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ORIGINAL RESEARCH

Contrasting effects of mixed farming on bats are mediated by local and landscape features and differ between seasons

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Abstract

Homogenisation of agricultural landscapes, driven by intensive farming, is one of the key drivers of biodiversity decline in Europe. Whilst government schemes to address this have benefitted some invertebrate species, they have been less successful for bats, which require a landscape-scale approach due to their high mobility. 'Mixed farming', where livestock are integrated into arable crop rotation, has been proposed as a landscape-scale approach to counteract biodiversity loss and could benefit bats via increased diversity of foraging habitats, both spatially and temporally (e.g. in the autumn when arable fields are ploughed, pasture may provide an alternative source of insect prey). We used structural equation models to investigated direct and indirect effects of mixed farming on bat activity and how these effects change between seasons. Bat activity was quantified on 26 farms in Scotland (UK) in summer 2022 and in autumn 2023 and 2024 using acoustic methods. On mixed farms, bats avoided arable fields in favour of grassland or woodland. Woodland edge density – which was higher on mixed than on arable farms – was positively associated with the occurrence of *Myotis* species. The activity of *Pipistrellus* and *Myotis* species was also positively associated with the height of treelines and hedgerows (which were marginally shorter on mixed farms than on arable farms). Bat responses differed between seasons, with habitat diversity becoming more important for *Pipistrellus pipistrellus* in the autumn, highlighting the importance of monitoring bats across the seasons to identify factors influencing bat activity.

Introduction

In Europe, 40% of land use is agricultural, the majority of which is managed intensively (European Union 2025), characterised by homogenisation and specialisation of agricultural landscapes. Whilst the total area of land dedicated to agriculture has varied very little over recent centuries, many parts of the world have seen a rapid increase in the use of intensive farming techniques following the industrial revolution. This trend was further accelerated

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after the second world war, largely driven by agricultural policies such as the Common Agricultural Policy in Europe and the US Farm Bill in the United States of America (Garrett et al. 2020). For example, across Europe large areas of semi-natural grasslands, that were traditionally grazed with low numbers of livestock, were converted to improved pasture or arable land between 1960 and 2013 (Aune et al. 2018; Cousins and Eriksson 2008). Agricultural intensification has also resulted in many farmers now specialising in one or two crops or in livestock production (Garrett et al. 2020), leading to large areas of extensive crop monocultures or intensive livestock farming. Additionally, removal of woodlands, hedgerows and treelines, which provide important shelter and landscape connectivity for a variety of taxonomic groups (Boutin et al. 2011; Finch et al. 2020; Fuentes-Montemayor et al. 2013) has historically been associated with intensive farming and has added to landscape homogenisation (Downey et al. 2025). Intensive agriculture is also associated with the use of synthetic inputs such as fertilisers, herbicides and pesticides which are known to be detrimental to insects (Dupont et al. 2018; Pisa et al. 2015), with evidence of bioaccumulation of insecticides occurring in animals at higher trophic levels (Eng et al. 2019; Valdespino and Sosa 2017). Thus, there is strong evidence that intensive agriculture is a key driver of global biodiversity declines (Outhwaite et al. 2022).

Bats can play an important role in agri-ecosystems. Insectivorous bats can consume up to 30% of their body weight in one night (Pimentel et al. 2022), with evidence that some species are able to reduce crop damage from insect pests (Sierra-Durán et al. 2025; Tuneu-Corral et al. 2024). However, bats are known to respond negatively to intensive farming, in particular to the loss of woody habitat and homogenisation of agricultural landscapes (Monck-Whipp et al. 2017; Put et al. 2019). In addition, bats are vulnerable to bioaccumulation of pesticides (Zhao et al. 2020). Government financial incentives to increase wildlife on farms (Agri-Environment Schemes - AES) are beneficial for some taxa such as moths and beetles (Fuentes-Montemayor et al. 2011a; Thomas et al. 2002) but have had limited advantages for bats, with higher bat activity recorded on farms that were not implementing such schemes in comparison to those that were (Fuentes-Montemayor et al. 2011b), though hedgerows managed under AES can increase bat activity in some cases (Froidevaux et al. 2019). Due to their high mobility, bats may respond better to landscape-scale changes in agricultural practices rather than field-scale schemes.

Mixed farming, where livestock are integrated into the crop rotation, has been suggested as a more sustainable approach than 'arable' farming, where livestock are absent and was once a widespread farming practice across the globe (Lemaire et al. 2015; Sylvester and Cunfer 2008). On a local scale, mixed farming can reduce the need for synthetic inputs that are harmful to insects via natural nutrient input from dung and natural weed-control from grazing (MacLaren et al. 2019; Schlegel et al. 2015). Grazing livestock can also directly increase bat activity on mixed farms by attracting or disturbing insect prey (Ancillotto et al. 2023; Downs and Sanderson 2010). However, management of hedgerows on mixed farms may be different to arable farms because: hedgerows on mixed farms are traditionally used to contain livestock and are usually subjected to regular trimming (Venturi et al. 2022). Furthermore, hedges or young trees may become damaged or altered from livestock browsing (Love et al. 2009; Schmitz et al. 2007). Given that linear woody features such as hedgerows and tree lines provide shelter and foraging for bats in otherwise very open agricultural landscapes (Finch et al. 2020), farming type may indirectly affect bats via hedgerow management practices.

At the landscape-scale, mixed farming may provide greater habitat diversity than arable farms, with a mix of cropland, pasture and woodland (that may often be retained as shelter for livestock). Indeed, bats have been found to avoid foraging over arable fields with some species preferring to forage over pasture or woodlands (Nicholls and Racey 2006a, b; Russ and Montgomery 2002). Greater landscape diversity may become even more important for bats in the autumn at a time of year when bats are feeding-up in preparation for hibernation, but when most arable fields will be ploughed over, reducing the abundance of insects (Thorbek and Bilde 2004), whilst pasture fields may continue to provide food resources and shelter for insects.

Thus, the effects of mixed farming on bats are likely to be complex and could be both indirect (via differences in local and landscape attributes) or direct (via the presence of livestock attracting insects) and may change between seasons. Here, we assess the habitat preferences of foraging bats on mixed and arable farms. We also take a whole-system approach using structural equation modelling to disentangle the direct and indirect effects of mixed farming systems on bat activity or occurrence in Eastern Scotland. Specifically, we address the following questions:

Q1. Do bat habitat preferences of bats differ between arable and mixed farms, and if so, how?

Q2. Does mixed farming benefit bats, either directly or indirectly via landscape composition and configuration? If so, do these effects vary between peak activity (summer) and pre-hibernation (autumn) periods?

Q3. On mixed farms, is bat activity higher adjacent to pasture than in arable areas? And is this influenced by pasture management (e.g. livestock stocking rates)?

Methods

Site selection

Our study sites were situated in Eastern Scotland (Fig. 1) between latitudes of 56.2 and 57.6 which is a highly agriculturally productive area of the UK, with fertile soils capable of growing a wide range of arable crops (Scottish and Government 2009). Cereals such as barley and wheat are the most common crops in this area, as well as potatoes and brassicas (mainly oilseed rape). We selected 13 mixed and 13 arable farms via contacts at Scotland's Rural College and using farmer recommendations, with each mixed farm being paired with a nearby arable farm (mean distance: 9.5 km; min = 3 km; max = 16 km) Here, we define an 'arable farm' as a crop-only farm with no livestock integrated into the crop rotation. We define a 'mixed' farm as having grazing livestock integrated into the crop rotation, either through rotation of temporary grassland and/or by grazing cover crops or herbal leys. For simplicity, we limited mixed farms to those that kept cattle only or cattle with some sheep grazing over the winter months. No other livestock types were present on mixed farms. Cattle were grazed between the months of April to November then kept indoors for the winter months as is common practice in the UK. Cattle were also administered with anthelmintic wormers on all farms and none of the farms (including arable farms) were managed organically. Whole-farm cattle stocking rate was calculated using the number of livestock units (LUs) and the total area of pasture available, with one LU approximately equivalent to one

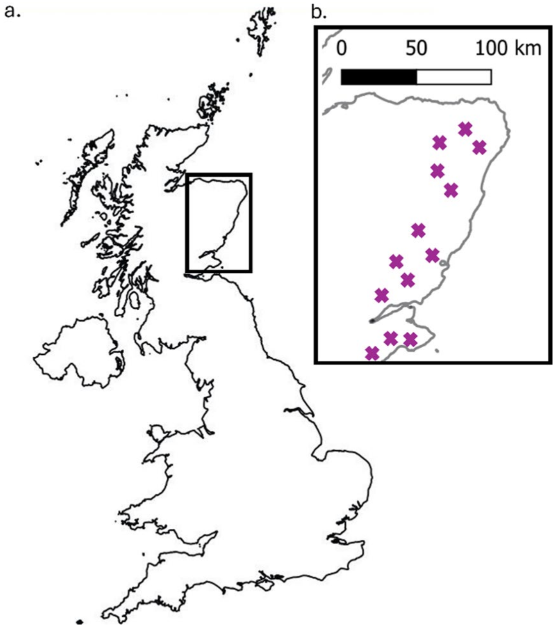

Fig. 1 Map showing location of study sites (approximate locations marked with 'X' for each pair of farms)

beef cow and calf (SAC Consulting 2024). We were unable to obtain accurate information on stocking rate of sheep for all farms where they were present, thus we noted presence or absence of sheep integrated into the rotation. Farms were situated in lowland areas with a mean altitude above sea level of 80 m (min: 9 m, max: 190 m) and had a mean size of 200 ha (min 73 Ha, max 483 Ha).

Bat surveys

Two methods were used to survey bats: walked transects and static detectors. All surveys were conducted in a paired design so that farms within the same pair were surveyed simultaneously to ensure similar weather conditions. All bat surveys were conducted on dry nights with a minimum temperature of 8 °C and a wind speed of less than 4 on the Beaufort scale (Fuentes-Montemayor et al. 2011b).

Walked transects

To assess habitat selection by bats in arable farms and mixed farms (research question Q1) foraging activity was recorded along transects once on each farm between June and July 2022 using a pair of hand-held Echo Meter 3 acoustic detectors (Wildlife and Acoustics 2011) with GPS unit to log the location of each bat pass recorded. The Echo Meters were set to 256 kHz sample rate, high enough to detect the frequencies of all bat species found in Scotland. Detectors were held at elbow height and aimed upwards at a 45° angle from the ground. Transects were walked on 20 out of the 26 participating farms, with three pairs unable to be surveyed due to logistical constraints. Surveys started 40 min after sunset to avoid peak emergence times (Fuentes-Montemayor et al. 2011b) and continued for a mean of 68 min (min = 45 min, max = 106 min). Transects were designed to cover as many habitat types on each farm as possible, with a mean transect length of 3.3 km (min 1.6 km; max 4.5 km) and a mean walking pace of 3.1 km hr^{-1}. The same two surveyors were used for almost all farm pairs, with the individual and detector alternating between farm types. To avoid disturbance to crops and livestock, transects followed field edges which were often lined with hedgerows or lines of trees, or bordered by woodland edge; the mean percentage of transect that was adjacent to these woody features was similar between farm types at 48% for arable farms (min 31%; max 80%) and 47% for mixed farms (min 18%; max 74%).

Static detectors

To assess the direct and indirect effects of farm type on bat activity, potentially mediated by local and landscape attributes (Q2), we carried out fixed-point surveys using Audiomoth acoustic recording devices (Hill et al. 2019) on the same pairs of farms as for walked transects, plus an additional three pairs ($n=26$ farms). Two different survey periods were chosen. Firstly, 28th June to 7th August 2022, which is during peak activity season for bat species in the north of the UK (Russ et al. 2003) and prior to crop harvesting. We then returned to the same farms between 26th September and 10th October 2023, which corresponds to the pre-hibernation period reported for bats at similar latitudes (Frafjord 2021; Meier et al. 2022) and is after the main crop harvest period. Due to very cold and wet weather in autumn 2023, we were unable to survey all farms (total farms surveyed in 2023 was 14). We therefore returned to the remaining 12 farms between 10th September 2024 and 4th October 2024. Static detectors were scheduled to begin recordings half an hour after sunset and stop recording half an hour before sunrise (settings are provided in table S.1). To increase the number of nights that could be recorded during longer autumn nights, we limited autumn recordings to two hours in the evening (starting half an hour after sunset) and two hours at the end of the night (ending half an hour before sunrise), as this is when bats have been found to be most active (Cel'uch and Kropil 2008). This meant that recording time for summer nights (mean duration = 4.5 h) was similar in length to autumn recordings. Detectors were deployed for a mean of 5.5 nights during the summer period (min = 4, max = 7) and for a mean of 3.4 nights in the autumn (min = 1 (only one location), max = 7), giving a total of 621 detector nights in the summer months and 368 detector nights in the autumn. Variation was due to SD cards becoming full more quickly in locations where more sound was recorded in comparison to quieter areas. During autumn deployment, temperature occasionally fell below 8 degrees Celsius ($n=7$ nights), as measured by temperature loggers. These nights were subsequently removed prior to data analysis ($n=7$ nights).

Three static detectors were deployed on each farm between two crop fields, hereafter called 'crop-crop' field margins (Fig. 2). Detector arrangement was designed to cover as much of the farm as possible, with a minimum distance of 100 m between the nearest detectors. Farms were relatively small (mean = 200 ha) so this approach enable good coverage. Since linear features are important for bats in agricultural landscapes (Finch et al. 2020) we placed static detectors along a hedgerow, line of trees or woodland strip (hereafter called 'woody features') approximately halfway along the field edge and at a height of 1.6 m. A visual estimate of maximum woody feature height was noted within 15 m either side of the detector. To examine the effects of pasture presence and livestock management on bat activity (Q3), we placed an additional three detectors on mixed farms in crop fields (oriented towards the crop field) adjacent to pasture or 'crop-pasture' margins (Fig. 2), resulting in

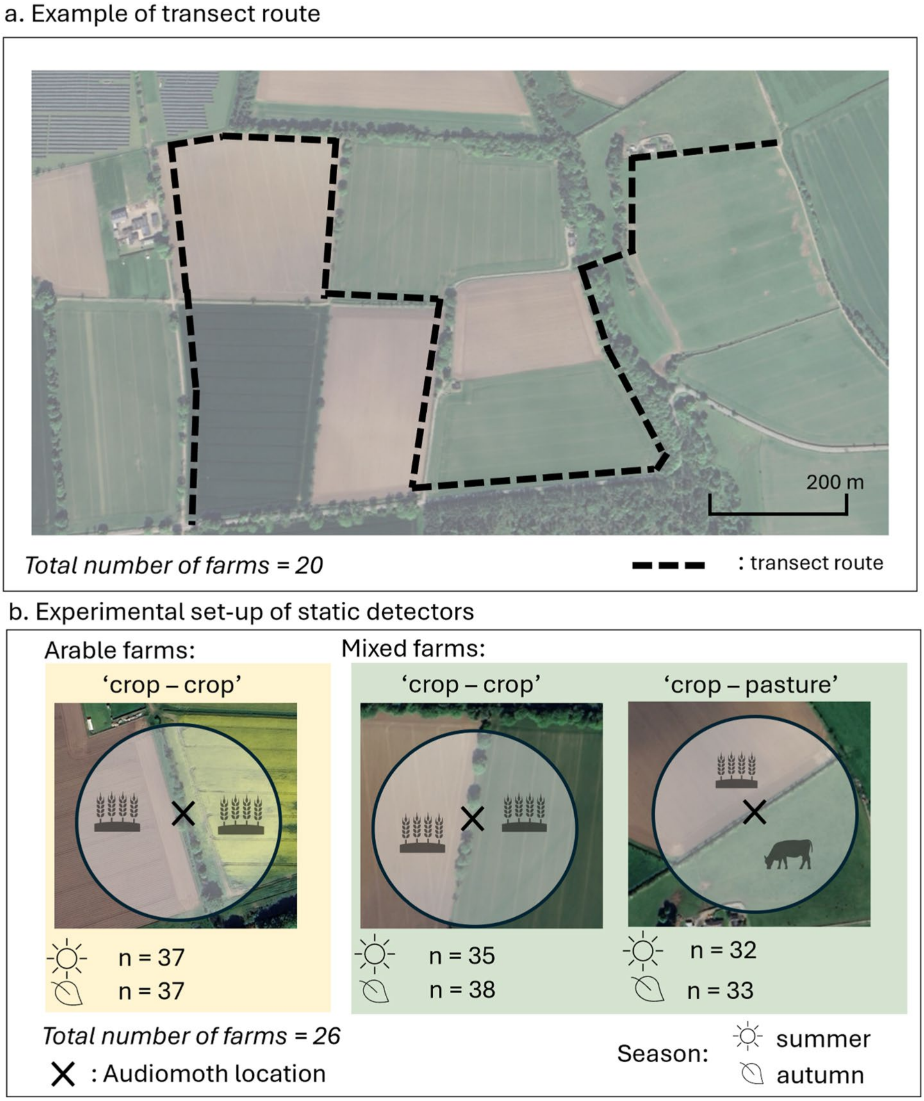

Fig. 2 Example of transect route design (**a**) and set up of static detectors (**b**). 'n' designates the total number of static detectors deployed in summer and autumn in each margin type ('crop-crop' on arable and mixed farms and 'crop-pasture' on mixed farms only)

three sampling points for every arable farm and six sampling points for every mixed farm. On mixed farms livestock were always present on the farm during sampling. However, livestock were not always present in fields adjacent to detectors, and were sometimes moved between fields during the deployment period.

Acoustic analysis

All acoustic files were split into five second files so that any continuous bat activity could be divided into five second passes, with one pass defined as at least two pulses (Azam et al. 2015; Millon et al. 2015) within a 5 s file. In the study area *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* are the most common species, with *Pipistrellus nathusii*, *Plecotus auritus*, *Myotis nattereri*, and *Myotis daubentonii* also present. Whilst *Nyctalus noctula* and *Nyctalus leisleri* are present in Scotland, they do not occur in the study area. We used Kaleidoscope (Wildlife Acoustic Inc, 2024) to carry out automatic identification of bats recorded on static detectors (settings are provided in Table S2). Manual checks were then carried out on all files flagged by the software as *Myotis* spp. or *Plecotus auritus* as the software identifies these species with low accuracy (Rydell et al. 2017). All species from the genus *Myotis* were grouped as *Myotis* spp., as identification to species level for this genus is unreliable using acoustic methods (Rydell et al. 2017; Walters et al. 2012). Kaleidoscope's auto-identification feature cannot identify feeding buzzes, a rapid decrease in the distance between pulses that is associated with bats attempting to catch prey (Griffin et al. 1960). Therefore, we identified feeding buzzes manually (whilst also checking the accuracy of the software to identify pipistrellus species correctly) on a subset of data ($n = 40$ nights across all farms). Feeding activity correlated positively with the number of bat passes for both *P. pipistrellus* (Pearson = 0.70, $P < 0.001$) and *P. pygmaeus* (Pearson = 0.80 $P < 0.001$, Fig. S1) thus we used the number of passes as a proxy for bat feeding activity in all models. Auto identification software correctly identified over 95% of *P. pipistrellus* and *P. Pygmaeus* calls within the subset, therefore no more manual checks were made across the remaining recordings.

Adjacent habitat and landscape analysis

Habitat adjacent to transects

GPS locations of each pass were loaded into QGIS version 3.28.1. (Development Team 2021). Habitat adjacent to transects was categorised as arable land (fields where arable crops were grown), pasture, woodland, buildings (including both farm buildings and residential buildings), water or semi-natural (scrub, heathland and semi-natural grassland combined) using a combination of farm maps provided by farmers and ground-truthing. Woodland habitat largely comprised mixed and broadleaf woodland, with riparian and coniferous woodland only representing 0.05% and 0.04% respectively of total transect proportion, therefore all woodland types were grouped together for analysis. Each bat pass was then assigned to the adjacent habitat type (within 20 m of GPS location). Where there was more than one habitat type within 20 m of the bat pass, the pass was split across the number of habitat types present as in Fuentes-Montemayor et al. (2011b). To obtain a measure of habitat availability on each farm, we manually measured the total length of each habitat type adjacent to the transect in QGIS.

Landscape analysis

To obtain measures of landscape configuration and composition surrounding each static detector, we used The Centre for Ecology and Hydrology Land Cover Map (Marston et al. 2022) reclassified into biotypes (Table S3). Buffers of 500, 1000, 1500, 2000, 2500 and 3000 m were created around each static detector location in QGIS. For each scale, we then used the landscapemetrics package (Hesselbarth et al. 2019) in R version 4.4.2. (Core Team 2023) to extract landscape attributes that have been found in previous studies to be important for bats, including the proportion of arable land, proportion of semi-natural (scrub and semi-natural grassland combined), woodland edge density, mean Euclidean nearest neighbour (ENN) for all woodland and Shannon's index of habitat diversity (Fuentes-Montemayor et al. 2011b, 2013; Walsh and Harris 1996a) using biotypes (woodland, arable land, grassland, freshwater, buildings, semi-natural, coastal). However, the mean proportion of semi-natural area was very low at all scales, (even at the largest scale of 3000 m maximum semi-natural cover recorded was just 0.09, with a mean of 0.02) and was not considered in further analysis. In addition, we measured proximity of each static detector to the nearest freshwater body as well as proximity to the nearest building using data from OS MasterMaps® (Ordnance Survey 2023).

Statistical analysis

Habitat preference on mixed and arable farms

To assess habitat preference of foraging bats (Q1) we used transect data to compare actual and expected use of habitat. This was conducted separately for *P. pipistrellus* and *P. pygmaeus* and for mixed and arable farms. There were insufficient passes of *Myotis* spp. for analysis of this group. The proportion of observed habitat use for each habitat type was calculated by dividing the number of bat passes assigned to each habitat type by the total number of bat passes. To calculate the proportion of expected use we assumed that habitat types were being used in proportion to their availability. Thus, we multiplied the proportion of each habitat available by the total number of bat passes recorded of each species. Passes associated with 'water' were removed from analysis as the expected number of passes was less than 5 (Neu et al. 1974). To assess if bat activity was equally distributed across all habitat types we ran a chi-squared test (χ^2) in base R. We then assessed the statistical significance of habitat selection or avoidance for each habitat type, by calculating simultaneous confidence intervals (using Bonferroni's inequality) around each proportion of observed habitat use, following the same method as Glendell and Vaughan (2002) (Bailey's method which is less prone to type II errors than other methods (Cherry 1996). We used a significance level of $P<0.05$. If the lower limit of the confidence interval was higher than the proportion of expected use, bats were deemed to be selecting for that habitat type. Conversely, if the upper limit of the confidence interval was below the proportion of expected use, bats were deemed to be avoiding that habitat type.

Structural equation modelling: exploring direct and indirect effects of farm type

To explore the direct effects and indirect effects of farm type on bats, mediated by local and landscape attributes (Q2) we used structural equation models (SEMs). SEMs are a multivariate technique to statistically test whether hypothesised causal pathways (based on ecological theory) are supported by the observed data. For this analysis static detector data from crop-crop margins on arable farms and mixed farms and across both seasons was used (summer $n = 72$, autumn $n = 75$).

Prior to building structural equation models (SEMs), we evaluated which landscape features and at which spatial scales explained the greatest amount of variation in bat activity (and probability of occurrence for *Myotis* spp.). Generalised linear models (GLMs) were built, with number of passes for each pipistrelle species as a response variable. Activity of *Myotis* spp. was low so occurrence was used as a response variable. Separate models were built for each landscape attribute (proportion of arable land, habitat diversity index, woodland edge density, mean woodland Euclidean Nearest Neighbour) at each spatial scale (500, 1000, 1500, 2000, 2500 and 3000 m). We also modelled summer and autumn data separately to understand if there were any differences in the importance of landscape attributes and scales at different times of year. *Pipistrellus pygmaeus* models were built using a Poisson distribution using the lme4 package (Bates et al. 2015), whilst *P. pipistrellus* models showed overdispersion so we used a negative binomial distribution using the MASS package (Venables and Ripely 2002). Occurrence of *Myotis* spp. was modelled using a binomial distribution. An offset to account for the number of nights recorded (log-transformed) was included in all GLMs. A pseudo r squared value (r^2), for non-normally distributed data, was then calculated for each landscape variable at each different scale (Fig. S.2.). Some landscape metrics were strongly correlated (Table S.4.). Thus, we selected one metric of landscape configuration (either woodland edge density or mean woodland ENN, whichever had the highest r^2 value (Fig. S.3.), plus one metric of habitat composition (either proportion of arable land or habitat diversity index, again based on r^2 value) for inclusion in subsequent SEMs (Fig. 3).

SEMs were built using the piecewiseSEM package (Lefcheck 2016) which allows for the use of random effects and non-normal distributions. In addition to the landscape variables with the highest r^2 value, woody feature height was included in all models as this can influence bat activity (Froidevaux et al. 2019; Heim et al. 2016). For *P. pygmaeus* and *Myotis* spp. models we also included proximity to freshwater, since *P. pygmaeus and M. daubentonii* prefer foraging over water or riparian habitats (Bellamy and Altringham 2015; Nicholls and Racey 2006a, b). For *P. pipistrellus* we included proximity to buildings since this species is known to make opportunistic use of buildings for roosting and foraging (Bellamy and Altringham 2015; Hale et al. 2012). Finally, we included mean temperature at sunset in all SEMS to account for weather differences between deployment periods., *Pipistrellus pipistrellus* and *P. pygmaeus* models did not converge when modelling with count data. Thus, we averaged bat passes to number of passes per night (to account for different number of deployment nights between detectors). Data were then log-transformed, as this showed better model fit than untransformed data, and modelled using a Gaussian distribution. We acknowledge that log-transforming and averaging bat activity data can potentially introduce bias into SEMs (e.g. changing the estimation of relationships among variables within the SEM paths) that could have been avoided if the data did not need transforming (Mendes and Luskin 2025). However, biases with relative abundance data mainly occur when data is zero inflated (which our data was not) and the SEM package used in our study (piecewiseSEM) handles relative abundance data well in comparison to other SEM packages available (Mendes and Luskin 2025). *Myotis* spp. occurrence (across all nights) was modelled as a binomial distribution. A random effect of 'site' was used in all models to account for multiple sample locations per site. For autumn models, a random effect of 'year' was ini-

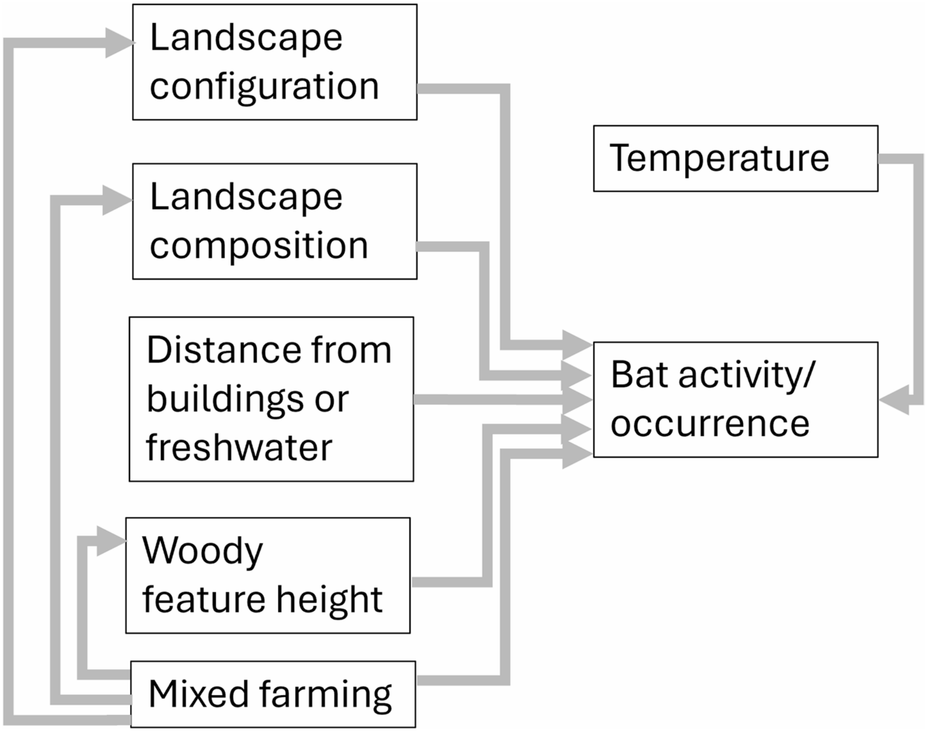

Fig. 3 Metamodel showing hypothesised pathways between variables. Grey arrows indicate a hypothesised directional relationship that was modelled in SEMs

tially included to account for sampling across two years. However, variances for year were very small so this was subsequently removed. In addition, continuous predictor variables in the *Myotis* spp. autumn model were scaled and centred around the mean to aid with model convergence. Each sub-model was checked for good model fit (using qq plots), overdispersion and zeroinflation using the DHARMa package (Hartig 2024). We then checked for missing pathways in SEMs using tests of directed separation (Shipley 2000). Pathways were subsequently included as correlated errors if they were found to be significant ($P<0.05$) and overall SEM fit was verified using Fisher's C statistic (with $P>0.05$ value confirming that model is supported by the data).

Effects of pasture presence and management on mixed farms

To test the effect of pasture presence and management (i.e. livestock stocking rate and sheep presence) on bat activity (Q3), we used data collected on mixed farms. Separate generalized mixed effects models (GLMMs) were constructed for each bat species/group and for the summer and autumn sampling periods. All continuous predictor variables were scaled and centred around the mean as variables were on very different scales. Predictor variables included in GLMMs were cattle stocking rate (for *P. pipistrellus* this was included as a quadratic effect as the relationship showed signs of non-linearity), occurrence of sheep on the farm and margin type ('crop-crop' or 'crop-pasture). We also included woody feature height as this varied within each farm. 'Site' was included as random effect and 'number of nights' (log transformed) as an offset to account for unbalanced sampling. *Myotis* spp. occurrence (across all nights) was modelled using a binomial distribution, whilst *P. pipistrellus* and *P. pygmaeus* activity was modelled as count data (total passes per detector across all nights) using a Poisson distribution, unless overdispersion was detected, in which case a negative binomial distribution was used. In autumn models, zero-inflation was detected for both *Pipistrellus* species. Therefore, zero-inflated models were built using the glmmTMB package (Brooks et al. 2017). We then used corrected Akaike's Information Criterion (AICc) for small sample size to compare the zero inflated model with non-zero inflated Poisson and non-zero inflated negative binomial models (Bolker et al. 2024). The model with the lowest AICc was retained as the final model. All GLMMs were checked for goodness of fit using the DHARMa package.

Results

Across a total of 67 km of walked transects and 20 farms we recorded 485 *P. pipistrellus* passes, 486 *P. pygmaeus* passes and 10 *Myotis* spp. passes. *Pipistrellus pygmaeus* was recorded on all farms, whilst *P. pipistrellus* was recorded on all but two farms. However, *Myotis* spp. was only recorded at five sites (two arable and three mixed farms).

Across all static detectors deployed during the summer months ($n=113$ across 26 farms), we recorded a total of 72, 407 *P. pipistrellus* passes and 128, 419 *P. pygmaeus* passes. During autumn deployment ($n=116$) a total of 8,320 *P. pipistrellus* and 28, 856 *P. pygmaeus* passes were recorded across all detectors. *Myotis* spp. was recorded on 55 detectors in the summer and 19 detectors in the autumn. *Plecotus auritus* was confirmed on a small number of recordings ($n=10$) but data was not sufficient for statistical analysis.

Habitat preferences of foraging bats in mixed and arable farms

Bats selected for certain habitat categories for foraging on mixed farms (for *P. pipistrellus* $\chi^2=46.59$, df=3, $P<0.0001$, for *P. pygmaeus* $\chi^2=81.93$, df=3, $P<0.0001$). This was also true for *P. pipistrellus* on arable farms ($\chi^2=16.5$, df=3, $P=0.009$) but not for *P .pygmaeus* on arable farms ($\chi^2=2.79$, df=3, $P=0.4$).

Pipistrellus pipistrellus selected for grassland and avoided arable fields on mixed farms but not on arable farms, and they selected for farmland buildings on both farm types, with observed *P. pipistrellus* activity around twice as high than expected (Table S.5.). *Pipistrellus pygmaeus* showed no habitat preference or avoidance on arable farms but strongly selected for woodland on mixed farms (with observed passes almost twice as high as expected). *Pipistrellus pygmaeus* also strongly avoided arable fields on mixed farms (with observed passes half that of the expected value) and slightly avoided buildings on both farm types Fig. 4).

Effects of mixed farming, landscape and local attributes on bats

Mixed farms had significantly higher woodland edge density than arable farms at larger scales of 1500 m and 2500 m (Fig. 5). Habitat diversity was also significantly higher on mixed farms but only at the 500 m scale. Mixed farming had lower mean ENN for woodland

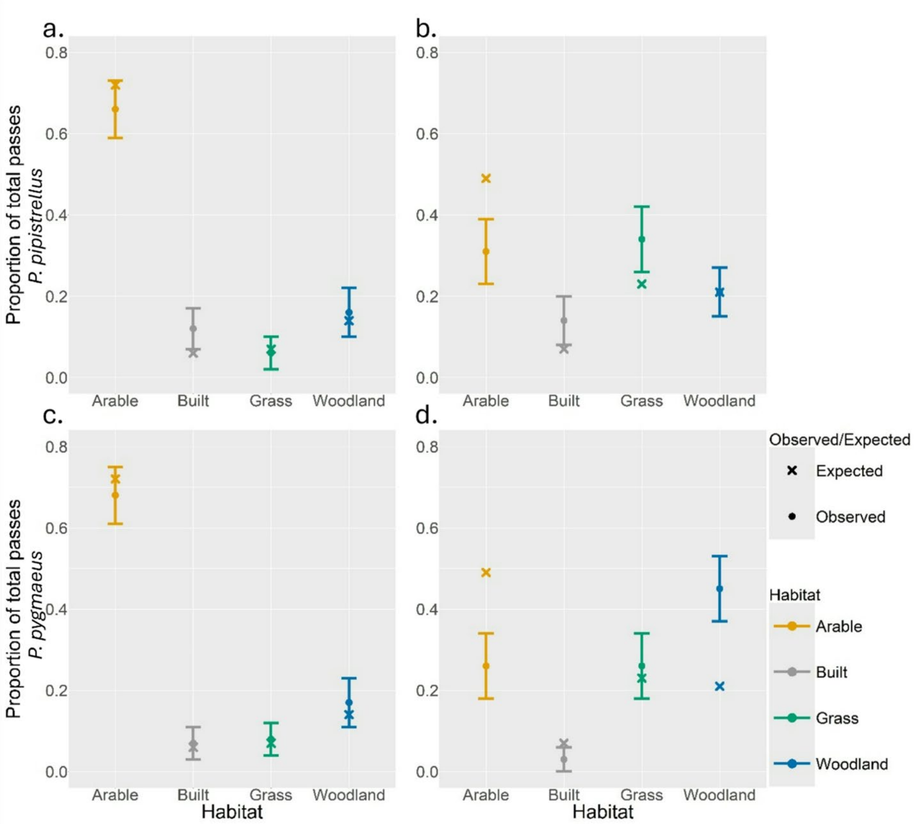

Fig. 4 Habitat selection of *P. pipistrellus* on arable (**a**) and mixed (**b**) farms and of *P. pygmaeus* on arable (**c**) and mixed (**d**) farms. The proportion of expected passes given the proportion of habitat available is shown with an 'x', whilst points and associated error bars show the proportion of observed passes with 95% confidence intervals. Where the proportion of expected passes lies above error bars this is interpreted as habitat avoidance, whilst habitat selection is deemed to occur where the proportion of expected passes lies below the error bars

patches at scales of 1000 and 1500 m (i.e. woodland patches tended to be closer together on mixed farms than on arable farms; Fig. 5), though this was marginally non-significant (P value greater than 0.05 but less than 0.1). Woody feature height tended to be lower on mixed farms though this effect was also marginal, only explained 6% of the variation in woody feature height and was not significant in autumn models, for which the subset of farms sampled differed slightly to that in summer.

Pipistrellus pipistrellus activity was unaffected by landscape composition or configuration in the summer months. Distance from buildings and local woody features were the only significant predictors of *P. pipistrellus* summer activity. Activity was higher closer to buildings, declining by 13.5% with every 50 m increase in distance from buildings. Local-scale woody features were also important, with an increase of two meters in woody feature height associated with an increase of 13.2% *P. pipistrellus* activity. As woody feature height was marginally lower on mixed farms, this resulted in an overall negative effect of mixed farming on *P. pipistrellus*. In the autumn, woody feature height and distance from build-

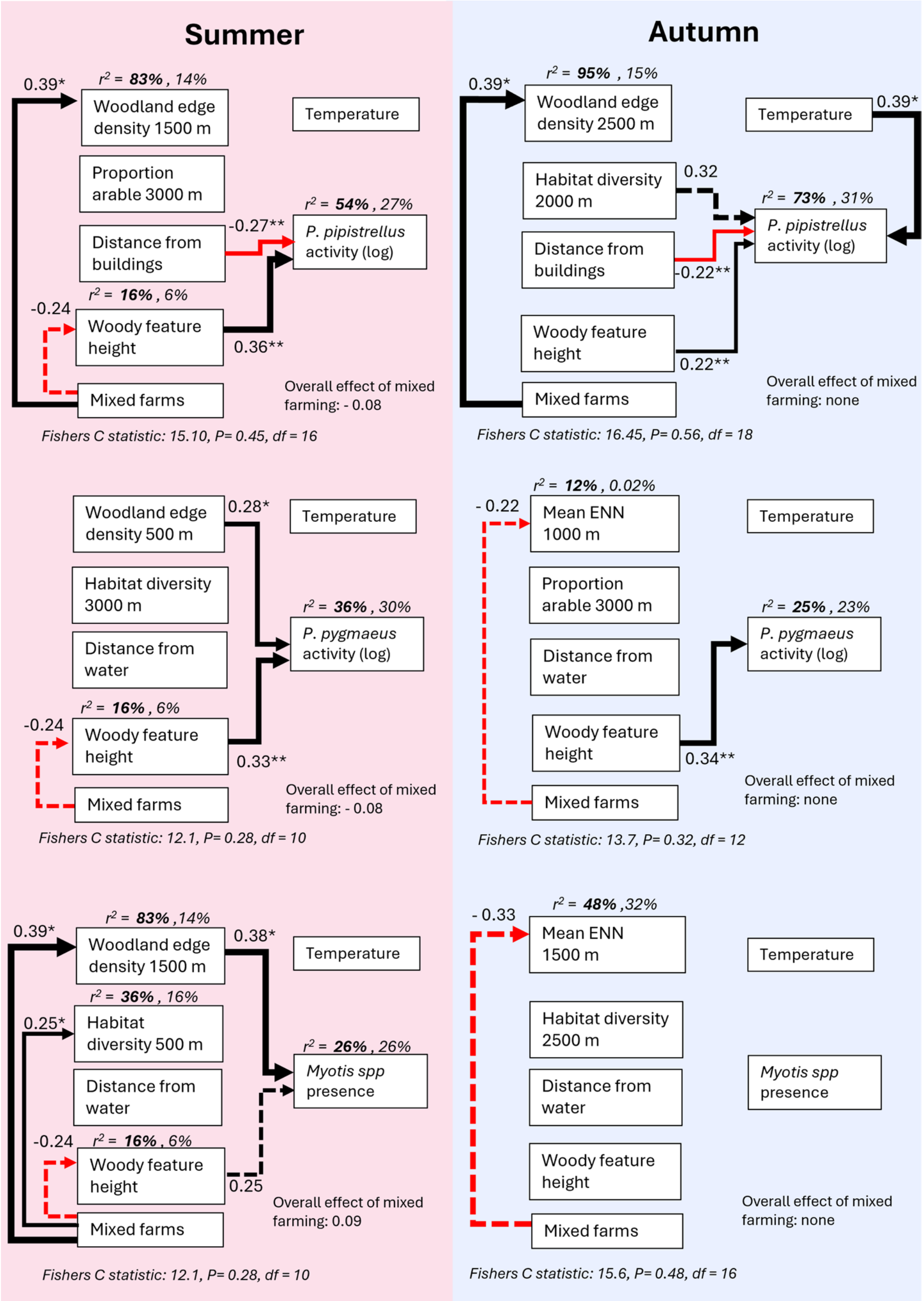

Fig. 5 SEM path diagrams for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp. for summer (pink) and autumn (blue). Black arrows show a positive effect whilst red arrows show a negative effect. Full arrows show a significant effect ($P<0.05$) and dashed arrows show a marginal effect ($0.05<P<0.1$). Standardized coefficients for each pathway are given with significance stars associated (significance codes: '*' $p\leq0.05$, '**' $p\leq0.01$, '*** $p\leq0.001$). Conditional r^2 (in bold-italic) and marginal r^2 (italic) values are given above each variable with significant or marginal pathways. Correlated errors and all p-values are given in Table S6. The selection of landscape variables included in each SEM is based on r^2 value (Sect. 2.5.2)

ings remained significant predictors of *P. pipistrellus* activity, an increase of 2 m in woody feature height was associated with an increase of 20% *P. pipistrellus* activity, whilst activity declined by 24% with every 50 m increase in distance from buildings. Additionally, *P. pipistrellus* activity was marginally ($P=0.06$) higher in landscapes with higher habitat diversity within 2000 m in autumn.

Pipistrellus pygmaeus responded to both local and landscape features in the summer months. Woodland edge density at the 500 m scale was positively associated with *P. pygmaeus* activity, which increased by 10% with every additional 10 m of woodland edge per hectare. On a local scale, an increase in woody feature height of 2 m was associated with an increase in activity of just over 11% in the summer months, leading to a marginal negative effect of mixed farming. This positive effect of woody feature height persisted in the autumn, with every 2 m increase in woody feature height associated with an increase of over 23% activity, however, this effect was not associated with farm type. We did not detect any effects of landscape composition or configuration on this species during the autumn.

In summer, *Myotis* spp. was positively associated with increasing woodland edge density at the 1500 m scale, with an increase of 10 m of woodland per hectare increasing the chance of recording *Myotis* spp. by 39%. We also detected a marginally non-significant positive effect of woody feature height (marginally shorter in mixed farms). An increase in woody feature height of 2 m was associated with an increased chance of recording *Myotis* spp. of 12%. Overall, the positive effect of mixed farming on *Myotis* spp. via woodland edge density outweighed the marginal negative effect of mixed farming mediated by lower woody feature height. No effects of farming type, local or landscape features were detected for *Myotis* spp. in autumn.

Effects of pasture presence and livestock management

Within mixed farms, there were no significant differences in bat activity between crop-crop or crop-pasture margins for *P. pipistrellus*, *P. pygmaeus* or *Myotis* spp. either during the summer months or autumn (Fig. S5). *Pipistrellus pipistrellus* activity had a non-linear significant relationship with cattle stocking rate in autumn but not in the summer, with lower activity associated with farms with less than 1.5 LU Ha^{-1} (Fig. 6b.). *Pipistrellus pygmaeus* activity levels were positively and linearly associated with cattle stocking rate in the autumn but not in the summer (Figs. 5d and 6c), with a small increase of 0.5 *P. pygmaeus* passes per night associated with an increase of 1 LU Ha^{-1} (the equivalent of one additional cow and calf per hectare). Autumn *P. pygmaeus* activity was also significantly higher on farms where sheep were present (+1.7 passes per night; $P=0.0004$). We found a marginally non-significant positive effect of cattle stocking rate on *Myotis* spp. occurrence in the summer. Overall GLMMs explained a reasonable amount of the variation in bat activity or occurrence on mixed farms ranging from 26% to 69% (Table S.7).

Discussion

To our knowledge, this is the first time that the impacts of mixed farming on bat foraging activity and habitat preferences have been investigated. We found that habitat selection of bats differed between farm type, with bats preferring woodland or grassland habitat on

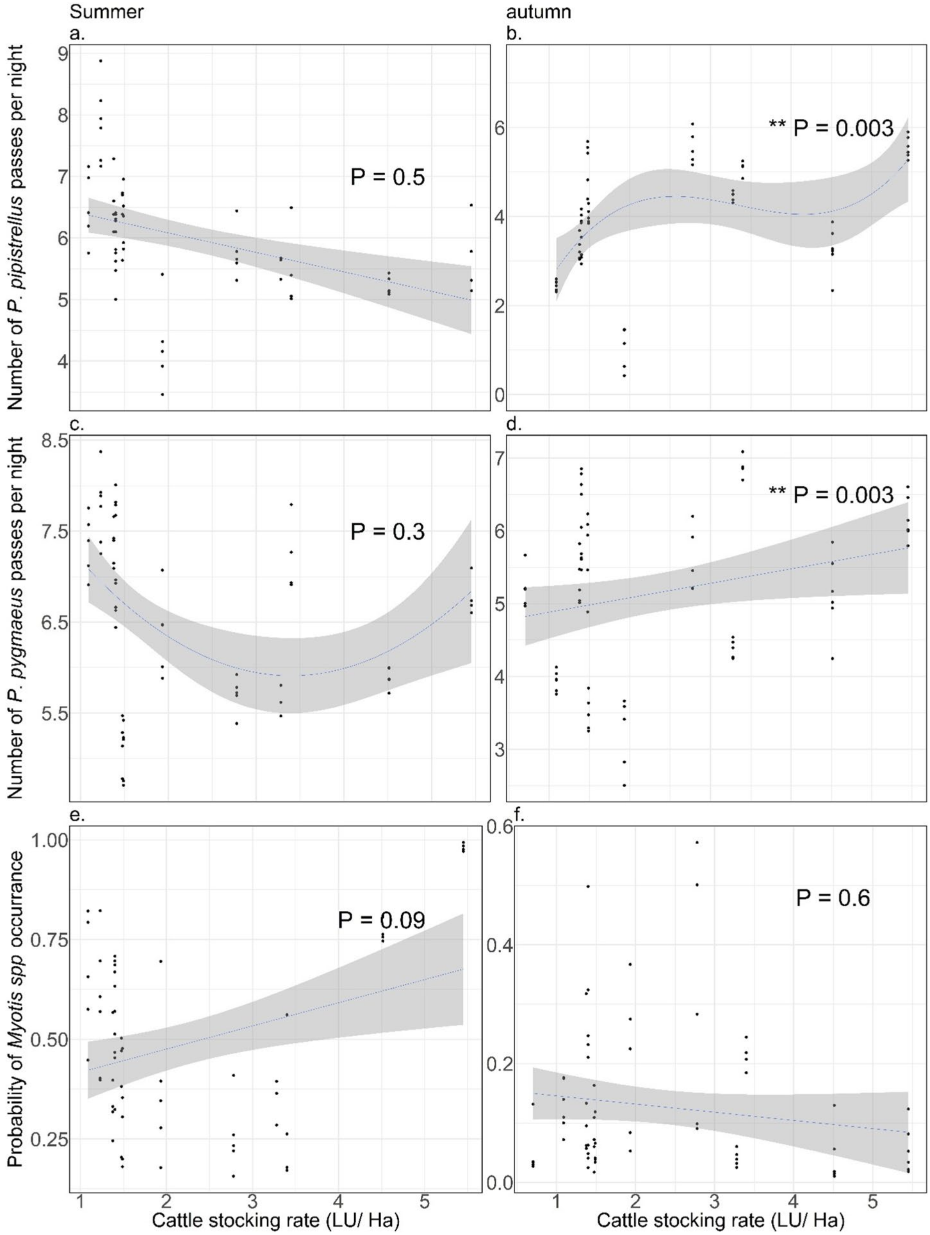

Fig. 6 Predicted change in *P. pipistrellus* and *P. pygmaeus* activity and *Myotis* spp. occurrence with cattle stocking rate

mixed farms but not on arable farms. In our whole-system approach we found no direct benefits of mixed farming compared to arable farming. Instead, bat activity or occurrence was influenced by local and /or landscape attributes. However, we found differences in landscape attributes of mixed and arable farms, which resulted in a higher probability of *Myotis* spp. occurrence in mixed farms (which have higher woodland edge density). Studies on the response of bats to agricultural practices often focus on bat activity during the summer months. However, this overlooks activity during the autumn, an important time of year for year bats feeding up pre-hibernation. Indeed, we found that the effects of mixed farming and livestock management on bat activity differed between seasons, highlighting the importance of monitoring bat response at different times of year.

Bat habitat preferences differ between mixed and arable farms

We detected no significant habitat selection or avoidance by bats on arable farms. In contrast, both *P. pipistrellus* and *P. pygmaeus* avoided arable fields on mixed farms (but not on arable farms), with *P. pipistrellus* selecting for grassland and *P. pygmaeus* selecting for woodland in mixed farms. The avoidance of arable fields and selection of grassland and woodland has been found in other studies (Nicholls and Racey 2006a, b; Russ and Montgomery 2002) suggesting that whilst both species can forage over arable land, they avoid it and show preference for other habitats when these are available, potentially due to lower insect abundances in arable fields compared with pasture or woodland (Evans et al. 2007; Garrett et al. 2022). These differing habitat preferences between farm types could also be driven by differences in the wider landscape (Sect. 4.3.).

Preference of buildings by *P. pipistrellus* on both farm types shows that this is an important resource in the agricultural matrix for this species. Some studies have found that livestock sheds can provide insect resources for bats (Dietz et al. 2013; Nosal et al. 2019). However, the selection of buildings by *P. pipistrellus* on both farm types in our study suggest that buildings are important regardless of livestock presence, likely by providing sheltered areas for insects and foraging bats in otherwise very open agricultural landscapes or important roosting sites for *P. pipistrellus*. Although our sampling design avoided peak emergence times, *P. pipistrellus* is known to increase regularity of feeding bouts during lactation (Davidson-Watts and Jones 2006), which coincides with the survey period for transects (June – July) and could explain higher activity around buildings with maternity roosts even after peak emergence.

Importance of landscape composition and configuration

We found significant associations between farming type and landscape composition and configuration. Mixed farming was associated with higher woodland edge density at larger scales (1500 and 2500 m) but not at smaller scales (500 m), and higher habitat diversity at smaller scales (500 m). It is possible that the presence of pasture habitat on mixed farms could contribute to higher habitat diversity on mixed farms at smaller scales (500 m). However, woodland configuration associated with mixed farming at larger scales (but not smaller scales) suggests that this is unlikely to be a causal effect of mixed farming, particularly given that mean farm size was only 200 Ha.

Pipistrellus pipistrellus activity was not influenced by landscape composition or configuration during the summer months. However, there was more activity in landscapes with higher habitat diversity in the autumn. The higher abundance of insects between June and July could mean that this generalist species isn't particularly affected by habitat configuration or composition during the summer months when food availability is high. However, in the autumn when crops have been harvested and temperatures drop, insects become less active (Welti et al. 2022) and may be concentrated in certain habitat types such as woodlands (Rigot et al. 2013). The positive effect of habitat diversity on *P. pipistrellus* activity found only in the autumn shows that this species can make use of a variety of habitats when insects are scarce. Our findings that the activity of *P. pipistrellus* increased closer to buildings in both summer and autumn, agrees with findings from our transect data that farmland buildings are an important landscape feature for this species. Whilst use of buildings by *P. pipistrellus* for roosting is well known (Hale et al. 2012), to our knowledge this is the first time that their importance as foraging features in agricultural landscapes has been found.

Woodland edge density was important for both specialist species (*P. pygmaeus* and *Myotis* spp.) during the summer months at scales similar to the known foraging/colony ranges for these species (Encarnação et al. 2006; Mordue et al. 2023; Nicholls and Racey 2006a, b). The positive effects of woodland edge density for *P. pygmaeus* and *Myotis* spp. corresponds with findings from Davidson-Watts and Jones (2006); Nicholls and Racey (2006a, b) and could be in part due to preferences for roosting in woodland for *P. pygmaeus* or near water bodies that are often associated with woodland for *M. daubentonii* (Encarnação et al. 2006; Lučan et al. 2009). In addition, these species are edge-adapted, preferring to forage along woodland edges (Walsh and Harris 1996b). Woodland configuration (as measured by mean woodland ENN) had no significant effect on these two specialist species in the autumn. *Myotis* spp. presence was very low in the autumn, recorded on just 19 out of 116 static detectors and with no effect of landscape composition or configuration found. This may have been influenced by *M. daubentonii* entering the hibernation period before the end of our survey period (Meier et al. 2022). Thus, presence of *Myotis* spp. in September and October may be more related to the location of suitable hibernacula rather than any of the landscape variables we measured.

Importance of local woody features

Activity of both pipistrelle species increased with woody feature height across both seasons measured, and *Myotis* spp probability of occurrence increased with increasing woody feature height during the summer months. Whilst we cannot disentangle the effects of woody feature height from other hedgerow characteristics that were not measured, our findings are similar to those found in Froidevaux et al. (2019). Similarly, trees incorporated into hedgerows have been found to increase pipistrelle activity (Finch et al. 2020; Tarcy et al. 2025). Similar benefits of hedgerows have also been found in other agroecosystems such as vineyards in Europe (Chavez et al. 2025). However, to our knowledge, this is the first time the positive effect of woody feature height has been found across seasons. Whilst current agricultural policies in Scotland support the retention of trees within hedgerows, management prescriptions that aim to manage and restore hedgerows for wildlife (Scottish and Government 2023) encourage regular trimming (every 2–3 years) and set a very low minimum hedgerow height (1.5 m) which is unlikely to be beneficial for bats, given that in our study peak activity was recorded adjacent to woody features that were 15 m high for *P. pipistrellus* and 25 m for *P. pygmaeus*. Though mixed farms in our study had marginally lower woody features in comparison to arable farms, farm type explained a very low amount of the variation in woody feature height ($r^2 = 6\%$) and the effect was not significant in autumn models (likely due to changing the location of some detectors between summer and autumn sampling). Marginally lower woody features on mixed farms could be due to management of hedgerows to contain livestock and/or hedgerow height may be reduced by browsing livestock in adjacent fields. Regardless of the drivers of woody feature height, taller hedgerows and treelines are likely to benefit both *Pipistrellus* spp. and *Myotis* spp. on both arable farms and mixed farms.

Stocking rate is more important than pasture presence for bat activity on mixed farms

We found no difference in bat activity between crop-crop and crop-pasture margins. Whilst this lack of difference is expected during the summer months when insects are abundant, it is surprising that we found no effect in the autumn when arable fields are generally bare following harvest and pasture could provide a more permanent habitat for insects. The lack of higher bat activity adjacent to pasture could be because livestock were not present in all pasture fields during autumn surveys (only eight out of the 31 crop-pasture margins where detectors were placed contained cattle at time of surveys) as this is the time of year when cattle are moved into barns in our study area. This is consistent with findings from Downs and Sanderson (2016) where bat activity was higher over fields containing cattle than over empty pasture where dung was present. Therefore, it could be that the pasture itself does not provide an important insect resource in the autumn but that the presence of livestock is more important. Indeed, we found a positive effect of cattle stocking rate on both pipistrelle species in the autumn (non-linear for *P. pipistrellus*, plateauing at around 2 LUs) and a positive effect of sheep presence on *P. pygmaeus* in the autumn, though the increase in bat activity associated with stocking rate was very small for both pipistrelle species. Evidence of bats feeding around livestock and a non-linear association has been previously reported by (Ancillotto et al. 2017). Our findings of increasing activity with higher stocking rates only in the autumn suggest that higher livestock numbers may be providing small additional insect resources on mixed farms during the pre-hibernation period.

Management recommendations

We investigated whether mixed farming is beneficial for foraging bats in comparison to arable farming. Mixed farming did not directly benefit bats in our study, although it was associated with landscape composition and configuration attributes that are beneficial for bats, such as higher woodland edge density, woodland patches closer together and higher habitat diversity. Greater woodland edge density was positively associated with the activity or occurrence of all three bat species/ groups. In addition, pipistrelle bats avoided arable fields in favour of woodland and grassland where these were available on mixed farms. Therefore, maintaining or increasing the cover of these semi-natural habitats on farmland regardless of farm type, is likely to be beneficial for foraging bats. *Pipistrellus pipistrellus* selected for buildings, which also provided important foraging grounds across the seasons. Policies that encourage bat-friendly farmland buildings could further enhance the use of these important features for *P. pipistrellus.* Positive effects of habitat diversity on *P. pipistrellus* were only apparent in the autumn, suggesting that this generalist species is able to make use of a variety of habitat types at a time of year when insects are scarce. Future agricultural policies that aim to benefit bats at a landscape scale should take into account habitat requirements at different times of year. Higher farm-level cattle stocking rates were only associated with a slight increase in pipistrelle activity in the autumn, suggesting that greater numbers of livestock are only providing a small benefit to bats, potentially via additional insect resource at a time when insects are scarcer. Taller woody features were associated with higher foraging activity or probability of occurrence of all species/groups studied, suggesting that increasing the minimum hedgerow height requirement for future Agri-Environment Schemes could encourage greater foraging activity of bats on farms.

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Author contributions RK: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. EF-M: Writing – review & editing, Validation, Supervision, Resources, Methodology, Conceptualization. Project administration. KJP: Writing – review & editing, Validation, Supervision, Resources, Project administration. NL: Writing – review & editing, Validation, Supervision, Software, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

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Data availability Data and R scripts used for analysis are available at The University of Stirling's DataSTORRE; [http://hdl.handle.net/11667/262](http:/hdl.handle.net/11667/262).

Declarations

Competing interests The authors declare no competing interests.

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