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- 1 Implications of transformation to irregular silviculture for woodland birds: a stand
- 2 wise comparison in an English broadleaf woodland
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- 11

## 12 Summary

13 Woodland birds in Britain have undergone significant long term declines since the late 1960s, associated in particular with changes in woodland structure in general, 14 15 and loss of early successional vegetation. Irregular, continuous canopy broadleaf 16 management is a form of selective logging, very recently adopted in UK that produces 17 woodlands with open canopies and substantial mid- and understorey growth. We examined spring and late winter bird densities, estimated using distance sampling, at 18 19 310 points in irregular, transitional (that being managed towards irregular), limited 20 intervention, and coppice stands within a large working broad-leaf woodland in 21 lowland southern Britain. Almost all understorey and canopy vegetation measures 22 differed significantly across stand types. Ten of 20 species had highest spring 23 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, 24 25 irregular and transitional, while no species preferred coppice. Densities differed little

26 across seasons except in Paridae where abundances increased in late winter during 27 which limited intervention stands were used more by this group. Birds generally 28 occupied similar niche positions and had similar niche breadths across seasons. Compared to under-managed woodlands, irregular silviculture in UK's broadleaf 29 woodlands is likely to enhance habitat quality for woodland birds, including several 30 species of conservation concern e.g. marsh tit Poecile palustris which was twice as 31 abundant in irregular stands as in any other stand type. 32 Keywords: Continuous cover forestry, Semi-natural woodland, Irregular silviculture, 33 Stand management, Understorey characteristics, Woodland bird communities. 34 \* Corresponding author. 35

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## 39 **1. Introduction**

Within the European forestry sector there is growing support for continuous cover 40 forestry (CCF). These systems embrace a diversity of approaches but all seek to 41 retain a continuous woodland cover, as opposed to large scale clear-felling (Mason et 42 al. 1999, Mason 2007). CCF systems, sometimes referred to as 'irregular forestry', are 43 often advocated on the basis of having economic, ecosystem service and ecological 44 advantages (Susse et al. 2011, Lõhmus et al. 2016, Pukkala et al. 2016). They form 45 one strand of silvicultural alternatives to even-aged forestry which also include 46 'ecological forestry' or 'close-to-nature forestry' (Seymour & Hunter 1999, Bürgi 47 2015, Puettmann et al. 2015). All of these systems emphasise avoidance of clear-48 cutting, the use of mixtures of tree species, natural regeneration and small-scale 49 structural variability (Puettmann et al. 2015). Improved understanding of the 50 responses of biodiversity to a shift towards CCF from other systems such as clear-51 cutting and rotational coppicing (Harmer & Howe 2003) have become increasingly 52 important to forest managers (Puettmann *et al.* 2015, Quine *et al.* 2007). Using an 53 'irregular' selective felling system, canopy opening is patchy and can resemble 54 natural woodland processes, with canopy gaps leading to localised seedling 55 regeneration, while developing a continuum of tree and shrub ages from young 56 thicket stage to mature trees in each stand (Susse *et al.* 2011). This structure is 57 58 expected to create a different range of ecological resources to those present within 59 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 60 61 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 62 (see for example Forsman *et al.* 2010). In beech dominated woodlands in the Belgian 63

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).

71 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 72 73 of birds, several species of woodland birds in Britain have undergone striking contractions of range and decreases in abundance in recent decades. The species 74 affected vary in taxonomy and ecology, though a disproportionately high number of 75 long-distance migrants have declined (Hewson et al. 2007, Hewson & Noble 2009, 76 77 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 78 79 management that occurred during the 20<sup>th</sup> century (Fuller *et al.* 2007). Towards the end of that century much woodland had become heavily shaded, with associated 80 reduction of understorey complexity, partly as a result of the demise of coppicing and 81 82 partly due to canopy-closure in plantations within afforestation and existing broadleaf woodland (Hopkins & Kirby 2007, Mason 2007). Concurrently, numbers of 83 deer also increased in Britain with similar consequences for woodland structure as 84 lack of management (Gill & Fuller 2007). These factors have led to interest in new 85 regimes for woodland management that reflect both biodiversity concerns and which 86 87 adapt to changes in woodland product demand (Fuller 2013).

88 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 89 90 conservation priority focuses mainly on retaining old forest stands (Wesołowski 2005, Roberge *et al.* 2008). In Britain, however, the restoration of some form of 91 woodland management including CCF Forestry, to unmanaged woods is widely 92 regarded as potentially beneficial for conservation (Fuller *et al.*2007). This reflects 93 the fact that most unmanaged woodland does not consist of 'near natural' stands but 94 is woodland that had formerly been harvested especially by a long tradition of 95 coppicing (Buckley & Mills 2015), and currently exists in a neglected often 96 97 structurally homogenous condition (Peterken & Mountford 2017, Mason 2007). 98 Therefore, woodland management, which we define here as sustainable harvesting of 99 standing timber of varying age classes, may enhance habitat quality for a range of 100 scarce and declining vertebrate and invertebrate species associated with early 101 successional habitats; many of these species are ones that have been adapted to a 102 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 103 104 example being marsh tit *Poecile palustris* (Broughton & Hinsley 2015) and invertebrates that depend on features such as standing deadwood (Sterling & 105 Hambler 1988). 106

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.

117 **2. Methods** 

118

## 119 2.1 Location and general description

120

The study was conducted on 442 ha broadleaf woodland and statutorily protected 121 Site of Special Scientific Interest (SSSI) spread across nine contiguous blocks on the 122 Rushmore Estate, in southern England (110-190 m a.s.l; 395724.26 E, 117963.15 N; 123 Figure 1). The principal National Vegetation Classifications (NVC) are W8 (ash-field 124 maple) associated with base-rich soils with some W10 (oak-birch) on slightly acidic 125 soils, that fall within the broad category of lowland mixed decidous woodlands on 126 fertile soil with several sub-categories around the former (Rodwell et al .1991, B. 127 Edwards *pers. comm.* 2017). The dominant tree and shrub species are ash *Fraxinus* 128 excelsior, pedunculate oak Quercus robur, field maple Acer campestre, silver birch 129 Betula pendula, downy birch Betula pubescens, hazel Corylus avellana, spindle 130 *Euonymus europaeus*, hawthorn *Crataegus monogyna*, sallow *Salix cinerea*, goat 131 willow Salix caprea, dogwood Cornus sanguinea and blackthorn Prunus spinosa. There 132 133 is scattered mature and veteran whitebeam *Sorbus aria*, and more locally distributed beech Fagus sylvatica and sycamore Acer pseudoplatanus. There are a significant 134 135 number of veteran trees particularly of oak, ash and field maple along with whitebeam and 19<sup>th</sup> Century beech plantings (Poore 2016). 136



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**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.

144

145 *2.2 Descriptions of Stand types* 

- 147 The following broadleaf stand management types and prescriptions are described (A.
- 148 Poore pers. comm. 2017; see Table 1 and Figure 2).
- 149 '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
- 151 intervention. Some of the limited intervention stands have developed from open
- 152 canopy high forest and have higher understorey densities.

153 'Coppice stands' have few canopy trees (<10% canopy cover) and include both simple 154 coppice and coppice with standards with up to 25% cover of standard trees. Coppice 155 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 156 coppice managed on two rotations of pure birch (c.19 ha) cut at 3-4 years for horse 157 jumps or revetment faggots and the remaining 50 ha hazel-birch mix on 25-30 year 158 cycles for wood fuel. (There was a broad representation of growth stages with a mean 159 age of coppice during the study of 9.4 years (SD  $\pm$  6.7) with 0-5 years (n = 25), 6-9 160 years (n = 37), 10-15 (n = 21), years and 15-30 years (n = 18)). At each cutting the 161 entire panel between 0.5-1.5 ha of underwood is removed leading to even-aged 162 regrowth (Harmer & Howe 2003). 163

164

'Irregular High Forest stands' (continuous cover forestry) have been transformed 165 166 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 167 weaker growing specimens along with cutting of the understorey to increase light 168 levels reaching the woodland floor. The aim is to increase incremental growth of 169 170 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 171 172 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 173 the range 17-24 m<sup>2</sup> ha<sup>-1</sup> whilst those classified as 'low stocking' are in the range 10-16 174 m<sup>2</sup> ha<sup>-1</sup>. Understorev stocking varies with past management and the effects of deer, 175 and can be dense in places yet patchily distributed. 176

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

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

186 \* Area in active rotation currently 85 ha.

## 187 Table 1

188 Areas of semi-natural broadleaved woodland stand types within the Rushmore Estate and number of

189 sample plots where habitat structural measures and bird community data were collected.

190



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

195

196 2.3 Data Collection

197

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
201 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 randomcompass bearing.

207 Within 30 m plots, the following habitat measurements were made: number of trees 208 >50 cm dbh, number of woody stems (coppice and individual trees) of dbh 7.5- $\leq$ 17.5 cm and 17.5-≤50 cm dbh, and the five trees with the largest dbh. These five were 209 210 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. 211 212 Percentage canopy openness was measured with a spherical convex mirror 213 densiometer (Lemmon 1956). Basal area (m<sup>2</sup> ha<sup>-1</sup>) was measured at each plot centre using the relascope principle (Bitterlich 1984) with each tree >7.5 cm dbh counted in 214 a 360<sup>0</sup> sweep at each sample point centre. A minimum number of ten trees are 215 required to give precision (Bitterlich 1984). The relascope application MOTI was 216 used (Rosset et al. 2014), calibrated for the basal area factor and camera in a 217 218 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 219 220 50 x 30 cm chequer board with 10 x 10 cm squares (Fuller & Henderson 1992). 221 Scores were taken at 0.5 m and 2.0 m above ground to assess variation at different 222 levels. Dead trees and dead branches (snags) over 20 cm diameter were counted at 223 each plot (Charman *et al.* 2010). Percentage means were calculated at each plot for bramble *Rubus fruticosus* cover and area of bare ground. 224

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

229 the spring visits, and 11h00 for winter visits. Counts took place during fine weather 230 avoiding periods of persistent rain and wind (Bibby *et al.* 1998). The distance to each 231 bird or group on first encounter was measured using a laser rangefinder and distances were estimated to singing/calling birds obscured by vegetation. Birds 232 beyond 50 m of the plot centre were ignored, as were birds flying into or over the 233 plot. Birds flying away were only recorded if they were believed to be 'within' the 234 plot, and the distance to their original position could be measured (Buckland 2006). 235 All fieldwork was carried out by DA. 236

237

238 2.4 Data analyses

239

240 Given the spatial arrangement of woodland stands (Figure 2), it is reasonable to 241 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 242 243 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 244 245 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 246 247 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 255 256 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 257 258 hundred metres from each other (Figure 2). Second, numbers of survey points per stand were fairly even (mean =  $5.7 \pm 3.9$  SD) with only five of the 53 stands having 259 260 more than ten survey points. Any issue in pseudoreplication in the Distance analysis 261 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'. 262

To compare across stand types, density estimates (individuals km<sup>-2</sup>), coefficients of 263 variation (% SE) and 95% confidence limits were produced in DISTANCE version 6, 264 (Thomas et al. 2010). Data were truncated removing the furthest 5% of bird records 265 266 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 267 functions for spring and winter were very different, reflecting both the profound 268 changes in visual detectability caused by leaf-fall in the largely deciduous woodland, 269 270 and changes in vocalisation patterns between breeding and non-breeding seasons. 271 While covariates (see below) can be added to alter parameters in the detection 272 function to account for variation in vegetation coverage across plots but within 273 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 274 winter. The Multiple Covariate Distance Sampling (MCDS) engine was used with 275 understorey density included as a covariate likely to influence detection probability 276

(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.

280 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

282 bird species plotted on these axes. The differences between mean 'niche positions'

283 (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).

288

# 289 **3. Results**

290

291 *3.1 Habitat differences between stand types* 

292

293 Fifteen of the 17 vegetation habitat variables differed significantly across stand types

294 (Table 2). Only dbh of largest tree did not differ significantly between stands.

295 Understorey densities were highest in coppice and irregular with coppice having

296 markedly higher density at 2.0 m. Bramble cover was highest in irregular while the

297 area of bare-ground was significant in limited intervention. Basal areas were lowest

in both irregular and coppice compared to limited intervention and transitional

Habitat Variable	Copp	ice (n 101)	Irreg	gular (n 73)	Limite	ed (n 61)	Trans	ition (n 75)	Random	Fixed
Basal Area	18.0	(11-22) L	18.0	(15-22) <b>L</b>	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) <b>I</b>	50.6	(44 <b>-</b> 56) <b>C</b>	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) <b>L</b> T	56.0	(19 <b>-</b> 75) <b>L</b> T	7.0	(3-22) <b>C I</b>	20.0	(11-36) I C	0.001	< 0.001
Understorey density 2m	52.5	(30-76) <b>I L T</b>	23.8	(8-39) <b>C</b>	13.8	(5-28) <b>C</b>	17.5	(9-28) <b>C</b>	0.001	< 0.001
No. stems ≤3 cm dbh	9.2	(5-18) <b>I L</b> T	2.8	(1-7) <b>C</b>	0.6	(0-2) <b>C</b>	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) <b>C</b>	0.8	(1-2) <b>C</b>	2.2	(0-4)	0.001	< 0.001
No. trees 7.5-17.5 cm dbh	9.0	(1-39) <b>L</b>	9.0	(1-21) <b>L</b>	69.0	(43-88) <b>C I</b> T	21.0	(7-59) L	0.001	< 0.001
No. trees 17.5-50 cm dbh	2.0	(0-4) <b>L</b> T	5.0	(2-7) L	11.0	(5-16) I <b>C</b>	7.0	(3-12) C	0.001	< 0.001
No. trees ≥50cm dbh	1.0	(0-2)	2.0	(1-3) <b>C</b> T L	2.0	(1-3)	1.0	(1-2)	0.001	0.10
Bramble % cover	2.8	(0-19) <b>I</b>	30.0	(5-56) <b>C T L</b>	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) <b>L</b>	26.0	(13-59) <b>I</b>	12.6	(6-35)	0.001	0.008

stands. Canopy openness was much greater in irregular plots than in other stands.

300

301	Table 2
302	Median values of habitat variables measured across the four stand types; lower and upper
303	quartiles in parenthesis and results of ANOVA tests for random effects (stand number) and fixed
304	effects (stand type) Pairwise comparisons usingTukey's <i>post-hoc</i> test, for stands; C - coppice, I -
305	Irregular, L - Limited intervention and T - Transitional; those in bold are highly significant P <
306	0.005.
307	
308	

309 *3.2 Bird densities across stand types and season* 

311	Across the 310 points, we accumulated 4,994 bird records of 38 species. We
312	calculated density estimates for 16 resident species and four spring migrants (Table
313	3). Three from the 20 species went unrecorded in limited intervention stands, and
314	two of the species were spring migrants (willow warbler Phylloscopus trochilus and
315	garden warbler <i>Sylvia borin</i> ). Six and five species had density estimates > 100
316	individuals km <sup>-2</sup> in at least one stand type in spring and winter respectively. Blue tit
317	<i>Cyanistes caeruleus</i> and wren <i>Troglodytes troglodytes</i> had estimates > 100 individuals
318	km <sup>-2</sup> in all stand types in spring, and blue tit and great tit <i>Parus major</i> in all stand
319	types in Winter.
320	

Spring					Winter				
			Limited				Limited		
	Coppice	Irregular	intervention	Transitional	Coppice	Irregular	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)
222								

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322
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323 Table 3

324 Density estimates (individuals km<sup>-2</sup> ± CV), 95% confidence intervals and numbers of encounters for

325 resident and spring migrant woodland birds by season and stand type. Also shown are results of

**326** Tukey's Range Test pairwise comparisons of density across stand types, where > indicates pairs differ

327 at P<0.05 and >> P<0.005. Direction of sign denotes which density estimate is larger. C = coppice; I =

328 irregular; L = limited intervention; T = transitional.

- 330 The mean variation in densities across stand types in spring (the percentage
- difference between pairs of stand wise densities) was  $31.2\% \pm 23.0$  (SD; n = 96). For

winter, variation was 29.8% ± 20.8 (n = 96), these figures not differing significantly 332 (W = 4640, p = 0.94). There were significant differences in across-stand densities for 333 334 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 335 than in Low intervention stands, and three being significantly higher than in both 336 transitional and coppice. Marsh tit *Poecile palustris* and all four summer warblers had 337 significantly higher densities in irregular over limited intervention. Coppice had five 338 species with highest spring densities, and these included three of the four migrant 339 warblers. All five species occurred in densities within coppice that were significantly 340 higher than in limited intervention, transitional, or both. There were far fewer 341 342 significant differences in densities across stand types in winter. Irregular stands had 343 higher densities of four species than coppice, limited intervention, or both, while 344 transitional was significant compared to coppice for two species.

345

#### 346 3.3 Habitat gradients and bird niche positions from ordination

347

348 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 349 350 gradient from open canopy mainly oak woodland with scattered large trees (>50 cm 351 dbh) associated with irregular stands to more closed woodland with relatively high 352 tree and stem density aligned closely to limited intervention stands. These denser 353 woodlands were composed of small saplings and shoots (3-7 cm dbh), small to 354 medium (7-17.5 cm dbh), and larger (17.5-50 cm) trees. Factor 2 was associated 355 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</li>
correlated with high scores for medium-large diameter sized trees within limited
intervention stands.

359

360



361

**Fig. 4.** Ordination of sample plots on PCA Factors 1 and 2 with vectors showing contribution of

363 individual habitat variables. Ordinations show mean positions of stand management types and bird

364 species during the spring. B – blackbird, BC – blackcap, BT – blue tit, CH – chaffinch, CC, chiffchaff, CT –

365 coal tit, D – dunnock, GC – goldcrest, GS –great spotted woodpecker, GT – great tit, GW – garden

366 warbler, LT – long-tailed tit, MT – marsh tit, NH – nuthatch, R – robin, ST – song thrush, TC –

367 treecreeper, WP – woodpigeon, WR – wren, WW – willow warbler.

369 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; 370 371 bottom-left quadrant). Garden warbler and willow warbler were particularly 372 associated with coppice, and treecreeper Certhia familiaris, blue tit and chaffinch with irregular-type stands. Woodpigeon *Columba palumbus* was the only species 373 strongly associated with dense plots characteristic of limited intervention 374 management. There was no systematic pattern of seasonal niche position shifts 375 across species (Figure 3a; F1: V = 64, p = 0.85, n = 16; F2: V = 51, p = 0.40, n = 16). 376 Five species 'shifted' to increasingly open woodland in winter - notably dunnock, 377 already associated with open woodland, and wren associated with dense 378 understorey. Great spotted woodpecker Dendrocopos major showed the greatest 379 380 niche position shift, being associated with open woodland and dense understorey in 381 spring and closed canopy plots (limited intervention) in winter. There was no 382 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). 383

Variables (axes F1 and F2: 44.33 %)



385 a.

-	1	
Woodpigeon	1.88	1.94
Wren	1.97	2.04
Treecreeper	1.72	2.00
Song thrush	1.89	1.96
Robin	1.93	2.08
Nuthatch	2.00	2.11
Marsh tit	1.92	1.85
Long-tailed tit	2.04	1.94
Great tit	1.99	1.94
Great spotted wpkr	1.95	1.78
Goldcrest	1.69	1.93
Dunnock	1.69	2.04
Coal tit	1.82	1.94
Chaffinch	2.04	1.86
Blue tit	1.86	2.01
Blackbird	2.01	2.12

1.54	1.56
1.53	1.46
1.29	1.51
1.47	1.56
1.56	1.52
1.41	1.30
1.37	1.77
1.53	1.45
1.37	1.53
1.27	1.50
1.42	1.55
1.48	1.55
1.56	1.60
1.55	1.73
1.59	1.55
1.64	1.50

386 b.

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

391

# 392 4. Discussion

393 *4.1 Differences between stand types* 

394

395 There were clear differences between stand types in both bird communities and woodland structure. Unlike other stand types, irregular management was 396 397 characterised by more open woodland with larger trees and an uneven mix of ages. 398 Spring bird densities were highest or second highest in irregular for 15 of the 20 399 species examined. In contrast, limited intervention had the lowest or second lowest 400 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 401 402 low numbers of warblers in transitional stands suggesting the understorey was insufficiently developed. As expected from previous studies in the UK, three of four 403 summer migrant warbler species had highest densities in coppice (e.g. Fuller & 404 Henderson 1992, MacColl et al. 2014) but all had second highest densities in irregular 405 406 stands with blackcap Sylvia atricapilla more abundant. In winter, for all species, the highest abundances occurred in irregular, transitional and limited intervention 407 408 stands, although there were fewer differences in bird abundances between stand 409 types than in spring.

410 Previous European studies of birds in CCF stands have generated mixed findings 411 although importantly these are not in pure broadleaf woodlands as in our study. 412 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 413 clear-fells. However, in Belgium, du Bus de Warnaffe and Deconchat (2008) reported 414 that in beech and conifer forests, no clear differences in bird communities were 415 evident between CCF and clear-cut systems. In North America, a meta-analysis by 416 Forsman *et al.* (2010) found that silviculture creation of small gaps did not result in 417 418 clear negative impacts on bird communities relative to unlogged forest.

419

### 420 *4.2 Seasonal differences*

421

422 There were fewer differences between bird densities across stand types in winter 423 than in spring, presumably because resource use patterns differ in the former and 424 latter (Fuller et al. 2012). In winter, many species, especially titmice, Paridae, 425 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 426 427 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 428 habitats in winter (Bilke 1984). Although we did not look at demographic variation in 429 our study it is known that several species differ in their seasonal responses to 430 understorey age, coppice especially, depending on whether they are adult or 431 juveniles (MacCol et al. 2014). Four species (blue tit, blackbird Turdus merula, wren 432 and dunnock Prunella modularis) had significantly higher winter densities in 433

434 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 435 436 irregular stands provides increased protection from predation risk and thermal variation (Holt et al. 2014). Although we found no statistically significant niche shifts 437 from spring to winter for resident species, there were a few notable changes in 438 habitat/niche use. Wren and dunnock were both significantly more abundant in 439 irregular stands during the breeding season, and this association strengthened 440 during the winter, presumably as they sought increased protection in the denser 441 shrub-layer. Bramble *Rubus fruticosus* cover was significantly higher in irregular 442 stands and contributed to the understorey density values at 0.5 m above ground 443 444 which was strongly associated with this stand type. Winter marsh tit densities were 445 highest in limited intervention, although its density in irregular stands were only a 446 little lower, perhaps reflecting a widening of home range and differential use of 447 habitats between the breeding and winter periods (Broughton et al. 2014). This is 448 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 449 450 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. 451

452

## 453 4.3 Implications for woodland bird conservation

454

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 458 in lowland British woodland, especially in spring, and that for some species it may 459 460 even provide preferred habitats. In combination with previous studies referred to 461 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 462 acknowledged. Firstly, the effects may be context dependent according to region, 463 forest type and the exact stand types being compared. Secondly, some early 464 successional bird species may prefer either coppice or young clear-fells which can 465 provide larger areas of young-growth than are found with CCF (Calladine *et al.* 2015). 466 For example, in our study we found tree pipit Anthus trivialis exclusively in recent 467 clear-fell gaps outside of the stand types under question. 468

The value of coppicing to early successional birds and other species associated with 469 dense understorey is well documented (Fuller & Warren 1991, Fuller 1992, Macoll et 470 471 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. 472 473 2017). Other than government grant-fundingtargeted at sites of high nature conservation value, woodfuel produce is likely to be the main economic driver 474 475 sustaining coppice management (Fuller 2013, Buckley & Mills 2015). However, 476 irregular stand management as a more widely economically viable system appears to provide resources for most woodland birds associated with both understorey and old 477 growth here in southern England. Furthermore, proponents of CCF point out the 478 multiple benefits it can offer in terms of meeting sustainability measures (Bürgi 479 2015). 480

481 No single silvicultural system can provide the preferred habitat of all woodland birds. 482 In practice, therefore, a conservation strategy that embraces a dynamic range of 483 management interventions is desirable to enhance habitat heterogeneity and complexity at varying spatial and temporal scales (Fuller et al. 2007, 2012). Irregular 484 CCF forestry clearly has the potential to play an important role in developing this 485 heterogeneity. However, there is a question about whether it can meet the 486 requirements of all early successional species. In this respect, further work is needed 487 to assess how varying gap sizes within different variants of CCF affect biodiversity 488 (Puettmann et al. 2015). 489

490 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 491 492 species. Both the irregular stands and the coppiced stands held higher densities of 493 breeding birds than the limited intervention stands, typical of much neglected 494 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 495 496 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 497 notable that the spring abundance of marsh tit in irregular stands was approximately 498 499 twice that in the other stand types. Broughton and Hinsley (2015) cautioned that 500 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 501 research is needed to draw firm conclusions. An integrated approach to forest 502 management which incorporates stand-level targets to attain biodiversity attributes 503 e.g. deadwood, as shown by Susse et al.(2012) is an exciting option; particularly if it 504

505 can be adapted to include measures that provide important functional resources used
506 by woodland birds in the UK including those associated with understorey.

507

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509

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