



Bird species distributions across woodland canopy structure gradients

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Abstract: The tree canopy characteristics of two broadleaved woods in southern England were quantified in terms of two independent measures of structure, canopy height (calculated using heights ≥ 1 m) and percentage canopy cover (derived using heights < 1 m), using airborne Light Detection and Ranging. The woods differed strikingly in structure due to their management systems; one was predominantly mature oak and the other coppice, comprising a patchwork of growth stages. Fine-scale relationships between breeding bird species distributions, determined by mapping censuses, and canopy height and canopy cover were assessed. Despite the differences in structure, species showed great consistency between the woods in their rank positions across gradients of canopy height (rank correlation between woods, $r = 0.77$, $p < 0.001$) and canopy cover ($r = 0.61$, $p = 0.003$). In both woods, and especially the mature oak ($R^2 > 0.90$, $p < 0.001$), there was a positive correlation across bird species between the mean values of canopy height and canopy cover associated with the mapped locations of each species. We suggest that canopy height acts as an effective surrogate of woodland structure and can be applied as a predictor of woodland bird composition and distribution, at least in lowland British conditions. Species associated with young growth were more restricted by habitat structure, as measured by differences in canopy height and canopy cover between the two woods, than were species associated with taller canopies. Remote sensing of canopy height potentially offers a simple, effective way of assessing habitat availability for many species, at both woodland and landscape scales. This may be especially relevant for species dependent on highly transient vegetation structures associated with the early pre-canopy closure stages of forest growth.

Abbreviations: DCHM – Digital canopy height model, DSM – Digital surface model, DTM – Digital terrain model, LiDAR – Light detection and ranging.

Nomenclature: The British List (British Ornithologists' Union) for birds.

Introduction

Physical attributes of vegetation profoundly affect the richness and species composition of bird communities and the total abundance of birds in temperate forest stands. Major variation is also associated with tree species composition, especially the relative quantities of broadleaved and coniferous trees (James and Wamer 1982, Moskát and Fuisz 1995, Easton and Martin 1998). Understanding the nature of these relationships is fundamental to predicting the effects of forest management on bird communities. Several studies have sought to identify broad relationships between the structural complexity of vegetation, measured in various ways, and diversity of bird communities (e.g., Karr and Roth 1971, Willson 1974, Mills et al. 1991, Korňan and Adamík 2007). Whilst it appears that such relationships exist across diverse

vegetation types, it is unclear to what extent they are evident within forest environments (Willson 1974). The concept of vegetation structural complexity is also difficult to translate into specific properties of stand structure that have meaning in the context of forest management. More informative approaches have either focused on comparisons of particular management treatments (Annand and Thompson 1997, Del-lasala et al. 1996, Fuller and Green 1998, Robinson and Robinson 1999), experimental manipulations (Gram et al. 2003, Hayes et al. 2003), or on modelling avian community relationships with multiple measurements of forest structure and tree species composition (James and Wamer 1982, Rice et al. 1984, Verner and Larson 1989, Canterbury et al. 2000). Most relevant quantitative studies have been undertaken in North America; knowledge of effects of forest management in

Europe is far less advanced (Moskát and Fuisz 1994, Fuller et al. 2007, Quine et al. 2007).

Not surprisingly, a diverse array of habitat variables has been identified as ecologically significant determinants of bird community attributes. At the level of individual species, the list of apparently important variables becomes enormous. Nonetheless, two broad elements of vegetation structure appear to be especially influential for avian species composition, richness and/or abundance. The first is understorey density. Many species, in both European and North American forests, select habitats on the basis of resources provided by understorey structures and are likely to be affected by processes that alter these structures (Fuller and Henderson 1992, Moskát and Fuisz 1994, Willson and Comet 1996, McShea and Rappole 2000, Fuller 2001, Hinsley et al. 2007). Secondly, a large number of studies have indicated that a suite of canopy characteristics is associated with major variation in bird assemblages. These include canopy height, crown volume and canopy cover (James and Wamer 1982, Helle and Fuller 1988, Verner and Larson 1989, Germaine et al. 1997, Fuller 2000, Moorman and Guynn 2001). These two structural elements are not necessarily independent because canopy characteristics can exert a strong influence on understorey density through shading.

Canopy characteristics, especially height and canopy cover, are strongly affected by management practices. This is most obviously observed in rotational felling systems (clear-cutting and coppice) which typically create patchworks of stands at different stages of growth varying in tree height and canopy cover. The structural changes accompanying stand development are often paralleled by large bird community changes (Helle 1985, Fuller et al. 1989, Helle and Mönkkönen 1990, Fuller and Henderson 1992, Donald et al. 1998). In such systems, canopy height may be a useful indicator of bird community structure and species composition by acting as a surrogate variable for a complex of vegetation attributes that change with stand development. Hinsley et al. (2002) have also suggested that canopy height acts as a surrogate for canopy density which is likely to be one factor determining habitat quality for canopy-feeding insectivorous species. Knowledge of how species respond to canopy characteristics is, therefore, of potential value in predicting effects of forest management on the composition of bird communities.

For canopy characteristics to be useful as predictors of distributions, species would need to display reasonably consistent relationships with the measured variables. In this paper, we examine fine-scale spatial relationships between breeding bird species and canopy height and canopy cover in two woods in southern Britain to assess the consistency of the bird species responses to canopy structure. These woods had very different habitat structures because of their contrasting management systems. We expected there to be a general positive relationship across species in the relationship between canopy height and canopy cover – that is, species would select different phases of the successional gradient.

Turnover rates of bird species across successional gradients tend to be highest in the early stages, although this is difficult to quantify (Helle and Mönkkönen 1990). This may imply that bird species typical of young-growth are more tightly bound to particular habitat structures than species associated with the more mature stages. Studies of the dynamics of British coppiced woodland indicate that species associated with early growth stages are more strongly constrained in their distributions across vegetation gradients compared with species reaching peak abundances later (Fuller et al. 1989). Migrants in particular tend to be confined to early growth stages (Helle and Fuller 1988, Fuller et al. 1989, Fuller and Henderson 1992). By comparing habitat use patterns in contrasting woods, we assess whether species associated with young growth stages are more conservative in their relationships with canopy structure than species associated with later stages.

Canopy characteristics are extremely difficult to measure by ground-based methods. This paper is novel in that airborne remote sensing (Light Detection and Ranging, LiDAR) was used to assess how canopy structure varied within two woods of strikingly different structures. This information was combined with locational data on birds derived from spot mapping to assess patterns of habitat association. Airborne LiDAR techniques are especially valuable for determining attributes of vegetation canopy structure because they provide high resolution data at the scale of whole woods or landscapes. The technology has great potential for quantifying landscape and habitat structure (Lefsky et al. 2002, Lim et al. 2003, Næseth 2004) and parameterizing predictive organism-habitat models (e.g., Hinsley et al. 2002, Hill et al. 2004, Bradbury et al. 2005, Broughton et al. 2006, Hinsley et al. 2006, Goetz et al. 2007, Vierling et al. 2008). We highlight the potential of such techniques to monitor habitat availability, and especially for species dependent on highly ephemeral vegetation structures.

Methods

Study sites and their management

The study sites comprised Bradfield Woods (52°11' N, 0°50' E) in Suffolk, eastern England and Sheephouse Wood (51°54' N, 0°58' W) in Buckinghamshire, east central England (Fig. 1). Both are ancient semi-natural woods (Peterken 1993), but are managed in different ways. Both contain networks of paths and both are isolated woods surrounded by open farmland, although an active land-fill site flanks the western edge of Sheephouse beyond the railway line visible in Figure 1.

Bradfield Woods is a rare example of managed mixed-species coppice (Peterken 1993) dominated by common ash (*Fraxinus excelsior*), hazel (*Corylus avellana*), birch (*Betula* spp.) and alder (*Alnus glutinosa*) which is typically cut on a rotation of 20 to 25 years. In 2003, the year of the study, the total area under active coppice management was 56.5 ha (total woodland area was 70.0 ha). The total number of manage-

ment compartments was 53. The mean area of the compartments was 1.07 ± 0.64 ha, and the range 0.20 – 3.70 ha. Of the 53, two (1.38 and 2.47 ha) have been allowed to regener-

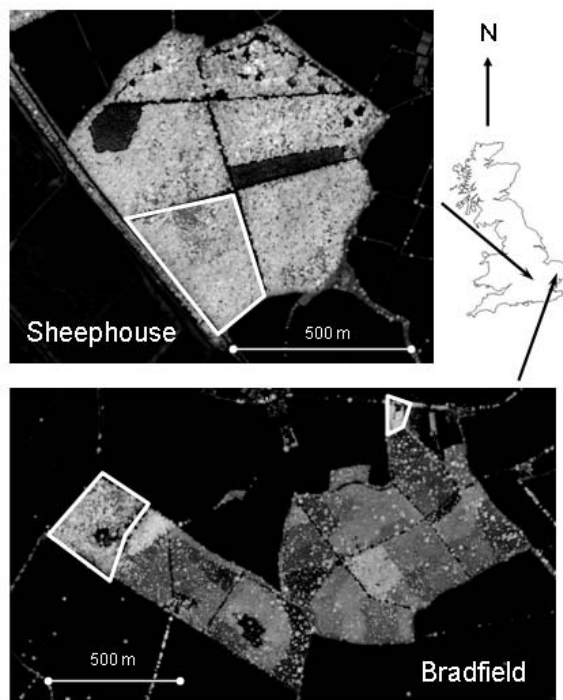


Figure 1. Locations and overall structures of Bradfield Woods and Sheephouse Wood. Images are digital canopy height models with increasing height indicated by lighter shading. In Sheephouse Wood, the clear-cuts, main rides and scalloping are clearly visible as darker areas and the largely closed canopy by the evenness of the light grey shading. In Bradfield Woods, the different ages/heights of the coppice compartments are clearly visible with the crowns of the standards appearing as white spots. The three areas outlined in white, and the railway line along the western edge of Sheephouse Wood, were not included in the bird census.

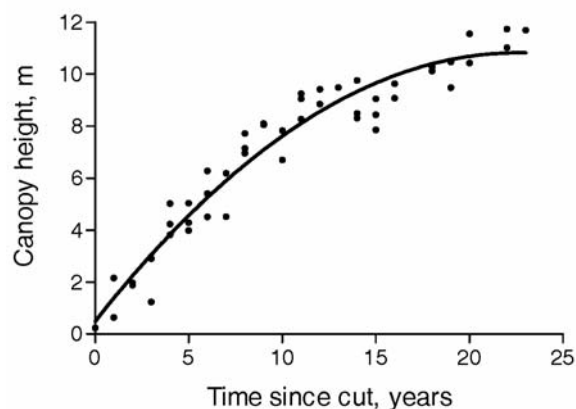


Figure 2. Relationship between coppice compartment age, i.e., time in years since last cut, and canopy height in Bradfield Woods. Line is fitted using a second order polynomial relationship; canopy height = $0.486 + 0.916 \text{ age} - 0.020 \text{ age}^2$, $R^2 = 0.934$, $p < 0.001$, $n = 48$.

ate to mature woodland for about 50 years. Of the remaining 51 compartments, between one and three (and exceptionally four in 1999) were coppiced each year from 1980 to 2003. The mean area cut each year was 1.08 ± 0.51 ha, and the range 0.20 – 3.00 ha, which was $1.07 \pm 0.64\%$ (range 0.20 – 3.70%) of the total area under coppice management. Scattered standard trees (non-coppiced, mature trees) were present in all compartments (Figure 1) and were predominantly pedunculate oak (*Quercus robur*) and birch. The standards tend to be widely spaced with large gaps between their canopies. The relationship between compartment age, i.e., time since cutting, and top canopy height for coppice regrowth is shown in Figure 2. The total area covered by the bird census (see below) in 2003 was 63.5 ha and comprised the active coppice compartments plus some additional mature woodland.

Sheephouse Wood was predominantly hazel-pedunculate oak (Peterken 1993) with some areas dominated by common ash and field maple (*Acer campestre*). Much of the wood had not been actively managed for several decades and the canopy was largely closed. However, two clear-cuts were made and maintained, one in 1983 (1.8 ha) and the other in 1988 (1.6 ha), and several group fells and ride scallops (each < 0.2 ha) have also been cut, mainly in 1985. The area of the wood was 59.4 ha of which 44.4 ha forms the bird census area.

Woodland structural data

Woodland canopy height and the occurrence of gaps in the canopy were measured using airborne LiDAR. This is an active technique in which a scanning laser rangefinder is used to measure the heights of points within a swath beneath the flight path of an aircraft (Lefsky et al. 2002, Lim et al. 2003, Næsset 2004). The laser used in this study fires high frequency short duration pulses of near infrared light (1064 nm) at the ground and a detector records the timing of the return signals backscattered from the ground itself and/or any surface features such as trees, hedges and buildings (Wehr and Lohr 1999). From the timing of the returns, and on-board measurement of the aircraft's position and orientation (using telemetry from an Inertial Navigation System combined with differential GPS recordings), the 3D positions of the ranged points can be calculated and geo-referenced (Ackermann 1999). These measurements can then be used to derive a digital model of the surface of the ground and of the surface of the vegetation and hence a canopy height model (Popescu et al. 2003).

LiDAR data for both woodland sites were acquired on 9th September 2003 using an ALTM 3033 (Optech Inc.). The ALTM is a small footprint (< 25 cm on the ground), discrete return system supplying the first and last significant return per laser pulse. These data were acquired at an average flying altitude of 1,100 m with a 33 kHz pulse repetition rate, a scan angle of $\pm 12^\circ$ and an average post spacing of one hit per 0.7 m^2 .

Note that because of the distance between the two sites, the two data acquisitions made use of different base stations (both operated by the Ordnance Survey).

Processing of the LiDAR data involved a similar approach for Bradfield and Sheephouse Woods. Both the first and last return data were interpolated into a Digital Surface Model (DSM) by triangulation and subsequent gridding, rendering a 0.5 m pixel size (i.e., 0.25 m²). The creation of a Digital Terrain Model (DTM) at each site made use of the last return data, which had a higher likelihood of ground hits (Reutebuch et al., 2003). This involved a process of minimum filtering, varying the size of the filter according to local variance calculated over different spatial scales (Gaveau and Hill 2003). For any given point, the size of the filter that could be used to extract a minimum elevation was dictated by the level of canopy closure and therefore the rate of laser penetration to the ground surface (Petzold et al. 1999). This varied both across and between each woodland site, hence the need for an adaptive filtering approach. The extracted local elevation minima were used to interpolate a complete terrain surface (or first-pass DTM). This DTM was then compared with the last return DSM and points within a 0.5 m elevation threshold were added into the mask of local elevation minimum. This was then interpolated by triangulation into a second-pass DTM. The process of minimum filtering, analysis of local variance and comparison with the last return DSM then continued iteratively on each generated DTM. At each iteration, the filter sizes were reduced and additional data were retained in the ground mask thereby achieving a closer match between the DTM and the ground data present in the last return DSM. The iterations completed when no additional data were included in the ground mask within the specified thresholds for local variance and surface difference.

Having produced a DTM for each site, a Digital Canopy Height Model (DCHM) was produced by the per-pixel subtraction of the DTM from the first return DSM. At both woodland sites, the DSMs, DTM and DCHM all had a pixel size of 0.25 m² (i.e., 0.5 m × 0.5 m).

Bird census

The breeding birds of Bradfield and Sheephouse Woods were censused in 2003 (as part of a longer-term study) using a territory mapping technique (spot mapping) (Bibby et al. 1992). Bradfield Woods was censused eight times and Sheephouse Wood six times from the beginning of April to the beginning of June. All parts of the woods included in the census were visited to within at least 50 m. The locations of all birds [except woodpigeon (*Columba palumbus*), pheasant (*Phasianus colchicus*), jackdaw (*Corvus monedula*) and carrion crow (*Corvus corone*)] encountered were recorded on detailed maps with an accuracy of ± 10 m. Bird species with 20 or more registrations in either wood were included in the analysis (20 being selected as a suitable sample size indicative of breeding). This selected 23 species in both Bradfield and Sheephouse, of which 22 were common to both woods.

In addition, nightingale (*Luscinia megarhynchos*) occurred only in Bradfield Woods and nuthatch (*Sitta europaea*) only in Sheephouse Wood, giving an overall total of 24 species. However, some species were relatively scarce in one or the other wood (Table 1).

Comparison of woodland structure

The canopy height and canopy gap characteristics of the two woods were sampled using 15 m radius circles located at the intersections of a 30 m grid laid across each wood, the starting points of the grids being selected at random. A total of 709 sample circles were located in Bradfield Woods and 660 in Sheephouse Wood. The occurrence of gaps in the canopy was defined as the percentage of each circle with a vegetation height of < 1 m. Canopy gap was then converted to canopy cover as: (100 – canopy gap)%. The mean height for each circle was calculated excluding those portions where the vegetation height was < 1 m. Therefore, these two measures of woodland structure were independent of each other. For circles at the edges of the woods, those with their centres outside the boundary were excluded. Circles with their centres inside the boundary were included and the portions falling outside the boundary, as well as inside, were included in the calculations of percentage gap and mean height as defined above. Woodland edge is an important bird habitat; this protocol allowed it to be sampled and also treated internal and external edges equally.

Bird-habitat analysis

Bird habitat associations were assessed for each of the 24 species by measuring (as above) the percentage of gap, converted to canopy cover, and the mean height within 15 m radius circles centred on each bird registration. Sections of circles falling outside the woodland boundary were included in the calculations for the same reasons as described above for woodland structure. The average canopy height associated with each species was then summarised as a mean value for each species for each wood. The average canopy cover was also summarised for each species for each wood. For Bradfield Woods, overall mean heights were also calculated for each species excluding the contribution, if any, of the standard trees (defined as canopy heights > 13 m) to the calculations of the mean heights of the individual registration sample circles. This was to investigate a previous finding that most bird species within coppiced woodland distributed themselves according to characteristics of the predominant coppice regrowth rather than of the standard trees (Fuller and Henderson 1992). For Sheephouse Wood, to examine bird responses to mature woodland structure alone, overall mean heights and percentage canopy cover were also calculated for each species excluding any bird registrations in the two clear-cuts.

Individual bird registrations, rather than estimates of territory locations, were used to sample bird habitat associations because this entailed the minimum of assumptions about habitat use by species. It also allowed a high level of spatial

Table 1. Effects of the exclusion of the standard trees from the calculation of species mean canopy heights in Bradfield Woods and of the exclusion of the clear-cuts from the calculation of species mean canopy heights and mean percentage canopy cover in Sheephouse Wood. Without the standards in Bradfield, mean heights were reduced; without the clear-cuts in Sheephouse, mean heights and canopy cover were either unchanged (for species absent from the clear-cuts) or increased. Figures in brackets show the percentage change. *Willow warbler only occurred in the clear-cuts in Sheephouse. G Spotted Wdpk = great spotted woodpecker, Green Wdpk = green woodpecker, L-tailed Tit = Long-tailed tit.

Bradfield Woods				Sheephouse Wood			
Species	N	Change in mean height without standards, m		Species	N	Change in mean values without clear-cuts Height, m	Cover, %
Nightingale	<i>Luscinia megarhynchos</i>	65	-0.5 (8)	Nuthatch	16	0	0
Stock Dove	<i>Columba oenas</i>	7	-0.7 (7)	<i>Sitta europaea</i>	72	0	0
Goldcrest	<i>Regulus regulus</i>	10	-0.7 (8)	Treecreeper	200	0	0
Garden Warbler	<i>Sylvia borin</i>	116	-0.9 (13)	G Spotted Wdpk	21	0	0
Chiffchaff	<i>Phylloscopus collybita</i>	345	-0.9 (12)	Stock Dove	11	0	0
Willow Warbler	<i>Phylloscopus trochilus</i>	181	-1.0 (13)	Jay	89	0	0
Robin	<i>Erithacus rubecula</i>	484	-1.0 (11)	Blackbird	16	0	0
G Spotted Wdpk	<i>Dendrocopos major</i>	57	-1.0 (11)	Robin	304	0.1 (0.3)	0.1 (0.1)
Song Thrush	<i>Turdus philomelos</i>	43	-1.1 (13)	Chaffinch	132	0.1 (0.7)	0.4 (0.4)
Blackbird	<i>Turdus merula</i>	165	-1.1 (13)	Blackcap	87	0.2 (1.7)	0.5 (0.6)
L-tailed Tit	<i>Aegithalos caudatus</i>	73	-1.1 (14)	Coal Tit	60	0.2 (1.5)	0.6 (0.6)
Blackcap	<i>Sylvia atricapilla</i>	238	-1.2 (14)	Green Wdpk	29	0.2 (1.7)	0.1 (0.1)
Bullfinch	<i>Pyrrhula pyrrhula</i>	35	-1.2 (13)	L-tailed Tit	23	0.3 (2.4)	2.3 (2.6)
Marsh Tit	<i>Poecile palustris</i>	73	-1.2 (12)	Blue Tit	201	0.3 (2.0)	1.0 (1.0)
Blue Tit	<i>Cyanistes caeruleus</i>	187	-1.2 (13)	Goldcrest	33	0.3 (2.1)	0.3 (0.3)
Great Tit	<i>Parus major</i>	163	-1.3 (13)	Great Tit	200	0.4 (3.1)	1.4 (1.5)
Dunnock	<i>Prunella modularis</i>	42	-1.3 (17)	Marsh Tit	52	0.4 (3.1)	1.1 (1.2)
Wren	<i>Troglodytes troglodytes</i>	409	-1.4 (16)	Song Thrush	40	0.5 (3.5)	1.5 (1.6)
Jay	<i>Garrulus glandarius</i>	20	-1.4 (14)	Chiffchaff	102	0.5 (4.6)	1.6 (1.9)
Coal Tit	<i>Pariparus ater</i>	51	-1.5 (14)	Wren	216	0.6 (5.3)	1.0 (1.1)
Chaffinch	<i>Fringilla coelebs</i>	150	-1.7 (17)	Dunnock	22	0.9 (9.9)	3.6 (4.7)
Treecreeper	<i>Certhia familiaris</i>	69	-2.0 (18)	Garden Warbler	27	3.5 (44.7)	10.2 (13.4)
Green Wdpk	<i>Picus viridis</i>	9	-3.1 (27)	Willow Warbler	16	*	*

precision in the matching of bird locations with canopy characteristics. Although many of the same territorial birds would have been recorded on some or even most visits, their locations on each visit were unambiguous samples of the breeding habitat used by that species. The analyses were repeated using 30 m radius sample circles, but this made little difference to the results and they are not presented here.

Results

Woodland structure

The difference in the height distributions of the top canopies of the two woods is clearly shown in Figure 3. For Bradfield Woods, 60% of the 709 15 m radius sample circles had a mean height in the range of 7.1 to 11 m whereas in Sheephouse Wood, 64% of 660 samples had a mean height range of 13.1 to 17 m. This difference in the height distributions was to be expected given the management histories of the two woods. The secondary peak in the height distribution in Sheephouse Wood at 2.1 to 3.0 m was due to the two clear-felled areas. The overall difference in mean heights between the two woods was 3.96 m (Bradfield = $9.33 \pm$ (sd) 2.65 m, $n = 709$; Sheephouse = $13.29 \pm$ (sd) 3.51 m, $n = 660$; difference = 3.96 m, $se_{diff} = 0.17$, $t = -23.4$, $p < 0.001$).

In contrast to canopy height, the distribution of canopy cover was broadly similar between the two woods (Fig. 4), with Sheephouse having a slightly greater frequency of maximal (> 95%) or complete cover. There was almost no overall difference in mean canopy cover between the two

woods (Bradfield = $87.2 \pm$ (sd) 16.4%, $n = 709$; Sheephouse = $87.4 \pm$ (sd) 18.0%, $n = 660$). This suggested that the occurrence of gaps in both woods was influenced more by the presence of edges, i.e., internal rides and the external edge, rather than by effects of the contrasting management practices. The minimum canopy cover values of c. 50% in both woods were due to sample circles at the edges of the woods. However, the relationships between canopy cover and mean height for each wood did show a substantial management effect. In Sheephouse Wood, canopy cover increased with increasing height as might be expected due to tree maturation and canopy closure (Fig. 5). In contrast, in Bradfield Woods, height had much less influence on canopy cover (Fig. 5), the more frequent occurrence of large values of canopy cover at relatively low heights probably being due to dense coppice regrowth coupled with our definition of gap as vegetation height of < 1 m. Furthermore, in the most recently cut compartments where low values of canopy cover would be expected to be associated with low coppice heights, mean heights were increased by the presence of the standards. These differences in structure, and the effects of the standards, are examined in more detail below in the bird species relationships between canopy height and cover.

Bird species associations with height

The mean heights associated with species locations in the two woods are shown in Figure 6. Despite the large differences in the structure of the two woods, the order of the species across the gradient of increasing height was similar (rank

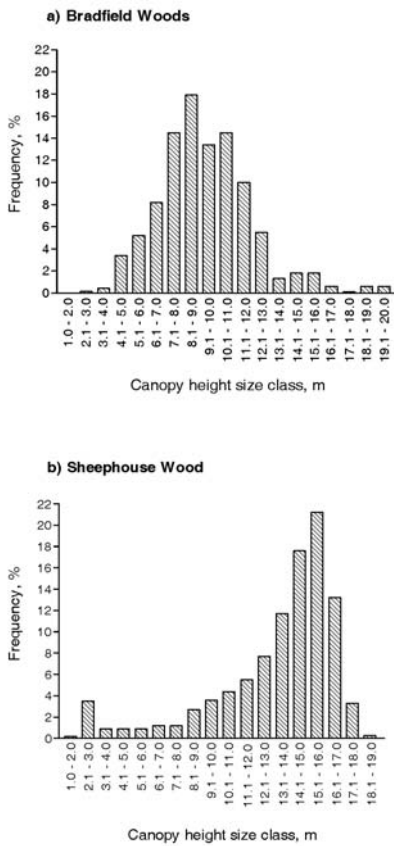


Figure 3. Canopy height (m) distributions for **a**: Bradfield and **b**: Sheephouse Woods. Numbers of 15 m radius sample circles: Bradfield n = 709; Sheephouse n = 660.

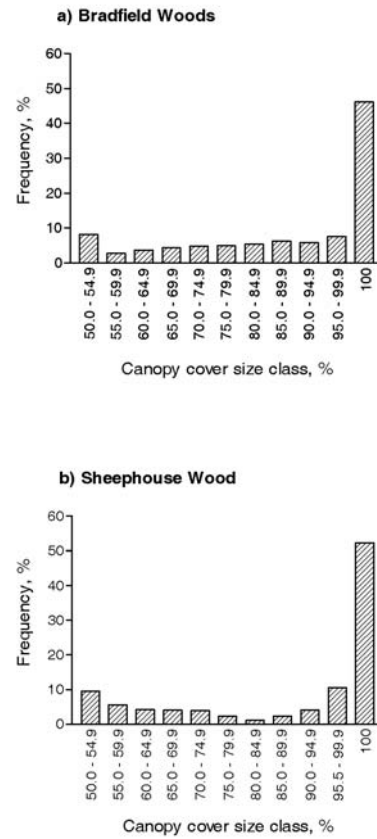


Figure 4. Canopy cover (%) distributions for **a**: Bradfield and **b**: Sheephouse Woods. Numbers of 15 m radius sample circles: Bradfield n = 709; Sheephouse n = 660.

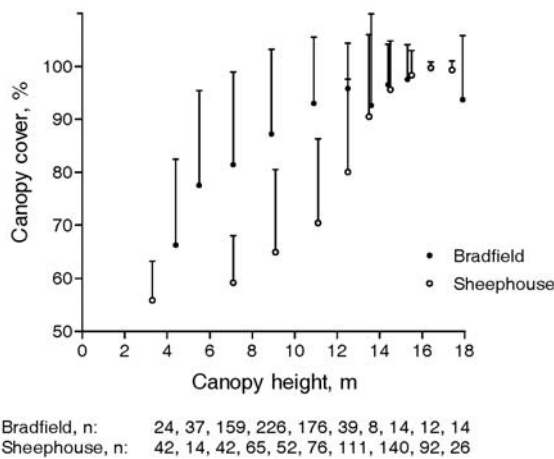


Figure 5. Relationship between canopy height (m) and canopy cover (%) in Bradfield and Sheephouse Woods showing greater cover at lower heights in Bradfield. Data are grouped into height intervals (usually 1-2 m) for clarity; bars show + 1 sd. Numbers of 15 m radius sample circles: Bradfield n = 709; Sheephouse n = 660. Note that 46% of circles for Bradfield and 52% for Sheephouse had a canopy cover value of 100%.

correlation of height order, $r = 0.77$, $p < 0.001$). As expected, species associated with low cover had the lowest mean heights and those associated with mature trees the highest. With the exclusion of willow warbler (see below), the overall mean difference in mean heights for the 21 species common to both woods was 3.34 ± 1.26 m, which was similar to the overall mean height difference between the two woods of 3.96 m.

In general, the species occupied habitat with the same relative height characteristics in both woods, but with a shift in absolute height in accordance with the taller structure of Sheephouse. However, the differences between the two woods in the species mean heights did vary between species (Fig. 7). Overall, species associated with relatively dense cover of low or medium height showed the smallest differences in mean heights whereas those more strongly associated with trees showed the largest differences.

Effects of the clear-cuts in Sheephouse Wood

Three species in Sheephouse Wood, dunnock, garden warbler and especially willow warbler, showed a relatively large association with low canopy height (Fig. 6) due to their presence in the two clear-cut areas. Willow warblers only oc-

occurred in the clear-cuts and 44% and 14% of registrations for garden warblers and dunnocks respectively also occurred in this habitat for which there was no direct equivalent in Bradfield. Recently cut coppice compartments in Bradfield are the

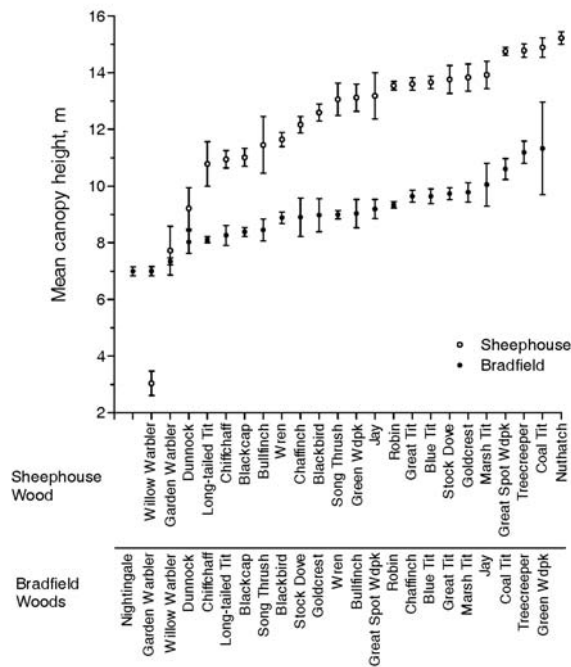


Figure 6. Mean heights (\pm SE) associated with species locations in Bradfield and Sheephouse Woods in 2003. The species are arranged in order of increasing mean height: Sheephouse Wood, open circles; Bradfield Woods, closed circles. Nightingale did not occur in Sheephouse, and nuthatch did not occur in Bradfield.

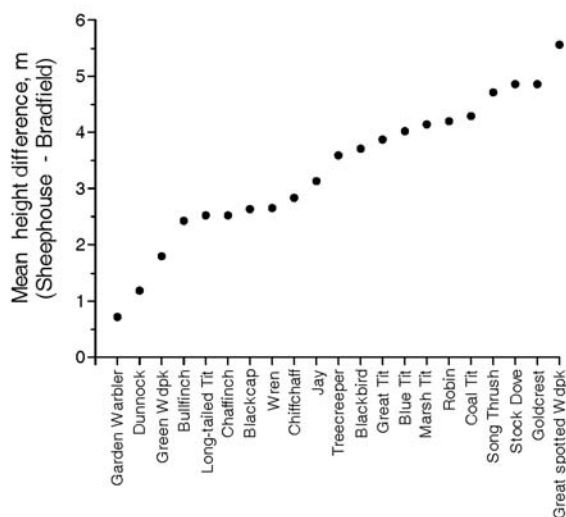


Figure 7. Differences in species mean heights between Bradfield Woods and Sheephouse Wood (calculated as Sheephouse - Bradfield) for the species common to both woods. The results for willow warbler are omitted.

closest structural equivalent to the clear-cuts in terms of height, but they lack low cover and hence have few associated birds (Fuller and Henderson 1992). Rapid coppice growth provides cover and attracts willow warblers, garden warblers and dunnocks, but the growth increases the mean height and hence generated the different pattern for these species in the two woods. In Sheephouse, removing registrations in the clear-cuts from the calculations of mean heights increased the mean for garden warbler by 3.45 m (45%) and for dunnock by 0.91 m (10%), but had little effect on any other species (Table 1).

Removing the influence of the clear-cuts in Sheephouse Wood from the calculation of percentage canopy cover had most influence on willow warbler because it only occurred in the clear-cuts, and on garden warbler (percentage canopy cover increased from 76.0 to 86.2%) and dunnock (increased from 77.1 to 80.7%). There was little or no change for any other species (Table 1).

Effects of the standards in Bradfield Woods

When excluding the standards, species mean heights in Bradfield Woods decreased by $13.4 \pm 4.0\%$, range 7.4 – 27.2%, $n = 23$ (Table 1). The smallest decreases were for nightingale (-0.54 m, 7.7%), stock dove (-0.66 m, 7.4%) and goldcrest (-0.69 m, 7.7%), and the largest decreases for green woodpecker (-3.08 m, 27.2%) and treecreeper (-2.0 m, 17.6%). In general, and as expected, excluding the standards had least effect on species associated with low or dense cover and most effect on those associated with mature trees. The relatively large effect on green woodpecker is detailed in the discussion. An additional effect of the standards in relation to height and canopy cover is also discussed below (see *Bird species canopy height/canopy cover relationships*)

Bird species associations with canopy cover

The mean percentage canopy cover associated with species locations in the two woods are shown in Figure 8 (rank correlation of canopy cover order, $r = 0.61$, $p = 0.003$). The order of the distribution of the species across the gradient of increasing percentage cover, i.e., less gap, indicated a negative association between the use of low cover by a species and the amount of canopy cover; species typical of low cover were associated with the smallest amounts of canopy cover. This trend was less well marked in Bradfield Woods where both willow warbler and nightingale had higher canopy cover values than might have been expected from their selection of relatively low canopy heights. The three species most strongly associated with the clear-cuts in Sheephouse (willow warbler, garden warbler and dunnock) showed the largest differences in canopy cover between the two woods. There were also clear differences for chiffchaff, blackcap and bullfinch (Fig. 9). This was probably because the complex understorey structures that these latter species generally require were available in Bradfield within the coppice compartments up to and just beyond canopy closure (Fuller and Henderson 1992). In contrast, such structures in Sheephouse

were largely confined to the clear-cuts and the edges of rides and group-fells and hence associated with gaps in the canopy and relatively low percentage canopy cover.

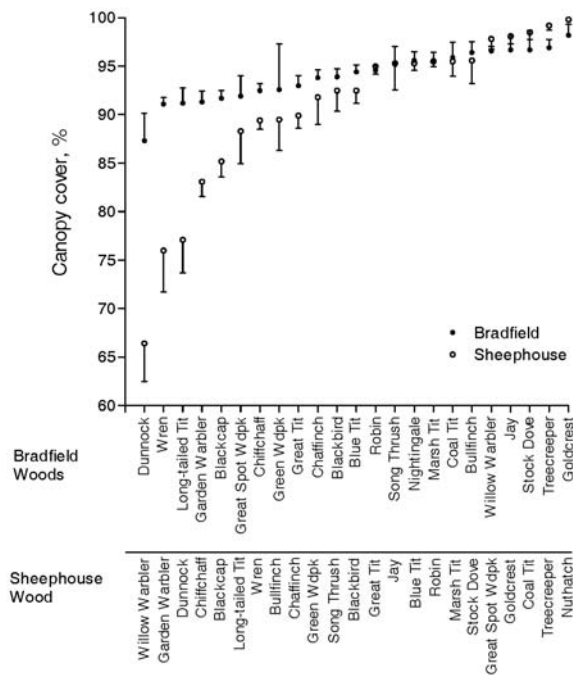


Figure 8. Mean (\pm SE) percentage canopy cover associated with species locations in Bradfield and Sheephouse Woods in 2003. The species are arranged in order of increasing cover: Sheephouse Wood, open circles; Bradfield Woods, closed circles. Nightingale did not occur in Sheephouse, and nuthatch did not occur in Bradfield. The species showing the largest difference between the two woods is willow warbler. For clarity, SE shown as + in Bradfield and - in Sheephouse.

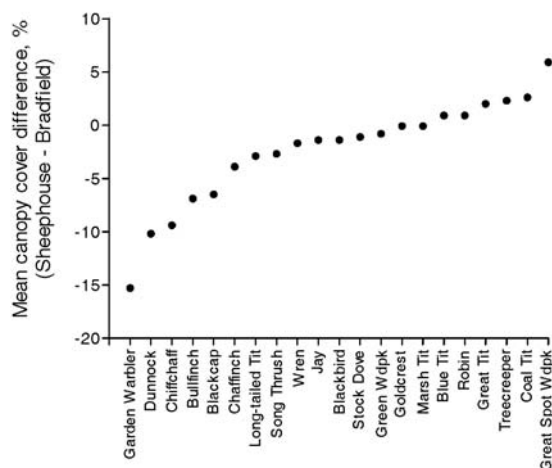


Figure 9. Differences in species mean canopy cover between Bradfield Woods and Sheephouse Wood (calculated as Sheephouse - Bradfield) for the species common to both woods. The results for willow warbler are omitted.

Considering the differences between the two woods in the species mean heights (Fig. 7) and mean canopy covers (Fig. 9), the order of the species was similar (rank correlation of species order, $r = 0.72$, $p < 0.001$). However, whereas the largest differences in mean heights were found for species associated with mature trees (Fig. 7), the largest differences in canopy cover were for species associated with dense, low cover (Fig. 9).

Bird species canopy height/canopy cover relationships

In terms of both physical structure and bird species associations with canopy characteristics, an increase in canopy cover with tree height (i.e., with maturation and canopy closure) would be expected. In Sheephouse Wood, an increase in species canopy cover with height was indeed strongly represented (species mean canopy cover = $54.1 + 2.99$ species mean hgt, $R^2 = 0.95$, $p < 0.001$, $n = 23$) because the structure of the wood was dominated by mature, closed canopy. The effect remained strong even when the influence of willow warbler (low canopy cover, low canopy height) on the relationship was removed by excluding the clear-cuts (Fig. 10a; species mean canopy cover = $49.1 + 3.36$ species mean hgt, $R^2 = 0.91$, $p < 0.001$, $n = 22$). The strength of this relationship suggested that, in closed canopy woodland, tree canopy height can act as an effective determinant of avian species assemblage. In Bradfield Woods, although species canopy cover tended to increase with increasing mean heights, the relationship was not significant (species mean canopy cover = $88.7 + 0.594$ species mean height, $R^2 = 0.07$, $p = 0.217$, $n = 23$) presumably due to the more complex spatial structure of the wood. For example, low, but dense, coppice regrowth acting to increase canopy cover and tall, but well spaced, standard trees contributing to height, but not to canopy closure (see Figs. 3, 4 and 5). However, after removing the influence of the standard trees from the calculations of species mean heights, the relationship became significant (species mean canopy cover = $83.3 + 1.38$ species mean hgt, $R^2 = 0.21$, $p = 0.028$, $n = 23$, Fig. 10b). This indicated that the canopy height of the coppiced structures beneath the standards did influence bird species assemblage. Furthermore, on removal of the four species known to be heavily influenced by cover at low heights, i.e., willow warbler, garden warbler, dunnock, and nightingale, the relationship for the remaining species was stronger again (species mean canopy cover = $77.0 + 2.15$ species mean hgt, $R^2 = 0.37$, $p = 0.006$, $n = 19$) and more closely resembled that found for Sheephouse Wood.

Discussion

Despite the large physical differences between the two woods, the distributions of bird species in relation to two simple measures of structure - canopy height and canopy cover - were similar in both woods. Tree height in particular appeared to be able to function as a general indicator of woodland bird species composition, at least in lowland Brit-

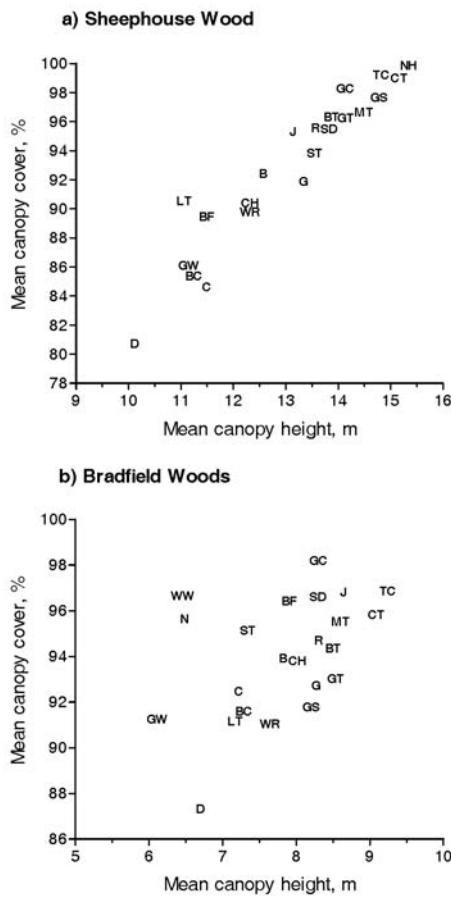


Figure 10. Species associations with canopy height and canopy cover in **a):** Sheephouse Wood and **b):** Bradfield Woods. Results for canopy height and cover for Sheephouse are calculated excluding the clear-cuts and for Bradfield the results for canopy height are calculated excluding the standards. Species are coded as follows: D: dunnoek, C: chiffchaff, BC: blackcap; GW: garden warbler, BF: bullfinch, LT: long-tailed tit, G: green woodpecker, B: blackbird, ST: song thrush, J: jay, R: robin, SD: stock dove, BT: blue tit, GT: great tit, MT: marsh tit, GS: great spotted woodpecker, GC: goldcrest, CT: coal tit, TC: tree-creeper, NH: nuthatch, WW: willow warbler, N: nightingale.

ish woodland. We are not aware that this has been demonstrated so clearly before.

The order of species across the height gradients in the two woods was most similar at the two extremes, i.e., the species most closely associated with early successional growth with the lowest mean heights, and those closely associated with mature trees with the highest. Removing the influence of the standards in Bradfield on the species mean heights did not change this general pattern. If anything, it concentrated species associated with trees, notably the tits, at the upper end of the height gradient as might be expected in Bradfield with its more limited availability of mature trees. Removing the standards from the data had most effect on the results for green woodpecker (Table 1), probably because this species frequently feeds on the ground in the open and thus might be expected to use the younger coppice compartments where the

difference in height between the standards and the coppice canopy was large.

The plots of species in graphical space defined by mean canopy cover and mean height (Fig. 10) produced an order of species which again progressed from those associated with dense, low cover (e.g., garden warbler, dunnoek) through to those associated with shrubby understorey cover (e.g., blackcap, bullfinch, long-tailed tit) to those associated with mature trees (e.g., tree-creeper, coal tit, nuthatch). Although the relationship was evident in both woods (after removing the effects of standard trees in Bradfield) it was strongest in Sheephouse. This difference probably was a consequence of the contrasting structures of the two woods; there was a much tighter relationship between the height and cover of the canopy in Sheephouse (Fig. 5). The higher proportion of internal edges in Bradfield Woods, e.g., between coppice compartments of different ages/heights, was also likely to have increased the variation in the calculated mean heights and values of canopy cover per 15 m radius sample circle. Nonetheless, this finding suggests that the habitat distribution of species can be effectively delineated in terms of a small number of structural metrics. Habitat quality may ultimately depend on the presence of key micro-features providing nest sites, shelter or feeding resources, but potential habitat may be identified using simple measures of canopy structure.

The ability of tree canopy height to act as an indicator of bird species composition is probably a consequence, at least in part, of the relationship between tree height and a complex of variables that change with forest maturity. These include canopy openness, crown density and understorey density. Hinsley et al. (2002) found that remote-sensed (LiDAR) tree height was positively correlated with field-based estimates of tree canopy density (canopy density index = $-0.826 + 2.54 \log_{10} \text{canopy height}$, $R^2 = 0.86$, $p < 0.001$, $n = 36$), which again probably reflected increasing crown volume with age. Sub-canopy foliage structure depends on canopy closure as well as canopy height. As shown here, remote-sensing can quantify canopy cover. We defined gaps as heights below 1 m, but definitions can be user-defined to suit particular circumstances. For example, in Bradfield, defining gaps as heights below 2 m would have reduced the percentage of canopy cover at low mean heights and probably increased the similarity of species responses in the two woods. Decisions how to define gaps could be based on canopy height distributions.

Although the distribution of bird species across the height gradients was similar in both woods, the absolute differences in species mean heights was greatest for species associated with mature woodland (Fig. 7). In part, this was a consequence of the overall height of Sheephouse Wood being greater than that of Bradfield Woods (Fig. 3). However, it also implied that bird species associated with mature trees were less sensitive to variation in tree structure over and above some threshold stage of tree development or woodland maturity. That the absolute differences in species mean can-

opy cover (Fig. 9) were least for species associated with mature trees was consistent with the notion that beyond a certain growth threshold, relatively small changes occur in structure. In contrast, the distribution of species associated with young growth was more tightly keyed into one part of the height gradient. These species also showed the greatest differences in mean canopy cover between the two woods, probably in part due to the greater availability of low, bushy cover in Bradfield (Fig. 5), but also because structure changed more rapidly with increasing height in the earlier stages of growth. Temporal availability of niche space of early successional species, therefore appears to be less than for late successional species. This is consistent with the observation that rates of species turnover are generally highest in early succession (Helle and Mönkkönen 1990) and with previous observations of the distribution of birds in relation to coppice dynamics (Fuller et al. 1989, Fuller and Henderson 1992).

Thus, small differences in height within early successional habitats are associated with relatively large changes in habitat structure. Understorey complexity changes rapidly with relatively small increases in canopy height, whereas once the canopy closes and the understorey is shaded out or stabilises, there can be quite large changes in canopy height with little change in foliage diversity profile. This is illustrated well by the growth dynamics of coppice woodland for the first 30 years of growth as described by Fuller and Henderson (1992). Tree height and stem diameter show an almost linear growth pattern throughout this period, but low foliage density peaks at about 3 years and declines rapidly thereafter as the canopy becomes fully closed by about 6 years. Extremely low foliage density would persist for many decades in the absence of further management such as felling or thinning. Thus habitat complexity does not change linearly with increasing canopy height. The consequence for bird assemblages is that species requiring complex understorey structures are frequently restricted to a shorter phase of habitat development than are those associated with more mature woodland.

The relatively transient nature of early successional vegetation structures and their bird assemblages should be a general feature of forest habitats, not just the English lowland deciduous woods of our study. For example, in a study of forest birds at the Hubbard Brook Experimental Forest in New Hampshire, USA, most of a reported decline in bird abundance in a long-term census plot was due to habitat maturation decreasing numbers of three species of Neotropical migrants favouring early to mid successional stages (Holmes and Sherry 2001, Holmes 2007). In Britain, early successional species may also be under pressure as a consequence of reduced habitat availability (Fuller et al. 2007). In 1947, 49% of British broadleaved woodland was classed as scrub or coppice and only 51% as high forest (Hopkins and Kirby 2007, Mason 2007). However, in recent decades, woodland management has declined, woods have matured and by 2003, 97% of woodland was classed as high forest. Population trends of UK woodland birds are complex, with some species increasing and others decreasing, and a

range of factors, in addition to structural changes associated with woodland maturation, appear to be involved (Fuller et al. 2005, Hewson et al. 2007). However, in recent years, reductions in the population sizes of birds associated with young growth, including several species of long-distance migrants, have become of conservation concern (Amar et al. 2006). Two of the three species most closely associated with low growth in both Bradfield and Sheephouse Woods - willow warbler and garden warbler - have shown strong national declines in the UK since the 1980s (Hewson et al. 2007).

Conclusions

In the UK and elsewhere, much deciduous woodland now occurs in relatively small patches. This makes management to maintain early successional habitat more difficult because many woods are too small to contain effective amounts of a range of age classes. Recreating coppice management without commercial incentive will be expensive, but the current interest in wood fuels as a carbon-neutral energy source has potential to revitalise woodland management (Fuller et al. 2007). Selective thinning and small group-fells may help to open up closed canopy woodland, encouraging successional growth without overall loss of woodland and landscape character or of the bird communities of mature woodland. Airborne LiDAR, using canopy height as a surrogate for woodland maturation, could provide a means of monitoring the distribution and abundance of different woodland age classes at a landscape-scale, facilitating regional management strategies. This would be especially valuable in assessing the extent of ephemeral scrub and young-growth woodland habitats which are particularly important for a suite of declining long-distance migrant birds. This type of approach is likely to be most effective in regions such as western Europe where woodland bird species tend not to show close associations with plant communities and are primarily distributed according to preferred vegetation structures (e.g., Helle and Mönkkönen 1990, Moskát and Fuisz 1994, Fuller and Green 1998).

We must also emphasize the importance of landscape context. Early successional habitats are critically important for biodiversity in cultural landscapes such as those of western Europe. Active management through grazing, cutting or burning vegetation is necessary to maintain these structures and their associated biological communities. However, these circumstances apply to landscapes with a long history of sustained human modification. The situation is very different in more pristine landscapes and old-growth forests where the bird species most at risk from intervention are those associated with old growth (Wesołowski 2005). Modification of such habitats may initially increase diversity, but the species which increase or invade are often generalists and edge species of lesser conservation value (Lovejoy et al. 1984, Saunders et al. 1991).

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