at 20 m). This ensured that all measured points within 10 m of the scanner were collected at a higher spatial resolution than required for division into 1 cm^3 voxels. Point spacing began to exceed 10 mm at distances of 13 m from the scanner. At 25 m from the scanner, point spacing from any single scanning location was 33 mm, sufficient to enable broad-scale description of canopy structure.

The scanner was placed at 10-m intervals along each edge of the transect, offset by 5 m on alternate sides, giving a minimum of 11 scans per transect. This ensured complete coverage within the plot of <1·0 cm beam spacing up to 10 m from scan locations. The default scanner height was 1·3 m, although this was reduced as necessary when obstacles prevented a clear line of sight. In order to register all of the scans in a single point cloud, targets were positioned throughout the survey area, placed so as to be visible from adjacent scan locations. Three targets were used to link adjacent scans, two outside the plot (to reduce shadowing of points) and one inside. Purpose-built targets were used at approximate heights of 50, 100 and 125 cm.

Full colour panoramic photographs were recorded at each scan location using the FARO Focus 3D internal camera and used for visual comparison with the computer reconstructions to ensure that they had accurately captured the overall structure.

DATA PROCESSING

An approach to data processing was taken which minimised manual input and allowed extraction of relevant features of forest structure using only a standard desktop computer. Data were initially filtered to remove isolated points or those with low reflectance values using the default filters in FARO Scene 4.8 (FARO Technologies, Lake Mary, FL, USA). Datasets were then trimmed to include only points within the 10×50-m transect. An initial digital terrain model (DTM) was created in ArcMap based upon the lowest recorded points within coarse 3-m grid cells, which were judged to represent the ground surface, and from which a triangulated irregular network was generated. This was repeated with a finer 0·5 m grid. Where dense understory is present, laser beams may not penetrate to the ground surface, and overestimation of ground height can occur (Ashcroft, Gollan & Ramp 2014). To identify these areas, the difference between the coarse and fine grids was examined, and those smaller grid squares for which a height increase exceeding 5 cm was observed were visually inspected. If dense understorey vegetation was the likely cause then the value from the larger square was used to generate the DTM, otherwise the finer grid value was taken. The DTM was used to convert all points from a height relative to the scanner to height above-ground, facilitating structural analysis. Points representing survey apparatus were removed manually.

A specimen plot is shown in Fig. 1; note the intrusion of canopies from outside the vertical edges of the plot. Where points could be matched with visual spectrum returns they have been coloured to aid inspection.

Point clouds were resampled to 1 cm^3 voxels using Pointools v1.5 (Bentley Systems Inc., Exton, PA, USA). They were processed in 10-cm height bands, divided into five 10 × 10 m

Fig. 1. Illustration of typical output obtained from terrestrial laser scanning in Ampfield wood (compartment 3), an oak-dominated stand in the Weald, c. 50 years old, managed, with high deer density. Points are coloured based on visual spectrum returns. Points which could not be matched with a colour are shown as white.

subsections to capture within-plot variance. Classification of voxels as stem or leaf was based on the expected higher density of returns in the vertical axis from stems relative to leaves (Côté *et al.* 2009) using the point density tool within ArcGIS (ESRI version 10.3, Redlands, CA, USA). Voxels were assessed within 10-cm vertical columns. Those with a point density of at least 4·0 were classified as stem material, those below as leaves. Selection of this parameter was a manual, iterative process, validated by comparison with visual spectrum returns (see Appendix S2 for further details).

The basic level of analysis was the subplot slice, giving a volume of $10 \times 10 \times 0{\cdot}1$ m $= 10$ m^3 and counting the number of filled voxels within. Note that the density of stem points is an estimate of stem surface area rather than volume. This means that it is not a straightforward estimate of total woody biomass as it can be confounded by stem size distributions and the angles of branches, especially at greater heights. Its interpretation is based upon the assumption that, because the composition of stands was broadly similar, trees in all plots would exhibit similar growth forms. Our intention was to capture the habitat surface area as experienced by birds and other organisms rather than tree biomass.

The vertical profile was split into subsections for initial analysis. Returns below 50 cm in height were considered unreliable due to occlusion by overlapping layers of dense foliage, and also contained very high variance, making patterns among plots difficult to discern. They were therefore excluded, which means that all subsequent interpretation is based on material above 50 cm. The remainder of the profile was split into height classes defined as understorey (0·5–2 m), shrub layer (2–5 m), subcanopy (5–10 m) and canopy (>10 m). These classes were chosen based on disjunctions in the variance profile with height across all plots (see Fig. 2).

With our methodology it is not possible to distinguish voxels which are empty from those which are occluded. Results from higher in the canopy are therefore likely to be confounded by the blocking effect of material at lower levels. Furthermore, the intensity of scanning means that, from 13 m above-ground, not all 1 cm^3 voxels will have been scanned. The results should therefore be seen as effectively complete for layers up to 10 m but a partial sample above. This still enables overall patterns to be assessed, and in more detail than permitted by conventional ground-based methods.

Full-canopy profiles are not directly comparable between plots as variation in total height overwhelms internal differences in structure. Whole canopy structures were therefore compared on the basis of height-adjusted profiles, scaled from 0 to 1, with the maximum height taken as the mean of the highest 10 points in each subplot. Points below 50 cm were removed, and points with relative heights above 1 excluded to avoid distortion by extreme outliers.

STATISTICAL ANALYSIS

Variation in maximum canopy height among subplots was assessed using a linear mixed-effects model with main effects and two-way interactions among region, deer and management, and a random effect of plot.

The distribution of foliage and stem material thoughout the vertical profile of woodlands follows a nonlinear pattern for which there was no *a priori* expectation. These trends were therefore analysed within a Generalised Additive Mixed Modelling (GAMM) framework using the mgcv package in R3.3.1 (Wood 2006; Zuur *et al.* 2009; R Core Team 2016), in which a flexible penalised regression spline was fit to the vertical trend with an arbitrarily high number of potential degrees of freedom. Models investigated whether a consistent spline was present in all forests, or whether splines varied with region, deer density or management practices. Main effects of region, deer density and management were also considered to assess overall changes in total foliage or stem, and interactions among these main effects. Numbers of returns per slice were $\log_{10}(x+1)$ transformed. Models included random intercepts for each plot, and a variance covariate for the interaction between region and deer density. Multiple variance covariates were considered but the region × deer effect consistently provided the greatest improvement to the fit of models (this reflects the division of plots as shown in Fig. S1). The basic model can be expressed as:

$$D_{ijk} = \alpha + f_x(\mathrm{height}_k) + \mathrm{deer}_j + \mathrm{management}_j + \mathrm{region}_j + a_j + \varepsilon_{ijk}$$
$$\varepsilon_{ijk} \sim (0, \sigma^2_{\mathrm{region}\times\mathrm{deer}})$$

where D is the density of returns per subplot slice, i is the subplot slice, j is the plot, α is a random intercept and k is the canopy height. The smoothing function f_x allows for different smoothers per factor group x (one of either height, deer or management). Analyses first considered whether different smoothers between factor groups were supported, and selected the best-performing model using Akaike's information criterion. This process was then repeated for all main effects. Table 1 presents a summary of the final best-fit models. Full model output for all main effects is provided in Appendix S3. In the results we show model estimates for foliage and stem density combined with empirical measurements at each height band. Graphs of GAMM smoothers display relative density of foliage or stem with height compared to the average value for the height range under study. This provides a clearer representation of differences in the shapes of smoothers between factor groups and is shown for comparison in Appendix S4.

Results

Scans revealed that plots contained a median density of leaves of 523 cm^3 m^{-3} [457–615 inter-quartile range (IQR)], or 0·052% of the total forest volume, as measured by the occupied 1 cm^3 voxels. This is a minimum estimate given that leaves higher in the canopy may not have been detected due to the blocking effect of material beneath them. Median stem surface density across plots was an order of magnitude lower at 49 cm^3 m^{-3} (43–61 IQR).

Forest stands varied in average height from 29·4 m (Wyre Main Block 1) to 16·5 m (West Blean Block 4). No differences in overall height were found between managed and unmanaged plots [likelihood ratio (LR) <0·1, d.f. = 1, $P = 0{\cdot}944$], and although forests in the Welsh Marches were slightly taller than those in the Weald (22·8 ± 0·8 m to 21·0 ± 0·9 m, means ± SE), this was only a marginal effect (LR = 3·9, d.f. = 1, $P = 0{\cdot}048$). A much greater difference in height was observed between high and low deer density forests. High-deer forests averaged 24·4 ± 0·8 m in height, whereas low-deer forests

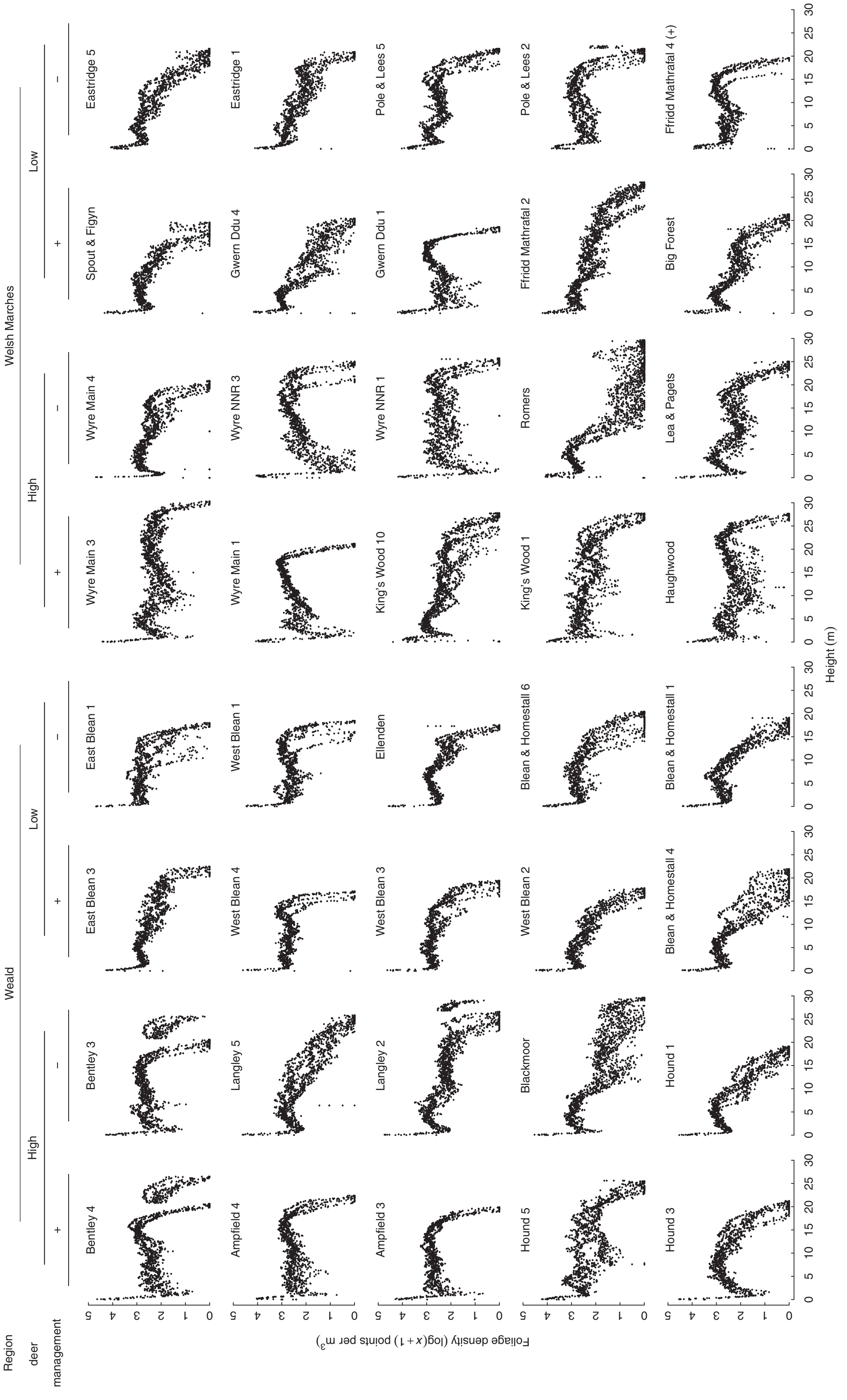

Fig. 2. Foliage density (number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$ scale with increasing height in the canopy of each plot; each 0·1 m height band is represented by five 10 × 10 × 0·1 m slices. Plot names as Table S1. Note that Ffrith Mathrafal 4 was managed.

Table 1. Summary of Generalised Additive Mixed Model outputs for foliage and stem distribution within height bands (0·5–2 m understorey; 2–5 m shrub layer; 5–10 m subcanopy; >10 m canopy) and across the whole canopy profile (normalised by total height). Each GAMM contained a single factor determining spline shape, marked with a dot, plus tests for main effects of deer, region and management. Differences in the best-supported model are given as percentage change relative to the intercept (low deer, Weald, unmanaged). W.M., Welsh Marches. Full details of final model outputs for all main effects are shown in Appendix S3 with GAMM smoothers plotted in Appendix S4

		Splines			Main effects			
Height (m)	Feature	Deer	Region	Management	Deer (high)	Region (W.M.)	Management	R^2
0·5–2	Foliage		•		−68%			0·373
0·5–2	Stem		•					0·124
2–5	Foliage	•						0·065
2–5	Stem	•					−19%	0·161
5–10	Foliage			•		−32%		0·171
5–10	Stem		•					0·216
>10	Foliage	•			+119%			0·264
>10	Stem		•		+137%			0·157
Full profile	Foliage	•						0·212
Full profile	Stem		•					0·435

were 5 m shorter at 19·4 ± 0·6 m (LR = 23·0, d.f. = 1, $P < 0·001$). The absence of a significant interaction between region and deer in the final model demonstrates that this pattern was consistent in both regions. High- and low-deer sites did not differ in soil nutrient regime ($F_{1,39} = 0·44$, $P = 0·512$); nor were there any differences between the two regions ($F_{1,39} < 0·01$, $P \approx 1·000$). A similar pattern emerged with soil moisture regime, which did not differ between deer densities ($F_{1,39} = 0·01$, $P = 0·941$) nor regions ($F_{1,39} = 0·39, P = 0·539$).

Overall patterns for foliage (Fig. 2) and stem material (Fig. 3) indicated the presence of substantial variation across the height range as well as among plots. Initial analyses therefore focussed on sections of the full height profile. These were defined as understorey (0.5–2 m), shrub layer (2–5 m), subcanopy (5–10 m) and canopy (>10 m).

VERTICAL SECTIONS

Median foliage densities were broadly comparable in the understorey (438 $cm^3\ m^{-3}$, 219–710 IQR), shrub layer (614 $cm^3\ m^{-3}$, 354–901 IQR) and subcanopy (398 $cm^3\ m^{-3}$, 210–656 IQR) across all plots. The trend was somewhat different for stem surfaces, for which values declined markedly from understorey (101 $cm^3\ m^{-3}$, 69–137 IQR) to shrub layer (62 $cm^3\ m^{-3}$, 42–86 IQR) and subcanopy (19 $cm^3\ m^{-3}$, 7–38 IQR). Overall values in the canopy cannot readily be compared due to heterogeneity in maximum height both between and within plots.

The final model for understorey foliage from 0·5 to 2 m above-ground included different smoothers for forests in the Weald and the Welsh Marches (Fig. 4a,b) and a greater overall quantity of foliage in low-deer forests (Table 1). This was evident from a predicted understorey foliage volume of 189 $cm^3\ m^{-3}$ in high-deer plots compared to 607 $cm^3\ m^{-3}$ in low-deer plots (back-transformed model means; see Appendix S3 for estimates with associated errors). There were no significant overall effects of either region or management on total foliage quantity. The final model explained over a third of the variance within the data (estimated $R^2 = 37·3\%$).

The analysis for understorey stem data provides a useful comparator. No differences were anticipated with deer density because deer do not directly browse stem material. In line with this expectation, there was once again a difference between regions in the shape of the smoother for stem distribution with height (Fig. 4c,d) but no significant main effect of deer on overall quantity of stem material, nor of either region or management. The explanatory power of the model was weak, in accordance with the limited number of effects exhibited (estimated $R^2 = 12·4\%$).

In the shrub layer, from 2 to 5 m in height, there were significantly different smoothers for foliage density in forests with high and low deer density (Table 1). There were, however, no overall changes in the amount of foliage with region, deer or management, and the model had limited explanatory power (estimated $R^2 = 6·5\%$). A similar pattern emerged for stem material within the same height range, with differences among deer densities in the pattern of distribution. In this case, however, there was also a significant main effect of management, with slightly lower amounts of stem in managed plots. The explanatory power of the model was, however, modest (estimated $R^2 = 16·1\%$).

From 5 to 10 m, representing the subcanopy, models suggest different smoothing functions for foliage in woodlands with or without records of recent management (Table 1). An additional main effect of region highlighted a lower total quantity of foliage in plots in the Welsh Marches. When considering stem material, different smoothers were supported in each region, but no main effects of any variable were detected. Models in each case were of reasonable explanatory power, accounting for 17·1% and 21·6% of the variance, respectively, reflecting

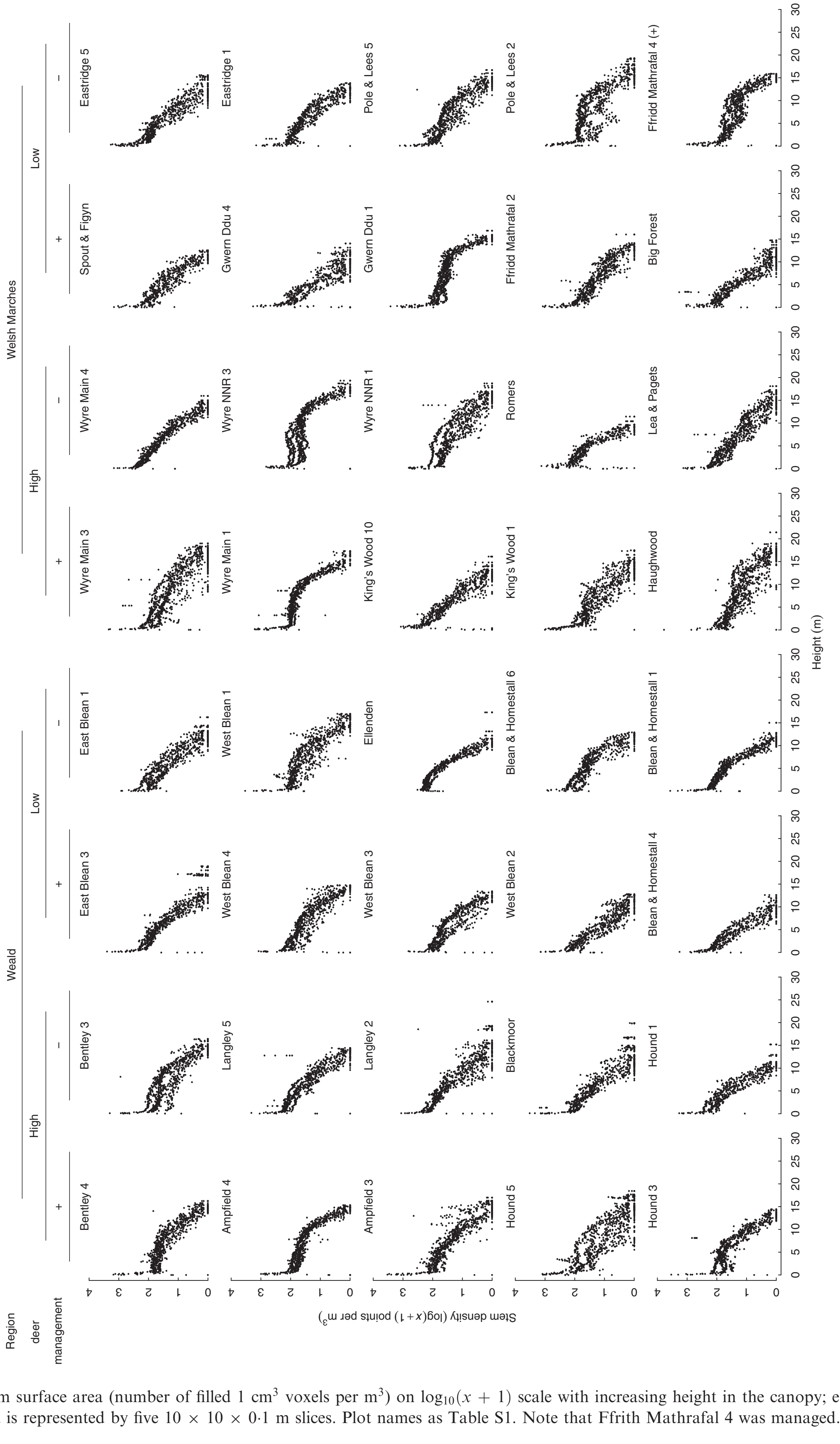

Fig. 3. Stem surface area (number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$ scale with increasing height in the canopy; each 0·1 m height band is represented by five 10 × 10 × 0·1 m slices. Plot names as Table S1. Note that Ffrith Mathrafal 4 was managed.

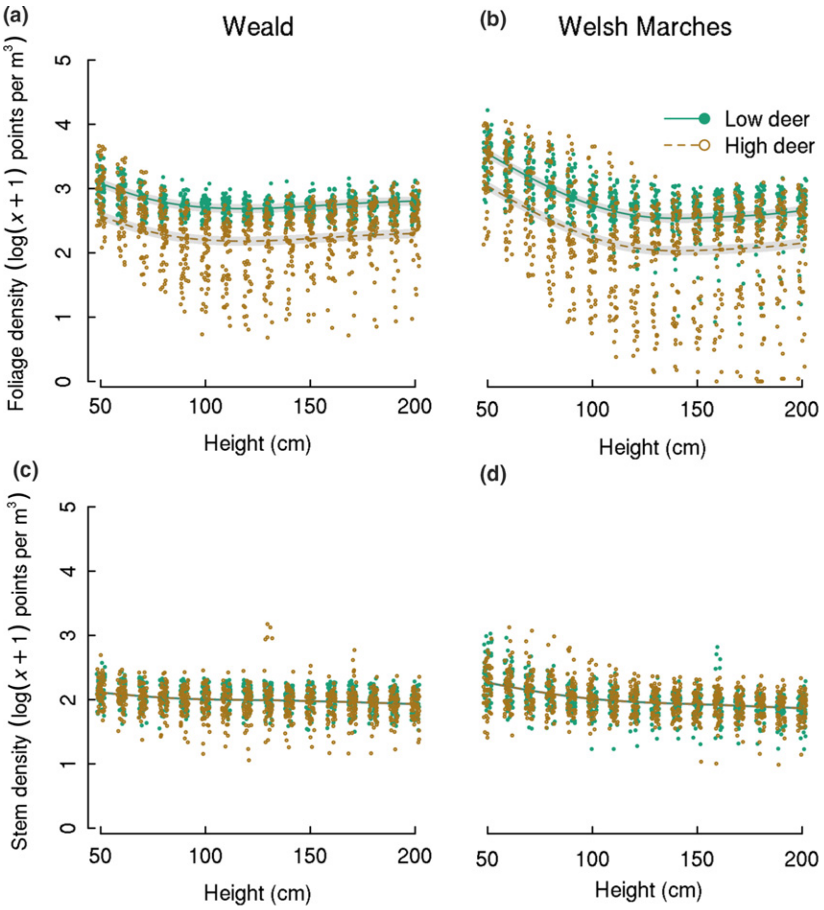

Fig. 4. Density of (a, b) foliage and (c, d) stem in the understorey layer (0·5–2 m above-ground) of each woodland plot, comparing woodlands in (a, c) the Weald with (b, d) the Welsh Marches. Density (measured as number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$ scale with increasing height; each 0·1 m height band is represented by five replicate 10 × 10 × 0·1 m slices in each of 40 woodland plots. Lines show model mean ± SE, and empirical data as dots, with horizontal jitter added for clarity.

a degree of consistency across plots in overall subcanopy structure.

Caution must be expressed in interpreting patterns higher in the canopy (see Materials and methods). Despite this caveat, returns still provide a sample of higher canopy layers from which trends can be discerned. A more even distribution of foliage occurred in high-deer areas, and the total amount of foliage more than doubled (Table 1). These patterns are likely to be artefacts of increased canopy height. No other main effect was detected. The distribution of stem density above 10 m was determined more strongly by region, with sites in the Weald maintaining a higher stem density in the upper layers than those in the Welsh Marches. Owing to sampling constraints this is difficult to interpret structurally. As with foliage, the total amount of stem surface area detected was more than twofold higher in high-deer areas. In both cases models explained a modest proportion of the total variance (estimated $R^2 = 26{\cdot}4\%$ and 15·7%).

FULL CANOPY PROFILES

The distribution of foliage and stem across the whole vertical canopy profile was rescaled by maximum height of each plot to facilitate comparisons of overall structure. The best-supported model for full foliage profiles included separate splines for high- and low-deer forests, most clearly evident from a decrease in the relative amount of foliage detected in the understorey and shrub layer, with a pronounced relative increase in the upper half of the profile (Fig. 5a). This pattern alone accounted for 21·2% of the variance in the dataset. There were no main effects of deer, region or management (Table 1).

Whole-canopy profiles of stem density revealed differences between the two regions, with a greater relative surface area of stem detected in the lower half of the profile in the Welsh Marches, while in the Weald the balance was weighted more towards the shrub layer and upper canopy (Fig. 5b). This cannot be attributed to consistent differences in composition (Table S1). Regional differences in stem distribution accounted for 43·5% of the total variance in the dataset. There were no significant differences in total stem with management, region or deer density (Table 1).

Discussion

Through TLS we have revealed a marked difference in the foliage profile of high-deer forests which extends beyond the understorey. A two-thirds lower surface area of foliage occurred from 0·5 to 2 m above-ground, and full-canopy profiles suggest that differences in forest structure extended throughout the canopy, with overall foliage distribution varying consistently between high- and

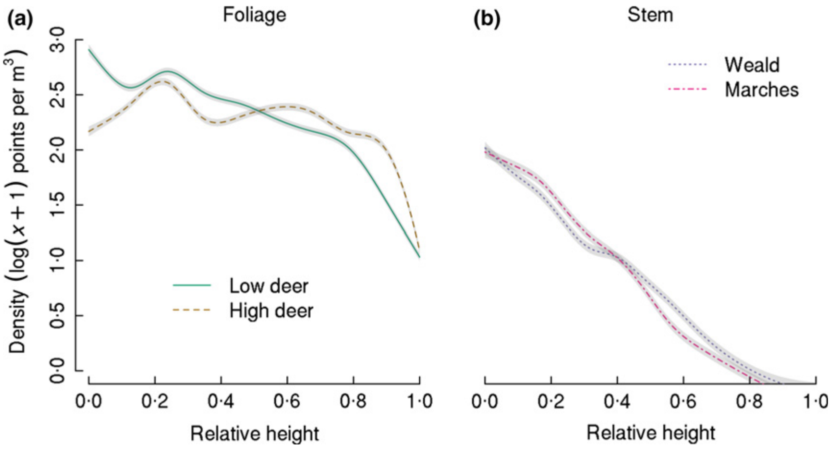

Fig. 5. Density of (a) foliage and (b) stem across the full canopy profile for all woodland plots, adjusted for maximum height from 0 (0·5 m above-ground) to 1 (top of canopy). Panels comparing woodlands (a) with high vs. low deer density and (b) in the Weald vs. the Welsh Marches. Density measured as number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$ scale with increasing relative height. Lines show model means ± SE based on 20 plots each. Empirical data are excluded for clarity.

low-deer forest sites. High-deer forests were also 5 m taller than low-deer sites.

Considering the large quantity of data and inherent heterogeneity of forest structures, the statistical models provided reasonable representations of the patterns present, based on only a single smoothing function and in some cases a further main effect on absolute densities of foliage or stem. This implies consistency in forest structural forms across regions and landscapes.

Reductions in understorey foliage strongly suggest a browsing effect in areas of high deer density, an inference which was strengthened by the lack of a similar trend in the density of stem material. This is consistent with previous work documenting alterations in the distribution of foliage in the understorey up to a browse line at a height of 2 m (Putman *et al*. 1989). While Putman *et al*. (1989) noted a near-total removal of foliage at some heights relative to full exclosure plots, we quantify this directly as a reduction by 68% in foliage from 0·5 to 2 m compared to low deer density sites (c. 1 km^{-2}).

Further differences between high- and low-deer forests were detected in the distribution of both foliage and stem in the shrub layer from 2 to 5 m, although the explanatory power of these models was weak, symptomatic of the large degree of heterogeneity both within and between woods. Nevertheless, such patterns may be consistent with the fourfold increase in density of small saplings observed following 20 years of deer exclusion in a North American forest (McGarvey *et al*. 2013), and the near-total failure of palatable tree species to recruit as saplings under heavy deer browsing (White 2012).

It is unclear how deer density might be related to structural differences at levels above 5 m, including the greater overall height of high-deer woods. Patterns were consistent in both regions, and we found no evidence that underlying edaphic factors were driving a common response in both deer and canopy height. Active choice by deer might play some part, perhaps driven by factors including species composition, availability of food sources, security from predation or shelter from adverse weather conditions (Gill & Morgan 2010; Ewald *et al*. 2014). Given the ranges of individual deer, however, landscape-level factors are more likely to determine their densities.

Nevertheless, the alternative explanation that high deer densities result in taller forests with distinct structural profiles remains conceivable given that forest stands with prolonged deer browsing are known to be altered in tree size distributions (Putman *et al*. 1989; Peltzer *et al*. 2014), rates and trajectories of succession (Côté *et al*. 2004; Long, Pendergast & Carson 2007) and overstorey composition (Putman *et al*. 1989; Côté *et al*. 2004). Deer browsing might influence foliage profiles above 2 m through compensatory responses by browsed or damaged trees or by reducing recruitment of regenerating stems into higher canopy layers (Long, Pendergast & Carson 2007; Gill & Morgan 2010). Although we recorded instantaneous deer densities, we do not have evidence that they have been consistent over time periods commensurate with the processes governing forest regeneration, nor data on stand ages.

Apparent increases in foliage and stem detection at higher canopy levels in high-deer sites might have arisen because reduced densities in the understorey allowed greater laser beam penetration. On the other hand, the greater canopy height of high-deer sites could have caused leaves higher in the canopy to remain undetected. While methodological artifacts cannot be entirely excluded, a comparison between foliage and stem returns demonstrates that each correlates with a distinct set of variables.

These differences are likely to have broad implications for forest ecosystems in which many species and processes respond to forest structure. Cascading impacts of high deer density have been detected among invertebrates, bird and small mammals (reviewed in Côté *et al*. 2004). Within the UK, high deer densities have been shown to correlate with declines in a number of bird species at both local (Holt, Fuller & Dolman 2014) and landscape scales (Newson *et al*. 2012). Likewise, the long-term decline in a number of understorey songbird species in North America has been linked to rising deer populations (Chollet & Martin 2013). On regional scales a reduction in productivity and carbon storage in high-deer forests could have major repercussions for climate models (White 2012).

While regional differences determined smoothing functions in half of the models, including canopy stem profiles, effects of management were limited. The only impacts detected were a minor reduction in the density of stem returns in the shrub layer (2–5 m) and an altered distribution of foliage in the subcanopy (5–10 m). Managed and unmanaged stands did not differ in overall height, and showed no evidence of variation in the overall distribution of foliage or stem across whole vertical profiles. The lack of consistent patterns with management may reflect only minor interventions within these old-growth stands or inconsistencies in timing, execution and intensity. It also suggests that management as practiced over the last 20 years in these sites has had relatively minor impacts on forest structures compared to those of deer. This contrasts with the results of McMahon *et al.* (2015), who used a vertical laser to detect legacies of management on canopy structure extending for at least 70 years in a UK woodland. These, however, reflected strong contrasts between stands which had regrown from either cleared sites or former coppice. Interventions in our stands are likely to have been less extreme; in most cases stand thinning has been carried out, which will have altered shrub and subcanopy layers but with limited effects on canopy openness. A greater number of recently cut stumps were detected in managed plots (see appendix 4.4 in Fuller *et al.* 2014).

Although we found no interactions among main effects in our analysis, synergies between forest management and deer have been found in other studies, and the pattern may vary between regions or ecological contexts. In the Czech Republic a variety of invertebrate groups show greater richness and the presence of species of conservation concern in managed woodlands with low deer density (Spitzer *et al.* 2008), while models of forest dynamics in North America suggest that the impacts of high deer density on forest composition are greatest when gap-forming disturbances occur (Holm *et al.* 2013). In managed woodlands there are likely to be trade-offs among canopy openness, deer densities and resultant understorey complexity (Fuller 2013), meaning that management decisions should be taken within a site-level context, encompassing factors including browsing pressure and the dependence of species of conservation concern on particular microhabitats.

There remain challenges for the implementation of TLS in forest surveying, and caveats regarding the detection of forest elements need to be borne in mind when interpreting observed patterns. At distances beyond 13 m from each scanner, distance between captured points began to increase beyond 10 mm, meaning that not all 1 cm^3 voxels were sampled from every scan location. This is an important consideration for any assessment of structure above this height, although overlap between sight lines from multiple scanners provides some compensation. While higher resolution data could in principle have been collected, this generates ever greater quantities of data, leading to increased time for both scanning and processing. Moreover, our primary interest was in forest structure below the canopy, and sampling was therefore designed to ensure accurate and efficient capture at these levels. Finally, at increasing heights in the canopy, obstruction by lower foliage levels becomes a more important constraint than scan resolution. Compensating for attenuation by foliage depends more on a large number of scan positions than improved resolution of any single scan.

Conclusions and applications

Through the application of terrestrial laser scanning to 40 woodland plots, we reveal that high deer densities are associated with a reduction in understorey foliage of 68%, with further differences observed throughout whole-canopy profiles. High-deer forests were on average 5 m taller and contained a distinctive vertical distribution of foliage, even above the browse line. The application of TLS provides new insights into forest structural organisation, allowing management to be directed towards creating the three-dimensional habitats required by species of conservation concern. For example, density of understorey foliage and canopy height are important predictors of the distributions of woodland birds (Hinsley *et al.* 2009). Our results imply that reduction of deer populations to low levels (c. 1 km^{-2}) is the most effective means of directing whole stand structures towards desired states, especially to increase the density of understory foliage. Previous work has shown that deer exclusion benefits birds which forage in the understorey and shrub layer, with no evidence of negative effects on any bird species (Holt *et al.*, 2014). On regional scales there is a strong association between deer densities and decline in understorey bird species (Newson *et al.* 2012). In contrast, low-intensity stand thinning was not associated with differences in overall structures in our plots, and is not thought to open canopies sufficiently to influence the understorey (Fuller 2013). In regions where browsing pressure is high, interventions to promote understorey vegetation are unlikely to succeed unless combined with deer exclusion.

Authors' contributions

M.P.E., M.J.S., G.M.S. and R.J.F. conceived the ideas and designed the methodology; J.R. and R.M.A.G. collected the data; M.P.E. and J.R. analysed the data; M.P.E. led writing of the manuscript and all authors contributed critically to drafts.

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Data accessibility

Post-processing data comprising the density of foliage and stem material, as used in the statistical analyses, can be found in the Dryad Digital Repository https://doi.org/10.5061/dryad.cd6tv (Eichhorn *et al.* 2017).

References

Ashcroft, M.B., Gollan, J.R. & Ramp, D. (2014) Creating vegetation density profiles for a diverse range of ecological habitats using terrestrial laser scanning. *Methods in Ecology and Evolution*, **5**, 263–272.

Chollet, S. & Martin, J.M. (2013) Declining woodland birds in North America: should we blame Bambi? *Diversity and Distributions*, **19**, 481–483.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics*, **35**, 113–147.

Côté, J.F., Widlowski, J.L., Fournier, R.A. & Verstraete, M.M. (2009) The structural and radiative consistency of three-dimensional tree reconstructions from terrestrial lidar. *Remote Sensing of Environment*, **113**, 1067–1081.

Dassot, M., Constant, T. & Fournier, M. (2011) The use of terrestrial LiDAR technology in forest science: application fields, benefits and challenges. *Annals of Forest Science*, **68**, 959–974.

Davies, A.B. & Asner, G.P. (2014) Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology and Evolution*, **29**, 681–691.

Dolman, P.M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research*, **35**, 202–214.

Eichhorn, M.P., Ryding, J., Smith, M.J., Gill, R.M.A., Siriwardena, G.M. & Fuller, R.J. (2017) Data from: Effects of deer on woodland structure revealed through terrestrial laser scanning. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.cd6tv.

Ewald, M., Dupke, C., Heurich, M., Muller, J. & Reineking, B. (2014) LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. *Forests*, **5**, 1374–1390.

Fuller, R.J. (2013) Searching for biodiversity gains through woodfuel and forest management. *Journal of Applied Ecology*, **50**, 1295–1300.

Fuller, R.J., Bellamy, P.E., Broome, A., Calladine, J., Eichhorn, M.P., Gill, R.M.& Siriwardena, G.M. (2014) Effects of woodland structure on woodland bird populations: an assessment of the effects of changes in woodland structure on bird populations as a result of woodland management practices and deer browsing. *Defra Project*, WC0793, http://randd.defra.gov.uk/.

Fuller, R.J. & Gill, R.M.A. (2001) Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, **74**, 193–199.

Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis*, **149**, 261–268.

Gill, R.M.A. (1992) A review of damage by mammals in north temperate forests. *Forestry*, **65**, 363–388.

Gill, R.M.A. & Morgan, G. (2010) The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry*, **83**, 53–63.

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

Holm, J.A., Thompson, J.R., McShea, W.J. & Bourg, N.A. (2013) Interactive effects of chronic deer browsing and canopy gap disturbance on forest successional dynamics. *Ecosphere*, **4**, 144.

Holt, C.A., Fuller, R.J. & Dolman, P.M. (2014) Exclusion of deer affects responses of birds to woodland regeneration in winter and summer. *Ibis*, **156**, 116–131.

Kirby, K. & Watkins, C.W., eds. (2015) *Europe's Changing Woods and Forests: From Wildwood to Managed Landscapes*. CAB International, Wallingford, UK.

Long, Z.T., Pendergast, T.H. & Carson, W.P. (2007) The impact of deer on relationships between tree growth and mortality in and old-growth beech-maple forest. *Forest Ecology and Management*, **22**, 230–238.

McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005) Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, **218**, 1–24.

McGarvey, J.C., Bourg, N.A., Thompson, J.R., McShea, W.J. & Shen, X. (2013) The short and long term effects of twenty year deer exclusion on woody vegetation at four life-history stages in a mid-Atlantic temperate deciduous forest. *Northeastern Naturalist*, **20**, 451–468.

McMahon, S.M., Bebber, D.P., Butt, N., Crockatt, M., Kirby, K., Parker, G.G., Riutta, T. & Slade, E.M. (2015) Ground based LiDAR demonstrates the legacy of management history to canopy structure and composition across a fragmented temperate woodland. *Forest Ecology and Management*, **335**, 255–260.

McShea, W.J. (2012) Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences*, **1249**, 45–56.

Newnham, G.J., Armston, J.D., Calders, K., Disney, M.I., Lovell, J.L., Schaaf, C.B., Strahler, A.H. & Danson, F.M. (2015) Terrestrial laser scanning for plot scale forest measurement. *Current Forestry Reports*, **1**, 239–251.

Newson, S.E., Johnston, A., Renwick, A.R., Baillie, S.R. & Fuller, R.J. (2012) Modelling large-scale relationships between changes in woodland deer and bird populations. *Journal of Animal Ecology*, **49**, 278–286.

Newton, A. (2007) *Forest Ecology and Conservation: A Handbook of Techniques*. Techniques in Ecology and Conservation Series. Oxford University Press, New York, NY, USA.

Peltzer, D.Q., Allen, R.B., Bellingham, P.J., Richardson, S.J., Wright, E.F., Knightbridge, P.I. & Mason, N.W.H. (2014) Disentangling drivers of tree population size distributions. *Forest Ecology and Management*, **331**, 165–179.

Putman, R.J., Edwards, P.J., Mann, J.C.E., How, R.C. & Hill, S.D. (1989) Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation*, **47**, 13–32.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rackham, O. (2003) *Ancient Woodland: Its History, Vegetation and Uses in England*. 2nd edn. Castlepoint Press, Dalbeattie, UK.

Royo, A.A. & Carson, W.P. (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research*, **36**, 1345–1362.

Spitzer, L., Konvicka, M., Benes, J., Tropek, R., Tuf, I.H. & Tufova, J. (2008) Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. *Biological Conservation*, **141**, 827–837.

Stephenson, A.C. & Harrison, R.J. (1992) Ancient forests in Spain: a model for land-use and dry forest management in south-west Spain from 4000 BC to 1900 AD. *Proceedings of the Prehistorical Society*, **58**, 227–247.

Takatsuki, S. (2009) Effects of sika deer on vegetation in Japan: a review. *Biological Conservation*, **142**, 1922–1929.

Tanentzap, A.J., Bazely, D.R., Koh, S., Timciska, M., Haggith, E.G., Carleton, T.J. & Coomes, D.A. (2011) Seeing the forest for the deer: do reductions in deer-disturbance lead to forest recovery? *Biological Conservation*, **144**, 376–382.

White, M.A. (2012) Long-term effects of deer browsing: composition, structure and productivity in a northeastern Minnesota old-growth forest. *Forest Ecology and Management*, **269**, 222–228.

Wood, S. (2006) *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, London, UK.

Zuur, A., Ieno, E., Walker, N., Savaliev, A. & Smith, G. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY, USA.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Map of regions for woodland structural surveys.

Table S1. Details of woodland plots surveyed.

Appendix S1. Summary of deer surveys.

Appendix S2. Differentiating wood and leaf material.

Appendix S3. Model summary tables.

Appendix S4. Figures illustrating GAMM smoothers.