Biological Conservation 267 (2022) 109476

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Research article

Tree size, microhabitat diversity and landscape structure determine the value of isolated trees for bats in farmland

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ARTICLE INFO

Keywords:
Acoustic sampling
Agricultural landscapes
Bat conservation
Landscape heterogeneity
Remnant trees
Scattered trees

ABSTRACT

Isolated trees are increasingly recognised as playing a vital role in supporting biodiversity in agricultural landscapes, yet their occurrence has declined substantially in recent decades. Most bats in Europe are tree-dependent species that rely on woody elements in order to persist in farmlands. However, isolated trees are rarely considered in conservation programs and landscape planning. Further investigations are therefore urgently required to identify which trees – based on both their intrinsic characteristics and their location in the landscape – are particularly important for bats. We acoustically surveyed 57 isolated trees for bats to determine the relative and interactive effects of size, tree-related microhabitat (TreM) diversity and surrounding landscape context on bat activity. Tall trees with large diameter at breast height and crown area positively influenced the activity of *Pipistrellus pipistrellus* and small *Myotis* bats (*Myotis* spp.) while smaller and thinner trees favoured *M. myotis* activity. The diversity of TreMs that can be used as roosts had a positive effect on (i) *Barbastella barbastellus* activity only when trees were relatively close (<50 m) to woody patches, (ii) *Pipistrellus nathusii/kuhlii* activity only in the most heterogeneous landscapes, and (iii) *Myotis* spp. activity only in the most forested environment (>10% within 100 radius scale). The potential benefits of isolated trees for bats result from ecological mechanisms operating at both tree and landscape scales, underlining the crucial need for implementing a multi-scale approach in conservation programs. Maintaining the largest and most TreM-diversified trees located in the most heterogeneous agricultural landscapes will provide the greatest benefits.

1. Introduction

Isolated trees are prominent features of farmlands worldwide (Prevedello et al., 2018). The key defining feature of isolated trees is the dispersed spatial distribution of the trees throughout the landscape matrix (Dunn, 2000; Manning et al., 2006). These dispersed elements are also referred to as scattered trees (Manning et al., 2006), pasture trees (Poltz and Zotz, 2011), paddock trees (Fischer and Lindenmayer, 2002), or remnant trees (Barth et al., 2015). Despite the relatively recent interest in isolated trees for both ecosystem function and conservation issues, their importance as "keystone ecological structures" has been widely recognised (Manning et al., 2006; Gibbons et al., 2008). They provide disproportionately diverse ecological functions for biodiversity relative to their small spatial extent, including food resources, shelters or nest sites for a large range of vertebrate, arthropod and plant taxa (Prevedello et al., 2018). The presence of scattered trees is especially beneficial to wildlife in agricultural landscapes, increasing both species abundance and richness (Dunn, 2000; DeMars et al., 2010). Moreover, scattered trees provide multiple ecosystem services that benefit farmers and crop production, such as soil maintenance, pollination of crops, shading for cattle, regulation of nitrogen dynamics, carbon sequestration, and wood provision (Barton et al., 2016; Cuni Sanchez and Lindsell, 2017; Hartel et al., 2017).

Isolated trees also increase spatial heterogeneity and forest

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https://doi.org/10.1016/j.biocon.2022.109476
Received 22 October 2021; Received in revised form 13 January 2022; Accepted 31 January 2022

connectivity allowing enhanced species dispersal by acting as stepping stones for mobile and tree-dependent species such as bats (Fischer and Lindenmayer, 2002; Manning et al., 2009; Rocha et al., 2021). Most bat species are highly dependent on woody elements such as forest edges, woodlands, hedgerows and scattered trees which confer navigational reference during commuting, and also provide shelter from wind and protection from predators within the agricultural matrix (Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2013; Kalda et al., 2015; Lacoeuilhe et al., 2018; Froidevaux et al., 2019). Tall trees with large canopies may act as better acoustic landmarks than small ones for bats in farmlands (Frey-Ehrenbold et al., 2013). At the local scale, tree-related microhabitats (TreMs) may favour bats either through enhancing the abundance of insect prey or by providing suitable diurnal and maternity roosting sites – even though the influence of TreMs on bats has so far only been assessed in forests (Regnery et al., 2013; Paillet et al., 2018; Larrieu et al., 2019; Basile et al., 2020).

At the landscape level, the diversity of habitat types in the surrounding matrix irrespective of their spatial arrangement (i.e. landscape compositional heterogeneity) and the spatial arrangement of patches irrespective of habitat types (i.e. landscape configurational heterogeneity) influence bat activity and species richness in farmland through several processes including landscape complementation (Ancillotto et al., 2017; Monck-Whipp et al., 2018; Rodríguez-San Pedro et al., 2019; Laforge et al., 2021). In contrast to less human-altered landscapes, intensively managed farmland is relatively homogeneous, so improving landscape compositional and/or configurational heterogeneity at different spatial scales through farming systems and management practices represents a great opportunity for biodiversity conservation (Tscharntke et al., 2021). Furthermore, bat activity may increase with habitat connectivity and matrix quality in the surrounding landscape (Hale et al., 2012), and this relationship is largely scale-dependent (Mendes et al., 2017). For instance, Le Roux et al. (2018) demonstrated that the number of bat species and their activity around scattered trees were significantly reduced in urban areas compared to semi-natural landscapes. Therefore accounting for matrix composition is critical to understand how bats respond to the distribution of isolated trees in farmland.

Scattered woody features are disappearing from many agricultural landscapes worldwide (Gibbons and Boak, 2002; Orłowski and Nowak, 2007; Fischer et al., 2010b; Lindenmayer, 2017), often being perceived as incompatible with current farming practices and intensification/mechanization (Gibbons et al., 2008). Meanwhile, isolated trees are rarely considered in conservation programs and landscape planning (Prevedello et al., 2018; Wintle et al., 2019). There is an urgent need to help retain isolated trees in agricultural landscapes, since agricultural intensification accompanied with a loss of established trees in farmland is extremely detrimental to bat populations (Azam et al., 2016). It is therefore critical to know which isolated trees, based on both their intrinsic characteristics and their location in the landscape, should be prioritised for retention when conflicts of interest between biodiversity conservation and food productivity occur (Le Roux et al., 2018). To fulfil this need, we investigated how the local tree characteristics and their surrounding landscapes influence insectivorous bats at isolated trees in farmlands.

The main objectives of our study were twofold: (i) to evaluate how tree size, tree-related microhabitat (TreM) diversity and surrounding landscape context influence bat activity around isolated trees in farmlands; and (ii) to assess the interactive effects of TreM diversity and landscape-level variables on bats. More precisely, we tested the predictions that (i) larger tree size and higher TreM diversity increase bat activity at isolated trees; (ii) bat use of isolated trees with high microhabitat diversity decreases with distance to woodlands and hedgerows, and in less heterogeneous landscape; and (iii) edge density positively influences edge specialist bats while other bat species benefit mostly from increasing habitat diversity in the surrounding landscape.

2. Material and methods

2.1. Study area and sampling design

The study was conducted in the east of France, in Doubs district (Bourgogne Franche-Comté region; Fig. 1). We selected a subunit of the first plateau of the Jura mountains (c. 47°12′N, 6°32′E), namely the "plateaux d'Aissey/Sancey/Feule et d'Orsans à Terre-de-Chaux" (407 km^2, 389–859 m a.s.l.). The landscape of this rural area consists of a mosaic of patchily distributed habitats including native forests (49%), grassland (45%), arable land (5%), small urban areas (1%, the largest village has <1500 inhabitants), and wetlands (<1%).

Using Google Earth 2017, we identified all isolated trees that were present in the study area. We defined for this study an isolated tree as a single tree located at least 20 m from any other woody habitat patch such as other isolated trees, hedgerows, orchards, and forests. We used this 20 m threshold to minimise recording bats from other habitats and because it represents for many bat species a distance after which the probability of crossing a gap between woody patches substantially decreases (Hale et al., 2015; Pinaud et al., 2018). We then randomly selected trees that were situated at least 1 km apart (to minimise the likelihood of counting the same bats at different sites), 50 m from asphalt roads (to avoid any road edge effect) and located in farmland. We ground checked all selected trees and identified the main agricultural land type surrounding the trees (grassland vs. cropland). As most of the trees selected were in cattle-grazed pastures and meadows, trees in croplands were disregarded.

We classified trees into three categories, namely oak trees (pedunculate oak, *Quercus robur*), fruit trees and other trees. Fruit trees mainly consisted of cherry (*Prunus avium*) and apple (*Malus domestica*) while other trees comprised ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), maple (*Acer pseudoplatanus* and *A. campestre*), and linden (*Tilia* spp.). We applied a final tree selection by considering diameter at 1.30 m (hereafter referred to as "diameter at breast height - DBH") and distance between trees and the nearest woody habitat patches to obtain similar gradients of tree size and habitat connectivity among tree categories. This resulted in a selection of 57 single, isolated trees in grassland, comprising 21 oak trees, 16 fruit trees and 20 other trees (Fig. 1).

2.2. Tree assessment

We assessed tree size by using measurements of DBH, tree height, and tree crown area. Tree height was measured with a laser distance meter (Tacklife LDM03; Shenzen Temie Technology Co., Shenzen, China). To calculate tree crown area, we measured the distance between the edge of the tree crown and the tree trunk at the four cardinal points (i.e. north, east, south, west) and four intercardinal points (i.e. NE, SE, SW, NW). We then we derived the coordinates of these eight sampling points and used ArcGIS Desktop v10 (ESRI, Redlands, CA, USA) to create a polygon around the tree and calculate its area.

We surveyed tree-related microhabitats (TreMs) at each tree following the typology of Larrieu et al. (2018). We only considered TreMs that could potentially enhance bat prey abundance and/or provide suitable summer roosts for bats based on expert knowledge and existing literature (Regnery et al., 2013; Larrieu et al., 2018). Thus, we inventoried the presence/absence of 12 TreM types (Appendix S1). All observations were performed by the same surveyor. The number of tree-related microhabitat types is subsequently referred to as TreM diversity. We counted the number of microhabitat types that could potentially enhance prey abundance ("TreM-prey diversity"), and the number of microhabitat types that can be used as roosting sites ("TreM-roost diversity", see Appendix S1).

2.3. Bat echolocation call recording and identification

We sampled bats acoustically at all 57 trees between June and

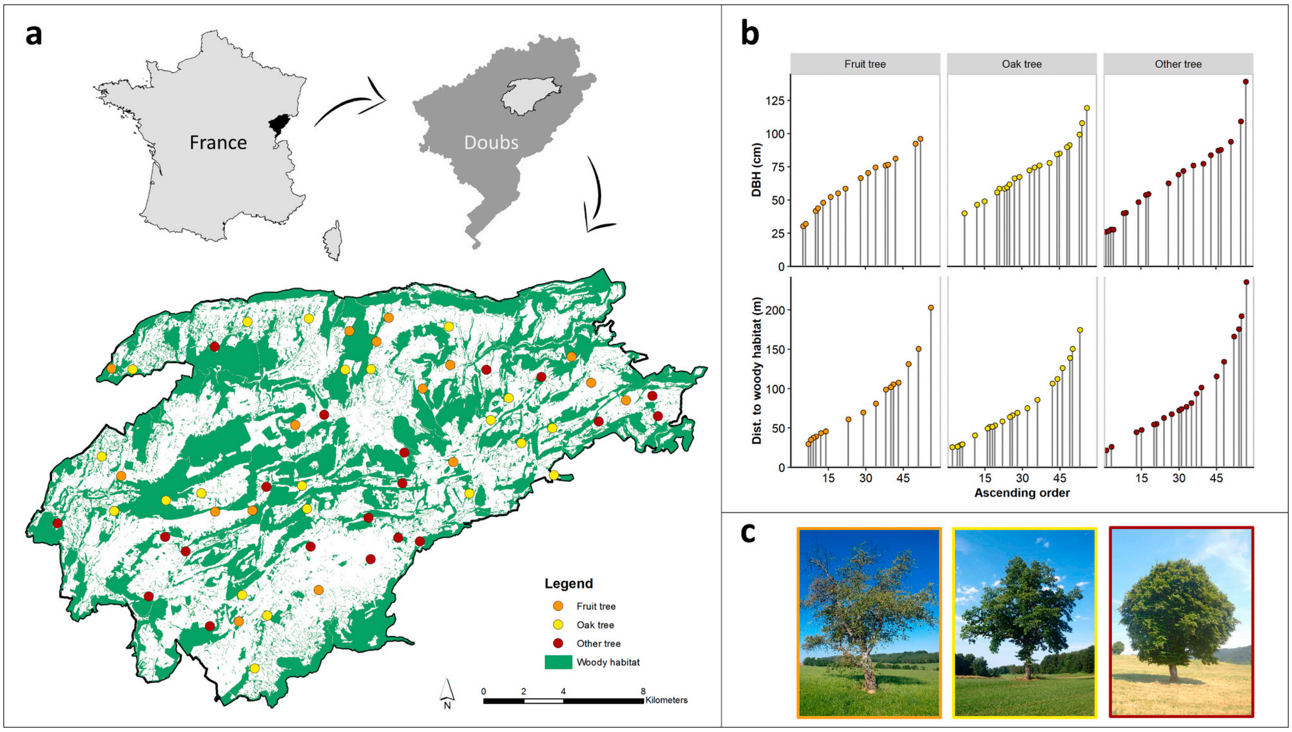

Fig. 1. (a) Map of the study area displaying the location of the 57 single, isolated trees in the grassland-dominated agricultural matrix. Tree species categories are represented with different colours (orange: fruit tree, yellow: oak tree, red: other tree), and woody habitat patches are displayed in green. (b) Tree species categories classed according to their diameter at breast height (DBH) and distance to the nearest woody habitat. (c) Examples of trees surveyed (left: cherry tree, centre: oak tree, right: linden tree). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

August 2017 using Song Meter SM2BAT+ recorders (sampling rate: 384 kHz) connected to SMX-U1 omnidirectional ultrasonic microphones (Wildlife Acoustics, Concord, USA). At each tree, we attached the recorder around the bare tree trunk or a branch at 1.8 m height and installed a data logger (RC-5; accuracy: 0.5 °C; Elitech, London, UK) to monitor temperature at night every 15 min. Recording was triggered automatically when sounds in the frequency range 12–192 kHz with a signal-to-noise-ratio level $\geq$12 dB were detected, and continued for 15 s. Sampling took place during one full night, from 30 min before sunset to 30 min after sunrise, and only when meteorological conditions were suitable for bats to forage, i.e., dry and calm nights with wind speed $<$30 km/h and temperature at sunset $>$ 12 °C. Before each sampling night, we randomly selected between one and six trees to sample simultaneously depending on logistical constraints and landowner permission. We used the number of bat passes per night as a measure of bat foraging and commuting activity. Each bat pass (i.e. a series of minimum two echolocation calls with interpulse intervals $<$1 s) present within each 15 s recording was identified using a semi-automatic approach. In brief, we used BatScope 3.2 (Obrist and Boesch, 2018) to detect and sort recordings containing bat calls and automatically extract call parameters. We then manually identified each bat pass to the lowest taxonomic level (see full details in Appendix S2).

2.4. Landscape analysis

We extracted landscape characteristics around each isolated tree at different spatial scales. We created five buffers (100, 250, 500, 1000, 2000 m radii) around the trees using ArcGIS Desktop v10. Larger spatial scales were not considered to minimise the likelihood of landscapes overlapping as most trees were located $<$2 km apart (mean: 1.6 km; range: 1.0–3.1 km), even though overlapping landscapes do not themselves represent a violation of independence (Zuckerberg et al., 2020). While the smaller spatial scales allow us to describe the environment close to the trees, the larger ones represent the mean daily foraging movement of many bat species present in the study area (Laforge et al., 2021). Using land use data compiled at 10 m spatial resolution for a previous study (Tournant et al., 2013), we quantified within each buffer the (i) landscape composition using the proportion of forest (which was negatively correlated with the proportion of grassland across the five spatial scales, $|r| > 0.7$), (ii) landscape configuration using the edge density (i.e. total length of all edge segments between multiple habitat patches in the buffer divided by the buffer area, m/ha) because many bat species use habitat patch edges to forage and commute, and (iii) landscape compositional heterogeneity using Shannon's diversity index calculated across all the reclassified habitat types ($n = 10$; Appendix S3). These variables were calculated with the “landscapemetrics” R-package (Appendix S4). We finally calculated the distance between trees and the nearest woody habitat patch (i.e. forests and hedgerows only) and used this metric as a proxy of habitat connectivity that is easily interpretable by land managers (Frey-Ehrenbold et al., 2013).

2.5. Statistical analysis

We conducted a series of generalized linear mixed-effect models (GLMMs; “glmmTMB” package) to assess the effects of tree and landscape attributes on bat taxon-specific activity. The response variable was the number of bat passes per night for species or group of species. Because bat activity is count data, GLMMs were fitted with a negative binomial error distribution due to over-dispersion and coupled with a logit link function.

Variables related to tree characteristics, tree connectivity, and landscape context were included as fixed effects and tree category was considered as random effect. We also added mean temperature at night and Julian day as covariates. All fixed variables were continuous and scaled (mean = 1; SD = 0) to enable direct comparisons. All analyses were conducted in R version 3.4.3 (R Development Core Team, 2017) and references of packages used are presented in Appendix S5.

We took a multi-step approach before building our final full models that included (i) a Principal Component Analysis (PCA) on DBH, tree height, and tree crown area, (ii) a selection of the best “scale of effect” for each landscape variable, and (iii) a selection of most relevant interaction between TreM diversity and landscape variables (see Appendix S6 for full details). Thus, for each species or group of species the full model included as fixed effects (i) the first PCA axis summarizing information on tree size, (ii) TreM type diversity, (iii) the interaction between TreM type diversity (either TreM-prey or TreM-roost) and one landscape variable (at its most relevant scale for buffer-dependent metric), (iv) the three area-based landscape variables at their most relevant scales, (v) the distance to the nearest woody habitat, and (vi) two covariates (i.e. mean temperature at night and Julian day). We examined collinearity among predictors present within the full models using the Spearman's correlation coefficient and the variance inflation factors (VIFs) and results did not highlight collinearity issues ($|r| < 0.7$, VIF < 3).

We conducted model selection based on the full models. We generated all possible models (“MuMIn” package) and ranked the most parsimonious ones based on *AICc* (Burnham and Anderson, 2002). We conducted a model-averaged procedure of most parsimonious models (i.e. those with $\Delta AICc < 2$), accounting for model selection uncertainties (Grueber et al., 2011) and report the full model average estimates. The significance of the effects was evaluated using 95% confidence intervals (Nakagawa and Cuthill, 2007). When a significant interaction between TreM type diversity and landscape variable was found, we undertook a spotlight analysis to explore the nature of the interaction effect using the “emmeans” package. In this analysis, we investigated the effects of TreM type diversity on bat activity at specific values (mean, mean − SD, mean + SD) of the selected landscape metric. Details on model validation can be found in Appendix S7.

Finally, as it became apparent that TreM-roost and tree size were key factors driving bat activity around isolated trees, we built a generalized linear mixed-effect model to investigate the relationship between TreM-roost diversity (response variable) and tree size (explanatory variable). We used the same random structure as described above and model was fitted with a Poisson distribution since no overdispersion was detected.

3. Results

We recorded 4091 bat passes around 57 isolated trees in agricultural grasslands (Appendix S8). The bat assemblage was dominated by *Pipistrellus pipistrellus* with 2305 bat passes (56.3% of the total bat activity), followed by small *Myotis* bats (12.1%, *Myotis* spp.), nyctaloids (11.5%, *Eptesicus/Nyctalus/Vespertilio* spp.), *Barbastella barbastellus* (5.1%), *Pipistrellus nathusii/kuhlii* (4.5%), *Myotis myotis* and *Rhinolophus hipposideros* (both 2.2%), *Plecotus* spp. (1.4%), *Miniopterus schreibersii* (0.6%), and *Rhinolophus ferrumequinum* (<0.1%; Appendix S8). We could not attribute with certainty <5% of the bat passes to a species or species/genus group. We were able to model the activity of *P. pipistrellus*, *P. nathusii/kuhlii*, *B. barbastellus*, *M. myotis*, *Myotis* spp., *Plecotus* spp., *R. hipposideros* and nyctaloids with a total variance explained ranging from 42 to 79% (i.e. R^2 marginal: proportion of variance explained by the fixed effects; Table 1).

3.1. Effects of isolated tree characteristics on bats

The effect of tree size on TreM-roost diversity was significant (estimate ± SE: 0.41 ± 0.15, lower 95% confidence interval: 0.12, higher 95% CI: 0.70). The diversity of TreM-roost increased with increasing tree height, crown area and DBH.

Our analyses confirmed that the size (DBH, tree height, and tree crown area) of isolated trees significantly influence bat activity. More precisely, we found that tall trees with large DBH and crown area significantly enhanced the activity of *P. pipistrellus* and *Myotis* spp. while the activity of *M. myotis* was positively associated with smaller trees (Table 1, Fig. 2). The diversity of TreM-roost was selected in our best

Table 1

Standardized, model-averaged parameter estimates with associated standards errors (SE) and 95% confidence intervals of the best GLMMs ($\Delta AICc < 2$) relating the effects of tree and landscape attributes on bat taxon-specific activity. Variables in bold represent influential variables for which 95% CI did not overlap zero. Marginal R^2 (variance explained by the fixed effects only) of the full models is given.

Variables	*Barbastella barbastellus*	Nyctaloids	*Pipistrellus pipistrellus*	*Pipistrellus nathusii/kuhlii*	*Myotis myotis*	*Myotis* spp.	*Plecotus* spp.	*Rhinolophus hipposideros*
Julian day	/	−0.25 ± 0.16 (−0.56, 0.05)	**0.35 ± 0.15** **(0.04, 0.65)**	0.17 ± 0.17 (−0.16, 0.50)	/	**0.34 ± 0.11** **(0.12, 0.55)**	0.18 ± 0.20 (−0.21, 0.57)	−0.37 ± 0.25 (−0.86, 0.12)
Temperature	0.50 ± 0.30 (−0.08, 1.08)	**0.28 ± 0.12** **(0.03, 0.52)**	0.19 ± 0.17 (−0.14, 0.52)	/	**0.75 ± 0.23** **(0.29, 1.21)**	**0.41 ± 0.12** **(0.17, 0.65)**	0.16 ± 0.24 (−0.31, 0.62)	/
Tree size	0.37 ± 0.29 (−0.19, 0.92)	/	**0.60 ± 0.13** **(0.34, 0.86)**	/	**−0.60 ± 0.23** **(−1.06, −0.14)**	**0.39 ± 0.12** **(0.15, 0.63)**	/	/
TreM-prey	/	/	/	/	/	/	/	0.15 ± 0.25 (−0.34, 0.63)
TreM-roost	−0.11 ± 0.30 (−0.71, 0.48)	0.23 ± 0.14 (−0.06, 0.51)	0.21 ± 0.16 (−0.09, 0.52)	0.19 ± 0.20 (−0.20, 0.58)	**0.84 ± 0.21** **(0.43, 1.26)**	0.15 ± 0.12 (−0.08, 0.39)	/	/
Dist. woody edge	−0.78 ± 0.41 (−1.58, 0.02)	/	/	/	0.36 ± 0.26 (−0.14, 0.87)	/	**−0.63 ± 0.31** **(−1.24, −0.03)**	−0.15 ± 0.29 (−0.72, 0.42)
Edge density	−0.60 ± 0.31 (−1.21, 0.01)^{4}	/	**0.53 ± 0.19** **(0.14, 0.92)**^{4}	0.25 ± 0.23 (−0.19, 0.70)^{1}	/	/	/	−0.49 ± 0.26 (−0.99, 0.02)^{3}
% of forest	−0.36 ± 0.29 (−0.93, 0.21)^{1}	**0.30 ± 0.14** **(0.03, 0.57)**^{1}	/	/	**−0.40 ± 0.22** **(−0.82, 0.03)**^{2}	−0.17 ± 0.18 (−0.52, 0.17)^{1}	0.20 ± 0.28 (−0.35, 0.45)^{1}	**0.48 ± 0.23** **(0.04, 0.93)**^{1}
SHDI	**0.95 ± 0.37** **(0.22, 1.67)**^{5}	**0.45 ± 0.16** **(0.14, 0.76)**^{5}	0.30 ± 0.20 (−0.10, 0.69)^{4}	0.33 ± 0.21 (−0.08, 0.74)^{1}	**0.72 ± 0.23** **(0.28, 1.17)**^{5}	0.21 ± 0.17 (−0.13, 0.55)^{1}	0.41 ± 0.32 (−0.22, 1.04)^{1}	−0.40 ± 0.27 (−0.92, 0.13)^{2}
TreM:Dist. woody edge	**−1.23 ± 0.41** **(−2.03, −0.43)**	/	/	/	/	/	/	**0.58 ± 0.24** **(0.11, 1.05)**
TreM:Edge density	/	/	/	/	/	/	/	/
TreM:% of forest	/	0.24 ± 0.18 (−0.12, 0.60)	/	/	/	**0.53 ± 0.16** **(0.22, 0.84)**^{1}	/	/
TreM:SHDI	/	/	/	**0.65 ± 0.21** **(0.23, 1.07)**^{1}	/	/	/	/
R^2 marginal	*0.79*	*0.50*	*0.55*	*0.48*	*0.68*	*0.63*	*0.42*	*0.43*

Spatial scales: ^{1}100 m radius scale, ^{2}250 m radius scale, ^{3}500 m radius scale, ^{4}1000 m radius scale, ^{5}2000 m radius scale.

TreM: tree-related microhabitats. SHDI: Shannon's diversity index calculated across all the reclassified habitat types.

models for six out eight taxa while TreM-prey diversity was only retained in the most parsimonious models on *R. hipposideros* (Table 1). TreM-roost diversity had only a significant positive effect on *M. myotis* activity (Table 1) and the effects of TreM diversity on the other taxa largely depended on the landscape context.

3.2. *Interactive effects of TreMs and landscape structure*

Our models revealed significant interactions between TreM-roost diversity and different landscape features (Table 1). Thus, the positive effect of TreM-roost diversity was significant on (i) the activity of *B. barbastellus* only when isolated trees were relatively close (<50 m) to a woody habitat patch (i.e. forest or hedgerow), (ii) *P. nathusii/kuhlii* spp. activity only in the most heterogeneous landscapes, and (iii) on *Myotis* spp. activity only in the most forested environment (Fig. 3). TreM-prey diversity was positively associated with *R. hipposideros* activity only when isolated trees were located away (>100 m) from a woody feature (Fig. 3).

3.3. *Influence of landscape composition and configuration on bats*

At the landscape level, significant effects of edge density and landscape compositional heterogeneity (i.e., Shannon diversity of habitats) were always positively associated with bat activity. Edge density at 1 km radius scale positively influenced *P. pipistrellus* activity, while Shannon diversity of habitats at 2 km radius scale had a positive effect on the activity of nyctaloids, *M. myotis* and *B. barbastellus* (Table 1). The proportion of forest surrounding isolated trees had a more contrasting effect on bats, whose responses were taxon-specific: the activity of nyctaloids and *R. hipposideros* increased with forest cover while the opposite was true for *M. myotis*. Finally, we also found that the activity of *Plecotus* spp. decreased significantly with the distance to the nearest woody habitat (Table 1).

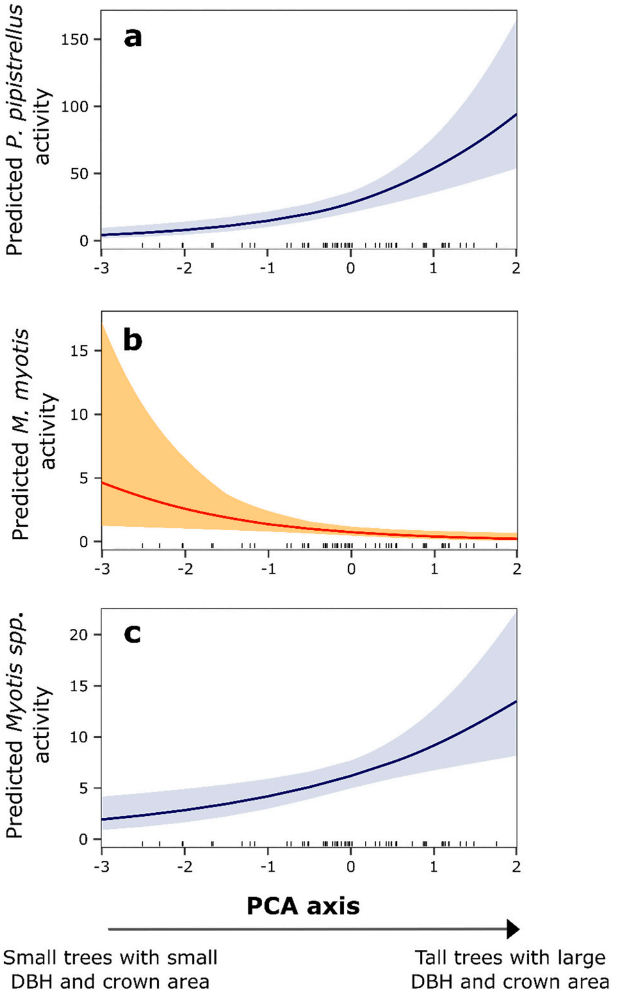

Fig. 2. Predicted bat responses to tree size with the 95% confidence interval (obtained from our best models): (a) predicted *P. pipistrellus* activity (i.e. number of bat passes per night); (b) predicted *M. myotis* activity; (c) predicted *Myotis* spp. activity. The tick marks on the x-axis are observed data points.

4. Discussion

Disregarded for a long time, the potential importance of isolated trees for wildlife has recently gained more attention (see meta-analysis of Prevedello et al., 2018). Yet, it can be difficult to identify the key mechanisms underlying the attractiveness of such isolated habitats within the agricultural matrix. Here, we demonstrate that the ecological importance of isolated trees for bats is determined by tree-related microhabitat diversity, tree size and landscape heterogeneity. More specifically, we found additive and interactive effects of local (i.e. tree characteristics) and landscape (i.e. both composition and configuration) factors on bats recorded around isolated trees. While retaining isolated trees is extremely important and should be urgently included in conservation planning (Le Roux et al., 2018) (e.g. through agri-environment schemes), our results shine a light on the isolated tree attributes and landscape contexts likely to contribute the most to bat conservation in farmland mosaic landscapes.

4.1. *Species and guild-specific responses of bats to tree size*

In line with our predictions, tall trees with large DBH and crown area enhanced the activity of edge-specialist (here *P. pipistrellus*) and clutter-adapted (here *Myotis* spp.) bat species but did not influence open-space forager activity (here nyctaloids). These three taxa accounted for more than 80% of the total bat activity recorded in the study area. However, contrary to our expectation, our results also revealed a negative relationship between tree size and *M. myotis* activity. Overall, our results do not corroborate the findings of Le Roux et al. (2018) who found no effect of tree size on insectivorous bats in Australia, probably because their studies included very contrasting and diverse landscapes with features that may have masked any effects of tree size on bat activity. Nevertheless, Polyakov et al. (2019) found similar results to ours around isolated trees located in Californian vineyards, with larger trees increasing the activity of edge-specialist bats.

As observed with other woody features embedded within the agricultural matrix such as hedgerows (Froidevaux et al., 2019), several mechanisms may explain the positive effects of tree size on edge-specialist and clutter-adapted species. First, tall trees with large canopies may act as better acoustic landmarks than smaller ones, especially for these species that mainly rely on woody features for commuting (Frey-Ehrenbold et al., 2013). Thus, large isolated trees may serve as stepping stones between forests and hedgerows and ultimately increase landscape connectivity (Saura et al., 2014). Second, bats may benefit from greater foraging opportunities around large trees. While we did not assess prey abundance along a tree size gradient, larger trees are likely to provide more shelter for bat insect prey in temperate farmland (Merckx et al., 2010). Prey aggregations around large trees are more likely to benefit relatively manoeuvrable edge-specialist and clutter-adapted bats (Denzinger and Schnitzler, 2013). Third, larger trees may offer more roosting sites for tree-dwelling bat species compared to smaller ones (Tillon et al., 2016). Diameter at breast height is one of the main driver of TreM diversity (Larrieu et al., 2014; Kozák et al., 2018; Asbeck et al., 2019) and TreM formation accelerates as trees grows (Courbaud et al., 2017). This is also confirmed for isolated trees by the positive and significant relationship we found between tree size and the diversity of TreM-roosts.

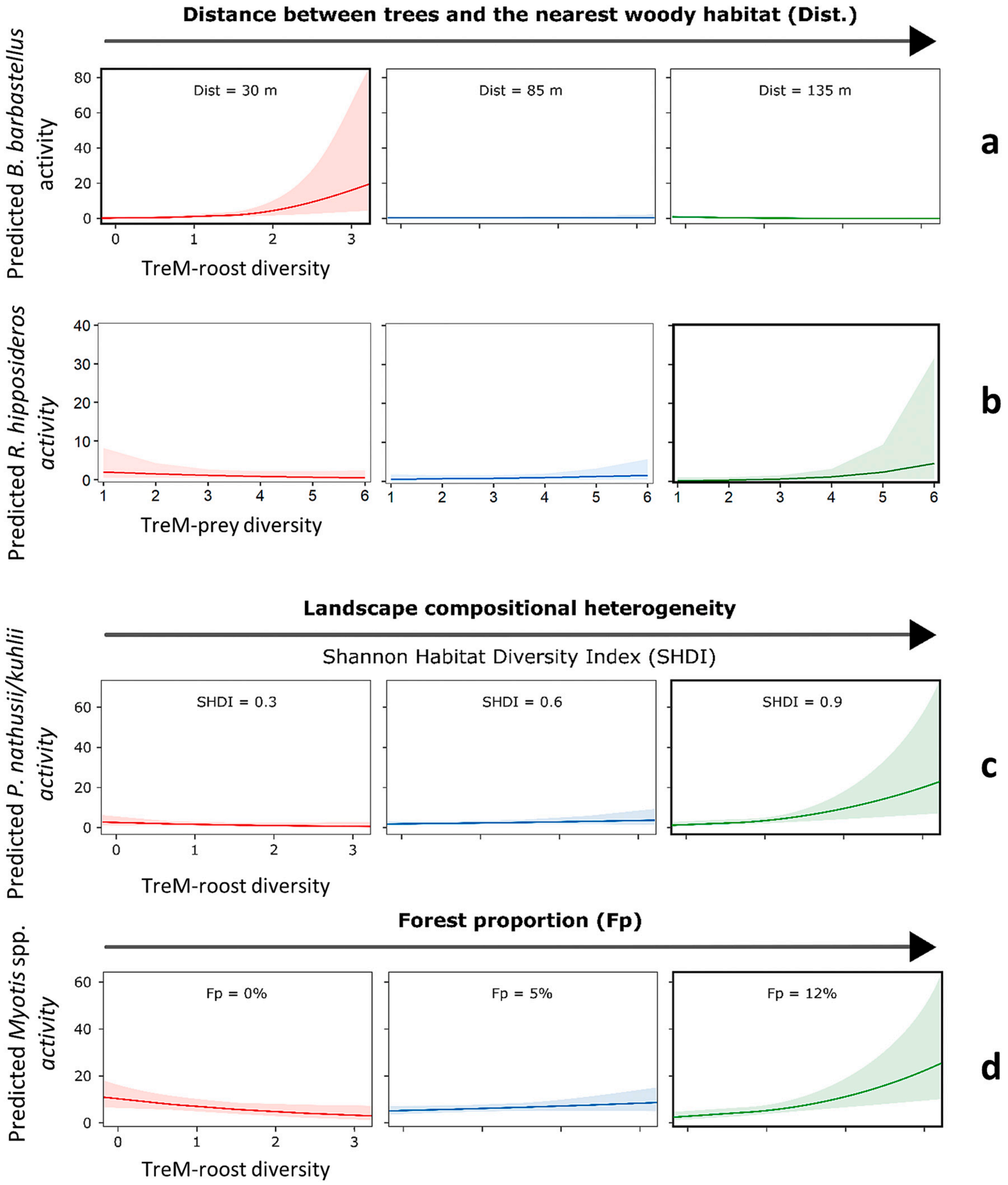

Fig. 3. Predicted bat responses to the number of tree-related microhabitat types (TreM-roost: TreM that can be used as roosting sites; TreM-prey: TreM that can enhance prey abundance) with the 95% confidence interval within different landscape contexts: predicted (a) *Barbastella barbastellus* activity (i.e. number of bat passes per night) and (b) *Rhinolophus hipposideros* activity, at three distances between trees and the nearest woody habitat; (c) *Pipistrellus nathusii/kuhlii* activity at three levels of landscape heterogeneity calculated within 100 m radius around trees; and (d) *Myotis* spp. activity at three levels of forest proportion calculated within 100 m radius around trees. We investigated the effects of TreM type diversity on bat activity at specific values (mean, mean − SD, mean + SD) of the selected landscape metric. Bold frames represent significant slopes (i.e. 95% confidence interval not overlapping zero).

4.2. Effects of microhabitat diversity on bats depend on the landscape context

The level of habitat use by bats may vary depending on a range of local and landscape factors (Mendes et al., 2017). We found that the activity of *B. barbastellus* increased with increasing TreM-roost diversity only around trees close to (<50 m) woody habitat patches. *Barbastella barbastellus* is a tree-dwelling species and this pattern most likely describes spillover effects of individuals from adjacent woody habitat such as forests and hedgerows to isolated trees when the latter are of higher quality (i.e. with high diversity of potential suitable roosts). Moreover, our findings suggest that *P. nathusii/kuhlii* and *Myotis* spp. were more active at trees bearing a high diversity of TreM-roost only in the most heterogeneous and forest-covered landscapes, respectively. These significant interactions were found at the smallest landscape scale considered in this study (i.e. 100 m), which represents the landscape context at the vicinity of the trees. Landscape compositional heterogeneity at such scales may promote the activity of *P. nathusii/kuhlii* through increasing overall landscape permeability as these edge-specialist species may better access to trees that are isolated in the agricultural matrix when this matrix is diverse. Similarly, as many *Myotis* spp. are clutter-adapted species, an increase of forest cover at the vicinity of the isolated trees may enhance the potential access to isolated trees. Depending on both the landscape context and the ecological requirements of the different *Myotis* bat species occurring in the study area, isolated trees bearing a relative high diversity of TreMs may be considered as both roosting habitats and secondary foraging habitats. We hypothesize that *Myotis* bats which mainly forage in forests may use isolated trees as foraging grounds in response to (i) higher inter or intra-specific competition in forests (Lewanzik et al., 2019), and (ii) potential asynchrony in the nightly emergence of insects among different habitats (e.g. between forest and isolated trees) (Ruczyński et al., 2020) arising from less buffered microclimatic conditions around trees. Finally, only *R. hipposideros* responded to the diversity of TreM-prey, with more activity detected around the most TreM-diversified trees that are located further away (>100 m) from woody habitat patches. This slow-flying forager highly relies on woody features for commuting, and crossing an open area can represent a potential risk (e.g. predation). We therefore stipulate that the cost-benefit ratio of crossing an open habitat to access isolated foraging sites is only advantageous for this species when the latter are of high quality (i.e. prey-rich patches). Interestingly, *M. myotis* activity was enhanced by TreM-roost diversity. Although our models on TreM-prey were not retained, this attic-dwelling species may not benefit from roosting opportunities but by enhanced prey resources around isolated trees.

4.3. *Influence of the surrounding environment*

Landscape compositional heterogeneity is known to enhance bat activity and species richness in farmland (Ancillotto et al., 2017; Monck-Whipp et al., 2018; Rodríguez-San Pedro et al., 2019). Our study corroborates these findings as we found that landscape heterogeneity (here defined as the Shannon diversity of habitats) positively influenced the activity of three taxa (nyctaloids, *M. myotis* and *B. barbastellus*). Landscape compositional heterogeneity is likely to benefit bats through an enhanced process of non-substitutable resource complementation (Dunning et al., 1992; Monck-Whipp et al., 2018). In line with other studies (Mendes et al., 2017; Rodríguez-San Pedro et al., 2019), our results further suggested that edge density between multiple habitat patches (i.e. a proxy of landscape configuration) at a 1 km radius scale positively influenced the activity of the most abundant edge-specialist species *P. pipistrellus*. Finally, we found that bat responses to forest cover at the landscape scale were species-specific, depending on roosting and foraging habitat preferences. Bat species that rely on forests for roosting or foraging (such as *Nyctalus* spp. and *R. hipposideros*, respectively) were positively associated with forest cover whereas *M. myotis*, an attic-dwelling species known to mainly forage above meadows, was negatively affected.

4.4. *Implications for conservation and recommendations for management practices*

Widely recognised as a keystone ecological structure (Manning et al., 2006) due to the disproportionate roles they provide for many species (Fischer et al., 2010a), isolated trees also represent an important landscape feature for bats in farmland (Le Roux et al., 2018; Polyakov et al., 2019). In accordance with other studies (Gibbons et al., 2008; Manning et al., 2009; Prevedello et al., 2018), our findings highlight the crucial need of maintaining a diversity of isolated trees within the agricultural matrix for both biodiversity conservation and ecosystem functioning. The contrasting response of bats to tree size implies that maintaining isolated trees with varying tree size should benefit the whole bat community (Wood et al., 2017). Our results also highlight the importance of maintaining a wide diversity of tree species in farmland to hinder near-future extensive tree losses (Fischer et al., 2010b) and to preserve a large range of tree shapes and structures, as well as continuous amount of dead and decaying trees within grassland at various locations in the wider landscape. While we advocate the preservation of isolated trees for the benefit of the entire bat community, our results also provide relevant information to be applied for species-specific conservation actions. For instance, the preservation of large trees in close vicinity of hedgerows and forest edges appears to be important for the conservation of the near-threatened barbastelle bat. Nevertheless, integrating the retention of such small features in conservation planning within farmlands might be challenging as their inventory have been neglected in many countries. Fortunately, remote sensing technologies offer substantial opportunities for both inventorying and monitoring trees in farmland (Malkoç et al., 2021).

The potential benefits of isolated trees to bats result from mechanisms that operate at both tree and landscape scales, and our results suggest that trees located in heterogeneous landscapes (in terms of both composition and configuration) will provide the greatest benefits. Finally, as isolated trees are often perceived as incompatible with most current farming practices (Gibbons et al., 2008), it would also be of great value to assess the potential of these trees in enhancing the biodiversity benefits for farmers. Such benefits include suppression of pest insects by bats in farmland (Russo et al., 2018), but also the various ecological functions fulfilled by isolated trees as well as the cultural ecosystem services they provide to agricultural landscapes.

Data availability

Data collected for this study are available to download at https://doi.org/10.5281/zenodo.5956938.

CRediT authorship contribution statement

JSPF conceived the ideas, designed the methodology, and collected the data; JSPF and PCF analysed the acoustic data; AF led the statistical analysis with the support of JSPF; LL formulated the hypotheses on tree-related microhabitats; JSPF and AL led the writing of the manuscript; JSPF and GJ secured the funding; All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

Authors report no conflicts of interest.

Acknowledgments

Acknowledgements We thank the landowners for granting permission to access their lands. We thank Jean-Christophe Foltête (Université Bourgogne Franche-Comté) for sharing land-use data and Antoine Brin (EI de Purpan) for his revision. We thank the associate editor and two anonymous reviewers who made valuable comments and suggestions that helped to improve an earlier version of the manuscript. This study was funded by the Biotechnology and Biological Sciences Research Council through the South West Biosciences Doctoral Training Partnership (grant number: 1576874).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109476.

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