



Assessing the importance of field margins for bat species and communities in intensive agricultural landscapes

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ABSTRACT

Landscape simplification and degradation through agricultural intensification is widely recognized as a main driver of biodiversity loss. In intensively used agricultural landscapes, patches of semi-natural habitats and particularly connections between them are of high importance for many taxa. Vegetated connections like hedgerows are especially important for foraging and commuting of mobile taxa such as bats. However, the interest of another treeless linear habitat – herbaceous field margins – remains unstudied for insectivorous bats. Field margins are nevertheless known as an important habitat for other taxa, including bat prey. Here we assessed the importance of field margins for bats compared to other landscape variables. We measured bat activity based on a repeated passive acoustic monitoring during 17 complete nights in summer on 112 study sites in an intensively used agricultural landscape. Each night, we sampled bat species activity and community metrics (i. e. species richness and community habitat specialization index) at different distances to field margins, and along a gradient of relative density of field margins. To compare field margin effects with other landscape variables, the sampled sites were selected by keeping a large variability in these other variables (land-cover Shannon diversity index, forests, hedgerows, water bodies, main roads, urban areas, grasslands, number of crops and rapeseed percentage). Only *Myotis* sp. were affected by herbaceous field margins. Specifically, the *Myotis* group activity decreased with the distance to herbaceous field margins (i.e. towards field crop cores), and positively correlated with relative density of herbaceous field margins, for which the effect size was comparable to other landscape variables. However, other landscape variables such as the proportion of and the distance to forests, the relative density of and the distance to hedgerows or land-cover Shannon diversity index, affected species richness, community specialization index, and bat activity of species from open, edge and narrow-space foragers, including the *Myotis* group as well. Our results highlight that herbaceous field margins have a positive effect on the activity of narrow-space bat foragers as *Myotis* species, but do not replace other landscape variables that drive the activity of the whole community.

1. Introduction

The global land area is dominated by agricultural landscapes (37%, World Bank Open Data; <https://data.worldbank.org/>), and the general trend towards the conversion of natural habitats into agricultural land is recognized as one of the main drivers of biodiversity decline (Maxwell et al., 2016). In addition to land conversion, landscape simplification appears to be a second process affecting biodiversity in agricultural landscapes. It consists in (i) a reduction of crop diversity within a

landscape, (ii) a decrease in diversity and amount of semi-natural habitats (e.g. ponds, small woodland, groves of trees, hedgerows, fallows), (iii) a progressive fragmentation of the remaining natural vegetation, and (iv) a removal of key structural elements (e.g. hedgerows; Benton et al., 2003; Gaston et al., 2003; Sirami et al., 2019). These changes lead to a reduction of crop varietal diversity and an intensification of farming practices (i.e. through tillage, fertilizer, pesticides; Robinson and Sutherland, 2002). Indeed, such changes are well known to deeply affect biodiversity by reducing the abundance and diversity of species (e.g.

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Peeters et al., 2004; Flynn et al., 2008; Flohre et al., 2011), their interactions (e.g. Tschamtko et al., 2005; Tamburini et al., 2016) and homogenizing communities towards those best adapted to poorly diversified and open landscapes (e.g. Filippi-Codaccioni et al., 2009; Ekroos et al., 2010). Thus, the more landscapes are intensively farmed, the more remaining patches of semi-natural habitats and connections between them by linear landscape elements (e.g. hedgerows, grass strips, wetlands) are of high importance for the persistence of many taxa (Michel et al., 2007; Diekötter et al., 2008; Schippers et al., 2008; Gil-Tena et al., 2014; Haenke et al., 2014; Correa Ayram et al., 2016).

Especially, linear landscape elements influence species dispersal across the farming matrix (Joyce et al., 2007; Runge et al., 2014), in particular for mobile species such as bats (Lookingbill et al., 2010; Boughey et al., 2011a, 2011b; Frey-Ehrenbold et al., 2013; Pinaud et al., 2018). Among studies dealing with the importance of linear habitats for bats, hedgerows have been identified as a key element because they provide prey insects and they also facilitate bat commuting across the farming matrix (Verboom and Huitema, 1997; Pinaud et al., 2018; Froidevaux et al., 2019).

Surprisingly, the importance of other treeless linear landscape elements such as herbaceous field margins for bats has received no attention. However, herbaceous field margins surrounding crops are linear habitats widely present in agricultural landscapes, and have been identified as a key habitat for numerous taxa of both flora and fauna, from arthropods to birds (Pffinner and Luka, 2000; Marshall and Moonen, 2002; Von Arx et al., 2002; Vickery et al., 2009). Indeed, spontaneous or sown herbaceous field margins host an important proportion of farmland plant diversity (Wuczyński et al., 2014), and many species of conservation concern had disappeared or seriously decreased in the field core but still persist in herbaceous field margins (Fried et al., 2009). Field margins also host a significant farmland insect diversity (Frouz and Paoletti, 2000; Meek et al., 2002; Olson and Wäckers, 2007; Smith et al., 2008; Smith et al., 2008; Merckx et al., 2009; Kuussaari et al., 2011). Through the diversity of plants and invertebrates they host, field margins provide a wide range of food resources for higher taxa in the food chain like birds in both summer and winter periods (Vickery et al., 2002; Wuczyński et al., 2014; Šálek et al., 2018). In addition, field margins are also known for playing a role as a refuge, a habitat and a corridor for small mammals (Hof et al., 2012; Redon (de) et al., 2015) and can even help to improve crop yields by providing natural pest control thanks to sheltered predators (Marshall and Moonen, 2002; Pywell et al., 2015). Nevertheless, the interest of herbaceous field margins for bats has not been assessed yet.

The aim of the study was to measure the role of herbaceous field margins for bats compared to other landscape variables in agricultural landscapes. Insectivorous bats forage arthropod orders (e.g. *Diptera*, moths; Vaughan, 1997) whose abundance is known to be enhanced with the presence of herbaceous field margins surrounding crops (Frouz and Paoletti, 2000; Meek et al., 2002; Olson and Wäckers, 2007; Merckx et al., 2009; Kuussaari et al., 2011). We therefore assume that herbaceous field margins are an interesting source of food for bats, as it is already documented for birds (Vickery et al., 2009). Thus, considering potential roles of herbaceous field margins for concentrating prey resources, we hypothesized that bat species activity or bat community diversity would be (i) higher close to herbaceous field margins compared to (crop) field cores and (ii) positively correlated with the density of herbaceous field margins. As bats have varied ecological requirements, they use landscape structures in different ways depending on their foraging and commuting strategies (Korine and Pinshow, 2004). In particular, narrow-space foragers fly very close to vegetation structures and can be distinguished from open-space foragers that tend to commute and forage further away in open space. Thus, we also hypothesize that the positive effect of herbaceous field margins would be stronger for narrow-space foragers, known to fly closer to vegetation and to mainly follow linear landscape habitats, as *Myotis* or *Plecotus* species do (Denzinger and Schnitzler, 2013). We finally expected that other

landscape variables, such as hedgerows, forests or water bodies, should have at least equivalent or even stronger effects on bat activity compared to herbaceous field margins, as these are widely recognized as strong drivers of the composition and activity of the entire bat community (e.g. Heim et al., 2017a, 2017b).

In order to assess the importance of herbaceous field margins for bats, we used passive acoustic sampling of bats in an intensive agricultural landscape by simultaneously recording species activity and community diversity at different distances to herbaceous field margins, and along a gradient of relative density of herbaceous field margins. We also compared respective effects of herbaceous field margins with other landscape variables.

2. Material and methods

2.1. Study area

The study was conducted in France, in the Île-de-France region (Yvelines, Essonne and Seine-et-Marne departments; Fig. 1a) in an intensively used agricultural landscape. This region is covered by 59% agricultural areas, 22% forests and semi natural areas, 18% artificial surfaces and 1% water bodies (Corine Land Cover data from 2016; <https://www.data.gouv.fr/en/datasets/corine-land-cover-occupation-des-sols-en-france>). The agricultural areas were dominated by arable land (90%) for intensive cropping (73% of rapeseed, 7% of wheat, 3% of barley, based on manual mapping during the experiment in a 100 m radius around sampling sites). Crops were harvested before the study between the end of June and the beginning of July.

We defined field margins as an herbaceous linear structure with only spontaneous vegetation, without fertilizers or pesticides immediately applied, without trees or bushes, 2 ± 1 m wide, and that were surrounding fields.

2.2. Sampling design

The aim of the study was to investigate the potential of field margins to support bat activity compared to other landscape variables in agricultural landscapes. As a consequence, we chose the location of sampling sites in a way that limited correlations between field margins and other landscape variables to avoid statistical issues (see Statistical analysis section), and to maximise the gradient of each (Table S1; see also Fig. S1 for more information about gradients of landscape variables). The weather was highly stable and favourable to bats throughout the sampling period (see Table S2). We recorded bat activity on 112 sampling sites along a gradient of distances from 0 to 447 m from field margins (median: 60 m, median absolute deviation: 57 m) and along a gradient of relative density of field margins ranging from 0 to 64 m/ha (computed in different sizes of buffers around sampling sites, from 250 m to 4,000 m, see Landscape variable and Statistical analysis sections for more details about buffer sizes) (Fig. S1a). Each night, we sampled simultaneously three to 11 sites at different densities of and distances from field margins (see Fig. 1b and c for examples of sampling nights and Table S3 for more details about the field margin gradient each night), in order to limit potential correlations with temporal variables (i.e. weather, moon). Each site was sampled one time and echolocation calls were recorded on sites separated by at least 230 m from each other to avoid simultaneous recordings (see acoustic sampling section). Recorders were associated with a single microphone throughout the study and were homogeneously distributed between distances to the field margin and relative densities of field margins, in order to limit potential correlations between recorders and field margins variables (Table S4).

2.3. Acoustic sampling

Sampling was carried out over 17 nights from the 8th of July to the 2nd of August 2015, during the seasonal peak in bat activity. Recordings

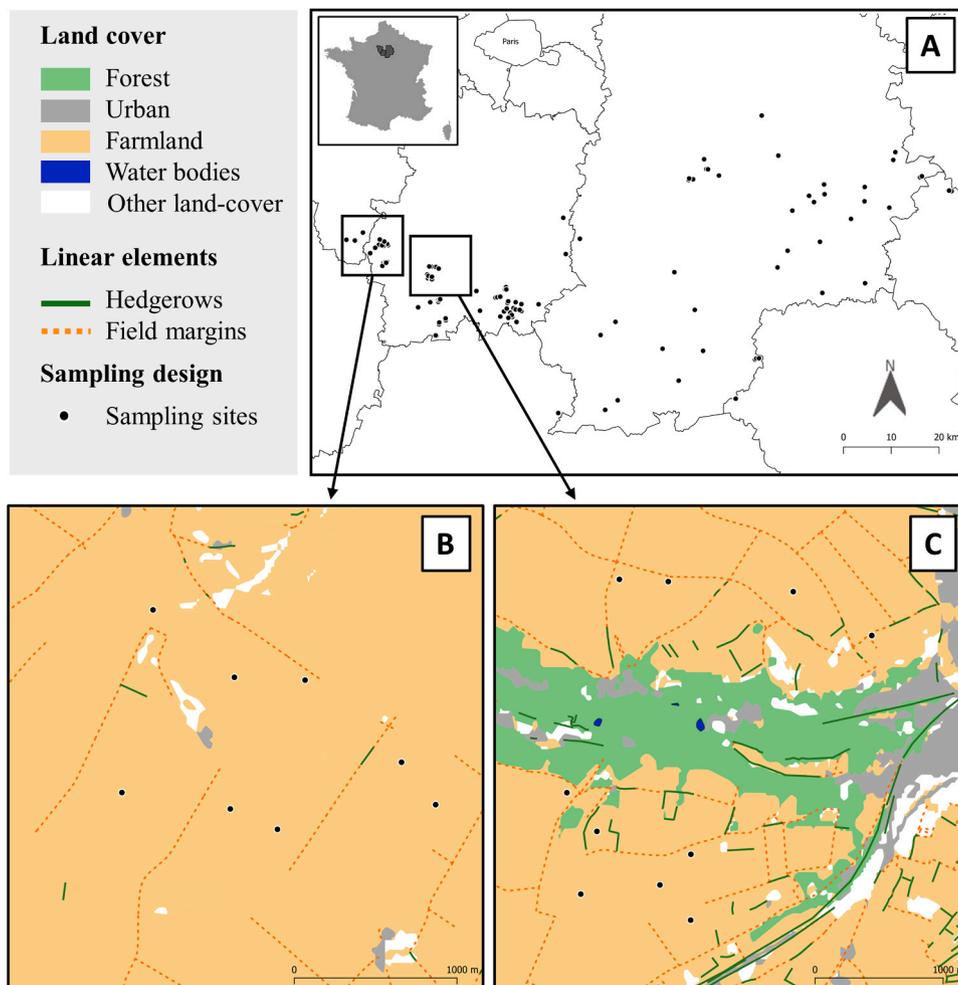


Fig. 1. Land cover map of the study area showing sampled sites (A) and examples of two sampling nights: one in a low diversified landscape (land-cover Shannon diversity index of 0.07; B) and one in a more diversified landscape (land-cover Shannon diversity index of 1.08; C).

were performed during the entire night, from 30 min before sunset to 30 min after sunrise. Standardized acoustic bat survey was carried out using Song Meter SM2Bat+ and omnidirectional microphones SMX-US (Wildlife Acoustics Inc., Concord, MA, USA) put horizontally at one meter above the ground on a pole and pointed perpendicularly to the field margin. Recording was triggered automatically by ultrasounds between eight and 192 kHz, using a trigger level set to 6 dB Signal Noise Ratio and set to continue recording until two seconds after last trigger event, and a 384 kHz sampling rate, as widely used in many previous studies (e.g. Azam et al., 2016; Barré et al., 2017, 2019).

As it is currently impossible to distinguish individual bats from their echolocation calls, it is not possible to count bat abundance. Instead, we used the number of bat passes recorded during a night as a measure of bat activity (however this metric is correlated to the abundance, see Mimmet et al., 2020). We defined a bat pass as one or more echolocation call within a 5-second interval, which is a commonly accepted standard in Europe (Stahlschmidt and Brühl, 2012; Millon et al., 2015; Kerbiriou et al., 2018a, 2018b, 2019; Put et al., 2019).

We used the software TADARIDA (Bas et al., 2017) to automatically detect sound events and assign bat passes (11,324 bat passes for a total of ~450,000 calls) to the most accurate taxonomic level associated to a confidence score calculated by the software (i.e. the probability that a bat pass has been assigned to the right species). Two species groups were firstly constructed in order to limit identification errors: (i) a *Myotis* group (including *Myotis nattereri*, *Myotis myotis*, *Myotis mystacinus* and *Myotis daubentonii*) and (ii) a *Plecotus* group (including *Plecotus austriacus* and *Plecotus auritus*). In addition to these species-groups, we

considered four species: (i) *P. pipistrellus* that are edge space foragers, (ii) *Nyctalus leisleri* and (iii) *Nyctalus noctula* that are open space foragers, and (iv) *Eptesicus serotinus*, that are edge space foragers (Robinson and Stebbins, 1997).

Given that automated identification can generate high error rates at species level, we followed the Barré et al. (2019) approach proposing a cautious method to ensure results robustness against automated identification errors. The method allows to model the error rate for each species or group, according to confidence scores of automated identifications provided by the software TADARIDA (Bas et al., 2017). This method allows to perform statistical analyses based on two levels of maximum error rate tolerance: first on a 0.5 maximum error rate tolerance and then by confirming results on a safer threshold of 0.1 maximum error rate tolerance. Indeed, each threshold of error rate tolerated in data involve different caveats which potentially induce biases in acoustic data (i.e. false positives and false negatives). The 0.5 maximum error rate tolerance keeps high number of bat passes for analysis including false positives, while a more restrictive 0.1 threshold limits false positives, but at the cost of discarding more true positives, which thus induce a loss of statistical power. As a consequence, checking the consistence in results whatever the threshold considered ensures robust conclusions (see Barré et al. 2019 for more details).

2.4. Computing community metrics

In addition to bat species activity (i.e. a relative abundance metric), we used community metrics: the species richness and the community

specialization index (CSI). Both metrics were calculated from species level activity.

The species richness was computed as the total number of species recorded during one sampled night for each site.

The CSI follows a community trait-based approach already used for bats (Regnery et al., 2013; Kerbiriou et al., 2018a, 2018b; Lacoëuilhe et al., 2018). It is calculated as the arithmetic mean of the 'Species Specialization Index' (SSI) weighted by the standardized number of bat species passes (Eq. (1)), as follows:

$$CSI_j = \frac{\sum_{i=1}^n a_{ij}(SSI_i)}{\sum_{i=1}^n a_{ij}} \quad (1)$$

where n is the total number of species recorded, a_{ij} is the number of bat passes of the species in a given site j , and SSI_i is the species specialization index.

The SSI is computed as the coefficient of variation of the number of bat passes across 20 habitat classes over France (ratio of the standard deviation to the mean, expressed as a percentage; Julliard et al., 2006). A high SSI corresponds to a species specialized to a specific habitat, and in turn a high CSI means that the community tends to be composed of species specialized to a specific habitat. For the calculation we used data based on 3,596 sites from the French Bat Monitoring Program (<http://www.vigienature.fr/fr/chauves-souris>), for more details on SSI calculation see Supplementary material S1.

2.5. Landscape variables

In order to assess the effect of field margin distance and density on bat activity in comparison with other landscape variables, we focused on the importance of six landscape variables known to affect bat activity: hedgerows (Lacoëuilhe et al., 2016; Froidevaux et al., 2017), forests (Boughey et al., 2011a, 2011b; Heim et al., 2017a, 2017b), water bodies (Sirami et al., 2013; Heim et al., 2017a, 2017b; Conno (De) et al., 2018), main roads (Berthinussen and Altringham, 2012; Fensome and Mathews, 2016), urban areas (Dixon, 2012; Azam et al., 2016), grassland (Lentini et al., 2012; Roeleke et al., 2016; Froidevaux et al., 2017). These variables are reported as key habitats for bats by facilitating foraging or commuting between foraging sites and roosts (Charbonnier et al., 2014; Pinaud et al., 2018). We distinguish main roads from field margins, which can also be on the edge of dirt pathways or between two crops.

We computed environmental variables using (i) the Euclidean distance in meters from the sampling site to the nearest hedgerow, forest, main road, urban area and water body, (ii) the relative density of a linear element in meters per hectare for hedgerows and main roads, and (iii) the percentage of land covered by forests, urban areas and grasslands in different buffer sizes (see below). Variables on forests, grasslands, urban areas and water bodies were calculated from the CES OSO land cover map 2016 (Derksen et al., 2020) and main road variables from the French National Institute of Geography (www.ign.fr; BD CARTO map) using R and QGIS 3.10 software. Hedgerows and field margins data were provided by the French Institute of Development and Urbanism of the Ile-de-France region (www.iau-idf.fr; ECOLINE map), and were validated by checking of aerial images and completed manually if needed. In addition, with the aim to take into account landscape diversity, we computed a land-cover Shannon diversity index known to affect bat activity in agricultural contexts (Monck-Whipp et al., 2018), calculated from water bodies, urban, forests, grasslands, arable lands, orchard/vineyard and moorlands cover (i.e. all land cover habitats available from CES OSO map). Depending on the context, Shannon's index applied to landscape metrics can be used as a fragmentation metric (Su et al., 2014) or as a diversity metric (Li et al., 2005). As the study area was an intensive agricultural landscape, crops covered the biggest part of land around each sampling site. Thus, in our study case, we interpreted an increase of land-cover Shannon diversity index (e.g. by switching from the landscape in Fig. 1b to the landscape in Fig. 1c) as an increased of

semi-natural habitat amount and diversity in the landscape. Furthermore, we added two other supplementary covariates to account for the agricultural context: the number of different crops and the percentage of rapeseed crops. These two variables were manually mapped during the experiment in a 100 m radius around each site at the sampling date. Concerning the rapeseed percentage, we choose to include it as this was the highly dominant crop type around sampling sites ($73.30 \pm 35.97\%$) known to concentrate much more *diptera* that are widely consumed by bats (Vaughan, 1997) than other types of crops (Holland et al., 2012).

Given that bat response to landscape variables at different scales (e.g. Boughey et al., 2011a, 2011b; Kalda et al., 2015; Lacoëuilhe et al., 2016; Put et al., 2019), we computed the land-cover Shannon diversity index, density and proportion variables at 250, 500, 750, 1000, 1,500, 2,000 and 4,000 m radii around each sampling site. The 250 m radius was the smallest one maintaining enough variability to perform analysis, while the 4,000 m one covered the foraging area of the most common bat species *Pipistrellus pipistrellus* (Nicholls and Racey, 2006). Thus, the land-cover Shannon diversity index and each density and proportion variables were calculated on seven buffer sizes for each sampling site (Table S1), in order to use the best scale for each variable in statistical analysis (see statistical analysis section). According to Zuckerman et al. (2020) the risk of pseudo-replication related to this method due to potential overlapping landscapes between sites does not constitute a violation of independence.

2.6. Statistical analysis

We performed generalized linear mixed models (GLMM, R package *lme4*) to test for potential differences in bat activity among a continuous gradient of distances to field margins and relative density of field margins. We also tested for landscape composition (see Sampling design and Landscape variables sections for a description of gradients). We built full models using bat activity (i.e. the number of bat passes) as response variable for each group or species, associated to a negative binomial error distribution in order to avoid overdispersion (the ratio of deviance to the number of degrees of freedom was between 0.82 and 1.20 for full models). As the distance to field margins and the relative density of field margins were correlated (r spearman = -0.6) we built for each species two full models, one (i) including the distance to field margins as fixed effect and another (ii) including the relative density of field margins as fixed effect. For both, we included standardized (i.e. by subtracting the mean and dividing by the standard deviation) landscape covariates (i.e. water bodies, hedgerows, main roads, grasslands, forests, urban areas, rapeseeds, number of different crops and land-cover Shannon diversity index variables). For each of these variables and each group or species we previously selected the radius having the smaller corrected Akaike Information Criterion (AICc) using univariate GLMMs, in order to include only one scale of each variable in full models. We also checked the potential need for adding quadratic effect by visual inspection of generalized additive models, i.e. in case of non-linear relationship (GAM, R package *mgcv*; see Tables 1 and 2 for variables which required

Table 1

Number of bat passes per species/groups and the corresponding percentage of total passes and occurrences (i.e. percentage of sites with at least one bat pass of the considered species) according to the maximum error risk tolerance applied for data selection (maximum error risk tolerance of 0.5 and 0.1).

Species	Number of passes recorded		% of total passes		Occurrence (%)	
	0.5	0.1	0.5	0.1	0.5	0.1
<i>Pipistrellus pipistrellus</i>	8,039	7,215	81	86	92	91
<i>Nyctalus leisleri</i>	531	433	5	5	45	39
<i>Myotis</i> sp.	305	205	3	2	45	34
<i>Eptesicus serotinus</i>	397	247	4	3	43	33
<i>Nyctalus noctula</i>	166	136	2	2	35	31
<i>Plecotus</i> sp.	56	23	< 1	< 1	27	13

Table 2

Results of the relationship between the number of bat passes and the distance to field margins or the relative density of field margins and other landscape covariates, using a multi-model inference averaging of candidate models in a delta AICc < 2.

Variables	Distance to field margin model			Relative density of field margin model		
	Estimate ± SE	p-value	Relative importance value	Estimate ± SE	p-value	Relative importance value
<i>Eptesicus serotinus</i>						
Intercept	-0.345 ± 0.590	0.559		-0.340 ± 0.590	0.564	
Distance to field margin	0.186 ± 0.175	0.289	0.08			
Distance to water bodies	-0.137 ± 0.169	0.417	0.06	-0.137 ± 0.169	0.417	0.07
Distance to hedgerow	0.197 ± 0.180	0.274	0.63	0.196 ± 0.181	0.280	0.60
Distance to main road	-0.069 ± 0.146	0.635	0.30	-0.069 ± 0.146	0.635	0.33
Distance to forest	-1.665 ± 0.522	0.001	1.00	-1.682 ± 0.524	0.001	1.00
Distance to forest ²	1.123 ± 0.404	0.005	1.00	1.137 ± 0.406	0.005	1.00
Distance to urban area	0.304 ± 0.180	0.092	0.86	0.298 ± 0.180	0.099	0.85
Relative density of hedgerow - 750 m	-0.174 ± 0.202	0.390	0.37	-0.174 ± 0.202	0.390	0.40
Relative density of main roads - 4000 m	0.148 ± 0.170	0.382	0.70	0.146 ± 0.171	0.392	0.67
Urban area land cover - 500 m	0.247 ± 0.191	0.195	0.14	0.247 ± 0.191	0.195	0.15
Grassland land cover - 4000 m	0.136 ± 0.167	0.414	0.06	0.136 ± 0.167	0.414	0.07
Land-cover Shannon diversity index - 250 m	0.687 ± 0.825	0.405	0.68	0.641 ± 0.839	0.445	0.65
Land-cover Shannon diversity index ² -250 m	-1.394 ± 0.651	0.032	0.55	-1.386 ± 0.656	0.035	0.51
<i>Myotis</i> group						
Intercept	-0.062 ± 0.265	0.814		-0.150 ± 0.196	0.445	
Distance to field margin	-0.626 ± 0.226	0.006	1.00			
Distance to hedgerow	-0.534 ± 0.255	0.036	1.00	-1.139 ± 0.685	0.097	1.00
Distance to hedgerow ²				1.137 ± 0.666	0.088	0.57
Distance to forest	-0.543 ± 0.318	0.087	0.73	-0.857 ± 0.273	0.002	1.00
Distance to urban area				0.192 ± 0.191	0.315	0.23
Relative density of field margins - 250 m				0.656 ± 0.191	< 0.001	1.00
Relative density of main roads - 1, 000 m	0.476 ± 0.179	0.008	1.00	0.394 ± 0.153	0.010	1.00
Urban area land cover - 250 m				-0.144 ± 0.139	0.298	0.23
Land-cover Shannon diversity index - 500 m	1.830 ± 0.626	0.003	1.00			
Land-cover Shannon diversity index ² -500 m	-1.531 ± 0.566	0.007	1.00			
Rapeseed percentage	-0.382 ± 0.250	0.127	0.53	-0.346 ± 0.167	0.038	0.91
Number of different crops	-0.389 ± 0.267	0.145	0.35			
<i>Nyctalus leisleri</i>						
Intercept	-0.013 ± 0.583	0.982		-0.017 ± 0.581	0.977	
Distance to field margin	0.229 ± 0.151	0.129	0.43			
Distance to water bodies	-0.120 ± 0.158	0.448	0.08	-0.102 ± 0.158	0.520	0.07
Distance to forest	-1.087 ± 0.389	0.005	1.00	-1.101 ± 0.386	0.004	1.00
Distance to forest ²	0.970 ± 0.301	0.001	1.00	0.976 ± 0.300	0.001	1.00
Relative density of hedgerow - 2000 m	-0.133 ± 0.158	0.400	0.12	-0.093 ± 0.159	0.560	0.07
Relative density of main roads - 750 m	0.067 ± 0.126	0.595	0.04	0.067 ± 0.126	0.595	0.07
Grassland land cover - 4000 m	0.159 ± 0.165	0.337	0.10	0.154 ± 0.167	0.359	0.09
Land-cover Shannon diversity index - 250 m	0.236 ± 0.161	0.143	0.40	0.210 ± 0.161	0.190	0.31
Rapeseed percentage	-0.337 ± 0.161	0.037	0.82	-0.334 ± 0.167	0.045	0.78
Number of different crops	0.251 ± 0.162	0.121	0.32	0.257 ± 0.163	0.114	0.40
<i>Nyctalus noctula</i>						
Intercept	-0.556 ± 0.459	0.226		-0.483 ± 0.425	0.256	
Distance to field margin	0.441 ± 0.240	0.066	0.70			
Distance to water bodies	-0.684 ± 0.236	0.004	1.00	-0.686 ± 0.245	0.005	1.00
Distance to main road	-0.261 ± 0.189	0.169	0.29	-0.230 ± 0.196	0.239	0.22
Distance to urban area				-0.115 ± 0.194	0.555	0.05
Relative density of hedgerow - 250 m	-1.235 ± 0.541	0.022	1.00	-1.268 ± 0.558	0.023	1.00
Relative density of hedgerow ² -250 m	1.284 ± 0.488	0.009	1.00	1.284 ± 0.508	0.011	1.00
Relative density of main roads - 4000 m	0.337 ± 0.261	0.196	0.22	0.346 ± 0.271	0.201	0.26
Forest land cover - 500 m	0.584 ± 0.232	0.012	0.82	0.524 ± 0.233	0.025	0.65
Urban area land cover - 250 m	0.318 ± 0.212	0.133	0.36	0.301 ± 0.236	0.203	0.36
Land-cover Shannon diversity index - 250 m	0.627 ± 0.220	0.004	0.18	0.527 ± 0.237	0.026	0.29
<i>Pipistrellus pipistrellus</i>						
Intercept	3.831 ± 0.269	< 0.001		3.830 ± 0.270	< 0.001	
Distance to hedgerow	-0.299 ± 0.107	0.005	1.00	-0.296 ± 0.106	0.005	1.00
Distance to main road	0.051 ± 0.094	0.591	0.24	0.050 ± 0.094	0.593	0.28
Distance to forest	-0.442 ± 0.291	0.128	0.87	-0.501 ± 0.289	0.084	0.91
Distance to forest ²	0.458 ± 0.235	0.051	0.74	0.491 ± 0.240	0.041	0.83
Distance to urban area	-0.117 ± 0.111	0.292	0.21	-0.115 ± 0.111	0.299	0.21
Relative density of field margins - 1000 m				-0.135 ± 0.101	0.181	0.35
Relative density of main roads - 2000 m	-0.136 ± 0.123	0.269	0.76	-0.131 ± 0.123	0.288	0.72
Forest land cover - 250 m	0.056 ± 0.103	0.583	0.13	0.056 ± 0.103	0.583	0.09
Urban area land cover - 1500 m	-0.172 ± 0.117	0.141	0.79	-0.186 ± 0.118	0.114	0.79
Grassland land cover - 4000 m	0.266 ± 0.122	0.029	1.00	0.270 ± 0.121	0.026	1.00
Rapeseed percentage	-0.345 ± 0.132	0.009	1.00	-0.345 ± 0.132	0.009	1.00
<i>Plecotus</i> group						
Intercept	-1.130 ± 0.217	< 0.001		-1.118 ± 0.216	< 0.001	
Distance to field margin	0.227 ± 0.170	0.182	0.32			
Distance to hedgerow	-0.383 ± 0.212	0.071	0.75	-0.384 ± 0.210	0.068	0.79
Distance to main road	0.413 ± 0.747	0.581	0.20	-0.206 ± 0.191	0.280	0.12
Distance to main road ²	-1.173 ± 0.855	0.170	0.12			

(continued on next page)

Table 2 (continued)

Variables	Distance to field margin model			Relative density of field margin model		
	Estimate \pm SE	p-value	Relative importance value	Estimate \pm SE	p-value	Relative importance value
Relative density of field margins - 750 m				-0.155 \pm 0.180	0.390	0.18
Relative density of main roads - 750 m	0.251 \pm 0.173	0.148	0.24	0.255 \pm 0.176	0.147	0.38
Forest land cover - 250 m	0.502 \pm 0.346	0.146	1.00	0.372 \pm 0.143	0.009	1.00
Forest land cover ² -250 m	-0.525 \pm 0.378	0.165	0.25			
Urban area land cover - 2000 m	-0.689 \pm 0.296	0.020	1.00	-0.682 \pm 0.295	0.021	1.00
Grassland land cover - 4000 m	0.399 \pm 0.165	0.016	1.00	0.384 \pm 0.165	0.020	1.00
Rapeseed percentage	0.130 \pm 0.207	0.530	0.05	0.130 \pm 0.207	0.530	0.08

For each group or species estimates from scaled variables, associated standard errors (SE), significance and relative importance value are shown. Distances are in meters, relative density in meters per hectare and habitat land cover in percentage. Variables not presented were not selected in the multi-model inference averaging. Significant effects are shown in bold.

quadratic effects). According to the sampling design (i.e. simultaneous recordings of bat activity at 3–11 sites on the same night), we included the date in models as a random effect to account for inter-night variations. For each landscape covariate we never included distance and proportion/density variations of the same variable in the same models as they were highly correlated (i.e. an $r > 0.7$ for forests, main roads, urban areas and hedgerows; see Table S5). We also checked for Spearman correlations between covariates (Table S5), and we never included simultaneously in the model two variables with an $r > 0.7$. In addition, no variable was correlated with the sampling date (Table S5). Then, we checked for multicollinearity problems by calculating variance inflation factors (VIF) using the *check_collinearity* function (R package *performance*) on each full model. All variables showed a VIF value < 2 , meaning there was no evidence of multicollinearity (Chatterjee and Hadi, 2015). These steps allowed to build two full models (i.e. one including the distance to field margins and another including their relative density) per group or species.

Based on each full model, we generated a set of candidate models containing all possible variable combinations ranked by corrected Akaike Information Criterion (AICc) using the *dredge* function. It should be noted that while we used the *dredge* function, we did not follow a “data dredging” approach, because we initially used variables known to drive bat activity from literature while selecting their more relevant scale of computing. Variables and their scale of computing were thus not randomly selected. So, we used the *dredge* function in our workflow in order to (i) never simultaneously include together correlated covariates mentioned above in a same model, (ii) avoid overparameterization due to a limited dataset (112 sites) by forcing each candidate model not to exceed ten degrees of freedom. Then, if spatial autocorrelation in residuals of each best model (R package *spatial*, Moran’s I test) was detected, we took it into account by adding a spatial correction variable to the full model (*autocov_dist* function, R package *spatial*). For each set of candidate models, we did multi-model inference averaging on a delta AICc < 2 using the *model.avg* function to obtain an averaged regression coefficient, associated standard error and p-value for each fixed effect (R package *MuMIn*; Barton, 2015). From multi-model inference averaging we also extracted the relative importance value for each variable defined as the sum of model weights over all candidate models including the variable (Barton, 2015). All averaged candidate models always had much lower AICc than null models (i.e. a difference of 8–52 points between candidate models AICc and null models AICc; Table S6). We compared effect size of field margins with other variables when significant using estimates from models. We only compared comparable variables, i.e. the relative density of field margins with other density/proportion variables having comparable gradients (Fig. S1).

Finally, in order to check if results were the same when considering constant radius size for variables calculation instead of best ones based on AIC, we re-ran analysis for species significantly affected by field margins by fixing calculation of each landscape covariates at the same buffer size as the relative density of field margin. Although we carried out the study in a way that limited biases (i.e. under stable and favourable weather conditions (Table S2) which were accounted for by

including date as a random effect, and by randomizing bat recorder identifier throughout the field margin gradient (Table S4)), we re-ran the modelling procedure by including recorder identifier as a random effect and the maximum wind speed and minimum temperature as fixed effects to ensure these do not change results. All analyses were performed using a significant threshold of 5% in R statistical software v.3.6.2.

3. Results

Results presented below are based on the 0.5 maximum error rate tolerance threshold and are consistent when applying a 0.1 threshold (Tables S7 and S8).

3.1. Bat monitoring

We recorded 11,445 bat passes in the 112 study sites. The most abundant species was *P. pipistrellus*, representing 81% of the total activity and occurring in 92% of sites. Other groups or species were less abundant, each of them having an activity representing less than 6% of the total bat activity. *N. leisleri* and the *Myotis* group were detected in 45% of sites and *E. serotinus*, *N. noctula* and *Plecotus* group in 43%, 35% and 27% of sites, respectively (Table 1). Across all sites, the mean species richness was 4.8 (standard deviation: 2.6).

3.2. Effect of distance to field margins

The activity of the *Myotis* group decreased with the distance to field margins (Table 2; Fig. 2). Models detected a 50% loss of the *Myotis* group activity at 117 m compared to 0 m from field margins, while this distance was 303 m when we looked at the *Myotis* group response to hedgerows (Table 2; Fig. S2). The community metrics and the activity of species other than *Myotis* sp. were not affected by field margins (Tables 1 and 2). Except for the *Myotis* group, the distance to field margins exhibited low relative importance values, and was thus rarely selected in candidate models with higher Akaike weights (Tables 1 and 2).

3.3. Effect of relative density of field margins

We found a significant positive effect of the relative density of field margins on the activity of the *Myotis* group while no effect was found for the other species and community metrics (Tables 1 and 2; Fig. 2). Except for *Myotis* group, the relative density of field margins variable exhibited low relative importance values and was thus little selected in candidate models (Tables 1 and 2).

The effect size of the relative density of field margins for the *Myotis* group was higher than other density or proportion of other landscape variables (i.e. the relative density of main roads, the proportion of urban areas and the rapeseed percentage) (Table 1; Fig. 3).

When all proportion and density covariates were fixed to the same buffer size as the best one selected for the relative density of field margins, results (i.e. model estimates) were the same as those for which

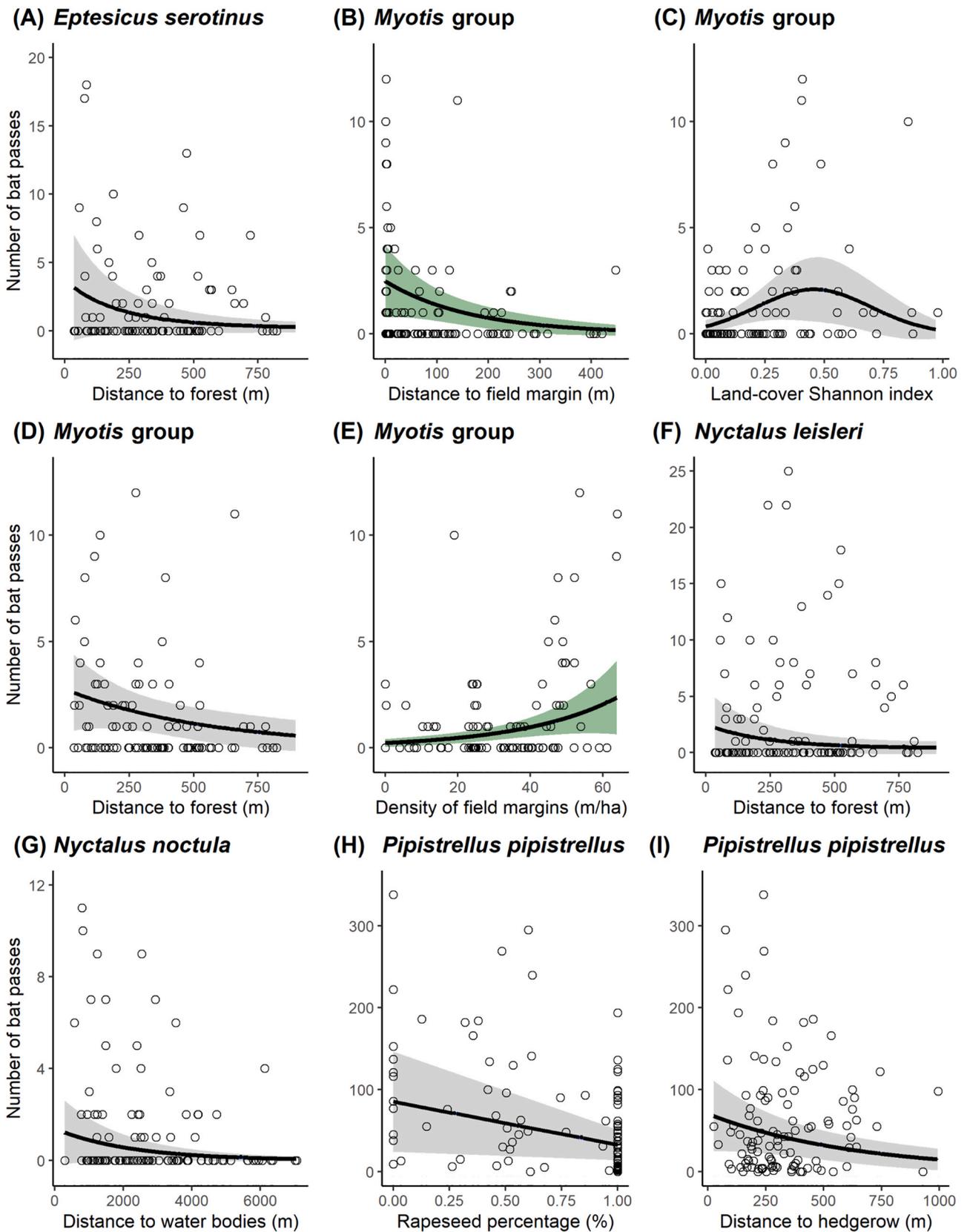


Fig. 2. Predicted relationships between the number of bat passes per night and the distance to field margins (B), the relative density of field margins in a 250 m buffer size (E) and others significant environmental covariates with a p-value < .01 (A, C-D, F-I) for *E. serotinus* (A), *Myotis* group (B-E), *N. leisleri* (F), *N. Noctula* (G) and *P. pipistrellus* (H-I); and associated 95% confidence intervals from best models of the multi-model inference averaging. Green plots show results on field margins.

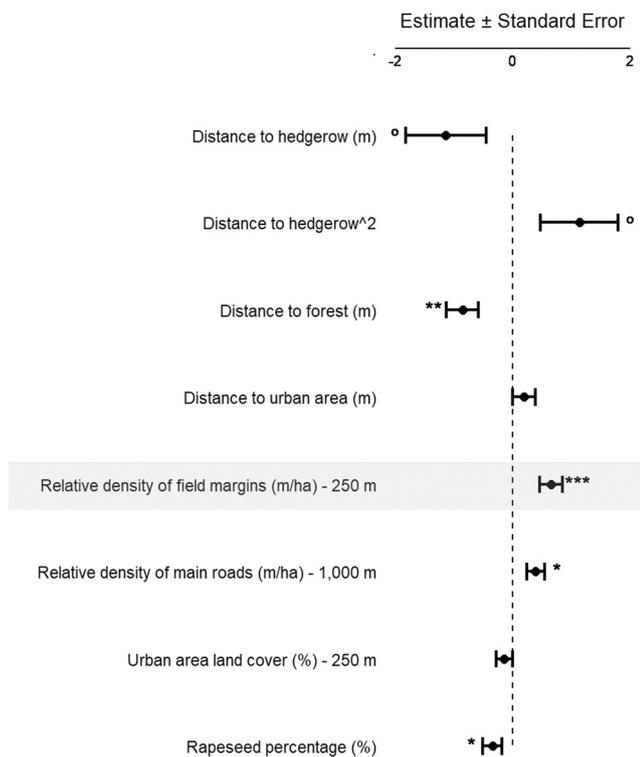


Fig. 3. Results of the effect of the relative density of field margins and other environmental covariates on the activity of *Myotis* group. Estimates, standard errors and p-values (*** $p < .001$, ** $p < .01$, * $p < .05$, ° $p < .1$) come from an averaging of candidate models with a delta AICc < 2 using the procedure of multi-model inference averaging (see Statistical analysis section for more details).

variables were calculated in the most appropriate buffer size (Table S9).

3.4. Effect of other environmental covariates

Concerning the influence of the other landscape covariates on open-space forager activity, *N. noctula* activity decreased with the distance to water bodies and the density of hedgerows, while we found the activity of this species increased with the proportion of forest land cover and the land-cover Shannon diversity index (Table 2; Fig. 2). *N. leisleri* and *E. serotinus* activity decreased with the distance to forests and the rapeseed percentage, while *E. serotinus* activity increased with the land-cover Shannon diversity index (Table 2; Fig. 2).

Concerning the influence of these landscape variables on the activity of edge-space foragers, *P. pipistrellus* activity decreased with the distance to hedgerow, the distance to forest and the rapeseed percentage while we found the activity of this species increased with the proportion of grassland land cover (Table 2; Fig. 2).

We found narrow-space foragers activity to be also affected by these landscape variables, given that the *Myotis* group activity decreased with the distance to forests, the distance to hedgerows and the rapeseed percentage (Table 2; Fig. 2). We also found that the *Plecotus* group activity decreased with the proportion of urban land cover and increased with the proportion of grassland land cover (Table 2). Finally, we found that the *Myotis* group activity increased with the land-cover Shannon diversity index and the relative density of main roads (Table 2; Fig. 2).

Concerning community metrics, we found that the Community Specialization Index increased with the proportion of forest land cover, the distance to hedgerow and the land-cover Shannon diversity index, and decreased with the proportion of grassland cover (Table 3; Fig. 4). We also found that the species richness increased with the proportion of forest land cover, the land-cover Shannon diversity index and is

maximised by a balanced percentage of rapeseed (~50%), and decreased with the distance to water bodies and hedgerows (Table 3).

Regarding the overall bat community, some landscape covariates such as those related to forests, hedgerows or land-cover Shannon diversity index almost systematically exhibited high relative importance values, and were thus often selected in candidate models unlike field margin variables (Tables 1 and 2). In addition, these variables also almost systematically drove bat activity, species richness and community specialization index: forests significantly affected four out of six species and both community metrics, hedgerows and land-cover Shannon diversity index significantly affected three out of six species and both community metrics (Tables 1 and 2).

Finally, including recorder identifier as a random effect and the maximum wind speed and minimum temperature as fixed effects did not change results (Table S10).

4. Discussion

Among six species-group's activity levels and two community metrics, we only found an effect of field margins on the activity of the *Myotis* group (i.e. narrow-space foragers). Specifically, the *Myotis* group activity decreased with distance to field margins (i.e. towards field crop cores), and increased with relative density of field margins. These responses had a comparable or even a higher effect size than other landscape variables such as the distance to forest, the relative density of main roads, the proportion of urban areas or the rapeseed percentage. However, results also showed that unlike field margins, other landscape covariates such as forests, hedgerows or land-cover Shannon diversity index almost systematically drove bat activity, species richness and community specialization index. Our results thus highlight that herbaceous field margins can have a positive effect on the activity of narrow-space bat foragers, but do not replace other landscape variables that almost systematically drive bat activity, community richness and specialization of bat community to specific habitat.

Even though results about the relative density of field margins were highly consistent when we checked it at the lower maximum error rate tolerance in data, the effect of the distance to field margins switched from a significant to a close to the significant p-value. We thus have to be cautious with these results as the change in p-value could either be due to an environmental bias in our acoustic data or to a too great loss of occurrence when applying the maximum error rate tolerance of 0.1 (Barré et al., 2019) which discarded one third of passes in this study. Thus, the effect of the distance to field margins on the activity of the *Myotis* group should be confirmed in further studies with greater data set.

4.1. Mechanism hypotheses and limitations

The effect of herbaceous field margins on bats was so far unknown. We only found an effect for the *Myotis* group, which mostly commute and forage by flying close to semi-natural habitats (Denzinger and Schnitzler, 2013; Roemer et al., 2019). To explain this response, we could hypothesize that herbaceous field margins can increase the abundance of prey such as moths (Merckx et al., 2009; Kuussaari et al., 2011) or *Coleoptera* (Smith et al., 2008), which are consumed by *Myotis* species (Vaughan, 1997; Ware et al., 2020). However, such prey are also widely consumed by other bat species, especially *Plecotus* group. Further studies are thus needed to understand why we did not detect any effect on this genus.

A second hypothesis to explain these field margins effects could be that the presence of field margins mostly induces a physical break between field crops and other landscape elements. Indeed, when a field margin is located at the edge of a crop there is potentially a difference in vegetation height between these two elements, which generates a relief that could facilitate orientation by echolocation for bats that would in turn move along it. This is especially true for narrow-space foragers,

Table 3

Results of the relationship between community metrics and the distance to field margins or the relative density of field margins and other landscape covariates, using a multi-model inference averaging of candidate models in a delta AICc < 2.

Variables	Distance to field margin model			Relative density of field margin model		
	Estimate ± SE	p-value	Relative importance value	Estimate ± SE	p-value	Relative importance value
<i>Community Specialization Index</i>						
Intercept	0.068 ± 0.006	< 0.001		0.068 ± 0.006	< 0.001	
Distance to hedgerow	0.003 ± 0.004	0.553	0.53	0.026 ± 0.014	0.057	0.95
Distance to hedgerow ²				-0.026 ± 0.013	0.038	0.89
Distance to main roads	0.001 ± 0.004	0.823	0.35	0.000 ± 0.004	0.950	0.70
Distance to forests				0.001 ± 0.004	0.781	0.45
Distance to urban area	-0.001 ± 0.004	0.729	0.13	-0.002 ± 0.004	0.566	0.45
Relative density of field margins - 4000 m				0.005 ± 0.004	0.238	0.15
Relative density of hedgerows - 4000 m	0.002 ± 0.004	0.683	0.47	0.001 ± 0.004	0.864	0.05
Relative density of main roads - 250 m	-0.004 ± 0.004	0.344	0.65	-0.004 ± 0.004	0.366	0.70
Forest land cover - 2000 m	0.015 ± 0.005	0.002	1.00	0.013 ± 0.005	0.007	0.55
Urban area land cover - 2000 m	0.005 ± 0.004	0.175	0.87	0.006 ± 0.004	0.110	0.55
Grassland land cover - 1000 m	-0.014 ± 0.004	0.001	1.00	-0.025 ± 0.014	0.064	1.00
Grassland land cover ² - 1000 m				0.018 ± 0.010	0.076	0.64
Landcover Shannon diversity index - 2000 m				0.022 ± 0.005	< 0.001	0.45
Rapeseed percentage	0.006 ± 0.004	0.186	0.36	0.005 ± 0.004	0.219	0.18
<i>Species richness</i>						
Intercept	4.209 ± 0.440	< 0.001		4.205 ± 0.437	< 0.001	
Distance to water bodies	-0.399 ± 0.202	0.048	0.84	-0.392 ± 0.201	0.051	0.86
Distance to hedgerow	-0.368 ± 0.172	0.033	1.00	-0.368 ± 0.172	0.033	1.00
Distance to forest	-0.233 ± 0.190	0.220	0.90	-0.233 ± 0.189	0.218	0.91
Relative density of field margins - 250 m				0.169 ± 0.177	0.339	0.11
Relative density of main roads - 750 m	0.249 ± 0.160	0.120	1.00	0.248 ± 0.160	0.122	1.00
Forest land cover - 500 m	0.540 ± 0.179	0.003	0.10	0.540 ± 0.179	0.003	0.09
Urban area land cover - 4000 m	-0.442 ± 0.237	0.062	1.00	-0.455 ± 0.239	0.057	1.00
Grassland land cover - 4000 m	0.455 ± 0.246	0.065	0.72	0.463 ± 0.248	0.062	0.75
Landcover Shannon diversity index - 500 m	0.519 ± 0.196	0.008	0.90	0.512 ± 0.198	0.010	0.91
Rapeseed percentage	1.398 ± 0.703	0.047	0.35	1.398 ± 0.703	0.047	0.31
Rapeseed percentage ²	-1.553 ± 0.724	0.032	0.35	-1.553 ± 0.724	0.032	0.31

For each group or species estimates from scaled variables, associated standard errors (SE), significance and relative importance value are shown. Distances are in meters, relative density in meters per hectare and habitat land cover in percentage. Variables not presented were not selected in the multi-model inference averaging. Significant effects are shown in bold.

which fly closer to vegetated structures (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013) and preferentially use linear structures to move from one habitat patch to another (Frey-Ehrenbold et al., 2013; Pinaud et al., 2018), and rarely fly over crop field cores (Wickramasinghe et al., 2003).

For the *Plecotus* group, which consists of narrow-space foragers, we cannot exclude that the absence of response to field margins could be linked to a lack of data (0.5 passes per site in average). Thus, further studies should investigate the response to field margins in a study area where this group is more abundant. Concerning results about edge-space foragers such as *P. pipistrellus*, the main taxa they consumed, *Diptera* (Beck, 1995), is reported to be enhanced by field margin areas at larval state, but not at flying adult state eaten by bats (Frouz and Paoletti, 2000). Concerning edge to open-space foragers, we did not detect any effect while we could expect a positive one on *E. serotinus*. Further studies are needed to explore the links between their diet and agricultural habitats. They are more specialized on big prey from different *Coleoptera* families (e.g. *Scarabaeidae*, *Carabidae*, *Cerambycidae*; Vaughan, 1997) whose abundance is potentially lower at field margins than wooded habitats or crops (e.g. French and Elliott, 1999; Spector and Ayzama, 2003). In addition, one study found field margins to be less attractive for smaller *Coleoptera* than field crops (Olson and Wäckers, 2007). Concerning open-space foragers, *N. leisleri* and *N. noctula*, the absence of field margin effect may be due to their call detection distance by recorders. These species fly high and fast, and their echolocation calls can easily carry to more than 100 m (while, in comparison, it is only 15 m for *Myotis* group; Denzinger and Schnitzler 2013; Barataud, 2015). Thus, a bat pass from *Nyctalus* species detected by the recorder can therefore correspond to a bat close to the recorder (and in turn close to the field margin), or to a bat 100 m further away (i.e. far from the field

margin). It is difficult to distinguish at this scale the effects of the different local habitats. Another non-exclusive hypothesis is that the flight height niche of open-space foragers may explain the absence of response to field margins for this guild. Indeed, to forage at field margins bats are likely forced to fly close to the ground, while open-space foragers forage at high altitude and likely do not exploit insects at field margins (Roemer et al., 2017).

Overall, our study does not provide information on how bats deal with field margins in term of behavioural reactions, which could help in further studies to better understand the significant responses and no responses. Indeed, the number of bat passes does not necessarily provide a full picture of responses since bat activity metric does not allow to distinguish foraging from commuting (Charbonnier et al. 2014).

Finally, other landscape variables we used as covariates in our models affected bats similarly to what is known in the literature. Indeed, the activity of species or groups and the species richness were found to be positively correlated with the proportion of grasslands (Froidevaux et al., 2017), the relative density of hedgerows (Lacoeuilhe et al., 2016) and the land-cover Shannon diversity index (Monck-Whipp et al., 2018); and negatively correlated with the proportion of urban areas (Azam et al., 2016) and the distance to water bodies (Heim et al., 2017a, 2017b), to forests (Heim et al., 2017a, 2017b) and to hedgerows (Lacoeuilhe et al., 2016). Such congruence reinforces our finding about the similar size effect of the relative density of field margins compared to the relative density of main roads, the proportion of urban areas and the rapeseed percentage. At the bat community level, some landscape covariates (i.e. variables related to forests, hedgerows and the land-cover Shannon diversity index) almost systematically affected species activity and community metrics, unlike field margin variables which only affected *Myotis* group. In comparison, hedgerows even drove

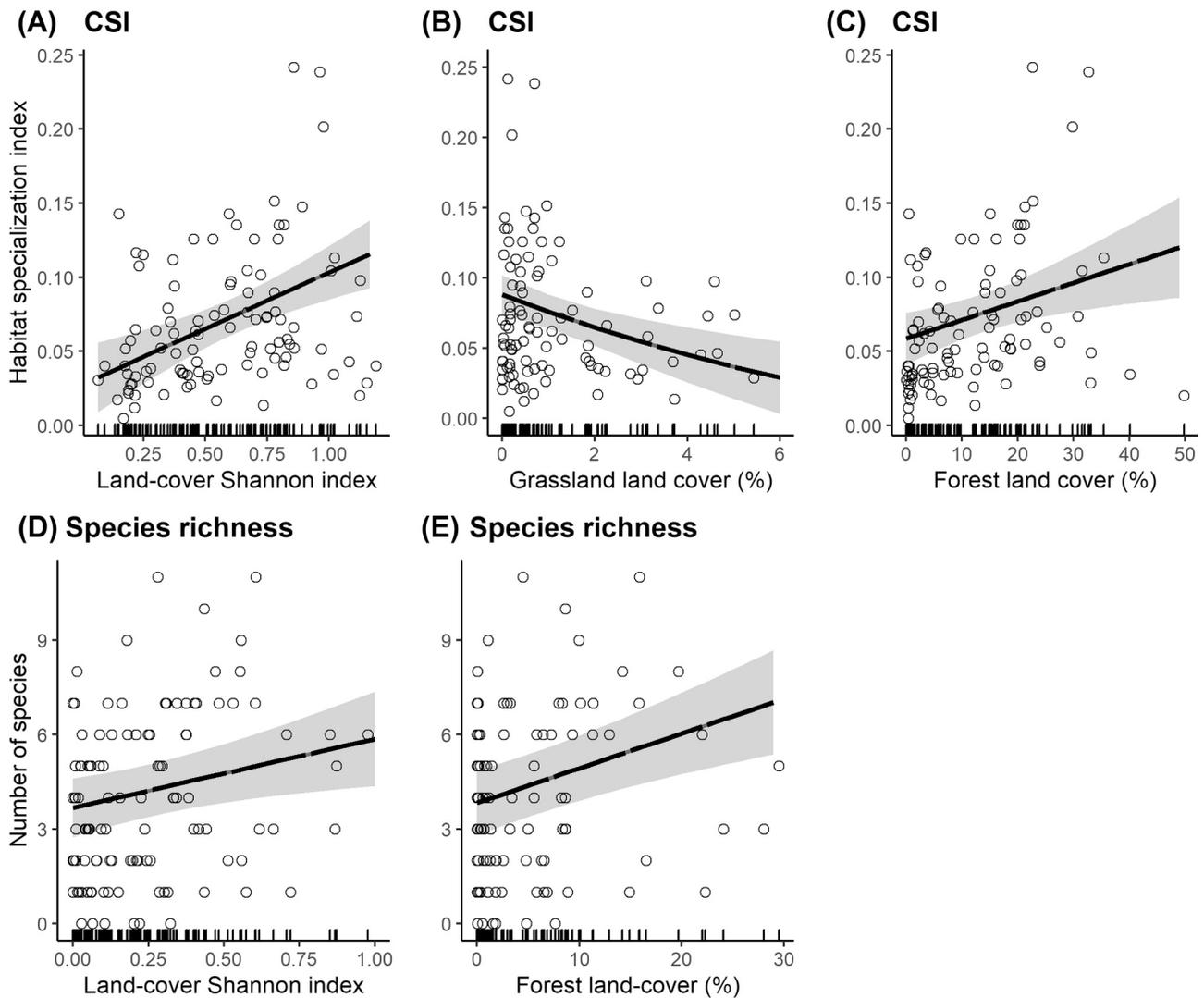


Fig. 4. Predicted relationships between the Community Specialization Index (CSI; A-C) or the species richness (D-E) and most significant environmental covariates (p -value < .01), and associated 95% confidence intervals from best models of the multi-model inference averaging.

the *Myotis* group activity at a much greater distances than field margins (i.e. a difference of 186 m; Fig. S2). We also found that when the land-cover Shannon index or the proportion of forest land cover increase, or when the proportion of grassland decreases, the community tends to be composed of species specialized in a specific habitat. We cannot compare these results with other studies since, to our knowledge, none have tested such relationships. Given that we assume that an increase in the land-cover Shannon index would mainly induce an increase of the proportion of forest land cover, we hypothesize that in turn it would enhance the activity of narrow-space foragers (*Plecotus* and *Myotis* groups) having higher Species Specialization Indices (see Supplementary Material S1). Concerning grasslands, the results could be explained by their positive effect on the dominant species activity (*P. pipistrellus*) which have a low species specialization index (see Supplementary Material S1). Finally, it should be noted that found positive effects of main roads are likely the reflect of road margin characteristics (e.g. the presence of vegetation or physical break with adjacent habitat), which could enhance foraging or commuting of bats along it though greater food resource or easier echolocation.

4.2. Perspectives and implications

Our study demonstrates that when studying bat responses to

landscape variables and hence to composition of intensive agricultural landscapes, incorporating information about herbaceous field margins in addition to other key landscape variables could help to improve the understanding of, at least, narrow-space forager activity. Moreover, although field margins constitute one of the easier ways to improve landscape attractiveness for *Myotis* sp., thanks to their low monetary cost (e.g. 5–25 times less expensive than hedgerows, BASF SE, 2018; PNRHL, 2014) and constraints (e.g. little shadow over crops, little management required and little growth delay), they have a lower – quite marginal – interest for the whole bat community compared to other habitats such as hedgerows, forests or water bodies. Although field margins can be useful at least for narrow-space foragers, they cannot be considered as an equivalent alternative to these other key landscape variables, which, unlike field margins, almost systematically drove bat activity and community.

CRedit authorship contribution statement

K.B. conceived the ideas, designed the methodology and collected the data. C.B., K.B., C.K. and I.L. analysed and interpreted results; all authors led the writing of the manuscript. All authors contributed to the drafts and gave their final approval for publication.

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.

Data Availability

Data used for analyses are available at <https://doi.org/10.48502/hssh-5194>.

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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.2021.107494](https://doi.org/10.1016/j.agee.2021.107494).

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