Alder, DC, Fuller, RJ and Marsden, SJ (2018) Implications of transformation to irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland. Forest Ecology and Management, 422. pp. 69-78. ISSN 0378-1127

DOI: https://doi.org/10.1016/j.foreco.2018.04.004

Publisher: Elsevier

Implications of transformation to irregular silviculture for woodland birds: a stand wise comparison in an English broadleaf woodland

Daniel C Alder [a,b*], Robert J. Fuller [c,d] & Stuart J Marsden [b]

[a] *Dorset Environmental Records Centre, Dorset History Centre, Bridport Road, Dorchester, Dorset DT1 1RP*

[b] *School of Science & the Environment, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, UK*

[c] *British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU;*

[d] *School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ*

Summary

Woodland birds in Britain have undergone significant long term declines since the late 1960s, associated in particular with changes in woodland structure in general, and loss of early successional vegetation. Irregular, continuous canopy broadleaf management is a form of selective logging, very recently adopted in UK that produces woodlands with open canopies and substantial mid- and understorey growth. We examined spring and late winter bird densities, estimated using distance sampling, at 310 points in irregular, transitional (that being managed towards irregular), limited intervention, and coppice stands within a large working broad-leaf woodland in lowland southern Britain. Almost all understorey and canopy vegetation measures differed significantly across stand types. Ten of 20 species had highest spring abundance in irregular woodland, five in coppice, three in transitional, and just two in limited intervention. In winter, 5-6 species preferred each of limited intervention, irregular and transitional, while no species preferred coppice. Densities differed little across seasons except in Paridae where abundances increased in late winter during which limited intervention stands were used more by this group. Birds generally occupied similar niche positions and had similar niche breadths across seasons. Compared to under-managed woodlands, irregular silviculture in UK's broadleaf woodlands is likely to enhance habitat quality for woodland birds, including several species of conservation concern e.g. marsh tit *Poecile palustris* which was twice as abundant in irregular stands as in any other stand type.

Keywords: Continuous cover forestry, Semi-natural woodland, Irregular silviculture, Stand management, Understorey characteristics, Woodland bird communities.

* Corresponding author.

E-mail addresses: da.conservation@gmail.com (D.C. Alder), rob.fuller@bto.org (R.J.Fuller), s.marsden@mmu.ac.uk (S.J. Marsden)

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1. Introduction

Within the European forestry sector there is growing support for continuous cover forestry (CCF). These systems embrace a diversity of approaches but all seek to retain a continuous woodland cover, as opposed to large scale clear-felling (Mason *et al*. 1999, Mason 2007). CCF systems, sometimes referred to as 'irregular forestry', are often advocated on the basis of having economic, ecosystem service and ecological advantages (Susse *et al*. 2011, Lõhmus *et al*. 2016, Pukkala *et al*. 2016). They form one strand of silvicultural alternatives to even-aged forestry which also include 'ecological forestry' or 'close-to-nature forestry' (Seymour & Hunter 1999, Bürgi 2015, Puettmann *et al*. 2015). All of these systems emphasise avoidance of clear-cutting, the use of mixtures of tree species, natural regeneration and small-scale structural variability (Puettmann *et al*. 2015). Improved understanding of the responses of biodiversity to a shift towards CCF from other systems such as clear-cutting and rotational coppicing (Harmer & Howe 2003) have become increasingly important to forest managers (Puettmann *et al.* 2015, Quine *et al.* 2007). Using an 'irregular' selective felling system, canopy opening is patchy and can resemble natural woodland processes, with canopy gaps leading to localised seedling regeneration, while developing a continuum of tree and shrub ages from young thicket stage to mature trees in each stand (Susse *et al*. 2011). This structure is expected to create a different range of ecological resources to those present within clear-felling and coppice systems with consequent shifts in the composition of bird communities (Quine *et al*. 2007, Fuller *et al*. 2012). In Europe there have been few comparisons of bird communities in stands managed under CCF with those in stands managed under other regimes, though more data are available for North America (see for example Forsman *et al*. 2010). In beech dominated woodlands in the Belgian

Ardenne, bird abundances were higher in uneven stands compared with even-aged (du Bus de Warnaffe and Deconchat, 2008). However, the effects of stand composition (conifer vs broadleaf) was more explicitly demonstrated where management for uneven-aged conifer did not enhance bird diversity. Understorey development from conifer stands undergoing CCF management, important to several species of conservation concern, has highlighted the value of this management type in the UK (Calladine *et al.* 2015).

There is a more specific question concerning the wider adoption of new irregular forestry – can it assist in the recovery of declining woodland biodiversity? In the case of birds, several species of woodland birds in Britain have undergone striking contractions of range and decreases in abundance in recent decades. The species affected vary in taxonomy and ecology, though a disproportionately high number of long-distance migrants have declined (Hewson *et al*. 2007, Hewson & Noble 2009, Fuller *et al*. 2013). There are several potential causes of these declines, one of which is reduction in habitat quality as a result of progressive shifts in woodland management that occurred during the 20th century (Fuller *et al*. 2007). Towards the end of that century much woodland had become heavily shaded, with associated reduction of understorey complexity, partly as a result of the demise of coppicing and partly due to canopy-closure in plantations within afforestation and existing broadleaf woodland (Hopkins & Kirby 2007, Mason 2007). Concurrently, numbers of deer also increased in Britain with similar consequences for woodland structure as lack of management (Gill & Fuller 2007). These factors have led to interest in new regimes for woodland management that reflect both biodiversity concerns and which adapt to changes in woodland product demand (Fuller 2013).

Britain lacks most of the specialist species dependent on late forest successional stages that can be found, for example, in eastern Europe and Fennoscandia where the conservation priority focuses mainly on retaining old forest stands (Wesołowski 2005, Roberge *et al*. 2008). In Britain, however, the restoration of some form of woodland management including CCF Forestry, to unmanaged woods is widely regarded as potentially beneficial for conservation (Fuller *et al.*2007). This reflects the fact that most unmanaged woodland does not consist of ‘near natural’ stands but is woodland that had formerly been harvested especially by a long tradition of coppicing (Buckley & Mills 2015), and currently exists in a neglected often structurally homogenous condition (Peterken & Mountford 2017, Mason 2007). Therefore, woodland management, which we define here as sustainable harvesting of standing timber of varying age classes, may enhance habitat quality for a range of scarce and declining vertebrate and invertebrate species associated with early successional habitats; many of these species are ones that have been adapted to a very long history of human exploitation of British woodlands (Fuller 2013, Hinsley *et al*. 2015). However, not all species may benefit from reintroducing coppicing, an example being marsh tit *Poecile palustris* (Broughton & Hinsley 2015) and invertebrates that depend on features such as standing deadwood (Sterling & Hambler 1988).

The results presented here provide, as far as we are aware, the first assessment of the responses of birds to CCF within temperate broadleaved stands in Europe. Our aim was to compare bird abundance and relevant vegetation attributes across four stand types in a large ancient semi-natural woodland: coppice; limited intervention (formerly managed, now neglected); irregular high forest; and transitional high forest. The latter consisted of stands undergoing initial management towards irregular. Having examined differences in habitat structure between these four broadleaf management types, we then compare bird densities both in spring and winter across stand types, and identify contrasts in habitat use across species and seasons.

2. Methods

2.1 Location and general description

The study was conducted on 442 ha broadleaf woodland and statutorily protected Site of Special Scientific Interest (SSSI) spread across nine contiguous blocks on the Rushmore Estate, in southern England (110-190 m a.s.l; 395724.26 E, 117963.15 N; Figure 1). The principal National Vegetation Classifications (NVC) are W8 (ash-field maple) associated with base-rich soils with some W10 (oak-birch) on slightly acidic soils, that fall within the broad category of lowland mixed decidous woodlands on fertile soil with several sub-categories around the former (Rodwell *et al* .1991, B. Edwards *pers. comm.* 2017). The dominant tree and shrub species are ash *Fraxinus excelsior*, pedunculate oak *Quercus robur*, field maple *Acer campestre*, silver birch *Betula pendula*, downy birch *Betula pubescens*, hazel *Corylus avellana*, spindle *Euonymus europaeus*, hawthorn *Crataegus monogyna*, sallow *Salix cinerea*, goat willow *Salix caprea*, dogwood *Cornus sanguinea* and blackthorn *Prunus spinosa*. There is scattered mature and veteran whitebeam *Sorbus aria,* and more locally distributed beech *Fagus sylvatica* and sycamore *Acer pseudoplatanus.* There are a significant number of veteran trees particularly of oak, ash and field maple along with whitebeam and 19th Century beech plantings (Poore 2016).

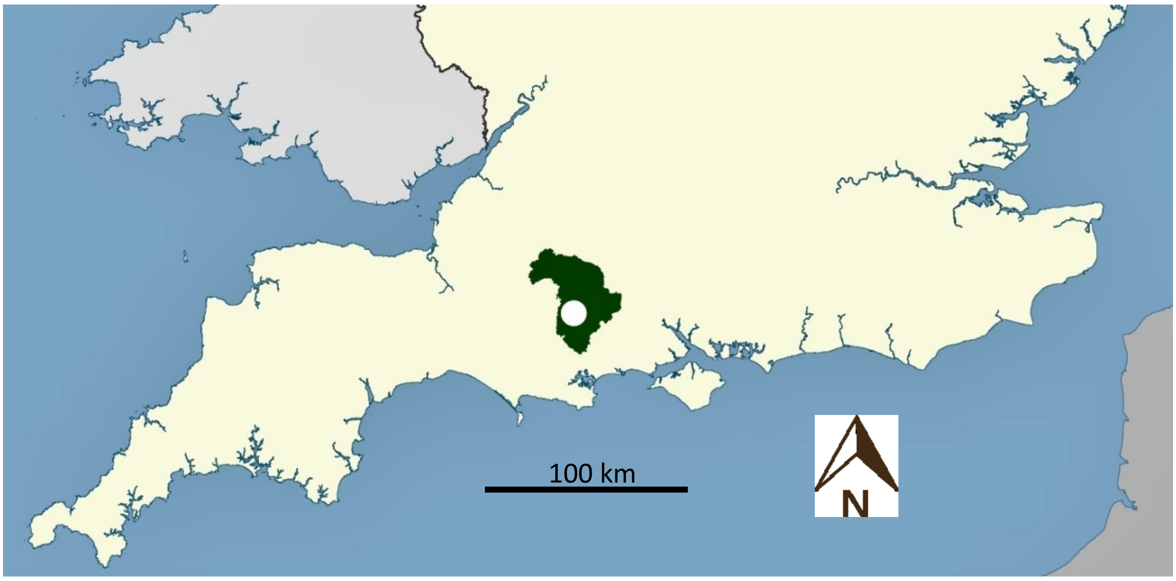


Fig. 1. Location of Cranborne Chase and study area, Dorset-Wiltshire border, southern England, UK.

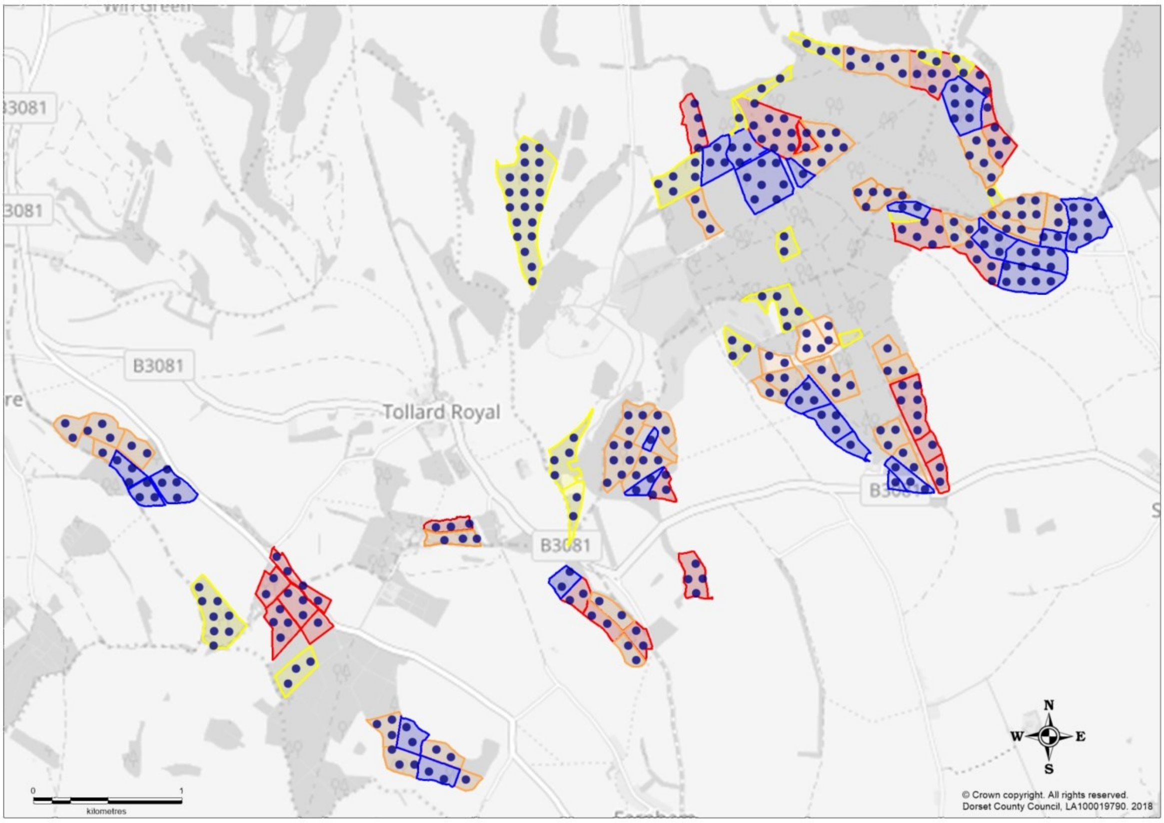


Fig. 2. Sampling points within stand types; orange – coppice, blue – transitional high forest, yellow - limited intervention, and red – irregular high forest.

2.2 Descriptions of Stand types

The following broadleaf stand management types and prescriptions are described (A. Poore pers. comm. 2017; see Table 1 and Figure 2).

'Limited intervention' stands were those with a closed canopy, high tree density, and limited understorey due to a long period (>30 years) without formal silvicultural intervention. Some of the limited intervention stands have developed from open canopy high forest and have higher understorey densities.

‘Coppice stands’ have few canopy trees (<10% canopy cover) and include both simple coppice and coppice with standards with up to 25% cover of standard trees. Coppice cycle lengths vary depending on uses with hazel dominated, (covering c.15 ha), cut every 8-12 years for hurdle fencing, thatching materials and bean poles. Birch coppice managed on two rotations of pure birch (c.19 ha) cut at 3-4 years for horse jumps or revetment faggots and the remaining 50 ha hazel-birch mix on 25-30 year cycles for wood fuel. (There was a broad representation of growth stages with a mean age of coppice during the study of 9.4 years (SD ± 6.7) with 0-5 years (n = 25), 6-9 years (n = 37), 10-15 (n = 21), years and 15-30 years (n = 18)). At each cutting the entire panel between 0.5-1.5 ha of underwood is removed leading to even-aged regrowth (Harmer & Howe 2003).

‘Irregular High Forest stands’ (continuous cover forestry) have been transformed from unmanaged coppice or even-aged stands to a selective irregular management for at least 30 years. This involves selective removal of harvestable trees, and of weaker growing specimens along with cutting of the understorey to increase light levels reaching the woodland floor. The aim is to increase incremental growth of retained trees to enhance their silvicultural and economic value, promote natural regeneration of trees and shrubs and establish a range of tree age classes. Selection of the trees best adapted to site conditions (phenotypes) is a key objective (Susse *et al* 2011). Stands with ‘moderate stocking’ have stand basal areas (> 7.5 cm dbh) in the range 17-24 m^2 ha^{-1} whilst those classified as ‘low stocking’ are in the range 10-16 m^2 ha^{-1}. Understorey stocking varies with past management and the effects of deer, and can be dense in places yet patchily distributed.

'Transitional High Forest' stands are intermediate between coppice and irregular High Forest and are developing towards irregular from former coppice or even-aged high forest. Transitional stands have undergone initial interventions within the previous 10-20 years but are yet to develop the range of irregular stand elements i.e. mixed age and height classes of trees and saplings but often with a developed understorey. They are variable with regard to both canopy and understorey density. However, they broadly separate into two categories depending on whether large trees or pole-stage trees form the canopy (Poore 2016).

Woodland type	**Stand Type**	**Area (ha)**	**% Broadleaf Wood**	**Number of Sample plots**
Semi-Natural Broadleaved Woodland	Irregular High Forest	137.1	31	73
	Transitional High Forest	97.4	22	75
	Limited intervention	102	23	61
	Coppice	106.1*	24	101
Total		442.6	100	310

* Area in active rotation currently 85 ha.

Table 1

Areas of semi-natural broadleaved woodland stand types within the Rushmore Estate and number of sample plots where habitat structural measures and bird community data were collected.

Fig. 3. Examples of stand types used in study shown clockwise from top left; limited intervention, coppice, transitional and irregular.

2.3 Data Collection

A plot-based stratified sampling approach was used (Bibby et al 1998, Kent 2012) for 310 plots derived from grid coordinates generated in MapInfo (Pitney Bowes Ltd 2014) representative of the four stand types. Plots were a minimum distance of 100 m apart to minimise duplication in counts of birds (Table 1). To reduce the influence of proximate habitats, plots were located a minimum distance of 30 m from stand edges (Bibby *et al*. 2000). Each plot consisted of a 30 m diameter circle (0.07 ha) with five subplots of 3 m diameter within each (four located at the cardinal points at 10 m radii (see Hansen & Hounihan 1995) and one at 2 m off-centre along a random compass bearing.

Within 30 m plots, the following habitat measurements were made: number of trees >50 cm dbh, number of woody stems (coppice and individual trees) of dbh 7.5-≤17.5 cm and 17.5-≤50 cm dbh, and the five trees with the largest dbh. These five were identified to species and mean dbh also calculated. At each 3 m subplot, the number of saplings and coppice stems <3 cm, and >3-7.5 cm dbh were counted if >0.5 m tall. Percentage canopy openness was measured with a spherical convex mirror densiometer (Lemmon 1956). Basal area (m^2 ha^{-1}) was measured at each plot centre using the relascope principle (Bitterlich 1984) with each tree >7.5 cm dbh counted in a 360^0 sweep at each sample point centre. A minimum number of ten trees are required to give precision (Bitterlich 1984). The relascope application MOTI was used (Rosset *et al.* 2014), calibrated for the basal area factor and camera in a Samsung Galaxy S2 smart-phone. To calculate understorey density, a percentage score of obscuration to the nearest 5% was estimated at each cardinal point using a 50 x 30 cm chequer board with 10 x 10 cm squares (Fuller & Henderson 1992). Scores were taken at 0.5 m and 2.0 m above ground to assess variation at different levels. Dead trees and dead branches (snags) over 20 cm diameter were counted at each plot (Charman *et al*. 2010). Percentage means were calculated at each plot for bramble *Rubus fruticosus* cover and area of bare ground.

Bird occurrence and abundance was recorded using 5 minute point counts (Bibby *et al*. 2000) at the 310 survey plots across three visit periods: early spring (28 April to 16 May 2014), late spring (21 May to 13 June 2014) and late winter (10 February to 12 March 2015). Counts started one hour after sunrise and completed by 09h30 for the spring visits, and 11h00 for winter visits. Counts took place during fine weather avoiding periods of persistent rain and wind (Bibby *et al*. 1998). The distance to each bird or group on first encounter was measured using a laser rangefinder and distances were estimated to singing/calling birds obscured by vegetation. Birds beyond 50 m of the plot centre were ignored, as were birds flying into or over the plot. Birds flying away were only recorded if they were believed to be ‘within’ the plot, and the distance to their original position could be measured (Buckland 2006). All fieldwork was carried out by DA.

2.4 Data analyses

Given the spatial arrangement of woodland stands (Figure 2), it is reasonable to expect some non-independence of sampled survey plots because they are nested within 53 stands. These stands have their own ecological signature, arising both from their geography and its effect on soil, isolation etc, but also through their history of management. The issue of pseudoreplication has received much attention from ecologists and statisticians (e.g. Hulbert 1984), with a great deal of debate as to how important the issue is, and how to best address it (Oksanen 2001; Davies & Gray 2015).

In an attempt to overcome the effect of non-independence in the across stand type habitat analysis, we “partialled out” the unwanted effect of stand number (the random effect; Davies & Gray 2015). Differences in individual habitat measures were tested across stand type (the Fixed effect) using a generalised linear mixed model in package 'lme4' with Stand number (1-35) as a random factor. The significance of the fixed effect and random effect were calculated using the ANOVA in 'lmerTest', along with Tukey's post hoc pairwise comparisons across stand types.

In the bird density analysis, we did not consider stand number as a factor for two reasons. First, points were spaced 100 m apart and positioned in stands which themselves were often just 100-300 m long/wide and usually less than a few hundred metres from each other (Figure 2). Second, numbers of survey points per stand were fairly even (mean = 5.7 ± 3.9 SD) with only five of the 53 stands having more than ten survey points. Any issue in pseudoreplication in the Distance analysis due to two visits to each survey point in the Summer are accounted for in the analysis by lumping data from the two visits to each point under 'effort=2'.

To compare across stand types, density estimates (individuals km^{-2}), coefficients of variation (% SE) and 95% confidence limits were produced in DISTANCE version 6, (Thomas *et al*. 2010). Data were truncated removing the furthest 5% of bird records to minimise the influence of outliers in the model. Data were entered as groups with 'exact' distances to encounters, with encounters of flying birds removed. Detection functions for spring and winter were very different, reflecting both the profound changes in visual detectability caused by leaf-fall in the largely deciduous woodland, and changes in vocalisation patterns between breeding and non-breeding seasons. While covariates (see below) can be added to alter parameters in the detection function to account for variation in vegetation coverage across plots but within season, we thought it safer to conduct separate seasonal analyses as the actual family of detection model (e.g. Uniform, Half-normal) was likely to differ between spring and winter. The Multiple Covariate Distance Sampling (MCDS) engine was used with understorey density included as a covariate likely to influence detection probability

(Marques *et al*. 2007). Density estimates for each species in each stand type were compared using ANOVA (seasons analysed separately) and significant differences between pairs of stand types identified with Tukey's range tests.

Principal components analysis (PCA) was used to condense the habitat variables onto two component axes/factors (Jolliffe 2002) and centroids for stand type and each bird species plotted on these axes. The differences between mean 'niche positions' (coordinates of plots at which each bird species was recorded) on factors 1 and 2 in spring and winter were tested using Wilcoxon matched pairs tests. Niche widths of species on the two factor axes were calculated as the standard deviations of Factor 1 and 2 scores for 'positive' plots for each species. We then examined any widening or narrowing of habitat associations between seasons (Lloyd & Marsden 2008).

3. Results

3.1 Habitat differences between stand types

Fifteen of the 17 vegetation habitat variables differed significantly across stand types (Table 2). Only dbh of largest tree did not differ significantly between stands. Understorey densities were highest in coppice and irregular with coppice having markedly higher density at 2.0 m. Bramble cover was highest in irregular while the area of bare-ground was significant in limited intervention. Basal areas were lowest in both irregular and coppice compared to limited intervention and transitional stands. Canopy openness was much greater in irregular plots than in other stands.

Habitat Variable	Coppice (n 101)		Irregular (n 73)		Limited (n 61)		Transition (n 75)		Random	Fixed
Basal Area	18.0	(11-22) **L**	18.0	(15-22) **L**	29.0	(24 -33) T	22.0	(18-27) L	0.001	< 0.001
Canopy Openness	10.4	(8-19)	21.3	(14-29) L	9.9	(8-14) I	10.9	(8-21)	0.001	0.06
Mean dbh	36.0	(24-49) **I**	50.6	(44-56) **C**	42.8	(34-53)	39.4	(34- 50)	0.001	0.001
Largest dbh	61.0	(46-79)	71.0	(58-82)	67.0	(52-83)	62.0	(51-70)	0.02	0.07
No. Oak	1.0	(0-2)	1.0	(0-2)	0.0	(0- 0)	1.0	(0-2)	0.001	0.10
No. Ash	1.0	(0-2) I L	3.0	(2-4) C	2.0	(1-3) C	2.0	(1-4)	0.001	0.002
No. deadwood snags	8.0	(4-12)	13.0	(7-17)	8.0	(6-12)	8.0	(6-16)	0.001	0.07
Logs (m) per plot	0.0	(0-4) L	0.0	(0-4)	3.0	(0-8) C	1.0	(0-4)	0.001	0.02
Understorey density 0.5m	48.0	(25-85) **L** T	56.0	(19-75) **L** T	7.0	(3-22) **C I**	20.0	(11-36) I C	0.001	<0.001
Understorey density 2m	52.5	(30-76) **I L T**	23.8	(8-39) **C**	13.8	(5-28) **C**	17.5	(9-28) **C**	0.001	<0.001
No. stems ≤3 cm dbh	9.2	(5-18) **I L** T	2.8	(1-7) **C**	0.6	(0-2) **C**	5.4	(2-10) C	0.001	<0.001
No. stems 3-7.5 cm dbh	3.2	(1-7) **I L**	0.2	(0-1) **C**	0.8	(1-2) **C**	2.2	(0-4)	0.001	<0.001
No. trees 7.5-17.5 cm dbh	9.0	(1-39) **L**	9.0	(1-21) **L**	69.0	(43-88) **C I** T	21.0	(7-59) L	0.001	<0.001
No. trees 17.5-50 cm dbh	2.0	(0-4) **L** T	5.0	(2-7) L	11.0	(5-16) I **C**	7.0	(3-12) C	0.001	<0.001
No. trees ≥50cm dbh	1.0	(0-2)	2.0	(1-3) **C** T L	2.0	(1-3)	1.0	(1-2)	0.001	0.10
Bramble % cover	2.8	(0-19) **I**	30.0	(5-56) **C T L**	0.0	(0-4) **I**	0.0	0-7 **I**	0.001	<0.001
Bare ground %	8.4	(0-29) I	1.4	(0-12) **L**	26.0	(13-59) **I**	12.6	(6-35)	0.001	0.008

Table 2

Median values of habitat variables measured across the four stand types; lower and upper quartiles in parenthesis and results of ANOVA tests for random effects (stand number) and fixed effects (stand type) Pairwise comparisons usingTukey's *post-hoc* test, for stands; C - coppice, I - Irregular, L - Limited intervention and T - Transitional; those in bold are highly significant P < 0.005.

3.2 Bird densities across stand types and season

Across the 310 points, we accumulated 4,994 bird records of 38 species. We calculated density estimates for 16 resident species and four spring migrants (Table 3). Three from the 20 species went unrecorded in limited intervention stands, and two of the species were spring migrants (willow warbler *Phylloscopus trochilus* and garden warbler *Sylvia borin*). Six and five species had density estimates > 100 individuals km^{-2} in at least one stand type in spring and winter respectively. Blue tit *Cyanistes caeruleus* and wren *Troglodytes troglodytes* had estimates > 100 individuals km^{-2} in all stand types in spring, and blue tit and great tit *Parus major* in all stand types in Winter.

	Spring				Winter			
	Coppice	Irregular	Limited intervention	Transitional	Coppice	Irregular	Limited Intervention	Transitional
Woodpigeon *Columba palumbus*	60.1 ± 10 49-73(86) > I	32.4 ± 17 23-45(33)	74.2 ± 12 59-94(62) > I	66.0 ± 11 53-82(71) > I	17.0 ± 35 9-33(12)	20.0 ± 33 10-39(10)	38.1 ± 22 25-59(16)	47.2 ± 21 31-71(25) > C
Great spotted woodpecker *Dendrocopos major*	10.4 ± 27 6-18(15)	12.7 ± 31 7-23(13)	7.1 ± 47 3-17(6)	9.2 ± 34 5-18(10)	5.4 ± 50 2-14(4)	19.0 ± 34 10-36(10)	22.8 ± 30 13-41(10)	16.2 ± 36 8-33(9)
Goldcrest *Regulus regulus*	25.9 ± 27 15-44(16)	27.2 ± 29 16-48 (12)	27.7 ± 32 15-51(10)	60.1 ± 19 42-87(28) > C I	48.8 ± 28 28-84(15)	68.8 ± 30 38-124(15)	93.3 ± 27 55-159(17)	47.9 ± 30 27-86(11)
Blue tit *Cyanistes caeruleus*	124.7 ± 12 99-158(66)	135.1 ± 13 115-175(51)	129.4 ± 15 96-174(40)	120.5 ± 14 92-158(48)	173.3 ± 10 142-211(74)	244.5 ± 9 206-290(74) > C	197.7 ± 13 153-255(50)	200.5 ± 11 161-249(64)
Great tit *Parus major*	92.4 ± 22 61-141(27)	115.2 ± 24 72-184(24)	128.9 ± 24 81-206(22)	86.4 ± 25 53-141(19)	155.9 ± 19 107-228(29)	182.1 ± 20 123-269(24)	236.0 ± 19 163-343(26)	194.2 ± 22 126-299(27)
Coal tit *Periparus ater*	22.5 ± 24 14-36(21)	27.0 ± 24 17-44(18)	9.2 ± 45 4-22(5)	17.1 ± 30 10-30(12)	17.3 ± 43 8-39(7)	59.3 ± 25 36-96(17)	62.6 ± 26 37-105(15)	66.1 ± 24 41-105(20) > C
Marsh tit *Poecile palustris*	65.1 ± 21 43-99(29)	122.8 ± 19 86-176(39) > C L T	53.8 ± 27 32-91(14)	34.9 ± 29 20-63(12)	63.1 ± 22 41-96(21)	76.4 ± 24 48-122(18)	86.3 ± 27 51-146(17)	68.4 ± 23 43-108(17)
Long-tailed Tit *Aegithilos caudatus*	66.0 ± 36 33-130(13) > L	56.5 ± 46 24-133(8) > L	0 0	33.5 ± 50 13-86(5) > L	77.7 ± 37 39-157(10)	65.7 ± 45 28-153(6)	78.7 ± 44 34-182(6)	41.6 ± 53 15-112(4)
Chiffchaff *Phylloscopus collybita*	98.4 ± 11 80-122(82)	82.5 ± 14 63-108(49)	34.9 ± 23 23-55(17)	35.0 ± 21 23-52(22)				

	>> L T	> L T						
Willow warbler *Phylloscopus trochilus*	19.3 ± 62 7-64(10) > L	5.4 ± 89 1-25(2) > L	0 0	3.0 ± 113 0.5-16(1) > L				
Blackcap *Sylvia atricapilla*	101.1 ± 12 81-127(79) >L T	120.2 ± 13 94-154(67) >>L T	50.4 ± 21 33-77(23)	49.3 ± 19 34-71(29)				
Garden warbler *Sylvia borin*	30.3 ± 20 21-45(38) > L T	18.9 ± 28 11-33(17) > L	0 0	7.4 ± 38 4-15(7) > L				
Nuthatch *Sitta europaea*	24.4 ± 32 9-32(16)	31.4 ± 35 16-61(16)	27.9 ± 37 14-57(17)	29.7 ± 33 16-56(17)	20.8 ± 23 13-33(16)	29.4 ± 24 18-47(16)	37.3 ± 21 25-56(17)	29.6 ± 23 19-47(17)
Treecreeper *Certhia familiaris*	9.4 ± 32 5-18(10)	30.2 ± 21 20-46(23) > C	25.6 ± 25 16-41(16)	21.1 ± 24 13-34(17)	20.4 ± 31 11-37(10)	48.9 ± 22 31-76(17)	34.4 ± 33 18-66(10)	24.6 ± 32 13-46(9)
Wren *Troglodytes troglodytes*	108.6 ± 8 92-128(121)	221.6 ± 6 195-252(176) >> C L	148.0 ± 8 126-172(96)	180.1 ± 8 154-211(151) >> C	77.9 ± 15 58-105(43)	163.5 ± 13 126-212(64) >> C > L	88.7 ± 19 62-128(29)	106.6 ± 18 74-153(44)
Blackbird *Turdus merula*	56.2 ± 10 46-68(78)	53.6 ± 12 43-68(53)	46.9 ± 14 36-62(38)	63.2 ± 11 51-79(66)	60.1 ± 16 44- 83(36)	82.4 ± 19 56-121(35) > L	31.0 ± 28 18-54(11)	49.2 ± 21 33-74(22)
Song thrush *Turdus philomelos*	29.2 ± 15 22-39(41) > L	24.0 ± 19 17-35(24)	11.0 ± 36 6-22(9)	24.6 ± 18 17-35(26)	24.3 ± 24 15- 39(19)	21.7 ± 27 13-37(12)	19.5 ± 31 11-36(9)	27.4 ± 23 18-43(16
Robin *Erithacus rubecula*	134.0 ± 9 112-161(109)	87.9 ± 13 68-114(51)	132.6 ± 12 106-167(61)	150.3 ± 10 125-182(92) > I	80.9 ± 13 62-105(54)	76.1± 15 56-103(36)	96.1 ± 14 73-127(38)	104.2 ± 11 83-131(52)
Dunnock *Prunella modularis*	51.8 ± 20 35-77(34)	61.9 ± 22 40-96(29)	20.9 ± 40 10-45(8)	26.3 ± 29 15-46(13)	67.3 ± 23 43-105(30)	107.6 ± 20 72-160(34) > L	15.1 ± 50 6-39(4)	57.0 ± 27 34-97(19)
Chaffinch *Fringilla coelebs*	16.1 ± 20 11-24(25)	29.8 ± 17 22-41(34)	25.3 ± 22 17-39(23)	19.7 ± 21 13-30(23)	26.7 ± 23 17-42(21)	25.2 ± 24 16-41(14)	23.7 ± 31 13-43(11)	35.8 ± 22 23-55(21)

Table 3

Density estimates (individuals km^{-2} ± CV), 95% confidence intervals and numbers of encounters for resident and spring migrant woodland birds by season and stand type. Also shown are results of Tukey's Range Test pairwise comparisons of density across stand types, where > indicates pairs differ at $P<0.05$ and >> $P<0.005$. Direction of sign denotes which density estimate is larger. C = coppice; I = irregular; L = limited intervention; T = transitional.

The mean variation in densities across stand types in spring (the percentage difference between pairs of stand wise densities) was 31.2% ± 23.0 (SD; n = 96). For winter, variation was 29.8% ± 20.8 (n = 96), these figures not differing significantly (W = 4640, p = 0.94). There were significant differences in across-stand densities for twelve species in spring and six in winter (Table 3). Ten species had highest spring density estimates in Irregular stands, with seven of these being significantly higher than in Low intervention stands, and three being significantly higher than in both transitional and coppice. Marsh tit *Poecile palustris* and all four summer warblers had significantly higher densities in irregular over limited intervention. Coppice had five species with highest spring densities, and these included three of the four migrant warblers. All five species occurred in densities within coppice that were significantly higher than in limited intervention, transitional, or both. There were far fewer significant differences in densities across stand types in winter. Irregular stands had higher densities of four species than coppice, limited intervention, or both, while transitional was significant compared to coppice for two species.

3.3 Habitat gradients and bird niche positions from ordination

PCA identified two woodland structural gradients which accounted for 44.3% of the variance within 15 original habitat variables (Figure 3). Factor axis 1 represented a gradient from open canopy mainly oak woodland with scattered large trees (>50 cm dbh) associated with irregular stands to more closed woodland with relatively high tree and stem density aligned closely to limited intervention stands. These denser woodlands were composed of small saplings and shoots (3-7 cm dbh), small to medium (7-17.5 cm dbh), and larger (17.5-50 cm) trees. Factor 2 was associated with greater understorey density at both 0.5m and 2.0m height and had high density of stems (<3 cm dbh) associated with coppice stands. These variables are negatively correlated with high scores for medium-large diameter sized trees within limited intervention stands.

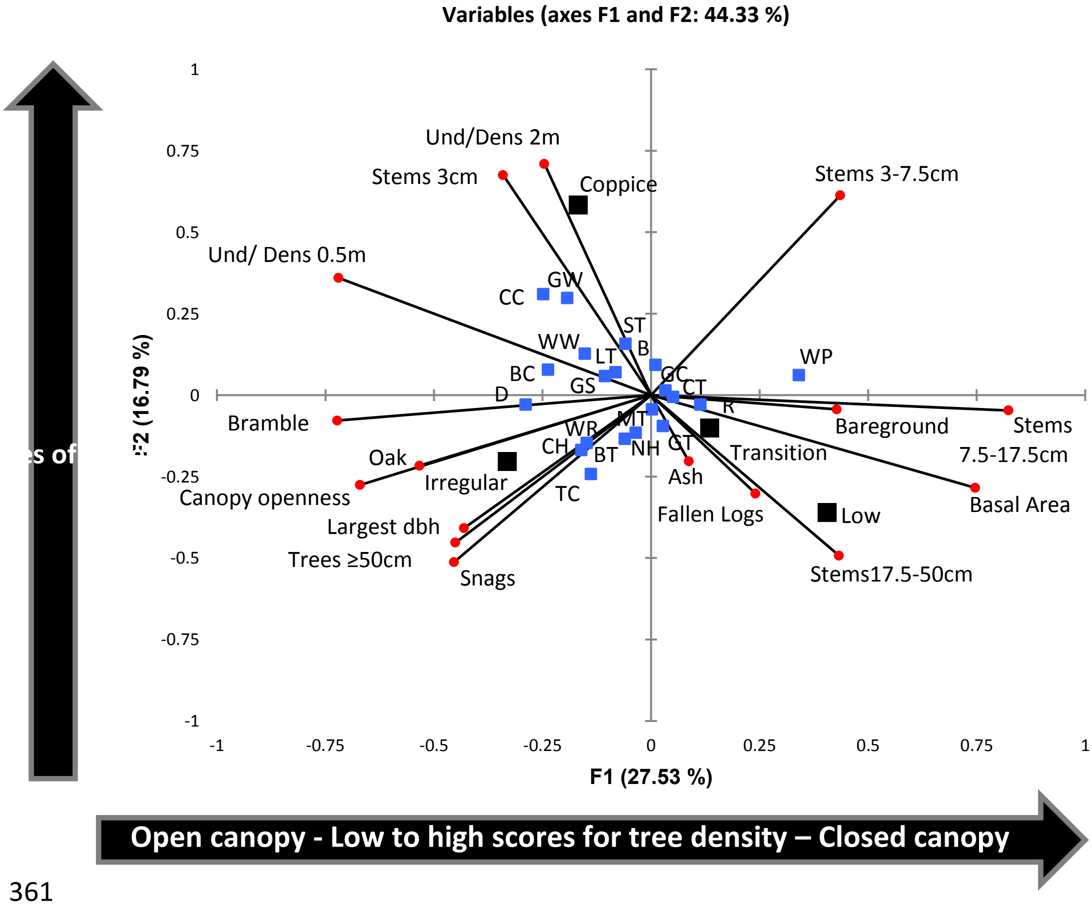
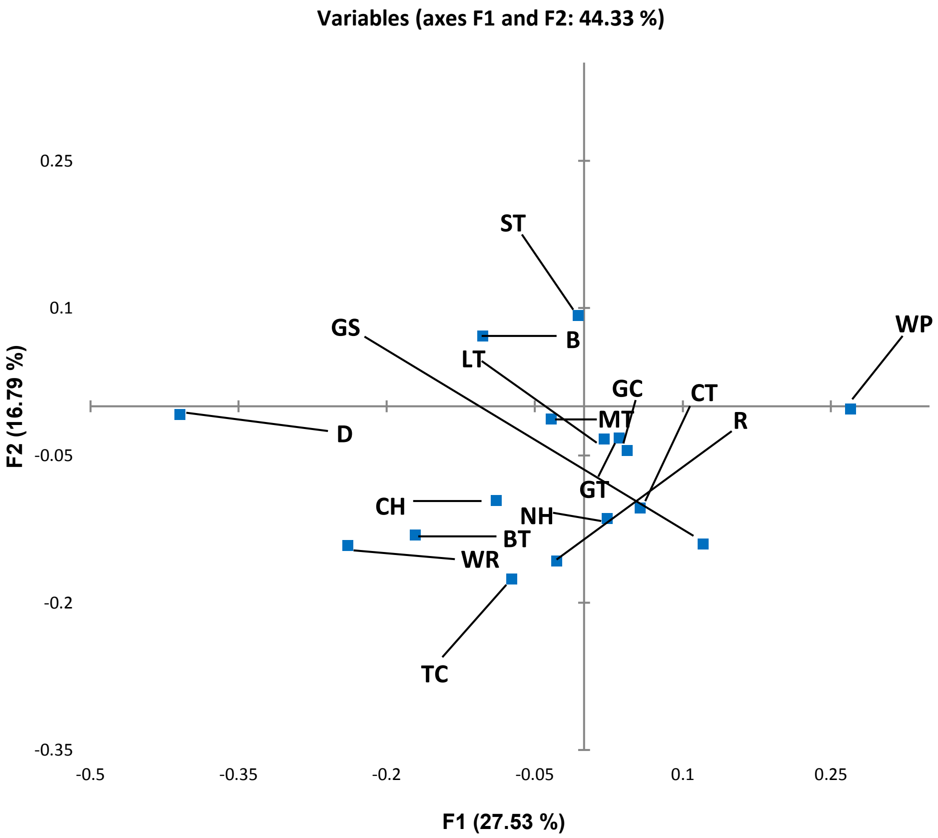
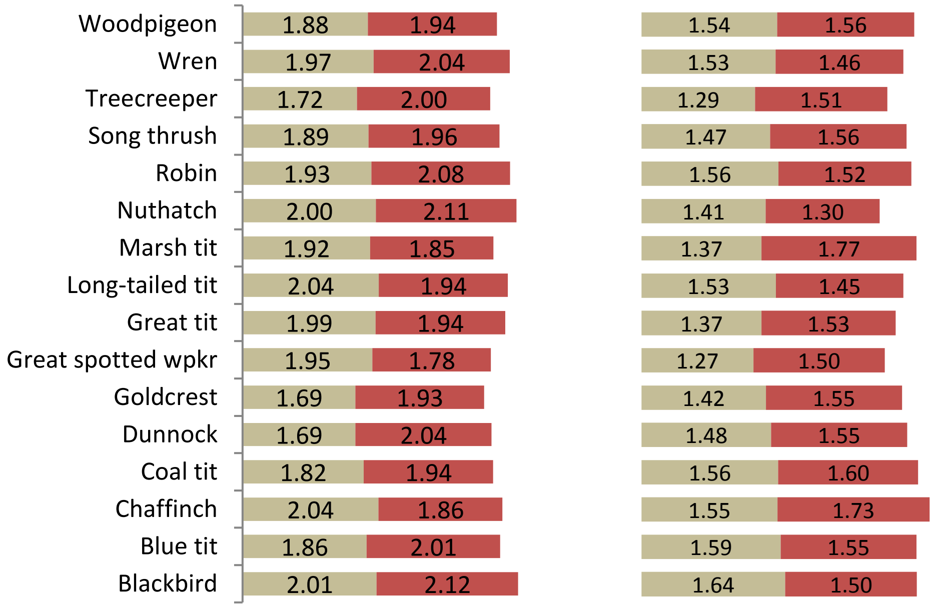


Fig. 4. Ordination of sample plots on PCA Factors 1 and 2 with vectors showing contribution of individual habitat variables. Ordinations show mean positions of stand management types and bird species during the spring. B – blackbird, BC – blackcap, BT – blue tit, CH – chaffinch, CC, chiffchaff, CT – coal tit, D – dunnock, GC – goldcrest, GS –great spotted woodpecker, GT – great tit, GW – garden warbler, LT – long-tailed tit, MT – marsh tit, NH – nuthatch, R – robin, ST – song thrush, TC – treecreeper, WP – woodpigeon, WR – wren, WW – willow warbler.

The majority of bird species were associated with either coppice-like plots (dense understorey; top-left quadrant of Figure 4) or irregular-type plots (open canopy; bottom-left quadrant). Garden warbler and willow warbler were particularly associated with coppice, and treecreeper *Certhia familiaris*, blue tit and chaffinch with irregular-type stands. Woodpigeon *Columba palumbus* was the only species strongly associated with dense plots characteristic of limited intervention management. There was no systematic pattern of seasonal niche position shifts across species (Figure 3a; F1: V = 64, p = 0.85, n = 16; F2: V = 51, p = 0.40, n = 16). Five species 'shifted' to increasingly open woodland in winter - notably dunnock, already associated with open woodland, and wren associated with dense understorey. Great spotted woodpecker *Dendrocopos major* showed the greatest niche position shift, being associated with open woodland and dense understorey in spring and closed canopy plots (limited intervention) in winter. There was no significant increase or decrease in niche breadths between spring and winter (F1: V = 35, p = 0.10, n = 16 F2: V = 38, p = 0.13, n = 16) (Figure 3b).


Variables (axes F1 and F2: 44.33 %)
F2 (16.79 %)
F1 (27.53 %)
0.25
0.1
-0.05
-0.2
-0.35
-0.5
-0.35
-0.2
-0.05
0.1
0.25
ST
GS
B
WP
LT
GC
CT
MT
R
D
GT
CH
NH
BT
WR
TC

a.


Woodpigeon
1.88
1.94
1.54
1.56
Wren
1.97
2.04
1.53
1.46
Treecreeper
1.72
2.00
1.29
1.51
Song thrush
1.89
1.96
1.47
1.56
Robin
1.93
2.08
1.56
1.52
Nuthatch
2.00
2.11
1.41
1.30
Marsh tit
1.92
1.85
1.37
1.77
Long-tailed tit
2.04
1.94
1.53
1.45
Great tit
1.99
1.94
1.37
1.53
Great spotted wpkr
1.95
1.78
1.27
1.50
Goldcrest
1.69
1.93
1.42
1.55
Dunnock
1.69
2.04
1.48
1.55
Coal tit
1.82
1.94
1.56
1.60
Chaffinch
2.04
1.86
1.55
1.73
Blue tit
1.86
2.01
1.59
1.55
Blackbird
2.01
2.12
1.64
1.50

b.

Fig. 4. Spring and winter niche characteristics for resident woodland birds. a. niche position shifts from spring (letter codes; see Fig.4.) to Winter – (blue points); b. niche breadth changes from Spring to Winter on Factor 1 and Factor 2 scores left and right respectively.

4. Discussion

4.1 Differences between stand types

There were clear differences between stand types in both bird communities and woodland structure. Unlike other stand types, irregular management was characterised by more open woodland with larger trees and an uneven mix of ages. Spring bird densities were highest or second highest in irregular for 15 of the 20 species examined. In contrast, limited intervention had the lowest or second lowest spring densities for 14 of 20 species, with notably low abundances for species, such as the warblers, that require complex understorey structures. There were generally low numbers of warblers in transitional stands suggesting the understorey was insufficiently developed. As expected from previous studies in the UK, three of four summer migrant warbler species had highest densities in coppice (e.g. Fuller & Henderson 1992, MacColl *et al*. 2014) but all had second highest densities in irregular stands with blackcap *Sylvia atricapilla* more abundant. In winter, for all species, the highest abundances occurred in irregular, transitional and limited intervention stands, although there were fewer differences in bird abundances between stand types than in spring.

Previous European studies of birds in CCF stands have generated mixed findings although importantly these are not in pure broadleaf woodlands as in our study. Working in spruce plantations in upland Britain, Calladine *et al.* (2015) found that most ‘mature forest’ bird species reached higher abundance in CCF than in rotational clear-fells. However, in Belgium, du Bus de Warnaffe and Deconchat (2008) reported that in beech and conifer forests, no clear differences in bird communities were evident between CCF and clear-cut systems. In North America, a meta-analysis by Forsman *et al*. (2010) found that silviculture creation of small gaps did not result in clear negative impacts on bird communities relative to unlogged forest.

4.2 Seasonal differences

There were fewer differences between bird densities across stand types in winter than in spring, presumably because resource use patterns differ in the former and latter (Fuller *et al*. 2012). In winter, many species, especially titmice, Paridae, nuthatch *Sitta europaea* and treecreeper become increasingly mobile, gleaning insect larvae from bark and buds in stands with higher tree density (Fuller 1995). In our study, this group of birds associated least with coppice in winter. Previous studies have shown these resident species associated with a broader range of woodland habitats in winter (Bilke 1984). Although we did not look at demographic variation in our study it is known that several species differ in their seasonal responses to understorey age, coppice especially, depending on whether they are adult or juveniles (MacCol *et al.* 2014). Four species (blue tit, blackbird *Turdus merula*, wren and dunnock *Prunella modularis*) had significantly higher winter densities in irregular than in limited intervention stands. For those species associated with foraging close to the woodland floor, it seems likely that the denser understorey of irregular stands provides increased protection from predation risk and thermal variation (Holt *et al.* 2014). Although we found no statistically significant niche shifts from spring to winter for resident species, there were a few notable changes in habitat/niche use. Wren and dunnock were both significantly more abundant in irregular stands during the breeding season, and this association strengthened during the winter, presumably as they sought increased protection in the denser shrub-layer. Bramble *Rubus fruticosus* cover was significantly higher in irregular stands and contributed to the understorey density values at 0.5 m above ground which was strongly associated with this stand type. Winter marsh tit densities were highest in limited intervention, although its density in irregular stands were only a little lower, perhaps reflecting a widening of home range and differential use of habitats between the breeding and winter periods (Broughton *et al.* 2014). This is likely to be true of several species although there was little evidence of systematic movement of niches. Great spotted woodpecker was associated with open woodland during spring (see Calladine *et al*. 2015) and moved into stands with a greater abundance of fallen deadwood, closed canopy and higher basal area in winter.

4.3 Implications for woodland bird conservation

We are unaware of any similar research in lowland broadleaved woodland in Britain or Europe where stands have undergone a transformation to an irregular high-forest management system, a type of CCF. Taken overall, the findings suggest that irregular forestry can provide suitable woodland habitats for a high proportion of bird species in lowland British woodland, especially in spring, and that for some species it may even provide preferred habitats. In combination with previous studies referred to above, our research suggests that CCF is likely to be either beneficial or neutral in terms of its effects on bird communities. However, two important caveats should be acknowledged. Firstly, the effects may be context dependent according to region, forest type and the exact stand types being compared. Secondly, some early successional bird species may prefer either coppice or young clear-fells which can provide larger areas of young-growth than are found with CCF (Calladine *et al*. 2015). For example, in our study we found tree pipit *Anthus trivialis* exclusively in recent clear-fell gaps outside of the stand types under question.

The value of coppicing to early successional birds and other species associated with dense understorey is well documented (Fuller & Warren 1991, Fuller 1992, Macoll *et al*. 2014) while it has a strong cultural association with many ancient semi-natural woods such as those found in Cranborne Chase (Rackham 1990, A. Poore pers. comm. 2017). Other than government grant-fundingtargeted at sites of high nature conservation value, woodfuel produce is likely to be the main economic driver sustaining coppice management (Fuller 2013, Buckley & Mills 2015). However, irregular stand management as a more widely economically viable system appears to provide resources for most woodland birds associated with both understorey and old growth here in southern England. Furthermore, proponents of CCF point out the multiple benefits it can offer in terms of meeting sustainability measures (Bürgi 2015).

No single silvicultural system can provide the preferred habitat of all woodland birds. In practice, therefore, a conservation strategy that embraces a dynamic range of management interventions is desirable to enhance habitat heterogeneity and complexity at varying spatial and temporal scales (Fuller *et al.* 2007, 2012). Irregular CCF forestry clearly has the potential to play an important role in developing this heterogeneity. However, there is a question about whether it can meet the requirements of all early successional species. In this respect, further work is needed to assess how varying gap sizes within different variants of CCF affect biodiversity (Puettmann *et al*. 2015).

Finally, the results of this study support the notion that in a British context, management of neglected woodland benefits the numbers of many woodland bird species. Both the irregular stands and the coppiced stands held higher densities of breeding birds than the limited intervention stands, typical of much neglected woodland in lowland Britain. Restoration of such stands to a structurally more complex state through opening up the canopy to stimulate the understorey would be beneficial and, if conducted on a sufficiently large scale, could potentially assist in the recovery of some woodland bird populations at a regional level. In this context, it is notable that the spring abundance of marsh tit in irregular stands was approximately twice that in the other stand types. Broughton and Hinsley (2015) cautioned that large scale management by coppicing could be detrimental to habitat quality for this species, but it appears that irregular stand management may benefit it, though more research is needed to draw firm conclusions. An integrated approach to forest management which incorporates stand-level targets to attain biodiversity attributes e.g. deadwood, as shown by Susse *et al*.(2012) is an exciting option; particularly if it can be adapted to include measures that provide important functional resources used by woodland birds in the UK including those associated with understorey.

Acknowledgements

Andy Poore (Consultant Forest Manager) provided background information on stand management and suitable locations for the study. Ian Burt (Rushmore Estate) and Rhiannon Rogers, Jon Corkill (Dorset Environmental Records Centre) helped with fieldwork and GIS support. For access to the woodlands we are grateful to the Trustees of the Rushmore Estate and particularly support from the managing agents Philip Gready and Ruth Mason, along with Andy Taylor, Robert Taylor and Don Taylor for their practical assistance. We are particularly grateful to Dr Annabel King for the recommendation and assistance given during the planning stages. The fieldwork was funded by the Golden Bottle Trust, Henry Hoare Charitable Trust and Forestry Commission (England). The study formed part of a multi-taxon study of the effects of transformation of broadleaf woodland overseen by Dr Phil Sterling (Dorset County Council) and Andy Poore. There are no declarations of conflicts of interests.

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