Environ Monit Assess (2023) 195:1480
https://doi.org/10.1007/s10661-023-12090-z

RESEARCH

Changes in diversity and species composition in the assemblage of live and dead bats at wind farms in a highly diverse region

**Sergio A. Cabrera-Cruz · José Luis Aguilar López ·
Pedro A. Aguilar-Rodríguez · Marco T. Oropeza-Sánchez ·
Oscar Muñoz Jiménez · Rafael Villegas Patraca**

Received: 22 May 2023 / Accepted: 2 November 2023 / Published online: 16 November 2023

Abstract Besides direct mortality, wind farms also affect aerial fauna by modifying their communities, reducing species diversity and richness through disturbance. During three consecutive years, we used mist nets and acoustic recorders, and conducted carcass searches, to characterize the assemblage of bat species and to estimate bat mortality at two nearby wind farms sited <5 km apart in a highly biodiverse region. We asked whether the diversity, richness and evenness of the assemblages varied yearly, predicting it would decrease through time. Richness and evenness did not change, but the diversity of species recorded acoustically, 96% being aerial insectivores, was significantly lower the third year. We estimate 4 – 15.7 fatalities/MW/year by wind farm, with 63% of species found as carcasses being aerial insectivores. We found >40% of dissimilarity in the species composition of bat assemblages between wind farms despite the short distance between them, with species turnover accounting for more than half of the dissimilarity every year. Similarly, species turnover accounted for >15% of the dissimilarity in the composition of the assemblage of live bats (captured and recorded acoustically) and the assemblage obtained through carcass searches. Our findings suggest that nearby wind farms impact bat communities differentially and aerial insectivores disproportionally. Long term, multi-method surveys are needed to characterize bat communities in highly diverse regions and to evaluate the post-construction effects that wind farms have on them.

Keywords Bat mortality · Community structure · Diversity · Isthmus of Tehuantepec · Mexico · Wind energy

Introduction

Wind farms are currently one of the most important renewable energy sources globally, with fewer

---

Sergio A. Cabrera-Cruz and José Luis Aguilar López contributed equally to this work.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10661-023-12090-z.

S. A. Cabrera-Cruz (✉) · J. L. Aguilar López ·
O. Muñoz Jiménez · R. Villegas Patraca (✉)
Unidad de Servicios Profesionales Altamente
Especializados (USPAE), Instituto de Ecología A.C.
(INECOL), Coatepec, Veracruz 91520, México
e-mail: sergio.cabrera@inecol.mx

R. Villegas Patraca
e-mail: rafael.villegas@inecol.mx

P. A. Aguilar-Rodríguez
Instituto de Investigaciones Forestales, Universidad
Veracruzana, Xalapa, Veracruz 91070, México

M. T. Oropeza-Sánchez
Instituto de Investigaciones en Ecosistemas y
Sustentabilidad (IESS), Universidad Nacional Autónoma
de México, Morelia, Michoacán 58190, México

negative effects on the health of the planet than fossil fuels due to their nil emission of greenhouse gases and low consumption of water (Saidur et al. 2011). A growing number of countries are adopting this form of energy production, and the number of installed wind turbines is estimated to increase (Veers et al. 2019). Wind energy developments, however, do have environmental impacts (Katzner et al. 2019), particularly notorious on aerial vertebrates given their direct mortality by collision or barotrauma (Baerwald et al. 2008; Marques et al. 2014).

Beyond mortality, wind farms impact fauna in ways that are more subtle and harder to detect and that relate to the disturbance caused by wind turbine operation, such as changes in the attributes of their communities (Santos et al. 2010). For example, bird and mammal communities are less rich, even and diverse within than outside wind farms, and these differences may exacerbate through time (Keehn and Feldman 2018; Kumara et al. 2022).

Of the two extant groups of aerial vertebrates, impacts on bats have raised serious concerns given their high fatality rates, which may threaten the viability of entire populations (Frick et al. 2017). The high mortality of bats at wind farms relates in part to their attraction to wind turbines (Guest et al. 2022), which is evidenced by the higher activity of some species within than outside wind farms (e.g., Richardson et al. 2021). Indeed, before wind turbines, bat mortality in relation to tall anthropogenic structures was rare (Cryan and Barclay 2009). Some other species, however, reduce their activity within (Millon et al. 2018) or in proximity to wind farms and small wind turbines (Barré et al. 2018; Minderman et al. 2012, 2017), suggesting avoidance rather than attraction.

Attraction and avoidance of bats to wind turbines, as well as the differential activity levels of some species within and outside wind farms, suggests that these facilities affect the communities of this biological group too. For example, bat species richness decreased after a wind farm was retrofitted from one- to three-blade turbines, presumably increasing the negative effects of the turbines (Ferri et al. 2016). Similarly, species richness as well as functional and phylogenetic diversity of understory bats decreased between the pre- and early post-construction periods of a wind farm, with those parameters later returning to pre-construction levels, suggesting a recovery of the community attributes (Briones-Salas et al. 2017).

In this work, we aimed to characterize the assemblage of bat species at wind farms and to evaluate if their diversity, richness and evenness varied through time. To do this, we surveyed bat activity and mortality through mist netting, ground-based acoustic recordings, and carcass searches. These surveys were part of the post-construction monitoring of two wind farms located in the Isthmus of Tehuantepec, a region in tropical Mexico where at least 63 bat species occur (García-Grajales and Buenrostro-Silva 2012), 21 of which have been recorded as carcasses (Bolívar-Cimé et al. 2016; Cabrera-Cruz et al. 2020). Bat diversity and richness are good indicators of disturbance in the Neotropics (Medellín et al. 2000), so we expected that diversity, richness and evenness of the assemblages would decrease through time. In highly diverse regions, the species composition of bat assemblages can vary at local scales (500 m – 1000 m; Avila-Cabadilla et al. 2012), and bat species found during carcass searches may not be detected through mist netting or acoustic recordings (e.g. Torres-Morales et al. 2014). Hence, we compared in detail the composition of the bat assemblages recorded between wind farms, as well as between the assemblages of bats recorded live and as carcasses. We found that the assemblage of species in this and maybe other highly diverse regions may differ even between close-by locations, and that mist-nets and ground-based acoustic recorders may not register all of the species that have fatal interactions with wind turbines. We also provide new mortality estimates at wind farms in the Neotropics, a region with fast-paced growth in wind energy developments but few accounts of aerial fauna mortality at such facilities (Agudelo et al. 2021).

Materials and methods

Each month from April to November 2016 – 2018, we surveyed bat communities at two wind farms in southern Mexico (Fig. 1) using mist nets, acoustic surveys, and conducting carcass searches. We identified bats to species as described below for each method, and then we updated and standardized all scientific names following the taxonomy in Simmons and Cirranello (2022). We assigned each species to a feeding or foraging guild following Denzinger and Schnitzler (2013), Kalko and Handley (2001), and Meyer and Kalko (2008).

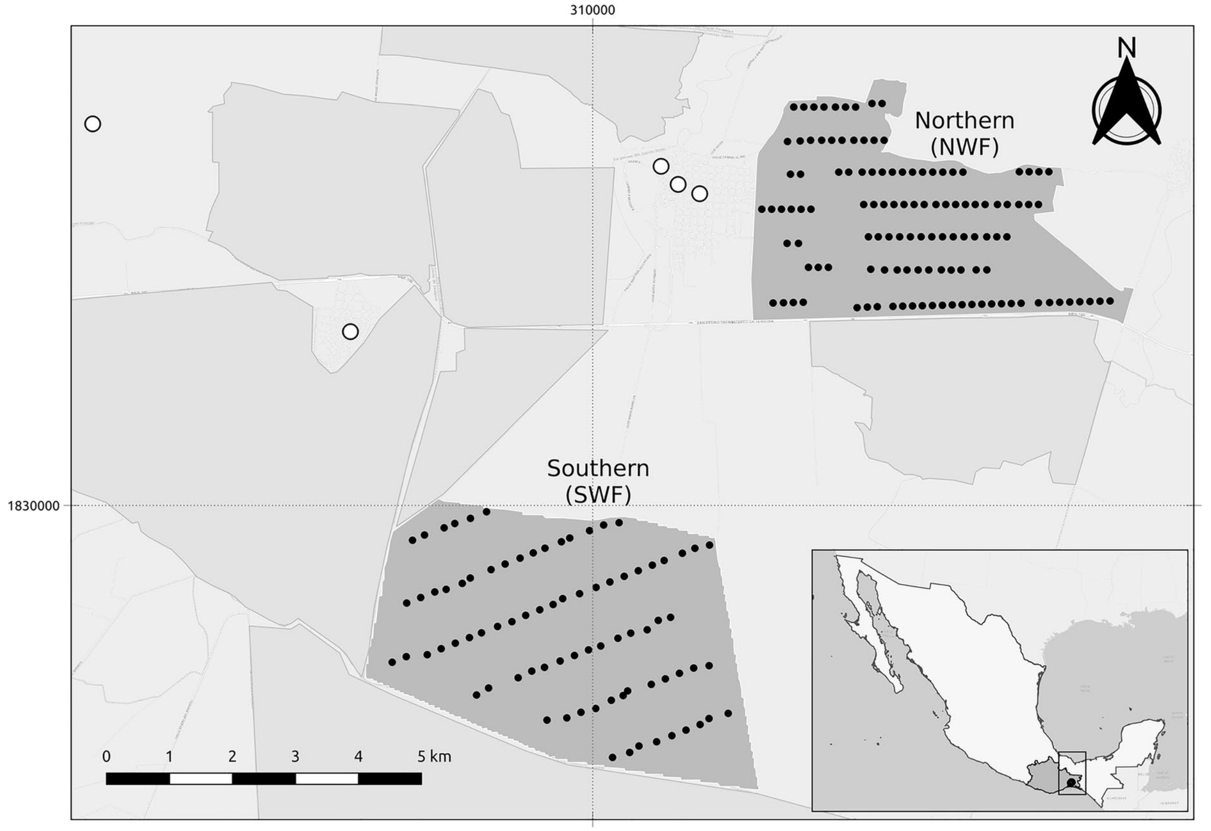

Fig. 1 Wind turbines (black dots) and footprints (dark gray polygons) of the Northern (NWF) and Southern (SWF) wind farms in southern Mexico showing nearby wind farms (light-gray polygons) and bat roosts (white circles). Inset shows Mexico in white, the state of Oaxaca in dark gray, the Isthmus of Tehuantepec within a black rectangle, and the location of the wind farms as a black dot.

Study area

The Northern and Southern wind farms (hereafter NWF and SWF) are located in the coastal plains of the Isthmus of Tehuantepec, southeast of the state of Oaxaca, Mexico (Fig. 1). This region harbors Mexico's highest wind energy potential (Alemán-Nava et al. 2014), and the first large wind farm of the country, built in 2006 with a capacity of 83.3 MW (Juárez-Hernández and León 2014). Up to 2020, the region had an installed capacity of ~3200 MW (Alonso and Beltrán 2021). NWF and SWF started operations in 2012 and 2014 with a capacity of 102.85 MW/year and 160 MW/year respectively (CRE 2022). Both wind farms have turbines on monopole towers, but with different turbine height and capacity, as well as distance between turbines (Table 1).

SWF is <5 km to the southwest of NWF (Fig. 1), and NWF is located directly east of a community where we have identified three small bat roosts

Table 1 Wind turbine attributes by wind farm.

Wind farm	Turbines (n)	Height to nacelle (m)	Maximum height (m)	Service area dimensions (m)	Turbines per access road (n)	Distance between turbines (m)	Capacity (MW)
SWF	80	80	125	60 × 30	6 – 23	240	2
NWF	121	43	69	40 × 15	9 – 29	160 - 1115	0.85

of different species in roofs of private residences (*Tadarida brasiliensis,* ~110 individuals; *Molossus molossus,* ~60 individuals; *M. rufus,* undetermined number of individuals; see Acknowledgments). Approximately 10 km from SWF and NWF there is a bat colony within a communal protected area home to at least 32 bat species belonging to 6 taxonomic families (Briones-Salas et al. 2013).

Diversity, richness, and evenness

Mist netting

Between April and November 2016 – 2018 and at each wind farm, we operated 4 – 8 mist nets (12 m long × 2.5 m high, 33 mm mesh, Avinet Inc., Dryden, New York) during 1 – 4 nights each month, placing them at least five meters apart. We located mist nets near areas with vegetation within the wind farms. Each net was installed a few centimeters above the ground and was active for 5 hours starting at sunset. All nets were checked every 15 or 20 minutes. We identified each captured individual following Medellín et al. (2008) and Álvarez-Castañeda et al. (2015). We calculated sampling effort as the area netted during the sampling hours (m^2net/h; Costa Straube and Vigiano Bianconi 2002), and the annual Relative Abundance (RA) of each species by wind farm, by dividing the number of individuals of each species by the sampling effort at each wind farm and year (García-Luis and Briones-Salas 2017).

Acoustic detection

We recorded bat vocalizations using one ultrasonic bat detector (Wildlife Acoustics Echo Meter EM3+) operating at a 384-kHz sampling rate, during 1 – 6 night/month at each site using two modes of sampling that we termed active and semiactive. During active sampling, we walked along rows of wind turbines (~1.2 – ~5.3 km-long), taking 90 minutes to walk the entirety of each road regardless of their length, during which time we recorded continuously. Semi-active sampling, on the other hand, consisted of 5 minutes of continuous recording from wind turbine service areas (i.e., 5-min recording near wind turbines).

We analyzed all recordings using BatSound Pro v.3.3 (Peterson Elektronik AB, Uppsala, Sweden) with a 1-s tracking unit (i.e., obtaining 60 screens/minute of recording). We generated spectrograms, selected call sequences with at least five consecutive pulses (attributable to one bat passing), and manually measured the initial and final frequency of one pulse per sequence, the interval between pulses, call duration, and peak frequency while checking for feeding buzzes (i.e., sequential echolocation calls that indicate the pursuit of prey by insectivorous bats). We visually identified phonic types to species following Arita and Fenton (1997), Torres-Morales (2007), and Rizo-Aguilar (2008), as well as the advice of an expert in bioacoustics of Mexican bat species (see Acknowledgments).

Analysis

During preliminary analysis, we detected differences in species composition of the bat assemblages at each wind farm; thus, we tested our predictions separately on each of them. For each wind farm and year, we estimated the first three Hill numbers ($q0$, $q1$ and $q2$; Chao et al. 2014) from mist netting and acoustic recordings data. Each Hill number provides a different measure of diversity, namely: species richness, Shannon entropy, and inverse Simpson entropy respectively. We compared the diversity of the bat assemblage at each wind farm between years by estimating 84% CI for each Hill number from 1000 bootstrap iterations of our data; for this we resampled from our mist-net data the number of individuals captured, and from our acoustic data the number of sampling nights. Non-overlapping CI represent statistically significant differences between samples with $\alpha = 0.05$ (MacGregor-Fors and Payton 2013). Before estimating Hill numbers, however, we evaluated the sample coverage for each wind farm and year with the Chao non-parametric estimator (Chao et al. 2014) using species abundance data from mist nets and presence-absence data from acoustic recordings. In case the coverage did not reach 100% even after extrapolating samples to double their size, we used standardized sample coverages (Chao et al. 2020). These analyses were done in R (R Development Core Team 2022) with the 'iNEXT' package (Hsieh et al. 2020).

Whittaker plots, also known as rank-abundance curves, illustrate species richness as the number of data points that make up the curve (i.e., how many species are ranked), and community evenness as the steepness of the curve. Steep curves indicate low evenness, as one or a few species have much higher abundances than the rest; shallow curves, on the other hand, indicate similar abundances among species and hence high community evenness. We built, for each wind farm and year, separate Whittaker plots for species captured with mist nets and recorded acoustically. We inspected those plots to assess whether species richness of bats captured and recorded acoustically, as well as the community evenness, changed through time. Whittaker plots for acoustic data were based on the number of vocalizations, hence they do not represent an actual measure of species abundances but a proxy of their activity levels.

Besides the difference in species composition between wind farms, we also observed differences between the assemblage of live bats (i.e., species recorded through mist nets and acoustic recordings) and the assemblage obtained through carcass searches. We explored differences in species composition between wind farms and between the 'live' and 'dead' assemblages through pair-wise dissimilarity analysis. Beta diversity, the extent of change in community composition, or degree of community differentiation (Koleff et al. 2003), can be driven by two different mechanisms: species turnover and species nestedness. Turnover refers to the replacement of species from site to site while nestedness refers to a subset of species from the richest site being present on the poorest site, and these processes describe all situations in which communities are not identical (Almeida-Neto et al. 2008; Baselga 2012).

We estimated the pair-wise dissimilarity between species compositions using the 'beta.pair' function from the R package 'betapart' (Baselga et al. 2022), estimating the total dissimilarity with the Jaccard index (β_{jac}) as well as its two components, species turnover (β_{jtu}) and species nestedness (β_{jne}), thus revealing the mechanisms driving the estimated dissimilarity. The total dissimilarity (β_{jac}) ranges between 0 – 1, with zero indicating identical species composition and a value of 1 indicating completely dissimilar sites or samples. When sites or samples are not identical or completely dissimilar, β_{jne} and β_{jtu} indicate the proportion of dissimilarity explained by nestedness or turnover respectively.

Mortality

The number of carcasses found at wind farms reflect only a portion of the actual number of fatalities. The difference is affected by the efficiency of searchers at finding carcasses, the frequency of the searches, the carcass persistence probability (i.e., the probability of carcasses not being removed by scavengers), and because not all killed animals fall or remain in the areas searched (Bernardino et al. 2013; Gauthreaux 1996). We searched for bat carcasses at SWF and NWF between 2016 and 2018, visiting wind farms with different frequencies and during periods of different length each year (Table 2). In order to incorporate the different carcass-searching efforts, we estimated bat mortality separately by year and wind farm.

For each wind farm and year, we estimated bat mortality using the function 'estimateN' from the package 'carcass' (Korner-Nievergelt et al. 2015) in R (R Development Core Team, 2022), in which we specified the following (italics denoting the name of the function's arguments in R): the number of carcasses found (*count*); an estimate for carcass

Table 2 Carcass search effort by year and wind farm. *Dates* = date of first and last search. *Days* = total number of days between first and last carcass search. *Searches* = Total number of searches in the year. *Interval* = average number of days between two searches. Italicized codes in parenthesis correspond with argument names used in the function 'estimateN' from the R package 'carcass' (Korner-Nievergelt et al., 2015).

	NWF				SWF			
Year	Dates	Days	Searches (*n*)	Interval (*d*)	Dates	Days	Searches (*n*)	Interval (*d*)
2016[a]	-	-	-	-	05 Apr – 08 Dec	247	75	3.3
2017[a]	May 1 – Nov 14	197	18	11.6	-	-	-	-
2018	Jan 25 – Nov 02	281	29	10	04 Jun – 27 Nov	176	46	3.9

[a] At NWF in 2016 and SWF in 2017, searchers only recorded days when carcasses were found. Consequently, for those wind farms in those specific years, we do not have reliable measures of the parameters reported in this table and we were unable to estimate mortality.

persistence probability (*s*); an estimate for searcher efficiency *(f)*; the proportion of carcasses in the search area (*a*); the search interval (i.e. the number of days between two searches; *d*); the number of searches (*n*); and the maximal possible number of animals killed for which a posterior probability is estimated (*maxn*).

'estimateN' first uses *s*, *f*, *d*, and *n* to estimate the probability (p) of finding a carcass. We specified "korner" as the method (*pform*) to estimate p. By also specifying the lower and upper limits of the 95% confidence intervals (CI) of parameters *s*, *a*, and *f*, 'estimateN' returns the median and 95% CI of p, thus also estimating uncertainty around each mortality estimate. We detail below the values used for arguments *s, a, f*, and *maxn*, but for search interval (*d*) and number of searches (*n*) see Table 2.

Carcass searches (count)

Land tenure in the Isthmus of Tehuantepec and in most of southern Mexico is characterized by small properties typically fenced and managed by different owners, some of which denied access to their properties due to conflicts with wind energy companies (e.g., Huesca-Pérez et al. 2016). Given the complications to access land surrounding wind turbines, we limited our searches to service roads (roads connecting wind turbines) and service areas (rectangular areas surrounding wind turbines, including pads). Under these conditions, we searched for carcasses on ground surfaces approximately 2017 m^2 and 3138 m^2 around each wind turbine of NWF and SWF respectively (Fig. S1). Service roads facilitate the transit of vehicles within wind farms and are permanently devoid of vegetation. Only the area immediately adjacent to the turbine tower (the pad, a subset of the service area) is covered with gravel, while the rest of the service area is covered either by grass, weed, bare ground, or a combination of these elements. Thus, the major proportion of the area searched was bare ground (service roads and some service areas), followed by grassy/weedy surfaces (most of the service areas), and a small proportion of gravel.

Every search started on the first turbine of a service road, from where 2 – 3 searchers walked along the road spacing themselves so that they could "sweep" the ground visually. When searchers arrived at a service area, they entered it in front of the turbine, positioned themselves parallel to each other facing the far end of the service area, and walked in that direction searching for carcasses. In order to effectively cover the whole area, searchers had to repeat this operation twice. After completing the search within the service area, searchers returned to the service road and continued searching on the road while walking to the next wind turbine and service area, where the procedure was repeated. Once reached the end of the service road (i.e., the row of turbines), searchers moved to another row and proceeded in the same way as described above. The starting point of the searches (end side of the service road), the position of searchers, and which road was searched changed every searching session.

When searchers found a carcass, they collected the specimen and identified it to species or genus either *in situ* or later with the aid of field guides and measuring instruments. For each carcass, searchers recorded: the wind farm where it was collected, GPS coordinates, date, ID number of closest turbine, name of the searcher, and a unique identifier to the carcass.

Proportion of carcasses in the search area (a)

The area searched for carcasses was limited (see *Carcass searches (count)* above), representing ~6.5% and ~10% of the areas defined by circular buffers with a 100 m radius around NWF and SWF wind turbines respectively, but most of each searched area was concentrated around turbines (Fig. S1). Carcass distribution is typically denser close to turbine towers (e.g., Choi et al. 2020), and when estimating mortality from carcass searches it is recommended to use an estimate of the proportion of carcasses that fall in the searched area rather than the searched area itself (Maurer et al. 2020). Dimensions of service areas searched for this work are similar (NWF) or exactly the same (SWF) as those of the 'western' and 'eastern' wind farms in Cabrera-Cruz et al. (2020) respectively; thus, we used their estimates of *a* (0.52 and 0.35 for SWF and NWF respectively).

Persistence probability (s)

The average time for the removal of bat carcasses at another nearby wind farm (second to the west of NWF in Fig. 1) is 2 days, with vegetation type around carcasses not affecting the time it takes to be removed by a scavenger (Villegas-Patraca et al. 2012). Then, for each year and wind farm, we estimated annual mortality using a persistence probability of 0.5. For details on the estimation of scavenger removal rates and carcass persistence see Villegas-Patraca et al. (2012).

Searcher efficiency (f)

One of the wind farms in this work (SWF) is the same as in Cabrera-Cruz et al. 2020 (code-named there as the "eastern" wind farm). Since some of our searchers were evaluated for that study (see Acknowledgments), and the search areas in this and that other study had similar characteristics, we used data from that study to estimate an efficiency at finding bat carcasses lying on bare ground of 0.55 (95% CI = 0.32 – 0.76).

Maximal possible number of animals killed (maxn)

Previous studies of annual bat mortality at nearby wind farms report upper 95% CI of 779 and 3576 individuals (Bolívar-Cimé et al., 2016) and of 2819 and 3464 individuals (Cabrera-Cruz et al., 2020). Thus, we set a *maxn* = 3520, the average of the two highest 95% CI in the literature.

Bat mortality estimates

After estimating bat mortality with 'estimateN', we calculated the expected number of fatalities/MW by dividing the mortality estimate of each year and wind farm by their respective nominal production capacity. We further extrapolated this to 365 days, to estimate a broad approximation of bat fatalities/MW/year. We did not estimate mortality for SWF in 2017 and for NWF in 2016 because searchers only recorded days when carcasses were found, and hence we could not estimate parameters *n* and *d*.

Results

In total, considering both wind farms and all methods (mist netting, acoustic recordings, and carcass searches), we recorded 41 bat species belonging to 23 genera and five families (Table S1).

On average, we mist-netted 10 nights/year at each wind farm, capturing 517 bats of 16 species. The most abundant species captured was *Artibeus jamaicensis* (Phyllostomidae; *n* = 247 individuals, 48% of captures). Almost half of the species captured were represented by ≤10 individuals (Fig. 2a). Annual sampling effort in m^2net/h ranged between 12,000 – 14,400 at SWF and 3,200 – 9,600 at NWF (Table S2).

We collected >12,000 minutes of acoustic recordings (5,400 min at SWF and 6,885 at NWF), with bat detections in 18.64% of this time (1,789 minutes at NWF and 1,205 minutes at SWF) containing a total of 129,147 bat passes (pulse sequences of the same phonic type) emitted by 29 species. *Pteronotus fulvus* (Mormoopidae) had the highest number of total vocalizations recorded in all years, being present in 9.61% of all minutes recorded (*n* = 1,180). The total number of minutes recorded, bat detections, vocalizations, and species recorded at SWF and NWF varied by year (Table S2).

All species recorded acoustically were either aerial insectivores or trawlers (*n* = 28 and 1 respectively) and 11 out of 15 species captured in mist nets were frugivorous or nectarivorous gleaners (Table S1).

Diversity, richness, and evenness

According to the Chao estimator, the level of inventory completeness derived from mist netting at both wind farms reached >99% during all years, allowing inter-annual comparisons. We did not find significant differences in bat diversity between 2016 and 2018 at either wind farm from mist net data (Fig. 3a and b). However, all Hill numbers at NWF were significantly lower in the second year compared to the first, and showed a general tendency to decrease from the first to the third year (Fig. 3a) suggesting a decrease in diversity of bats captured with mist nets through time.

Inventory completeness derived from acoustic recordings did not reach 100% even after extrapolating with twice as much data. Consequently, we implemented a standardized sample coverage of 86% of bat assemblages at both wind farms in all three years. All Hill numbers at both wind farms decreased annually and were significantly lower in the last year compared to the first (Figs. 3c and d), showing a decrease in diversity of bats recorded acoustically.

There was little variation in the identity of the most abundant species captured with mist nets every year at both wind farms, with *Artibeus lituratus* and *A. jamaicensis* being consistently the two most abundant

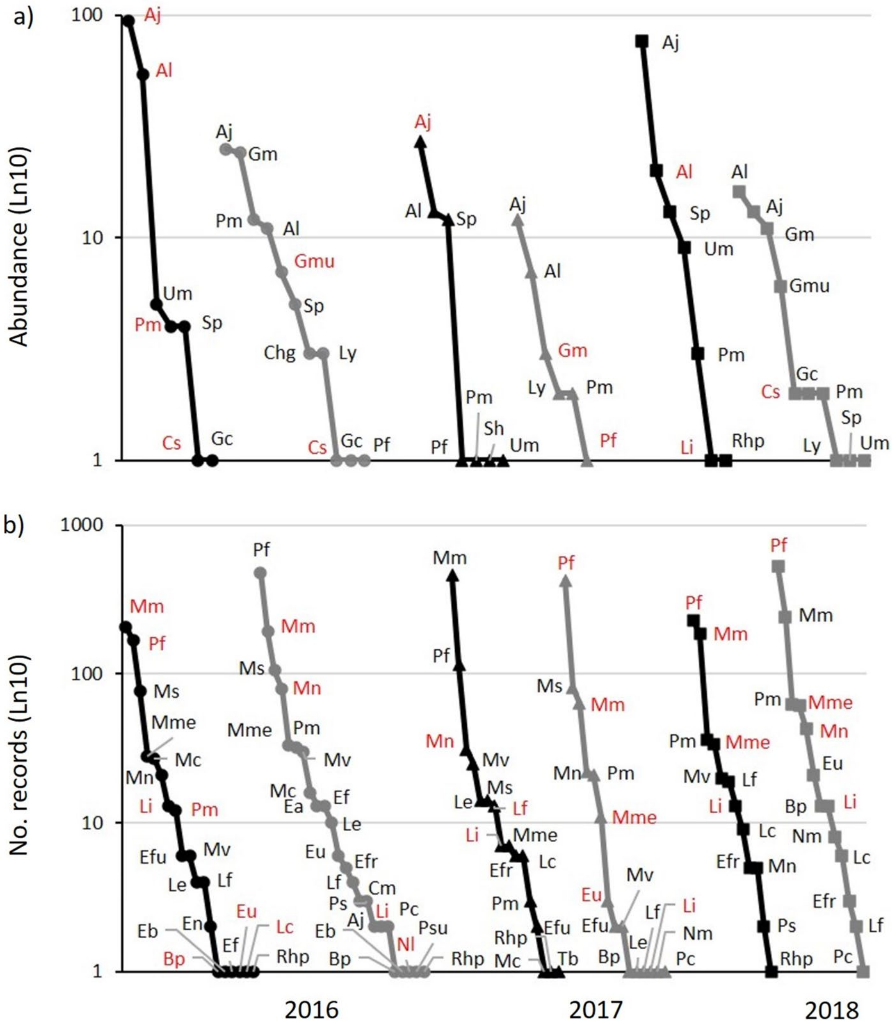

Fig. 2 Whittaker plots showing the structure of the bat assemblages sampled with **a**) mist nets and **b**) acoustic recorders each year. Black and gray lines: SWF and NWF respectively. Data points are linked to species codes available in Table S1. Red-colored species codes represent species also found as carcasses in the corresponding wind farm and year. Color version of this figure available online

species at SWF, and among the top three most abundant at NWF (Fig. 2a). Similarly, two species (*Pteronotus fulvus* and *Molossus molossus*) consistently had the highest number of vocalizations recorded at both wind farms in all years (Fig. 2b). The shape of the Whittaker plots from each wind farm, and the number of points in each plot, did not vary visibly with year, indicating that community evenness and species richness did not change through time at either site (Fig 2a and b).

Mortality

At both wind farms, all years included, we found a total of 123 carcasses belonging to 19 species, 12 genera and five families (Table S1). We identified 74 carcasses to species, 13 to genus, and 36 could not be identified due to advanced decomposition. Most of the species (63%) were aerial insectivores while the rest were frugivorous or nectarivorous gleaners. The three genera with the highest number of carcasses were *Lasiurus* (22), *Molossus* (15), and *Centurio* (10); accordingly, the taxonomic families with most carcasses were Phyllostomidae, Molossidae (26 each) and Vespertilionidae (22). Identified species with the highest numbers of carcasses were *Lasiurus intermedius* (Vespertilionidae, $n = 17$) and *Centurio senex* (Phyllostomidae, $n = 10$).

We identified 15 and 13 species from 70 and 54 carcasses found at SWF and NWF respectively. In 2018, the only year when we searched for carcasses at both wind farms, we found carcasses of two species

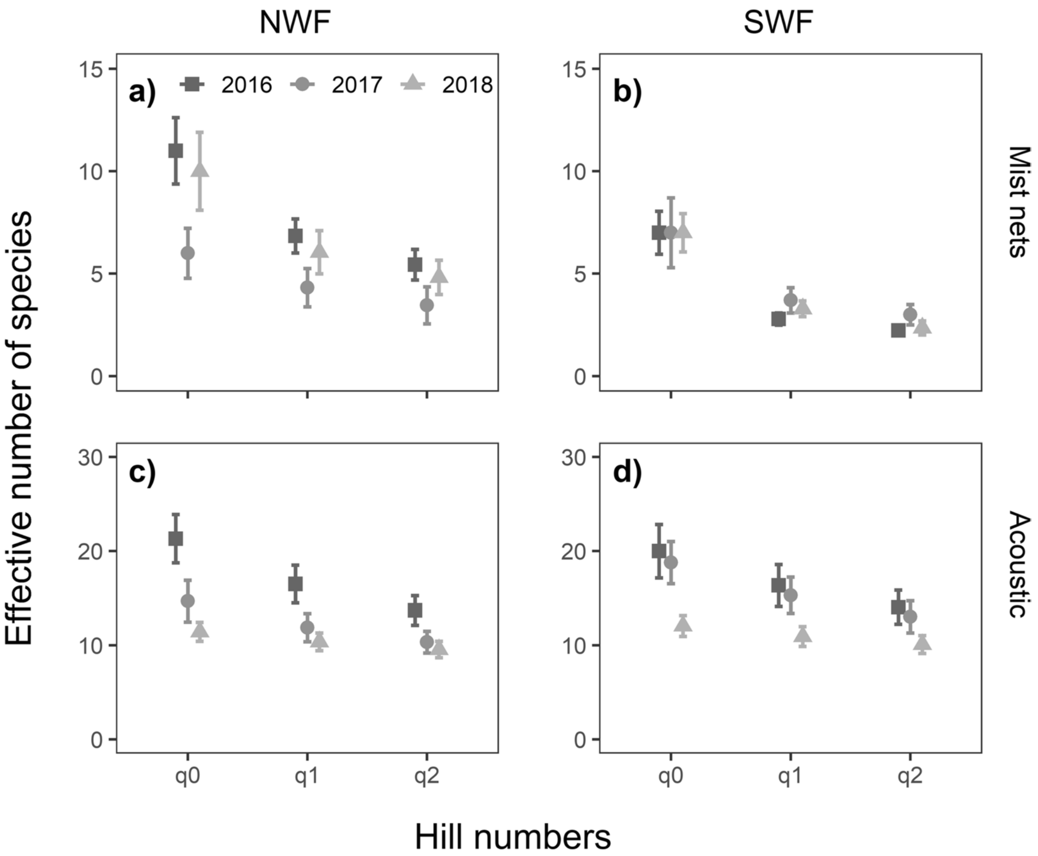

Fig. 3 Average (mid points) and 84% confidence intervals (whiskers) of Hill numbers (X-axis: q0 = species richness, q1 = Shannon entropy, q2 = inverse Simpson entropy) derived 1000 bootstrap iterations of our mist netting (top) and acoustic recordings (bottom) data at the NWF (left) and SWF (right) wind farms in southern Mexico between 2016 – 2018

at each wind farm that did not occur in the other. Specifically, we found at SWF carcasses of *Artibeus lituratus* and *Molossus molossus* but not at NWF, while *Lasiurus ega* and *Molossus nigricans* occurred as carcasses at NWF but not at SWF. Similarly, two species and their genera (*Balantiopteryx plicata* and *Enchistenes hartii*) occurred as carcasses in SWF but not in NWF. However, we were not able to identify to species or genus 13 and 8 carcasses from NWF and SWF. Nevertheless, the only member of the Emballonuridae family found as carcass occurred at NWF. Overall, these results suggest that bat communities might be impacted differentially by these wind farms despite the short distance between them (<5 km between their closest wind turbines). We estimate a median annual bat mortality ranging between 15.41 – 15.72 bats/MW/year at NWF, and between 3.97 and 4.32 bats/MW/year at SWF (Table 3).

Pair-wise dissimilarity

We found >40% of dissimilarity in the species composition of the bat assemblages recorded at each wind farm, with species turnover consistently accounting for more than half of the dissimilarity each year (Fig. 4a). When comparing assemblages recorded at each wind farm by method, we found >50% and >40% of dissimilarity in the composition of species captured with mist nets and recorded acoustically respectively, with species turnover also accounting for an important proportion of the dissimilarity (Fig. S2).

Except for NWF in 2017, the composition of species identified from carcasses was not a proper subset of the bat assemblage. We found that species turnover accounts for 10% – 30% of the dissimilarity in species composition between live bats and carcasses, both wind farms and all years considered (Fig. 4b), but for up to 60% of the dissimilarity at SWF in 2017 (Fig. S3). Furthermore, we recorded two species (*Enchisthenes hartii* and *Phyllostomus discolor*) as carcasses only but not in mist nets or acoustic recordings. Similarly, 3, 3, and 1 species found as carcasses at SWF in 2016, 2017 and 2018 respectively were not recorded in live bats, while at NWF in 2016 and 2018 we found one species as carcass that was not detected by neither monitoring method. Overall, between 19% and 36% of the species recorded live each year were represented as carcasses (Table 4).

Discussion

In both wind farms, the diversity of bats recorded acoustically was significantly lower at year three compared to year one, and the diversity of bats captured with mist nets tended to decrease at one of the wind farms. Surprisingly, despite being <5 km

Table 3. Number of carcasses found (n) and estimated median mortality at NWF and SWF (Estimate). We were unable to estimate mortality at NWF in 2016 and SWF in 2017 (see Methods and Table 2).

	NWF				SWF			
	n	Estimate (95% CI)	Estimate / MW	Estimate / MW / Year	n	Estimate (95% CI)	Estimate / MW	Estimate / MW / Year
2016	17	-	-	-	34	430 (244– 832)	2.69	3.97
2017	14	874 (411 – 1901)	8.49	15.72	12	-	-	-
2018	23	1222 (626 – 2506)	11.86	15.41	23	333 (178 – 671)	2.08	4.32
Total	54				69			

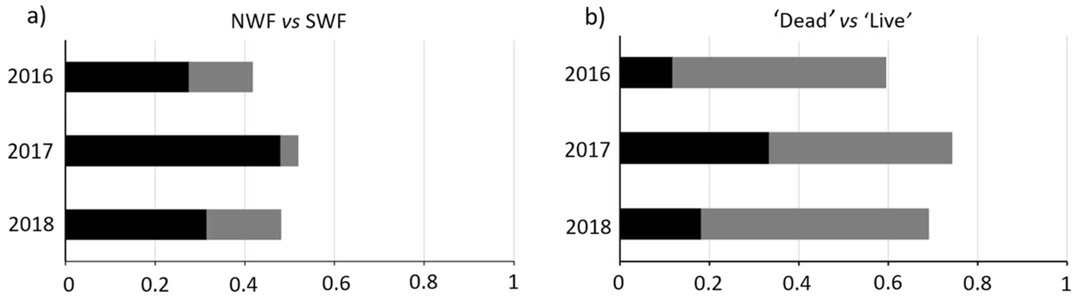

Fig. 4 Annual difference in species composition (β_{jac}, full bar) between **a**) wind farms, with species detected by mist netting and acoustic recordings pooled together by wind farm; and **b**) between species recorded as carcasses and those recorded live (captured and recorded acoustically), with species from both wind farms pooled together. Black: proportion of difference due to species turnover (β_{jtu}), gray: proportion due to species nestedness (β_{jne}). Also see Figures S1 and S2

Table 4. Number of species identified as carcasses ('*Dead*'), and through mist nets and acoustic recordings ('*Live*'), and their proportion of *Dead / Live*.

	NWF			SWF		
	Dead	Live	Proportion	Dead	Live	Proportion
2016	7	32	21.9	9	25	36.0
2017	6	19	31.6	4	21	19.0
2018	5	22	22.7	5	16	31.2

apart, we detected 25% – 45% of species turnover in the composition of bat assemblages between the two wind farms, and not all species documented as carcasses were captured or detected acoustically. These results have several implications for evaluations of the effect that wind farms in highly diverse regions have on bats.

First, that the operation of wind farms might affect bat guilds differentially. The diversity of bats detected acoustically decreased consistently through time at both wind farms, most of which were aerial insectivores and nearly 65% of the species found as carcasses belonged to this guild. Hence, mortality might play a role in decreasing the diversity of aerial insectivores. On the contrary, the diversity of bats captured with mist nets (mostly gleaners) remained similar through the years except for NWF where it was significantly lower at year 2 but bounced back the following year. When we started our surveys, the SWF and NWF had been operating for 2 and 4 years respectively, hence the community of low-flying species might have recovered and stabilized after the first years of operation (Briones-Salas et al. 2017). Further work is needed to assess whether mortality affects bat guilds differentially in this region, since differential impacts could alter the structure and function of local bat communities.

It should be noted that by having surveyed bat assemblages a few years after the wind farms became operational, we may have missed the period when the greatest changes in diversity might be expected (e.g. Briones-Salas et al. 2017). Furthermore, the composition of bat assemblages can vary through time (e.g. Aguirre et al. 2003) and three-year-long surveys may be insufficient to detect long-term, continuing trends in diversity changes. Moreover, since our surveys only included years when the wind farms were already operational and from within their area of influence, we can't unequivocally conclude that the observed changes in guild diversity are directly attributable to wind farm operation. Hence, our results should be interpreted as just an indication of a potential decline of aerial insectivore bats, probably attributable to wind farm operations. Future similar surveys at wind farms in highly diverse regions should ideally encompass the pre-construction period and the very first years of operation, longer term efforts, and consider surveying multiple sites including controls outside wind farms. Alternatively, analyses should incorporate longer-term data, including those from early periods; in order to facilitate this, wind energy companies should make all their data derived from environmental surveys publicly accessible (e.g. Salguero et al. 2023).

A second implication is that species that tend to fly at low altitudes may be at higher risk than one would expect. The susceptibility of 28 European bat species to collide with wind turbines is higher for high-altitude flying species that includes open space aerial foragers, and lower for low-altitude flying species including gleaning foragers (Roemer et al. 2017). Gleaner bats forage in the vegetation, which in our study area has mean heights ranging from 4.1m to 6.8 m – 7.9 m (Gallardo et al. 2005; Silva-Aparicio et al. 2018), well below the minimum altitude of the rotor-swept area (16 and 35 meters at NWF and SWF respectively). Hence, one could expect that gleaner bats at our study sites would have a low vulnerability of mortality. However, over a third of the species that we identified in carcasses belong to this guild. Land cover at the coastal plains of the Isthmus and at both wind farms is a mosaic of cattle pastures, cropland, secondary vegetation, and patches of tropical deciduous and sub-deciduous forest (Muñoz-Jiménez et al. 2019). Gleaner bats may get exposed to collisions when moving between patches of vegetation, as other species in North America seem to get exposed during their migratory movements (Arnett et al. 2008).

Since bat assemblages differed between wind farms, a third implication of our results is that every single wind energy project proposed at highly diverse regions should be surveyed intensively to characterize the bat community. Five bat species reported at another wind farm ≤5km away from SWF and NWF (Bolívar-Cimé et al. 2016) were not recorded here, while we report 16 species missing in that study even though the same survey methods were used in both studies during a similar amount of time. We acknowledge, however, that differences in the species composition of bat assemblages may relate to seasonal fluctuations as recorded in dry forests in the Neotropics (Aguirre et al. 2003; Avila-Cabadilla et al. 2014), or to differences in land cover (Avila-Cabadilla et al. 2012), or to nearby bat roosts (Fig. 1). Future studies should look into the phenology of bat species and assemblages in the region.

Implementing minimum distances between proposed wind turbine sites and potential roosts or maternity colonies could be an important management tool (Lehnert et al. 2014). Where wind turbines have already been erected, such as in NWF and SWF, it remains to be investigated whether and to what extent nearby roosts (Fig. 1) contribute to the bat assemblages recorded at each wind farm. Most importantly, it should be evaluated whether mortality at wind farms affects the viability of local roosts; this would be of particular relevance for wind farms sited within distribution ranges of endemic bat species (e.g. Bennett et al. 2022).

The potentially transient presence of some species in the region may also affect both the differences between wind farms and the detectability of the species. We documented the presence of *Tadarida brasiliensis* only once, acoustically and with no carcasses. This species occurs in North, Central, and South America (Wilkins 1989) and is commonly killed at wind farms in southern US (Weaver et al. 2020) where it is migratory. *Tadarida brasiliensis* migrates during the boreal winter mostly to northern and central Mexico, but some populations from southeastern US and northeastern Mexico go as far south as Chiapas (Wiederholt et al. 2013), the Mexican state east of Oaxaca. Chiapas harbors a colony with ~2500 individuals of this species nearly 300 km from our study sites, but it is not clear whether those individuals perform migratory movements (Llaven-Macías et al. 2021). Similarly, *Artibeus lituratus*, one of the most abundant species in our mist nets, is known to perform long-distance movements in other tropical regions (Arnone et al. 2016). However, migratory movements of bats in the Neotropics remain poorly understood (Fraser et al. 2010).

Another implication of our results is that even three years of mist netting and ground-based acoustic recordings are not enough to get a full picture of the bat species that might have fatal interactions with turbines at highly diverse regions. The combined use of mist nets and ground-based acoustic recorders for monitoring Neotropical bat communities identifies more species than using a single method (MacSwiney et al. 2008; Pech-Canche et al. 2010). Thus, we expected that our surveys would capture most of the species present in the area. In fact, the 41 bat species that we recorded represent up to 73% of those documented in the Isthmus (García-Grajales and Buenrostro-Silva 2012). However, ground-based recordings may fail at detecting species that move at high-altitudes (Voigt et al. 2021). This might explain, for example, why we recorded a single individual of *Nyctinomops laticaudatus* acoustically, since some *Nyctinomops* species commute and forage up to 200 m above the ground (Griffin and Thompson 1982, cit. by MacSwiney et al. 2020). Nevertheless, not all of the low abundances recorded here can be attributed to methodological limitations. Respectively, *Enchistenes hartii* and *Phyllostomus discolor* are herbivorous and gleaning insectivorous species (Jones et al. 2009; Kwiecinski 2006) that can be considered low-altitude fliers (e.g., Pereira et al. 2010) and are typically captured in mist nets (Arroyo-Cabrales and Owen 1997; Kwiecinski 2006). However, we only registered them as carcasses.

The species and genera with the highest number of carcasses differed between wind farms, and two species found as carcasses at SWF were not identified at NWF. Hence, in the future it should not be assumed that the impacts documented at a wind farm in a highly diverse region will be the same as for another nearby site. We acknowledge, however, that not all carcasses found were identified to genus or species. It would be desirable the use molecular methods to identify bat carcasses (Chipps et al. 2020). This would allow to unequivocally assess what species get killed at wind farms and would be particularly useful in tropical areas where decomposition is fast due to high temperatures. Nevertheless, we did not find carcasses of species of the Emballonuridae family in NWF but, after pooling data from both wind farms, that family was among the top five in numbers of carcasses found; hence we suggest to assume that differences exist, and that careful evaluations should be made at all wind energy facilities. This is especially relevant considering that up to 36% of the species in the assemblage had fatalities at these wind farms (average = 27%, all years and both wind farms considered), and that up to 56% of the species recorded in other tropical area were killed at a single wind farm (Barros et al. 2015).

Our estimated fatality/MW/year for SWF is much lower than previous estimates for the same wind farm in 2015 (Cabrera-Cruz et al., 2020). In that study, authors set the argument ‘*maxn*’ = 10000 in the R function ‘*estimateN*’, while we set ‘*maxn’* = 3520. As an exercise, we re-ran our estimates setting ‘*maxn*’ = 10000 and the result did not change, hence this might not be the reason for the difference. This opens the question of whether the difference relates to our observed reduction in diversity of aerial insectivores through time and to the higher mortality of bats in that guild. On the other hand, our estimated mortality/MW/year is higher at NWF even though we found fewer carcasses there, placing it among the highest when compared to other wind farms in the USA (Strickland et al. 2011).

Mortality estimates are as good as the values of the parameters fed to the R function 'estimateN'. In this work, the parameters *a* (proportion of carcasses in the search area), *f* (searcher efficiency), and *s* (persistence probability) are based on previously published work rather than on estimates made during the surveys reported here. Consequently, our median mortality estimates would have been different had we used other values of *a*, *f*, and *s*. For example, a lower persistence of carcasses on the ground, a lower efficiency of our searchers, or a smaller area searched, would have resulted in higher mortality estimates. On the contrary, a higher carcass persistence, higher searcher efficiency, or a larger area searched would have contributed towards lower mortality estimates.

As an additional exercise, we re-ran our mortality estimates with different parameter values, finding that decreasing *a*, *f*, or *s* by just 10% of the values used for the analysis reported in Table 3, increased mortality estimates to up to 23.82 bat fatalities/MW/year in NWF and to up to 6.39 fatalities/MW/year in SWF (Table S3). On the contrary, increasing the value of those parameters by 10% lowered our mortality estimates to up to 10.34 fatalities/MW/year in NWF and to up to 2.81 fatalities/MW/year in SWF (Table S4). In both cases, the modification of parameter *s* resulted in mortality estimates with the greatest difference when compared to our results.

The parameter values we used for our mortality estimates were calculated for sites near NWF and SWF. Consequently, we consider that our estimates represent a fair approximation of the true bat mortality occurring at NFW and SWF. We also acknowledge, however, that our mortality estimates at both sites might be biased low given the limited area searched; this might be especially true for NWF given the long intervals between carcass searches (Smallwood 2017).

The installed capacity of wind energy in the coastal plains of the Isthmus of Tehuantepec has increased >30 fold since the construction of the first large wind farm in the region and is expected to continue growing throughout the country (SENER 2018). Similarly, the installed capacity of wind-energy production in Latin America is poised to continue growing (IEA 2021). The results presented here indicate the necessity for long-term, multi-method and intensive surveys for evaluating the post-construction effects that wind farms have on bats in highly diverse regions.

Conclusions

We found a significant decrease in the diversity of bats recorded acoustically, most of which were aerial insectivores, but not of bats captured with mist nets, the majority of which were gleaners. Furthermore, most of the species identified from carcasses were aerial insectivores. Hence, wind farms in this region might affect bat guilds differentially. However, over a third of species found as carcasses were gleaners, hence even species that tend to fly at low altitudes have a non-negligible risk of mortality. Turnover consistently explained an important proportion of the dissimilarity in species compositions between wind farms and between the 'live' and 'dead' communities, hence nearby wind farms at highly diverse regions impact different sets of species. Long-term, intensive surveys are necessary to identify all bat species that can have fatal interactions with turbines in highly diverse regions.

Acknowledgements We want to thank Dr. Antonio Guillén for his help identifying some species from acoustic recordings. Guillermo Rodriguez Aguilar shared his observation of bat roosts in Santo Domingo Ingenio, Oaxaca. Christian Alavez contributed with valuable comments on bat taxonomy. César Gallo helped with the study area figure. Guillermo Rodríguez Aguilar and José Domingo Cú Vizcarra processed acoustic recordings and identified calls to species. Special thanks two anonymous reviewers who helped improve this manuscript and to the many searchers without whom this work would not have been possible (italics indicate searchers that participated in previous studies, see main text): Alex Coronel, Alma Patricia Degante González, Angela Marlene Soto Calderón, Ana Ramírez, *Anayani Rivera*, Aressia García, *Carlos Corona*, Citlalli Fernández Reyes, *Delfino Santiago, Dulce Santiago*, Fátima del Carmen García Salinas, Griselda Jorge, Isabel García, Israel Lozano, Jazmín Ramírez Ramírez, Jonathan Sulvararan, José Luis Ponce, Mariana Del Valle, Martha Santiago, Mauricio Rodríguez Vázquez, Miguel Demeneghi, Miriam Escobar, Paola Figueroa Islas, Roberto Rodríguez, Tereso Hernández, Víctor López, William Ramos Arreola.

Author Contributions José Luis Aguilar López and Sergio A. Cabrera-Cruz designed this manuscript and contributed equally to its development. Material preparation and analysis were performed by José Luis Aguilar López, Marco T. Oropeza-Sánchez, Pedro A. Aguilar-Rodríguez, and Sergio A. Cabrera-Cruz. Rafael Villegas Patraca and Oscar Muñoz Jiménez conceived and coordinated data collection. The first draft of the manuscript was written by Sergio A. Cabrera-Cruz with input from José Luis Aguilar López. All authors commented early versions of the manuscript and approved its final form.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author.

Declarations

Competing Interests RVP and OMJ were responsible for the post-construction surveys at NWF and SWF during the period of this study. SACC, JLAL, RVP and OMJ current affiliation is with the institution in charge of conducting the surveys and declare no other interests. PAAR and MTOS declare they have no interests to disclose. Actual wind farm names not disclosed due to privacy reasons.

References

Agudelo, M. S., Mabee, T. J., Palmer, R., & Anderson, R. (2021). Post-construction bird and bat fatality monitoring studies at wind energy projects in Latin America: A summary and review. *Heliyon, 7*(6), e07251. https://doi.org/10.1016/j.heliyon.2021.e07251

Aguirre, L. F., Lens, L., van Damme, R., & Matthysen, E. (2003). Consistency and variation in the bat assemblages inhabiting two forest islands within a neotropical savanna in Bolivia. *Journal of Tropical Ecology, 19*(4), 367–374. https://doi.org/10.1017/S0266467403003419

Alemán-Nava, G. S., Casiano-Flores, V. H., Cárdenas-Chávez, D. L., Díaz-Chavez, R., Scarlat, N., Mahlknecht, J., et al. (2014). Renewable energy research progress in Mexico: A review. *Renewable and Sustainable Energy Reviews, 32*, 140–153. https://doi.org/10.1016/j.rser.2014.01.004

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Jr., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos, 117*(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Alonso, A. A., & Beltrán, Y. G. (2021). Diagnóstico y riesgos de la energía eólica en México. *Revista de Geografía Agrícola, 67*, 27–45. https://doi.org/10.5154/r.rga.2021.67.02

Álvarez-Castañeda, S. T., Álvarez, T., & González-Ruiz, N. (2015). Guía para la identificación de los mamíferos de México en campo y laboratorio. *Centro de Investigaciones Biológicas del Noroeste, SC, Asociación Mexicana de Mastozoología, AC Ciudad de México, México*.

Arita, H. T., & Fenton, M. B. (1997). Flight and echlocation in the ecology and evolution of bats. *Trends in Ecology & Evolution, 12*(2), 53–58. https://doi.org/10.1016/S0169-5347(96)10058-6

Arnett, E. B., Brown, W. K., Erickson, W. P., Fiedler, J. K., Hamilton, B. L., Henry, T. H., et al. (2008). Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management, 72*(1), 61–79. https://doi.org/10.2193/2007-221

Arnone, I. S., Trajano, E., Pulchério-Leite, A., & Passos, F. de C. (2016). Long-distance movement by a great fruit-eating bat, *Artibeus lituratus* (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica, 16*(1), e0026. https://doi.org/10.1590/1676-0611-BN-2015-0026

Arroyo-Cabrales, J., & Owen, R. D. (1997). Enchisthenes hartii. *Mammalian Species, 546*, 1–4. https://doi.org/10.2307/3504135

Avila-Cabadilla, L. D., Sanchez-Azofeifa, G. A., Stoner, K. E., Alvarez-Añorve, M. Y., Quesada, M., & Portillo-Quintero, C. A. (2012). Local and landscape factors determining occurrence of Phyllostomid bats in tropical secondary forests. *PLOS ONE, 7*(4), e35228. https://doi.org/10.1371/journal.pone.0035228

Avila-Cabadilla, L. D., Stoner, K. E., Nassar, J. M., Espírito-Santo, M. M., Alvarez-Añorve, M. Y., Aranguren, C. I., et al. (2014). Phyllostomid bat occurrence in successional stages of Neotropical dry forests. *PLOS ONE, 9*(1), e84572. https://doi.org/10.1371/journal.pone.0084572

Baerwald, E. F., D'Amours, G. H., Klug, B. J., & Barclay, R. M. R. (2008). Barotrauma is a significant cause of bat fatalities at wind turbines. *Current Biology, 18*(16), R695–R696. https://doi.org/10.1016/j.cub.2008.06.029

Barré, K., Le Viol, I., Bas, Y., Julliard, R., & Kerbiriou, C. (2018). Estimating habitat loss due to wind turbine avoidance by bats: Implications for European siting guidance. *Biological Conservation, 226*, 205–214. https://doi.org/10.1016/j.biocon.2018.07.011

Barros, M. A. S., de Magalhães, R. G., & Rui, A. M. (2015). Species composition and mortality of bats at the Osório Wind Farm, southern Brazil. *Studies on Neotropical Fauna and Environment, 50*(1), 31–39. https://doi.org/10.1080/01650521.2014.1001595

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography, 21*(12), 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baselga, A, Orme, D., Villeger, S., Bortoli, J.D., Leprieur, F., Logez, M., et al. (2022). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. https://CRAN.R-project.org/package=betapart. Accessed 13 May 2022

Bennett, E. M., Florent, S. N., Venosta, M., Gibson, M., Jackson, A., & Stark, E. (2022). Curtailment as a successful method for reducing bat mortality at a southern Australian wind farm. *Austral Ecology, 47*(6), 1329–1339. https://doi.org/10.1111/aec.13220

Bernardino, J., Bispo, R., Costa, H., & Mascarenhas, M. (2013). Estimating bird and bat fatality at wind farms: a practical overview of estimators, their assumptions and limitations. *New Zealand Journal of Zoology, 40*(1), 63–74. https://doi.org/10.1080/03014223.2012.758155

Bolívar-Cimé, B., Bolívar-Cimé, A., Cabrera-Cruz, S. A., Muñoz-Jiménez, Ó., & Villegas-Patraca, R. (2016). Bats in a tropical wind farm: species composition and importance of the spatial attributes of vegetation cover on bat fatalities. *Journal of Mammalogy, 97*(4), 1197–1208. https://doi.org/10.1093/jmammal/gyw069

Briones-Salas, M., Lavariega, M. C., & Moreno, C. E. (2017). Effects of a wind farm installation on the understory bat community of a highly biodiverse tropical region in Mexico. *PeerJ, 5*, e3424. https://doi.org/10.7717/peerj.3424

Briones-Salas, M., Peralta-Pérez, M., & García-Luis, M. (2013). Acoustic characterization of new species of bats for the State of Oaxaca, Mexico. *Therya, 4*(1), 15–32. https://doi.org/10.12933/therya-13-106

Cabrera-Cruz, S. A., Cervantes-Pasqualli, J., Franquesa-Soler, M., Muñoz-Jiménez, Ó., Rodríguez-Aguilar, G., & Villegas-Patraca, R. (2020). Estimates of aerial vertebrate mortality at wind farms in a bird migration corridor and bat diversity hotspot. *Global Ecology and Conservation, 22*, e00966. https://doi.org/10.1016/j.gecco.2020.e00966

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs, 84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., Kubota, Y., Zelený, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., et al. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research, 35*(2), 292–314. https://doi.org/10.1111/1440-1703.12102

Chipps, A. S., Hale, A. M., Weaver, S. P., & Williams, D. A. (2020). Genetic approaches are necessary to accurately understand bat-wind turbine impacts. *Diversity, 12*(6), 236. https://doi.org/10.3390/d12060236

Choi, D. Y., Wittig, T. W., & Kluever, B. M. (2020). An evaluation of bird and bat mortality at wind turbines in the Northeastern United States. *Plos One, 15*(8), e0238034. https://doi.org/10.1371/journal.pone.0238034

Costa Straube, F., & Vigiano Bianconi, G. (2002). Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de redes-de-neblina. *Chiroptera Neotropical, 8*(1–2), 150–152.

CRE. (2022). (Comisión Reguladora de Energía). Lista de permisos y autorizaciones otorgados en materia de electricidad. *Micrositio de Permisos en materia de Generación de Energía Eléctrica*. Government. http://www.gob.mx/cre/acciones-y-programas/micrositio-de-permisos-en-materia-de-generacion-de-energia-electrica. Accessed 25 March 2022

Cryan, P. M., & Barclay, R. M. R. (2009). Causes of bat fatalities at wind turbines: hypotheses and predictions. *Journal of Mammalogy, 90*(6), 1330–1340. https://doi.org/10.1644/09-MAMM-S-076R1.1

Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology, 4*(164), 1–15. https://doi.org/10.3389/fphys.2013.00164

Ferri, V., Battisti, C., & Soccini, C. (2016). Bats in a Mediterranean mountainous landscape: Does wind farm repowering induce changes at assemblage and species level? *Environmental Management, 57*(6), 1240–1246. https://doi.org/10.1007/s00267-016-0686-2

Fraser, K. C., McKinnon, E. A., & Diamond, A. W. (2010). Migration, diet, or molt? Interpreting stable-Hydrogen isotope values in Neotropical bats. *Biotropica, 42*(4), 512–517. https://doi.org/10.1111/j.1744-7429.2009.00608.x

Frick, W. F., Baerwald, E. F., Pollock, J. F., Barclay, R. M. R., Szymanski, J. A., Weller, T. J., et al. (2017). Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation, 209*, 172–177. https://doi.org/10.1016/j.biocon.2017.02.023

Gallardo, J. A., Pérez, E. A., & Meave, J. A. (2005). Estructura, composición y diversidad de la selva baja caducifolia del Cerro Verde, Nizanda (Oaxaca), México. *Boletín de la Sociedad Botánica de México, 76*, 19–35.

García-Grajales, J., & Buenrostro-Silva, A. (2012). Revisión al conocimiento de los murciélagos del estado de Oaxaca. *Therya, 3*(3), 277–293.

García-Luis, M., & Briones-Salas, M. (2017). Composición y actividad de la comunidad de murciélagos artropodívoros en parques eólicos del trópico mexicano. *Revista Mexicana de Biodiversidad, 88*(4), 888–898. https://doi.org/10.1016/j.rmb.2017.10.018

Gauthreaux, S. A. (1996). Suggested practices for monitoring bird populations, movements and mortality in wind resource areas. In *Proceedings of the National Avian-Wind Power Planning Meeting II* (pp. 88–110). Washington, DC: National Wind Coordinating Committee/RESOLVE.

Guest, E. E., Stamps, B. F., Durish, N. D., Hale, A. M., Hein, C. D., Morton, B. P., et al. (2022). An updated review of hypotheses regarding bat attraction to wind turbines. *Animals, 12*(3), 343. https://doi.org/10.3390/ani12030343

Hsieh, T. C., Ma, K. H., & Chao, A. (2020). iNEXT: Interpolation and Extrapolation for Species Diversity. https://CRAN.R-project.org/package=iNEXT. Accessed 23 May 2022

Huesca-Pérez, M. E., Sheinbaum-Pardo, C., & Köppel, J. (2016). Social implications of siting wind energy in a disadvantaged region – The case of the Isthmus of Tehuantepec, Mexico. *Renewable and Sustainable Energy Reviews, 58*, 952–965. https://doi.org/10.1016/j.rser.2015.12.310

IEA. (2021). *Renewables 2021. Analysis and forecasts to 2026* (p. 173). France: International Energy Agency. https://www.iea.org/reports/renewables-2021. Accessed 14 December 2022

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., et al. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology, 90*(9), 2648–2648. https://doi.org/10.1890/08-1494.1

Juárez-Hernández, S., & León, G. (2014). Energía eólica en el istmo de Tehuantepec: desarrollo, actores y oposición social. *Problemas del Desarrollo, 45*(178), 139–162. https://doi.org/10.1016/S0301-7036(14)70879-X

Kalko, E. K. V., & Handley, C. O. (2001). Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology, 153*(1), 319–333. https://doi.org/10.1023/A:1017590007861

Katzner, T. E., Nelson, D. M., Diffendorfer, J. E., Duerr, A. E., Campbell, C. J., Leslie, D., et al. (2019). Wind energy: An ecological challenge. *Science, 366*(6470), 1206–1207. https://doi.org/10.1126/science.aaz9989

Keehn, J. E., & Feldman, C. R. (2018). Disturbance affects biotic community composition at desert wind farms. *Wildlife Research, 45*(5), 383–396. https://doi.org/10.1071/WR17059

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology, 72*(3), 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Korner-Nievergelt, F., Behr, O., Brinkmann, R., Etterson, M. A., Huso, M. M. P., Dalthorp, D., et al. (2015). Mortality estimation from carcass searches using the R-package carcass — a tutorial. *Wildlife Biology, 21*(1), 30–44. https://doi.org/10.2981/wlb.00094

Kumara, H. N., Babu, S., Rao, G. B., Mahato, S., Bhattacharya, M., Rao, N. V. R., et al. (2022). Responses of birds and mammals to long-established wind farms in India. *Scientific Reports, 12*(1), 1339. https://doi.org/10.1038/s41598-022-05159-1

Kwiecinski, G. G. (2006). Phyllostomus discolor. *Mammalian Species, 801*, 1–11. https://doi.org/10.1644/801.1

Lehnert, L. S., Kramer-Schadt, S., Schönborn, S., Lindecke, O., Niermann, I., & Voigt, C. C. (2014). Wind farm facilities in Germany kill Noctule bats from near and far. *Plos One, 9*(8), e103106. https://doi.org/10.1371/journal.pone.0103106

Llaven-Macías, V., Ruíz-Montoya, L., López-González, C., Rico, Y., & Naranjo, E. J. (2021). Monthly fluctuation of colony size and composition of the free-tailed bat *Tadarida brasiliensis* in the southernmost roost of Mexico. *Mammal Research, 66*(2), 339–348. https://doi.org/10.1007/s13364-021-00559-6

MacGregor-Fors, I., & Payton, M. E. (2013). Contrasting diversity values: Statistical inferences based on overlapping confidence intervals. *Plos One, 8*(2), e56794. https://doi.org/10.1371/journal.pone.0056794

MacSwiney, M. C., Ávila-Flores, R., & Pech-Canché, J. M. (2020). Richness and activity of arthropodophagous bats in an arid landscape of central México. *Therya*, *11*(1), 23–31. DOI: 10.12933/therya-20-900 ISSN 2007-3364

MacSwiney, M. C., Clarke, F. M., & Racey, P. A. (2008). What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology, 45*(5), 1364–1371. https://doi.org/10.1111/j.1365-2664.2008.01531.x

Marques, A. T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M. J. R., Fonseca, C., et al. (2014). Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. *Biological Conservation, 179*, 40–52. https://doi.org/10.1016/j.biocon.2014.08.017

Maurer, J. D., Huso, M., Dalthorp, D., Madsen, L., & Fuentes, C. (2020). Comparing methods to estimate the proportion of turbine-induced bird and bat mortality in the search area under a road and pad search protocol. *Environmental and Ecological Statistics, 27*(4), 769–801. https://doi.org/10.1007/s10651-020-00466-0

Medellín, R. A., Equihua, M., & Amin, M. A. (2000). Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology, 14*(6), 1666–1675. https://doi.org/10.1111/j.1523-1739.2000.99068.x

Medellín, R., Arita, H. T., & Sánchez, O. (2008). *Identificación de los murciélagos de México, guía de campo*. Instituto de Ecología, UNAM. México. 80p.

Meyer, C. F. J., & Kalko, E. K. V. (2008). Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography, 35*(9), 1711–1726. https://doi.org/10.1111/j.1365-2699.2008.01916.x

Millon, L., Colin, C., Brescia, F., & Kerbiriou, C. (2018). Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. *Ecological Engineering, 112*, 51–54. https://doi.org/10.1016/j.ecoleng.2017.12.024

Minderman, J., Gillis, M. H., Daly, H. F., & Park, K. J. (2017). Landscape-scale effects of single- and multiple small wind turbines on bat activity. *Animal Conservation, 20*(5), 455–462. https://doi.org/10.1111/acv.12331

Minderman, J., Pendlebury, C. J., Pearce-Higgins, J. W., & Park, K. J. (2012). Experimental evidence for the effect of small wind turbine proximity and operation on bird and bat activity. *PLOS ONE, 7*(7), e41177. https://doi.org/10.1371/journal.pone.0041177

Muñoz-Jiménez, O., Acosta, J. C. L., & Patraca, R. V. (2019). Diversidad y estructura vegetal en un paisaje antropizado de La Venta, Juchitán, Oaxaca, México. *Acta Botanica Mexicana*, (126), e1413. 10.21829/abm126.2019.1413

Pech-Canche, J. M., MacSwiney, C., & Estrella, E. (2010). Importancia de los detectores ultrasónicos para mejorar los inventarios de murciélagos Neotropicales. *Therya, 1*(3), 221–227. https://doi.org/10.12933/therya-10-17

Pereira, M. J. R., Marques, J. T., & Palmeirim, J. M. (2010). Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. *Current Zoology, 56*(4), 469–478. https://doi.org/10.1093/czoolo/56.4.469

R Development Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org

Richardson, S. M., Lintott, P. R., Hosken, D. J., Economou, T., & Mathews, F. (2021). Peaks in bat activity at turbines and the implications for mitigating the impact of wind energy developments on bats. *Scientific Reports, 11*(1), 3636. https://doi.org/10.1038/s41598-021-82014-9

Rizo-Aguilar, A. (2008). *Descripción y análisis de los pulsos de ecolocación de 14 especies de murciélagos insectívoros aéreos del estado de Morelos* (M.S. Thesis). Instituto de Ecología A. C., Xalapa, México.

Roemer, C., Disca, T., Coulon, A., & Bas, Y. (2017). Bat flight height monitored from wind masts predicts mortality risk at wind farms. *Biological Conservation, 215*, 116–122. https://doi.org/10.1016/j.biocon.2017.09.002

Saidur, R., Rahim, N. A., Islam, M. R., & Solangi, K. H. (2011). Environmental impact of wind energy. *Renewable and Sustainable Energy Reviews, 15*(5), 2423–2430. https://doi.org/10.1016/j.rser.2011.02.024

Salguero, M. M. del, De la Cruz, A., Muñoz, A.-R., & Muñoz Arroyo, G. (2023). Bat mortality in wind farms of southern Europe: temporal patterns and implications in the current context of climate change. *Biodiversity and Conservation*. https://doi.org/10.1007/s10531-023-02674-z

Santos, M., Bastos, R., Travassos, P., Bessa, R., Repas, M., & Cabral, J. A. (2010). Predicting the trends of vertebrate species richness as a response to wind farms installation in mountain ecosystems of northwest Portugal. *Ecological Indicators, 10*(2), 192–205. https://doi.org/10.1016/j.ecolind.2009.04.014

SENER. (2018). (Secretaria de Energia). Prospectiva de energías renovables 2018-2032. *Prospectivas del sector energético*. http://www.gob.mx/sener/documentos/prospectivas-del-sector-energetico. Accessed 2 May 2023

Silva-Aparicio, M., Castro-Ramírez, A. E., Castillo-Campos, G., Perales Rivera, H., Silva-Aparicio, M., Castro-Ramírez, A. E., et al. (2018). Estructura de la vegetación leñosa en tres áreas con Selva Baja Caducifolia en el Istmo-Costa de Oaxaca, México. *Revista de Biología Tropical, 66*(2), 863–879. https://doi.org/10.15517/rbt.v66i2.33419

Simmons, N. B., & Cirranello, A. L. (2022). Bat Species of the World: A taxonomic and geographic database. https://batnames.org/. Accessed 20 January 2023

Smallwood, K. S. (2017). Long search intervals underestimate bird and bat fatalities caused by wind turbines. *Wildlife Society Bulletin, 41*(2), 224–230. https://doi.org/10.1002/wsb.774

Strickland, M. D., Arnett, E. B., Erickson, W. P., Johnson, D. H., Johnson, G. D., Morrison, M. L., et al. (2011). *Comprehensive guide to studying wind energy/wildlife interactions* (p. 281). Washington, D. C., U.S.A.: National Wind Coordinating Collaborative.

Torres-Morales, L. (2007). *Patrones de uso de los hábitats por los murciélagos insectívoros del valle del río Los Pescados, Veracruz* (M.S. Thesis). Instituto de Ecología A. C., Xalapa, México.

Torres-Morales, L., Rodríguez-Aguilar, G., Cabrera-Cruz, S. A., & Villegas-Patraca, R. (2014). Primer registro de *Eumops nanus* (Chiroptera: Molossidae) en Oaxaca, México. *Mastozoología Neotropical, 21*(2), 373–378.

Veers, P., Dykes, K., Lantz, E., Barth, S., Bottasso, C. L., Carlson, O., et al. (2019). Grand challenges in the science of wind energy. *Science, 366*(6464), eaau2027. https://doi.org/10.1126/science.aau2027

Villegas-Patraca, R., Macías-Sánchez, S., MacGregor-Fors, I., & Muñoz-Robles, C. (2012). Scavenger removal: Bird and bat carcass persistence in a tropical wind farm. *Acta Oecologica, 43*, 121–125. https://doi.org/10.1016/j.actao.2012.06.004

Voigt, C. C., Russo, D., Runkel, V., & Goerlitz, H. R. (2021). Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. *Mammal Review, 51*(4), 559–570. https://doi.org/10.1111/mam.12248

Weaver, S. P., Jones, A. K., Hein, C. D., & Castro-Arellano, I. (2020). Estimating bat fatality at a Texas wind energy facility: implications transcending the United States–Mexico border. *Journal of Mammalogy, 101*(6), 1533–1541. https://doi.org/10.1093/jmammal/gyaa132

Wiederholt, R., López-Hoffman, L., Cline, J., Medellín, R. A., Cryan, P., Russell, A., et al. (2013). Moving across the border: modeling migratory bat populations. *Ecosphere, 4*(9), art114. https://doi.org/10.1890/ES13-00023.1

Wilkins, K. T. (1989). Tadarida brasiliensis. *Mammalian Species, 331*, 1–10. https://doi.org/10.2307/3504148