Wind energy and insects: reviewing the state of knowledge and identifying potential interactions

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ABSTRACT

In 2023 the wind industry hit a milestone of one terawatt of installed capacity globally. That amount is expected to double within the next decade as billions of dollars are invested in new wind projects annually. Wildlife mortality is a primary concern regarding the proliferation of wind power, and many studies have investigated bird and bat interactions. Little is known about the interactions between wind turbines and insects, despite these animals composing far more biomass than vertebrates. Turbine placement, coloration, shape, heat output, and lighting may attract insects to turbines. Insects attract insectivorous animals, which may be killed by the turbines. Compiling current knowledge about these interactions and identifying gaps in knowledge is critical as wind power grows rapidly. We reviewed the state of the literature investigating insects and wind energy facilities, and evaluated hypotheses regarding insect attraction to turbines. We found evidence of insect attraction due to turbine location, paint color, shape, and temperature output. We provide empirical data on insect abundance and richness near turbines and introduce a risk assessment tool for comparing wind development with suitable climate for insects of concern. This understudied topic merits further investigation as insects decline globally. Compiling information will provide a resource for mitigation and management strategies, and will inform conservation agencies on what insects may be most vulnerable to the expansion of wind technologies.

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INTRODUCTION

Tumultuous events throughout the early 2020s reinvigorated global interest and commitment to renewable energy and energy independence (*Hutchinson & Zhao, 2023*). Countries worldwide have invested billions of dollars into wind energy technology leading to the milestone of one terawatt (TW) of global installed capacity in 2023, produced by ~400,000 individual turbines. The Global Wind Energy Council estimates that a second terawatt of capacity could be installed within a decade (*Hutchinson & Zhao, 2023*). China, the United States and Europe have driven most growth; however, markets in Southeast Asia, Africa and the Middle East are forecasted to diversify the global land-based wind

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market (*Hutchinson & Zhao, 2023*). Electricity generation from wind represented >20% of total energy generation for several countries in 2022, proving that wind energy can be a reliable source of electricity (*Wiser et al., 2023*). Land-based wind is well-established and accounts for ~88% of the global capacity added in 2022 (*Hutchinson & Zhao, 2023*). Wind technology as a cost-effective, renewable energy source is a focal point in many nations' agendas to lower emissions and carbon footprints.

The production of electricity using wind centers around the use of wind turbines. Turbines have rotors with large, airfoil-shaped blades that spin when wind flows over them. The rotation of blades converts wind power into electricity through rotation of a generator. Electricity production using wind provides several environmental benefits over coal and gas. Wind power uses less water in terms of consumption (water being permanently removed from its source) and withdrawal (water being diverted from its source) than most other forms of electricity generation. This occurs because wind energy does not require fuel extraction or processing, and only uses water in manufacturing, construction, and maintenance (*Meldrum et al., 2013*). Wind power produces fewer greenhouse gases (*i.e.*, carbon dioxide) and other sources of pollution (*e.g.*, mercury and sulfur dioxide) compared to fossil fuels, which emit these pollutants during combustion (*Allison et al., 2019*; *Saidur et al., 2011*). It is estimated that wind energy reduced CO^2 emissions in the U.S. by 132 million metric tons in 2015, and water consumption by 73 billion gallons in 2013 (*Wiser et al., 2015*). Wind installations have adverse effects as well. Wind facilities can harm or disturb vertebrate wildlife populations and their habitats. The most thoroughly investigated subjects are bat and bird fatalities caused by turbine collisions and mitigation strategies to prevent collisions (*Schuster, Bulling & Koppel, 2015*). Concerns are due to obvious evidence (*i.e.*, carcasses in wind facilities) and the threat to vulnerable or protected species such as the northern long-eared bat, *Myotis septentrionalis*, and golden eagle, *Aquila chrysaetos* (*Allison et al., 2019*; *Schuster, Bulling & Koppel, 2015*). Conversely, almost nothing is known about how insects are affected by turbines and more investigation is necessary to understand how invertebrate wildlife interact with wind facilities (*Elzay, Tronstad & Dillon, 2017*).

There is strong evidence of regional declines in insect populations, and global declines in insect abundance and diversity during recent decades (*Grixti et al., 2009*; *Hallmann et al., 2017*; *Harvey et al., 2023*; *Potts et al., 2010*). Butterfly (*Nakamura, 2011*; *Swengel et al., 2011*; *Van Dyck et al., 2009*; *Warren et al., 2021*) moth (*Bell, Blumgart & Shortall, 2020*; *Fox, 2013*; *Green et al., 2021*) and wild bee species (*Goulson, Lye & Darvill, 2008*; *Potts et al., 2010*) are experiencing strong declines in abundance. The total biomass of flying insects declined by >75% in some areas (*Hallmann et al., 2017*). Reasons for insect declines may include widespread pesticide use, disease, changes in climate, and habitat loss (*Goulson et al., 2015*). Insects are the most abundant group of animals on the planet (*May, 1988*) and perform ecosystem services including pollination, decomposition, nutrient cycling, suppression of pests, and forage for numerous vertebrate species (*Morse, 1971*; *Prather et al., 2013*). Because of their abundance and diversity, insects are useful as indicators of ecosystem change (*Kremen et al., 1993*). Furthermore, many agricultural ecosystems rely on animal pollination; the transport of pollen is primarily performed by insects, and 80% of wild plants depend on insect pollination to reproduce (*Potts et al., 2010*). Declines in the abundance and diversity of insect pollinators could have far-reaching effects on industries reliant on pollination other than agriculture, such as forestry, trade, resource extraction, and power generation (*Chopra, Bakshi & Khanna, 2015*). While insect ecologists have progressed in understanding how many human activities negatively affect native insect populations, the extent to which renewable energy sources, such as wind turbines, are influencing these dynamics is unknown.

Wind energy facilities kill large numbers of insects (*Trieb, Gerz & Geiger, 2018*), potentially because insects are attracted to wind turbines. If insects are attracted to and more abundant at wind facilities, turbines may attract vertebrates that forage on insects, such as birds and bats, which are vulnerable to striking turbines. We know insects are attracted to the standardized white paint color used for most turbines (*Crawford et al., 2023a*; *Long, Flint & Lepper, 2010*), but turbines may also attract insects by acting as a source of ambient heat, luring them with flashing lights, or *via* contrast against the sky (*Ashfaq et al., 2005*; *Dudek, Dudek & Tryjanowski, 2015*; *Hauptfleisch, 2015*; *Seelig & Jayaraman, 2013*). Trillions of insects strike turbine blades annually (*Trieb, Gerz & Geiger, 2018*) and beyond conservation concerns, insect debris accumulated on blades can halve the expected power output by decreasing the aerodynamic performance of the blades (*Corten & Veldkamp, 2001*). Thus, siting, managing, and operating wind facilities while considering insects would benefit wildlife and allow wind facilities to produce more power.

Publications that investigated insect interactions with wind energy highlight topics that require further research including insect attraction to wind facilities, identification of vulnerable species, effects on insect populations, and how turbine design, siting and management can be improved to decrease insect fatalities (*Voigt, 2021*). We compiled current knowledge on insect physiology and behavior related to wind energy into a comprehensive review of the literature to address these questions. Specifically, we review how turbines change the abiotic environment, how insects may be affected by these changes, methods for surveying insects and what data they provide, insect orders vulnerable to collisions, how techniques for mitigating vertebrate fatalities may be used for insects, and the potential for trophic cascades at wind energy facilities. We present a case study investigating the potential influences of turbines on the abundance and richness of bees. Our questions included; (1) do abiotic factors influenced by turbines (*i.e.*, wind speed and temperature) influence bee abundance or richness, (2) does proximity to wind turbines influence bee abundance or richness, (3) are more bees and bee genera found near turbine bases as opposed to upwind or downwind of them, and (4) are there different assemblages of bees found at wind facilities compared to surrounding, undeveloped areas? Finally, we introduce a method to estimate potential overlap of wind energy development and suitable climate for species of concern that could be used to target areas of conservation interest. Our goal is to inform management practices, aid conservation efforts, and stimulate further research. As the proliferation of wind energy rapidly increases globally, investigating the industry's effects on wildlife, and mitigating impacts to align with climate and biodiversity goals is critical.

METHODS

Literature review

We reviewed the literature to interpret knowledge on interactions between insects and wind energy, and identify gaps. We discuss relevant technical aspects of turbine design, operation, and siting. We identified hypotheses about insect attraction to onshore turbines in the literature, and hypotheses about insect perception, behavior, and physiology (*e.g.*, hilltopping, attraction to light, attraction to heat). We related these hypotheses to knowledge about insect interactions with relevant abiotic stimuli such as visual cues, heat, light, and wind with a focus on anthropogenic sources. Our review summarized the evidence supporting hypotheses while highlighting topics that required further research. We reviewed literature regarding turbines' effects on insect habitat and forage to assess potential impacts to taxa of concern, specifically pollinators, and presented our results in figures and tables.

We compiled data from studies that identified insects caught at different altitudes and reviewed methods to survey insects in the atmosphere to evaluate how well each method explained patterns of insect presence. We discuss the methodologies to survey insects in the air and at wind turbines, and how that may confound our synthesis of results. We used literature detailing insect surveys conducted aerially and at ground level, and diet analyses of bats found near turbines to pinpoint which insect taxa are the most at-risk for striking turbines.

We cited >250 documents for this review. We used the Web of Science and Google Scholar databases to access international peer-reviewed articles discussing how wind turbines and wind energy facilities are known or hypothesized to interact with wildlife. Our review also includes information from secondary sources including textbooks on wind energy and entomology, and reports from U.S. government agencies. We used key words including wind energy, wind power, wind turbines, wildlife mortality, insects, invertebrates, insect vision, insect flight, insect monitoring, anthropogenic noise, infrasound, and microclimate, individually and in combination, to conduct a search of the literature. Resources were individually screened for relevancy, and cited works within retrieved articles were used when relevant. Additionally, we used Tethys Knowledge Base, developed to support the U.S. Department of Energy's Wind Energy Technologies Office and Water Power Technologies Office. The knowledge base contained many resources and we evaluated what sources are used by project developers, regulatory agencies, researchers, and other interested parties. Note that most resources about onshore turbines are based on research conducted in the United States and Western Europe; however, we attempted to integrate information from as many areas globally as possible.

Case study

We monitored insects at an operational wind facility, reference site, and sites that were slated for future wind development, with plans to conduct post-development surveys, and analyze trends in insect abundance and richness. Approval for this work was granted by the United States Bureau of Land Management (#L21AC10148-00) and PacifiCorp. In our

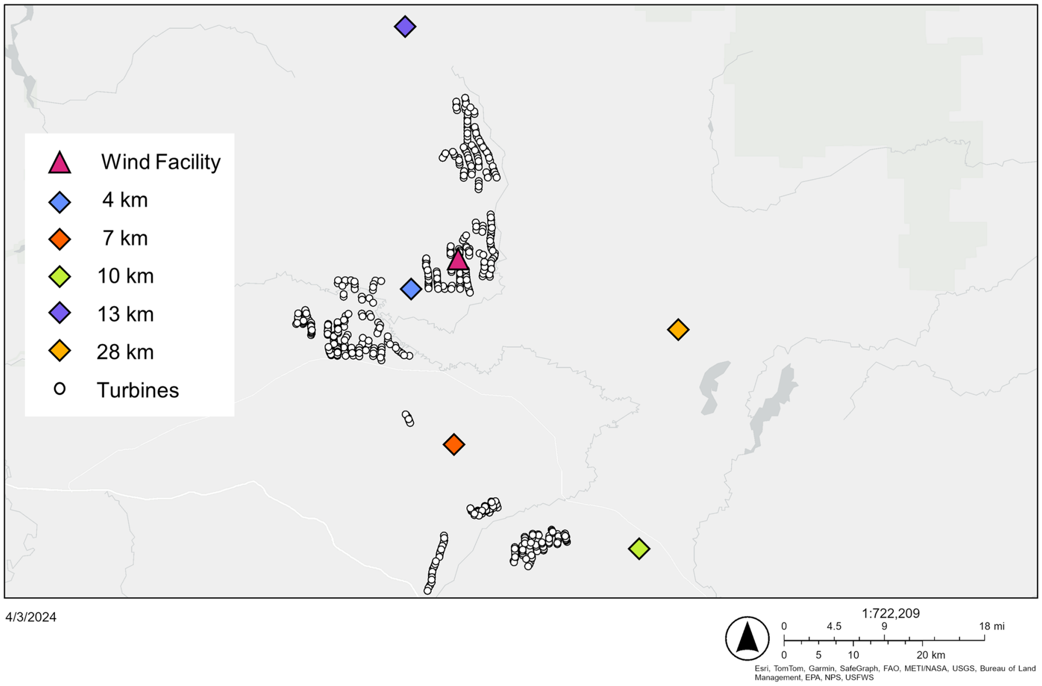

Figure 1 2022 sampling sites in relation to wind turbine locations. Location of six sampling sites in southeastern Wyoming, U.S., where insects were collected *via* vane trap and active netting for our case study in 2022. Distances in the legend indicate how far each site was from the closest operating turbine. Turbine location data provided by the US Wind Turbine Database. See Dataset S2. Basemap accessed on 4/3/2024. Basemap source: Esri. Data for basemap provided by: Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS and USFWS.
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first season we set out 83 vane traps and conducted 13 active netting sessions across six field sites in southeast Wyoming, U.S. from May to July 2022. Three to six traps were placed at each site twice per month. Traps were deployed for ~10 h, sometimes extending to 48 h, and abundance was reported as insects/hour. We secured traps to rebar and hung them <0.5 m above ground level at the height of surrounding vegetation. Sites included an operational wind energy facility on private land and five other locations on public land ranging from ~3.7 to ~28 km from turbines (Fig. 1). Sites and nearby habitat were classified as mixed-grass prairie and sagebrush steppe. The farthest site was a reference not proposed for development at the time of the study. Distances between traps and the closest turbine were calculated in R Studio using coordinates retrieved from the U.S. Turbine Database data layer in ArcGIS. Additionally, we walked two to three transects per site to target net bees and butterflies (38 cm diameter and 1 m handle). Active netting sessions lasted 30 to 83 min. Temperature and wind speed were measured using a Kestrel weather meter at the beginning and end of active netting events and upon deployment and collection of vane traps. Because bees made up the majority of our catch, we used that taxa for statistical power. Bees were identified to genus using a key modified from *Michener, McGinley & Danforth (1994)*. Bumble bees were identified to species using *Williams et al. (2014)* and sweat bees of the genera *Agapostemon* and *Halictus* were identified to species using

Tronstad & Dillon (2019). We used a non-metric multidimensional scaling (NMDS) analysis to compare assemblages of bee genera collected at each site using the vegan package (*Oksanen et al., 2022*). We removed genera that were only found on a single date or site and those that were rare (*i.e.*, individuals made up <0.1% of the total sample size). We used Program R (*R Core Team, 2022*) to analyze data and the plyr package (*Wickham, 2011*) to summarize data.

To measure if insect abundances and assemblages were influenced by proximity to turbines, we measured differences in bee catch (bees/hr) and bee genus richness with distance from turbines using generalized linear models (GLM). We calculated bee catch by dividing the number of bees caught in a trap by the length of time the trap was deployed, and we summed catch among vane traps per site and date. We calculated cumulative richness among all vane traps for each site and date. Our statistical models included wind speed, air temperature, and Julian date to account for abiotic factors affecting insect flight and seasonality of insects. We analyzed insect data within an operating wind facility (50–100 m upwind, near the tower, or 50–100 m downwind; $n = 24$ vane traps over four collection days at eight different turbines throughout the facility) using mixed effect models (GLMM). We combined this with similar data originally reported by *Dority (2019)* and reanalyzed it for this review, using study as a random variable for our models. Our model included wind speed, air temperature and Julian date along with position relative to the turbines. Our data were not normally distributed, so we used a gamma distribution with a log link to analyze our data after inspecting the histograms of our response variable and assessing fit using the fitdistrplus package (*Delignette-Muller & Dutang, 2015*).

To provide supporting evidence for the influence of temperature and wind speed on insect abundance, we conducted a case study that combined original data on insect catch rates and diversity with data that was previously reported by *Dority (2019)* and *Crawford et al. (2023a)* and reanalyzed it. We measured differences in catch rate using GLMMs. We included air temperature, wind speed and trap type as fixed effects and study as a random effect. We used a gamma distribution with a log link and scaled temperature and wind speed. We used estimated marginal means *via* the emmeans package to calculate the effect of trap types on the catch rate (*Lenth, 2024*). We used the lme4 package (*Bates et al., 2015*) to run our models and the ggplot2 package (*Wickham, 2016*) to visualize our data.

Risk assessment

We used nationwide Dakota Skipper, *Hesperia dacotae*, and Regal Fritillary, *Argynnis idalia*, observations from the Butterflies and Moths of North America (BAMONA) database to create a Maximum Entropy (Maxent) species distribution model (SDM) for both species. SDMs use species observations and environmental data to map geographic distribution (*Franklin, 2010*) and to understand how various environmental aspects may influence distribution (*Guisan & Thuiller, 2005*). Data were provided by Metalmark Web and Data, LLC and the many participants who contribute to its Butterflies and Moths of North America project (*Lotts & Naberhaus, 2023*). We used 51 unique points to model the potential distribution of the Dakota Skipper, and 864 unique points to model Regal Fritillary potential distribution. Ten thousand randomly selected locations across the U.S.

were used as background sites. We created two models with 21 potential CHELSA bioclimatic variables (*Karger et al., 2017*, *2018*). Predictors were chosen on overall contribution, jackknife contribution, and low correlation. The top six predictors were used to generate the Dakota Skipper model, and the top 10 predictors were used to create the Regal Fritillary model.

We binned the results of the SDMs into five climate categories based on the values of the model output with five representing the highest probability of species occurrence. These bins were combined with land-use and land cover data from the National Renewable Energy Laboratory (NREL) that show the potential for wind turbine installation in different siting regimes: open access, reference access, and limited access (*Lopez et al., 2021*). Each of these regimes uses a combination of siting constraints including existing infrastructure, regulations, and physical obstructions such as water, mountains, and steep slopes. The limited access regime applies the most constraints, while the open access regime applies the fewest, only considering physical barriers to development, protected land, and conservation easements. The reference access scenario represents a balance between siting considerations and uses widespread, common development practices. According to *Lopez et al. (2021)*, the most significant consideration for the limited access regime is the setback requirement to infrastructure. In the limited access regime, the tallest turbines would have a setback (distance from the turbine to the nearest railroad, road, building or property line) of 705 m. The amount of land available for wind energy development that overlapped with each climate category was calculated in square kilometers and mapped. Areas where suitable climate and development potential overlapped were classified as having some risk, while areas with no overlap were classified as no risk. We used the terra and raster packages in Program R to analyze the data and produce our maps (*R Core Team, 2022*; *Hijmans, 2023a*, *2023b*).

RESULTS

Turbine history, function and design

As wind energy regained prominence as an alternative energy option, the engineering of turbines changed significantly since the first verified use of windmills in the 9th century A.D. Initial machines converted wind power to mechanical power to mill grain and move water. In the 19th century turbines were developed to generate electricity. The first wind turbines were smaller and blades resembled airplane propellers more than today's highly engineered airfoils (*Manwell, McGowan & Rogers, 2010*). Modern turbines are about three times larger in terms of height and area covered by the blades. Taller turbines capture more energy from high-speed winds, while faster tip speeds and thinner blades reduce the amount of kinetic rotational energy lost to wind passing through them. Therefore, taller, faster turbines produce energy more efficiently because less wind can freely pass between the blades.

Modern turbines use a design called horizontal axis wind turbine (HAWT) in which the axis of rotation is parallel to the ground. The basic components of a HAWT turbine include the rotor, which consists of blades and a hub that connects the rotor to the nacelle. The nacelle is the housing for the controls, drive train, and generator. Underneath the

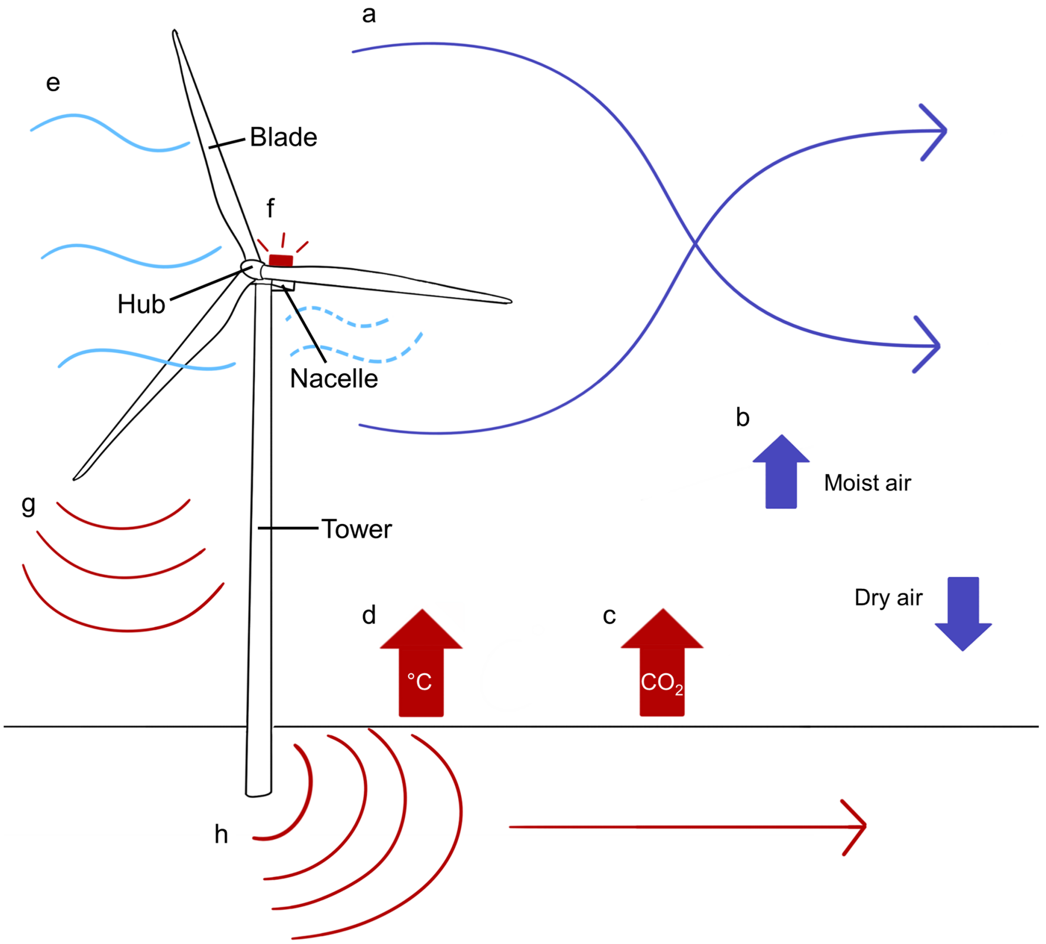

Figure 2 **Ways turbines influence the abiotic environment of the habitat they are sited in.** The main components of a horizontal axis wind turbine (HAWT). Turbines can influence the abiotic environment *via* (a) vertical mixing of air layers and increased turbulence, (b) changes in humidity, (c) increased carbon dioxide respiration, (d) warming of near-surface air temperatures at night, (e) reduction in wind speed at hub height, (f) light pollution from obstruction lighting, (g) production of audible noise, and (h) production of infrasound. Graphics credit: Michelle Weschler *via* Sketchbook.

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nacelle is the main frame, which mounts the drive train and the yaw system using a large bearing and sometimes motors and brakes to align rotors with the wind. The tower is typically made of steel, concrete, or a lattice that supports the primary components (Fig. 2). Finally, onshore turbine towers are installed into a concrete foundation (*Manwell, McGowan & Rogers, 2010*).

Turbine designs differ including designs for upwind or downwind placement, number of blades, blade design, rotor configurations, tower size and design, generator types, and more. In the U.S., the average wind turbine in 2022 was 3.2 MW capacity HAWT with three blades, a hub height ≥98 m, and a rotor diameter of 131.6 m. These average sizes indicate a 73% increase in height and 173% increase in rotor diameter since 1998–1999; a trend that is predicted to continue (*Wiser et al., 2023*). The towers are usually a steel tube painted pure white or light grey.

The function of wind turbines is to convert wind power into electricity. Wind flows over the blades of the turbine, generating lift forces (in most turbines) making them spin. The rate of rotation is often sped up by the drive train from tens of rotations per minute to thousands of rotations per minute that work better with the generator. Modern turbines are designed to capture and convert wind power as efficiently as possible while minimizing fatigue and stress on the turbine components. As blades turn, they exert torque on the wind passing through the blades that causes some rotational kinetic energy. This rotational energy is not being captured by the turbine, so one engineering goal is to reduce rotation, which is achieved with faster rotating turbines. Faster blades absorb more of the wind's kinetic energy, however; faster rotation is associated with increased noise created by blade tips. Turbine manufacturers limit blade speed to keep noise levels at an acceptable level.

Siting

Siting is the placement of turbines on the landscape, and is considered on a broad scale (entire wind facilities) and on a small scale (individual turbines within wind facilities; micrositing). The goal of siting turbines is to maximize potential energy production while minimizing cost, potential impacts on the environment, and disturbances to human communities (*Manwell, McGowan & Rogers, 2010*). Topography and landscape features (*e.g.*, distance to forests and water sources) can alter potential interactions with flying wildlife such as bats (*Roemer et al., 2019*). Furthermore, turbine siting is increasingly subject to local regulations and constraints (*Lopez et al., 2021*, *2023*).

Proposed locations for wind development undergo numerous evaluations before selection including compiling data about the landscape and topography, wind pattern variation over space and time, grid connections, and potential environmental impacts. Generally, utility-scale turbines (>1 MW) are placed where average wind speed is ≥21 km/h. Rounded hilltops, mountain gaps that funnel wind, and open plains without obstacles are the most favorable terrains for turbines (*Wiser et al., 2022*). Most turbine projects in the U.S. are in the Electric Reliability Council of Texas (ERCOT), Midcontinent Independent System Operator (MISO), and Southwest Power Pool electric grids (SPP), which are in the center of the country. China, Germany, and India have the highest cumulative wind power capacity internationally; China consistently has the largest increases in capacity annually (*Wiser et al., 2022*). Siting in these countries is subject to specific restrictions based on region or state, but usually involves setbacks from infrastructure and protected natural areas (*Jung, Schindler & Grau, 2018*). China has a "highly concentrated deployment tendency" wherein many of their new onshore wind facilities are being built within 10 km of existing ones (*Deng, Yu & Liu, 2011*). It is unclear how the density of turbines may augment wildlife interactions.

The *U.S. Fish and Wildlife Service (2012)* published a tiered set of guidelines for evaluating potential wind energy sites based on impacts to species of concern and vulnerable habitats. Each tier provides questions to be answered with credible data to inform decision-makers about the environmental risk of the project, specifically with regards to species of concern including plants, bats, and birds. Insects and invertebrates are not mentioned in this document, pointing to an important blind spot when it comes to conservation-focused siting guidance.

Wind facilities require larger amounts of land than most other energy facilities. For example, a facility being built in Wyoming, U.S. will host ~600 turbines on ~130,000 hectares of land and supply an estimated 3,000 MW of power (*Power Company of Wyoming, 2024*). Land surrounding turbines can be used for agriculture (*e.g.*, grazing or crop production). The proportion of that land precluded from these uses is 3–5% in the United States, and lower in Europe (*Manwell, McGowan & Rogers, 2010*).

How do turbines affect the abiotic environment?

Microclimate

Wind turbines alter the microclimates within and downwind of wind facilities based on field experiments and modeling. Microclimates result from a combination of influences, including operating turbines and infrastructure, topography, land use, soil composition, and vegetation. In some cases, landscape characteristics have larger effects on microclimate than turbines (*Moravec et al., 2018*). Turbines can change the stability of the atmospheric boundary layer (ABL) (*Zhou et al., 2012*) by vertically mixing stratified air (see a et Fig. 2). During the day, air temperatures are cooler at higher altitudes and the opposite occurs at night because of convective cooling of the air directly above ground level, flipping the temperature gradient with respect to elevation. Turbines can disrupt this natural phenomenon (*Armstrong et al., 2016*; *Baidya Roy & Traiteur, 2010*); this effect could be mitigated by siting turbines in areas that naturally experience high turbulence. Similarly, facilities with many turbines can affect humidity by lifting moist air up and sending dry air towards the ground (*Adkins & Sescu, 2022*; see b et Fig. 2). Turbine wakes and pressure changes in soil, especially at night, can alter carbon dioxide and water fluxes. Specifically, soil microbes respire more carbon dioxide downwind of turbines (*Rajewski et al., 2014*, *2013*; see c et Fig. 2). Shifts in microclimate may affect carbon cycling and plant-soil interactions (*Armstrong et al., 2014*). Moreover, microclimate effects may extend several kilometers downwind from turbines.

Temperature

Changes in local and downwind air temperatures near the ground are understudied compared to other climate effects of wind energy. Turbines influence local meteorology and can alter air temperatures near the ground at wind energy facilities (*Baidya Roy & Traiteur, 2010*; see d et Fig. 2). For example, near-ground air temperatures downwind of a turbine were higher during the night and morning, and lower during the day (*Baidya Roy & Traiteur, 2010*). The Crop Wind Energy Experiment investigated industrial scale wind energy facilities that were combined with agricultural land and found that turbines increased upward heat flux during the night (*Rajewski et al., 2013*).

Characteristics of wind energy sites may influence temperature effects. For example, larger facilities, and those in cropland and grassland showed stronger nighttime warming than smaller facilities and those in forests (*Qin et al., 2022*). The effects of a single turbine on daytime surface temperatures can be overridden by ecological factors

(*Moravec et al., 2018*). Overall, larger wind energy facilities sited on land with low natural turbulence and topographic homogeneity may have the strongest effects on ground-level air temperature. Notably, turbines radiate heat, increasing surfaces temperatures by >2 °C compared to the surrounding ground (*Dudek, Dudek & Tryjanowski, 2015*).

Wind and atmospheric conditions

The average wind turbine in the U.S. has blades ~30–140 m above ground-level within the ABL (*Wiser et al., 2022*) and mix layers of air while operating. Turbines affect the early evening transition, which occurs a few hours before and after sunset each day. During the transition, there is a strong reduction in turbulence near the ground, which slowly extends upward into the atmospheric layers during night. During this period, turbulence from turbines has stronger influences than natural turbulence, altering natural processes (*Rajewski et al., 2020*).

While turbulence increases downwind of turbines, wind speed is reduced at hub-height, according to models and wind-tunnel experiments (*Chamorro & Porte-Agel, 2009*; *Rajewski et al., 2020*; see e et Fig. 2). This effect can persist far downwind of turbines, reducing power output in the wake (*Miller & Kleidon, 2016*). Turbines operating since 2021 in the U.S. were sited in areas with lower average wind speed (8 m/s at 100 m) than the previous 7 years. The average wind speed of developed sites will likely continue decreasing in the future. Turbine hub heights and rotor diameters are increasing; they can capture wind higher than 100 m above the ground despite being sited in areas with lower wind speeds (*Wiser et al., 2022*).

Light

Obstruction lighting on wind turbines is required by the U.S. Federal Aviation Administration (FAA) (see f et Fig. 2). Currently these lights must be aviation red (FAA L-864) in color, and pulse, flash, or strobe continuously at night or in low-visibility conditions (*e.g.*, fog). The number and placement of lights depend on the size and configuration of the wind facility, and turbine size (*Federal Aviation Administration (FAA), 2015*).

Aircraft detection lighting systems (ADLS) are an innovation to reduce the negative effects of artificial lighting at wind facilities on neighboring homes and communities. Lights are off until aircraft are detected nearby, activating obstruction lights (Terma A/S). Widespread use of ADLS would reduce light pollution and reduce wildlife attraction to wind facilities; however, ADLS are not practical for every wind energy facility because of the added costs from installation, maintenance, updates, and monitoring (*Weigel, Viebahn & Fischedick, 2022*).

Rotating turbine blades cause the shadow cast by turbines to "flicker" or flash when the sun is low in the sky. This happens at certain times of the day and year for short periods and has mainly been investigated concerning its potential influence on humans (*van Kamp & van den Berg, 2018*, *2021*) and less frequently on vertebrate animals (*Lovich & Ennen, 2013*; *Nopp-Mayr et al., 2021*). Nothing is known about how flicker could alter insect behavior or abundance.

Sound

Turbines can produce noise from high (6–8 kHz) to low (<200 Hz) frequencies (*Ryunosuke, 2008*; see g et Fig. 2) and frequencies below the range of human hearing (<20 Hz) called infrasound (*Zajamšek et al., 2016*; see h et Fig. 2). Noise produced by wind energy facilities can travel long distances (≤90 km) under certain atmospheric conditions (*Marcillo et al., 2015*). The propagation of turbine noise is dependent upon the environmental and topographical conditions of the site and seasonality. *Whalen et al. (2019)* found that turbine noise levels at 296 Hz were greater in May than March, increased with high wind speeds, and decreased when hilly topography was present. Furthermore, turbine noise tends to travel further downwind than upwind (*Whalen et al., 2019*). Usually, the intensity of noise produced by turbines is similar to the sound of an urban residence at ground level (*U.S. Department of Labor, 2022*) and the infrasound produced is not audible to humans even when near turbines (*D'Neal, Hellweg & Lampeter, 2011*). There are concerns about increased noise production and propagation as turbines become larger and more numerous.

No connection between turbine noise and human health was found beyond annoyance (*van Kamp & van den Berg, 2018*, *2021*); however; several vertebrate species were affected by turbine noise, but few studies with a only a small number of species have investigated these phenomena thus far. Birds, such as Dupont's lark, *Chersophilius duponti*, altered their vocalizations when exposed to turbine noise, possibly to prevent their calls from being masked by similar frequencies produced by turbines (*Gómez-Catasús et al., 2022*). Male Japanese tree frogs, *Dryophytes japonicus*, increased their call rate when exposed to turbine noise, potentially leading to greater energy investment and impaired immunity over time (*Park & Do, 2022*). Cortisol levels in badgers, *Meles meles*, and young domestic geese, *Anser anser f. domestica*, were greater in individuals that remained closer to turbines than in individuals located father away, which could be attributed to infrasound exposure (*Agnew, Smith & Fowkes, 2016*; *Mikołajczak et al., 2013*). Methods to reduce turbine noise are being investigated including changes to blade design such as serrated trailing edges, pointed tips, porous surfaces, and low-noise airfoil designs (*Van Treuren, 2018*).

Surveying flying insects

The insect flight boundary layer is a point within the ABL, below which insect flight speed is higher than the wind speed, and above which insects are moved downwind (*Taylor, 1974*). This level occurs 1–10 m above the ground depending on the species and environmental conditions of the habitat (*Taylor, 1974*). Insects may lift themselves above their flight boundary layer to move long distances, aided by wind. Aerial trapping collected many orders of arthropods at heights throughout the ABL, which is ~1 km thick (*Chapman et al., 2004*; *de Jong et al., 2021*; *Freeman, 1945*; *Hardy & Milne, 1938*; Fig. 3). Diptera, Hemiptera, Hymenoptera, Coleoptera, and Araneae were the most abundant orders across several aerial trapping studies performed in the UK (*Chapman et al., 2004*), making those orders vulnerable to turbines. Coleoptera (*Jeffries et al., 2013*) and Lepidoptera (*Gibo, 1981*) have been observed above the ABL.

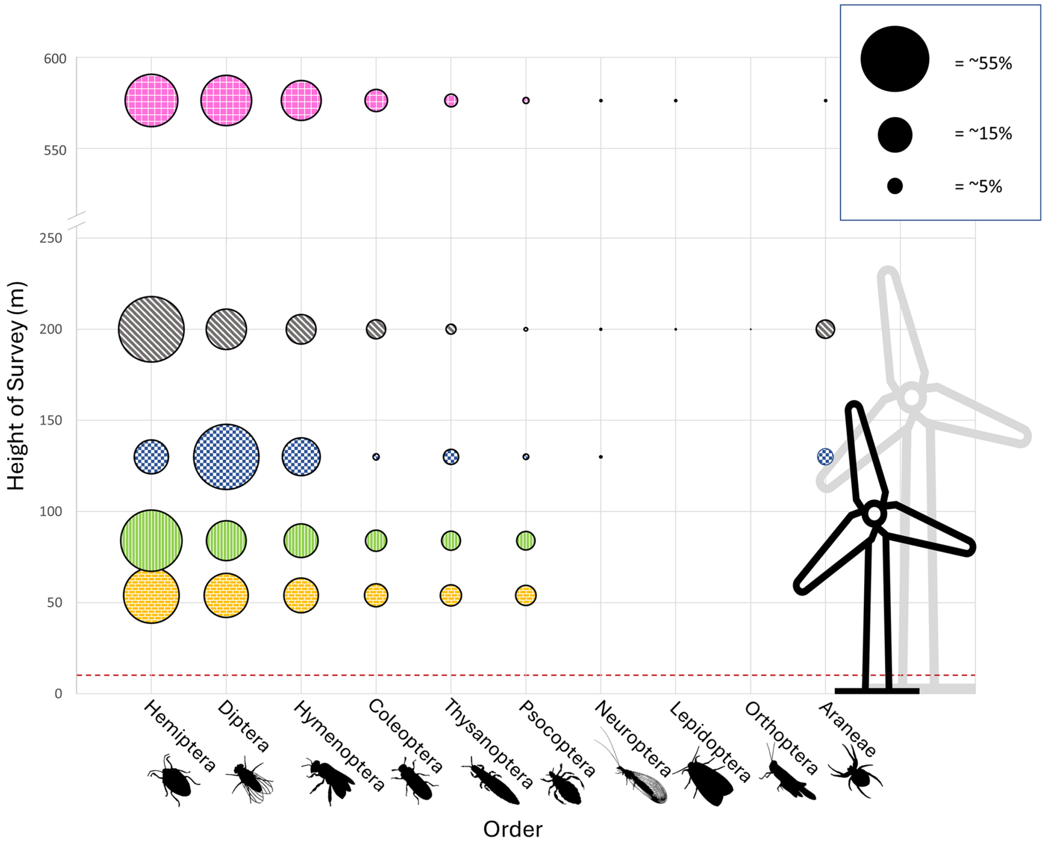

Figure 3 **The presence of insect orders found in aerial insect surveys taken at different heights in the atmosphere.** Patterns and colors represent different aerial surveys. The area of each bubble is relative to the proportion of each order found in the survey. The black turbine represents the average total height for turbines in the United States in 2022 (164 m) The grey turbine represents the maximum total height of turbines under construction in the United States as of 2022 (225 m). The red dashed line represents the average insect flight boundary level (10 m). Survey data from *Chapman et al. (2004)*, *de Jong et al. (2021)*, *Freeman (1945)*, and *Hardy & Milne (1938)*. All invertebrate silhouettes were sourced from https://www.phylopic.org and have been dedicated to the public domain. The wind turbine icon was provided by Microsoft.

Full-size DOI: 10.7717/peerj.18153/fig-3

Estimating arthropod density and identity in the atmosphere is difficult but several techniques have been developed with varying strengths and weaknesses. Surveying at high altitudes employs a variety of methodologies including netting, sticky traps, or suction traps on structures, airplanes or balloons which provide abundance and richness information, but not behavior (*Chapman, Reynolds & Smith, 2004*; *de Jong et al., 2021*; *Rydell et al., 2016*).

Monitoring insect movement across a vertical stratum is viable with radar (*i.e.*, radio waves) and lidar technology (*i.e.*, lasers or light waves). Vertical looking radars provide information on size, shape, wing-beat frequency, and orientation of flying insects at ~1 km scale; however, radar usually cannot identify insects, especially when sparse (*Chapman, Drake & Reynolds, 2011*). Radar provides insight into the magnitude of insect migrations and behavioral adaptations; however, radar is complemented by aerial trapping to identify arthropods. Lidar provides high precision observations of individual insects and swarms.

In fact, lidar detected insects swarming consistently at the tops of turbines at sunset (*Jansson et al., 2020*).

Bat activity and diet provides insight about flying insects near turbines, because bats actively forage at wind energy facilities at night. DNA barcoding of bat stomach contents and fecal pellets are used to assess insect presence and frequency around turbines (*Foo et al., 2017*; *Rydell et al., 2016*; *Scholz & Voigt, 2022*). Lepidoptera, Orthoptera, Coleoptera, Diptera, Hemiptera, Trichoptera, Neuroptera and Psocodea are being predated upon by bats at turbines in decreasing order of abundance. Insects collected at night in the immediate vicinity of wind turbines at ground level closely correlate with bat stomach contents, suggesting that flying insects collected near the bottom of turbine towers are comparable to insects flying at heights that bats forage (*Foo et al., 2017*).

How do turbines affect insects?

Case study results

The abundance of insects, primarily bees, did not differ with distance from turbines. We captured 1,614 insects, 95% of which were bees. The abundance and richness of bee taxa captured in vane traps did not vary with distance to turbine across the landscape at the scales we investigated. Bee catch appeared uniform across the landscape (glm, $\beta = -0.04$, $t = -0.13$, $p = 0.89$; Fig. 4A), which did not support our hypothesis that insects are more abundant at turbines; however, the insects captured in our traps at ground level were not necessarily the taxa we expected to interact with blades. We expect that other habitat characteristics (*e.g.*, number of blooming flowers) may help explain some of the variance observed.

Generic richness did not vary with distance from turbines (glm, $\beta = -0.03$, $t = -0.3$, $p = 0.76$; Fig. 4B). The two sites farthest from turbines were not directly downwind and we collected more genera there on average, suggesting that the direction from turbines may help explain variance. Expectedly, we caught more bees (glm, $\beta = 1.08$, $t = 3.096$, $p = 0.006$) and observed more genera (glm, $\beta = 0.29$, $t = 2.49$, $p = 0.02$) at higher temperatures. Higher wind speeds did not affect the number of bees captured (glm, $\beta = -0.17$, $t = -0.56$, $p = 0.58$), but we captured slightly fewer genera (glm, $\beta = -0.18$, $t = -1.74$, $p = 0.09$) suggesting not all bees fly at high wind speeds. Capture rate (glm; $\beta = -0.02$, $t = -1.53$, $p = 0.14$) and richness (glm; $\beta = 0.004$, $t = 0.83$, $p = 0.41$) did not vary with Julian date.

The abundance and richness of bees did not vary based on position within wind facilities at the scale we measured. The catch rate of insects within wind facilities expectedly increased as temperature increased (glmer; $\beta = 0.34$, $t = 7.97$, $p < 0.001$) and decreased as wind speed increased (glmer; $\beta = -0.23$, $t = -4.43$, $p < 0.001$). Position did not explain variance in catch rate (glmer; $p > 0.1$; Fig. 5A). There was a weak correlation between position and number of genera caught, with lower generic richness near turbine towers rather than upwind or downwind (glmer; $\beta = -0.17$, $t = -1.92$, $p = 0.05$; Fig. 5B).

Polygons representing the insect assemblages overlapped at most sites, but the wind energy facility and prairie (distance ~10 km downwind) differed by the largest degree. The most stable NMDS solution was 2D (stress = 0.15). The prairie and wind facility sites occupied the broadest space while the other sites had much smaller polygons (Fig. 6).

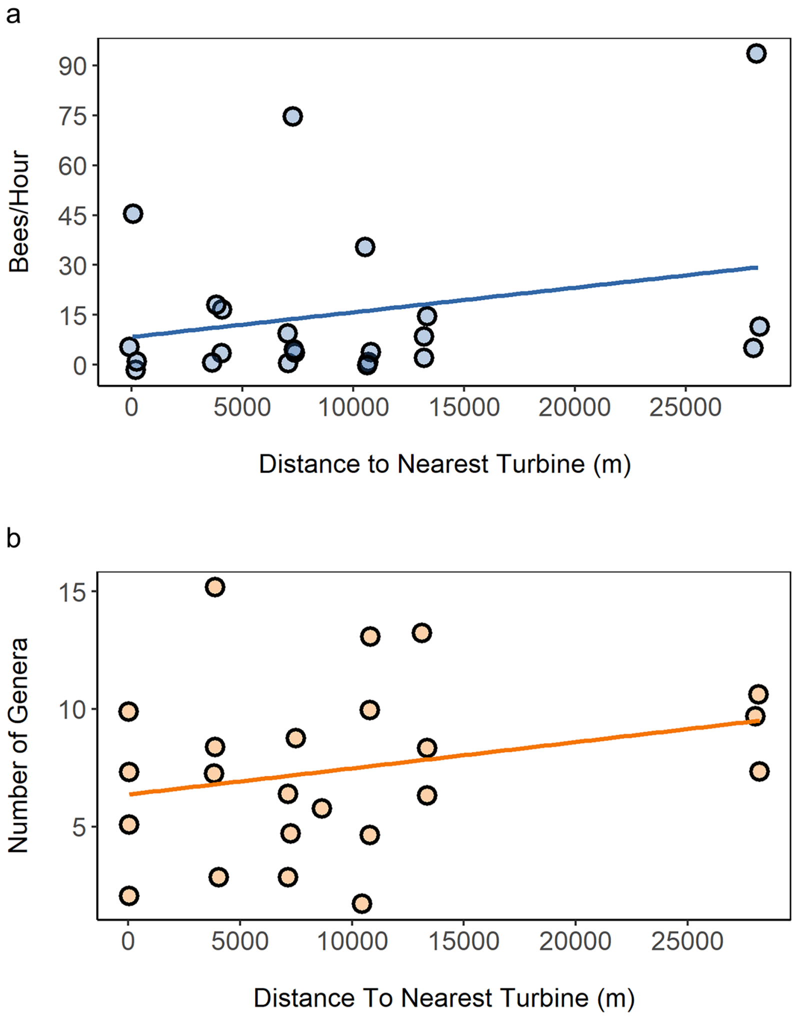

Figure 4 **Distance to turbines did not influence measures of insect populations.** (A) Catch rate of bees at different distances to the nearest turbine where each point represents the sum of catch rates for traps placed at the same site on the same day (three to six traps). (B) Number of bee genera caught at different distances to turbines where each point represents the sum of genera caught in traps placed at the same site on the same date (three to six traps). All data comes from the 2022 case study. See Dataset S2.

Full-size DOI: 10.7717/peerj.18153/fig-4

Dissimilarity rank showed no differences among sites and very low dissimilarity (ANOSIM, R = −0.014, p = 0.5). Surveying at multiple operating wind facilities along with similar areas at varying distances downwind over multiple years could reveal stronger trends and provide information about the relationship between insects that live in the boundary layer at wind facilities. For example, our results suggest that the bee genera *Melissodes*, *Dianthidium*, and *Halictus* were more closely associated with the wind facility, while Diptera and bees in the genera *Perdita* and *Megachile* were correlated with the downwind, highly-grazed prairie site. Our reference site (~28 km from the nearest turbine) overlapped with all sites and occupied a small space, supporting our models suggesting that habitat characteristics likely play a larger role in species richness and assemblages.

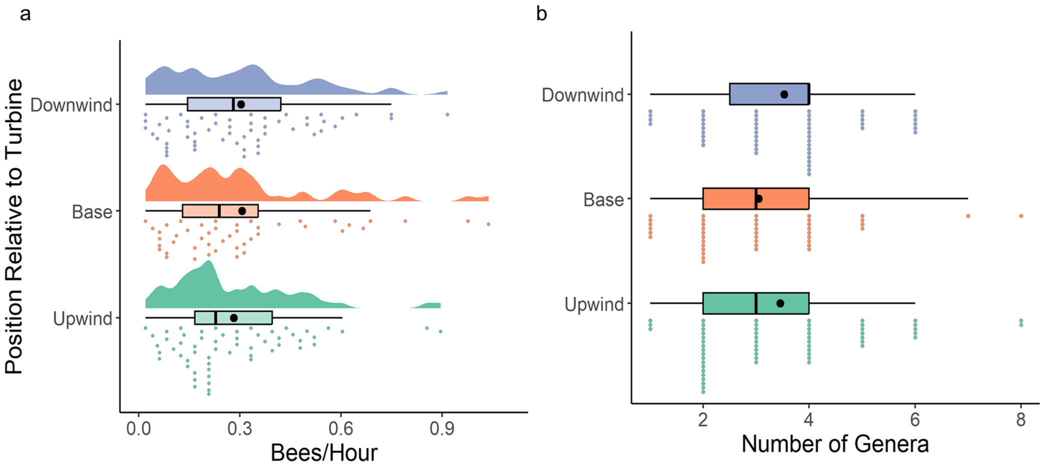

Figure 5 **Results for catch rate and generic richness locally around turbines at ground level.** (A) The catch rate of bees within the wind energy facility did not differ significantly based on differing placement of traps (upwind, downwind, or adjacent to the base of the turbine tower). (B) The number of genera caught did not differ significantly bases on differing placement of traps; however traps adjacent to the base of the tower tended to catch a slightly lower number of genera. The black dots indicate mean values. These results combine data collected from the case study and Dority (2019). Upwind and downwind traps were 30–110 m away from turbines in Dority (2019), and 50–100 m away in our case study. Traps at the base were <5 m away for both studies. See Dataset S2. Full-size DOI: 10.7717/peerj.18153/fig-5

Microclimate

Microclimates created within and around wind energy facilities could attract or deter insect species. *Pustkowiak et al. (2018)* found that pollinator abundance, richness and diversity did not differ between sites with turbines and grasslands without turbines, but these metrics were lower in adjacent cropland without turbines. Furthermore, bees preferred sites around turbines while flies showed no preference. Towers of turbines surrounded by cropland may be novel habitats for wild pollinators and plant species in a homogenous landscape due to flowering weeds; however, they could be managed for pollinator conservation, connecting pollinators populations in a fragmented landscape (*Pustkowiak et al., 2018*). Similarly, concrete foundations of turbines, roads within energy facilities, transformers and substations may act as novel habitats for basking or nesting. Increases in beneficial and pest insects around turbines may occur as wind energy within agricultural ecosystems are developed (*Dudek, Dudek & Tryjanowski, 2015*; *Pustkowiak et al., 2018*).

Most insects are subjected to fine-scale changes in microclimates on horizontal and vertical scales. The appropriate scale to consider for insect microclimates is ~20 cm (*Pincebourde & Woods, 2020*), because most insects are small (<5 mm) (*May, 1988*); however, a larger scale may be used for larger insects or insects that disperse quickly among habitats. Knowing that insects experience microclimate on a different scale than humans or other vertebrates is crucial to assess their behaviors and habitat needs. For example, investigations into microclimates at wind energy facilities have focused on local (*i.e.*, changes in air temperature, wind speed, and humidity) rather than fine-scale microclimates such as the surface temperature of vegetation, which may be more relevant

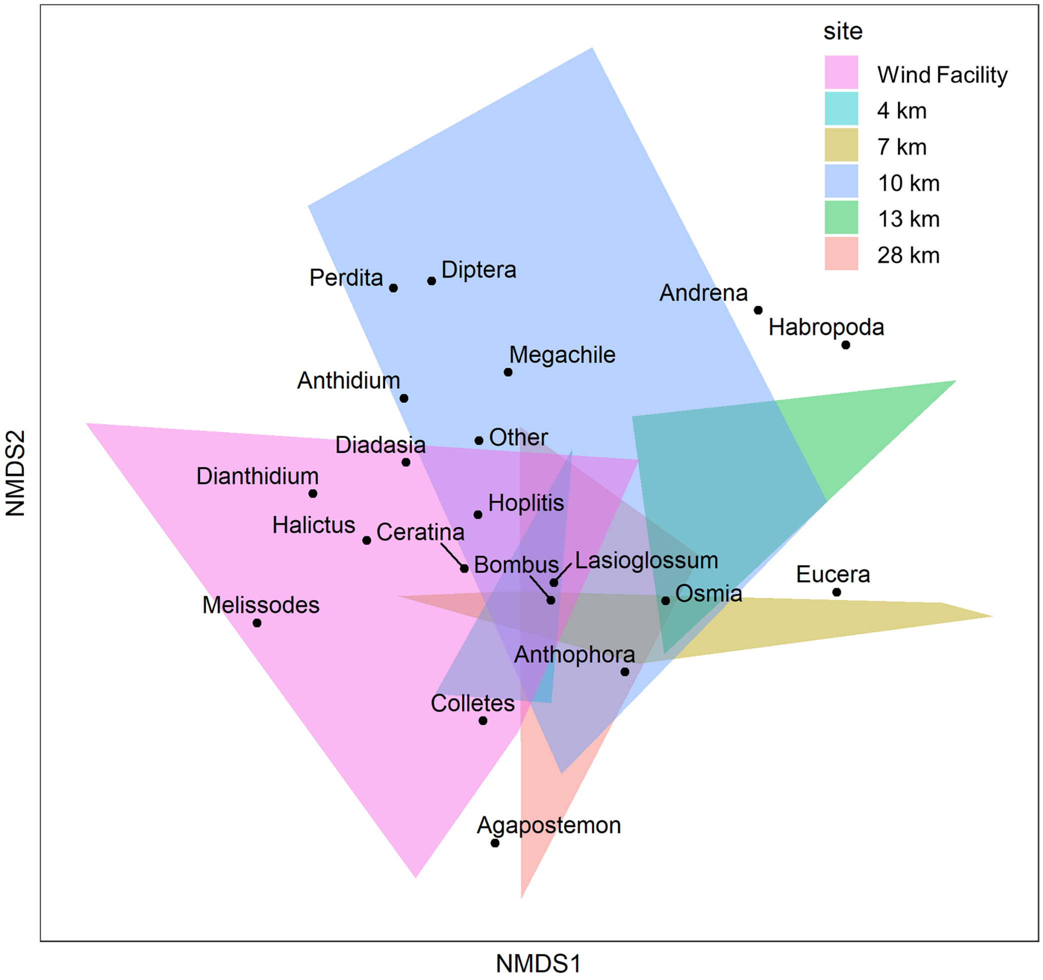

Figure 6 **NMDS showing insect assemblages collected at six field sites.** Sites are organized in the legend by their distance to turbines, with the wind energy site being the closest and the reference site being the farthest away (~28 km). The 10 km site and wind energy site show the most difference among other sites, however all sites show some overlap with others, showing general similarity. The axes are arbitrary, the differences between species and sites can be interpreted from distance between points and polygons. See Dataset S2. Full-size DOI: 10.7717/peerj.18153/fig-6

to insects and can differ from ambient temperatures (*Stoutjesdijk, 1977*). Microclimates are an increasingly important topic in insect conservation because they provide habitats that buffer insects from extreme environmental conditions caused by climate change (*Pincebourde & Woods, 2020*). Local changes inherently influence fine-scale microclimates, but we are not aware of any literature investigating fine-scale microclimates at wind energy facilities.

Temperature

Insects use external sources of heat to maintain a constant body temperature which may be found at turbines. Development, foraging, diapause, and many other aspects of insect behavior hinge upon proper ambient temperatures occurring for the proper amount of time (*Atkinson, 1994*; *Gérard et al., 2022*; *Matthews & Matthews, 2009*). Insects display

Table 1 **Insect sensory organs potentially affected by stimuli produced or altered by wind turbines.**

Stimuli produced or altered by turbines	Impacted sense organs	Potential effects	Supporting literature
Light/color/shape	Compound eyes and ocelli	Attraction to turbines; congregation around turbines	*Kriska et al. (2008)*, *Long, Flint & Lepper (2010)*, *Seelig & Jayaraman (2013)*, *Park & Lee (2017)*, *Crawford et al. (2023a)*
Acoustic noise	Tympanal ears; hairs; antennae	Alterations to calls; hindrance to mate location	*Morley, Jones & Radford (2014)*, *Orci, Petróczki & Barta (2016)*, *Gurule-Small & Tinghitella (2018)*, *Duarte et al. (2019)*
Vibration (seismic noise)	Antennae; mechanoreceptors throughout body	Disruption of vibratory signals; increased stress; reduced offspring	*Yack (2016)*, *Phillips et al. (2020)*, *Velilla et al. (2021)*
Temperature	Thermoreceptors in antennae	Attraction to turbine towers; deterrence of some species	*Dudek, Dudek & Tryjanowski (2015)*, *Rydell et al. (2016)*
Wind	Antennae, mechanoreceptors	Increased abundance near nacelle; dispersal of kariomones; migration interference	*Dority (2019)*, *de Jong et al. (2021)*

heightened thermal sensitivity during processes such as competition, communication and mating (*Leith et al., 2021*).

Insects use thermoreception to find places to feed, take refuge, thermoregulate, and oviposit. Therefore, temperature is inherently related to insect habitat selection, even at fine scales. For example, plant surfaces in tree canopies are generally warmer than other microhabitats within a forest, but experience more variation in temperature. Therefore, temperature generalists rather than high-temperature specialists typically live in tree canopies (*Kaspari et al., 2015*). Wake effects from turbines influence the air and ground temperatures at wind energy facilities, and could create selective temperature conditions that differ from those in surrounding environments, thereby attracting, or deterring certain species (Table 1).

The high surface area to volume ratio of small insects makes them particularly vulnerable to fluctuations in air temperature, because they lose and gain heat quickly. Some insects thermoregulate by basking on warm or sunny surfaces (*e.g.*, turbine towers) or selecting for specific microhabitats. Other insects, such as bees, can rapidly vibrate their wing muscle to raise the temperature of their thorax. Thermoregulation is particularly important for flying insects as they must reach a certain minimum body temperature to initiate flight, and typically only fly when ambient temperatures are >15 °C (*Cox & Dolder, 1995*; *Krogh & Zeuthen, 1941*; *Taylor, 1963*).

We combined our case study results of catch rates of flying insects with data from two comparable studies in southeastern Wyoming, U.S. in 2016 and 2017. These combined results support the literature that flying insects are usually active at temperatures >15 °C. Furthermore, catch rate increased as temperature increased (glm, $\beta = 0.106$, $t = 6.507$, $p < 0.0001$; *Crawford et al., 2023a*; *Dority, 2019*; Fig. 7A), but results depended on the method of capture.

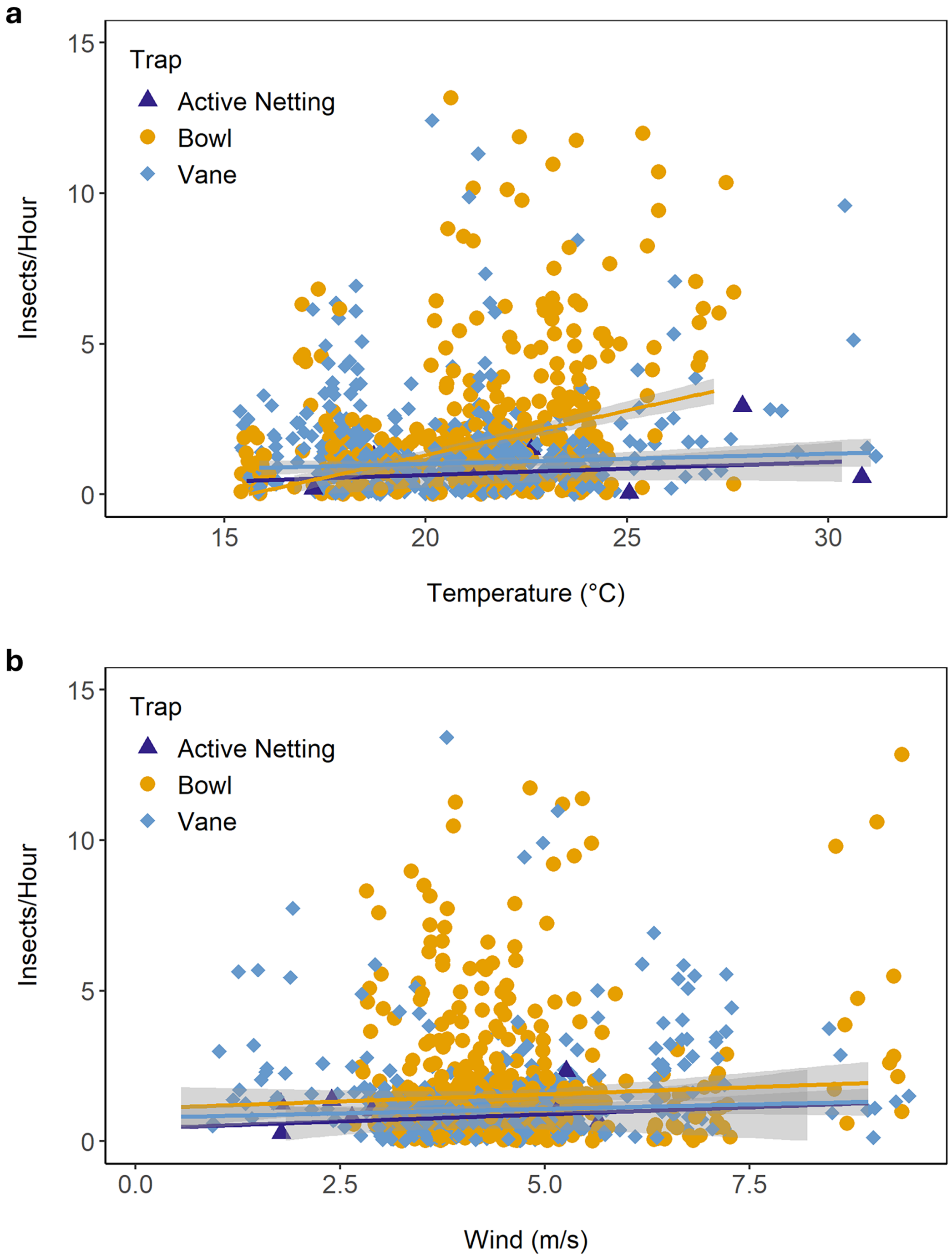

Figure 7 Method of capture influenced catch rate in combined study data. Insect catch rate per trap for active netting, and vane traps and pan traps set out at different (A) temperatures and (B) wind speeds in three studies in southeast Wyoming, U.S. from 2016, 2017, and 2022. Each point represents a different trap or session of netting. Includes data from case study, *Dority (2019)* and *Crawford et al. (2023a)*. See Dataset S2.

Full-size DOI: 10.7717/peerj.18153/fig-7

The heat that turbines radiate may make them an attractive spot to thermoregulate. *Harmonia axyridis*, an Asian species of lady beetle, used turbines as an overwintering site in Poland where they are invasive. This behavior was attributed to attraction to the warmth of turbine towers and the protection they provide from wind (*Dudek, Dudek & Tryjanowski, 2015*). Large flies, such as blowflies, flesh-flies, and houseflies, were observed resting and basking on the surfaces of wind turbines, sometimes in large numbers despite making them more vulnerable to predation (*Rydell et al., 2016*). This is consistent with aerial surveys reporting a large percentage of Diptera in the atmosphere (*Chapman, Reynolds & Smith, 2004*).

Wind, atmosphere and flight

Insects typically fly at low wind speeds although the threshold for flight can vary among species and areas (*Taylor, 1974*). Wind can influence flying insects by making maneuverability more difficult in the air and on host plants. Wind turbulence can limit the flight speeds of insects by increasing drag, and high wind variability can cause instability leading to loss of control (*Combes & Dudley, 2009*). Not all insects respond to wind equally. Small-bodied insects are particularly vulnerable to changes in wind speed and direction, and tend to fly at dusk or night when the atmosphere is more stable (*Peng, Fletcher & Sutton, 1992*). Flying in high wind speeds requires increased energetic costs and can influence the dispersal and migration capabilities of many species; however, some insects have mechanisms that orient them based on wind direction or stabilize themselves during flight, such as euglossine bees extending their hind legs to reduce the acceleration of their side-to-side rolls (*Combes & Dudley, 2009*).

Our analysis of three studies, including out case study, in southeastern Wyoming, U.S. suggested that insects may be more abundant during intermediate wind speeds (~4.5 m/s) than previously thought. Overall, insect catch rate increased slightly as wind speed increased (glm, $\beta = 0.057$, $t = 3.436$, $p = 0.0005$; Fig. 7B). Bowl traps placed at ground level tended to catch more insects at wind speeds >3 m/s than vane traps places ~0.5 m above ground, likely because many insects were crawling rather than flying; however, some vane traps still had higher catch rates at high wind speeds. This may be because flying insects were searching for cover or were flying between wind gusts. Generally, vane traps tend to catch more insects (particularly bees) and more genera than bowl traps (*Bell, Tronstad & Hotaling, 2023*; *Short et al., 2023*). These results may indicate that more insects are actively flying during higher winds than previously described, especially in areas with higher average wind speeds, such as Wyoming (*Dority, 2019*; *Crawford et al., 2023a*).

Wind conditions may affect pollination, herbivory, and predator-prey interactions. For example, wind speed can affect the herbivory of larval insects by influencing where individuals reside on the host plant (*Shao et al., 2020*). High wind speeds may influence insect predator-prey interactions by delaying the onset of predation because of increased plant movement and impaired predator mobility, thereby indirectly increasing the abundance of the prey species (*Barton, 2014*; *Chen et al., 2018*). Furthermore, air turbulence affects the dispersal of insect pheromones (*e.g.*, kariomones) and other chemicals that alter insect behavior. When turbines reduce wind speeds near the hub and create increased turbulence throughout the facility, these zones could be more attractive to flying insects, making them vulnerable to colliding with spinning blades. Indeed, *de Jong et al. (2021)* found that insect abundance was negatively correlated with wind speed at turbines at nacelle height. Furthermore, the recent trend of turbines sited at locations with lower average wind speeds could increase the number of insects that are interacting with wind energy facilities.

Insects have diverse wing structures and flight types that may alter how vulnerable they are to colliding with turbines. For example, reduced wind speeds downwind of turbines and directly behind blades could create a refuge for insects that are weaker fliers. The size of insect wingspans ranges from <1 mm to >25 cm. Flying insects possess one or two pairs of wings which may or may not operate independently during flight (*Grodnitsky, 1995*). Wing morphology plays a role in individual flight ability. For example, monarch butterflies that migrate long distances have longer, larger wings (*Flockhart et al., 2017*), and the hind wings of migrating and nonmigrating dragonflies differ in shape and size (*Johansson, Söderquist & Bokma, 2009*; *Sacchi & Hardersen, 2013*). Furthermore, insects have two types of flight muscles: synchronous and asynchronous. Synchronous flight muscles respond directly to individual nerve inputs in a 1:1 ratio. Conversely, contractions in asynchronous flight muscles do not correspond directly to nerve inputs which are possessed by many bees, wasps, beetles, flies, true bugs and most flying insects (*Dudley, 1991*). Asynchronous flight muscles probably allow for high-frequency movements at a lower energy expenditure.

One common way to detect and monitor insects in flight is by observing wing-beat frequency, which is a proxy for the speed of insect wing beats. Wing-beat frequency can range from 10 to 1,000 Hz and is generally inversely proportional to the size of the insect. Wing-beat frequency is influenced by environmental conditions such as temperature and humidity (*Parmezan et al., 2021*), both of which can be locally altered by wind turbines.

In birds, flight types (*e.g.*, hovering, soaring, flapping) may influence which species are more likely to collide with turbines (*Balmori-de la Puente & Balmori, 2023*). When birds are flying to forage or mate (*i.e.*, active soaring, hovering, and song-flights) they may not perceive threats such as turbines resulting in a higher collision risk. Similarly, insects use a variety of flight types, which may put specific taxa at higher risk. The probability of insects interacting with turbines is higher during hilltopping, swarming, and migration flights (*Voigt, 2021*).

Hilltops are an aggregation site for hundreds of insect species and more insects may use hills with a highly visible landmark, such as a wind turbine. Hilltopping is a flight behavior where males and virgin females seek higher ground to find mates. The behavior is innate in species and individuals travel hundreds of meters (both horizontal and vertical) to reach summits. Hilltopping has been observed in Diptera, Hymenoptera, and Lepidoptera (*Skevington, 2008*). Hilltops are preferable sites for turbines because of their position above topography that naturally disrupts wind speeds.

Swarming usually occurs along with mating or migration. Like hilltopping, mating insects aggregate as a swarm at a marker. Swarms of males either wait for females to arrive or move to sites where females are emerging or feeding. Swarming behavior is enhanced by the spread of pheromones, which may be affected by turbine wake depending on the insects' position around turbines (*e.g.*, upwind or downwind). Migrating swarms are often larger than mating swarms and move together to find shelter and food. One common example is honey bee swarms that form when one colony splits into two, and a proportion of workers follow a queen to a new nest site (*Dublon & Sumpter, 2014*).

Migrating insects may be the most vulnerable to turbines collisions, because insect flight evolved to travel at higher altitudes and across long distances. Insects are inherently at risk when they migrate, exposing themselves to predation or poor weather conditions; however, species that migrate benefit from accessible resources, more persistent genetic lineages, and relief from parasites (*Roff & Fairbairn, 2007*). Various taxa can migrate using thermal drafts and wind currents above their flight boundary layer, and microinsects (insects <2 mm long) predominate daytime wind-borne migrants (*Gatehouse, 1997*).

Many taxa use wind currents above the insect flight boundary layer to migrate long distances during the day, night or both, depending on the species (*Chapman, Drake & Reynolds, 2011*). Daytime fliers use updrafts in the convective boundary layer while nocturnal migrants use the more stable nocturnal boundary layer to transverse up to hundreds of kilometers. These flight behaviors are influenced by seasonality and weather patterns; for example, migratory moths use winds that follow cold fronts (*Krauel, Westbrook & McCracken, 2015*). Nocturnal migrants can be limited by air temperature in different climates, forcing them into specific altitudes where the air is warmest and suitable for flight. Migrating moths can choose their flight altitude and often fly at higher altitudes where the wind is fastest to maximize their displacement (*Chapman, Drake & Reynolds, 2011*). Many insects fly in the evening when turbines have the largest influence on the ABL. Therefore, the flight of insects downwind of turbines may experience increased turbulence and temperature mixing within the ABL.

Vision

The way that insects visually perceive turbines may play a prominent role in their attraction to them (Table 1); however, not all insects distinguish objects the same way. For example, most adult insects have compound eyes, but their structure differs among taxa. Compound eyes are composed of ommatidia, tapered, hexagonal units that include photoreceptor cells, pigment cells, axons, a corneal lens, and more (Fig. 8A). Light is focused through the lenses of individual ommatidia, which each provide a small part of the larger field of view that is compiled by the central nervous system. Most insects, even those with a relatively small number of ommatidia, have a nearly panoramic field of view thanks to their eye curvature (Figs. 8B, 8C). Some insects have zones within a compound eye where differences in structure increase acuity or sensitivity to aid flying, hunting, and mating (*Land, 1997*). For example, the dorsal half of a dragonfly's eye has larger facets and smaller inter-ommatidial angles enabling them to track small flying prey against the sky (*Olberg et al., 2007*). Eye adaptations can be sexually dimorphic; many male Diptera have regions of heightened acuity to find and pursue females. Greater visual acuity in psyllids (Hemiptera) may be correlated with higher mobility including frequent movements among microhabitats (*Farnier et al., 2015*).

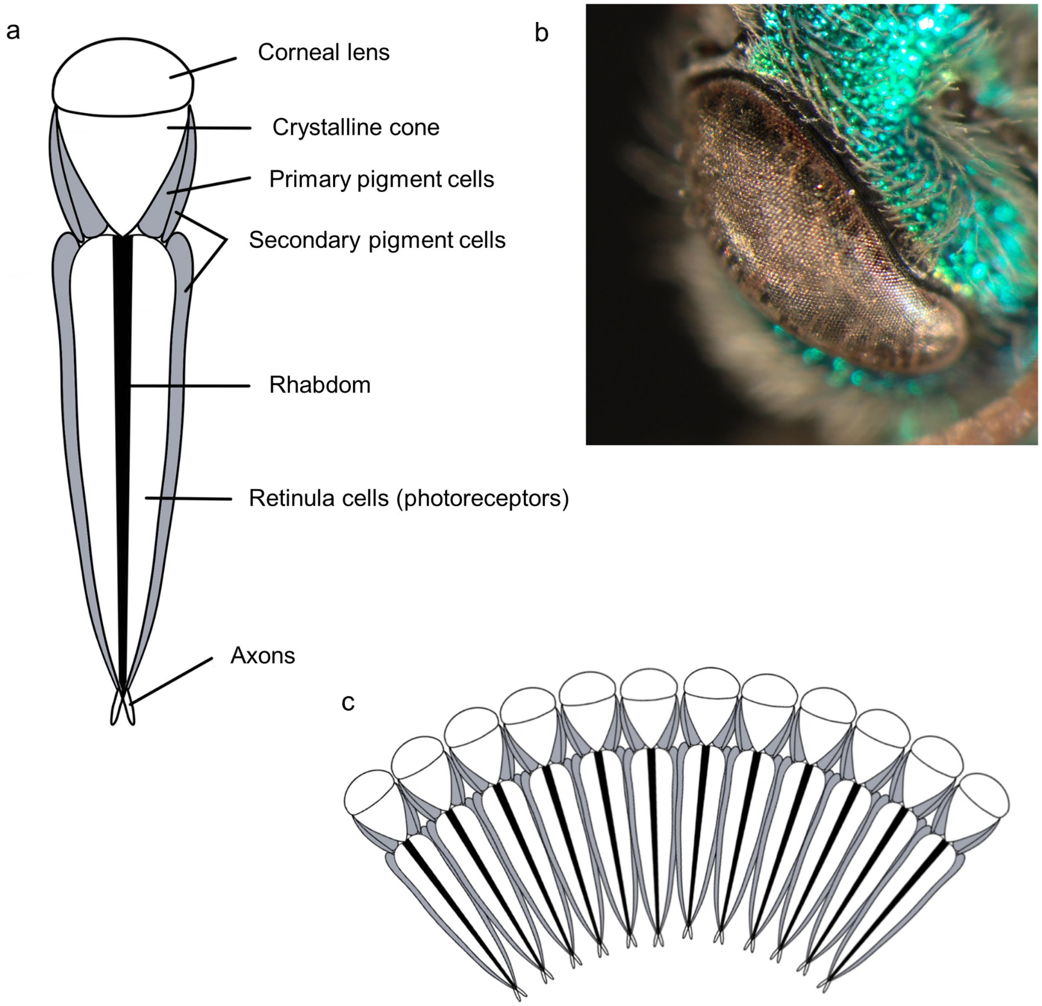

Figure 8 **Ommatidia make up the compound eye of an insect.** The structure of an (A) individual ommatidia in the compound eye, (B) a close-up image of the compound eye of a bee, and (C) many ommatidia fitting together to make up part of a compound eye. Photo credit: Michelle Weschler. Graphics credit: Michelle Weschler *via* Sketchbook. Full-size DOI: 10.7717/peerj.18153/fig-8

The way rods and cones absorb and convert light waves varies among insects. Apposition eyes isolate and dim light coming into each ommatidia with layers of pigment cells, while optical superposition eyes allow light from neighboring lenses to hit individual rhabdoms (*i.e.*, rod-like structures that receive and transfer light to the brain). Optical superposition eyes generally trade resolution for dramatically increased sensitivity to light, which is why they are commonly found on nocturnal moths and beetles (Table 2). Nocturnal and crepuscular insects with superposition eyes have lower visual and spatial acuity making them more vulnerable to turbine collisions because they must be relatively close to objects before they are resolved (*Stöckl et al., 2017*). Furthermore, birds may collide with turbines due to visual blurring of moving blades (*May et al., 2020*). Insects, even those with high visual acuity, experience strong motion blur when moving at high speeds. Insects often rely on mechanosensation with their antennae to avoid obstacles

Table 2 Morphological characteristics of the compound eye in well-studied insect orders with flying species.

Order	Apposition (A) or Superposition (S)	# of ommatidia per eye	Interommatidial angles	Color vision	# of photoreceptor types
Lepidoptera	A and S (mostly nocturnal)	5,000–17,000	0.9–3	Trichromatic and tetrachromatic	3–15
Diptera	S	600–6,400	0.6–5.8	–	5
Odonata	A	<30,000	0.24–1.2	Trichromatic	4–5
Hymenoptera	A	40 (some ant workers)–5,500 (honey bee workers)	0.41–4	Mostly Trichromatic	2–4
Orthoptera	A	510	0.9	Trichromatic	3
Coleoptera	S and A	40–1,380	1.5–7	Trichromatic	2–4
Neuroptera	S	600	1.4–2.4	–	2
Hemiptera	A and S (homopteran)	820	1.65–2.1	Trichromatic	3

Note:
Ranges are given for orders where data for multiple species exists. Sections where evidence is lacking or unclear are denoted with "-" (*Anastasia, Meyer-Rochow & Alexey, 2019*; *Dander & Jander, 1994*; *Giglio et al., 2022*; *Hao et al., 2023*; *Labhart & Nilsson, 1995*; *Stukenberg & Poehling, 2019*; *Taylor, 1981*; *Yang, Lin & Wu, 1998*).

(*Zurek & Gilbert, 2014*); however, insects touching a spinning turbine blade with their antennae are in the process of colliding with blades.

Many adult flying insects have three simple eyes known as ocelli that occur at the top of the head in addition to compound eyes. Ocelli have large fields of vision and are very sensitive to changes in light. Ocelli produce images that are blurry and low-resolution, although some insects such as dragonflies can focus their median ocellus. Ocelli are thought to help insects orient and stabilize themselves during flight, specifically to assess their position relative to the horizon (*Stange & Howard, 1979*). Wind turbines could affect this functionality by casting shadows, reflecting light due to their coloration, and altering the appearance of the horizon.

Color

Insects use color vision for phototaxis, navigation, detecting shelters, identifying landmarks, finding resources, spotting breeding sites, selecting mates, and more (*van der Kooi et al., 2021*). Most studied insects have trichromatic vision, meaning they have photoreceptors that are sensitive to three colors. While humans are sensitive to green, blue, and red, trichromatic insects are sensitive to green, blue, and UV wavelengths which has significant implications for how insects perceive color. For example, trichromatic insects can see UV patterns on flowers that are invisible to the human eye (*Silberglied, 1979*).

Color and reflectance likely influence an insect's decisions to visit wind facilities. Insects respond to the reflectivity of specific colors (*Crawford et al., 2023a*). Bees and other flying insects are attracted to colors with higher reflectance within a preferred range of wavelengths (*Acharya et al., 2022*, *2021*; *Vrdoljak & Samways, 2012*). Two colors commonly used to paint turbines ('Pure White' and 'Light Grey' from Reichs-Ausschuss für Lieferbedingungen; RAL) are more attractive to insects than other color options (*Long, Flint & Lepper, 2010*). When the effect of coloration was studied using turbine mimics, green and dark grey attracted the fewest insects, while white attracted the most

(*Crawford et al., 2023a*). White is highly reflective at all wavelengths, visible to a diversity of insects with differing color vision, and a common flower color. Most turbines in the world are painted white to better blend into the sky, remain visible to aircraft during the day, and gain less heat from solar radiation (*Long, Flint & Lepper, 2010*).

Some insects orient towards or swarm around highly contrasting vertical structures such as trees and buildings (*Kriska et al., 2008*; *Seelig & Jayaraman, 2013*). Similarly, insects swarm around the nacelles of turbines directly behind the spinning blades (*Jansson et al., 2020*). These structures may be markers for some insects, highly visible spots that swarming insects can use to congregate (*Savolanien, 1978*). Therefore, white, or light grey turbine towers may contrast against the landscape and act as markers for insects to orient toward and gather. This behavior likely leads to collisions because of the large diameter of turbine rotors. More investigations are needed to estimate the degree to which insects gather at turbines and if painting turbine towers a different color than white or grey would reduce insect abundance around them.

Light

Artificial light and light pollution have known influences on insect behavior and are hypothesized to contribute to regional insect declines (*Owens et al., 2020*). Certain insect species exhibit positive phototactic behaviors (attraction to and subsequent movement towards light), while others may be repelled by different types of lighting. The most well-known example of phototaxis in insects is nocturnal moths. The wavelength, intensity, and length of exposure to artificial lights may impact how individual species react in the presence of light. For example, higher intensity, longer exposure, and shorter wavelengths generally attract more insects (*Gullan & Cranston, 2014*; *Martin, Perez & Ferrer, 2021*).

Some castes of the ant, *Lasius niger*, were sensitive to red light and changed their aggregation behavior under its influence despite previous literature suggesting red light was invisible to certain Hymenoptera (*Depickere, Fresneau & Deneubourg, 2004*). Therefore, insects presumed unable to perceive red wavelengths may be influenced by red light. While red light-emitting diodes (LEDs), the market standard for obstruction lighting, attract fewer insects than incandescent lighting at low wattages (*Justice & Justice, 2016*), some species have specific attraction to red LED lights (*e.g.*, pest species of beetles and moths) (*Park & Lee, 2017*). In fact, recent research investigated LEDs for monitoring and trapping pests in agricultural settings (*Miyatake et al., 2016*; *Pan, Liang & Lu, 2021*; *Wee et al., 2021*; *Zhang et al., 2020*).

Ambient levels of artificial light alter positive phototaxis. Insects are more attracted to artificial sources of light in areas with less artificial light (*Hauptfleisch, 2015*). This could enhance the attractiveness of obstruction lighting to insects at wind facilities located in rural, undeveloped areas. Artificial turbine lighting could be uniquely attractive because turbines require open space and are usually located away from development; however, ADLS would mitigate effects by keeping obstruction lighting off most of the time.

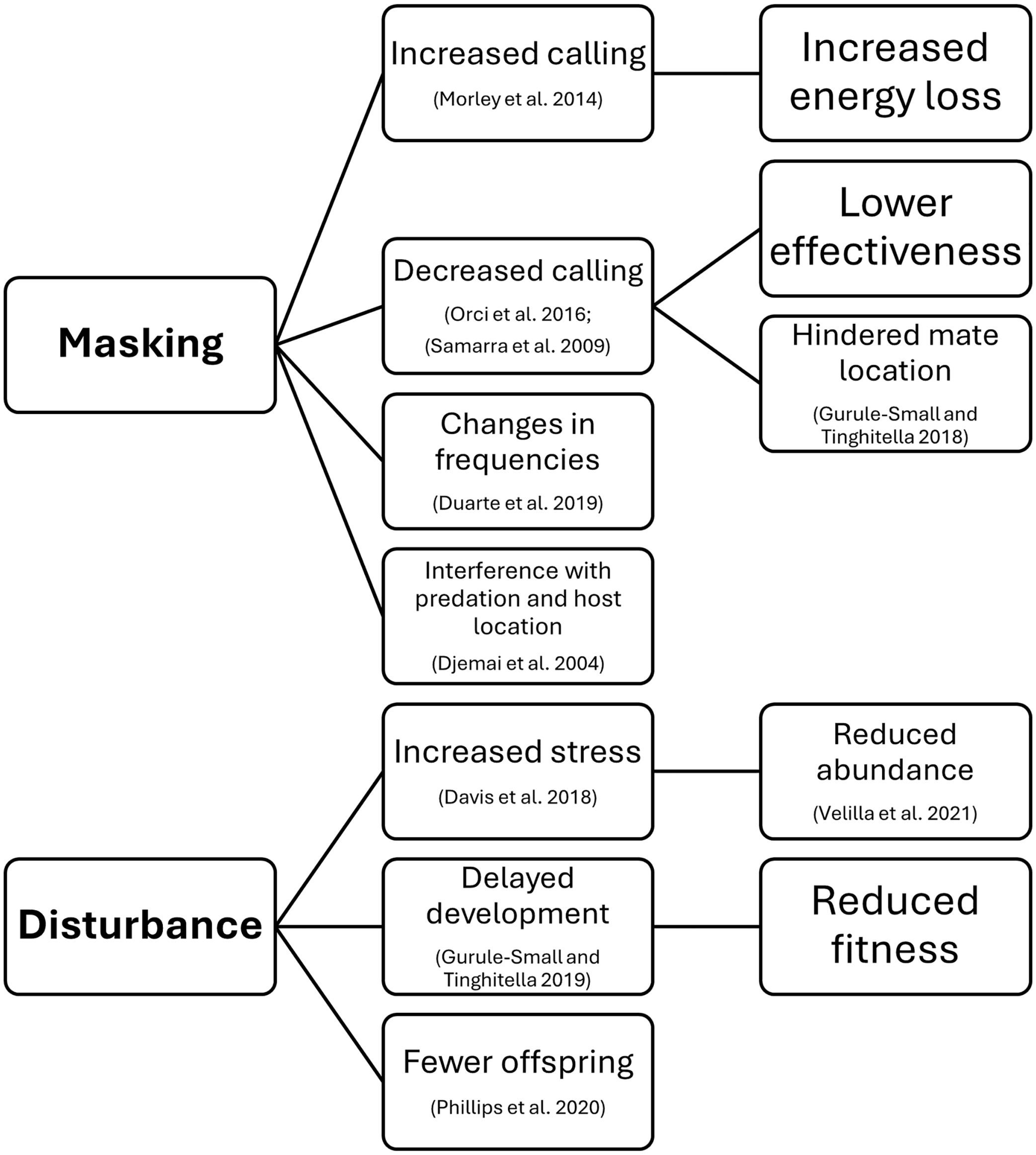

Figure 9 **Potential negative influences of anthropogenic noise on insect behavior and physiology.**
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Sound

Sound from turbines may influence insects in two major ways: by masking information-carrying noise such as calls, or by disturbing the environment and causing stress (Fig. 9; Table 1). Insects produce sound to avoid predation, locate and attract mates, and convey aggression (*Morley, Jones & Radford, 2014*) and anthropogenic noise pollution can interfere with insect communication. *Morley, Jones & Radford (2014)* highlighted the importance of evaluating the effects of anthropogenic noise on insects. Specifically, they suggest that many insects have a hearing range that overlaps in frequency with road traffic, a common source of anthropogenic noise pollution and, unlike humans, some insects (*e.g.*, Diptera and Hymenoptera) can sense the particle velocity of sound waves (*Morley, Jones &*

Radford, 2014). Some insects displayed shorter echemes (chirps with multiple syllables) and pauses in calls in areas with variable, sudden anthropogenic noise, such as traffic, which may conserve energy when calls risk of being masked (*Duarte et al., 2019*; *Orci, Petróczki & Barta, 2016*). *Gurule-Small & Tinghitella (2018)* found that exposure to anthropogenic noise during rearing hindered mate location in crickets, *Teleogryllus oceanicus*. How changes to calls may interfere with overall fitness is unknown.

Underground sound vibration may affect insects because many species burrow, overwinter, and raise brood in soil, but studying insects below the surface is difficult. *Velilla et al. (2021)* showed that earthworm abundance decreased as vibratory noise from turbines increased suggesting that soil invertebrates may not tolerate turbine infrasound. Substrate-vibration is a more ubiquitous and primitive form of insect communication used in a variety of ways by most insect orders. Like acoustic signaling, insect vibratory signals are used for mating and reproduction, predator avoidance, and group interactions (*Yack, 2016*). Insects receive information about their environment from inter- and intraspecies vibratory signals, and signals from abiotic factors, such as wind and rain (*Yack, 2016*). Furthermore, adults, larvae, and pupae can create and respond to vibrational signals (*Kojima, Takanashi & Ishikawa, 2012*). Insects can be negatively affected by anthropogenic noise and vibrations. For example, burying beetles, *Nicrophorus marginatus*, are sensitive to low-frequency seismic noises which lowered brood mass and offspring number upon exposure (*Phillips et al., 2020*). Insects that spend time underground during any life stage could experience communication masking or negative influences on fitness because of turbine vibrations. Effects on vibration signaling, brood development, or overwintering insects is an important knowledge gap in our understanding of turbine effects on insects.

Infrasound may alter the interactions between pollinators and plants. For example, subterranean vibrations altered self-pollination frequency in Plains Pricklypear, *Opuntia polyacantha*, likely decreasing their genetic diversity in and near wind energy facilities (*Crawford et al., 2023b*). Conversely, changes in plant communities downwind of turbines could change the abundance of insects, especially pollinating and herbivorous species. Protecting habitats and interactions between pollinators and plants is critical to maintaining genetic diversity in plant populations for the perpetuation of bees and butterflies and should be a main concern with regards to insect conservation efforts.

Risk assessment

Regal Fritillary butterflies are declining across their range in the U.S. after experiencing dramatic contractions in the eastern part of their range (*Debinskl & Kelly, 1998*; *Swengel & Swengel, 2016*; *Wagner et al., 1997*) and they are currently petitioned for federal protection under the U.S. Endangered Species Act (ESA). Our Regal Fritillary SDM model had good fit (AUC = 0.86). The model predicted that areas with suitable climate were affected by the mean precipitation of the warmest quarter (28.3%), mean temperature of the driest quarter (23.4%), growing degree days above 0 °C (16.7%), mean temperature of the coldest quarter (14.8%), mean temperature of the warmest quarter (6.3%), isothermality (4.8%), mean temperature of the wettest quarter (2.5%), precipitation seasonality (2%), mean diurnal

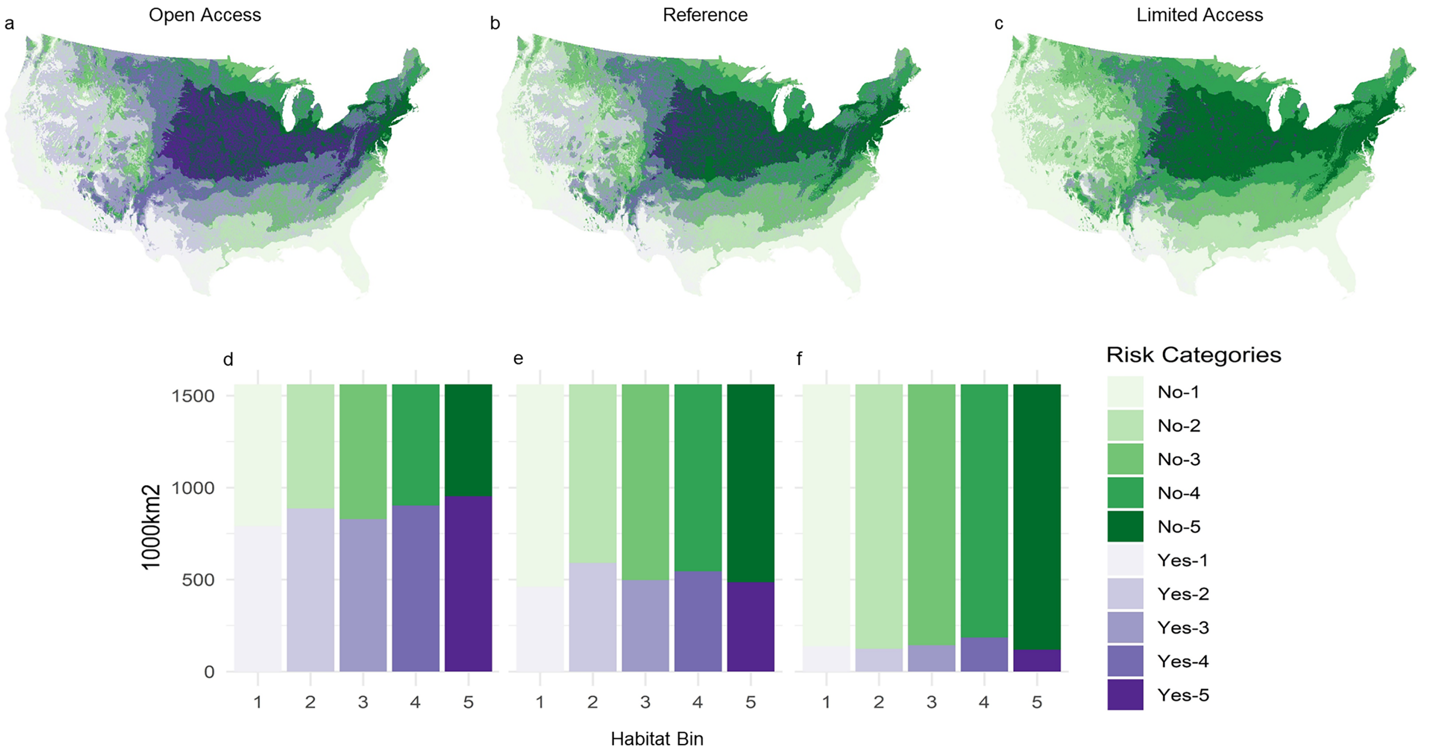

Figure 10 The overlap of potential wind development with suitable climate for the Regal Fritillary butterfly. Overlaps between Regal Fritillary climate and wind development are shown in purple for the (A) open access scenario, (B) reference scenario and (C) limited access scenario while areas of no overlap are shown in green. The darkest shades represent the most suitable climate. Histograms show the amount of land in units of 1,000 km^2 that has the potential for wind energy development in the (D) open access scenario, (E) reference scenario and (F) limited access scenario in purple. Green represents area that is not at risk to be developed within each scenario. See linked online supplemental dataset. Map shapefile source: U.S. Census Bureau.

Full-size DOI: 10.7717/peerj.18153/fig-10

temperature range (0.7%) and temperature seasonality (0.4%). Our model predicted suitable climate mostly in the midwestern and northeastern U.S.

The Dakota Skipper butterfly was listed as threatened under the ESA in 2014, and the U. S. Fish and Wildlife Service finalized a recovery plan to conserve the species' native prairie habitat (*U.S. Fish and Wildlife Service, 2021*). The Dakota Skipper SDM model fit well (AUC = 0.97). The model predicted that areas with suitable climate were affected by temperature seasonality (71.7%), mean temperature of the driest quarter (16.1%), precipitation seasonality (5.6%), isothermality (3.4%) and mean precipitation amount of the driest quarter (3.2%). Our model suggested that the most suitable climate is in the north central part of the U.S., centered on North and South Dakota.

Our assessment for Regal Fritillaries showed that the risk of wind development to areas with suitable climate varied greatly depending on the level of restriction used for potential wind energy development. The limited access regime, the most restrictive, indicated ~120,000 km^2 (~1.5% of the potential range according to our model) with the most suitable climate for Regal Fritillaries in the U.S may be developed for wind energy (see c and f et Fig. 10). In the least restrictive, open access scenario, ~950,000 km^2 (~12.2%) of their most suitable climate may be developed (see a and d et Fig. 10). The reference

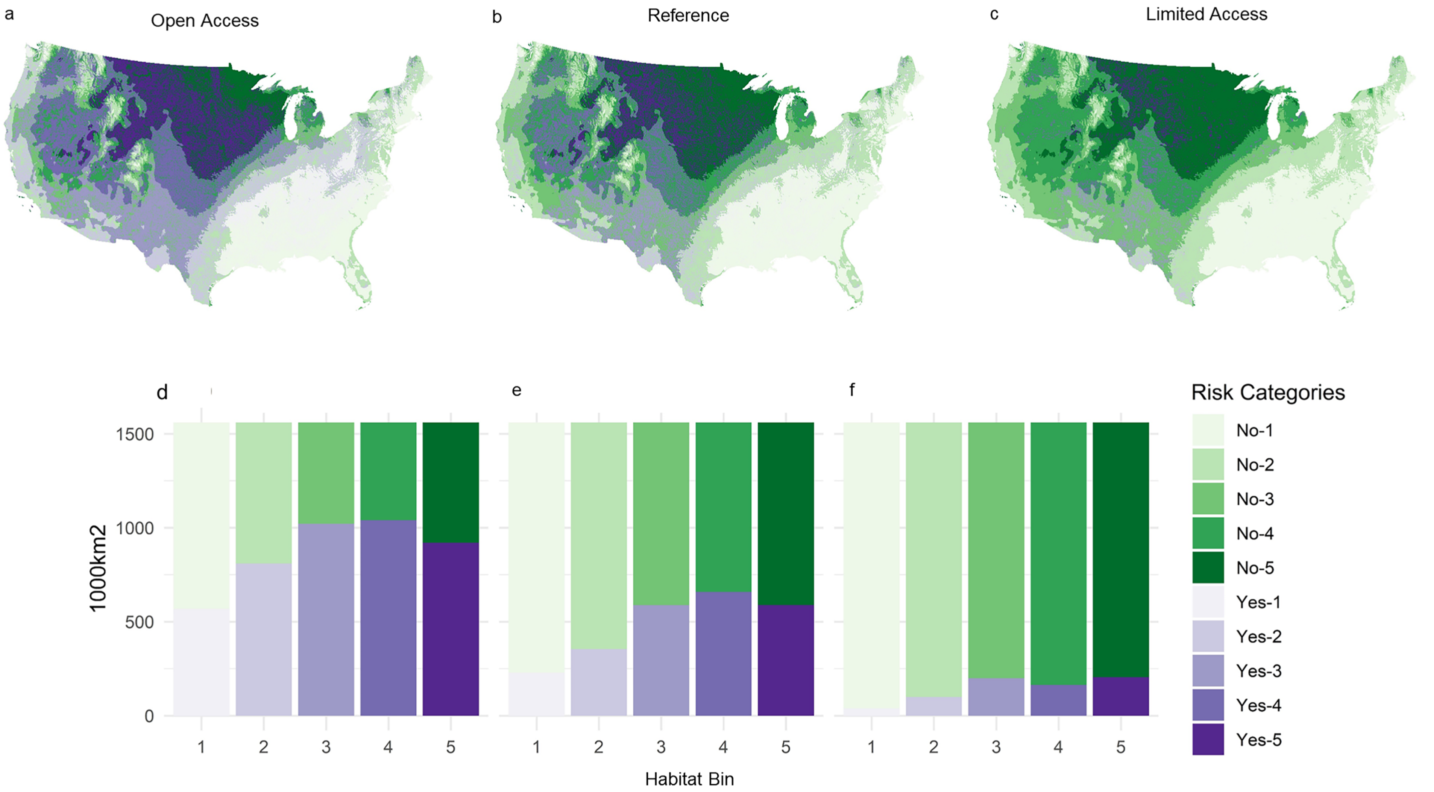

Figure 11 **The overlap of potential wind development with suitable climate for the Dakota Skipper butterfly.** Overlaps between Dakota Skipper climate and wind development are shown in purple for the (A) open access scenario, (B) reference scenario and (C) limited access scenario while areas of no overlap are shown in green. The darkest shades represent the most suitable climate. Histograms show the amount of land in units of 1,000 km^2 that has the potential for wind energy development in the (D) open access scenario, (E) reference scenario and (F) limited access scenario in purple. Green represents area that is not at risk to be developed within each scenario. See linked online supplemental dataset. Map shapefile source: U.S. Census Bureau.

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scenario, which is based on common management practices, predicts ~440,000 km^2 (~5.6%) of their suitable climate is at risk (see b and e et Fig. 10).

The risk of wind development in areas with suitable climate for Dakota Skippers varied among development scenarios. The limited access scenario indicated ~200,000 km^2 (~2.6% of the modeled range) with the most suitable climate is at risk (see c and f et Fig. 11). The at-risk areas with suitable climate in the open access scenario (~920,000 km^2; ~11.8%; see a and d et Fig. 11) were larger than the reference scenario (~590,000 km^2; ~7.5%; see b and e et Fig. 11).

The area identified as the most suitable climate for the Regal Fritillary and Dakota Skipper that overlaps with areas predicted to be developed for wind energy is relatively low for the most restrictive scenarios but increases drastically with less regulated siting. Furthermore, the inclusion of land cover data into the models could show significant increases in risk to suitable areas. Successful recovery and protection of these species will hinge on efficient conservation and management of key native habitats. These models may be a tool for facilitating this conservation moving forward.

Mitigation

Some negative effects of wind energy development on wildlife can be avoided or reduced through mitigation strategies. Mitigation for wind energy can range from avoiding areas with sensitive species, establishing physical barriers and installing deterring devices to removing particularly hazardous turbines. The main goal of mitigation thus far is reducing vertebrate (particularly bat and raptor) collisions with turbines by reducing attraction. Mitigation strategies can be implemented throughout the planning, construction, and life cycle of wind turbines. Several strategies are effective at reducing the mortality of specific taxa, promoting ongoing advocacy for widespread implementation (*Gartman et al., 2016*; *Voigt et al., 2022*). Some strategies could be investigated for preventing insect attraction and mortality.

Operational curtailment is the practice of stopping turbines from operating under specific conditions. Curtailment can be used for individual turbines or sections of a facility that pose a higher risk to wildlife. Curtailment is used during specific weather conditions, or times of the day or year that correlate with peak bat or bird activity or migration. Bat mortality decreases sharply when operational curtailment is practiced. Curtailment strategies may improve using algorithms that account for landscape features, weather, seasonality, and wind turbine function (*Barré et al., 2023*). Because bats often feed near turbines, the conditions that lead to algorithmic curtailment could include many of the same environmental conditions that affect insect presence near turbines. Seasonal curtailment along migration paths could prevent collisions of insect species that migrate at high altitudes, such as the Monarch butterfly, *Danaus plexippus*, (*Reppert & De Roode, 2018*) and noctuid moths like the adult army cutworm, *Euxoa auxiliaris* (*Hendricks, 1998*).

Facilities can alter their cut-in speed, the wind speed at which blades begin to turn, which reduced bat collisions (*Bennett et al., 2022*; *Good et al., 2022*; *Smallwood & Bell, 2020*; *Voigt et al., 2022*) and may conserve flying insects that are most abundant at low wind speeds. Bat mortality can be reduced by 50% when cut-in speeds are raised 1.5–3.0 m/s (*Arnett et al., 2011*). Net production of wind energy is low at these wind speeds, so company losses when employing this mitigation technique should be minimal.

Finally, painting turbine blades or towers can provide visual contrast that helps birds avoid collisions and potentially insects too. Painting a single blade black to reduce motion smear, and painting the bottom of towers green reduced bird mortality (*Dürr, 2011*; *May et al., 2020*). This mitigation technique may reduce insect attraction based on the studies that investigated insect attraction to turbine color (*Long, Flint & Lepper, 2010*) and turbine mimics (*Crawford et al., 2023a*).

DISCUSSION

In 2021, the average wind speed at sites of new wind projects in the U.S. was lower than the previous 8 years (*Wiser et al., 2022*). The trend of development in areas with lower wind speeds could potentially increase turbine-insect interactions because wind speed and flying insect abundance are usually inversely related. Unless cut-in speeds are managed and operational curtailment is an option, we can expect an increase in insect fatalities at wind facilities. Siting, particularly micrositing, is considered for vertebrate conservation

(*Schuster, Bulling & Koppel, 2015*), but we do not understand how micrositing could affect insect populations or influence habitat selection and use. For example, insects can be most abundant at mid-slopes or ridges depending on the site (*DePaolo, 2015*) and such information could help with siting decisions. The long-term trend of taller turbines with larger rotors will change the effect of wind energy on insects. Rotors occupying more space in the ABL will increase potential interactions with high-flying insects; however, the increased efficiency of those rotors may reduce the total number of turbines necessary to reach energy goals. Additionally, turbines are recycled or disposed of at the end of their life cycle, and we know little about how that may affect the habitats of insects and other wildlife.

Information about insects at wind facilities is limited. For example, 0.1% of publications in the Pacific Northwest National Laboratory's database on wind energy (*i.e.*, Tethys Knowledge Base) investigated invertebrate interactions with land-based wind energy. We lack information about how wind energy facilities can be sited and managed to conserve insects (*U.S. Fish and Wildlife Service, 2012*); a review of wind energy impacts on wildlife included insects only as attractive forage for birds and bats around turbines (*Schuster, Bulling & Koppel, 2015*). Ultimately, the lack of data on insect interactions with turbines matches the general lack of data on the life history of many insect species. Indeed, one of the few studies investigating turbine effects on specific species focused on the well-studied honey bee, *Apis mellifera*, and found no significant impact on colony health (*Fourrier et al., 2023*). Most insect orders exhibit wide variation in behavior and morphology based on their life histories, from predator avoidance (*Denno et al., 2002*) to flight morphology (*Tercel, Veronesi & Pope, 2018*). Therefore, investigating specific families, genera, and species is necessary to fill this knowledge gap. The literature exhibits shifting techniques for monitoring and assessing species diversity, density, and distribution, making conclusions more difficult. There is a need for consistent and standardized monitoring to assess the risk of energy development to specific species and groups of insects based on the variety of aerial sampling techniques. A combination of methods deployed in tandem will be necessary to ascertain data for the conservation of diverse insect species.

Our case study results suggest wind facilities and the surrounding, undeveloped habitat have an equal abundance of bees and richness of bee genera, regardless of distance from turbines. Our wind facility site also had a similar assemblage of bees compared to other sites. Finally, we did not find a difference in richness or abundance of bees based on relative position to turbines within a wind facility. These results could indicate adult bees are less influenced by turbines than other taxa, and that they are not deterred by the presence of turbines. Because it is difficult to keep conditions consistent over the distance that downwind effects may be present, interpretation from our results is limited. Our case study is one basic example of how insects at wind facilities may be investigated, and these methods could be used in conjunction with other studies. Ultimately, we recommend insect sampling techniques that capture a wider variety of taxa, monitoring over several years, and using models that take more habitat information into account for more accurate, actionable results.

We can begin to broadly assess which insect groups may be most vulnerable to colliding with turbines by considering the physiology of specific insect taxa along with their responses to abiotic factors (Table S1). We included orders that have been found in the air at or above turbine height or in the stomach contents of bats killed at turbines. We compiled literature about how species within each order respond to changes in their abiotic environment such as heat, wind, noise, and light. We also evaluated flight behaviors. Based on this information, we suggest insects in the orders Lepidoptera, Coleoptera, Diptera and Hemiptera may be the most vulnerable to colliding with turbine blades. These orders exhibit high-altitude flight through migration, swarming, or hilltopping. Furthermore, these groups thermoregulate by basking, and some hemipterans and dipterans are acutely heat sensitive, attracting them to turbine towers. The families Noctuidae and Nymphalidae (Leidoptera) are of particular concern because of their high-altitude migrations that use wind as a means of dispersal and often include large numbers of individuals (*Hendricks, 1998*; *Krauel, Westbrook & McCracken, 2015*; *Lingren et al., 1995*; *Rydell et al., 2010*). Coccinellidae (Coleoptera) species have been observed on turbines and engage in wind-mediated high-altitude migration (*Dudek, Dudek & Tryjanowski, 2015*; *Jeffries et al., 2013*). Tabanidae (Diptera) flies are particularly heat sensitive, may be attracted to the color white, and may rest on turbines and swarm near the blades (*Crawford et al., 2023a*; *Jansson et al., 2020*; *Rydell et al., 2016*; *Thorsteinson, 1958*). These observations serve as a baseline for what orders may be most at risk within wind energy facilities. Notably, these insect orders contain pollinating species. For example, moths (Lepidoptera) are a main contributor to nocturnal pollination (*Anderson, Rotheray & Mathews, 2023*). Hoverflies (Diptera), though often left out of discussions about pollination, are frequent flower visitors, efficient crop pollinators and pest predators (*Li, Wyckhuys & Wu, 2023*; *Rader et al., 2016*; *Sánchez et al., 2022*). Ladybugs (Coleoptera) visit and pollinate a wide variety of crops (*Rader et al., 2016*). Big-eyed bugs (Hemiptera) inadvertently pollinate while predating on thrips (*Kondo et al., 2016*). Monitoring and conserving specific species will need to occur on a case-by-case basis based on location, local insect populations, and environmental variables.

Species of special concern such as Monarch butterflies may be especially vulnerable to turbines. They migrate at high altitudes through the central U.S., which has the highest potential for current and future development of wind energy (*Reppert & De Roode, 2018*). Temporary turbine shutdowns have been proposed during periods of high bat activity or avian migration (*Smallwood & Bell, 2020*) and a similar strategy could be used for Monarchs. Many insects that migrate at high altitudes do so at specific times of day or on a seasonal basis, making temporary shutdowns an option for insect conservation. Considering how renewable energy impacts insect survival is critical as more insects are being petitioned for federal protection and listed under the U.S. Endangered Species Act. Additionally, invasive and destructive insect species can be attracted to turbines and use them as refuge. Disturbed or highly modified areas (*e.g.*, re-seeded habitat around turbines) could be vulnerable to invasive species, which merits additional investigation, especially when turbines are sited near agricultural lands.

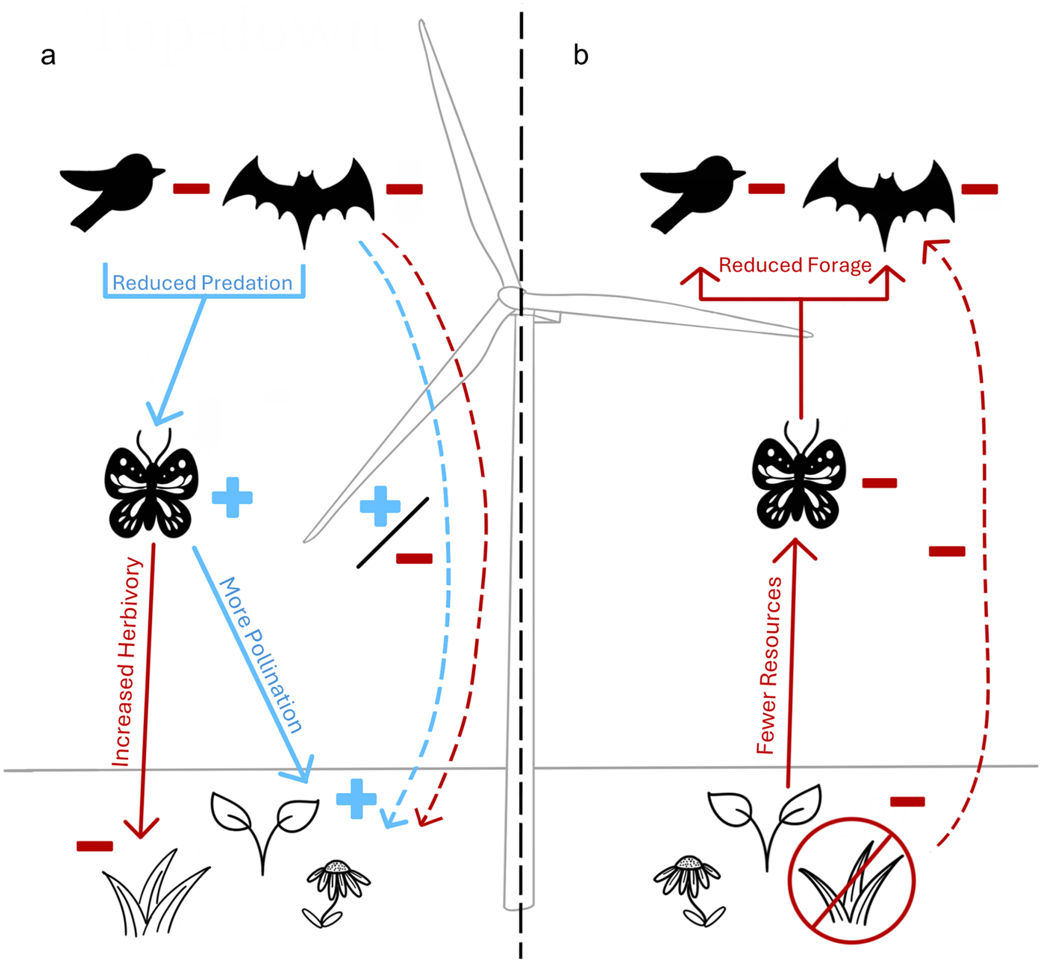

Figure 12 **Turbines may cause understudied trophic cascades.** (A) Top-down and (B) bottom-up trophic cascades influenced by wind turbine presence and operation showing both direct (solid line) and indirect (dashed line) effects. Negative influences are shown in red; positive interactions are shown in blue. Graphic credit: Michelle Weschler *via* Sketchbook. Full-size DOI: 10.7717/peerj.18153/fig-12

Considerable efforts to understand and reduce the effects of wind energy facilities on vertebrate species, especially raptors and bats, have occurred (*Schuster, Bulling & Koppel, 2015*); however, insects remain largely unstudied. Operational curtailment, color changes, and acoustic deterrents may reduce turbine-related avian and bat fatalities (*Arnett et al., 2013*; *May et al., 2020*; *Smallwood & Bell, 2020*; *Stokke et al., 2020*). These mitigation strategies could reduce effects to insects. Other changes that could benefit insects include cultivating host plant species and reducing herbicide use in wind facilities (*Pustkowiak et al., 2018*). Furthermore, our risk assessments suggest that large swaths of area with suitable climate for insects of concern could be developed for wind energy. These SDM-based risk assessments could be refined and used to make siting decisions nationally or at smaller scales based on specific species of concern.

Turbine presence and operation may influence insect populations indirectly through top-down and bottom-up trophic effects (Fig. 12). Bat species that are vulnerable to turbine collisions in North America and Europe frequently consume pest insects and insects from a wide variety of habitats (*Scholz & Voigt, 2022*), showing potential impacts to food webs and ecosystems beyond where turbines are sited. Passerines (songbirds) composed >50% of the avian deaths due to collisions with turbines (*Erickson et al., 2014*) and most passerines are insectivores. These birds consume ~400–500 million tons of insect prey annually (*Nyffeler, Şekercioğlu & Whelan, 2018*). Declines in pest-controlling bat and bird species can lead to arthropod outbreaks resulting in increased herbivory and crop damage (*Böhm, Wells & Kalko, 2011*; *Boyles et al., 2011*; *Hooks, Pandey & Johnson, 2003*; *Maas et al., 2016*). Some bat species exhibit an avoidance effect wherein habitat that is suitable around wind turbines is less attractive or not used (*Gaultier et al., 2023*) which may temporarily cause increases in insect populations due to fewer predators. Greater abundances and diversity of insect pollinators could benefit plant species in wind energy facilities, especially if they experience pollen limitation (*Castro et al., 2021*; *Gómez et al., 2010*).

Plant assemblages may be positively (*Xu et al., 2019*) or negatively (*Tang et al., 2017*) affected by disturbances caused by the construction of turbines and their operation (*Qin et al., 2022*). Surface temperature (*Walsh-Thomas et al., 2012*), precipitation, and soil moisture (*Wang, Li & Liu, 2023*) can be affected by operating turbines. These alterations in the abiotic environment likely influence plant-soil interactions such as nutrient cycling (*Armstrong et al., 2014*) and evapotranspiration. Lower diversities of rare, imperiled and endemic plants were observed in areas disturbed by wind power compared to areas without wind energy development (*Urziceanu et al., 2021*), and vegetation may be negatively affected by turbines. Plant diversity and abundance is foundational in food webs and is correlated with the abundance of terrestrial insects (*Scherber et al., 2010*). Beyond herbivory, insects use plant material to escape predators, avoid harsh environmental conditions, nest and raise offspring (*Gullan & Cranston, 2014*). Rare and endemic plants host a variety of insect species and increase insect diversity (*Hernández-Teixidor et al., 2020*). Robust plant-pollinator networks comprise both generalist and specialist interactions (*Taki & Kevan, 2007*), and loss of rare and endemic plants could result in the disappearance of those specialist interactions. In some insect communities, plant biomass and nutrition can influence top-down effects on a species. For example, suppression of planthoppers, *Prokelisia dolus* and *P. marginata*, by wolf spiders depended on plant nutrition and structure (*Denno et al., 2002*). How insect species respond to novel trophic effects initiated by wind energy is worth further investigation given their importance in food webs and ecosystem services.

Conserving insect abundance and diversity goes hand in hand with conserving habitats. Protected areas managed with insect conservation in mind are a “non-negotiable” according to *Samways (2018)*, but agro-ecological strategies that are insect-friendly can be important, such as wildflower margins and semi-natural habitat around agricultural land (*Grab et al., 2018*; *McCullough, Angelella & O’Rourke, 2021*). A single species of insect can require diverse resources that may span multiple habitats (*Knight et al., 2005*); thus, understanding insect habitat selection and needs is an essential element for conservation. Further investigations into turbine effects on surrounding landscapes, vegetation, and habitat will be crucial in forming effective management and siting strategies.

Lingering questions remain regarding how turbines affect population dynamics and habitat use of wildlife on a broad scale. The key role that insects play in agricultural ecosystems globally and trophic interactions points to a growing need for entomological research that is robust and targets a diverse array of species. Loss of insects due to wind energy is inevitable; however, mitigation may minimize loss. Ultimately, the threats to insect biodiversity due to climate change likely outweigh those presented by wind energy development. Higher temperatures projected over the next decades in conjunction with other anthropogenic change may increase extinction risk for ectotherms globally (*Duffy, Gouhier & Ganguly, 2022*; *Thomas et al., 2004*). Pollinators may be at risk due to the increased frequency and intensity of weather phenomena such as heatwaves and drought caused by climate change (*Halsch et al., 2021*; *Melone, Stuligross & Williams, 2024*). For example, warm winter temperatures decrease the weight of and prompt earlier emergence for some wild bees (*Fründ, Zieger & Tscharntke, 2013*). Bumble bees in North America and Europe risk extirpation in areas where climate anomalies fall outside species' tolerance levels (*Soroye, Newbold & Kerr, 2020*). Finally, pollinator abundance is lower in cropland with temperature anomalies than natural habitats without temperature increases, suggesting an important intersection between climate change and land use (*Millard et al., 2023*, *Outhwaite, McCann & Newbold, 2022*). While some species show resiliency and adaptability by expanding their range, climate change is driving population-level changes (*Martay et al., 2017*). The renewable energy sector demonstrated the ability to adapt and mitigate harm to vertebrate wildlife; the same can be done for insects. The impacts of renewable energy development and production will grow and compound as countries across the globe strive to reduce their dependence on finite energy resources. Accessible and globally diverse sources of data on lower trophic levels are necessary to assess these impacts to advance energy technology in a truly sustainable direction.

KNOWLEDGE GAPS

Gaps in our understanding of insect interactions with turbines outnumber what we know; however, we suggest prioritizing a few topics for future research. The most critical gap is that we do not know which taxa are killed by wind turbines or in what numbers besides total insect biomass estimates in a single country (*Trieb, Gerz & Geiger, 2018*). We have used information on insect physiology and behavior to identify which orders and families may be most vulnerable; however, there may be high variability even within these taxa (*e.g.*, at the genus or species level). Furthermore, abiotic conditions vary among wind energy facilities and investigations on a finer scale are necessary to accurately evaluate the risk to specific taxa. Analysis of insect debris on turbine blades at facilities using eDNA metabarcoding may be a good place to start (*Voigt, 2021*).

Basic knowledge about the effects of wind turbines on insects remains uninvestigated. Nothing is known about the availability or quality of insect nesting sites within wind energy facilities. Pesticides and herbicides are used to maintain graveled areas around turbines which could pose further risk to insects (*Pustkowiak et al., 2018*). No information has been published about how wind energy influences immature insects (*e.g.*, vibrations affecting developing insects in soil). Understanding how turbines influence insect survival at immature stages is critical to form and prioritize conservation strategies. Investigating microclimates and microhabitats on a fine scale, such as vegetation and soil temperatures, could fill gaps. Linking insect fatalities at turbines to potential influences on source populations is also necessary to fully understand if wind energy acts as a biodiversity sink, through insect fatalities or through the loss of higher trophic levels such as insectivorous bats and birds.

Mitigation strategies for insects interacting with turbines have not been investigated. Including insect monitoring in current and future studies of proposed wind development and mitigation techniques for bats and birds could be an effective way to evaluate methods for reducing insect fatalities and serve as a jumping-off point for insect-specific mitigation techniques. Investigating the mitigation of insect fatalities could provide data on reducing blade-soiling and potentially reduce overall maintenance needs of turbines. The creation of regional models that pinpoint temperatures, wind speeds, and times of year flying insects are active could be useful when planning curtailment strategies.

Most studies investigating wildlife and wind turbines come from North America and Europe. China, which has the highest cumulative and annual capacity additions of wind power in the world (*Wiser et al., 2022*), lacks much published research into wildlife interactions with turbines. As the U.S. and many other countries aim for more dependence on wind energy, information about effects on wildlife in a country with 3-times the operational capacity of any other would help guide management strategies. Furthermore, insect diversity, ecology and conservation strategies vary across continents. Learning differences and similarities among continents concerning wind energy effects on invertebrate wildlife is critical as wind energy grows globally.

CONCLUSIONS

Despite a lack of data on most insect interactions with wind facilities, our review revealed future avenues of research and knowledge gaps. Wind turbines kill insects in large numbers, especially in temperate zones. Turbines do not kill insects merely by obstructing their flightpaths, but likely by being attractive to insects' visual and thermal senses (Table 1). Insects may be most vulnerable to striking turbines during key parts of their life cycles, such as migration and mating. Turbines likely affect insects by altering aspects of the abiotic and biotic environment around them, such as temperature and plant diversity. Furthermore, insect attraction to and loss due to turbines may negatively influence vertebrate communities.

Scientists have been sounding the alarm on insect declines due to shifts in land use and how they will be exacerbated by climate change; however, insects are a novel afterthought in discussions of conservation issues related to infrastructure for wind energy. *Donkersley et al. (2022)* suggested that shifts in public perception and political protection of insects is needed to address meaningful changes to biodiversity loss. Recently, the role of insect pollinators became more widely understood, but non-native, managed honeybees tend to be the focus (*Donkersley et al., 2022*). Entomologists need to engage with the public about the variety of ecosystem services insects provide, and the threats to insect biodiversity and conservation that exist. Engaging with governments on these issues is equally vital. An uneven political approach to insect conservation is apparent, especially in the U.S. where several states do not include insects in their definition of wildlife. Government protections or directives on insects would begin conversations about managing and conserving insects as wind energy grows and fill knowledge gaps.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Author Contributions

- Michelle Weschler conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Lusha Tronstad conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.

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Field experiments were contracted and approved by the Bureau of Land Management. Permission to conduct research and sample on private land was given by PacifiCorp.

Data Availability

The following information was supplied regarding data availability:

The case study data and code are available in the Supplemental File.

The risk assessment code and data are available at Zenodo: Weschler, M. (2023). Risk Assessment for Insects of Concern Based on Wind Energy Potential [Data set]. Zenodo. https://doi.org/10.5281/zenodo.10836442.

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