



HAL
open science

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

Jérémy S.P. Froidevaux, Alexis Laforge, Laurent Larrieu, Luc Barbaro, Kirsty Park, Penelope Fialas, Gareth Jones

► To cite this version:

Jérémy S.P. Froidevaux, Alexis Laforge, Laurent Larrieu, Luc Barbaro, Kirsty Park, et al.. Tree size, microhabitat diversity and landscape structure determine the value of isolated trees for bats in farmland. *Biological Conservation*, 2022, 267, pp.109476. 10.1016/j.biocon.2022.109476 . hal-03619557

HAL Id: hal-03619557

<https://hal.inrae.fr/hal-03619557v1>

Submitted on 22 Jul 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

Jérémy S. P. Froidevaux^{1,2,3,¥,*}, Alexis Laforge^{3,4,*}, Laurent Larrieu^{5,6}, Luc Barbaro^{4,5}, Kirsty Park²,
Penelope C. Fialas¹, Gareth Jones¹

¹ University of Bristol, School of Biological Sciences, Life Sciences Building, Bristol, UK.

² University of Stirling, Biological and Environmental Sciences, Faculty of Natural Sciences, Stirling, UK

³ Centre d'Ecologie et des Sciences de la Conservation (CESCO, UMR 7204), CNRS, MNHN, Sorbonne-Université, Concarneau/Paris, France.

⁴ Université de Toulouse, Ecole d'Ingénieurs de PURPAN, UMR DYNAFOR, Toulouse, France.

⁵ CRPF-Occitanie, Tarbes, France.

* These authors contributed equally to this study

¥ Corresponding author:

Jérémy S. P. Froidevaux

E-mail: jeremy.froidevaux@stir.ac.uk

Author contributions

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.

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

3
4
5 **Abstract**

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

23

24 **Keywords**

25 Acoustic sampling; agricultural landscapes; bat conservation, landscape heterogeneity; remnant trees;
26 scattered trees.

27

28 **1. Introduction**

29 Isolated trees are prominent features of farmlands worldwide (Prevedello et al., 2018). The key
30 defining feature of isolated trees is the dispersed spatial distribution of the trees throughout the
31 landscape matrix (Dunn, 2000; Manning et al., 2006). These dispersed elements are also referred to as
32 scattered trees (Manning et al., 2006), pasture trees (Poltz & Zotz, 2011), paddock trees (Fischer &
33 Lindenmayer, 2002), or remnant trees (Barth et al., 2015). Despite the relatively recent interest in
34 isolated trees for both ecosystem function and conservation issues, their importance as “keystone
35 ecological structures” has been widely recognised (Manning et al., 2006; Gibbons et al., 2008). They
36 provide disproportionately diverse ecological functions for biodiversity relative to their small spatial
37 extent, including food resources, shelters or nest sites for a large range of vertebrate, arthropod and
38 plant taxa (Prevedello et al., 2018). The presence of scattered trees is especially beneficial to wildlife
39 in agricultural landscapes, increasing both species abundance and richness (Dunn, 2000; DeMars et al.,
40 2010). Moreover, scattered trees provide multiple ecosystem services that benefit farmers and crop
41 production, such as soil maintenance, pollination of crops, shading for cattle, regulation of nitrogen
42 dynamics, carbon sequestration, and wood provision (Barton et al., 2016; Cuni Sanchez & Lindsell,
43 2017; Hartel et al., 2017).

44 Isolated trees also increase spatial heterogeneity and forest connectivity allowing enhanced
45 species dispersal by acting as stepping stones for mobile and tree-dependent species such as bats
46 (Fischer & Lindenmayer, 2002; Manning et al., 2009, Rocha et al., 2021). Most bat species are highly
47 dependent on woody elements such as forest edges, woodlands, hedgerows and scattered trees which
48 confer navigational reference during commuting, and also provide shelter from wind and protection
49 from predators within the agricultural matrix (Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al.,
50 2013; Kalda et al., 2015; Lacoeuilhe et al., 2018; Froidevaux et al., 2019). Tall trees with large canopies
51 may act as better acoustic landmarks than small ones for bats in farmlands (Frey-Ehrenbold et al., 2013).
52 At the local scale, tree-related microhabitats (TreMs) may favour bats either through enhancing the
53 abundance of insect prey or by providing suitable diurnal and maternity roosting sites – even though

54 the influence of TreMs on bats has so far only been assessed in forests (Regnery et al., 2013; Paillet et
55 al., 2018; Larrieu et al., 2019; Basile et al., 2020).

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

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

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

90

91 **2. Material and methods**

92 **2.1. Study area and sampling design**

93 The study was conducted in the east of France, in Doubs district (Bourgogne Franche-Comté
94 region; Fig. 1). We selected a subunit of the first plateau of the Jura mountains (c. 47°12'N, 6°32'E),
95 namely the “plateaux d'Aissey / Sancey / Feule et d'Orsans à Terre-de-Chaux” (407 km², 389-859 m
96 a.s.l.). The landscape of this rural area consists of a mosaic of patchily distributed habitats including
97 native forests (49%), grassland (45%), arable land (5%), small urban areas (1%, the largest village has
98 < 1500 inhabitants), and wetlands (<1%).

99 Using Google Earth 2017, we identified all isolated trees that were present in the study area.
100 We defined for this study an isolated tree as a single tree located at least 20 m from any other woody
101 habitat patch such as other isolated trees, hedgerows, orchards, and forests. We used this 20 m threshold
102 to minimise recording bats from other habitats and because it represents for many bat species a distance
103 after which the probability of crossing a gap between woody patches substantially decreases (Hale et
104 al., 2015; Pinaud et al., 2019). We then randomly selected trees that were situated at least 1 km apart
105 (to minimize the likelihood of counting the same bats at different sites), 50 m from asphalt roads (to
106 avoid any road edge effect) and located in farmland. We ground checked all selected trees and identified
107 the main agricultural land type surrounding the trees (grassland vs. cropland). As most of the trees
108 selected were in cattle-grazed pastures and meadows, trees in croplands were disregarded.

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

117

118 **2.2. Tree assessment**

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

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

134

135 **2.3. Bat echolocation call recording and identification**

136 We sampled bats acoustically at all 57 trees between June and August 2017 using Song Meter
137 SM2BAT+ recorders (sampling rate: 384 kHz) connected to SMX-U1 omnidirectional ultrasonic
138 microphones (Wildlife Acoustics, Concord, USA). At each tree, we attached the recorder around the
139 bare tree trunk or a branch at 1.8 m height and installed a data logger (RC-5; accuracy: 0.5°C; Elitech,
140 London, UK) to monitor temperature at night every 15 min. Recording was triggered automatically
141 when sounds in the frequency range 12–192 kHz with a signal-to-noise-ratio level ≥ 12 dB were
142 detected, and continued for 15 s. Sampling took place during one full night, from 30 min before sunset
143 to 30 min after sunrise, and only when meteorological conditions were suitable for bats to forage, i.e.,
144 dry and calm nights with wind speed < 30 km/h and temperature at sunset > 12 °C. Before each sampling
145 night, we randomly selected between one and six trees to sample simultaneously depending on logistical
146 constraints and landowner permission. We used the number of bat passes per night as a measure of bat
147 foraging and commuting activity. Each bat pass (i.e. a series of minimum two echolocation calls with
148 interpulse intervals < 1 s) present within each 15 s recording was identified using a semi-automatic
149 approach. In brief, we used BatScope 3.2 (Obrist & Boesch, 2018) to detect and sort recordings
150 containing bat calls and automatically extract call parameters. We then manually identified each bat
151 pass to the lowest taxonomic level (see full details in Appendix S2).

152

153 **2.4. Landscape analysis**

154 We extracted landscape characteristics around each isolated tree at different spatial scales. We
155 created five buffers (100, 250, 500, 1000, 2000 m radii) around the trees using ArcGIS Desktop v10.
156 Larger spatial scales were not considered to minimise the likelihood of landscapes overlapping as most
157 trees were located < 2 km apart (mean: 1.6 km; range: 1.0 – 3.1 km), even though overlapping
158 landscapes do not themselves represent a violation of independence (Zuckerberg et al., 2020). While
159 the smaller spatial scales allow us to describe the environment close to the trees, the larger ones
160 represent the mean daily foraging movement of many bat species present in the study area (Laforge et
161 al., 2021). Using land use data compiled at 10 m spatial resolution for a previous study (Tournant et al.,
162 2013), we quantified within each buffer the (i) landscape composition using the proportion of forest
163 (which was negatively correlated with the proportion of grassland across the five spatial scales, $|r| >$

164 0.7), (ii) landscape configuration using the edge density (i.e. total length of all edge segments between
165 multiple habitat patches in the buffer divided by the buffer area, m/ha) because many bat species use
166 habitat patch edges to forage and commute, and (iii) landscape compositional heterogeneity using
167 Shannon's diversity index calculated across all the reclassified habitat types (n = 10; Appendix S3).
168 These variables were calculated with the "landscapemetrics" R-package (Appendix S4). We finally
169 calculated the distance between trees and the nearest woody habitat patch (i.e. forests and hedgerows
170 only) and used this metric as a proxy of habitat connectivity that is easily interpretable by land managers
171 (Frey-Ehrenbold et al. 2013).

172

173 **2.5. Statistical analysis**

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

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

184 We took a multi-step approach before building our final full models that included (i) a Principal
185 Component Analysis (PCA) on DBH, tree height, and tree crown area, (ii) a selection of the best "scale
186 of effect" for each landscape variable, and (iii) a selection of most relevant interaction between TreM
187 diversity and landscape variables (see Appendix S6 for full details). Thus, for each species or group of
188 species the full model included as fixed effects (i) the first PCA axis summarizing information on tree
189 size, (ii) TreM type diversity, (iii) the interaction between TreM type diversity (either TreM-prey or
190 TreM-roost) and one landscape variable (at its most relevant scale for buffer-dependent metric), (iv) the
191 three area-based landscape variables at their most relevant scales, (v) the distance to the nearest woody

192 habitat, and (vi) two covariates (i.e. mean temperature at night and Julian day). We examined
193 collinearity among predictors present within the full models using the Spearman's correlation
194 coefficient and the variance inflation factors (VIFs) and results did not highlight collinearity issues ($|r|$
195 < 0.7 , $VIF < 3$).

196 We conducted model selection based on the full models. We generated all possible models
197 ("MuMIn" package) and ranked the most parsimonious ones based on $AICc$ (Burnham & Anderson,
198 2002). We conducted a model-averaged procedure of most parsimonious models (i.e. those with $\Delta AICc$
199 < 2), accounting for model selection uncertainties (Grueber et al., 2011) and report the full model
200 average estimates. The significance of the effects was evaluated using 95% confidence intervals
201 (Nakagawa & Cuthill, 2007). When a significant interaction between TreM type diversity and landscape
202 variable was found, we undertook a spotlight analysis to explore the nature of the interaction effect
203 using the "emmeans" package. In this analysis, we investigated the effects of TreM type diversity on
204 bat activity at specific values (mean, mean - SD, mean + SD) of the selected landscape metric. Details
205 on model validation can be found in Appendix S7.

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

211

212 **3. Results**

213 We recorded 4,091 bat passes around 57 isolated trees in agricultural grasslands (Appendix S8).
214 The bat assemblage was dominated by *Pipistrellus pipistrellus* with 2,305 bat passes (56.3% of the total
215 bat activity), followed by small *Myotis* bats (12.1%, *Myotis* spp.), nyctaloids (11.5%,
216 *Eptesicus/Nyctalus/Vespertilio* spp.), *Barbastella barbastellus* (5.1%), *Pipistrellus nathusii/kuhlii*
217 (4.5%), *Myotis myotis* and *Rhinolophus hipposideros* (both 2.2%), *Plecotus* spp. (1.4%), *Miniopterus*
218 *schreibersii* (0.6%), and *Rhinolophus ferrumequinum* ($< 0.1\%$; Appendix S8). We could not attribute

219 with certainty <5% of the bat passes to a species or species/genus group. We were able to model the
220 activity of *P. pipistrellus*, *P. nathusii/kuhlii*, *B. barbastellus*, *M. myotis*, *Myotis* spp., *Plecotus* spp., *R.*
221 *hipposideros* and nyctaloids with a total variance explained ranging from 42 to 79% (i.e. R^2 marginal:
222 proportion of variance explained by the fixed effects; Table 1).

223

224 **3.1. Effects of isolated tree characteristics on bats**

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

228 Our analyses confirmed that the size (DBH, tree height, and tree crown area) of isolated trees
229 significantly influence bat activity. More precisely, we found that tall trees with large DBH and crown
230 area significantly enhanced the activity of *P. pipistrellus* and *Myotis* spp. while the activity of *M. myotis*
231 was positively associated with smaller trees (Table 1, Fig. 2). The diversity of TreM-roost was selected
232 in our best models for six out eight taxa while TreM-prey diversity was only retained in the most
233 parsimonious models on *R. hipposideros* (Table 1). TreM-roost diversity had only a significant positive
234 effect on *M. myotis* activity (Table 1) and the effects of TreM diversity on the other taxa largely
235 depended on the landscape context.

236

237 **3.2. Interactive effects of TreMs and landscape structure**

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

245

246 **3.3. Influence of landscape composition and configuration on bats**

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

255

256 **4. Discussion**

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

267

268 **4.1. Species and guild-specific responses of bats to tree size**

269 In line with our predictions, tall trees with large DBH and crown area enhanced the activity of
270 edge-specialist (here *P. pipistrellus*) and clutter-adapted (here *Myotis* spp.) bat species but did not
271 influence open-space forager activity (here nyctaloids). These three taxa accounted for more than 80%
272 of the total bat activity recorded in the study area. However, contrary to our expectation, our results also
273 revealed a negative relationship between tree size and *M. myotis* activity. Overall, our results do not

274 corroborate the findings of Le Roux et al., (2018) who found no effect of tree size on insectivorous
275 bats in Australia, probably because their studies included very contrasting and diverse landscapes with
276 features that may have masked any effects of tree size on bat activity. Nevertheless, Polyakov et al.,
277 (2019) found similar results to ours around isolated trees located in Californian vineyards, with larger
278 trees increasing the activity of edge-specialist bats.

279 As observed with other woody features embedded within the agricultural matrix such as
280 hedgerows (Froidevaux et al., 2019), several mechanisms may explain the positive effects of tree size
281 on edge-specialist and clutter-adapted species. First, tall trees with large canopy may act as better
282 acoustic landmarks than smaller ones, especially for these species that mainly rely on woody features
283 for commuting (Frey-Ehrenbold et al., 2013). Thus, large isolated trees may serve as stepping stones
284 between forests and hedgerows and ultimately increase landscape connectivity (Saura et al., 2014).
285 Second, bats may benefit from greater foraging opportunities around large trees. While we did not assess
286 prey abundance along a tree size gradient, larger trees are likely to provide more shelter for bat insect
287 prey in temperate farmland (Merckx et al., 2010). Prey aggregations around large trees are more likely
288 to benefit relatively manoeuvrable edge-specialist and clutter-adapted bats (Denzinger & Schnitzler,
289 2013). Third, larger trees may offer more roosting sites for tree-dwelling bat species compared to
290 smaller ones (Tillon et al., 2016). Diameter at breast height is one of the main driver of TreM diversity
291 (Larrieu et al., 2014; Kozák et al., 2018; Asbeck et al., 2019) and TreM formation accelerates as trees
292 grows (Courbaud et al., 2017). This is also confirmed for isolated trees by the positive and significant
293 relationship we found between tree size and the diversity of TreM-roosts.

294

295 **4.2. Effects of microhabitat diversity on bats depend on the landscape context**

296 The level of habitat use by bats may vary depending on a range of local and landscape factors
297 (Mendes et al., 2017). We found that the activity of *B. barbastellus* increased with increasing TreM-
298 roost diversity only around trees close to (<50 m) woody habitat patches. *Barbastella barbastellus* is a
299 tree-dwelling species and this pattern most likely describes spillover effects of individuals from adjacent
300 woody habitat such as forests and hedgerows to isolated trees when the latter are of higher quality (i.e.
301 with high diversity of potential suitable roosts). Moreover, our findings suggest that *P. nathusii/kuhlii*

302 and *Myotis* spp. were more active at trees bearing a high diversity of TreM-roost only in the most
303 heterogeneous and forest-covered landscapes, respectively. These significant interactions were found
304 at the smallest landscape scale considered in this study (i.e. 100 m), which represents the landscape
305 context at the vicinity of the trees. Landscape compositional heterogeneity at such scales may promote
306 the activity of *P. nathusii/kuhlii* through increasing overall landscape permeability as these edge-
307 specialist species may better access to trees that are isolated in the agricultural matrix when this matrix
308 is diverse. Similarly, as many *Myotis* spp. are clutter-adapted species, an increase of forest cover at the
309 vicinity of the isolated trees may enhance the potential access to isolated trees. Depending on both the
310 landscape context and the ecological requirements of the different *Myotis* bat species occurring in the
311 study area, isolated trees bearing a relative high diversity of TreMs may be considered as both roosting
312 habitats and secondary foraging habitats. We hypothesize that *Myotis* bats which mainly forage in
313 forests may use isolated trees as foraging grounds in response to (i) higher inter or intra-specific
314 competition in forests (Lewanzik et al., 2019), and (ii) potential asynchrony in the nightly emergence
315 of insects among different habitats (e.g. between forest and isolated trees) (Ruczyński et al., 2020)
316 arising from less buffered microclimatic conditions around trees. Finally, only *R. hipposideros*
317 responded to the diversity of TreM-prey, with more activity detected around the most TreM-diversified
318 trees that are located further away (>100 m) from woody habitat patches. This slow-flying forager
319 highly relies on woody features for commuting, and crossing an open area can represent a potential risk
320 (e.g. predation). We therefore stipulate that the cost-benefit ratio of crossing an open habitat to access
321 isolated foraging sites is only advantageous for this species when the latter are of high quality (i.e. prey-
322 rich patches).

323 Interestingly, *M. myotis* activity was enhanced by TreM-roost diversity. Although our models
324 on TreM-prey were not retained, this attic-dwelling species may not benefit from roosting opportunities
325 but by enhanced prey resources around isolated trees.

326

327 **4.3. Influence of the surrounding environment**

328 Landscape compositional heterogeneity is known to enhance bat activity and species richness
329 in farmland (Ancillotto et al., 2017; Monck-Whipp et al., 2018; Rodríguez-San Pedro et al., 2019). Our

330 study corroborates these findings as we found that landscape heterogeneity (here defined as the Shannon
331 diversity of habitats) positively influenced the activity of three taxa (nyctaloids, *M. myotis* and *B.*
332 *barbastellus*). Landscape compositional heterogeneity is likely to benefit bats through an enhanced
333 process of non-substitutable resource complementation (Dunning et al., 1992; Monck-Whipp et al.,
334 2018). In line with other studies (Mendes et al., 2017; Rodríguez-San Pedro et al., 2019), our results
335 further suggested that edge density between multiple habitat patches (i.e. a proxy of landscape
336 configuration) at a 1 km radius scale positively influenced the activity of the most abundant edge-
337 specialist species *P. pipistrellus*. Finally, we found that bat responses to forest cover at the landscape
338 scale were species-specific, depending on roosting and foraging habitat preferences. Bat species that
339 rely on forests for roosting or foraging (such as *Nyctalus* spp. and *R. hipposideros*, respectively) were
340 positively associated with forest cover whereas *M. myotis*, an attic-dwelling species known to mainly
341 forage above meadows, was negatively affected.

342

343 **4.4. Implications for conservation and recommendations for management practices**

344 Widely recognized as a keystone ecological structure (Manning et al., 2006) due to the
345 disproportionate roles they provide for many species (Fischer et al., 2010a), isolated trees also represent
346 an important landscape feature for bats in farmland (Le Roux et al., 2018; Polyakov et al., 2019). In
347 accordance with other studies (Gibbons et al., 2008; Manning et al., 2009; Prevedello et al., 2018), our
348 findings highlight the crucial need of maintaining a diversity of isolated trees within the agricultural
349 matrix for both biodiversity conservation and ecosystem functioning. The contrasting response of bats
350 to tree size implies that maintaining isolated trees with varying tree size should benefit the whole bat
351 community (Wood et al., 2017). Our results also highlight the importance of maintaining a wide
352 diversity of tree species in farmland to hinder near-future massive tree losses (Fischer et al., 2010b) and
353 to preserve a large range of tree shapes and structures, as well as continuous amount of dead and
354 decaying trees within grassland at various locations in the wider landscape. While we advocate the
355 preservation of isolated trees for the benefit of the entire bat community, our results also provide
356 relevant information to be applied for species-specific conservation actions. For instance, the
357 preservation of large trees in close vicinity of hedgerows and forest edges appears to be important for

358 the conservation of the near-threatened barbastelle bat. Nevertheless, integrating the retention of such
359 small features in conservation planning within farmlands might be challenging as their inventory have
360 been neglected in many countries. Fortunately, remote sensing technologies offer substantial
361 opportunities for both inventorying and monitoring trees in farmland (Malkoç et al., 2021).

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

370 **Data availability**

371 Data collected for this study will be available to download on Figshare.

372

373 **REFERENCES**

374

- 375 Ancillotto, L., Ariano, A., Nardone, V., Budinski, I., Rydell, J. & Russo, D. (2017) Effects of free-ranging
376 cattle and landscape complexity on bat foraging: implications for bat conservation and
377 livestock management. *Agriculture, Ecosystems & Environment*, **241**, 54-61.
- 378 Asbeck, T., Pyttel, P., Frey, J. & Bauhus, J. (2019) Predicting abundance and diversity of tree-related
379 microhabitats in Central European montane forests from common forest attributes. *Forest
380 Ecology and Management*, **432**, 400-408.
- 381 Azam, C., Le Viol, I., Julien, J.-F., Bas, Y. & Kerbirou, C. (2016) Disentangling the relative effect of light
382 pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale
383 monitoring program. *Landscape Ecology*, **31**, 2471-2483.
- 384 Barth, B.J., FitzGibbon, S.I. & Wilson, R.S. (2015) New urban developments that retain more remnant
385 trees have greater bird diversity. *Landscape and Urban Planning*, **136**, 122-129.
- 386 Barton, D.N., Benjamin, T., Cerdán, C.R., DeClerck, F., Madsen, A.L., Rusch, G.M., Salazar, Á.G.,
387 Sanchez, D. & Villanueva, C. (2016) Assessing ecosystem services from multifunctional trees
388 in pastures using Bayesian belief networks. *Ecosystem Services*, **18**, 165-174.
- 389 Basile, M., Asbeck, T., Jonker, M., Knuff, A.K., Bauhus, J., Braunisch, V., Mikusiński, G. & Storch, I.
390 (2020) What do tree-related microhabitats tell us about the abundance of forest-dwelling
391 bats, birds, and insects? *Journal of Environmental Management*, **264**, 110401.
- 392 Burnham, K.P. & Anderson, D.R. (2002) A practical information-theoretic approach. *Model selection
393 and multimodel inference*.
- 394 Courbaud, B., Pupin, C., Letort, A., Cabanettes, A. & Larrieu, L. (2017) Modelling the probability of
395 microhabitat formation on trees using cross-sectional data. *Methods in Ecology and
396 Evolution*, **8**, 1347-1359.
- 397 Cuni Sanchez, A. & Lindsell, J.A. (2017) The role of remnant trees in carbon sequestration, vegetation
398 structure and tree diversity of early succession regrowing fallows in eastern Sierra Leone.
399 *African Journal of Ecology*, **55**, 188-197.
- 400 DeMars, C.A., Rosenberg, D.K. & Fontaine, J.B. (2010) Multi-scale factors affecting bird use of
401 isolated remnant oak trees in agro-ecosystems. *Biological Conservation*, **143**, 1485-1492.
- 402 Denzinger, A. & Schnitzler, H.-U. (2013) Bat guilds, a concept to classify the highly diverse foraging
403 and echolocation behaviors of microchiropteran bats. *Frontiers in physiology*, **4**, 164.
- 404 Dunn, R.R. (2000) Isolated trees as foci of diversity in active and fallow fields. *Biological
405 Conservation*, **95**, 317-321.
- 406 Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in
407 complex landscapes. *Oikos*, 169-175.
- 408 Fischer, J. & Lindenmayer, D.B. (2002) The conservation value of paddock trees for birds in a
409 variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones.
410 *Biodiversity & Conservation*, **11**, 833-849.
- 411 Fischer, J., Stott, J. & Law, B.S. (2010a) The disproportionate value of scattered trees. *Biological
412 Conservation*, **143**, 1564-1567.
- 413 Fischer, J., Zerger, A., Gibbons, P., Stott, J. & Law, B.S. (2010b) Tree decline and the future of
414 Australian farmland biodiversity. *Proceedings of the National Academy of Sciences*, **107**,
415 19597-19602.

416 Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R. & Obrist, M.K. (2013) Landscape connectivity, habitat
417 structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied*
418 *Ecology*, **50**, 252-261.

419 Froidevaux, J.S.P., Boughey, K.L., Hawkins, C.L., Broyles, M. & Jones, G. (2019) Managing hedgerows
420 for nocturnal wildlife: do bats and their insect prey benefit from targeted agri-environment
421 schemes? *Journal of Applied Ecology*, **56**, 1610-1623.

422 Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M. & Park, K.J. (2013) Fragmented
423 woodlands in agricultural landscapes: the influence of woodland character and landscape
424 context on bats and their insect prey. *Agriculture, Ecosystems & Environment*, **172**, 6-15.

425 Gibbons, P. & Boak, M. (2002) The value of paddock trees for regional conservation in an agricultural
426 landscape. *Ecological Management & Restoration*, **3**, 205-210.

427 Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P. &
428 Barrett, G. (2008) The future of scattered trees in agricultural landscapes. *Conservation*
429 *Biology*, **22**, 1309-1319.

430 Grueber, C., Nakagawa, S., Laws, R. & Jamieson, I. (2011) Multimodel inference in ecology and
431 evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699-711.

432 Hale, J.D., Fairbrass, A.J., Matthews, T.J. & Sadler, J.P. (2012) Habitat composition and connectivity
433 predicts bat presence and activity at foraging sites in a large UK conurbation. *PLoS ONE*, **7**,
434 e33300.

435 Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G. & Sadler, J.P. (2015). The ecological impact of city
436 lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology*
437 **21**, 2467-2478.

438 Hartel, T., Réti, K.-O. & Craioveanu, C. (2017) Valuing scattered trees from wood-pastures by farmers
439 in a traditional rural region of Eastern Europe. *Agriculture, Ecosystems & Environment*, **236**,
440 304-311.

441 Kalda, O., Kalda, R. & Liira, J. (2015) Multi-scale ecology of insectivorous bats in agricultural
442 landscapes. *Agriculture, Ecosystems & Environment*, **199**, 105-113.

443 Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larrieu, L., Nagel, T.A., Begovič, K., Čada, V. &
444 Diku, A. (2018) Profile of tree-related microhabitats in European primary beech-dominated
445 forests. *Forest Ecology and Management*, **429**, 363-374.

446 Lacoëuilhe, A., Machon, N., Julien, J.-F. & Kerbiriou, C. (2018) The relative effects of local and
447 landscape characteristics of hedgerows on bats. *Diversity*, **10**, 72.

448 Laforge, A., Archaux, F., Coulon, A., Sirami, C., Froidevaux, J.S., Gouix, N., Ladet, S., Martin, H., Barré,
449 K., Claireau, F., Kerbiriou, C., Roemer, C., Barbaro, L., (2021) Landscape composition and life-
450 history traits influence bat movement and space use: analysis of 30 years of published
451 telemetry data. *Global Ecology and Biogeography*, **30**, 2442-2454.

452 Larrieu, L., Cabanettes, A., Brin, A., Bouget, C. & Deconchat, M. (2014) Tree microhabitats at the
453 stand scale in montane beech–fir forests: practical information for taxa conservation in
454 forestry. *European Journal of Forest Research*, **133**, 355-367.

455 Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M.,
456 Gosselin, M., Ladet, S. & Savoie, J.-M. (2019) Assessing the potential of routine stand
457 variables from multi-taxon data as habitat surrogates in European temperate forests.
458 *Ecological Indicators*, **104**, 116-126.

459 Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B.
460 & Vandekerckhove, K. (2018) Tree related microhabitats in temperate and Mediterranean
461 European forests: A hierarchical typology for inventory standardization. *Ecological*
462 *Indicators*, **84**, 194-207.

463 Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2018) The value of scattered
464 trees for wildlife: contrasting effects of landscape context and tree size. *Diversity and*
465 *Distributions*, **24**, 69-81.

- 466 Lewanzik, D., Sundaramurthy, A.K. & Goerlitz, H.R. (2019) Insectivorous bats integrate social
467 information about species identity, conspecific activity and prey abundance to estimate
468 cost–benefit ratio of interactions. *Journal of Animal Ecology*, **88**, 1462-1473.
- 469 Lindenmayer, D.B. (2017) Conserving large old trees as small natural features. *Biological
470 Conservation*, **211**, 51-59.
- 471 Malkoç, E., Rüetschi, M., Ginzler, C. & Waser, L. (2021) Countrywide mapping of trees outside forests
472 based on remote sensing data in Switzerland. *International Journal of Applied Earth
473 Observation and Geoinformation*, **100**, 102336.
- 474 Manning, A.D., Fischer, J. & Lindenmayer, D.B. (2006) Scattered trees are keystone structures–
475 implications for conservation. *Biological Conservation*, **132**, 311-321.
- 476 Manning, A.D., Gibbons, P. & Lindenmayer, D.B. (2009) Scattered trees: a complementary strategy
477 for facilitating adaptive responses to climate change in modified landscapes? *Journal of
478 Applied Ecology*, **46**, 915-919.
- 479 Mendes, E.S., Fonseca, C., Marques, S.F., Maia, D. & Pereira, M.J.R. (2017) Bat richness and activity in
480 heterogeneous landscapes: guild-specific and scale-dependent? *Landscape Ecology*, **32**, 295-
481 311.
- 482 Merckx, T., Feber, R.E., Mclaughlan, C., Bourn, N.A., Parsons, M.S., Townsend, M.C., Riordan, P. &
483 Macdonald, D.W. (2010) Shelter benefits less mobile moth species: the field-scale effect of
484 hedgerow trees. *Agriculture, Ecosystems & Environment*, **138**, 147-151.
- 485 Monck-Whipp, L., Martin, A.E., Francis, C.M. & Fahrig, L. (2018) Farmland heterogeneity benefits
486 bats in agricultural landscapes. *Agriculture, Ecosystems & Environment*, **253**, 131-139.
- 487 Nakagawa, S. & Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a
488 practical guide for biologists. *Biological Reviews*, **82**, 591-605.
- 489 Obrist, M.K. & Boesch, R. (2018) BatScope manages acoustic recordings, analyses calls, and classifies
490 bat species automatically. *Canadian Journal of Zoology*, **96**, 939-954.
- 491 Orłowski, G. & Nowak, L. (2007) The importance of marginal habitats for the conservation of old
492 trees in agricultural landscapes. *Landscape and Urban Planning*, **79**, 77-83.
- 493 Paillet, Y., Archaux, F., Du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F. &
494 Guilbert, E. (2018) The indicator side of tree microhabitats: a multi-taxon approach based on
495 bats, birds and saproxylic beetles. *Journal of Applied Ecology*, **55**, 2147-2159.
- 496 Pinaud, D., Claireau, F., Leuchtman, M. & Kerbiriou, C. (2018) Modelling landscape connectivity for
497 greater horseshoe bat using an empirical quantification of resistance. *Journal of Applied
498 Ecology*, **55**, 2600-2611.
- 499 Poltz, K. & Zotz, G. (2011) Vascular epiphytes on isolated pasture trees along a rainfall gradient in the
500 lowlands of Panama. *Biotropica*, **43**, 165-172.
- 501 Polyakov, A.Y., Weller, T.J. & Tietje, W.D. (2019) Remnant trees increase bat activity and facilitate
502 the use of vineyards by edge-space bats. *Agriculture, Ecosystems & Environment*, **281**, 56-63.
- 503 Prevedello, J.A., Almeida-Gomes, M. & Lindenmayer, D.B. (2018) The importance of scattered trees
504 for biodiversity conservation: a global meta-analysis. *Journal of Applied Ecology*, **55**, 205-
505 214.
- 506 Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F. & Kerbiriou, C. (2013) Tree microhabitats as
507 indicators of bird and bat communities in Mediterranean forests. *Ecological Indicators*, **34**,
508 221-230.
- 509 Rocha, É.G.d., Brigatti, E., Niebuhr, B.B., Ribeiro, M.C. & Vieira, M.V. (2021) Dispersal movement
510 through fragmented landscapes: the role of stepping stones and perceptual range.
511 *Landscape Ecology*, **36**, 3249-3267
- 512 Rodríguez-San Pedro, A., Rodríguez-Herbach, C., Allendes, J.L., Chaperon, P.N., Beltrán, C.A. & Grez,
513 A.A. (2019) Responses of aerial insectivorous bats to landscape composition and
514 heterogeneity in organic vineyards. *Agriculture, Ecosystems & Environment*, **277**, 74-82.

515 Ruczyński, I., Hałat, Z., Zegarek, M., Borowik, T. & Dechmann, D.K. (2020) Camera transects as a
516 method to monitor high temporal and spatial ephemerality of flying nocturnal insects.
517 *Methods in Ecology and Evolution*, **11**, 294-302.

518 Russo, D., Bosso, L. & Ancillotto, L. (2018) Novel perspectives on bat insectivory highlight the value of
519 this ecosystem service in farmland: research frontiers and management implications.
520 *Agriculture, Ecosystems & Environment*, **266**, 31-38.

521 Saura, S., Bodin, Ö. & Fortin, M.J. (2014) Stepping stones are crucial for species' long-distance
522 dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, **51**,
523 171-182.

524 Tillon, L., Bresso, K. & Aulagnier, S. (2016) Tree selection by roosting bats in a European temperate
525 lowland sub-Atlantic forest. *Mammalia*, **80**, 271-279.

526 Tournant, P., Afonso, E., Roué, S., Giraudoux, P. & Foltête, J.-C. (2013) Evaluating the effect of
527 habitat connectivity on the distribution of lesser horseshoe bat maternity roosts using
528 landscape graphs. *Biological Conservation*, **164**, 39-49.

529 Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C. & Batáry, P. (2021). Beyond organic farming –
530 harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, **36**, 919-930.

531 Wood, H., Lindborg, R. & Jakobsson, S. (2017) European Union tree density limits do not reflect bat
532 diversity in wood-pastures. *Biological Conservation*, **210**, 60-71.

533 Zuckerberg, B., Cohen, J.M., Nunes, L.A., Bernath-Plaisted, J., Clare, J.D., Gilbert, N.A., Kozidis, S.S.,
534 Nelson, S.B.M., Shipley, A.A. & Thompson, K.L. (2020) A Review of overlapping Llandscapes:
535 pseudoreplication or a red herring in landscape ecology? *Current Landscape Ecology Reports*,
536 1-9.
537
538

Table 1. Standardized, model-averaged parameter estimates with associated standards errors (SE) and 95% confidence intervals of the best GLMMs ($\Delta AIC_c < 2$) 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.

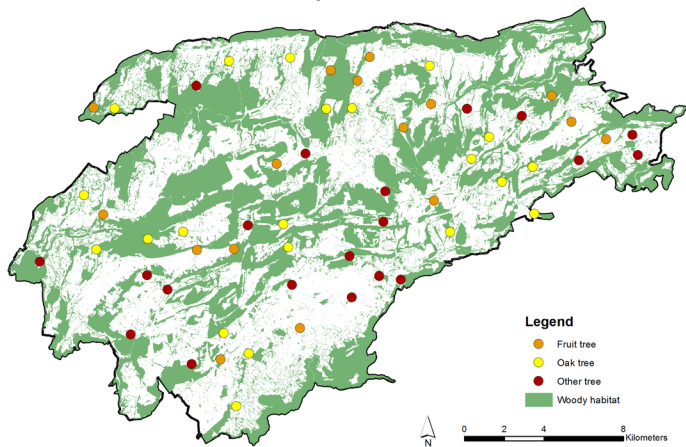
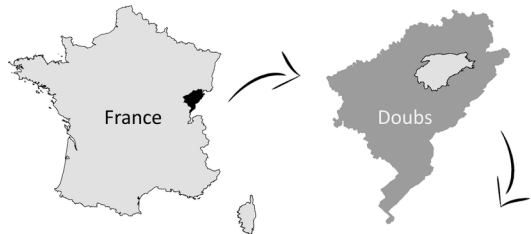
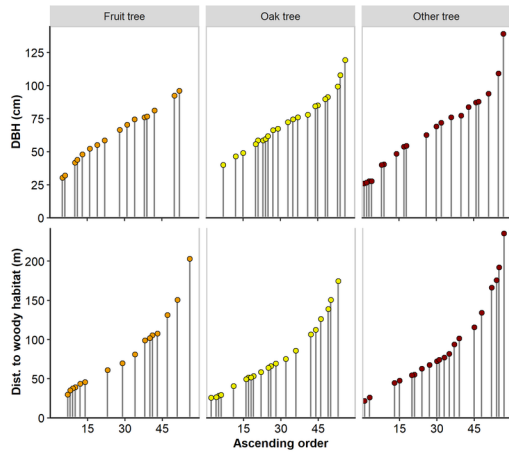
Variables	<i>Barbastella barbastellus</i>	Nyctaloids	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus nathusii/kuhlii</i>	<i>Myotis myotis</i>	Small <i>Myotis</i> spp.	<i>Plecotus</i> spp.	<i>Rhinolophus hipposideros</i>
Julian day	/	-0.25 ± 0.16 (-0.56, 0.05)	0.35 ± 0.15 (0.04, 0.65)	0.17 ± 0.17 (-0.16, 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	/	/	/	/
<i>R</i> ² marginal	0.79	0.50	0.55	0.48	0.68	0.63	0.42	0.43

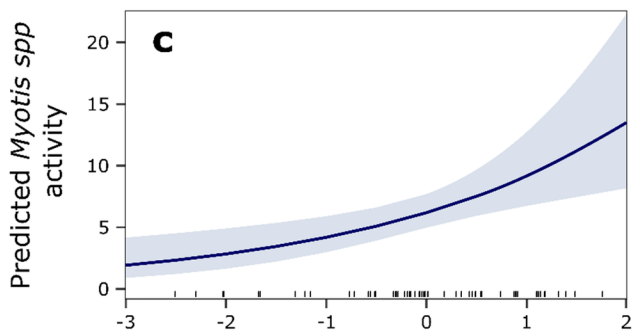
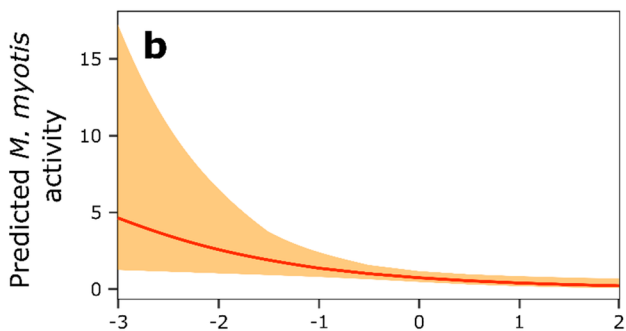
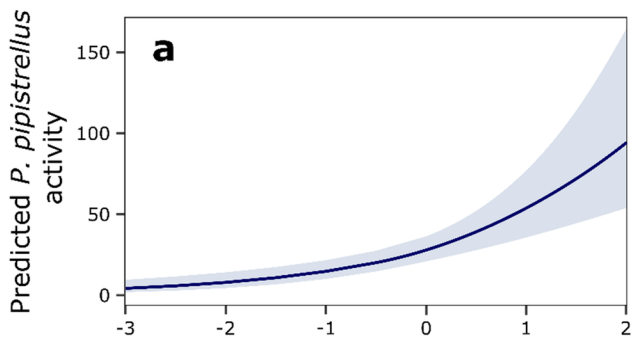
Spatial scales: ¹ 100 m radius scale, ² 250 m radius scale, ³ 500 m radius scale, ⁴ 1000 m radius scale, ⁵ 2000 m radius scale.
TreM: tree-related microhabitats. SHDI: Shannon's diversity index calculated across all the reclassified habitat types.

Figure 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).

Figure 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.

Figure 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).

a**b****c**



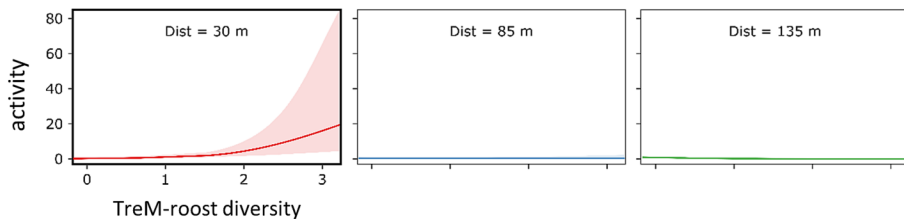
PCA axis

Small trees with small
DBH and crown area

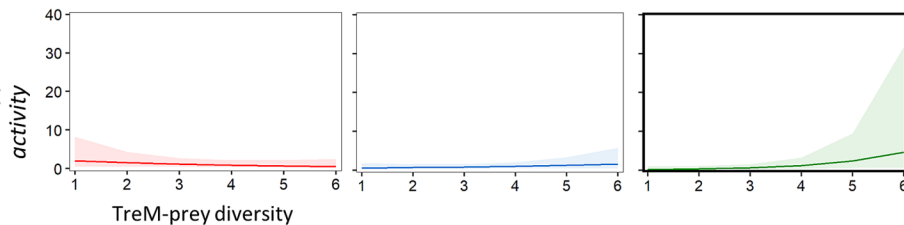
Tall trees with large
DBH and crown area

Distance between trees and the nearest woody habitat (Dist.)

Predicted *B. barbastellus* activity

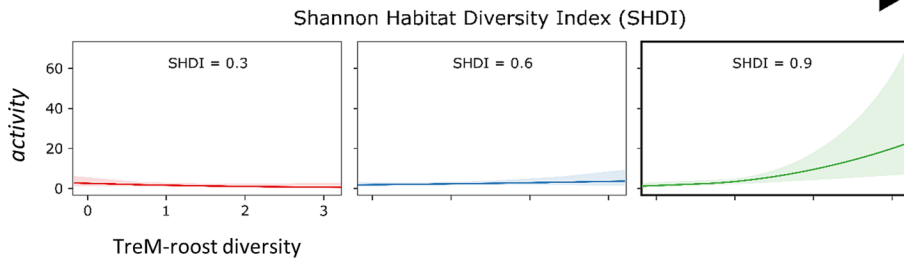


Predicted *R. hipposideros* activity



Landscape compositional heterogeneity

Predicted *P. nathusii/kuhlii* activity



Forest proportion (Fp)

Predicted *Myotis* spp. activity

