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Contributed Paper

Effects of development of wind energy and associated changes in land use on bird densities in upland areas

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Abstract: *Wind energy development is the most recent of many pressures on upland bird communities and their habitats. Studies of birds in relation to wind energy development have focused on effects of direct mortality, but the importance of indirect effects (e.g., displacement, habitat loss) on avian community diversity and stability is increasingly being recognized. We used a control-impact study in combination with a gradient design to assess the effects of wind farms on upland bird densities and on bird species grouped by habitat association (forest and open-habitat species). We conducted 506 point count surveys at 12 wind-farm and 12 control sites in Ireland during 2 breeding seasons (2012 and 2013). Total bird densities were lower at wind farms than at control sites, and the greatest differences occurred close to turbines. Densities of forest species were significantly lower within 100 m of turbines than at greater distances, and this difference was mediated by habitat modifications associated with wind-farm development. In particular, reductions in forest cover adjacent to turbines was linked to the observed decrease in densities of forest species. Open-habitat species' densities were lower at wind farms but were not related to distance from turbines and were negatively related to size of the wind farm. This suggests that, for these species, wind-farm effects may occur at a landscape scale. Our findings indicate that the scale and intensity of the displacement effects of wind farms on upland birds depends on bird species' habitat associations and that the observed effects are mediated by changes in land use associated with wind-farm construction. This highlights the importance of construction effects and siting of turbines, tracks, and other infrastructure in understanding the impacts of wind farms on biodiversity.*

Keywords: bird guilds, displacement, habitat modification, land-use change, uplands, wind farms, wind turbines

Efectos del Desarrollo de la Energía Eólica y los Cambios Asociados al Uso de Suelo sobre las Densidades de Aves en Tierras Altas

Resumen: *El desarrollo de la energía eólica es la más reciente de muchas presiones ejercidas sobre las comunidades de aves de tierras altas y sus hábitats. Los estudios sobre aves en relación con el desarrollo de la energía eólica se han enfocado en los efectos de la mortalidad directa, pero la importancia de los efectos indirectos (p. ej.: desplazamiento, pérdida de hábitat) sobre la diversidad y estabilidad de las comunidades aviares cada vez se reconoce más. Usamos un estudio de control-impacto combinado con un diseño de gradiente para evaluar los efectos de los campos eólicos sobre las densidades de aves de tierras altas y sobre las especies de aves agrupadas por asociación de hábitat (especies de bosque y de hábitat abierto). Realizamos 506 censos de conteo por puntos en 12 sitios de campos eólicos y 12 sitios control en Irlanda durante dos temporadas de reproducción (2012 y 2013). Las densidades de aves totales fueron más bajas en los campos eólicos que en los sitios control, con las diferencias más importantes ocurriendo cerca de las turbinas. Las densidades de las especies de bosque fueron significativamente más bajas a 100 m de las turbinas que a distancias mayores y esta diferencia estuvo mediada por modificaciones asociadas con el desarrollo de campos eólicos. De manera particular, las reducciones en la cobertura de bosque adyacente a las turbinas estuvieron vinculadas con la disminución observada en las densidades de las especies de bosque.*

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Las densidades de las especies de hábitat abierto fueron más bajas en los campos eólicos pero no estuvieron relacionadas con la distancia a las turbinas y tuvieron una relación negativa con el tamaño del campo eólico. Lo anterior sugiere que, para estas especies, los efectos del campo eólico pueden ocurrir a la escala de paisaje. Nuestros hallazgos indican que la escala y la intensidad de los efectos de desplazamiento de los campos eólicos sobre las aves de tierras altas dependen de las asociaciones de hábitat de las especies de aves y que los efectos observados están mediados por cambios en el uso de suelo asociados con la construcción de campos eólicos. Esto remarca la importancia de los efectos de construcción y el sitiado de las turbinas, pistas y demás infraestructura en el entendimiento de los impactos que tienen los campos eólicos sobre la biodiversidad.

Palabras Clave: cambio de uso de suelo, campos eólicos, desplazamiento, gremios de aves, modificación de hábitat, tierras altas, turbinas de viento

摘要: *风能的开发是山地鸟类群落面临的许多压力中最近出现的一种。关于鸟类与风能开发有关的研究主要集中于其直接导致鸟类死亡的影响, 但人们也逐渐认识到其对鸟类群落多样性和稳定性的间接影响 (如被迫迁徙、生境丧失) 的重要性。我们用控制-影响研究, 结合梯度设计, 来评估风电场对山地鸟类密度和按生境相关性分类的鸟类物种 (森林和开放生境的物种) 的影响。我们在 2012 年和 2013 年的两个繁殖季对爱尔兰 12 个风电场和 12 个对照位点对 506 个样点进行计数调查。结果显示, 风电场的鸟类总密度比对照位点低, 且差异最大的位置在涡轮机附近。在涡轮机附近 100 米内森林鸟类的密度显著低于离涡轮机更远的位置, 这一差异受到风电场建设相关生境改造的调控。特别是与观察到的森林鸟类密度下降与涡轮机附近森林覆盖的减少有关。风电场开放生境的物种密度也较低, 但这与距离涡轮机的远近无关, 而与风电场的大小呈负相关。这说明风电场对这些物种的影响可能发生在景观尺度上。我们的结果表明, 风电场导致山地鸟类被迫迁徙的影响尺度和强度取决于物种的生境相关性, 观察到的影响是由风电场建设相关的土地利用变化介导的。这强调了涡轮机、轨道和其它基础设施的施工效应及选址对于理解风电场对生物多样性影响的重要性。* **【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 鸟类同资源种团, 被迫迁徙, 生境改造, 土地利用变化, 山地, 风电场, 风力涡轮机

Introduction

In recent decades, development of wind energy has played a key role in efforts to mitigate climate change by reducing carbon emissions while meeting increasing energy demands. It is expected that by 2050, wind energy will provide 20% of global energy requirements (IPCC 2015). Although widely perceived as one of the most environmentally responsible and affordable energy sources, ongoing increases in development of wind energy have led to concerns about its potential environmental impacts (Leung & Yang 2012; Tabassum et al. 2014; Zwart et al. 2016). Large-scale installations can result in habitat loss and degradation, displacement of wildlife, and direct mortality of birds and bats (Kuvlesky et al. 2007; Pearce-Higgins et al. 2009; Northrup & Wittemyer 2013).

In many parts of the world, onshore wind farms are commonly built in areas with high elevation, sparse human populations, and relatively low levels of management and economic productivity. These areas are attractive for wind-energy development because they typically combine high wind yield with few economically competing land uses (Bright et al. 2008; Schuster et al. 2015). However, these upland areas are often also priority conservation areas with important bird assemblages, including generalists, upland specialists, and migratory birds. In Europe many of these bird species are of conservation concern; thus, their populations are sensitive to wind-farm development and expansion (e.g., Bright et al. 2008; Bonn et al. 2009; Wilson et al. 2017). Upland bird communities have been shaped by human activity, in particular habitat loss and degradation related to agricultural improvement, peat extraction, recreation, air pollution, and climate (Fielding & Haworth 1999; Pearce-Higgins et al. 2008). Because development of wind energy has been incentivized by policies aiming to reduce carbon emissions from energy production, its effects on upland birds can be regarded as an indirect consequence of climate change (Evans & Douglas 2014). The scale of wind-farm development in many upland areas has led to a growing demand for information on its potential impacts on birds to guide sustainable development of the wind energy sector (Katzner et al. 2013; Zwart et al. 2016).

Early studies of the effects of wind farms on birds most commonly assessed direct mortality associated with wind turbines (Leung & Yang 2012; Erickson et al. 2014; Smith & Dwyer 2016). Recently, the scope of studies has broadened to include assessments of secondary effects, such as disturbance and displacement, either through habitat loss or species avoidance of habitat (e.g., Pearce-Higgins et al. 2009; Astiaso Garcia et al. 2015; Shaffer & Buhl 2016). Research has also evaluated the impact of wind farms on a variety of bird breeding indices (e.g., Pearce-Higgins et al. 2012; Sansom et al. 2016; Rasran & Mammen 2017). Reviews on the displacement effect of wind farms on birds indicate that the existence and extent of impacts varies considerably across species, land cover, seasons, and geographic regions (e.g., Pearce-Higgins et al. 2009; Shaffer & Buhl 2016; Smith & Dwyer 2016). Despite this variability, the majority of studies have focused on a small number of endangered or charismatic species with already low abundances (e.g., De Lucas et al. 2008; Smith & Dwyer 2016). Although the displacement of key species can ultimately result in a shift in the structure of avian communities (Tabassum et al. 2014), there have been few publications on the impacts of wind farms at a multispecies scale. Furthermore, few studies take into account the interdependent effects of the presence of wind turbines and habitat modification or address ecosystem-level impacts of wind-energy development. Understanding whether, and to what extent, wind turbines affect bird communities as a whole is an essential step toward understanding the effects of wind farms at an ecosystem scale.

We designed an impact-control study to assess bird densities and changes in land use due to construction at a range of large, modern wind farms and paired control sites. By surveying points at a range of distances from turbines, we simultaneously assessed impact-gradient effects. We sought to compare bird densities between areas with and without a wind farm; determine the effects of distance from wind turbines and age and size of a wind farm on total bird densities; assess whether, and how, observed effects are related to changes to species groups with different habitat associations; and assess potential effects of changes in land use due to wind-farm development on total bird densities. Our study is one of the first to combine surveys of multiple wind farms and control sites with an impact-gradient approach to assess the effects of wind-energy development on upland birds in a multispecies context (review of studies in Shaffer and Buhl [2016]).

Methods

Survey Design

We surveyed 6 wind farms and 6 control sites in 2012 and a further 6 of each in 2013, all in upland habitats across Ireland. Irish uplands are characterized by a mosaic of open habitats (e.g., heath, bog, rough and improved grassland, scrub) and closed habitats (commercial forestry plantation and natural forests). To maximize the detection of effects, we selected large, modern wind farms with at least 8 turbines of similar design covering a broad geographical range (2–8 years since construction; 8–35 turbines with individual outputs of 850–2500 kW [Supporting Information]). For each wind-farm site, a control site was selected within 12 km in an area of similar size, habitat composition, and topography but without wind-farm development. The similarity between wind-farm and control-site habitat composition (preconstruction) was assessed by visual inspection of satellite images and topographical maps. To avoid confounding effects of yearly variations in bird densities, each wind farm and its corresponding control site were surveyed during the same breeding season.

At each wind farm, 27 survey points were selected at increasing distances from the nearest turbine (9 survey points within 100 m of turbines, 6 at 100–400 m, 6 at 400–700 m, and 6 at 700–1000 m). To avoid any confounding effects of multiple turbines, points farther than 100 m from individual turbines were selected only outside of the minimum polygon containing all turbine 100-m buffers. Within each distance band, survey points were selected to represent the range of habitats and human-made structures present within that band. All points were at least 200 m from the nearest neighboring point to avoid multiple detections of individual birds.

For each survey point at a wind farm, a matching survey point with similar habitat characteristics and elevation was selected at the corresponding control site. Our aim was to assess the overall effect of wind-farm development, including the presence of turbines and the effect of changes in land use associated with wind-farm construction. For this reason, habitat composition (percent cover, based on aerial photographs) at control points was matched with that of the survey point at the wind farm prior to construction (habitat types: pre-thicket forest, closed canopy, clearfell, grassland, scrub, peatland, or human altered). This was done with the aid of aerial photographs taken prior to wind-farm construction. All pairs of wind farm and control points were selected to contain the same habitat types in as similar percentage cover as possible (±5%). By matching control-point habitats with those of wind-farm points prior to construction we ensured that land-use and habitat changes due to wind-farm development could be assessed. As a result, we expected that habitat differences would be greatest for points located closest to wind farms, where habitats would be most affected by construction. To account for variation in bird densities due to elevation, control survey points were also selected to match the elevation of their corresponding wind-farm point.

Many upland bird species in Ireland are rare and occur at relatively low abundances. Because this could affect the observed trends in total bird densities, we also carried out an analysis of densities of the most common bird species. Because of the configuration of upland habitats in Ireland, the most common bird species are associated with either forest or open habitats. By analyzing densities of forest birds and open-habitat birds, we were able to study the effects of land-use changes associated with wind farms on bird groups linked to specific habitats.

Bird and Habitat Surveys

Breeding birds were surveyed using the point-count method following Bibby et al. (2000). Surveys were conducted on days without persistent rain or strong wind (<20 km/hour) during the breeding seasons (April to

June) and in the mornings (from 1 hour after dawn until noon). Each point was visited once for 5 minutes, during which time all birds detected by sight or sound within a 100-m radius were recorded and their distance from the observer noted. All data collection was carried out under license issued by the National Parks & Wildlife Service in Ireland in accordance with the Wildlife Act 1976. Flying birds were excluded from the data analysis unless they were actively foraging or singing. Distance estimates were made by experienced observers aided by scaled aerial photos. Because time of day or season can affect bird densities, point-count pairs (wind farm and control) were surveyed in succession. If this was not possible, they were visited within the next 2 days at the same time of day and under similar weather conditions. Distance software version 5.0 (Thomas et al. 2010) was used to derive species densities from field observations. For further details on survey methods and density estimate calculations, see Supporting Information.

Survey-point bird densities were calculated for individual species and summed to calculate total bird densities. Using information on avian ecology and habitat associations in Ireland (Nairn & O'Halloran 2012), we also classified the most commonly occurring species in our study as either forest species or open-habitat species. Forest species included Great Tit (*Parus major*), Coal Tit (*Periparus ater*), Chaffinch (*Fringilla coelebs*), and Goldcrest (*Regulus regulus*). Open-habitat species included Meadow Pipit (*Anthus pratensis*), Skylark (*Alauda arvensis*), and Wheatear (*Oenanthe oenanthe*).

Once the bird survey at each point was completed, habitats within the 100-m survey radius were categorized as pre-thicket forest, closed canopy, clearfell, grassland, scrub, peatland, or human altered (e.g., bare ground, buildings, tracks providing access for forestry operations or wind farms). Percent cover of habitats, point-count elevation, and distance from nearest wind turbine were calculated using ArcGIS 10 software (Environmental Science Research Institute, Redlands, California).

Of the 648 designated point counts, it was not possible to carry out surveys at 71 points due to land-access constraints. To maintain the paired design, their corresponding survey-point pairs were also excluded from analysis. This resulted in analysis of 506 survey points (253 points at wind farms, 253 points at control sites). The final distribution of wind-farm points was 68 within 100 m of the nearest turbine; 70 from 100 to 400 m; 56 from 400 to 700 m; and 59 from 700 to 1000 m.

Data Analyses

To assess how different factors affected bird densities, we used generalized linear mixed models (GLMMs) with a Gaussian distribution and identity link functions (Zuur et al. 2013). We followed a 3-step process to test the effects of wind-energy development on bird densities. First, we built a base model explaining total bird densities (i.e., density of all species combined) based on environmental factors (percent cover of each habitat type and elevation in meters) and retaining only significant variables (model A). We then added a categorical variable with 2 levels (wind farm or control) to this model to test the effect of wind-farm development on total bird densities (model B). Finally, we used a subset of data from wind-farm sites only to test the effects of distance to turbine (meters), age of wind farm (years), and size (number of turbines as a proxy for size) on total bird densities, on forest bird densities, and on open-habitat bird densities (models C). Thus, models A and B included data from all survey points ($n = 506$), whereas model C included data from wind-farm survey points only ($n = 253$). To control for site-specific patterns, we included site as a random factor in all models (factor with 12 levels, 1 for each wind-farm and control-site pair). To control for non-independence of survey-point pairs, pair was included as a random effect nested within site for models A and B. Spearman correlation coefficients were calculated for all variable pairs. All variables included in analyses had values of $|r| < 0.5$.

Preliminary analysis revealed that the effects of wind farms on habitat were greatest closest to wind turbines. Therefore, to further analyze the spatial nature of any effects, we calculated total, forest, and open-habitat bird densities at wind-farm points at increasing distance bands from turbines (0–100 m, 100–400 m, 400–700 m, and 700–1000 m) and compared them with the densities of their matching control points with Wilcoxon signed-rank tests. To detect differences in habitats between matched points that could be attributed to wind-farm development (habitats at control points were matched to those at wind-farm points prior to construction), we performed similar analyses comparing percentage of each habitat type between wind-farm points and their matched control points for each of the distance bands. All statistical analyses were performed using R version 3.4.3 (www.r-project.org). The GLMM analyses were performed with R packages lme4 and nlme.

Results

Fifty-six bird species and 3715 individual birds were recorded. Thirty-six percent of the species recorded ($n = 20$) are of conservation concern in Ireland at present (Colhoun & Cummins 2013). Mean densities across all sites were 2.99 birds/ha, with 0.99 forest birds/ha and 0.47 open-habitat birds/ha. At wind farms, mean densities were 2.80 birds/ha, 0.93 forest birds/ha, and 0.41 open-habitat birds/ha. At control sites, mean densities were 3.19 birds/ha, 1.04 forest birds/ha, and 0.52 open-habitat birds/ha. For a list of species recorded, their conservation statuses, and densities see Supporting Information.

Table 1. Summary of environmental effects on total bird densities at wind-farm and control sites (model A).*

Factor	*Estimate (SE)*	t	p
Intercept	5.677 (0.552)	10.29	<0.001
Closed canopy	0.024 (0.003)	7.08	<0.001
Pre-thicket	0.009 (0.004)	2.46	0.012
Peatland	−0.012 (0.003)	−4.01	<0.001
Elevation	−0.010 (0.001)	−5.74	<0.001

**Predicted total bird densities (birds/ha) at individual point counts (n= 506) at 12 wind farm and 12 control sites modeled as a function of environmental factors (land-cover type and elevation). Point-count pair nested within site was included as a random factor.*

Table 2. Summary of effects of wind-farm development on total bird densities at wind farm and control sites (model B).*

Factor	*Estimate (SE)*	t	p
Intercept	5.822 (0.555)	10.50	<0.001
Closed canopy	0.024 (0.003)	6.84	<0.001
Pre-thicket	0.008 (0.004)	2.25	0.024
Peatland	−0.012 (0.003)	−4.20	<0.001
Elevation	−0.010 (0.002)	−5.62	<0.001
Wind farm present	−0.313 (0.148)	−2.11	0.035

**Predicted bird densities (birds/ha) at individual point counts (n = 506) at 12 wind farm and 12 control sites modeled as a function of different land-cover types (percent), elevation (meters), and presence or absence of wind farms. Point-count pair nested within site was included as a random factor.*

Bird densities at all survey points (wind farm and matching control) were influenced by different habitat covers and elevation (model A, Table 1). However, point counts at wind farm sites showed significantly lower bird densities than point counts at control sites (model B, Table 2).

Tests of characteristics specific to wind farms revealed different effects on total, forest, and open-habitat bird densities (C models, Table 3). Distance to turbine was significantly and positively related to total bird densities, indicating an increase in densities at increasing distances from turbines. Densities of forest birds showed a similar significant positive effect of distance to turbine. However, for open-habitat birds, only size of the wind farm was significant; large wind farms held lower densities of open-habitat birds.

Differences in total bird densities were greatest for paired wind-farm and control points that were closest to wind turbines (Fig. 1a). When assessed by distance bands, these differences were significant between wind-farm points within 100 m of turbines and their paired control points ($z = 1043.5, p < 0.001$) (Fig. 1b) but not for other distance bands. Densities of forest birds were significantly lower at wind-farm points within 100 m of wind turbines than at matching control points ($z = 553.5$, $p = 0.009$) (Fig. 1c) but not for other distance bands. Densities of open-habitat bird species were significantly lower at wind-farm sites than control sites ($z = 2910.0$, $p = 0.008$), but this difference was not significant for any specific distance band (Fig. 1d).

Comparison of habitat composition at wind-farm and control points highlighted significant differences for 3 habitat types attributed to construction effects: human-altered (bare ground, tracks, and buildings), clearfelled forest, and closed canopy forest (Fig. 2). Human-altered habitats occurred more frequently at wind-farm points ($z = 4126.0$, $p < 0.001$) (Fig. 2a); differences were significant up to 700 m from turbines. Likewise, clearfelled forest occurred more frequently at wind-farm points ($z = 492.0$, $p = 0.039$) (Fig. 2b); differences were significant within 100 m from turbines. Closed canopy forest was less abundant at wind-farm points within 100 m of turbines than at their corresponding control points ($z = 636.5, p = 0.020$) (Fig. 2c).

Discussion

Total bird densities were lower at wind-farm sites than at control sites without wind-farm development. Because wind farms were generally located at high elevations, elevation decreased and bird densities increased at points farther from turbines and at matched control points (positive slope of both lines in Fig. 1a). However, bird densities close to wind turbines were lower than at matching control points, and we recorded a higher rate of elevation-related increase at wind-farm than at control sites (lower y-intercept and steeper slope of wind-farm average density represented by the dark grey line in Fig. 1a). This indicates a gradient effect of wind farms on bird densities. Maximum differences in bird densities were recorded between wind-farm points within 100 m of turbines and their corresponding control point pairs (Fig. 1b). These findings are consistent with other studies showing the displacement of birds in areas within a few hundred meters of turbines (Pearce-Higgins et al. 2009; Stevens et al. 2013; Sansom et al. 2016; Shaffer & Buhl 2016). The magnitude of these displacement effects are shown by model estimate values indicating that total bird densities were 0.313 birds/ha (SE 0.148) lower at wind farms than control sites (Table 2). At wind-farm sites, total densities increased by 0.001 birds/ha/m (SE 0.000) (or 1.3 birds/ha/km [SE 0.4]) from a wind turbine (Table 3). Although these values may seem low, in the context of upland bird densities (e.g., mean of 2.99 birds/ha in our study) changes of 0.3–1.3 birds/ha can have important effects at both bird species population and community scales.

Densities of forest species were lower at wind farms than at control sites; distance to turbine significantly explained this observed difference. Specifically, points within 100 m of wind turbines had significantly lower densities of forest species than paired control points. In contrast, densities of open-habitat species were lower

Table 3. Summary of effects of wind-farm development on total, forest, and open-habitat bird densities at wind-farm sites (models C).*

Response variable	*Factor*	*Estimate (SE)*	z	p
Total species density (birds/ha)	intercept	4.966 (0.988)	5.03	0.002
	closed canopy	0.022 (0.004)	5.31	<0.001
	peatland	−0.015 (0.003)	−4.73	<0.001
	elevation	−0.007 (0.003)	−2.72	0.006
	distance	0.001 (0.000)	3.26	0.001
	age	−0.035 (0.084)	−0.41	0.681
	size	−0.014 (0.012)	−1.14	0.254
Forest species density (birds/ha)	intercept	0.770 (0.201)	3.83	<0.001
	closed canopy	0.018 (0.003)	7.00	<0.001
	peatland	−0.006 (0.002)	−2.94	0.003
	distance	0.001 (0.000)	3.33	0.001
	age	−0.030 (0.030)	−1.01	0.315
	size	−0.005 (0.004)	−1.25	0.213
Open-habitat species density (birds/ha)	intercept	−0.324 (0.272)	−1.19	0.234
	closed canopy	−0.003 (0.002)	−2.03	0.043
	grassland	0.005 (0.001)	3.78	<0.001
	peatland	0.007 (0.001)	5.51	<0.001
	elevation	0.002 (0.001)	2.61	0.009
	distance	0.001 (0.000)	0.91	0.365
	age	0.010 (0.016)	0.55	0.581
	size	−0.007 (0.002)	−3.11	0.002

Predicted total, forest, and open-habitat bird densities (birds/ha) at individual point counts ($n = 253$) at 12 wind farms modeled as a function of different land-cover types (percent), elevation (meters), distance to turbine (meters), and age (years) and size of wind farm (number of turbines). Site was included as a random factor.

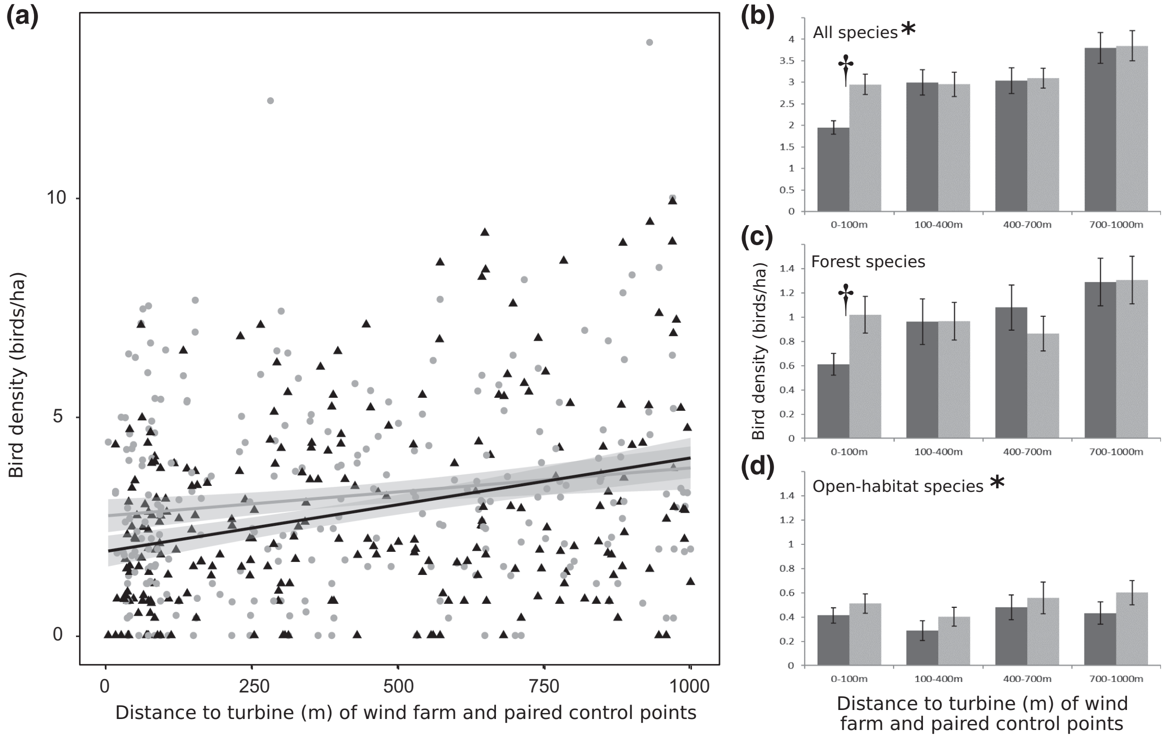

Figure 1. Bird densities recorded at 506 point counts at 12 wind farms (black) and 12 control sites (grey) in 2012 and 2013: (a) total bird densities at wind-farm point counts (triangles) and control point counts (circles) (lines, means; shading, 95% CI); (b) mean (SE) total bird densities in each distance band; (c) mean (SE) densities of forest bird species in each distance band; (d) mean (SE) density of open-habitat bird species in each distance band. Control point values are represented at the distance of their corresponding wind farm point pair (, statistical significance for that group independent of distance; †, statistical significance for that distance band).*

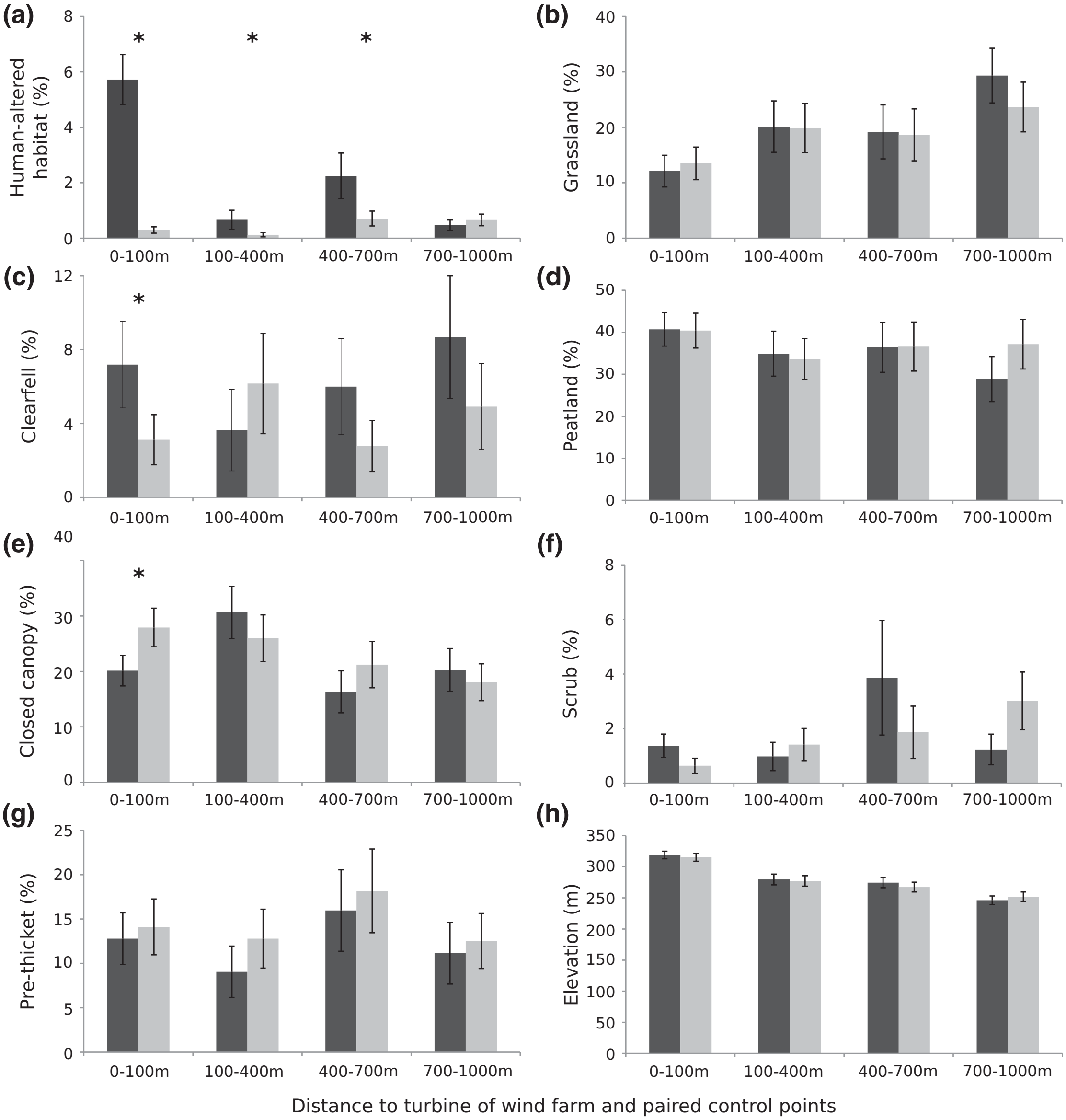

Figure 2. Mean (SE) (a–g) cover of different land-cover types and (h) elevations at wind farms (dark grey) and control sites (light grey) where bird point counts were conducted (, p < 0.05; values on x-axes differ). Control point values are represented at the distance of their corresponding wind-farm point pair.*

at wind farms independent of distance to turbines, although size of the wind farm was negatively related to their densities. These findings indicate a variation in the intensity and scale of the effects of wind-farm development that depends on the ecological association of bird species. Previous research suggests that sensitivity to displacement by wind turbines may be related to species' characteristics, such as their social behavior and habitat use (Stevens et al. 2013; Schuster et al. 2015).

Habitat changes resulting from wind-farm development may help explain the different responses of forest and open-habitat species. Because control survey points were selected to match the habitat and elevation of wind-farm points prior to wind-farm construction (Fig. 2), differences in habitat composition can be attributed to wind-farm construction. Wind-farm points close to turbines had proportionally less closed canopy cover and relatively more clearfell forest and human-altered habitats (bare ground, tracks, and buildings) than did matching control points. Ground clearing and clear felling are often undertaken to make space for wind-farm infrastructure or to maximize wind load (Nayak et al. 2010), whereas access roads increase the area of bare ground. These changes in land use had a net effect of decreasing natural habitat cover at wind farms. In our study, these changes particularly affected closed-canopy habitats, resulted in reductions of habitat for forest bird species, and ultimately led to lower recorded densities. Similar patterns have been observed in response to development of shale gas in forested areas, where changes in land use affect mature forest birds but not birds associated with early successional or disturbed habitats (Farwell et al. 2016). These patterns highlight the importance of planning the precise location of turbines, roads, and other infrastructure in determining which habitats and thus species will be affected by wind-energy development. Presence of wind turbines could also affect bird densities through blade noise, visual disturbance, increased predation risk, or human activity around these structures (Drewitt & Langston 2006; Helldin et al. 2012). Although our findings suggest that changes in land use played an important role, it is possible that these other indirect effects may have contributed to decreased forest bird densities.

Densities of open-habitat birds followed a different pattern from that of forest species. The lack of an apparent gradient in densities at increasing distance from turbines (Fig. 1d) could be explained if either the spatial scale of our study was insufficient (i.e., impact gradients occurred beyond 1000 m from turbines) or if these effects were occurring at a landscape scale. However, typical territory sizes of the open-habitat species are within this scale (Cramp 1988), and for forest species we detected gradient effects within 100 m of turbines. Therefore, it seems unlikely that our study scale was inappropriate, which suggests that for open-habitat birds, effects were operating at a landscape scale. Although there were no differences in extent of open habitat between wind-farm and control survey points (Fig. 2b, d), we did not assess the extent of these habitats in the wider landscape or their quality (e.g., plant species composition, vegetation height). Wind farms are typically located in areas of relatively low value for nature or where access is easy, which may in turn be associated with differences in habitat quality, land use, or habitat management. These, or other differences at a landscape scale that are indirectly linked to presence of wind farms, may play a role in determining bird densities (Lachance et al. 2005). Furthermore, the susceptibility of different species to disturbances (e.g., human activity, movement of turbine blades) may also determine the scale of the effect.

Previous research shows that the extent of wind-farm impacts on bird populations varies considerably across species and regions (Farfán et al. 2009; Pearce-Higgins et al. 2009; Sansom et al. 2016). Where reduced bird abundance at wind farms has been reported, this has generally been confined to areas close to turbines and has not extended into the wider landscape (Leddy et al. 1999; Drewitt & Langston 2006; Pearce-Higgins et al. 2009). Other studies report effects of wind farms specific to certain habitats or to their structure (Hale et al. 2014; Shaffer & Buhl 2016). However, these studies are typically restricted to a small number of species or wind farms, often with limited sample sizes, and efforts to assess impacts on multiple bird species across multiple sites have relied largely on meta-analyses or reviews (Drewitt & Langston 2006; Madders & Whitfield 2006).

Despite the large body of work on best practice for the assessment of effects of wind-energy development on wildlife in general, and birds in particular (Strickland et al. 2007; Astiaso Garcia et al. 2015; Schuster et al. 2015), few studies combine different assessment designs (i.e., before-after, control-impact, impact-gradient approaches) or cover multiple bird species, wind farms, or years (Shaffer & Buhl 2016). Our approach allowed us to compare areas with wind-farm development with control areas of similar environmental characteristics and avoid confounding temporal effects associated with before-after designs (Strickland et al. 2007). By combining this paired control-impact design with an impact-gradient approach, it was possible to evaluate the effects of wind turbine presence and changes in land use while maximizing our ability to detect displacement gradients (NRC 2007). Surveys of breeding birds targeting multiple species allowed detection of nonlethal effects on overall bird densities, as well as of differential effects dependent on species habitat associations.

Ours is one of the first studies to highlight differences in nonlethal effects of wind farms on different bird groups in relation to their ecological association and to demonstrate how the spatial scale of this response may be specific to each group (Pearce-Higgins et al. 2009, 2012). These findings are particularly relevant for planners and policy makers. The differential response of bird guilds reported here suggests that it is possible to locate wind farms and to plan changes in land use in accordance with conservation interests. Depending on regional conservation priorities, it may be possible to locate wind-farm infrastructure such that habitat changes will affect species and habitats of lower conservation concern or even benefit those in need of conservation action. Furthermore, consideration must be given to the ecological role of these habitats and species from a wider ecological perspective. Many of the birds recorded in our study are important prey for key flagship species such as Hen Harrier (*Circus cyaneus*), Merlin (*Falco columbarius*), or Short-eared Owl (*Asio flammeus*), predators that are the focus of considerable conservation effort (Glue 1977; Fernández-Bellon & Lusby 2011; Watson 2013). As such, understanding the effects of wind farms on prey populations and how this may influence these species' foraging habits near wind turbines is essential for their effective management and conservation.

Our study highlights the relevance of assessing the effects of wind farms or other developments on ecological communities or ecosystems as a whole, rather than solely on individual species. Further research into wind-farm impacts on birds should look beyond the effects of turbine presence and take into consideration effects of construction, associated infrastructure, and changes in land use and habitat composition. Similarly, wind-farm planners should consider these potential effects by taking into account not only the precise location of wind turbines, but also that of associated infrastructure (e.g., roads, buildings) and how changes in land use may affect wildlife. Understanding the ways in which land-use changes impact upland ecology is particularly important in the context of continued growth in wind-energy development in combination with other pressures such as afforestation, agricultural intensification, and climate change.

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Supporting Information

Details on site locations (Appendix S1), survey methods and density calculations (Appendix S2), and bird species recorded and their conservation status and densities (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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