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Hierarchical mixture models and high-resolution monitoring data can inform siting and operational strategies to mitigate bat fatalities at wind turbines

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ABSTRACT

Bats provide critical ecosystem services, but bat fatalities due to wind energy development may imperil some bat populations. Statistical models are used to estimate the total fatalities that occur based on carcasses observed during monitoring surveys. Current models often estimate fatalities aggregated across species, time, and/or turbines, but fall short of reliably informing siting and operational collision mitigation strategies that account for species-specific fatality patterns on a fine spatiotemporal scale. We developed a hierarchical mixture model for estimating species-specific covariate effects and total fatalities per species at each turbine on weekly intervals. We applied the model to a high-resolution dataset of bat carcasses found during turbine searches across nineteen wind facilities in Iowa over two years. Our model explains species-specific variation in bat fatalities at individual wind turbines according to turbine proximity to bat habitat, turbine design specifications, seasonal trends, and weather conditions such as nightly air temperature, air pressure, and wind speed. Turbines located on the edge of wind facilities had higher fatalities, and proximity to roosting and foraging habitat accounted for variation in species-specific fatality estimates. These insights into turbine placement effects can inform siting strategies. We also discovered species-specific relationships with average nightly wind speed and air temperature, among other weather conditions, that could inform operational mitigation strategies such as smart curtailment. Our model can transform observations of carcasses found during turbine searches across multiple facilities, years, and variable search efforts into estimates of total fatalities per species associated with species-specific spatial, temporal, and environmental covariate effects.

1. Introduction

Bats provide critical benefits to humans by suppressing disease vectors, regulating agricultural pest abundances, pollinating flowering plants, and their guano is an effective fertilizer for crops (Kunz et al., 2011; Ramírez-Fráncel et al., 2022). Yet, numerous stressors are threatening bat populations world-wide (Frick et al., 2020) and research suggests that 90% of North American bat populations are in decline (Adams et al., 2024). Loss of such vigorous contributors to ecosystems (Kunz et al., 2011) and the economy (Boyles et al., 2011) could have cascading effects on humans through unintended ecological disturbances. One of the most prominent stressors threatening bat populations are fatal collisions with rotating wind turbines (Arnett et al., 2016; O'Shea et al., 2016).

The first known mass mortality event of bats at a wind facility in North America occurred in 2003 (Kerns and Kerlinger, 2004), prompting an urgent response to determine how to effectively manage bat interactions with wind energy infrastructure (*Proceedings of the Wind*

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Energy and Birds/Bats Workshop: Understanding and Resolving Bird and Bat Impacts, 2004). Since then, scientific investigations into bat-wind interactions have grown globally, informing strategies to reduce impacts to bats (Voigt et al., 2024). Still, the precision and reliability of mitigation strategies are limited, even when taking a multi-faceted approach (Clerc et al., 2025). Despite over two decades of research, critical information gaps persist regarding species-specific patterns in bat fatalities, variation in mortality within and among facilities, and the implications for bat populations and management.

High-resolution data from carcass searches conducted during post-construction monitoring (PCM) at wind facilities can fill these information gaps. However, the number of carcasses observed during PCM searches are limited due to removal by decomposition or scavengers, survey effort constraints, and the difficulty of spotting small carcasses on the landscape. Heterogeneity in the environment presents further challenges, including variation among species' relationships to habitat and the non-static nature of environmental processes. However, these challenges can be addressed through field protocols, data management, and statistical methods. When these data are input into statistical models that account for detection probabilities and variation over space and time, the scope and precision of inference improve (Bennett et al., 2024).

GenEst (Dalthorp et al., 2018) and Evidence of Absence (EoA; Huso et al., 2015) are statistical estimators of total fatalities. GenEst and EoA are widely used but are not without limitation. GenEst was developed to address biases of earlier estimators, but this regression-based estimator is not ideal for estimating fatalities of rare species (Dalthorp et al., 2018). Alternatively, EoA estimates rare fatality events using Bayes' theorem to calculate a posterior distribution of fatalities (Huso et al., 2015). However, neither are well suited to infer turbine-specific fatality estimates due to aggregating carcass counts across turbines, time, and species. Aggregation reduces the ability to relate fine-scale covariate information, such as turbine placement and weather, to fine-scale fatality estimates. We propose pairing high-resolution carcass data with hierarchical mixture modeling to return new information with sufficient precision to inform siting and operational strategies that reliably reduce fatalities.

In this paper, we present a Bayesian hierarchical mixture model that infers turbine-level bat fatality estimates with species-specific covariate relationships while accounting for imperfect detection at sub-weekly intervals. We designed the model to incorporate a variety of covariates, including proximity to habitat, weather conditions, facility layouts, and turbine designs. We describe a method for aggregating predictions and generating estimates of total fatalities across facilities, species, and/or time, like GenEst. However, GenEst pools data into low-resolution subgroups, but our model estimates fatalities while retaining the full resolution of the data and simultaneously inferring species-specific covariate relationships hierarchically. By relating fine-scale habitat and weather data to turbine-specific fatality estimates, our approach can inform siting and operational mitigation strategies to help maximize energy production while minimizing wildlife impacts (Hayes et al., 2019).

2. Methods

Western Ecosystems Technology, Inc. (WEST) monitored bat fatalities at 19 wind facilities across Iowa that requested to remain unnamed. For each facility and survey season we were provided with survey protocols, estimates of carcass persistence and searcher efficiency, and the location, date, and species identification of each bat carcass found during PCM surveys.

2.1. Monitoring data

WEST conducted carcass searches in two phases. Nine facilities were monitored from December 1, 2014 to November 15, 2015, and 13 facilities from November 16, 2015 to November 16, 2016. Three facilities were monitored across both phases. During the first phase, all turbines were searched approximately every other week in the winter (December 1 – March 15) and approximately once per week otherwise. During the second phase, all turbines were searched approximately every other week in the winter (November 16 – March 15) and approximately twice per week otherwise. Monitoring at one facility during the second phase did not start until May 15, 2016. All facilities were operated without curtailment during the study to determine baseline fatality estimates. In Supplementary Fig. 1, we provide a map of Iowa overlaid with a kernel density layer representing approximate sampling effort while preserving the anonymity of the specific facilities included in the study, and in Supplementary Table 1, we summarize the average turbine size and the monitored year(s) at each facility.

Only two bat carcasses were observed over the winter, so we excluded winter from the analysis. We assumed modeling fatalities across the winter when there were no observed fatalities at eighteen out of nineteen facilities would be computationally expensive with little effect on total estimated fatalities. From here on, carcasses observed in 2015 refer to those found from March 16, 2015 to November 15, 2015, and in 2016, those found from March 16, 2016 to November 16, 2016. Detected bat species included the big brown bat (*Eptesicus fuscus*: EPFU), eastern red bat (*Lasiurus borealis*: LABO), evening bat (*Nycticeius humeralis*: NYHU), hoary bat (*Lasiurus cinereus*: LACI), Indiana bat (*Myotis sodalis*: MYSO), little brown bat (*Myotis lucifugus*: MYLU), silver-haired bat (*Lasionycteris noctivagans*: LANO), and tricolored bat (*Perimyotis subflavus*: PESU).

We processed the data to assign carcasses to search intervals, filtered out carcasses found outside the standard protocols, and removed Indiana bats from the analysis as only one carcass was observed. We did not have access to a list of dates when searches were conducted at each turbine. However, given the dates when carcasses were found and the number of times each turbine was searched per week, we imputed an approximate search history for each turbine. We assigned each carcass to a corresponding weekly or bi-weekly search interval and imputed zeros when no carcasses were observed. Further data processing details are in Supplementary Text (Section A). Supplementary Table 2 summarizes carcass counts after all filtering steps.

2.2. Search effort data

For PCM at wind facilities, detection probability is driven by searcher efficiency, carcass persistence, the effective search interval, and the probability that the carcass falls within the searched area (Huso, 2011). Searcher efficiency is the probability that a searcher will observe a carcass if present within the searched area. Carcass persistence is the probability a carcass remains unremoved by scavengers or other means from the searched area before the next scheduled search. The effective search interval adjusts for the proportion of the interval that is considered adequately monitored. Finally, the probability that the carcass falls within the searched area depends on the size and shape of the search plot relative to the distribution of bat carcasses around turbines (Dalthorp et al., 2018; Dalthorp et al., 2024). Details of how we estimated each of these are described in Supplementary Text (Section B).

2.3. Covariate data

We collected covariates varying across facilities, turbines, and search intervals. These covariates included facility layout and geometry, turbine specifications, turbine proximity to bat roosting and foraging habitats, and weather data across each search interval. A priori, we hypothesized these covariates may account for variation in fatalities among species based on previous research (e.g., Davy et al., 2021; Garvin et al., 2024; Moustakas et al., 2023). We aimed to capture variation among fine-scale turbine, habitat, and weather covariates that could inform species-specific risk profiles for turbine design, siting, and operation to better avoid and minimize bat fatalities. Additional details

Table 1
Covariates used in a hierarchical mixture model to estimate species-specific covariate effects and total fatalities per bat species at wind turbines with organization of covariates by groups, including the covariate names used to reference the values in the text and figures, and original data sources. ANN = average nearest neighbor.

Group	Covariate name	Source
Turbine specifications	Rotor swept area	Hoen et al., 2024
	Ground clearance	
	Edge turbine	
Facility specifications	ANN Distance	
	Area	
	Shape index	
Habitat	River distance	Hutchinson et al., 2010
	Lake distance	U.S. Fish and Wildlife Service, 2018
	Open water distance	
	Wetland distance	
	Forest distance	Wickham et al., 2023
Weather	Wind speed	Draxl et al., 2015
	Wind speed^2	
	Wind direction	
	Air pressure	
	Air temperature	
	Precipitation	Thornton et al., 2022
	Solar intensity	

about all covariates considered in this analysis can be found in Supplementary Text (Section C). To improve model convergence and reduce multicollinearity, we refined the initial list of proposed covariates using both ecological insights and statistical diagnostics, as described in Supplementary Text (Section D). Below, and in Table 1, we summarize the final set of covariates included in the model.

To represent turbine design and facility layout, we calculated relevant quantities after matching each turbine in the dataset with its corresponding record in the U.S. Wind Turbine Database (USWTDB; Hoen et al., 2024). Wind turbine size has been shown to influence fatal wildlife collisions (Garvin et al., 2024; Moustakas et al., 2023), and in this work we hypothesized that the layout and relative position of wind turbines in a facility may also influence fatalities. For each turbine, we calculated the rotor swept area (m^2), ground clearance (m), and a binary variable indicating whether the turbine was on the edge of the facility. We propose that rotor swept area is an intuitive metric for collision risk, as it directly describes the total area of airspace where wildlife are at risk of colliding with the turbine blades.

Additionally, to characterize facility layout, we calculated the density of the turbines via Average Nearest Neighbor (ANN) distance (m), total area of the facility (m^2), and shape index, which is a dimensionless metric of the ratio between area and perimeter. Because most of the facilities we studied were not immediately adjacent to other wind facilities, these metrics could be reliably calculated for each facility as an independent unit on the landscape.

Proximity to bat habitats has also been shown to influence bat fatalities at wind turbines (Davy et al., 2021; Ellerbrok et al., 2023; Moustakas et al., 2023). Davy et al. (2021) used a variety of metrics, including distances to and amount of bat habitats (woods, wetlands, rivers, lakes, etc.) surrounding wind turbines, to study relationships with landscape features. In our analysis, we considered both distances to and percentages of relevant land covers surrounding each wind turbine. However, due to the highly homogenous agricultural landscapes in Iowa, we found that distance-based measures were more informative for representing habitat proximity in this case. Based on these findings, we calculated the distance from each turbine to the nearest river, lake, open water, wetland, and > 3.4-ha forest patch to represent proximity to bat habitats (Yates and Muzika, 2006).

Bat fatalities often occur when wind turbines are operating at low wind speeds of approximately 3–6 m/s, a pattern that has led to curtailment becoming a primary strategy for reducing bat fatalities. Bats tend to be more active at low wind speeds (Arnett et al., 2005), potentially increasing their availability to collide with wind turbines. To quantify the relationship between bat fatalities and wind speed, we used the WTK-LED Climate dataset to estimate average nightly wind speed (m/s) and direction (degrees) over each search interval at each facility (Draxl et al., 2015; National Renewable Energy Laboratory (NREL), 2024).

We calculated wind speed and direction at the ground clearance height, which we propose is an ecologically relevant altitude for assessing collision risk of bats at wind turbines. We also hypothesized that a non-linear (quadratic) relationship may exist between wind speed and bat fatalities, and we considered the influence of additional weather covariates. Specifically, we calculated the average nightly air pressure at ground level (Pa) and air temperature at 2-m above the ground (C) across each search interval. From the Daily Surface Weather and Climatological Summaries dataset (DAYMET; Thornton et al., 2022), we also calculated average daily precipitation (mm) and incident shortwave radiation flux density (W/m^2) hereafter "solar intensity."

Measuring the percentage of time wind speeds exceeded each turbine's manufacturer-specified cut-in speed could more directly reflect turbine operation and potential collision risk. However, the WTK-LED Climate dataset provides simulated weather conditions based on downscaled meteorological observations that may not be accurate at the hourly resolution required for such calculations. While we are confident that the dataset reasonably represents average wind speeds over the search intervals, the dataset potentially lacks the precision needed to estimate turbine operational time. Turbine-specific operational data obtained directly from wind facilities are likely the most accurate data to determine when turbines were spinning, but these data are typically proprietary and inaccessible to external researchers.

2.4. Model

We developed a Poisson-binomial mixture model estimating the total fatalities N_{ftawvs} at facility f, turbine t during year a, week w, and interval v for species s according to:

$$Y_{ftawvs} \middle| N_{ftawvs}, p_{ftaz} \sim \text{Binomial}\left(N_{ftawvs}, p_{ftaz}\right)$$

$$N_{ftawvs} | \lambda_{ftawvs} \sim \text{Poisson}\left(\lambda_{ftawvs}\right)$$

The quantity Y_{ftawvs} represents the number of bat carcasses per species observed during each turbine search. The detection probability p_{ftaz}, which varies across facility, turbine, year and season z, relates the number of carcasses observed Y_{ftawvs} to the expected total fatalities that occurred N_{ftawvs}. The rate λ_{ftawvs} relates the expected total fatalities N_{ftawvs} to species-specific covariate effects based on a generalized linear mixed model.

Since the observations are conditionally independent, we can simplify the notation by assuming index i refers to each combination of facility, turbine, year, week, interval, and species observed in the data. Simplified, $Y_i | N_i, p_i \sim \text{Binomial}(N_i, p_i)$ and $N_i | \lambda_i \sim \text{Poisson}(\lambda_i)$.

Our model is an update to the bivariate Poisson formulation of an N-mixture model described by Dennis et al. (2015), which was designed to estimate the abundance of closed populations with repeated counts. Dennis et al. (2015) formulated their bivariate Poisson likelihood function with an N_i shared between replicate counts Y_{i1} and Y_{i2}. Specifically, they assume that (Y_{i1}, Y_{i2}) are correlated Poisson random variables conditional on λ_i and p_i for each i. However, the population of fatalities we studied was not closed over time. Fatality rates of bats at wind turbines change seasonally, with most fatalities occurring during the autumn migration period (Baerwald and Barclay, 2009). In our formulation, Y_i are independent Poisson random variables conditional on λ_i and p_i.

2.4.1. Fatality process

In ecology, Poisson-binomial mixture models are often used to estimate population abundance (Madsen and Royle, 2023). The abundance process estimates the number of individuals occupying a location, which would all be observed given perfect detection. In this case, we are applying a morbid view to the process and estimate the abundance of bat fatalities rather than the abundance of live individuals. This fatality process is driven by covariate relationships determining the mean of a Poisson distribution. We proposed several versions of generalized linear mixed models to apply to the mean λ_{ftawvs}.

2.4.1.1. Baseline model. The "Baseline" model is the underlying framework that is adapted in all subsequent versions. We applied a generalized linear mixed model to model the rate λ_{ftawvs}. Specifically, we assumed:

$$\log(\lambda_{ftawvs}) = x'_{ftawvs}\beta_s + \epsilon_{aws}$$

$$\epsilon_{aws} \mid \mu_{aw}, \rho_a, \rho_w, \sigma_1^2 \sim \text{Normal}\left(\mu_{aw} + \text{I}_{\{a>1\}}\rho_a\epsilon_{a-1,w,s} + \text{I}_{\{w>1\}}\rho_w\epsilon_{a,w-1,s}, \sigma_1^2\right)$$

where $\text{I}_{\{A\}}$ is an indicator function on condition A. Thus, the linear predictor consists of two components:

1. The fixed effects $x'_{ftawvs}\beta_s$, which may be time-varying covariates across turbines with species-specific slopes.
2. The time-varying species-specific random effect ϵ_{aws}, which captures temporally correlated variation in fatalities among species. These effects follow a first-order autoregressive AR(1) process within years with correlation ρ_w and variance σ_1^2. There is also correlation ρ_a between the same week among years to capture recurrent seasonal patterns in the residuals. These are normally distributed random variables marginally centered at week within year means μ_{aw}.

We used the following priors for the parameters in the Baseline model. In subsequent versions, we note when any priors are updated, otherwise, the priors remain the same. The species-specific coefficients β_s were assumed to have covariate-specific hypermeans ν (i.e., a global effect across species) and a shared scale parameter τ with the identity matrix $\text{I}_{n\times m}$ of dimension n by m where $\beta_s \sim \text{Normal}_{15}(\boldsymbol{\nu}, \tau^2\mathbf{I}_{15\times 15})$. We also assumed the following priors for additional hyperparameters:

$$\tau, \sigma \sim \text{Half-Cauchy}(0, 1)$$

$$\rho_a, \rho_w \sim \text{Uniform}(-1, 1)$$

$$\nu_j \sim \text{Normal}(0, 100)$$

$$\mu_{aw} \sim \text{Normal}(0, 100)$$

2.4.1.2. Scales model: covariate-specific scales. The "Scales" model was identical to the Baseline model, except for the scale parameter τ of the β_s parameters, which was allowed to be covariate specific. For this version, we assumed the β_s coefficients had the following prior:

$$\beta_s \sim \text{Normal}_{15}(\boldsymbol{\nu}, \boldsymbol{\tau}^2)$$

2.4.1.3. FCovar model: including facility-level covariates. The "FCovar" model was identical to the Baseline model but included several additional facility-level covariates. These covariates were ANN Distance, Area, and Shape index.

2.4.1.4. FRand model: including facility-level random effects. The "FRand" model was identical to the Baseline model, except for additionally including facility-level random effects ϵ_f in the rate λ_{ftawvs}. We assumed the ϵ_f random effects had the following priors:

$$\epsilon_f \sim \text{Normal}\left(\mu_f, \sigma_2^2\right)$$

$$\sigma_2 \sim \text{Half-Cauchy}(0, 1)$$

2.4.2. Observation process

Whether a Poisson-binomial mixture model is used to estimate the abundance of living or dead populations, the observation process controls how many individuals are likely to be detected by observers. Here, the observation process is dependent on the detection probability p_{ftaz}, which relates the number of carcasses that were observed at a turbine to the total number of bats that were killed by the turbine over the search interval.

In our model, we assume this detection probability is directly related to the quantity $\hat{g}$, the search effort correction factor described by Huso (2011). We estimate $\hat{g}_{ftaz}$, which varies by year and season for each turbine. It is a probability based on the product of searcher efficiency probability $\hat{g}_{se}$, carcass persistence probability $\hat{g}_{cp}$, effective search interval proportion $\hat{g}_{int}$, and the probability a carcass falls in the searched area around each turbine $\hat{g}_{dwp}$ for each year, turbine, and season as described in Supplementary Text (Section B). We used this correction factor to inform the prior distribution of each detection probability p_{ftaz}, such that:

$$p_{ftaz} \sim \text{Beta}\left(100^*\hat{g}_{ftaz}, 100^*\left(1-\hat{g}_{ftaz}\right)\right)$$

2.5. Bayesian Markov-chain Monte Carlo simulation

We performed Bayesian Markov-chain Monte Carlo (MCMC) simulation to estimate model parameters using the *cmdstanr* package (v0.8.1 with CmdStan v2.36.0) in R (v4.4.0). The *cmdstanr* package uses Stan, a software for Bayesian data analysis, which implements a marginalized sampling method based on the Hamiltonian Monte Carlo (HMC) algorithm (Yackulic et al., 2020). In addition to simulating posterior distributions via MCMC, we calculated the Gelman-Rubin ($\hat{R}$) and effective sample size (ESS) statistics for each parameter in the generalized linear mixed model on λ_{ftawvs}. It is recommended all parameters of interest have $\hat{R}$ values ≤ 1.01 to 1.1, and at least several hundred bulk and tail ESS iterations as evidence of convergence (Vehtari et al., 2021). We monitored our model runs and increased the number of iterations until we consistently achieved approximate convergence according to these metrics. For each model, we ran an MCMC simulation with 4 chains for 500 warmup iterations and 1000 sampling iterations. To select a best performing model, we compared the percent of divergent iterations, estimated Bayesian fraction of missing information (*E*-BFMI), lack of fit (LoF), and leave-one-out information criterion (LOOIC) statistics for the final runs of each model version.

2.6. Posterior distributions of total fatalities

Since Stan implements MCMC using the HMC algorithm, discrete parameters including the total fatalities N_i are marginalized out of the likelihood rather than simulated directly. Therefore, simulations for each N_i cannot be monitored and posterior estimates for these parameters are not included in the outputs from the sampler directly. Itô (2017) and Pullin et al. (2023) described how to approximate the posterior distribution for each N_i by generating quantities based on each iteration of previously generated MCMC samples. Since the total fatalities at each turbine over time are the primary quantity of interest in this analysis, we needed a method that could infer these values and aggregate them across turbines, facilities, or periods of time. We describe how we aggregated estimates in Supplementary Text (Section E).

Table 2
Convergence and fit statistics for model selection among the model versions used to estimate species-specific covariate effects and total fatalities per bat species at wind turbines, including the percent of divergent iterations, estimated Bayesian fraction of missing information (EBFMI), lack of fit (LoF), leave-one-out information criterion (LOOIC) and its standard error in parentheses. The best performing values of each statistic are in bold.

Model version	Divergent iterations	E-BFMI	LoF	LOOIC (SE)
Baseline	**0%**	0.828	1.029	25,908 (454)
Scales	13%	0.787	1.031	25,894 (454)
FCovar	**0%**	**0.840**	1.031	25,846 (453)
FRand	15%	0.822	**1.023**	**25,705 (452)**

3. Results

3.1. Model selection

The Baseline and FCovar models achieved the best convergence statistics. Both models had no divergent iterations and FCovar had the highest *E*-BFMI. According to the LoF and LOOIC statistics, the FRand model had the best fit, but it also had the highest number of divergent iterations (Table 2).

Based on these convergence and fit statistics, and ease of interpretation, we selected the Baseline version as our predictive model. While the LOOIC statistic for the FRand model was the lowest, the LOOIC statistics for the Baseline and FCovar models, which had the best convergence, fell within the standard error of the FRand model's LOOIC statistic. We preferred the Baseline model over the FCovar model because the turbine-level covariates were strongly confounded with the facility-level covariates, which made the interpretation of the turbine-level covariates more difficult while not substantially improving model fit when included.

3.2. Fatality estimates

Using the Baseline model, we predicted 67,007 fatalities (approximate 95% credible interval conditional on Y, λ, and p: 63,733–70,554 fatalities) at the monitored facilities over two years. Each facility had a different number of turbines, and only three facilities were monitored over both years. To standardize across facility sizes and monitoring periods, we estimated the mean number of annual fatalities per turbine at each facility (Fig. 1). Annual fatalities per turbine varied across facilities, with some facilities killing less than 20 bats per turbine, while others were estimated to kill at least twice as many bats.

We also used our species-specific model to estimate the mean annual fatalities per turbine for each species (Fig. 2). Eastern red bats and hoary bats consistently had the highest number of fatalities per turbine. Except for a few cases, fatalities of eastern red bats exceeded hoary bats, but both species often had about 5 to 20 annual fatalities per turbine across the monitored facilities. Big brown bats had about 2 to 10 annual fatalities per turbine, and silver-haired bats often had 1 to 6 annual fatalities per turbine with a few facilities closer to 10. There were usually less than 5 annual fatalities per turbine of little brown bats, evening bats, and tricolored bats each.

We included weekly species-specific random effects in our model to estimate fatalities of each species over time. Fatalities aggregated across all facilities show species may peak at different times (Fig. 3). Our model can also predict turbine-specific total fatalities. After aggregating over all species, we identified the five turbines that had the highest and lowest annual fatalities at each facility (Supplementary Fig. 2). For some facilities, the most-deadly turbines had more than twice the annual fatalities compared to the least deadly turbines.

3.3. Covariate effects

To account for variation in fatalities across turbines, we included a variety of turbine-level, habitat, and weather covariates in our model (Fig. 4). The hypermean coefficients of four covariates had credible effects, such that the 95% credible interval did not overlap zero. As turbine rotor swept area and average nightly air temperature increased, fatalities also increased. Turbines located along the edge of a facility were related to a higher number of fatalities. In contrast, increasing wind speed corresponded with decreases in fatalities. We summarize the numerical estimates for hypermean coefficients in Supplementary Table 3.

The covariates that had credible hypermean effects across all species often had consistent species-specific relationships as well (Fig. 5). For example, turbine rotor swept area had a credible positive relationship with the number of fatalities for each species except evening bat (Fig. 5A). However, credible species-specific relationships appeared for some species that were not revealed by the hypermean relationships. Both distance to habitat and meteorological covariates had variable relationships across species, with air pressure and distance to waterbodies showing both positive and negative effects across species (Fig. 5C and D). Fatalities increased at lower wind speeds for most species, especially big brown bat, eastern red bat, and hoary bat (Fig. 6). We

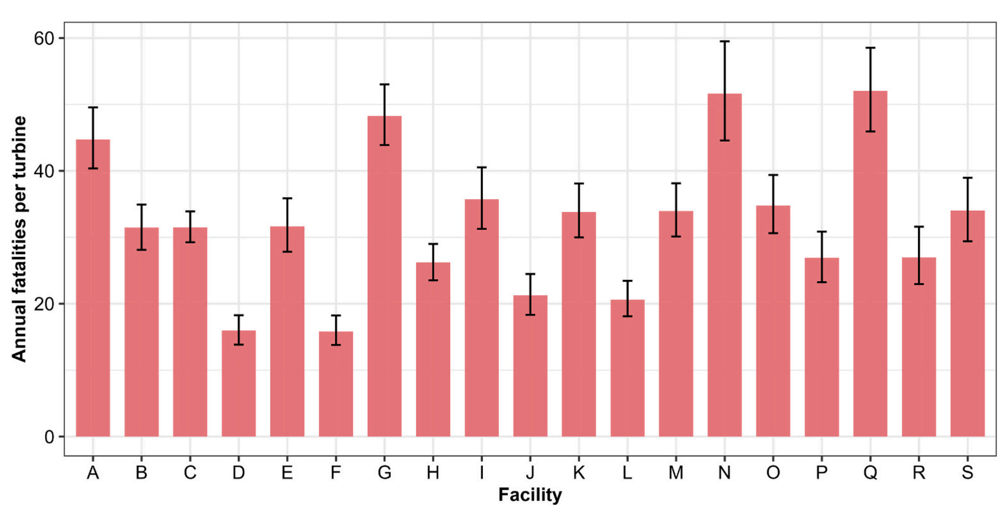

Fig. 1. The estimated mean annual bat fatalities per wind turbine (and approximate 95% credible interval of the posterior mean) for each facility. Nine facilities were monitored in 2015, and 13 facilities were monitored in 2014. Of these, three facilities were monitored across both years.

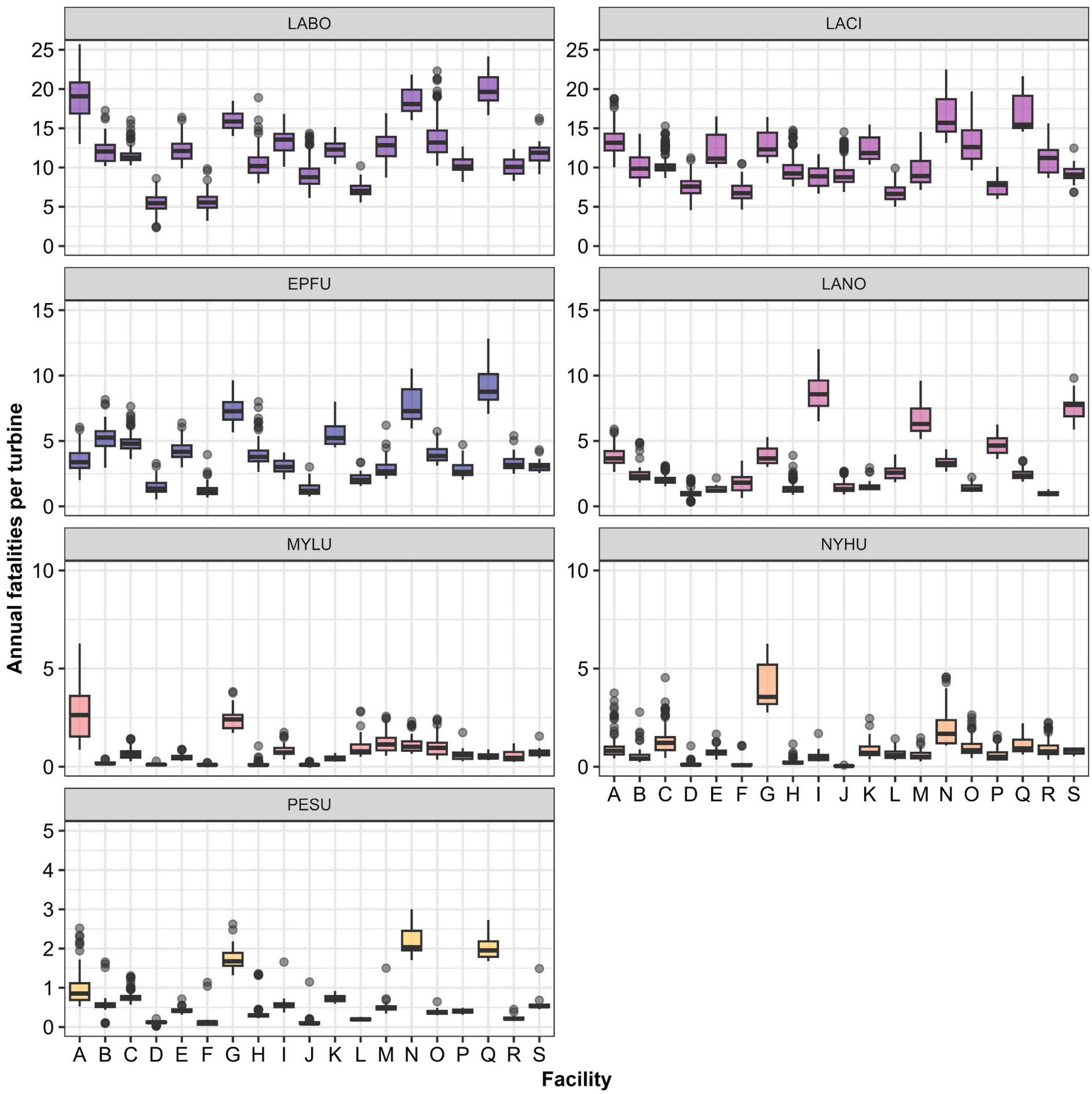

Fig. 2. The estimated annual fatalities per turbine for each species found across the monitored facilities in 2015 and 2016. Bat species are labeled by four-letter codes including big brown bat (EPFU), eastern red bat (LABO), hoary bat (LACI), silver-haired bat (LANO), little brown bat (MYLU), evening bat (NYHU), and tricolored bat (PESU). Box plots depict the first quartile, median, and third quartile, as well as minimum and maximum values within 1.5 times the interquartile range, with outliers depicted as single points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

summarize the numerical estimates for the species-specific coefficients in Supplementary Table 4.

We mapped the mean multiplicative effect of the habitat proximity hypermeans to predict relative bat fatality potential dependent on turbine siting across Iowa (Fig. 7). Formally, we considered the means of the posterior distributions for the estimated coefficients for river distance ($\overline{\beta}_r$), lake distance ($\overline{\beta}_l$), open water distance ($\overline{\beta}_o$), wetland distance ($\overline{\beta}_w$), and forest distance ($\overline{\beta}_f$) multiplied by the observed distances to these habitats (x) at hypothetical turbine locations such that the mean multiplicative effect was equal to: $\exp\left(x_r\overline{\beta}_r + x_l\overline{\beta}_l + x_o\overline{\beta}_o + x_w\overline{\beta}_w + x_f\overline{\beta}_f\right)$. We also mapped the effect based on the species-specific habitat proximity coefficients (Supplementary Figs. 3–9).

4. Discussion

We developed a hierarchical model to estimate species-specific bat fatalities at wind turbines in relation to fine-scale habitat and weather covariates on weekly intervals. Our model provides a framework for estimating wildlife fatalities at monitored wind turbines and revealing covariate relationships that may be used to inform siting and operational mitigation strategies to avoid or reduce bat fatalities. Compared to GenEst and its precursors derived from Huso (2011), our model is much more advanced. GenEst is designed to produce unbiased estimates of total fatalities after correcting for detection probability, but GenEst typically generates fatality estimates aggregated across turbines, species, and/or time. In contrast, our model retains the full resolution of the PCM data by estimating fatalities per species at each turbine on weekly intervals. Our model produces ecological insights that enable

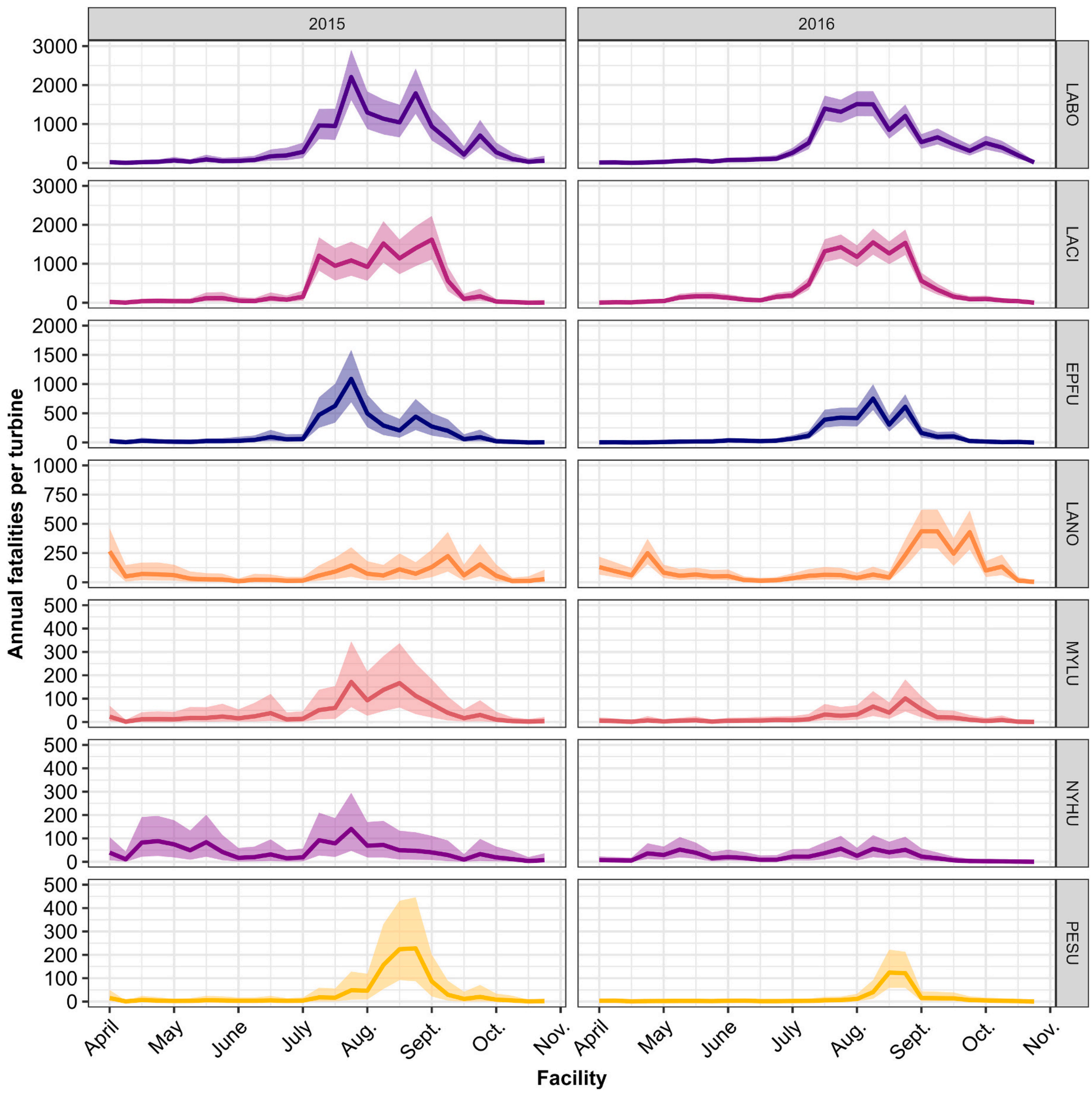

Fig. 3. Estimated species-specific wind-turbine fatalities per week in 2015 and 2016 aggregated across facilities with 95% approximate credible intervals. Bat species are labeled by four-letter codes including big brown bat (EPFU), eastern red bat (LABO), hoary bat (LACI), silver-haired bat (LANO), little brown bat (MYLU), evening bat (NYHU), and tricolored bat (PESU). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

meaningful interpretations of spatiotemporal patterns and species-specific risk factors of bat fatalities at wind turbines.

Applied to high-resolution PCM data from Iowa, our model predicted more bat fatalities than were estimated across the original PCM reports. Specifically, the aggregated posterior mean predicted 67,007 fatalities (approximate 95% credible interval conditional on Y, λ, and p: 63,733–70,554 fatalities), compared to a point estimate of 55,477 fatalities derived from the original reports based on the Huso (2011) method. We could not derive a comparable uncertainty interval from the original reports because the results for each facility were estimated separately without accounting for interfacility correlation. As a result, the estimates from the earlier approach are not directly comparable, but the advancements offered by our model are clear. Rather than estimating fatalities for each facility independently, our hierarchical model borrowed information across all 19 facilities and predicted total species-specific fatalities per turbine each week. Additionally, our model related these estimates to turbine- and species-specific risk factors, including weather conditions, turbine design, facility layout, and proximity to roosting and foraging habitats.

According to the covariate effects estimated by our model, edge turbines were credibly associated with higher fatalities for several observed bat species. To our knowledge, this study is the first report of edge turbines having a credible positive relationship with bat fatalities, although Arnett et al. (2008) mentioned the highest number of fatalities were often found near the end of strings of turbines. The edge turbine effect is likely not an artifact of survey effort since every turbine was monitored within each facility. We propose three nonexclusive hypotheses for the observed increase in bat fatalities at edge turbines: (1) bats entering a wind facility generally encounter edge turbines first, where they may be struck and removed prior to reaching core turbines; (2) bats generally encounter edge turbines more frequently than interior turbines because they must pass edge turbines when both entering and exiting a wind facility; (3) turbines located at the edge of a wind facility are generally closer to habitats with greater bat abundances (Ellerbrok et al., 2023). However, while our model accounted for distance to various waterbodies and forest patches, we could have failed to account for additional habitat conditions that were confounded with edge turbines, such as distance to buildings.

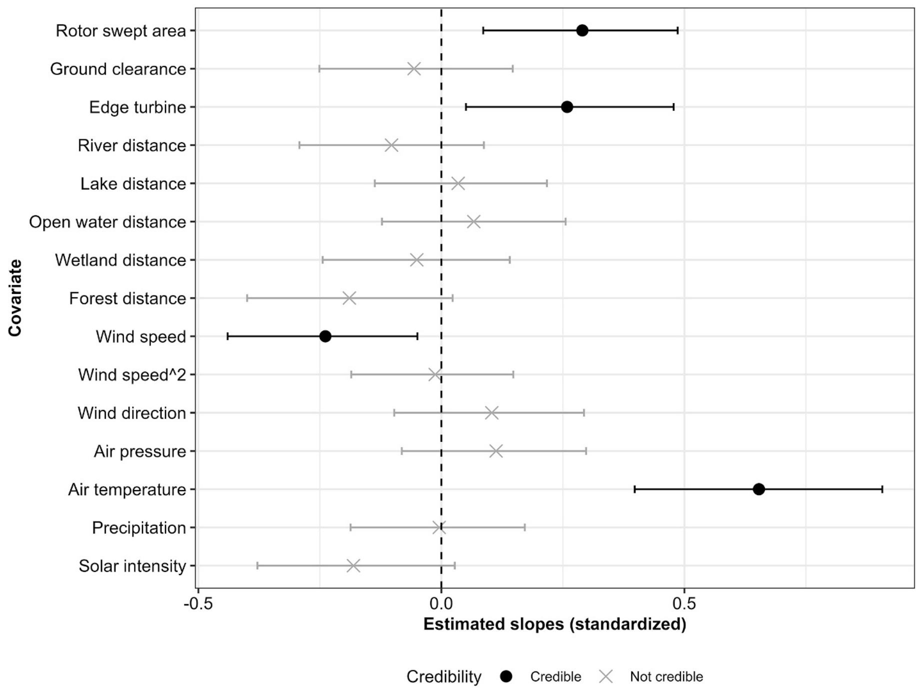

Fig. 4. Estimated hypermeans of the slopes of covariate effects across all bat species in 2015 and 2016 at the studied wind facilities with 95% credible intervals. Covariates with credible effects on wind turbine-associated bat fatalities did not include zero in within the 95% credible interval.

Our model is designed primarily for ecological inference rather than for forecasting fatalities at new sites. However, the model can be used to generate maps that highlight areas with high fatality potential in similar landscapes based on the inferred relationships with the studied habitat proximity coefficients. Maps generated from these coefficients demonstrated that the effects of turbine proximity to roosting and foraging habitats were not consistent across species and relative fatality potential varied considerably across Iowa. Locations close to forest, rivers, and wetland had higher bat fatality potential than locations further from these features.

The species-specific coefficients and maps also revealed evidence of variable habitat use patterns between species. For example, hoary bats travel great distances throughout agricultural landscapes (Morningstar and Sandilands, 2019). For hoary bat, our model did not estimate credible relationships for any habitat proximity effect. These estimates suggest hoary bats collided with wind turbines regardless of proximity to specific habitats. On the other hand, big brown bat fatalities increased at turbines closer to forest habitats. Big brown bats travel shorter distances than hoary bats and have strong affinity to forest habitat (Menzel et al., 2001). Higher forest density increases occupancy of several bat species (Starbuck et al., 2022), which could increase bat fatalities at wind turbines sited near forests. Our model also showed fatalities increased at turbines closer to various waterbody types for several species, which could be related to species-specific attraction to wetlands (Lookingbill et al., 2010). Considering both the effect of edge turbines and habitat proximity, we found evidence that turbine location had a strong relationship with fatalities, similar to results from Moustakas et al. (2023).

While not intended for precise fatality estimates at unmonitored turbines or proposed wind facilities prior to construction, the maps generated from our model could inform species-specific siting strategies by highlighting locations that may have higher fatality potential based on their proximity to bat foraging and roosting habitats. The primary purpose of our model is to infer ecological patterns rather than to forecast fatalities at new locations. Generating weekly, species-specific fatality estimates per turbine for additional facilities requires post-construction monitoring data collected there in the format described in this manuscript, including carcass counts and detection probabilities estimates. Nevertheless, the ecological insights generated from the model at studied turbines could reveal environmental and operational conditions associated with elevated fatality risk at proposed or operating wind facilities in similar landscapes.

Wind turbine design, such as rotor swept area and ground clearance, can affect fatality rates but Garvin et al. (2024) suggests this may vary by species. Our model showed rotor swept area had a credible positive relationship with bat fatalities for all species except evening bat. Arnett et al. (2008) similarly observed that larger rotor-swept area was related to higher bat fatalities, and Moustakas et al. (2023) found wind turbine power had a positive relationship with fatalities. In contrast, Garvin et al. (2024) reported that rotor diameter, a proxy for rotor swept area, was negligible for hoary bats, and found ground clearance was the strongest predictor of hoary bat fatalities, which also differed from our findings, where ground clearance had a negative relationship for only silver-haired bats and was negligible for all other species. These disparities could be an artifact of the turbine designs included in our study; there was very little variation both within and among turbine designs across the studied facilities while Garvin et al. (2024) analyzed PCM data from a broader geographic context. Additionally, only silver-haired bats had a credible positive relationship with the quadratic effect for wind speed, which may have affected estimates of other covariate effects for this species. We would recommend removing the quadratic effect for wind speed in future applications of this model.

We found peaks in fatalities during late summer through early autumn, but these peaks differed slightly by species. Previous research has shown bat fatalities at wind facilities vary seasonally (Lloyd et al., 2023) and with weather conditions (Arnett et al., 2008). Our model accounted for these temporal trends by estimating weekly random effects, but also incorporated average weather conditions, including nightly wind speed, over each search interval. Lower nightly wind speeds generally resulted in a higher number of bat fatalities, likely because bat activity increases at lower wind speeds (Arnett et al., 2005) and there may be more bats available to collide with rotating turbine blades. Higher nightly air temperatures were associated with higher bat fatalities across all analyzed species, except for silver-haired bats. High bat fatalities on warmer nights may be related to a positive association

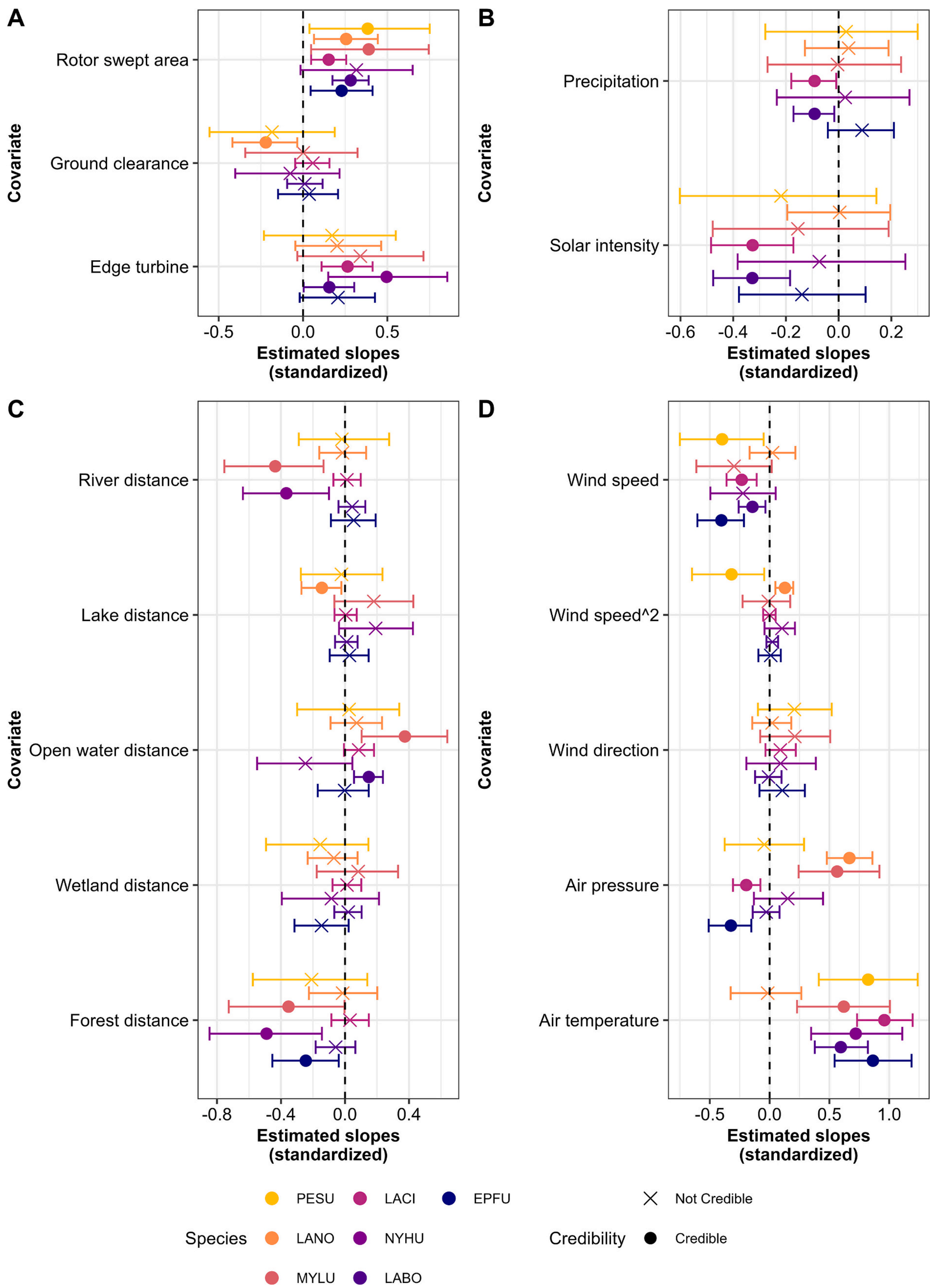

Fig. 5. Species-specific estimates of covariate effect slopes with 95% credible intervals. Covariates with credible effects on wind turbine-associated bat fatalities in 2015 and 2016 did not include zero within the 95% credible interval. Bat species are labeled by four-letter codes including big brown bat (EPFU), eastern red bat (LABO), hoary bat (LACI), silver-haired bat (LANO), little brown bat (MYLU), evening bat (NYHU), and tricolored bat (PESU). The covariates are grouped by (A) turbine specifications, (B) weather covariates measured daily, (C) habitat distances, and (D) weather covariates measured nightly. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

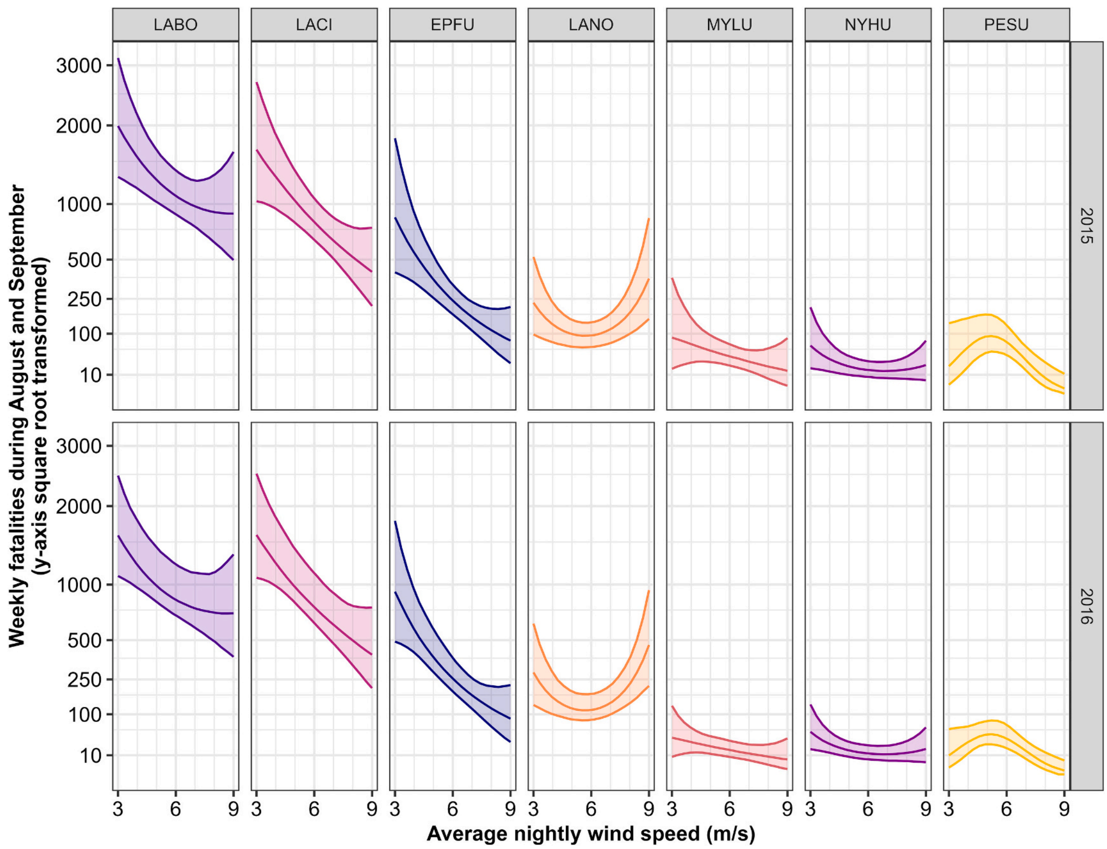

Fig. 6. The marginal relationship and approximate 95% credible interval of average nightly wind speed (m/s) with simulated total weekly wind turbine-associated bat fatalities in 2015 and 2016 across August 1 – September 30, which is commonly considered the period of the year with the highest collision rates of bats with wind turbines. Bat species are labeled by four-letter codes including big brown bat (EPFU), eastern red bat (LABO), hoary bat (LACI), silver-haired bat (LANO), little brown bat (MYLU), evening bat (NYHU), and tricolored bat (PESU). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between bat and insect activity, but this correlation can vary by species (Andreozzi et al., 2024). High numbers of fatalities during warmer nights may also be an artifact of seasonal bat activity patterns, but the random effects in our model should theoretically marginalize across temporal trends before accounting for additional covariate effects (Supplementary Fig. 10).

Results from our model provide evidence that differences in behavior, ecology, distribution and abundance could explain variation in mortality rates among species. Bats adapted for long distance migration in open environments, such as hoary bats, eastern red bats and silver haired bats, experience higher rates of mortality than species adapted for flight in much more cluttered environments (e.g., various myotis species; Fleming, 2019). Long distance migrants occupy expansive species ranges (National Atlas of the United States, 2011), move at a greater frequency than their counterparts (Fleming, 2019), and are anecdotally believed to be abundant, all of which may be linked to more encounters with wind turbines and therefore higher collision risk. Unfortunately, due to the cryptic nature of bats and challenges documenting populations (O'Shea and Bogan, 2003), too many information gaps exist to link species-specific behaviors, ecology, distribution, or abundance directly to variation in mortality with a reasonable level of certainty. Although the state of the science is rapidly advancing (Udell et al., 2025), we still lack status and trends for most North American bat species, and data to inform predictable movement and behavioral patterns are sparse at best.

Despite these uncertainties, smart curtailment strategies are used to reduce bat fatalities by avoiding turbine operation during periods when bat presence is detected or during conditions associated with higher activity (Adams et al., 2021; Hayes et al., 2019). Our model described temporal trends and environmental conditions that were linked with the highest number of fatalities, which could be combined to refine curtailment strategies. Similar to Whitby et al. (2024), our results indicated that increasing cut-in speeds from 3 m/s to 6 m/s could reduce fatalities by ~50% for some bat species. However, our model can provide additional information to inform smart curtailment which has not been available from other models of PCM data. The estimated species-specific weekly patterns of fatalities could be used to inform the seasonal timing of curtailment to target species-specific mitigation. Additionally, weather conditions including average wind speed, air temperature, and precipitation affected species-specific bat fatalities. Simulation studies of curtailment strategies relating our model estimates to historical weather data could quantify trade-offs between bat conservation and energy production over time, both generally and for endangered species specifically. Energy developers could use our model to study the environmental effects linked with the highest number of fatalities at their facilities and incorporate these predictors into automated smart curtailment algorithms to reduce fatalities on the highest risk nights. Our model could also inform spatially variable curtailment approaches, combining the habitat proximity effects with environmental conditions to identify specific turbines that may need to be curtailed more frequently or at higher wind speeds to reduce fatalities of certain species.

In conclusion, the nuanced interactions among turbines, habitat, and environmental covariates across species derived from our model highlight the utility of collecting, reporting, and collating high-resolution PCM data. Despite using data from multiple years and facilities, these results represent a relatively narrow spatiotemporal window – a common downfall of PCM analyses. Improving the scope, accuracy, and

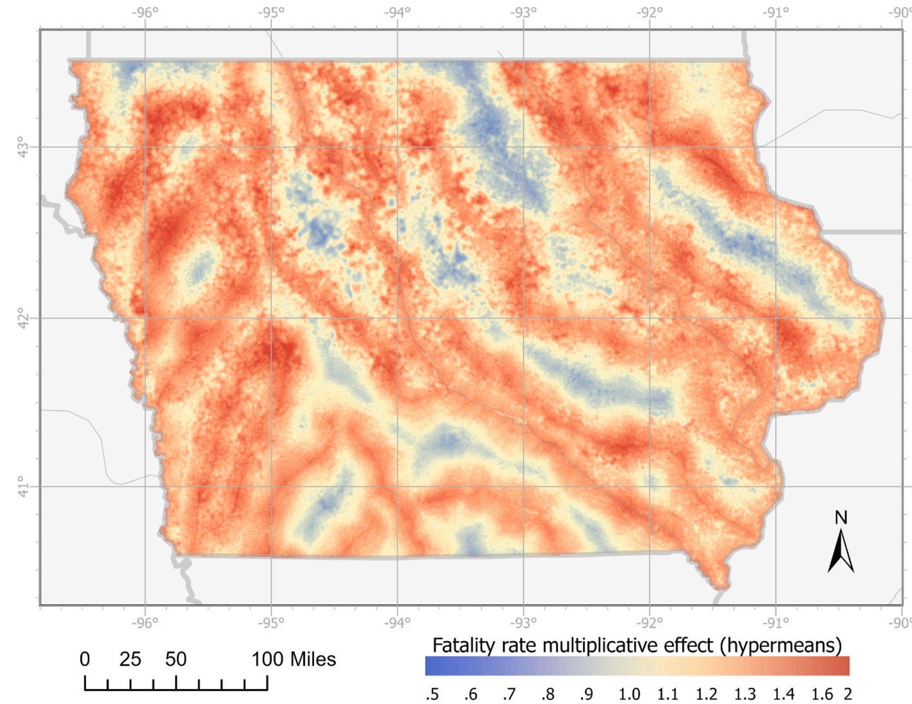

Fig. 7. A map of the mean multiplicative effect of the habitat proximity hypermean coefficients (river distance, lake distance, open water distance, wetland distance, and forest distance) across all species to predict relative bat fatality potential in 2015 and 2016 dependent on turbine siting across Iowa. The effects of all other covariates were marginalized. Locations of wind energy facilities used in this study are not shown because of their privileged nature. Basemap: Human Geography Detail (ESRI, 2025).

precision of pre-construction predictions requires compiling a dataset representative of the lifespan and distribution of both bats and wind infrastructure. Continuing to record species-specific carcass observations of bats found during individual turbine searches, along with detailed searcher efficiency, carcass persistence, and search effort, is essential for understanding bat-wind interactions. The utility of PCM data is maximized when made publicly available across space and time in a standardized format. The model we proposed can transform these data into valuable insights on species-specific patterns in fatalities within and among facilities, geographies, and seasons to inform species-specific mitigation strategies that include technology selection, siting and operation. Ultimately, this work highlights the utility of pairing standardized, high-resolution PCM data from uniform field protocols with advanced statistical modeling to discover insights that can better balance conservation and energy production.

CRediT authorship contribution statement

Charles Labuzzetta: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Arnold Johnsen:** Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis. **Amber Andress:** Investigation, Data curation, Conceptualization. **Teresa Bohner:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Alejandro Grajal-Puche:** Writing – review & editing, Writing – original draft, Investigation. **Megan Seymour:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Bethany Straw:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Wayne Thogmartin:** Writing – review & editing, Methodology, Conceptualization. **Bradley Udell:** Writing – review & editing, Methodology, Conceptualization. **Ashton Wiens:** Writing – review & editing, Methodology, Conceptualization. **Jay Diffendorfer:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors report no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2026.103652.

Data availability

The data and code supporting this analysis can be found at doi: https://doi.org/10.5066/P1HVFES6 (Labuzzetta et al., 2025).

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