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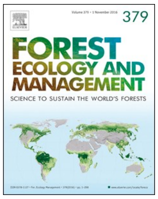

The effects of thinning management on bats and their insect prey in temperate broadleaved woodland

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ABSTRACT

Trees, woods, forests and associated biodiversity are being affected by anthropogenic climate breakdown, and need management to maintain delivery of a wide range of ecosystem services. Wood harvested from sustainably managed woodlands can be used to mitigate greenhouse gas emissions through carbon substitution, directly using biomass for bioenergy to replace fossil fuels or indirectly through the use of wood products instead of higher carbon footprint materials such as concrete and steel. However, it is also important to understand how managing woodlands to mitigate climate change affects biodiversity.

We tested the hypotheses that thinning woodland benefits bats and their insect prey by measuring bat species/species group richness and activity, and insect species/species group richness and biomass in 27 pairs of managed and under-managed broadleaved woodlands, and explored temporal responses to time since management. Sixteen woodland characteristics were measured to investigate how management affected woodlands, and to assess the relative importance of these characteristics to bats and their insect prey.

Woodland thinning significantly reduced five woodland characteristics known to be important for woodland-dwelling bats. Standing dead trees were three times more abundant, and tree cavities five times more frequent in under-managed woodland compared with managed paired sites.

Woodland thinning significantly increased bat richness and activity. Common and adaptable bat species, and those that forage along woodland edges (e.g. *Pipistrellus pipistrellus*), were positively affected by management, presumably exploiting less cluttered woodland interiors. Rarer bat species, and species that roost predominantly in trees (e.g. *Barbastella barbastellus*) were negatively affected by management, which reduced roosting opportunities. Overall bat activity and species richness were relatively low in woodland that had not been thinned for 30 years before increasing. Insect biomass peaked after 30 years of no thinning.

We recommend minimum intervention management to conserve rare bat species in woodlands, although common and adaptable bat species may benefit from intermediate to heavy thinning. Sustainably thinned woodland could be greatly improved for all bats by retaining or mimicking habitat characteristics that are more representative of old growth woodland such as (i) standing dead trees, (ii) tree cavities, (iii) heterogeneous canopy architecture, and (iv) an overall uncluttered below-canopy vegetation with pockets of densely cluttered shrubs.

1. Introduction

Trees, woods and forests, and associated biodiversity are thought to possibly deliver the greatest range of ecosystem services of any habitat type (UKNEA, 2011). However, to continue to do so, they need to adapt to anthropogenic climate breakdown. Woodlands are important wildlife habitat (Myers et al., 2000) and store carbon effectively (Pachauri and Meyer, 2014; Bastin et al., 2019). If woodlands successfully adapt to climate breakdown they can continue to be a part of the solution by mitigating it. Mitigation of climate change by forests is achieved via a combination of carbon sequestration by trees, carbon storage by forest ecosystems, especially soils, and utilisation of forest-derived products. Carbon substitution can also mitigate climate change directly by replacing fossil fuels with bioenergy, and indirectly through use of wood to substitute for higher carbon footprint materials. Reducing fossil fuel use and obtaining energy independence are major drivers for biomass commodity trading (WEC, 2016). Global woodfuel production is 1.86 billion m^3, equating to 50% of total roundwood (wood in its natural

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state as felled) production (FAO, 2018) and biomass derived from wood is becoming more established in industrial-scale electricity production. Managing woodland for conservation value may also use thinning interventions.

The economic and renewable energy benefits of wood-derived products are clear. The European Union recognises the value of biomass and the UK government is aiming to achieve an addition of 2 million tonnes of wood per annum to the wood fuel market by 2020 by bringing 50% of abandoned or under-managed woodland into production (FC, 2007; Renewables Obligation Order, 2015). The potential impact of bringing under-managed woodland into production on wildlife will be most pronounced in countries with low woodland cover due to its relative scarcity within the landscape.

The forestry sector highlights an urgent need for better evidence on which to base wildlife regulations (Starr et al., 2011). A concern is that regulations are deterring active woodland management and the evidence base used to determine how woodland management activities affect wildlife is incomplete, a view recognised by the UK government (Defra, 2012). Despite the acknowledged unknown effect of woodland management on biodiversity, landowners continue to be encouraged to bring under-managed woodland into production including strict forest reserves (Nelson, 2018).

Thinning to transform even-aged, simple structure clearfell and restocking forest stands into continuous cover forestry creates variation in structure, reduces vegetation clutter, creates canopy gaps, and allows sunlight through the canopy (FC, 2017). Woodland thinning is often viewed as beneficial to biodiversity (Defra, 2012; Peterken and Mountford, 2017) and although some taxa including butterflies (Taylor et al., 2013) and some Australian insectivorous bats (Blakey et al., 2016) respond positively to it relatively little is known for other taxa.

Bats account for more than 20% of the world's mammals with 1411 recognised species (Mammal Diversity Database, 2019). All European bats are insectivores and use woodland to some extent (Dietz and Kiefer, 2016) with woodland specialists such as *Barbastella barbastellus* (Schreber 1774) showing high dependence on forested habitats (Russo et al., 2004; Carr et al., 2018). Although forestry practices influence tree roost availability (Russo et al., 2016) and foraging opportunities (Lacki et al., 2007) the impact of thinning on bats needs rigorous scientific testing (Russo et al., 2016). Bats exhibit habitat specialisations making them vulnerable to anthropogenic habitat modification (Russo and Jones, 2015). Changes in woodland management affect the species richness and abundance of temperate bats and species-specific responses are evident (Patriquin and Barclay, 2003; Obrist et al., 2011; Fuentes-Montemayor et al., 2013; Cistrone et al., 2015). Research on the effects of forest thinning on bats in North America is extensive (see Patriquin and Barclay, 2003). In contrast, there has been limited research in Europe (*France*; Bouvet et al., 2016; *Germany*; Mehr et al., 2012; Kortmann et al., 2017; *Italy*; Cistrone et al., 2015). As forestry prescriptions vary globally (Law et al., 2015) more research is needed in Europe, and, as advised by Russo et al. (2010), managers should avoid focussing only on conserving prime habitat (i.e. primary and ancient woodland) and look to improve all woodland. As commercial forestry encroaches on under-managed woodland there is a critical need for applied research to determine the impacts of woodland management on bats, and to identify the woodland characteristics influencing the carrying capacity of bat populations (Russo et al., 2016).

Here we test the prediction that sustainable woodland thinning increases the richness and activity of bats and their insect prey when compared with under-managed (minimum intervention management, management prohibited and abandonment) woodlands. This might be expected if thinning creates more habitat for edge-feeding bats, and a greater range of microhabitats than are present in under-managed woodland. We identify important habitat characteristics that influence bat richness and activity, and investigate the relationship between time since last management and bats using chronosequence analysis.

The terms forest and woodland are interchangeable between countries and regions but typically forests are large continuously wooded areas, and woodlands are smaller fragmented areas (FAO, 2015). All broadleaved habitat in the UK can be considered highly fragmented but otherwise typical of large proportions of north western European broadleaved woodland habitat. In addition, with exceptions such as the New Forest and the Forest of Dean, UK woodland tends to be native broadleaf whereas forest tends to be commercial conifer. Throughout this paper, we use the term woodland and only specify 'forest' when considering particularly large continuously wooded habitat.

2. Materials and methods

2.1. Study area and site selection

Bats and insects were sampled between May 2014 and September 2016 within 27 managed, and 27 under-managed paired broadleaved woodlands in southern England and Wales (Fig. S1). The landscape consists of mosaic, fragmented habitats in an agricultural matrix within a temperate oceanic climate. All study sites were broadleaved woodland as categorised by the Forestry Commission Forestry Standard (FC, 2017), i.e. each site had a canopy cover of 20% or more with a minimum area of 0.5 ha with broadleaved trees accounting for at least 20% or more of the total tree cover, and conifer trees accounting for less than 10% of total tree cover. Sites consisted of upland or lowland broadleaved woodland and included *Quercus* spp. or *Fagus sylvatica* as the dominant species. The average woodland size was 86 ha (± 66 SD) with the minimum size of 10 and maximum 200 ha. Woodland sites were identified using a requested shape file of 'large natural reserves' supplied by the Forestry Commission. This was filtered to identify sites that were broadleaved woodland (as categorised above) and had areas that met 'managed' and 'under-managed' criteria (as described below). Site visits and discussions with woodland managers further identified suitable sites.

Each woodland was divided into management plots and categorised as managed or under-managed following UK Forestry Commission descriptions (FC, 2017) as follows:

1. Managed woodland: certified as sustainably managed (UKWAS, 2017). Management consisted of systematic thinning on 10–15 year rotations by intermediate to heavy thinning with retention of 55% to 65% canopy cover. Clear felling, small group felling or traditional woodland management (i.e. coppicing) were not included.
2. Under-managed woodland: had not received any systematic management for ≥ 20 years and included (i) neglected woodland, (ii) research sites i.e. management was strictly forbidden except for fencing to control for grazing, (iii) natural reserves i.e. no felling or planting of trees (UKWAS, 2017) and (iv) minimum intervention managed woodland i.e. no systematic felling or planting of trees. Permitted management included fencing, control of exotic plant species and vertebrate pests, maintenance of paths and rides and safety work.

Distance between pairs was minimum 250 m and maximum 1 km to increase the likelihood of recording independent data while ensuring similar geographic and landscape characteristics. Independence has been considered as adequate for distances as low as 200 m for bats along river systems (Vaughan et al., 1996). Woodland (or woodland plot) sizes were selected to be of similar size with the largest difference being six hectares. Pairing in this way controls for environmental factors because comparisons were made on the same nights within pairs and, therefore, weather, geographic location, landscape barriers and variation in landscape characteristics are similar within paired sites.

2.2. Bat and insect sampling

Bats were sampled during dry nights (> 5 °C) using static bat detectors. Echolocation calls were recorded using Song Meter SM2BAT recorders (one unit simultaneously in each woodland pair) (Wildlife Acoustics, Concord, USA) connected to SMX-US ultrasonic microphones mounted on a tree 2 m from the ground. Uncompressed WAV recordings were made from dusk until dawn through continuous monitoring for five nights at each site using the following settings: high pass filter 16 kHz; sampling frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 s; and trigger level 12 dB. An echolocation pass was documented and analysed when a series of echolocation calls lasting up to 15 s with less than 1 s inter-pulse duration were recorded.

Pipistrellus spp. calls were identified to species using automated software identification (BatClassify; https://bitbucket.org/chrisscott/batclassify). To ensure reliability 10% of *Pipistrellus* spp. calls were randomly selected and manually identified using BatSound 4.1.4 (Pettersson Elektronik, Uppsala Science Park, Sweden). All other recordings were manually identified using BatSound and assigned to species or genus using call parameters in a guide to the echolocation calls of British bat species (Russ, 2012). Ambiguous *Pipistrellus* calls with frequencies of most energy at 51 kHz, *Myotis* spp. and *Plecotus* spp. could not be confidently assigned to species and grouped by genus. 'Bat richness' therefore refers to species richness, although *Plecotus* spp. and *Myotis* spp. were included as single taxa. For consideration of responses of guilds, bats were categorised as short-range (SRE; including *B. barbastellus*, *Myotis* spp. and *Plecotus* spp.), mid-range (MRE; including *P. pipistrellus* and *P. pygmaeus*) and long-range echolocators (LRE; including *E. serotinus* and *N. noctula*) (Schnitzler et al., 2003; Froidevaux et al., 2016) (see Table 1 in Frey-Enrenbold et al. (2013) for details).

To consider the influence of potential prey on bat richness and activity insects were sampled in each woodland for one night using portable heath light traps with 6 W 12 V actinic bulbs (Sylvania, Wilmington, US) powered with 12 V batteries, activated 15 min after sunset and turned off at dawn. Light traps were deployed on the same nights as bat surveys but positioned approximately 20 m away from the acoustic bat detectors to avoid interference (Froidevaux et al., 2018). Insects were euthanased, stored at −18 °C, identified, dried to a constant weight at 60 °C for 48 h and weighed with a 0.1 mg readability Mettler Toledo AE200 analytical balance (Mettler Toledo LLC, Columbus, US). 'Insect richness' was measured with moths identified to species, beetles identified to genus, trichopterans identified to order, and dipterans identified to family.

2.3. Survey of woodland characteristics

To obtain comparable woodland characteristic variables, two 20 × 20 m quadrants were delimited within each woodland interior ($n = 108$). Measured characteristics included (i) tree height and standard deviation of tree height, (ii) basal area per hectare, (iii) illuminance, (iv) roosting opportunity, (v) temperature, and (vi) vegetation characteristics (Table S1). Each tree within a quadrant were (i) identified to species, (ii) classified as live or dead, (iii) measured for height, and (iv) surveyed for cavities using x10 magnification binoculars. Vegetation clutter was measured between 0 and 4 m in height at each point. Following a procedure used by Smith and Gehrt, (2010) and Lintott et al. (2015) a four-metre pole with sixteen 0.25 m subsections marked on it was placed at each of the 18 points. Any vegetation touching a subsection was counted and summed to provide a measure of clutter from 0 to 100%. Illuminance and temperature was measured at each of the 18 points during the day and one hour after sunset using a PeakTech 5025 lx meter (PeakTech, Ahrensburg, Germany) and a thermometer. Variation in weather conditions between sites was controlled by surveying on days considered not to be extreme i.e. high winds, rain or hot days. Shrub cover was assessed visually using the Domin scale. Floral richness was measured within two 2 × 2 m quadrants within each of the 20 × 20 m quadrant ($n = 216$). Recorded floral species included all woody and non-woody plants within the ground and field layer. To investigate the effect of time since last management on bats we identified the last documented systematic thinning intervention using a combination of site management plans provided by Forestry Commission and Woodland Trust and by communicating with woodland managers. Communication with each woodland manager proved important as thinning interventions often differed from adaptive management plans without being recorded as such.

2.4. Statistical analysis

2.4.1. Management type and woodland characteristics

To explore whether woodland characteristics differed significantly between managed and under-managed woodlands we undertook univariate analyses. Paired t-tests were performed for parametric data while permutation tests (10,000 randomisations) were performed for non-parametric data. To determine which woodland characteristics in combination were different between managed and under-managed woodlands, we performed generalized linear mixed models (GLMMs) using maximum likelihood estimations with a binary predictor variable (managed or under-managed) and a logit link function (lme4 package; R core team). Woodland pair was included as a random effect. Multicollinearity was assessed prior to model building using Spearman's correlation tests using a $|r| > 0.6$ coefficient threshold. Insect richness and biomass were highly correlated. Insect richness was removed from analysis as we considered insect biomass as a more suitable measure of prey availability. All other measured woodland characteristics were included as response variables (see Table 2 for measured woodland characteristics). To provide meaningful comparisons of effect size, data (x) were standardised by their means (μ) and standard deviation (σ) using the formula $(x - \mu)/\sigma$. To identify the most parsimonious model that also explained the largest amount of variance, Akaike's Information Criterion adjusted for small sample sizes (AICc) was used. A final model with only variables from the best fitting models using delta AICc ($\Delta I) \leq 2$ was selected.

2.4.2. Management, bats and their insect prey

To explore whether insect richness and biomass differed significantly between managed and under-managed woodland we undertook univariate analyses. To determine the influence of management type on response variables (i) bat richness and activity, (ii) species or species group activity, and (iii) insect richness and biomass, and to explore which of the measured predictor variables (i) management type, and (ii) measured woodland characteristics contributed most to explaining any observed differences in response variables, we performed a series of GLMMs with an appropriate distribution (i.e. Poisson or negative binomial family to handle overdispersion). Multicollinearity was assessed prior to model building, as were any non-linear relationships between response variables (e.g. bat richness) and predictor variables (e.g. vegetation clutter). Predictor variables considered to have a non-linear relationship with response variables (time since management) were analysed separately and those deemed to be highly correlated to one or more other predictor variables (insect richness) using Spearman's correlation $|r| > 0.6$ coefficient threshold were removed from analysis (see Section 2.4.1 for further model construction and assessment).

Nyctalus leisleri, Rhinolophus ferrumequinum, R. hipposideros, and ambiguous *Pipistrellus* spp. calls were not analysed as their overall detection between sites was considered sporadic (i.e. detection occurred in less than 50% of the 27 sites). The predictor variable 'time since management' had a non-linear relationship with response variables and was analysed separately (see Section 2.4.3. Time since management).

Table 1

Guild and species-specific bat activity (number of bat passes) in 27 paired managed and 27 under-managed broadleaved woodlands including the total number of sites each species or species group was recorded.

Taxa	Managed woodland	Unmanaged woodland	Total bat passes	% total passes	Number of paired sites
Pipistrellus pipistrellus[MRE]	16,369	3,997	20,366	62.28	27
Pipistrellus pygmaeus[MRE]	4,673	3,183	7,856	24.03	27
Myotis spp.[SRE,†]	1,357	862	2,219	6.79	27
Nyctalus noctula[LRE]	183	721	904	2.76	22
Barbastella barbastellus[SRE]	46	558	604	1.85	14
Plecotus spp.[SRE,††]	121	367	488	1.49	18
Eptesicus serotinus[LRE]	71	13	84	0.26	14
Rhinolophus hipposideros[SRE]	48	35	83	0.25	13
Nyctalus leisleri[LRE]	30	35	65	0.20	12
Rhinolophus ferrumequinum[SRE]	9	13	22	0.07	10
Pipistrellus spp.[MRE,†††]	7	1	8	0.02	4
TOTAL	22,914	9,785	32,699	100	

[†] Includes *M. alcathoe*, *M. bechsteinii*, *M. brandtii*, *M. daubentonii*, *M. mystacinus* and *M. nattereri* as identified from call features that could not be confidently categorised to species level.

[††] Includes *P. auritus* and potentially *P. austriacus* that could not be confidently identified to species level from call features.

[†††] Includes *P. pipistrellus*, *P. pygmaeus*, and *P. nathusii* that could not be confidently identified to species level from call features.

[SRE] Short-range echolocators.

[MRE] Mid-range echolocators.

[LRE] Long-range echolocators.

2.4.3. Time since management

To determine the influence of time since last management on bats and insects we performed a series of Generalized Additive Mixed-Effect Models (GAMMs; "gamm4" package; Wood and Scheipl, 2017) with a smooth term (See Section 2.4.1 for further model construction and assessment). The relationship between each response variable and time since management was plotted using model predictions.

All measurements of central tendency are presented as means ± SDs unless otherwise stated. Data distribution was tested for normality using Shapiro-Wilk tests prior to univariate analyses, and for all model 'response' variables. These tests determined which univariate analysis tests were used (permutation or t-test) and selected GLMM/GAMM distribution. All analyses were performed with R 3.3.2 (R Core Team 2013).

3. Results

3.1. Bat and insect sampling

Bat passes were recorded in managed ($n = 22,914$; average per site = 856 ± 1037) and under-managed woodland ($n = 9785$; average per site = 385 ± 498) (Table 1). *Pipistrellus pipistrellus* was detected most frequently and dominated the bat assemblage with 62% of all passes. Woodland specialist bat species including *Barbastella barbastellus* were recorded regularly i.e. at 14/27 sites. The mean number of insects captured per site was 28 (± 17) for managed and 41 (± 40) for under-managed woodland. Most insects (97%) were moths. Insect biomass was significantly greater in under-managed (median 0.8 ± 0.6 g IQR) than in managed woodland (median 0.3 ± 0.2 g IQR) ($n = 54$, perm, $p < 0.001$).

3.2. Management type and woodland characteristics

Univariate analysis identified seven of the 16 measured variables to be significantly different between managed and under-managed woodland (Table 2). Generalized linear mixed models ($\Delta I \leq 2$) identified basal area per hectare ($p = 0.004$), number of cavities ($p = 0.015$), amount of vegetation clutter ($p = 0.011$) and number of standing dead trees ($p = 0.007$) as significantly greater in under-managed woodland (Table S2). In contrast, day temperature was

Table 2

Habitat variables recorded from managed ($n = 27$) and under-managed ($n = 27$) woodland (refer to Table S1 for detail). Values of central tendency for normally distributed variables (+) are presented as mean ± standard deviation, and for non-normally distributed variables (−) as median ± inter-quartile range. ** $p < 0.01$ *** $p < 0.001$. ns = not significant. SD = standard deviation. lx = lux.

Variable	Managed woodland	Unmanaged woodland	p value	Distribution
Basal area per hectare[†]	16 ± 7	47 ± 24	***	+
Clutter (%)	22 ± 17	49 ± 23	***	+
Floral richness	5 ± 3	5 ± 3	ns	–
Invertebrate biomass (g)	0.3 ± 0.2	0.8 ± 0.6	***	–
Light level (day) (lx)	4069 ± 3496	1542 ± 2085	**	–
Light level (night) (lx)	0.0 ± 0.1	0.0 ± 0.0	ns	–
Management type	Categorical	Categorical	–	–
Number of cavities	3 ± 4	15 ± 13	***	–
SD tree height	2 ± 1	3 ± 1	ns	–
Shrub cover (%)	36 ± 38	36 ± 42	ns	–
Shrub richness	3 ± 1	2 ± 1	ns	–
Number of standing dead trees	0 ± 0	1 ± 1	***	–
Temperature (day) (°C)	21 ± 2	19 ± 2	ns	–
Temperature (night) (°C)	17 ± 1	16 ± 1	ns	–
Last thinning (years)	7 ± 5	44 ± 20	***	–
Tree height (m)	19 ± 2	18 ± 3	ns	+

[†] Basal area per hectare is a function of the number of trees and the size of trees. This measure of overall competition between trees is used to determine a thinning intervention.

Table 3
List of habitat variables from the best generalized linear mixed effects models ($\Delta I \leq 2$) relating to management type and habitat characteristics for guild and species-specific bat activity and insect richness (number of species/species groups) and biomass, including marginal R^2 (variance explained by the fixed effects only), effect size, standard error, z statistic and *p* value. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$. ns = not significant. Positive effects are plus numbers and negative effects are minus numbers in the effect size column.

Response variable	Independent variable	Effect size	± SE	z	*p*
Bat richness	Basal area per hectare	0.2	0.1	2.2	*
Marginal R^2: 0.17	Light level (day) (lx)	0.2	0.1	2.2	*
	Management	0.3	0.2	2.2	*
Bat activity					
All bats	Deadwood	0.4	0.2	1.9	ns
Marginal R^2: 0.46	Light level (day) (lx)	0.5	0.2	2.2	*
	Management	1.2	0.4	2.9	**
B. barbastellus[SRE]	Cavity	0.6	0.1	4.7	***
Marginal R^2: 0.56	Deadwood	0.3	0.1	3.0	**
	Light level (night) (lx)	0.9	0.2	4.4	***
	Management	−1.3	0.3	−4.5	***
	Shrub richness	0.4	0.2	2.9	**
Myotis spp.[SRE]	Clutter (%)	−0.7	0.2	−4.1	***
Marginal R^2: 0.25	Deadwood	0.4	0.2	2.5	*
	Shrub richness	0.4	0.2	2.8	**
Plecotus spp.[SRE]	Deadwood	0.6	0.3	2.4	*
Marginal R^2: 0.53	Management	−0.8	0.5	−1.6	ns
P. pipistrellus[MRE]	Light level (day) (lx)	0.5	0.2	2.2	*
Marginal R^2: 0.31	Management	1.5	0.3	4.4	***
	SD tree height	0.3	0.2	1.8	ns
	Temperature (night) (°C)	−0.4	0.8	−2.3	*
P. pygmaeus[MRE]	Cavity	0.5	0.2	2.3	*
Marginal R^2: 0.38	Light level (day) (lx)	0.3	0.2	1.5	ns
	Management	0.8	0.5	1.6	ns
E. serotinus[LRE]	Management	1.9	0.6	2.8	**
Marginal R^2: 0.32					
N. noctula[LRE]	Deadwood	0.9	0.3	3.1	**
Marginal R^2: 0.29	Light level (day) (lx)	0.6	0.3	2.2	*
	Management	−0.2	0.5	−0.4	ns
Insect					
Biomass	Clutter (%)	0.2	0.1	2.9	**
Marginal R^2: 0.32	Temperature (night) (°C)	−0.2	0.1	−3.2	**
	Tree height (m)	−0.1	0.1	−2.4	*
Richness	Clutter (%)	0.2	0.1	2.0	*
Marginal R^2: 0.38	Shrub cover (%)	−0.3	0.1	−3.2	**

[SRE] Short-range echolocators.
[MRE] Mid-range echolocators.
[LRE] Long-range echolocators. lx = lux.

significantly lower in under-managed woodland ($p = 0.038$) (Table S2).

3.3. Management, bats and their insect prey

Bat richness ($p = 0.029$), overall bat activity ($p = 0.003$), *P. pipistrellus* ($p < 0.001$) and *E. serotinus* ($p = 0.004$) activity were all positively influenced by management, and *P. pygmaeus* activity showed a positive trend. In contrast, *B. barbastellus* activity ($p < 0.001$) was negatively influenced by management, and *Plecotus* spp. and *N. noctula* showed negative trends (Table 3).

The number of standing dead trees positively influenced *B. barbastellus* ($p = 0.003$) (Fig. 1), *Myotis* spp. ($p = 0.011$) and *N. noctula* ($p = 0.002$) (Fig. 1) activity, and overall bat activity, and *Plecotus* spp. activity showed a positive trend. The number of available cavities positively influenced *B. barbastellus* ($p < 0.001$) (Fig. 1) and *P. pygmaeus* ($p = 0.024$) activity (Table 3).

Higher light levels positively influenced bat richness ($p = 0.020$), overall bat activity ($p = 0.016$), *B. barbastellus* ($p < 0.001$) (Fig. 1) (night levels only), *P. pipistrellus* ($p = 0.026$) and *N. noctula* ($p = 0.031$) activity, and *P. pygmaeus* activity showed a positive trend (Table 3).

Shrub species richness positively influenced *B. barbastellus* ($p = 0.004$) and *Myotis* spp. ($p = 0.005$) activity. Temperature negatively influenced *P. pipistrellus* activity ($p = 0.022$). *P. pipistrellus* activity also showed a positive trend in relation to increasing tree height standard deviation. Vegetation clutter negatively influenced *Myotis* spp. activity ($p < 0.001$) (Fig. 1) but positively influenced insect richness ($p = 0.042$) and biomass ($p = 0.003$) (Fig. 1). Night temperature negatively influenced insect biomass ($p = 0.007$). Tree height negatively influenced biomass ($p = 0.047$) and shrub cover negatively influenced insect richness ($p = 0.001$) (Table 3).

3.4. Time since last management

When assessing the influence of time since last management (1–65+ years), the best models predicted non-linear relationships with some response variables (Fig. 2). Bat species richness ($p = 0.016$) and overall bat activity levels ($p = 0.009$) initially started to decrease before increasing after 40 years of no management as did *P. pipistrellus* ($p < 0.001$), *P. pygmaeus* ($p = 0.003$), and *E. serotinus* ($p = 0.002$) activity. The relationship for all bat activity remained similar even after *Pipistrellus* data were removed (data not shown). *B. barbastellus* ($p < 0.001$) and *Plecotus* spp. ($p < 0.001$) activity showed a more linear increase in activity after management. Insect biomass ($p = 0.002$) and richness ($p = 0.001$) both initially increased after management although richness then began to fall after peaking at 15 years to a minimum at 50 years (Fig. 2).

4. Discussion

4.1. Influence of management type on woodland characteristics

Woodland thinning significantly altered basal area per hectare, number of dead trees and tree cavities, temperature and below-canopy clutter. Changes in these habitat characteristics influence the activity of woodland-dwelling bats (Obrist et al., 2011; Fuentes-Montemayor et al., 2013; Cistrone et al., 2015). From a forestry perspective 67% of the surveyed under-managed woodlands were fully stocked (i.e. stands where basal area is above the threshold value at which thinning is normally recommended, see Matthews and Mackie, 2006; FC, 2015), requiring thinning, making them suitable targets for extracting wood for use as biomass.

Per hectare standing dead trees were three times greater in under-managed woodland (4.9 ± 3.8 IQR) than in managed woodland (1.6 ± 0.7 IQR); and the number of cavities more than five times higher in under-managed woodland (37.5 ± 32.6 IQR) than in managed woodland (7.5 ± 10 IQR). Thinning therefore might degrade the quality of woodland for some bat species by limiting opportunities for protection, sociality and reproduction (i.e. roosting opportunity). Our finding that management reduces tree cavities is also evident in holm oak (*Quercus ilex*) woodlands where the density of trees with cavities has been observed 13 times higher in ageing woodland stands (> 90 years) than in recently cut stands (< 30 years) (Regnery et al., 2013). The importance of roosting opportunities for woodland-dwelling bats is evident in *B. barbastellus*, which selects roost sites within woodlands that possess relatively high frequencies of tree cavities (Russo et al., 2004; Carr et al., 2018).

Natural broadleaved forests are structurally heterogeneous (Bauhus et al., 2009). Managed European woodlands have historically been even-aged stands (Russo et al., 2016). We found that in managed woodland, canopy heterogeneity, shrub richness and cover, and floral richness were comparable with values for under-managed woodland. This highlights a positive outlook for sustainable forestry advancements for managing biodiversity and *P. pipistrellus* was indeed positively influenced by canopy heterogeneity, as occurs in *Pipistrellus* spp. in Germany (Renner et al., 2018).

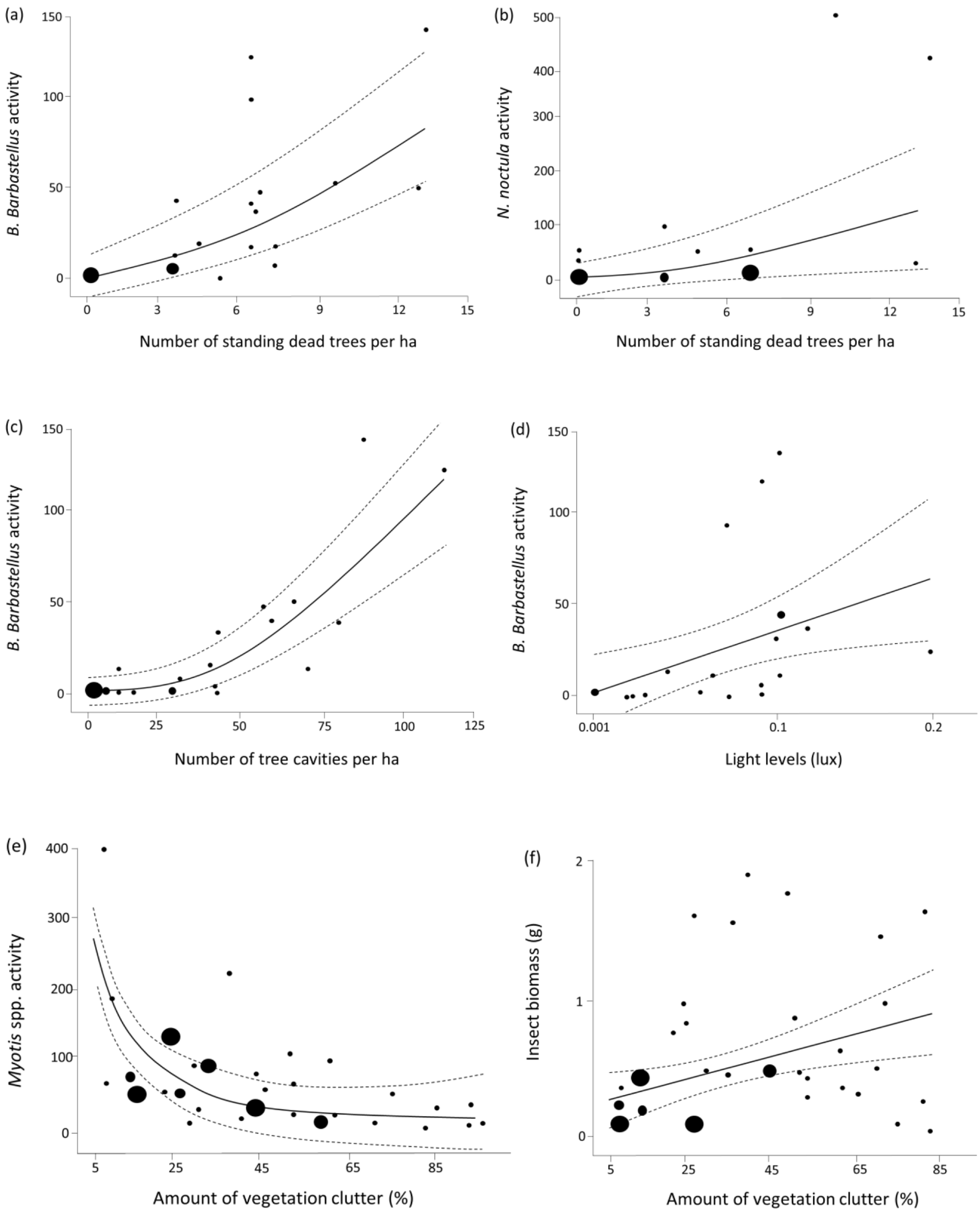

Fig. 1. Predicted relationships from the best Generalized Linear Mixed Models (GLMMs) between highly significant variables (a) *B. barbastellus* activity ($p < 0.01$); and (b) *N. noctula* activity ($p < 0.01$) and number of standing dead trees per hectare; (c) *B. barbastellus* activity and number of tree cavities per hectare ($p < 0.001$); (d) *B. barbastellus* activity and light levels ($p < 0.001$); and (e) *Myotis* spp. Activity ($p < 0.001$); and (f) Insect biomass activity ($p < 0.01$) and percentage of below-canopy vegetation clutter. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. Original data (number of passes recorded) are superimposed as black circles with diameter proportional to the number of sampling points where mean values occurred.

4.2. Influence of management type on bats and their insect prey

Bat richness and overall activity increased in managed woodlands probably because uncluttered understorey vegetation provided opportunity for edge and open foraging bats, in addition to woodland interior specialists. Increased bat richness in response to management has been observed in sweet chestnut (*Castanea sativa*) orchards in southern Switzerland (Obrist et al., 2011) and activity has shown to increase in managed loblolly pine (*Pinus taeda*) and shortleaf (*P. echinata*) forests in the US (Loeb and Waldrop, 2008) and at some sites in Italian high

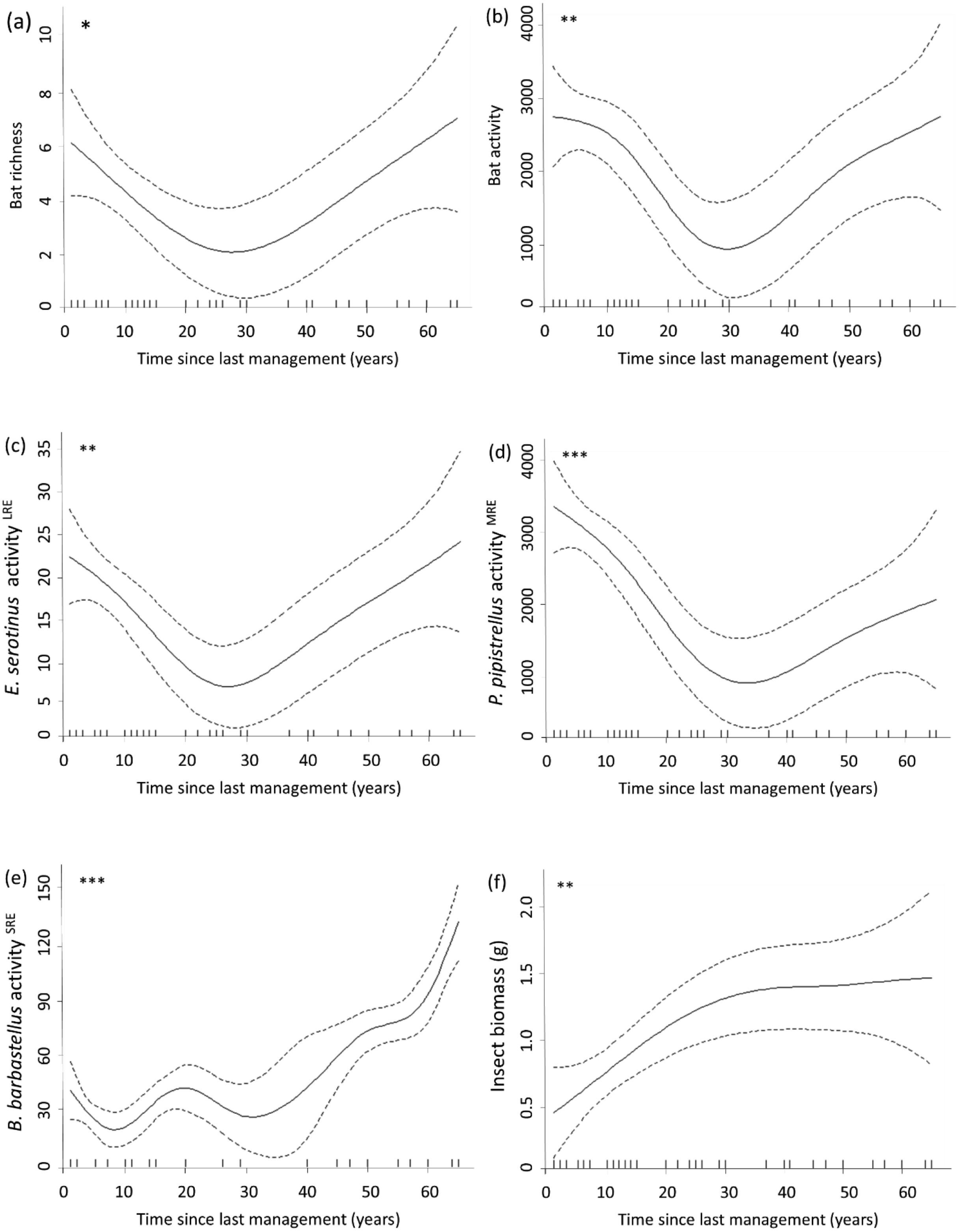

Fig. 2. Predicted significant relationships from the best generalized additive models (GAMMs) between (a) bat richness (number of species/species groups); (b) bat activity; (c) *P. pipistrellus* activity; (d) *P. pygmaeus* activity; (e) *E. serotinus* activity; (f) *N. noctula* activity; (g) *B. barbastellus* activity; (h) *P. auritus* activity; (i) insect biomass; (j) insect richness (number of species/species groups) and time since last systematic thinning intervention. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. The distribution of data points is represented by vertical lines on the x-axis. Significance values are taken from generalized additive mixed models (GAMMs) with woodland pair (managed and under-managed) as a random effect. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$. $^{\mathrm{SRE}}$short-range echolocator, $^{\mathrm{MRE}}$mid-range echolocator, $^{\mathrm{LRE}}$ long-range echolocator.

forests (Cistrone et al., 2015).

We found commonalities in bat responses to woodland characteristics. Overall activity and more than half of all bat species activity increased in relation to the amount of standing dead trees and number of available tree cavities. In agreement with Kirkpatrick et al. (2017) (*Pipistrellus* spp. in conifer plantations in Scotland), Russo et al. (2010) (*B. barbastellus* in beech woodlands in Italy) and Rueegger et al. (2018) (woodland dwelling bats in France), it is likely that roost availability, rather than other factors such as prey availability, constrains levels of bat activity in many wooded habitats. Indeed, we found prey availability did not influence activity at any level (i.e. family, genus or species). The hypothesis proposed by Russo et al. (2010) that increasing prey abundance alone is not a key factor for bat conservation in woodland habitats seems valid.

Bat species richness, overall activity and many bat species were positively influenced by increasing light. This can be interpreted in two ways; first that light penetrating the upper canopy will influence the temperature of tree roosts below, and second that increasing light below the canopy is directly related to the openness of the canopy. Although *B. barbastellus* is known to regulate roost temperature through socio-thermoregulatory behaviour (Russo et al., 2017) bats often select day roosts based, in part, on their thermal properties. Consequently, the amount of light within a woodland interior may influence roost use and activity (i.e. bats moving to and from roosts and engaging in social behaviour around a roost).

The more abundant and adaptable *P. pipistrellus* strongly influenced our statistical output when all bats were grouped together. Suggesting that thinning a woodland will be positive to all bats is misleading and habitat suitability studies for bats should be made at the species level when possible, or using guilds based on ecomorphology (Law et al., 2015) or echolocation call traits (Russo et al., 2016).

4.2.1. Species-specific responses

Short-range echolocators. *B. barbastellus* activity was greater in under-managed woodland, in fact they were often unrecorded in managed woodland. In central Italy both male and female *B. barbastellus* have been captured more often in under-managed woodland (Russo et al., 2010). At the landscape scale *B. barbastellus* is predicted to avoid production forests and favour dense areas of native woodland (Rebelo and Jones, 2010). We found *B. barbastellus* activity increased when the number of available cavities, the number of standing dead trees and light levels increased. In combination, these characteristics influence the amount and quality of roosting opportunity within woodland, which is the probable driver of woodland suitability for this species (Russo et al., 2004; Carr et al., 2018). Indeed, *B. barbastellus* activity increases in woodlands with relatively open canopies (Kortmann et al., 2017) and maternity roosts occur below gaps in the canopy (Carr et al., 2018).

Myotis spp. activity decreased as vegetation clutter increased suggesting their ability to deal with 'clutter' echoes (Schnitzler et al., 2003) from surrounding vegetation is limited. In contrast, the gleaning *Myotis nattereri* may benefit from a dense understorey clutter (Fuentes-Montemayor et al., 2013). This disagreement is probably due to grouping bats that frequently glean prey from vegetation with bats that often hunt by aerial hawking (e.g. *M. mystacinus*) (Siemers and Swift, 2006). The relatively low explanatory power of the *Myotis* spp. model further suggests that within-group diversity in wing morphology and echolocation traits potentially confounds interpretation of data for bats in the genus*Myotis*.

Plecotus spp. activity was greater in under-managed woodland with increasing quantities of standing dead trees. Thinning may be detrimental to interior hunting species such as *Plecotus auritus* by reducing clutter and presumably limiting the surfaces on which it can glean prey (Russo et al., 2016). We found that variation in vegetation clutter, shrub cover or species, floral richness or insect biomass did not explain activity, leaving the amount of standing dead trees as the only predictor variable among those measured.

Short-range echolocating bat activity was often greater in under-managed woodland and positively affected by the availability of standing dead trees and number of tree cavities. The density of tree cavities and number of standing dead trees sufficient to support populations of woodland dwelling bats are major knowledge gaps in bat conservation (Law et al., 2015; Russo et al., 2016). Our results suggest that woodland managers should aim to have higher amounts of standing deadwood than the minimum threshold 20 m^3 per hectare value recommended by current guidelines (e.g. UKWAS, 2017).

Mid-range echolocators. *P. pipistrellus* activity was greater in managed woodland with a relatively open and heterogenic canopy architecture. Canopy ruggedness increases *P. pipistrellus* activity (Froidevaux et al., 2016) and Müller et al. (2013) observed *Pipistrellus* spp. regularly foraging above the canopy in closed canopy mature woodland. *P. pygmaeus* responded positively to the number of available tree cavities which suggests *P. pygmaeus* continues to rely on roosts within trees in addition to roosts within buildings and may explain why the abundance of *P. pygmaeus* and not *P. pipistrellus* decreases with proximity to urban areas (Lintott et al., 2015).

Relatively open and structurally diverse canopy architecture is important for mid-range echolocating bats that often forage at habitat edges. Indeed, bats in this guild have shown to exploit the upper canopy of heterogeneous high forests, presumably to forage (Müller et al., 2013; Froidevaux et al., 2016).

Long-range echolocators. Long-range echolocating bats varied in their responses to management. The tree dwelling *N. noctula* negatively responded to management and positively responded to the amount of standing dead trees and increasing below canopy light levels, showing that roosting opportunity and possibly ambient temperature (determined through solar radiation) at roosting sites are drivers for their presence. In contrast, *E. serotinus* (a species rarely found roosting in trees (Tink et al., 2014)) was more active in less cluttered thinned woodland that provides foraging opportunities for larger bats, as observed in the relatively large *Eptesicus fuscus* (Cox et al., 2016) and open space foraging bats in Germany (Jung et al., 2012).

4.2.2. Insect responses

Although univariate analysis found insect biomass was significantly greater in under-managed woodland, linear modelling did not identify management type as affecting either biomass or richness. Insect richness and biomass increased with vegetation clutter, which was significantly higher in under-managed woodland. Captured insects consisted mostly of Lepidoptera (97%), hence our findings suggest that moths benefit from substantial amounts of below-canopy vegetation clutter. Fuentes-Montemayor et al. (2013) found the same response to clutter by flies. Generally then, woodlands with dense understorey vegetation are important habitats for prey of insectivorous bats.

Dense, below-canopy vegetation clutter may reduce predation pressure on insects by aerial insectivores such as bats and birds, although the increased abundance of insects at more cluttered sites is more probably the consequence of increased foliage providing more food for insect larvae (Root et al., 2017) or creating large amounts of suitable micro-habitat and micro-climate for insects (Merckx et al., 2012).

4.3. Influence of time since management on bats and their insect prey

Bat richness and activity followed non-linear temporal relationships; richness and activity was initially high in recently thinned uncluttered woodland, followed by a decrease in early succession cluttered woodland, followed by increases in reduced clutter, later stage, successional woodland. A reduction in bat activity and richness as habitat complexity increases has been observed in urban green spaces in

Austria (Suarez-Rubio et al., 2018) and similar non-linear temporal relationships have been observed in open forest foraging birds such as the Capercaillie (Braunisch et al., 2019). Woodlands often possess high levels of vegetation clutter below their canopies at 30 years of succession (Adams et al., 2009; Peterken and Mountford, 2017). The activity of LRE and MRE bats was minimal at and around 30 years after no management.

In contrast, insect richness and biomass started at a relatively low level, before peaking between 20 and 30 years after management supporting the hypothesis that insect richness and biomass may peak in woodlands with dense understorey vegetation.

Plecotus spp. and *B. barbastellus* activity did not reduce during early successional stage periods, instead showing a more linear increase in activity once management had stopped. The level of activity corresponds with increases in the number of trees with cavities in woodlands (Regnery et al., 2013) a likely causal association. In agreement with Adams et al. (2009) and Obrist et al. (2011) we suggest that thinning has a profound influence on bats which is best evidenced through the change in bat richness and activity over time once thinning management has ceased. We did not assess bat activity and richness, or insect richness and biomass prior to thinning.

5. Practical implications

While it is possible to extract woody biomass material by forestry thinning and increase bat richness and activity, rare woodland specialist bats benefit from abandoned and under-managed woodland. We consider the following recommendations as the most suitable and wide-ranging approach for bat conservation in temperate broadleaved woodland in Europe.

1. Encourage minimum intervention management

All bat species responded well to woodland characteristics that form in later successional stage woodlands including numerous standing dead trees and trees with cavities as a result of age or damage, an open canopy as a result of gap dynamics, heterogeneous canopy architecture and a reduction in overall below-canopy vegetation clutter. Promoting the natural succession of woodland using minimum intervention management will help to deliver sustained benefits by allowing the gradual development of these old growth characteristics, particularly for rarer bat species.

2. Improve production woodland

In agreement with Russo et al. (2010) we need to improve the value of intensively managed woodland for bats and our findings show some bat species respond positively to thinning. The characteristics that form in ancient woodland are well known and these characteristics may be achieved through managing woodland to facilitate natural succession. We believe that old growth woodland characteristics can be achieved in production woodlands independent of woodland habitat type. We recommend woodland managers should (i) increase the amount of bat roosting opportunity by using positive selection (i.e. removing trees that directly compete with trees marked to remain) over negative selection (i.e. removing all undesirable trees) during thinning operations, (ii) action forestry techniques that increase tree crevices in the long term such as ‘ring barking’ and use artificial bat habitat boxes in the short term (Griffiths et al., 2017), (iii) promote a relatively open and heterogeneous canopy that will allow light penetration though the canopy to warm roosts, encourage a species rich understorey and provide foraging opportunity at the canopy, and (iv) reduce overall below-canopy clutter to provide opportunity for open and edge foraging species to exploit the woodland interior, while leaving pockets of dense understorey clutter to benefit insects.

3. Improve plantation forests

Encourage the occurrence of minimal intervention forest patches in forest landscapes used for production such as planation forests. The creation of minimal intervention islands may act as stepping stones for woodland specialist bats as well as source hotspots from which bats and other forest organisms might colonise surrounding exploited forest.

6. Authors’ contributions

AC, GJ and AW designed the study and secured funding. AC collected and analysed field data. AC drafted the manuscript. GJ and AW edited the manuscript.

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

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