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RESEARCH ARTICLE

Distance to hedgerows drives local repulsion and attraction of wind turbines on bats: Implications for spatial siting

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Abstract

1. The exponential development of wind energy raises concerns regarding its impacts on airborne biodiversity. Evidence of wind turbine attraction and repulsion on bats, and underlying collision risks and habitats losses, are increasingly reported. Since bat activity strongly decreases with distance to optimal habitats such as woody edges, we hypothesize that the distance to these habitats could drive attraction and repulsion in the immediate vicinity of wind turbine. Although several studies have demonstrated wind turbine attraction and repulsion on bats separately, none have so far investigated the co-existence of both in the same landscape context and evaluated the underlying safe siting distance of wind turbines to bat habitats.
2. We assessed how wind turbines alter bat activity in their immediate vicinity when located at different distances from hedgerows. We acoustically quantified bat activity for two guilds (short-and long-range echolocators) and two species/species group (*Pipistrellus pipistrellus* and *Pipistrellus kuhlii/nathusii* from the mid-range echolocators guild) in open areas from 10 to 283 m from hedgerows using a paired sampling design (i.e. recordings conducted simultaneously in areas with and without wind turbines). Sixty-five pairs were sampled over 23 nights during the migration period (i.e. from late summer to late fall) in France.
3. Overall, in the absence of wind turbine, we found that bat activity decreased with increasing distance to hedgerows for all guilds, as widely reported in the literature. Yet, this pattern was no longer observed under wind turbine.
4. When looking at specific distances to hedgerows, we found the activity of all bat groups and species (except for *Pipistrellus kuhlii/nathusii*) near hedgerows (10–43 m) to be drastically lower under wind turbines than without wind turbine. In contrast, the activity of short-range echolocators was higher under wind turbines when located at 43–100 m from hedgerows, and it tended to be higher for long-range echolocators. Lastly, no effect was detected under wind turbines located at 100–283 m from hedgerows for any guild.

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5. *Synthesis and applications*. This study provides empirical evidence that wind turbines close to optimal habitats such as hedgerows strongly repel bats, while wind turbines located farther away in open areas could attract them. Increased risks of collisions and habitat losses near edges strengthen the importance of keeping wind turbines at a sufficient distance from woody edges (e.g. 200 m as recommended by EUROBATS guidelines).

KEYWORDS
acoustic monitoring, attractive effect, aversive effect, bat spatial distribution, collision risk, habitat loss, wind energy planning, woody edges

1 | INTRODUCTION

Habitat loss, either due to land use change or land consumption, is widely recognized as a major threat to global biodiversity (Maxwell et al., 2016). Over the past decades, infrastructure development (e.g. housing, power lines, roads, etc.) has largely contributed to direct effects on biodiversity by increasing mortality events through collisions with airborne animals (e.g. Loss et al., 2015) and habitat losses through destruction (August et al., 2002; Gaston et al., 2003). However, infrastructures can also generate in their vicinity indirect effects on biodiversity by affecting habitat use by species. This is especially true for wind energy facilities, which are characterized by a small ecological footprint compared to other infrastructures, but are not free from negative externalities on biodiversity through: (a) collisions which can threaten population viability of airborne taxa such as bats (Frick et al., 2017) and (b) a reduced attractivity of adjacent habitats (Barré et al., 2018; Millon et al., 2015; Millon et al., 2018; Minderman et al., 2012; Minderman et al., 2016).

In a context of accelerating biodiversity and climate change crises, reconciling the development of renewable energies and biodiversity conservation still appears as a major issue. Indeed, wind energy development is growing fast as part of climate change mitigation strategies (e.g. France has set an ambitious target of 20% of electricity produced by wind power by 2028, and has planned the installation of 6,500 wind turbines between 2018 and 2028). So far, most studies on bats and wind energy have focussed on mortality, contributing to define guidelines for considering bats in wind farm projects. For instance, European guidelines from UNEP/EUROBATS agreement (Rodrigues et al., 2015) advise that wind turbines should be placed at least 200 m away from any woody edges to avoid collisions. Indeed, woody edges represent optimal habitats for many bat species (Frey-Ehrenbold et al., 2013; Kelm et al., 2014), as they can serve as commuting routes and foraging sites (Froidevaux et al., 2019; Pinaud et al., 2018; Walsh & Harris, 1996). However, such guidelines generally do not account for wind turbine impacts on habitat use by bats. Specifically, the use of woody edges by bats was recently shown to strongly decrease until at least 1 km away from wind turbines (Barré et al., 2018). Hence, guidelines should account for both collision risks and changes in habitat use to build efficient siting recommendations.

When placed close to optimal habitats such as hedgerows, the presence of wind turbines negatively affects bat activity at such habitat (Barré et al., 2018; Figure 1a). More specifically, we expected these repulsion effects to mainly occur in the first 50 m from hedgerows to open area which concentrate most bat activity (Heim et al., 2017; Kelm et al., 2014; Figure 1b). In contrast, other studies have reported observations of individuals attracted to wind turbines placed far away from hedgerows (e.g. one to several hundreds of meters) in open habitat (Cryan et al., 2014; Figure 1a). Hypotheses to explain such attraction are that bats may misperceive turbines to be a tree and thus adopt roosting and mating behaviours, or may actively forage at turbine due to insect accumulation (Cryan et al., 2014; Foo et al., 2017; Kunz et al., 2007; Rydell et al., 2016). Following these studies, we hypothesized that a turbine located in open areas far from woody edges could potentially constitute a structural element for bats and a more valuable foraging site than open habitats in the immediate vicinity. We therefore expected bat activity to increase at the wind turbine's base in open area compared to a context without wind turbine (Richardson et al., 2021; Figure 1b). We finally expected these attraction effects to be more pronounced for edge- and open-space foragers as they spend more time in open areas than narrow-space foragers (Denzinger & Schnitzler, 2013), while repulsion effects should affect all bat guilds (Barré et al., 2018). Although assessing the effect of wind turbines on bat activity along a gradient of distance to woody edges is essential to provide relevant spatial siting guidance, no studies have so far investigated such a relationship.

The aim of the study was to unravel both repulsion and attraction effects generated by wind turbines on bats in relation to turbine siting distance from woody edges. We assessed bat activity by recording echolocation calls of three guilds (short-, mid- and long-range echolocators, corresponding to narrow space, edge space and open space foragers, respectively; Denzinger & Schnitzler, 2013) along a distance gradient of 10 to 283 m from hedgerows using a paired sampling design with and without a wind turbine. To ensure the robustness of the paired sampling design, we standardized within each pair other landscape variables known to either positively (e.g. forest and grassland proportion, water proximity or hedgerow density; Boughey et al., 2011a; Froidevaux et al., 2019; Heim et al., 2017; Sirami et al., 2013) or

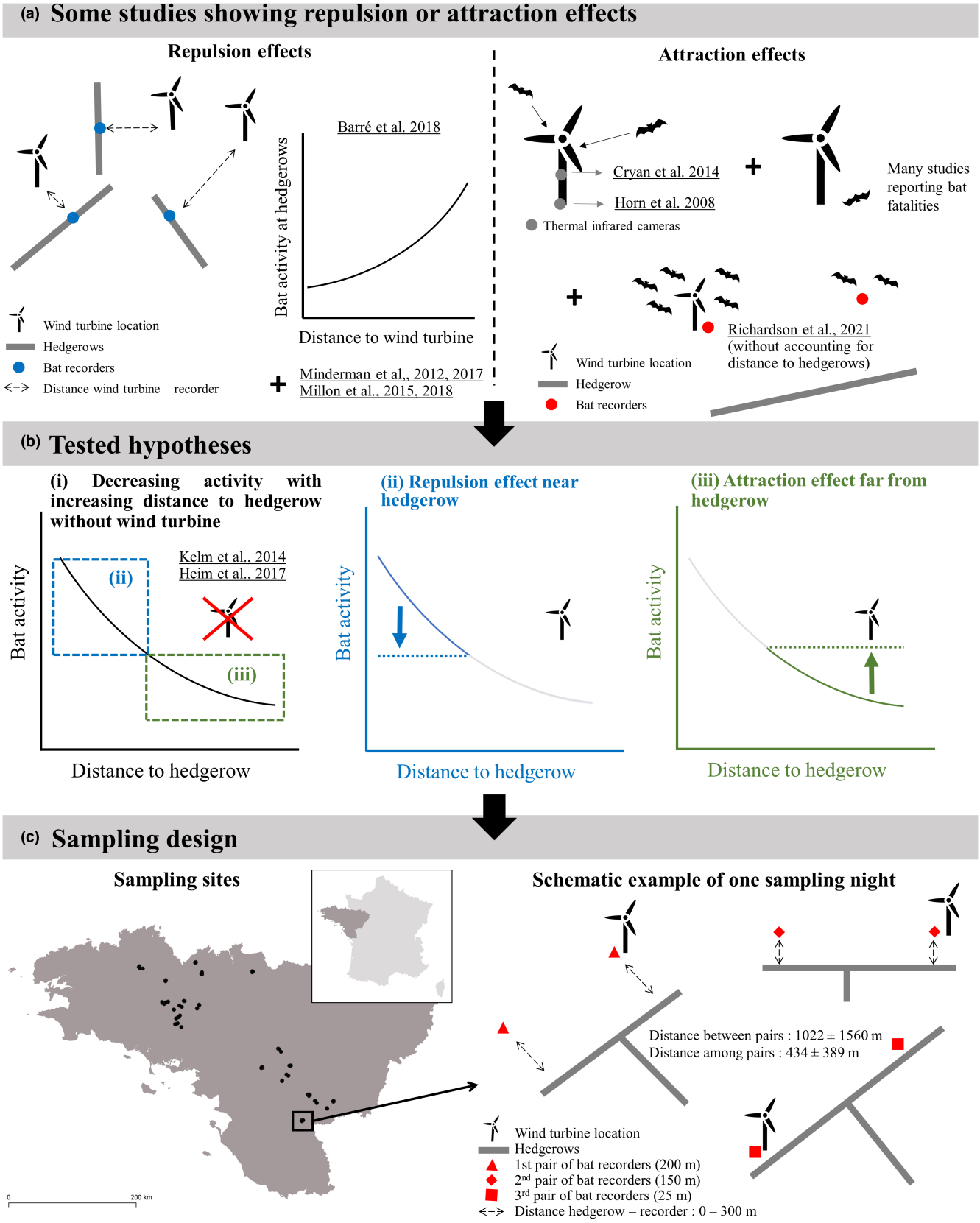

FIGURE 1 Synthesis of main knowledge about repulsion and attraction effects of wind turbines on bats (a), underlying tested hypotheses in this study (b) and sampling design performed to address it (c).

negatively (e.g. arable land proportion; Put et al., 2019) affect bat activity. We specifically predicted that: (a) without wind turbine bat activity should decrease with the increasing distance to hedgerows; (b) when a wind turbine is placed close to hedgerows (i.e. <50 m), the activity of all guilds would be much lower at the turbine's base due to repulsion in comparison with a context without wind turbine; and (c) when a wind turbine is placed far from hedgerows, the activity of edge- and open-space foragers at the turbine's base would be higher due to attraction compared to a context without wind turbine (Figure 1b). While worldwide policies are leading to an extensive development of wind energy to limit greenhouse gas emissions, this study provides practical recommendations for safe spatial siting to limit both bat fatalities (i.e. attraction effects) and habitat losses (i.e. repulsion effects).

2 | MATERIALS AND METHODS

2.1 | Study area

We collected data at 28 wind farms containing a total of 243 turbines (3–20 per farm, 7.7 in average) across two regions (Bretagne and Pays de la Loire) in northwest France, representing 26.7% of installed turbines in these regions. Wind turbines were in average 82 m (*SD* ± 11 m) in hub height and at each farm all turbines had the same height. Blade length was in average 41 m (*SD* ± 5 m). Main habitats of the study regions consisted of farmland (82.2%), with 48% of arable land and 34% of grassland. Urban areas covered 6% of the study area and were mainly characterized by villages and small towns, while forests and wetlands covered 11 and 1%, respectively.

2.2 | Sampling design

To investigate the effect of wind turbines on the relationship between bat activity and distance to hedgerows, we recorded bat activity through a paired sampling design using sites located under wind turbines at 4 m from the mast (treatment) paired with sites without wind turbines (control; Figure 1c), hereafter referred to as 'sampling pairs'. We sampled a gradient of distances to hedgerows from 10 to 283 m. For each pair, we standardized the sampled habitat (i.e. either cropland or grassland), distance to hedgerows and type of hedgerow (see Appendix S1). Moreover, we ensured that there were no differences in landscape composition between control and treatment sites (see Table S1 for paired Wilcoxon tests). Each night, we sampled one to three pairs simultaneously (2.8 in average) at contrasted distances to hedgerows (see Table S2). In total, 65 pairs were sampled during 23 nights from September 7th to October 8th, 2015. No ethical approval was required for data collection. When needed, fieldwork permissions were discussed and granted directly by the owner of the land plot.

2.3 | Landscape variables

Although our sampling design minimizes differences in landscape composition between control and treatment sites, we accounted for landscape composition around recording sites during the modelling procedure (see Statistical analysis section) to control for residual variations. We selected a set of environmental variables known to influence bat activity according to the literature either positively, including hedgerows (Heim et al., 2017; Lacoeuilhe et al., 2018), forests (Boughey et al., 2011b; Froidevaux et al., 2021), wetlands (Sirami et al., 2013), and grassland (Froidevaux et al., 2019; Walsh & Harris, 1996), or negatively including arable land (Put et al., 2019), or both (i.e. negatively or positively), depending on the context and the species, such as urban areas (Azam et al., 2016). Thus, we calculated the proportion of arable land, grassland and forest as well as hedgerow density around each sampling sites. These variables were calculated within four buffer sizes previously used in European studies (250, 500, 750 and 1,000 m radii; Kalda, Kalda, & Liira, 2015; Lacoeuilhe et al., 2016) to use the more relevant scale of each variable for bats to be included into the models (see Statistical analysis section). We also calculated the distance to the nearest urban areas, forests and wetlands for each site. All variables were calculated from 2016 data using ArcGIS 10.0. Landscape data were provided by the National Institute of Geography (https://geoservices.ign.fr): wetland data were extracted from BD Carthage, forests and urban areas data were extracted from BD TOPO and hedgerows were manually digitalized from aerial photography (BD ORTHO). Grasslands and arable lands were extracted from Graphical Parcel Register (RPG; www.data.gouv.fr).

2.4 | Acoustic sampling

We recorded bat echolocation calls on 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.) put horizontally at 1.5 m above the ground on a pole and pointed parallel to the hedgerow and the ground. Recorders automatically recorded all ultrasounds between 8 and 192 kHz, using a trigger level set to 6 dB signal noise ratio and set to continue recording until 2 s after last trigger event, as widely used in previous studies (e.g. Azam et al., 2016; Barré et al., 2018; Millon et al., 2015).

As it is currently impossible to distinguish individual bats from their echolocation calls, we used the number of bat passes recorded during a night as a measure of bat activity. We defined a bat pass as one or several echolocation call(s) within a 5-s interval, which is a commonly accepted standard in Europe (e.g. Millon et al., 2015; Put et al., 2019; Stahlschmidt & Brühl, 2012).

We used the software TADARIDA (Bas et al., 2017) to automatically detect sound events and assign each bat pass to the most accurate taxonomic level. Then, assigned species were pooled into three

guilds based on similar echolocation call structure and in turn similar foraging strategies (i.e. short-range echolocators (SRE): *Myotis* spp., *Barbastella barbastellus* and *Plecotus* spp.; mid-range echolocators (MRE): *Pipistrellus* spp.; and long-range echolocators (LRE): *Nyctalus* spp. and *Eptesicus serotinus*; Frey-Ehrenbold et al., 2013; Denzinger & Schnitzler, 2013). These guilds represent different levels of sensitivity to wind turbines; the short range echolocators being especially sensitive to the habitat loss generated by wind turbines, followed by the mid-range echolocators (Barré et al., 2018), although the underlying mechanisms remain unknown, while the long-range echolocators are known to be highly sensitive to collision risks due to the great part of the time they spend at height, followed by the mid-range echolocators (Roemer et al., 2019). Species grouping also allowed us to include some species that can be difficult to study individually, either because they are rare or because it is difficult to detect them. Moreover, this way allowed to avoid any identification errors from TADARIDA software by pooling together species whose echolocation calls can be confused (Barré et al., 2019). However, as *Pipistrellus pipistrellus* dominated the MRE guild with 61% of bat passes (see Table S3), we conducted the analysis for *P. pipistrellus* and for the rest of mid-range echolocators (i.e. *Pipistrellus kuhlii/nathusii* species complex) separately.

2.5 | Statistical analysis

The statistical workflow is presented hereafter and summarized in Figure S1.

2.5.1 | Model building

To model the effect of the presence of wind turbines on bat activity at specific distances to hedgerows, we first built a full model in which we included bat activity as response variable using Generalized Linear Mixed Models (GLMMs; R package GLMMTMB). Due to the nature of the response variable (i.e. bat activity), we used a negative binomial error distribution for each bat group and species (short- and long-range echolocators, *P. pipistrellus* and *P. kuhlii/nathusii* from mid-range echolocators). Since the sampling design was based on several pairs sampled per night (recordings conducted simultaneously in areas with and without wind turbines), we included the identifier of sampling pairs nested within the date as random intercept effect to control for inter-nights and inter-pairs variations in bat activity. We included as fixed effects the distance to hedgerows as categorical variable (see below for more details), type of site (i.e. control: absence of wind turbine; treatment: presence of wind turbine), and their interaction. Then, we also included as fixed effects three weather covariates (mean temperature and wind speed at night, and total precipitation) to consider weather variations between nights (see Table S4). Finally, we also included a maximum of three landscape covariates (to avoid model over-parameterization) among a set of seven landscape covariates (see Table S5) known to influence bat activity (see the Landscape variables section). We first defined the most relevant computing buffer size for each proportion/density covariate (Fuentes-Montemayor et al., 2011; Kalda, Kalda, Lõhmus, et al., 2015) by fitting a separate univariate GLMM including the same random structure described above for each of these buffer sizes and covariates (i.e. 16 models for each species/group; see Table S6). We then retained for each covariate and species/group the buffer size included in the GLMM with the lowest AICc. Secondly, we followed the same method by building seven more univariate GLMMs for each species/group (i.e. one per covariate) and selecting the three landscape covariates included in the GLMMs with the lowest AICc to include in each full model (see Table S6). All continuous explanatory variables were scaled in full models. Thus, full models were built in the following way:

$$\begin{aligned}&\text{Bat activity}\%\text{Distance to hedgerows}+\text{Control/Wind turbine}\\&+\text{Distance to hedgerows: Control/Wind turbine}\\&+\text{mean temperature}+\text{mean wind speed}+\text{total precipitation}\\&+3\text{ landscape covariates}+1\,|\,\text{Date/pair}.\end{aligned}$$

To test for the effect of wind turbine presence at specific distances from hedgerows, we transformed the continuous distance to hedgerows into a categorical variable. We split distances into three classes according to a quantile classification to maintain sufficient and balanced number of samples in each category: 10 to 43 m, 43 to 100 m and 100 to 283 m. Distance classes align with Kelm et al. (2014) who found that most bat activity was contained in the first 50 m from hedgerows.

From full models we ranked all possible model combinations by AICc (R package MuMIn), and retained the model containing at least all variables of interest (i.e. distance to hedgerows, type of site, and their interaction) with the lowest AICc, hereafter referred to as 'selected model'.

Then, we assessed differences in activity levels both between control and treatment sites at specific distances from hedgerows and between specific distances for control and for treatment sites using post-hoc pairwise comparisons on selected models and full models for validation (see results validation section).

Finally, we also performed this modelling with the continuous distance to hedgerows using generalized additive mixed models (GAMMs; R package MGCV and LME4) to visually inspect continuous and non-linear patterns (see Figure S2 for more details).

2.5.2 | Post hoc pairwise comparison tests

For each selected GLMM model, we performed three complementary post hoc pairwise comparisons (R package LSMEANS) using Tukey's method for *p*-value adjustment when performing multiple comparisons to prevent type I error inflation. To check our hypothesis that without wind turbine bat activity would decrease with increasing distance to hedgerows, and to assess whether this pattern would be altered in the presence of wind turbine, we first tested for differences

in bat activity levels between classes of distance to hedgerows for control and treatment sites separately. Second, to test whether bat activity at the turbine's base would decrease near hedgerows and would increase far from hedgerows, we tested for differences in bat activity levels between control and treatment sites within each class of distance from hedgerows. Finally, we conducted a third post hoc pairwise comparison test on the same model as for the previous test except that we removed the interaction term to assess the effect of wind turbine on bat activity regardless of the class of distance to hedgerows.

2.5.3 | Model diagnostic

We ensured that there was no correlation between all explanatory variables contained in the models by conducting Spearman's rank correlation test (i.e. a correlation coefficient < |0.7|, Dormann et al., 2013; *rcorr* function, R package Hmisc; see Table S7 for correlation matrix). We also checked that there was no collinearity issues in both full and selected models using the variance inflation factor (VIF; *check_collinearity* function, R package performance): all variables had a VIF < 3 and the mean of VIF values was always <2 meaning that there was no evidence of multicollinearity (Zuur et al., 2010). We checked that there was no overdispersion in both full and selected models (*testResiduals* function, R package DHARMa). Finally, we checked full and selected model assumptions by plotting the residuals using the package DHARMa (*simulateResiduals* function).

2.5.4 | Validation of results through alternative statistical approaches

Finally, we validated results using two alternative approaches based on results from the full model and from each plausible model. Thus, in addition to the three pairwise comparison tests performed on the selected model, we also conducted them on each full model for comparison. Finally, to ensure that selected models provided reliable results, we also (a) assessed how many times the interaction was retained among a set of candidate models within a ΔAICc <7 (i.e. all plausible models, Burnham et al., 2011), and (b) tested for differences in activity levels between control and treatment sites within each class of distance from hedgerows for each of these candidate models containing the interaction.

All analyses were performed using the statistical software R 3.6.2 (2019).

3 | RESULTS

In total, we recorded 15,407 bat passes, with 1,090 passes of short-range echolocators (SRE), 13,105 passes of mid-range echolocators (MRE; including 61% passes of *P. pipistrellus*) and 817 passes of long-range echolocators (LRE; see Table S3 for guild composition). SRE were recorded in 71.1% of sites, MRE in 90.6% and LRE in 30.5%.

3.1 | Model ranking and variable selection

The selected model (i.e. model containing all target variables—distance to hedgerows, the type of site, and their interaction—with the lowest AICc) was also the model with the lowest AICc among all models (i.e. regardless of the inclusion of the target variables) for *P. pipistrellus*, SRE and LRE guilds. Nevertheless, it was only the 57th model for *P. kuhlii/nathusii*.

For all response variables, the AICc of both selected and full models were much lower than the AICc of the null one (see Table S8).

For *P. pipistrellus*, SRE and LRE guilds, the interaction between the presence of wind turbines and distance to hedgerows was included in most models within a ΔAICc of 7. Specifically, the interaction was retained in 26 out of 54 models (representing 63% out of 94% of cumulative weights) for *P. pipistrellus*, 13 out of 14 models (representing 89% out of 90% of cumulative weights) for SRE guild, and 56 out of 63 models (representing 86% out of 88% of cumulative weights) for LRE guild (see Figure S3). In contrast, the first and the only model to contain all variables of interest for the *P. kuhlii/nathusii* group among the 67 candidate models within a ΔAICc of 7 was only the 57th model with the lowest AICc (ΔAICc of 6.12 compared to the best model). For landscape and weather covariate results, please refer to the summary of the models (see Tables S9 and S10) and to the Appendix S2.

3.2 | Bat activity in relation to distance to hedgerows without and with wind turbine

In the absence of wind turbine, we found that the activity of all bat groups and species decreased with distance to hedgerows (Figures 2 & S2; Table 1). Specifically, we found activity level to be higher in the closest class of distance to hedgerows (i.e. 10–43 m) compared to all others (i.e. 43–100 m and 100–283 m) for SRE, LRE and *P. pipistrellus*, and compared to the third one (i.e. 100–283 m) for the *P. kuhlii/nathusii* group (Table 1). We did not detect any differences for all bat groups and species between 43–100 m and 100–283 m classes.

In the presence of a wind turbine, these differences between distance classes to hedgerows for all bat groups and species are no longer observed (Figures 2 and S2; Table 1).

When conducting these same tests on full models, we still observed at least one significant comparison for *P. pipistrellus*, SRE and LRE guilds showing evidence for the negative relationship between their activity and the distance to hedgerows (Table S11). As well as for the selected model, this relationship was no longer observed for any of these bat groups and species in presence of wind turbine (Table S11). These results corroborate the ones obtained with the selected model.

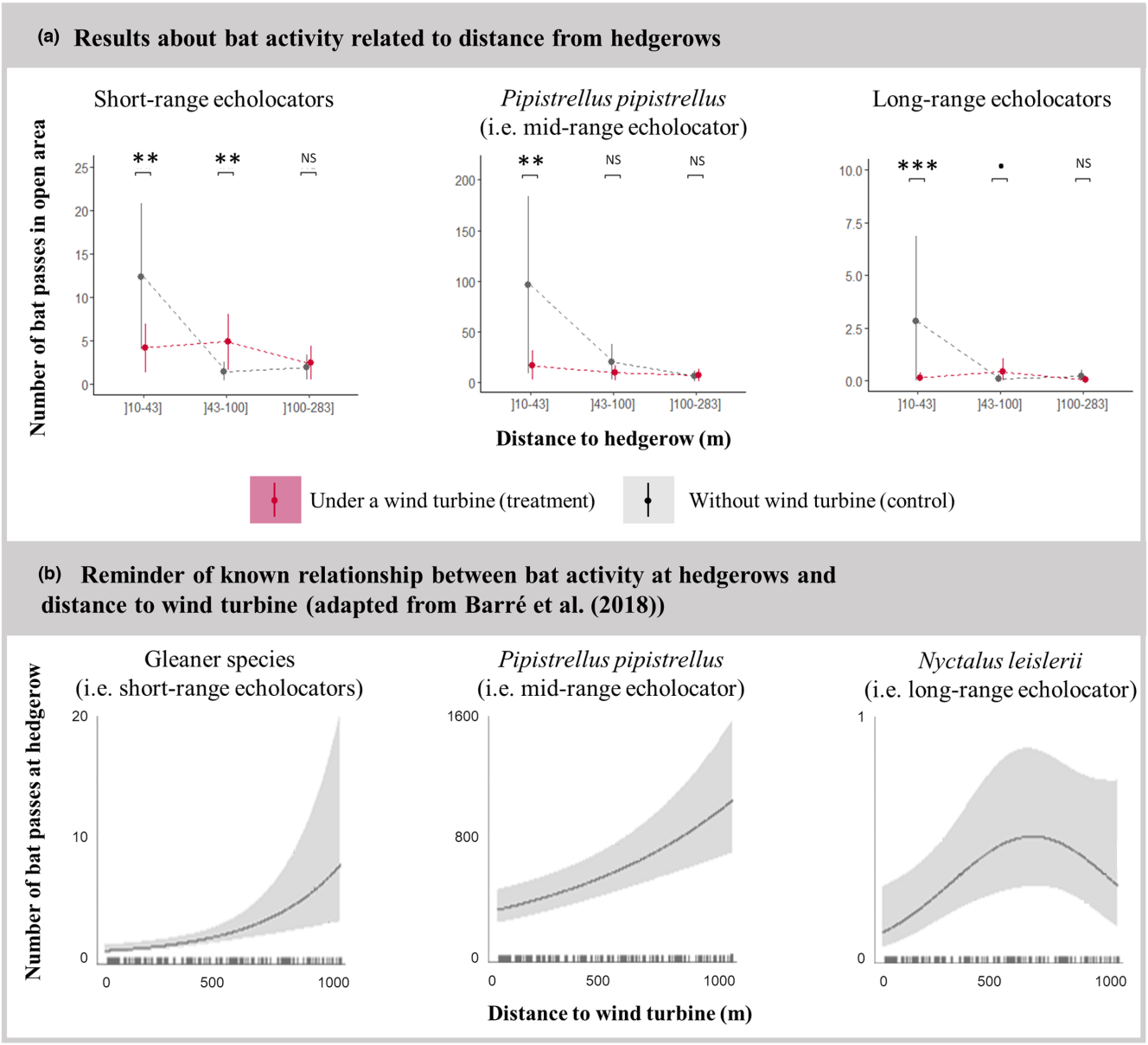

FIGURE 2 Predicted number of bat passes per night in open area in relation to distance from hedgerows for sites recorded under a wind turbine (red) and without wind turbine (grey) modelled from continuous distance to hedgerows using generalized additive mixed models (a). The panel (b) reminds known relationship between the number of bat passes at hedgerows in relation to distance from wind turbines showing long-distance repulsion on wooded habitat (adapted from Barré et al., 2018).

3.3 | Effect of wind turbine presence on bat activity within distance classes to hedgerows

Regarding activity level within the 10–43 m class of distance to hedgerows, the activity of SRE, *P. pipistrellus* and LRE was significantly lower in the presence of wind turbine (i.e. compared to site without wind turbine; Table 2), and the predicted activity was divided by 3.0, 5.6 and 18.6 respectively (Figure 2a). In contrast, we found SRE and LRE activity levels to be significantly higher (by 3.4 times) and nearly significantly higher (by 4.1 times), respectively, in the presence of wind turbine compared to control sites at 43–100 m from hedgerows. No effect was observed for *P. pipistrellus* and *P. kuhlii/nathusii*. No differences were found for all bat groups and species at 100–283 m (Table 2; Figure 2a; see Figure S4 for *P. kuhlii/nathusii*).

These results were confirmed when looking at the full models (Table S12), as well as at each candidate model including the variables of interests within a ΔAICc <7 (i.e. all plausible models considered as equivalent to the best one) with 100% of them showing in presence of wind turbine (a) a significantly reduced

TABLE 1 Estimates and *p*-values from pairwise comparison tests (using Tukey's method for *p*-value adjustment) on selected models containing the tested interaction (i.e. between the distance from hedgerows and the presence/absence of wind turbine) between classes of distance from hedgerows when 10–43 m class (a) and 43–100 m class (b) were used as intercept, for each bat guild and each modality (in absence of and under wind turbine). Significant *p*-values are shown in bold. See Table S9 for summary results of models (i.e. estimates, standard errors and *p*-values for each variable)

Bat foraging guild	Distance to hedgerows (m)	Absence of wind turbine		Under wind turbine	
		Estimates ± *SE*	*p*-value	Estimates ± *SE*	*p*-value
Short-range echolocators	(A) 10–43 versus 43–100	2.154 ± 0.480	**<0.001**	−0.157 ± 0.447	0.934
	(A) 10–43 versus 100–283	1.855 ± 0.477	**<0.001**	0.521 ± 0.501	0.554
	(B) 43–100 versus 100–283	−0.300 ± 0.492	0.815	0.679 ± 0.471	0.323
Pipistrellus pipistrellus	(A) 10–43 versus 43–100	1.563 ± 0.572	**0.020**	0.577 ± 0.546	0.543
	(A) 10–43 versus 100–283	2.697 ± 0.577	**<0.001**	0.881 ± 0.546	0.244
	(B) 43–100 versus 100–283	1.134 ± 0.553	0.105	0.304 ± 0.534	0.836
Pipistrellus kuhlii + *Pipistrellus nathusii*	(A) 10–43 versus 43–100	1.127 ± 0.636	0.183	1.223 ± 0.639	0.139
	(A) 10–43 versus 100–283	1.676 ± 0.647	**0.029**	1.444 ± 0.685	0.092
	(B) 43–100 versus 100–283	0.550 ± 0.642	0.669	0.221 ± 0.650	0.938
Long-range echolocators	(A) 10–43 versus 43–100	3.242 ± 0.887	**0.001**	−1.087 ± 0.900	0.451
	(A) 10–43 versus 100–283	2.610 ± 0.904	**0.013**	0.870 ± 1.065	0.693
	(B) 43–100 versus 100–283	−0.632 ± 0.956	0.786	1.958 ± 0.982	0.118

TABLE 2 Estimate and *p*-values from pairwise comparison tests on selected models containing the tested interaction (i.e. between the distance from hedgerows and the presence/absence of wind turbine) between bat activity under and without wind turbine (intercept) for each bat guild and each class of distance to hedgerows. Negative estimates mean a lower bat activity in presence of wind turbine compared to sites without wind turbine while positive estimates mean a higher activity in the presence of wind turbine compared to sites without wind turbine. Significant *p*-values are shown in bold. See Table S9 for summary results of models (i.e. estimates, standard errors and *p*-values for each variable)

Bat foraging guild	Class of distance to hedgerows (m)	Bat activity without versus under wind turbine	
		Estimates ± *SE*	*p*-value
Short-range echolocators	10–43	−1.096 ± 0.412	**0.009**
	43–100	1.215 ± 0.441	**0.007**
	100–283	0.237 ± 0.465	0.611
Pipistrellus pipistrellus	10–43	−1.721 ± 0.522	**0.001**
	43–100	−0.735 ± 0.508	0.151
	100–283	0.095 ± 0.446	0.831
Pipistrellus kuhlii/*Pipistrellus nathusii*	10–43	0.273 ± 0.546	0.618
	43–100	0.177 ± 0.582	0.762
	100–283	0.505 ± 0.587	0.391
Long-range echolocators	10–43	−2.92 ± 0.853	**<0.001**
	43–100	1.40 ± 0.773	0.072
	100–283	−1.19 ± 0.937	0.209

activity at 10–43 m from hedgerows for *P. pipistrellus*, SRE and LRE guilds and (b) a significantly increased activity at 43–100 m from hedgerows for SRE guild (Figure S5). Regarding LRE guild, 21% of candidate models, including the full model, showed also in presence of wind turbine a significantly increased activity at 43–100 m from hedgerows, and 55% showed a nearly significant (i.e. *p*-value between 0.05 and 0.1) increased activity (Figure S5).

3.4 | Effect of wind turbine presence on bat activity regardless of the distance to hedgerows

When looking at bat activity regardless of the distance to hedgerows on selected models (Table 3), we only detected a negative effect of wind turbine on *P. pipistrellus* activity. This effect became nearly significant when looking at full models (Table S13).

TABLE 3 Estimate and *p*-values from pairwise comparison tests on selected models without the interaction term (i.e. Distance to hedgerows:Wind turbine) between bat activity under and without wind turbine (intercept) for each bat guild. Negative estimates mean a lower bat activity in presence of wind turbine compared to sites without wind turbine while positive estimates mean a higher activity in presence of wind turbine compared to sites without wind turbine. Significant *p*-values are shown in bold. See Table S9 for summary results of models (i.e. estimates, standard errors and *p*-values for each variable)

	Bat activity without versus under wind turbine	
Bat foraging guild	**Estimates ± *SE***	***p*-value**
Short-range echolocators	0.058 ± 0.285	0.840
Pipistrellus pipistrellus	−0.696 ± 0.298	**0.021**
Pipistrellus kuhlii/Pipistrellus nathusii	0.317 ± 0.333	0.344
Long-range echolocators	−0.782 ± 0.579	0.180

4 | DISCUSSION

The coexistence of repulsive and attractive effects under wind turbines on bats in relation to their siting distance to commuting and foraging habitats such as hedgerows have so far received little attention. This study provides empirical evidence that under wind turbines placed close to hedgerows, bat activity is much lower compared to situations without wind turbine, while when placed in open area at an intermediate distance from hedgerows (between 43 and 100 m), bat activity can be higher. These results highlight the importance of keeping wind turbines far from optimal habitats to limit losses of habitat use due to repulsion effect. These results also highlight the need to limit attraction towards turbines in open areas and in turn collision risks by keeping wind turbines far enough from woody edges, for instance 200 m as recommended by EUROBATS guidelines.

Our results showed a negative relationship between bat activity and distance to hedgerows in the absence of wind turbine as shown in previous studies (Heim et al., 2016; Kelm et al., 2014), and revealed that this pattern was highly altered in the presence of wind turbine. Indeed, between 10 and 43 m from hedgerows, the activity of SRE, LRE and *P. pipistrellus* was negatively affected by the presence of wind turbines compared to a site without wind turbine at the same distance to hedgerows. In contrast, in open habitats between 43 and 100 m from hedgerows we observed a higher activity under wind turbines than without wind turbine for short-range and long-range echolocators, although the effect was marginal for this last guild (among the candidate models including the variables of interests within a ΔAICc <7, only 21% showed a significant effect and 55% a nearly significant effect). These results support the conclusions of Barré et al. (2018) (Figure 2b) and Richardson et al. (2021), which have shown repulsion near optimal habitat such as hedgerows and attraction in less optimal foraging habitat such as open areas, respectively. Our study also reveals the concomitance of these effects according to distance from hedgerows. Finally, we did not observe any significant difference in bat activity between control sites and treatment sites between 100 and 283 m from hedgerows, probably because of the low activity level in such homogenous agricultural landscape (Monck-Whipp et al., 2017). Lastly, the absence of wind turbine effect on *Pipistrellus kuhlii/nathusii*, at least near hedgerows, is consistent with the study of Barré et al., 2018. As the authors hypothesized in their study, this could reflect two opposite responses to wind turbines of these species due to different migratory status and in turn different flight behaviours.

Although no hypothesis was raised to explain the repulsion, there have been suggested that attraction of bats may be due to confusion with tall trees resulting in roosting and mating behaviours (Cryan, 2008; Cryan et al., 2014) or to insect and water accumulation which offers foraging and drinking opportunities (Foo et al., 2017; Jansson et al., 2020; McAlexander, 2013). These hypotheses could explain the higher activity in presence of wind turbine at 43–100 m from hedgerows. The fact that attraction was no longer detected at 100–283 m from hedgerows could suggest that below 100 m from hedgerows the costs for individuals located at hedgerows to come towards the turbine exceeds the benefits provided by the turbine. This could be explained by the higher energetic cost to cross such a distance, and by a reduced insect prey abundance at wind turbines located in such uniform agricultural area (Martin et al., 2020; Sirami et al., 2019). Moreover, 100 m from hedgerows in intensive croplands could be a threshold distance for some insects to disperse from hedgerows located at field margins (Morandin et al., 2014). We suggest that below 100 m from hedgerows wind turbines could no longer attract insects and consequently no bats. Since Richardson et al. (2021) detected wind turbine attraction on *Pipistrellus* species using sites at more than 532 m in average from total woodland in Great Britain, another explanation could be that bat activity become too low at more than 100 m from hedgerows in our study area to detect any significant effect.

4.1 | Perspectives and implications

Although the results on LRE are consistent with the effects observed for SRE, interpretations about distances at which effects occurred for this guild should be led cautiously since their detection range (up to 100 m according to Barataud, 2015) is larger than our first two distance classes. Then, as mechanisms involved in the responses we found cannot be inferred using bat activity level, we recommend the use of more accurate methods such as acoustic microphone array allowing for flight trajectory reconstruction to explore behavioural mechanisms. Nevertheless, our approach has revealed in a same spatial and temporal context the coexistence of two opposite phenomena (i.e. attraction and repulsion), which had been so far identified only separately in the literature.

Our results strongly emphasize the importance to consider distance to habitats when designing studies aiming to assess the effects of wind turbines on bat activity. Indeed, failing to account for

this variable could hamper the detection of wind turbine effects (i.e. attraction and repulsion) on bats (Table 3).

Our findings highlight new local stakes regarding the implantation of wind turbines near hedgerows by revealing the importance of considering both attraction and repulsion effects at the planned wind turbine location, in addition to the repulsion on surrounding habitats at a larger scale found by Barré et al. (2018) (Figure 2b). As a consequence, siting wind turbines too close to hedgerows (e.g. <50 m) will induce a strong reduction of activity locally and in turn habitat losses that are detrimental to species. We also conclude that a distance of at least 100 m between wind turbines and hedgerows should be kept to minimize attraction and in turn collision risks. Besides, although we did not find wind turbines to attract bats beyond 100 m from hedgerows, we recorded some activity meaning that there were still collision risks which should be addressed on a case-by-case basis depending on siting distance from woody edges. Indeed, in addition to sufficient distances between wind turbines and hedgerows, we also recommend addressing collision risks by wind turbine cut-in speed to prevent them from operating during peaks of bat activity.

Our conclusions are in line with current EUROBATS guidelines which recommend to avoid installing wind turbines at <200 m from hedgerows for minimizing attraction and repulsion effects locally (i.e. under a wind turbine). However, all these recommendations remain largely insufficient to avoid the loss of habitat use by bats on surrounding habitats at distance to wind turbines, which occurs in a perimeter of, at least, 1 km around wind turbines (Barré et al., 2018; Figure 2b). The fact that current EUROBATS guidelines cover only a part of distances of known impacts is even more worrying given that they are still often unapplied (Barré et al., 2018) with 89% turbines established in Northwest France not complying with it.

Finally, we draw attention to the crucial need for future studies about the impact of wind turbines on other attractive habitats for bats, like water bodies or forest, so that all major landscape elements for bats can be considered in wind energy planning.

AUTHORS' CONTRIBUTIONS

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

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the PNDB Data Repository https://doi.org/10.48502/rx37-fj67 (Leroux et al., 2022).

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