Living on the edge – utilising lidar data to assess the importance of vegetation structure for avian diversity in fragmented woodlands and their edges

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ABSTRACT

Context. In agricultural landscapes, small woodland patches can be important wildlife refuges. Their value in maintaining biodiversity may, however, be compromised by isolation, and so knowledge about the role of habitat structure is vital to understand the drivers of diversity. This study examined how avian diversity and abundance were related to habitat structure in four small woods in an agricultural landscape in eastern England.

Objectives. The aims were to examine the edge effect on bird diversity and abundance, and the contributory role of vegetation structure. Specifically: what is the role of vegetation structure on edge effects, and which edge structures support the greatest bird diversity?

Methods. Annual breeding bird census data for 28 species were combined with airborne lidar data in linear mixed models fitted separately at i) the whole wood level, and ii) for the woodland edges only.

Results. Despite relatively small woodland areas (4.9 – 9.4 ha), bird diversity increased significantly towards the edges, being driven in part by vegetation structure. At the whole woods level, diversity was positively associated with increased vegetation above 0.5 m and especially with increasing vegetation density in the understorey layer, which was more abundant at the woodland edges. Diversity along the edges was largely driven by the density of vegetation below 4 m.

Conclusions. The results demonstrate that bird diversity was maximised by a diverse vegetation structure across the wood and especially a dense understorey along the edge. These findings can assist bird conservation by guiding habitat management of remaining woodland patches.

Keywords: avian diversity, fragmentation, vegetation structure, lidar, forest edge, habitat structure, edge effect, biodiversity

1 INTRODUCTION

Habitat fragmentation has been shown to have negative impacts on species diversity across ecosystems (Donald et al. 2001; Mahood et al. 2012). A common example of a modern fragmented landscape is a mosaic of woodland patches scattered in an agricultural matrix. In such settings, fragmentation reduces the total extent of habitat for woodland species, increases patch isolation, and alters the habitat quality of individual patches, for example by changing the physical characteristics, including edge to interior ratios (Fuller 2012). Birds have been widely studied in this context because of the correlation demonstrated between their diversity and overall biodiversity (Kati et al. 2004; Gregory and van Strien 2010). Much previous work has shown direct effects of habitat fragmentation on bird distributions, abundance, diversity and reproductive success (Hinsley et al. 1996; Rodriguez et al. 2001; Turcotte and Desrochers 2003; Hinsley et al. 2009).

Bird diversity in fragmented woodland is influenced by the area, structure and composition of the woods themselves and by the configuration of the surrounding landscape (Opdam et al. 1985; Hinsley et al. 1995; Fletcher et al. 2007). Woodland edge habitat can provide resources such as nest sites for birds that typically forage in more open and agricultural landscapes (Benton et al. 2003; Fahrig et al. 2011; Wilson et al. 2017). In addition, the presence of connecting landscape features such as hedgerows and tree lines can offer additional habitat, cover and dispersal corridors for a range of species (Hinsley et al. 1995; Fuller et al. 2001). Partly due to these reasons, but also strongly influenced by vegetation structure (Fuller 1995; Batáry et al. 2014), higher densities of some bird species may be recorded at forest edges (Schlossberg and King 2008; Knight et al 2016).

The influence of vegetation structure across forest edges has been investigated using conventional field methods, such as ground-based vegetation and bird surveys, and more recently with remote sensing techniques. For example, in the Czech Republic, Hofmeister et al. (2017) assessed the role of fragment size, edge distance and tree species composition on bird communities using aerial imagery and land cover maps and found that both distance to the woodland edge and tree species composition had significant effects for majority of common bird species. In Canada, Wilson et al. (2017) used high-resolution aerial imagery and documented positive relationships between the presence of linear woody features and bird diversity among the forest-edge communities (models including the linear woody features were ranked best). In contrast, Duro et al. (2014) found low or moderate relationships between Landsat imagery based predictors and patterns of bird diversity in an agricultural environment (R^2 values between 0.28 and 0.3 for Landsat TM predictors and avian beta and gamma diversity). Thus, the drivers of diversity in fragmented woodlands, and especially in relation to edge habitat, may be too fine-scaled to be studied without sufficient consideration of the structural composition of vegetation.

While field methods and remote sensing imagery are limited in their ability to estimate the three-dimensional (3D) structure of vegetation, airborne laser scanning (ALS), utilising light detection and ranging (lidar), is ideal for this. The first studies to use lidar to characterize wildlife habitats were conducted on songbirds in the UK (Hinsley et al. 2002; Hill et al. 2004). Since then, the literature has grown considerably with many reviews showing the usefulness of lidar data in wildlife studies across different landscapes (e.g. Bradbury et al. 2005; Vierling et al. 2008; Davies and Asner 2014; Hill et al. 2014), and investigating data fusion and specific metrics with which lidar could assist in habitat modelling (Vogeler and Cohen 2016). Recent bird studies using lidar have assessed the effects of vegetation structure on plant, bird and butterfly species diversity (Zellweger et al. 2017), on grouse broods in boreal forests (Melin et al. 2016), and on habitat envelopes of individual forest dwelling bird species (Garabedian et al. 2017; Holbrook et al. 2015; Vogeler et al. 2013).

In Britain, Broughton et al. (2012) showed that occupation of forest edge by Marsh Tits (*Poecile palustris*) was lower than in the interior, which was associated with differences in habitat structure as assessed using airborne lidar data. Aside from this single species study, the technology has yet to be fully applied to species communities in habitat refuges within highly modified environments**.** This paper combines airborne lidar data with breeding bird census data for four small, isolated woods within an agricultural landscape to: 1) quantify the edge effect on bird species diversity in each wood; 2) determine the role of vegetation structure in any edge effect and how this might vary between the woods; and 3) assess how edge structure could be managed to enhance bird diversity and abundance in small woods.

2 MATERIALS AND METHODS

2.1 Study area

The study was conducted in Cambridgeshire, eastern England (52°25'19.3" N, 0°11'18.3" W), where four remnant patches of ancient woodland that once covered the area lie within ca. 8 km^2 in a landscape dominated by intensive arable agriculture (Figure 1). The four woods comprise Riddy Wood (9.4 ha), Lady's Wood (8.4 ha) Raveley Wood (7.2 ha) and Gamsey Wood (4.9 ha).

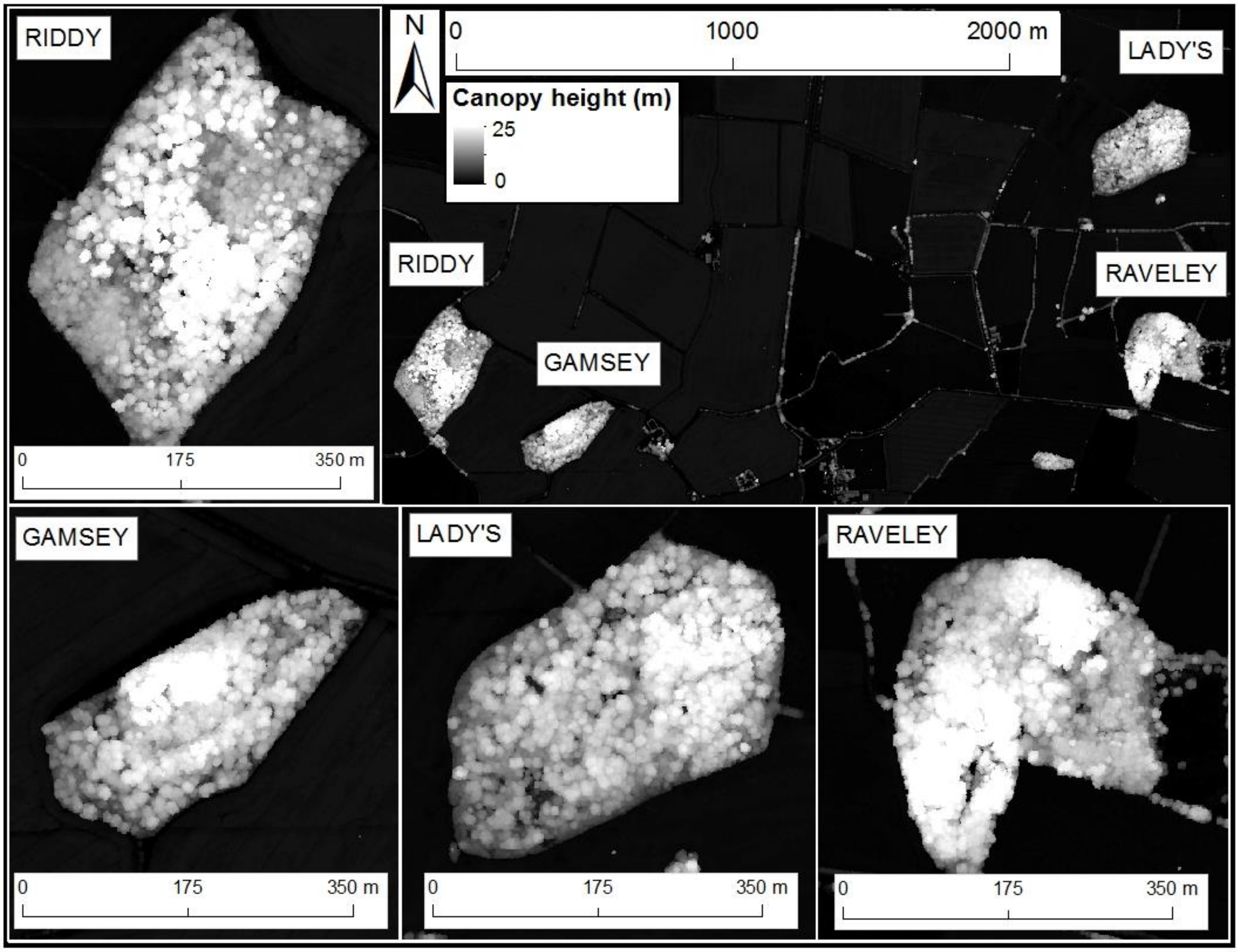

Figure 1. The study area and the four target woods displayed as Canopy Height Models, which show the top surface of the vegetation and its height (lighter shading indicates taller vegetation).

The woods are broadly similar in tree species composition and structure; no wood was being actively managed during the study period (except maintenance of rides and control of deer populations). All woods are dominated by Common Ash (*Fraxinus excelsior*), English Oak (*Quercus robur*), Field Maple (*Acer campestre*) and Elm (*Ulmus* spp.). Elm occurs in discrete patches within each wood among an admixture of the other species. The main shrub species are Common Hazel (*Corylus avellana*), Hawthorn (*Crataegus* spp.) and Blackthorn (*Prunus spinosa*), which are well mixed and common throughout the woods, although the exterior woodland edges are generally dominated by Blackthorn, particularly in Lady's Wood and Riddy Wood. The main differences between the four woods are related to their shape, area and growth-stage of the forest, with the vegetation at Lady's Wood being generally lower than in the other three.

All woods are located within 5 – 20 m above sea level with no steep topography (e.g. hills, ridges, ravines or other distinct topographical features) in the near vicinity. All the woods are similarly surrounded by an agricultural matrix and other larger woods are located ca. 1,200 m away. Individual ringed birds have been noted to move between these woods and the study woods, but there is no evidence for any systematic bias in such movements.

2.2 Bird data collection

As part of a larger, long-term study, the woods were surveyed annually in 2012 to 2015 to determine the abundance and distribution of their breeding bird populations. Each wood was visited four times per year from late March to late July. Visits started shortly after dawn and avoided weather conditions likely to depress bird activity (e.g. rain and strong winds).

Birds were recorded using a spot mapping technique (Bibby et al. 1992) based on the Common Birds Census method of the British Trust for Ornithology (Marchant 1983). Each wood was searched systematically using a route designed to encounter all breeding territories (Bellamy et al. 1996). Routes varied between visits, but always included walking around the perimeter. All birds seen or heard, and their activity, were recorded on a map of the wood and the mapped locations were later digitised into a GIS. Due to the small size of the woods, and the familiarity of the surveyors with the sites, the accuracy of the mapping was estmated to be ca. ± 10 m. Individuals were recorded only once, omitting any suspected repeat observations, and only the initial location of mobile individuals was included in analyses.

Only records of putative adults were included in the analysis because the locations of dependent young are not independent of their parents, and because juvenile habitat use is not necessarily related to breeding requirements or selection of the species concerned. In the event, the fourth visit was omitted entirely from the analysis because it contained a high proportion of juvenile records. Several species were also omitted: nocturnal species such as Owls (*Strix* spp.) because the census technique could not detect them reliably; game birds because their presence/absence was influenced by local rearing and release activities; species such as Grey Heron (*Ardea cinerea*) and Mallard (*Anas platyrhynchos*) which were associated with ponds; colonially breeding species such as Jackdaws (*Corvus monedula*); and ubiquitous Woodpigeons (*Columba palumbus*). In total, the bird data comprised 3506 observations of 28 species (Table 1).

Table 1. The number of bird observations recorded from each wood by species during three survey visits in each of four years (2012-15).

Species	Latin name	Number of observations				
		Raveley	Riddy	Lady's	Gamsey	Total
Blackbird	*Turdus merula*	36	72	60	49	217
Blackcap	*Sylvia atricapilla*	43	69	74	39	225
Blue tit	*Cyanistes caeruleus*	161	217	190	137	705
Bullfinch	*Pyrrhula pyrrhula*	3	7	18	10	38
Chaffinch	*Fringilla coelebs*	65	108	119	64	356
Chiffchaff	*Phylloscopus collybita*	16	28	40	17	101
Coal tit	*Periparus ater*	18	15	8	11	52
Crow	*Corvus corone*	7	2	1	8	18
Dunnock	*Prunella modularis*	9	8	23	10	50
Garden warbler	*Sylvia borin*	0	1	5	0	6
Goldcrest	*Regulus regulus*	2	1	1	0	4
Goldfinch	*Carduelis carduelis*	7	5	7	4	23
Great spotted woodpecker	*Dendrocopos major*	24	30	23	16	93
Great tit	*Parus major*	97	105	129	74	405
Green woodpecker	*Picus viridis*	7	17	14	17	55
Jay	*Garrulus glandarius*	4	3	8	4	19
Long-tailed tit	*Aegithalos caudatus*	28	30	23	25	106
Magpie	*Pica pica*	10	1	9	0	20
Marsh tit	*Poecile palustris*	19	15	1	8	43
Nuthatch	*Sitta europaea*	0	6	0	1	7
Robin	*Erithacus rubecula*	72	83	119	57	331
Song thrush	*Turdus philomelos*	1	5	5	12	23
Stock dove	*Columba oenas*	20	36	27	12	95
Treecreeper	*Certhia familiaris*	46	41	31	30	148
Whitethroat	*Sylvia communis*	2	8	5	4	19
Willow warbler	*Phylloscopus trochilus*	0	2	2	0	4
Wren	*Troglodytes troglodytes*	51	106	129	47	333
Yellowhammer	*Emberiza citrinella*	1	1	2	6	10
Total		749	1022	1073	662	3506

2.3 Airborne lidar data collection and pre-processing

The lidar data of the study area were collected with a Leica ALS50-II laser scanning system during leaf-on conditions on June 1st 2014. The bird survey years (2012-2015) were selected to be close to this year to ensure temporal compatibility with vegetation structure (Vierling et al. 2014). Bird survey data were not available for 2016.

The lidar sensor was mounted on a fixed-wing aircraft flown at an altitude of ca. 1600 m with a scan half angle of 10 degrees and a pulse repetition frequency of 143.7 MHz, resulting in a nominal sampling density of 1.9 pulses per m^2 and a footprint size of ca. 35 cm. Due to overlapping flight lines the average sampling density in the study area was 2.7 pulses per m^2, a density that has proven to be sufficient in describing vegetation structure when assessing wildlife habitats and forest structural profile in general (Zellweger et al. 2017; Melin et al. 2016; Hill et al. 2004). The ALS50-II device captures a maximum of four return echoes for one emitted laser pulse with an approximate vertical discrimination distance of 3.5 m between the echoes. All of the echo categories were used in this study. The lidar echoes were classified into ground or vegetation hits following the method of Axelsson (2000), as implemented in LAStools software. Next, a raster Digital Terrain Model (DTM) with a 1 m spatial resolution was interpolated from the classified ground hits using inverse distance weighted interpolation (IDW). This DTM was then subtracted from the elevation values (z-coordinates) of all the lidar returns to scale them to above ground height.

2.4 Calculating variables of diversity and vegetation structure

For analysis, the four woods were delineated into cells with an area of ca. 215 m^2. The cell size was chosen to account for potential inaccuracies in bird locations and to ensure sufficient lidar echoes within the cells to adequately calculate the 3D metrics of vegetation structure. The delineation was done with basic geoprocessing tools in QGIS. Cells were constrained to lie within the woodland boundary and hence cell shape was allowed to be irregular to ensure similar cell areas and to fit within the irregular boundaries of the woods. However, it was ensured that the cells, especially along the edges, were of approximately similar depth and shape so that differences would not introduce any systematic bias in relation to bird occurrence probabilities. Next, bird data (i.e. individual bird locations) and lidar data were extracted for each cell, which formed the research setting (Figure 2).

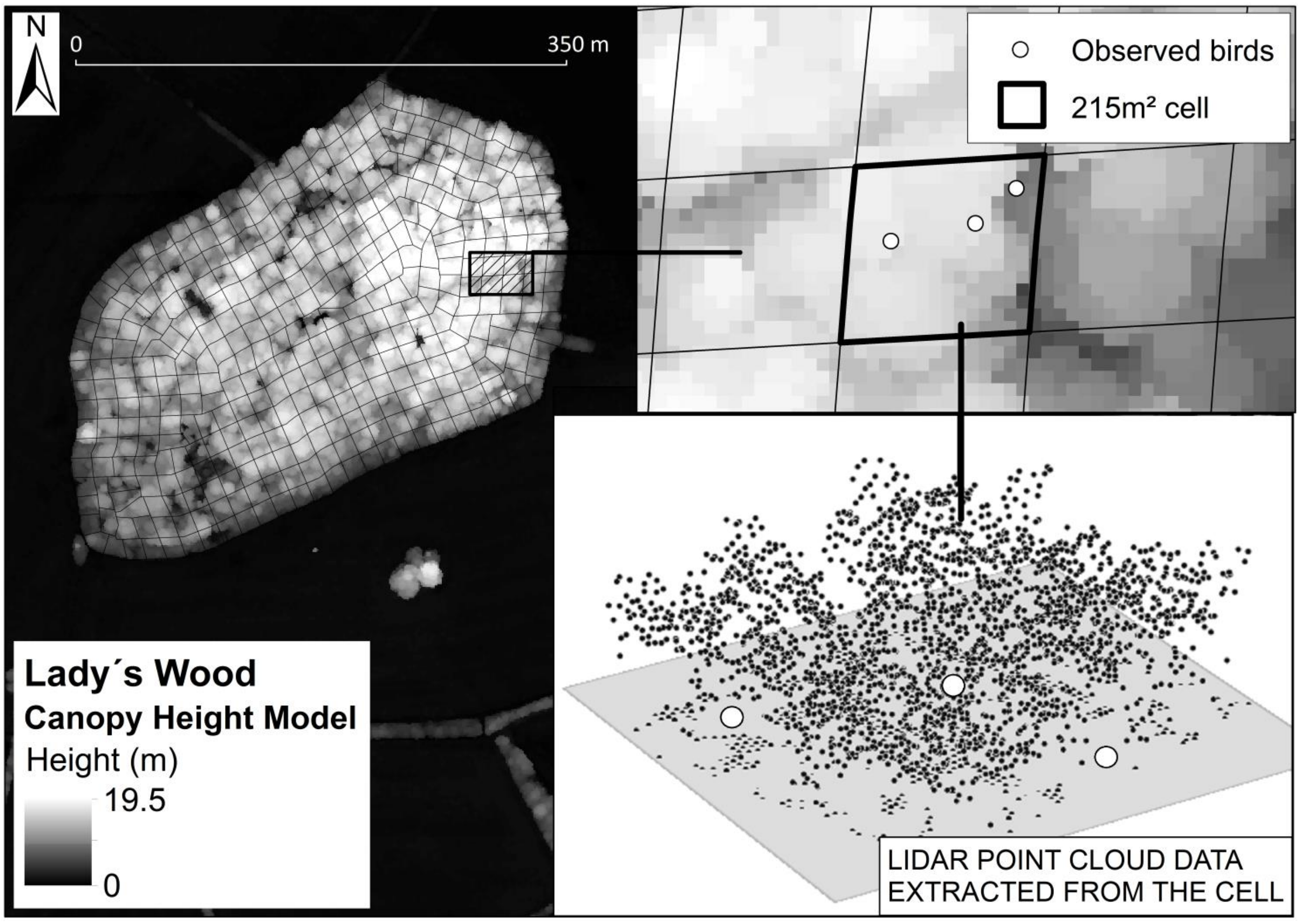

Figure 2. Lady´s Wood delineated into grid cells, showing the cell-level bird and lidar data.

Lidar data were used to obtain metrics of vegetation structure such as maximum and average canopy height and its standard deviation, proportion of vegetation above ground level (defined as > 0.5 m) , proportion of vegetation at different height levels of the overstorey (canopy) and understorey (shrub) layers, and Foliage Height Diversity (FHD) (see Table 2). FHD was calculated according to MacArthur and MacArthur (1961):

$$FHD = -\sum p_i * \log(p_i) \qquad (1)$$

where p_i is the proportion of lidar returns in zone i. The FHD was derived by binning the lidar returns into zones according to their height: 0.5 – 4 m, > 4 – 8 m, > 8 – 12 m, > 12 – 16 m, > 16 – 20 m and > 20 m. The division created six nearly equal height classes in terms of how the proportion of vegetation was spread throughout the vertical profile of the woods. The variable FHD has been estimated in a similar fashion from lidar data for bird habitat modeling in Clawges et al. (2008). The chosen variables have proven to be attainable from lidar data and useful in assessing vegetation structure and bird habitats, in particular (Hill et al. 2014).

Other cell-specific metrics included the Euclidean distance from the centroid of each cell to the nearest woodland-field edge, and for the edge cells only, the Euclidean distance to the nearest hedgerow and the aspect (i.e. the slope direction or bearing), which was calculated from the DTM. The purpose of aspect was to assess whether, for example, south-facing edges differ in their vegetation structure compared with north-facing ones due to different light conditions or degree of exposure. Distances to hedgerows were included because hedges may provide hedgerow-dwelling species with access points to the edges of small woods (Hinsley et al. 1995). The definition ‘nearest hedgerow’ included hedges adjoined to the woodland edge and also those within 300 m (the maximum distance to any hedge).

Finally, indices of bird diversity were derived for each cell as species richness (*SpeciesN*) calculated as the cumulative total number of species, bird abundance (*BirdN*) calculated as the maximum number of individual birds encountered in a cell in any one survey, and the Shannon index of diversity (Shannon 1948) (*ShannonD*). All the metrics are listed in Table 2.

Table 2. The cell-specific predictor and response variables used in the analysis

PREDICTOR VARIABLES	
Variable	**Description**
WoodID	Used as the random effect as the data were grouped into four woods.
FHD	Foliage Height Diversity. Calculated from all returns using equation [1]. FHD conveys the proportional distribution of vegetation throughout the full vertical profile of the forest.
p_veg	% of lidar returns coming from above 0.5 m (vegetation hits). A *p_veg* value of 0.55 would mean that 55% of returns from this cell came from above 0.5 m.
**p_canopy_X*	% of lidar returns coming from above X m in the vegetation profile, calculated from all the returns. A *p_canopy_8* value of 0.75 would mean that 75% of returns from this cell came from above 8 m.
**p_shrub_X*	% of lidar returns between 0.5 and X m, calculated only from the returns below X m. A *p_shrub_4* value of 0.6 would mean that 60% of the returns coming from below 4 m within this cell hit vegetation, not the ground.
h_max	Maximum height of the lidar returns per cell.
h_avg, hstdev	Average height of the lidar returns per cell and their standard deviation
EdgeDistance	The Euclidean distance (m) from the centroid of a cell to the nearest edge.
HedgeDistance 1 and 2	The Euclidean distance (m) from the centroid of a cell to the nearest hedgerow (calculated for the edge cells only). Assessed as a continuous variable (1) and as a categorical variable (2) divided into 25 m classes, i.e.: 0 – 25 m, > 25 – 50 m, etc.
Aspect	The slope direction of the cell (calculated for the edge cells only). Assessed as a categorical variable divided into eight classes, i.e. north, north-east, east etc.

RESPONSE VARIABLES	
Variable	**Description**
ShannonD	The Shannon index of diversity
BirdN	Bird abundance: the maximum number of individual birds observed in the cell during any single survey.
SpeciesN	Bird species richness: the cumulative total number of species observed within the cell.

**four cut-off values (4, 6, 8 and 10 m) were used for assessing the density of shrub- and canopy cover at different heights. This equals to eight different variables, four for shrub cover and four for canopy cover.*

2.5 Modeling bird diversity and abundance

The aim of the modeling was to examine which variables had the greatest effect on bird diversity and whether or not this differed between the four woods. Therefore, linear mixed-effects models were the chosen method. Mixed models extend the basic linear model such that they recognize grouped or nested structures in data via random effects. Here, the data were grouped into four separate woods with different areas and structures.

Altogether, two sets of models were fitted to the data. The first models quantified for cells across the whole wood the most significant predictors of bird diversity out of those listed in Table 2. The second models were fitted only to data from the row of cells immediately adjacent to the edge of each wood, corresponding to a width of approximately 14.7 m. This was to examine what drives bird diversity along the edge itself, i.e. establish what determines a favoured edge and how its vegetation might differ from sections of edges that are avoided. Variable selection was done by forward selection where the single most significant variable was first added to the model, after which the process was iterated until no more variables could be added; the final model included only significant ($p < 0.05$) variables. All modeling and analyses were conducted in R (R Core Team 2017) using the package *nlme* (Pinheiro et al. 2017) and *ggplot2* (Wickham 2009) for visualizations. Package *lmfor* (Mehtätalo 2017) were used to examine model residuals, which showed no non-linearity or heteroscedasticity. Multicollinearity among the final predictors was examined with the *vis* function from the package *car* (Fox and Weisberg 2011), and it was noted not to be an issue. Spatial autocorrelation (SAC) was examined individually for each wood and it was noted to be present in the immediate neighborhood of a cell. This was accounted for by using a linear SAC structure with the built-in functions available in the *nlme* package.

3 RESULTS

3.1. Bird diversity in the study area

The four woods differed in how many species they supported, and in individual species abundance. The most abundant generalists, such as the Blue Tit, Robin and Great Tit, followed a consistent pattern where they were less abundant in the two smaller woods (Gamsey and Raveley) than in the two larger woods (Riddy and Lady's). In contrast, some edge-preferring species, such as Yellowhammer and Whitethroat, were encountered more often in the smallest wood (Gamsey) than in the others (Table 1). Bird diversity and abundance per unit area were highest in Gamsey, followed by Lady's, Raveley and Riddy Woods (Table 3).

Table 3. Summary statistics of the cell-level bird diversity metrics in the four woods. *ShannonD* refers to Shannon Index, *BirdN* to the maximum number of birds encountered during one visit and *SpeciesN* to the number of different species encountered. *Avg.* refers to arithmetic mean, *Max.* to the maximum value and *Std.Dev* to standard deviation.

WoodID (and size)	***ShannonD***			***BirdN***			***SpeciesN***		
	Avg.	Std.Dev.	Max.	Avg.	Std.Dev	Max.	Avg.	Std.Dev.	Max.
Riddy (9.4 ha)	0.56	0.56	2.36	1.22	0.58	6	1.93	1.60	12
Lady's (8.4 ha)	0.62	0.59	2.15	1.33	0.58	4	2.13	1.72	9
Raveley (7.2 ha)	0.61	0.56	2.08	1.31	0.62	4	2.08	1.53	8
Gamsey (4.9 ha)	0.69	0.63	2.38	1.35	0.70	6	2.39	1.95	12

3.2 Forest structure in the woods and their edges

The decision to group the data by wood prior to the modeling was justified by the clear difference in the details of their structure (Figure 3A). Lady's Wood is dominated mostly by vegetation below 11 m in height and with all trees being below 20 m. In addition, Lady's Wood (together with Raveley) is more open than the other woods, as shown by a proportionally higher number of ground echoes (class 1 in Figure 3A). By contrast, Gamsey Wood has the lowest proportion of ground echoes and (together with Riddy Wood), the tallest canopies.

The differences are further evident at the woodland edges (Figure 3B). Lady's Wood is clearly different from the other woods by having over 80 % of its edge vegetation below 7 m. Also, the edge of Lady's Wood is the densest, having the lowest proportion of ground echoes (class 1 in Figure 3B). By contrast, Raveley Wood has the highest proportion of vegetation in the higher canopies (above 12 m) and the lowest amount below 8 m at its edge. Raveley Wood also has the most open edges (i.e. highest proportion of ground and near-ground echoes – class 1 in Figure 3B).

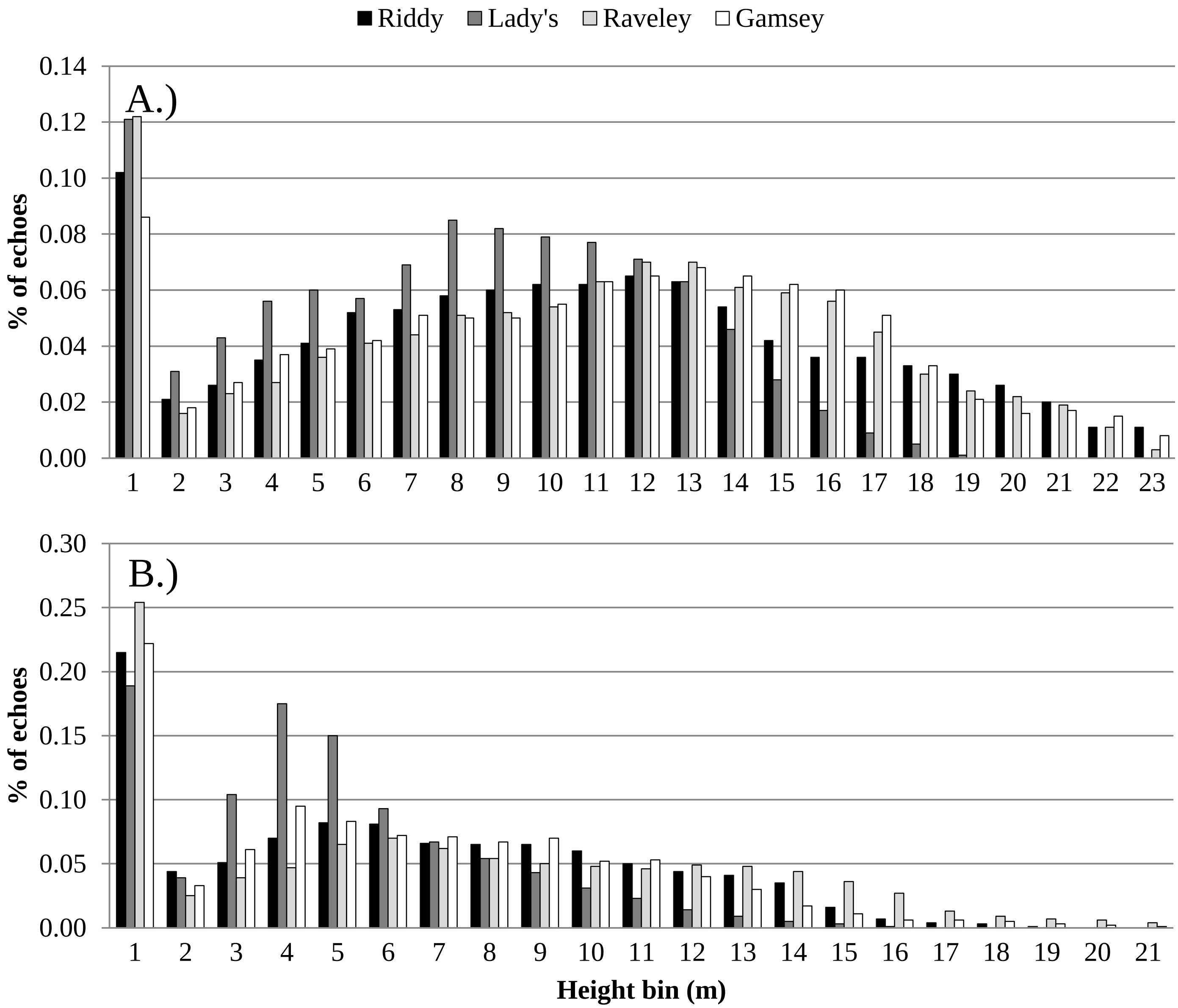

Figure 3. Histograms showing the proportion (Y-axis) of lidar echoes reflecting from vegetation heights in 1 m height bins in four whole woods (A.) and along their edges only (B.). The X-axis shows different height bins, where Class 1 includes echoes below 1 m, Class 2 includes those within 1 – 2 m, etc. In A. Class 23 includes all echoes above 22 m, and in B. Class 21 includes all echoes above 20 m.

3.3 Drivers of bird diversity and abundance in the woods

Three variables, *EdgeDistance*, *p_veg* and *p_canopy_6* (Table 2), were selected as the most significant predictors in all the 'whole wood' models, i.e. for all three response variables (*SpeciesN*, *BirdN*, *ShannonD*), while the amount of vegetation between the ground and 4 m was the single most significant predictor in the 'edge models' for all three response variables (Table 4). Thus, bird diversity and abundance decreased with increasing edge distance and increased with higher amounts of vegetation (*p_veg*). However, the relationships to a second variable, *p_canopy_6* (the amount of vegetation above 6 m), were negative indicating that bird abundance and diversity were negatively influenced by an increase in the amount of vegetation if it took place only in the top canopy and not at all in the shrub layer, i.e. below 6 m. Similar trends were also apparent within the model output for woodland edges, where the hotspots of avian abundance and diversity were the edges with the densest shrub cover (i.e. the highest amount of vegetation below 4 m). As all three tested bird metrics were highly consistent in their relationships with the predictor variables, only *SpeciesN* is shown for reference in Figures 4 and 5.

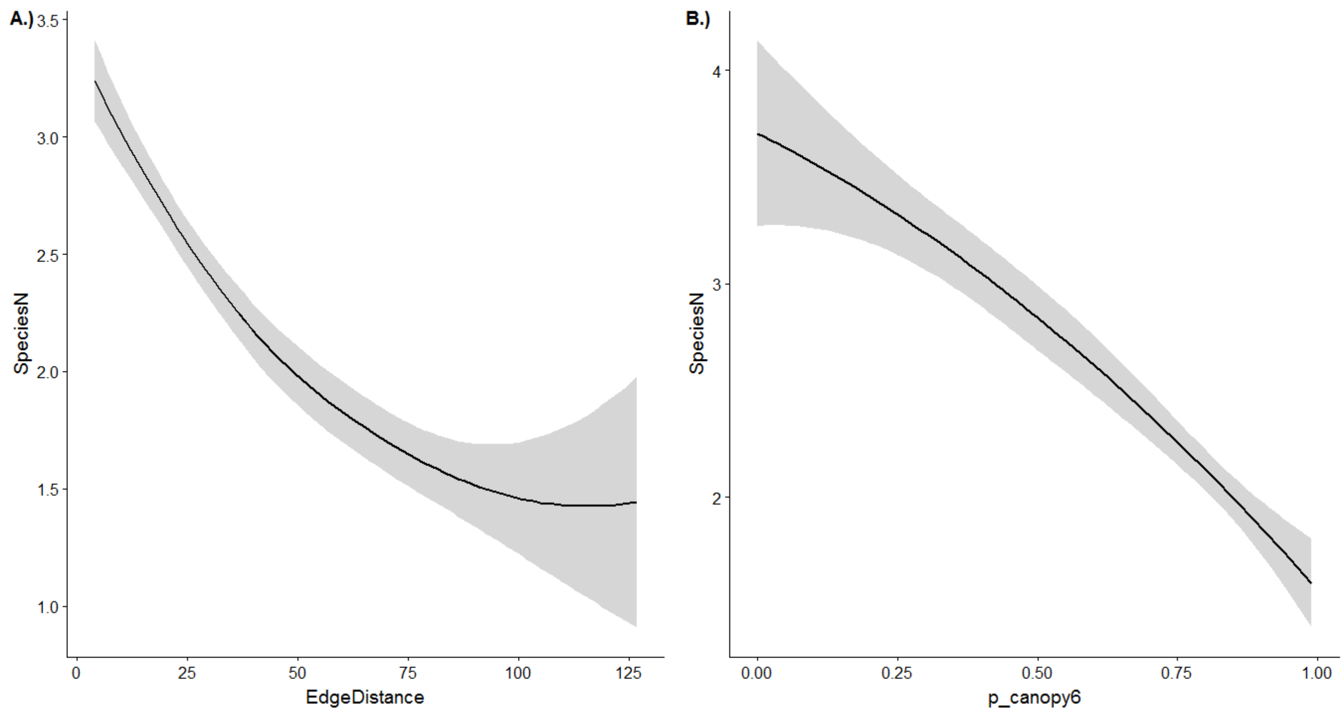

Figure 4. Illustration of the relationship between *EdgeDistance (A)* and *p_canopy_6 (B)* with species richness *(SpeciesN*) in the 'whole woods' (all woods combined). The grey polygons around the lines depict the standard errors. *EdgeDistance* is the Euclidean distance to the nearest woodland-field edge and *p_canopy_6* is the proportion of lidar echoes above 6 m.

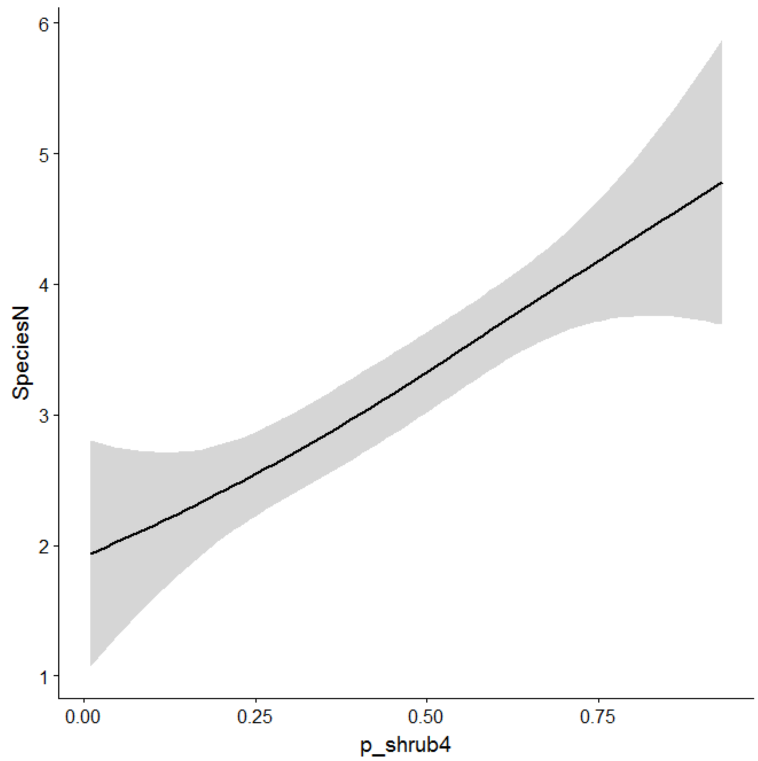

Figure 5. Illustration of the relationship between *p_shrub_4* and species richness *(SpeciesN*) in the woodland edges (all woods combined). The grey polygon around the line depicts the standard error. *p_shrub_4* is the proportion of echoes from below 4 m which hit vegetation.

It was notable that the effects of both distance from the woodland edge and shrub cover were consistent between the four woods and for all the diversity metrics, albeit varying in strength (Table 4). Gamsey Wood, despite its smallest size, had the highest average diversity and most bird species per unit area, followed by Lady's, Riddy and Raveley Wood. Similarly, the decrease in bird diversity as edge distance increased was evident in all woods, but due to its smallest size, the effect was the strongest in Gamsey Wood (Table 4A). Along the edge, there was no significant difference in bird diversity between the woods and the relationships of the diversity metrics were also consistent: as the amount of vegetation below 4 m increased, so did bird abundance and diversity (Table 4B).

Table 4. The mixed models of bird abundance and diversity in relation to vegetation structure in the four woods. The random ‘wood effects’ relate to corresponding intercept values from fixed effects. For instance, the wood effect of *Raveley* on the Shannon index (-0.14) is subtracted from the Intercept of 0.55, while that of *Gamsey* (0.19) is added to it. All parameter estimates were significant at $p < 0.05$.

A.) WHOLE WOOD MODELS

Fixed effects	**Model parameter estimates**							
Response	***Intercept***		***EdgeDistance***		***p_veg***		***p_canopy_6***	
	Estimate	Std.error	Estimate	Std. error	Estimate	Std.error	Estimate	Std.error
ShannonD	0.55	0.2	-0.01	0.002	0.75	0.25	-0.47	0.11
BirdN	1.47	0.21	-0.005	0.001	0.46	0.28	-0.22	0.09
SpeciesN	2.11	0.57	-0.02	0.01	2.18	0.71	-1.57	0.31

Random effects	**The wood effect**			**EdgeDistance**		
Wood	*ShannonD*	*BirdN*	*SpeciesN*	*Shannon*	*BirdN*	*SpeciesN*
Raveley	-0.14	0.004	-0.38	0.004	-0.0002	0.01
Riddy	-0.05	-0.03	-0.05	0.002	0.0002	0.004
Lady´s	0.01	0.02	0.01	-0.001	-0.002	0.0003
Gamsey	0.19	0.002	0.19	-0.01	-0.0004	-0.02
σ	0.15	0.03	0.43	0.004	0.0003	0.01
ε	0.53	0.58	1.47			

B.) EDGE MODELS

Fixed effects	**Model parameter estimates**			
Response	***Intercept***		***p_shrub_4***	
	Estimate	Std.error	Estimate	Std.error
ShannonD	0.57	0.1	0.86	0.18
BirdN	1.34	0.13	0.54	0.26
SpeciesN	1.77	0.34	3.24	0.61

Random effects	**The wood effect**		
Wood	*ShannonD*	*BirdN*	*Species*
Raveley	< 0.001	< 0.001	< 0.001
Riddy	< 0.001	< 0.001	< 0.001
Lady´s	< 0.001	< 0.001	< 0.001
Gamsey	< 0.001	< 0.001	< 0.001
σ	< 0.001	< 0.001	< 0.001
ε	0.61	0.39	2.06

Figure 6 further illustrates the relationship between bird diversity and shrub vegetation at two specific sites along the edge of Gamsey Wood with the lowest and the highest numbers of bird species respectively. Whereas the most diverse section in terms of avifauna (Figure 6B) had most of its vegetation spread between the ground and 4 m with comparably few ground echoes, the least diverse section (Figure 6A) was almost lacking vegetation in this same height stratum. This section of the edge has a high overstorey canopy, which continues down until the height of 4 m after which a clear majority of the lidar echoes hit the ground indicating a lack of vegetation below 4 m.

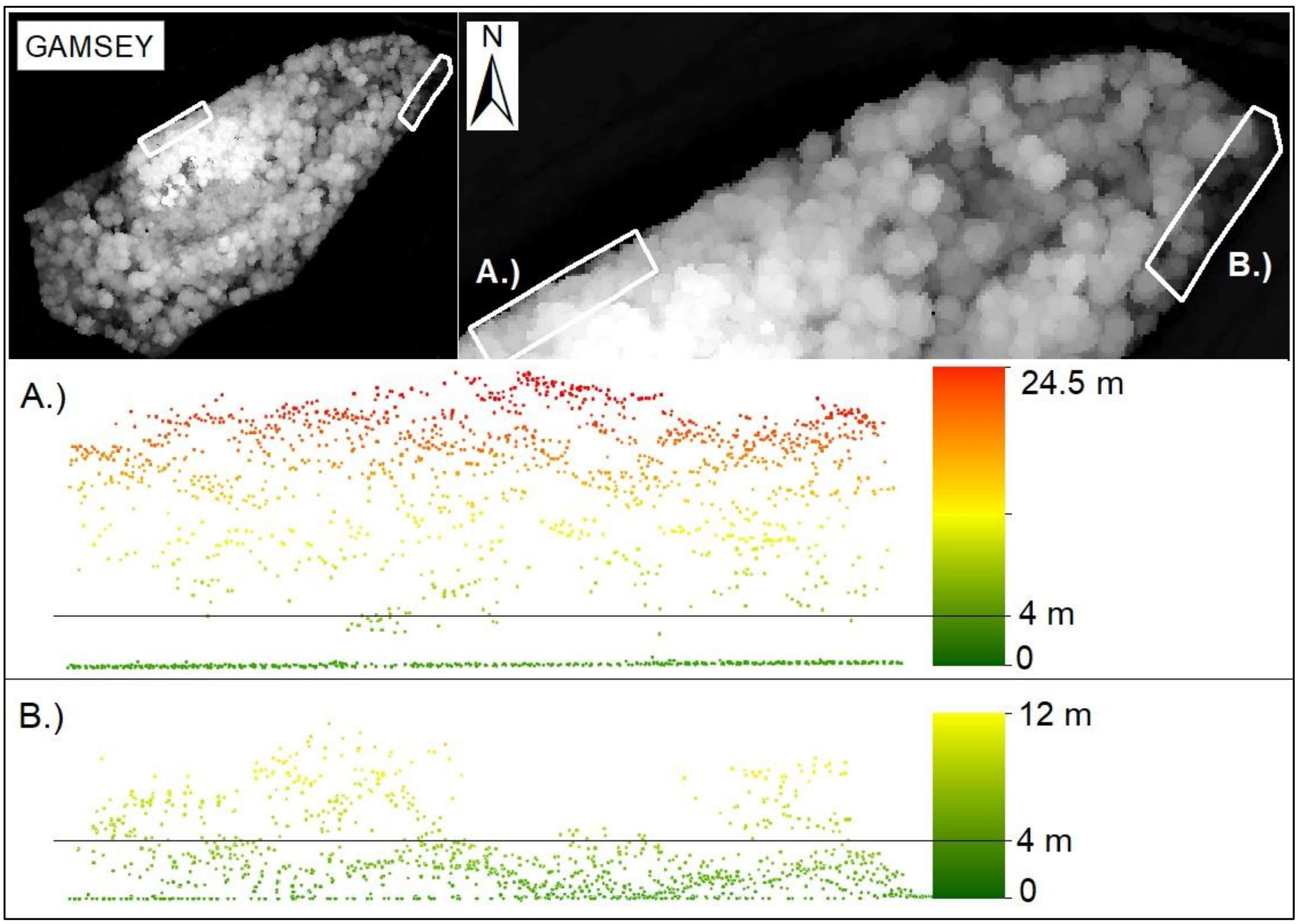

Figure 6. Visualization of the forest structure in two sites along the edge of Gamsey Wood with the lowest (A) and highest (B) species diversity. Both sections cover an area of ca. 15 x 40 metres. Section A had average values of 1.5 species per cell while Section B had average values of 10.3 species per cell.

4 DISCUSSION

This study examined the drivers of bird species diversity and abundance in relation to vegetation structure across four woods and, specifically, at their edges. Bird diversity and abundance were found to be positively affected by vegetation density, and the importance of the shrub layer for both whole woods and the edges was also revealed. These findings were achieved by combining lidar data with spot-mapped bird data, which allowed the examination of the spatial relationships between bird distributions and vegetation structure across the whole woods and in relation to the full vegetation height profile. The capabilities of the type of lidar data used, as well as the variables derived from it, in characterising 3D vegetation structure have been shown by many previous studies (Zellweger et al. 2017, Melin et al. 2016, Broughton et al. 2012, Vogeler et al. 2013, Hill et al. 2004). However, our results extend those of other studies where optical remote sensing data have been used to assess bird-edge relationships (Duro et al. 2014; Pfeifer et al. 2017), without the advantage of 3D data on vegetation structure. While field methods have quantified the importance of shrub vegetation in edge-habitats (Knight et al. 2016), lidar offers an efficient and, due to national scanning campaigns, an increasingly available method (Melin et al. 2017).

Small woods are often regarded as being composed of 'all edge', but our results showed a clear edge effect for all four woods, with a decline in bird diversity and abundance from the edges to the centres across a distance of 75 m or more (Figure 4). While both the number of species and abundance responded positively to increasing vegetation density throughout a wood, the main driver of this response was the density of vegetation below 6 m, i.e. within the shrub layer (Figure 4, Table 4A).

Vegetation density in the shrub layer was similarly important within the edges themselves (Figure 5), with all the edge models selecting vegetation heights of 4 m (variable *p_shrub_4*) as the single most significant driver of bird diversity and abundance (Table 4B). The distance to the nearest hedgerow had a mild negative effect on bird species richness (*SpeciesN*), but with a p-value of 0.07 it was dropped from the final models. Several bird species, including Dunnock, Goldfinch, Whitethroat and Yellowhammer, which are typical of hedgerow habitats in Britain (Fuller et al. 2001), will also nest in the edges of small woods (Hinsley et al. 1995) and occurred in small numbers in the study woods (Table 1). However, overall bird diversity at the edge was most strongly influenced by vegetation structure in the edges themselves, suggesting that such ‘hedgerow species’ (and others) may be absent from woodland edges in the absence of suitable vegetation structure.

The response of birds to edge habitat appears to be more complex than the edge effect proposed by Odum (1958), whereby species richness and abundance increased in the transition zone, or ecotone, between two habitat types. Instead, it seems to depend on a number of factors including the characteristics of the species community, the structure of the edges in relation to interior habitat, and perhaps most especially the structure (e.g. patch size and spatial arrangement) and history of the wider landscape (Baker et al. 2002). For example, a study of declining shrubland birds in the eastern United States (Schlossberg and King 2008) found that many species avoided edges and achieved higher densities in patch centres; their presence in forest edges being more a consequence of habitat scarcity than active preference. Why such bird species, often regarded as ‘early successional’ and hence potentially typical of shrubby forest edges (Fuller 2012), should actually avoid edges is unclear, but the more recent history of landscape change in the United States compared to Europe, and hence the time available for bird species to adapt, may have a role (Martin et al. 2012). Other factors including habitat quality, microclimate, competition, and parasitism or predation may also be involved (Murcia 1995), the latter effect being suggested as an ‘ecological trap’ (Gates and Gysel 1978; Chalfoun et al. 2002). Intensive landscape modification may, however, dilute the ‘ecological trap’ effect by reducing predator diversity and abundance (Batáry et al. 2014). At some scales, detection of strong external edge effects may be influenced by the frequency and distribution of internal edges. In a study of forest fragments (maximum size 255 ha) in the Czech Republic, Hofmeister et al. (2017) found that 60% of the forest area was within 50 m of an edge and only 10% at more than 150 m.

In intensive agricultural landscapes of the UK, and elsewhere in Europe, habitat edges, along with hedgerows, may constitute the majority of the shrubby vegetation available. Hence these habitats tend to attract woodland species requiring dense cover for nesting and/or foraging and open country species in search of nest sites, as well as early successional species. This general pattern was apparent in our study woods; species recorded more frequently (on average) within 40 m of the edge than elsewhere included woodland species (Wren, Chaffinch, Long-tailed Tit, Robin and Blackbird), open country species (Goldfinch and Yellowhammer), and early successional species (Garden Warbler, Whitethroat and Dunnock). Green Woodpecker was also more frequent near edges, which was consistent with its use of trees for nest holes whilst mostly foraging outside of woodland. The central areas of our study woods were not lacking a shrub layer, but the edges had a greater density of lower-level (i.e. below 4 m) shrub vegetation potentially offering more foraging resources and greater cover, and were accessible to the open country species mentioned above. These kinds of ecotonal woodland edges with relatively low bushy growth grading into taller shrub and tree cover are generally recommended as a management objective (Symes and Currie 2005; Blakesley and Buckley 2010). Other studies have also reported greater bird abundance and diversity at forest edges and ecotones, including both internal and external edges (Fuller 2000; Terraube et al. 2016).

Higher light intensity along unshaded bushy edges can promote greater vegetation density with concomitant greater potential to provide resources. For example, flowering shrubs in the woodland edge may provide important food resources in early spring and hence increased bird usage. In our woods, Blackthorn in flower attracted species such as tits, most notably Marsh Tits, which are more usually associated with mature trees. The dense structure of Blackthorn also provided nest sites for a range of species including Long-tailed Tit, Chaffinch, Blackcap and Dunnock, but some of these, particularly the former two, also foraged in mature trees within the wood. Our finding that both bird abundance and diversity had a similar relationship with edge distance and vegetation structure (*p_canopy_6* and *p_shrub_4*) was consistent with this hypothesis that the complexity of the vegetation offers greater niche diversity (more food, cover and nest sites supporting more individuals). Thus, woodland bird diversity seems to depend on the overall structural complexity of the wood: a patch of scrub without trees or a stand of trees lacking shrubs are both unlikely to support the range of species typical of structurally diverse woodland.

Previous work (Hinsley and Bellamy 1998) found that the co-occurrence of greater species richness and the abundance of individual bird species in small woods were influenced by their connectivity, the number of habitat types present within a wood and the density of vegetation in the shrub layer. The present study highlights the importance of the woodland edge in providing dense shrubby vegetation. Large tracts of woodland can contain complex networks of rides and glades with shrubby edge vegetation whilst retaining the overall essential structure of closed canopy woodland. In contrast, small woods are too small to support extensive internal structures without becoming disjointed, i.e. more open habitat with a greater resemblance to scrub than woodland. Thus, the external edges of small woods are a valuable resource, and especially so in intensive arable landscapes where the contrast between the patches of semi-natural habitat and the cropland tends to be abrupt and stark.

Although there seem to be few genuinely edge-dependent bird species, this may be largely a matter of how ‘edge’ is interpreted. For example, Skylarks (*Alauda arvensis*) and Meadow Pipits (*Anthus pratensis*) using mosaic habitats of heather and grassland would not usually be described as edge species, whereas Black Grouse (*Tetrao tetrix*) using complexes of woodland and moorland may be (Watson and Moss 2008). In fragmented forest, Holbrook et al. (2015) found both the area of harvested forest and vegetation structure influenced site occupancy of red-naped sapsuckers (*Sphyrapicus nuchalis*). Similarly, Flashpohler et al. (2010) found that fragment size and vegetation structure both affected bird species distributions. Also, even in the absence of a physical edge, there are many species requiring the young growth and/or dense low cover which is typical of a woodland edge (Fuller 2012), and the importance of shrub vegetation in general for birds has been well documented (Melin et al. 2016; Lindberg et al. 2015; Müller et al. 2010). It has been argued that the deforestation and fragmentation of Britain's woodlands happened so long ago that current conservation is being targeted to species already adjusted to patchy landscapes (Rackham 1986; Dolman et al. 2007), which further underlines the significance of knowing what features of vegetation are most important for birds. To maximize woodland bird diversity and abundance, management strategies should seek to create and maintain substantial low shrubby woodland edges in combination with good shrub cover beneath the tree canopy within woodlands (Fuller 1995; Broughton et al. 2012). In general, when planning habitat management, special care should be taken to first identify and then to preserve the features of habitat that act as determinants for diversity. This is especially critical within the agricultural mosaics where woodlands are already affected by fragmentation and isolation.

DATA ACCESSIBILITY

The lidar data used for this study is available from the Centre for Environmental Data Analysis at http://www.ceda.ac.uk/. The bird data is owned and maintained by the Centre of Ecology and Hydrology (https://www.ceh.ac.uk/).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

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