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# Diverse agricultural landscapes increase bat activity and diversity: Implications for biological pest control

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## ABSTRACT

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

Here, we tested the hypothesis that crop mosaics would provide a temporal continuity in prey availability for bats, ultimately resulting in higher biological control. We sampled bat activity and diversity, and the abundance and damage of three major pests of vineyards, maize, and pine plantations, in both simple and diverse landscapes mixing the three production types. Bat species richness and total activity were higher in vineyards and pine plantations located within diverse landscapes. Bat foraging activity also peaked within diverse landscapes. In vineyards, moth abundance decreased with bat species richness. In pine plantations, pest damage decreased with bat foraging activity. In maize fields, pest abundance and damage increased with bat richness and activity longer-term investigations would be necessary to assess their actual effectiveness. Our study advocates for promoting a diversity of coexisting crops within agricultural landscapes to enhance bat activity and diversity, which in turn would sustain higher biological control and bolster biodiversity conservation in farmland.

## 1. Introduction

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

Pest infestations are known to increase in monoculture landscapes, but it is also greater in more favourable landscapes, i.e., when the proportion of host crop cover is higher within the crop mosaic and/or is increasingly connected (Rand et al., 2014; Veres et al., 2013). Moreover, biological control of pests by their natural enemies tends to be less effective in simplified landscapes, i.e. crop-dominated landscapes, because the effect of local management often interacts with landscape complexity (Rusch et al., 2016). While the role of semi-natural habitats on biological control has been intensively studied, the benefits of crop diversity itself are less well understood (Veres et al., 2013). It is now widely established that landscape spatio-temporal heterogeneity enhances multitrophic abundance and diversity of natural enemies (Sirami et al., 2019) in part by promoting complementary resources for natural enemies, including foraging areas, food sources, shelter, nesting and overwintering sites (Bertrand et al., 2016; Schellhorn et al., 2015). However, the actual consequences in terms of biological pest control

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remain inconsistent across regions, sites and experiments, probably due to complex interactions between farming practices and landscape context leading to synergistic or antagonistic effects (Barbaro et al., 2017; Etienne et al., 2022; Muneret et al., 2019; Ricci et al., 2019). Although the relationship between natural enemy diversity and the effectiveness of biological pest control is generally positive, it can be substantially disrupted by, e.g., intra-guild predation within the natural enemy community (Letourneau et al., 2009; Martin et al., 2013).

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

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

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

Our first objective was to evaluate the effects of more diverse agricultural landscapes on bat community and its foraging activity. We predicted that in landscapes mixing the three crops, the presence of higher diversity of landscape elements favourable for bats would provide complementary resources, resulting in higher species richness and bat activity. Our second prediction is that bat guild-specific responses are expected because crop-diverse landscapes display higher diversity in habitat structures than crop-dominated ones.

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

## 2. Material and methods

### 2.1. Study area and site selection

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

Within this study area, we selected thirty-seven landscapes (a 563-m radius scale; Fig. 1) according to the predominance of one or all three target crop types. Thirty landscapes were dominated by only one of the three crops, i.e. 10 simplified landscapes dominated by vineyards (mean: 70%; range 57%–78%), maize fields (mean: 52%; range 21%–76%, without any other dominant crop) or pine plantations (mean: 79%; range 63%–100%), respectively. Seven landscapes were selected that had all three crop types in varying proportions but their total surface cover was at least 45% of the total area (hereafter referred to as ‘diverse landscapes’). Among the 17 vineyards sampled two were organically managed and maize fields were all conventionally managed.

### 2.2. Field sampling of targeted Lepidoptera and potential alternative prey

Vineyards (*Vitis vinifera* L.), maize (*Zea mays* L.) fields and pine plantations (mainly *Pinus pinaster*) dominate agricultural landscapes of South-western France. Key pests include the European grapevine moth *Lobesia botrana* Denis & Schiffernüller (Lepidoptera: Tortricidae), which cause direct losses in grape production (Delbac and Thiéry, 2016); the Mediterranean corn borer *Sesamia nonagrioides* Lefèbvre (Lepidoptera: Noctuidae), which is one of the most damaging pests of maize in early stages (Maine and Boyles, 2015); and the pine processionary moth *Thaumetopoea pityocampa* Denis & Schiffernüller (Lepidoptera: Notodontidae), which is the main defoliator of pines reducing growth of young trees (Jacquet et al., 2012). The flight peaks of these three species follow one another in time. The corn borer and the grape berry moth have between 2 and 4 generations per year, with a flight peak of the first generation at the end of April and the end of May, respectively. The control of the first generation is key to limit the abundance of the following generations. The pine processionary moth has one generation per year and a flight peak spread out between late June and early September. Current control of moth pests in crops consists of mating disruption, application of insecticide or *Bt* toxin but their effectiveness tends to decrease in a context of global warming and the appearance of resistance (Thiéry et al., 2018).

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

The same experimental set-up was conducted in May in 16 maize

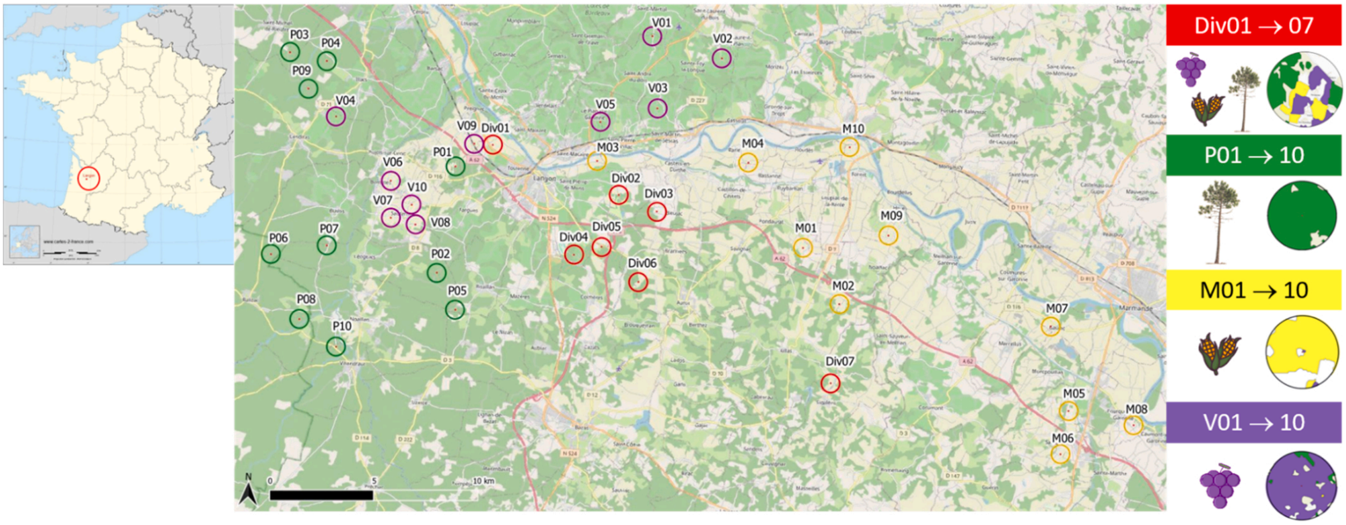

**Fig. 1.** Map of the study area showing the two landscape types: simplified landscapes depending on the targeted crop (P: pine or M: maize or V: vineyards) and diverse landscapes (Div: three crops were represented).

fields and in July in 17 pine plantations. The pheromone baited-traps specific to *S. nonagrioides* were placed from 18 to 27 May 2021 and specific to *T. pityocampa* from 28 June to 7 July 2021.

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

### 2.3. Bat monitoring

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

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

Species identification was supported by the Tadarida software, which classified calls to the most accurate taxonomic level with a confidence index value (https://github.com/YvesBas/Tadarida-C/; Bas et al., 2017). As automated identification can generate significant error rates, we followed the procedure by Barré et al. (2019) in order to find the best compromise limiting species identification errors and maintaining a relatively high number of bat passes. Then, we removed acoustic data with a maximum error rate tolerance (MERT) of 0.5 to minimize false positives while keeping a high number of bat passes. We checked the consistency of responses using a more restrictive MERT of 0.1 (detailed results are available in Appendix B), which limited false positives but discarded more true positives. Call identifications were grouped at genus level for *Plecotus* spp. and we distinguished small and large *Myotis* spp. (see Table 1). The number of species or complex of species were counted per site and per night. Species of regional conservation concern (SCC) were identified according to the Nouvelle-Aquitaine regional red list (see Table 1; Liste rouge des Chiroptères d'Aquitaine, 2019).

We also grouped bats according to their echolocation range into three guilds (Frey-Ehrenbold et al., 2013; Schnitzler and Kalko, 2001)

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

| Species | Complex of species | Guild | Status of species on the Nouvelle-Aquitaine red list* |
|---|---|---|---|
| *Nyctalus leisleri* | – | LRE | LC |
| *Nyctalus noctula* | – | LRE | VU |
| *Nyctalus lasiopterus* | – | LRE | VU |
| *Eptesicus serotinus* | – | LRE | LC |
| *Pipistrellus pipistrellus* | – | MRE | LC |
| *Pipistrellus kuhlii* | – | MRE | LC |
| *Pipistrellus nathusii* | – | MRE | NT |
| *Pipistrellus pygmaeus* | – | MRE | DD |
| *Hypsugo savii* | – | MRE | LC |
| *Miniopterus schreibersii* | – | MRE | EN |
| *Barbastella barbastellus* | – | SRE | LC |
| *Plecotus auritus* | *Plecotus* spp. | SRE | LC |
| *Plecotus austriacus* | | SRE | LC |
| *Myotis blythii* | Large *Myotis* spp. | SRE | EN |
| *Myotis myotis* | | SRE | LC |
| *Myotis emarginatus* | Small *Myotis* spp. | SRE | LC |
| *Myotis crypticus* | | SRE | NT |
| *Myotis mystacinus* | | SRE | DD |
| *Rhinolophus ferrumequinum* | – | SRE | LC |
| *Rhinolophus hipposideros* | – | 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 namely short-, mid- and long-range echolocators (SRE, MRE and LRE respectively - see Table 1).

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

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

### 2.4. Evaluation of specific damage in targeted crops

Specific damage was evaluated in maize and pine plantations to estimate the actual effects of bat predation on target lepidopterans. Damage in vineyards (glomerules on grape bunches) could not be assessed due to a frost episode that occurred at the beginning of April (2021) and greatly affected vegetative development of the grapevines.

Maize damage was evaluated the fortnight following bat sampling that corresponded to 10–15 days after 50% of the *S. nonagrioides* peak flying (maximum of adult emergence) and to the maximum of larvae at the crawler stage. Three transects of 100 maize plants were observed in each field and the plants showing wilting were counted to assess larvae densities per field and per 100 plants (maize densities equal in all our fields).

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

### 2.5. Landscape metrics

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

Part of the landscape metrics were then calculated for a 1 $km^2$ circle (i.e., inside a circular buffer with radius of 563 m, centred on the middle of the pheromone baited-trap and acoustic detector position). First, we used a descriptive variable (i.e. landscape type) to distinguish the type of landscape in which the measurements were made, i.e. either simplified (dominance of one targeted crop) or diverse (presence of all three crops).

To describe crop mosaic compositional heterogeneity, the proportion of each targeted crop (vineyards, maize fields and pine plantations) was assessed and the Shannon crop-diversity index was specifically calculated on those categories. Another Shannon diversity index was calculated for the whole landscape based on the proportion of each land cover (other habitats than crops such as deciduous woodlands, water bodies, building, hedgerows with mainly deciduous trees) but it was highly correlated with the Shannon crop-diversity index of specific crops (Pearson's coefficient $> 0.9$), and was therefore disregarded for the analysis. The compositional heterogeneity of the semi-natural habitats (SNH) was described using the proportion of SNH, which grouped hedgerows, woodlands and water bodies and we also calculated the total length of hedgerows, which represented an indicator of configuration heterogeneity. The proportion covered by artificial spaces (i.e. buildings, roads, commercial and industrial areas) was calculated to consider the potential effect of artificialization.

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

### 2.6. Statistical analysis

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

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

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

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

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

**Table 2**

Description of the landscape metrics, co-variables and random factors used for 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<br>%SNH<br>%Artificial<br>Length of hedgerows<br>Distance to the nearest building<br>Distance to the nearest hedgerow<br>Distance to the nearest riparian zone<br>Distance to the Garonne<br>Distance to the nearest forest edge | Biomass<br>Relative pest abundance (number of *L. botrana*) | (1\|Site) + (1\|Night) |
| Maize fields N = 32 (16 sites x 2 nights) | Shannon diversity of crops<br>%SNH<br>Length of hedgerows<br>Distance to the nearest building<br>Distance to the nearest riparian zone<br>Distance to the Garonne<br>Distance to the nearest forest edge<br>Distance to the nearest water body | Biomass<br>Relative pest abundance (number of *S. nonagrioides*) | (1\|Site) + (1\|Night) |
| Pine plantations N = 33 (17 sites x 2 nights[a]) | Shannon diversity of crops<br>%SNH<br>Length of hedgerows<br>Distance to the nearest hedgerow<br>Distance to the nearest water body | Relative pest abundance (number of *T. pityocampa*) | (1\|Site) + (1\|Night) |

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

## 3. Results

### 3.1. Bat, pest and plant damage

#### 3.1.1. Bat richness and activity

We recorded a total of 17,786 and 13,386 bat passes, considering a MERT of 0.5 and a MERT of 0.9, that belonged to 16 taxa (Table 3). The average species richness was 7.4 ( ± 1.8) species in vineyards; 6.4 ( ± 2.3) in maize fields and 6.1 ( ± 1.7) in pine plantations.

Bat activity was mainly represented by MRE guild (72%) with the *Pipistrellus* genus as most frequently detected (39% *Pipistrellus pipistrellus,* 29% *Pipistrellus kuhlii*). LRE and SRE guilds represented 22% and 6% of total bat activity; *Nyctalus leisleri* and *Eptesicus serotinus* represented each 11% of recorded activity.

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

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

**Table 3**

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

| Taxa | Vineyards | Maize fields | Pine plantations | *Total* |
|---|---|---|---|---|
| **Long-range echolocators - LRE** | **810** *(619)* | **531** *(358)* | **2 691** *(1 459)* | **4 032** *(2 436)* |
| *Nyctalus leisleri* | 679 *(589)* | 290 *(233)* | 1 047 *(804)* | 2 016 *(1 626)* |
| *Nyctalus noctula* | 4 *(1)* | 11 *(8)* | 0 | 15 *(9)* |
| *Nyctalus lasiopterus* | 0 | 14 *(0)* | 0 | 14 *(0)* |
| *Eptesicus serotinus* | 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)* |
| *Pipistrellus pipistrellus* | 1 209 *(1 104)* | 2 268 *(1 917)* | 3 415 *(3 052)* | 6 892 *(6 073)* |
| *Pipistrellus kuhlii* | 737 *(572)* | 1 302 *(903)* | 3 138 *(2 628)* | 5 177 *(4 103)* |
| *Pipistrellus nathusii* | 200 *(29)* | 286 *(14)* | 122 *(0)* | 608 *(43)* |
| *Pipistrellus pygmaeus* | 11 *(6)* | 2 *(0)* | 0 | 13 *(6)* |
| *Hypsugo savii* | 6 *(2)* | 10 *(0)* | 6 *(0)* | 22 *(2)* |
| *Miniopterus schreibersii* | 4 *(3)* | 1 *(0)* | 0 | 5 *(3)* |
| **Short-range echolocators - SRE** | **250** *(152)* | **456** *(323)* | **331** *(205)* | **1 037** *(680)* |
| *Barbastella barbastellus* | 78 *(73)* | 306 *(279)* | 117 *(72)* | 501 *(424)* |
| *Plecotus* spp. | 81 *(15)* | 123 *(31)* | 110 *(44)* | 314 *(90)* |
| Small *Myotis* spp. | 16 *(2)* | 3 *(0)* | 23 *(12)* | 42 *(14)* |
| Large *Myotis* spp. | 14 *(6)* | 14 *(6)* | 2 *(0)* | 30 *(12)* |
| *Rhinolophus ferrumequinum* | 9 *(9)* | 5 *(3)* | 59 *(58)* | 73 *(70)* |
| *Rhinolophus hipposideros* | 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)* |

#### 3.1.2. Pest abundance and alternative prey biomass

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

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

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

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

#### 3.1.3. Plant damage

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

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

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

### 3.2. Effects of landscape diversity on bat communities

Results exposed in this paragraph correspond to response variables

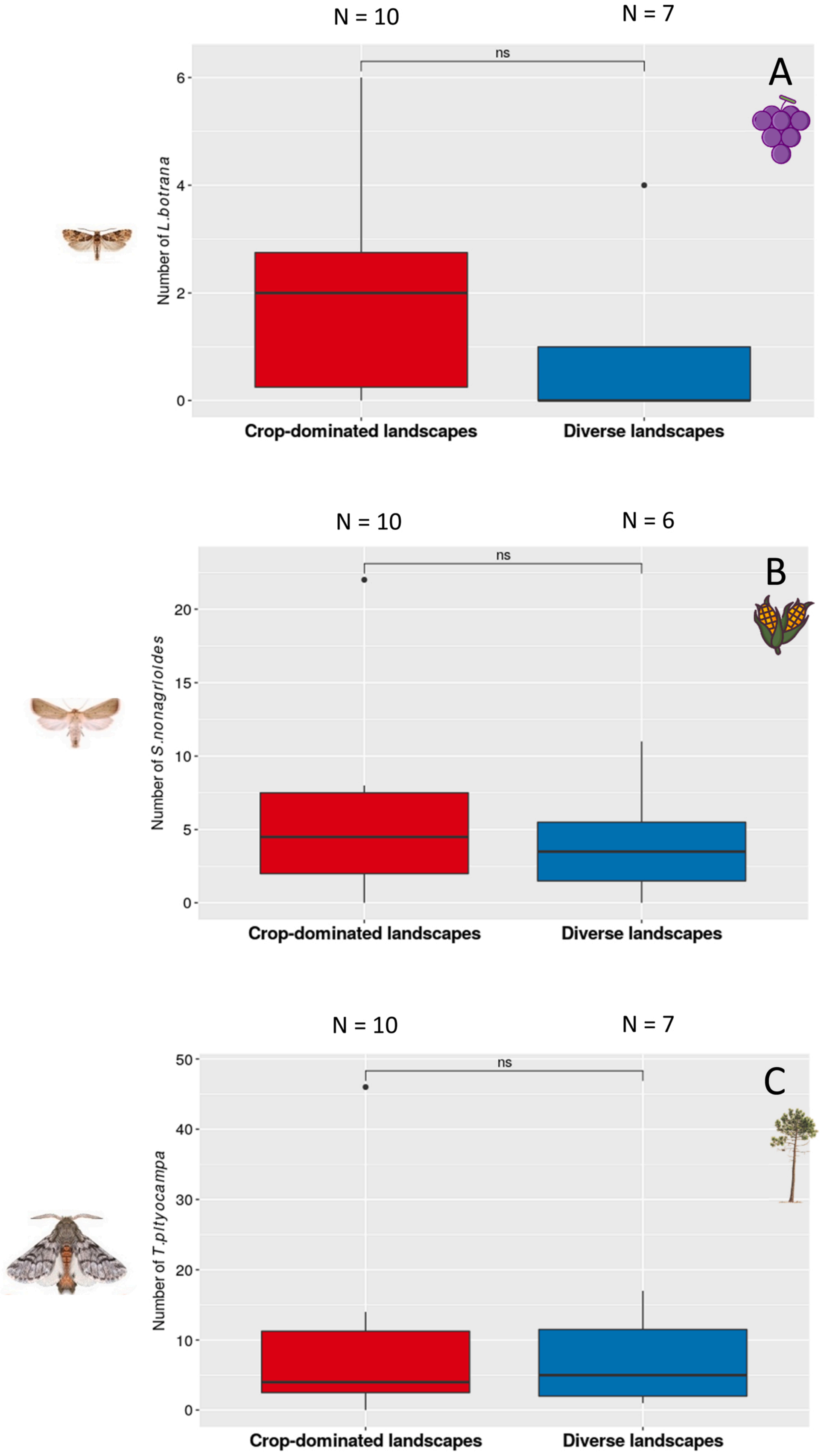

**Fig. 2.** Relative abundance of the three targeted moths in the crops they were specialist about. Respectively (A) in vineyards (April) for L. botrana; (B) in maize fields (May) for S. nonagrioides; (C) in pine plantations (July) for T. pityocampa. N corresponded to the number of landscapes considered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

using a MERTof 0.5 in automated identification (for MERT of 0.1 results, see Table B 1).

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

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

The total foraging activity, was not significantly influenced by the landscape type. However when considering guild foraging activity, SRE foraging activity was significantly longer in diverse landscapes.

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

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

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

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

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

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

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

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

Bat foraging activity was slightly but significantly positively influenced by the relative abundance of *S. nonagrioides* and negatively influenced by the distance to the main river. Considering foraging activity through guild classification, SRE foraging activity was negatively affected by the length of hedgerows and positively affected by the proportion of SNH and relative pest abundance. In addition, insect dry biomass and crop diversity had significant positive effects on LRE foraging activity (Fig. A 6; Table B 2).

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

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

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

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

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

## 4. Discussion

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

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

**Table 4**
Estimates and standards errors ( ± SE) of the effect of landscape type variable on species richness and bat activity (3 sampling periods combined, n = 99). MRE: Mid-Range Echolocators; SRE: Short-Range Echolocators; SCC: Species of Conservation Concern; BSD: Bat Sequence Duration.

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

Marginal $R^2$, i.e., variance explained by the fixed effects only, are given for GLMMs and * $p < 0.05$; * * $p < 0.01$ and * ** $p < 0.001$.

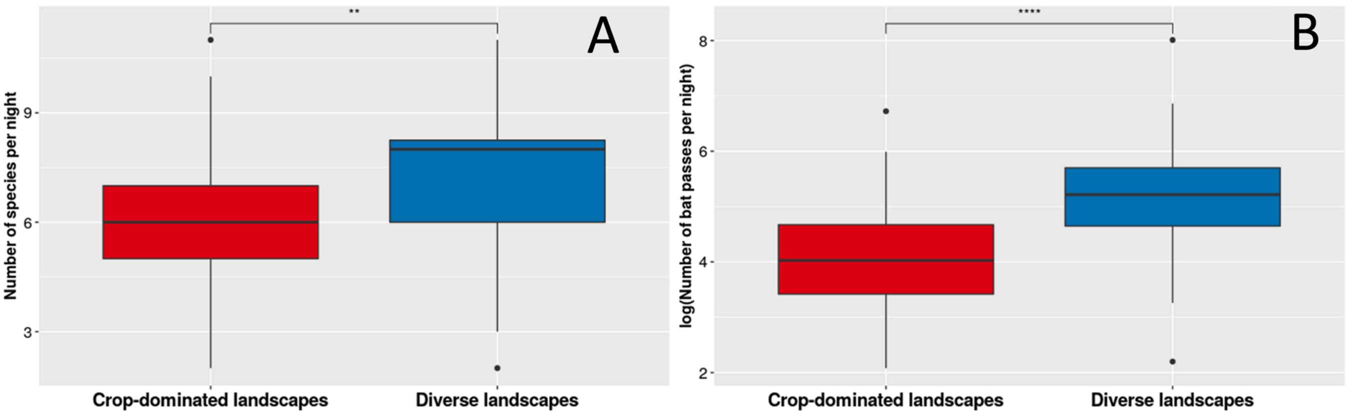

**Fig. 3.** Bat species richness (A) and total bat activity (B - data log transformed) depending on landscape type. (** $p < 0.01$, **** $p < 0.0001$).

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

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

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

In addition to the importance of a more diverse agricultural landscape in terms of crops, our study also showed the influence of the presence and the distance to semi-natural habitats, which is consistent with previous studies (e.g. Laforge et al., 2021). Surprisingly, we found that a higher length of hedgerows was associated with a bat species richness decrease at the local scale, maybe due to less foraging bats gathering in optimal areas when hedgerow availability is low at the landscape scale. Also, hedgerows may benefit more to some bat species depending on their structure (strata), plant diversity and even height. Lacoeuilhe et al. (2018), showed that bat species preferred wooded hedgerows dominating in agricultural landscapes rather than a diversity of hedgerow types. Hawking bat species such as *Pipistrellus* spp., benefit from wooded hedgerows due to their vegetation that shelters a large number of insects and allows dispersal away from the wind (Lewis and Dibley, 1970). Moreover, gleaning foragers, which are mainly species from SRE guild, were associated with more complex hedgerows with diversified strata. These results also point out that the quality of the hedgerow itself might be critical to explain its differentiated use by the different bat species (Froidevaux et al., 2019; Wickramasinghe et al., 2003).

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

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

Our study adds to the growing body of literature supporting the positive effects of diverse agricultural landscapes and woodlands on biocontrol agents such as bats resulting in higher pest regulation activity (Fill et al., 2022; Maas et al., 2016). We tried to find out the reciprocal benefits of different crop types already implanted in the region and all around the world. It appeared that crop association at the landscape scale offered benefits for each crop in terms of biological control of pests. In our study, grapevines and pine plantations indicate higher levels of biological control by bats in diverse landscapes than in landscapes dominated by a single crop. In vineyards, the abundance of moths decreased with the bat species richness. This represents an indicator of potential biological control, but the low moth population levels and the lack of damage measurements does not allow to affirm that this process is actually at play. However, in French vineyards, Charbonnier et al. (2021) highlighted the regulation role of bats on grape berry moths. Also the importance of adjacent forested semi-natural habitats near vineyards for prey availability was assessed in Central Chile vineyards which suggests that both semi-natural and vineyards may promote bat conservation and ressources (Chaperon et al., 2022). In pine plantations, in July, foraging activity (particularly MRE activity) was not correlated with the relative abundance of *T. pityocampa* but significantly and negatively with the index of damage on pine trees. These results partly corroborate those from previous studies showing that different species belonging to the three guilds are *T. pityocampa* predators without being independent on it in their diet (Garin et al., 2019) and that bats were efficient biological pest control agents for *T. pityocampa.* Bat foraging plasticity allowing them to concentrate their activity on local prey aggregates (Charbonnier et al., 2014), and the high mobility of pine

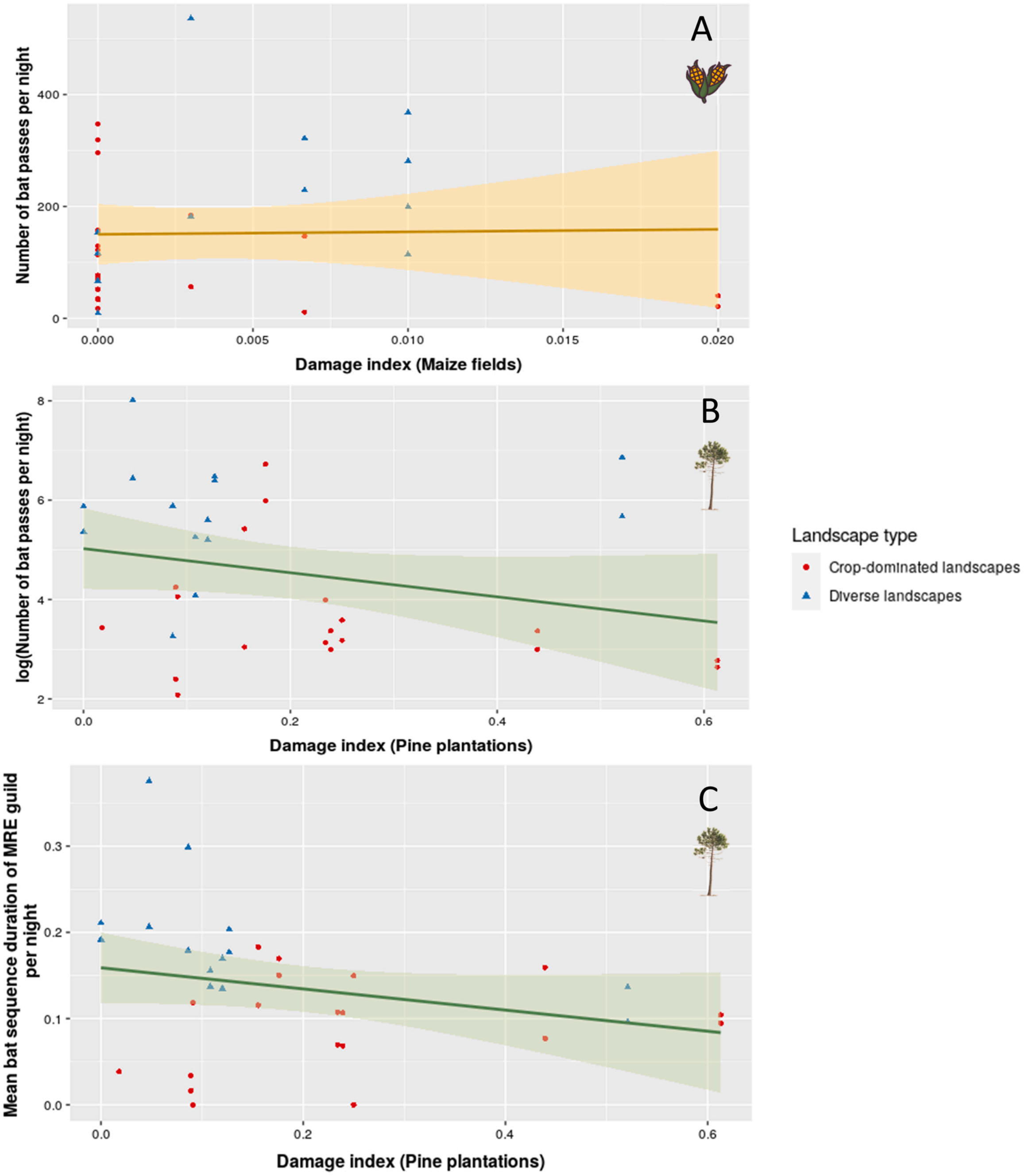

**Fig. 4.** Relationships between total bat activity and damage index in maize fields in May (A) and in pine plantations in July (B), especially MRE foraging activity (C). Red points represent sampled points in maize- or pine plantations- dominated landscapes while blue points represent sampled points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

processionary moths through the landscape may explain the non-detection of a relationship between bat activity and relative abundance of *T. pityocampa* (Battisti et al., 2015).

However, no difference of potential moth biological control was observed in maize between maize-dominated and diverse landscapes: while the abundance of moths seems to attract bats (in particular reflected by SRE and LRE foraging activities), the associated predator-prey dynamics does not allow for biological control. It is probably related to the rapid oviposition rate observed in *S. nonagrioides,* with a maximum of egg-laying on maize as soon as 30% of the moths have emerged. Although the role of bats as predators of corn pests has been demonstrated (Maine and Boyles, 2015; Whitby et al., 2020) bats probably predate moths after most of the eggs have already been laid on maize plants. While biological control of *S. nonagrioides* in maize does not seem to be directly and solely controlled by bats, other natural enemies, such as parasitoids, can be involved in the egg stages of this pest and be favoured by diverse landscapes (Gardiner et al., 2009; Landis and Haas, 1992). Additional agricultural practices, not recorded in our study, such as the use of pesticides, may also vary between fields and dampen relationships between moth abundances and observed damage (Paredes et al., 2021). Nevertheless, maize appears to provide moth prey that benefit bats at the landscape level, possibly translating into a higher biological pest control by the same bats in the other adjacent crop types.

Our study illustrates that the diversification of agricultural landscapes to favour biological control can be thought of by taking advantage of the dominant crops in the landscapes, as an alternative to the introduction of new crop species, then without fundamentally modifying the local value chains (Vialatte et al., 2021). Our study is in line with the results of recent meta-analyses that show that crop diversification promotes biodiversity, biological control and yields (Beillouin et al., 2021; Paiola et al., 2020; Tamburini et al., 2020). It complements this work, which is largely dominated by intra-plot diversification by showing that crop diversification at the landscape scale is also a lever for biological control. While semi-natural elements in landscapes are widely known to support biodiversity and biological control (Dainese et al., 2019; Karp et al., 2018) and in particular by bats (Chaperon et al., 2022; Pedro et al., 2021) crop mosaics appear to be a complementary way of diversification. In the face of the risk of pest outbreaks associated with global warming (Klapwijk et al., 2012), our results open up avenues of alternative agroecological management to conventional agriculture for globally important crops such as maize (world's second cereal, FAOSTAT, 2020), planted forests (conifers account for more than 55% of the world's forest plantation resource) and grapevines (Brockerhoff et al., 2017; Hannah et al., 2013).

### 4.3. *Conservation implications*

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

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

Mata et al. (2021) showed that a limited number of bat species, consisting of both common species such as *P. pipistrellus* and conservation concern species, are central in pest interaction networks and could be the focus of conservation strategies. The results of our study support that enhancing crop diversity by combining agricultural fields and forestry and also other landscape elements such as linear features promote complementary and more stable resources (e.g. roost, foraging, commuting), which will benefit to a large range of bat species with some positive effects on biological control in crop fields.

## 5. Conclusion

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

## Declaration of Competing Interest

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

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108318.

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