

Effects of deer on woodland structure revealed through terrestrial laser scanning

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Running title

Terrestrial laser scanning of woodlands

1 Summary

- 2 1. Terrestrial laser scanning (TLS) captures the three-dimensional structure of
3 habitats. Compared to traditional methods of forest mensuration it allows
4 quantification of structure at increased resolution, and the derivation of novel
5 metrics with which to inform ecological studies and habitat management.
- 6 2. Lowland woodlands in the UK have altered in structure over the last century
7 due to increasing abundance of deer and a decline in management. We
8 aimed to compare whole canopy profiles between woodlands with high (>
9 10 deer km⁻²) and low deer density (*c.*1 deer km⁻²), and in stands with and
10 without a record of management interventions in the last 20 years, providing
11 a test-case for the application of TLS in habitat assessment for conservation
12 and management.
- 13 3. Forty closed-canopy lowland woodlands (height range 16.5–29.4 m) were sur-
14 veyed using TLS in two regions of the United Kingdom, divided into areas
15 of high and low deer abundance, and between plots which had been re-
16 cently managed or were unmanaged. Three-dimensional reconstructions of
17 the woodlands were created to document the density of foliage and stem
18 material across the entire vertical span of the canopy.
- 19 4. There was a 68% lower density of understorey foliage (0.5–2 m above ground)
20 in high-deer woodlands, consistent in both regions. Despite this, total amounts
21 of foliage detected across the full canopy did not differ between deer density
22 levels. High-deer sites were 5 m taller overall and differed in the distribution
23 of foliage across their vertical profile. Managed woodlands, by contrast, ex-

24 hibited relatively minor differences from controls, including a lower quantity
25 of stem material at heights from 2–5 m, but no difference in foliage den-
26 sity. All main effects were replicated equally in both regions despite notable
27 differences in stand structures between them.

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

35 **Keywords**

36 Deer browsing; foliage profile; forest canopy; forest management; forest structure;
37 forest understorey; LiDAR; oak; woodland management

38 Introduction

39 Deer densities in north-temperate forests are at extraordinarily high levels (Côté
40 *et al.*, 2004; Takatsuki, 2009; McShea, 2012). This is due to a combination of
41 factors including the absence of large predators, a decline in hunting pressure,
42 concentration of populations in habitat fragments and the widespread invasion
43 of non-native, smaller deer species such as Chinese muntjac *Muntiacus reevesi*
44 (Côté *et al.*, 2004; Dolman & Wäber, 2008). In Britain, increases in woodland
45 area and autumn sowing of crops providing winter forage are likely to be locally
46 influential (Fuller & Gill, 2001). The increased density of deer has direct impacts
47 on the structure of forests, most markedly through the creation of browse lines
48 where edible foliage has been removed from the understorey, and the imposition
49 of severe recruitment limitation on trees, whose seedlings are damaged and unable
50 to establish (Côté *et al.*, 2004; Gill & Morgan, 2010). Damage is also often caused
51 to the bark of standing trees (Gill, 1992). The removal of gap-colonising seedlings
52 increases understorey light levels, favouring the growth of herbaceous plants that
53 subsequently impede tree regeneration (Royo & Carson, 2006).

54 Across Europe increasing deer densities have occurred alongside a decline in
55 woodland management, particularly over the course of the last century (Rackham,
56 2003). Within British woodlands there is concern that their structure may have
57 systematically altered, with reductions in understorey vegetation driven by an
58 interaction between increased deer browsing and greater shading from fully closed
59 canopies (Fuller *et al.*, 2007). Management to modify forest structure has been
60 carried out in Europe for at least 4,500 years (Stephenson & Harrison, 1992).
61 Traditional objectives were the promotion of favoured species for food, fuel and

62 timber. More recently there has been a growing focus on conservation and the
63 maintenance of traditional landscapes, and much discussion regarding the best
64 means of achieving conservation goals through woodland structural management
65 (Kirby & Watkins, 2015).

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

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

87 managers as to the impacts of interventions, disturbances or other drivers of forest
88 structure.

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

104 **Materials and Methods**

105 **Plot selection**

106 This work was undertaken as part of a broader project examining bird communities
107 and vegetation in 300 study plots in two regions of Britain — the Weald and the
108 Welsh Marches (see Fig. S1; Fuller *et al.*, 2014). A subsample of comparable

109 plots were identified as potentially suitable for TLS. Criteria for inclusion were
110 (a) mature, closed-canopy broad-leaved forest; (b) availability of an initial deer
111 density estimate and record of management interventions; (c) road access to allow
112 transport of survey equipment; and (d) a minimum 1 km distance among plots
113 to reduce spatial autocorrelation of main effects. Management was characterised
114 based on explicit documentation of interventions (or lack thereof) at the stand level
115 within the last 20 years; in the majority of cases this implied stand thinning, though
116 detailed records of protocols or intensity were seldom available. Deer densities were
117 initially classified as high or low.

118 From this subsample of plots a selection of 40 plots was made to enable a
119 fully factorial comparison among regions, management type and deer density. In
120 several cases a site was deemed unsafe to access on inspection in the field and was
121 therefore replaced with the nearest suitable plot from a predetermined shortlist.
122 This led to a minor imbalance in the factor groups (see Table S1 for plot details).
123 Although some plots were within the same named wood, the minimum distance of
124 1 km apart was a more important criterion, as in the Weald there were numerous
125 small woods close together. The majority of plots were in oak-dominated forest
126 (*Quercus* spp.; 35), with the remainder dominated by birch (*Betula* spp.; 2), ash
127 (*Fraxinus excelsior*; 2), or mixed (1).

128 High and low deer sites were confirmed by concurrent deer surveys (see Ap-
129 pendix S1). In four cases direct deer surveys did not take place in the woods
130 themselves (Ampfield, Ellenden, Haugh Wood, Lea and Pagets Wood); classifi-
131 cation was therefore based on proximity to other woods from which data were
132 available. High deer densities (> 10 deer km⁻²) were consistent with those re-
133 ported in other studies (e.g. Tanentzap *et al.*, 2011). Low deer densities did not

134 exceed 1.2 deer km⁻². Fallow deer *Dama dama* Linnæus 1758 were the dominant
135 species (>85%), although counts included roe *Capreolus capreolus* Linnæus 1758
136 and muntjac *Muntiacus reevesi* Ogilby 1839.

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

142 Survey protocol

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

148 Surveys were conducted using a FARO Focus 3D 125 scanner set to allow data
149 to be collected at a point separation of 7.67 mm at 10 m distance (beam diameter
150 was *c.*4 mm at 10 m and *c.*6 mm at 20 m). This ensured that all measured
151 points within 10 m of the scanner were collected at a higher spatial resolution
152 than required for division into 1 cm³ voxels. Point spacing began to exceed 10 mm
153 at distances of 13 m from the scanner. At 25 m from the scanner, point spacing
154 from any single scanning location was 33 mm, sufficient to enable broad-scale
155 description of canopy structure.

156 The scanner was placed at 10 m intervals along each edge of the transect, offset

157 by 5 m on alternate sides, giving a minimum of 11 scans per transect. This ensured
158 complete coverage within the plot of <1.0 cm beam spacing up to 10 m from scan
159 locations. The default scanner height was 1.3 m, although this was reduced as
160 necessary when obstacles prevented a clear line of sight. In order to register all of
161 the scans in a single point cloud, targets were positioned throughout the survey
162 area, placed so as to be visible from adjacent scan locations. Three targets were
163 used to link adjacent scans, two outside the plot (to reduce shadowing of points)
164 and one inside. Purpose-built targets were used at approximate heights of 50 cm,
165 100 cm and 125 cm.

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

170 **Data processing**

171 An approach to data processing was taken which minimised manual input and
172 allowed extraction of relevant features of forest structure using only a standard
173 desktop computer. Data were initially filtered to remove isolated points or those
174 with low reflectance values using the default filters in FARO Scene 4.8. Datasets
175 were then trimmed to include only points within the 10×50 m transect. An ini-
176 tial digital terrain model (DTM) was created in ArcMap based upon the lowest
177 recorded points within coarse 3 m grid cells, which were judged to represent the
178 ground surface, and from which a triangulated irregular network was generated.
179 This was repeated with a finer 0.5 m grid. Where dense understory is present, laser

180 beams may not penetrate to the ground surface, and overestimation of ground
181 height can occur (Ashcroft *et al.*, 2014). To identify these areas, the difference
182 between the coarse and fine grids was examined, and those smaller grid squares
183 for which a height increase exceeding 5 cm was observed were visually inspected.
184 If dense understorey vegetation was the likely cause then the value from the larger
185 square was used to generate the DTM, otherwise the finer grid value was taken.
186 The DTM was used to convert all points from a height relative to the scanner to
187 height above ground, facilitating structural analysis. Points representing survey
188 apparatus were removed manually.

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

192 Point clouds were resampled to 1 cm³ voxels using Pointools v1.5. They were
193 processed in 10 cm height bands, divided into five 10×10 m subsections to capture
194 within-plot variance. Classification of voxels as stem or leaf was based on the
195 expected higher density of returns in the vertical axis from stems relative to leaves
196 (Côté *et al.*, 2009) using the point density tool within ArcGIS (ESRI version 10.3).
197 Voxels were assessed within 10 cm vertical columns. Those with a point density
198 of at least 4.0 were classified as stem material, those below as leaves. Selection
199 of this parameter was a manual, iterative process, validated by comparison with
200 visual spectrum returns (see Appendix S2 for further details).

201 The basic level of analysis was the subplot slice, giving a volume of 10 × 10 ×
202 0.1 m = 10 m³ and counting the number of filled voxels within. Note that the
203 density of stem points is an estimate of stem surface area rather than volume. This
204 means that it is not a straightforward estimate of total woody biomass as it can

205 be confounded by stem size distributions and the angles of branches, especially
206 at greater heights. Its interpretation is based upon the assumption that, because
207 the composition of stands was broadly similar, trees in all plots would exhibit
208 similar growth forms. Our intention was to capture the habitat surface area as
209 experienced by birds and other organisms rather than tree biomass.

210 The vertical profile was split into subsections for initial analysis. Returns below
211 50 cm in height were considered unreliable due to occlusion by overlapping layers of
212 dense foliage, and also contained very high variance, making patterns among plots
213 difficult to discern. They were therefore excluded, which means that all subsequent
214 interpretation is based on material above 50 cm. The remainder of the profile was
215 split into height classes defined as understorey (0.5–2 m), shrub layer (2–5 m),
216 subcanopy (5–10 m) and canopy (>10 m). These classes were chosen based on
217 disjunctions in the variance profile with height across all plots (see Fig. 2).

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

226 Full-canopy profiles are not directly comparable between plots as variation in
227 total height overwhelms internal differences in structure. Whole canopy structures
228 were therefore compared on the basis of height-adjusted profiles, scaled from 0–
229 1, with the maximum height taken as the mean of the highest 10 points in each

230 subplot. Points below 50 cm were removed, and points with relative heights above
231 1 excluded to avoid distortion by extreme outliers.

232 **Statistical analysis**

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

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

$$D_{ijk} = \alpha + f_x(\text{height}_k) + \text{deer}_j + \text{management}_j + \text{region}_j + a_j + \varepsilon_{ijk}$$

$$\varepsilon_{ijk} \sim (0, \sigma_{\text{region} \times \text{deer}}^2)$$

252 where D is the density of returns per subplot slice, i is the subplot slice, j is the
253 plot, α is a random intercept, and k is the canopy height. The smoothing function
254 f_x allows for different smoothers per factor group x (one of either height, deer or
255 management).

256 Analyses first considered whether different smoothers between factor groups
257 were supported, and selected the best-performing model using Akaike's Informa-
258 tion Criterion (AIC). This process was then repeated for all main effects.

259 Table 1 presents a summary of the final best-fit models. Full model output for
260 all main effects is provided in Appendix S3. In the results we show model estimates
261 for foliage and stem density combined with empirical measurements at each height
262 band. Graphs of GAMM smoothers display relative density of foliage or stem
263 with height compared to the average value for the height range under study. This
264 provides a clearer representation of differences in the shapes of smoothers between
265 factor groups and is shown for comparison in Appendix S4.

266 Results

267 Scans revealed that plots contained a median density of leaves of $523 \text{ cm}^3\text{m}^{-3}$
268 (457–615 inter-quartile range (IQR)), or 0.052% of the total forest volume, as
269 measured by occupied 1 cm^3 voxels. This is a minimum estimate given that leaves

270 higher in the canopy may not have been detected due to the blocking effect of
271 material beneath them. Median stem surface density across plots was an order of
272 magnitude lower at $49 \text{ cm}^3\text{m}^{-3}$ (43–61 IQR).

273 Forest stands varied in average height from 29.4 m (Wyre Main Block 1) to
274 16.5 m (West Blean Block 4). No differences in overall height were found between
275 managed and unmanaged plots (Likelihood Ratio (LR) < 0.1 , $\text{df} = 1$, $P = 0.944$),
276 and though forests in the Welsh Marches were slightly taller than those in the
277 Weald (22.8 ± 0.8 m to 21.0 ± 0.9 m, $\text{means} \pm \text{SE}$), this was only a marginal effect
278 (LR = 3.9, $\text{df} = 1$, $P = 0.048$). A much greater difference in height was observed
279 between high and low deer density forests. High-deer forests averaged 24.4 ± 0.8 m
280 in height, whereas low-deer forests were 5 m shorter at 19.4 ± 0.6 m (LR = 23.0, df
281 = 1, $P < 0.001$). The absence of a significant interaction between region and deer
282 in the final model demonstrates that this pattern was consistent in both regions.
283 High- and low-deer sites did not differ in soil nutrient regime ($F_{1,39} = 0.44$, $P =$
284 0.512); nor were there any differences between the two regions ($F_{1,39} < 0.01$, $P \approx$
285 1.000). A similar pattern emerged with soil moisture regime, which did not differ
286 between deer densities ($F_{1,39} = 0.01$, $P = 0.941$) nor regions ($F_{1,39} = 0.39$, $P =$
287 0.539).

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

293 Vertical sections

294 Median foliage densities were broadly comparable in the understorey (438 cm³m⁻³,
295 219–710 IQR), shrub layer (614 cm³m⁻³, 354–901 IQR) and subcanopy (398 cm³m⁻³,
296 210–656 IQR) across all plots. The trend was somewhat different for stem surfaces,
297 for which values declined markedly from understorey (101 cm³m⁻³, 69–137 IQR)
298 to shrub layer (62 cm³m⁻³, 42–86 IQR) and subcanopy (19 cm³m⁻³, 7–38 IQR).
299 Overall values in the canopy cannot readily be compared due to heterogeneity in
300 maximum height both between and within plots.

301 The final model for understorey foliage from 0.5–2 m above ground included
302 different smoothers for forests in the Weald and the Welsh Marches (Fig. 4a,b) and
303 a greater overall quantity of foliage in low-deer forests (Table 1). This was evident
304 from a predicted understorey foliage volume of 189 cm³m⁻³ in high-deer plots
305 compared to 607 cm³m⁻³ in low-deer plots (back-transformed model means; see
306 Appendix S3 for estimates with associated errors. There were no significant overall
307 effects of either region or management on total foliage quantity. The final model
308 explained over a third of the variance within the data (estimated $R^2=37.3\%$).

309 The analysis for understorey stem data provides a useful comparator. No differ-
310 ences were anticipated with deer density because deer do not directly browse stem
311 material. In line with this expectation, there was once again a difference between
312 regions in the shape of the smoother for stem distribution with height (Fig. 4c,d)
313 but no significant main effect of deer on overall quantity of stem material, nor of
314 either region or management. The explanatory power of the model was weak, in
315 accordance with the limited number of effects exhibited (estimated $R^2=12.4\%$).

316 In the shrub layer, from 2–5 m in height, there were significantly different

317 smoothers for foliage density in forests with high and low deer density (Table 1).
318 There were, however, no overall changes in the amount of foliage with region,
319 deer or management, and the model had limited explanatory power (estimated
320 $R^2=6.5\%$). A similar pattern emerged for stem material within the same height
321 range, with differences among deer densities in the pattern of distribution. In this
322 case, however, there was also a significant main effect of management, with slightly
323 lower amounts of stem in managed plots. The explanatory power of the model was
324 however modest (estimated $R^2=16.1\%$).

325 From 5–10 m, representing the subcanopy, models suggest different smoothing
326 functions for foliage in woodlands with or without records of recent management
327 (Table 1). An additional main effect of region highlighted a lower total quantity of
328 foliage in plots in the Welsh Marches. When considering stem material, different
329 smoothers were supported in each region, but no main effects of any variable were
330 detected. Models in each case were of reasonable explanatory power, accounting
331 for 17.1% and 21.6% of the variance respectively, reflecting a degree of consistency
332 across plots in overall subcanopy structure.

333 Caution must be expressed in interpreting patterns higher in the canopy (see
334 Methods). Despite this caveat, returns still provide a sample of higher canopy
335 layers from which trends can be discerned. A more even distribution of foliage
336 occurred in high-deer areas, and the total amount of foliage more than doubled
337 (Table 1). These patterns are likely to be artefacts of increased canopy height.
338 No other main effects were detected. The distribution of stem density above 10 m
339 was determined more strongly by region, with sites in the Weald maintaining a
340 higher stem density in the upper layers than those in the Welsh Marches. Owing
341 to sampling constraints this is difficult to interpret structurally. As with foliage,

342 the total amount of stem surface area detected was more than twofold higher in
343 high deer areas. In both cases models explained a modest proportion of the total
344 variance (estimated $R^2 = 26.4\%$ and 15.7%).

345 **Full canopy profiles**

346 The distribution of foliage and stem across the whole vertical canopy profile was
347 rescaled by maximum height of each plot to facilitate comparisons of overall struc-
348 ture. The best-supported model for full foliage profiles included separate splines
349 for high and low-deer forests, most clearly evident from a decrease in the relative
350 amount of foliage detected in the understorey and shrub layer, with a pronounced
351 relative increase in the upper half of the profile (Fig. 5a). This pattern alone ac-
352 counted for 21.2% of the variance in the dataset. There were no main effects of
353 deer, region or management (Table 1).

354 Whole-canopy profiles of stem density revealed differences between the two
355 regions, with a greater relative surface area of stem detected in the lower half of
356 the profile in the Welsh Marches, while in the Weald the balance was weighted more
357 towards the shrub layer and upper canopy (Fig. 5b). This cannot be attributed
358 to consistent differences in composition (Table S1). Regional differences in stem
359 distribution accounted for 43.5% of the total variance in the dataset. There were
360 no significant differences in total stem with management, region or deer density
361 (Table 1).

362 Discussion

363 Through terrestrial laser scanning we have revealed a marked difference in the
364 foliage profile of high-deer forests which extends beyond the understorey. A two-
365 thirds lower surface area of foliage occurred from 0.5–2 m above ground, and full-
366 canopy profiles suggest that differences in forest structure extended throughout
367 the canopy, with overall foliage distribution varying consistently between high and
368 low-deer forest sites. High-deer forests were also 5 m taller than low-deer sites.

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

374 Reductions in understorey foliage strongly suggest a browsing effect in areas of
375 high deer density, an inference which was strengthened by the lack of a similar trend
376 in the density of stem material. This is consistent with previous work documenting
377 alterations in the distribution of foliage in the understorey up to a browse line at
378 a height of 2 m (Putman *et al.*, 1989). While Putman *et al.* (1989) noted a near-
379 total removal of foliage at some heights relative to full exclosure plots, we quantify
380 this directly as a reduction by 68% in foliage from 0.5–2 m compared to low deer
381 density sites ($c.1 \text{ km}^{-2}$).

382 Further differences between high and low deer forests were detected in the
383 distribution of both foliage and stem in the shrub layer from 2–5 m, though the
384 explanatory power of these models was weak, symptomatic of the large degree of
385 heterogeneity both within and between woods. Nevertheless, such patterns may be

386 consistent with the fourfold increase in density of small saplings observed following
387 20 years of deer exclusion in a North American forest (McGarvey *et al.*, 2013), and
388 the near-total failure of palatable tree species to recruit as saplings under heavy
389 deer browsing (White, 2012).

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

399 Nevertheless, the alternative explanation, that high deer densities result in
400 taller forests with distinct structural profiles, remains conceivable given that forest
401 stands with prolonged deer browsing are known to alter in tree size distributions
402 (Putman *et al.*, 1989; Peltzer *et al.*, 2014), rates and trajectories of succession
403 (Côté *et al.*, 2004; Long *et al.*, 2007) and overstorey composition (Putman *et al.*,
404 1989; Côté *et al.*, 2004). Deer browsing might influence foliage profiles above
405 2 m through compensatory responses by browsed or damaged trees or by reducing
406 recruitment of regenerating stems into higher canopy layers (Long *et al.*, 2007; Gill
407 & Morgan, 2010). Although we recorded instantaneous deer densities, we do not
408 have evidence that they have been consistent over time periods consistent with the
409 processes governing forest regeneration, nor data on stand ages.

410 Apparent increases in foliage and stem detection at higher canopy levels in high-

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

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

427 While regional differences determined smoothing functions in half of models,
428 including canopy stem profiles, effects of management were limited. The only im-
429 pacts detected were a minor reduction in the density of stem returns in the shrub
430 layer (2–5 m) and an altered distribution of foliage in the subcanopy (5–10 m).
431 Managed and unmanaged stands did not differ in overall height, and showed no
432 evidence of variation in the overall distribution of foliage or stem across whole
433 vertical profiles. The lack of consistent patterns with management may reflect
434 only minor interventions within these old-growth stands or inconsistencies in tim-
435 ing, execution and intensity. It also suggests that management as practiced over

436 the last 20 years in these sites has had relatively minor impacts on forest struc-
437 tures compared to those of deer. This contrasts with the results of McMahon *et al.*
438 (2015), who used a vertical laser to detect legacies of management on canopy struc-
439 ture extending for at least 70 years in a UK woodland. These however reflected
440 strong contrasts between stands which had regrown from either cleared sites or
441 former coppice. Interventions in our stands are likely to have been less extreme; in
442 most cases stand thinning has been carried out, which will have altered shrub and
443 subcanopy layers but with limited effects on canopy openness. A greater number
444 of recently-cut stumps were detected in managed plots (see Appendix 4.4 in Fuller
445 *et al.*, 2014).

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

458 There remain challenges for the implementation of TLS in forest surveying,
459 and caveats regarding the detection of forest elements need to be borne in mind
460 when interpreting observed patterns. At distances beyond 13 m from each scanner,

461 distance between captured points began to increase beyond 10 mm, meaning that
462 not all 1 cm³ voxels were sampled from every scan location. This is an important
463 consideration for any assessment of structure above this height, though overlap
464 between sight lines from multiple scanners provides some compensation. While
465 higher resolution data could in principle have been collected, this generates ever
466 greater quantities of data, leading to increased time for both scanning and process-
467 ing. Moreover, our primary interest was in forest structure below the canopy, and
468 sampling was therefore designed to ensure accurate and efficient capture at these
469 levels. Finally, at increasing heights in the canopy, obstruction by lower foliage
470 levels becomes a more important constraint than scan resolution. Compensating
471 for attenuation by foliage depends more on a large number of scan positions than
472 improved resolution of any single scan.

473 **Conclusions and applications**

474 Through the application of terrestrial laser-scanning to 40 woodland plots, we
475 reveal that high deer densities are associated with a reduction in understorey fo-
476 liage of 68%, with further differences observed throughout whole-canopy profiles.
477 High-deer forests were on average 5 m taller and contained a distinctive verti-
478 cal distribution of foliage, even above the browse line. The application of TLS
479 provides new insights into forest structural organisation, allowing management to
480 be directed towards creating the three-dimensional habitats required by species
481 of conservation concern. For example, density of understorey foliage and canopy
482 height are important predictors of the distributions of woodland birds (Hinsley
483 *et al.*, 2009). Our results imply that reduction of deer populations to low levels

484 ($c.1 \text{ km}^{-2}$) is the most effective means of directing whole stand structures towards
485 desired states, especially to increase the density of understory foliage. Previous
486 work has shown that deer exclusion benefits birds which forage in the understorey
487 and shrub layer, with no evidence of negative effects on any bird species (Holt
488 *et al.*, 2014). On regional scales there is a strong association between deer den-
489 sities and decline in understorey bird species (Newson *et al.*, 2012). In contrast,
490 low-intensity stand thinning was not associated with differences in overall struc-
491 tures in our plots, and is not thought to open canopies sufficiently to influence the
492 understorey (Fuller, 2013). In regions where browsing pressure is high, interven-
493 tions to promote understorey vegetation are unlikely to succeed unless combined
494 with deer exclusion.

495 **Authors' contributions**

496 MPE, MJS, GMS and RJF conceived the ideas and designed the methodology; JR
497 and RMAG collected the data; MPE and JR analysed the data; MPE led writing
498 of the manuscript and all authors contributed critically to drafts.

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510 Data accessibility

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

514

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624 **Supporting Information**

- 625 **Appendix Fig S1.** Map of regions for woodland structural surveys.
- 626 **Appendix Table S1.** Details of woodland plots surveyed.
- 627 **Appendix S1.** Summary of deer surveys.
- 628 **Appendix S2.** Differentiating wood and leaf material.
- 629 **Appendix S3.** Model summary tables.
- 630 **Appendix S4.** Figures illustrating GAMM smoothers.

631 **Table captions**

632 **Table 1.** Summary of Generalised Additive Mixed Model outputs for foliage and
633 stem distribution within height bands (0.5–2 m understorey; 2–5 m shrub layer; 5–
634 10 m subcanopy; > 10 m canopy) and across the whole canopy profile (normalised
635 by total height). Each GAMM contained a single factor determining spline shape,
636 marked with a dot, plus tests for main effects of deer, region and management.
637 Differences in the best-supported model are given as percentage change relative to
638 the intercept (low deer, Weald, unmanaged). Full details of final model outputs
639 for all main effects are shown in Appendix S3 with GAMM smoothers plotted in
640 Appendix S4.

641

Table 1:

Height (m)	Feature	Splines		Main effects		R^2
		Deer	Region	Deer (high)	Region (W.M.)	
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

642 **Figure captions**

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

648
649 **Figure 2.** Foliage density (number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$
650 scale with increasing height in the canopy of each plot; each 0.1 m height band
651 is represented by five $10 \times 10 \times 0.1$ m slices. Plot names as Table S1. Note that
652 Ffrith Mathrafal 4 was managed.

653
654 **Figure 3.** Stem surface area (number of filled 1 cm^3 voxels per m^3) on $\log_{10}(x + 1)$
655 scale with increasing height in the canopy; each 0.1 m height band is represented
656 by five $10 \times 10 \times 0.1$ m slices. Plot names as Table S1. Note that Ffrith Mathrafal
657 4 was managed.

658
659 **Figure 4.** Density of (a,b) foliage and (c,d) stem in the understorey layer (0.5–2
660 m above ground) of each woodland plot, comparing woodlands in (a,c) the Weald
661 with (b,d) the Welsh Marches. Density (measured as number of filled 1 cm^3 voxels
662 per m^3) on $\log_{10}(x + 1)$ scale with increasing height; each 0.1 m height band is
663 represented by five replicate $10 \times 10 \times 0.1$ m slices in each of 40 woodland plots.
664 Lines show model mean \pm SE, with empirical data as dots, with horizontal jitter
665 added for clarity.

666

667 **Figure 5.** Density of (a) foliage and (b) stem across the full canopy profile for
668 all woodland plots, adjusted for maximum height from 0 (0.5 m above ground)
669 to 1 (top of canopy). Panels comparing woodlands (a) with high versus low deer
670 density and (b) in the Weald versus the Welsh Marches. Density measured as
671 number of filled 1 cm³ voxels per m³) on $\log_{10}(x + 1)$ scale with increasing relative
672 height. Lines show model means \pm SE based on 20 plots each. Empirical data are
673 excluded for clarity.

674

Figure 1:



Figure 2:

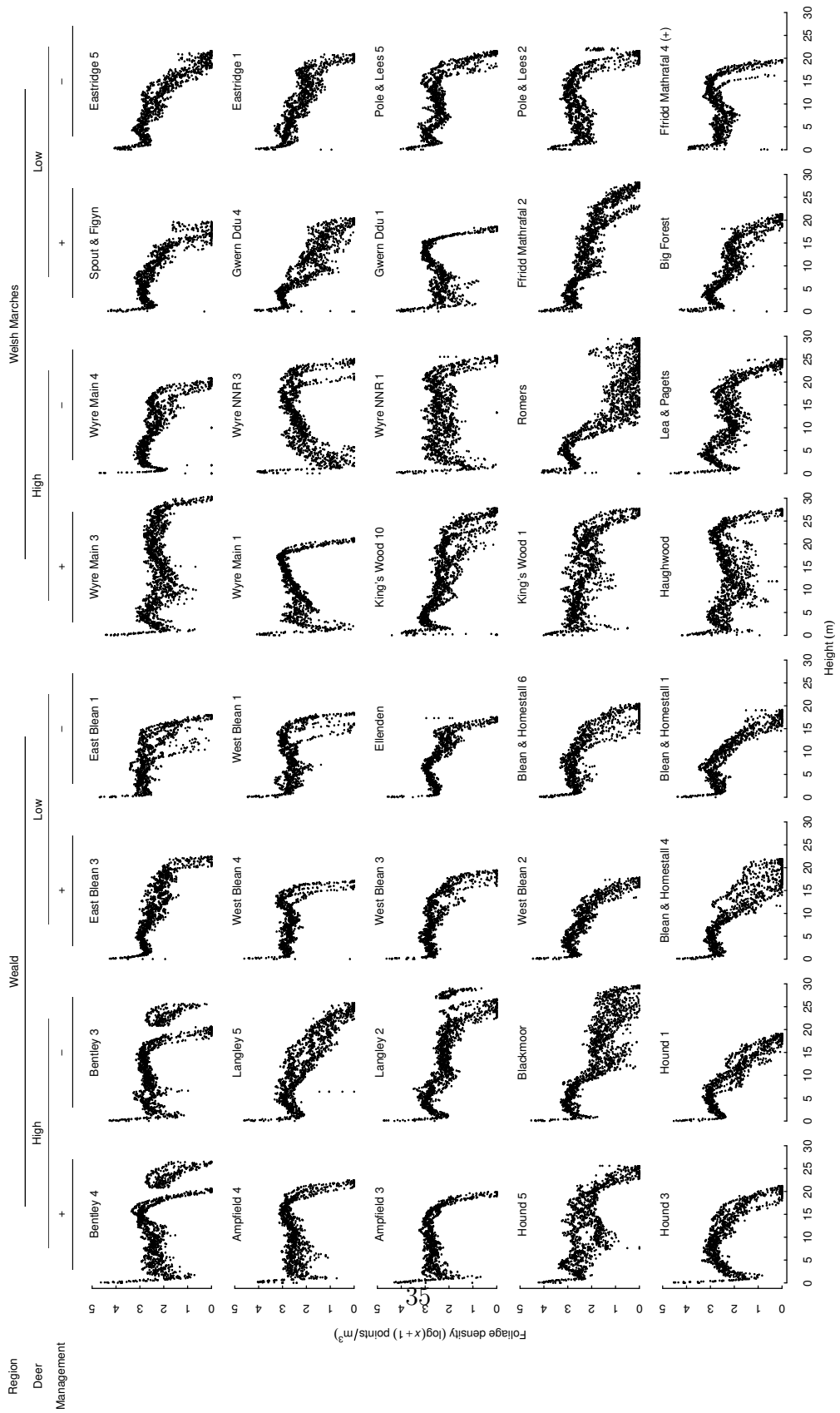


Figure 3:

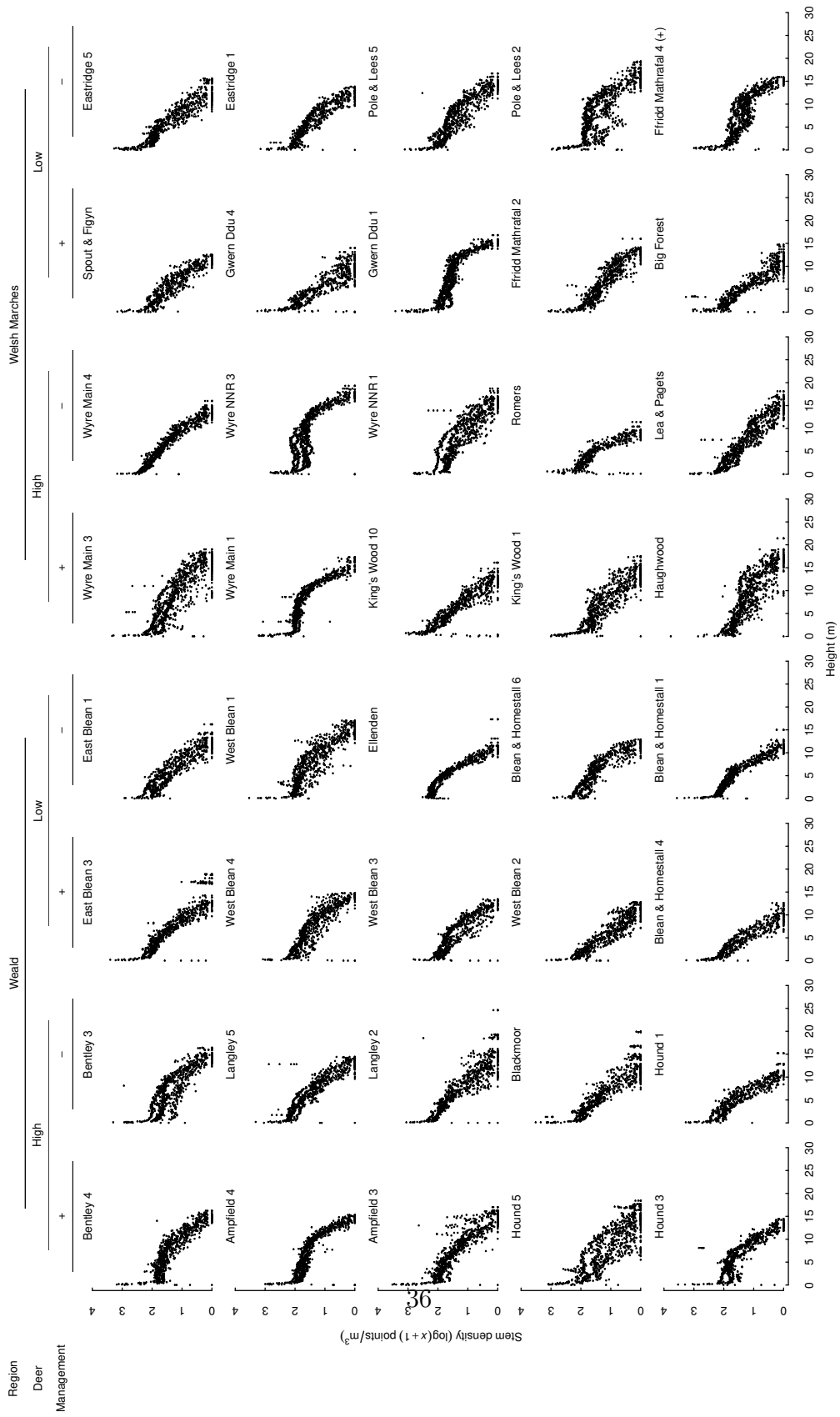


Figure 4:

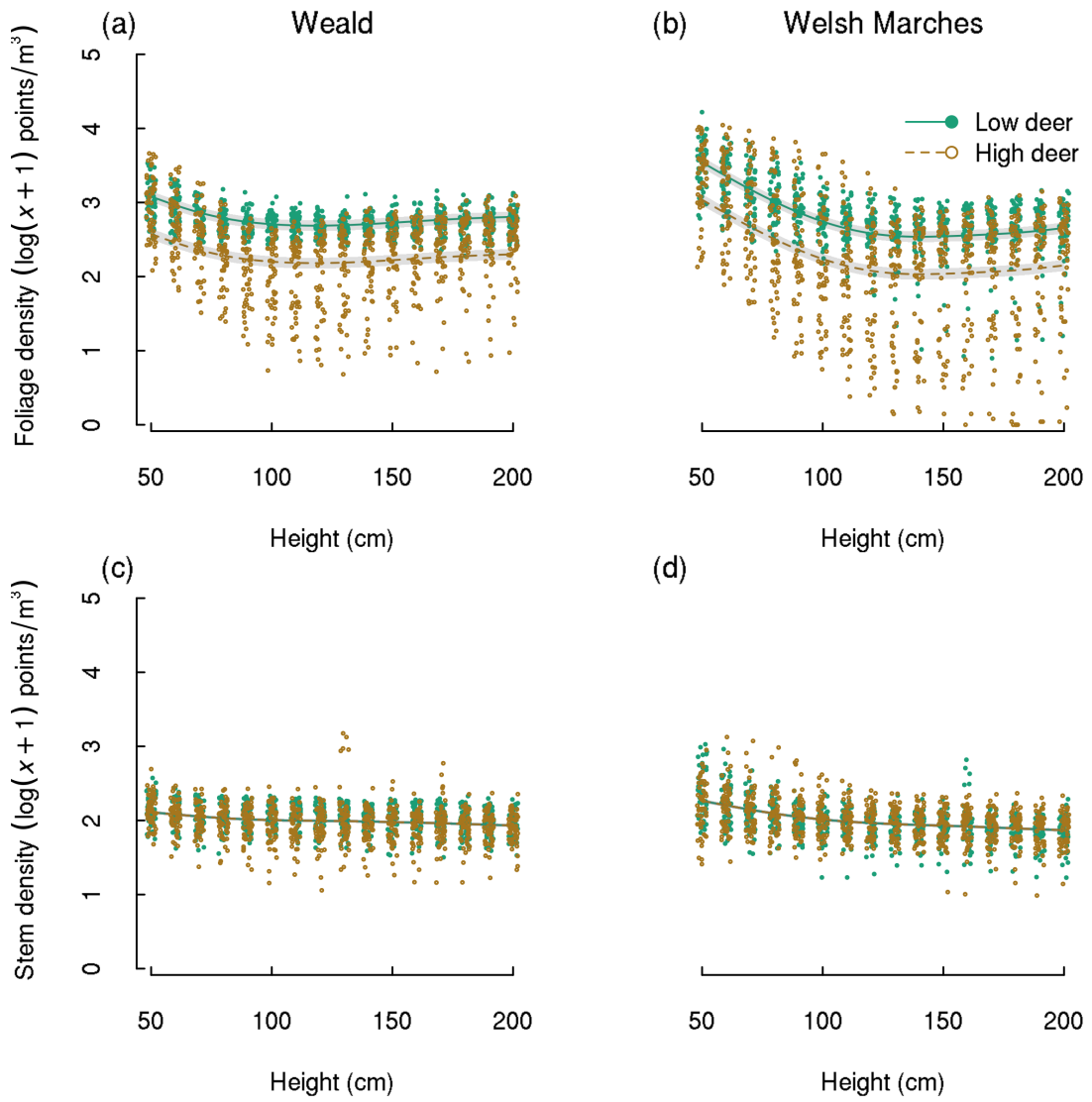


Figure 5:

