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1 Diverse agricultural landscapes increase bat activity and
2 diversity: implications for biological pest control.

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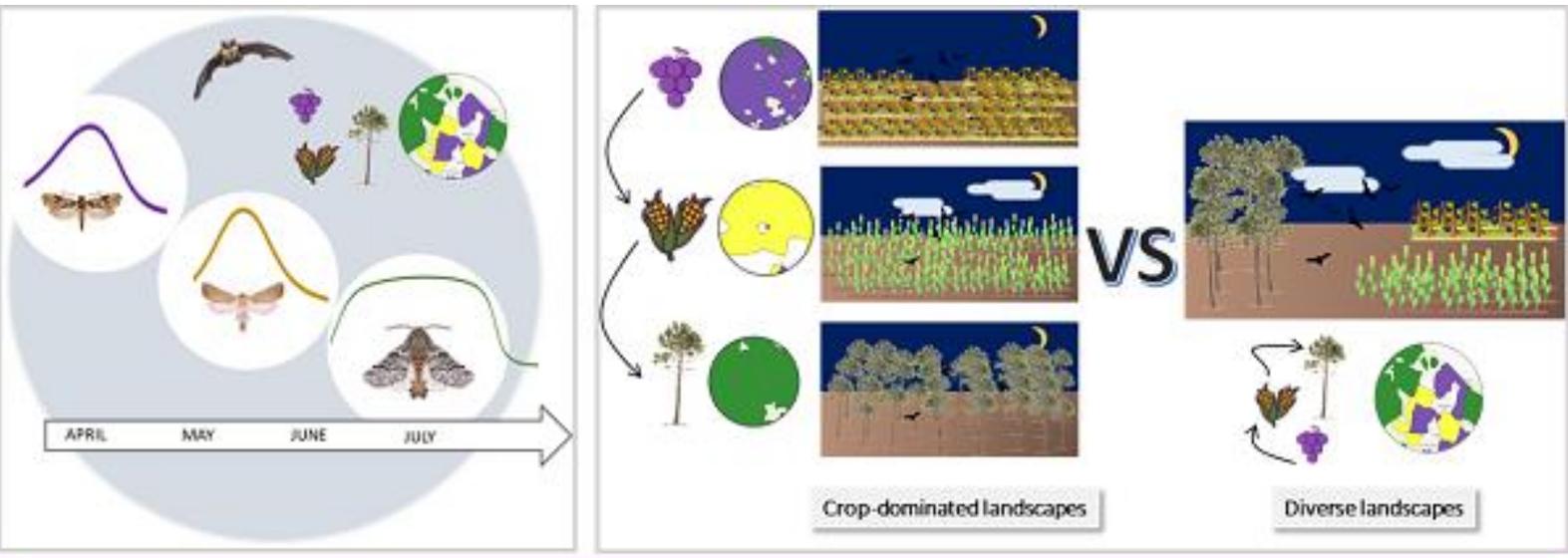
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22



Bat activity ?
Biological pest control ?

Simplified versus diversified landscapes, does the continuity of pest resources in diversified landscapes favour bats and biological control ?

24 **Abstract**

25 Diverse landscapes consisting of mixed crops are expected to support higher biological
26 control, while also contributing to maintain farmland biodiversity. Although bats are known
27 as predators of many farming pests, few studies to date have investigated how their
28 foraging activity may enhance natural pest control.

29 Here, we tested the hypothesis that crop mosaics would provide a temporal continuity in
30 prey availability for bats, ultimately resulting in higher biological control. We sampled bat
31 activity and diversity, and the abundance and damage of three major pests of vineyards,
32 maize, and pine plantations, in both simple and diverse landscapes mixing the three
33 production types. Bat species richness and total activity were higher in vineyards and
34 pine plantations located within diverse landscapes. Bat foraging activity also peaked
35 within diverse landscapes. In vineyards, moth abundance decreased with bat species
36 richness. In pine plantations, pest damage decreased with bat foraging activity. In maize
37 fields, pest abundance and damage increased with bat richness and activity longer-term
38 investigations would be necessary to assess their actual effectiveness.

39 Our study advocates for promoting a diversity of coexisting crops within agricultural
40 landscapes to enhance bat activity and diversity, which in turn would sustain higher
41 biological control and bolster biodiversity conservation in farmland.

42

43 **Keywords :** Farmland, crop mosaic, Chiroptera, conservation, pest insects,
44 *Lepidoptera*, *Lobesia botrana*, *Sesamia nonagrioides*, *Thaumetopoea pityocampa*.

45

46 **1. Introduction**

47 The intensification of agricultural production systems, by increased use of chemical
48 inputs, landscape simplification and homogenization of the crop mosaic, has led to a
49 dramatic decrease in farmland biodiversity (Benton et al., 2003; Flynn et al., 2009; Geiger
50 et al., 2010; Tilman et al., 2011; Tscharntke et al., 2005). These negative effects are
51 suspected to threaten the long-term stability of ecological processes involved in
52 ecosystem services limiting sustainability and resilience of agroecosystems (Cadotte et
53 al., 2011). It is therefore urgent to develop a form of agriculture that is more oriented
54 towards ecological intensification. In particular, farmland biodiversity supports many
55 ecosystem services such as pest control (Dainese et al., 2019; Tscharntke et al., 2012),
56 which has traditionally been a costly challenge for farmers given that pests are
57 responsible for around 20% of yield losses irrespective of crop types (Duflot et al., 2022;
58 Oerke, 2006). Arthropod pests are also acknowledged as a major threat to forest health,
59 and are likely to worsen with severe outbreaks due to global change (Simler-Williamson
60 et al., 2019).

61 Pest infestations are known to increase in monoculture landscapes, but it is also greater
62 in more favourable landscapes, i.e., when the proportion of host crop cover is higher
63 within the crop mosaic and/or is increasingly connected (Rand et al., 2014; Veres et al.,
64 2013). Moreover, biological control of pests by their natural enemies tends to be less
65 effective in simplified landscapes, i.e. crop-dominated landscapes, because the effect of
66 local management often interacts with landscape complexity (Rusch et al., 2016). While
67 the role of semi-natural habitats on biological control has been intensively studied, the
68 benefits of crop diversity itself are less well understood (Veres et al., 2013). It is now
69 widely established that landscape spatio-temporal heterogeneity enhances multitrophic
70 abundance and diversity of natural enemies (Sirami et al., 2019) in part by promoting
71 complementary resources for natural enemies, including foraging areas, food sources,

72 shelter, nesting and overwintering sites (Bertrand et al., 2016; Schellhorn et al., 2015).
73 However, the actual consequences in terms of biological pest control remain inconsistent
74 across regions, sites and experiments, probably due to complex interactions between
75 farming practices and landscape context leading to synergistic or antagonistic effects
76 (Barbaro et al., 2017; Etienne et al., 2022; Muneret et al., 2019; Ricci et al., 2019).
77 Although the relationship between natural enemy diversity and the effectiveness of
78 biological pest control is generally positive, it can be substantially disrupted by, e.g., intra-
79 guild predation within the natural enemy community (Letourneau et al., 2009; Martin et
80 al., 2013).

81 Insectivorous bats are efficient natural enemies of key pest arthropods in temperate
82 agroecosystems and forest ecosystems (Ancillotto et al., 2022; Blažek et al., 2021; Boyles
83 et al., 2011; McCracken et al., 2012). For instance, they are both efficient in annual crops
84 such as maize fields (Aizpurua et al., 2018; Maine & Boyles, 2015; Whitby et al., 2020)
85 and perennial crops such as vineyards and orchards or in plantation forests (Charbonnier
86 et al., 2014, 2021). In agricultural landscapes, most bat species rely on woody features
87 for commuting and foraging, depending on their wing morphology and echolocation
88 strategy (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2019; Garin et al., 2019), and
89 some bats can forage above crop fields (e.g., open-space foragers; Heim et al., 2015).
90 Higher landscape diversity and shorter distances between roosting sites and other
91 foraging habitats (e.g. water bodies, riparian zones) promote bat activity and species
92 richness (Monck-Whipp et al., 2018; Rainho & Palmeirim, 2011). Bats are also central-
93 place foragers as they used to return to the same site after foraging, with an average
94 distance between foraging areas and roost for many species most often less than 3 km
95 (Laforge et al., 2021), but occasionally up to ten of kilometres to reach high rewarding
96 areas (Bruun & Smith, 2003). Most insectivorous bats are generalist predators that are
97 able to maintain vital rates and stable populations by shifting to alternative prey and by

98 feeding on several adult moths. Although their foraging strategy and habitat selection (or
99 use) are different, species belonging to different guilds have been shown to feed on the
100 same pest moths (Garin et al., 2019).

101 Thanks to the development of new molecular analysis techniques such as DNA
102 metabarcoding, many moth pests of both annual and perennial crops have been detected
103 in bat diet (Aizpurua et al., 2018; Charbonnier et al., 2021). Nevertheless, these
104 qualitative approaches only highlight pest consumption and do not allow inference about
105 pest control (Russo et al., 2018). Several studies demonstrated the role of bats as
106 biological control agents in specific crops such as maize or rice, using (semi-)
107 experimental approaches (e.g. Maine & Boyles, 2015; Puig-Montserrat et al., 2015). Yet,
108 little is known regarding the influence of the landscape and the season on bat activity
109 resulting in more effective biological control.

110 Crop mosaic diversity at the landscape scale, i.e. agroecosystems mixing trees (forest
111 patches, hedgerows) and crop fields, may be particularly favourable to enhance pest
112 control provided by bats. Crop diversity is expected to increase the co-occurrence of
113 annual and perennial crops offering complementary food and roost resources both
114 temporally and spatially across the entire bat activity period, depending on variation in
115 seasonal energy demands. In addition, crop diversity may benefit a large range of bat
116 species including species with different echolocation, foraging strategies and
117 conservation concerns. Our study focuses on whether the complementarity of three crop
118 types, namely maize, vineyard and pine plantations, at the landscape scale, would affect
119 bat communities and their potential usefulness in terms of biological control, i.e., is the
120 mixture of these three crops at the landscape scale favourable to bats and does it favour
121 biological control of pests?

122 Our first objective was to evaluate the effects of more diverse agricultural landscapes on
123 bat community and its foraging activity. We predicted that in landscapes mixing the three

124 crops, the presence of higher diversity of landscape elements favourable for bats would
125 provide complementary resources, resulting in higher species richness and bat activity.
126 Our second prediction is that bat guild-specific responses are expected because crop-
127 diverse landscapes display higher diversity in habitat structures than crop-dominated
128 ones.

129 Finally, because we predicted that landscapes that are more diverse regarding co-
130 occurring crop types may offer a higher food resource continuity through the succession
131 of each lepidopteran pest biological cycle, we expected a higher foraging activity and less
132 crop damage in these landscapes. To account for the effects of plant resource availability
133 provided by the dominant crop on phytophagous insect abundances, we also directly
134 assessed the abundance of other moths and other alternative bat prey.

135

136 **2. Material and methods**

137 ***2.1. Study area and site selection***

138 The study area was located in the south west of France, between Gironde and Lot-et-
139 Garonne counties and near Langon (44° 33' 19.508" N 0° 14' 42.454" W). This area is
140 dominated by vineyards (Sauternes and Graves vineyards), maize fields and pine
141 plantations (mainly *Pinus pinaster*).

142 Within this study area, we selected thirty-seven landscapes (a 563-m radius scale; Figure
143 1) according to the predominance of one or all three target crop types. Thirty landscapes
144 were dominated by only one of the three crops, i.e. 10 simplified landscapes dominated
145 by vineyards (mean: 70%; range 57%-78%), maize fields (mean: 52%; range 21%-76%,
146 without any other dominant crop) or pine plantations (mean: 79 %; range 63%-100%),
147 respectively. Seven landscapes were selected that had all three crop types in varying
148 proportions but their total surface cover was at least 45% of the total area (hereafter

149 referred to as 'diverse landscapes'). Among the 17 vineyards sampled two were
150 organically managed and maize fields were all conventionally managed.
151

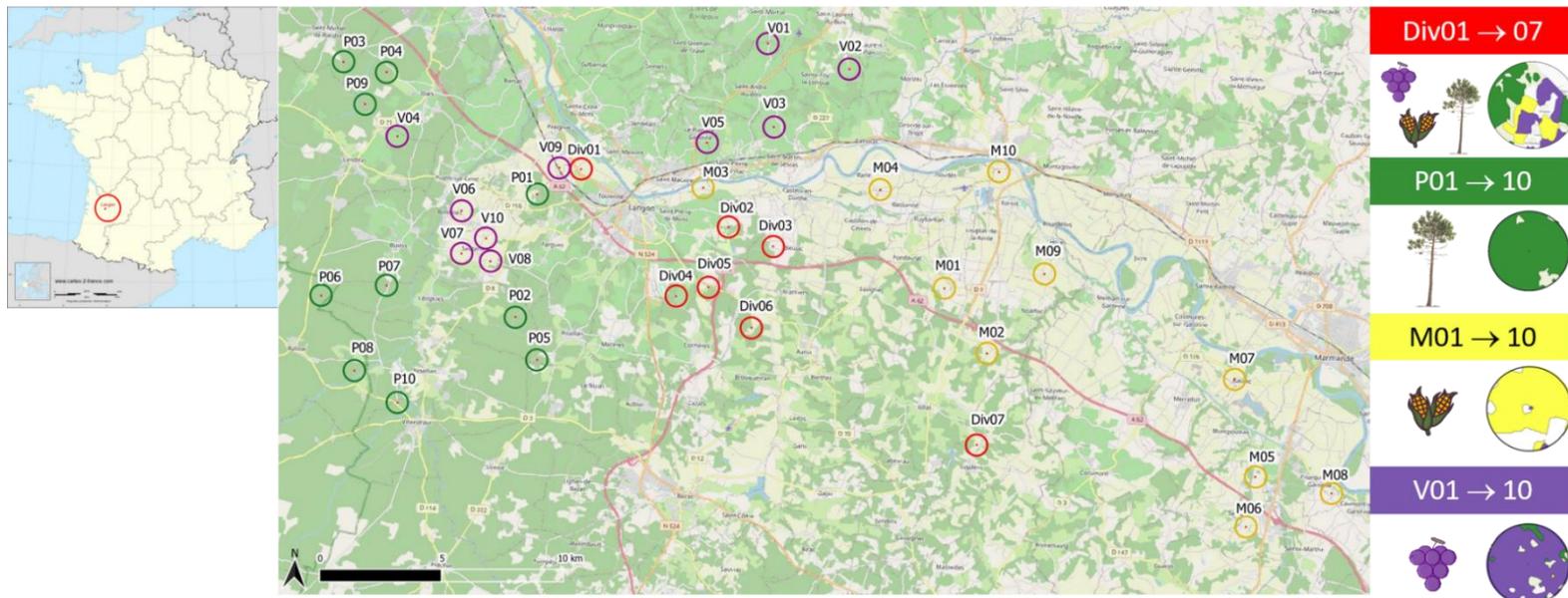


Figure 1 : Map of the study area showing the two landscape types: simplified landscapes depending on the targeted crop (P: pine or M: maize or V: vineyards) and diverse landscapes (Div: three crops were represented).

152 2.2. Field sampling of targeted *Lepidoptera* and potential alternative prey

153 Vineyards (*Vitis vinifera* L.), maize (*Zea mays* L.) fields and pine plantations (mainly *Pinus*
154 *pinaster*) dominate agricultural landscapes of South-western France. Key pests include
155 the European grapevine moth *Lobesia botrana* Denis & Schiffenüller (Lepidoptera:
156 Tortricidae), which cause direct losses in grape production (Delbac & Thiéry, 2016); the
157 Mediterranean corn borer *Sesamia nonagrioides* Lefèbvre (Lepidoptera: Noctuidae),
158 which is one of the most damaging pests of maize in early stages (Maine & Boyles, 2015);
159 and the pine processionary moth *Thaumetopoea pityocampa* Denis & Schiffenüller
160 (Lepidoptera: Notodontidae), which is the main defoliator of pines reducing growth of
161 young trees (Jacquet et al., 2012). The flight peaks of these three species follow one
162 another in time. The corn borer and the grape berry moth have between 2 and 4

163 generations per year, with a flight peak of the first generation at the end of April and the
164 end of May, respectively. The control of the first generation is key to limit the abundance
165 of the following generations. The pine processionary moth has one generation per year
166 and a flight peak spread out between late June and early September. Current control of
167 moth pests in crops consists of mating disruption, application of insecticide or *Bt* toxin but
168 their effectiveness tends to decrease in a context of global warming and the appearance
169 of resistance (Thiéry et al., 2018).

170 The data collection was carried out over three sampling periods in April, May and July
171 2021, according to the flight peaks of the targeted lepidopteran pests in each crop and in
172 the study region. The first sampling period was carried out in April 2021 in the 17
173 vineyards: 10 vineyards in vineyard-dominated landscapes and 7 vineyards in diverse
174 landscapes. We installed specific pheromone baited-traps of *L. botrana* alternatively
175 during 7 nights from 12 to 21 April 2021, 30 m inside the fields. We also placed food traps
176 containing diluted apple must in order to collect potential alternative prey (Figure A 1).
177 Food traps were located 50 m away from the pheromone baited-traps in the same fields.
178 After 7 nights, food traps were refilled and deployed for two more consecutive nights
179 during the bat sampling.

180 The same experimental set-up was conducted in May in 16 maize fields and in July in 17
181 pine plantations. The pheromone baited-traps specific to *S. nonagrioides* were placed
182 from 18 to 27 May 2021 and specific to *T. pityocampa* from 28 June to 7 July 2021.

183 All insects collected in food traps were stored in a 70% ethanol solution. Among the
184 collected insects, targeted moths, i.e. *L. botrana* or *S. nonagrioides* or *T. pityocampa*,
185 were counted and added to those counted on pheromone baited-traps. The total relative
186 abundance of moth species was determined in the targeted crop. The collected insects
187 stored in ethanol were then dried for 24 hours at 60° and weighted with a precision
188 balance. The total insect dry biomass for each site was determined.

189 **2.3. Bat monitoring**

190 The main activity period of bats ranges from spring to autumn and peaks during periods
191 of high energy demands. For instance, after hibernation, female bats have to fulfil their
192 reserves and ensure the rapid growth of their embryos. Therefore, pregnant females will
193 need more food resources to achieve their pregnancy in June-July (Laforge et al., 2021).
194 The lactation period is also a period of high energy demand, during which the females
195 tend to forage closer to their roost and until the young forage in their turn (Arthur &
196 Lemaire, 2015; O'Donnell, 2002).

197 Bats were recorded using an ultrasound bat detector model Elekon Batlogger A/A+
198 (Wigum GmbH, Germany); recording was triggered automatically when sounds in the
199 frequency range 8-192 kHz with a signal-noise-ratio level above 6 dB were detected.
200 Detectors were programmed to record from 30 min before sunset to 30 min after sunrise.
201 They were installed for two consecutive nights instead of the specific pheromone baited-
202 traps, i.e. vineyards in both landscape types were sampled between 19 and 23 April 2021;
203 maize fields between 25 and 29 May 2021; pine plantations between 5 and 9 July 2021.
204 Bats were recorded only in nights without rain, with low wind speed (< 30 km/h) and an
205 average minimum temperature at night of >10°C (Parsons, 2007).

206 Species identification was supported by the Tadarida software, which classified calls to
207 the most accurate taxonomic level with a confidence index value
208 (<https://github.com/YvesBas/Tadarida-C/>; Bas et al., 2017). As automated identification
209 can generate significant error rates, we followed the procedure by Barré et al. (2019) in
210 order to find the best compromise limiting species identification errors and maintaining a
211 relatively high number of bat passes. Then, we removed acoustic data with a maximum
212 error rate tolerance (MERT) of 0.5 to minimize false positives while keeping a high
213 number of bat passes. We checked the consistency of responses using a more restrictive
214 MERT of 0.1 (detailed results are available in Appendix B), which limited false positives

215 but discarded more true positives. Call identifications were grouped at genus level for
216 *Plecotus* spp. and we distinguished small and large *Myotis* spp. (see Table 1). The
217 number of species or complex of species were counted per site and per night. Species of
218 regional conservation concern (SCC) were identified according to the Nouvelle-Aquitaine
219 regional red list (see Table 1; Liste rouge des Chiroptères de Nouvelle-Aquitaine, 2019).
220 We also grouped bats according to their echolocation range into three guilds (Frey-
221 Ehrenbold et al., 2013; Schnitzler & Kalko, 2001) namely short-, mid- and long-range
222 echolocators (SRE, MRE and LRE respectively - see Table 1).

223 As acoustic sampling does not allow differentiating individual bats, we used bat activity
224 as a surrogate of bat abundance (e.g. Azam et al., 2016; Barré et al., 2019; Froidevaux
225 et al., 2017) which was calculated by summing the number of bat passes per site and per
226 night. Bat pass was defined as the detection of a single or several bat calls during a 5-s
227 interval, which was the best compromise between the risk to miss an individual and to
228 count several times the same one (Kerbirou et al., 2019; Millon et al., 2015). Global bat
229 activity (i.e. global activity) was calculated by summing nightly bat activity of each species
230 or complex of species. Guild activity (i.e. LRE , MRE or SRE activities) and SCC activity
231 were also calculated by summing the number of bat passes of species or complex of
232 species that constitute the guild and the number of bat passes of species from SCC
233 mentioned before (Table 1), respectively.

234 Finally, we quantified bat foraging activity through the mean bat sequence duration BSD
235 (Kerbirou et al., 2019) weighted by the number of bat sequences of each species or
236 complex of species and of each guild (i.e. LRE BSD, MRE BSD, SRE BSD). Bat sequence
237 duration corresponds to the total duration of a bat sequence (i.e. a series of bat calls),
238 considering two acoustic events separated by a time interval shorter than 2 seconds as
239 a same bat sequence. Longer bat sequences indicate that a bat is foraging while shorter
240 bat sequences would suggest that a bat is commuting (Kerbirou et al., 2019).

241 **Table 1: List of species sampled in the study and aggregation of species used in the**
 242 **statistical analyses.** Table shows the guild of each different sampled species (according to their
 243 echolocation range) and their conservation concern.

Species	Complex of species	Guild	Status of species on the Nouvelle-Aquitaine red list*
<i>Nyctalus leisleri</i>	-	LRE	LC
<i>Nyctalus noctula</i>	-	LRE	VU
<i>Nyctalus lasiopterus</i>	-	LRE	VU
<i>Eptesicus serotinus</i>	-	LRE	LC
<i>Pipistrellus pipistrellus</i>	-	MRE	LC
<i>Pipistrellus kuhlii</i>	-	MRE	LC
<i>Pipistrellus nathusii</i>	-	MRE	NT
<i>Pipistrellus pygmaeus</i>	-	MRE	DD
<i>Hypsugo savii</i>	-	MRE	LC
<i>Miniopterus schreibersii</i>	-	MRE	EN
<i>Barbastella barbastellus</i>	-	SRE	LC
<i>Plecotus auritus</i>	Plecotus spp.	SRE	LC
<i>Plecotus austriacus</i>		SRE	LC
<i>Myotis blythii</i>	Large <i>Myotis</i> spp.	SRE	EN
<i>Myotis myotis</i>		SRE	LC
<i>Myotis emarginatus</i>	Small <i>Myotis</i> spp.	SRE	LC
<i>Myotis crypticus</i>		SRE	NT
<i>Myotis mystacinus</i>		SRE	DD
<i>Rhinolophus ferrumequinum</i>	-	SRE	LC
<i>Rhinolophus hipposideros</i>	-	SRE	LC

LRE : Long-range echolocators; MRE : Mid-range echolocators; SRE: Short-range echolocators
 LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered; DD: Data deficient

244

245

246 **2.4. Evaluation of specific damage in targeted crops**

247 Specific damage was evaluated in maize and pine plantations to estimate the actual
 248 effects of bat predation on target lepidopterans. Damage in vineyards (glomerules on
 249 grape bunches) could not be assessed due to a frost episode that occurred at the
 250 beginning of April (2021) and greatly affected vegetative development of the grapevines.
 251 Maize damage was evaluated the fortnight following bat sampling that corresponded to
 252 10-15 days after 50% of the *S. nonagrioides* peak flying (maximum of adult emergence)
 253 and to the maximum of larvae at the crawler stage. Three transects of 100 maize plants
 254 were observed in each field and the plants showing wilting were counted to assess larvae
 255 densities per field and per 100 plants (maize densities equal in all our fields).

256 In early February 2022, we estimated the density of larval colonies of *T. pityocampa* by
257 counting the number of larval colonies on all pine trees located 100 m from the forest
258 edge and on the first two rows where the larval colonies are concentrated (Dulaurent et
259 al., 2012).

260

261 **2.5. Landscape metrics**

262 Using ArcGIS Desktop 10.5.1 software (ESRI, Redlands, CA, US), land cover was
263 digitized from OSO 2019 (Inglada et al., 2017) and annual crops were identified for the
264 study sites based on direct field observations.

265 Part of the landscape metrics were then calculated for a 1km² circle (i.e., inside a circular
266 buffer with radius of 563m, centred on the middle of the pheromone baited-trap and
267 acoustic detector position). First, we used a descriptive variable (i.e. landscape type) to
268 distinguish the type of landscape in which the measurements were made, i.e. either
269 simplified (dominance of one targeted crop) or diverse (presence of all three crops).

270 To describe crop mosaic compositional heterogeneity, the proportion of each targeted
271 crop (vineyards, maize fields and pine plantations) was assessed and the Shannon crop-
272 diversity index was specifically calculated on those categories. Another Shannon diversity
273 index was calculated for the whole landscape based on the proportion of each land cover
274 (other habitats than crops such as deciduous woodlands, water bodies, building,
275 hedgerows with mainly deciduous trees) but it was highly correlated with the Shannon
276 crop-diversity index of specific crops (Pearson's coefficient > 0.9), and was therefore
277 disregarded for the analysis. The compositional heterogeneity of the semi-natural habitats
278 (SNH) was described using the proportion of SNH, which grouped hedgerows, woodlands
279 and water bodies and we also calculated the total length of hedgerows, which represented
280 an indicator of configuration heterogeneity. The proportion covered by artificial spaces

281 (i.e. buildings, roads, commercial and industrial areas) was calculated to consider the
282 potential effect of artificialization.

283 As bats have a dispersal capacity from a breeding site to a foraging zone that may reach
284 several tens of kilometres depending on the species, we chose to consider the distance
285 to the nearest elements of the landscape with potentially significant effects on the
286 sampled bat community (Laforge et al., 2021). Then we used the distances to the nearest
287 water body, hedgerow, forest edge, riparian zone and building (Arthur & Lemaire, 2015;
288 Froidevaux et al., 2019; Laforge et al., 2021; Sirami et al., 2013). The distance to the
289 Garonne, the main water body of the study area, was also considered (Salvarina, 2016;
290 Salvarina et al., 2018). The distribution of landscape metrics is available in Appendix A
291 (Table A 2).

292

293 **2.6. Statistical analysis**

294 Spearman's correlations were performed on the different response variables in order to
295 evaluate potential redundancies. All rho coefficients were below 0.7, except between total
296 bat activity and MRE activity (Figure A 3).

297 To assess the influence of landscape type (monoculture vs three-type crop mosaic) on
298 bat community activity and foraging activity, we performed statistical analyses on both (i)
299 the pooled dataset of the three sampling periods, and (ii) each separate dataset
300 corresponding to the sampling in April, May and July respectively. Firstly, we tested
301 independently the relationships between all response variables (i.e. bat species richness,
302 global activity, SCC activity, guild activity and foraging activity) and the landscape type
303 (crop-dominated versus diverse), using Generalized Linear Mixed-Effect Models
304 (GLMMs; *lme4* package) with the appropriate distribution (Gaussian or Poisson or
305 negative binomial family) and considering site and night as random effects.

306 Secondly, independent variables (landscape metrics, biomass and relative pest
307 abundance) were standardized. Pearson's correlations ($|r| < 0.7$) and collinearity with
308 variation inflation factor (VIF values < 5) were tested using the *corvif* function (Zuur et al.,
309 2009) for each period. Then, we modelled relationships between the response variables
310 and different independent landscape variables depending on the landscape context of
311 each targeted crop (Table 2) and co-variables such as biomass or relative abundance of
312 targeted pest. We used GLMMs to create the full model, and then the *dredge* function
313 (*MuMin* package) was run with a maximum of three independent variables in the same
314 model to avoid model overparametrization, and site and night as random factors. We
315 selected models with a $\Delta AICc < 2$ and averaged coefficients were calculated using
316 *model.avg* function (*MuMin* package). Distance-dependence in all model residuals was
317 assessed using Moran's I test and appeared to be not spatially related (Moran's I test, all
318 $p > 0.05$).

319 Finally, Spearman's correlations were calculated between the relative pest abundance
320 and the index of damage for maize and pine plantations sampling periods. We also
321 investigated correlation relationships between variables describing bat community or
322 activity and relative pest abundances and the associated index of damage for each
323 sampling period. Wilcoxon's tests were performed for the different variables responses
324 and between landscape types.

325 All analyses were performed with R software version 3.6.3 (R Core Team, 2022).

326

327 **Table 2: Description of the landscape metrics, co-variables and random factors used for**
 328 **each analysis, according to the dataset.**

Dataset	Landscape metrics	Other co-variables	Random factor
All N= 99 (50 sites x 2 nights*)	Landscape type (crop-dominated landscapes VS landscapes with the three crops)	-	(1 Site) + (1 Night)
Vineyards n= 34 (17 sites x 2 nights)	Shannon diversity of crops %SNH %Artificial Length of hedgerows Distance to the nearest building Distance to the nearest hedgerow Distance to the nearest riparian zone Distance to the Garonne Distance to the nearest forest edge	Biomass Relative pest abundance (number of <i>L. botrana</i>)	(1 Site) + (1 Night)
Maize fields N= 32 (16 sites x 2 nights)	Shannon diversity of crops %SNH Length of hedgerows Distance to the nearest building Distance to the nearest riparian zone Distance to the Garonne Distance to the nearest forest edge Distance to the nearest water body	Biomass Relative pest abundance (number of <i>S. nonagrioides</i>)	(1 Site) + (1 Night)
Pine plantations N= 33 (17 sites x 2 nights*)	Shannon diversity of crops %SNH Length of hedgerows Distance to the nearest hedgerow Distance to the nearest water body	Relative pest abundance (number of <i>T. pityocampa</i>)	(1 Site) + (1 Night)

*Acoustic recording failed one night in pine plantations, therefore the total number of recording nights is 99 instead of 100.

330 **3. Results**

331 **3.1. Bat, pest and plant damage**

332 **3.1.1. Bat richness and activity**

333 We recorded a total of 17,786 and 13,386 bat passes, considering a MERT of 0.5 and a
334 MERT of 0.9, that belonged to 16 taxa (Table 3). The average species richness was 7.4
335 (± 1.8) species in vineyards; 6.4 (± 2.3) in maize fields and 6.1 (± 1.7) in pine plantations.
336 Bat activity was mainly represented by MRE guild (72%) with the *Pipistrellus* genus as
337 most frequently genus detected (39% *Pipistrellus pipistrellus*, 29% *Pipistrellus kuhlii*).
338 LRE and SRE guilds represented 22% and 6% of total bat activity; *Nyctalus leisleri* and
339 *Eptesicus serotinus* represented each 11% of recorded activity.

340 Keeping bat passes with an error rate of less than 50%, i.e. a MERT of 0.5, there were
341 14 bat passes of species of conservation concern compared to only two bat passes when
342 considering an identification error rate of less than 10%, i.e. a MERT of 0.1.

343 Foraging activity varied from 0.05s to 0.81s (mean for MERT of 0.5: 0.40s; LRE foraging
344 activity: 0.14s \pm 0.09; MRE foraging activity: 0.23s \pm 0.10; SRE foraging activity: 0.14s \pm
345 0.10).

346

347 **Table 3: Guild and species bat activity with a maximum error rate tolerance of 0.5 (and a**
 348 **maximum error rate tolerance of 0.1 in brackets), i.e. number of bat passes recorded for**
 349 **each sampling period.**

Taxa	Vineyards	Maize fields	Pine plantations	<i>Total</i>
Long-range echolocators - LRE	810 (619)	531 (358)	2 691 (1 459)	4 032 (2 436)
<i>Nyctalus leisleri</i>	679 (589)	290 (233)	1 047 (804)	2 016 (1 626)
<i>Nyctalus noctula</i>	4 (1)	11 (8)	0	15 (9)
<i>Nyctalus lasiopterus</i>	0	14 (0)	0	14 (0)
<i>Eptesicus serotinus</i>	127 (29)	216 (117)	1 644 (655)	1 987 (801)
Mid-range echolocators - MRE	2 167 (1 716)	3 869 (2 834)	6 681 (5 680)	12 717 (10 230)
<i>Pipistrellus pipistrellus</i>	1 209 (1 104)	2 268 (1 917)	3 415 (3 052)	6 892 (6 073)
<i>Pipistrellus kuhlii</i>	737 (572)	1 302 (903)	3 138 (2 628)	5 177 (4 103)
<i>Pipistrellus nathusii</i>	200 (29)	286 (14)	122 (0)	608 (43)
<i>Pipistrellus pygmaeus</i>	11 (6)	2 (0)	0	13 (6)
<i>Hypsugo savii</i>	6 (2)	10 (0)	6 (0)	22 (2)
<i>Miniopterus schreibersii</i>	4 (3)	1 (0)	0	5 (3)
Short-range echolocators - SRE	250 (152)	456 (323)	331 (205)	1 037 (680)
<i>Barbastella barbastellus</i>	78 (73)	306 (279)	117 (72)	501 (424)
<i>Plecotus</i> spp.	81 (15)	123 (31)	110 (44)	314 (90)
Small <i>Myotis</i> spp.	16 (2)	3 (0)	23 (12)	42 (14)
Large <i>Myotis</i> spp.	14 (6)	14 (6)	2 (0)	30 (12)
<i>Rhinolophus ferrumequinum</i>	9 (9)	5 (3)	59 (58)	73 (70)
<i>Rhinolophus hipposideros</i>	52 (47)	5 (4)	20 (19)	77 (70)
Total	3 227 (2 487)	4 856 (3 515)	9 703 (7 344)	17 786 (13 386)

351 3.1.2. *Pest abundance and alternative prey biomass*

352 The number of *L. botrana* counted on pheromone baited-traps in vineyards, in April 2021
353 ranged from zero to six individuals (mean: 0.23 ± 0.19 ; Figure 2A). Relative abundance
354 of *L. botrana* was the lowest among the three targeted lepidopteran pests. The mean dry
355 biomass was 0.25g (± 0.30).

356 In May 2021, *S. nonagrioides* counted in maize fields ranged from zero to 22 individuals
357 per site (mean: 3.50 ± 5.56 ; Figure 2B). The mean dry biomass measured was 0.23 g (\pm
358 0.19).

359 Finally, in July 2021, the number of *T. pityocampa* ranged from 0 to 46 individuals per site
360 (mean: 8.41 ± 11.11 ; Figure 2C). The mean dry biomass measured was 0.56 g (± 1.45)
361 and the highest among the three sampling periods.

362 There was no significant difference between the relative abundances of pests in crop-
363 dominated landscapes and in diverse landscapes (Figure 2), for each sampling period.

364

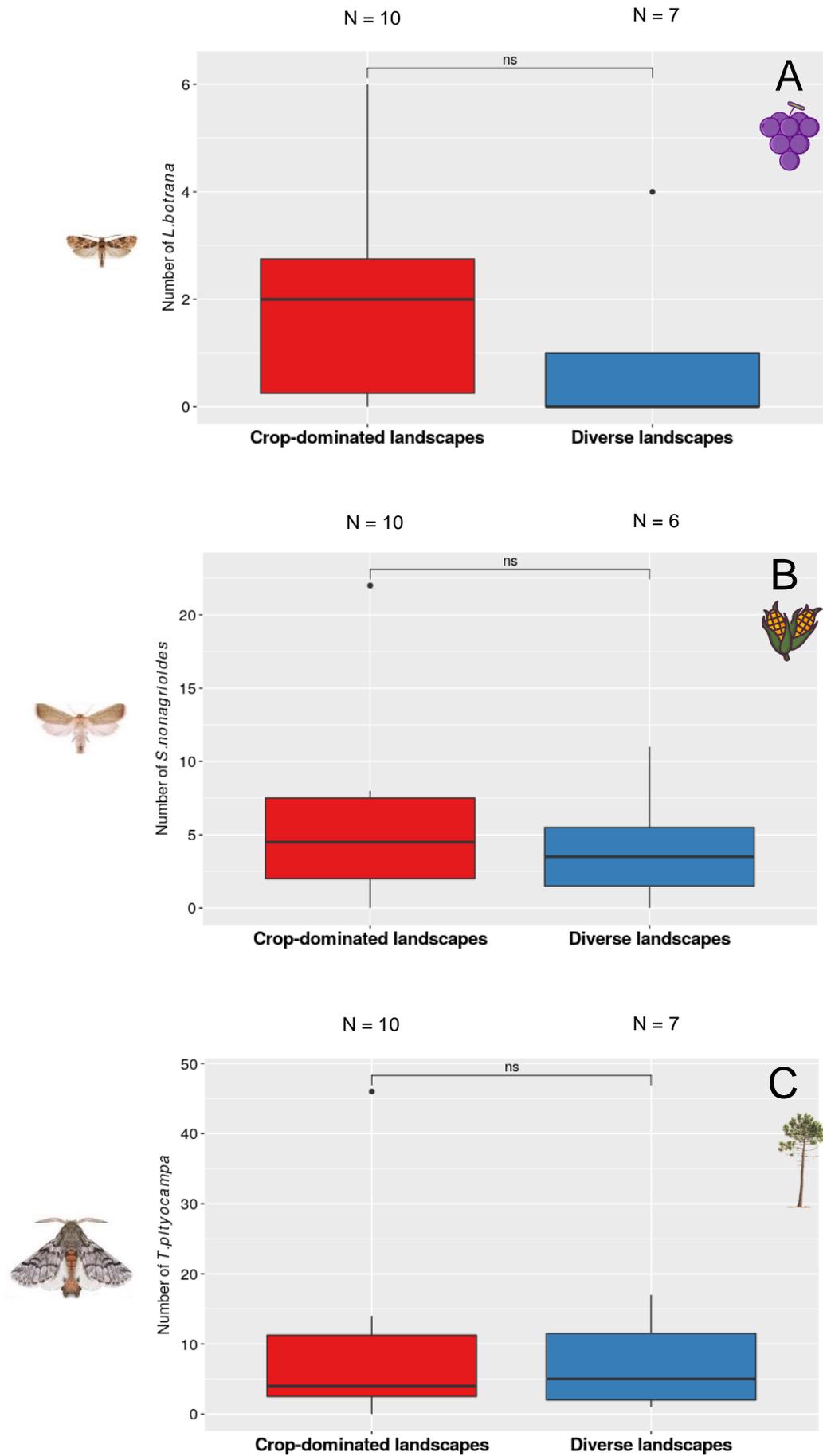


Figure 2 : Relative abundance of the three targeted moths in the crops they were specialist about. Respectively (A) in vineyards (April) for *L. botrana*; (B) in maize fields (May) for *S. nonagrioides*; (C) in pine plantations (July) for *T. pityocampa*. N corresponded to the number of landscapes considered for each modality.

366 *3.1.3. Plant damage*

367 The damage index measured on maize plants was very low ranging from zero to 0.02,
368 which corresponded to a maximum of six affected plants out of 300 observed.

369 The density of larval colonies of the pine processionary moth, varied among sites between
370 0 to 25 nests per site. Depending on the site, the total number of pines observed varied
371 from 21 to 108 trees, with an average around 50 trees per site, leading to an index of
372 damage ranging from zero to 0.61.

373 The index of damage calculated for pine plantations was significantly lower in diverse
374 landscapes than in pine-dominated landscapes (Wilcoxon's test: $W = 198$, $p\text{-value} =$
375 0.019).

376

377 ***3.2. Effects of landscape diversity on bat communities***

378 Results exposed in this paragraph correspond to response variables using a MERT of 0.5
379 in automated identification (for MERT of 0.1 results, see Table B 1).

380 Bat species richness was always higher in diverse than in simple landscapes (Table 4;
381 Figure 3).

382 Total bat activity was significantly influenced by landscape type (Table 4; Figure 3). It was
383 largely driven by the activity of MRE guild, which was also significantly higher in diverse
384 than simple landscapes, as well as activity of species of conservation concern (Table 4).

385 The total foraging activity, was not significantly influenced by the landscape type.

386 However when considering guild foraging activity, SRE foraging activity was significantly
387 longer in diverse landscapes.

388

389 Table 4: **Estimates and standards errors (\pm SE) of the effect of landscape type**
 390 **variable on species richness and bat activity (3 sampling periods combined, n =**
 391 **99)**. MRE: Mid-Range Echolocators; SRE: Short-Range Echolocators; SCC: Species of Conservation
 392 Concern; BSD: Bat Sequence Duration.
 393 Marginal R², i.e., variance explained by the fixed effects only, are given for GLMMs and * p <
 394 0.05; ** p < 0.01 and *** p < 0.001.

	Response variable	Estimate (\pm SE)	z-value or t-value	P-value	Marginal R ²
Bat community	Species richness Gaussian family	1.01 (\pm 0.43)	2.35	0.023*	0.07
Bat activity	Total activity Negative binomial family	0.60 (\pm 0.23)	2.61	0.009**	0.08
	MRE activity Poisson family	0.58 (\pm 0.28)	2.09	0.037*	0.04
	SCC activity Poisson family	1.23 (\pm 0.45)	2.75	0.006**	0.14
Foraging activity	SRE BSD Gaussian family	0.05 (\pm 0.02)	2.01	0.045*	0.06

395

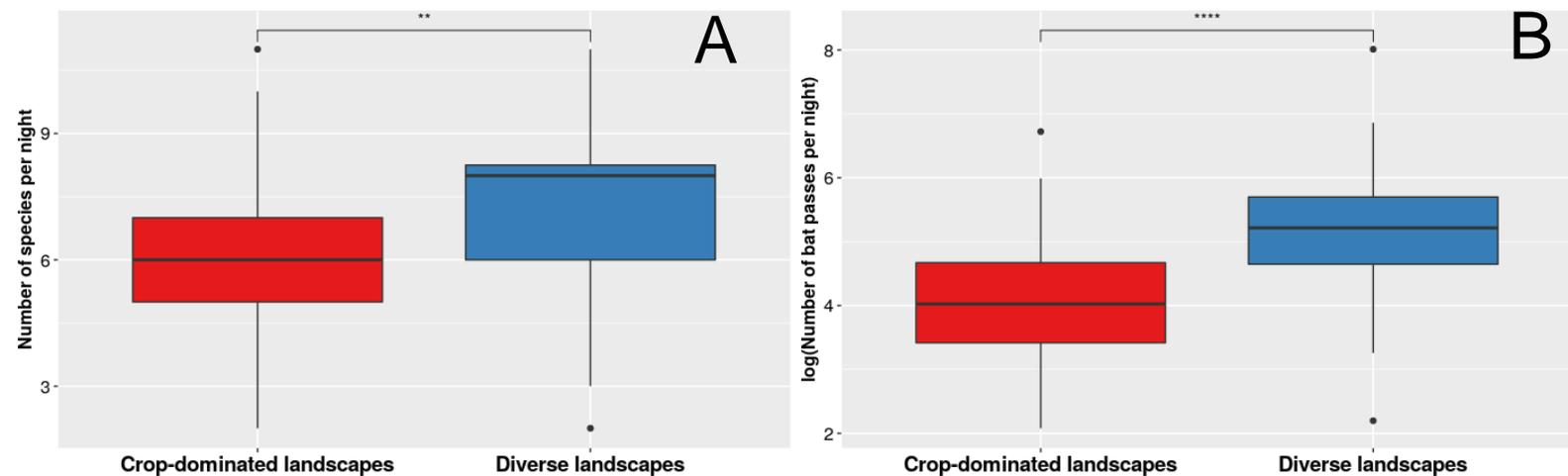


Figure 3: Bat species richness (A) and total bat activity (B - data log transformed) depending on landscape type. (** p < 0.01, **** p < 0.0001)

396

397 3.3. Effects of crop diversity and pest abundance on bat communities in vineyards

398 Bat activity in vineyards in April increased with crop diversity and decreased with distance
 399 to the nearest hedgerow (Figure A 4). Crop diversity had also a positive effect on
 400 endangered bat species.

401 MRE activity followed the same pattern as total bat activity and peaked in diverse
402 landscapes. LRE activity was positively related to the distance to the largest river and
403 negatively to the distance to the nearest hedgerow.

404 In addition, the relative abundance of pest *L. botrana* was negatively correlated with bat
405 species richness (Figure A 5; A 8) and SRE foraging activity.

406

407 ***3.4. Effects of crop diversity and pest abundance on bat communities in maize*** 408 ***fields, consequences on plant damage***

409 In maize fields in May, bat species richness was influenced positively by the proportion
410 of semi-natural habitats (SNH) and negatively by the total length of hedgerows (Figure A
411 6, Table B 2).

412 Total bat activity in maize fields significantly increased with the length of hedgerows and
413 closer to forest edges and decreased closer to the riparian zone (Figure A 6, Table B 2).

414 Bat guild activity was driven by MRE activity, which was influenced positively by the
415 distance to the nearest forest edge and negatively by the distance to the nearest riparian
416 zone. SRE activity significantly decreased with the total length of hedgerows (Figure A 6;
417 Table B 2). The activity of species of conservation concern in maize fields was significantly
418 and positively related to the distance to the nearest riparian zone. In addition, the
419 proportion of SNH and the crop diversity index had a significant positive effect on SCC
420 activity (Figure A 6; Table B 2).

421 Bat foraging activity was slightly but significantly positively influenced by the relative
422 abundance of *S. nonagrioides* and negatively influenced by the distance to the main river.

423 Considering foraging activity through guild classification, SRE foraging activity was
424 negatively affected by the length of hedgerows and positively affected by the proportion
425 of SNH and relative pest abundance. In addition, insect dry biomass and crop diversity
426 had significant positive effects on LRE foraging activity (Figure A 6; Table B 2).

427 The abundance of *S. nonagrioides* in sampled maize fields was positively correlated with
428 bat species richness (Figure A 6; A 8; Table B 3), SRE activity SRE and LRE foraging
429 activities. Total bat activity was not significantly correlated with the index of damage on
430 maize plants (Figure 4) whereas SCC activity and LRE foraging activity were positively
431 correlated to the maize damage index (Table B 4).

432

433 ***3.5. Effects of crop diversity and pest abundance on bat communities in pine*** 434 ***plantations, consequences for tree damage***

435 In pine plantations in July, bat species richness significantly increased with crop diversity
436 and decreased with the total length of hedgerows. Bat activity increased with crop
437 diversity and distance to the nearest hedgerow, while activity of endangered bats only
438 increased with crop diversity.

439 MRE activity was positively influenced in the same way as global bat activity. SRE activity
440 was positively influenced by the three-crops Shannon diversity index and negatively by
441 the total length of hedgerows (Figure A 7; Table B 2). The three-crops Shannon diversity
442 index affected positively the SCC activity (Figure A 7; Table B 2).

443 Bat foraging activity increased with the distance to the nearest hedgerow and crop
444 diversity index. Relative abundance of *T. pityocampa* in sampled pine plantations was
445 positively correlated with the index of damage measured on pine plantations but only in
446 pine-dominated landscapes (Table B 4). Total foraging activity and especially MRE
447 foraging activity were negatively correlated with the damage index (Figure 4, Table B 4).

448

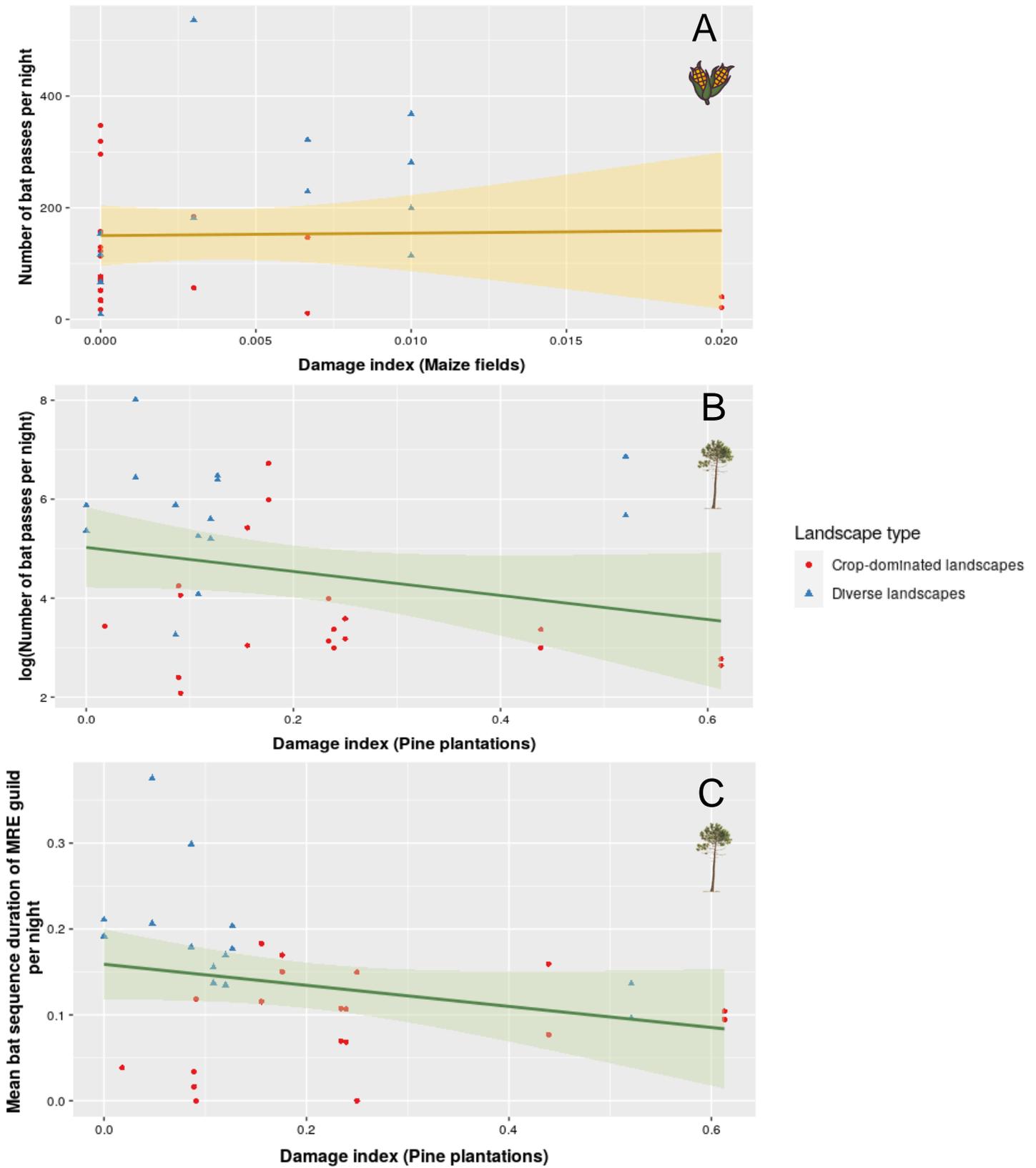


Figure 4: Relationships between total bat activity and damage index in maize fields in May (A) and in pine plantations in July (B), especially MRE foraging activity (C). Red points represent sampled points in maize- or pine plantations- dominated landscapes while blue points represent sampled points in diverse landscapes.

450 **4. Discussion**

451 While more and more studies highlight the importance of landscape complexity for bats
452 (e.g. Allegrini et al., 2022; Krings et al., 2022; Ocampo-Ariza et al., 2022), there are still
453 few studies that highlight their potential role in pest control within agricultural landscapes
454 (Russo et al., 2018).

455 This study provides evidence for the positive effect of the diversity of the crop mosaic at
456 the landscape scale on bat richness and activity. The novelty of the study relies in
457 focusing the approach on the biological control of three pests at key periods for bats in
458 agricultural landscapes, and allowed us highlighting their effective role in natural pest
459 control. In line with our hypotheses, our results suggest bat guild-dependent responses.
460 On the one hand, long-range echolocators foraging activity was higher with pest
461 abundance and damage index in maize fields. On the other hand, damage index on pine
462 trees decreased with mid-range echolocators activity. These findings highlight the
463 importance of landscape scale and pest control-centred approaches together with studies
464 analysing bat diet, in order to quantify the role of bats in agricultural landscapes and to
465 identify conservation actions.

466 **4.1. More diverse landscapes foster bat species richness and activity**

467 Our models revealed that species richness and bat activity, especially mid-range
468 echolocators activity (mainly *Pipistrellus* spp.) were higher in the more diverse landscapes
469 mixing more or less equally the three target crop types. These results corroborate with
470 Monck-Whipp et al. (2018), who found that diverse agricultural landscapes improved both
471 bat species richness and activity.

472 There are three main hypotheses explaining positive effects of crop diversity on species
473 richness, bat activity and to a lesser extent on foraging activity. First, more diverse
474 landscapes typically combined perennial and annual crops that may provide more diverse
475 and abundant prey spatially within the landscape and over the time, especially for highly

476 mobile taxa (Bertrand et al., 2016; Fahrig et al., 2015; Laforge et al., 2021). Particularly
477 in our study design we hypothesised a temporal continuity in abundance of moth pests,
478 whose flight peaks narrowly followed each other within the three crop types during the
479 entire bat activity period. In diverse landscapes, prey abundance is likely to be more
480 stable through the night as different species are active at different time in different habitats
481 (Rydell et al., 1996). Second, bats also depend on non-substitutable key resources, such
482 as daylight roosting sites. Diverse landscapes, especially those combining trees and
483 crops may provide these complementary resources year-on-year and then the proximity
484 of foraging and roosting habitats may benefit both species richness and bat activity.
485 Finally, the combination of annual and perennial crops, which have different phenologies
486 and varying cover heights, offers a three-dimensional structure of the landscape. It is
487 widely accepted that the different bat species do not commute and forage in the same
488 way within the landscape according to their wing morphology and echolocation
489 capabilities (Frey-Ehrenbold et al., 2013; Fuentes- Montemayor et al., 2011). Therefore,
490 landscapes with such three-dimensional structure may be favourable to a larger range of
491 bat species classified into different guilds and will increase their activity. Furthermore,
492 landscape elements such as forest edges or hedgerows contribute to landscape
493 connectivity especially for bats belonging to SRE guild, which includes species that are
494 relatively sensitive to landscape fragmentation and more active in well-connected
495 landscapes (Fill et al., 2022; Frey-Ehrenbold et al., 2013).

496 In addition to the importance of a more diverse agricultural landscape in terms of crops,
497 our study also showed the influence of the presence and the distance to semi-natural
498 habitats, which is consistent with previous studies (e.g. Laforge et al., 2021). Surprisingly,
499 we found that a higher length of hedgerows was associated with a bat species richness
500 decrease at the local scale, maybe due to less foraging bats gathering in optimal areas
501 when hedgerow availability is low at the landscape scale. Also, hedgerows may benefit

502 more to some bat species depending on their structure (strata), plant diversity and even
503 height. Lacoeyuilhe et al. (2018), showed that bat species preferred wooded hedgerows
504 dominating in agricultural landscapes rather than a diversity of hedgerow types. Hawking
505 bat species such as *Pipistrellus* spp., benefit from wooded hedgerows due to their
506 vegetation that shelters a large number of insects and allows dispersal away from the
507 wind (Lewis & Dibley, 1970). Moreover, gleaning foragers, which are mainly species from
508 SRE guild, were associated with more complex hedgerows with diversified strata. These
509 results also point out that the quality of the hedgerow itself might be critical to explain its
510 differentiated use by the different bat species (Froidevaux et al., 2019; Wickramasinghe
511 et al., 2003).

512 Our study is therefore in line with several others that highlight both the benefits of the
513 compositional heterogeneity of the crop mosaic but also its arrangement with other semi-
514 natural and woodland habitats resulting in promoting bat diversity and activity (Fill et al.,
515 2022; Maas et al., 2016; Monck-Whipp et al., 2018; Pedro et al., 2021; Puig-Montserrat
516 et al., 2015; Rodríguez-San Pedro et al., 2019).

517

518 ***4.2. Crops benefit from each other within the landscape in terms of biological*** 519 ***control of pests***

520 Our study adds to the growing body of literature supporting the positive effects of diverse
521 agricultural landscapes and woodlands on biocontrol agents such as bats resulting in
522 higher pest regulation activity (Fill et al., 2022; Maas et al., 2016). We tried to find out the
523 reciprocal benefits of different crop types already implanted in the region and all around
524 the world. It appeared that crop association at the landscape scale offered benefits for
525 each crop in terms of biological control of pests. In our study, grapevines and pine
526 plantations indicate higher levels of biological control by bats in diverse landscapes than
527 in landscapes dominated by a single crop. In vineyards, the abundance of moths

528 decreased with the bat species richness. This represents an indicator of potential
529 biological control, but the low moth population levels and the lack of damage
530 measurements does not allow to affirm that this process is actually at play. However, in
531 French vineyards, Charbonnier et al. (2021) highlighted the regulation role of bats on
532 grape berry moths. Also the importance of adjacent forested semi-natural habitats near
533 vineyards for prey availability was assessed in Central Chile vineyards which suggests
534 that both semi-natural and vineyards may promote bat conservation and resources
535 (Chaperon et al., 2022). In pine plantations, in July, foraging activity (particularly MRE
536 activity) was not correlated with the relative abundance of *T. pityocampa* but significantly
537 and negatively with the index of damage on pine trees. These results partly corroborate
538 those from previous studies showing that different species belonging to the three guilds
539 are *T. pityocampa* predators without being independent on it in their diet (Garin et al.,
540 2019) and that bats were efficient biological pest control agents for *T. pityocampa*. Bat
541 foraging plasticity allowing them to concentrate their activity on local prey aggregates
542 (Charbonnier et al., 2014), and the high mobility of pine processionary moths through the
543 landscape may explain the non-detection of a relationship between bat activity and
544 relative abundance of *T. pityocampa* (Battisti et al., 2015).

545 However, no difference of potential moth biological control was observed in maize
546 between maize-dominated and diverse landscapes: while the abundance of moths seems
547 to attract bats (in particular reflected by SRE and LRE foraging activities), the associated
548 predator-prey dynamics does not allow for biological control. It is probably related to the
549 rapid oviposition rate observed in *S. nonagrioides*, with a maximum of egg-laying on
550 maize as soon as 30% of the moths have emerged. Although the role of bats as predators
551 of corn pests has been demonstrated (Maine & Boyles, 2015; Whitby et al., 2020) bats
552 probably predate moths after most of the eggs have already been laid on maize plants.
553 While biological control of *S. nonagrioides* in maize does not seem to be directly and

554 solely controlled by bats, other natural enemies, such as parasitoids, can be involved in
555 the egg stages of this pest and be favoured by diverse landscapes (Gardiner et al., 2009;
556 Landis & Haas, 1992). Additional agricultural practices, not recorded in our study, such
557 as the use of pesticides, may also vary between fields and dampen relationships between
558 moth abundances and observed damage (Paredes et al., 2021). Nevertheless, maize
559 appears to provide moth prey that benefit bats at the landscape level, possibly translating
560 into a higher biological pest control by the same bats in the other adjacent crop types.
561 Our study illustrates that the diversification of agricultural landscapes to favour biological
562 control can be thought of by taking advantage of the dominant crops in the landscapes,
563 as an alternative to the introduction of new crop species, then without fundamentally
564 modifying the local value chains (Vialatte et al., 2021). Our study is in line with the results
565 of recent meta-analyses that show that crop diversification promotes biodiversity,
566 biological control and yields (Beillouin et al., 2021; Paiola et al., 2020; Tamburini et al.,
567 2020). It complements this work, which is largely dominated by intra-plot diversification
568 by showing that crop diversification at the landscape scale is also a lever for biological
569 control. While semi-natural elements in landscapes are widely known to support
570 biodiversity and biological control (Dainese et al., 2019; Karp et al., 2018) and in particular
571 by bats (Chaperon et al., 2022; Pedro et al., 2021) crop mosaics appear to be a
572 complementary way of diversification. In the face of the risk of pest outbreaks associated
573 with global warming (Klapwijk et al., 2012), our results open up avenues of alternative
574 agroecological management to conventional agriculture for globally important crops such
575 as maize (world's second cereal, FAOSTAT, 2020), planted forests (conifers account for
576 more than 55% of the world's forest plantation resource) and grapevines (Brockerhoff et
577 al., 2017; Hannah et al., 2013).

578

579 **4.3. Conservation implications**

580 It is widely recognised that habitat loss driven by the expansion of agriculture has led to
581 biodiversity declines (e.g. Billeter et al., 2008). One of the main challenges for biodiversity
582 conservation is therefore to maintain or enhance biodiversity by taking advantage of
583 existing production types by increasing the diversity of crops, as well as their spatial and
584 temporal arrangement at the scale of the wider landscape mosaic. This study highlights
585 that considering crop diversity and more precisely annual and perennial crops with
586 different ecological characteristics favourable for bats could represent an efficient
587 conservation strategy to promote bat species richness, and favour species of major
588 conservation concern in agricultural landscapes. Bat responses to landscape features
589 vary depending on their home range size, species-specific echolocation call
590 characteristics and foraging strategies that may explain the diversity of species identified
591 and the role of agricultural landscapes as foraging and commuting areas (Frey-Ehrenbold
592 et al., 2013; Laforge et al., 2021).

593 Finally, the activity of species of conservation concern was significantly and positively
594 related to the most diverse agricultural landscapes. We suggest that the diverse
595 landscapes mixing crops and forests studied here actually have a high conservation
596 potential due to their higher structural complexity (Harvey & González Villalobos, 2007;
597 Schroth, 2004) allowing a differentiated use by a large range of bat guilds. Moreover,
598 improving landscape compositional heterogeneity through an increase of the amount of
599 key habitats such as hedgerows or riparian zones, their spatial configuration and their
600 connectivity are of main importance (e.g. Froidevaux, Boughey, et al., 2017; Froidevaux,
601 Louboutin, et al., 2017; Fuentes- Montemayor et al., 2011; Heim et al., 2015; Monck-
602 Whipp et al., 2018).

603 Mata et al. (2021) showed that a limited number of bat species, consisting of both
604 common species such as *P. pipistrellus* and conservation concern species, are central in

605 pest interaction networks and could be the focus of conservation strategies. The results
606 of our study support that enhancing crop diversity by combining agricultural fields and
607 forestry and also other landscape elements such as linear features promote
608 complementary and more stable resources (e.g. roost, foraging, commuting), which will
609 benefit to a large range of bat species with some positive effects on biological control in
610 crop fields.

611 **5. Conclusion**

612 Because of their ability to disperse and as generalist predators, bats have been proved
613 to be particularly important in controlling pest outbreaks (Boyles et al., 2013). While more
614 and more studies are focusing on the diet of bats via metabarcoding methods, few studies
615 have been carried out to assess the role of bats for pest control (Russo et al., 2018), and
616 even fewer have considered the agricultural and forestry mosaic. Our study adds to the
617 growing body of literature by (i) showing the positive effects of more diverse agricultural
618 landscapes on bat richness and activity and (ii) supporting the efficacy of bats for the
619 biological control of crop and forest pests (Charbonnier et al., 2014; Maine & Boyles,
620 2015). Agricultural landscapes combining a diverse crop mosaic (in a broad sense,
621 including pine forestry) provide more stable resources over space and time for generalist
622 predators such as bats. Thus, more diverse landscapes can allow for win-win strategies
623 in each of the sampled crop increasing bat activity and biological pest control. In addition,
624 more diverse landscapes benefit to a large range of bat species from different guilds,
625 which may have a complementary predation on pests (Garin et al., 2019). These results
626 may benefit greatly to biocontrol conservation, especially in the context of diversifying
627 agricultural landscapes facing rapid global changes.

628

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641

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