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Research article

What drives bat activity at field boundaries?

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ABSTRACT

Field boundaries are important habitat for bats in agricultural landscapes, serving as commuting and foraging areas for many species. The goal of our study was to better understand the drivers of bat activity in agricultural landscapes to inform conservation policy and make specific recommendations for habitat management. We placed sixty-four full spectrum bat detectors at random recording locations, weekly, along field boundaries in North Somerset between July and October 2020. We used an automated classifier to analyse recordings and performed error rate modelling to account for and remove the majority of error in automated classifications. We used generalised additive models to explore bat response to recording location metrics, controlling for spatial-autocorrelation and temporal differences in sampling. We validated our models with k-fold cross-validation and explored the utility of our models for predicting bat activity at new sites. We found that field boundary characteristics better describe bat activity than adjacent field characteristics or measures of local landscape for the majority of species studied. Bat activity was higher along tall, wide, vegetated field boundaries containing trees; there was lower activity at arable recording locations. Still, bat activity was highly variable and predictive error was high. We found a large spatial effect driving activity patterns, meaning models are not able to predict activity beyond the extent of the study area. We recommend management strategies that give incentives to farmers for replacing fences with hedgerows, planting hedgerow trees, and maintaining tall and outgrown field boundaries.

1. Introduction

Modern intensive agriculture is a major driver of the current biodiversity crisis (e.g. Sánchez-Bayo and Wyckhuys, 2019). Low levels of habitat diversity associated with intensive farming are a primary cause of species declines (Benton et al., 2003; Robinson and Sutherland, 2002). As half of all habitable land globally has been converted to agriculture (UN Food and Agricultural Organization, 2021) there is a need to make agriculture compatible with biodiversity (in Western Europe the proportion of land converted to agriculture is much higher: for example, in England 75% of land is used for agriculture; Rae, 2017).

Increasing landscape heterogeneity has been proposed as a method to make agricultural landscapes functional for both wildlife and humanity, increasing the area of vegetated field boundaries is a key approach for achieving this (Benton et al., 2003; Kremen and Merenlender, 2018; Tscharntke et al., 2021). Hedgerows and woody field boundaries provide food, shelter and facilitate landscape connectivity for wildlife (Barr et al., 1999; Montgomery et al., 2020), while services provided by functional ecosystems, such as flood management, pollination, nutrient cycling, soil retention, windbreaks and pest control, can improve agricultural outputs (Bommarco et al., 2018; Fischer et al., 2008; Pereira et al., 2018).

Bats are valuable pest control agents (Kunz et al., 2011; Williams-Guillén and Perfecto, 2011) which benefit from vegetated field boundaries (Graham et al., 2018; Walsh and Harris, 1996). Vegetated field boundaries support a diverse array of invertebrate prey items for bats (Froidevaux et al., 2019; Graham et al., 2018; Merckx et al., 2009), and vegetation offers shelter from wind and predators (Jones et al., 1995; Verboom and Spoelstra, 1999). Vegetated field boundaries could also act as navigational aids for species with quiet or high frequency echolocation calls that attenuate quickly in air (Altringham, 2011), for example *Rhinolophus* spp. Vegetated field boundaries are known to be of particular importance for *Rhinolophus ferrumequinum*, (Dietz et al., 2013; Ransome, 1996), as demonstrated by a study in southern England that found 71% of *R. ferrumequinum* activity to be in close proximity to field boundaries, compared to centres of fields (Finch et al., 2020).

Although the importance of field boundaries is well known, the mechanisms by which field boundaries benefit bats are still being

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explored. Specific aspects of field boundary structure are important for different bat species, likely a function of how different species utilise field boundaries (Lacoeuilhe et al., 2018), based on their echolocation and morphological adaptations (Jacobs and Bastian, 2016). Species adapted to forage in cluttered environments (e.g. *Myotis bechsteinii*) will prefer large, overgrown field boundaries (Toffoli, 2016). Species that forage along edge habitats (e.g. *Pipistrellus* species) have not previously been found to respond to specific aspects of hedgerow structure, although *P. pygmaeus* may prefer boundaries with a greater number of trees (Boughey et al., 2011). In general, high numbers of trees in field boundaries has been found to promote activity of many species (Boughey et al., 2011; Finch et al., 2020; Heim et al., 2015; Lacoeuilhe et al., 2018). Free-flying aerial hawkers such as *Nyctalus* spp. and *Eptesicus* spp. have not previously been found to associate with field boundary structure (Boughey et al., 2011; Finch et al., 2020; Kelm et al., 2014; Toffoli, 2016; Verboom and Huitema, 1997) and instead are likely responding to characteristics of adjacent fields, or local landscape characteristics.

Although some studies have investigated the relationship between specific field boundary measurements and bat activity (e.g. Boughey et al., 2011; Lacoeuilhe et al., 2018; Toffoli, 2016), the relationship remains unclear for many species (e.g. *Rhinolophus* spp.). Understanding how boundary features are important for bats is essential to inform recommendations for effective field boundary and habitat management that enhances biodiversity. In the UK, for example, best practice guidelines lack detail on the specific relationships different bat species have with field boundaries (Hedgelink, 2022), and further research into the link with bats and hedgerows has been recommended (ADAS UK Ltd, 2004). To our knowledge, no study has compared the relative importance of field boundaries with other landscape characteristics in driving bat activity, despite the importance of this information for informing evidence-based conservation strategies.

Here we investigate the relationship between field boundary structure, surrounding habitat and bat activity, with the aim of making specific recommendations for field boundary management. We predict that there will be high bat activity at vegetated field boundaries, vegetation biomass (as measured by height, width, tree content) will be positively associated with bat activity, and this association will be most pronounced in gleaning and edge-foraging species. We also explore the utility of our modelling approach for predictive modelling of bat activity across a wider landscape.

2. Materials and methods

2.1. Study site

Fieldwork was conducted over 12 weeks in North Somerset, UK, between 9th July and October 1, 2020. The target species was *R. ferrumequinum*, however, as our recording equipment picked up all bat species present in the study area the decision was made to include more species in our analysis. Fieldwork was carried out within 4 km of two *R. ferrumequinum* maternity roosts: Brockley Hall Stables SSSI (ST470669) and Kings & Urchin Woods SSSI (ST452647). The study site was chosen to comprise the main foraging areas around the roosts (Jones

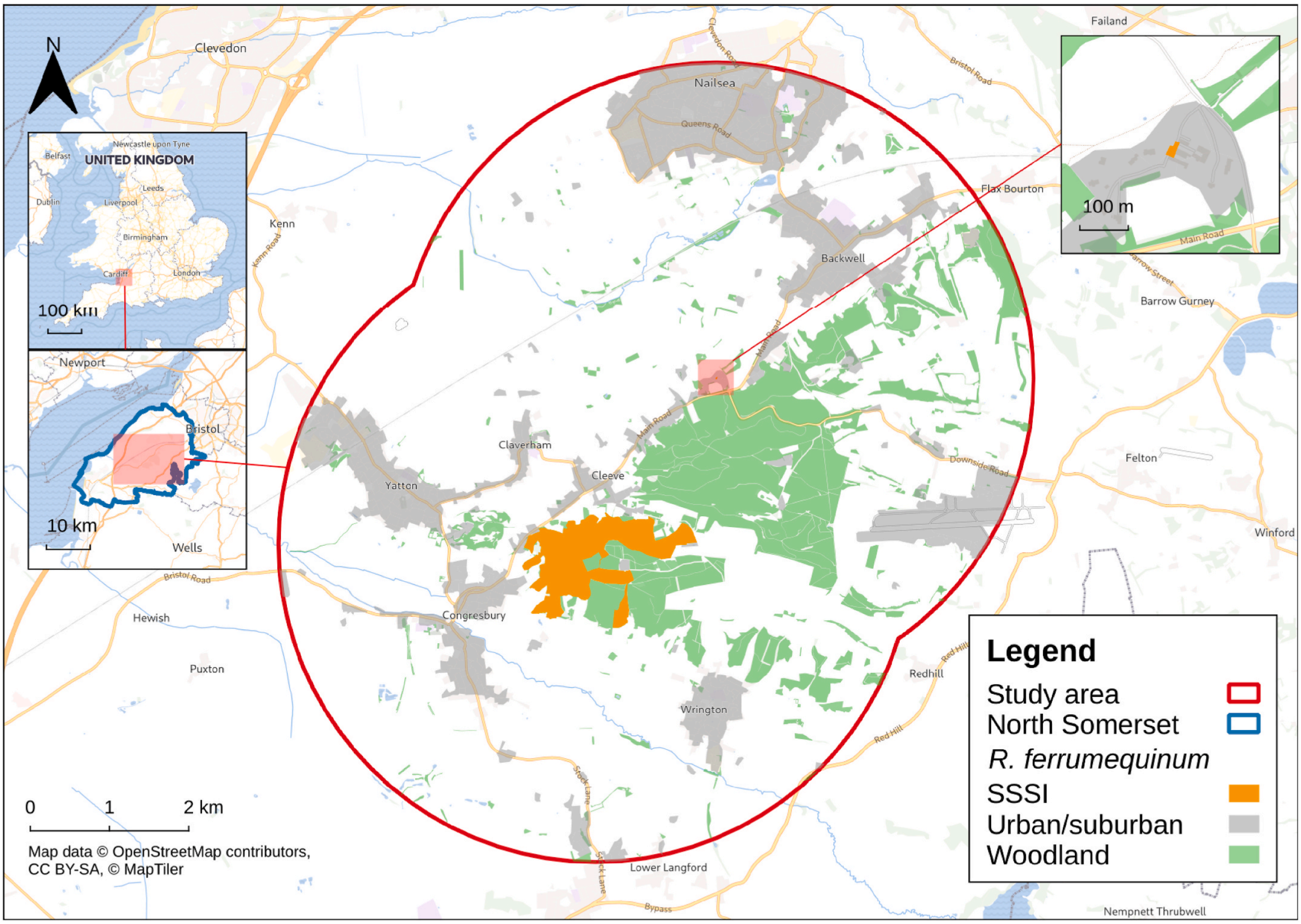

Fig. 1. Map showing location of study site (main image) within North Somerset (inset, lower left, and North Somerset in the UK (inset, top left). *Rhinolophus ferrumequinum* maternity roosts are located in the two SSSIs. The northernmost (inset, top right) is Brockley Hall SSSI, the southernmost is Kings and Urchin Woods SSSI.

et al. 1995; Billington, 2001; Burrows, 2018, Fig. 1). This set up gave us the additional opportunity to investigate how much the spatial component of bat activity depends upon knowledge of where the bats are roosting.

At 51° latitude, the study area has a wet and mild marine climate (Köppen classification *Cfb*). The topography of the area is diverse, encompassing the coastal plains of the North Somerset levels and limestone hills of the Lulsgate Plateau. Land cover in the study area comprises 14.4% broadleaf woodland, 0.8% coniferous woodland, 8.1% arable farmland, 58.9% grassland and 17.7% built-up areas and gardens (Morton et al., 2021). Arable crops include wheat and maize, while grassland is mainly grazed by cattle.

2.2. *Recording equipment*

We monitored bat activity using passive ultrasound detectors (Song Meter Mini Bat, Wildlife Acoustics Ltd, Manyard USA) placed along field boundaries (hedgerows, lines of trees, fences and ditches) in the study area. All detectors were new from the manufacturer and microphones were manufacturer-calibrated. We attached detectors to fenceposts or branches 1–2 m above the ground using cable ties, facing the length of the field boundary. We set detectors to record bat activity from 15 min before sunset to 15 min after sunrise, using a 20 kHz minimum trigger threshold and a maximum recording length of 1 min.

2.3. *Sampling design*

A stratified random sampling approach was employed whereby 32 recording locations were generated randomly along field boundaries each week, with 50% of locations within a 2 km buffer of the roosts and 50% between 2 and 4 km. This sampled the area closer to the roost at higher density and allowed for spatial stratification of detectors avoiding spatial temporal bias in sampling with regard to distance from the roost.

Detectors were moved to new recording locations every week after a minimum of six nights (Fig. 2), the minimum duration to ensure the detection of common species (Mathews et al., 2016). Different field boundary types (hedgerows, lines of trees, fences and ditches) were surveyed in proportion to their availability. We placed detectors in pairs where possible, one either side of each field boundary. An individual field boundary was defined as ending at the point of connection between two or more field boundaries, following DEFRA hedge survey guidelines (2007). Each recording location was surveyed only once. Spatial autocorrelation between recording locations was controlled for in the statistical analysis (section 2.6 below).

2.4. *Recording location characteristics*

Field boundary characteristics and habitats of adjacent fields were recorded at each recording location (Table 1). A field was defined as adjacent if the detector was able to pick up bats in that field, e.g. a detector on a thickly vegetated field boundary would only pick up bats on

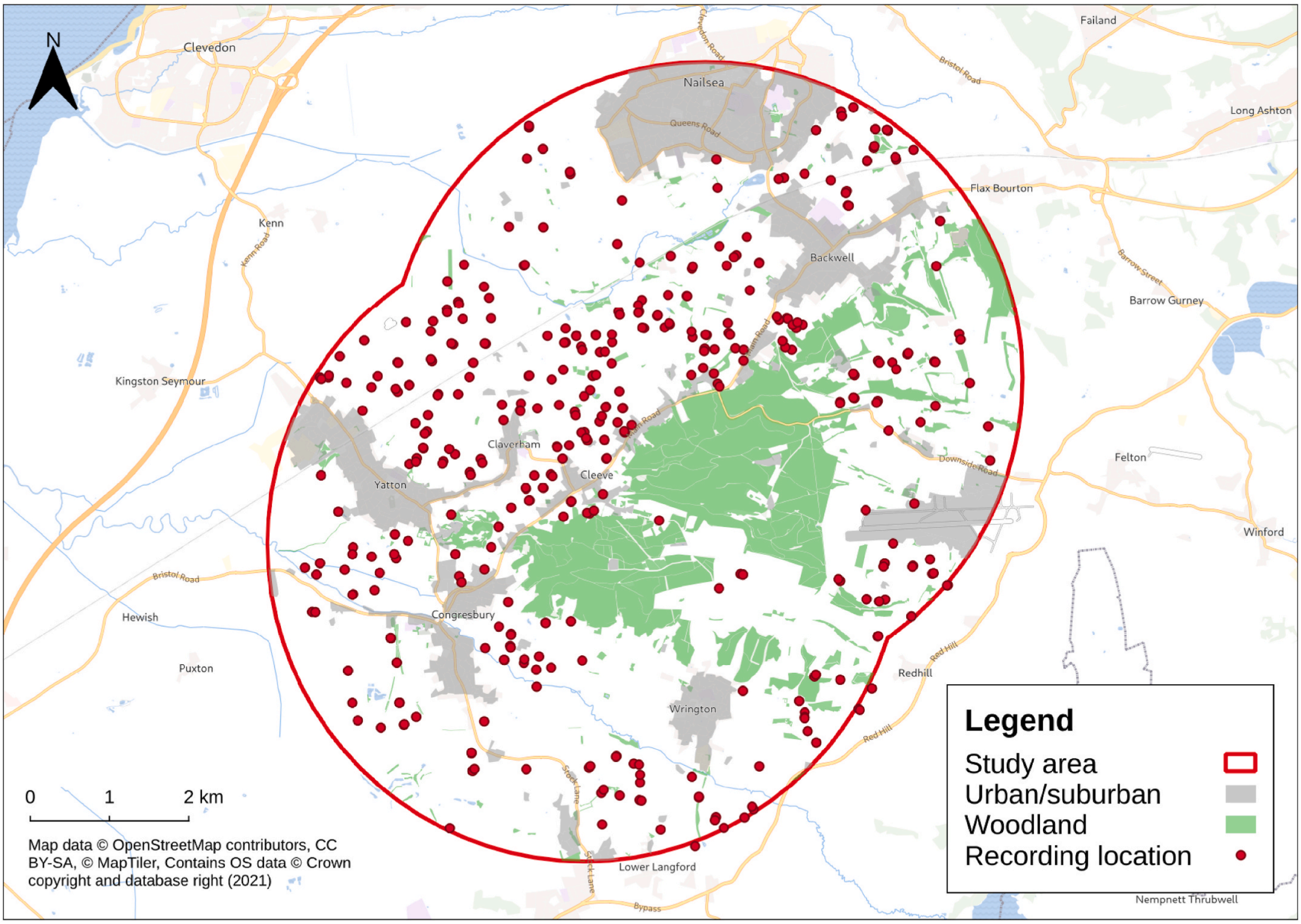

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Fig. 2. Map of study area and recording locations in North Somerset, UK.

Fig. 3. Photos of example recording locations.

the same side as the detector, whereas a detector placed on a bare fence would pick up bats in fields either side of the fence. Three adjacent field habitat types were surveyed: arable, improved grassland and road/track. Images of example recording locations are presented in Fig. 3.

To assess the impact of local landscape features on bat activity we created a 250 m buffer around each recording location and quantified local landscape metrics in QGIS (QGIS.org, 2022; Table 1). A number of different sized buffers (up to 4 km) were considered, at 500 m and above variables started to become collinear due to close proximity of recording locations. A 250 m buffer was the largest scale that was feasible to model and represents the immediate surroundings that may influence activity at the recording location.

2.5. *Bat activity*

2.5.1. *Acoustic analysis and error rate modelling*

Automated species identification was necessary as manual classification would have been prohibitively time consuming. We used BatClassify (Scott, 2012) to classify bat calls by species or species groups. Consistent with recommendations (López-Baucells et al., 2019; Russo and Voigt, 2016; Rydell et al., 2017) we manually verified the automated analysis following Barré et al. (2019) to quantify classification error rates (see supplementary material for detail of error rate modelling approach).

It was not possible to reliably differentiate *Myotis* spp. in the manual verification due to similarity in call structure between species in this genus, so these species were grouped. *Nyctalus* spp. and *Eptesicus* spp. are grouped by BatClassify. *Pipistrellus nathusii* is not classified by BatClassify so were grouped with *P. pipistrellus*. The decision was taken not to include *Plecotus* spp. in the statistical analyses on the basis that acoustic monitoring is not an effective survey method for these species, as their calls are often too quiet to be detected (Flaquer et al., 2007). *Barbastella barbastellus* was not included in statistical analyses due to low numbers of recordings.

2.5.2. *Acoustic activity index*

We quantified bat activity at recording locations according to Miller (2001). Every minute in which a bat species is present was counted as one occurrence, the total occurrences were then divided by the total time the detector was recording, creating an activity index (AI). The AI thus represents the rate of bat occurrences over the whole period the detector was recording (approximately one week, mean 6.8 nights). This allows us to account for variation in night length over the study period and to compare activity between recording locations with differing recording effort.

Rather than providing positive and negative classifications for recordings, error rate modelling returns a probability of a correct classification (by species). Following Barré et al. (2019) we excluded all classifications below a 50% probability. We then weighted classifications by their probability, so a classification with a 90% probability would count as an activity index of 0.9. This meant classifications with a higher probability contributed more towards the final analysis.

2.6. *Statistical analysis*

We conducted statistical analyses in R (R Core Team, 2022). We fitted models for six different species/species groups using a generalised additive model (GAM) with a negative binomial error distribution in the *mgcv* package (Wood, 2011).

For each species we first fitted a global model to explore the relationship between predictors and bat activity (*bat activity* ~ *predictors*). We then assigned predictors from the global model to one of three 'scenario' models, dependent upon their scale of action (Table 1). This allowed us to gauge the relative importance of different aspects of landscape structure (field boundaries, adjacent fields and local landscape) in driving bat activity. The first model contained descriptors of field boundary structure (field boundary model), the second contained descriptors of the field adjacent to the detector (adjacent field model). The third model contained descriptors of local landscape measured in GIS (local landscape model).

Table 1
All variables included in analysis (global model). 'Scenario model' column shows which scenario model each variable was assigned to.

Variable	Detail	Scenario model
Vegetated field boundary	Hedge, lines of trees etc. = yes; fence, ditch etc. = no	Field boundary
Number of trees per 100 m	Only included trees above 15 cm diameter at breast height	Field boundary
Field boundary height	Mean calculated from three representative points measured using either a tape measure or geometry (following West, 2009), depending on height.	Field boundary
Field boundary width	Width was defined as the widest point of the boundary cross-section. Measured at three representative points along the field boundary with a tape measure and calculated the mean.	Field boundary
Improved grassland	Yes/no	Adjacent field
Arable	Yes/no	Adjacent field
Livestock (cows, sheep, horses)	Livestock present or evidence of recent livestock presence (fresh faeces)? Yes/no	Adjacent field
Environmental stewardship scheme	Yes/no – is the land managed under an environmental stewardship scheme?	Adjacent field
Artificial light at night (ALAN)	Measured in 250 m buffer from satellite imagery (Earth Observation Group, NOAA/NCEI)	Local landscape
Normalised difference vegetation index (NDVI)	Measured in a 250 m buffer from satellite imagery (LandSat 8) using imagery acquired during the study period (September 20, 2020)	Local landscape
Percentage woodland cover	Percentage woodland cover calculated in a 250 m buffer from Ordnance Survey data (OS Open Map Local). Includes both coniferous and broadleaf (study area is 92% broadleaf) and any patch size	Local landscape
Percentage urban/suburban cover	Percentage of land classified as urban/suburban in CEH Land Cover Map 2015 (Rowland et al., 2017) calculated in a 250 m buffer	Local landscape
Easting and northing	British National Grid format	Control variable (all scenarios)
Week of study	1–12	Control variable (all scenarios)
Average nightly minimum temperature	Mean nightly minimum temperature for all nights the detector was recording (taken from detector internal thermometer or average of all other detectors out at the same time if not available)	Control variable (all scenarios)
Average nightly rainfall	Mean nightly rainfall (mm), obtained from the Environment Agency station no. 417635 (Barrow Gurney, grid ref. ST5377167950, 7.75 km NEE from centre of study site)	Control variable (all scenarios)

Continuous data were scaled and centred. Smooth terms were included for geographic coordinates (Duchon spline; *bs = "ds", k = 250*) and week of study (thin plate regression spline; *bs = "tp", k = 12*) to account for spatial autocorrelation and temporal differences in sampling, respectively. All other variables were included as linear predictors (Table 1). Model fit was assessed by visual inspection of residuals and diagnostic plots. We tested all models for multicollinearity and concurvity (the equivalent of multicollinearity for GAMs) and we removed recording locations with less than four nights data.

We optimised global and scenario models by searching all possible combinations of variables using the *dredge* function from the *MuMIn* package (Bartoń, 2020), with the control variables fixed. AICc of the best model identified by *dredge* was used to compare competing scenario models. We performed model averaging on the global model, using all models <2 ΔAICc of the best model (Burnham and Anderson, 2002), calculating the model averaged coefficients and z-values in the *MuMIn* package. Effect size was assessed by calculating the percentage change in variables. The modelling procedure is summarised in Fig. 4.

2.7. Model validation and predictive power

We tested the ability of models to predict bat activity at new sites. We performed 10-fold cross validation and fitted a GLM with predicted vs actual values, calculating McFadden's pseudo-R^2 to assess how well predictions match the actual data.

To assess the relative magnitude of the effect of predictor variables compared with the spatial component of the model, we also fitted models with 1) only control variables; 2) only control variables and no spatial smooth; 3) control variables, no spatial smooth, only one predictor variable, 'distance to *R. ferrumequinum* roosts at the centre of the study site'.

Predicted activity maps were made for three species at a 10 m resolution using three predictor variables: vegetated boundaries, habitat type (improved grassland or arable). Within the study site most field boundaries represent the edge of a land parcel and can therefore be mapped with reasonable accuracy using OS Master Map land parcel boundaries. We used LIDAR data from the National LIDAR Programme (Environment Agency, 2022), masked with OS MasterMap boundaries, to map vegetated field boundaries. Arable sites were mapped from sites identified during the survey period.

3. Results

Detectors were deployed at 380 locations, which equated to 26,557 recording hours, or 2656 10-h nights (mean night length = 9.82 h). In total over 1.6 million files were recorded, yielding 484,795 bat classifications. A total of eight species/species groups were identified (mean = 6.8 per site). Bats were detected on average just over 11 min (±8.2 s.d.) in every hour (Table 2, Fig. 5).

3.1. Scenario model comparison

The field boundary model was best supported for *P. pipistrellus*, *P. pygmaeus*, *R. ferrumequinum* and *R. hipposideros* (Table 3). The local landscape model was best supported for *N. noctula/N. leisleri/E. serotinus* while the adjacent field model received some support for this species group. All three models were highly supported for *Myotis* spp.

3.2. Global model

A total of 4095 models were examined by dredge for each species. The number of models ranked in the top model set (<2 ΔAICc) for each species were as follows: *Myotis* spp. n = 15, *N.* spp./*E. serotinus* n = 2, *P. pipistrellus* n = 2, *P. pygmaeus* n = 5, *R. ferrumequinum* n = 5, *R. hipposideros* n = 13. Model selection tables detailing all models used in model averaging for each species are included in the supplementary material.

3.2.1. Field boundary characteristics

Activity of *R. ferrumequinum*, *R. hipposideros*, *P. pipistrellus* and *N.* spp./*E. serotinus* was higher along vegetated field boundaries, compared to non-vegetated field boundaries (145%, 307%, 123% and 33% higher, respectively; $p < 0.001$, $p < 0.001$, $p < 0.001$, $p = 0.01$; Table 6–7, Fig. 6). *R. ferrumequinum* and *P. pygmaeus* activity was higher at boundaries with trees (2% and 3% increase in activity per tree per 100 m; $p < 0.001$ and $p = 0.01$, respectively). *P. pipistrellus* and *P. pygmaeus* activity was higher at field boundaries with tall vegetation (a 9% and 15% increase in activity for every extra metre of height, respectively; both $p < 0.001$, Fig. 7). *Myotis* spp. activity was higher at wide

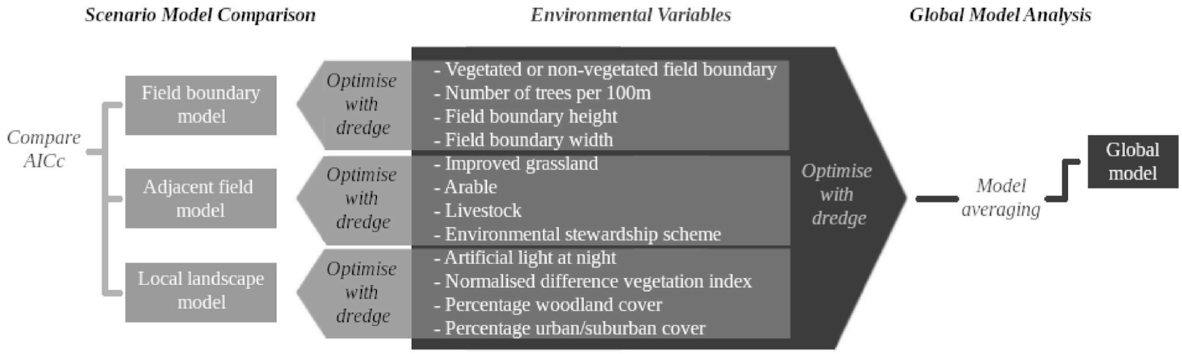

Fig. 4. Graphical representation of the modelling procedure.

Table 2
Mean activity index (AI) across recording locations. AI was calculated as the number of minutes in which a bat was recorded per hour of survey. Note that this is weighted by the confidence in the species classification, as described in section 2.5.2. Species not included in the statistical analysis are denoted with *.

Species	Mean Activity Index	Standard Deviation
*Barbastella barbastellus**	0.01	0.02
Nyctalus noctula/N. leisleri/Eptesicus serotinus	3	2.95
Plecotus spp*	0.1	0.13
Pipistrellus pipistrellus	4.76	4.8
Pipistrellus pygmaeus	0.69	1.25
Rhinolophus ferrumequinum	0.65	1.04
Rhinolophus hipposideros	0.13	0.3
Myotis spp.	2.05	2.62
All species	11.39	8.19

Table 3
Model ranking of competing scenario models. Units are ΔAICc between models, meaning the best performing scenario model has the lowest ΔAICc. Models with ΔAICc <10 (i.e. all models with some level of empirical support; Burnham and Anderson, 2002, pg. 70) are highlighted in bold.

Species/species group	field. boundary	adjacent. field	local. landscape
Rhinolophus ferrumequinum	**0.00**	15.83	24.40
Rhinolophus hipposideros	**0.00**	12.21	20.87
Pipistrellus pipistrellus	**0.00**	18.62	41.32
Pipistrellus pygmaeus	**0.00**	67.02	69.93
Myotis spp.	**0.74**	**0.09**	**0.00**
Nyctalus spp./*Eptesicus serotinus*	17.47	**5.54**	**0.00**

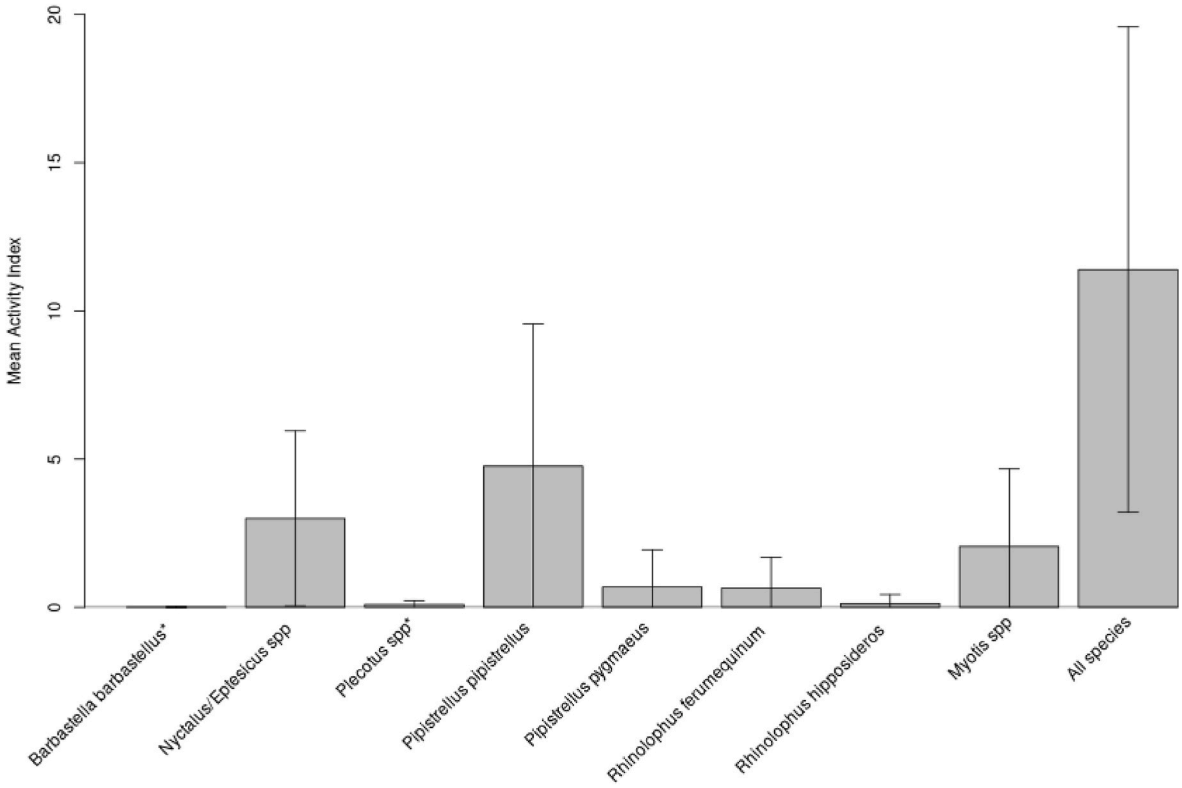

Fig. 5. Mean activity index (AI) across recording locations in North Somerset, UK, showing standard deviation. AI was calculated as the number of minutes in which a bat was recorded per hour of survey. Note that this is weighted by the confidence in the species classification, as described in section 2.5.2. Species not included in the statistical analysis are denoted with *.

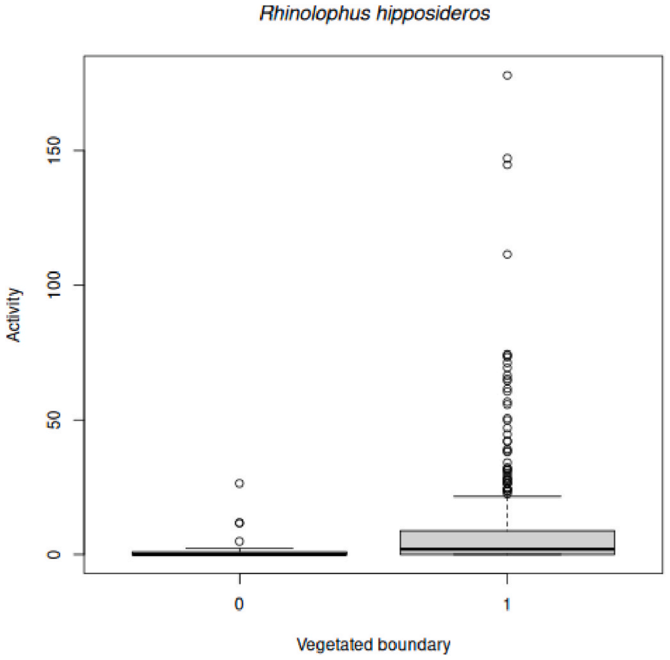

Fig. 6. Boxplot showing *Rhinolophus hipposideros* activity at vegetated/non-vegetated field boundaries in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

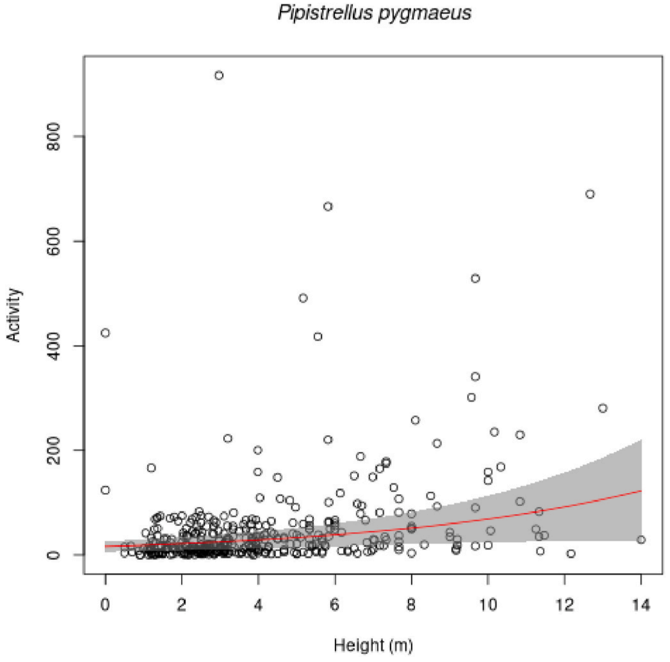

Fig. 7. Partial effects plot showing the effect of field boundary height on *Pipistrellus pygmaeus* activity (red line, 95% c. i. shaded) in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

boundaries (4% increase in activity for every extra metre of width; $p < 0.001$).

3.2.2. Adjacent field characteristics

R. hipposideros activity was 149% higher at field boundaries bounded by improved grassland ($p < 0.001$, Tables 6–7), whereas *P. pipistrellus* activity was lower (42%; $p < 0.001$). *R. ferrumequinum* and *P. pipistrellus* activity was lower at field boundaries bounded by arable land (46% and 48%; both $p < 0.001$, Fig. 9). *Myotis* spp. activity was lower at recording locations managed under an environmental stewardship scheme (39%; $p = 0.01$). *P. pipistrellus*, *P. pygmaeus* and *N. noctula/N. leisleri/E. serotinus* activity was higher at recording locations with livestock, compared to recording locations without (26%, 34% and 26% respectively; $p = 0.02$, $p = 0.03$ and $p < 0.001$; Tables 6–7, Fig. 8).

3.2.3. Local landscape characteristics

R. hipposideros and *N.* spp./*E. serotinus* activity increased with woodland cover in a 250 m buffer (both 2% increase in activity for every 1% increase in woodland cover; $p = 0.004$ and $p < 0.001$ respectively; Tables 6–7). *N.* spp./*E. serotinus* activity increased with urban/suburban cover in a 250 m buffer (1.4% increase in activity for every 1% increase in urban/suburban cover; $p < 0.001$). *P. pygmaeus* and *Myotis* spp. activity decreased with higher levels of ALAN in a 250 m buffer of the recording site (8% and 5% decrease in activity for every 1 increase in radiance; $p = 0.01$, $p = 0.03$, respectively).

3.3. Model validation and predictive power

We found a large spatial component explaining activity patterns – removing predictor variables did relatively little to reduce the deviance explained (Table 4) or the predictive power of the models (Table 5) when compared with the effect of removing the spatial smooth. For *R. ferrumequinum*, part of this was explained by proximity to the roost (Tables 4 and 5). Predicted activity maps for *Nyctalus* spp./*E. serotinus, P. pipistrellus* and *R. ferrumequinum* (Fig. 10) show spatial activity patterns recorded in the study period. There is a clear concentration of *R. ferrumequinum* activity around the roost at Brockley hall, while *Nyctalus* spp./*E. serotinus* and *P. pipistrellus* activity hotspots are more dispersed (although locations of roosts of these species is unknown)..

4. Discussion

For many animal species, field boundaries represent important slivers of habitat in an otherwise inhospitable agricultural landscape. Here, we demonstrate the value of field boundaries for bats and identify

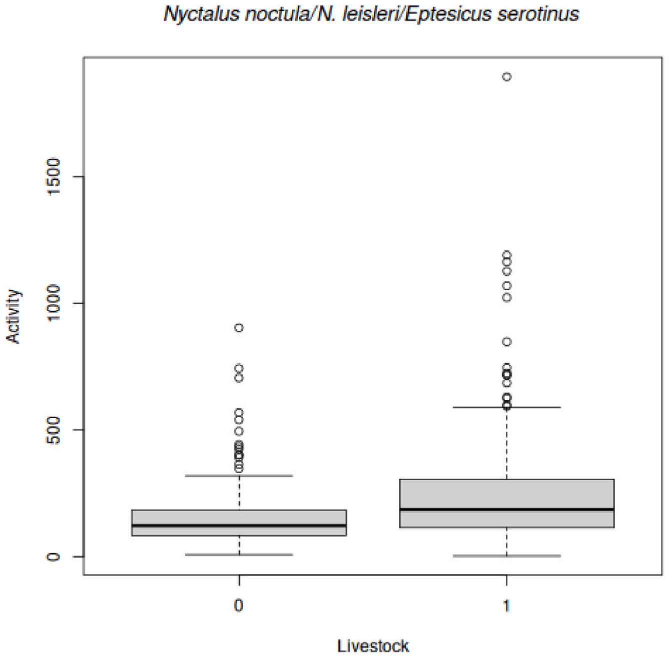

Fig. 8. Boxplot showing *Nyctalus* spp./*Eptesicus serotinus* activity at recording locations with/without livestock in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

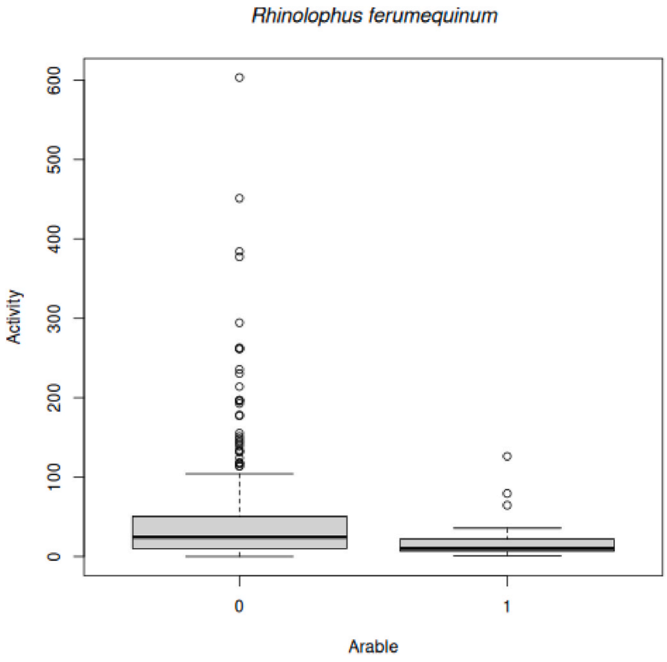

Fig. 9. Boxplot showing *Rhinolophus ferrumequinum* activity at arable/non-arable recording locations in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

Table 4

Percentage deviance explained by models. Comparison between the global model with all predictor variables (global), a model with only control variables (control.only), a model with only control variables but lacking the spatial control (control.non.spatial), and a model with only control variables, no spatial control but with the variable 'distance to R. ferrumequinum roosts at centre of study site' added (control.non.spatial.with.roost).

	global	control. only	control.non. spatial	control.non. spatial.with.roost
Rhinolophus ferrumequinum	85.07	79.50	18.19	35.51
Rhinolophus hipposideros	39.79	34.95	8.98	9.06
Pipistrellus pipistrellus	77.06	63.11	14.09	14.84
Pipistrellus pygmaeus	67.09	62.64	4.19	4.60
Myotis spp.	55.47	48.69	7.09	8.00
Nyctalus spp./ *Eptesicus serotinus*	81.36	83.00	23.77	23.84

Table 5

McFadden's pseudo-R^2 of predicted vs actual values from cross validation, measuring how well model predictions match the actual data. Comparison between the global model with all predictor variables (global), a model with only control variables (control.only), a model with only control variables but lacking the spatial control (control.non.spatial), and a model with only control variables, no spatial control but with the variable 'distance to R. ferrumequinum roosts at centre of study site' added (control.non.spatial.with.roost).

	global	control. only	control.non. spatial	control.non. spatial.with.roost
Rhinolophus ferrumequinum	0.42	0.39	0.07	0.26
Rhinolophus hipposideros	0.15	0.13	0.05	0.05
Pipistrellus pipistrellus	0.31	0.25	0.09	0.10
Pipistrellus pygmaeus	0.25	0.23	0.02	0.02
Myotis spp.	0.13	0.09	0.01	0.02
Nyctalus spp./ *Eptesicus serotinus*	0.46	0.42	0.17	0.17

specific characteristics of agricultural landscapes that are associated with bat activity in six species/species groups. Our results have direct application in landscape management and for the specification of environmental stewardship schemes.

We show that field boundary characteristics are better than local landscape or adjacent field characteristics at describing activity patterns in four of the six species studied (*P. pipistrellus*, *P. pygmaeus*, *R. hipposideros* and *R. ferrumequinum*) and that vegetated field boundaries are associated with significantly higher activity than non-vegetated boundaries (*P. pipistrellus*, *N.* spp./*E. serotinus*, *R. hipposideros* and *R. ferrumequinum*). Our results reiterate the importance of vegetated field boundaries for bats in agricultural landscapes – increasing activity by over 300% for *R. hipposideros* – and demonstrate that increasing the area of vegetated field boundaries can enhance the biodiversity value of farmland.

The importance of tall, overgrown hedgerows for *R. ferrumequinum* was previously known (Ransome, 1996), however, here we provide new evidence that the number of field boundary trees is the most important aspect of field boundary structure for this species. This builds on previous research that found high *R. ferrumequinum* activity along tree lines (Finch et al., 2020) and affords an easily-implemented approach to improving habitat quality for *R. ferrumequinum*. We also found trees to be important for *P. pygmaeus*, a finding reported previously (Boughey et al., 2011). Coupled with the finding that *Myotis* spp. activity was higher at wide field boundaries and *P. pipistrellus* and *P. pygmaeus* activity was higher at tall field boundaries, our results add to the body of evidence that planting field boundary trees and allowing existing hedgerows to outgrow will benefit a number of bat species (Boughey et al., 2011; Heim et al., 2015; Lacoeuilhe et al., 2018; Toffoli, 2016; Wickramasinghe et al., 2003).

Nyctalus spp./*E. serotinus* activity was better explained by local landscape characteristics than field boundary or adjacent field characteristics. These species forage above the height of vegetated field boundaries or at pace over open areas, targeting large free-flying prey items using loud, low-frequency echolocation (Jones, 1995; Waters et al., 1999). *Nyctalus* spp./*E. serotinus* would not therefore be expected to interact with field boundaries the same way as gleaning bats, or species with low-intensity or high-frequency echolocation calls that attenuate quickly in air. In this respect, our findings support previous studies (Boughey et al., 2011; Finch et al., 2020; Kelm et al., 2014; Toffoli, 2016; Verboom and Huitema, 1997). In contrast, we found higher *Nyctalus* spp./*E.* serotinus activity along vegetated field boundaries than non-vegetated boundaries, although the effect size is small compared to that of other species (Table 7). Our interpretation of this is that while *Nyctalus* spp./*E.* serotinus are not selecting for field boundary characteristics directly, they may still benefit from the increased landscape heterogeneity provided by vegetated field boundaries. This view is supported as both increased woodland and urban/suburban cover had a positive impact on activity for this species group.

Activity of *Nyctalus* spp./*E.* serotinus was higher in fields with livestock. Dung beetles (Geotrupidae, Scarabaeidae) comprise a significant portion of the diet of this group, which likely explains this finding (Jones, 1995; Shiel et al., 1998; Waters et al., 1999; Whitaker and Karataş, 2009). Activity of both *Pipistrellus* species was also higher in fields with livestock, likely because livestock attract prey items such as midges and mosquitoes that are important for *Pipistrellus* species (Ancillotto et al., 2017, 2021).

Activity of *R. ferrumequinum* and *P. pipistrellus* activity was negatively associated with arable fields (either in current crop production or fallow), a finding reported in previous studies (Dietz et al., 2013; Flanders and Jones, 2009; Walsh and Harris, 1996; Wickramasinghe et al., 2003). Additionally, *R. hipposideros* activity was higher in improved grassland. Arable farming requires greater amounts of agrochemicals than pasture, which have been shown to negatively impact bat activity (Kahnonitch et al., 2018; Wickramasinghe et al., 2003), while traditionally managed semi-natural grassland can support relatively high

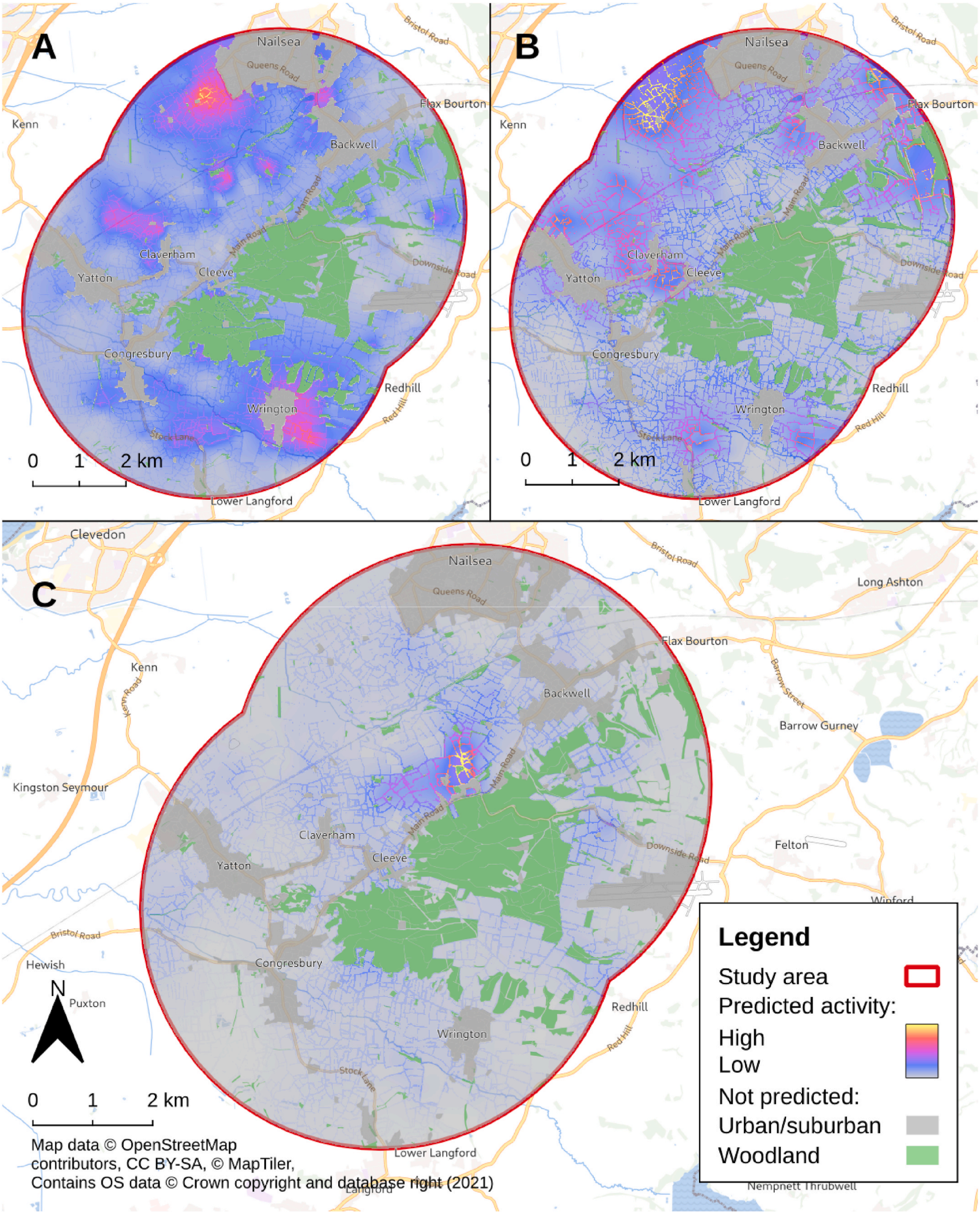

Fig. 10. Predicted activity outside woodland and urban areas in North Somerset, UK for A) *Nyctalus* spp./*Eptesicus serotinus*, B) *Pipistrellus pipistrellus*, C) *Rhinolophus ferrumequinum*.

Table 6
Estimates, (adjusted) standard errors and p-values for all variables in global model. Variables not included in the final optimised models are denoted with -.

	Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	Pipistrellus pipistrellus	Pipistrellus pygmaeus	*Myotis* spp.	*Nyctalus* spp./*Eptesicus serotinus*
Vegetated/non-veg. field boundary	**0.894 (±0.159), <0.001***	**1.402 (±0.337), <0.001***	**0.8 (±0.158), <0.001***	0.109 (±0.241), 0.65	–	**0.285 (±0.109), 0.01***
Trees per 100 m	**0.149 (±0.047), <0.001***	0.149 (±0.14), 0.29	–	**0.169 (±0.067), 0.01***	0.036 (±0.054), 0.51	–
Height	–	−0.112 (±0.167), 0.5	**0.234 (±0.05), <0.001***	**0.374 (±0.081), <0.001***	–	–
Width	–	0.208 (±0.123), 0.09	–	–	**0.165 (±0.056), <0.001***	–
Improved grassland	0.079 (±0.158), 0.62	**0.914 (±0.262), <0.001***	**−0.542 (±0.152), <0.001***	−0.419 (±0.249), 0.09	−0.022 (±0.085), 0.79	–
Arable	**−0.624 (±0.202), <0.001***	–	**−0.656 (±0.187), <0.001***	−0.479 (±0.298), 0.11	−0.039 (±0.125), 0.76	–
Livestock	–	−0.381 (±0.222), 0.09	**0.231 (±0.1), 0.02***	**0.29 (±0.134), 0.03***	−0.082 (±0.108), 0.45	**0.232 (±0.068), <0.001***
ESS	–	−0.091 (±0.2), 0.65	–	−0.065 (±0.168), 0.7	**−0.499 (±0.178), 0.01***	–
ALAN	–	−0.023 (±0.07), 0.74	−0.132 (±0.08), 0.1	**−0.262 (±0.093), 0.01***	**−0.174 (±0.082), 0.03***	−0.031 (±0.056), 0.59
NDVI	–	0.003 (±0.027), 0.91	0.083 (±0.084), 0.32	0.011 (±0.04), 0.79	0.02 (±0.052), 0.7	0.098 (±0.058), 0.09
Woodland cover	−0.031 (±0.06), 0.6	**0.199 (±0.097), 0.04***	−0.023 (±0.049), 0.64	−0.008 (±0.035), 0.82	–	**0.156 (±0.053), <0.001***
Urban/suburban cover	−0.081 (±0.07), 0.25	–	0.098 (±0.086), 0.25	–	0.075 (±0.078), 0.34	**0.143 (±0.051), <0.001***

Table 7
Percentage change in activity for every one unit of predictor in global model. For binary variables this is the difference between true/false (e.g. arable/not arable). Note NDVI is very high because it is calculated on a scale of −1 to 1, so an increase in one unit represents a large change, i.e. equivalent to the difference between bare rock and tropical rainforest.

	Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	*Pipistrellus pipistrellus*	*Pipistrellus pygmaeus*	*Myotis* spp.	*Nyctalus* spp./*Eptesicus serotinus*
Vegetated/non-veg. field boundary	144.58	306.52	122.57	11.52	–	32.94
Trees per 100 m	2.45	2.45	–	2.79	0.58	–
Height	–	−4.22	9.43	15.45	–	–
Width	–	5.23	–	–	4.14	–
Improved grassland	8.22	149.38	−41.82	−34.26	−2.22	–
Arable	−46.41	–	−48.09	−38.05	−3.79	–
Livestock	–	−31.70	26.01	33.65	−7.86	26.17
ESS	–	−8.67	–	−6.27	−39.29	–
ALAN	–	−0.73	−4.07	−7.92	−5.33	−0.96
NDVI	–	7.34	599.94	27.96	60.46	890.30
Woodland cover	−0.33	2.16	−0.24	−0.09	–	1.69
Urban/suburban cover	−0.78	–	0.95	–	0.73	1.40

insect diversity (Green, 1990). Encouraging the establishment of species rich, permanent pasture with low-intensity management would be beneficial for these species.

P. pipistrellus activity was negatively associated with improved grassland, in comparison to the reference group, roads. While roads have been shown to have a negative effect on bat activity, in our study area roads comprise small country lanes or farm tracks, rather than major roads that have been the focus of previous studies (motorways, Berthinussen and Altringham, 2012; dual carriageways, Claireau et al., 2019). The benefit of roads for bats our study was likely that there was almost always a hedgerow and/or tree line either side of the road. Hedgerows and tree lines are important for edge-foraging *Pipistrellus* species, as they provide shelter from wind and predators, high surface area of vegetation and high densities of insects (Froidevaux et al., 2019; Oakeley and Jones, 1998; Verboom and Huitema, 1997). Our findings corroborate this as the field boundary model best explained activity in both *Pipistrellus* species, and vegetated boundaries had significantly higher *P. pipistrellus* activity. Our results further highlight the value of vegetated field boundaries for *Pipistrellus* species.

Environmental stewardship schemes (ESS) award a subsidy to landowners for managing their land for the benefit of wildlife and the environment. ESS were not positively associated with bat activity in our study. Instead we found reduced *Myotis* activity at recording locations managed under ESS. It may be that survey locations under ESS are unsuitable for *Myotis* spp. for unmeasured reasons, however this requires further investigation.

Assessing the frequency of feeding buzzes (increased repetition rate of echolocation calls associated with the bat honing in on a prey item) was beyond the scope of this study, however future work would benefit from the extra insight this would provide into how bats are using field boundaries.

4.1. *Using models for prediction*

We found a large spatial effect driving activity patterns, which would make models unsuitable for predicting outside the study area where the spatial component is unknown. We found that part of the spatial effect for *R. ferrumequinum* was explained by proximity to known roosts, demonstrating that the location of species-centric landmarks plays a large part in dictating spatial activity patterns.

Bat activity is known to be highly variable and difficult to predict (Langton et al., 2010; Richardson et al., 2019; Silva et al., 2017). High variation in activity levels meant that predictions at best had an R^2 value of 0.45 when regressed with the actual values (for *Nyctalus* spp./*E. serotinus*), but for most species this was considerably less (Table 5).

The predicted activity maps generated in this study (Fig. 10) describe spatial activity patterns during our study period, albeit a smoothed-over version of true activity. It is unclear whether this would be representative of activity at the same sites in subsequent years, although there is evidence to suggest that activity hotspots change over time (Medinas et al., 2021). Border et al. (2022) used a similar modelling and mapping approach to ours, but treated bat activity as a proxy of habitat suitability. While there almost certainly is a link between habitat suitability and bat activity levels, based on our findings we would not recommend using predictive modelling of bat activity as a substitute for habitat suitability until the relationship between the two has been better characterised.

5. Conclusions

Our results add to a growing understanding of the value of field boundaries for bats. We shed new light on the specific aspects of field boundary structure that benefit bats and identify a number of measures that could be used for habitat restoration and species conservation. We show that increasing the area of vegetated field boundaries, planting hedgerow trees and developing tall and outgrown hedgerows will enhance agricultural landscapes for many species. Our results show how field boundaries can be a valuable tool in developing biodiversity-friendly agricultural landscapes.

Authors' contributions

Thomas Foxley: Methodology, Investigation, Project administration, Data Curation, Formal analysis, Software, Validation, Visualization, Writing - Original Draft; *Paul Lintott:* Writing- Reviewing and Editing; *Emma Stone:* Conceptualization, Funding acquisition, Writing- Reviewing and Editing, Supervision.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.117029.

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