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Bat use of commercial coniferous plantations at multiple spatial scales: Management and conservation implications

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Highlights

1. Many studies have demonstrated active avoidance by bats of non native conifer plantations.
2. We found a wide range of bat species using Sitka Spruce plantations, particularly *Pipistrellus* species.
3. A high proportion of the *Pipistrellus* spp. captured were lactating females.
4. Responses to local and landscape-scale habitat characteristics differed between species and foraging guilds.
5. Increasing roost provision and maintaining thinning should benefit bat populations in plantations.

Abstract

Commercial plantations are primarily managed for timber production, and are frequently considered poor for biodiversity, particularly for mammalian species. Bats, which constitute one fifth of mammal species worldwide, have undergone large declines throughout Europe, most likely due to widespread habitat loss and degradation. Bat use of modified landscapes such as urban or agricultural environments has been relatively well studied, however, intensively managed plantations have received less attention, particularly in Europe. We assessed three of the largest, most intensively managed plantations in the UK for the occurrence of bats, activity levels and relative abundance in response to environmental characteristics at multiple spatial scales, using an information theoretic approach. We recorded or captured nine species; *Pipistrellus pipistrellus* and *P. pygmaeus* were the most commonly recorded species on acoustic detectors and female *P. pygmaeus* were the most commonly captured. The influence of environmental characteristics on bat activity varied by species or genus, although all bat species avoided dense stands. Occurrence and activity of clutter and edge adapted species were associated with lower stand densities and more heterogeneous landscapes whereas open adapted bats were more likely to be recorded at felled stands and less likely in areas that were predominantly mature conifer woodland. In addition, despite morphological similarities, *P. pipstrellus* and *P. pygmaeus* were found foraging in different parts of the plantation. This study demonstrates that with sympathetic management, non-native conifer plantations may have an important role in maintaining and supporting bat populations, particularly for *Pipistrellus spp.*

1. Introduction

Unsustainable exploitation of native forests is considered one of the greatest threats to biodiversity and has led to the fragmentation and degradation of forests worldwide (Anon., 2011). Demand for wood-based products is likely to increase in the future and there is a growing need for this to be met by sources other than primary forests. Plantation forests, defined as cultivated forest ecosystems established by planting and/or seeding in the process of afforestation and reforestation, are economically important worldwide as sustainable sources of wood fibre become more necessary (Carnus et al., 2003). Widespread historical deforestation, post war planting initiatives and a need for wood products meant many countries established plantations during the 20th Century. Globally, plantation forests cover 54.3 million hectares with temperate regions such as the US, Japan, Oceania and Europe accounting for more than 50% of plantation areas and demand for wood products is predicted to increase (FSC, 2012; Honnay, 2004). Due to their lack of structural complexity, intensive management, and often single or low species composition, plantations are often considered to be devoid of biodiversity (Bremer and Farley, 2010) although there is evidence that for some taxa this is not the case (Humphrey et al., 2003).

Maintaining and restoring biodiversity is a key tenet in sustainable ecosystem management, the paradigm currently guiding habitat management practices across Europe, North America and Australasia (Ober and Hayes, 2010; Paquette and Messier, 2009). This is driven by concern about world-wide declines in species and populations across a range of taxa (Dirzo et al., 2014) and recognition that much of this is driven by habitat loss and fragmentation, caused by anthropogenic change (Thomas et al., 2004). In many countries the timber industry has responded by shifting focus from purely timber production to one which encourages sustainable practices that promote both wildlife conservation and sustainable timber yields (FSC, 2012). In Europe this has been driven by policy change initiated as a result of the Convention of Biological Diversity, requiring explicit consideration of environmental, economic and social objectives and a multi-purpose approach to forestry (Watts et al., 2008)

Previous studies have suggested that species diversity will be positively influenced if management operations such as felling mimic natural disturbances, for example by creating multi-aged rather than even aged plantations (Bardat and Aubert, 2007). Multi-aged forest systems can support a higher diversity of species through the provision of different habitats for a wide range of flora and fauna, from those reliant on early successional habitats e.g. some song birds (Sweeney et al., 2010) to species dependent on mature habitats e.g. canopy dwelling Coleoptera (Ohsawa, 2007). As a result, many forest managers are moving away from practices such as clear felling (the removal of all trees within a stand, a forestry unit denoting a distinct area of woodland that is composed of uniform group of trees in terms of species composition, age class distribution and size class distribution) to more targeted harvesting approaches such as continuous cover forestry (Lindenmayer and Hobbs, 2004; Pawson et al., 2006). Other forest management practices such as retention of stands with longer rotations, leaving dead wood (Humphrey et al., 2003) and restructuring plantations have had positive impacts for a wide range of taxa (e.g. Oxbrough et al. 2010).

Bats have undergone major historical declines across many temperate regions, in part due to widespread habitat loss (Walsh et al., 1996). The majority of temperate bat species rely on forest for at least part of their life cycle (Altringham, 2013), but while bat associations with native woodlands are well established (e.g Boughey et al., 2011; Dietz et al., 2009), less is known about use of plantation habitats. This paucity of research is perhaps in response to many habitat studies showing active avoidance of plantations by individual species (Boughey et al., 2011; Russo and Jones, 2003; Smith and Racey, 2008; Walsh et al., 1996). However, there is growing evidence from Europe (Charbonnier et al., 2016; Cistrone et al., 2015; Cruz et al., 2016; Mortimer, 2006; Pereira et al., 2016; Russo et al., 2010), New Zealand and Australia (Borkin and Parsons, 2011; Borkin et al., 2011; Burgar et al., 2015) and North America (Morris et al., 2010; Patriquin and Barclay, 2003) that suggests that bat use of plantations may be more widespread than previously assumed. While management for biodiversity and protection of European Protected Species is a key requirement for European forestry management (Boye & Dietz 2005), the lack of broad scale studies in European plantation forests means that there is currently insufficient information for forest managers to ensure sufficient and appropriate mitigation is carried out (Russo et al., 2016). Understanding whether there are general patterns that underpin how highly mobile species make use of plantations may be an important strategy for protecting against future species declines.

Here, we examine the extent to which bat species use plantation woodlands in northern Britain by assessing the influence of various environmental characteristics on bat abundance and activity at multiple spatial scales. Specifically, our objectives were to:

1. Assess the composition of bat populations in commercial coniferous plantations.
2. Identify local and landscape scale variables which influence occurrence, abundance and activity, and how this varies between species.
3. Compare how two morphologically similar species (*Pipistrellus pipistrellus* and *P. pygmaeus*) respond to plantation characteristics.
4. Use these findings to give appropriate management recommendations.

Nine of the seventeen species resident in Britain occur within the study area, including *Myotis*, *Nyctalus* and *Pipistrellus spp.* These can be categorised into different foraging "guilds", bats with similarities in morphology, hunting technique and echolocation call structure (Schnitzler et al., 2003). Bats in the genus *Nyctalus* forage primarily in open spaces (open adapted) compared to *M. nattereri* (clutter adapted) or *P. pipistrellus* (edge adapted) and are therefore likely to respond differently to both local and landscape scale characteristics. *Pipistrellus pipistrellus* and *P. pygmaeus* are of particular interest as they are common, sympatric species which share morphological and dietary similarities (Barlow, 1997) and may use habitat selection as a mechanism for resource partitioning.

2. Methods

The study was conducted in three plantation forests in Central and Southern Scotland and Northern England (Figure 1). We chose forests for their large size (ranging from 30,000 ha in Cowal and Trossachs to 60,000 ha in Kielder and 114,000 ha in Galloway), high productivity and the predominance of *Picea sitchensis* (Sitka spruce), the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each forest, multiple sites were selected using a Forestry Commission sub-compartment database within a Geographic Information System (GIS) (ArcMap 10.1, ESRI) based on stand age and species composition (Figure 1).

In total, seven sites were surveyed in Cowal and Trossachs, 12 in Galloway Forest and 12 in Kielder Forest. Where possible, a stand of trees at each management stage (from a total of six management stages: see appendix 1) were selected in each site, which was a maximum of 2km^2 in size and at least 4km from another site. Not all sites had all stands of each management stage resulting in an unbalanced design of between four and six stands per site and a total of 285 stands across 31 sites (Figure 1).

2.1 Bat abundance surveys

For some species identification from echolocation calls is not possible (Schnitzler et al., 2003), therefore capturing individuals for inspection in the hand can be the only way to confirm species occurrence, while also allowing confirmation of reproductive status (Hill and Greenaway, 2005). We assessed relative bat abundance (number of captures per site) by placing an Austbat harp trap (2.4 x 1.8m) and three Ecotone mist nets (2.4 x 6m) at one location in each site to trap bats. The location was selected based on ease of access and nets were placed across potential flight lines (e.g. tracks or rides) between either two mature stands or extending from the edge of a mature stand into felled stands. Nets were placed at least 50m from each other, with placement dictated by the plantation structure and deliberately chosen to maximise capture rates. We used an acoustic lure (The Autobat, Sussex University, Brighton, UK) with four different synthesised bat calls (*Pipistrellus* spp mix, a mixture of *Myotis* sp., *Nyctalus leisleri* and *M. nattereri*), which has been demonstrated to greatly improve capture rates (Hill and Greenaway, 2005) and attracts a variety of different bat species present in the study area (following Lintott et al. 2014). Each call was played at each trap for 15 minutes, with the lure moved between traps every 30 minutes. Traps were checked every 15 minutes and any captured bats were identified to species, weighed, measured, aged, sexed, assessed for reproductive status and marked temporarily by fur clipping. All captures were carried out under licences 19584 and 20131093 (Scottish Natural Heritage, Natural England)

2.2 Bat acoustic surveys

All surveys were carried out between 12th June and 3rd September 2013. We surveyed all the stands within a site simultaneously and for a single night, starting 30 minutes after sunset to ensure that recorded individuals would be actively foraging rather than commuting from roosts. Surveys finished 4 hours later as this represents the length of the shortest night in this area during summer. Bat activity was quantified using a SongMeter SM2 Bat+ (Wildlife Acoustics, Inc., Concord, MA) using two microphones at a height of 1m and positioned at a 45 degree angle. One microphone was placed at the stand edge pointing towards adjacent tracks or rides; the other was positioned 20 – 40m into the trees (depending on ease of access) pointing towards the stand interior, allowing simultaneous recording of both the stand edge and interior.

2.3 Bat call analysis

We identified all calls manually to species or genus and counted the number of bat passes (defined as at least 2 echolocation calls within one second of each other) resulting in a measure of activity per four-hour recording period at each stand edge and interior. *Pipistrellus* species can be separated due to differences in the characteristic frequency of the call (Fc = frequency of the right hand end of the flattest part of the call; Russ, 2012) and the call shape. Bats in the genus *Myotis* have a similar call structure and as such were identified only to genus. It can be difficult to distinguish between *Nyctalus* calls in cluttered environments (Schnitzler et al., 2003), so again these were only identified to genus. *Plecotus auritus* have very quiet calls, so their occurrence will be underestimated by using acoustic recordings alone. Due to low activity levels of *Nyctalus* and *Myotis* species, we were unable to analyse activity and assessed presence / absence instead.

2.4 Local habitat characteristics

We carried out vegetation surveys in two 0.01 ha plots around each microphone point within two weeks of bat surveys. Due to the homogenous nature of stands these plots were considered representative of the stand as a whole. At each plot we recorded the total number of trees with diameter at breast height greater than 7 cm (stand density), and recorded the dominant ground cover according to the following categories: bare, needle, moss, grass, tussock, bracken, flowering plant. We also recorded the total number of standing dead trees (snags) in each plot, as these can be associated with higher species richness and abundance of a variety of taxa in managed forests and provide potential roost sites for bats (Elmore et al., 2005). However, it was very rare to see standing dead wood that was appropriate for bat roosts at any of our study sites. We assessed the amount of dead wood on the forest floor using the following scale: 0 – no coarse woody debris, 1 – small twigs, 2 – large twigs and branches over 7cm in diameter, 3 – both large and small branches. Understory vegetation height (defined as all ground vegetation not including trees) was measured at 10 evenly spaced points across the radius of the circle and canopy cover was recorded at each point using a sighting tube with an internal crosshair; if the crosshair intersected with any canopy vegetation presence of canopy cover was recorded and converted to a percentage cover score (Lintott et al., 2015). We also recorded stand age (as years since planting).

2.5 Landscape analysis

We used Arcmap 10.1 to determine landscape scale features within 250, 500, 1000, 2000, 3000 and 4000m of the centre point of each site. The smaller scale allows the extraction of site-specific characteristics, whereas the larger scale reflects the home range of low and intermediate vagility species such as *P. pygmaeus* (Lintott et al., 2015). Data from the OS Mastermap (EDINA, 2014) was combined with a high resolution Forestry Commission database specific to the study areas to reclassify the landscape within each specified distance into the following eight categories: 1. Human infrastructure (e.g. buildings), 2. Felled (recently felled or conifers < 5 years old), 3. Broadleaved trees, 4. Thicket conifer (between 5 and 20 years old), 5. Closed canopy conifer (> 20 years old), 6. Water (tidal or inland), 7. Open (heathland, upland areas, scree), 8. Tracks and roads. Fragstats 4.2 (Mcgarigal, 2014) was used to calculate the proportion of land covered by each category and Shannon's diversity index (a measure of landscape heterogeneity which increases as the number of different patch types increases) within each buffer. Additionally, the Largest Patch Index (a measure of habitat dominance, LPI is the percentage of the landscape comprising the largest patch of any of the habitats outlined above), Euclidian Nearest Neighbour distance (ENN, mean value of ENN distances between all patches of a type in a landscape), and total Edge Density (ED, the sum of the lengths of all stand edge segments divided by the total landscape area) were calculated as previous studies have shown these influence bat foraging activity (Fuentes-Montemayor et al., 2013; Lintott et al., 2015). Additional features were measured as proxies for either water, roost or food availability (Hayes and Loeb, 2007), the full list of local and landscape variables considered in analyses is outlined in appendix 2.

2.6 Statistical analysis

All analysis was carried out in R Studio using R version 3.2.2 (R core development team), using the lme4, effects, MuMIn, ggplot2, arm and glmmADMB packages. Analysis involved four stages:

1). To select the ***local characteristics*** to be entered into the maximal model, we constructed species- or genus-specific models, which explained variation in bat responses (occurrence, activity or abundance of each species or genus separately) between stands. A generalised linear mixed effect model (GLMM), with site nested in forest as a random effect was used to account for differences due to geographical location, with the error structure dependent on the species or genus being tested (see step 4 for more details). We tested models consisting of either stand type or quantitative descriptors of stand type (e.g. stand density, % canopy cover, supplementary data, appendix 2), selecting those with the highest F statistic to be entered into the maximal model (step 4).

2). To select the ***landscape variables*** to be entered into the maximal model we tested land cover type parameters (e.g. proportion of land cover and LPI, appendix 2) at multiple spatial scales (250m – 4km; see section 2.5) on bat response variables (occurrence, activity or abundance of each species or genus separately) using linear regression models, as no random factor was required. Individual models for each landscape parameter at each scale were performed and R^2 values calculated to quantify the amount of variation in the data explained; the variables with the highest R^2 at the relevant scale were chosen for inclusion.

3). All predictor variables selected for inclusion in the maximal model were tested for collinearity, retaining those which were not collinear (Pearson's correlation < 0.5). See appendix 3 for description of model construction.

4). ***Maximal models***; all continuous predictors included in the maximal models were scaled and centred around a mean of zero with a standard deviation of 1 to allow direct comparisons between the estimates regardless of differences in scale. All possible combinations of variables within the maximal model were ranked using Akaike's Information Criterion adjusted for small samples (AICc) (Burnham and Anderson, 2002). Model fit was assessed using change in AIC and Akaike weights. As there was no single best model (change in AIC greater than 4), we accounted for model uncertainty by computing model averaged predictions and standard errors across the models retained within a 95% Akaike weights confidence set (Burnham and Anderson, 2002). The full model averaged coefficients with shrinkage are presented to reduce model selection bias from parameters which do not appear in all the "best" models (Burnham and Anderson, 2002). Where possible, the marginal R^2 is presented following Nakagawa & Schielzeth 2013, which quantifies the proportion of variance explained by the fixed effects without considering the random effects. Predictions from model outputs are given as means with 95% confidence intervals. Using a mixed effect generalised linear modelling approach allows us to account for a lack of independence between stands within sites, while controlling for other influential variables, and the model averaging approach allows assessment of the influence of variables across multiple models when no single best model is found.

We only modelled abundance for *P. pygmaeus,* as we caught insufficient numbers of other bat species. *Pipistrellus pygmaeus* abundance was modelled using a Poisson distribution, *P. pygmaeus* and *P. pipstrellus* activity using negative binomial distributions, and *Nyctalus* and *Myotis* occurrence using binomial GLMMs (objective 2) as activity was low for these species. R^2 was used as a measure of explanatory power for all models except those with negative binomial error distributions, for which we used F statistics.

We assessed differential responses to plantation management for the two *Pipistrellus* spp. due to an ecological interest in understanding how morphologically similar species may partition resources (objective 3). We used a GLMM with a binomial distribution to determine the relative effects of landscape and local characteristics on *P. pygmaeus* in comparison to *P. pipistrellus.* The model was run with the proportion of *P. pygmaeus* to total identified *Pipistrellus* passes at each stand location. An equal proportion of *P. pipistrellus* and *P. pygmaeus* passes indicates stands where activity was similar and unequal proportions where one species dominates compared to the other. After examining the data, we included an interaction between stand type and distance with water, in addition to other measures as previous work has shown *P. pygmaeus* have a preference for riverine habitats compared to *P. pipistrellus* (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006). We also included stand age as a quadratic term to allow for a non linear relationship and an interaction between temperature and altitude as bats may forage at higher altitude in warmer weather. In summary, models were constructed for the following bat responses: *P. pygmaeus* abundance; *P. pygmaeus* and *P. pipistrellus* activity (passes per four hour period); occurrence of *Myotis* and *Nyctalus*; proportion of *P. pygmaeus* to *P. pipistrellus* activity.

Finally, we tested the influence of the acoustic lure on our bat capture rates using Wilcoxon's paired test.

3. Results

3.1 Bat use of commercial coniferous plantations

We caught a total of 85 bats between May and August 2013 (sites = 31, Table 1); capture rates were considerably improved by use of an acoustic lure (Wilcoxon's paired test, n= 31, w = 665, p = 0.006). Over 80% of bats were *P. pygmaeus* (41 adults, 28 juveniles). Of the adult bats the majority (28) were females, of which 84% were either pregnant, lactating or post lactation. We also caught a small number of other species including *P. pipistrellus* and *N. leisleri* lactating females (Table 1) and juvenile *N. noctula, N. leisleri, P. pygmaeus* and *M. nattereri.*

We recorded a total of 19,222 passes during 1,104 hours of acoustic sampling (Table 1); bats were recorded within all stand types and at all sites. The majority of calls were *Pipistrellus* spp. (some could not be identified to species), but we also recorded *Myotis* and *Nyctalus.* In addition both *P. auritus* and *P. nathusius* were recorded in plantations but in very low numbers, and were excluded from further analysis (Table 1).

3.2 Factors affecting bat abundance and activity in coniferous plantations

Pipistrellus pygmaeus abundance was highest in sites closer to buildings (Figure 2D), with mean captures falling from 3.9 (95% Confidence Interval 2.3 – 7.4) in sites within 400m of buildings to 0.8 (0.3 – 1.6) in sites more than 2km from buildings. There was a trend towards higher abundance in sites with a higher landscape heterogeneity but the effect size was small (Table 2). Both local and landscape scale factors influenced *P. pygmaeus* activity in coniferous plantations (Table 3)*;* activity was highest at stand edges and stands surrounded by a relatively low proportion of open ground, falling by 90% as the percentage of surrounding open space increased from 30 to 65% (Figure 2A). Activity of *P. pygmaeus* decreased with increasing stand density falling from 29 (16 – 53) passes in stands of less than 50 trees ha^{-1}, to 7 (3 – 15) passes in stands of 3000 trees ha^{-1} (Figure 2B). Activity was also lower (11; 5 – 23 passes) in stands over 50 years old, compared to 25 (14 – 44) passes in clear felled stands (Figure 2C).

Pipistrellus pipistrellus was most influenced by stand type, with the highest activity occurring in felled areas and at stand edges compared to stand interiors, apart from at felled stands where *P. pipistrellus* used both stand edges and stand interiors (Table 3).

The probability of recording *Myotis* sp. was greater at stand edges compared to interiors (Table 4) and was strongly influenced by stand density; there was a 0.7 (0.5 – 0.9) likelihood of recording *Myotis* in stands with fewer than 50 trees ha^{-1} which fell to a 0.3 (0.1 – 0.6) in denser stands (>2750 trees ha^{-1}).

Occurrence of *Nyctalus* in plantations was influenced by both local and the landscape factors; this group were most likely to be recorded at the edge of felled stands and least likely to be recorded in stand interiors, particularly stands where canopy closure has occurred ("mature" and "thinned" stands; see appendix 1). At the landscape scale, as distance between patches of closed canopy conifer increased, the likelihood of recording *Nyctalus* species also increased from 0.1 (0.0 – 0.3) in stands within 100m of closed canopy cover to 0.7 (0.3 – 0.9) in stands with more than 1km between mature conifer stands (Figure 3A). *Nyctalus* were also less likely to be recorded in stands in which water is the largest patch in the surrounding landscape (Table 4). *Nyctalus* species responded negatively to the built environment; in less populated areas (fewer than 50 houses within 4km) there was a 60% (28 – 85%) likelihood of recording *Nyctalus* but this fell to 2% (0.2 – 32%) likelihood of recording *Nyctalus* in stands with more than 1500 buildings within 4km (Figure 3B).

3.3 Differential use of plantations by P. pygmaeus and P. pipistrellus

Proximity to broadleaved woodland was the most influential variable explaining differences in activity between *P. pygmaeus* and *P. pipistrellus* (Table 5). At stands close to broadleaved woodland (< 1km), approximately 40% (20 – 62) of activity was *P. pygmaeus* compared to *P. pipistrellus,* rising to nearer 80% (60 – 91) in stands further away (~ 4km) from broadleaved woodland (4A). A higher proportion of *P. pygmaeus* to *P. pipistrellus* calls was predicted in felled or freshly planted stands (< 5 years) and older (60+ years) stands but was approximately equal for those between 20 to 40 years

(Figure 4B). Stands close to buildings had higher *P. pygmaeus* activity (0.68; 0.46 – 0.84) compared to those over 2.5km from buildings which had higher *P. pipistrellus* activity (0.36; 0.18 – 0.59, Figure 4C). Finally, there was a trend for *P. pygmaeus* to dominate in stands close to water, and *P. pipistrellus* in stands > 1km from water, particularly in felled areas (Table 5; Figure 4D).

4. **Discussion**

Plantation woodlands have been viewed as "green deserts", often presumed to be hostile to wildlife and of little intrinsic value for biodiversity (Gardner, 2012). However, as most bat species rely on forests during their life cycle, understanding how forestry management impacts bat use of plantations is highly important for bat conservation (Russo et al., 2016), particularly as plantation landscapes are receiving growing interest as sites of alternative energy generation. In this study we found a wide diversity of bat species used commercial plantations, with edge, clutter and open adapted foragers detected. However, the extent of plantation use depended on both local and landscape habitat composition, and varied between species and species' guilds.

4.1 Composition of bat populations in commercial coniferous plantations:

Relative abundance, assessed through captures, was generally low in comparison to studies in a similar geographical area (Fuentes-Montemayor et al. 2013; Lintott et al. 2015). Despite the fact that levels of activity of *P. pygmaeus* and *P. pipistrellus* were very similar, *P. pipistrellus* was under represented in the capture records. Lintott et al (2014) found comparable capture rates when using a lure for both *P. pygmaeus* and *P. pipistrellus* in a similar geographical region, therefore it is unlikely that the difference in capture rate in this study is due to capture bias from the acoustic lure. Rather this may be in part due to higher *P. pipistrellus* activity in felled and open areas which we did not target for catching due to the lack of clearly defined flight lines. Nevertheless, it is evident that we cannot use capture data for *P. pipistrellus* to infer relative abundance. Analyses using the capture data have been restricted to *P. pygmaeus*, as a previous, larger scale, study indicated that measures of abundance using the lure was complementary to activity levels; Lintott et al. 2014.

This study indicates that plantation woodlands support the foraging activities of breeding populations of *P. pygmaeus* (and potentially *P. pipistrellus and N. noctula*), which are likely to roost in nearby buildings (Altringham et al., 1996) as we caught relatively high numbers of lactating females. However, we found no evidence that breeding colonies of forest specialist bats such as *Myotis* and *Plecotus* species are using plantation woodlands. The lack of woodland specialists in plantations has been reported from other studies and has been attributed to the paucity of appropriate natural roost structures such as tree cavities (Bender et al., 2015; Burgar et al., 2015; Pereira et al., 2016; Rodríguez-San Pedro and Simonetti, 2015; Russo et al., 2010). Although standing dead wood is retained as part of forestry operations, we saw no evidence of any standing dead wood being appropriate for roosting. In addition, we saw no evidence of any tree holes, rot or damage in *Picea sitchensis* which could be used as a potential roost, and found no evidence of lactating female *P. pygmaeus* using (*Picea sitchensis*) as temporary roosts, as part of a later radio tracking study (Kirkpatrick, unpublished data). *Myotis* species such as *M. nattereri*, *M. daubentoni* and *M. mystacinus* roost switch regularly and use a combination of tree holes, man-made structures such as bridges, and occasionally bat boxes (Altringham et al., 1996), which were uncommon in the plantations surveyed for this study (pers. obs). Therefore, it is highly likely that the lack of appropriate roosting structures for forest specialist bats is responsible for the sex specific differences in bat diversity and abundance we observed.

4.2 Responses of bats to features at the local scale:

In this study, although bat associations with plantation habitat features separated into two broad guilds (those using more complex habitats such as *P. pygmaeus* and *Myotis* spp., and open space foragers such as *Nyctalus* and to some extent *P. pipistrellus*), all species preferentially used stand edges. Edges may allow both clutter tolerant and clutter sensitive bats access in and around different areas of the plantation (Heer et al., 2015; Hein et al., 2009; Rodríguez-San Pedro and Simonetti, 2014), provide protection from wind for weak flying Diptera or act as windbreaks collecting airborne insects blown in from adjacent open or felled areas and also provide protection from predators (Nicholls and Racey, 2006a; Verboom and Spoelstra, 1999). The exception was at felled stands which were used by both open and edge-space foragers such as *Nyctalus* and *P. pipistrellus*. *Pipistrellus pygmaeus* foraged more near water and in older stands compared to *P. pipistrellus* which more commonly used areas near to broadleaved woodland, further from buildings or water, particularly felled stands. Whilst there are small differences in the diet of the two pipistrelle species (Barlow 1997), both primarily feed on Nematoceran Diptera; a parallel study not presented here (Kirkpatrick, unpublished data) found no difference in the abundance of this group between stand types within plantations. Therefore, prey abundance does not appear to be driving the within plantation differences in foraging activity we see here. Rather, a high dipteran abundance may attract *Pipistrellus spp.* to plantations, but within plantations the two different species segregate based on local stand characteristics and different foraging styles, such as the well documented association of *P. pygmaeus* with riverine habitats (Davidson-Watts and Jones, 2005; Nicholls and Racey, 2006).

Activity of *P. pygmaeus* and occurrence of *Myotis* spp. decreased with increasing stand density, being highest at felled stands and decreasing at thin and thicket aged stands which are harder to negotiate (Dietz et al., 2009; Jung et al., 2012). Adams and Law (2011) suggested that thinning to a threshold of below 1100 stems ha^{-1} would benefit bat species in Australian plantation forests, with other studies from Australia and America supporting this recommendation (Bender et al., 2015; Blakey et al., 2016; Cistrone et al., 2015; Cox et al., 2016; Morris et al., 2010; Patriquin and Barclay, 2003). We were unable to directly test the impacts of thinning as mechanical thinning was rare in our study system but as the average density of mature stands was 1200 stems ha^{-1} and *P. pygmaeus* activity was predicted to fall by a third in stands over 1000 stems ha^{-1}, it is likely that thinning would be beneficial.

4.3 Responses of bats to features at the landscape scale

In general, bat species or genera had stronger responses to local rather than landscape features. However, *P. pygmaeus* responded strongly and negatively to the proportion of open land within 3 km, which was strongly correlated with increased landscape heterogeneity. Firstly, *P. pygmaeus* distinguished between open ground (i.e. moorland or upland) compared to felled land. Structurally, felled stands and open areas are similar, so access to prey and exposure to predators will be similar in both land cover types. However, felled stands may support different prey abundance and diversity than open areas. Felling causes soil disturbance and results in a boggy environment which may be a better breeding ground for Nematoceran Diptera (Blackwell et al., 1994). Landscapes with a higher proportion of open ground may have a lower proportion of suitable edge habitats and linear features which *P. pygmaeus* may use for commuting into and through plantations (Law et al., 2015). Bender et al (2015) found that most species specific bat occupancy and activity was related to stand level, rather than landscape level features, similarly to Erickson et al (2003). The lack of strong associations with landscape at larger spatial scales may reflect the fact that bats do not perceive different management stages in plantations as inhospitable habitat (Bender et al., 2015; Heer et al., 2015), compared to woodland patches within an agricultural or urban matrix (e.g. agricultural dominated landscape; Fuentes-Montemayor et al., 2013; urban dominated landscape; Lintott et al., 2015). In contrast, the likelihood of detecting *Nyctalus* was higher in stands surrounded by a lower proportion of mature conifer. *Nyctalus* are large, fast flying bats which forage by gleaning in open habitats and will avoid cluttered habitats such as mature conifer (Russ, 2012).

4.4 Management implications for commercial coniferous plantations

The lack of information regarding bat use of commercial plantations in Europe means that current management recommendations are sparse and predominantly drawn from research in America and Australia (e.g. Bender et al., 2015; Blakey et al., 2016; Borkin and Parsons, 2011; Heer et al., 2015). Although plantation management regimes can vary markedly between countries resulting in differences in composition and structure, we have outlined a number of recommendations likely to benefit bat species across a range of plantation forests:

1. Increasing roost availability: it is likely that roost rather than food availability is constraining the use of commercial plantations for many bat species. We saw no evidence of suitable roosting features in stands of *Picea sitchensis*, although other conifer species such as *Pinus nigra* can house maternity colonies of *M. nattereri* (Mortimer, 2006). Therefore, although felling operations have been shown to reduce colony size and available roosting habitat in *Eucalyptus* plantations in New Zealand (Borkin et al., 2011), it is unlikely that felling directly causes roost loss or increased mortality in *Picea sitchensis* plantations. In fact, in the current study *Pipistrellus* and *Nyctalus* species preferentially foraged in these areas. Installing bat boxes in riparian areas, near broadleaved woodland or in stands not included in felling schedules should allow more bat species, particularly lactating females, to make use of plantation areas without impacting forest operations. Other studies have demonstrated accelerated uptake of bat boxes adjacent to plantation woodlands, probably as a result of the lack of alternative roosting possibilities (Ciechanowski, 2005; López-Baucells et al., 2016; Russo et al., 2010; Smith and Agnew, 2002). It is unlikely that boxes will be used by *P. pygmaeus* maternity colonies, although harem formation in late summer and autumn would be expected (Park et al., 1996). However, for forest specialist bats such as *M. nattereri*, bat boxes may be appropriate for the formation of maternity colonies (Mortimer, 2006). Long term monitoring of mitigation such as installing bat boxes is essential to assess the effectiveness of installing bat boxes in commercial plantations and should be built into any management plan (Russo et al., 2016).

2. Enhancing plantation heterogeneity: We found that the presence and activity of different species or genera was impacted at multiple spatial scales. Plantations can cover huge areas as contiguous forest; maintaining a variety of stand types and ages will allow species such as *P. pygmaeus* which preferred the edges of mature or felled stands as well as *Nyctalus* species which preferred felled stands to both make use of plantation landscapes.

3. Reducing stand density: In line with various other studies across temperate zone plantations, maintaining and enhancing thinning programs where possible may allow stands to reach similar densities to mature stands at a younger age, which will benefit edge and clutter adapted species (Bender et al., 2015; Blakey et al., 2016; Cox et al., 2016; Morris et al., 2010). In addition,

felling creates new foraging patches for open and edge adapted species. Studies which have found no effect of thinning may not have thinned sufficiently; Blakey et al (2016) found that felling to densities below 1100 stems ha^{-1} resulted in greater bat activity whereas Patriquin and Barclay (2003) found no impact of thinning to 1250 stems ha^{-1}. Adams et al (2011) recommend thinning to below a threshold of 1100 stems ha^{-1} where appropriate. We found a 30% increase in activity in stands below 1000 stems ha^{-1}, although the mean density of mature stands in our dataset was 1260 stems ha^{-1}, which may still be too dense for even clutter adapted bats to make use of.

4. Improving feeding opportunities: the presence of bats in plantations is likely a reflection of food availability, as Nematoceran Diptera were abundant across all stand types and dominated invertebrate diversity (Kirkpatrick, unpublished data). Shifts in plantation management toward continuous cover forestry and maintaining riparian habitat will support a wider diversity of invertebrates (Kerr, 1999), benefiting species that forage on other invertebrates. In addition, continuous cover forestry may benefit clutter adapted bat species such as *M. nattereri* and even *P. auritus* which are gleaning foragers, while maintaining clear felling will benefit open adapted species. Both *P. pipistrellus* and *Nyctalus* associated strongly with freshly felled areas. Felling operations resulting in a change in land use should be aware that bats may be using these areas in greater numbers post felling and ensure that the new operations are not likely to harm bat species.

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Tables:

Table 1. Total adult abundance and the number of passes recorded for species / genera in three forests. Numbers in parentheses indicate adult females. We were unable to identify some *Pipistrellus* calls to species and were removed from further analysis. We caught *Myotis nattereri, M. daubentoni* and *M. mystacinus* in the plantations but due to echolocation similarities we did not differentiate between their call types. We caught *Nyctalus leisleri* and *N. noctula* but again recorded occurrence at the genus level. We caught *Plecotus auritus* and recorded *Pipistrellus nathusii* in very low numbers and present these results here for interest. Sites at which species were present was determined by both acoustic and capture data.

Species/species group	Total abundance (of which females)	Total passes recorded	% of bat calls	Kielder (%)	Galloway (%)	Cowal and Trossachs (%)	Sites present (total n = 31)
Pipistrellus pygmaeus	42 (26)	6569	34.17	17.59	9.23	7.35	31
Pipistrellus pipistrellus	1 (1)	6333	32.95	28.58	2.47	1.90	30
Pipistrellus spp.	0	4849	25.23	12.22	7.26	5.75	31
Myotis spp.	3 (0)	737	3.83	2.93	< 1 %	< 1 %	30
Nyctalus spp.	1 (1)	540	2.81	< 1 %	2.20	< 1 %	20
Plecotus auritus	2 (0)	117	< 1 %	< 1 %	< 1 %	< 1 %	23
Pipistrellus nathusii	0 (0)	77	< 1 %	< 1 %	< 1 %	0.00	7

Table 2. Best approximating GLMM models (with shrinkage) using an information theoretic approach based on Akaike's Information Criterion (AICs) adjusted for small sample sizes for *P. pygmaeus* abundance. Listed are the parameters and their respective influence on *P. pygmaeus* abundance in commercial plantations. Parameters in bold have a large effect size. $R^2 = 0.27$.

GLM Model	Habitat parameters	Estimate	Error	Z value
Abundance of				
P. pygmaeus spp.	(Intercept)	-29.7	12.6	0.22
(poisson)	**Distance to buildings**	**-0.51**	**0.18**	**-2.74**
	Total buildings within 4km	**0.23**	**0.11**	**2.114**
	Shannon's diversity index (Landscape heterogeneity)	**0.28**	**0.14**	**1.96**
	% ASNW within 4km	-0.15	0.17	0.37
	Date	0	0	0.69
	Temperature	0.18	0.11	0.11

Table 3. Best approximating GLMM models (with shrinkage) using an information theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc) for both Pipistrelle species. Listed are the parameters and their respective influence on (a) *P. pygmaeus* (intercept is for stand edge), and (b) *P. pipistrellus* (intercept is stand edge at felled stands). It is not possible to calculate R^2 for negative binomial mixed effects models. Bold indicates parameters where the error of the estimate does not cross zero. ASNW is ancient semi natural woodland

GLMM Model	Structural parameters	Estimate	Error	Z value
(a)	*Local characteristics*			
P. pygmaeus	**(Intercept)**	**3.06**	**0.28**	**10.79**
activity (negative binomial)	**Stand interior**	**-1.46**	**0.21**	**-6.83**
	Stand density (ha)	**-0.42**	**0.12**	**-3.59**
	Stand Age	**-0.30**	**0.12**	**-2.58**
	Altitude (m)	-0.09	0.16	0.56
	Landscape characteristics			
	% Open land (3km)	**-0.57**	**0.18**	**-3.14**
	Distance to broadleaved woodland (m)	-0.14	0.19	-0.70
	Distance to water (m)	0.00	0.05	0.07
	% ASNW (4km)	-0.06	0.14	-0.39
	Total buildings	0.21	0.21	1.08
	Environmental characteristics			
	Temperature (°C)	0.10	0.15	0.53
(b)	*Local characteristics*			
P. pipistrellus	**Intercept**	**3.58**	**0.70**	**5.05**
activity (negative binomial)	**Stand Interior**	**-1.64**	**0.21**	**-7.79**
	Stand type: Mature	**-1.88**	**0.33**	**-5.68**
	Stand type: Thicket	**-1.63**	**0.34**	**-4.78**
	Stand type: Thin	**-0.96**	**0.37**	**-2.60**
	Stand type: Young	**-1.12**	**0.32**	**-3.43**
	Altitude (m)	-0.23	0.23	-0.98
	Landscape characteristics			
	Edge density	-0.01	0.11	-0.11
	Distance to water (m)	0.25	0.18	1.36
	Distance to nearest building (m)	0.09	0.07	0.60
	% Felled land (3km)	0.16	0.21	0.76
	% ASNW (4km)	-0.05	0.16	-0.34
	ENN distance to closed canopy conifer (m)	-0.40	0.23	-1.77
	Environmental characteristics			
	Temperature (°C)	**0.54**	**0.25**	**2.14**

Table 4. Best approximating GLMM models (with shrinkage) using an information theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc) for both *Myotis* and *Nyctalus* occurrence in commercial coniferous plantations. Listed are the parameters and their respective influence on (a) *Myotis spp* (marginal R^2 = 0.29). (b) *Nyctalus* (marginal R^2 = 0.86). Bold indicates parameters where the error of the estimate does not cross zero.

GLMM Model	Habitat parameters	Estimate	Error	Z value
Occurrence of Myotis spp.	*Local scale*			
	Intercept	0.54	0.50	1.09
Presence (binomial)	**Stand interior**	**-1.30**	**0.31**	**-4.22**
	Stand density per hectare	**-0.60**	**0.17**	**-3.45**
	Altitude (m)	0.00	0.10	0.01
	Stand age	-0.05	0.12	-0.40
	Landscape scale			
	Distance to water (m)	-0.20	0.19	-1.72
	Shannons diversity index	0.08	0.15	0.53
	LPI (open land within 250 m)	0.06	0.14	0.46
	% ASNW (4km)	-0.08	0.20	-0.41
	Environmental variables			
	Mean nightly temperature (°C)	0.02	0.10	0.21
Occurrence of Nyctalus	*Local scale*			
	Intercept	-0.53	0.65	0.82
Presence (binomial)	**Stand interior**	**-1.46**	**0.39**	**-3.73**
	Stand type: Mature	**-2.04**	**0.70**	**-2.90**
	Stand type: Thicket	**-1.39**	**0.65**	**-2.13**
	Stand type: Thin	**-1.71**	**0.67**	**-2.53**
	Stand type: Young	-0.93	0.60	-1.53
	Altitude (m)	-0.03	0.17	-0.19
	LPI (open water within 500m)	**-4.85**	**1.43**	**-3.38**
	Shannon's diversity index	0.26	0.32	0.81
	Distance to water (m)	-0.07	0.17	-0.44
	% ASNW (4km)	-0.09	0.32	-0.27
	Total buildings	**-1.58**	**0.65**	**-2.44**
	ENN distance to nearest patch of closed canopy conifer (m)	**1.00**	**0.31**	**3.21**
	Environmental variables			
	Temperature	**1.66**	**0.40**	**4.12**

Table 5. Best approximating binomial distributed generalised linear mixed models (GLMM's) for the differential responses of *P. pygmaeus* and *P. pipistrellus* to local and landscape scale habitat parameters. Presented are the best approximating models (with shrinkage) using an information theoretic approach based on Akaike's Information Criterion adjusted for small sample sizes (AICc). Listed are the parameters and their respective impact on *P. pygmaeus* activity proportional to *P. pipistrellus* activity. Positive estimates predict a higher probability of recording *P. pygmaeus,* negative estimates predict a higher probability of recording *P. pipistrellus.* No response does not necessarily indicate that neither species was impacted but could mean both respond in the same way. Marginal R^2 = 0.09. Bold indicates parameters where the error of the estimate does not cross zero.

GLMM Model	Habitat parameters	Estimate	Error	Z value
Proportion of P. pygmaeus to	*Local scale*			
P. pipistrellus	Intercept	0.15	0.45	0.35
Activity (binomial)				
	Mature* stand interior	-0.44	0.44	-1.02
	Thicket* stand interior	-0.28	0.19	-1.45
	Thin* stand interior	**-1.45**	**0.25**	**-5.64**
	Young* stand interior	0.26	0.13	2.12
	Mature* distance to water	**0.55**	**0.07**	**7.15**
	Thicket* distance to water	**0.32**	**0.09**	**3.28**
	Thin* distance to water	**0.23**	**0.08**	**2.58**
	Young* distance to water	**0.40**	**0.08**	**4.89**
	Stand age (quadratic term)	**0.19**	**0.04**	**4.68**
	Landscape scale			
	Distance to nearest building (m)	**-0.32**	**0.06**	**-5.50**
	% felled land (3km)	-0.24	0.17	-1.42
	Distance to broadleaved woodland (m)	**0.55**	**0.05**	**9.96**
	Environmental variables			
	Temperature*Altitude	-0.36	0.07	-4.25

Figures:

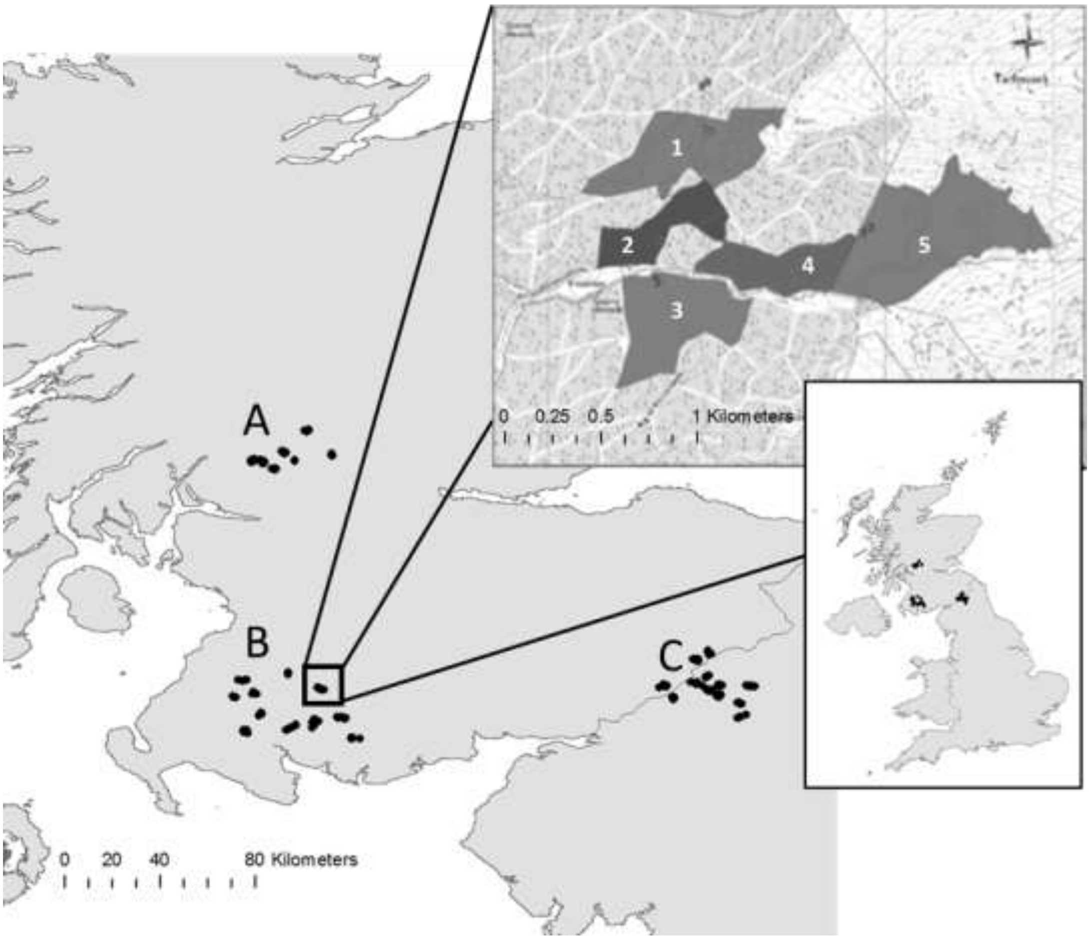

Figure 1. Location of field sites at three different study areas in (A) Cowal and Trossachs, South West Scotland, (B) Galloway, South West Scotland and (C) Kielder, Northern England. Stand types were as follows: Clearfell (felled less than 5 years ago, 1), Young (planted between 5 and 10 years ago, 2), Thicket (planted between 10 and 20 years ago, 3), Thin (planted between 20 and 40 years ago, 4), Mature (planted more than 40 years ago, 5).

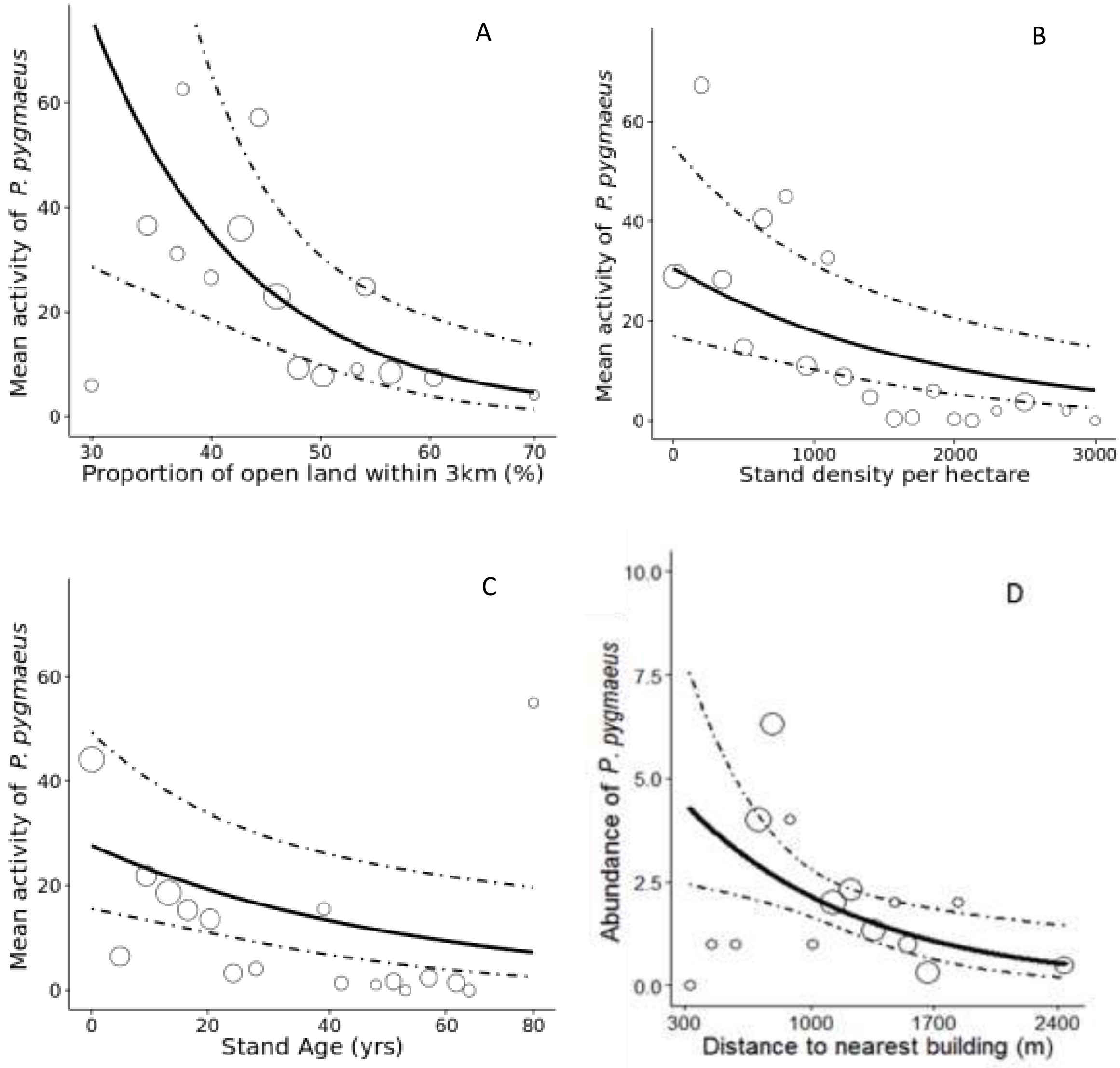

Figure 2A – C. Estimated mean *P. pygmaeus* activity against (A) Proportion of open land within 3km radius of sampling point, (B) Stand tree density per hectare and (C) Stand age (years), using model averaged estimates. Original data on activity (number of passes in a four hour sampling period) are superimposed as grey circles with diameter proportional to the number of sampling points where mean activity occurred. Bold line indicates line of best fit from the top model set. Dashed lines represent 95% confidence intervals around the predictions. Figure 2D. Estimated probability of *P. pygmaeus* abundance in relation to distance to nearest building (m), using model averaged estimates. Original data on abundance (number of individuals caught) are superimposed as grey circles with diameter proportional to the number of sampling points where mean abundance occurred. Bold line indicates line of best fit from the top model set. Dashed lines represent 95% confidence intervals around the predictions.

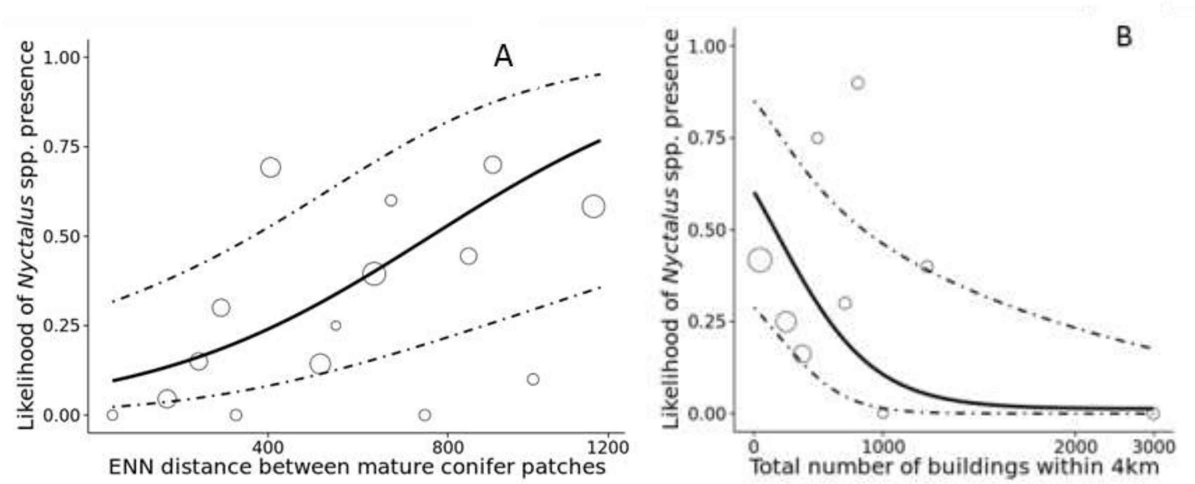

Figure 3. Estimated probability of recording *Nyctalus* with (A) increasing Euclidean distance (ENN) between closed canopy conifer patches, (B) Total number of buildings within 4km. Original data on activity (number of passes in a four-hour sampling period) are superimposed as grey circles with diameter proportional to the number of sampling points where mean activity occurred. Bold line indicates line of best fit from the top model set.

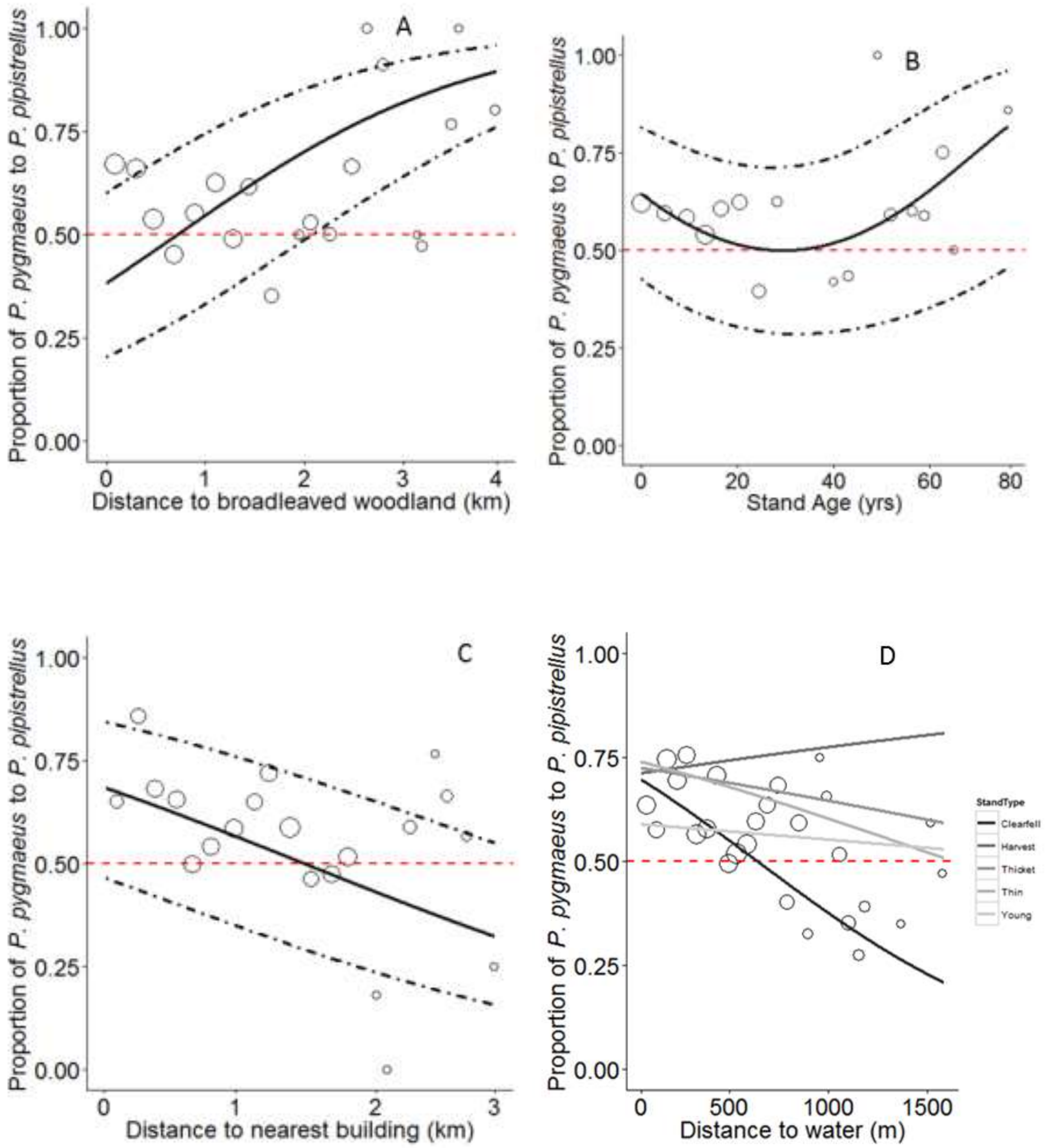

Figure 4 A - D Model averaged estimated probability of *P. pygmaeus* activity proportional to *P. pipistrellus* activity in relation to (A) Distance to broadleaved, (B) Stand age (quadratic term), (C) Distance to nearest building (D) Stand type and distance to water. Original data on the proportion of *P. pygmaeus* to *P. pipistrellus* are superimposed as grey circles with diameter proportional to number of sampling locations where proportional activity was recorded. Dashed red line indicates the proportion at which *P. pygmaeus* and *P. pipistrellus* activity was equal. Bold line indicates line of best fit from the top model set.