# Species mobility and landscape context determine the importance of local and landscape-level attributes: Insights from a large-scale natural experiment

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Running head: Local & landscape factors influence bats

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## ABSTRACT:

Conservation strategies to tackle habitat loss and fragmentation require actions at local (e.g. improving/expanding existing habitat patches) and landscape level (e.g. creating new habitat in the matrix). However, the relative importance of these actions for biodiversity is still poorly understood, leading to debate on how to prioritise conservation activities. Here, we assess the relative importance of local *vs*. landscape-level attributes in determining the use of woodlands by bats in fragmented landscapes; we also compare the role of habitat amount in the surrounding landscape *per se vs*. a combination of both habitat amount and configuration and explore whether the relative importance of these attributes varies with species mobility and landscape context. We conducted acoustic surveys in 102 woodland patches in the UK which form part of the WrEN project (www.wren-project.com), a large-scale natural experiment designed to study the effects of 160 years of woodland creation on biodiversity and inform landscape-scale conservation. We used multivariate analysis and a model-selection approach to assess the relative importance of local (e.g. vegetation structure) and landscape-level (e.g. amount/configuration of surrounding land types) attributes on bat occurrence and activity levels. Species mobility was an important trait determining the relative importance of local *vs*. landscape-level attributes for different bat species. Lower mobility species were most strongly influenced by local habitat quality; the landscape became increasingly important for higher mobility species. At the landscape-scale, a combination of habitat amount and configuration appeared more important than habitat amount alone for lower mobility species, whilst the opposite was observed for higher mobility species. Regardless of species mobility, landscape-level attributes appeared more important for bats in a more homogeneous and intensively farmed landscape. Conservation strategies involving habitat creation and restoration should take into account the mobility of target species and prioritise landscape-level actions in more homogeneous and intensively farmed landscapes where habitat loss and fragmentation have been more severe.

Keywords: Bats, Chiroptera, connectivity, ecological networks, fragmentation, landscape-scale conservation, natural experiment, woodland creation, WrEN project.

## 1. INTRODUCTION:

Habitat loss and fragmentation are amongst the main threats to biological diversity (Haddad *et al*. 2015). Reversing these trends is therefore a high conservation priority, and becoming increasingly important with the need to make species populations more resilient to climate change (e.g. by facilitating inter-population movements and providing more resources to support population recovery; Newson *et al.* 2014). Conservation strategies to tackle habitat fragmentation often include creating new habitat patches, expanding, connecting and restoring existing patches, and increasing the permeability of the surrounding matrix to increase the persistence and movement of species across the landscape (Lawton *et al.* 2010). This approach requires actions at both the local and landscape level. However, the relative importance of these actions is still poorly understood and much debated (e.g. Hodgson *et al.* 2011; Fahrig 2013; Hanski 2015). This hampers the translation of ecological theory into practice and highlights the urgent need for scientific evidence to inform conservation and ensure that habitat creation and restoration activities are implemented in the most effective manner to benefit biodiversity.

Studies on habitat fragmentation can provide insights into what factors are likely to be important for habitat creation and restoration (e.g. Humphrey *et al.* 2015). However, their focus is mainly on the capacity of species to persist in habitat fragments, rather than on their ability to colonise and capitalise on new patches. Therefore, there is a need for ecological studies informing landscape-scale conservation to investigate the effects of habitat restoration and creation. Additionally, such studies should focus on landscapes at sufficiently large spatial scales to ensure ecological realism and incorporate appropriately long time scales to account for the considerable lag in ecosystem development and colonisation associated with habitat restoration and creation (Watts *et al.* 2016).

The WrEN project (Watts *et al.* 2016) is a large-scale natural experiment designed to study the effects of 160 years of woodland creation on biodiversity in UK landscapes; WrEN aims to inform conservation activities by quantifying the relative effects of different local and landscape-level attributes on woodland biodiversity. Historically, woodland has been severely affected by habitat loss and fragmentation, with worldwide deforestation resulting in a 50% decrease in woodland cover over the last three centuries (Ramankutty & Foley 1999; ‘woodland’ is the term commonly used in the United Kingdom to describe any forested area, for convenience we use this term hereafter in the paper). More recently, deforestation rates have slowed down; net woodland loss has halved over the last 25 years and woodland extent has increased in many countries, particularly in temperate regions, largely through deliberate planting often encouraged through the provision of financial incentives to landowners (Keenan *et al.* 2015). It is often assumed that creating new woodlands will benefit biodiversity. However, despite an overall increase in woodland area over recent decades, many species (particularly those associated with native semi-natural woodland) continue to undergo severe population declines in many places (e.g. Burns *et al.* 2013). A sound ecological knowledge of the factors likely to enhance biodiversity in newly planted woodlands is of key importance to inform future conservation strategies if these are to benefit biodiversity. However, slow rates of vegetation succession, together with significant time lags in species colonisation and capitalisation of new habitat patches, have resulted in a lack of empirical studies assessing the long-term value of woodland creation and the relative importance of local (e.g. patch size and quality) *vs*. landscape-level (e.g. degree of connectivity) characteristics for biodiversity.

In the UK, long-term deforestation has been so severe that woodland cover dropped from a post-glacial high of 70% to a low of 5% in 1900 (Watts 2006). Since then it has increased to 13%, mainly as a result of woodland planting and restoration programmes that started in the mid-19th century and increased in the 20th century (Quine *et al.* 2013). These historical changes in woodland cover have resulted in landscapes containing new woodland patches of varying ages, sizes and degrees of isolation. Many of these new woodlands were established on agricultural land without remnant woodland biodiversity. Therefore, the occurrence and relative abundance of species within these sites represents successful colonisation, presumably mediated by attributes of the sites themselves and the landscapes around them. This array of new woodland sites forms the basis of the WrEN project (Watts *et al.* 2016).

We have selected bats as one of the WrEN taxonomic study groups because many bat species are woodland specialists (i.e. are strongly dependent on woodland for roosting and/or foraging) whilst others frequently use woodland for roosting, foraging or as commuting habitat alongside other land types (Lacki, Hayes & Kurta 2007). Therefore, bats have been badly affected by worldwide deforestation (Mickleburgh, Hutson & Racey 2002) and fragmentation (e.g. Meyer & Kalko 2008). Many bat species are highly mobile and so are influenced by both woodland extent and configuration at relatively large spatial scales (e.g. up to 5 km; Klingbeil & Willig 2009; Boughey *et al.* 2011a; Fuentes-Montemayor *et al.* 2013). Bats' responses to habitat fragmentation often depend on species life-history traits, such as roosting and foraging ecology. In general, slow-flying species adapted to forage in cluttered environments, are particularly sensitive to habitat fragmentation (e.g. Meyer & Kalko 2008), whilst fast-flying species adapted to forage in uncluttered environments are relatively tolerant of fragmentation processes (e.g. Klingbeil & Willig 2009). Local woodland attributes (e.g. vegetation structure) are also important in determining the availability and quality of habitat for bats. In general, mature broadleaved woodlands with high availability of large diameter snags and dense canopy cover are associated with high bat activity levels (Lacki, Hayes & Kurta 2007).

We studied temperate bat assemblages in historic woodland creation sites as part of the WrEN project. Our objectives were to:

i) Assess the relative importance of local *vs*. landscape-level habitat characteristics on species occurrence and activity levels.

ii) Compare the role of habitat amount in the surrounding landscape *per se vs*. a combination of both habitat amount and configuration in determining species occurrence and activity levels.

iii) Examine how variables identified in i) and ii) vary between bat species with differing mobility.

We expect the relative importance of local *vs*. landscape-level attributes to depend on species mobility (hypothesis 1), with higher mobility species being more strongly influenced by their surrounding landscape than lower mobility species for which local woodland character might be more important (Meyer & Kalko 2008; Fuentes-Montemayor *et al.* 2013). At the landscape scale, we expect amount of surrounding woodland to be more important for higher mobility species, whereas a combination of surrounding woodland amount and configuration will be more important for lower mobility species (hypothesis 2), as the latter are more limited by dispersal and often reluctant to fly across open spaces (Entwistle, Racey & Speakman 1996; Frey-Ehrenbold *et al.* 2013).

Additionally, we identify specific local (e.g. woodland patch size and vegetation structure) and landscape-level (e.g. proportion of different habitat types in the surrounding matrix) attributes influencing the occurrence and/or activity levels of temperate bats. Finally, we use our findings to provide recommendations to inform landscape-scale conservation strategies which aim to combat habitat loss and fragmentation.

## 2. MATERIALS AND METHODS:

### 2.1. Study area and site selection protocol:

The WrEN woodland sites are located in two study areas in Scotland (*ca*. 7,335 km$^2$) and England (*ca*. 8,570 km$^2$) (Figure 1). Both areas are dominated (>70%) by agricultural land and represent fairly typical lowland landscapes in these countries. We used digital maps within a GIS environment (ArcGIS 10.2; ESRI) and a systematic site-selection process to identify 102 broadleaved woodland patches (>80% broadleaved canopy cover according to the National Forest Inventory; Forestry Commission 2012) created over the past 160 years on what was previously agricultural land (see Watts *et al.* 2016 for a detailed description of the site-selection protocol). These sites were selected to range in area (0.5 to 30 ha), age (10 to 160 years old), amount of woodland within the surrounding landscape (0.4 to 17% broadleaved woodland within a 3 km buffer) and isolation from the next nearest broadleaved woodland (10 to 1570 m). We surveyed woodlands of different character evenly throughout the duration of the field seasons and across the study areas, avoiding any seasonal or spatial bias. The majority of study sites were at least 3 km (a minimum of 1 km) from each other.

### Figure 1 approximately here ###

### 2.2. Characterisation of local-level attributes:

We conducted field surveys to characterise the vegetation structure of all woodland patches. Vegetation surveys were conducted along edge-to-interior transects. We established points every 15 m along each transect and used the point-centred quarter method to collect the following data: tree species richness, tree density and tree diameter at breast height (DBH; only trees ≥ 7 cm DBH were measured). Each point also served as the corner of a 10 m × 10 m quadrat which was used to visually assess understory cover (%). Canopy cover (%) was assessed using a sighting tube with an internal crosshair; if the crosshair intersected canopy vegetation, presence of canopy was recorded (Fuentes-Montemayor *et al.* 2013). This was repeated 10 times at 1 m intervals perpendicular to each of the transect-points. We used the OS historic maps collection (EDINA 2013) to determine the age of each woodland patch (i.e. the time period when each woodland patch ‘appeared’ in maps - see Watts *et al.* 2016 for further details). We used digital maps (National Forest Inventory) and GIS software to measure the area and shape (patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area; McGarigal & Cushman 2002) of each woodland. We also used Land Cover Map 2007 data (Morton *et al.* 2011) to measure the proportion of woodland edge adjacent to each of the following land cover types: 1) agricultural areas (i.e. arable land or agriculturally improved grassland), 2) semi-natural vegetation (e.g. rough-grassland and scrub), 3) urban areas (e.g. buildings and roads) and 4) water. Improved grassland is distinguished from semi-natural grasslands based on its higher productivity and lack of winter senescence. The proportion of woodland edge adjacent to water approximated zero and was excluded from further analyses.

### 2.3. Characterisation of landscape-level attributes:

We used GIS software to create buffers of different sizes (100, 250, 500, 1000, 1500, 2000, 2500 and 3000 m) around each of the 102 woodland patches. These spatial scales were selected to represent distances travelled during foraging trips (i.e. from a roost to a feeding site) by low (e.g. *Plecotus auritus*), intermediate (e.g. *Pipistrellus pygmaeus*) and higher mobility bat species (e.g. *Pipistrellus pipistrellus*; Entwistle, Racey & Speakman 1996; Nicholls & Racey 2006) in agricultural landscapes. Within each buffer category we measured the proportion of land covered by woodlands of the following categories: 1) any woodland (including broadleaved, conifer and mixed woodland), 2) broadleaved woodland (>80% canopy covered by broadleaved trees) and 3) ancient woodland (i.e. native woodland areas which have remained woodland since at least 1600 in England and 1750 in Scotland). We also calculated a measure of inter-patch connectivity between our study sites and surrounding woodland patches of each of the woodland categories outlined above. This measure is based on the Incidence Function Model (Hanski 1994; Moilanen & Hanski 2001; Moilanen & Nieminen 2002). The sum contribution from all surrounding woodland patches of each category was calculated based on their size and distance from the target patch (i.e. each of our study sites), assuming that 5% of dispersers would potentially reach each of the previously defined buffer sizes (i.e. 100, 250, 500, 1000, 1500, 2000, 2500 and 3000 m). Thus the contribution from each surrounding patch declines along a negative exponential dispersal function to the target patch. We also measured the Euclidean distance to the nearest woodland of each category. For woodland categories 1) and 2) we used data from the National Forest Inventory and for 3) we used the Ancient Woodland Inventory (Forestry Commission 2011). In addition, we used Land Cover Map 2007 (Morton *et al.* 2011) data to quantify the proportion of land covered by agricultural areas, semi-natural vegetation, urban areas and water bodies (as described in Section 2.2) in the matrix surrounding each woodland patch within each buffer size.

### 2.4. Bat surveys and sound analyses:

We conducted bat surveys between June and August in 2013 (in Scotland n=31) and 2014 (Scotland n=35; England n=36) using ultrasonic detectors which recorded simultaneously at the edge and ‘interior’ (i.e. 50m away from the edge) of each woodland patch. Each site was surveyed once, starting 45 minutes after sunset (to avoid recording bats commuting to feeding sites) and finishing 4 hours later. We recognise that a single visit to each woodland provides only a coarse description of local bat assemblages and that species with low detectability (e.g. *P. auritus*) might have been missed at some sites; we adopted this approach in order to maximise the number/range of sites surveyed and statistical power, and because previous work has indicated that it can successfully identify influential habitat characteristics (e.g. Fuentes-Montemayor *et al*. 2013; Lintott *et al*. 2015). SongMeter SM2BAT+ and SongMeter SM3 detectors (Wildlife Acoustics Inc.) were used in 2013 and 2014 respectively. Whilst the performance of the two detector types might differ, woodlands of different character (e.g. sizes, shapes and degree of isolation) were evenly surveyed throughout the two field seasons and across the study areas to avoid any seasonal or spatial bias. Sound files were recorded in WAC format and later converted to zero crossing for sound analysis using AnalookW 4.1 (Titley Electronics). Files which required further inspection for species identification were converted to WAV format and analysed using BatSound 4.2 (Pettersson Elektronik AB). We analysed all bat recordings manually to identify bat species and quantify activity (numbers of bat passes, ≥ 2 echolocation calls within 1 s of each other; Walsh & Harris 1996). Of the six bat genera present in the study area *Pipistrellus, Plecotus* and *Barbastella* were identified to species; *Myotis, Nyctalus* and *Eptesicus* were identified to genus due to similarities in call structure between species. *Eptesicus serotinus* calls can sometimes be difficult to distinguish from *N. leisleri*; when this was the case these two species were grouped into a single category but due to small sample size (<50 bat passes in total) were later excluded from analyses. *Barbastella* and *Eptesicus* only occur in England (Richardson 2000).

### 2.5. Statistical analyses:

All statistical analyses were conducted in R v3.2.2 within Rstudio v0.99.484 using the MASS v7.3-43 and MuMIn v1.15.1 packages (Barton 2015; R Core Team 2015; RStudio Team 2015; Venables & Ripley 2002). We ran separate analyses for the two study areas given that:

1) the relative abundance of different bat species differs in England and Scotland (Richardson 2000); and 2) land-use intensity is higher in England than in Scotland (e.g. higher proportion of farmland tilled annually and lower proportion of land covered by woodland in England than in Scotland; Robinson & Sutherland 2002; Watts 2006).

### 2.5.1. Selection of landscape-level variables:

Given the high degree of collinearity between proportions of land covered by a particular land type across different spatial scales, we conducted Generalised Linear Models (GLMs) using bat activity of each species per site as a response variable (species presence in the case of *P. auritus* due to low activity levels) and the proportion of land covered by each land type category at each spatial scale as the only explanatory variable in each model. Models were fitted using Negative Binomial error distributions (except for *P. auritus* where a Binomial error distribution was used; Crawley 2013). For each land type category (i.e. any woodland, broadleaved woodland, ancient woodland, agricultural, semi-natural, urban and water; for descriptions see Section 2.2) we selected the spatial scale with the largest coefficient to be included in further analyses.

### 2.5.2. Principal components analysis:

We used Principal Components Analysis (PCA) to reduce the number of explanatory variables to be included in statistical models. We adopted this approach because we were primarily interested in the relative influence of local *vs*. landscape-level attributes on different bat species, depending on their mobility, rather than on the effects of specific variables which have already been identified as predictors of bat occurrence/activity in fragmented landscapes (e.g. Fuentes-Montemayor *et al*. 2013). To test hypothesis 1, we conducted a PCA for all local-level attributes (described in Section 2.2 and Table 1) and separate PCAs for landscape-level attributes (described in Sections 2.3, 2.5.1 and Table 1). To test hypothesis 2, we conducted two sets of landscape-level PCAs, one incorporating metrics relating to the amount of surrounding woodland, and the other to woodland inter-patch connectivity (as described in Section 2.3) to account for both amount and configuration of surrounding woodland. Variables in PCAs were scaled to standardise the weights of components. Details of PCA analyses are presented in Appendix S1.

### Table 1 approximately here ###

### 2.5.3. Model specification and selection approach:

We conducted GLMs to quantify the relative importance of local *vs*. landscape-level attributes on activity levels or presence of each species. Data recorded at woodland 'edge' and 'interior' were pooled. Full models incorporated Principal Components (PCs; see Section 2.5.2) explaining ≥ 10% variation in the data for either 'local', 'landscape' or both 'local and landscape' level attributes. In addition, date (days since first bat survey of the season) and minimum temperature per night (data obtained from Met Office) were included as covariates in the full models. For Scotland, year (2013 or 2014) was included as a factor; however, preliminary analyses indicated that temperature in Scotland was significantly lower in 2014 than in 2013 ($t = -3.90$; coefficient ± SE = -2.83 ± 0.73; $P = <0.001$); therefore only one of these two predictors was included in each model at a time during the model selection procedure. We then followed an information-theoretic model-selection approach based on AICc (Akaike Information Criterion corrected for small sample sizes) to compare all candidate models (i.e. all possible combinations of predictors included in a particular model) to identify the best model (i.e. lowest AICc value) for each response variable (Burnham & Anderson 2002). In the Results section we report ΔAICc (relative to the model with the lowest AICc within a particular set of models) and $R^2$ values (Likelihood-ratio based pseudo-$R^2$; not adjusted). For illustrative purposes, we also present parameter estimates (±SE) and *P* values obtained from the best models for each response variable; these were not used during the model-selection process.

## 3. RESULTS:

We surveyed a total of 66 sites in Scotland and 36 sites in England; we detected six species/genera and counted 56,543 bat passes during a total of 816 recording hours. These were soprano pipistrelles (*Pipistrellus pygmaeus*; 48.1% of all bat passes), common pipistrelles (*Pipistrellus pipistrellus*; 41.0%), *Myotis* sp. (2.1%), *Nyctalus* sp. (1.0%), brown long-eared bats (*Plecotus auritus*; 0.2%), Nathusius pipistrelles (*Pipistrellus nathusii*; 0.1%) and barbastelle bats (*Barbastella barbastellus*; <0.1%) (Table 2). *Myotis nattereri* and *M. daubentonii* were identified to species level in some cases, but these data were insufficient for species-specific analyses and were pooled to genus level for further analyses. Due to small sample size *P. nathusii* and *B. barbastellus* were excluded from analyses. Models with the lowest AICc for each response variable usually explained between 35% and 66% of data variation, except for *P. auritus* in Scotland ($R^2$ = 17%) and *Myotis* sp. ($R^2$ Scotland = 16%; $R^2$ England = 25%) which had lower explanatory power (Figure 2).

### Table 2 approximately here ###

### Figure 2 approximately here ###

### 3.1. Relative importance of local *vs*. landscape-level habitat characteristics:

In Scotland, models which included only local-level variables were better (i.e. had lower AICc and higher $R^2$ values) than those including only landscape-level variables for *P. auritus*, *P. pygmaeus* and *P. pipistrellus* (Figure 2a,c,e); the opposite was observed for *Myotis* sp. (Figure 2g). In England, local-only models were better than landscape-only models for *P. auritus* and *P. pipistrellus* (Figure 2b,f), but the opposite was observed for *P. pygmaeus, Myotis* sp. and *Nyctalus* sp. (Figure 2d,h,i). However, in both study areas the best models (i.e. lowest AICc and highest $R^2$ values) for most bat species included both local and landscape-level predictors, except for *P. auritus* (Scotland) where the best model included local variables only and *Myotis* sp. (England) where the best model included landscape variables only (Figure 2). Where landscape-level variables were retained in the best models, these usually incorporated woodland inter-patch connectivity metrics, except for *P. pipistrellus* (Scotland) and *Myotis* sp. (Scotland and England), where the proportion of woodland in the landscape provided a better model fit (Table 3).

### Table 3 approximately here ###

**3.2.Effects of specific local and landscape-level habitat characteristics on bats:**

In the majority of cases, PCs 1-4 explained ≥10% of variation in the data (for both local and landscape-level PCAs) and were therefore included in further analyses; in two cases (for *P. pipistrellus* Scotland and *Nyctalus* sp. England) Landscape-PC5 was also included. Total variance explained by these ranged from 66% to 79% in Scotland and 74% to 86% in England (see Appendix S1 for species-specific figures illustrating the most influential PC axes). Since we conducted two sets of landscape-level PCAs (see Section 2.5.2), in the following paragraphs we differentiate between 'Landscape-PCs (amount)' (i.e. PCs incorporating metrics relating to the amount of surrounding woodland) and 'Landscape-PCs (configuration)' (i.e. PCs incorporating woodland inter-patch connectivity metrics).

After accounting for the effects of year, date and temperature, the occurrence of *P. auritus* was negatively related to Local-PC2 in Scotland (although model $R^2$ was low) and to Local-PC3 in England (Table 3; Appendix S1), mainly indicating a higher probability of occurrence in woodlands bordering agricultural land rather than semi-natural habitat (in Scotland) and a relatively open canopy, low tree densities and low proportion of urban edge (in England). Local-PC4 and Landscape-PC3 (configuration) were also marginally related (positively and negatively, respectively) to the occurrence of *P. auritus* in England, indicating that this species is more likely to occur in woodlands with large amounts of understorey, relatively small trees (i.e. small DBH mean), that primarily border agricultural land and with larger amounts of water within 250m.

Activity levels of *P. pygmaeus* in Scotland were related to Local-PC1 (negatively) and Landscape-PC1 and PC2 (configuration) (positively and negatively, respectively), indicating higher activity in older woodlands with lower tree densities, larger trees (large DBH mean) and high degree of variation in tree size (large tree DBH SD) and in woodlands with larger amounts of semi-natural vegetation within 1 km and larger amounts of well-connected broadleaved and ancient woodlands within 1 and 3 km respectively. In England, *P. pygmaeus* activity was negatively related to Local-PC3 and Landscape-PC4 (configuration) indicating higher activity levels in woodlands with a relatively open canopy, lower tree densities, relatively low proportions of urban edge and large amounts of water within 2 km.

The activity of *P. pipistrellus* in Scotland was negatively related to Local-PC1 and PC4 and to Landscape-PC5 (amount), indicating higher activity levels in older woodlands with larger trees (large DBH mean), high degree of variation in tree size (large tree DBH SD), lower tree densities, relatively little understorey, a large proportion of urban edge and low amounts of ancient woodland within 500 m. In England, *P. pipistrellus* activity levels were negatively related to Local-PC1 and Landscape-PC3 (configuration), indicating similar patterns to those observed in Scotland at the local scale (i.e. higher activity in older woodlands with larger trees, high degree of variation in tree size and lower tree densities) and also higher activity levels in woodlands farther away from ancient woodland and with a larger proportion of water within 100 m.

*Myotis* bats activity levels in Scotland were only significantly related (negatively) to Landscape-PC4 (amount) indicating higher activity in woodlands with a larger proportion of water within 100 m and closer to other broadleaved woodland. In England, a positive relationship with Landscape-PC3 (amount) indicated mainly higher activity in woodlands with a smaller proportion of urban areas within 1500 m, a larger proportion of agricultural land within 1500 m and closer to other woodland, particularly broadleaved.

The activity of *Nyctalus* bats in England was negatively related to Local-PC3 and PC1 and Landscape-PC3 and PC1 (configuration), indicating higher activity in older woodlands with larger trees and higher variation in tree size, with a relatively open canopy, lower tree densities and smaller proportion of urban edge, and in woodlands with larger amounts of water within 2500 m and poorly connected woodland in the surrounding landscape (particularly ancient woodland within 250 m and broadleaved woodland within 1000 m).

## 4. DISCUSSION:

In this study we assessed bat occurrence and activity levels in secondary woodland patches created over the last 160 years as part of a large-scale natural experiment in two distinct study landscapes. Our primary interest was to evaluate the relative influence of local (i.e. woodland patch size, age and characteristics/quality) *vs*. landscape-level attributes (i.e. woodland amount, degree of isolation and nature of the surrounding matrix) on bats (objective i). Very few studies have simultaneously incorporated this full range of factors likely to influence biodiversity in fragmented woodland landscapes (<30% of studies have assessed five or more of these variables in tandem; Humphrey *et al.* 2015). We also compared the role of habitat amount in the surrounding landscape *per se vs*. a combination of both habitat amount and configuration in determining species occurrence and activity levels (objective ii). Finally, we explored the influence of species mobility on the relative importance of these factors for bats (objective iii). Bat species detected during our study ranged from relatively low (e.g. *P. auritus*) to high (e.g. *Myotis* sp.) mobility. In accordance with our hypotheses, this trait was important in determining the relative importance of local *vs*. landscape-level attributes for different bat species (hypothesis 1) and, at the landscape-scale, of woodland amount *vs*. configuration (hypothesis 2). Although we did not formally assess landscape-moderated effects (e.g. Tscharntke *et al*. 2012), our findings support the idea that the effects of habitat fragmentation/restoration processes depend on the landscape context (e.g. vary in landscapes with different proportions of suitable habitat; Andrén 1994). In general, our study sites in England were embedded in more intensively farmed landscapes with a lower proportion of semi-natural vegetation and lower degree of woodland connectivity than our study sites in Scotland (Watts *et al.* 2016), where landscapes tend to be more heterogeneous. These differences were consistently reflected in a higher importance of landscape-level attributes for bats in England than in Scotland.

### 4.1 Bat mobility and the relative importance of local *vs*. landscape-level attributes:

The occurrence of *P. auritus* was influenced largely by local-level attributes. These are relatively low mobility bats spending most of their time foraging within 500 m from their roosts (Entwistle, Racey & Speakman 1996), mainly in woodlands with large amounts of well-developed understorey (Murphy, Greenaway & Hill 2012). Their higher habitat specificity and lower mobility in comparison to other bat species might explain the relatively low importance of the surrounding landscape; as these bats are often reluctant to fly across open spaces and are restricted to woodland remnants, local habitat characteristics become more important. The best model for *P. auritus* in Scotland included only local variables, whilst the best model for England included local and landscape-level variables (although only local variables were significant predictors), which suggests the relative importance of the surrounding landscape is higher in more intensive agricultural landscapes such as central England.

Activity levels of pipistrelle bats (*P. pygmaeus* and *P. pipistrellus*) in both study areas were best explained by models including both local and landscape-level components. These species have intermediate mobility (e.g. the maximum straight-line distance a bat has been recorded from a roost during foraging trips in agricultural landscapes is 2300 m for *P. pygmaeus* and 3700 m for *P. pipistrellus*; Nicholls & Racey 2006). Our findings are in accordance with previous studies showing that these species are influenced by both local habitat attributes (e.g. woodland vegetation structure and patch configuration) and the surrounding landscape (e.g. amount of surrounding woodland; Fuentes-Montemayor *et al.* 2013). For both pipistrelle species the amount of data variation explained by landscape-level metrics relative to that explained by local-level attributes was higher in England than in Scotland, suggesting that the relative importance of the surrounding landscape is higher where fragmentation is more severe and land-use more intensive. Therefore, both species require a conservation approach involving habitat creation and management at local and landscape scales, but managing the landscape seems particularly important in more homogenous landscapes of intensive agriculture.

The activity of *Myotis* bats was mainly influenced by landscape-level attributes. Previous work carried out in woodlands within our study area in Scotland (Fuentes-Montemayor *et al.*

2013) suggests that most of the *Myotis* bats recorded during our surveys are likely to be *M. nattererii*. Whilst the specific foraging habitat preferences of different *Myotis* species present in the area might differ, these are all relatively high mobility species which can commute long distances from their roosts to their foraging sites (e.g. *M. nattereri* up to 6000 m; Smith & Racey 2008). Although the best models for these species did not retain any significant local-level woodland attributes, previous studies have shown that the activity of *Myotis* bats is influenced by some local habitat characteristics (e.g. higher activity levels in woodlands with higher tree densities), but that the importance of these is lower than that of landscape-level attributes (Fuentes-Montemayor *et al.* 2013). Similar to *Pipistrellus* species, for *Myotis* bats the amount of data variation explained by the landscape relative to that explained by local-level attributes was much higher in England than in Scotland.

Activity levels of *Nyctalus* bats were influenced by both local and landscape-level components. These bats display highest activity levels over lakes, rivers and intensive cattle grazing land (Vaughan, Jones & Harris 1997), while radio-tracking studies suggest a preference for pasture and broadleaved woodland areas (Waters, Jones & Furlong 1999; Mackie & Racey 2007). *Nyctalus* bats roost predominantly in tree cavities (Ruczyński & Bogdanowicz 2008) and are highly mobile, often foraging further than 6000 m from their roosts (Mackie & Racey 2007). This high mobility might explain why they were influenced by their surrounding landscape. However, information on these species' habitat associations at the local scale is scarce (although they are selective when choosing tree roosts; Ruczyński & Bogdanowicz 2008) which makes it harder to interpret the observed influence of local-level attributes on these species.

## 4.2 Woodland amount *vs*. amount and configuration:

For most bat species, a combination of woodland amount and configuration in the surrounding landscape (measured as inter-patch connectivity) appeared to be more important than a measure of only woodland amount in the landscape, except for *P. pipistrellus* (Scotland) and *Myotis* sp. (Scotland and England) for which the opposite was observed. Our findings suggest that lower mobility species respond strongly to habitat configuration (Hanski 2015), whereas for higher mobility species the amount of habitat in a landscape outweighs the importance of habitat configuration (Fahrig 2013). Higher mobility species, which are able to fly longer distances across a variety of land cover types (such as *P. pipistrellus*), are likely to find suitable foraging sites as long as they have a sufficient amount of woodland in the landscape, even if it is poorly connected. Despite the amount of woodland being more important than configuration for *P. pipistrellus* in Scotland, these bats often make use of linear landscape elements (e.g. tree lines and hedgerows) which might enhance woodland connectivity in the landscape and allow access to feeding sites over wider areas (Boughey *et al.* 2011b; Frey-Ehrenbold *et al.* 2013). Interestingly, however, woodland configuration did appear to be more important for *P. pipistrellus* in England than Scotland; this difference might be a result of the landscape in England being more dominated by intensive agricultural land with a lower proportion of woodland cover, making the effects of woodland fragmentation stronger (Andrén 1994).

As expected, woodland configuration was more important than woodland amount *per se* for lower mobility species such as *P. auritus* and *P. pygmaeus.* Short-range echolocating bats such as *P. auritus* have been shown to focus foraging activity in well-connected landscapes (Frey-Ehrenbold *et al.* 2013). *Pipistrellus pygmaeus* have also been shown to be influenced by habitat connectivity; for instance, they make use of hedgerows, particularly if these contain trees and are relatively close to woodland areas (Boughey *et al.* 2011b). Woodland connectivity at large spatial scales (e.g. within 3 km) has also been shown to increase the probability of occurrence of *P. pygmaeus* relative to that of other more mobile species such as *P. pipistrellus* (Lintott *et al.* 2016).

For *Nyctalus* bats, woodland configuration also appeared more important than just the amount of woodland in the surrounding landscape; this association was negative, however, indicating higher activity levels in poorly connected landscapes. This contrasts with previous studies showing higher activity levels of these species in well-connected landscapes (Frey-Ehrenbold *et al.* 2013), although other studies suggest that these species' preference for specific foraging sites is unlikely to be affected by connectivity (Mackie & Racey 2007).

### 4.3 Bat species-specific responses to local woodland character and surrounding landscape:

Most bat species were influenced by local woodland characteristics in a similar way. For instance, *P. pygmaeus*, *P. pipistrellus* and *Nyctalus sp.* all displayed higher activity levels or were more likely to occur in older woodlands with larger trees, higher structural heterogeneity (i.e. larger variability in tree diameter), lower tree densities and a relatively open canopy. Activity of both *Pipistrellus* species was higher in woodlands with relatively little understorey, whilst *P. auritus* was marginally more likely to be present in woodlands with larger amounts of understorey. Our findings are consistent with these species' habitat preferences, which include foraging in woodlands with low tree densities and open understorey (for *P. pygmaeus* and *P. pipistrellus*; Fuentes-Montemayor *et al.* 2013), old forests with native tree species and a dense and diverse understorey (for *P. auritus*; Murphy, Greenaway & Hill 2012) and roosting in woodlands with old, tall and thick trees (for *Nyctalus* bats; Ruczyński & Bogdanowicz 2008). Our findings also suggest that there might be long time lags before newly created woodlands (which are slowly-developing ecosystems) reach successional stages with a habitat structure likely to provide suitable resources for bats. In addition, the activity or probability of occurrence of most species (i.e. *P. auritus, P. pygmaeus* and *Nyctalus sp.*) was higher in woodlands with a lower proportion of urban edge, although the opposite was observed for *P. pipistrellus*. Previous studies have reported the avoidance of urban areas by *Nyctalus* bats (i.e. *N. leisleri*; Waters, Jones & Furlong 1999), whilst high amounts of urban development around woodlands have been shown to decrease the probability of occurrence of *P. pygmaeus* when compared to *P. pipistrellus* (which seem better adapted to urban environments; Lintott *et al.* 2015, 2016).

Bats' responses to landscape-level attributes were species-specific and more variable. In general, bat activity was higher in woodlands with larger amounts of water in the surrounding landscape. These findings are consistent with many bat species' preference for water/riparian areas (e.g. *P. pygmaeus*, Nicholls & Racey 2006; *Myotis* bats, Russ & Montgomery 2002; *Nyctalus* bats, Vaughan, Jones & Harris 1997). Woodland, particularly broadleaved woodland, has been described as one of the most important habitats for many bat species (e.g. Walsh & Harris 1996; Vaughan, Jones & Harris 1997). However, previous studies have reported negative associations between activity levels of some species (e.g. *P. pipistrellus*) and the amount of woodland in the landscape, suggesting that bats might use woodland more intensively in areas where it is scarce (Fuentes-Montemayor *et al.* 2013).

### 4.4. Conservation and management implications:

Bats' responses to local and landscape-level attributes were dependent on species mobility; lower mobility species were most strongly influenced by local habitat quality, whilst the surrounding landscape became increasingly important for higher mobility species (sections 3.1 & 4.1). Therefore, actions to enhance bat populations in fragmented landscapes should involve both local and landscape-scale habitat creation and management. We identified specific local and landscape-level habitat characteristics influencing the occurrence and activity levels of different bat species (section 3.2 & 4.3). Our findings provide evidence to suggest that:

- Local habitat quality should be enhanced, for instance by protecting mature woodlands, managing younger woodlands to promote the development of large trees, relatively low tree densities and open canopies, and maintaining low levels of urbanisation in the immediate surroundings of woodland patches. Increasing understorey cover would benefit gleaning bats but negatively affect aerial hawkers; this highlights the importance of ensuring structural heterogeneity (either within or between patches) to benefit a wider range of species.
- The surrounding landscape should be improved by increasing the amount of broadleaved woodland in the landscape. However, our findings indicate that whilst this might be an adequate conservation strategy for higher mobility species, improving woodland configuration (for example by spatially targeting woodland planting or creating wooded linear corridors between habitat patches to increase connectivity) seems particularly important for lower mobility species (section 4.2). Maintaining and enhancing the amount and quality of ponds and rivers in the landscape would also benefit most bat species.
- Landscape-scale management will be particularly important in more homogeneous and intensively farmed landscapes where woodland loss and fragmentation have been more severe.

Our findings provide evidence on the local and landscape-level factors likely to enhance biodiversity in newly planted woodlands and are highly relevant to conservation actions focused on the creation and restoration of habitats to reconnect fragmented landscapes. Many of the patterns we observed in bats are broadly similar to those displayed by other taxa (e.g. birds; Dolman *et al.* 2007) and our recommendations are likely to create woodland patches valuable not only for bats, but also for other species. Current work by the authors (e.g. Watts *et al.* 2016) focuses on surveying WrEN sites for a wide range of taxa with different life-history traits whose populations are likely to respond differently to changes in the structure, management and spatial configuration of woodlands and their surrounding landscape, and at different spatial and temporal scales. Using this approach we hope to identify potential differences in the requirements of different taxonomic or functional groups, as well as attempt to draw out general recommendations for conserving woodland biodiversity.

### 4.5. Conclusion:

Conservation strategies to tackle habitat fragmentation require actions at both local and landscape level. However, the relative importance of these actions is still poorly understood and much debated, hampering the translation of ecological theory into practice. Using a large-scale natural experiment (WrEN), we assessed the relative influence of local *vs*. landscape-level attributes on the occurrence and activity levels of a range of bat species of different mobility, and within two distinct study landscapes of varying land-use intensity. Our results indicate that species mobility is an important trait determining the relative importance of local *vs*. landscape-level attributes for different bat species; lower mobility species are most strongly influenced by local habitat quality, whilst the surrounding landscape becomes increasingly important for higher mobility species. In addition, for lower mobility species a combination of amount and configuration of habitat in the surrounding landscape appears more important than habitat amount only, whilst the opposite was observed for higher mobility species. Our results also show that, regardless of species mobility, landscape-level attributes appear more important for bats in more homogeneous and intensively farmed landscapes. Our findings are highly relevant to inform landscape-scale conservation, and suggest that conservation strategies involving habitat creation and restoration activities should take into account the mobility of target species and prioritise landscape-level actions in more homogeneous landscapes where woodland loss and fragmentation have been more severe.

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For further information and updates on the WrEN project visit http://wren-project.com/.

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**Table 1.** Local and landscape-level attributes measured for all woodland sites and included in PCAs.

| ID | Variable type | Variable | Description | Obtained from |
|---|---|---|---|---|
| 1 | Local | Tree species richness | Number of tree species. | Field surveys |
| 2 | Local | Tree density | Number of trees per hectare. | Field surveys |
| 3 | Local | Tree DBH (mean) | Tree diameter at breast height (average value; used as indicator of tree size). | Field surveys |
| 4 | Local | Tree DBH (SD) | Tree diameter at breast height (standard deviation; used as indicator of structural heterogeneity). | Field surveys |
| 5 | Local | Understorey cover | Proportion of understorey cover in 10x10 m quadrats (average value). Uses Domin scale. | Field surveys |
| 6 | Local | Canopy cover | Proportion of vegetation cover in canopy (average value). | Field surveys |
| 7 | Local | Patch age | Years since woodland patch appeared on historic maps. | Historic maps |
| 8 | Local | Patch area | Area of woodland patch (ha). | Digital maps / GIS |
| 9 | Local | Patch shape | Patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area. | Digital maps / GIS |
| 10 | Local | Agricultural edge % | Proportion of woodland edge adjacent to agricultural land. | Digital maps / GIS |
| 11 | Local | Semi-natural edge % | Proportion of woodland edge adjacent to semi-natural habitats. | Digital maps / GIS |
| 12 | Local | Urban edge % | Proportion of woodland edge adjacent to urban areas. | Digital maps / GIS |
| 13 | Landscape | Woodland (any type) % [a] | Proportion of landscape covered by woodland of any type. | Digital maps / GIS |
| 14 | Landscape | Woodland (broadleaved) % [a] | Proportion of landscape covered by broadleaved woodland. | Digital maps / GIS |
| 15 | Landscape | Woodland (ancient) % [a, b] | Proportion of landscape covered by ancient woodland. | Digital maps / GIS |
| 16 | Landscape | Woodland (any type) - Inter-patch connectivity [a] | Connectivity index based on the distance between the target woodland patch and all surrounding woodland patches (of any type) weighted by their area. | Digital maps / GIS |
| 17 | Landscape | Woodland (broadleaved) - Inter-patch connectivity [a] | Connectivity index based on the distance between the target woodland patch and all surrounding broadleaved woodland patches weighted by their area. | Digital maps / GIS |
| 18 | Landscape | Woodland (ancient) - Inter-patch connectivity [a, b] | Connectivity index based on the distance between the target woodland patch and all surrounding ancient woodland patches weighted by their area. | Digital maps / GIS |
| 19 | Landscape | Distance to nearest woodland (any type) | Distance (m) to nearest woodland of any type. | Digital maps / GIS |
| 20 | Landscape | Distance to nearest woodland (broadleaved) | Distance (m) to nearest broadleaved woodland. | Digital maps / GIS |
| 21 | Landscape | Distance to nearest woodland (ancient) | Distance (m) to nearest ancient woodland. | Digital maps / GIS |
| 22 | Landscape | Agricultural matrix % [a] | Proportion of landscape covered by agricultural land. | Digital maps / GIS |
| 23 | Landscape | Semi-natural matrix % [a] | Proportion of landscape covered by semi-natural habitats. | Digital maps / GIS |
| 24 | Landscape | Urban matrix % [a] | Proportion of landscape covered by urban areas. | Digital maps / GIS |
| 25 | Landscape | Water matrix % [a] | Proportion of landscape covered by water bodies. | Digital maps / GIS |

[a] Calculated within buffers of 100, 250, 500, 1000, 1500, 2000, 2500 and 3000 m.

[b] Native woodland areas which have remained woodland since at least 1600 in England and 1750 in Scotland; excludes plantations on ancient woodland sites.

**Table 2.** Bat species/genera detected in woodland sites through acoustic surveys.

| | Number of sites detected [b] | Total bat passes | Bat passes (% of total) |
|---|---|---|---|
| *Pipistrellus pygmaeus* | 95 | 27,183 | 48.07 |
| *Pipistrellus pipistrellus* | 92 | 23,014 | 40.70 |
| *Pipistrellus* sp.[a] | 85 | 4,363 | 7.72 |
| *Myotis* sp. | 70 | 1,171 | 2.07 |
| *Nyctalus* sp. | 31 | 582 | 1.03 |
| *Plecotus auritus* | 26 | 95 | 0.17 |
| *Pipistrellus nathusii* | 5 | 52 | 0.09 |
| *Barbastella barbastellus* | 3 | 9 | 0.02 |
| Other / unidentified | 32 | 74 | 0.13 |
| Total | 102 | 56,543 | 100 |

[a] Includes *Pipistrellus* bats (i.e. *P. pygmaeus*, *P. pipistrellus* and *P. nathusii*) which could not be confidently identified to species level.

[b] A total of 102 sites surveyed; at least one bat pass was detected in all sites.

**Table 3.** Parameter estimates (± SE) obtained from GLMs using local and landscape-level Principal Components as predictors and bat activity or species presence as response variables. Only top models (i.e. lowest AICc) are shown. All models were fitted using Negative Binomial error distributions (except for *P. auritus* where a Binomial error distribution was used).

| | Local | Landscape |
|---|---|---|
| *P. auritus* occurrence | | |
| Scotland | PC2 (-0.59 ± 0.29) * | - |
| England | PC3 (-2.42 ± 1.22) * | PC1-configuration (-2.20 ± 1.30) $^{\dagger}$ |
| | PC4 (1.60 ± 0.95) $^{\dagger}$ | PC3-configuration (-1.90 ± 1.19) $^{\text{ns}}$ |
| *P. pygmaeus* activity | | |
| Scotland | PC1 (-0.23 ± 0.09) ** | PC1-configuration (+0.20 ± 0.08) * |
| | | PC2-configuration (-0.33 ± 0.12) ** |
| England | PC3 (-0.47 ± 0.20) * | PC4-configuration (-0.75 ± 0.22) *** |
| *P. pipistrellus* activity | | |
| Scotland | PC1 (-0.66 ± 0.12) *** | PC5-amount (-1.05 ± 0.29) *** |
| | PC4 (-0.47 ± 0.18) ** | |
| England | PC1 (-0.69 ± 0.12) *** | PC3-configuration (-0.70 ± 0.17) *** |
| *Myotis* sp. activity | | |
| Scotland | PC1 (-0.19 ± 0.13) $^{\text{ns}}$ | PC4-amount (-0.58 ± 0.21) ** |
| England | - | PC3-amount (+0.94 ± 0.24) *** |
| *Nyctalus* sp. activity | | |
| Scotland | NA | NA |
| England | PC1 (-0.27 ± 0.11) * | PC1-configuration (-0.25 ± 0.12) * |
| | PC3 (-0.57 ± 0.16) *** | PC3-configuration (-0.64 ± 0.18) *** |

Significance values: ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$ and $^{\dagger}\, p \leq 0.1$, $^{\text{ns}}\, p \geq 0.1$. NA: insufficient data for analyses.

**Figure 1.** Map showing the location of the two study landscapes and woodland sites within them.

**Figure 2.** Summary of GLMs using ‘local’, ‘landscape’ and ‘local and landscape’ level Principal Components as predictors and bat activity or species presence as response variables. Bars represent model $R^2$ and dots are ΔAICc values (relative to model with the lowest AICc for that response variable). Only top models are shown for each category.

Figure 1.


Stirling
Edinburgh
Glasgow
N
0 5 10 20 Miles
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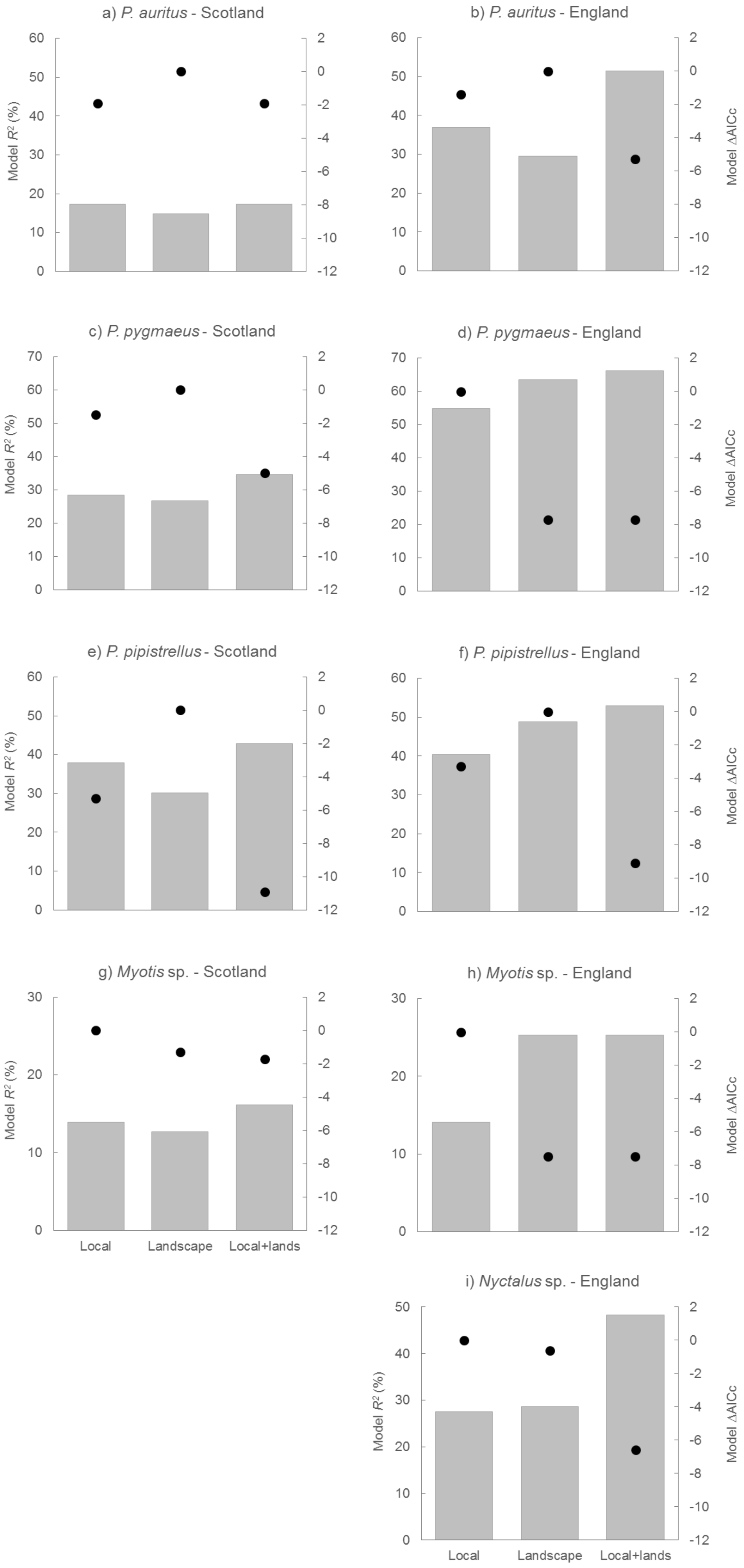
Nottingham
Leicester
Peterborough
Birmingham
Northampton
N
0 5 10 20 Miles
Esri, HERE, DeLorme, Mapmy India, © OpenStreetMap contributors, and the GIS user community

Figure 2.


a) P. auritus - Scotland
b) P. auritus - England
c) P. pygmaeus - Scotland
d) P. pygmaeus - England
e) P. pipistrellus - Scotland
f) P. pipistrellus - England
g) Myotis sp. - Scotland
h) Myotis sp. - England
i) Nyctalus sp. - England
Model R² (%)
Model ΔAICc
0
10
20
30
40
50
60
70
2
0
-2
-4
-6
-8
-10
-12
Local
Landscape
Local+lands