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Research article

Wind turbines in managed forests partially displace common birds

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ABSTRACT

Wind turbines are increasingly being installed in forests, which can lead to land use disputes between climate mitigation efforts and nature conservation. Environmental impact assessments precede the construction of wind turbines to ensure that wind turbines are installed only in managed or degraded forests that are of potentially low value for conservation. It is unknown, nevertheless, if animals deemed of minor relevance in environmental impact assessments are affected by wind turbines in managed forests. We investigated the impact of wind turbines on common forest birds, by counting birds along an impact-gradient of wind turbines in 24 temperate forests in Hesse, Germany. During 860 point counts, we counted 2231 birds from 45 species. Bird communities were strongly related to forest structure, season and the rotor diameter of wind turbines, but were not related to wind turbine distance. For instance, bird abundance decreased in structure-poor (−38%) and monocultural (−41%) forests with wind turbines, and in young (−36%) deciduous forests with larger and more wind turbines (−24%). Overall, our findings suggest that wind turbines in managed forests partially displace common forest birds. If these birds are displaced to harsh environments, wind turbines might indirectly contribute to a decline of their populations. Yet, forest bird communities are locally more sensitive to forest quality than to wind turbine presence. To prevent further displacement of forest animals, forests of lowest quality for wildlife should be preferred in spatial planning for wind turbines, for instance small and structure-poor monocultures along highways.

1. Introduction

Wind energy is among the major alternatives to promote a change from fossil fuels to renewable energy sources (Dehler-Holland et al., 2022; Veers et al., 2019). If renewable energy sources are prioritized in future, 25–40% of the world's energy will need to come from wind energy to achieve net-zero emissions by 2050 (BNEF, 2021). This assumes an additional demand of 500–800 TW-hours of wind energy per year (BNEF, 2021). Yet, constructing and operating wind turbines requires large areas of land (Diffendorfer et al., 2019; Kiesecker et al., 2019), which creates land use conflicts in populated regions around the globe (Brannstrom et al., 2017; Huesca-Pérez et al., 2016; Rand and Hoen, 2017; Wüstenhagen et al., 2007). A potential solution is to construct onshore wind turbines in remote areas far from residential areas. In Europe, where forests cover 38% of area (Gallaun et al., 2010), and in some countries even more than 65% of area (Global Forest Watch, 2014), constructing wind turbines far from residential areas has recently led to an accelerated expansion of wind turbines in managed forests (Fig. 1) (Enevoldsen, 2016).

Wind turbines in managed forests can produce energy as effectively as wind turbines in marine environments (Enevoldsen and Valentine, 2016). Wind turbines in managed forests, however, endanger the biodiversity and quality of forest ecosystems, creating a 'green-green conflict' between nature conservation and climate change mitigation (Kati et al., 2021; Katzner et al., 2019; Rehbein et al., 2020; Schöll and Nopp-Mayr, 2021; Voigt et al., 2019). Causalities due to collision with rotor blades or barotrauma have become a major issue in the protection of animals (Drewitt and Langston, 2006; Kunz et al., 2007; Lehnert et al., 2014; Voigt, 2021), in particular that of large and migratory species (Thaxter et al., 2017). Large species usually have long generation times, low rates of reproduction and small population sizes, so wind turbines pose a particular threat to their populations (Carrete et al., 2009; Frick et al., 2017; Katzner et al., 2017; Mattsson et al., 2022). Apart from collisions, wind turbines can negatively affect animals and the forest environment in other direct and indirect ways. Constructing wind turbines and their infrastructure causes habitat loss, edge effects and

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Fig. 1. Wind turbines in managed forests far from residential areas and animal migration routes, as a model for minimizing land use conflicts among society, nature conservation and climate change mitigation. Photo by S. Rösner.

fragmentation of forests (Diffendorfer et al., 2019; Haddad et al., 2015). Wind turbine construction alters the forest structure, leading to a loss of microhabitats important for foraging or nesting animals (Fernández-Bellon et al., 2019). Wind turbines can further block flyways of foraging and migrating animals, and disturb animals through the noise or shadowing of their rotating blades (Larsen and Madsen, 2000; Zwart et al., 2016). Forest degradation resulting from wind turbine construction may not directly kill animals, but may displace animals from otherwise suitable habitats (Ellerbrok et al., 2022; Hötker, 2017). If animals are forced to migrate from benign to harsher forest environments with more competitors or fewer resources (Kolk et al., 2020, 2022; Thiel et al., 2008), wind turbines might indirectly lead to fitness and population declines of the displaced animals.

To reduce potential conflicts between nature conservation and climate change mitigation, environmental impact assessments (EIA) commonly precede the construction of wind turbines in forests (Glasson et al., 2019; Morgan, 2012). EIA ensure that construction sites are limited to forests of low priority for nature conservation. Such forests include (i) small, fragmented, degraded and structurally-poor forests, (ii) forests not located along migratory routes of animals and (iii) forests that lack endangered species or species known to be sensitive to wind turbine collision or disturbance (Barrios and Rodríguez, 2004; Buchholz et al., 2021; Bunzel et al., 2019; Liechti et al., 2013). Wind turbines are consequently often constructed in managed or degraded forests. Previous studies found, however, that EIA could not always anticipate and mitigate post-construction effects of wind turbines on animals (Ferrer et al., 2012; Lintott et al., 2016). This is partly related to a lax implementation of EIA in practice (Morgan, 2012). Another possible reason for the inefficiency of EIA for reducing post-construction effects of wind turbines on animals could be that national or regional species lists mostly consider large bird species sensitive to wind turbines (Coppes et al., 2020; Mattsson et al., 2022). Small bird species are usually of minor importance during EIA (Allison et al., 2019), but can be similarly sensitive to wind turbines (Aschwanden et al., 2018; Erickson et al., 2014). It has yet to be extensively investigated whether wind turbines operating in managed forests disturb bird communities and lead to the displacement of common bird species.

In this study, we investigated the post-construction impact of wind turbines in forests on local bird communities in 24 temperate forests located in Hesse, Germany. Over a period of two years, an impact-gradient design was employed with point counts of all forest birds at distances between 80 and 700 m from one wind turbine in each forest. In addition, at the point count locations, characteristics of forest structure important for forest birds were assessed to account for differences in the habitat quality of forests (James and Wamer, 1982; Willson and Comet, 1996). Furthermore, we investigated whether the size of rotor blades explain differences in the local bird communities among forests. Wind turbines with large rotor blades are now commonly used for the construction of new turbines and the repowering of old turbines, as they produce more energy than wind turbines with smaller blades (Enevoldsen and Xydis, 2019; Lacal-Arántegui et al., 2020). A drawback is that they can also produce more noise (Møller and Pedersen, 2011) and increase collision risk of birds (Therkildsen et al., 2021), potentially increasing the negative effects of wind turbines on bird communities (Francis and Barber, 2013).

We expected negative post-construction effects of wind turbines on common forest birds. Consequently, we hypothesized that (H1) abundance and species richness of forest birds increase with increasing distance to a wind turbine; (H2) abundance and species richness of forest birds decrease with increasing rotor diameter; but (H3) the responses of birds to wind turbines and rotor diameter will be species-specific and thus, there will be changes in bird community composition with wind turbine distance and increasing rotor diameter.

2. Materials and methods

2.1. Study area

Our study was conducted in Hesse, a federal state in central Germany with one of the highest proportions of forest area (42%) in the country (HMUELV, 2012). Thirty-eight percent of these forests are owned by the state, 36% by communities, and 25% by private forest owners (HMUKLV, 2015). In Hesse, owners have to manage their forests in a sustainable way, so that multiple functions of the forest are maintained simultaneously, i.e. forest production, nature conservation and recreation (HMUKLV, 2018). Forest owners strive to avoid large-scale clear-cutting and the use of pesticides, and promote silvicultural practices that ensure long-term sustainability of forest production and protection (HMUKLV, 2018). Most of the managed forests in Hesse are either mixed deciduous forests dominated by beech (*Fagus sylvatica*, 31%), and oak (*Quercus* sp., 14%), or mixed coniferous forests dominated by spruce (*Picea abies*, 22%) (HMUELV, 2012). Currently, there are 472 wind turbines in Hesse's managed forests (1115 in total) and almost all of them were constructed in the last decade (FA Wind, 2022). The study sites were located at 24 managed forests with wind farms, with 12 sites each in deciduous and coniferous forests (Fig. 2, Table S1). The wind farms consisted of on average 6.3 (range: 3–12) wind turbines. Mean diameter of the rotor blades was 111.3 m (82 m–126 m) and mean turbine height was 194.3 m (145 m–212 m). Mean time since turbine construction was 5.1 years (2–13.5 years). Across study sites, the rotor diameter, the height, number and age of wind turbines were correlated ($r \geq 0.7$ in all but one comparison). Mean height of tree canopy was 17.8 m (9.6–28.2 m).

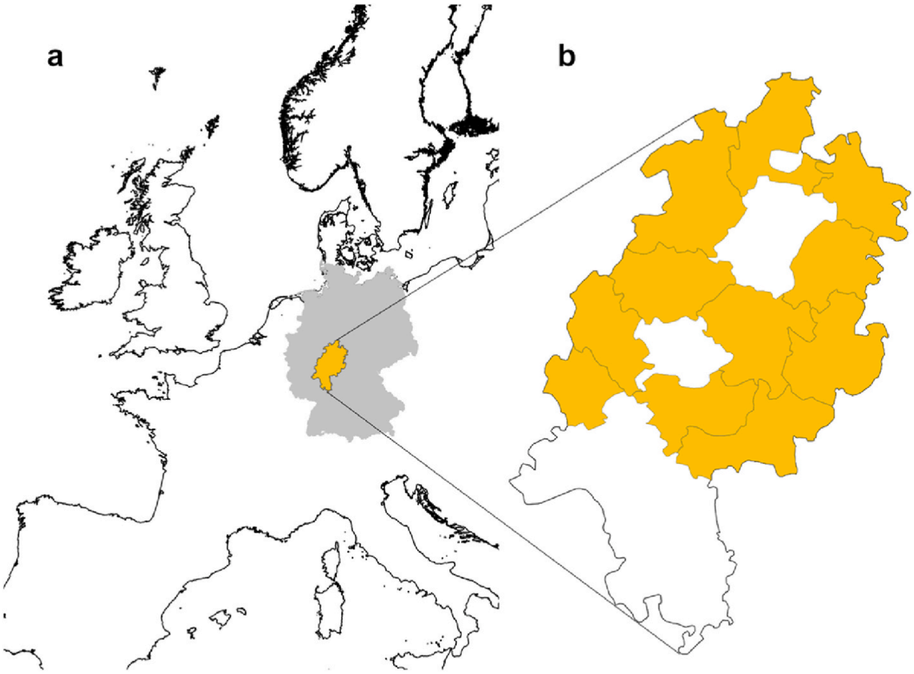

Fig. 2. Map showing the area of the 24 study sites in managed forests with wind turbines in (a) Germany and (b) Hesse in yellow. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. Forest bird monitoring

The abundance, species richness, composition and species-specific occurrence of forest birds in relation to wind turbine distance was assessed using an impact-gradient design (Ellis and Schneider, 1997). At each study site, one wind turbine at the edge of the wind farm was selected as the starting point for the impact gradient. The impact gradient was designed to ensure that the forest structure within study sites was relatively homogeneous and located far from roads and other wind turbines. The birds were monitored at five point locations, located at a distance of 80 m, 130 m, 250 m, 450 m and 700 m from the wind turbine (with some deviations due to forest structure). Point counts at each location were performed four times in both study years (2020 and 2021): March 11–31 (‘March’), April 1–30 (‘April’), May 1–20 (‘May’), and May 21 – June 20 (‘June’) (Südbeck et al., 2005). Point counts were performed between sunrise and 11 a.m. on days without rain and with low wind speed, and by the same observer throughout the study period. For each point count, all birds heard or seen within a period of 10 min and within a radius of 20 m around the point location were counted. Birds flying over the tree canopy were not included. The chosen study design is especially suited to record the local abundance of common songbirds, but not that of raptors, night-active birds or birds sensitive to human presence. Because we assumed that turbine operation may disturb birds we further recorded whether the wind turbine was operating during the point counts (‘operation status’). The order of study sites and direction of the distance gradient were randomly selected. Out of 960 planned observations (24 study sites × 5 distance points × 4 months × 2 years), data from 860 point counts (89.6%) were used in this study. In the other 100 cases, birds were not counted or the data were not included because (i) the forest was actively managed (2 point counts), (ii) it was too windy at the designated time (2 point counts), (iii) the distance gradient was incomplete due to clearings (16 point counts) and (iv) the forest at two study sites was logged after the first study year (80 point counts). Wind turbines were operating during 740 of the 860 point counts (86.0%).

2.3. Forest characteristics

Three forest characteristics were assessed that are known to influence the abundance and diversity of forest bird communities: forest composition (coniferous, deciduous and mixed forest), vertical vegetation heterogeneity and stand age. The trees within a radius of 250 m around each point count location were separated into deciduous and coniferous trees based on a land cover map from Copernicus (Copernicus Sentinel data 2018, for Sentinel data) using QGIS (version 3.4.13). In the following, forest composition describes the fraction of coniferous forest. As a proxy for the structural richness of forests, the vertical vegetation heterogeneity was assessed by estimating the vegetation cover at different heights (0 m, 0.5 m, 1 m, 2 m, 4 m, 8 m, 16 m and 32 m above ground) within a 5-m radius around each point count location between May and June each year. The Shannon-Weaver index at a point count location was calculated for each year and averaged. As a proxy for forest stand age, the diameter at breast height was measured for all tree individuals with a diameter ≥1 cm within a 10 m-radius around each point count location, and averaged.

2.4. Data analysis

2.4.1. Bird abundance and species richness analysis at community level

The relationship between total bird abundance and season, wind turbines and forest characteristics was analyzed using one generalized linear mixed model with a negative binomial distribution and a log link to account for overdispersion. In the model, the total abundance of forest birds served as the response variable, study sites as the random factor and the operation status of the wind turbines, the distance to the wind turbines, forest composition, vertical vegetation heterogeneity, log-transformed stand age, study year (2020 vs. 2021) and study months (March, April, May, June) as fixed factors. In addition, the two-fold interactions of wind turbine distance, year and month were tested. As wind turbines were operating or not operating randomly over time and sites, the interaction between wind turbine distance and operation status was tested, but not the interactions of operation status and year or month. Because total bird abundance was higher in mixed forests than in forests dominated by coniferous or deciduous trees, a quadratic term of forest composition was included to test for a non-linear relationship. Multicollinearity among fixed factors was checked, and all continuous fixed factors were z-transformed before the statistical analyses. The relationship between the species richness of forest birds and season, wind turbine distance and forest structure was analyzed by applying the model structure used in the analysis of bird abundance. A generalized Poisson distribution with a log link was applied to account for underdispersion.

2.4.2. Community composition

The relationship between bird community composition at a point count location and wind turbine distance and forest structure was analyzed using a permutational analysis of variances (PERMANOVA) (Anderson, 2017). The PERMANOVA was based on the maximum number of observations of bird species at the point count locations. The abundance of bird species was Hellinger-transformed before the analysis to assign low weight to rare species. The Bray-Curtis index was calculated as a dissimilarity measure. Wind turbine distance, forest composition, vertical vegetation heterogeneity and log-transformed stand age served as fixed factors. All continuous fixed factors were z-transformed before statistical analyses. To account for the nested structure of the data, the point counts were permutated among study sites, with 9999 permutations used to calculate a quasi-F statistic. Differences among forest bird communities at point count locations were visualized using nonmetric multidimensional scaling. The homogeneity of multivariate dispersion was determined (PERMDISP) (Anderson, 2017), and a Spearman rank correlation was used to check for differences in the dispersion of continuous variables.

2.4.3. Bird species analysis

Investigating total abundance of forest birds pooled for all species might hide changes in the abundance of certain bird species. However, we did not analyze bird abundance at the species level, because ≤3 bird individuals per species were documented at ~85% of the point count location, and the data distribution was highly right-skewed. Instead, we investigated whether the occurrence of forest bird species at point count locations was affected by wind turbines. For this, all point counts at a location were pooled across months and years. When a bird species was present during at least one of the eight point counts at a location, it was considered present at this point count location; otherwise it was absent. A generalized linear mixed model with the presence/absence of a bird species at point count locations served as the response variable, study site as a random factor, and wind turbine distance, forest composition, vertical vegetation heterogeneity and log-transformed stand age as fixed factors. A binomial error distribution and a logit link were used and all continuous fixed factors were z-transformed before statistical analyses. This binomial model structure was applied twice: (i) the first model included bird species identity and their interactions with distance, vertical vegetation heterogeneity and stand age as random factors, i.e. the largest possible random effect structure (Barr et al., 2013). This model tested whether there was a generally positive or negative relationship between bird occurrence and fixed factors, independent of the identity of the bird species; (ii) the second model included bird species and their interactions with forest composition, vertical vegetation heterogeneity, stand age and wind turbine distance as fixed factors. This model tested whether the occurrence of a certain bird species (for example the blackbird *Turdus merula*) was negatively or positively related to certain factors. Operation status was not part of the analysis because all wind turbines were in operation during the study period and the point counts were pooled over the study period. Only bird species were included in the models that were observed at a minimum of 15 point count locations and five study sites to guarantee a sufficient sample size for the analyses (n = 22 bird species in forests with wind turbines with only large rotors, and n = 15 bird species in deciduous forests with wind turbines of different rotor diameter, see 2.4.4).

2.4.4. Performing analyses with different subsets of wind turbines

The 22 wind turbines and their rotor diameters were non-randomly distributed across forest types, as there were no wind turbines with small rotors in coniferous forests (Fig. S1). This could have led to confounding effects when the effect of wind turbines (operation, distance, rotor diameter) was investigated in forest birds that did not occur in forests with wind turbines with small rotors. Therefore, the statistical analysis was split into two parts: first, the relationship between bird communities and the distance to wind turbines with only large rotor blades (diameter >100 m) was examined in deciduous, mixed and coniferous forests (H1), as described above. Second, the relationship between bird communities and rotor diameter as well as the distance × rotor diameter interaction was examined, but only in deciduous forests (H2). In the latter analyses, the model structure was the same as that used in the analysis of H1, but the linear and quadratic terms of forest composition were not included as fixed factors.

All statistical analyses were done with R program version 4.1.1 (R Core Team, 2021). Generalized linear mixed models were constructed using the R-package ‘glmmTMB’ version 1.1.2 (Brooks et al., 2017). Significance values were obtained using Wald-χ^2-tests in the package ‘car’ version 3.0–12 (Fox and Weisberg, 2019). Model performance was evaluated using the R-package ‘DHARMa’ version 0.4.5 (Hartig, 2021). The permutation analysis was conducted using the R-packages ‘vegan’ version 2.5–7 (Oksanen et al., 2020) and ‘RVAideMemoire’ version 0.9-81-2 (Hervé, 2022).

3. Results

3.1. Bird abundance and species richness in forests with wind turbines

During the two-year study, 2231 bird individuals from 45 species were observed during 860 point counts, with an average of 3.6 bird individuals (95% confidence interval: 2.9–4.5) from 2.8 (2.3–3.5) bird species per point count. The most abundant bird species was the common chaffinch (*Fringilla coelebs,* 10.5%), followed by the blue tit (*Cyanistes caeruleus*, 8.9%), the great tit (*Parus major*, 8.9%), the coal tit (*Periparus ater*, 8.2%) and the European robin (*Erithacus rubecula*, 7.7%). Five species were observed only once (bird species list in Table S2).

At the community level, the abundance and species richness of birds in forests with wind turbines was strongly related to the observation period (month and year) and forest structure (forest composition, vegetation heterogeneity and stand age, Table 1, Fig. 3, Fig. S2). For example, bird abundance was 68% greater in mixed forests (n = 3.2 ± 0.7) than in forests dominated by either deciduous (1.9 ± 0.4) or coniferous (1.9 ± 0.5) trees (Fig. 3a). Likewise, bird abundance increased by 63% with increasing heterogeneity of vertical vegetation structure in forests (2.6 vs. 4.2, Fig. 3b; by 109% in deciduous forests, 1.6 vs. 3.4), and by 60% with increasing age of deciduous forests (1.8 vs. 2.8, Fig. 3c). When a wind turbine was operating, bird abundance was reduced by 21.7%, and bird species richness by 22.8% (Table 1, Fig. 3d). There was no general relationship between the abundance or species richness of forest birds and wind turbine distance, nor was this relationship associated with the operation status of a wind turbine (Table 1, Fig. 3e). The relationship between forest bird abundance or species richness and wind turbine distance differed significantly, albeit inconsistently, across months and to a lesser extent also across years (Table 1). For example, forest bird abundance was higher in March than in the later months and did not change with distance. Forest bird abundance close to wind turbines was roughly similar during April, May and June but increased with wind turbine distance in April, did not change with wind turbine distance in May and decreased with wind turbine distance in June. The species richness pattern of forest bird communities was qualitatively similar to the pattern of bird abundance (Fig. S2). Forest bird abundance or species richness was negatively related to the rotor diameter of wind turbines in deciduous forests (Fig. 3f). For example, 2.7 bird individuals and 1.9 bird species were counted at small wind

Table 1

Mixed-model analyses of variance of the relationship between the abundance and species richness of forest bird communities in temperate forests and forest structure [the proportion of conifers (forest composition), vertical heterogeneity in vegetation structure (vegetation structure), mean DBH of trees (forest stand age)], temporal factors (year, month) and wind turbine characteristics (operation status, wind turbine distance, rotor diameter).

		Windfarms with large rotors in all forests				Windfarms with small and large rotors in deciduous forests			
		Abundance		Species richness		Abundance		Species richness	
	DF	Wald-χ^2	p	Wald-χ^2	p	Wald-χ^2	p	Wald-χ^2	p
Forest structure									
Forest composition	1	6.40	**0.011**	18.58	**< 0.001**				
Forest composition^2	1	16.79	**< 0.001**	7.52	**0.006**				
Vegetation structure	1	9.65	**0.002**	4.60	**0.032**	23.52	**< 0.001**	20.01	**< 0.001**
Stand age (log)	1	0.39	0.531	2.34	0.126	12.64	**< 0.001**	6.33	**0.012**
Temporal factors									
Year	1	0.02	0.894	2.02	0.155	0.71	0.400	1.35	0.245
Month	3	34.09	**< 0.001**	5.03	0.169	20.84	**< 0.001**	3.61	0.307
Year × Month	3	22.76	**< 0.001**	11.60	**0.009**	10.11	**0.018**	9.32	**0.025**
Wind turbine factors									
Operation status	1	9.72	**0.002**	13.80	**< 0.001**	4.99	**0.026**	8.77	**0.003**
Turbine distance	1	1.80	0.180	0.89	0.347	0.04	0.837	0.70	0.404
Turbine × Year	1	2.32	0.128	2.47	0.116	5.40	**0.020**	2.78	0.095
Turbine × Month	3	10.57	**0.014**	8.43	**0.038**	13.57	**0.004**	8.44	**0.038**
Turbine × Operation	1	1.21	0.272	<0.01	0.983	0.11	0.735	0.30	0.586
Rotor diameter	1					5.95	**0.015**	4.27	**0.039**
Rotor × Year	1					3.14	0.076	2.38	0.123
Rotor × Month	3					1.52	0.677	2.78	0.427
Turbine × Rotor	1					0.20	0.654	0.01	0.920

Note: Because the rotor diameter of the wind turbines was non-randomly distributed with respect to forest composition, the analysis was conducted twice, with different subsamples of wind turbines (see Methods).

turbines (diameter = 82 m), but only 2.1 bird individuals (−24.4%) and 1.68 bird species (−12.5%) in forests with large wind rotor diameter (diameter = 126 m). The negative relationship between rotor diameter and bird abundance tended to be more pronounced in the study year 2021 than 2020 (i.e. rotor diameter × year interaction, $0.05 < p < 0.1$, Table 1). There was no relationship between bird abundance or species richness and the interaction of rotor diameter and wind turbine distance in deciduous forests (Table 1).

3.2. *Bird community composition in forests with wind turbines*

In deciduous, mixed and coniferous forests, bird community composition (based on the maximum abundance of a bird species at a point count location) changed with the forest composition ($r^2 = 0.127$, quasi-$F_{1,\ 85} = 14.23$, $p = 0.035$), vertical vegetation heterogeneity ($r^2 = 0.025$, quasi-$F_{1,\ 85} = 2.85$, $p = 0.028$) and forest stand age ($r^2 = 0.037$, quasi-$F_{1,\ 88} = 4.19$, $p = 0.001$) (Fig. 4). For example, while the red crossbill (*Loxia curvirostra*) was associated with relatively young, coniferous forests, the wood warbler (*Phylloscopus sibilatrix*) and the nuthatch (*Sitta europaea*) were associated with older, deciduous forests (Fig. 4a). Similar significant relationships between bird community composition and vertical vegetation heterogeneity ($r^2 = 0.036$) or stand age ($r^2 = 0.052$) were also found in only deciduous forests (Table S2).

Bird community composition was not related to wind turbine distance (both $r^2 = 0.012$–0.013, all forests: quasi-$F_{1,\ 85} = 1.35$, $p = 0.158$, Fig. 4e; deciduous forests: quasi-$F_{1,\ 59} = 0.90$, $p = 0.482$). However, the bird community composition was marginally related to the rotor diameter of wind turbines (deciduous forests: $r^2 = 0.040$, quasi-$F_{1,\ 59} = 2.87$, $p = 0.074$, Fig. 4f), and the variation in the community composition of forest birds among point count locations increased with the rotor diameter of the wind turbines ($\rho = 0.64$, $p = 0.018$, i.e. increasing point spread with increasing rotor diameter, Fig. 4f, Fig. S3). For example, the two very frequent bird species, the common chaffinch (*Fringilla coelebs*) and the marsh tit (*Poecile palustris*), were mainly associated with forests with wind turbines with small rotors. In contrast, many different, partly less frequent bird species were associated with forests with wind turbines with large rotors. There was no relationship between bird community composition and the wind turbine × rotor diameter interaction (deciduous forests: $r^2 = 0.012$, quasi-$F_{1,\ 59} = 0.82$, $p = 0.472$, Table S2).

3.3. *Bird occurrence in forests with wind turbines*

At the point count locations, the occurrence of bird species was positively related to locations with a vertically heterogenous vegetation structure (all forests: Wald-$\chi^2 = 3.06$, $p = 0.080$; deciduous forests: Wald-$\chi^2 = 9.05$, $p = 0.003$). The occurrence of bird species was higher in mixed forests than in forests dominated by either deciduous or coniferous trees (i.e. quadratic term of forest composition, Wald-$\chi^2 = 11.31$, $p = 0.001$), but bird occurrence was not generally related to forest stand age ($p > 0.05$, Table S3). Similarly, there was no general trend in the relationship between bird occurrence and wind turbine distance (all forests: Wald-$\chi^2 = 0.08$, $p = 0.774$, deciduous forests: Wald-$\chi^2 = 0.48$, $p = 0.490$), rotor diameter (Wald-$\chi^2 = 1.03$, $p = 0.310$), nor the wind turbine × rotor diameter interaction (Wald-$\chi^2 = 1.51$, $p = 0.219$, Fig. 5). However, significant differences were observed in the occurrence of certain bird species as a function of rotor diameter (Wald-$\chi^2 = 26.76$, $p = 0.021$), but not wind turbine distance (all forests: Wald-$\chi^2 = 18.23$, $p = 0.634$, deciduous forests: Wald-$\chi^2 = 7.82$, $p = 0.898$) or their interaction (Wald-$\chi^2 = 12.24$, $p = 0.587$) when bird species was used as a fixed factor in the analyses (grey and colored lines in Fig. 5, see also Figs. S4 and S5).

4. Discussion

Our study showed that the observation period (month, year) and local forest structure (forest composition, vertical heterogeneity of the vegetation, stand age) strongly influenced the abundance, species richness and community composition of forest birds. For instance, the abundance and species richness of common forest birds was higher in mixed, structure-rich and old forests. Although fewer birds were counted during wind turbine operation, there was no difference in the occurrence of 22 common forest bird species with wind turbine distance. Accordingly, the local abundance and species richness of the forest bird community was not influenced by wind turbine distance, in contrast to our expectation (H1). As the radius for point counting birds was only 20 m, it is unlikely that quietly singing birds were missed during point counts. Thus, the lower abundance of counted birds when wind turbines were operating suggests that forest birds might have become silent or inactive, due to differences in noise (Zwart et al., 2016), weather (Robbins,

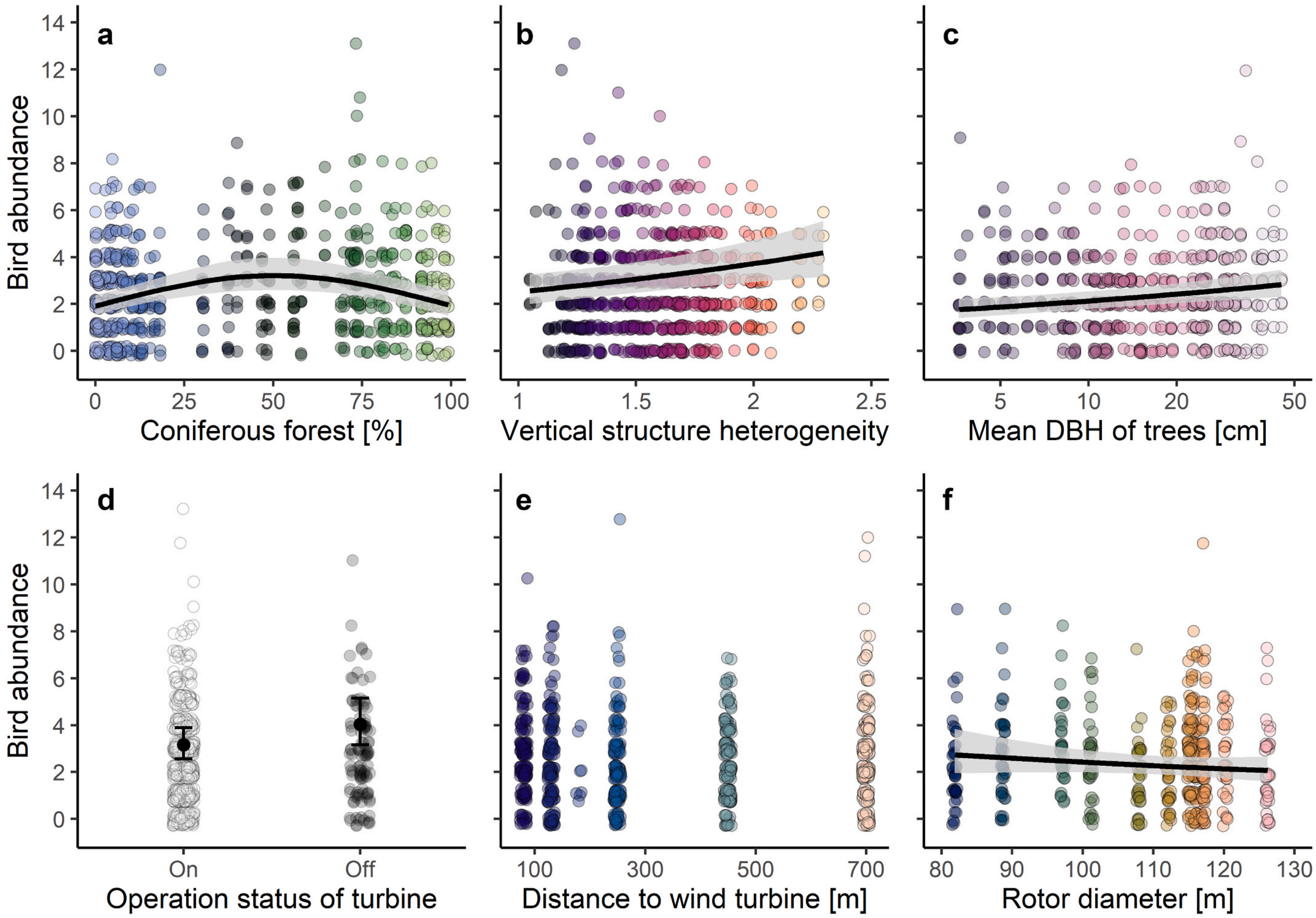

Fig. 3. Relationship between bird abundance during point counts and characteristics of (a, b, c) forest structure and (d, e, f) wind turbines. In (a, b, d, e), results are shown for point counts in forests with wind turbines with large rotors in deciduous, mixed and coniferous forests, and (c, f) for point counts in forests with wind turbines with small and large rotors in deciduous forests. In (a, b, d, e), one outlier (n = 25 individuals) is not shown. In (c), mean DBH of trees refers to the diameter of trees at breast height, i.e. a surrogate for forest stand age. Mean ± 95% prediction interval. The color schemes for characteristics of the forest and wind turbine at a point count location represent distinct gradients and are consistent in Fig. 4 and Fig. S2. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

1981; Wolf and Walsberg, 1996) or climate (Armstrong et al., 2016). However, as expected (H2), the rotor diameter of the turbines was associated with differences in the occurrence of certain bird species, changes in the community composition, and an overall decrease in bird abundance at the community level. This decrease in bird abundance was largely explained by a partial displacement of four abundant bird species in forests with larger rotor diameter (in line with H3), namely the common chaffinch (*Fringilla coelebs*), the marsh tit (*Poecile palustris*), the nuthatch (*Sitta europaea*) and the coal tit (*Peripatus ater*). Although observed locally, displacement effects by wind turbines may have far reaching consequences for common birds. In anthropogenic landscapes, where the remaining forests are often small and fragmented, places of refuge decrease as wind turbines are increasingly built in forests. If forest birds are displaced to harsh environments of high competition or low resource availability, their populations might be at risk.

A suite of studies have found relatively strong negative effects of wind turbines on the local abundance of birds, especially in open habitats (Leddy et al., 1999; Pearce-Higgins et al., 2009; Sansom et al., 2016; Shaffer and Buhl, 2016; Stevens et al., 2013). In contrast, our finding suggests that effects of wind turbines on birds in managed forests are not very pronounced, as the effect sizes were relatively small in comparison to those of the forest structure. Furthermore, wind turbines do not seem to lead to a complete local displacement of common forest birds. The relatively small impact of wind turbines on forest birds in this study may have been due to the following not mutually exclusive reasons: (1) Small post-construction effects of wind turbines, (2) a high tolerance of generalist birds towards wind turbines in managed forests, (3) potential positive effects of clearings around turbines on birds in the forest edges close to wind turbines, and (4) a potential lack of power to detect wind turbine effects on forest birds in a study that lasted only two years.

(1) In forest habitats, changes in habitat quality during wind turbine construction often account for larger differences in bird abundance or occurrence than the effects of operating wind turbines after construction (Fernández-Bellon et al., 2019; Pearce-Higgins et al., 2012). For example, the logging of forest remnants, road construction and other modifications of the environment during wind turbine construction were related to reduced abundances of forest birds in a recent study (Fernández-Bellon et al., 2019). Because our study only examined the post-construction effect of operating wind turbines on forest birds, this could partially explain the weak relationships between forest bird abundance and wind turbine distance.

(2) In Germany, wind turbine construction must be preceded by an environmental impact assessment (EIA) to guarantee that only forests of low priority for nature conservation are selected and that no species sensitive to wind turbines are present in the area (BfN, 2011). As a consequence, in managed forests or in forests with high levels of degradation, populations of bird species that may be sensitive to wind

turbines are likely to have been lost before wind turbine construction (e.g. the black stork *Ciconia nigra*) (Smeraldo et al., 2020). In fact, the studied forests were small and fragmented, highly degraded, intensively managed or a combination thereof. For example, most of the included forests were fragmented by roads, one study site was located in the vicinity of a highway, and at least seven sites were actively managed during the study period. In line with this, forest specialist birds (*sensu* Gregory et al., 2007), which are on the Red List in Hesse (HMUKLV,

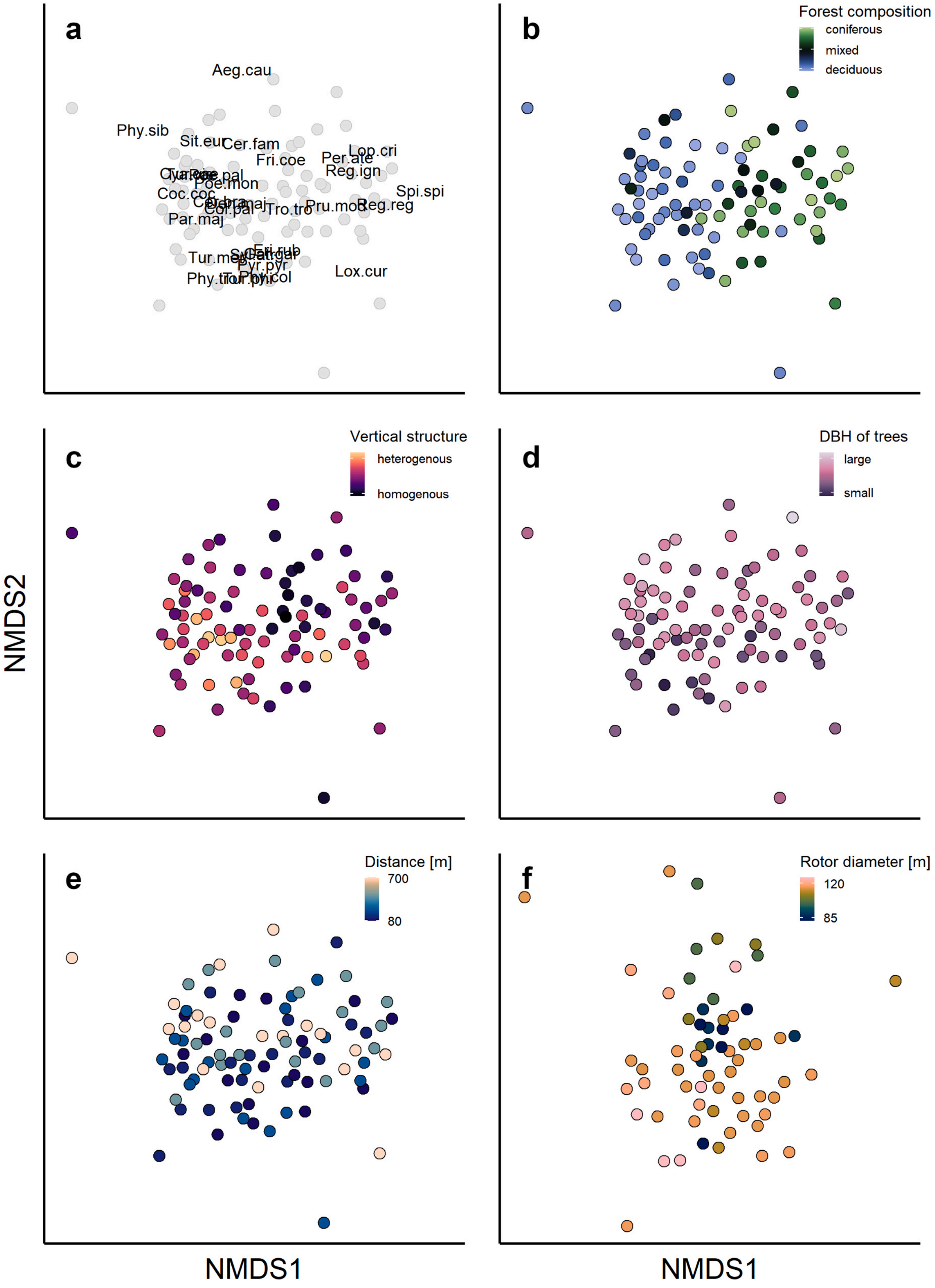

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Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination of point count locations based on Bray-Curtis dissimilarities of max abundances of 45 bird species in managed forests containing wind turbines in Hesse, Germany. (a) The location of bird species in deciduous, mixed and coniferous forests with wind turbines with only large rotors. Each circle represents the bird community at one point count location. Bird species and point-count locations far from each other in the panel were strongly dissimilar in their bird community composition. (b, c, d, e) The dissimilarity of bird communities at point-count locations in deciduous, mixed and coniferous forests containing wind turbines with large rotors (n = 90, n study sites = 18). A directed shift in bird communities at point-count locations ($p < 0.05$, Table S2) was associated with (b) forest composition, (c) vertical vegetation heterogeneity and (d) the diameter of trees at breast height (i.e. a surrogate for forest stand age), but not with (e) wind turbine distance ($p > 0.05$). (f) The dissimilarity of bird communities at point-count locations in deciduous forests containing wind turbines with small and large rotors (n = 65, n study sites = 13). With increasing rotor diameter there was only weak directed change in bird community composition ($0.05 < p < 0.1$), but bird communities became more heterogeneous in their composition with larger rotors (i.e. the variation in dissimilarity among point counts increased, $p < 0.05$). The color schemes for characteristics of the forest and wind turbine at a point count location represent distinct gradients and are consistent in Fig. 3 and Fig. S2. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

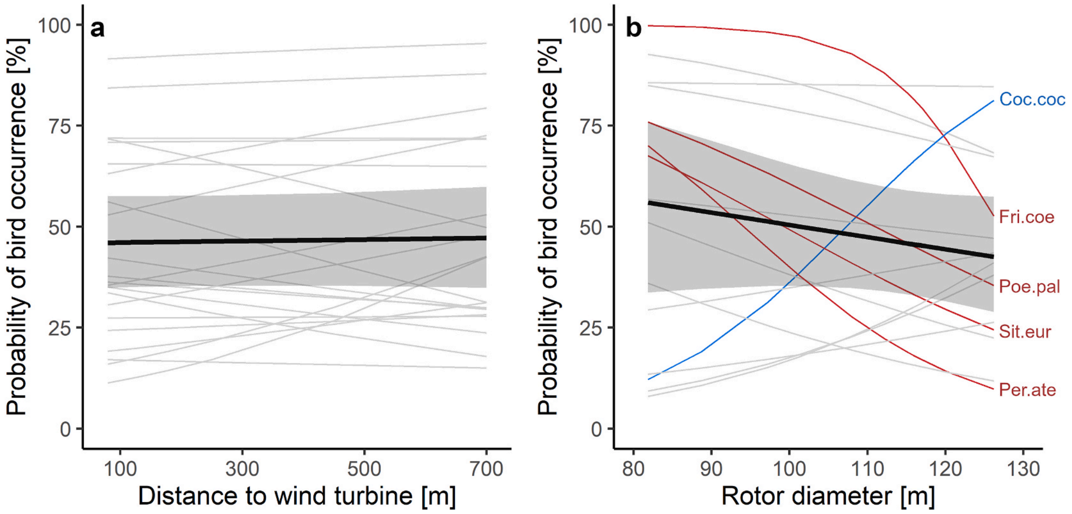

Fig. 5. (a) Relationship between the occurrence of common forest bird species at point count locations and the distance to wind turbines in deciduous, mixed and coniferous forests; (b) Relationship between bird occurrence and the diameter of wind turbine rotors in deciduous forests. The solid black line indicates the mean ± 95% prediction interval. Grey lines illustrate the relationships of each of (a) 22 and (b) 15 bird species, respectively, when bird species were included as a fixed factor in the statistical analyses. Only in (b), differences among bird species were significant ($p < 0.05$) and most pronounced in the hawfinch *Coccothraustes coccothraustes* ('Coc.coc'), the chaffinch *Fringilla coelebs* ('Fri.coe'), the marsh tit *Poecile palustris* ('Poe.pal'), the nuthatch *Sitta europaea* ('Sit.eur') and the coal tit *Periparus ater* ('Per.ate'). Further information on the relationships of bird species is provided in Figs. S4 and S5.

2016), were observed very rarely (three observations of the tree pipit *Anthus trivialis*) or not at all (seven species). Only up to two woodpecker species, which are indicators of forest health and bird diversity (Drever et al., 2008; Mikusiński et al., 2001), were recorded at the study sites, underlining the relatively low ecological value of the managed forests. Instead, the forest bird communities were dominated by small-bodied forest- and diet-generalist species (Devictor et al., 2008; Farwig et al., 2017), such as tits or thrushes (Table S2). Generalist bird species are known to tolerate even harsher conditions than those in the studied managed forests, for instance the noisy and light-polluted environment of cities (Ciach and Fröhlich, 2017; Evans et al., 2010; Nordt and Klenke, 2013). Therefore, the low ecological value of the managed forests, the lack of sensitive species, and the occurrence of mainly generalist species possibly contributed to the lack of a negative relationship between forest bird abundance and wind turbine distance.

(3) Particularly strong negative effects of wind turbines have often been identified very close to the turbines, i.e. at 0–200 m (Leddy et al., 1999; Pearce-Higgins et al., 2009; Stevens et al., 2013). Although we counted birds at distances of 80 m and 130 m to the wind turbines, birds closer to the wind turbines were not counted because at all study sites the forest at those distances was cleared. These clearings very close to the wind turbines, in turn, might have even attracted birds due to improved foraging opportunities in forest gaps compared to forest interiors (Albrecht et al., 2013; Berg, 1997), and increased the abundance of birds at the forest edges close to the wind turbines (80 m). Such edge effects of forests close to wind turbines might have compensated a potential decrease of bird populations close to wind turbines.

(4) We only counted birds over a two-year period, which may have been too short to detect consistent trends in either direction. Studying long-term responses of forest animals to wind turbines in their vicinity may be a promising area of future research (Madsen and Boertmann, 2008). However, birds are highly mobile and the potential displacement effect of wind turbines on animals should take place immediately (Larsen and Madsen, 2000). It has been further reported that abundances of forest birds within species vary much stronger between years than the total abundance of forest birds pooled across species (Blüthgen et al., 2016). Consequently, even if the effect size of wind turbines on single bird species largely varies among years, it would have been likely to detect effects of wind turbines on total bird abundance if many bird species responded in a similar pattern. But there was no such relationship between wind turbine distance and total abundance of forest birds in both study years. Overall, these findings suggest that the abundance of the usually small-bodied, common forest birds of managed forests is most sensitive to differences in forest structure, but may not be very sensitive to wind turbines in the proximity.

As bird singing at low frequencies is important for territorial defense, noise pollution by wind turbines may increase competition within and among bird species (Zwart et al., 2016). We had therefore expected that wind turbine noise would cause bird species to avoid the vicinity of wind turbines with large rotor diameter, as these produce more noise than wind turbines with small rotor diameter (Møller and Pedersen, 2011). In line with this, we found evidence of a general decrease in bird abundance and species richness, and changes in bird community composition with increasing rotor diameter of wind turbines. Four abundant bird species were partially displaced and the bird community composition among study sites became more heterogeneous in forests with wind turbines of increasing rotor diameter. Simultaneously, however, bird species did not generally occur less likely in forests with larger rotor diameter. Overall, decreases in bird abundance with increasing rotor diameter (−24.4%) were twice as large as those in species richness (−12.5%). This indicates that larger rotors might have, indeed, increased the negative effects of operating wind turbines on bird singing or activity. However, as point-counting birds relies on detecting singing birds, a decrease in bird singing would mask simultaneous decreases in bird abundances. Thus, more studies are needed to demonstrate whether large rotors keep more forest birds from singing, or whether forest birds generally become less abundant.

Differences in the community composition of birds in the presence of larger wind turbines may be related to the effects of not only rotor diameter, but also the age, height or number of wind turbines (Fig. S6), as these wind turbine features were correlated. For example, the observed changes in bird communities in forests with larger rotor diameter could also be due to birds generally avoiding forests with more or taller wind turbines (Skov et al., 2018). Similarly, wind turbine height can determine the distance of rotor blades to forest canopy. Small wind turbines might have led to disappearance of bird species preferentially occurring in the forest canopy layer (e.g. the hawfinch *Coccothraustes coccothraustes*, Fig. S5) (Perea et al., 2014). As *C. coccothraustes* is a bird species very effective in predating seeds of plants, the natural regeneration of the predated plants (e.g. *Fagus sylvatica*, or fleshy-fruited plants as *Prunus* sp.) will be limited in forests with large rotors. Thus, larger or more wind turbines will not only change the community composition of birds, but will also change the natural regeneration of plant communities due to indirect effects on seed dispersal and seed predation (Rehling et al., 2022; Simmons et al., 2018). However, it remains unknown which wind turbine feature, whether rotor diameter, age, turbine height or number of turbines, was the decisive factor for the observed changes in the bird communities in forests with large wind turbines.

5. Conclusion

Our study shows that the usually small, common forest birds in managed forests are more sensitive to the forest structure than to wind turbines in their proximity, possibly as the birds are locally not wary of wind turbines and fly at low heights. Nonetheless, common forest birds are displaced by wind turbine presence due to the age, height or number of turbines, or the size of their rotor blades, reducing bird abundance and species richness in managed forests with newer, larger and more wind turbines. If forest birds are displaced to harsh environments, wind turbines might indirectly lead to fitness and population declines of the displaced animals. Consequently, negative ecological impacts of wind turbines on forest ecosystems may prevail despite performing environmental impact assessments before wind turbine construction.

To ensure that the relatively small extent of animal displacement at wind turbines at the local scale will not become ecologically significant at larger scales, we recommend to further minimize the impact of wind turbines on forest animals. We see two potential ways forward: First, compensatory measures for constructing wind turbines should account for indirect effects of wind turbines on their environment. Secondly, the spatial planning for wind turbines in forests should prioritize forests most impacted by humans, for instance small and fragmented monocultures close to highways. Assessing forest characteristics related to forest quality (forest size, stand age, vertical vegetation heterogeneity, forest composition) will be useful in identifying the most degraded forests for the construction of wind turbines.

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Declaration of competing interest

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

Data availability

The original contributions and R code presented in the study will be made available online in the Dryad Digital Repository https://doi.org/10.5061/dryad.rfj6q57d8

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.116968.

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