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The location and vegetation physiognomy of ecological infrastructures determine bat activity in Mediterranean floodplain landscapes

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ABSTRACT

Ecological infrastructures (EI), defined as natural or semi-natural structural elements, are important to support biodiversity and could play a crucial role in counteracting the well-known impacts of intensive agriculture. Yet, the importance of EI remains largely unexplored in Mediterranean agricultural landscapes and for species providing essential ecosystem services such as bats. Here, we evaluated the role of different EI types – in terms of location (riparian vs terrestrial) and vegetation physiognomy (woody vs non-woody) – in shaping bat guild activity in crop fields located in the floodplains of the Iberian Peninsula. We recorded 60,732 bat sequences in 96 crop fields and characterised 106 EI patches via an adaptation of the Biodiversity Potential Index (BPI). We found that the activity of mid-range echolocators (MRE) and long-range echolocators (LRE) was twofold higher when the nearest EI patch was riparian (i.e., contiguous to a watercourse) than when it was terrestrial. When assessing changes in bat activity in crop fields in relation to a gradient distance from EI types, our results revealed both distinct and similar effects of the location and vegetation physiognomy of the EI on bat guilds. For instance, while only the LRE guild positively responded to the proximity of woody EI, both MRE and LRE showed a marked increase of activity when increasing distances to non-woody EI, thus suggesting low bat activity levels near these features. Our habitat quality assessment also revealed that woody EI and riparian EI had higher biodiversity potential and related habitat quality, thus contributing to our understanding of bat responses to EI type in crop fields. As riparian areas are rarely targeted in biodiversity-friendly measures in farmland, we strongly recommend including riparian EI (especially the woody type) in conservation planning as they are crucial for both biodiversity conservation and ecosystem functioning.

1. Introduction

Agricultural systems occupy large areas worldwide, meaning that their ability to maintain fauna and flora diversity is crucial for the future of biodiversity conservation (Perrings et al., 2006; Egli et al., 2018). Past and current intensification of agricultural systems have increased the global food supply, but have also resulted in soil degradation, water scarcity and quality deterioration, habitat loss, degradation and fragmentation, turning this activity into one of the main causes of biodiversity losses worldwide (Green et al., 2005; Kehoe et al., 2017). Nevertheless, depending on their management, agricultural landscapes can still offer habitat opportunities for many species (Tscharntke et al., 2021). For instance, the promotion of ecological infrastructures (EI) – which represent key landscape elements such as hedgerows, field margins, and small woody features (Boller et al., 2004) – could play a crucial role in maintaining and enhancing habitat heterogeneity, biodiversity and ecosystem services in agricultural landscapes (Dainese et al., 2017; Poschlod and Braun-Reichert, 2017; Barrios et al., 2018; Rosas-Ramos et al., 2018; Rosas-Ramos et al., 2019; Tscharntke et al., 2021).

In Mediterranean floodplains, EI not only occur between cultivated areas but also along water features. Decades of water deviation from rivers and storage reservoirs for agriculture have drastically changed many lowland Mediterranean landscapes. Opposing to the natural flood pulse (high winter floods and long-lasting summer droughts), flow

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regulation and water redistribution onto crops and along the year have determined novel patterns of water connectivity and rearranged the location and maintenance of water patches and associated EI across Mediterranean landscapes (Tockner and Stanford, 2002; Cooper et al., 2013; Aguiar et al., 2016; Fernandes et al., 2020). This new-fangled reorganisation of water availability may promote, in some areas, habitat heterogeneity and biodiversity in the arid Mediterranean environment. However, despite the well-known ecological importance of EI in temperate agroecosystems, their roles in biodiversity conservation remain largely unexplored in Mediterranean agricultural landscapes (Schmitz et al., 2017; Montgomery et al., 2020). Surprisingly, this is even true for species providing essential ecosystem services in farmland, such as bats.

Due to their insectivorous diet, European bats represent efficient natural enemies of many pest insects (Aizpurua et al., 2018; Herrera et al., 2021) that could potentially exert top-down pest control (Russo et al., 2018). However, bats have shown marked population declines that are believed to have occurred during the second half of the twentieth century in Europe (Browning et al., 2021) and many species are still threatened with extinction (IUCN, 2021). One of the primary causes of the decline and threats posed to bats can be attributed to the intensification of farming practices (Frick et al., 2020; Browning et al., 2021). Agricultural intensification has led to the loss and fragmentation of commuting and foraging habitats in farmland (Park, 2015) but also to increased exposure to toxic levels of several pesticides (Torquetti et al., 2020; Oliveira et al., 2021). Since bats play an important role in pest suppression and are legally protected across Europe (European Union Habitats Directive 92/43/EEC), it is of utmost importance to mitigate the negative effects arising from agricultural intensification (Park, 2015). Among the different conservation actions and initiatives, the maintenance, restoration, and management of EI within the agricultural landscapes offer promising opportunities to reconcile food production and bat conservation.

Many bat species use crop fields for foraging (Heim et al., 2016, 2017) but the intensity of habitat use depends on several factors. At the farm scale, field size and management practices are key determinants of bat activity, with higher activity found in smaller fields (Monck-Whipp et al., 2018) and fields under wildlife-friendly management (Barré et al., 2018). Nevertheless, landscape attributes are generally more important for bats than local management (Froidevaux et al., 2017). Thus, at larger scales, landscape compositional diversity (in terms of land-cover variety, including crop type diversity) and configurational heterogeneity (number, size and arrangement of habitat patches) positively influence bat activity, as heterogeneous agricultural landscapes provide greater diversity of resources (Mendes et al., 2017; Monck-Whipp et al., 2018). Furthermore, many studies demonstrated that bats can only thrive in crop fields thanks to the occurrence of key landscape features in the surrounding environment, including freshwater bodies (Lisón and Calvo, 2011; Stahlschmidt et al., 2012; Sirami et al., 2013; Cruz et al., 2016; Froidevaux et al., 2017; Heim et al., 2018) and woody EI such as remnants isolated trees, hedgerows, and woodlands (Frey-Ehrenbold et al., 2013; Kelm et al., 2014; Heim et al., 2015; Kalda et al., 2015; Lacoeuilhe et al., 2018; Froidevaux et al., 2019).

Despite the growing interest in bat conservation in agricultural landscapes, there are several research gaps on the role of EI in enhancing bat activity in farmland that still need to be addressed, namely (i) determining the relative importance of woody (e.g., hedgerows and isolated or small groups of trees) and non-woody EI (e.g., herbaceous field margins) for bats, (ii) understanding to which extent the location of the EI in the wider landscape could determine their benefits to bats, and (iii) assessing whether the use of EI by bats depends on their quality. Furthermore, most of the studies on bats in Mediterranean farmland have so far focused on the management of vineyards (Kelly et al., 2016; Froidevaux et al., 2017; Rodríguez-San Pedro et al., 2018; Polyakov et al., 2019) and olive orchards (Herrera et al., 2015; Costa et al., 2020; Puig-Montserrat et al., 2021). Yet, other crops occurring mostly in Mediterranean floodplains have received little attention, and the role of EI to promote bats in such agricultural fields still need to be further explored to ultimately provide adequate management recommendations towards bat conservation.

In this study, we aimed to assess the role of different EI types in shaping bat activity in floodplain Mediterranean crop fields. This purpose led us to formulate the following three hypotheses:

H1–*EI vegetation physiognomy-based hypothesis*

In H1 we hypothesized that the vegetation physiognomy (woody vs non-woody) of the EI would influence bat activity in crop fields. We predicted that the relationship between bat activity and vegetation physiognomy of the EI would depend on species' eco-morphological traits, including echolocation call design and flight manoeuvrability, which determine their foraging and commuting strategies (Denzinger and Schnitzler, 2013). Thus, such effects should be specific for guilds consisting of short- (SRE), mid- (MRE) and long- (LRE) range echolocators (Frey-Ehrenbold et al., 2013). We predicted that woody EI would benefit both SRE (i.e. narrow-space foragers flying close to the vegetation) and MRE (i.e. edge-specialist flying along woody edges) but not LRE (i.e. open-space foragers). We also predicted that SRE activity would be higher near non-woody EI as observed in temperate croplands (Blary et al., 2021).

H2–*EI location influence-based hypothesis*

In H2 we further hypothesized that the EI location (riparian vs terrestrial) would affect bat activity in crop fields. We predicted that proximity to riparian EI would have a stronger effect than proximity to terrestrial ones since bats use freshwater sites for both drinking and foraging (Salvarina, 2016) and because freshwater is one of the most limited resource in the Mediterranean area during summer (Amorim et al., 2018).

H3–*EI habitat quality-based hypothesis*

In H3 we hypothesized that the habitat quality of the EI patches would contribute to understanding the responses of bats to EI types. We forecasted a higher habitat quality in woody patches, particularly in the riparian vegetation ones. Woody patches have a higher strata complexity providing a higher number of microhabitats when comparing with the herbaceous patches. On the other hand, riparian patches are located in areas with higher water availability, thus providing higher foraging habitat resources for many bat species, when comparing with the terrestrial patches.

2. Material and methods

2.1. Study area and sampling design

The study was conducted in 2019 in two agricultural landscapes located in the floodplains of the Tagus and Sorraia rivers, in central Portugal (Western Europe) (Fig. 1). Both study areas are situated in the alluvial zones where irrigated maize and rice pads are the most common crop types. The region has a Mediterranean climate characterised by mild winters, hot dry summers and recurrent interannual fluctuations of precipitation. The Tagus study area extends over 84.736 km^2, the Sorraia area 54.494 km^2, and both areas show evidence of long-term degradation by intensive agriculture (riparian habitat fragmentation, fine sediments and nutrient pollution in the river system). Nevertheless, these agricultural landscapes present relevant greening remnant patches considered key habitats for the provision of biodiversity and ecosystems services (Lee et al., 2014; Sun et al., 2020).

To characterise the EI habitat quality, a stratified sampling design was applied by randomly selecting 106 patches considering the distinct types of EI (Tagus: 52, Sorraia: 54) given their location and vegetation physiognomy. For the bat surveys, we randomly selected 96 sites in crop fields (Tagus: 44, Sorraia: 52) located at least 500 m from each other to minimize potential autocorrelation biases (Fig. 1; Appendix S1).

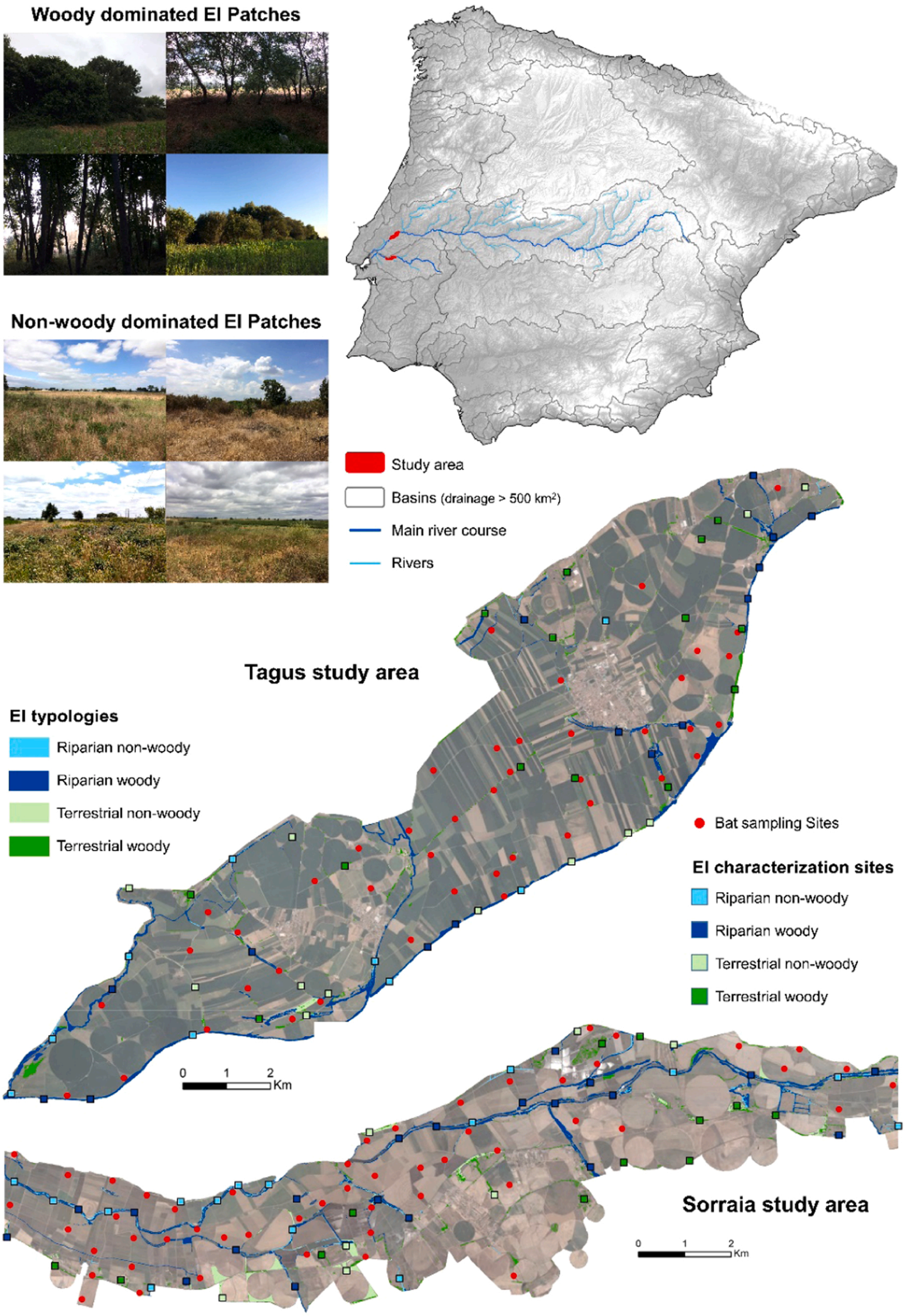

Fig. 1. Geographic location of the Tagus and Sorraia study areas in the context of the European Biogeographical regions. EI patches per typology are represented in both study areas using polygons of distinct colours (Terrestrial non-woody: light green; Terrestrial Woody: dark green; Riparian non-woody: light blue; Riparian woody: dark blue). Red dots indicate the geographic location of the sampling points. Squares indicate the geographic location of EI characterisation sampling sites per typology (expressed by the aforementioned colours).

2.2. *Ecological infrastructure data*

Ecological infrastructure data were mapped using an image-based approach, supported by a Geographic Information System (GIS). All the homogeneous patchescorresponding to vegetation remnants (i.e. patches clearly different, in origin and dynamics, from the surrounding agricultural landscape), were manually and individually digitised through a visual analysis of the Esri World Imagery layer (1:1000 scale). The Minimum Gap (MG) considered between EI patches was 10 m, while the Minimum Mapping Unit (MMU) was 200 m^2 (Ferreira et al., 2005; Wasser et al., 2015). These thresholds represent the minimum distance between EI patches and the smallest patch size, respectively. The EI vegetation patches were then classified according to the vegetation physiognomy, i.e., those dominated by trees and shrubs (hereafter referred to as “woody EI”) and those where trees were absent or rare, including open areas with scarce vegetation or dominated by herbaceous plants and low bushes (hereafter referred to as “non-woody EI”). We also classified EI vegetation patches according to their location, i.e., those located contiguous to a watercourse (hereafter referred to as “riparian EI”) and those that were non-contiguous to a watercourse (hereafter referred to as “terrestrial EI”).

Information concerning the geographic location of water features (rivers and water channels) were obtained by manually improving a Portuguese river network layer, produced based on a 25 m resolution DEM (available at the Portuguese Environment Agency). Small tributaries and headwater streams were added to the previous vector data using visual analysis of high spatial resolution (0.6 m) Esri World Imagery layer (ArcGIS Online data, Copyright © Esri) obtained in 2018.

Then, using the ESRI ArcGIS® Proximity Toolbox we calculated the Euclidean distances from every sampling site to the nearest woody, non-woody, riparian and terrestrial EI patch. Table 1 summarizes the variables used in the following statistical analysis, as explanatory aspects for bat activity.

2.3. *Habitat quality assessment*

Ecological infrastructure patches were characterised concerning their biodiversity potential, derived from a general habitat quality perspective. A stratified sampling design was applied by randomly selecting 106 patches considering the distinct types of EI (riparian: N = 61, terrestrial: N = 45; woody: N = 63, non-woody: N = 43) For this assessment, we adapted the method from the Biodiversity Potential Index (Larrieu and Gonin, 2008) which evaluates indicators of biodiversity that are potentially related to vegetation features, associated habitats and vegetation management within the EI. The index methodology was applied to areas with a minimum width of 5 m and minimum area of 200 m^2, covering 16 metrics of biodiversity potential from four categories: (i) vegetation structure, used to detail the quality of the vegetation considering species origin (includes the number of different native tree species present, coverage by invasive species, number of vertical strata); (ii) vegetation habitats, describing the habitats present in the woody strata vegetation, like type and abundance of microhabitats, dead wood, features in large dead and living trees, tree-related microhabitats and others; (iii) associated habitats, to detail the diversity of foraging habitats relying on rocky features or water availability (includes the presence of natural and artificial rocky and wetland features); (iv) vegetation management, quantifying the degree of impactful vegetation management (including woody cuts; shrub and herbaceous management; pruning and thinning). Each metric was classified using three score ranks (1, 3, 5), ordinal values indicating an increasing potential to promote biodiversity (see Appendix S2 for further details). EI characterisation, patch location, limits and shape were verified and validated during field surveys. The overall percentage of each scoring rank was compiled considering the sampled woody vs non-woody and riparian vs terrestrial EI patches.

Table 1

Explanatory variables considered for the statistical analysis, including a description of each variable and an indication of which were included in the models after data exploration and validation. Variable type: (1) target variable, (2) covariate.

Variable	Description	Units	Included in models (yes/no)	Type	Source references
Dist. EI	Euclidean distance to the closest EI patch	meters	n	1	Fonseca et al. (2020); Fonseca et al. (2021)
Dist. non-woody EI	Euclidean distance to the closest non-woody EI patch	meters	y	1	Fonseca et al. (2020); Fonseca et al. (2021)
Dist. woody EI	Euclidean distance to the closest woody EI patch	meters	y	1	Fonseca et al. (2020); Fonseca et al. (2021)
Dist. riparian EI	Euclidean distance to the closest riparian EI patch	meters	y	1	Fonseca et al. (2020); Fonseca et al. (2021)
Dist. non-riparian EI	Euclidean distance to the closest terrestrial EI patch	meters	y	1	Fonseca et al. (2020); Fonseca et al. (2021)
Woody vs non-woody EI	Categorical variable depicting the vegetation physiognomy of the EI	/	n	1	Fonseca et al. (2020); Fonseca et al. (2021)
Riparian EI vs terrestrial EI	Categorical variable depicting the location of the EI	/	y	1	Fonseca et al. (2020); Fonseca et al. (2021)
Dist. urban area	Euclidean distance to the closest urban area using level 4 of COS 2018 layer	meters	y	2	COS 2018 layer (www.dgterritorio.pt)
Dist. forest	Euclidean distance to the closest forest patch using level 1 of COS 2018 layer	meters	n	2	COS 2018 layer (www.dgterritorio.pt)
Dist. water	Euclidean distance to the closest water feature (rivers and water channels)	meters	n	2	Fonseca et al. (2020); Fonseca et al. (2021)
% Cropland (1 km)	Percentage of cropland area in the 1 km buffer radius contained within the study area (obtained by excluding EI and urban areas in this buffer)	%	y	2	obtained usingFonseca et al. (2020); Fonseca et al. (2021) and the COS 2018 layer (www.dgterritorio.pt)
Temperature	Mean hourly temperature at night	°C	y	2	obtained via the Portuguese National Information System on Hydric Resources

(*continued on next page*)

Table 1 (*continued*)

Variable	Description	Units	Included in models (yes/no)	Type	Source references
					(www.snirh.apambiente.pt)
Wind velocity	Mean hourly wind velocity at night	km/h	y	2	obtained via the Portuguese National Information System on Hydric Resources (www.snirh.apambiente.pt)

2.4. Bat echolocation call recording and identification

Bat surveys took place in 36, 26 and 34 sampling sites during May, June and July 2019, respectively, when weather conditions in terms of temperature, precipitation and wind velocity were suitable for insect flight and consequently for bats to forage (see Appendix S3 for more information on weather conditions and moon illumination). Bats were acoustically sampled using AudioMoth devices (stationary automatic ultrasound recording systems; Hill et al., 2018), installed on a tripod at approximatively 1.7 m height. No trigger was used, and sounds were continuously recorded during the full night (from sunset to sunrise) using a sampling rate of 254 kHz and medium gain. To minimise recording several bat species within the same audio file, each sound file was set to last for two seconds.

We used the number of bat sequences per night as a measure of bat foraging and commuting activity (i.e., a surrogate of bat abundance). A bat sequence was defined as one or several echolocation calls recorded within a 2-second interval. In fact, it was not possible to manually count each true bat pass due to the high number of files recorded. For the same reason, we applied a semi-automatic approach (Appendix S4) using Kaleidoscope Pro (v.5.1.8, Wildlife Acoustics, Massachusetts, USA) to classify bats in three general guilds reflecting their echolocation range and clutter avoidance (Schnitzler and Kalko, 2001; Schnitzler et al., 2003), namely short-range echolocators (SRE; *Barbastella barbastellus*, *Rhinolophus* spp., *Myotis* spp. and *Plecotus* spp.), mid-range echolocators (MRE; *Miniopterus schreibersii*, *Pipistrellus* spp. and *Hypsugo savii*) and long-range echolocators (LRE; *Eptesicus* spp., *Nyctalus* spp. and *Tadarida teniotis*). This guild approach has been successfully used in understanding the responses of different functional bat groups to habitat connectivity (Frey-Ehrenbold et al., 2013), forest structure (Froidevaux et al., 2016), presence of roads (Medinas et al., 2019), different types of street light (Bolliger et al., 2020), and varying levels of urbanization (Villarroya-Villalba et al., 2021).

2.5. Covariates

We only considered the most ecologically relevant covariates, thus avoiding model overparameterization and overfitting. The proportion of intensive agriculture in the landscape is considered as one of the main anthropogenic drivers altering bat activity (Azam et al., 2016). We quantified this variable using the proportion of the landscape under crop production within a 1 km buffer radius. We defined the spatial grain of the landscape by considering the mean daily foraging movement of European bat species (Laforge et al., 2021) while minimizing overlapping buffers. Besides representing important drinking sites, freshwater bodies are also crucial for foraging and orientation (Greif and Siemers, 2010; Lisón and Calvo, 2011; Salvarina, 2016). Thus, we used the river and stream features developed for the EI methodology along with a layer of the irrigation canals existing in the Sorraia study area (layer provided by the farmers association) to compute the minimum distance of the sampling sites to freshwater sites. While bat activity in a given habitat largely depends on the proximity to roosting sites (Rainho and Palmeirim, 2011), exhaustive maps of bat roosts do not exist. Considering that most European bat species occurring in non-karstic areas roost either in human-made structures or in trees (Dietz et al., 2009), we considered the distance to the nearest urban area and forest as a rough proxy of distance to the nearest roosting sites. The inclusion of distance to urban area also permitted to account for the effects of artificial light at night on bat activity as most sources of artificial illumination are located within urban areas (Azam et al., 2016). It is important to point out that all sampling sites were located at least > 40 m from urban area with most sites ($>95\%$) located > 100 m. Finally, although bat surveys were conducted during good weather conditions, small variations in temperatures and wind velocity may influence insect abundance and consequently bat activity. Thus, we calculated for each survey night the mean hourly temperature and wind velocity.

2.6. Statistical analysis

We first evaluated multicollinearity among predictors with Spearman's correlation test. We found that the distance to riparian EI was correlated with distance to water ($r = 0.82$) and with distance to forest ($r = 0.66$), and therefore only retained the distance to riparian EI in the subsequent analysis. Similarly, we excluded the distance to EI as it was highly correlated with the distance to woody EI ($r = 0.96$). As such, we kept distances to the four types of EI to be included in the models. No multicollinearity issue was found among the other continuous predictors ($|r| \leq 0.60$; Appendix S5). Second, we checked if the numbers in the different classes of the two categorical variables were balanced. We observed that the numbers were balanced for the variable depicting the EI location (44 riparian EI vs 52 terrestrial EI) but not for the variable depicting the EI vegetation physiognomy (87 woody EI vs 9 non-woody EI). Thus, we excluded the latter variable from the analysis.

To assess whether the location and vegetation physiognomy of the ecological infrastructures could shape guild-specific bat activity, we performed generalized linear mixed models (GLMMs) with the "glmmTMB" package. Bat activity (i.e., number of bat sequences per night) being count data,models were fitted with a negative binomial distribution to handle over-dispersion. The eight pre-selected predictors (Table 1) were included as fixed factors and all continuous ones were standardized (i.e., rescaled to the same unit) to enable comparisons of effect magnitude. We applied an information-theoretic approach using the Akaike information criterion corrected for small sample size (*AICc*) to test the statistical relevance of including crop types (maize fields, rice pads, and other crops) and sampling months (May, June, and July) alone or together as random effects to account for the sampling design.

Validation of the full multivariate models was carried out using the "DHARMa" and "performance" packages with the help of diagnostic plots. We removed one outlier from the SRE activity. We examined spatial autocorrelation of response variables and model residuals using Moran's I statistic, calculated with the 'spdep' package. We found no significant spatial autocorrelation ($p > 0.10$), except for LRE activity (Moran's I: 0.17 $p < 0.001$). We, therefore, accounted for spatial autocorrelation in the model on LRE by including a spatial autocovariate into the models.

We generated all possible models based on the full ones and performed model selection with the "MuMIn" package. When the *AICc* of the most parsimonious candidate models (delta $AICc < 2$) was more than two AICc units lower than the null one, we computed standardized, model-averaged estimates with associated standard errors (SE) and 95% confidence intervals across the "substantially" supported models (Burnham and Anderson, 2002). To do so, we used the mean of regression coefficients weighted by the *AICc* weight (w_i) from each model including that variable (Grueber et al., 2011). We also derived the relative importance of a predictor which represented the sum of *AICc* weights of all top models containing that variable. The significance of the effects was evaluated using 95% confidence intervals (Nakagawa and Cuthill, 2007).

All analyses were conducted in R v.4.0.2. (R Development Core Team, 2021) and references of packages used are presented in Appendix S6.

3. Results

3.1. Ecological infrastructure characterisation

We digitised 1699 EI patches (riparian: N = 538, terrestrial: N = 1161; woody: N = 1236 woody, non-woody: N = 463), 813 in the Tagus study area (riparian: N = 200, terrestrial: N = 613; woody: N = 643 woody, non-woody: N = 170) and 887 in the Sorraia study area (riparian: N = 339, terrestrial: N = 548; woody: N = 594, non-woody: N = 293). The total area of the EI represented 4.9% of the total landscape area considered for this study. Though less numerous, riparian patches were on average larger than terrestrial ones thus showing dominance (64.7%) in terms of the total occupied area (Table 2). Regarding the vegetation physiognomy, woody patches were on average more abundant and larger than the non-woody ones, representing 82.8% of the EI total area (Table 2).

Concerning the habitat quality assessment, the woody EI patches presented higher average values than non-woody EI patches (Table 2). Regarding the “vegetation structure” category, woody EI had an overall higher percentage of score ranks 3 and 5, except for the metric focused on invasive species. For the second characterising category “vegetation habitats”, non-woody EI had on average a higher percentage associated with score rank 1 (82.5%), with score rank 5 representing on average just 3.1%. For woody EI, percentages were more balanced between all scoring ranks, with ranks 1 (39.4%) and 5 (36.0%) having close average values. Regarding the “associated habitats” category, non-woody EI had a higher percentage associated with rank 1 (58.72%), with woody EI having a good balance between all scoring ranks (34.5%, 34.1% and 31.6%, from scoring ranks 1–3, respectively). In terms of “vegetation management”, both EI types had higher values for scoring rank 5, with non-woody and woody EI presenting respectively 86.0% and 70.7% of EI on average ranked like this.

As for the location attributes, the riparian EI patches revealed higher biodiversity potential and related habitat quality when compared with the terrestrial EI patches (Table 2). In the vegetation structure category, though the scoring rank with the highest percentage is always the same for both types, riparian patches tend to be classified more frequently with higher scoring ranks. For the “vegetation habitats” category, though the scoring rank 1 for “microhabitats at trees (>3 m)” is dominant in both types, terrestrial EI patches (20.0%) reveal a higher percentage of patches with a scoring rank 5. Despite this, all the other sub-categories reveal that riparian EI patches have in general higher percentages for the scoring ranks 3 and 5, especially for the “microhabitats at trees (<3 m)”, “dead trunks” and “large living trees” sub-categories. About the third category "associated habitats", the marked difference in terms of the "aquatic habitats" sub-category was to be expected. The sub-categories on "rocky habitats" show similarities between the two types of EI but, in terms of the “shade” sub-category, the riparian EI have the scoring rank 2 with the highest percentage (44.3%), while the terrestrial EI have the scoring rank 1 (46.7%). Concerning "vegetation management", both EI types reveal elevated percentages for the scoring rank 5, though for the "understorey clearing" sub-category there is a marked difference between them because the scoring rank 2 has a relevant percentage in the case of terrestrial EI patches (40.0%).

3.2. Bat activity

We recorded 60,732 bat sequences in the 96 sites located in irrigated agricultural landscapes (Table 3), with 46,205 bat sequences in the Sorraia study area (N = 52) and 14,527 in the Tagus study area (N = 44). July was the month with the highest bat activity (32,620 bat sequences, N = 36). Overall, species belonging to the MRE guild dominated the bat assemblage (80.6%; 48,971 bat sequences), followed by those of the LRE guild which represented 18.9% (11,495 bat sequences) of the whole bat activity

Table 2

Landscape descriptors and biodiversity potential characterisation of the Ecological Infrastructure (EI) patches existing in the study areas considering their location (riparian vs terrestrial) and vegetation physiognomy (woody vs non-woody). Percentage values for each scoring rank for all metrics used to characterise the EI patches sampled in terms of their biodiversity potential (bold formatting indicates the scoring rank with the highest percentage). The increasing value of scoring rank indicates a further potential of habitat quality and biodiversity.

Landscape descriptors	**Woody EIs**			**Non-woody EIs**			**Riparian EI**			**Terrestrial EI**		
Number of patches	1236			463			538			1161		
Total area (ha)	564.95			117.54			441.55			240.95		
Mean Patch size (ha)	0.46			0.25			0.82			0.21		
Sampling size	63			43			61			45		
	% per Score Category						**% per Score Category**					
Biodiversity potential	**1**	**3**	**5**	**1**	**3**	**5**	**1**	**3**	**5**	**1**	**3**	**5**
1. Vegetation structure (mean)	*5.3*	***57.7***	*37.0*	*25.6*	***51.2***	*23.3*	*11.5*	***52.5***	*36.1*	*16.3*	***58.5***	*25.2*
1.1. Native tree species	3.2	**87.3**	9.5	48.8	**51.2**	0.0	16.4	**77.0**	6.6	28.9	**66.7**	4.4
1.2. Invasive species	12.7	27.0	**60.3**	2.3	27.9	**69.8**	9.8	23.0	**67.2**	6.7	33.3	**60.0**
1.3. Vertical strata	0.0	**58.7**	41.3	25.6	**74.4**	0.0	8.2	**57.4**	34.4	13.3	**75.6**	11.1
2. Vegetation habitats (mean)	***39.4***	*24.6*	*36.0*	***82.6***	*14.3*	*3.1*	***52.2***	*23.2*	*24.6*	***63.3***	*16.7*	*20.0*
2.1. Microhabitats at trees (>3 m)	**60.3**	15.9	23.8	**100.0**	0.0	0.0	**77.0**	13.1	9.8	**75.6**	4.4	20.0
2.2. Microhabitats at trees (<3 m)	4.8	7.9	**87.3**	**90.7**	4.7	4.7	34.4	4.9	**60.7**	**46.7**	8.9	44.4
2.3. Standing dead trees	**82.5**	14.3	3.2	**100.0**	0.0	0.0	**86.9**	11.5	1.6	**93.3**	4.4	2.2
2.4. Dead trunks	39.7	19.0	**41.3**	**86.0**	7.0	7.0	**44.3**	18.0	37.7	**77.8**	8.9	13.3
2.5. Large living trees	**47.6**	33.3	19.0	**100.0**	0.0	0.0	**60.7**	27.9	11.5	**80.0**	8.9	11.1
2.6. Leaf litter	1.6	**57.1**	41.3	18.6	**74.4**	7.0	9.8	**63.9**	26.2	6.7	**64.4**	28.9
3. Associated habitats (mean)	***34.5***	*34.1*	*31.3*	***58.7***	*14.0*	*27.3*	*33.2*	***35.2***	*31.6*	***56.1***	*16.7*	*27.2*
3.1. Shade	3.2	**65.1**	31.7	**93.0**	0.0	7.0	34.4	**44.3**	21.3	**46.7**	31.1	22.2
3.2. Aquatic habitats	33.3	**61.9**	4.8	**46.5**	44.2	9.3	4.9	**83.6**	11.5	**84.4**	15.6	0.0
3.3. Rocky habitats (natural)	**93.7**	6.3	0.0	**90.7**	9.3	0.0	**91.8**	8.2	0.0	**93.3**	6.7	0.0
3.4. Rocky habitats (artificial)	7.9	3.2	**88.9**	4.7	2.3	**93.0**	1.6	4.9	**93.4**	0.0	13.3	**86.7**
4. Vegetation management (mean)	*10.6*	*19.0*	***70.4***	*2.3*	*11.6*	***86.0***	*6.0*	*12.6*	***81.4***	*8.9*	*20.7*	***70.4***
4.1. Tree clearing	3.2	11.1	**85.7**	2.3	0.0	**97.7**	1.6	6.6	**91.8**	4.4	6.7	**88.9**
4.2. Understorey clearing	17.5	25.4	**57.1**	0.0	30.2	**69.8**	9.8	18.0	**72.1**	11.1	40.0	**48.9**
4.3. Tree pruning	11.1	20.6	**68.3**	4.7	4.7	**90.7**	6.6	13.1	**80.3**	11.1	15.6	**73.3**

Table 3
Total, mean, maximum and minimum bat activity registered in the two study areas for each month. MRE: medium-range echolocators; LRE: long-range echolocators; SRE: short-range echolocators.

		Sorraia May (N = 17)	June (N = 16)	July (N = 19)	Tagus May (N = 17)	June (N = 10)	July (N = 17)
MRE	**Total**	6579	8830	22,162	5584	611	5205
	Mean	387	551.9	1166.40	328.5	61.1	306.2
	Max	2296	3923	3956	3216	118	932
	Min	13	37	127	14	30	53
LRE	**Total**	2511	2990	3037	709	113	2135
	Mean	147.7	186.9	159.8	41.7	11.3	125.6
	Max	495	601	428	258	25	592
	Min	8	24	51	4	1	13
SRE	**Total**	25	21	50	127	12	31
	Mean	1.5	1.3	2.6	7.5	1.2	1.8
	Max	11	6	13	110	4	7
	Min	0	0	0	0	0	0

(Table 3). The SRE group was less represented with only 266 bat sequences (0.4%) detected, and there were 34 bat sequences for which guild identification could not be achieved.

3.3. Effects of the location and vegetation physiognomy of the ecological infrastructures on bat activity

The effects of the location and vegetation physiognomy of the EI were relevant for both MRE and LRE guilds but not for SRE. The *AICc* value of all top candidate models (delta *AICc* < 2) on MRE and LRE activity but not on SRE activity was more than two *AICc* units lower than the null model (Appendix S7). Top candidate models on SRE activity were considered equivalent to the null model, thus indicating a lack of fit.

When investigating whether bat activity in crop fields was influenced by the nearest EI type, we found that the variable depicting the location of the EI was retained in all the most parsimonious models on MRE and in most models on LRE (Table 4). Our models suggest that the activity of the two guilds was twofold higher when the nearest EI patch was riparian (i.e., contiguous to a watercourse) than when it was terrestrial (Fig. 2).

When assessing changes in bat activity in crop fields in relation to a gradient distance from multiple EI types, our results revealed both distinct and similar effects of the location and vegetation physiognomy of the EI on the two dominant bat guilds (MRE and LRE). Firstly, we detected significant negative effects of the increasing distance from the nearest terrestrial EI on MRE and LRE activity, indicating that bat activity decreased with increasing distance (Fig. 3). The strengths of the two relationships (indicated by the effect size) were relatively similar ($|\beta| = 0.36$ and $|\beta| = 0.25$, respectively) but weaker than the other significant variables present in the models ($|\beta| > 0.40$; Table 4). For LRE guild, the upper limit of the 95% confidence interval was very close to zero, thus meaning that the variable could be irrelevant. We further found a negative relationship between MRE activity and distance to riparian EI (Table 4). It is important to point out that distance to riparian EI was highly correlated with distance to water and forest (Appendix S5). Secondly, our models suggest that the LRE guild was significantly more active in fields near woody EI (Fig. 3). This variable was found to be highly correlated with distance to any EI. In contrast, MRE activity was not affected by the proximity of woody EI. This variable was retained in the most parsimonious models but the 95% confidence interval around the estimate overlapped zero. Finally, we found that distances to the nearest non-woody EI were retained in our best models for both MRE and LRE activity. We detected significant, positive relationships between the distance to the nearest non-woody EI and the activity of MRE and LRE, suggesting lower activity in fields near non-woody EI (Fig. 3). While the strength of the relationship was relatively weak for LRE ($|\beta| = 0.32$), it was strong for MRE ($|\beta| = 0.61$) in comparison to other significant variables (Table 4).

Table 4
Standardized, model-averaged parameter estimates (Est.) and associate standard error (SE) and 95% confidence intervals of the variables present in the most parsimonious models (ΔAICc < 2) relating the effects of location and vegetation physiognomy of the ecological infrastructures (EI) on the activity of the two dominant bat guilds: mid- and long-range echolocators (MRE and LRE, respectively). Marginal R^2 values (variance explained by the fixed effects only) of the full model are provided. Explanatory variables displayed in bold represent significant variables for which 95% CI did not overlap zero. Relative importance (RI) of a predictor represents the sum of AICc weights of all most parsimonious models containing that variable.

Response variable	Explanatory variable	Est. (± SE)	95% CI	RI
MRE activity	**Terrestrial vs riparian EI**	**-0.60 (± 0.24)**	**(−1.08, −0.12)**	**1.00**
$R^2 = 0.37$	**Dist. non-woody EI**	**0.61 (± 0.12)**	**(0.36, 0.85)**	**1.00**
	Dist. woody EI	-0.14 (± 0.11)	(−0.36, 0.08)	0.25
	Dist. riparian EI	**-0.37 (± 0.15)**	**(−0.66, −0.08)**	**1.00**
	Dist. terrestrial EI	**-0.36 (± 0.12)**	**(−0.60, −0.13)**	**1.00**
	% Cropland (1 km)	0.14 (± 0.09)	(−0.04, 0.33)	0.45
	Dist. urban area	-0.19 (± 0.13)	(−0.44, 0.06)	0.45
	Temperature	**0.45 (± 0.11)**	**(0.22, 0.68)**	**1.00**
	Wind velocity	-0.12 (± 0.11)	(0.36, 0.08)	0.22
LRE activity	**Terrestrial vs riparian EI**	**-0.85 (± 0.25)**	**(−1.33, −0.37)**	1.00
$R^2 = 0.65$	Spatial autocovariate	-0.07 (± 0.12)	(−0.31, 0.17)	1.00
	Dist. non-woody EI	**0.32 (± 0.09)**	**(0.14, 0.50)**	**1.00**
	Dist. woody EI	**-0.30 (± 0.11)**	**(−0.51, −0.09)**	**1.00**
	Dist. terrestrial EI	**-0.25 (± 0.12)**	**(−0.49, −0.01)**	**0.75**
	% Cropland (1 km)	-0.09 (± 0.10)	(−0.28, 0.10)	0.23
	Temperature	**0.39 (± 0.11)**	**(0.18, 0.60)**	**1.00**
	Wind velocity	**-0.60 (± 0.11)**	**(−0.81, −0.39)**	**1.00**

3.4. Effects of covariates on bat activity

Mean hourly temperature and wind velocity at night and the amount of cropland in the surrounding landscape were retained in the top candidate models on LRE activity whereas all four covariates were retained on models on MRE activity. Yet only weather variables had a

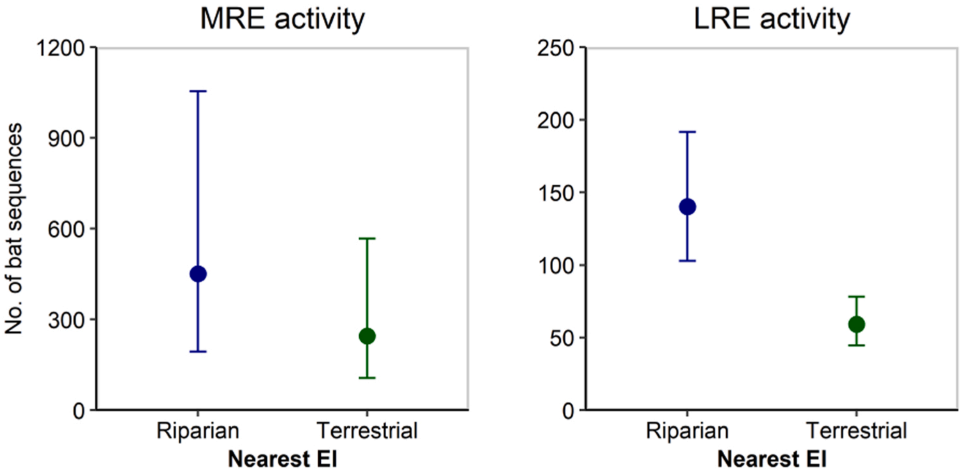

Fig. 2. Predicted responses of the two dominant bat guilds (mid- and long-range echolocators, MRE and LRE) in crop fields depending on whether the nearest EI was riparian (i.e., contiguous to a watercourse) or terrestrial (i.e., non-contiguous to a water course). Model predictions and associated 95% confidence intervals are depicted with full circle and error bars, respectively.

significant effect on bat activity. The activity of the two guilds was positively associated with temperature while wind velocity negatively affected LRE activity (Table 4). We did not find any statistical evidence of an effect of distance to the nearest urban area and amount of cropland at 1 km radius scale on bat activity.

4. Discussion

The potential importance of ecological infrastructures (EI) for biodiversity conservation in Mediterranean agricultural landscapes has been poorly documented (Rosas-Ramos et al., 2018), yet maintaining areas out of production is crucially needed for promoting biodiversity and ecosystem services in farmland (Grass et al., 2019; Tscharntke et al., 2021). Here, we demonstrated that EI location and vegetation physiognomy shape bat activity in floodplain crop fields of the Iberian Peninsula. More specifically, we revealed that the two most abundant bat guilds (MRE and LRE, accounting for 99.5% of total bat activity) responded similarly to the proximity of non-woody EI and to some extent to terrestrial EI, and highlighted guild-specific responses to the proximity of woody and riparian EI. We also confirmed previous findings that crop fields located in the close vicinity of riparian habitats and the existence of a network of EI patches close to one another may support higher bat activity levels.

4.1. Bat responses to woody and non-woody ecological infrastructures

Woody elements provide a multitude of benefits to bats in agricultural landscapes, including shelter from wind, protection from predators, buffered micro-climatic conditions enhancing prey availability, and acoustic landmark for commuting (Verboom and Huitema, 1997; Boughey et al., 2011; Feber et al., 2019; Froidevaux et al., 2019). In intensive landscapes where woody patches are scarce, it is thus expected that the activity of bats foraging in narrow spaces (i.e., SRE guild) and along woody edges (i.e., MRE guild) declines with increasing distances to woody patches (Kelm et al., 2014; Heim et al., 2015, 2018; Kalda et al., 2015; Froidevaux et al., 2017; Finch et al., 2020). In this study, we recorded an extremely low number of bat sequences from the SRE guild in crop fields (<0.5% of total bat activity) and could not establish a direct link between SRE activity and the distance to woody EI. Nevertheless, our results based on acoustic data suggest that SRE do not thrive in such intensive agricultural landscapes, even with the occurrence of remnant woody patches of relatively high quality. Their high sensitivity to landscape disturbances is likely to be the main reason behind this finding (Duchamp and Swihart, 2008). Surprisingly, our models indicated that – unlike MRE – LRE guild activity markedly declined with increasing distance to woody EI. While LRE can be recorded as far as 200 m from the detectors (Barataud, 2015), this finding cannot solely be attributed to a potential detection bias. Other studies have demonstrated a similar pattern on LRE with distance to forest edges (Heim et al., 2018; Blary et al., 2021) and Mendes et al. (2017) revealed a strong positive relationship between open-space foragers and the proportion of forests at 1.5 km radius scale in Portugal. Based on the EI characterisation, we can speculate that greater roost availability and insect abundance at woody EI could explain our findings, but the mechanisms underlying such effect remain to be explored.

Non-woody EI had a strong influence on both MRE and LRE. Most bat sequences were recorded away (>500 m) from non-woody EI, thus suggesting a marked avoidance of this EI type by bats. Studies assessing the effects of non-woody EI such as field margins are scarce in the literature (but see Blary et al., 2021) and the activity patterns we found have not been described in any agroecosystems. Our EI habitat quality assessment highlighted that non-woody EI were of lower quality compared to woody EI. Non-woody EI patches are less numerous and on average smaller than woody EI, which for elongated patches as those commonly found in agricultural landscapes translates into areas with high edge effects. In human-dominated landscapes, larger EI patch sizes generally represent higher habitat availability for species while smaller edge effects promote the existence of a core area that may help support more complex biological communities (Fahrig, 2003). Habitat heterogeneity (i.e., having a diverse EI) within intensive agricultural landscapes enhances species richness and abundance (Šálek et al., 2018) but the quality and quantity of these EI also influence the aforementioned parameters and improves the ecosystem services provided (Badenhausser et al., 2020). EI habitat quality characterisation indicates that concerning vertical strata, non-woody EI patches have generally less complexity than woody EI, and the same applies to the quality and quantity of habitats associated with vegetation (e.g., deadwood, large trees, tree-related microhabitats, leaf litter) or with rocky and water features. Though non-woody EI were established as those where trees are scarce or inexistent, these could exist along with other dominant vegetation strata such as herbs and shrubs. However, fieldwork revealed that shrubby vegetation is scarce or at least not abundant in non-woody EI patches, which are mostly dominated by grasses (Poaceae), where giant reed (*Arundo donax*) is generally dominant. In Mediterranean agricultural landscapes, the presence of native woody elements (trees and shrubs) has been linked to nocturnal insect abundance (Chaperon et al., 2022). Given this, the lower complexity and habitat potential of non-woody EI seems to be related to lower plant richness and a smaller

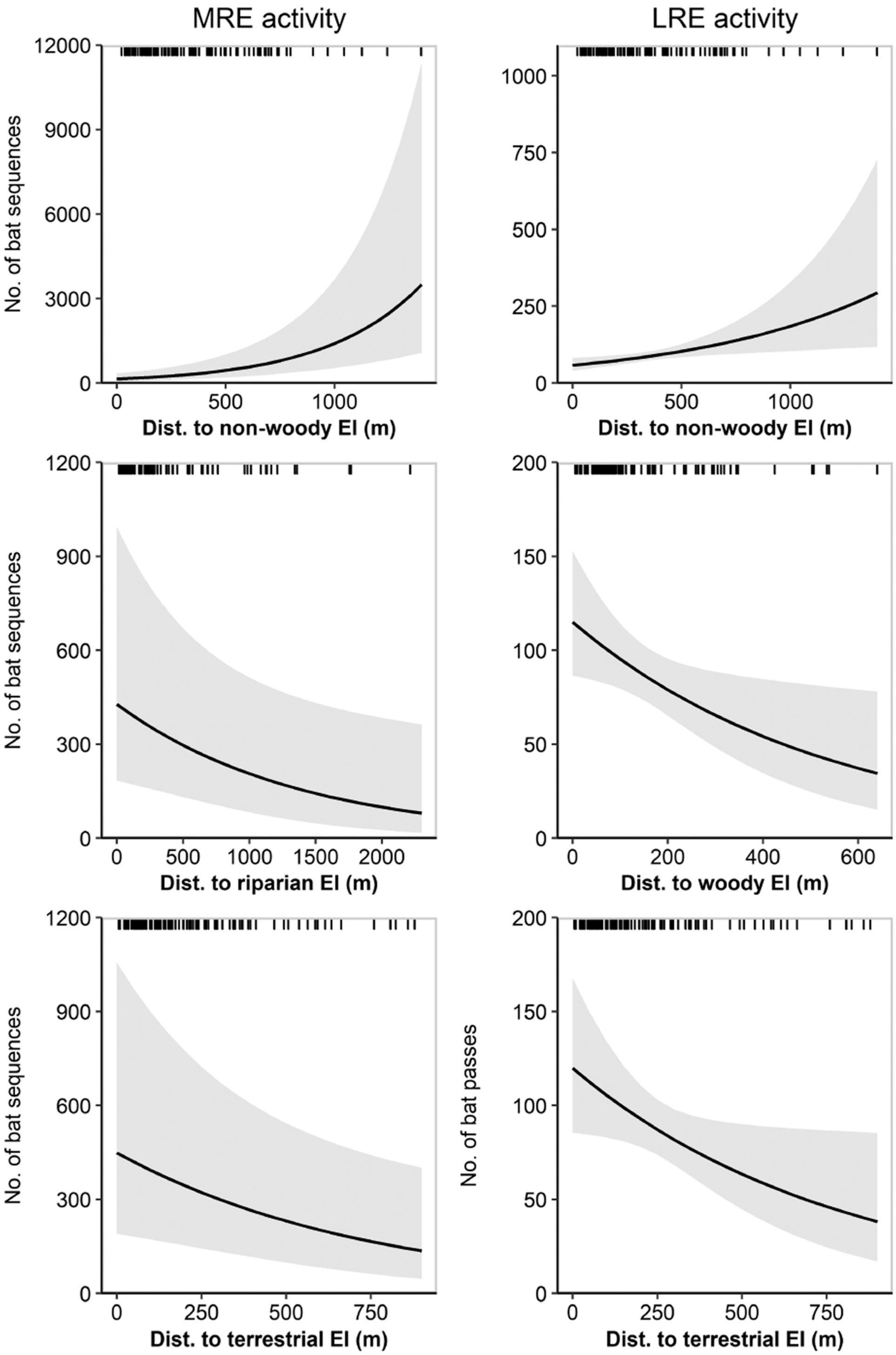

Fig. 3. Predicted responses of the two dominant bat guilds (mid-and long-range echolocators, MRE and LRE) in relation to (i) distance to the nearest woody and non-woody ecological infrastructure (EI), and (ii) distance to the nearest riparian and terrestrial EI in floodplain crop fields. Model predictions from GLMMs and associated 95% confidence intervals are represented by the solid lines and shaded areas, respectively.

heterogeneity of other habitat features, which may hamper insect species richness in these areas, and thus affect the activity of insectivorous bat species. This concurs with the work of McHugh et al. (2019) who revealed when comparing different field margin management that species present in these structures determine species-specific bat activity.

4.2. The importance of riparian and terrestrial ecological infrastructures

Freshwater sites and associated bankside vegetation provide important foraging habitats for many bat species (Fukui et al., 2006) and can serve as commuting corridors in the wider landscape (Salvarina, 2016). Our findings strengthen the crucial role of water and associated riparian vegetation in enhancing bat activity in agricultural landscapes and consolidate previous studies conducted in other Mediterranean habitats (Kahnonitch et al., 2018) including vineyards (Froidevaux et al., 2017) and eucalypt plantations (Cruz et al., 2016). For both MRE and LRE guilds, we found that bat activity in crop fields was twofold higher when the nearest EI patch was riparian than when it was terrestrial. Nevertheless, it is difficult to disentangle the respective role of riparian vegetation and water, as the former is by definition strongly associated with the latter. While there was no statistical support for an effect of the distance to riparian EI on LRE activity, the importance of riparian habitats to bats was further illustrated by the significant negative relationship found between MRE activity and distance to riparian EI that indicated higher activity levels near riparian EI. The comparison of EI location attributes indicated that riparian EI should have a higher ability to support species and ecosystems services, both due to the spatial attributes and the biodiversity potential. Riparian EI, despite their intrinsic linear nature, tend to be larger and less fragmented than their terrestrial counterparts. As mentioned previously, these spatial attributes often translate into higher habitat availability for species and smaller edge effects (Fahrig, 2003). Concerning the ability to support biodiversity, riparian EI revealed an overall higher heterogeneity and complexity in terms of vegetation, while also presenting a higher quantity and quality in most other habitat features (e.g., microhabitats, dead and large living trees, rocky and water features). As expected, vegetation in the terrestrial EI experiences a higher intervention and management, though nevertheless low for both types. Despite this, incremental distances to terrestrial EI seem to be detrimental to MRE and LRE activity. Given than terrestrial EI are mainly located in crop field boundaries, these results suggest that large crop fields may hamper bat activity. This is concurrent with studies highlighting that smaller crop fields positively affect biodiversity (Fahrig et al., 2015; Šálek et al., 2018) including bats (Monck-Whipp et al., 2018), but also with others indicating that bats highly benefit from a dense network of woody EI elements in agricultural landscapes (Heim et al., 2015; Mendes et al., 2017).

4.3. Perspectives and implications for bat conservation in floodplain crop fields

Our findings highlight the need for maintaining a dense network of EI patches in floodplain crop fields, especially riparian and woody, for reconciling food production and bat conservation. For nearly the last 30 years, the EU has provided financial aid to agricultural production methods that help protect the environment (Plieninger et al., 2012; Desjeux et al., 2015). The 2013 reform introduced the Common Agricultural Policy Greening, i.e., a set of measures to motivate farmers to adopt agricultural practices beneficial for the climate and the environment (European Union, 2013). This includes a specific and subsidised measure that encourages farmers to set aside a share of arable land to improve biodiversity and ecological benefits, the Ecological Focus Areas (EFA). In general, terrestrial EI (woody and non-woody) can be included in one of the multiple EFA typologies but riparian EI tend to be excluded from such schemes in many countries (including Portugal) since these are not considered as part of the farmlands. Given our findings, changes in subsidising schemes aiming to promote adequate management of riparian EI and the enhancement of its biodiversity and ecosystem services should prove beneficial for agricultural landscapes. Moreover, we also recommend including riparian EI (especially the woody patches) in conservation planning as they are essential for both biodiversity conservation and ecosystem functioning (Naiman et al., 1993; Carrasco-Rueda and Loiselle, 2019; Riis et al., 2020). To better designing adequate management actions to enhance bat activity in farmland, we also underline the need to explore and identify the intrinsic characteristics of woody EI – such as shape, height, plant species composition – and their location in the wider agricultural landscape. As highly disturbed landscapes such as intensive farmlands can be hostile to the SRE guild (that include many species of major conservation concern), other conservation actions are required to promote these species in such landscapes. For instance, large-scale restoration of native woody habitats in the landscapes (e.g., hedgerow planting, woodland creation) as well as increasing cropland heterogeneity could benefit many bat species (Fuentes-Montemayor et al., 2017; Monck-Whipp et al., 2018) and beyond (Tscharntke et al., 2021). Furthermore, to better understand the role of non-woody EI in shaping bat activity we strongly encourage future studies to explore this relationship in other agroecosystems. Assessing the intrinsic characteristics of non-woody EI would be of great value. Finally, in line with Blary et al. (2021), we highlight the importance of considering non-woody EI such as field margins when studying bats in farmland.

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 availavility

Data collected for this study are available to download at https://doi.org/10.5281/zenodo.6322159.

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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.2022.107929.

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