Forest Ecology and Management 544 (2023) 121214

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Seeing the wood for the trees, irregular silviculture supports bat populations in conifer plantations

Patrick Cook [a,*], Daniel Alder [b], Lisbeth Hordley [a], Stuart E. Newson [c], David Pengelly [d]

[a] *Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, UK*
[b] *Independent Ecologist, 12 Elm Close, Motcombe, Shaftesbury, Dorset SP7 9HN, UK*
[c] *British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK*
[d] *Consultant Forester, SelectFor Ltd, Barrow Hill House, Wood Lane, Stalbridge, Dorset DT10 2QZ, UK*

ARTICLE INFO

Keywords:
Bats
Continuous cover forestry
Habitat structure
Irregular forestry
Landscape context
Woodland management

ABSTRACT

Conifer plantations are a major land use globally and provide a range of social, economic and environmental benefits, particularly the provision of timber. There is a growing interest in alternative forestry techniques, such as irregular silviculture, to create more sustainable and resilient plantations in response to climate change. Plantations are often considered poor for bats due to limited structural diversity. Irregular forestry increases structural diversity and reduces growing stocks, with potentially positive effects on bats, but this remains poorly understood in conifer plantations. At two estates in south-west Britain, we specifically tested whether bat species richness and activity respond to (1) the surrounding landscape cover types (2) habitat structure within irregular stands and (3) increasing progress along the transformation continuum in three continuous cover forestry stands undergoing transformation including irregular high forest. Stands further progressed along the transformation continuum had lower basal area, higher mean tree diameter, higher levels of fallen deadwood and greater canopy cover of broadleaf trees. A total of 13 species of bat, equivalent to 76% of the UK resident species were recorded. The activity of six species was significantly influenced by the proportion of four land use types (two positive and two negative associations with conifer woodland, one positive and one negative association with broadleaved woodland, two positive associations with improved grassland and two negative associations with arable) in the surrounding landscape at three spatial scales (500 m, 1500 m and 3000 m around each survey plot). Four species showed significant positive associations with habitat structural features including larger mean tree diameter, greater canopy openness, higher vertical structural complexity, higher quantities of standing and fallen deadwood, and higher canopy cover of broadleaved trees. Many of these habitat features were more prevalent in stands further progressed towards irregular high forest. We did not detect any significant differences in bat species richness or activity levels between the three stand stages, except for *Plecotus auritus/austriacus* which had higher activity in the Stage 3 stand compared to Stage 2, as the limited replication of our study may have precluded detection of any differences. Our study helps inform us on how bats populations respond to novel management of conifer plantations. Further research to determine thresholds for deadwood and broadleaved trees to further support bats in plantations would be beneficial.

1. Introduction

Forest ecosystems are globally important for biodiversity and ecosystem services (FAO & UNEP, 2020). Forest biodiversity, particularly forest specialist species, continues to decline at continental and national scales, with both intensification and under-management of forests a contributing factor in this decline (DEFRA, 2020; Reid et al., 2021; PECBMS, 2023). The response of biodiversity to forest management is often highly context dependent, varying between species according to habitat preferences (Paillet et al., 2010; Boch et al., 2013; Kirby et al., 2017; Kaufmann et al., 2018), the history of management within a stand and previous land use legacies (Dupouey et al., 2002; Hermy and Verheyen, 2007; Ellis et al., 2021).

Woodlands in the United Kingdom (UK) have a long history of management, primarily through coppicing to produce poles and timber (Rackham, 2015; Kirby et al., 2017). After the First World War

---

* Corresponding author at: Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, UK.
E-mail address: pcook@butterfly-conservation.org (P. Cook).

https://doi.org/10.1016/j.foreco.2023.121214
Received 22 March 2023; Received in revised form 9 June 2023; Accepted 12 June 2023

(1914–1918) the demand for timber increased, which led to the formation of the Forestry Commission in 1919 and planting of thousands of hectares of commercial, plantation forestry (Gambles, 2019). Fast growing, non-native soft-wood conifers, such as Sitka spruce *Picea sitchensis* and Douglas fir *Pseudotsuga menziesii*, were selected to establish new plantations across a range of sites (Savill, 2015). Currently in the United Kingdom, conifer woodland, including native pinewoods *Pinus sylvestris,* covers 1,650,000 ha and represents an important source of economic revenue (Forest Research, 2022).

Conifer plantations have a legacy of even-aged structure in the UK due to management using clear-fell and replant. Cohorts of trees are harvested in coupes of varying size, during the stem exclusion phase, on a rotation of approximately 30–60 years for conifers (Mason et al, 1999; Mason, 2000). Post-harvesting, felled areas are restocked at high densities, creating homogeneous, even aged stands, often comprised of a single species. This technique is criticised for the negative impacts it has on biodiversity (Kuuluvainen et al., 2012; Borkin et al., 2014) due to high disturbance levels, although it can support a community composition of species associated with open woodland habitats (Calladine et al., 2015; Kirkpatrick et al., 2017b).

It is increasingly recognised that commercial forests should deliver multi-functional benefits, beyond timber production, including ecosystem services, greater resilience to climate change and the provision of habitat for biodiversity (Law et al., 2016; Peura et al., 2018; Forestry Commission, 2020; Gustafsson et al., 2020). Driven by the need to deliver these multi-functional benefits and adapt to climate change there is a growing interest in alternative silvicultural techniques, such as continuous cover forestry (CCF). Whilst widely implemented across continental Europe, CCF has been adopted on a limited scale in the UK and will likely expand (Wilson, 2013; Puettmann et al., 2015). Adoption has remained limited in the UK due to limited experience in the forestry sector of transformation and managing forests using CCF, economic models tailored towards processing high volumes of medium sized timber classes and challenges around effective deer control to facilitate natural regeneration (Larsen et al., 2022; Mason et al., 2022; D. Pengelly pers.comm. 2023). Irregular silviculture, a CCF silvicultural technique (Pommerening & Murphy, 2004; Susse et al., 2011) involves the selective removal of individual trees or small group felling and maintenance of a permanent irregular canopy (Sanchez, 2017). Vertical structure develops as lower and spatially dispersed tree stocking allows light to reach the forest floor facilitating natural regeneration and development of a varied understorey (Susse et al., 2011; Muscolo et al., 2014). Over time, stand heterogeneity and vertical structural diversity increase, which alongside the promotion of mixed stands of conifer and broadleaf tree species, is expected to benefit biodiversity at the stand and landscape scale (Schall et al., 2018; Alder et al., 2021). Irregular silviculture is particularly likely to benefit groups associated with mature forest, small scale disturbances and specific habitat features such as open canopy (Alder et al., 2021).

Bats are an important vertebrate group that display an affinity for woodland, with all UK species at least partially using woodlands (Altringham, 2003). Bat populations are influenced by stand habitat structural variables, such as clutter of the understorey, tree species composition and deadwood availability (Jung et al., 2012; Müller et al., 2012; Charbonnier et al., 2016a; Langridge et al., 2019). Our understanding of the response of bats to alternative woodland management techniques, including irregular forest management remains limited particularly in conifer plantations (Alder et al., 2021). As adoption of CCF in plantations increases, even-aged stands undergo transformation to irregular stands. Further work is needed to consolidate habitat features associated with bat species and activity in irregular conifer plantations to maximise opportunities for habitat use within stand interiors. Irregular stands potentially provide habitat features of importance to bats, compared to even-aged stands, but no study has compared species richness and activity levels across stands at different stages of transformation in conifer plantations. Bats are also influenced by the quantity of habitats or land cover types found in the surrounding landscape, such as broadleaved woodland and open water (Fuentes-Montemayor et al., 2013; Kalda et al., 2015; Gili et al., 2020). Conifer plantations are often considered to be poor environments for bats, although stand management can influence habitat for roosting and foraging (Kirkpatrick et al., 2017a, Kirkpatrick et al., 2017b). Unlike even-aged stands, conifer plantations managed using irregular silviculture could also provide benefits to bat species at the landscape scale.

To address this gap in the research we investigated the response of bats to management under irregular silvicultural principles in a lowland, conifer plantation. We explore how bats responded to habitat attributes at two spatial scales; firstly, at the stand level and secondly the landscape cover types surrounding these stands. Studied stands were surveyed at three varying stages of forest transformation, from regular structure towards irregular high forest where we specifically explore (1) the differences in habitat structure amongst the stand stages. We also explored how bat species richness and activity responds to (2) four land cover types in the wider landscape at three spatial scales, (3) habitat structural variables within a stand and (4) increasing stage of stand transformation towards irregular high forest.

2. Materials and methods

2.1. Study sites

The study was undertaken on the Stourhead (Western) Estate (SWE) and National Trust (NT) Stourhead Estate in southern England (51°06′46.1″N 2°21′32.2″W; 141 m – 239 m a.s.l; Fig. 1). Underlying geology of the site is Greensand and Gault Clay. Conifer plantations are comprised of species such as Douglas fir and Sitka spruce. Plantations were planted in the 18th to early 20th century on grassland and common land. SWE has adopted an innovative silvicultural approach and began a more formal transition towards permanently irregular structures in 1997.

2.2. Stand descriptions

Three spatially distinct stands were selected for the study (Fig. 1). Each selected stand is comprised of a smaller set of sub-compartments with each sub-compartment reflecting an area of historical planting with trees (Fig. S1). Stands represented three points along a transformation continuum from having relatively regular (even-aged) to irregular (mixed-age and species) structure. Stands progress from Stage 1 (Preparatory Stage), through Stage 2 (Regeneration Initiation Stage) to finally Stage 3 (Structural Development Stage) (Fig. 2). At the end of Stage 3, stand structure stabilises around an equilibrium. Stages represent an idealised model of forest development dependent on basal area of the stand which influences the development of stand structural elements (A. Poore pers.comm. 2023; Fig. 2). In our study there were some discrepancies from the idealised model, for instance at the south end of the stand selected to represent Stage 1 some plots had an understorey indicating a transition towards Stage 2.

2.3. Habitat measures

A total of thirty-two, 30 m diameter, sample plots were selected across the three treatments with eight plots in Stage 1, eight plots in Stage 2 and sixteen plots in Stage 3. All sample plots were located a minimum distance of 30 m from the nearest major forest edge (defined as an agricultural boundary, a major ride > 8 m wide or a road), with each plot a minimum of 85 m from the next nearest plot.

Habitats measures were adapted from Khanaposhtani et al. (2012) and Alder et al. (2018). At each 30 m sample plot the following habitat measurements were gathered in July 2021.

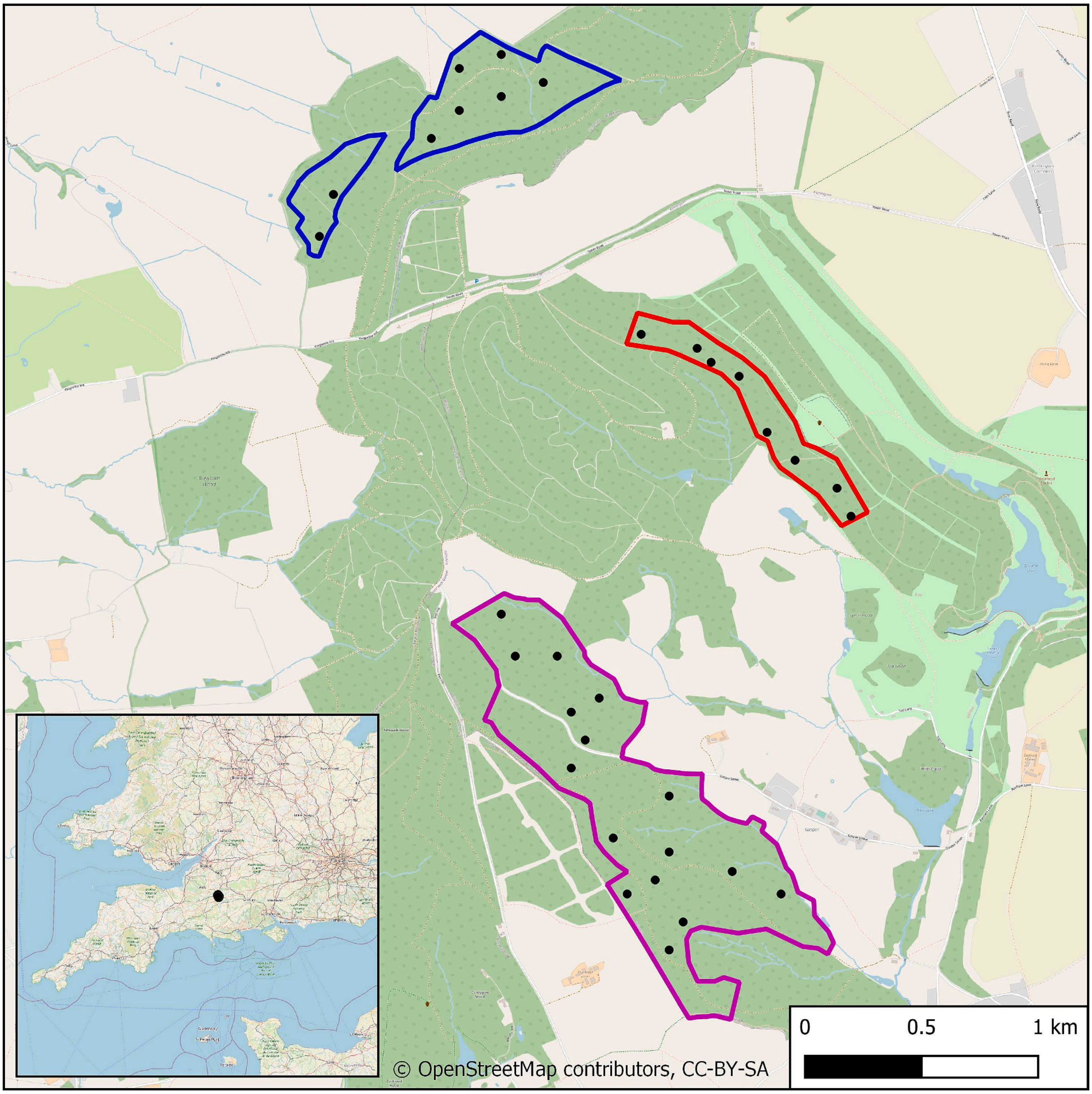


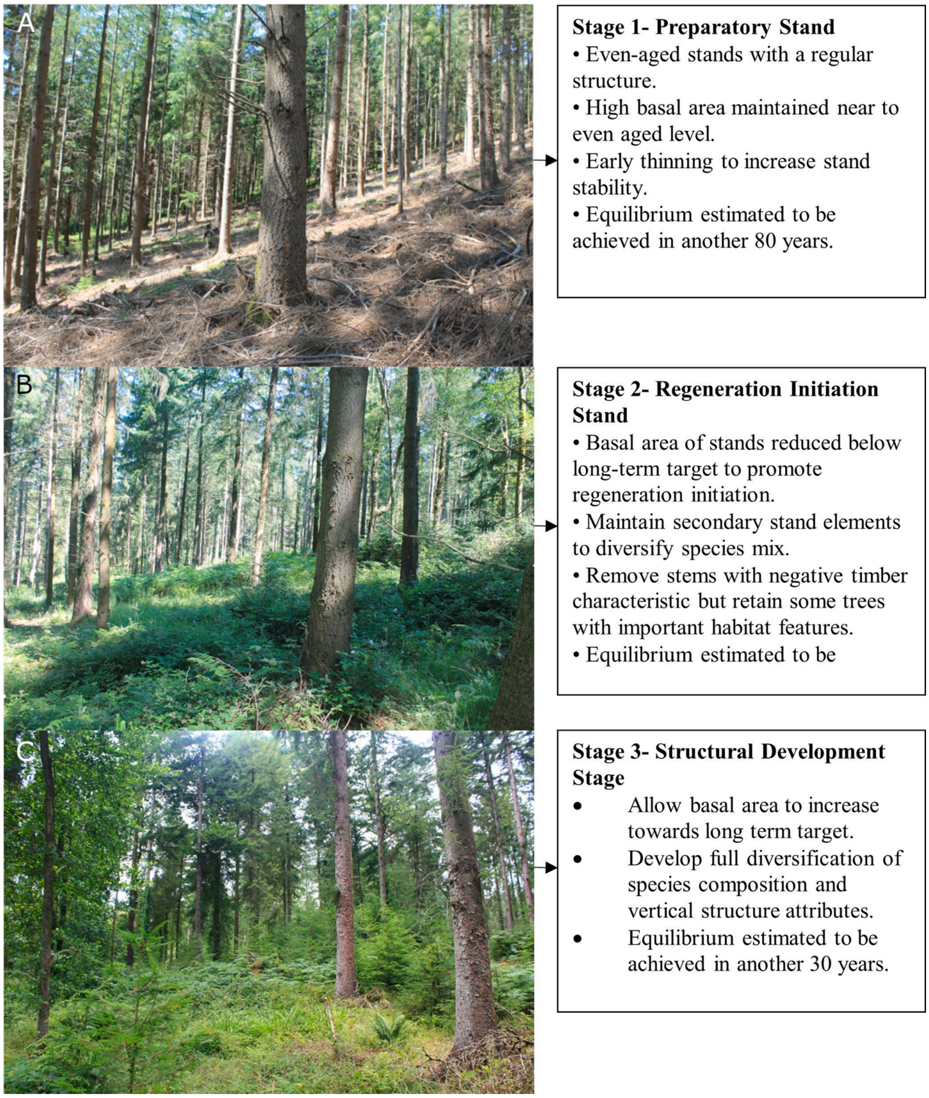
Fig. 1. Location of the study sites in southern England. Stands surveyed in this study are outlined. The polygon with a red outline represents the Stage 1 (Preparatory Stage) stand, dark blue outline represents the Stage 2 (Regeneration Initiation) stand and purple outline represents the Stage 3 (Structural Development) stand. Black dots represent the location of sample plots of acoustic bat surveys. Base map © OpenStreetMap contributors CC BY-SA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

- Basal area in m^2ha which represents the growing stock of each plot. Basal area was calculated by conducting a 360° sweep from the plot centre, with a basal factor of 2 and a minimum of ten trees, in the relascope (forestry tool to calculate basal area) MOTI application (Rosset et al., 2015).
- Mean diameter at breast height (DBH) was calculated from the five largest trees in the plot.
- Percentage broadleaved canopy cover.
- Length of fallen deadwood > 1 m in length and > 20 cm in diameter.
- Frequency of deadwood snags > 1 m in length and > 10 cm in diameter. This includes dead branches on a tree and standing dead trees.
- Percentage canopy openness using a spherical convex mirror densiometer.

The forest structure was divided into five categories for data collection; canopy, subcanopy, tall understorey (2.5–6 m), low shrub (1–2.5 m) and ground/field layer (0–1 m). We calculated cover for dominant field layer species using the DOMIN scale (Kent, 2011). Four percentage categories (0–10 %, 11–20 %, 21–50 % and > 50 %) were used to estimate the tree cover of the canopy, sub-canopy, tall understorey and shrub layer with scores later converted to a 1–4 scale to calculate habitat complexity scores. Scores for the four categories were merged to calculate an overall vertical habitat structural complexity score with high classified as ≥ 5 and low as < 5.

2.4. *Bat sampling*

Bats were surveyed acoustically in 2021, with one night between the 10th and 17th of August and a second night between the 18th and 26th August 2021, using four Song Meter SM3Bat recorders (Acoustics, 2021). In any individual night of recording, a total of one to two



Stage 1- Preparatory Stand

- Even-aged stands with a regular structure.
- High basal area maintained near to even aged level.
- Early thinning to increase stand stability.
- Equilibrium estimated to be achieved in another 80 years.

Stage 2- Regeneration Initiation Stand

- Basal area of stands reduced below long-term target to promote regeneration initiation.
- Maintain secondary stand elements to diversify species mix.
- Remove stems with negative timber characteristic but retain some trees with important habitat features.
- Equilibrium estimated to be

Stage 3- Structural Development Stage

- Allow basal area to increase towards long term target.
- Develop full diversification of species composition and vertical structure attributes.
- Equilibrium estimated to be achieved in another 30 years.

Fig. 2. The three forest transformation stages used in the study. (A) Stage 1, (B) Stage 2, and (C) Stage 3. Descriptions provide detail of the idealised model of stand transformation for each stage (D. Pengelly pers.comm. 2023).

SM3Bat's were placed in each of the three treatments. Surveys were conducted on nights without rain, wind speeds below force 4 on the Beaufort Scale and temperatures above 7 °C (Froidevaux et al., 2014). Microphones were pole-mounted at a height of 3.0 m and a minimum of 1.5 m from dense vegetation (Alder et al., 2021).

Bat detectors were deployed before sunset and detectors set to switch on and record 15 min after sunset until 15 min before sunrise the following day (Froidevaux et al., 2014). The bat detectors were set to record with a sample rate of 384 kHz, a trigger threshold of 12 dB and to use a high pass filter of 8 kHz which defined the lower threshold of the frequencies of interest for the triggering mechanism. Recording was set to continue until no trigger is detected for a 2.0 s period up to a maximum of 5.0 s (Newson et al., 2015). Each triggered event was categorised as a pass for each species. A first analysis of bat recordings was carried out using the BTO Acoustic Pipeline (https://bto.org/pipeline).

Following recommendations by Barré et al. (2019), identifications with a probability of <0.5 (50%) were not considered further. For the remaining recordings, verification of species identification was carried out through the manual checking of spectrograms using the software SonoBat 4.1 (https://sonobat.com/) which was used as an independent check of the original species identities assigned by the classifier. This was carried out for recordings of all species, except for *Pipistrellus pipistrellus* which were the most encountered species where a sample of c.20% was manually checked to confirm identification.

Criteria for distinguishing *Myotis mystacinus* and *Myotis brandtii* are very subtle and poorly defined. Because these two species are extremely difficult to distinguish acoustically, as are *Plecotus auritus and P. austriacus* we treat these species here as species pairs respectively.

2.5. Data analysis

To understand how the structural habitat measures vary across the three stand types for hypothesis one, we composed mixed effects models with each habitat measure as our response variable, stand stage as our explanatory variable, and sub-compartment as a random effect to account for similarities within sub-compartments (Fig. S1). We used a mixture of Generalised Linear Mixed-effects Models (GLMMs) with Poisson distribution and zero-inflated GLMMs for count data and LMMs for continuous data using packages "lme4" (Bates et al., 2015) and "glmmTMB" (Brooks et al., 2017). Models were followed by Tukey's post hoc multiple comparison test using the "multcomp" package (Hothorn et al., 2008) to examine pairwise differences between stand types.

For the subsequent hypotheses, we calculated bat species richness and bat activity at each survey plot in each of the two visits. Bat activity was calculated as the proportions of 10-minute periods during a night, within which the bat species was recorded at least once, following Alder et al. (2021). Four species did not occur frequently enough and were removed from the activity analysis (*Nyctalus leisleri*, *Pipistrellus nathusii*, *Rhinolophus ferrumequinum*, and *Rhinolophus hipposideros*).

To understand the influence of the surrounding landscape on bat species richness and activity for hypothesis two, we used the CEH Land Cover Map 2015 (Rowland et al., 2017) to extract the proportions of four land cover types ((1) arable and horticulture, (2) broadleaf, yew and mixed woodland, (3) coniferous woodland, and (4) improved grassland) within three buffers (500 m, 1500 m, and 3000 m) around each sampling plot. The spatial scales were chosen to cover the home ranges of low (e.g. *P. auritus/austriacus*), intermediate (e.g. *Pipistrellus pygmaeus*), and highly mobile bat species (e.g. *P. pipistrellus*; Entwistle et al., 1996; Nicholls & Racey, 2006). Selected land cover types were important in the surrounding landscape of the study site with previously documented influences on bat populations (Fuentes-Montemayor et al., 2013; Border et al., 2017). We assessed the importance of the surrounding landscape by using GLMMs with Poisson distribution for bat species richness and binomial GLMMs for bat species activity levels as the response variables with visit as a coviarate and subcompartment as a random intercept (Fig. S1). We fitted individual models to each land cover type at each spatial scale separately and calculated R^2 values to quantify the amount of variation in the data explained by each land cover type.

To examine the effect of structural habitat variables on bat activity for hypothesis three, we fitted GLMMs with species richness or each species activity as the response variable, and six habitat variables as explanatory variables: mean DBH, basal area, canopy openness, complexity score, length of fallen deadwood, and frequency of deadwood snags, hereafter termed 'habitat models'. We fitted the same distributions as mentioned above, including visit and distance to nearest edge as a covariate, and subcompartment as a random intercept. All continuous variables were standardised to zero mean and one standard deviation. To account for the surrounding landscape in these models, we selected the spatial scale (500 m, 1500 m or 3000 m) for each land cover type which had the highest R^2 value. We added each land cover type at the selected spatial scale to the 'habitat models' separately. A correlation matrix of all explanatory variables was created to check for collinearity between variables. We considered variables to be correlated if $r \geq 0.7$. Frequency of deadwood snags and percentage broadleaf canopy were highly correlated and the variable that was least correlated with the response variable was removed from the model. Model assumptions (including overdispersion) were verified using the DHARMa R package (Hartig, 2022). We compared the 'habitat model' without any land use parameters, to each habitat model with a land cover type variable added (hereafter 'landscape model') to assess whether a particular land cover type provided a better fit to the data, by comparing AIC values between models. A model was considered to provide a better fit to the data if the differences between AIC values was ≥ 2.

Finally, for hypothesis four, GLMMs with Poisson distribution were used to analyse the differences in bat species richness between stand types and binomial GLMMs were used to analyse the differences in bat species activity levels between stand types. We included distance to edge and visit as a covariate and sub-compartment was included as a random intercept (Fig. S1). The models were followed by Tukey's post hoc multiple comparison tests.

3. Results

3.1. Habitat structure across the development stage stands

Habitat features overlapped greatly between the stand stages particularly Stage 1 and 3, but six significant differences were detected (Fig. 3, Table S1). Basal area declined across the stand development stages being lowest in Stage 3. Other characteristics of the Stage 3 stand included higher mean DBH and complexity score compared to the Stage 2 stand, and higher percentage canopy cover of broadleaf trees and higher levels of fallen deadwood compared to the Stage 1 stand.

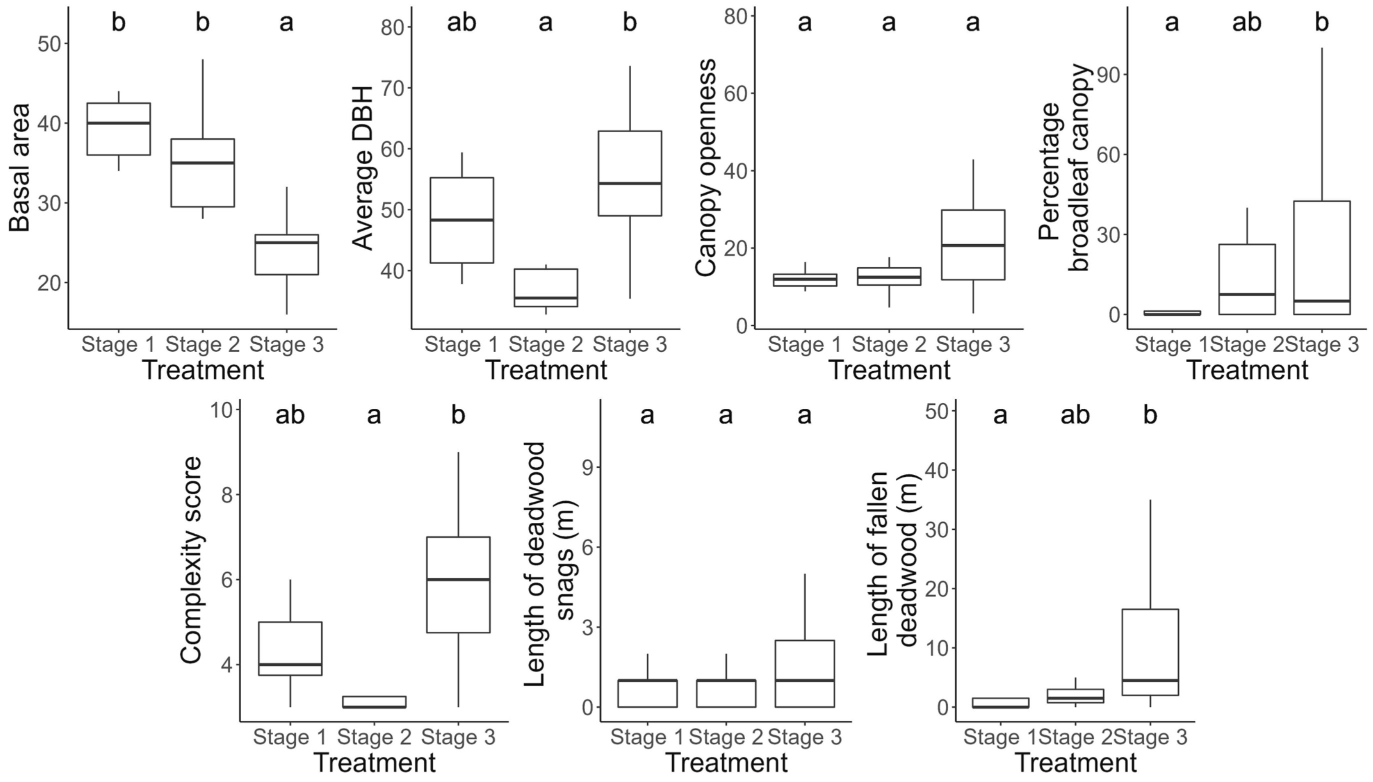


Fig. 3. Habitat variables amongst the three stand development stages.

3.2. Bat data

A total of 13 bat species and 5940 bat registrations were recorded during the sampling period (Table 1). Bat species recorded included species considered scarce in the UK such as *Barbastella barbastellus*, *R. ferrumequinum* and *R. hipposideros*. *Pipistrellus pipistrellus* accounted for 41.9% of all recorded bat registrations, followed by *P. pygmaeus* with 26.8% of all bat registrations. Four other species recorded>100 registrations including *M. mystacinus/brandtii*, *Nyctalus noctula*, *B. barbastellus*, and *P. auritus/austriacus*.

3.3. Landscape cover type associations

The proportion of conifer woodland declined at larger spatial scales whereas improved grassland and arable increased. In the 500 m buffer conifer woodland was the most common land cover type, whereas in the 1500 m buffer and particularly the 3000 m buffer improved grassland was the most common land cover type (Table S2). The surrounding landscape within 1500 m of sampling plots had the highest R^2 value, i.e. explained the most variation in species' activity levels, for five bat species, followed by two species each in the 500 m and 3000 m categories. Conifer cover and improved grassland had the highest R^2 for three species, followed by two species for broadleaf woodland and one species for arable (Table 2). Conifer cover also had the highest R^2 for total bat species richness.

Incorporating surrounding landscape metrics into the habitat models improved the model fit for five species (*B. barbastellus*, *Myotis daubentonii*, *P. pipistrellus*, *P. pygmaeus* and *N. noctula*; Table S3). All four land cover types were found to influence the activity of six bat species (Table 2). *Eptesicus serotinus* and *P. pipistrellus* were negatively associated with the quantity of arable in a 1500 m buffer. *Myotis mystacinus/brandtii* had a strong positive association with broadleaved woodland cover at the 3000 m level whereas *P. pygmaeus* was negatively associated at the 500 m level. *Nyctalus noctula* and *P. pipistrellus* were positively associated with conifer cover in the 1500 m buffer. *M. daubentonii* and *Myotis mystacinus/brandtii* were negatively associated with conifer cover at the 1500 m and 3000 m spatial scale. *Myotis daubentonii and P. pygmaeus* were positively associated with improved grassland at the 500 m spatial scale.

3.4. Stand habitat associations

Bat species richness and activity of individual bat species were significantly influenced by seven habitat structural variables; mean DBH, canopy openness, complexity score, deadwood snags, distance to edge, fallen deadwood and percentage broadleaved canopy cover (Fig. 4: Table 3, Table S4). Total bat species richness was positively associated with mean DBH of tree species at the plot level (Fig. 4a) and one species, *P. pygmaeus* also had higher activity levels in plots with greater mean DBH (Fig. 4b). Activity levels of two species (*P. pipistrellus* and *P. pygmaeus*) were strongly associated with plots that had greater canopy openness in the forest stands (Fig. 4c and Fig. 4d). *Pipistrellus pipistrellus* had higher activity levels in plots which had higher vertical structural complexity when we accounted for the proportion of broadleaf habitat within 3000 m of the plots (Fig. 4e). *Pipistrellus pipistrellus* and *P. pygmaeus* had higher levels of activity in plots with higher frequencies of deadwood snags (Fig. 4f and Fig. 4g) and greater quantities of fallen deadwood (Fig. 4h and Fig. 4i). Total bat richness and activity levels of three species, *P. pipistrellus*, *P. pygmaeus* and *P. auritus/austriacus* were negatively associated with distance from the nearest edge (Table 3). *Myotis mystacinus/brandtii* had activity levels strongly positively associated with increasing levels of broadleaved canopy cover (Fig. 4j).

Table 1
Recorded bat registrations and percentage of total bat registrations per species.

Species	Registrations	Percentage (%) of total registrations
Pipistrellus pipistrellus	2486	41.85
Pipistrellus pygmaeus	1593	26.82
Myotis mystacinus/brandtii	612	10.30
Nyctalus noctula	582	9.80
Barbastella barbastellus	243	4.09
Plecotus auritus/austriacus	198	3.33
Myotis nattereri	82	1.38
Eptesicus serotinus	65	1.09
Myotis daubentonii	63	1.06
Rhinolophus hipposideros	6	0.10
Nyctalus leisleri	4	0.07
Rhinolophus ferrumequinum	4	0.07
Pipistrellus nathusii	2	0.03
Total	5940	100

3.5. Bat activity across stand development stages

There was no difference in bat species richness amongst the three stand stages (Table S5). Similarly, no differences were detected for individual species activity rate amongst the three stand stages, except for *Plecotus auritus/austriacus* which had higher activity in the Stage 3 stand compared to Stage 2 (Table S5).

4. Discussion

Increasing bat populations in conifer plantations depends on the implementation of more ecologically sensitive management techniques. Adoption of irregular silviculture is likely to increase in the future, as forest managers look to adapt and increase forest resilience to climate change. Our understanding of the potential benefits to bats at the stand and landscape scale of transforming conifer plantations to irregular structures remains limited. We found bat richness and activity was positively associated with six habitat features in conifer plantations. Bat activity was positively and negatively influenced by the proportion of broadleaved woodland and conifer woodland, positively influenced by improved grassland, whereas only negative associations were detected with arable cover in the surrounding landscape.

4.1. Landscape analysis

The proportion of four landscape cover types influenced bat species activity in our study area. Given the limited spatial replication of our study we are cautious with the interpretation of these results as we cannot exclude the possibility that the distribution of existing roost sites could bias the results. *Pipistrellus pygmaeus* and *P. pipistrellus* activity was influenced by stand structure and habitat availability in the wider landscape. *Pipistrellus pygmaeus* had associations to two habitat types (improved grassland and broadleaved woodland) at the 500 m spatial scale, whereas *P. pipistrellus* had associations with two habitat types (arable and conifer) at the 1500 m spatial scale. All detected associations for *P. pygmaeus* were within the smallest buffer size, which corresponds with the lower mobility of this species compared to *P. pipistrellus* which responded at the 1500 m scale (Nicholls & Racey, 2006, Kirkpatrick et al., 2018). *Pipistrellus pipistrellus* and *E. serotinus* had a negative relationship with arable farmland, a possible reflection of the limited food availability in this land use, which can be influenced by the suitability of specific agri-environment schemes (Fuentes-Montemayor et al., 2011; McHugh et al., 2019). *Nyctalus noctula* and *E. serotinus* are species that can fly high above the ground often foraging above the canopy in open space (Jones, 1995; Catto et al., 1996; Müller et al., 2013; Roeleke et al., 2016, O'Mara et al., 2019). The response to land cover types rather than stand characteristics in this study reflects these attributes. *Myotis daubentonii* and *M. mystacinus/brandtii* had a negative relationship with conifer woodland cover. *Myotis mystacinus/brandtii* also had a strong

Table 2
Summary table of the influence of landscape context on bat activity. Selected spatial scale (500 m, 1500 m, or 3000 m), parameter estimates, standard error (in brackets) and R^2 are provided. For statistical significance levels a * indicates a significant p value < 0.05, ** highly significant p value < 0.01, and *** very highly significant p value < 0.001. The spatial scale of the selected model is provided in brackets beneath the R^2. Colour and depth of shading indicate the direction and significance of the relationship with deeper blue and deeper red shades indicating more significant positive and negative relationships respectively.

Bat Species	Arable	Broadleaved	Conifer	Improved Grassland
B. barbastellus	-1.61(4.05) 0.40% (3000 m)	-2.94(1.70) 2.11% (500 m)	2.55(1.44) 3.35% (500 m)	-3.86(2.75) 3.36% (1500 m)
E. serotinus	**-3.58(1.79)*** **4.27%** **(1500 m)**	5.87(3.44) 3.53% (1500 m)	3.73(1.96) 3.55% (1500 m)	2.58(2.55) 1.93% (3000 m)
M. daubentonii	4.64(2.50) 1.97% (3000 m)	1.19(1.97) 0.29% (500 m)	**-4.96(1.77)**** **4.81%** **(1500 m)**	**3.73(1.60)*** **3.26%** **(500 m)**
M. mystacinus/brandtii	-5.11(2.83) 5.68% (1500 m)	**30.03(13.83)*** **5.42%** **(3000 m)**	**-36.14(11.42)**** **8.77%** **(3000 m)**	3.55(2.36) 3.31% (1500 m)
M. nattereri	5.01(3.20) 1.51% (500 m)	-2.79(1.44) 2.91% (500 m)	0.91(1.13) 1.06% (500 m)	1.70(2.15) 1.02% (3000 m)
N. noctula	-8.77(4.45) 1.87% (500 m)	2.82(1.78) 1.38% (1500 m)	**3.75(1.07)***** **2.60%** **(1500 m)**	-1.57(1.06) 1.37% (1500 m)
P. auritus/austriacus	-8.43(5.01) 1.87% (500 m)	12.12(6.44) 1.91% (3000 m)	-1.40(0.96) 1.85% (500 m)	-2.71(1.91) 1.59% (3000 m)
P. pipistrellus	**-4.39(2.17)*** **6.27%** **(1500 m)**	21.85(11.92) 5.48% (3000 m)	**5.18(2.18)*** **5.21%** **(1500 m)**	-4.31(2.61) 6.01% (1500 m)
P. pygmaeus	4.01(3.57) 1.17% (3000 m)	**-2.93(0.99)**** **2.22%** **(500 m)**	-10.50(11.28) 1.01% (3000 m)	**5.21(1.23)***** **5.71%** **(500 m)**
Total richness	0.52(1.07) 0.94% (3000 m)	2.99(3.19) 1.98% (3000 m)	1.18(0.73) 4.51% (1500 m)	-0.80(0.49) 4.49% (1500 m)

positive association to broadleaved cover at the 3000 m scale, reflecting preferences found at the stand level in this study. *Myotis daubentonii* and *M. mystacinus/brandtii* can respond positively to irregular silviculture in broadleaved woodlands (Alder et al., 2021) so perhaps the negative association found here with conifer woodlands reflects limited suitable foraging areas and roosting sites (Boonman, 2000; Müller et al., 2012) compared to more open habitats and broadleaved woodland in the landscape.

4.2. Response of bats to habitat features

Total species richness and activity of *P. pygmaeus* had weak and moderate, positive associations with larger mean tree diameter. Trees of greater diameter, including conifer species in our study (Erickson & West, 2003), develop characteristics and micro-habitats, such as snags, cavities and peeling bark, suitable for a wider range of roosting bat species including scarcer species (Kalcounis-Rüppell et al., 2005; Dietz et al., 2018; Paillet, et al., 2018; Singer et al., 2021). The greater spacing between wider trees provides diverse foraging opportunities in cluttered and uncluttered environments, the latter particularly important for edge species like *P. pygmaeus* (Jung et al., 2012; Müller et al., 2012; Charbonnier et al., 2016b; Wood et al., 2017).

Broadleaved canopy cover influences bat populations at multiple spatial scales (Charbonnier et al., 2016a, Charbonnier et al. 2016b; Border et al., 2017; Barbaro et al., 2019), with some species actively selecting broadleaved woodland over conifer woodland (Entwistle et al., 1996). Conifer plantations are often considered poor for bats so we would expect the presence of broadleaf trees to positively influence bat activity within the stands (Charbonnier et al., 2016a; Border et al., 2017). Our study found *M. mystacinus/brandtii* had a strong positive association with broadleaved canopy cover, supporting findings from other studies in the UK (Border et al. 2017). Broadleaved trees provide both foraging and roosting opportunities for bats (Boughey et al., 2011; Singer et al., 2021), which can often be depauperate in even-aged conifer woodlands (Kirkpatrick et al., 2017a). The suitability of broadleaf trees for bats will depend on the woodland structure, proportion and composition of species, and further work is required in our study area to determine this.

Open canopy gaps promote the development of habitats important to bat populations including vertical structure (Renner et al., 2018) and uncluttered areas for edge specialist species to forage (Kaňuch et al., 2008., Erasmy et al., 2021). Total bat richness and the activity of eight bat species (strongly significant for *P. pipistrellus and P. pygmaeus*), more than any other variable in our study, had a positive association with canopy openness, which aligns with similar studies in temperate European Forests (Tillon et al., 2018; Carr et al., 2020a; Alder et al., 2021). In this study we also found *P. pipistrellus* had a weak positive association with vertical structural complexity score. Development of forest vertical structure is facilitated by patchy openings in the canopy allowing light to reach the plantation floor and subsequent understorey development. Canopy gaps are rare in plantations in the UK and limits bat activity to edges (Kirkpatrick et al., 2017a). The variable and patchy canopy openness characteristic of irregular high forest, e.g., Stage 3 stand of our study site, allows edge foraging bats such as *P. pipistrellus and P. pygmaeus* to utilise habitat within the stand interior (Müller et al., 2013; Alder et al. 2021). Open canopy areas and developed vertical structural complexity provide suitable food sources for these species with a high abundance of invertebrates dependent on understorey (Müller et al.,

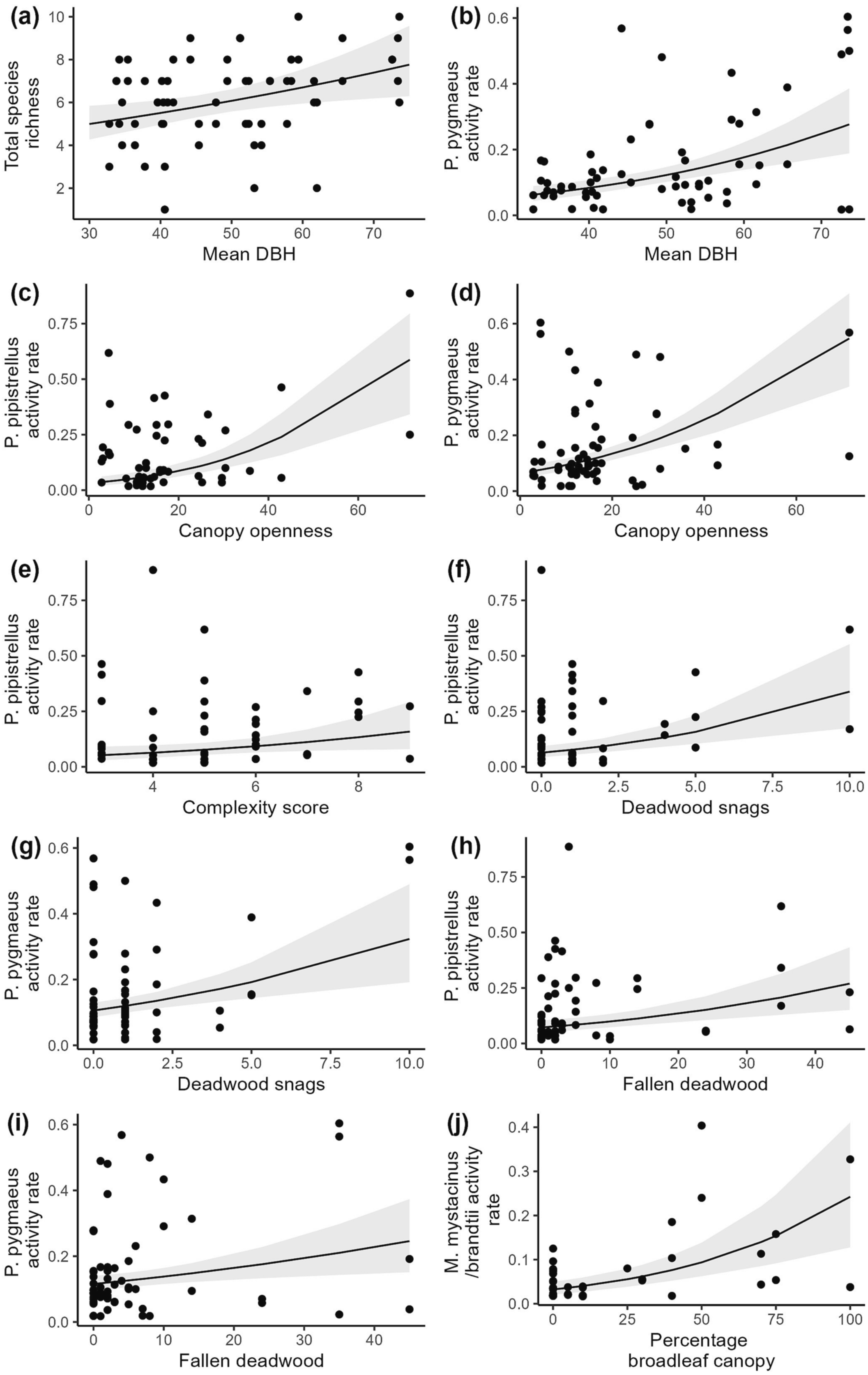


Fig. 4. The response of activity rate of individual bat species and total bat species richness to habitat structural variables.

Table 3
Summary table of the influence of habitat structure on bat richness and activity. Parameter estimates and standard error are provided. For statistical significance levels a * indicates a significant p value < 0.05, ** highly significant p value < 0.01, and *** very highly significant p value < 0.001. Colour and depth of shading indicate the direction and significance of the relationship with deeper blue and deeper red shades indicating more significant positive and negative relationships respectively. A dash is provided where either deadwood snags or broadleaf canopy was removed from the model due to a high correlation (r ≥ 0.7) between these two variables.

Response variable	**Best Fit Model**	**Mean DBH**	**Basal area**	**Canopy openness**	**Complexity score**	**Deadwood snags**	**Distance to edge**	**Fallen deadwood**	**Percentage broadleaf canopy**
Barbastella barbastellus	Conifer 500m	0.16(0.25)	0.12(0.29)	0.47(0.26)	-0.08(0.25)	0.50(0.26)	-0.33(0.23)	-0.13(0.19)	-
Eptesicus serotinus	Habitat only	-0.1(0.26)	0.11(0.26)	0.41(0.21)	0.18(0.29)	-	0.25(0.29)	-0.05(0.22)	-0.08 (0.19)
Myotis daubentonii	Conifer 1500m	-0.07(0.39)	0.11(0.29)	0.21(0.31)	0.29(0.39)	-	0.11(0.38)	-0.05(0.27)	-0.08(0.34)
Myotis mystacinus/brandtii	Habitat only	-0.33(0.20)	-0.23(0.23)	-0.05(0.2)	0.40(0.21)	-	0.20(0.18)	-0.16(0.14)	**0.66(0.14)***
Myotis nattereri	Habitat only	-0.14(0.22)	-0.18(0.22)	0.17(0.17)	-0.09(0.20)	0.06(0.22)	0.03(0.25)	-0.27(0.24)	-
Nyctalus noctula	Grassland 1500m	-0.20(0.12)	-0.20(0.16)	0.14(0.12)	0.13(0.13)	-	-0.002(0.13)	-0.05(0.09)	0.15(0.09)
Pipistrellus pipistrellus	Broadleaf 3000m	0.03(0.19)	0.02(0.18)	**0.76(0.14)***	**0.35(0.17)***	**0.44(0.11)***	**-0.30(0.13)***	**0.41(0.11)***	-
Pipistrellus pipistrellus	Conifer 1500m	-0.09(0.2)	0.007(0.21)	**0.64(0.17)***	0.31(0.21)	**0.40(0.12)****	-0.26(0.14)	**0.41(0.13)****	-
Pipistrellus pygmaeus	Grassland 500m	**0.52(0.12)***	0.18(0.11)	**0.54(0.09)***	0.08(0.12)	**0.29(0.08)****	**-0.27(0.10)****	**0.22(0.08)****	-
Plecotus auritus/austriacus	Habitat only	0.26(0.15)	-0.01(0.16)	0.25(0.16)	0.06(0.14)	-	**-0.43(0.17)***	-0.05(0.13)	0.17(0.11)
Total richness	Habitat only	**0.12(0.04)****	0.05(0.05)	0.09(0.05)	0.06(0.05)	-	**-0.11(0.05)***	-0.003(0.04)	0.02(0.04)

2012; Carr et al., 2020b), which can influence bat activity across the forest area (Kirkpatrick et al., 2017a).

Deadwood availability influences bat activity at it provides roosting locations and foraging opportunities on emergent saproxylic invertebrates (Tillon et al., 2016; Alder et al., 2021). Similar to Tillon et al. (2016) where *P. pygmaeus* responded to fallen deadwood and *P. pipistrellus* to standing deadwood we found both species had a weak to moderate positive association to fallen and standing deadwood. This reflects the ability of these species to use deadwood such as snags and peeling bark for roost locations (Dietz et al., 2018). In the UK *P. pygmaeus* rarely use conifer trees for roosting (Kirkpatrick et al., 2018), although this is likely to reflect the age at which trees are harvested before valuable roosting characteristics develop (Węgiel et al., 2019). Irregular silviculture is a flexible technique that allows the retention of trees with high value deadwood characteristics, which over time is likely to increase roosting opportunities within stand interiors. Contrary to expectations we did not detect associations between other bat species and deadwood availability (Tillon et al., 2016; Dietz et al., 2018; Alder et al., 2021). This reflects the comparatively low volumes of deadwood compared to old growth forests (Müller & Bütler, 2010; Tillon et al., 2016). Studies determining the volume of deadwood required to increase bat activity and roosting in conifer plantations would be extremely valuable (Müller & Bütler, 2010).

The finding that *P. auritus/austriacus* activity was negatively associated with distance from external edges suggests the species is actively using plots closer to major rides and edges within the woodland. This contrasts with habitat use in native broadleaved and conifer woodlands where the woodland interior is preferentially used for foraging around understorey clutter (Entwistle et al. 1996; Murphy et al., 2012; Alder et al., 2021). *Plecotus auritus/austriacus* likely adapts its behaviour to use openings and rides within plantations, a habitat type generally avoided by this species in favour of broadleaved woodland (Entwistle et al. 1996; Ancillotto et al., 2022). Edge habitat in dense conifer plantations provides understorey structure for foraging compared to plantation interiors and increases accessibility by facilitating less energy intensive commuting to stands (Entwistle et al. 1996; Ancillotto et al., 2022). We detected higher activity of *P. auritus/austriacus* in the Stage 3 stand compared to Stage 2, where the understorey is more developed. As the Stage 3 stand continues to develop, *P. auritus/austriacus* activity could increase in the plantation interior in response to the accessible, developing understorey and prey availability (Alder et al., 2021).

4.3. Bat activity across stand development stages

The limited spatial replication of our study with one replicate of each stage type means we interpret our results with caution for this section. It was expected that activity would be higher in the Stage 3 stand, which is further progressed along the transformation continuum towards irregular high forest, due to the presence of habitat features important in influencing bat activity (Jung et al., 2012; Müller et al., 2012). Contrary to our hypothesis bat species richness and activity rates were not higher in stands further along the transformation continuum, except for *P. auritus/austriacus* which had higher activity in the Stage 3 stand than Stage 2. This is likely to reflect (1) the limited spatial replication in our study which if conducted across more sites may allow a difference amongst stand stages to be detected, (2) the differences between stand stages were not completely distinct (Fig. 3), unlike Alder et al. (2021), due to ongoing development with the Stage 3 stands yet to reach equilibrium and (3) the difficulty of selecting a suitable Stage 1 stand in the study area with the chosen stand having more variation than would be predicted in an idealised model (A. Poore pers.comm. 2023). Further studies with higher spatial replication would be extremely useful for determining differences between stand development stages.

5. Conclusions

Conifer plantations can support a surprising level of bat species and activity if managed at low basal areas with an open canopy and developing understorey. Habitat features at the stand level that enhanced the number of bat species and activity in conifer plantations included larger diameter trees, higher canopy cover of broadleaf trees, higher canopy openness and greater quantities of deadwood. The transformation of existing conifer plantations to irregular high forest, alongside existing management techniques, will enhance such habitat features at a local scale and increase habitat heterogeneity at the landscape scale for bat populations. Further work is needed to identify roosting locations in plantations, the importance of the composition, proportion and structure of broadleaf elements within conifer stands and the influence of management in surrounding land cover types adjacent to forest stands.

Funding

This study was funded by donations from Natural England, the Henry

Hoare Charitable Trust, the Barbara Whatmore Charitable Trust and a private individual.

CRediT authorship contribution statement

Patrick Cook: Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Daniel Alder:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – review & editing. **Lisbeth Hordley:** Validation, Formal analysis, Data curation, Writing – review & editing, Visualization. **Stuart E. Newson:** Methodology, Software, Validation, Data curation, Writing – review & editing. **David Pengelly:** Conceptualization, Writing – review & editing.

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.

Acknowledgements

We wish to thank the Stourhead Western Estate and National Trust Stourhead Estate for allowing access to conduct the research, in particular Nick Hoare, Henry Hoare and Kim Portnell. Forest manager, David Pengelly, provided important background information regarding the history of the stands, stand selection for the study and management of the stands. We also thank colleagues at Butterfly Conservation for advice on study design.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121214.

References

Wildlife Acoustics., 2021. Song Meter 3. viewed 5/1/21, <https://www.wildlifeacoustics.com/>.

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

Alder, D.C., Poore, A., Norrey, J., Newson, S.E., Marsden, S.J., 2021. Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland. For. Ecol. Manage. 483, 118786 https://doi.org/10.1016/j.foreco.2020.118786.

Altringham, J.D., 2003. British Bats. Harper Collins, London.

Ancillotto, L., Palmieri, A., Canfora, C., Nastasi, C., Bosso, L., Russo, D., 2022. Spatial responses of long-eared bats *Plecotus auritus* to forestry practices: Implications for forest management in protected areas. For. Ecol. Manage. 506, 119959 https://doi.org/10.1016/j.foreco.2021.119959.

Barbaro, L., Allan, E., Ampoorter, E., Castagneyrol, B., Charbonnier, Y., De Wandeler, H., Kerbiriou, C., Milligan, H.T., Vialatte, A., Carnol, M., Deconchat, M., De Smedt, P., Jactel, H., Koricheva, J., Le Viol, I., Muys, B., Scherer-Lorenzen, M., Verheyen, K., van der Plas, F., 2019. Biotic predictors complement models of bat and bird responses to climate and tree diversity in European forests. Proc. R. Soc. B 286 (1894), 20182193.

Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S.E., Julien, J.-F., Claireau, F., Kerbiriou, C., Bas, Y., Zamora-Gutierrez, V., 2019. Accounting for automated identification errors in acoustic surveys. Methods Ecol. Evol. 10 (8), 1171–1188.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.-D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic Appl. Ecol. 14 (6), 496–505.

Boonman, M., 2000. Roost selection by noctules *(Nyctalus noctula*) and Daubenton's bats *(Myotis daubentonii*). J. Zool. 251 (3), 385–389. https://doi.org/10.1111/j.1469-7998.2000.tb01089.x.

Border, J.A., Newson, S.E., White, D.C., Gillings, S., 2017. Predicting the likely impact of urbanisation on bat populations using citizen science data, a case study for Norfolk, UK. Landsc. Urban Plan. 162, 44–55. https://doi.org/10.1016/j.landurbplan.2017.02.005.

Borkin, K.M., Parsons, S., Russo, D., 2014. Effects of clear-fell harvest on bat home range. PLoS One 9 (1), e86163.

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. https://doi.org/10.1016/j.biocon.2011.06.008.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, 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.

Calladine, J., Bray, J., Broome, A., Fuller, R.J., 2015. Comparison of breeding bird assemblages in conifer plantations managed by continuous cover forestry and clearfelling. For. Ecol. Manage. 344, 20–29. https://doi.org/10.1016/j.foreco.2015.02.017.

Carr, A., Weatherall, A., Fialas, P., Zeale, M.R., Clare, E.L., Jones, G., 2020a. Moths consumed by the Barbastelle *Barbastella barbastellus* require larval host plants that occur within the bat's foraging habitats. Acta Chiropterologica 22 (2), 257–269. https://doi.org/10.3161/15081109ACC2020.22.2.003.

Carr, A., Weatherall, A., Jones, G., 2020b. The effects of thinning management on bats and their insect prey in temperate broadleaved woodland. For. Ecol. Manage. 457, 117682 https://doi.org/10.1016/j.foreco.2019.117682.

Catto, C.M.C., Hutson, A.M., Raccey, 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. https://doi.org/10.1111/j.1469-7998.1996.tb05419.x.

Charbonnier, Y.M., Barbaro, L., Barnagaud, J.Y., Ampoorter, E., Nezan, J., Verheyen, K., Jactel, H., 2016b. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. Oecologia 182 (2), 529–537. https://doi.org/10.1007/s00442-016-3671-9.

Charbonnier, Y., Gaüzère, P., van Halder, I., Nezan, J., Barnagaud, J.Y., Jactel, H., Barbaro, L., 2016a. Deciduous trees increase bat diversity at stand and landscape scales in mosaic pine plantations. Landsc. Ecol. 31 (2), 291–300. https://doi.org/10.1007/s10980-015-0242-0.

Forestry Commission, 2020., Climate Change and Resilient Woodlands, Forestry Commission, viewed 21/1/22. < https://www.gov.uk/government/collections/climate-change-and-resilient-woodlands#:~:text=Even%20with%20very%20ambitious%20actions,be%20part%20of%20our%20response.>.

DEFRA, 2020., *Wild bird populations in the UK 1970 to 2019*. Department for Environment, Food and Rural Affairs, accessed 24.11.21, < https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/938262/UK_Wild_birds_1970-2019_final.pdf>.

Dietz, M., Brombacher, M., Erasmy, 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. https://doi.org/10.3161/15081109ACC2018.20.1.008.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83 (11), 2978–2984. https://doi.org/10.1890/0012-9658(2002)083[2978:IIOPLU]2.0.CO;2.

Ellis, E.C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D.Q., Gill, J.L., Kaplan, J.O., Kingston, N., Locke, H., McMichael, C.N.H., Ranco, D., Rick, T.C., Shaw, M.R., Stephens, L., Svenning, J.-C., Watson, J.E.M., 2021. People have shaped most of terrestrial nature for at least 12,000 years. Proc. Natl. Acad. Sci. 118 (17) https://doi.org/10.1073/pnas.2023483118.

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. https://doi.org/10.1098/rstb.1996.0085.

Erasmy, M., Leuschner, C., Balkenhol, N., Dietz, M., 2021. Shed light in the dark–How do natural canopy gaps influence temperate bat diversity and activity? For. Ecol. Manage. 497, 119509 https://doi.org/10.1016/j.foreco.2021.119509.

Erickson, J.L., West, S.D., 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biol. Conserv. 109 (1), 95–102. https://doi.org/10.1016/S0006-3207(02)00141-6.

FAO & UNEP. 2020. *The State of the World's Forests 2020. Forests, biodiversity and people*. FAO and UNEP, Rome. DOI: 10.4060/ca8642en.

Forest Research Forestry Statistics 2021, Forest Research: Edinburgh 2022 viewed 7/12/21.

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. https://doi.org/10.1002/ece3.1296.

Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011. Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. Biol. Conserv. 144 (9), 2233–2246. https://doi.org/10.1016/j.biocon.2011.05.015.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. Agr Ecosyst Environ 172, 6–15. https://doi.org/10.1016/j.agee.2013.03.019.

Gambles, I., 2019. British Forests: the Forestry Commission 1919–2019. Profile Books, London.

Gili, F., Newson, S.E., Gillings, S., Chamberlain, D.E., Border, J.A., 2020. Bats in urbanising landscapes: habitat selection and recommendations for a sustainable future. Biol. Conserv. 241, 108343 https://doi.org/10.1016/j.biocon.2019.108343.

Gustafsson, L., Bauhus, J., Asbeck, T., Augustynczik, A.L.D., Basile, M., Frey, J., Gutzat, F., Hanewinkel, M., Helbach, J., Jonker, M., Knuff, A., Messier, C., Penner, J., Pyttel, P., Reif, A., Storch, F., Winiger, N., Winkel, G., Yousefpour, R., Storch, I., 2020. Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. Ambio 49 (1), 85–97.

Hartig, F., 2022. DHARMa: residual diagnostics for hierarchical (multi-level /mixed) regression models. R package version (4), 6. https://CRAN.R-project.org/package=DHARMa.

Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Sustainability and Diversity of Forest*. In: Nakashizuka, T. (Ed.), Sustainability and Diversity of Forest Ecosystems. Springer Japan, Tokyo, pp. 361–371.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal: Journal of Mathematical Methods in Biosciences 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Jones, G., 1995. Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. J. Zool. 237 (2), 303–312. https://doi.org/10.1111/j.1469-7998.1995.tb02764.x.

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. https://doi.org/10.1111/j.1365-2664.2012.02116.x.

Kalcounis-Rüppell, M.C., Psyllakis, J.M., Brigham, R.M., 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildl. Soc. Bull. 33 (3), 1123–1132. https://doi.org/10.2193/0091-7648(2005)33[1123:TRSBBA]2.0.CO;2.

Kalda, O., Kalda, R., Liira, J., 2015. Multi-scale ecology of insectivorous bats in agricultural landscapes. Agr Ecosyst Environ 199, 105–113. https://doi.org/10.1016/j.agee.2014.08.028.

Kaňuch, P., Danko, Š., Celuch, M., Krištín, A., Pjenčák, P., Matis, Š., Šmídt, J., 2008. Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). Mamm. Biol. 73 (2), 147–155. https://doi.org/10.1016/j.mambio.2006.12.001.

Kaufmann, S., Hauck, M., Leuschner, C., Gilliam, F., 2018. Effects of natural forest dynamics on vascular plant, bryophyte, and lichen diversity in primeval Fagus sylvatica forests and comparison with production forests. J. Ecol. 106 (6), 2421–2434.

Kent, M., 2011. Vegetation Description and Data Analysis: A Practical Approach. Wiley-Blackwell.

Khanaposhtani, M.G., Kaboli, M., Karami, M., Etemad, V., 2012. Effect of habitat complexity on richness, abundance and distributional pattern of forest birds. Environ. Manag. 50 (2), 296–303. https://doi.org/10.1007/s00267-012-9877-7.

Kirby, K.J., Buckley, G.P., Mills, J., 2017. Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland. Folia Geobot. 52 (1), 5–13. https://doi.org/10.1007/s12224-016-9252-1.

Kirkpatrick, L., Maher, S.J., Lopez, Z., Lintott, P.R., Bailey, S.A., Dent, D., Park, K.J., 2017a. Bat use of commercial coniferous plantations at multiple spatial scales: management and conservation implications. Biol. Conserv. 206, 1–10. https://doi.org/10.1016/j.biocon.2016.11.018.

Kirkpatrick, L., Oldfield, I.F., Park, K., 2017b. Responses of bats to clear fell harvesting in Sitka Spruce plantations, and implications for wind turbine installation. For. Ecol. Manage. 395, 1–8. https://doi.org/10.1016/j.foreco.2017.03.033.

Kirkpatrick, L., Graham, J., McGregor, S., Munro, L., Scoarize, M., Park, K., Yue, B.-S., 2018. Flexible foraging strategies in *Pipistrellus pygmaeus* in response to abundant but ephemeral prey. PLoS One 13 (10), e0204511.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio 41 (7), 720–737. https://doi.org/10.1007/s13280-012-0289-y.

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. https://doi.org/10.1016/j.foreco.2019.04.053.

Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., Konczal, A., Kuuluvainen, T., Mason, B., Motta, R., Pötzelsberger, E., Rigling, A., Schuck, A., 2022. Closer-to-Nature Forest Management. From Science to Policy 12. European Forest Institute. DOI: 10.36333/fs12.

Law, B., Park, K.J., Lacki, M.J., 2016. Insectivorous bats and silviculture: balancing timber production and bat conservation. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham, pp. 105–150.

Mason, W.L., 2000. Silviculture and stand dynamics in Scots pine forests in Great Britain; implications for biodiversity. Investigacion Agraria. Systema y Recursos Forestals 1, 175–197.

Mason, W.L., Kerr, G., Simpson, J., 1999. *What is continuous cover forestry?* Forestry Commission Information Note 29. Forestry Commission, Edinburgh.

Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2022. Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. Forestry: An International Journal of Forest Research 95 (1), 1–12. https://doi.org/10.1093/forestry/cpac008.

McHugh, N.M., Bown, B.L., Hemsley, J.A., Holland, J.M., 2019. Relationships between agri-environment scheme habitat characteristics and insectivorous bats on arable farmland. Basic Appl. Ecol. 40, 55–66. https://doi.org/10.1016/j.baae.2019.09.002.

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. https://doi.org/10.1016/j.foreco.2013.06.043.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129 (6), 981–992. https://doi.org/10.1007/s10342-010-0400-5.

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. https://doi.org/10.1007/s00442-011-2247-y.

Murphy, S.E., Greenaway, F., Hill, D.A., Bennett, N., 2012. Patterns of habitat use by female brown long-eared bats presage negative impacts of woodland conservation management. J. Zool. 288 (3), 177–183.

Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R., 2014. A review of the roles of forest canopy gaps. J. For. Res. 25 (4), 725–736. https://doi.org/10.1007/s11676-014-0521-7.

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. https://doi.org/10.1016/j.biocon.2015.06.009.

Nicholls, B., Racey, P.A., 2006. Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. Behav. Ecol. Sociobiol. 61 (1), 131–142. https://doi.org/10.1007/s00265-006-0244-7.

O'Mara, M.T., Wikelski, M., Kranstauber, B., Dechmann, D.K., 2019. Common noctules exploit low levels of the aerosphere. R. Soc. Open Sci. 6 (2), 181942 https://doi.org/10.1098/rsos.181942.

Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E., Firn, J., 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.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L.U.C., Fuhr, M., Grandin, U.L.F., Kanka, R., 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, **24**(1), pp.101-112, DOI: 10.1111/j.1523-1739.2009.01399.x.

Pecbms PanEuropean Common Bird Monitoring Scheme 2023 viewed 23/2/2023, <https://pecbms.info/trends-and-indicators/indicators/>.

Peura, M., Burgas, D., Eyvindson, K., Repo, A., Mönkkönen, M., 2018. Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. Biol. Conserv. 217, 104–112. https://doi.org/10.1016/j.biocon.2017.10.018.

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77 (1), 27–44. https://doi.org/10.1093/forestry/77.1.27.

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged forest management-what limits global adoption? Forest Ecosystems 2 (1). https://doi.org/10.1186/s40663-015-0031-x.

Rackham, O., 2015. Woodlands. William Collins, London.

C. Reid K. Hornigold E. McHenry C. Nichols M. Townsend K. Lewthwaite M. Elliot R. Pullinger A. Hotchkiss E. Gilmartin I. White H. Chesshire L. Whittle J. Garforth R. Gosling T. Reed M. Hugi viewed 7/12/21, < 2021 Woodland Trust Grantham.

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. https://doi.org/10.1016/j.foreco.2018.02.028.

Roeleke, M., Blohm, T., Kramer-Schadt, S., Yovel, Y., Voigt, C.C., 2016. Habitat use of bats in relation to wind turbines revealed by GPS tracking. Sci. Rep. 6 (1), 1–9. https://doi.org/10.1038/srep28961.

Rosset, C., Brand, R., Wuillemin, E., Gollut, C., Caillard, I., Fiedler, U., 2015. MOTI, forest inventories in the pocket. Forêt-Entreprise 220, 30–33.

C.S. Rowland R.D. Morton L. Carrasco G. McShane A.W. O'Neil C.M. Wood Land Cover Map 2015 (vector 2017 NERC Environmental Information Data Centre GB) 10.5285/6c6c9203-7333-4d96-88ab-78925e7a4e73.

Sanchez, C., 2017. Pro Silva Silviculture: Guidelines on Continuous Cover Forestry/Close to Nature Forestry Management Practices. Forêt Wallonne, Namur, Belgium.

P. Savill High forest management and the rise of even-aged stands C.A.B.I. Publishing Europe's Changing Woods and Forests 2015 London 93 106.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., Mori, A., 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.

Singer, D., Hondong, H., Dietz, M., 2021. Habitat use of Bechstein's Bat (*Myotis bechsteinii*) and woodpeckers reveals the importance of old-growth features in European beech forests. For. Ecol. Manage. 498, 119547 https://doi.org/10.1016/j.foreco.2021.119547.

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, p. 144p.

Tillon, L., Bouget, C., Paillet, Y., Aulagnier, S., 2016. How does deadwood structure temperate forest bat assemblages? Eur. J. For. Res. 135 (3), 433–449. https://doi.org/10.1007/s10342-016-0944-0.

Tillon, L., Langridge, J., Aulagnier, S., 2018. Bat Conservation Management in Exploited European Temperate Forests. In: Bats. IntechOpen, London, pp. 63–79.

Węgiel, A., Grzywiński, W., Ciechanowski, M., Jaros, R., Kalcounis-Rüppell, M., Kmiecik, A., Kmiecik, P., Węgiel, J., 2019. The foraging activity of bats in managed pine forests of different ages. Eur. J. For. Res. 138 (3), 383–396. https://doi.org/10.1016/j.foreco.2009.08.002.

Wilson, S.M.G., 2013. Adoption of alternative silvicultural systems in Great Britain: a review. QJ Forest 100, 279–293.

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. https://doi.org/10.1016/j.biocon.2017.04.001.