

# Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland

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## ABSTRACT

Changing economics in the 20th century led to losses and fragmentation of semi-natural woodland in Britain and to a reduction in active woodland management with many becoming increasingly neglected, even-aged and with closed canopy. Lack of woodland management is known to contribute to declines in some taxonomic groups, for example birds. However, the response of bats to changes in woodland structure are poorly understood. We compared two measures of bat activity, derived from static acoustic recorders across 120 sample plots in coppice, irregular high forest (uneven-aged, continuous cover) and limited intervention (under-managed, even-aged) management stands, within a large tract of ancient woodland in southern England. Bat species richness was highest in irregular high forest stands, and there were significant differences in occupancy rates for most bat species across stand management types. Coppice recorded low activity of several bat species and irregular high forest showed high occupancy rates, including for *Barbastella barbastellus*, which is IUCN listed as near threatened. The occupancy rates in stand management types differed for some bat species between mid- and late summer counts, suggesting seasonal variation in habitat use. Within stands, most bat species were associated with opened canopy, lower growing stocks and reduced densities of understorey, and to a lesser extent, with large-girthed trees and presence of deadwood snags. In some cases, species responded to a given habitat variable similarly across the three stand management types, whereas in others, the response differed among stand management types. For example, increased numbers of large-girthed trees benefitted a number of bat species within coppice where these were least common, but not in irregular stands. Irregular silviculture high forest appears to provide many of the structural attributes that positively influence occupancy of several woodland bat species, including *Barbastella barbastellus*.

## 1. Introduction

Developing strategies for forest and woodland resilience in the face of climate change and increasing exploitation of forest resources is seen as a global priority (Pastur et al. 2020, Brang et al. 2014, Bussotti et al. 2015, Thompson et al. 2009). Structural and functional change following intensive silvicultural interventions (e.g. clear felling) can compromise woodland resilience and reduce the range of ecosystem services woodlands and forests support at multiple scales (Felipe-Lucia et al. 2018). Simplification of forest habitats has led to losses of biodiversity (Lelli et al. 2019) and in turn is likely to have impacted upon the ecological functioning and economic productivity of forest systems

(Liang et al. 2016). During the 20th Century, many European woodlands became structurally more homogeneous as a result of clear-fell silviculture followed by abandonment and the rise of plantations or neglect (Hopkins & Kirby 2007, Savill 2015, Russo et al. 2016). In Britain many semi-natural woods were heavily exploited during both World Wars then abandoned due to the economic demise of coppice management after the Second World War (Hopkins & Kirby 2007). Many ancient woodlands in Britain (those present since at least 1600AD; Spencer & Kirby 1992) had been subject to traditional management regimes, particularly coppicing, for >650 years (Rackham 1986). The structural homogenisation of these woodlands following abandonment and the widescale conversion to coniferous plantation transformed Britain's

landscape during the 20th Century (Harmer et al. 2010) and ancient woodlands that were spared degradation are seen as relics of high historical/cultural (Rackham 2003) and nature conservation value (Fuller & Warren 1993). In these remaining semi-natural stands, however, there has been a long-term, natural process of structural change leading to increasing density of trees and declining density of underwood. Climate induced reduction in temperate forest health in Europe (Senf et al. 2018), and the ecological consequences of tree pests and pathogens e.g. *Hymenoscyphus fraxineus* on Ash, *Fraxinus excelsior*, are expected to increase in the absence of mitigation (Mitchell et al. 2014, Hill et al. 2019, Forestry Commission 2019).

Continuous cover forest management (CCF; Mason et al. 1999), is a relatively new woodland management system for the UK (Kerr 1999). Silvicultural management using CCF systems are likely to be important where adaptive responses to ecological change are essential (Wilson et al. 2018). Irregular silviculture is one strand of CCF, which aims at permanently irregular high forest structures. It emphasises natural processes and seeks to develop complex habitat structures with a range of different size-classes of trees and an understorey partly comprised of tree saplings (Susse et al. 2011, Kerr 1999). This approach has been advocated because it provides a range of ecological benefits and ecosystem services (Pukkala 2016, Kerr 1999) while providing economic return (Löhmuus et al. 2016, Pastur et al. 2020). Using a stem-by-stem or group harvesting system, canopy opening is patchy and can resemble natural woodland processes (Bürgi 2015, Kuuluvainen 2009), 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 (Sanchez 2017, Susse et al. 2011). Semi-natural stands are highly variable in the level and spatial distribution of their growing stock and in the spatial distribution of individual trees with high biodiversity or economic values (Susse et al. 2011). Unlike irregular silviculture, even-aged silviculture constrains within stand complexity (Puettmann et al. 2015, Sanchez 2017). Finally, Irregular Silviculture involves moderate change and provides benign environments for vulnerable stand elements such as standing deadwood (Sanchez 2017). Despite the potential of irregular management to support keystone species (Gustafsson et al. 2020, Basile et al. 2020), there remains a significant knowledge gap of the effects on biodiversity following its introduction within temperate forests (Storch et al. 2020). Recent research as part of our wider study has highlighted positive effects of irregular silviculture on woodland birds (Alder et al. 2018).

All 17 species of bats found in Britain use woodlands (Altringham 2003) and several, including *Barbastella barbastellus*, are reliant upon semi-natural broadleaf woodlands (Dietz et al. 2018, Zeale et al. 2012). Broadleaf woodland provides keystone resources on which many species depend (Mendes et al. 2017, Boughey et al. 2011). Bats are an important indicator of changes in the structure and function of managed temperate woodlands (Jones et al. 2009, Kalda et al. 2015) and provide important forest ecosystem services (Garin et al. 2019). The availability of insect prey (Tillon et al. 2018), the ability of bats to forage effectively (Müller et al. 2012, Adams et al. 2009), microhabitat features important for roost availability (Regnery et al. 2013, Tillon et al. 2015, Russo et al. 2016), and abundance of standing deadwood (Carr et al. 2019, Tillon et al. 2018, Dietz et al. 2018, Lučan et al. 2009, Russo et al. 2004), can influence bat abundance and are all affected by woodland management. Bat species within the same guild face competitive challenges that they must overcome in the way they respond to the often variable, complex vegetation structures of temperate woodland (Langridge et al. 2019, Denzinger & Schnitzler 2013). Partitioning of resources may be achieved through choice of prey, avoiding direct competition by feeding at different periods, selecting different habitat patches and through behavioural differences (Swift & Racey 1983).

While our knowledge of the habitat associations of European bats is good (Downs & Racey 2006, Tillon et al. 2018) we know little about the effects of different silvicultural management options across a range of broadleaf woodlands, and in particular as a result of manipulating high

forest structures (Russo et al. 2016). Furthermore, caution has been urged over the restoration of traditional coppice management on *Plecotus auritus* (Murphy et al. 2012). Excessive levels of harvesting in high-forest stands are known to negatively affect bats (Tillon et al. 2018, Russo et al. 2016).

Studies in mixed broadleaf stands in western Europe have highlighted the positive influence on bats, in woodland managed sensitively to produce a varied structure (Jung et al. 2012) and through the introduction of innovative selective silviculture (Cistrone et al. 2015). Conversely, a comparison across even-aged, uneven-aged and unmanaged beech *Fagus sylvatica* forest by Schall et al. (2018) identified similar bat diversity. However, we are unaware of a direct comparison between management types in British woodlands that include irregular silviculture amongst the management options in ancient semi-natural broadleaf stands, and the effects on bats of creating diverse high forest structures. We compared a range of structural habitat measures across three management types and assessed bat species richness and activity of each species across coppice, limited intervention, and irregular high forest stands. We used two metrics of bat activity from acoustic recorders; (1) an encounter rate of number of passes through the night; (2) one reflecting the proportion of ten-minute periods during which each species was recorded at least once. We then looked within woodland stand management types to identify structural attributes influenced by woodland management and associated these with bat activity.

## 2. Methods

### 2.1. Study area and stand types

The study was conducted within 442 ha of semi-natural broadleaf woodland, mostly statutorily protected Site of Special Scientific Interest (SSSI), across two contiguous blocks on the Rushmore Estate, in southern England (110–190 m a.s.l.; 395724.26 E, 117963.15 N; Fig. 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 deciduous woodland on fertile soil with several sub-categories around the former (Rodwell et al. 1998, B. Edwards pers. comm. 2019). 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*, willow *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, those identified as having biological and cultural importance (Read 2000); particularly of oak, ash and field maple and 19th Century beech *Fagus sylvatica* plantings (Alder et al. 2018, Poore 2016).

### 2.2. Descriptions of broadleaf stand types

We evaluated three broadleaf stand management types (A. Poore pers. comm. 2019; Fig. 2). Silviculture is either high forest with trees derived from seed on long felling rotations 50–200 years or coppice, referring to cyclical cutting of regenerated stems on short rotations (Harmer et al. 2010). We define woodland management as the harvesting of woody material and the stand as the silvicultural unit at which forest management was undertaken.

*Limited intervention stands* (43.4 ha) 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 developed from open canopy high forest and had higher understorey densities. Limited intervention stands originate from three starting points which were typical in lowland Britain following reductions in broadleaf management (Mason 2007).



Fig. 1. Location of study area within Cranborne Chase on the Dorset-Wiltshire border, southern Britain, UK. © Natural England copyright 2012. Contains Ordnance Survey data © Crown copyright and database right 2012.

- Stands which had a more varied structure when management ceased and where a somewhat more complex structure persists.
- Stands which had a more uniform coppice structure at the point of abandonment.
- Stands which came out of a wood pasture structure with less underwood but where some remnant scrub persists.

*Coppice stands* (59.0 ha) include both simple coppice and coppice with standards with up to 20% cover of upper canopy trees. However, effective underwood production requires a maximum cover of 10% upper canopy trees. Underwood cycle lengths vary with use: hazel dominated coppice cut every 8–12 years, birch coppice was managed on two rotations, with pure birch cut at 3–4 years and the remaining on > 25 year cycles for wood fuel. There was a broad representation of growth stages across our study site, with a mean age of coppice during the study of  $7.3 \pm 3.9$  (SD) years with 0–5 years ( $n = 10$ ), 6–9 years ( $n = 19$ ), and 12–15 years ( $n = 11$ ). At each cutting, the entire panel (felling) between 0.5 and 1.5 ha of underwood is removed leading to even-aged regrowth (Harmer & Howe 2003).

*Irregular High Forest stands* (52.9 ha) were transformed to high forest (tree recruitment into canopy) from unmanaged coppice or developing high forest stands to an irregular stand structure for at least 30 years. This involved selective removal of harvestable trees and of weaker growing specimens and cutting the understorey to increase light levels reaching the woodland floor. The aim was to increase incremental growth of retained trees to enhance their economic value, promote natural regeneration of trees and shrubs and establish a range of tree age classes. Stands with ‘moderate stocking’ have stand basal areas (>7.5 cm diameter at breast height, (dbh)) in the range 17–24  $m^2 ha^{-1}$  whilst ‘low stocking’ are in the range 10–16  $m^2 ha^{-1}$ . Understorey stocking was dense in places yet patchily distributed as influenced by management and the effects of deer browse. Species diversity was encouraged and individual trees with particular biodiversity values retained, including senescent and standing deadwood (Susse et al. 2011). A feature of irregular high forest stands at Rushmore was the high densities of retained deadwood and trees with cavities.

The coppice and irregular stand types in the south-west of our study were not chosen being unrepresentative of the age-classes of each; coppice here was mostly advanced in-cycle and the irregular was more recently transformed < 30 years ago.

### 2.3. Collection of acoustic data

Bats were sampled acoustically during the summer over two periods 24 June – 22 July and 31 July – 2 September 2015 using six Song Meter 3 (SM3) acoustic recorders fitted with a single omnidirectional

microphone (Wildlife Acoustics Inc. USA). Microphones were pole-mounted at 3 m height to avoid reflected sounds from the ground, facing downwards at an angle of  $45^\circ$ , and placed a minimum of 1.5 m from dense leafy growth to reduce reflection from vegetation (Müller et al. 2012).

Full spectrum audio using an 8 kHz high pass filter was used to reduce the chance of recording low frequency sounds not made by bats (Newson et al. 2015). SM3s were programmed to switch on 15 mins before sunset and off 15 mins after sunrise, and record throughout the night (Froidevaux et al. 2014) using a trigger threshold above 12 dB and recording set to continue until no trigger was detected for a 2.0 s period (Newson et al. 2015). Each triggered event was categorised as a bat pass for each species identified following Newson et al. (2015). We adopted a stratified sampling procedure with simultaneous recording made using two SM3 units in each of the three stand types, each sampling night (Humes et al. 1999) with each plot sampled twice across the two periods with a minimum interval of 3 weeks between each visit (Frey-Ehrenbold et al. 2013). Plots were located a minimum of 30 m from the edges of each stand to reduce the effects from proximate habitats (Humes et al. 1999). There were 40 sampling plots (a total 120 plots) in each stand type across 26 individual stands Fig. 3. Acoustic sampling was conducted on nights without rain, wind speeds below force 4 on the Beaufort scale and temperatures above  $7^\circ C$  (Froidevaux et al. 2014).

### 2.4. Sound identification of bats

Bats were identified according to a two-step procedure following Newson et al. (2017) whereby recordings were firstly filtered through species classifiers built by one of us (SEN) using the software TADARIDA (Bas et al. 2017), which assigns bat calls to species. This automatically detects and extracts acoustic features of the recorded echolocation calls and classifies them to species using a Random Forest algorithm (Claireau et al. 2019). Manual verification (step 2) of all bat calls following TADARIDA was made using Sonobat 4.1 software ([www.sonobat.com](http://www.sonobat.com)) producing 35,230 confirmed bat passes from 137,018 sound files. Of these, 10,992 bat passes were not assigned to species as manual verification could not be identified with confidence to species (Russ 2012). *Myotis mystacinus* and *M. brandtii*, and *Plecotus auritus* and *P. austriacus* are particularly difficult to identify acoustically, and were treated as species pairs, therefore *M. mystacinus* / *brandtii* and *P. auratus* / *austriacus* respectively (Starik et al. 2018). ‘Guilds’ for each species identified are used; SRE – short range echolocators, MRE – medium range echolocators, LRE – long range echolocators (adapted from Denzinger & Schnitzler (2013)).

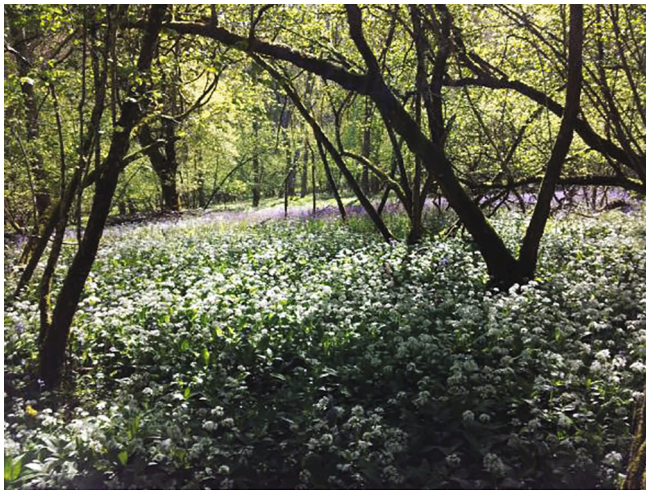


Fig. 2. Examples of stand types sampled in the study from top to bottom: limited intervention, coppice and irregular high forest.

## 2.5. Habitat measures

At each sample plot measurements of woodland structure were collected within a 30 m diameter circle (0.07 ha) with five sub-plots of 3 m diameter within each (four located at the cardinal points at 10 m radii and one at 2 m off-centre along a random compass bearing (Alder et al. 2018)).

Within 30 m plots and 3 m sub-plots, the following habitat

measurements were made:

- **Number of trees/stems in each 30 m plot** > 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 of **canopy openness** was measured at each 3 m sub-plot with a spherical convex mirror densiometer (Lemmon 1956).
- **Growing stock density** (basal area (m<sup>2</sup> ha<sup>-1</sup>)) was measured at each plot centre using the relascope principle (Bitterlich 1984) where each tree > 7.5 cm dbh is counted in a 360° 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 for this (Rosset et al. 2014), calibrated for the basal area factor and camera and was used 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 of the 30 m plot using a 50 × 30 cm chequer board with 10 × 10 cm squares (Alder et al. 2018).
- **Standing deadwood**, dead trees and dead branches (snags) over 20 cm diameter (as a proxy for cavity availability (Paillet et al. 2018)) were counted around each 30 m plot centre (Charman et al. 2010)
- **Length of fallen logs** over 20 cm diameter were measured entirely within each 30 m plot (Lush et al. 2012).
- **Percentage cover** was calculated at within 30 m plot for dominant vegetation; bramble *Rubus fruticosus* cover, and area of bare ground.

All fieldwork was carried out by DA.

## 2.6. Data analyses

Structural habitat measures were compared across stand types using a mixed effect models and pairwise comparisons with stand number as a random factor to account for nestedness in samples within stands. Measured continuous variables were analysed using Linear mixed model using the package “nlme” (Pinheiro et al. 2020) or GLMM with a gamma distribution. Count data was analysed with a GLMM with Poisson distribution. For percentage data an arcsine transformation was applied to the data and analysed using a Linear Mixed effects Model (see table × in supplementary material). GLMM models were performed using the “LME4” package (Bates et al. 2015). Tukey’s post-hoc multiple comparison tests were used to make comparisons across management stand types. Spearman’s rank correlations (supplementary file S 4) were used to select habitat variables to include in bat habitat association models and to compare across and within stand types.

We calculated bat species richness at each plot in each survey period. We expressed bat activity across stand types and survey periods using two different metrics. First, ‘overall encounter rates’ were calculated as the mean number of bat passes per hour, to give an overall indication of activity during the sampling night. For encounter rate we excluded the first and last 30 min of each night, to avoid issues associated with high numbers of bats moving to and from roost sites (Wood et al. 2017). The second, ‘occupancy or activity rates’, was calculated as the proportions of 10-minute periods during a night, within which the bat species was recorded at least once. Using the proportion of 10-minute periods, which differed across nights of different length (in our study period it varied between 7.5 h and 10.5 h), allowed us to account for night length differences in our activity metric.

A GLMM with Poisson distribution was used to analyse species richness across stand types. A GLMM with a binomial distribution was used to analyse activity level (proportion of possible 10-minute periods each species was active per night) between the stand types. Because sampling plots were nested within woodland stands (n = 30) we included stand number as a random factor in all models (Zuur et al.

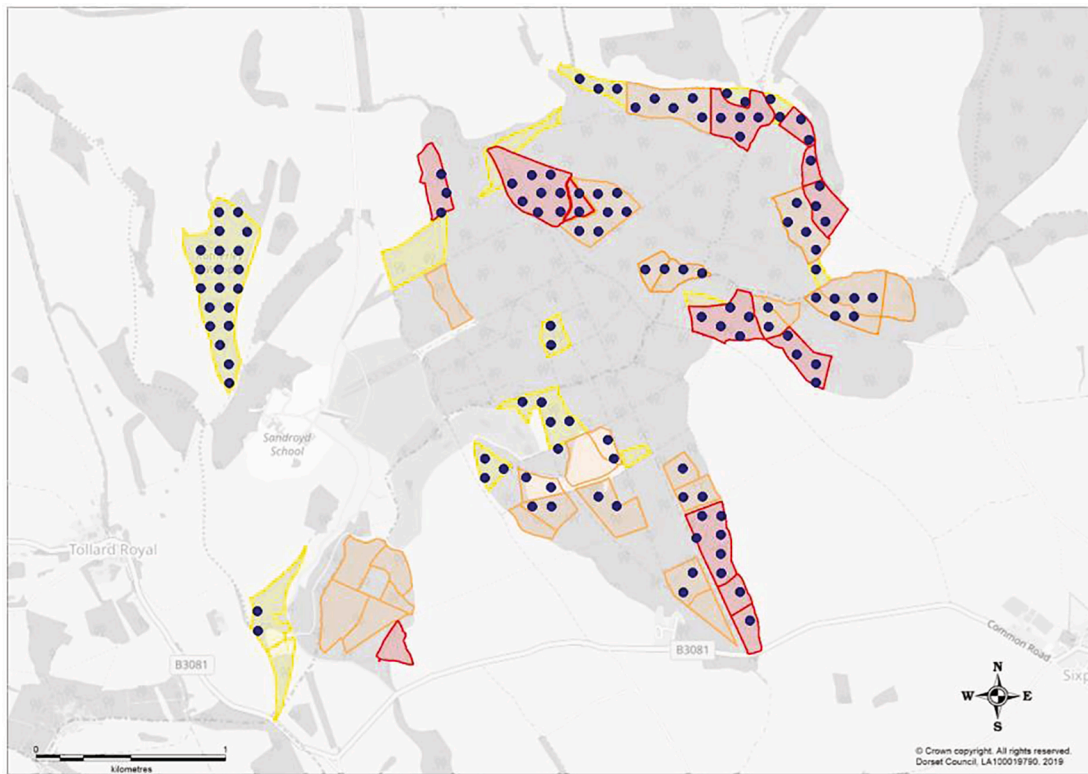


Fig. 3. Location of sample points within three stand management types; orange coppice, yellow limited intervention and red irregular. Average nearest plot distances within stand types was 117 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2009). Encounter rate data (mean number of bats per hour) being continuous and including zeros were analysed using a zero-inflated mixed effects model with a gamma distribution using the package 'glmmTMB' (Brooks et al. 2017). Models were run for each species with management stand type and an interaction with survey period and stand type as predictors.

To examine the effect of habitat variables on species activity within each habitat type separately, three GLMM's with binomial distribution were applied with canopy openness, general stem density, mean DBH and snag frequency as predictors. Habitat variables were based on gradients of openness, stem size and density and standing deadwood and selected by examining collinearity between all habitat variables collected. Model averaging using the package "MuMIn" (Barton, 2020) was used to identify the relative importance of each habitat variable on each species within the three stand types.

### 3. Results

#### 3.1. Bat species data

Eleven bat species were identified (Table 1). *Pipistrellus pipistrellus* dominated the sample, making up 78% of records from 90% of plots. Three other species, *Barbastella barbastellus*, *P. pygmaeus* and *Myotis mystacinus/brandtii* all had >1,000 bat passes. *Myotis mystacinus/brandtii* group comprised 1,733 records and were recorded on 63% of plots. *P. nathusii* (22 records; <2% of plots) and *Nyctalus leisleri* (52 records; 14% of plots) were deemed too rare for further analysis. Species richness differed between irregular and coppice stand types with higher species richness in the irregular stands (Copp-Irr, estimate  $\pm$  se, Z, p:  $-0.4 \pm 0.1$ ,  $-2.6$ , 0.03; see Supplementary file S 2). Seven of the nine species were more often recorded in the second survey period than the first. However, there were no significant differences across survey periods, or interaction between period and stand management type.

Table 1

Bat passes and percentage of occupied survey plots for eleven bat species recorded over two survey periods.

Species/Guild	Bat Passes			% of total	% Plots used	
	Period one	Period two	All		Period one	Period two
<i>Plecotus auritus/austriacus</i> <sup>SRE</sup>	63	187	250	0.7	28.3	31.7
<i>Barbastella barbastellus</i> <sup>SRE</sup>	234	789	1023	2.9	40.0	37.5
<i>Myotis nattereri</i> <sup>SRE</sup>	278	268	546	1.6	51.7	50.0
<i>Pipistrellus pipistrellus</i> <sup>MRE</sup>	9,881	17,660	27,541	78.0	89.2	90.8
<i>Pipistrellus pygmaeus</i> <sup>MRE</sup>	1,669	1,192	2,861	8.1	61.7	68.3
<i>Pipistrellus nathusii</i> <sup>MRE</sup>	22	0	22	0.1	2.5	0.8
<i>Myotis mystacinus/brandtii</i> <sup>MRE</sup>	715	1,018	1,733	4.9	63.3	62.5
<i>Myotis daubentonii</i> <sup>MRE</sup>	147	316	463	1.3	42.5	49.2
<i>Eptesicus serotinus</i> <sup>LRE</sup>	181	247	428	1.2	50.0	56.7
<i>Nyctalus noctula</i> <sup>LRE</sup>	256	55	311	0.9	49.2	32.5
<i>Nyctalus leisleri</i> <sup>LRE</sup>	21	31	52	0.2	19.2	9.2
Total	13,467	21,763	35,230	100	96	96

#### 3.2. Bat activity metrics across stand management types

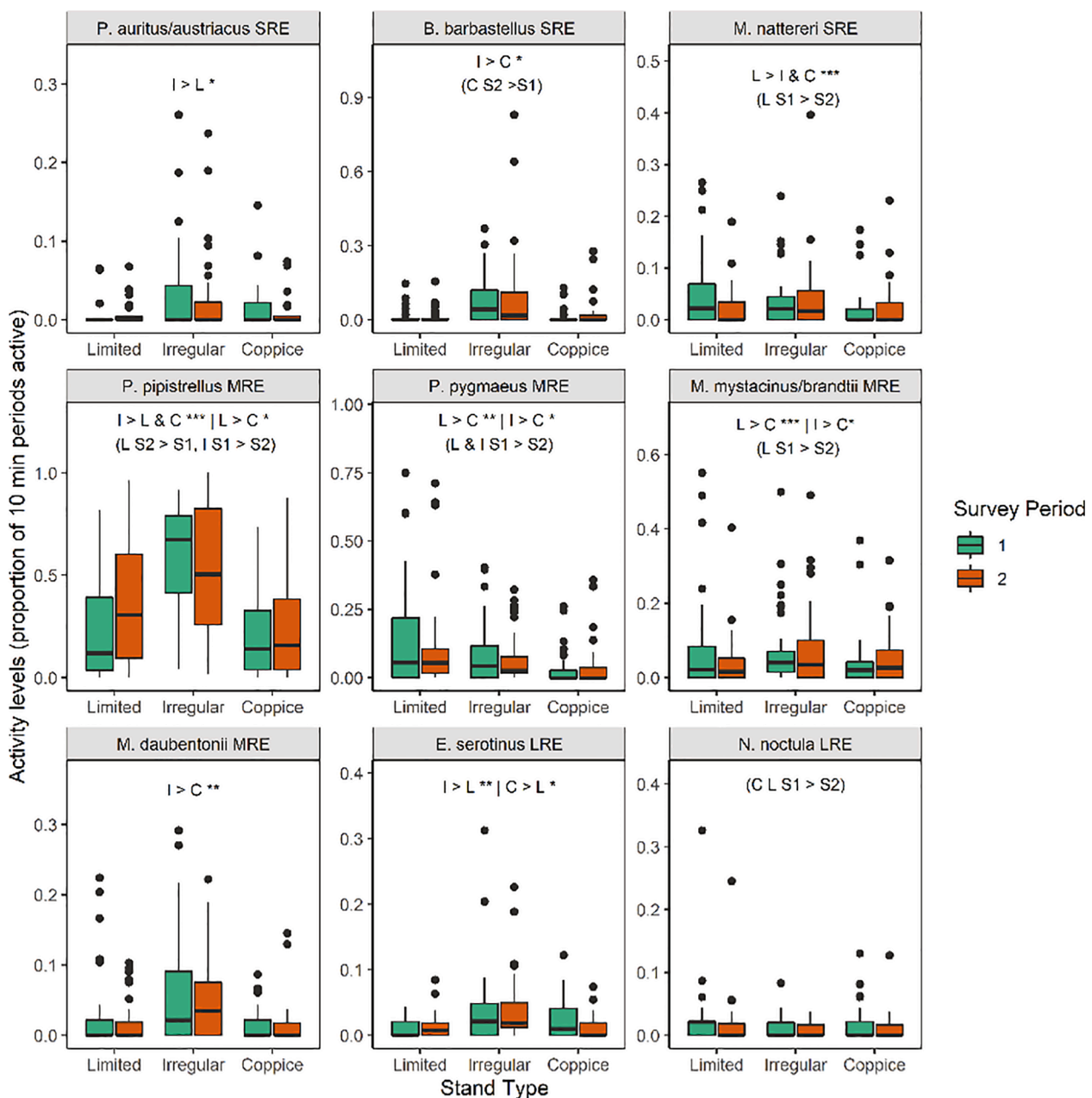
Although encounter rates and occupancy metrics were correlated ( $r = 0.73$ ,  $n = 2160$ ,  $p < 0.001$ , across all species / survey period / and plots), occupancy indicated more significant differences among stands

or between survey periods (24 significant differences), than ‘encounter rates’ (10 significant differences). We describe our rationale for selection of each metric in the Discussion but here, we focus on the results of the latter (encounter rate results appear alongside occupancy rates in [Supplementary file S1](#)).

Activity for two of the three short-range echolocators was greatest in Irregular, for two of four MREs, and one of two LRE. We expand on differences in activity between species sharing similar traits in the discussion. Six of nine bat species ([Fig. 4](#)) had significantly greater occupancy in irregular high forest than in at least one of the other stand management types. *Eptesicus serotinus* and *P. auratus/austriacus* were most active compared to limited intervention; whereas *M. daubentonii*, *M. mystacinus/M. brandtii*, *P. pygmaeus* and *B. barbastellus* were encountered more than in Coppice (*P. pipistrellus* higher than in both).

Only *M. nattereri*, was significantly more likely to be recorded in limited stand management type over both coppice and irregular high forest. The results highlight the generally low occupancy rates in coppice stands. *M. nattereri*, *P. pipistrellus* and *P. pygmaeus*, and *M. mystacinus/brandtii* selected limited intervention over coppice, with *E. serotinus* more common in coppice than limited intervention.

Six of nine species showed significantly different levels of occupancy of the stand management types between the survey period. Two taxa, *P. pipistrellus* and *M. mystacinus/brandtii*, increased usage during period 2 in one stand type (limited intervention and coppice respectively) over another stand type (irregular high forest and limited intervention), suggesting a change in habitat use within the study area according to season. In contrast *P. pygmaeus* and *N. noctula* used two stand types less in period 2, which along with the general lack of records from period 2



**Fig. 4.** Bat activity (proportion of possible 10-minute periods each species was active per night) as a measure of occupancy throughout the sample night. Where significant, management code I = Irregular, C = Coppice, L = Limited were combined with < (less than) or > (greater than) and \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), and \*\*\* ( $p < 0.001$ ) to show significant difference in management type. For survey period and management type interactions that were significant (S1 = Survey period 1, S2 = Survey period 2) were combined with management codes (above) and < and > with asterisks (see above) to show direction of difference and significance level.

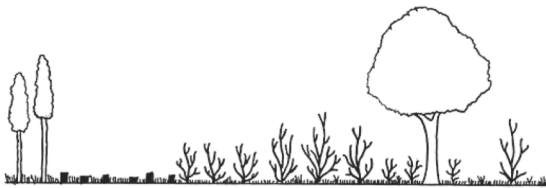
(Table 1) suggest a movement out of the study site post-breeding. *M. nattereri*, although preferring limited intervention stands overall, reduced its use of this stand management type in period 2, while *B. barbastellus* used coppice stands more in period 2.

### 3.3. Stand habitat characteristics

There were 19 habitat variables which showed significant differences in pairwise comparisons of stand management types (Supplementary file S 3). Fig. 5 shows a schematic of the three stand management types labelled with key habitat features.

### 3.4. Habitat associations

Of the four habitat variables considered (see Supplementary file S 4 correlations of all habitat variables), canopy openness was significantly associated with bat occupancy rates in eleven species/stand type cases (Fig. 6), stem density in six, and DBH and snags five each. In nine of the eleven cases, it was high values of canopy openness that were positively associated with bat occupancy rates, while in all six cases, low stem density was associated with high occupancy rates. In general, larger DBHs and frequent snags promoted bat occupancy (Fig. 6).



Coppice: low tree stocking, dense understorey or no understorey if recently cut; few large trees; heavy moss cover



Irregular High Forest: patchy open canopy, range of tree sizes including large trees; variable understorey with low, dense bramble cover; combines many characteristics of coppice and limited intervention



Limited Intervention: High tree stocking with high stem density; few oaks; closed canopy; sparse understorey and bare ground; high volume of fallen dead wood.

Fig. 5. Significant structural characteristics identified within each stand.

For some species, associations of occupancy with individual habitat measures was very similar across different stand management types. For example, *B. barbastellus* was strongly positively associated with the most open plots in all three stand management types, and *P. pygmaeus* generally negatively associated with stem density, regardless of stand type. The generalist/edge species *E. serotinus* had no significant associations with any of the habitat variables which was consistent across stand management types.

In other cases, species appeared to respond differently to the same habitat variable in different stand management types. So, there was a stronger likelihood of a species having a positive relationship with Mean DBH in the coppice, and to a lesser extent, limited intervention, than in irregular stands where Mean DBH was higher. Nevertheless, there were several differences in species-specific responses across stand management types. Several of these involve the closely related species *P. pipistrellus* and *P. pygmaeus* despite sharing similar morphological characteristics the two Pipistrelles exhibit differences in habitat use. *P. pygmaeus* used closed canopy more than *P. pipistrellus* which is more of an edge species. In other cases, it may be that the rarity of a bat species in one or more of the stand management types is affecting models. – essentially the habitat is far from suitable in terms of that individual habitat measure so changing values as they appear across our plots is having little effect on overall suitability.

## 4. Discussion

### 4.1. Species response to stand management

We found clear differences in bat occupancy among three stand management types. Irregular high forest, had the highest species richness, and highest occupancy rates for most bat species, including the IUCN ‘near-threatened’ *B. barbastellus* (Piraccini et al. 2016). Activity across three foraging guilds was higher in irregular than in either coppice or limited intervention stands. Coppice had lower bat activity for four species, *B. barbastellus*, *E. serotinus*, *M. daubentonii*, and *P. pipistrellus* and lower species richness compared with irregular stands. This may reflect the coppice age structure sampled with 10% at 0–3 years. Four plots in closed-canopy coppice (c14 years) where no bats were recorded, suggested that short-range echolocating (SRE) species including *M. nattereri* avoided densest clutter (Rainho et al. 2010, Froidevaux et al. 2016, Arlettaz et al. 2001).

Broadleaf stands which have undergone thinning can positively influence bats (Blakey et al. 2016) although recent research found rarer species benefitted from non-intervention compared to managed stands (Carr et al. 2019). However, the choices of silviculture management available to forest managers are diverse, reflecting site conditions and past management histories (Adams et al. 2009, Langridge et al. 2019). Irregular silviculture is very different from even-aged management (Bürgi 2015, Löhmus et al. 2016). Our study suggests variable retention of tree size classes, deadwood, understorey, open canopy and larger tree size associated with irregular seems to benefit multiple bat species across foraging guilds (Renner et al. 2018).

Structural complexity in irregular stands is likely to influence habitat quality for bats including accessibility to abundant invertebrate prey associated with denser low understorey (Starik et al. 2018, Tillon et al. 2018, Charbonnier et al. 2016, Plank et al. 2012, Adams et al. 2009). Differences in three-dimensional structure of vegetation influences the composition of bat species assemblages (Adams et al. 2009, Jung et al. 2012, Kirkpatrick et al. 2017). Work on woodland birds within our study area (Alder et al. 2018) indicated that irregular silviculture can provide several functional resources for species reliant on early successional growth and old growth features. Where woodland management constrains levels of decaying trees, the presence of keystone cavity makers like woodpeckers can be important (Remm & Löhmus, 2011). Great Spotted Woodpecker *Dendrocopos major* had highest spring densities in irregular stands in our study area where deadwood snags were frequent

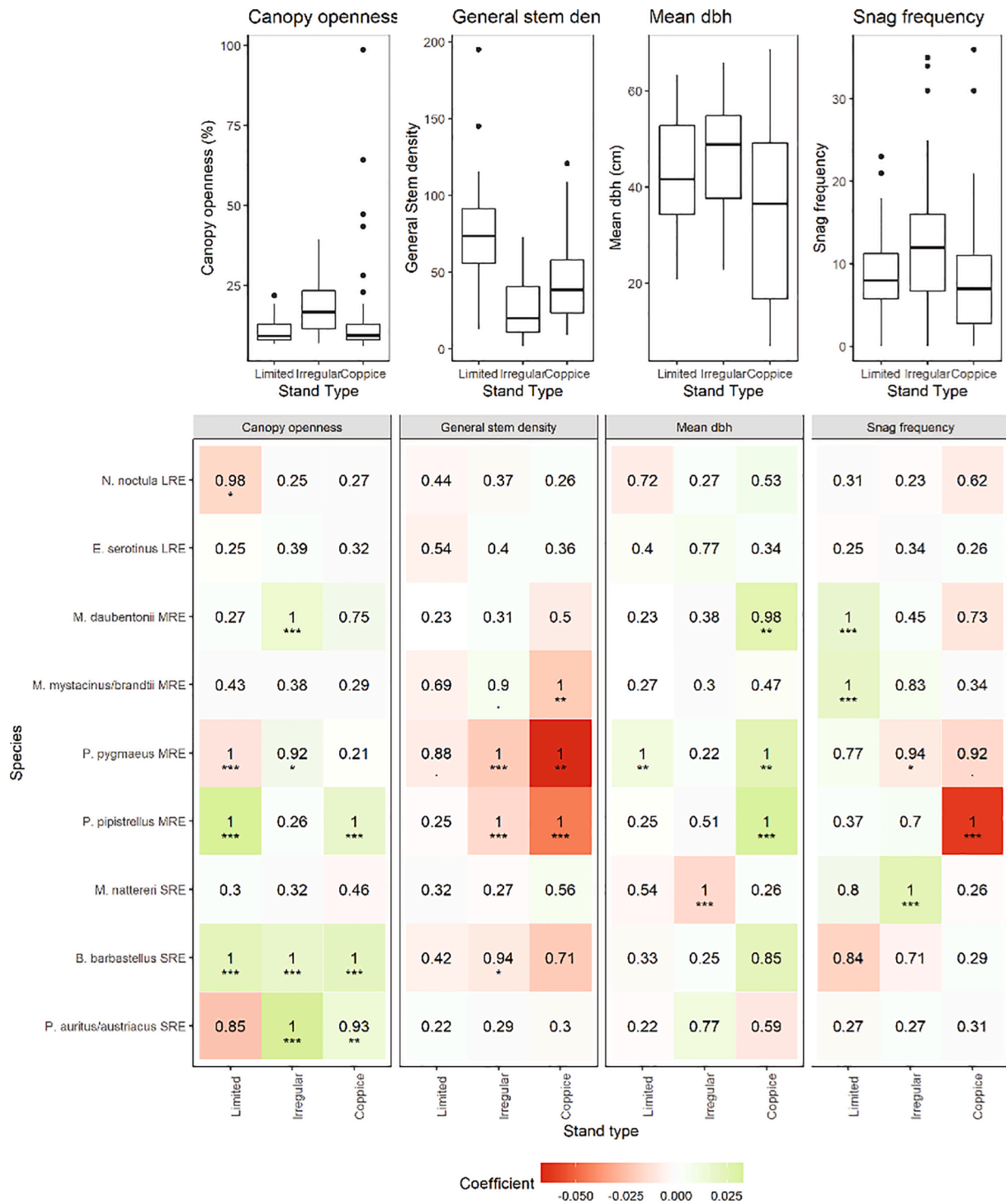


Fig. 6. Habitat attributes across stands (upper) and bat species associations within each stand management type (lower) taken from a GLMM with binomial distribution and model averaging. The number shown in the individual panes are the sums of 'Akaike weights' over all models with Delta AICc < 6. The colour indicates the direction and strength of the fixed effect variable. Significance is indicated by \* (p < 0.05), \*\* (p < 0.01), and \*\*\* (p < 0.001).

(Alder et al. 2018). Importantly, irregular silviculture creates benign conditions for retaining trees with special biodiversity features (Sanchez 2017).

*B. barbastellus*, a SRE, low-level foraging bat (Rainho et al. 2010, Plank et al. 2012, Denzinger & Schnitzler 2013), was significantly associated with more open canopy areas in all stand management types with highest occupancy in irregular high forest. Within coppice stands *B. barbastellus* was significantly associated with larger trees and strongly correlated to the presence of snags in all stand types (See Supplementary

file S 3). Dead wood availability is important for *B. barbastellus* (Russo et al. 2004, Carr et al. 2019) because individuals frequently switch roosting locations (Russo et al. 2005). Their higher occupancy in irregular stands potentially reflects the abundance of retained deadwood (Görföl et al. 2019) and feeding habitat across patches of dense understorey (Zeale et al. 2012, Hill & Greenaway 2008). We found a negative association in limited intervention stands with deadwood snags; interestingly Tillon et al. (2016) did not identify a relationship between *B. barbastellus* and deadwood presence. Moreover, there may be



thermophilic benefits for *B. barbastellus* utilising open and sheltered interiors of irregular stands (Carr et al. 2019, Dietz et al. 2018).

*Eptesicus serotinus* occupancy was higher also in irregular and coppice stands. Accessible prey is possibly a key factor; *E. serotinus* is an adaptable forager (Catto et al. 1996) using forest interiors where structural heterogeneity enables manoeuvrability (Langridge et al. 2019, Plank et al. 2012). It is associated with deadwood (Tillon et al. 2016) and tree roost woodpecker cavities (Langridge et al. 2019).

*Nyctalis noctula*, a LRE (Langridge et al. 2019), was encountered across all stand types, most in limited intervention but not significantly. It was negatively associated with canopy openness in limited intervention stands in our habitat models. *N. noctula* uses open-space flight-lines above the woodland canopy over which it can hawk flying insects (Müller et al. 2013).

Several *Myotis* species are morphologically similar yet differ in echolocation, enabling each to exploit different vegetation structures (Siemers & Schnitzler 2004). *M. daubentonii*, an edge species (Müller et al. 2012), had highest occupancy in irregular high forest, significantly so over coppice and a positive association with canopy openness. Plank et al. (2012) found this species flew at ground level in uncluttered woodland which explains its low occupancy in coppice. Snag frequency within limited intervention stands was important, perhaps because open understorey enables *M. daubentonii* to exploit snags as roosts. The species is known to use cavity roosts which develop in humid conditions associated with closed-canopy woods (Boonman 2000).

*M. mystacinus/brandtii* stand-wise occupancy was highest within limited intervention followed by irregular high forest over coppice. Our models showed strong avoidance of highest stem densities typical of dense coppice and accords with a association with woodland edges (Müller et al. 2013). The species group utilises lower height stratum beneath canopy in accessible forest interiors, (Cel'uch & Kropil, 2008, Froidevaux et al. 2016). Despite high tree densities in limited intervention stands the open understorey enables the species to manoeuvre at heights below 10 m (Bačkor 2016).

*M. nattereri* with highest occupancy in limited intervention over coppice and irregular high forest suggest it is able to exploit a range of closed canopy environments including all but the densest clutter where it gleans arthropods from foliage (Swift & Racey 2002, Tillon et al. 2016). The negative relationship with mean dbh and positive with deadwood snags suggests avoidance of open habitats with larger trees. *M. nattereri* as a SRE exploits closed-canopy woods using very broadband echolocation to forage in cluttered conditions (Siemers & Schnitzler 2000, Müller et al. 2012, Plank et al. 2012).

Although recorded in our study area we did not identify *Myotis bechsteinii*. This species exploits tree canopies and can go undetected (Plank et al. 2012). *M. bechsteinii* difficult to distinguish acoustically from other *Myotis* species (Russ 2012), particularly in cluttered woodlands. It is possible that recordings were missed during auditing.

*Plecotus auritus/austriacus* was significantly associated with irregular stands compared with limited intervention stands, less so in coppice stands. *Plecotus auritus/austriacus* occupancy was positively associated with mean tree dbh in irregular stands. *P. auritus* is known to avoid wide gaps (Entwistle et al. 1996, Murphy et al. 2012) which may explain the negative association with mean dbh in coppice. We found *Plecotus* spp used coppice more than limited intervention. There have been concerns over the widespread reintroduction of coppice for *P. auritus* which appears to prefer well-developed understorey and more heterogenous canopy structure (Murphy et al. 2012). In the absence of natural disturbances, creating the desired understorey requires silvicultural intervention which we suggest irregular silviculture could satisfy (Mölder et al. 2019, Horak et al. 2014).

Both *Pipistrellus* species tended to avoid the cluttered environment in coppice reflecting their similar morphology as MRE (Nicholls & Racey 2006a, Carr et al. 2019). There was a positive habitat association with canopy openness in coppice and limited intervention stands for *P. pipistrellus* yet a negative association within limited intervention for

*P. pygmaeus* which may reflect habitat partitioning (Nicholls & Racey 2006b, Davidson-Watts et al. 2006).

#### 4.2. Conservation and research implications

Although *P. pipistrellus* and *P. pygmaeus* made up 86% of all bat passes, we recorded over 200 passes for nine species, at > 25% of plots. The proportion of ten-minute periods with at least one pass, provided a useful measure of intensity of habitat use through the night (Gorresen et al. 2008).

Most European bats can be recorded beneath tree canopy (Müller et al. 2012) although differences in canopy height and vegetation structure may affect detection probabilities across stand types (Gorresen et al. 2008). Except for *Plecotus* species, the difference in detection distance between extremes of recording in open environments and dense forest understorey is about 5-m or less (Barataud 2015). In practice, the difference in detection distance between stands is less because the influence of understorey heights and densities varies depending upon the growth stage.

We identified important associations between bat species and woodland structures, but these do not fully describe the complex needs of individual species (Langridge et al. 2019). Linking activity patterns of bats to three dimensional models of habitat complexity, (e.g. using LIDAR data), are exciting developments, particularly for the study of volant animals within complex forest habitats (Froidevaux et al. 2016, Russo et al. 2016, Renner et al. 2018). Despite including stand number as a random effect in models, we acknowledge habitat use across stand types will be blurred especially in ancient woodlands with intricate habitat mosaics (Hilmers et al. 2018).

Irregular silviculture in our study appeared to promote structural features which positively influence bat activity (Kusch et al. 2004, Wood et al. 2017, Starik et al. 2018). In managed temperate high-forests habitat complexity increases in stands under irregular silviculture (Jung et al. 2012, Gustafsson et al. 2020). Understorey density, at 0.5 m was similar between irregular and coppice yet considerably less in irregular at 2 m (Supplementary file S 3), and combined with a varied distribution of tree sizes and open canopy suggests irregular maybe more accessible to foraging bats across guilds which our results indicate (Adams et al. 2009, Titchenell et al. 2011, Wood et al. 2017).

Our study area within a complex patchwork reflects historical changes in woodlands over much of lowland Britain (Peterken 2015). Differences between irregular high forest and limited intervention here are less than is often encountered in managed high forest (Peterken & Mountford 2017). Coppice had low tree densities and reduced deadwood, typical of managed coppice (Harmer & Howe 2003, Buckley & Mills 2015, Buckley 2020), limiting roost availability. Irregular silviculture incorporates structural similarities of both young coppice and old growth stands and appears to cater for several species associated with each (Alder et al. 2018). Further research on habitat selection for rare bats like *B. barbastellus* will be beneficial, particularly elucidating knowledge of moth prey between stand management types including irregular high forest.

Transformation to heterogenous irregular high forest appears to enhance habitat quality for woodland bats (Tillon et al. 2018, Ketzler et al. 2018). Large trees provide important foraging resources including saproxylic invertebrates (Siitonen et al. 2015) and roosting features (Dietz et al. 2018). Structural diversity is likely to become an important ambition for forest managers (Forestry Commission 2019), which potentially establishes a range of resources benefitting woodland bats (Langridge et al. 2019, Tillon et al. 2015). The biodiversity value of successional gradients within temperate European forests is clear (Hilmers et al. 2018, Kuuluvainen 2009). Stand manipulation provides an opportunity to create dynamic, mixed structures, enhancing habitat quality for a range of species (Lelli et al. 2019, Dieler et al. 2017) including bats within temperate broadleaf woodland (Carr et al. 2019).

Non-intervention as the appropriate woodland management

treatment for bat conservation may not be broadly applicable without an understanding of the structural characteristics required by bats, which is more useful to forest managers (Law et al. 2016, Langridge et al. 2019). Each woodland has its own historical signature reflecting past exploitation; many unmanaged woodlands today lack the mix of characteristics found in both old growth woodlands and in-cycle coppice (Amar et al. 2010, Peterken & Mountford 2017; Buckley, 2020). Interventions are often necessary to transform even-aged or neglected woodland to create such conditions (Ketzler et al. 2018, Law et al. 2016, Jung et al. 2012, Patriquin et al. 2003, Susse et al. 2011). Irregular silviculture in temperate woodlands may offer a sustainable and cost-effective option for the conservation of woodland biodiversity.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118786>.

## References

- Adams, M.D., Law, B.S., French, K.O., 2009. Vegetation structure influences the vertical stratification of open-and edge-space aerial-foraging bats in harvested forests. *For. Ecol. Manage.* 258 (9), 2090–2100.
- Alder, D.C., Fuller, R.J., Marsden, S.J., 2018. Implications of transformation to irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland. *For. Ecol. Manage.* 422, 69–78.
- Altringham, J. D. (2003). *British Bats* (Collins New Naturalist Library, Book 93) (Vol. 93). HarperCollins.
- Amar, A., Smith, K.W., Butler, S., Lindsell, J.A., Hewson, C.M., Fuller, R.J., Charman, E. C., 2010. Recent patterns of change in vegetation structure and tree composition of British broadleaved woodland: evidence from large-scale surveys. *Forestry* 83 (4), 345–356.
- Arlettaz, R., Jones, G., Racey, P.A., 2001. Effect of acoustic clutter on prey detection by bats. *Nature* 414 (6865), 742.
- Bačkor, P., 2016. The activity of bats in the Badínský Prales primeval forest. *Folia Oecologica* Vol. 43, no. 1.
- Barataud, M., 2015. Acoustic ecology of European bats. Species, identification, study of their habitats and foraging behaviour. Biotope, Mèze.
- Bas, Y., Bas, D., Julien, J.F., 2017. Tadarida: A toolbox for animal detection on acoustic recordings. *Journal of open research software* 5 (1).
- Basile, M., Asbeck, T., Pacioni, C., Mikusiński, G., & Storch, I. (2020). Woodpecker cavity establishment in managed forests: relative rather than absolute tree size matters. *Wildlife Biology*, (1).
- Barton, K., 2020. MuMIn: Multi-Model Inference. R package version 1 (43), 17. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1).
- Bitterlich, W., 1984. The relascope idea. Relative measurements in forestry. Commonwealth Agricultural Bureaux.
- Blakey, R.V., Law, B.S., Kingsford, R.T., Stoklosa, J., Tap, P., Williamson, K., 2016. Bat communities respond positively to large-scale thinning of forest regrowth. *J. Appl. Ecol.* 53 (6), 1694–1703.
- Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biol. Conserv.* 144 (9), 2300–2310.
- Boonman, M., 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). *J. Zool.* 251 (3), 385–389.
- Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Bončina, A., Chauvin, C., Drössler, L., García-Güemes, C., Heiri, C., Kerr, G., Lexer, M.J., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* 87 (4), 492–503.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* 9 (2), 378–400.
- Buckley, P., & Mills, J. (2015). Coppice silviculture: from the Mesolithic to the 21st century. Europe's changing woods and forests: from wildwood to managed landscapes; Kirby K, Watkins C (Eds). Cabi Int, Oxfordshire, UK, 77-92.
- Buckley, P., 2020. Coppice restoration and conservation: a European perspective. *Journal of Forest Research* 1–9.
- Bürgi, M. (2015). Close-to-nature forestry. Europe's changing woods and forests: from wildwood to managed landscapes; Kirby K, Watkins C (Eds). Cabi Int, Oxfordshire, UK, 107-115.
- Bussotti, F., Pollastrini, M., Holland, V., Brueggemann, W., 2015. Functional traits and adaptive capacity of European forests to climate change. *Environ. Exp. Bot.* 111, 91–113.
- Carr, A., Weatherall, A., Jones, G., 2019. The effects of thinning management on bats and their insect prey in temperate broadleaved woodland. *For. Ecol. Manage.* 457, 117682.
- Catto, C.M.C., Hutson, A.M., Racey, P.A., Stephenson, P.J., 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool.* 238 (4), 623–633.
- Cel'uch, M., Kropil, R., 2008. Bats in a Carpathian beech-oak forest (Central Europe): habitat use, foraging assemblages and activity patterns. *Folia Zool.* 57 (4), 358.
- Charbonnier, Y.M., Barbaro, L., Barnagaud, J.Y., Ampoorter, E., Nezan, J., Verheyen, K., Jactel, H., 2016. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. *Oecologia* 182 (2), 529–537.
- Charman, E.C., Smith, K.W., Gruar, D.J., Dodd, S., Grice, P.V., 2010. Characteristics of woods used recently and historically by Lesser Spotted Woodpeckers *Dendrocopos minor* in England. *Ibis* 152 (3), 543–555.
- Cistrone, L., Altea, T., Matteucci, G., Posillico, M., De Cinti, B., Russo, D., 2015. The effect of thinning on bat activity in Italian high forests: the LIFE+“ ManFor C. BD.” experience. *Hystrix, the Italian J. Mammal.* 26 (2), 125–131.
- Claireau, F., Bas, Y., Pauwels, J., Barré, K., Machon, N., Allegrini, B., Puechmaile, S.J., Kerbiriou, C., 2019. Major roads have important negative effects on insectivorous bat activity. *Biol. Conserv.* 235, 53–62.
- Davidson-Watts, I., Walls, S., Jones, G., 2006. Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biol. Conserv.* 133 (1), 118–127.
- Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T., Pretzsch, H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *Eur. J. Forest Res.* 136 (4), 739–766.
- Dietz, M., Brombacher, M., Erasmý, M., Fenchuk, V., Simon, O., 2018. Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest. *Acta Chiropterologica* 20 (1), 117–127.
- Denzinger, A., Schnitzler, H.U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front. Physiol.* 4, 164.
- Downs, N.C., Racey, P.A., 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterologica* 8 (1), 169–185.
- Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 351 (1342), 921–931.
- Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M.M., Bauhus, J., 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. *Nat. Commun.* 9 (1), 1–11.
- Forestry Commission (2019) *Managing England's woodlands in a climate emergency. A guide to help foresters and agents implement adaptation actions. Version 1.* Forestry Commission. Online. Date accessed 8/12/2019. <https://www.gov.uk/government/publications/managing-englands-woodlands-in-a-climate-emergency>.
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.* 50 (1), 252–261.
- Froidevaux, J.S., Zellweger, F., Bollmann, K., Obrist, M.K., 2014. Optimizing passive acoustic sampling of bats in forests. *Ecol. Evol.* 4 (24), 4690–4700.
- Froidevaux, J.S., Zellweger, F., Bollmann, K., Jones, G., Obrist, M.K., 2016. From field surveys to LiDAR: shining a light on how bats respond to forest structure. *Remote Sens. Environ.* 175, 242–250.
- Fuller, R.J., Warren, M.S., 1993. Coppiced woodlands: their management for wildlife. Joint Nature Conservation Committee, London.
- Garin, I., Aihartza, J., Goiti, U., Arrizabalaga-Escudero, A., Noguera, J., Ibáñez, C., 2019. Bats from different foraging guilds prey upon the pine processionary moth. *PeerJ* 7, e7169.
- Gorresen, P.M., Miles, A.C., Todd, C.M., Bonaccorso, F.J., Weller, T.J., 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. *J. Mammal.* 89 (1), 11–17.

- Görföl, T., Haga, K., Dombi, I., 2019. Roost selection of barbastelle bats (*Barbastella barbastellus*) in an intensively managed floodplain forest: implications for conservation. *North-Western Journal of Zoology* 15 (2), 184–186.
- Gustafsson, L., Bauhus, J., Asbeck, T., Augustyniczik, A.L.D., Basile, M., Frey, J., Gutzat, F., Hanewinkel, M., Helbach, J., Jonker, M., Knuff, A., 2020. Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. *Ambio* 1–13.
- Harmer, R., Howe, J., 2003. The silviculture and management of coppice woodlands. Forestry Commission, Edinburgh.
- Harmer, R., Kerr, G., Thompson, R., 2010. Managing native broadleaved woodland. The Stationary Office Ltd (TSO).
- Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. *J. Appl. Ecol.* 55 (6), 2756–2766.
- Hill, D.A., Greenaway, F., 2008. Conservation of bats in British woodlands. *British Wildlife* 19 (3), 161.
- Hill, L., Hemery, G., Hector, A., Brown, N., 2019. Maintaining ecosystem properties after loss of ash in Great Britain. *J. Appl. Ecol.* 56 (2), 282–293.
- Hopkins, J.J., Kirby, K.J., 2007. Ecological change in British broadleaved woodland since 1947. *Ibis* 149, 29–40.
- Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. *For. Ecol. Manage.* 315, 80–85.
- Humes, M.L., Hayes, J.P., Collopy, M.W., 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. *J. Wildl. Manag.* 553–561.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* 8 (1–2), 93–115.
- Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., Kalko, E.K., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J. Appl. Ecol.* 49 (2), 523–531.
- Kalda, R., Kalda, O., Lõhmus, K., Liira, J., 2015. Multi-scale ecology of woodland bat the role of species pool, landscape complexity and stand structure. *Biodivers. Conserv.* 24 (2), 337–353.
- Kerr, G., 1999. The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. *Forestry* 72 (3), 191–205.
- Ketzler, L.P., Comer, C.E., Twedt, D.J., 2018. Bat community response to silvicultural treatments in bottomland hardwood forests managed for wildlife in the Mississippi Alluvial Valley. *For. Ecol. Manage.* 417, 40–48.
- Kirkpatrick, L., Oldfield, I.F., Park, K., 2017. Responses of bats to clear fell harvesting in Sitka Spruce plantations, and implications for wind turbine installation. *For. Ecol. Manage.* 395, 1–8.
- Kusch, J., Weber, C., Idelberger, S., Koob, T., 2004. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zoologica Praha* 53 (2), 113–128.
- Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe. The complexity challenge. *Ambio* 38 (6), 309–315.
- Langridge, J., Pisanu, B., Laguet, S., Archaux, F., Tillon, L., 2019. The role of complex vegetation structures in determining hawking bat activity in temperate forests. *For. Ecol. Manage.* 448, 559–571.
- Law, B., Park, K. J., & Lacki, M. J. (2016). Insectivorous bats and silviculture: balancing timber production and bat conservation. *Bats in the Anthropocene: Conservation of bats in a changing world*, 105-150.
- Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I., Nascimbene, J., Tottrup, A.P., Rahbek, C., Heilmann-Clausen, J., 2019. Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. *For. Ecol. Manage.* 432, 707–717.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354 (6309), aaf8957.
- Lõhmus, A., Nellis, R., Pullerits, M., Leivits, M., 2016. The potential for long-term sustainability in seminatural forestry: a broad perspective based on woodpecker populations. *Environ. Manage.* 57 (3), 558–571.
- Lučan, R.K., Hanák, V., Horáček, I., 2009. Long-term re-use of tree roosts by European forest bats. *For. Ecol. Manage.* 258 (7), 1301–1306.
- Lush, M.J., Hewins, E.J., Lush, C.E., Peterken, G.F., 2012. Woodland Conservation Condition Survey Handbook: A method for assessing the nature conservation condition on non-statutory woodlands. Version 1.0. exeGesIS SDM Ltd. 65, pp.
- Mason, W., Kerr, G., Simpson, J., 1999. What is continuous cover forestry? Information Note, Forestry Commission, Edinburgh, p. 8.
- Mason, W.L., 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis* 149, 41–52.
- Mendes, E.S., Fonseca, C., Marques, S.F., Maia, D., Pereira, M.J.R., 2017. Bat richness and activity in heterogeneous landscapes: guild-specific and scale-dependent? *Landscape Ecol.* 32 (2), 295–311.
- Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., 2014. Ash dieback in the UK: a review of the ecological and conservation implications and potential management options. *Biol. Conserv.* 175, 95–109.
- Mölder, A., Meyer, P., Nagel, R.V., 2019. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *For. Ecol. Manage.* 437, 324–339.
- Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.J., Brandl, R., 2012. Aggregative response in bats: prey abundance versus habitat. *Oecologia* 169 (3), 673–684.
- Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Veith, M., Fenton, B., 2013. From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height. *For. Ecol. Manage.* 306, 179–184.
- Murphy, S.E., Greenaway, F., Hill, D.A., 2012. Patterns of habitat use by female brown long-eared bats presage negative impacts of woodland conservation management. *J. Zool.* 288 (3), 177–183.
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biol. Conserv.* 191, 38–49.
- Newson, S.E., Evans, H.E., Jarrett, D., Raynor, R., Wilson, M.W., 2017. Large-scale citizen science improves assessment of risk posed by wind farms to bats in southern Scotland. *Biol. Conserv.* 215, 61–71.
- Nicholls, B., Racey, P.A., 2006a. Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. *Behav. Ecol. Sociobiol.* 61 (1), 131–142.
- Nicholls, B., Racey, P.A., 2006b. Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography* 29 (5), 697–708.
- Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E., 2018. The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles. *J. Appl. Ecol.* 55 (5), 2147–2159.
- Patriquin, K.J., Barclay, R.M., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *J. Appl. Ecol.* 40 (4), 646–657.
- Pastur, G.J.M., Vanha-Majamaa, I., Franklin, J.F., 2020. Ecological perspectives on variable retention forestry. *Ecological Processes* 9 (1), 1–6.
- Peterken, G. F. (2015). *18 Woodland History in the British Isles—An Interaction of Environmental and Cultural Forces. Europe's changing woods and forests: from wildwood to managed landscapes*; Kirby K, Watkins C (Eds). Cabi Int, Oxfordshire, UK, 265.
- Peterken, G., Mountford, E., 2017. *Woodland Development: A Long-term Study of Lady Park Wood*. CABI.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R. C., 2020. nlme: linear and nonlinear mixed effects models. R package version 3 (1-148), 2020.
- Piraccini, R., 2016. *Barbastella barbastellus*. The IUCN Red List of Threatened Species 2016: e.T2553A22029285. <http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T2553A22029285.en>. Date accessed 14th November 2019.
- Plank, M., Fiedler, K., Reiter, G., 2012. Use of forest strata by bats in temperate forests. *J. Zool.* 286 (2), 154–162.
- Poore, A., 2016. *Rushmore Estate Woods; management plan 2016-2026*. Estate Office, Tollard Royal, Wiltshire.
- Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Putz, F. E., 2015. Silvicultural alternatives to conventional even-aged forest management—what limits global adoption? *Forest Ecosystems* 2 (1), 8.
- Pukkala, T., 2016. Which type of forest management provides most ecosystem services? *Forest Ecosystems* 3 (1), 9.
- Rackham, O., 2003. *Ancient woodland, its history, vegetation and uses in England*, 2nd edn. Castlepoint Press, Dalbeattie, UK.
- Rackham, O. (1986). *The history of the countryside*. J M Dent & Sons.
- Rainho, A., Augusto, A.M., Palmeirim, J.M., 2010. Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. *J. Appl. Ecol.* 47 (4), 850–858.
- Read, H., 2000. *Veteran Trees A guide to good management*. English Nature, Peterborough (United Kingdom).
- Renner, S.C., Suarez-Rubio, M., Kaiser, S., Nieschulze, J., Kalko, E.K., Tschapka, M., Jung, K., 2018. Divergent response to forest structure of two mobile vertebrate groups. *For. Ecol. Manage.* 415, 129–138.
- Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecol. Ind.* 34, 221–230.
- Remm, J., Lõhmus, A., 2011. Tree cavities in forests—the broad distribution pattern of a keystone structure for biodiversity. *For. Ecol. Manage.* 262 (4), 579–585.
- Rodwell, J. S. (Ed.). (1998). *British plant communities: volume 1, woodlands and scrub* (Vol. 1). Cambridge University Press.
- Russ, J.M., 2012. *British Bat Calls: A Guide to Species Identification*. Pelagic Publishing, UK.
- Rosset, C., Brand, R., Caillard, I., Fiedler, U., Gollut, C., Schmocker, A., Weber, D., Wuillemin, E. and Dumollard, G., (2014). MOTI-L'inventaire forestier facilité par le smartphone. Haute école des sciences agronomiques, forestières et alimentaires HAFL.
- Russo, D., Cistrone, L., Jones, G., Mazzoleni, S., 2004. Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biol. Conserv.* 117 (1), 73–81.
- Russo, D., Cistrone, L., Jones, G., 2005. Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats *Barbastella barbastellus*. *Ecography* 28 (6), 769–776.
- Russo, D., Billington, G., Bontadina, F., Dekker, J., Dietz, M., Gazaryan, S., Jones, G., Meschede, A., Rebelo, H., Reiter, G., Ruczyński, I., 2016. Identifying key research objectives to make European forests greener for bats. *Frontiers in Ecology and Evolution* 4, 87.
- Sanchez, C., 2017. *Pro Silva Silviculture: Guidelines on Continuous Cover Forestry/Close to Nature Forestry Management Practices*. Forêt Wallonne, Namur, Belgium.
- Savill, P. (2015). *High forest management and the rise of even-aged stands. Europe's changing woods and forests: from wildwood to managed landscapes*; Kirby K, Watkins C (Eds). Cabi Int, Oxfordshire, UK, 93-106.

- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Buscot, F., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55 (1), 267–278.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* 9 (1), 4978.
- Siitonen, J., & Ranius, T. (2015). The Importance of Veteran Trees for Saproxylic Insects. Europe's changing woods and forests: from wildwood to managed landscapes; Kirby K, Watkins C (Eds). Cabi Int, Oxfordshire, UK, 140.
- Siemers, B.M., Schnitzler, H.-U., 2000. Natterer's bat (*Myotis nattereri* Kuhl, 1818) hawks for prey close to vegetation using echolocation signals of very broad bandwidth. *Behavioural Ecology & Sociobiology* 47, 400–412.
- Siemers, B.M., Schnitzler, H.U., 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429 (6992), 657–661.
- Spencer, J.W., Kirby, K.J., 1992. An ancient woodland inventory for England and Wales. *Biol. Conserv.* 62, 77–93.
- Starik, N., Göttert, T., Heitlinger, E., Zeller, U., 2018. Bat Community Responses to Structural Habitat Complexity Resulting from Management Practices Within Different Land Use Types—A Case Study from North-Eastern Germany. *Acta Chiropterologica* 20 (2), 387–405.
- Storch, I., Penner, J., Asbeck, T., Basile, M., Bauhus, J., Braunisch, V., Dormann, C.F., Frey, J., Gärtner, S., Hanewinkel, M., Koch, B., 2020. Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of Central Europe using an interdisciplinary, multi-scale approach. *Ecol. Evol.* 10 (3), 1489–1509.
- Susse, R., Allegrini, C., Bruciamacchie, M., Burrus, R., (2011). Management of Irregular Forests: developing the full potential of the forest. Association Futaie Irreguliere. English translation P. Morgan, 144p.
- Swift, S.M., Racey, P.A., 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool.* 200 (2), 249–259.
- Swift, S., Racey, P., 2002. Gleaning as a foraging strategy in Natterer's bat *Myotis nattereri*. *Behav. Ecol. Sociobiol.* 52 (5), 408–416.
- Thompson, I., Mackey, B., McNulty, S., & Mosseler, A. (2009). Forest resilience, biodiversity, and climate change. In Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43. 1-67. (Vol. 43, pp. 1-67).
- Tillon, L., Bresso, K., Aulagnier, S., 2015. Tree selection by roosting bats in a European temperate lowland sub-Atlantic forest. *Mammalia* 80 (3), 271–279.
- Tillon, L., Bouget, C., Paillet, Y., Aulagnier, S., 2016. How does deadwood structure temperate forest bat assemblages? *Eur. J. Forest Res.* 135 (3), 433–449.
- Tillon, L., Langridge, J., Aulagnier, S., 2018. Bat Conservation Management in Exploited European Temperate Forests. In *Bats*, IntechOpen.
- Titchenell, M.A., Williams, R.A., Gehrt, S.D., 2011. Bat response to shelterwood harvests and forest structure in oak-hickory forests. *For. Ecol. Manage.* 262 (6), 980–988.
- Wilson, E., Short, I., Ni Dhubhain, A., 2018. Continuous Cover Forestry: The rise of transformational silviculture. *Forestry Journal* 288, 38–40.
- Wood, H., Lindborg, R., Jakobsson, S., 2017. European Union tree density limits do not reflect bat diversity in wood-pastures. *Biol. Conserv.* 210, 60–71.
- Zeale, M.R., Davidson-Watts, I., Jones, G., 2012. Home range use and habitat selection by barbastelle bats (*Barbastella barbastellus*): implications for conservation. *J. Mammal.* 93 (4), 1110–1118.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.