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Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey

Elisa Fuentes-Montemayor*, Dave Goulson, Liam Cavin, Jenny M. Wallace, Kirsty J. Park

Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, Scotland, FK9 4LA, UK

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ABSTRACT

Agricultural expansion has led to the widespread destruction of habitats and the creation of fragmented landscapes. Woodland has been severely affected by habitat loss; remaining woodland is often highly fragmented and degraded, immersed in an agricultural matrix. Woodland is one of the most important habitats for bats because it offers roosting and feeding opportunities for many species. A number of agri-environment schemes aim to increase the amount and quality of woodland on agricultural land; however, little is known about how woodland character relates to bat abundance/activity and recommendations for woodland creation and management for foraging bats are scarce. We studied temperate bat communities and examined bat foraging activity and relative abundance (and insect prey availability) in 34 woodland fragments in agricultural landscapes using two complementary methods (acoustic monitoring and trapping assisted by an acoustic lure). We evaluated the relative importance of woodland vegetation character, patch configuration and surrounding landscape in order to assess the importance of local- vs. landscape-scale woodland management to bat populations. Bat abundance and activity were influenced by both local and landscape-level attributes. At the local scale, woodland vegetation character appeared more important than patch configuration. High activity levels of aerial hawkers (e.g. *Pipistrellus* species) were related to low tree densities and an open understory, while gleaning species (e.g. *Myotis* bats) showed the opposite trend. Areas of cluttered vegetation were associated with high insect (mostly Diptera) abundance and could act as sources of prey for certain bat species. Bats' responses to the surrounding landscape depended on species mobility. For relatively low mobility species (e.g. *Pipistrellus pygmaeus*), local woodland character was more important than the landscape context, whereas the opposite was observed for higher mobility species (e.g. *Pipistrellus pipistrellus* and *Myotis* bats). Higher bat activity levels were observed in small and isolated woodland fragments, and in sparsely wooded landscapes. This may reflect a more intensive use of woodland in landscapes where this habitat is scarce, where woodland creation should be prioritised. Woodland management and creation schemes should encourage habitat heterogeneity to fulfil the requirements of different bat species.

1. Introduction

Agricultural expansion has led to the widespread destruction of habitats and the creation of fragmented landscapes. Forest systems have been severely affected by habitat loss and their cover has been reduced by ca. 50% worldwide in the last three centuries (Groom et al., 2006). Remaining woodlands are often highly fragmented and degraded, consisting of a large number of relatively small and isolated patches immersed in an agricultural matrix. Vegetation structure and spatial configuration are usually altered in fragmented woodlands, which can affect biological communities by e.g. creating dispersal barriers and edge effects (Groom et al., 2006). Although species responses to habitat fragmentation are variable (depending on life-history traits such as specialisation and mobility; Groom et al., 2006), this process is regarded by many as one of the greatest threats to biological diversity (e.g. Fahrig, 2003).

Woodland is one of the most biologically diverse systems on Earth and one of the most important habitats for bats because it offers roosting and feeding opportunities for many species (Lacki et al., 2007). Therefore, worldwide deforestation has resulted in many bat species suffering severe population declines (Mickleburgh et al., 2002). Woodland vegetation structure is of great importance in determining habitat quality and availability for bats. Although the concept of 'quality' depends on the specific requirements of a particular species, in general, mature hardwood forest stands with high availability of large diameter snags,

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* Corresponding author. Tel.: +44 01786 467009.
E-mail address: ef12@stir.ac.uk (E. Fuentes-Montemayor).

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dense canopy cover and reduced clutter (e.g. low tree density and understory cover) are often associated with high bat activity levels because they provide roosting and foraging opportunities for bats (Lacki et al., 2007).

The configuration and extent of a woodland patch can also have a strong influence on bat communities. Island biogeography theory (IBT; MacArthur and Wilson, 1967) suggests that the number of species inhabiting an island depends on its size and isolation. Its conceptual framework has been extended from real islands to terrestrial ecosystems in order to understand the effects of habitat loss and fragmentation on biodiversity. Patterns of bat species richness on real islands are consistent with those predicted by IBT (i.e. positively related to area and negatively related to isolation; Frick et al., 2008). In terrestrial ecosystems, however, large woodland patches do not necessarily support more species or larger populations of bats than small patches (Law et al., 1999; Estrada and Coates-Estrada, 2002). Relatively small woodland fragments may provide roosting opportunities and support populations of many bat species, especially if they are located relatively close to other fragments and have a high structural diversity (Estrada and Coates-Estrada, 2002; Meyer and Kalko, 2008; Boughey et al., 2011). However, the response of bats to woodland fragmentation can vary between species. Fast-flying species adapted to forage in uncluttered environments are relatively tolerant to habitat fragmentation, and may show higher abundance and activity levels in small and isolated fragments (Estrada-Villegas et al., 2010) or in sparsely wooded landscapes (Klingbeil and Willig, 2009). In contrast, slow-flying and highly manoeuvrable species are usually more sensitive to habitat isolation and show positive associations with woodland availability (Law et al., 1999; Meyer and Kalko, 2008). Roosting ecology and edge-affinity have also been identified as good predictors of bat species' sensitivity to habitat fragmentation; 'woodland interior' species (often tree-roosting bats) are negatively affected by fragmentation, as opposed to species which show affinity for woodland edges (often roosting in human-made structures; e.g. Meyer et al., 2008). Many bat species are highly mobile; therefore, it is likely that they will be influenced not just by the local character of a woodland patch, but also by the surrounding landscape at relatively large spatial scales (e.g. within 5 km; Klingbeil and Willig, 2009).

As a consequence of long-term deforestation, woodland cover in the United Kingdom (UK) has been drastically reduced. At the beginning of the 20th century woodland comprised a mere ca. 5% of the UK's land area, but programmes of afforestation over the last 50 years have increased this figure to approximately 12% (Mason, 2007). Much of this consists of forestry plantations, which in many cases have low species richness and structural diversity, and which provide fewer roosting and feeding opportunities for bats than ancient semi-natural woodland (Altringham, 2003; but see Mortimer, 2006). The remaining woodland is highly fragmented and consists of a large number of relatively small patches (<100 ha) within agricultural landscapes (Watts, 2006). Currently in the UK, a number of agri-environment schemes (AES; financial incentives used in Europe and North America for farmers to adopt less intensive, environmentally-sensitive agricultural practices) aim to increase the amount and quality of woodland on agricultural land. Despite the importance of woodland habitat for all UK bat species (e.g. Walsh and Harris, 1996; Vaughan et al., 1997), little is known about how woodland character relates to prey availability and bat abundance and diversity (but see Hill and Greenaway, 2008). To date, most studies assessing the effects of woodland character and fragmentation on bats have been conducted in tropical ecosystems and/or predominantly forested areas, and only rarely in farmland-dominated landscapes where the effects of woodland fragmentation are likely to be stronger (Andrén, 1994). As a result, recommendations for the creation and management of farm woodland to improve habitat for wildlife in many temperate countries seldom take the needs of bats and their insect prey into consideration; therefore, management guidelines for bats are scarce, and the ones that exist focus on creating/maintaining roosting opportunities rather than enhancing good foraging habitat (Anonymous, 2005; but see Entwistle et al., 2001). Furthermore, studies that investigate the effect of woodland character at several spatial scales, incorporating local character and surrounding landscape effects on bat populations are few (e.g. Erickson and West, 2003).

Here, we assess the response of a temperate bat community, and their insect prey, within an agricultural landscape to woodland fragmentation at several spatial scales. In particular, we address four specific questions:

1. Does insect prey availability relate to woodland characteristics and, if so, to which specific attributes?
2. Do bat abundance and activity levels relate to woodland vegetation character (e.g. tree density) and patch configuration (size and shape) and, if so, to which specific attributes?
3. Does the surrounding landscape (e.g. proportion of woodland cover) influence bat abundance and activity levels in woodland patches and, if so, to what spatial extent?
4. What is the relative importance of woodland vegetation character, patch configuration and surrounding landscape for bats (i.e. is local management of woodlands sufficient to enhance bat populations or is a landscape-scale management approach important)?

We expect certain bat species to be more strongly affected by woodland fragmentation than others, according to differences in their ecology (Table 1). In addition, we expect the relative importance of woodland vegetation character, patch configuration and surrounding landscape to differ between bat species: lower mobility species should be more influenced by the local habitat (e.g. vegetation character), and by patch isolation, compared to higher mobility species which may be more affected by landscape factors at large spatial scales.

2. Methods

This work was conducted in the same sites and parallel to a study assessing the influence of woodland character on moth assemblages. Therefore, only essential information on site selection and vegetation survey methods is presented here; for further details see Fuentes-Montemayor et al. (2012).

2.1. Site selection and study design

Thirty-four woodland patches of different size (0.1–30 ha) and shape (ranging from compact to complex) within agricultural land in central Scotland, UK (Appendix A) were surveyed for vegetation, nocturnal insects and bats once during the summers of 2009 (June to August, 20 sites) and 2010 (May to July, 14 sites). Woodlands consisting purely of conifer plantations were excluded from the site selection process because they are often composed mainly of exotic tree species and are of comparatively low conservation value to biodiversity (Mason, 2007). Bat surveys and nocturnal insect sampling occurred simultaneously and were only conducted in dry weather, when temperature was $\geq 8\,^{\circ}$C and wind force $\leq$ Beaufort scale 4.

2.2. Tree vegetation surveys

Surveys were conducted along transects 100 m in length (number of transects per site depended on woodland size) with points

Table 1
Scoring system used to quantify the expected effect of woodland fragmentation on different bat species common in Scotland, according to their ecological traits (scored as 1 = weak, 2 = moderate, 3 = strong[a]). Overall scores range from 4 to 12 (4–6 = weak, 7–9 = moderate, 10–12 = strong). Consulted references indicated as superscript letters are as follows: [e] Altringham (2003); [f] Dietz et al. (2009); [g] Entwistle et al. (1996); [h] Kapfer et al. (2008); [i] Nicholls and Racey (2006); [j] Smith and Racey (2008).

Bat species[b]	Foraging habitat preference[e,f]		Foraging ecology[e,f]		Roosting ecology[e,f]		Mobility[d]		Expected effect of woodland fragmentation	
P. pipistrellus	Ubiquitous (woodland, water, hedgerows, grassland, farmland, suburban and urban areas)	1	Aerial hawking	1	Mainly buildings; also tree holes	1	3700 m [i]	2	Weak	5
P. pygmaeus[c]	Mainly riparian woodland and water; woodland edge, tree lines, hedges, suburban gardens and parks also used	2	Aerial hawking	1	Buildings and tree holes	2	2300 m [i]	3	Moderate	8
M. daubentonii	Over water bodies; woodland and parkland also used if located nearby water.	2	Gleaning from water surface and aerial hawking	2	Tree holes, underground sites and occasionally buildings. Always close to water	2	3500 m [h]	2	Moderate	8
M. nattereri	Mainly woodland; occasionally parkland and gardens	3	Gleaning from vegetation and aerial hawking	2	Buildings and tree holes	2	6000 m [j]	1	Moderate	8
P. auritus[c]	Mainly woodland; occasionally parkland and gardens	3	Gleaning from vegetation	3	Trees and old buildings close to wooded areas	3	2800 [g]	3	Strong	12

[a] Score criteria for 'foraging habitat preference': 1 for 'ubiquitous' species, 2 for species frequently using woodland, 3 for species strongly dependent on woodland; for 'foraging ecology': 1 for aerial hawkers, 2 for species hunting by both aerial hawking and gleaning, 3 for gleaning species; for 'roosting ecology': 1 for species frequently roosting outside woodland, 2 for species using woodland and non-woodland habitats, 3 for species strongly associated with woodland; for 'mobility': 1 for species travelling > 5000 m from roosts, 2 for >3000 m from roosts, 3 for <3000 m from roosts.

[b] *P. nathusii*, *M. mystacinus*, *N. noctula* and *N. leisleri* are also present in Scotland, but are classed as uncommon or rare (Bat Conservation Trust, 2010).

[c] Classed as UK Biodiversity Action Plan (BAP) priority species (Joint Nature Conservation Committee, 2011).

[d] Maximum straight-line distance a bat has been recorded from a roost during foraging trips.

established every 15 m to assess tree density and understory cover (%). In addition, canopy cover (%) was assessed using a sighting tube with an internal crosshair; if the crosshair intersected canopy vegetation, presence of canopy was recorded (Jennings et al., 1998). This was repeated 10 times at 1 m intervals perpendicular to each of the transect-points. Vegetation surveys were conducted no more than two weeks before the nocturnal surveys.

2.3. *Nocturnal insect sampling*

Diptera and Lepidoptera are amongst the most important components in the diet of bat genera commonly present in the study area (Table 1), the former being the main component in the diet of *Pipistrellus* bats and an important component in the diet of *Myotis* bats, and the latter being also an important constituent in the diet of *Myotis* bats and the main component in the diet of *Plecotus* bats (Vaughan, 1997). Diptera were collected using a 9-in.-diameter Johnson–Taylor insect suction trap (Johnson and Taylor, 1955) operated at the maximum speed (1500 rpm), powered by an electric generator and positioned >30 m from the woodland edge. To avoid disturbance to bats from the noise produced by the electric generator, the suction trap was located at sufficient distance (i.e. where the generator could not be heard by surveyors nor recorded by ultrasonic detectors) from the bat trapping points described in Section 2.4. The trap was activated 15 min after sunset and switched off 4 h later. After the surveys, the collecting cone was removed from the trap and placed in a sealed zip-lock bag; insects were euthanized by dropping a cotton pad soaked with ethyl acetate into the bag and left overnight. Insects were later placed in sample bottles and stored in 70% ethanol for later identification to Order (suborder for Diptera) following Chinery (1993). Lepidoptera were surveyed as described by Fuentes-Montemayor et al. (2012); results relating to the influence of woodland character on this group are presented therein.

2.4. *Bat surveys*

Bat surveys started 45 min after sunset to avoid peak emergence times for different bat species (and therefore avoid recording bats commuting to feeding sites) and finished 4 h later. Two complementary methods (sound recording and trapping) were simultaneously used to assess species presence, bat abundance and bat activity at each woodland patch.

2.4.1. *Sound recording and analysis*

Bat activity was assessed using a frequency division bat detector (Anabat SD1, Titley Electronics) mounted on a 1 m high pole with the microphone pointing upwards. The detector was positioned in the interior of each woodland patch (as far away from the edges as possible) and moved between four different points (≥20 m from each other; located adjacent to the trapping points described in Section 2.4.2; Fig. B.1 in Appendix B) every 30 min to maximise the area surveyed. We analysed all bat recordings manually using AnalookW (Corben, 2006). We identified bat species and counted total numbers of bat passes (defined as at least two echolocation calls within 1 s of each other; Walsh and Harris, 1996). There are four bat genera present in the study area (*Pipistrellus*, *Myotis*, *Nyctalus* and *Plecotus*; Richardson, 2000), and all can be identified based on characteristics of their search-phase echolocation calls. The *Pipistrellus* species present in the UK can be distinguished on the basis of the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben, 2006) of their search-phase echolocation calls. However, in the other cases it is difficult to distinguish between species within a genus due to similarities in call structure (especially in cluttered environments; Schnitzler and Kalko, 2001). Such is the case for the *Myotis* (*Myotis daubentonii*, *Myotis nattereri* and *Myotis mystacinus*) and *Nyctalus* (*Nyctalus noctula* and *Nyctalus leisleri*) species found in the area. These species were identified to genus level for analysis. *Plecotus* is represented by only one species in the area (*Plecotus auritus*), but it is rarely recorded because of its quiet echolocation calls. Therefore, for *Myotis*, *Nyctalus* and *Plecotus* species the best way to confirm their presence within a site is by capturing and examining individuals in the hand.

2.4.2. *Bat trapping*

Bats can be extremely difficult to capture in woodlands. Therefore, an acoustic lure for bats – a bat call synthesiser (the Sussex AutoBat; Hill and Greenaway, 2005) – was used. This lure, which only attracts bats in the immediate vicinity (<20 m), offers huge potential for surveying bats in conditions under which ultrasonic detectors perform poorly (e.g. cluttered woodland) and species with quiet echolocation calls (Hill and Greenaway, 2005). An Austbat harp trap (2.4 m × 1.8 m) and three mist nets (2.4 m × 6 m each) were located in the interior (as far away from the edges as possible) of the woodland patch $\geq$ 20 m from each other (Fig. B.1 in Appendix B). The AutoBat was positioned next to one of the nets/trap and moved along to the next one every 30 min in a sequence that ensured it was not playing at the same trap as the bat detector was recording. Four different synthesised bat call types (which were switched every 15 min and played in the same order every night) were used to attract a wide variety of bat species (F. Greenaway, personal communication). All nets were checked every 15 min to extract any captured bats, which were then identified to species (following Dietz and von Helversen, 2004), sexed, aged, weighed and temporarily marked by fur clipping; morphometric measures, pictures and ultrasonic recordings were taken before releasing each bat to aid with species identification. We used numbers of bats captured as a relative index of their abundance within woodlands (hereafter referred to as 'bat abundance'). Occasionally (seven times), bat surveys lasted <4 h due to heavy rain or malfunction of the AutoBat's internal battery (minimum survey length = 2 h). Data from bat activity and bat captures were combined to obtain records of species presence for each woodland patch.

In addition, point counts (10 min duration) were conducted at different locations within and around each woodland patch using a frequency division bat detector (Anabat SD1, Titley Electronics) to compare bat activity at the woodland interior, edge and surrounding matrix (pasture/arable; >20 m from the woodland edge). At each patch, an equal number of point counts were conducted at the interior (as far away from the edges as possible) and the edge of the woodland; the total number of points per site depended on the size of the woodland; 2 interior, 2 edge and 2 matrix points were used for patches of 0.1–3 ha, 3 interior, 3 edge and 2 matrix points for patches of 3–10 ha, and 4 interior, 4 edge and 2 matrix points for patches of 10–30 ha (Fig. B.2 in Appendix B). These point counts were conducted simultaneously to the bat recording and trapping described in Sections 2.4.1 and 2.4.2. Bat recordings were analysed as described in Section 2.4.1.

2.5. *Landscape analysis*

We used ArcGIS 9.2 (ESRI Inc., 2006) to create circles of 250, 500, 1000, 1500, 2000, 2500 and 3000 m radii around the centre of each woodland patch. The smallest of these scales represents site-specific characteristics, whereas the others cover the home ranges of low (e.g. *P. auritus*) and intermediate (e.g. *P. pygmaeus*) mobility species; the largest scale approximates an upper limit to home range sizes of more mobile bat species (e.g. *P. pipistrellus*; Entwistle et al., 1996; Nicholls and Racey, 2006). We used data from OS MasterMap Topography Layer (EDINA, 2010) to reclassify the landscape within each circle into five biotopes: (i) urban areas (buildings, structures and roads); (ii) farmland; (iii) water (inland and tidal water); (iv) semi-natural environment (rough grassland, scrub and scattered trees); and (v) woodland (coniferous, deciduous and mixed trees). Despite potential differences in habitat suitability for bats, different woodland types were grouped together into a single category. Patches of one type are often adjacent to (or immersed in) patches of a different type; therefore, the calculation of fragmentation metrics (see below) for particular woodland types would not result in useful information. We used Fragstats 3.3 (McGarigal et al., 2002) to calculate the proportion of land covered by each biotope and a landscape heterogeneity index (Shannon diversity) within each circle. Based on published literature on bat ecology, we considered 'woodland' and 'water' as the most important biotopes for bats; we therefore calculated an additional selection of landscape metrics for these two biotopes, including largest patch index (LPI, percentage of the landscape comprising the largest patch of a type), Euclidean nearest neighbour distance (ENN, mean value of ENN distances between all patches of a type within the landscape) and total edge density (ED, the sum of the lengths of all woodland edge segments divided by the total landscape area; calculated for woodland only).

2.6. *Data analysis*

Statistical analyses were conducted using R version 2.11.1 (R Development Core Team, 2010) and the packages lme4 and MASS. We constructed Generalised Linear Models (GLMs) to determine the influence of woodland character on bats and nocturnal insects. For nocturnal insects, we used total abundance per site ($n = 32$ due to breakdown of the generator on two occasions) as a response variable. For bat abundance and activity, we used mean values per survey hour as response variables ($n = 34$); mean values resulting in decimal places were re-scaled (i.e. rounded-up to the nearest integer) and expressed in bins (e.g. 0–1, 1–2, 2–3 bat captures per hour). This allowed for the data to be treated as counts. All continuous variables were standardised following Schielzeth (2010) in order to allow meaningful comparisons of the relative importance of predictors within a model. Models were fitted using Poisson errors when the response variables were counts (e.g. bat abundance/activity; negative binomial errors were used if count data were overdispersed; Table 2) and binomial errors for species presence-absence data (Crawley, 2007). Based on previous knowledge on the ecology of woodland bats, we selected the following potential explanatory variables to be included in the starting models: (i) vegetation character variables: woodland type (broadleaved or broadleaved-conifer mix), tree density, understory cover (%), canopy cover (%), surrounding matrix type (arable, pastoral or mixed) and presence/absence of in-site grazing, and (ii) patch configuration variables: woodland patch shape (patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area; equals 1 when the patch is maximally compact and increases as shape becomes more irregular; McGarigal et al., 2002) and a woodland proximity index (focal patch area (m^2) divided by the edge-to-edge distance squared (m^2) between the focal patch and the nearest patch $\geq$ 0.2 ha; log transformed to achieve a better fit; modified from McGarigal et al., 2002). 'Year' was included as a factor to account for potential variation between the two sampling periods. Date and temperature at sunset were included as covariates. A correlation matrix of all potential explanatory variables (excluding landscape metrics) was created to check for possible collinearity between predictors (Pearson correlation coefficient $\leq$ 0.6 in all cases). A backwards step-wise model selection approach based on AIC was adopted (Zuur et al., 2009). All models were validated by visual examination of residuals (e.g. plotting residuals vs. fitted values to check for constant variance; Crawley, 2007). These models are referred to as 'woodland character' models hereafter.

Table 2
Summary table showing the influence of woodland character and landscape context on bats and nocturnal insects. Parameter estimates (±SE; standardised for continuous variables) and models' goodness of fit (model R^2) are shown. Directions of effects for categorical variables are discussed in the text. Significance codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$, '·' $p \leq 0.1$, "–" $p \geq 0.1$. The influence of the surrounding landscape was only assessed for bats; these values are not available (NA) for insect abundance.

Response variable	Vegetation character									
	Model error[a]	Year	Date	Temp	Matrix type	Grazing	Wood type	Tree density	Canopy cover	Understory cover
Insect abundance[b]	NB	−0.63 (0.31)*	0.37 (0.16)*	–	–	–	−0.51 (0.27)$^{\cdot}$	0.32 (0.13)*	−0.52 (0.13)***	0.50 (0.14)***
P. pipistrellus (activity)	NB	2.03 (0.46)***	–	–	$A > (M = P)^{***}$	3.17 (0.53)***	–	–	–	−0.47 (0.23)*
P. pygmaeus (abundance)	P	–	–	0.32 (0.13)*	–	–	–	–	–	–
P. pygmaeus (activity)	NB	1.40 (0.41)***	0.52 (0.20)*	0.33 (0.17)$^{\cdot}$	–	–	1.11 (0.37)**	−1.04 (0.21)***	–	–
Myotis spp. (abundance)	P	–	–	–	–	0.97 (0.52)$^{\cdot}$	–	0.49 (0.16)**	–	–
Myotis spp. (activity)	NB	–	0.29 (0.17).	0.34 (0.20)$^{\cdot}$	–	1.68 (0.41)***	–	0.51 (0.16)**	–	–
P. auritus (presence)	B	–	–	–	–	–	1.23 (0.73)$^{\cdot}$	–	–	–

Response variable	Patch configuration			Landscape			
	Wood proximity	Wood shape	Model $R^{2\,a,c}$	Most relevant metrics (scale)	Parameter estimates (SE)	Significance of model fit Δ[d]	Model $R^{2\,a,d}$
Insect abundance[b]	–	–	45.8%	NA	NA	NA	NA
P. pipistrellus (activity)	–	–	67.7%	Woodland % (3 km)	−0.85 (0.23)	**	76.6%
P. pygmaeus (abundance)	–	–	15.8%	–	–	–	–
P. pygmaeus (activity)	−0.61 (0.18)***	–	62.0%	Heterogeneity (250 m) Water LPI (2 km)	−0.48 (0.17) 0.30 (0.16)	*	69.3%
Myotis spp. (abundance)	–	–	27.6%	Water ENN (1.5 km)	0.35 (0.20)	.	36.4%
Myotis spp. (activity)	−0.41 (0.20)*	–	57.6%	Wood LPI (2 km) Urban % (3 km)	−0.63 (0.36) −0.52 (0.24)	**	72.9%
P. auritus (presence)	–	–	64.7%	Semi-natural % (250 m)	−0.89 (0.63)	.	70.6%

[a] For models with a Poisson (P) or negative binomial (NB) error distribution R^2 = (deviance explained by model/null deviance) × 100 (Zuur et al., 2009). For binomial (B) models R^2 = proportion of correct predictions of presence/absence derived from the model (a probability of 0.5 was used as a cut-point threshold; >0.5 = presence; <0.5 = absence; Fielding and Bell, 1997).

[b] Refers to nocturnal insects collected with suction trap (mostly Diptera). See Appendix C for details.

[c] R^2 values for 'woodland character' models.

[d] R^2 values and significance of change in model fit after incorporating landscape metrics into the 'woodland character' models.

The effect of the surrounding landscape on bats was assessed in two steps: firstly, linear regression analyses were used to evaluate the effect of the surrounding landscape on bats. Individual models (one for each landscape parameter at each spatial scale) were constructed and R^2 values calculated to quantify the amount of variation in the data explained by each landscape parameter. These models are referred to as 'landscape' models hereafter and were used to select the most important landscape parameter at the most important spatial scale (i.e. highest R^2 value) for each response variable. This approach was followed given the high degree of collinearity between landscape metrics (i.e. between different biotope types, and between proportions of one particular biotope type and its fragmentation metrics) within and across different spatial scales. When several landscape parameters seemed equally important (i.e. < 5% difference from the highest R^2 value) they were all selected, providing they were not strongly correlated (Pearson correlation coefficient < 0.6 and $p > 0.05$ used as threshold). For strongly correlated variables, only the parameter with the highest R^2 value (from 'landscape' models) was selected. We then added the selected landscape parameters to the final 'woodland character' models (see above) and compared the models without any landscape metrics against the new models incorporating landscape metrics to assess whether they provided a better fit to the data, based on differences in deviance values between models (χ^2 tests; Zuur et al., 2009).

In addition, Generalised Linear Mixed-effects Models (GLMMs; Zuur et al., 2009) with a Poisson error distribution were conducted to assess differences in bat activity between woodland interior ($n = 96$), woodland edge ($n = 96$) and surrounding matrix ($n = 68$). 'Location' – interior, edge or surrounding matrix – and 'year' were included in the model as fixed factors, whereas 'site' was used as a random factor (to account for variation between sites). Date and temperature were included as covariates. Because the number of point counts per site depended on 'location' and the size of the woodland, this value was included in this model as an offset. The total number of bat passes (for each species/genus) per 'location' was used as a response variable ($n = 102$; i.e. 3 types of 'location' × 34 woodlands).

3. Results

Vegetation character varied widely between sites; for instance, tree density ranged from 181 to 2512 trees per ha. Further details on the character of woodland sites are presented in Appendix A.

3.1. Nocturnal insects

We collected a total of 3367 insects from 32 samples in 128 h of sampling. The most abundant insect Order collected was Diptera (97.5% of all insects; Appendix C). Insect abundance was influenced by woodland vegetation character, but not by patch configuration variables. More insects were collected in woodlands with higher tree densities, dense understory cover and open canopy cover; based on median fitted values, insect abundance was 50% lower in mixed (conifer-broadleaved mix) than in broadleaved woodlands (Table 2).

3.2. Bats

We recorded a total of 13,723 bat passes and captured a total of 184 bats during 127 h of monitoring. Six bat species were identified; these were *P. pygmaeus*, *P. pipistrellus*, *P. auritus*, *M. nattereri*, *M. daubentonii* and *M. mystacinus* (Table 3). Abundance of the latter two species was insufficient to conduct any analysis at species level; therefore, abundance of all *Myotis* species was pooled together and analysed at the genus level. The use of the acoustic lure for bats

Table 3
Summary table for numbers of bats/bat passes per species and detection method.

Bat species	Detection method	Mean per site (±SE)	Total	% of total	Sites detected	
P. pygmaeus	Trapping	3.6 ± 0.6	126	68.5	27	34
	Acoustic	252.2 ± 93.0	8575	62.5	34	
P. pipistrellus	Trapping	0.2 ± 0.1	5	2.7	3	28
	Acoustic	131.3 ± 47.7	4464	32.5	28	
Myotis spp.	Trapping	1.2 ± 0.3	41[a]	22.3	19	26
	Acoustic	3.9 ± 1.2	133	1.0	21	
P. auritus	Trapping	0.4 ± 0.1	12	6.5	8	15
	Acoustic	0.3 ± 0.1	11	0.1	8	
All species	Trapping	5.4 ± 0.7	184	100.0	33	34
	Acoustic	389.8 ± 105.9[b]	13,723[b]	100.0	34	

[a] 38 *M. nattereri*, 2 *M. daubentonii* and 1 *M. mystacinus*.

[b] Includes unidentified bat calls (mostly *Pipistrellus* sp.).

considerably increased the number of individuals captured during our surveys. Seventy-one percent (131 out of 184) of bats were captured using the acoustic lure, which represents a 185% increase in capture rate relative to the 25% (46 out of 184) of bats expected by chance given that the lure was operating at 1 out of 4 traps at any given time. Bat abundance and activity were significantly correlated for *P. pygmaeus* (Pearson coefficient = 0.42, $p = 0.012$) and *Myotis* spp. (Pearson coefficient = 0.48, $p = 0.004$). However, because analyses using abundance and activity yielded somewhat different results, here we present both. For *P. pipistrellus*, only five individuals were caught in the nets/traps and for this reason only activity was used as a response variable in subsequent analyses. For *P. auritus*, few individuals were caught (12 bats) and few were recorded (11 passes; Table 3); therefore, we combined both detection methods and used species presence/absence as a response variable.

3.2.1. Effects of woodland vegetation character and woodland patch configuration on bats

After accounting for the effects of year, date and temperature, bats were significantly influenced by variables relating to both woodland vegetation character and woodland patch configuration. Woodland vegetation character consistently had a stronger influence (i.e. more significant associations and higher standardised parameter estimates) on bat abundance and activity than woodland patch configuration (Table 2). Tree density, woodland type, woodland proximity (incorporating patch size and isolation) and presence of grazing stock in a woodland patch were amongst the most important predictors for bat activity/abundance, although bat responses to woodland character were species-specific. Standardised parameter estimates are presented in Table 2 (for continuous variables); magnitudes of effects are given in the text (as differences in median fitted values) for categorical variables. A selection of relevant figures is presented in Appendix D.

P. pipistrellus activity was higher in woodland patches with little understory cover, and was influenced by in-site grazing (97% lower activity at sites with no grazing relative to sites with grazing) and matrix type (90% and 43% lower activity at sites surrounded by mixed and pastoral land, respectively, relative to sites surrounded by arable land; but note that $n = 4$ for 'arable'). *P. pygmaeus* activity was higher in woodlands with lower tree densities and 'proximity' values (i.e. small and isolated patches), and was influenced by woodland type (56% higher activity in broadleaved-conifer mix than in broadleaved-only woodlands). *P. pygmaeus* abundance was not related to any of the woodland characteristics assessed. The abundance and activity levels of *Myotis* spp. were higher in woodlands with high tree densities and where grazing stock was present (54% fewer bats and 78% lower activity at sites with no grazing); woodland 'proximity' had a negative effect on *Myotis* spp. activity, indicating higher activity levels in small and isolated woodland patches. The presence of *P. auritus* in a site was only related (marginally) to woodland type (100% higher probability of presence in broadleaved-conifer mix than in broadleaved-only woodlands).

3.2.2. Effects of the surrounding landscape on bats

All bat species were influenced by the surrounding landscape to some extent. However, the spatial scale and magnitude of effects of specific metrics varied between species (Appendix E). In general, metrics relating to woodland and water were amongst the most important landscape parameters influencing bat abundance and activity; landscape heterogeneity and percentage cover of semi-natural environment and urban areas were also important for some species (Appendix E).

After incorporating the most relevant landscape metric(s) for each bat species into the 'woodland character' models, the new models provided a better fit to the data (i.e. lower deviance and higher R^2 values than models without landscape metrics) for most response variables (Table 2). For *P. pipistrellus*, woodland cover within 3000 m was the most important landscape metric significantly related (negatively) to this species' activity levels; this metric remained significant and increased the model fit (by nearly 9%) after being incorporated into the 'woodland character' model. *P. pygmaeus* activity was most strongly related (negatively) to landscape heterogeneity within 250 m and to water LPI within 2000 m; these metrics remained significant and increased the model fit by ca.7% after being incorporated into the 'woodland character' model. For *P. pygmaeus* abundance, none of the landscape metrics contributed significantly to the 'woodland character' model. *Myotis* spp. activity was related (negatively) to woodland LPI within 2000 m and to urban cover within 3000 m; both remained significant predictors and increased the model fit by ca. 15% after being incorporated into the 'woodland character' model. *Myotis* spp. abundance was most strongly related (positively) to water ENN within 1500 m, which remained marginally significant and increased the model fit by ca. 9% after being incorporated into the 'woodland character' model. The presence of *P. auritus* was not significantly influenced by any landscape parameters; semi-natural environment cover within 250 m had the strongest influence on this species presence ($p = 0.085$; $R^2 = 12.6\%$), and it remained marginally significant while increasing the model fit by 6% after being incorporated into the 'woodland character' model.

For reasons described in Section 2.5, all woodland types were pooled together into a single category for landscape analyses purposes. However, a more detailed examination indicated that woodland in the surrounding landscape (within 5 km of field sites) was primarily coniferous (ca. 54% of woodland area), with mixed and broadleaved woodland comprising 18% and 28% of woodland area, respectively. In addition, coniferous patches were, on average, larger (mean ± SE: 2.51 ± 0.04 ha) than either mixed or broadleaved woodland patches (1.28 ± 0.03 ha and 0.65 ± 0.01 ha, respectively).

3.2.3. *Use of woodland interior, woodland edge and surrounding matrix by bats*

In total, 260 point counts (10 min each) were conducted at different locations within and around each woodland patch and 2657 bat passes – 1810 *P. pygmaeus*, 719 *P. pipistrellus*, 33 *Myotis* spp., 6 *P. auritus* and 89 unidentified (mostly *Pipistrellus* sp.) – were recorded. Bat activity in woodland was substantially higher than in the surrounding matrix for all species, but preference for woodland interior or edge was species-specific (Fig. 1). *P. pipistrellus* activity was similar in woodland interior and edge ($p = 0.706$) and lower in the surrounding matrix, representing only 11% and 10% of the activity recorded in woodland interior and edge, respectively ($p \leq 0.001$; model $R^2 = 79.0\%$; Fig. 1a). *P. pygmaeus* activity was higher in woodland interior than in woodland edge – although difference in median fitted values was relatively small (i.e. 16% fewer bat passes at edge vs. interior; $p \leq 0.001$) – and much lower in the surrounding matrix, representing only 8% and 10% of the activity recorded in woodland interior and edge, respectively ($p \leq 0.001$; model $R^2 = 63.7\%$; Fig. 1b). The activity of *Myotis* species was higher in woodland interior than at either woodland edge ($p = 0.045$; 57% lower than in interior) or surrounding matrix ($p = 0.013$; 85% lower than in interior); the activity of this group did not differ between woodland edge and surrounding matrix ($p = 0.269$; model $R^2 = 33.3\%$; Fig. 1c). *P. auritus* data were insufficient for analysis.

4. Discussion

4.1. *Nocturnal insects*

Most of the insects collected were Diptera. These insects are the main component in the diet of *Pipistrellus* bats and an important component in the diet of *Myotis* bats (Vaughan, 1997). Insect abundance in woodlands was influenced by vegetation character, and was higher in cluttered woodlands (i.e. those with high tree densities and abundant understory cover), but with relatively little canopy cover; these characteristics may represent woodlands in relatively early successional stages (e.g. densely arranged trees which have not fully developed their canopies), or neglected woodlands which have not been actively managed (e.g. by thinning). Insect abundance was higher in broadleaved than in mixed woodlands, probably reflecting the more diverse insect communities supported by deciduous tree species (Kirby, 2001). However, patterns observed in insect abundance in relation to woodland character were not reflected by bat abundance/activity patterns, indicating that food availability for bats is determined by the foraging ecology of each species (e.g. aerial hawkers requiring open spaces to hunt despite higher insect abundance in cluttered areas). A parallel study conducted at the same sites indicated that Lepidoptera – the main component in the diet of *P. auritus* and an important constituent in the diet of *Myotis* species (Vaughan, 1997) – show strong associations with woodland vegetation character and patch configuration; these findings suggest that food availability for moth-eating bats is higher in large and well connected woodland patches with a dense understory cover (Fuentes-Montemayor et al., 2012). Accordingly, a well-developed woodland understory has been linked to the occurrence of moth-eating bat species (e.g. *Barbastella barbastellus*; Hill and Greenaway, 2008).

4.2. *Bats*

Bats were captured and/or recorded in all woodland sites and all common bat species in Scotland were detected during our surveys.

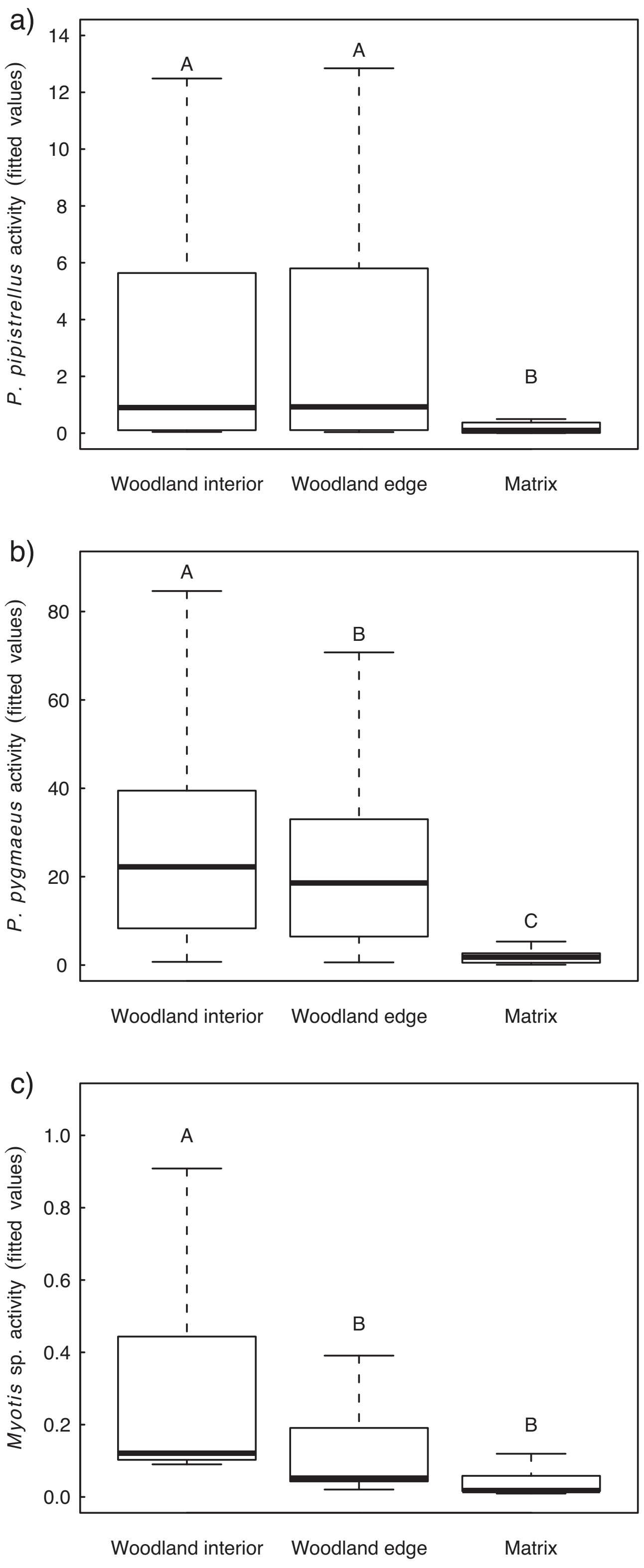

Fig. 1. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for the activity (number of bat passes per point count type) of (a) *P. pipistrellus*, (b) *P. pygmaeus*, and (c) *Myotis* spp. at woodland interior, woodland edge and surrounding matrix. Fitted values predicted by GLMMs are used. Capital letters indicate significant differences between groups at $p \leq 0.05$.

In addition, one species classed as rare (*M. mystacinus*) was captured in one of the sites, this record being the most northerly ever reported in the UK (Richardson, 2000). Complete descriptions of bat assemblages generally require the simultaneous use of multiple methods (MacSwiney et al., 2008). In this study, we used two complementary techniques – sound recording and trapping (assisted by an acoustic lure for bats). By using both methods we were able to detect species which responded poorly to one of the methods (e.g. *P. pipistrellus* which was rarely caught but often recorded, and *P. auritus* which was caught in some sites and recorded in others) and to unequivocally identify *Myotis* species which are difficult to distinguish from ultrasonic recordings. *M. nattereri* comprised more than 90% of *Myotis* bats abundance during our surveys; hence, results referring to '*Myotis* spp.' mainly reflect this species' associations. The use of the acoustic lure for bats considerably increased the number of individuals captured during our surveys.

4.2.1. *Effects of local woodland character on bats*

In general, the effects of woodland vegetation character on bat abundance and activity were stronger than those of woodland patch configuration. Bats showed species-specific associations with woodland vegetation character. High activity levels of *Pipistrellus* species were related to relatively low tree densities (<1000 trees per hectare; for *P. pygmaeus*) and an open understory cover (for *P. pipistrellus*), which is consistent with findings for other *Pipistrellus* species (e.g. *Pipistrellus subflavus*; Yates and Muzika, 2006) and reflects these species' hunting habits (aerial hawking in uncluttered spaces). In contrast, *Myotis* species' abundance and activity were higher in dense woodlands, contrasting with previous findings of negative associations between tree density/clutter and *Myotis* spp. activity (e.g. Brigham et al., 1997) and reflecting their ability to forage in more cluttered environments, gleaning invertebrates from vegetation. These species-specific and conflicting responses to vegetation structure suggest that habitat heterogeneity is needed to meet the requirements of different bat species. Woodlands with conifer and broadleaved trees had higher *P. pygmaeus* activity and (marginally) higher probability of *P. auritus* occurrence than woods with broadleaved trees only. This contrasts with work regarding broadleaved woodland as a higher quality habitat for bats than coniferous or mixed woodland (Walsh and Harris, 1996; but see Mortimer, 2006). The presence of grazing stock in a woodland was associated with higher activity levels of *P. pipistrellus* and *Myotis* spp. Grazing has been linked to changes in woodland vegetation structure, such as reduced sapling recruitment, shrub and herb cover (Hester et al., 1996); reduced clutter caused by grazing might potentially facilitate hunting for aerial hawkers (Schnitzler and Kalko, 2001). In addition, large amounts of dung are associated with high numbers of insects (McCracken et al., 1995); hence, the presence of grazing stock might result in higher food availability for some bat species (although we did not detect this effect on insect abundance). However, in-site grazing has strong negative effects on moth abundance (Fuentes-Montemayor et al., 2012), which might reduce foraging resources for moth-eating bats. Higher activity levels were observed for *P. pygmaeus* and *Myotis* species in smaller and more isolated woodland patches. Although this may seem counter intuitive, it was consistent with patterns observed at the landscape scale (see relevant discussion in Section 4.2.3).

4.2.2. *Effects of the surrounding landscape on bats*

The surrounding landscape had a relatively strong influence on most bat species, with individual landscape parameters explaining ca. 10–40% of variation in bat abundance and activity, and contributing 0–15% further to the variation explained by local woodland character. For lower mobility species, such as *P. auritus* and *P. pygmaeus*, the landscape context was of relatively low importance when compared to local woodland character. This goes in accordance with these species' relatively small foraging ranges (Entwistle et al., 1996; Nicholls and Racey, 2006) and previously reported weak responses to the surrounding landscape, which occur at small spatial scales (<500 m; Fuentes-Montemayor et al., 2011). Higher mobility species showed stronger associations with the landscape context, and at larger spatial scales, compared to the local woodland character. *P. pipistrellus* was significantly influenced by woodland % cover at a large spatial scale (within 3000 m); this landscape metric had higher importance than any of the local woodland characteristics. These larger-scale landscape effects are in accordance with *P. pipistrellus* relatively large home ranges (~1500 ha; Nicholls and Racey, 2006) and strong responses to the surrounding landscape (reported up to 3 km; Fuentes-Montemayor et al., 2011). Surprisingly, this species relation to woodland % cover was negative (for further discussion see Section 4.2.3). *Myotis* species were also influenced by the surrounding landscape (marginally by water proximity, and significantly by woodland largest patch index and urban % cover) at large spatial scales (1500–3000 m); for *Myotis* species activity (but not abundance), the landscape metrics were more important than any other variables relating to local woodland characteristics. This is consistent with the ability of many *Myotis* species (e.g. *M. nattereri*) to travel long distances to their foraging sites (Smith and Racey, 2008). In addition, *M. nattereri* has previously been shown to be more strongly associated with the landscape at large (within 4 km) than at small (within 1 km) spatial scales (Boughey et al., 2011). The negative relation of *Myotis* activity to woodland largest patch index indicated higher bat activity in landscapes with smaller patches in the surroundings, which is consistent with the negative relation of *Myotis* activity to the woodland proximity index observed at the local scale (see below).

Given that the response of bats (particularly *P. pipistrellus* and *Myotis* spp.) to the surrounding landscape was strong even at large spatial scales (up to 3000 m as assessed in our study, although it might extend further), a wide-landscape-scale management approach seems crucial to benefit highly mobile bat species.

4.2.3. *Local and landscape scale effects of woodland extent and fragmentation on bats*

Positive effects of woodland fragmentation have been reported for some bat species, in particular those adapted for hunting in open areas (Klingbeil and Willig, 2009; Estrada-Villegas et al., 2010). In other studies, these effects have been linked to increases in woodland edge density (Grindal and Brigham, 1999), which along with other linear landscape features (e.g. hedgerows) is intensively used by many bat species as a navigational reference, source of insect prey, shelter from wind, and protection from predators (Morris et al., 2010). However, our results showed that woodland edge density was negatively related to the activity of *Pipistrellus* and *Myotis* species, and that *P. pygmaeus* and *Myotis* spp. activity was higher in woodland interior than in woodland edge. There is strong evidence supporting the importance of woodland habitat for British bats (e.g. Walsh and Harris, 1996; Vaughan et al., 1997) and our own results show that bat activity is much higher in woodland patches than in the surrounding matrix; therefore, such negative relations of bat activity to the woodland proximity index at the local scale, and negative relations to woodland % cover and LPI at the landscape scale may seem counter intuitive. These effects of habitat fragmentation were observed for several bat species (i.e. *Pipistrellus* and *Myotis*), were consistent at different spatial scales (i.e. local and landscape) and reflected by various fragmentation metrics (e.g. woodland extent and isolation). Given that ca. 70% of woodland within 5 km around our field sites was either coniferous or mixed, the total proportion of woodland in the landscape is likely to be dominated by conifer plantations, which is usually regarded as a lower quality habitat for bats than broadleaved woodland (Walsh and Harris, 1996; but see Mortimer, 2006). It is also possible that the higher bat activity levels detected for some species in small and isolated woodland fragments (at the local scale) might reflect a more intensive use of woodland in areas where this habitat is scarce. Similar findings have been reported for other taxa (e.g. birds; Vanhinsbergh et al., 2002). For bats, flight is energetically expensive (Thomas and Suthers, 1972) and intensively managed agricultural land is a hostile (low permeability) matrix which is avoided by many species (Walsh and Harris, 1996). Therefore, bats might 'choose' to use nearby resources more intensively rather than commute long distances to remote foraging areas. This suggests that woodland creation is more important (and should be prioritised) in sparsely wooded areas. Other studies support the idea that the benefits bats gain from an increase in woodland extent would be higher in landscapes with little existing woodland cover (e.g. <20% within 1 km; Boughey et al., 2011). In addition, tree lines, hedgerows and riparian corridors linking otherwise isolated woodland patches might act as commuting routes for bats (e.g. Verboom and Huitema, 1997) and allow access to feeding sites over a wider area.

5. Conclusion

Bat populations in woodland patches within an agricultural landscape were influenced by both local and landscape-level attributes. At the local scale, woodland vegetation character was more important than patch configuration. Given that habitat associations were species-specific, habitat heterogeneity (within or between woodland patches) seems essential to fulfil the foraging requirements of different bat species. Aerial hawkers (e.g. *Pipistrellus* species) would benefit from relatively open areas (low tree densities and scarce understory cover), whilst species with gleaning habits (e.g. some *Myotis* species) forage more intensively in more cluttered environments; areas of cluttered vegetation (i.e. dense understory cover and high tree densities) were associated with high insect (mostly Diptera) abundance and could act as sources of insect prey. Bat activity was higher in woodlands than in the surrounding matrix, highlighting the importance of this habitat for bats in agricultural areas. Apparent positive effects of woodland fragmentation on bats might reflect a more intensive use of woodland in landscapes where this habitat is limited. This suggests that woodland creation should be prioritised in more scarcely wooded landscapes. For lower mobility species (e.g. *P. pygmaeus*), local woodland character was more important than the surrounding landscape, highlighting the importance of habitat management at the local scale to create good quality woodland for bats. For highly mobile bat species (e.g. *P. pipistrellus* and *Myotis* species), the landscape context was more important than local woodland characteristics; these species were influenced by the surrounding landscape at large spatial scales (up to 3000 m) and would benefit from woodland creation and management at a landscape-scale. Our results provide relevant information to be applied by land managers and policy makers involved in woodland management and creation schemes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.03.019.

References

Altringham, J.D., 2003. British Bats. The New Naturalist Library – Harper Collins Publishers, London.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Anonymous, 2005. Woodland management for bats. Forestry Commission – England, Forestry Commission – Wales, Bat Conservation Trust, Countryside Council for Wales & English Nature.

Bat Conservation Trust, 2010. The National Bat Monitoring Programme. Annual Report 2010. Bat Conservation Trust, London.

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, 2300–2310.

Brigham, R.M., Grindal, S.D., Firman, M.C., Morissette, J.L., 1997. The influence of structural clutter on activity patterns of insectivorous bats. Can. J. Zool. 75, 131–136.

Chinery, M., 1993. Collins Field Guide: Insects of Britain and Northern Europe. HarperCollins, London.

Corben, C., 2006. AnalookW for bat call analysis using ZCA, version 3.3f. <www.hoarybat.com>.

Crawley, M.J., 2007. The R Book. John Wiley & Sons, West Sussex.

Dietz, C., von Helversen, O., 2004. Illustrated identification key to the bats of Europe. Electronic Publication, version 1.0, Tuebingen & Erlangen.

Dietz, C., von Helversen, O., Nill, D., 2009. Bats of Britain, Europe and Northwest Africa. A & C Black Publishers Ltd., London.

EDINA Digimap Ordnance Survey Service, OS MasterMap Topography Layer. <http://edina.ac.uk/digimap> (accessed February 2010).

Entwistle, A.C., Harris, S., Hutson, A.M., Racey, P.A., Walsh, A., Gibson, S.D., Hepburn, I., Johnston, J., 2001. Habitat Management for Bats: a Guide for Land Managers, Land Owners and their Advisors. Joint Nature Conservation Committee, Peterborough.

Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. Philos. Trans. R. Soc. B 351, 921–931.

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, 95–102.

ESRI Inc., 2006. ArcGIS 9.2. <http://www.esri.com>.

Estrada-Villegas, S., Meyer, C.F.J., Kalko, E.K.V., 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. Biol. Conserv. 143, 597–608.

Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biol. Conserv. 103, 237–245.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

Frick, W.F., Hayes, J.P., Heady Iii, P.A., 2008. Island biogeography of bats in Baja California, Mexico: patterns of bat species richness in a near-shore archipelago. J. Biogeogr. 35, 353–364.

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, 2233–2246.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2012. Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes. Biol. Conserv. 153, 265–275.

Grindal, S.D., Brigham, R.M., 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. EcoScience 6, 25–34.

Groom, M.J., Meffe, G.K., Carroll, C.R., 2006. Principles of Conservation Biology, 3rd ed. Sinauer Associates, Inc., Massachusetts.

Hester, A.J., Mitchell, F.J.G., Kirby, K.J., 1996. Effects of season and intensity of sheep grazing on tree regeneration in a British upland woodland. For. Ecol. Manage. 88, 99–106.

Hill, D.A., Greenaway, F., 2005. Effectiveness of an acoustic lure for surveying bats in British woodlands. Mammal Rev. 35, 116–122.

Hill, D.A., Greenaway, F., 2008. Conservation of bats in British woodlands. Brit. Wildlife 19, 161–169.

Jennings, S.B., Brown, N.D., Sheil, D., 1998. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72, 59–73.

Joint Nature Conservation Committee, 2011. UK BAP priority terrestrial mammal species. <http://www.ukbap.org.uk/TerrestrialMammals.aspx> (accessed July 2011).

Johnson, C.G., Taylor, L.R., 1955. The development of large suction traps for airborne insects. Ann. Appl. Biol. 43, 51–61.

Kapfer, G., Rigot, T., Holsbeek, L., Aron, S., 2008. Roost and hunting site fidelity of female and juvenile Daubenton's bat Myotis daubentonii (Kuhl, 1817) (Chiroptera: Vespertilionidae). Mammal Biol. 73, 267–275.

Kirby, P., 2001. Habitat Management for Invertebrates: a Practical Handbook, 2nd ed. Royal Society for the Protection of Birds, Sandy.

Klingbeil, B.T., Willig, M.R., 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J. Appl. Ecol. 46, 203–213.

Lacki, M.J., Hayes, J.P., Kurta, A. (Eds.), 2007. Bats in Forests: Conservation and Management. The Johns Hopkins University Press, Baltimore.

Law, B.S., Anderson, J., Chidel, M., 1999. Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. Biol. Conserv. 88, 333–345.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, New Jersey.

MacSwiney, M.C., Clarke, F.M., Racey, P.A., 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. J. Appl. Ecol. 45, 1364–1371.

Mason, W.L., 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. Ibis 149, 41–52.

McCracken, D.I., Foster, G.N., Kelly, A., 1995. Factors affecting the size of leatherjacket (Diptera: Tipulidae) populations in pastures in the west of Scotland. Appl. Soil Ecol. 2, 203–213.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst.

Meyer, C.F.J., Fründ, J., Lizano, W.P., Kalko, E.K.V., 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. J. Appl. Ecol. 45, 381–391.

Meyer, C.F.J., Kalko, E.K.V., 2008. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. J. Biogeogr. 35, 1711–1726.

Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. Oryx 36, 18–34.

Morris, A.D., Miller, D.A., Kalcounis-Rueppell, M.C., 2010. Use of forest edges by bats in a managed pine forest landscape. J. Wildlife Manage. 74, 26–34.

Mortimer, G., 2006. Foraging, roosting and survival of Natterer's bats, Myotis nattereri, in a commercial coniferous plantation, Ph.D. Thesis, University of St Andrews, St Andrews.

Nicholls, B., Racey, P.A., 2006. Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. Behav. Ecol. Sociobiol. 61, 131–142.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. Foundation for Statistical Computing, Vienna, Austria.

Richardson, P., 2000. Distribution Atlas of Bats in Britain and Ireland 1980–1999. Bat Conservation Trust, London.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Method Ecol. Evol. 1, 103–113.

Schnitzler, H.-U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. Bioscience 51, 557–569.

Smith, P.G., Racey, P.A., 2008. Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. J. Zool. 275, 314–322.

Thomas, S.P., Suthers, R.A., 1972. The physiology and energetics of bat flight. J. Exp. Biol. 57, 317–335.

Vanhinsbergh, D., Gough, S., Fuller, R.J., Brierley, E.D.R., 2002. Summer and winter bird communities in recently established farm woodlands in lowland England. Agr. Ecosyst. Environ. 92, 123–136.

Vaughan, N., 1997. The diets of British bats (Chiroptera). Mammal Rev. 27, 77–94.

Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. Appl. Ecol. 34, 716–730.

Verboom, B., Huitema, H., 1997. The importance of linear landscape elements for the pipistrell *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecol. 12, 117–125.

Walsh, A., Harris, S., 1996. Foraging habitat preferences of vespertilionid bats in Britain. J. Appl. Ecol. 33, 519–529.

Watts, K., 2006. British forest landscapes: the legacy of fragmentation. Q. J. Forest. 100, 273–279.

Yates, M.D., Muzika, R.M., 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. J. Wildlife Manage. 70, 1238–1248.

Zuur, A.F., Ieno, E.N., Walker, N.J., Savaliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science+Bussiness Media, New York.