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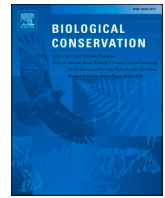
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Context-dependent effects of wind turbines on bats in rural landscapes

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ABSTRACT

Rural landscapes are undergoing widespread changes, of which homogenization and the installation of wind turbines are important components. To keep track of the impacts of homogenization and the presence of wind turbines on biodiversity, the responses of vulnerable organisms should be assessed considering their combined effects. We have tested the response of bat activity to the interaction between agricultural landscape gradients reflecting the degree of homogenization (parcel size, parcel diversity and density of hedges), and the presence of wind turbines. To do this, we combined acoustic sampling data gathered from 2014 to 2020 throughout continental France with land use and wind turbine siting data. GLMMs showed that each echolocation guild (LRE: long, MRE: mid, and SRE: short-range echolocators) responded to different gradients. Increasing parcel sizes and lower densities of hedges correlated negatively with the activity of MRE and SRE bats. Activity of LRE and SRE bats was lower, and that of MRE bats (mostly Common Pipistrelles *Pipistrellus pipistrellus*) was higher, when wind turbines were present. In landscapes containing wind turbines, hedge density correlated positively with LRE activity, and parcel diversity fostered SRE activity. Therefore, increasing hedge densities, or dividing large monocultures into more diverse cropland configurations, may compensate for negative effects of wind turbine presence on bat activity. Siting of new wind turbines should still avoid high-quality locations where bat activity and diversity are currently high, as the negative impact is bound to include not only habitat loss, but also enhanced mortality by collision.

1. Introduction

Land conversion into agricultural surfaces (Chase et al., 2020; Hoekstra et al., 2004), and the development of energy infrastructure (Niebuhr et al., 2022; Voigt et al., 2019) are important components of global anthropogenic change (Ellis et al., 2010; Foley et al., 2005). Within rural landscapes, structure is changing by ongoing homogenization, whereby parcels are fused together (Benton et al., 2003; Clough et al., 2020). This entails the loss of marginal structures such as hedgerows (Cornulier et al., 2011; Sklenicka et al., 2009; Van Den Berge et al., 2019). Indeed, homogenization of rural landscapes decreases beta diversity through habitat loss and landscape complementation loss (Denac and Kmecl, 2021; Gámez-Virrués et al., 2015; Sálek et al., 2018).

Concomitant to changes in agriculture, a growing use of renewable sources for the production of electricity has often been found to conflict with biodiversity conservation (Rehbein et al., 2020; Schöhl and Nopp-Mayr, 2021; Smith and Dwyer, 2016). This conflict is referred to as the “green-green dilemma”, whereby the transition toward renewable energy sources with a low carbon footprint entails biodiversity losses (Pörtner et al., 2021; Powell and Lenton, 2013; Rusch et al., 2022). Wind energy is a key element in this transition with a large potential for growth (Bórawski et al., 2020; Dammeier et al., 2019; Fawzy et al., 2020). Onshore wind energy capacity in the European Union is expected to increase between 2023 and 2027 by 70.4 GW (IEA, 2021), which implies, assuming an average 3 MW capacity per turbine, the installation of more than 23,400 turbines. However, wind turbines induce habitat

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loss and mortality by collision in birds and bats (Barré et al., 2018a; Laranjeiro et al., 2018; Minderman et al., 2012).

The strategy to achieve no net loss of biodiversity involves a mitigation hierarchy, whereby actions against negative impacts are considered in the following order of priority: avoidance, reduction and offsetting (Arlidge et al., 2018; Rainey et al., 2015; Ten Kate et al., 2018). To inform this strategy in the context of expanding wind energy production, there is a need for knowledge on the context-dependency of wind turbines' impact on biodiversity. Pinpointing the landscape characteristics where impacts are higher can help to decide on which criteria to prioritize when a siting choice is at hand (e.g. Kati et al., 2021), or quantify an expected loss of biodiversity to be offset. Land use planning may follow two criteria: (1) concentrate impacts – land sparing, or (2) a sparse distribution of impacts, extensively across landscapes – land sharing (Caryl et al., 2016; Fischer et al., 2014; McManamay et al., 2021). But beyond this, land use allocation should consider whether a particular activity has a disproportionate impact when placed on certain landscape types (Edwards et al., 2014; Law et al., 2015).

This study assesses whether rural landscape homogenization influences the impact of wind turbines on bat activity. Insectivorous bats are often used as bioindicators (Pocock and Jennings, 2008; Russo and Jones, 2015), and provide ecosystem services to agriculture, namely in the form of pest control (Boyles et al., 2011; Ramírez-Francel et al., 2022). Bats are affected by landscape composition and configuration, where heterogeneous and connected landscapes show higher activity (Kalda et al., 2015; Monck-Whipp et al., 2018). Notably, linear structures such as hedges play a central role in a rural landscape's connectivity and foraging resources for bats (Kelm et al., 2014; Lacoëuilhe et al., 2016; Toffoli, 2016). Wind turbines either induce bat mortality by collision or habitat loss by deterrence (Barré et al., 2018a; Leroux et al., 2022; Rydell et al., 2010). However, bat responses to landscape composition and configuration, as well as to wind turbines, depend on the ecology of the species involved. Bat species can be grouped into functional guilds that reflect their flight modes and foraging ecologies (Denzinger and Schnitzler, 2013), and that indeed show different sensitivities to landscape composition-configuration (Frey-Ehrenbold et al., 2013) and wind turbines (Leroux et al., 2022; Roemer et al., 2017).

We hypothesized that landscape homogenization and wind turbines have a negative impact on bat activity, and that the impact of wind turbines is influenced by the degree of local landscape homogenization, represented by agricultural parcel sizes, diversity of parcel use, and density of hedges. We therefore expected bat activity to decrease (1) in more homogeneous landscapes, (2) with wind turbine presence, and (3) comparatively more in the presence of wind turbines within heterogeneous landscapes. To test this, we fitted parametric models of bat activity per echolocation guild (long-, mid- and short-range echolocators), built upon thousands of acoustic samples collected in a citizen science initiative aiming for a standardized bat survey throughout France.

2. Methods

2.1. Study area

We analyzed data from the citizen science bat monitoring program Vigie-Chiro (<https://www.vigienature.fr/fr/chauves-souris>). This standardized, passive acoustic monitoring protocol is performed by volunteers throughout the French territory. Passive acoustic bat detector devices are placed at the ground level, and record all sounds between 8 and 192 kHz, from 30 min before sunset to 30 min after sunrise. Volunteers are asked to perform the protocol in nights when no rain is expected, and maximum wind speed is not expected to be over 30 km/h. Different device models have been used in this program (see Supplementary material Fig. S14), with device-specific settings to ensure data comparability.

We compiled data from sampling positions throughout continental France, following the haphazard distribution of participants in the Vigie-

Chiro program. Given our aim to study the interacting effects of rural landscape homogenization and wind turbine presence, we selected sampling sites surrounded by a surface cover of at least 25 % agricultural lands (see "Choice of buffer landscape scale" subsection below). We excluded surveys carried out above 1000 m altitude to avoid biases due to high mountain environmental conditions. To limit spatial autocorrelation, we randomly selected points no closer than 1 Km from each other. For each point, one to nine nights of recordings were performed, although a majority of points (55 %) present only one night (Supplementary material Table S2). We restricted our study to the period spanning from 15 May to 15 October, which includes yearly bat activity peaks in temperate regions, associated to breeding and subsequent dispersal or migration (Ciechanowski et al., 2007; Goldenberg et al., 2021; Gorman et al., 2021). Our dataset was thus made up of 1923 nights in 993 sites, covering the period from 2014 to 2020 (Fig. 1 left).

2.2. Bat activity

Bat species were pooled into three functional guilds (Supplementary material Table S1) as previously done elsewhere (Frey-Ehrenbold et al., 2013; Leroux et al., 2022). These guilds are based on similarities in echolocation call structures, and imply similar foraging modes: long-range echolocators (LRE), mid-range echolocators (MRE) and short-range echolocators (SRE). LRE are prone to collisions with wind turbines due to the large amount of time they spend flying at height (Roemer et al., 2017), but it is the abundant MRE *Pipistrellus pipistrellus* which presents the greatest fraction of fatalities in Europe (Rydell et al., 2010). Furthermore, each guild is expected to respond differently to landscape configuration: bats with shorter echolocation call range and lower mobility may be more vulnerable to connectivity loss than the more mobile LRE, which rather respond to habitat amount (Fuentes-Montemayor et al., 2017). SRE are particularly sensitive to connectivity loss or fragmentation within agricultural landscapes (Frey-Ehrenbold et al., 2013; Pinaud et al., 2018; Reiter et al., 2013), and thus expected to respond most drastically to landscape variables reflecting rural homogenization.

We analyzed total recorded night activity, in terms of number of bat passes, separately per guild. We defined a bat pass as each event where at least one echolocation call was recorded within a five-second time window (Kerbiriou et al., 2019; Millon et al., 2015). Each bat pass was automatically classified to the lowest possible taxonomic level using the Tadarida software (Bas et al., 2017).

2.3. Environmental variables

2.3.1. Wind turbines

Wind turbines within a buffer area around the acoustic sampling point were considered as a presence/absence factor. To avoid inconsistencies in the amount of missing data due to the varying accessibility and update frequency of governmental geographic databases, the positions of wind turbines were obtained from the OpenStreetMap database (openstreetmap.org). Preliminary checks by photointerpretation had proven the accuracy of this database compared to governmental sources of information. The date of creation of a map feature representing a wind turbine was taken as an approximation to its start of operation.

2.3.2. Landscape variables

Landscape variables of interest were the median parcel area as a measure of configurational heterogeneity, Shannon's diversity index for crop types and pastures among parcels as a measure of compositional heterogeneity, similarly as in Bertrand et al. (2016), as well as hedge density. Hedge density is expected to provide landscape complementation, for instance as foraging habitat and a support to commuting flight (Heim et al., 2018; Verboom and Huitema, 1997). By "parcel" we refer to all crop fields and pastures. The Pearson correlation coefficient

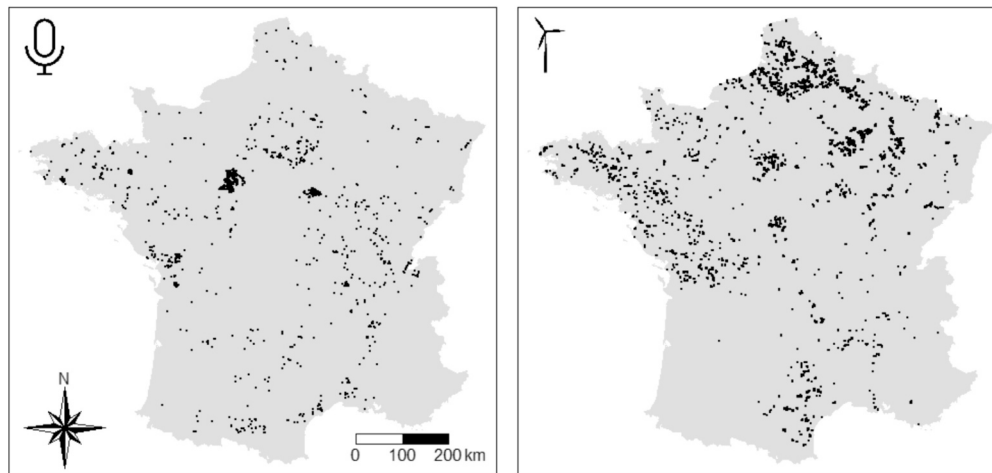


Fig. 1. Distribution of 993 acoustic sampling points in rural areas (LEFT) and 8582 wind turbines (as of the latest date of acoustic sampling, RIGHT) in continental France.

between these three landscape variables never exceeded an absolute value of 0.29 (Supplementary material Figs. S3; S8–10).

Data on parcel structure and crop types was sourced from the RPG (<https://geoservices.ign.fr/rpg>). This public database is provided by the national geographical institute (IGN), and includes the outline of individual agricultural parcels throughout France, with information of their reported use, including main crops.

Other landscape variables known to drive bat activity were included as covariates: density of roads (Claireau et al., 2019) and railroads (Vandeveldt et al., 2014), density of water courses, including lake, pond and reservoir margins (Heim et al., 2018; Rainho and Palmeirim, 2011; Sirami et al., 2013), and the proportion of agricultural cover. Data on roads was obtained from the 2021 edition of the Route500 dataset (<https://geoservices.ign.fr/route500>), produced by IGN. Data on water courses and bodies were obtained from the OSO layer (<https://www.th.eia-land.fr/en/product/land-cover-map/>): a 10-meter land use raster dataset based on the analysis of satellite imagery from the Copernicus Program (Derksen et al., 2020). We downloaded the 2020 version, and considered all cells in category 23 (“water”) as water courses. The density of linear features (hedges, roads and water courses) was calculated as the sum of total feature lengths divided by the buffer area (m/m^2). Agricultural cover was calculated as a proportion of total surface within the buffer (0–1).

2.4. Choice of landscape scale

Given that the effect of a landscape variable on bat activity may vary according to the spatial scale considered (Lacoëuilhe et al., 2016; Monck-Whipp et al., 2018), landscape variables included in our analyses were calculated for 10 nested buffers ranging from 0.5 to 5 km (similarly to Put et al., 2019), in accordance with reported bat home ranges (Laforge et al., 2021). A single buffer radius per variable and bat guild was selected by fitting negative binomial regression models of nightly bat activity per guild against the variable in question. We selected the buffer size corresponding to the model with lowest AIC to be used in multivariate models (Supplementary material Table S3 and Fig. S6).

2.5. Weather

Weather variation, known to influence bat activity (Ciechanowski et al., 2007), was accounted for by including the daily mean temperature, a Boolean factor indicating whether precipitation took place, and mean wind speed for the date when the night started. Weather variables were sourced from the E-Obs dataset, in the Copernicus database (surfobs.climate.copernicus.eu). We downloaded version 25.0e of 0.1-

degree gridded data on daily mean temperature, precipitation sums and mean wind speed. For each acoustic sampling point, data from the closest position in the weather grid were assigned. Acoustic sampling took place under favorable weather conditions (Dubos et al., 2021): no rain expected, wind speeds under 5 m/s, and temperatures above 12 °C (Supplementary material Fig. S2).

2.6. Statistical analysis

A generalized linear mixed model was fit, assuming a negative binomial distribution of residuals, for bat activity as the total number of bat passes by site-night, by guild (SRE, MRE, LRE). All 3 models contained as explanatory variables the presence of wind turbines and the above-defined landscape variables: parcel size, parcel diversity, hedge density, road and railroad density, watercourse density and agricultural cover. They also included the weather variables temperature, precipitation and wind speed, as well as the Julian date, with a linear and quadratic component to account for phenological changes in activity along the summer season. The interactions between the presence of wind turbines and the rural landscape variables of interest (parcel size, parcel diversity and hedge density) were included and retained only if significant.

A considerable amount of recorded nights displayed 0 bat passes: 20 % of site-nights for LRE, 2 % for MRE, and 14 % for SRE. Following diagnostic, a zero-inflation component was incorporated to all models, including the weather parameters as explanatory variables for the probability of presence against the absence of bat passes in a night. The significance of interactions and fixed effects was tested by means of type III Wald Chi-squared tests. Explanatory variables were never found to be collinear: Pearson correlation coefficients remained below 0.5 (Supplementary material Figs. S8–10), and variance inflation factors remained below 2. Prior to model fitting, all variables were scaled and centered.

Although variation in detection range was minimized using device-specific trigger settings recommended by the Vigie-Chiro program, we included the device brand as a random effect to account for remaining between-brand variation. We also added random effects between 12 administrative regions, which vary consistently in climate, orography and main land uses, as well as between years (Supplementary material Fig. S14).

Data analysis was performed on R 4.1. Landscape variables were treated with package *sf* (Pebesma, 2018). Wind turbine positions were downloaded using package *osmdata* (Padgham et al., 2017) and their creation date was obtained using package *rvest* (Wickham, 2022). Package *glmmTMB* was used for model fitting (Brooks et al., 2017).

Wald tests were run with package car (Fox and Weisberg, 2019), zero-inflation, overdispersion and homoscedasticity were tested using package DHARMA (Hartig, 2022). Plots were drawn using packages ggplot2 (Wickham, 2016) and gridExtra (Auguie, 2017).

3. Results

Bat activity was dominated by MRE, which accounted for 85 % of all bat passes, with 0 to 11,455 bat passes per night (median 263). LRE accounted for only 5 %, and their activity fluctuated between 0 and 2283 bat passes (median 6). The remaining 10 % pertained to SRE, counting between 0 and 5103 bat passes (median 10; Supplementary material Fig. S1). The Common Pipistrelle *Pipistrellus pipistrellus* was the most abundant species, accumulating 76 % of recorded MRE bat passes. The Lesser Noctule *Nyctalus leisleri* was the most frequent LRE, with 42 % of bat passes within this guild, while the Greater Horseshoe Bat *Rhinolophus ferrumequinum* and Daubenton's Bat *Myotis daubentonii* were the most common SRE with 30 % and 29 % of bat passes in this guild respectively (Supplementary material Table S1).

Trends in AIC relative to buffer radii were apparent for most landscape variables (Supplementary material Fig. S7). Some were however not sensitive to scale, for instance the turbine presence and parcel size for MRE. Landscape variables affected the activity of each guild mostly at different scales, and no guild showed a consistently larger or smaller effect radius. For example, in the case of wind turbine presence, SRE showed responses at a larger scale (3 Km) than LRE and MRE (1.5 Km), while the response to hedge density was at a larger scale in LRE (4.5 Km) and SRE (1.5 Km) than in MRE (0.5 Km). Watercourses presented strong model fit values at 0.5 Km for all 3 guilds (Supplementary material Table S3).

3.1. Bat activity models

Wind turbines correlated with reduced bat activity when present within 1.5 Km for LRE, and within 3 Km for SRE. Conversely, MRE activity was positively correlated with the presence of wind turbines. LRE bats were unaffected by parcel size and diversity. Hedge density correlated positively with LRE activity, but only in the presence of wind turbines, antagonizing their deterrence effect. Model predictions for this interaction between wind turbine presence and hedge density cannot be interpreted at the higher end of the hedge density gradient, where few sites are found having wind turbines in the vicinity, and model confidence intervals are very wide. MRE activity decreased with parcel size and diversity, and increased with hedge density. For this guild, no significant interactions were found between wind turbines and landscape variables. SRE activity decreased with parcel size and increased with the

density of hedges. However, parcel diversity antagonized the negative effect of wind turbine presence, similarly to the trend observed between hedge density and LRE bat activity (Figs. 2 & 3).

All model covariates correlated with the activity of at least one guild. The density of watercourses stands out among the landscape covariates, as it relates to increases in the activity of all 3 guilds. Road and railroad density correlated positively with LRE and negatively with SRE activity, while agricultural cover correlated negatively with the activity of LRE and SRE, but positively with that of MRE (Fig. 2, Supplementary material Fig. S12).

Responses to weather varied between guilds, where warmer temperatures increased the activity of LRE and MRE but decreased that of SRE, precipitation hindered the activity of LRE, and wind speed only had a slight effect on MRE activity. Wind speeds in our sample range from 0.35 to 8.99 m/s, with 75 % of nights showing values below 3.4 m/s, while the full period registered wind speeds up to 14.05 m/s. Finally, SRE activity first increased with the Julian date, levelled off mid-season and decreased toward the end of the period (Fig. 2, Supplementary material Fig. S13).

4. Discussion

The responses of bat activity to landscape homogenization, quantified as parcel size, parcel diversity and hedge density, were heterogeneous among three different echolocation guilds representing different foraging strategies. The activity of long-range echolocating bats, which forage at high altitude, was independent of the aforementioned variables in the absence of wind turbines. Guilds with shorter detection ranges, MRE and SRE, showed higher activity in landscapes with small parcels (cf. Monck-Whipp et al., 2018) and elevated hedge density (cf. Boughey et al., 2011; Lacoëuilhe et al., 2016). Wind turbines decreased the activity of LRE and SRE bats, as expected based on previous results at a narrower geographical context (Barré et al., 2018b; Leroux et al., 2022). Here, we provide an unprecedented description of antagonistic interactions between the presence of wind turbines and hedge density in the case of LRE activity, and with parcel diversity for SRE.

MRE bats, mainly *P. pipistrellus*, showed enhanced activity in landscapes containing wind turbines. Current literature shows no consensus on the responses of this guild: while avoidance has been reported (Barré et al., 2018a), attraction has often been observed in the immediate vicinity of turbines (Cryan et al., 2014; Leroux et al., 2022) and highlighted for *P. pipistrellus* (Richardson et al., 2021). However, and in contrast with the cited research, acoustic detectors in our study were most often placed further than 100 m away from any wind turbine (Supplementary material Fig. S11).

Rural landscape variables did not always act in the expected

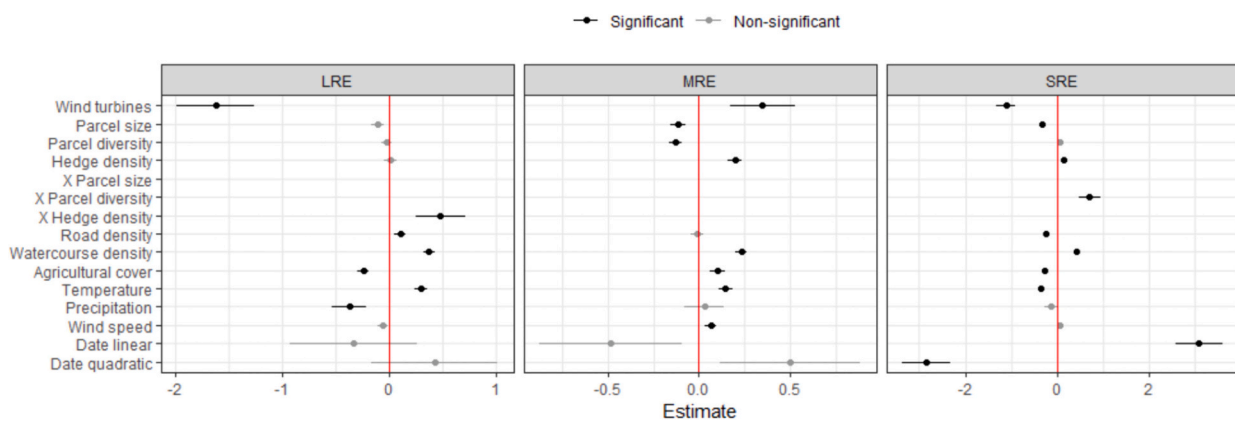


Fig. 2. Model coefficient estimates by guild. Interactions between the presence of wind turbines and agricultural landscape components are represented by “X name of landscape component”. “Date” refers to the Julian date. Only significant interaction coefficients are represented. Lines represent the estimates’ 95 % confidence intervals.

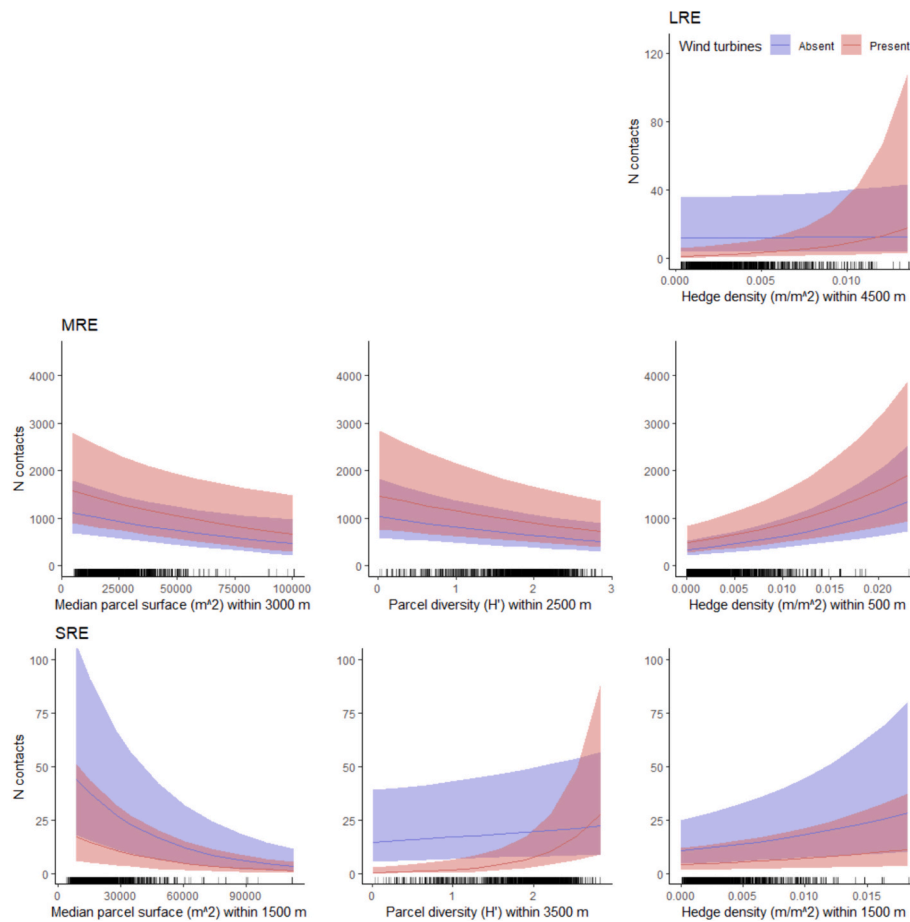


Fig. 3. Model predictions for activity by guild against median parcel surface (LEFT), parcel diversity (CENTER) and hedge density (RIGHT), in absence or presence of wind turbines.

direction. As hypothesized, the deleterious effect of wind turbines on the activity of LRE and SRE did interact with variables reflecting landscape homogenization. However, wind turbine impact was not smaller in homogenized landscapes, but it rather seems that heterogeneous configurations compensated for deterrence by wind turbines. In the case of LRE bats, hedge density was the compensating variable. The activity detected around hedges may either represent uses by this guild other than for hunting (commuting, shelter from wind), or enhanced food resources that counter the tendency to avoid areas with wind turbines. While there is consensus on the positive effect of hedges on activity levels of MRE and SRE bats (Froidevaux et al., 2019; Lacoëuilhe et al., 2016; Pinaud et al., 2018), the response of LRE bats is more context dependent: Boughy et al. (2011) reported no effects on the activity levels of *Nocules* (LRE), but Barré et al. (2019) as well as Lacoëuilhe et al. (2016) detected positive effects. The use of roads and watercourses for commuting between roosting and foraging habitats may explain the positive relationships between these features and bat activity (Kerbiouri et al., 2018), but the fact that the total agricultural cover had a negative effect (see also Put et al., 2019) may as well imply that these elements also drive local trophic resource availability.

With an objective of minimum bat activity loss at the landscape level, a land sparing criterion may be followed for new wind turbine installation, by prioritizing areas with larger parcel size and lower hedge density, where MRE and SRE bat activity levels are lower. A land sharing interpretation would foster hedge densities and crop diversification in areas where wind turbines are already present, to compensate for the deterrence effect of turbines on LRE and SRE bats.

Our results suggest far-reaching effects of wind turbine presence, as well as of landscape variables related to rural homogenization, with

most variables showing a best fit for areas of 1.5 to 4.5 Km around the sampling site. We therefore recommend calculating landscape variables at different buffer radii up to 5 km when evaluating landscape effects on the expected impact of wind turbine placement. The landscape scale of bat deterrence effects by wind turbines remains poorly understood. Barré et al. (2018a) suggested that this effect spans beyond 1 Km in a rural context, while Gaultier et al. (2023) estimate an effect radius of 0.6 Km for *E. nilssonii* and 0.8 Km for *Myotis* spp. in forests. Considering that wind turbines affect bat activity at distances over 1 Km means that, to avoid impacts on protected or sensible areas, such distances should be respected. Furthermore, evidence for large scale landscape effects on mortality due to wind turbines was provided by Moustakas et al. (2023), who propose scales of at least 5 km.

Mortality should indeed be considered together with habitat loss when evaluating impacts. Attraction of some bats such as *Pipistrelles* to wind turbines may increase collision risks (Jameson and Willis, 2014). *Pipistrelles* are the main bat group affected by mortality due to wind turbines in Europe (Rydell et al., 2010), but the high-flying LRE bats are as well exposed to collisions (Roemer et al., 2017). If hedge density promotes levels of LRE bat activity in the presence of wind turbines, it should be evaluated whether they also increase activity within collision risk areas, by gathering bat detection data at the relevant heights and with the appropriate devices (Barré et al., 2023; Voigt et al., 2021).

Finally, grouping observations into echolocation guilds is useful for large-scale ecological analyses of bat responses to landscape variables. It allows for comparisons across biogeographical boundaries, and avoids bias due to misidentification between phenotypically close species (e.g. different *Myotis* spp.). However, for preliminary impact assessment, it cannot substitute an evaluation of the presence of locally rare and

endangered species, whose responses are bound to be masked by variation in the activity of the most common species within each guild (e.g. variation in MRE activity is fundamentally variation in *P. pipistrellus* and *P. kuhlii*).

The multiple factors and scales involved in anthropogenic change hinder the impact assessment of a single human activity type. Agricultural homogenization is associated to the broader process of intensification (e.g. Put et al., 2019), which involves agrochemical use, resulting in the loss of foraging resources for bats, thus reducing their local abundance (Barré et al., 2018b; Wickramasinghe et al., 2003). To disentangle landscape composition and structure effects from the impacts of agrochemical use, data on agricultural practices need to be made publicly available (see Galimberti et al., 2020). Only then may an offsetting approach be undertaken to mitigate biodiversity loss due to wind energy production through gains obtained by changes in agricultural landscape structure, as here proposed, and practices (see Millon et al., 2021).

CRedit authorship contribution statement

Alejandro Sotillo: Writing – original draft, Formal analysis. **Isabelle le Viol:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Kévin Barré:** Writing – review & editing, Methodology, Conceptualization. **Yves Bas:** Software, Resources, Data curation. **Christian Kerbiriou:** Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110647>.

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