Disturbance affects biotic community composition at desert wind farms

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Abstract

Context. The global benefits of increased renewable energy production may come at a cost to local biotic communities and even regional ecosystems. Wind energy developments, in particular, are known to cause bird and bat mortalities, and to fragment habitat for terrestrial vertebrates within developed project areas. Effects on species sensitive to wind turbines (and increased prevalence of species tolerant to this disturbance) might alter community-level patterns of occurrence, with potentially detrimental changes to wildlife habitat and ecosystem health.

Aims. The present study assessed whether wind energy developments produced downstream ecological costs. Specifically, community composition and diversity were compared between wind farms and nearby areas without energy development.

Methods. Traditional diversity measures and non-metric multidimensional scaling (NMDS) were used to map ecological dissimilarity across four wind farms and five reference (control) areas in Southern California, USA.

Key results. Wind farms had more noise and road disturbance than sites without turbine installations. Noise and disturbance were correlated with reduced plant richness, particularly for endemic plant species and, conversely, with increased non-native plant richness. Animal communities at wind farms were less diverse, with fewer species and lower evenness relative to reference areas with minor or no disturbances. Wind farms had fewer rare and unique species and, for some species of avian predators, encounter rates were lower at wind farms.

Conclusions. Renewable wind energy may indeed cause shifts in local communities. Although wind farms still supported many of the same species found in natural areas, suggesting that renewable wind energy facilities can provide useable habitat for some wildlife, these communities were also less rich and diverse.

Implications. Non-native species were more prevalent at wind farms, which may then facilitate further invasions into surrounding habitats. In addition, reduced overall plant and predator diversity at wind farms, and lower encounter rates for specific taxa (particular birds), may significantly affect community structure and function.

Additional keywords: anthropogenic disturbance, community diversity, renewable energy, wind turbines.

Introduction

Human activities affect more than 80% of the terrestrial surface of our planet, resulting in dramatically altered patterns of global biodiversity (McDaniel and Borton 2002; Sanderson *et al*. 2002; Shochat *et al*. 2010). Currently, 5 to 20% of species on earth are threatened with extinction resulting from habitat loss and degradation, exotic species invasions, pollution and global climate change (Pimm *et al*. 1995; Chapin *et al*. 2000). Of these threats, researchers predict that land-use change will be the strongest driver of biodiversity loss over the next century, followed closely by global climate change (Sala *et al*. 2000). Reducing carbon emissions responsible for climate change will require substantial investment in renewable energy technologies. Renewable energy is an intensive land-use strategy, requiring on average from 3.6 to 34.5 ha for each MW produced by solar and wind, respectively (Denholm *et al*. 2009; McDonald *et al*. 2009;

Ong *et al*. 2013). Although renewable energy may help to reduce greenhouse gas emissions, the dramatic changes in land-use associated with these developments may create immediate and long-term losses in biodiversity (Pearce-Higgins *et al*. 2009; Lovich and Ennen 2011, 2013; Jones *et al*. 2015).

Wind energy is an attractive strategy for sustainable energy production in the south-western deserts of the USA, a region with high potential for solar and wind energy development (Pocewicz *et al*. 2011; Lopez *et al*. 2012). Relative to solar energy technology (photovoltaics), wind energy costs less for consumers, is more efficient to produce with fewer limitations and greater availability, produces less atmospheric pollution, requires less water consumption and is often considered to be more socially acceptable (Evans *et al*. 2009). And yet, the south-western desert region supports diverse plant communities, with at least 20% of species endemic to the region (McLaughlin 1986)

and high concentrations of species of conservation priority (Dobson *et al*. 1997). Furthermore, desert communities are slow to recover following anthropogenic disturbance; these arid regions may demonstrate altered patterns of community structure and function for centuries after disturbance activities have ceased (Lovich and Bainbridge 1999). Thus, wind farm developments may threaten large tracts of viable wildlands that have been identified as important habitats or habitat corridors for wildlife (Kiesecker *et al*. 2011; Stoms *et al*. 2013). Given the high risk of biodiversity loss in deserts, responsible development requires an understanding of the inherent risks to biota from changing habitat quality at energy production sites.

Whether wind farms act as suitable wildlife habitats depends upon the diverse responses of individual species to disturbances, including construction, operation and maintenance of turbines and associated infrastructure (Drewitt and Langston 2006; Lovich and Ennen 2013). Although wind farms require larger tracts of land (34.5 ha per MW of installed capacity) relative to other renewable energy production strategies (Gagnon *et al*. 2002; Denholm *et al*. 2009; McDonald *et al*. 2009), the direct physical footprint of energy production infrastructure may be less than 1% of the total project area (Denholm *et al*. 2009). Unlike solar farms, facility grounds are not often cleared of vegetation, leaving behind native flora and creating a matrix of usable habitat within the project area (Menzel and Pohlmeyer 1999; Lovich and Ennen 2011). Some studies indicate no apparent decline for terrestrial wildlife at wind farms (Menzel and Pohlmeyer 1999; de Lucas *et al*. 2005; Łopucki and Mróz 2016), including species of conservation priority (Agha *et al*. 2015*a*, 2015*b*). Wind farms may increase suitability of habitat for some wildlife via reduced traffic volume, enhanced resource availability and decreased predator abundances relative to nearby areas with unrestricted public access (Orloff and Flannery 1992; Lovich *et al*. 2011*b*; Agha *et al*. 2015*a*, 2017).

Potential consequences of wind farm development include increased direct mortality risk for volant species such as birds and bats (McCrary *et al*. 1986; Kuvlesky *et al*. 2007; Chatfield *et al*. 2009; Cryan and Barclay 2009). These risks can be mitigated by designing and actively managing wind farms to reduce collision rates (Baerwald *et al*. 2009; May *et al*. 2015). Additional risks include effects of low-frequency noise from generators and blade movements that may disrupt acoustic communication for mammals or birds (Rabin *et al*. 2006). Habitat fragmentation and increased human activity may disrupt habitat composition and alter patterns of habitat use for apex predators or long-lived species (Orloff and Flannery 1992; Lovich and Daniels 2000; Pearce-Higgins *et al*. 2009; Veiberg and Pedersen 2010). Access roads for machinery and vehicles can increase mortality risk for slow-moving species (Andrews *et al*. 2008; Lovich *et al*. 2011*a*; but see Agha *et al*. 2015*a*) while promoting invasive plant establishment and increasing foraging activity for scavengers and mesocarnivores (Orloff and Flannery 1992; Gelbard and Belnap 2003; Smallwood *et al*. 2010; Lovich and Ennen 2013; Agha *et al*. 2017). At the regional scale, wind farms may affect habitat composition by altering macroclimate wind and temperature patterns (Roy and Traiteur 2010).

In the present study, we examine community composition and diversity at wind farm sites relative to nearby natural areas.

We hypothesise that wind farms will be more disturbed than nearby sites without turbines, and will thus display reduced diversity, resulting in unique community assemblages dominated by disturbance-tolerant species of plants and animals (Johnson *et al*. 1975; Traveset and Richardson 2006; Croci *et al*. 2008; Fischer *et al*. 2012; Sol *et al*. 2014). We test this prediction by characterising patterns of diversity and species composition at sites with and without wind energy developments in the San Gorgonio Pass Wind Resource Area (SGWRA) of Southern California, USA. We focus on communities of commonly encountered predators from four taxonomically divergent guilds (mammals, reptiles, birds and arachnids), as well as primary producers, because diversity within these two groups can influence ecosystem function in desert systems (Polis 1991; Johnson *et al*. 1996; Gordon 1998; Ayal 2007; Sergio *et al*. 2008; Fischer *et al*. 2012;). Few studies have addressed the biodiversity consequences of renewable wind energy developments on terrestrial vertebrate communities (de Lucas *et al*. 2005; Santos *et al*. 2010; Łopucki and Mróz 2016; Lovich and Ennen 2017); we are unaware of any studies that consider effects of wind farms on floral diversity.

Materials and methods

Study area

The SGWRA is near Palm Springs, California (33°56′N, 116°34′W). It was developed for wind energy production starting in the mid-1980s and is currently one of the country's largest wind production regions (Pasqualetti 2001). The wind resource area covers over 18 000 ha, with more than 3000 individual turbines providing 615 MW of installed energy (NRC 2007). The area (Fig. 1) is a transition zone between the Sonoran and the Mojave Deserts, and is dominated by a sparse shrub community of creosote brush (*Larrea tridentata*), brittlebush (*Encelia farinosa*) and white bursage (*Ambrosia dumosa*), with lower abundances of other annual and perennial plants.

Study sites covered a gradient of habitats within the SGWRA (Fig. 1; Table 1). We selected four study sites at wind farms: Mesa (ME); Painted Hills (PH); Dillon (DI); and Mountain View (MV). Sites ME and PH were developed in the mid-1980s, with high densities of smaller turbines with lattice tower bases. Sites DI and MV were developed in the mid-2000s and these sites have tall, monopole-mounted turbines at lower densities with fewer access roads. Additional anthropogenic disturbances (e.g. electrical transmission lines or proximity to high-traffic roads, see Fig. 1) were also evident at wind farm sites (Table 1).

Our original intent was to pair wind-turbine sites with adjacent non-turbine sites. However, the combination of land access and extensive disturbance at adjacent sites made this infeasible. Therefore, we selected five reference study sites (Fig. 1; Table 1) that matched the variation in abiotic and biotic conditions at the four turbine sites as closely as possible, including elevation, slope, aspect, substrates and overall plant communities. We also attempted to match levels of disturbance at turbine sites by intentionally selecting reference sites along a gradient of low to high disturbance intensity: Mission (MI); San Gorgonio (SG); Whitewater (WW); Desert Hot Springs (DH);
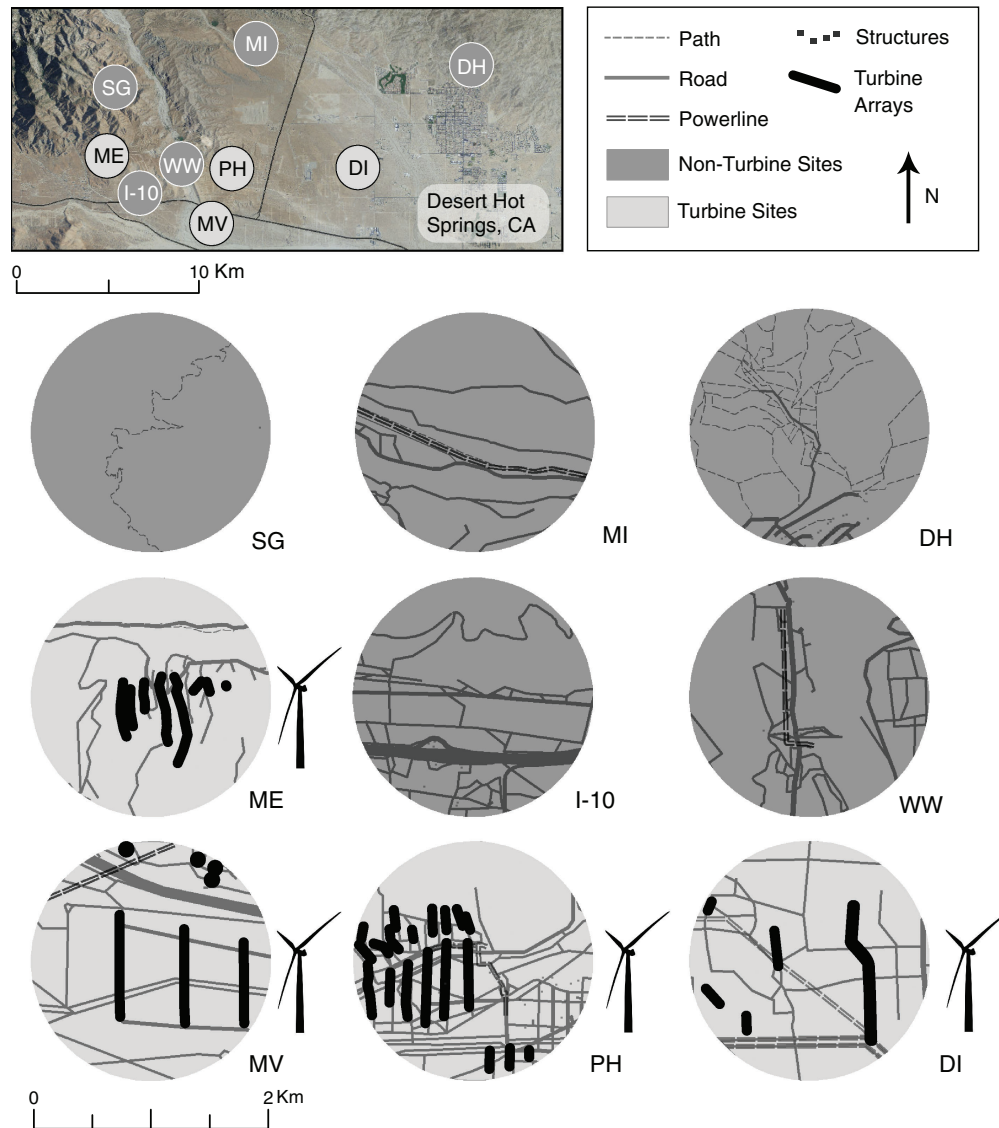
Fig. 1. Nine study sites in the San Gorgonio Pass Wind Resource Area (SGWRA) in southern California, near Desert Hot Springs, north of Palm Springs. Five study areas lack turbines (dark grey) and were used as reference sites, while four sites contained turbines (light grey) and were considered as treatments. Insets show land-use at each study area: paths (dashed line), roads (grey lines; thickness reflects road traffic volume), transmission lines (double-dashed line), buildings (squares) and turbine arrays (black) indicate the types of human disturbances present at each site. Vegetation survey plots (40 × 40 m) were centred at these sites, and animal surveys began at vegetation plots and wandered up to 1 km from vegetation plots.

and Interstate 10 (I-10). Sites MI and SG were low-disturbance areas at least 2.4 km away from any paved road disturbances, with limited human activity (however, site SG experienced substantial erosion and soil disturbance over the course of the study from illegal grazing). Sites WW and DH were moderately disturbed areas, with nearby paved roads used frequently for access to recreation opportunities (WW), and substantial human activity such as hiking and dog walking (DH). Finally, site I-10 was highly disturbed, 420 m north of a rest stop on a major highway, the I-10. There was substantial traffic noise, off-road vehicle use, human activity, and multiple transmission line corridors at this site. This gradient

of disturbance at turbine and non-turbine sites allowed us to assess the effects of anthropogenic disturbance on diversity and community composition, although our ability to isolate the influence of the wind turbines *per se* was weakened because we were unable to strictly pair wind farms with adjacent reference sites.

Site disturbance, habitat and climate characteristics

For each of the nine study sites, we used field surveys and GIS data to identify disturbance history, habitat and climate characteristics (Table 1). We measured anthropogenic disturbance

Table 1. Disturbance, habitat, and climate characteristics of predator and plant community study areas in the San Gorgonio Pass Wind Resource Area (SGWRA) in southern California, near Palm Springs

Study site	Latitude, longitude	Disturbance index[A]	Avg. noise levels (dBA)	Bare ground cover (%)	Shrub density (# per m²)	Shrub canopy cover (%)	Shrub canopy height (m)	Slope (degrees)	Elevation (m)	Avg. annual rainfall (cm)	Avg. wind speed (km h⁻¹)
No turbines											
SG (−)	33.9775, −116.6719	2.61	41.16	84	0.06	2.95	0.61	17.40	822.73	43.05	6.12
MI (−)	34.0009, −116.6037	22.82	45.45	63	0.38	27.50	0.56	5.84	640.74	35.20	5.86
WW (−)	33.9385, −116.6406	40.23	47.62	75	0.15	17.43	0.66	2.72	468.75	35.53	9.09
DH (−)	33.9903, −116.4975	24.17	48.17	82	0.11	18.92	0.97	4.12	500.99	27.48	4.15
I-10 (−)	33.9266, −116.6610	67.47	54.43	72	0.14	19.81	0.85	8.67	390.74	30.00	21.13
Turbines											
ME (+)	33.9440, −116.6791	26.48	47.92	76	0.23	12.97	0.62	8.84	711.98	46.81	13.52
PH (+)	33.9393, −116.6179	59.97	66.37	85	0.14	13.00	0.70	13.21	464.42	34.09	13.28
MV (+)	33.9134, −116.6268	49.89	60.49	87	0.09	3.88	0.48	1.92	366.12	38.76	16.33
DI (+)	33.9394, −116.5540	34.53	49.85	90	0.07	12.83	1.01	1.51	318.03	16.69	11.01
−Avg. +/− s.d.		31.46±24.15	47.37±4.82	75±8.0	0.17±0.12	17.32±8.93	0.73±0.17	7.75±5.83	564.79±170.21	34.26±5.99	9.27±6.86
+Avg. +/− s.d.		42.72±15.05	56.16±8.77	85±6.0	0.13±0.07	10.67±4.53	0.70±0.22	6.37±5.67	465.14±175.48	34.09±12.73	13.53±2.19

[A]Disturbance Index: total length of road (weighted by 0.5 for footpath, 1.0 for two-track, 3.0 for residential, 5.0 for secondary and 10.0 for highway) within a 1000 m radius from plant richness study plots; digitised in ArcMap from 1 m resolution California National Agriculture Imagery Program (NAIP) imagery.

as (1) an index of physical road disturbance (DISTURB), calculated as the sum of road lengths (digitised in ArcMap from 1-m resolution California National Agriculture Imagery Program (NAIP) imagery) within a 1000-m buffer of the 40×40 m (1600 m²) plant study plots (see below). To better account for differences in disturbance level across road types, we weighted road lengths as 0.5 for footpaths, 1.0 for dirt roads, 3.0 for residential roads, 5.0 for secondary roads and 10.0 for primary highways (e.g. Brady *et al.* 2009). We also calculated (2) noise level (NOISE) as an average a-weighted decibels (dB$_A$) reading from a random sample of 10 readings taken with a MS6708 digital sound level meter (Mastech, Coral Gables, FL) at plant study plots in June and July (2015) when turbines were running and wind was ≤ 3.5 mph (readings of wind noise interfered with turbine noise during high wind conditions).

We quantified differences in habitat characteristics using data from three 100-m point-line-intercept surveys (Herrick *et al.* 2005) completed in July of 2014 at plant study plots. We calculated non-canopy cover (COVER) using the proportion of random points at each meter interval per transect that did not intersect a plant canopy. We completed three 100-m belt transects to estimate the number of shrubs within 2 m of the transect line, which we then used to calculate shrub density (SHRUBS) as the number of shrubs per m². We estimated the percentage of the study area with a shrub canopy (SHRUB. CANOPY), determined from measured shrub diameters (d) obtained during belt-transect surveys, calculated as: $\pi\left(\frac{d}{2}\right)^{2}$. We estimated the average height of the shrub canopy (CANOPY.HEIGHT) from measured shrub heights.

We used slope (SLOPE), elevation (ELEV) and precipitation (PRECIP) to approximate community differences resulting from climate variation. We obtained slope and elevation from a 2013 digital elevation model (DEM) raster at 1/3 arc-second resolution, retrieved from the USGS National Elevation Dataset (USGS 2013). Extracted values characterised average conditions for each 1600 m² plant study plot at the centre of the predator survey area. We extracted average precipitation values for each plant study plot from precipitation models generated by the PRISM Climate Group (PRISM Climate Group 2004), averaged across the winter months of November through February, 2012–2015. We also calculated the average wind speed (WIND) recorded using a 3000 pocket wind meter (Kestrel, Boothwyn, PA) during predator encounter surveys in June and July of 2014.

Field surveys

We recorded predator encounter rates as an index of abundance and diversity using data collected during meandering field surveys (0.75 to 4.88 h long, average: 2.55 h). We used the vegetation study plot for each site as the central starting point for each survey, limiting the search region to areas representative of the plant study plot for each site (similar disturbance type, disturbance magnitude and habitat type). From June to late July of 2014, observers (five possible surveying in 1–2 person teams for each target guild independently) conducted surveys by searching for animals within suitable habitat for each guild. Survey conditions and total survey effort were similar at wind farms and at reference sites (see Table S1 available as

Supplementary Material to this paper). Surveys targeted a subset of 32 common predatory taxa consisting of reptile, bird, mammal and arachnid guilds (Table S2).

During reptile surveys, an observer searched during mid-morning hours for individuals active on the surface or beneath suitable cover objects. During bird surveys, we detected species in early morning hours using auditory and visual surveys. For mammal surveys, we used scat (a species observation was recorded if at least one scat pile was detected over a 10-min search period) and direct observations of animals or physical remains. We did not record tracks or burrow activity due to differences in soil characteristics across study sites. For arachnid surveys, we searched under suitable cover objects for inactive adults and included silk-lined burrows or webs as observations.

We estimated plant species richness within study plots centred at each of the nine established sites during mid-March of 2015. Each plot was 40×40 m (1600 m^2). We surveyed each site by systematically searching the study plot for undetected species until no new species were encountered for a 15-min search interval. This method ensured that we detected all common species (although, it may have introduced some bias against small or rare plants). We identified specimens to species (except for the following genera: *Logfia*, *Rafinesquia*, *Pectocarya*, *Caulanthus*, *Cuscuta*, *Dudleya* and *Schismus*) in accordance with the nomenclature of the Jepson Desert Manual and dichotomous keys therein (Baldwin *et al*. 2002). We confirmed our identifications using pressed specimens maintained in herbaria at the University of Nevada, Reno, Museum of Natural History and the Boyd Deep Canyon Desert Research Center, or by comparison with photos maintained in the CalPhotos database (CalPhotos 2011). For an annotated list of plants encountered, see Table S3.

Analyses

We predicted that loss of disturbance-intolerant species and guilds (in favour of disturbance exploiters) would result in lower diversity due to declines in richness and community evenness. We tested this prediction by comparing overall patterns of richness and diversity between sites with and without wind farms ('treatments'). For predator communities, we calculated richness (R), diversity (Shannon Diversity Index; H) and evenness (E). For plant communities, we calculated richness of plants by species. We then compared differences in richness, diversity (of species and genera within plant families) and evenness (of species within plant families) between reference and treatment sites using Mann–Whitney *U*-tests in R v3.2.2 (R Core Team 2015).

Next, we used ordination techniques to look at patterns of community composition. We predicted that community composition would reflect variables describing anthropogenic disturbance, or variables describing confounding variation from habitat or climate characteristics of the study sites. We visualised plant and predator community diversity using non-metric multidimensional scaling (NMDS) to characterise relationships between turbine and non-turbine communities. This indirect ordination technique optimises the physical arrangement of sites (rows) and species (columns) along a specified number of axes, such that communities with similar species composition are close together in ordination space. NMDS does not assume an underlying model of species distributions (McCune and Grace 2002).

We performed all ordinations in R v3.2.2, using the default settings of the *metaMDS* function from the 'vegan' package v2.3 (Oksanen *et al*. 2011). The *metaMDS* function follows the ordination approach outlined in Minchin (1987). In this method, up to 20 random starting configurations are allowed until a stable, global solution is reached (which requires that the same minimum stress value is returned in two consecutive iterations). We used the Bray–Curtis (Sørensen) distance estimator to quantify community dissimilarity (Faith *et al*. 1987; McCune and Grace 2002). We compared final stress of ordinations with 2 and 3 axes to identify the simplest solution with a stress of less than 20%, and determined that a 2-dimensional solution was sufficient in all cases (McCune and Grace 2002). We assessed the strength of ordination solutions using a Shepard diagram. Output diagrams were centred, scaled to half-change units and rotated so that the first axis maximised the variation between groups of sites with and without turbines to best represent differences resulting from the treatment effect.

We used NMDS to visualise community structure independently for plant and predator datasets. For plants, ordinations were generated using presence/absence data and for predators, ordinations used the encounter rate per unit of search effort for each species (ranging from 4.3 to 12.8 h per site). In each ordination, we used a permutation-based analysis of variance (ANOVA; using the *adonis* function in 'vegan' with 1000 runs) to test whether a significant amount of variation in the distance matrix was explained by the treatment effect of turbine presence or absence (Oksanen *et al*. 2011).

We used *envfit* ('vegan') to identify correlations between ordination structure, community diversity and measured abiotic and biotic variables. The *envfit* function calculates correlation between site location in ordination space and selected variables using a permutation test ($n = 1000$) to estimate a coefficient of determination (R^2) and an α value (Oksanen *et al*. 2011). We looked for correlations between ordination structure and richness (RICH), diversity (DIVERSE) and evenness (EVEN). We also calculated correlations between ordinations and disturbance, habitat and climate variables. We *z*-standardised all variables (mean = 0.0, s.d. = 1.0) to account for scale of measurement when comparing the effects of parameters.

We used 'vegan' *envfit* to identify individual predator taxa with strong gradients in abundance along NMDS Axis 1 (with one dimension, this is identical to a linear regression with abundance as a function of Axis 1 score). For plant presence and absence data, this objective was achieved using logistic regression. We used R^2 (linear regression, predators) or pseudo-R^2 (logistic regression, plants) values to identify species where probability of presence or abundance was explained by Axis 1 score. For plant communities, we predicted that species prevalence at wind farms would be explained by shared life-history traits indicating sensitivity to anthropogenic disturbance (Lavorel *et al*. 1999); we used ANOVA to identify coefficient and standard deviation values for *a priori* taxa groups on NMDS Ordination Axis 1. We classified species by origin as

native, non-native or endemic to California and northern Baja California in the western USA (Stylinski and Allen 1999; Rejmánek 2000; Vamstad and Rotenberry 2010; Slatyer *et al.* 2013); and by life-form groups of shrubs, annual herbs, annual grasses, succulents and perennial herbs or grasses. We omitted two species classified as ferns from group response analyses, but not from ordination or diversity calculations (Table S3).

Results

Predator communities

We observed 32 target taxa 884 times. An average of 13.3 taxa were encountered per site (range: 10–16), at a rate of 13.5 observations per hour (range: 7.5–20). Abundance of predators at non-turbine sites was higher, on average, relative to predator abundance at turbine sites; we found higher relative abundances of arachnids at non-turbine sites (+46.2%), mammals (+21.4%), raptors (+70.1%), and songbirds (+61.5%). Only lizard and corvid relative abundances were lower at reference sites compared with turbine sites (−18.9% and −7.4%, respectively). Overall, turbine sites were 13.4% less rich ($r = 12.3$, s.d. $= 1.7$; $W = 16.5$, $P = 0.133$), 14.3% less diverse ($H = 1.8$, s.d. $= 0.2$; $W = 19$, $P = 0.036$) and 11% less even

($E = 0.70$, s.d. $= 0.06$; $W = 18$, $P = 0.065$) than non-turbine sites (Fig. 2), which had an average of 14.2 (s.d. $= 1.3$) taxa, Shannon diversity of 2.1 (s.d. $= 0.2$) and evenness of 0.81 (s.d. $= 0.07$). Of the taxa encountered, four were present at all sites (bobcat, coyote, loggerhead shrike and western whiptail). These taxa (as well as common raven, zebra-tailed lizard and tarantula sign) were encountered with more than 0.75 observations per hour per site, on average.

Eleven taxa were unique to a single site – two taxa unique to turbine sites (sidewinder rattlesnake, spotted leaf-nosed snake), and nine taxa unique to non-turbine sites (Great Basin collared lizard, western fence lizard, California kingsnake, speckled rattlesnake, red diamond rattlesnake, golden eagle, grey fox, American badger and western black widow). Four of these unique taxa were observed at one high elevation non-turbine site, SG (western fence lizard, speckled rattlesnake, golden eagle and grey fox).

The final 2-dimensional NMDS solution had a stress value of 8.25%. There was a strong correlation between site dissimilarity and ordination distance for standardised data (non-metric $R^2 = 0.99$, linear $R^2 = 0.97$; Fig. 3). The presence of turbines explained 11% of the variation in Bray–Curtis distance between sites (Permutation ANOVA, $F_{1,7} = 0.90$, $P = 0.534$).
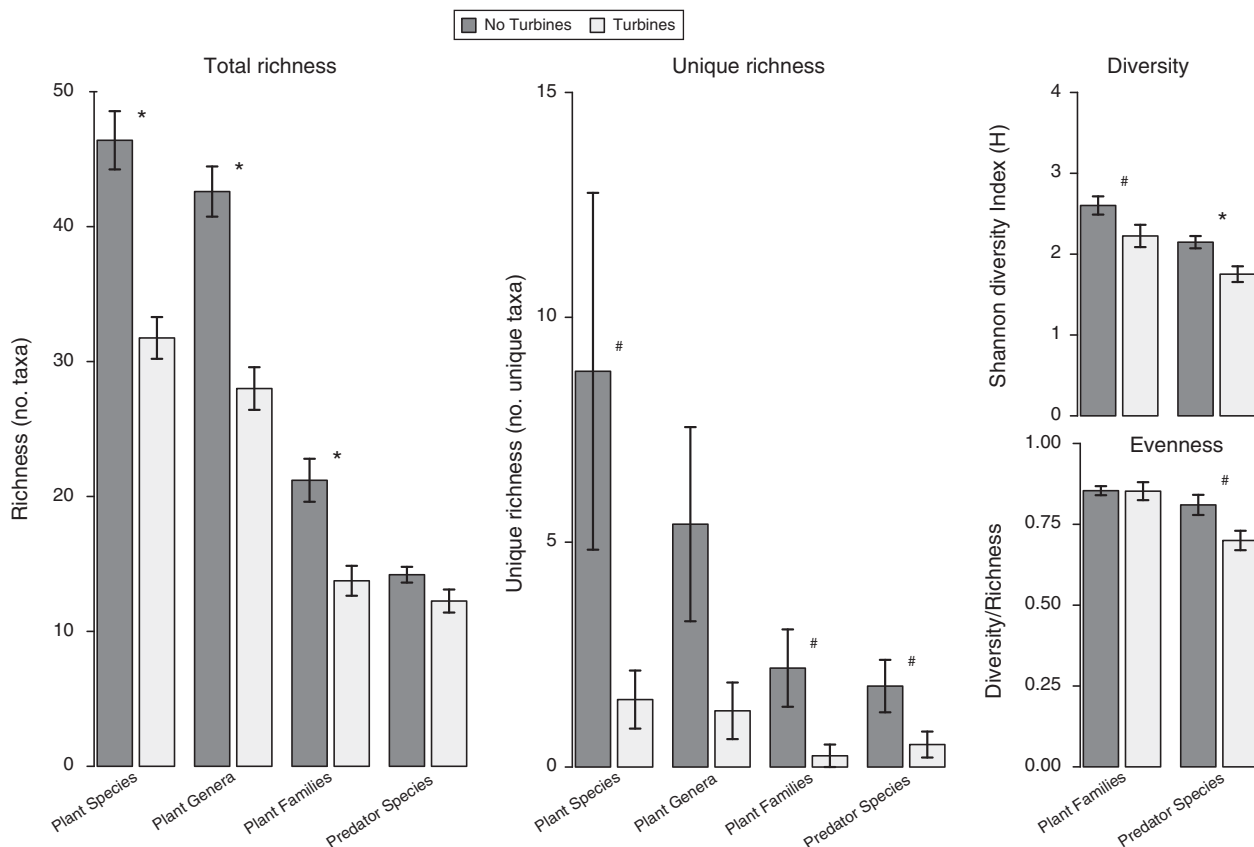

Fig. 2.   Total richness (left), number of unique taxa (middle), diversity (top right), and evenness (bottom right) of plant and predator communities surveyed at reference sites without turbines (dark grey) and sites with wind turbines (light grey) in the San Gorgonio Pass Wind Resource Area (SGWRA). Bars represent the mean values, with standard error bars indicating variation among sites. Significance differences (Mann–Whitney U-test) between non-turbine and turbine sites indicated as follows: * $P < 0.05$; # $P = 0.06$–0.10. Diversity and evenness measures for plants represent the distribution of plant species within plant families, rather than abundances of individual species.
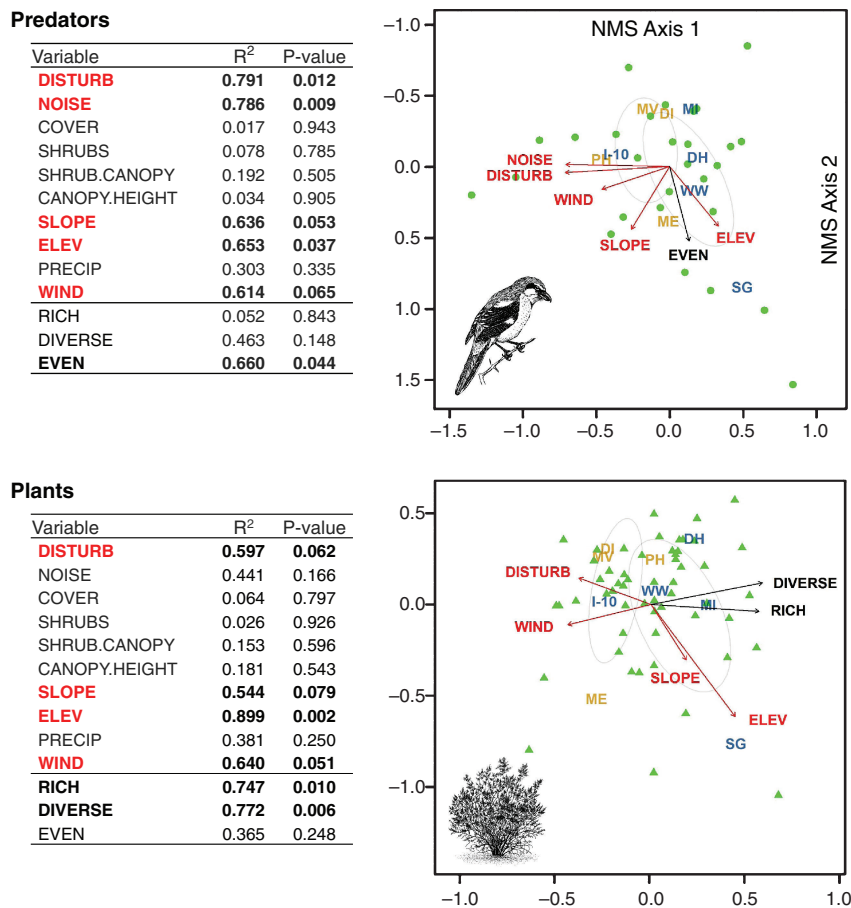
Predators

Variable	R^2	P-value
DISTURB	**0.791**	**0.012**
NOISE	**0.786**	**0.009**
COVER	0.017	0.943
SHRUBS	0.078	0.785
SHRUB.CANOPY	0.192	0.505
CANOPY.HEIGHT	0.034	0.905
SLOPE	**0.636**	**0.053**
ELEV	**0.653**	**0.037**
PRECIP	0.303	0.335
WIND	**0.614**	**0.065**
RICH	0.052	0.843
DIVERSE	0.463	0.148
EVEN	**0.660**	**0.044**

Plants

Variable	R^2	P-value
DISTURB	**0.597**	**0.062**
NOISE	0.441	0.166
COVER	0.064	0.797
SHRUBS	0.026	0.926
SHRUB.CANOPY	0.153	0.596
CANOPY.HEIGHT	0.181	0.543
SLOPE	**0.544**	**0.079**
ELEV	**0.899**	**0.002**
PRECIP	0.381	0.250
WIND	**0.640**	**0.051**
RICH	**0.747**	**0.010**
DIVERSE	**0.772**	**0.006**
EVEN	0.365	0.248

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of predator encounter rate surveys and plant richness surveys at nine study sites in the San Gorgonio Pass Wind Resource Area (SGWRA). Left panels show correlations between site variables (see Table 1), diversity measures, and NMDS solution ($P < 0.10$ in bold). Right panels show final NMDS solution for predator taxa (green circles) and plant taxa (green triangles) at turbine (yellow text) and non-turbine sites (blue text). Plotted vectors are scaled relative to the maximum variance explained for predators (DISTURB) and plants (ELEV).

Of the external variables tested, EVEN ($R^2 = 0.660$, $P = 0.044$), DISTURB ($R^2 = 0.791$, $P = 0.01$), NOISE ($R^2 = 0.786$, $P = 0.01$), SLOPE ($R^2 = 0.636$, $P = 0.05$), ELEV ($R^2 = 0.653$, $P = 0.004$) and WIND ($R^2 = 0.614$, $P = 0.07$) were correlated with the 2-dimensional NMDS solution (Fig. 3). When the solution was rotated to maximise the difference between turbine and non-turbine sites along the treatment axis, DISTURB (78.7%), NOISE (78.6%) and WIND (46.6%) were negatively correlated with Axis 1, while EVEN (64.6%), ELEV (57.2%) and SLOPE (52.6%) correlated positively with Axis 2 (Fig. 3). The resulting solution defined community structure by gradients of anthropogenic disturbance and associated high wind levels (Axis 1, 'treatment axis'), and by gradients in site climate characteristics associated with greater evenness (Axis 2, 'elevation axis'). Cover (canopy height, shrub and bare ground canopy cover and shrub density) and precipitation did not explain significant variation in predator community structure.

Predator encounter rates were positively correlated ($R^2 > 0.4$), with ordination scores on the treatment axis for two of the 32 target taxa. For loggerhead shrike and red-tailed hawk, encounter

rates increased as disturbance declined. The treatment axis explained 49.9% ($P = 0.02$) and 57.2% ($P = 0.004$) of variation in encounter rates for these species (see Table 3 for correlations in remaining taxa).

Plant communities

We detected 119 plant species from 91 genera and 36 families, resulting in an average species richness of 2.5 species per 100 m^2 (range: 1.8–3.3). Of these species, 15 were endemic to California and Baja California, while 13 were non-native. On average, wind farms plant richness was 0.8% lower for endemic and 124% higher for non-native plant species. Richness of plants increased at non-turbine sites relative to turbine sites for succulents (+380%), shrubs (+67%), annual grasses (+14.3%), annual herbs (+34%), ferns (none at turbine sites) and perennial herbs and grasses (+50%). In total, turbine sites had 31.5% fewer species ($r = 31.8$, s.d. $= 3.1$; W $= 20$, $P = 0.019$) than non-turbine sites ($r = 46.4$, s.d. $= 4.8$) (Fig. 2). These species comprised 34.7% fewer genera at turbine sites

($r = 28.0$, s.d. $= 3.2$; $W = 20$, $P = 0.016$) than at non-turbine sites ($r = 42.6$, s.d. $= 4.2$), and 34.9% fewer plant families per site ($r = 13.8$, s.d. $= 2.2$; $W = 18.5$, $P = 0.048$) than at non-turbine sites ($r = 21.2$, s.d. $= 3.6$) (Fig. 2).

We recorded 50 plant species that were each present at one site only. Only six (average $= 1.5$ per site) of these were found at turbine sites: three native annual herbs (one endemic); two native shrubs (one endemic); and one non-native annual herb. The remaining 44 unique taxa were located at control sites (average $= 8.8$ per site), including nine (60%) of the recorded endemic species (four annual herbs, four perennial herbs and one shrub), four non-native plants (two annual grasses and two annual herbs), and 31 native plants (14 annual herbs, nine shrubs, six perennial herbs, one fern and one succulent). Of the 44 unique observations at non-turbine sites, 24 were observed at one high elevation non-turbine site, 'SG', which accounted for six of the nine recorded endemic species at control sites. Seven species were found at all nine sites (two non-native annual herbs, four native annual herbs and one non-native grass).

The final NMDS ordination (stress of 8.42%) showed strong agreement between site dissimilarity and ordination distance (non-metric $R^2 = 0.99$, linear $R^2 = 0.97$, Fig. 3). The presence of turbines explained 16% of the variation in Bray–Curtis distance between sites (Permutation ANOVA, $F_{1,7} = 1.39$, $P = 0.239$). Of the external variables tested, RICH ($R^2 = 0.747$, $P = 0.01$), DIVERSE ($R^2 = 0.772$, $P = 0.01$), DISTURB ($R^2 = 0.597$, $P = 0.06$), SLOPE ($R^2 = 0.544$, $P = 0.08$), ELEV ($R^2 = 0.899$, $P = 0.002$) and WIND ($R^2 = 0.640$, $P = 0.05$) were correlated with the 2-dimensional solution (Fig. 3). When the solution was rotated, Axis 1 ('treatment axis') was positively correlated with RICH (74.1%) and DIVERSE (71.1%) and negatively correlated with DISTURB (50.0%) and WIND (56.1%). ELEV (75.8%) and SLOPE (47.7%) were negatively correlated with Axis 2 ('elevation axis'). Overall, community structure was negatively correlated with disturbance and associated high wind levels, with lower diversity and richness at high-disturbance sites. Abiotic characteristics were important drivers of community trends as well (Fig. 3). Cover and precipitation variables did not explain significant variation in community structure.

Plants showed segregation of group means by plant status (native, non-native and endemic) along the treatment axis (Fig. 3). Presence of endemic plants was associated with low disturbance and low noise along the treatment axis ($P = 0.001$). Similarly, scores for non-native plants were associated with high noise and disturbance on the treatment axis ($P = 0.02$). The coefficient for native plants was not significant. There were no differences between group means for plant habit levels on NMDS Axis 1 when assessed using ANOVA models (Table 2). Nonetheless, when richness was partitioned by plant habit category, average richness per site at non-turbine sites always exceeded that at turbine sites.

Of the 119 encountered plants, presence or absence was strongly explained ($R^2 > 0.4$) by ordination scores on the treatment axis for 10 species. Probability of presence increased with high noise and high disturbance on the treatment axis for non-native annual herbs *Oncosiphon piluliferum*, *Sisymbrium irio*, and for the native, perennial herb *Stephanomeria pauciflora*. Probability of presence increased with low noise and disturbance values on the treatment axis for native annual herbs *Eucrypta chrysanthemifolia*, *Eulobus californicus*, *Salvia columbariae* and *Phacelia minor* (endemic), as well as natives *Selaginella bigelovii* (endemic fern), *Mirabilis laevis* (perennial herb) and *Bahiopsis parishii* (shrub) (Table 3).

Discussion

Development of renewable energy infrastructure remains a top priority in efforts to mitigate global climate change (Panwar *et al.* 2011). To maximise the net conservation gain realised from renewable wind energy production, best land-management practices should aim to reduce biodiversity loss associated with development. Collision mortality may represent only a fraction of the cumulative effects that wind farms have on biotic community function and health (Kuvlesky *et al.* 2007). Here, we addressed whether wind farms affected biodiversity with a focussed study of plant and predator communities in relation to nearby reference areas.

Diversity and community composition trends between sites

We found that wind farm sites were less rich, even and diverse (Fig. 2). Low diversity is often encountered in habitats that are less stable, trophically complex, productive or disturbance resistant than areas with high levels of diversity, suggesting that wind farms may provide lower quality habitats for local

Table 2. Results of analysis of variance (ANOVA) models of variation in taxa scores on non-metric multidimensional scaling (NMDS) Ordination Axis 1 (variation between turbine and non-turbine sites) explained by affinity to plant community functional groups

Bold indicates significant ($P < 0.05$) effect of functional group category

Community grouping	Functional level	Coefficient	Standard error	P-value
Origin $F_{(2,116)} = 2.79$ **P = 0.07**	native	−0.145	0.093	0.121
	non-native	**−0.294**	**0.124**	**0.020**
	endemic	**0.289**	**0.086**	**0.001**
Life form $F_{(4,112)} = 1.02$ $P = 0.40$	annual herb	−0.151	0.169	0.374
	annual grass	0.252	0.164	0.128
	perennial herb/grass	0.010	0.181	0.957
	shrub	−0.127	0.177	0.476
	succulent	−0.082	0.232	0.724

Table 3. Linear correlations between non-metric multidimensional scaling (NMDS) Ordination Axis 1 scores (treatment axis) and predator abundances, and between NMDS Ordination Axis 1 and plant species presence or absence

A positive correlation (+) indicates higher predator encounter rates or that probability of plant species presence increases at high values of Axis 1 (non-turbine sites; quiet, low disturbance); a negative correlation (−) indicates higher predator encounter rates or that probability of plant species presence increases at low values of Axis 1 (turbine sites; loud and high disturbance). Note that all predators are shown, but only plant species with $R^2 \geq 0.10$ and that occurred more than once (and not at all sites) are shown. Bold indicates strong correlation of greater than 0.40. The R^2 value for plants is McFadden's Pseudo-R^2 statistic

Predator species	Direction	R^2	Plant species	Direction	R^2
Red-tailed Hawk	+	**0.572**	*Bahiopsis parishii*	+	**0.77**
Loggerhead Shrike	+	**0.499**	*Oncosiphon piluliferum*	−	**0.77**
Golden Eagle	+	0.394	*Eulobus californicus*	+	**0.60**
Western Fence Lizard	+	0.394	*Sisymbrium irio*	−	**0.60**
Speckled Rattlesnake	+	0.394	*Eucrypta chrysanthemifolia*	+	**0.56**
Gray fox	+	0.394	*Phacelia minor*	+	**0.56**
Prairie Falcon	−	0.384	*Stephanomeria pauciflora*	−	**0.56**
Sidewinder	−	0.345	*Selaginella bigelovii*	+	**0.44**
Bobcat	+	0.280	*Mirabilis laevis*	+	**0.43**
Wolf Spider	+	0.249	*Salvia columbariae*	+	**0.43**
Great Basin Collared Lizard	−	0.211	*Stephanomeria exigua*	−	0.39
Western Black Widow	−	0.211	*Emmenanthe penduliflora*	+	0.37
Rock Wren	+	0.202	*Phacelia distans*	+	0.31
Scorpion	−	0.189	*Gilia stellata*	+	0.30
Coyote	+	0.177	*Senegalia greggii*	+	0.30
Western Whiptail	−	0.120	*Encelia farinosa*	+	0.27
Cactus Wren	−	0.082	*Malacothrix glabrata*	−	0.26
Northern Mockingbird	+	0.072	*Crassula connata*	−	0.23
Red Diamond Rattlesnake	+	0.060	*Cryptantha angustifolia*	−	0.18
Greater Roadrunner	−	0.052	*Eriogonum thurberi*	−	0.17
Yellow-backed Spiny Lizard	+	0.049	*Sonchus oleraceus*	−	0.16
California Kingsnake	+	0.046	*Cryptantha micrantha*	−	0.16
Common Raven	−	0.040	*Loeflingia squarrosa*	−	0.16
Leaf-nosed Snake	−	0.035	*Amsinckia intermedia*	+	0.14
American Badger	+	0.033	*Artemisia californica*	+	0.14
American Kestrel	+	0.029	*Chorizanthe brevicornu*	−	0.14
Zebra-tailed Lizard	+	0.017	*Dichelostemma capitatum*	+	0.14
Sun Spider	−	0.014	*Euphorbia polycarpa*	−	0.14
Burrowing Owl	+	0.013	*Echinocereus engelmannii*	+	0.10
Coachwhip	−	0.008	*Hilaria rigida*	+	0.10
Domestic Dog	+	0.005			
Tarantula	+	0.004			

biota (Paine 1966; Johnson *et al*. 1996; McCann 2000; Santos *et al*. 2010; but see Agha *et al*. 2015*a*, 2017).

Because we were unable to strictly pair reference and wind farm sites by habitat or climate (Table 1), our observed diversity trends may also reflect additional confounding variation. For example, turbine sites tended to be windier than reference sites (Table 1). Sites also varied in elevation, which can be an important driver of diversity trends (Richerson and Lum 1980), including within the SGWRA (Agha *et al*. 2017), because many abiotic factors (e.g. temperature and precipitation) change rapidly along elevational gradients, particularly in desert communities (Beatley 1975, Ehleringer and Cooper 1988). Regardless, after accounting for the potentially confounding effects of variation in habitat and climate traits (elevation axis) on community structure in NMDS ordinations, results still indicated an effect of total disturbance intensity (treatment axis correlated with road

density and noise level) on diversity trends at wind farms sites relative to reference areas. The observed losses of diversity at wind farms were comparable in magnitude with diversity losses reported for natural gas extraction (Jones *et al*. 2014), grazing (James 2003), or for linear disturbances such as aqueducts (Berry *et al*. 2015), utility corridors (Lathrop and Archbold 1980), or roads (Bury *et al*. 1977). Reference sites harboured more diversity than wind farm sites, despite grazing activities, close proximity to housing developments, or paved roadways with moderate traffic volume in these areas. These types of disturbances were also sometimes present at wind farms, and may have contributed synergistically towards the overall diversity losses at these sites.

We also found strong correlations between variables in the NMDS ordination solutions, which may explain the importance of predictors such as average wind speed (correlated with disturbance at Pearson's $r = 0.70$, $P = 0.037$; and with noise

level at $r = 0.66$, $P = 0.054$) and slope (correlated with elevation at $r = 0.67$, $P = 0.048$). Elevation and anthropogenic disturbance were more important predictors of ecological distances than variables describing relative site productivity (bare ground cover, precipitation and shrub canopy cover, density and height). Relative to reference sites, wind farms had higher average wind speeds (correlated with disturbance at Pearson's $r = 0.70$, $P = 0.037$; and with noise at $r = 0.66$, $P = 0.054$) and were more disturbed (lower score on NMDS disturbance axis) than all control areas except for site I-10, which was characterised by close proximity to a major interstate and high levels of off-road vehicle use.

We also found some evidence that wind farm communities were more homogeneous than communities at non-turbine control sites. In both predator and plant datasets, fewer unique species observations occurred at wind farm sites relative to nearby control areas. Homogenised communities often result from high intensity of human disturbance (Proppe *et al*. 2013), where altered abiotic conditions can cause local extirpations of rare species with low densities, or endemic species with limited geographic ranges (McKinney and Lockwood 1999). Further research is needed to address whether low encounter rates may have affected study results, because a number of species thought to be commonly distributed in the SGWRA (Lovich 2011, 2015; Agha *et al*. 2017) were encountered as unique species observations in this study.

Predator community composition

Prior predator work at the Mesa (ME) wind farm found that mesopredators (coyotes, grey foxes, bobcats and western spotted skunks) were encountered less frequently at camera trapping sites placed at desert tortoise (*Gopherus agassizii*) burrows near wind turbines; however, mesopredators were also more active at burrows near roadways (Agha *et al*. 2017). In our study, wind farm sites were also characterised by greater road densities; thus, we were unable to identify the contribution of individual effects of either disturbance type on predator community structure trends. Predator diversity declined at disturbed wind farm sites, with no significant association between the treatment axis and mesopredator taxa encounter rates in the NMDS ordination.

As a group, predator community composition trend differences across study sites were best explained by noise and road disturbance at wind farm sites, after accounting for existing habitat and climate variation among sites. This is an important finding because predator diversity is often associated with ecosystem function (Finke and Denno 2004). Similarly, changes in plant composition and richness were detected at wind farm sites, including more frequent encounters of exotic species. Invasions may alter the structure and function of entire biotic communities; for example, when plant invasions reduce the abundance of host plants that are important as food or as habitat (de Groot *et al*. 2007). Reduced plant diversity can also accelerate exotic species establishment, further altering the stability of plant communities and resulting in rapid declines in ecosystem diversity and function (Lyons and Schwartz 2001; Tilman *et al*. 2006).

Of the 32 predatory taxa included in this study, encounter rates were significantly lower in high disturbance areas (negative

values along the treatment axis) for red-tailed hawks and loggerhead shrikes. On average, an individual hawk was encountered every 25.8 h and a shrike every 3.2 h at wind farm sites, compared with more frequent encounters of every 2.3 and 0.9 h at non-turbine sites, respectively. These species are moderately tolerant of human disturbances (Minor *et al*. 1993; Michaels and Cully 1998), and both have been documented using wind farm habitats in California wind resource areas including SGWRA (Smallwood *et al*. 2009; Lovich 2015; Agha *et al*. 2017). Yet, these species may also experience high mortality rates at wind farm facilities (Orloff and Flannery 1992; Smallwood *et al*. 2009; Pagel *et al*. 2013; Lovich 2015).

Of the eleven targeted avian species, burrowing owls, American kestrels and loggerhead shrikes were less abundant or absent from old generation turbine sites relative to sites with newer turbine models. At the Altamont Pass Wind Resource Area in California, these species had higher than average wind turbine collision mortality rates relative to other bird species, and all three were shown to have greater mortality rates at old-generation turbine sites (Smallwood and Karas 2009). Relative to newer turbine models, old-generation turbines may also suppress abundance for avian species with behaviour or habitat affinities that increase turbine-induced mortality risks (Remeš 2000).

Plant community composition

Wind farm sites supported plant communities with diverse life-history characteristics, which may be of greater importance than total plant richness for overall ecosystem function (Hector *et al*. 1999). However, in this study, we documented increased invasive plant richness at wind farm sites. Of the 13 invasive species encountered, a majority (69%) were present at turbine sites. While one or more non-native plants were detected at all sites, ordination scores for non-native plants, and in particular for London rocket (*Sisymbrium irio*), were significantly correlated with the treatment axis (non-native plants were more commonly encountered at wind farm sites and non-turbine sites with high disturbance). At these sites, high road density and heavy human traffic may provide an avenue for invasive plant dispersal and establishment (Trombulak and Frissell 2000).

Conversely, there was clear evidence that disturbed areas supported fewer plant species endemic to deserts within the California floristic province. Only four of the 15 endemic species encountered were present at disturbed sites. In particular, wild Canterbury bells (*Phacelia minor*) and Bigelow's moss fern (*Selaginella bigelovii*) showed the strongest negative association with the disturbance axis (less common at wind farms and disturbed areas). Endemic species are often characterised by narrow niche breadths – traits that may inhibit persistence in disturbed habitats (Slatyer *et al*. 2013). These species may mature late, produce few seeds, produce seeds infrequently, or produce seeds that disperse short-distances; altogether, these characteristics reduce the pace of recolonisation after severe disturbances such as road clearing or electrical fires (McIntyre and Lavorel 1994; Brown and Boutin 2009). Endemics with slow life-history characteristics or narrow habitat preferences may also be less able to compete with invasive species, which were

more common at disturbed non-turbine sites and wind farm sites (Seabloom *et al.* 2003).

Conclusions

Wind farm sites were correlated with low plant richness, particularly for endemic species. Probability of non-native species presence increased at wind farms, an effect that may create a detrimental stepping-stone for invasion into surrounding natural habitats (e.g. Gelbard and Belnap 2003). Predator communities at wind farms were less rich, even and diverse than communities from nearby natural areas. Several avian species showed reduced encounter rates at wind farm sites, which were characterised by fewer unique species relative to nearby communities with lower disturbance intensity. These results indicate that wind farm developments may negatively affect local communities. However, strategies exist to minimise the potential for biodiversity loss at wind energy facilities. Primarily, managers should promote development strategies that reduce permanent physical footprints in local habitats (particularly when rare and endemic or conservation priority species may be affected). Ideally, wind farms should be constructed in areas of low conservation priority, and not in pristine areas or areas sensitive to disturbance (Kiesecker *et al.* 2011). The results from this study indicate that local diversity is affected by wind farm developments and so, in order to avoid significant diversity loss by developing in natural, un-altered habitats, wind farms may instead be situated in areas being used concurrently for ranching, farming, or resource extraction (McDonald *et al.* 2009; Kiesecker *et al.* 2011). By comparing diversity across alternative wind farm siting locations, managers can identify areas where energy development will be the least detrimental. Managers should continue to enforce facility design and management protocols that reduce avian mortality risk, particularly for high-risk taxa such as raptors. For vertebrates, the potential for behavioural avoidance of wind energy facilities should be carefully considered, especially in species that demonstrate ecological interactions that are important for overall ecosystem health (Drewitt and Langston 2006; Pearce-Higgins *et al.* 2009; but see Agha *et al.* 2015*a*).

Wind farms provide a valuable source of renewable energy that can substantially reduce dependence on finite carbon fuels. Yet, this research suggests that wind energy developments affect local biodiversity. With the lowest land-use intensity of any renewable technology (McDonald *et al.* 2009; Ong *et al.* 2013), wind farms provide remnant patches of habitat that are capable of supporting most of the same species found in less-developed areas. It is possible that low land-use intensity allows for greater biologically sustainability of wind farms relative to other renewable technologies. Similar research addressing biodiversity loss at solar, hydroelectric and geothermal facilities is needed to assess the validity of this claim. In sensitive desert habitats where utility-scale renewable energy developments would create substantial risks for local biodiversity, the potential for decentralised energy production strategies needs to be considered (Van Der Schoor and Scholtens 2015).

Conflicts of interest

The authors declare no conflicts of interest.

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