

1 **Bird and bat species' global vulnerability to collision mortality with wind farms revealed**
2 **through a trait-based assessment**

3 Chris B. Thaxter*¹ chris.thaxter@bto.org

4 Graeme M. Buchanan² graeme.buchanan@rspb.org.uk

5 Jamie Carr³ jamie.carr@iucn.org

6 Stuart H. M. Butchart^{4,6} stuart.butchart@birdlife.org

7 Tim Newbold⁵ t.newbold@ucl.ac.uk

8 Rhys E. Green⁶ reg29@hermes.cam.ac.uk

9 Joseph A. Tobias⁷ j.tobias@imperial.ac.uk

10 Wendy B. Foden⁸ fodenw@gmail.com

11 Sue O'Brien⁹ Sue.O'Brien@jncc.gov.uk

12 James W. Pearce-Higgins^{1,6} james.pearce-higgins@bto.org

13 ¹British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK / The David
14 Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK.

15 ²RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, 2 Lochside View,
16 Edinburgh Park, Edinburgh, EH12 9DH, UK.

17 ³International Union for Conservation of Nature, the David Attenborough Building, Pembroke Street,
18 Cambridge, CB2 3QZ, UK.

19 ⁴BirdLife International, David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK.

20 ⁵Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and
21 Environment, University College London, Gower Street, London, WC1E 6BT, UK.

22 ⁶Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street,
23 Cambridge CB2 3EJ, UK.

24 ⁷Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Rd, Ascot SL5
25 7PY, UK

26 ⁸Department of Botany and Zoology, University of Stellenbosch, P/Bag X1, Matieland, 7602
27 Stellenbosch, South Africa.

28 ⁹Joint Nature Conservation Committee, Inverdee House, Baxter Street, Aberdeen, AB11 9QA, UK.

29 *Corresponding author: telephone: +44(0)1842 750050; fax: +44(0)1842 750030

30

31 Running title: Bird and bat vulnerability to wind farms

32

33 **Keywords**

34 Biodiversity, climate change, impact, meta-analysis, phylogeny, renewable energy

35

36

37

38 **Abstract**

39 Mitigation of anthropogenic climate change involves deployments of renewable energy worldwide,
40 including wind farms, which can pose a significant collision risk to volant animals. Most studies
41 into the collision risk of species with wind turbines, however, have taken place in industrialised
42 countries. Potential effects for many locations and species therefore remain unclear. To redress this
43 gap, we conducted a systematic literature review of recorded collisions of birds and bats with wind
44 turbines within developed countries. We related collision rate to species-level traits and turbine
45 characteristics to quantify the potential vulnerability of 9,538 bird and 888 bat species globally.
46 Avian collision rate was affected by migratory strategy, dispersal distance and habitat associations
47 and bat collision rates were influenced by dispersal distance. For birds and bats, larger turbine
48 capacity (megawatts) increased collision rates, however, deploying a smaller number of large
49 turbines with greater energy output, reduced total collision risk per unit energy output, although bat
50 mortality increased again with the largest turbines. Areas with high concentrations of vulnerable
51 species were also identified, including migration corridors. Our results can therefore guide wind
52 farm design and location to reduce the risk of large-scale animal mortality. This is the first
53 quantitative global assessment of the relative collision vulnerability of species groups with wind
54 turbines, providing valuable guidance for minimising potentially serious negative impacts on
55 biodiversity.

56

57 **1. Introduction**

58 In response to projected impacts of climate change on the environment, human society and health
59 [1], political consensus at the 21st Conference of Parties of the United Nations Framework
60 Convention on Climate Change (UNFCCC) led to agreement to hold the increase in global
61 temperatures to below 2°C, above pre-industrial levels, and pursue efforts to limit the increase to
62 1.5°C [2]. Achieving this ambition depends on global emissions peaking around 2020, with
63 negative emissions in the second half of this century [3], requiring large-scale and rapid deployment
64 of renewable energy technologies. Wind farms are the most well-developed, cheapest, widely
65 available and feasible renewable energy technologies for electricity generation [4], and are likely to
66 form an important component of renewable electricity generation strategies.

67 Wind farms can have negative impacts upon biodiversity [5], including direct collision
68 mortality, displacement from feeding or nesting areas, barrier effects to movement and habitat
69 degradation or loss [6]. For volant species such as birds and bats, the risk of collision is a serious
70 concern [5], and large numbers of birds and bats have been shown to be killed by turbines [5,7,8],
71 particularly aggregation sites, such as migratory bottlenecks or near breeding colonies [9]. It has
72 been suggested anecdotally that some species groups, such as migratory bats, raptors and seabirds,
73 may be particularly impacted [9,10], which may at least be partly linked to visual acuity [11].

74 Collision mortality with wind turbines may reduce populations, particularly of long-lived,
75 slow-reproducing species [12,13] and wide-ranging or migratory species [12,14]. Consequently,
76 there is an urgent need to quantify species' vulnerability across as wide a range of species and
77 geography as possible. Further, a recent review highlighted most studies to date have focused on the
78 developed world [5]. The need to identify species' vulnerability, however, is crucial for countries in
79 the developing world, where wind farms may be rapidly deployed to achieve climate change
80 mitigation targets. This paper describes analyses designed to improve our understanding of the
81 factors influencing the collision vulnerability of species to onshore wind turbines, and to inform
82 future wind farm location and design in areas and for species for which this has been little studied.
83 We model the extent to which ecological, morphological and life-history traits, are likely to

84 influence encounter rates with turbines, accounting for variation in parameters that differ between
85 studies. We also consider other factors, such as turbine size, that might affect the likelihood of
86 collision [15,16], to examine the extent which wind farm design may reduce collision rates.

87

88 **2. Methods**

89 **(a) Literature review and data structure**

90 We conducted meta-analyses using Web of Science, Google Scholar[®] and Google[®] to search for
91 peer- and non-peer reviewed literature. Given the known differences in terminology for ‘wind
92 farms’, we used the following search terms: (bird* OR avian) AND wind AND (farm* OR energy
93 OR windfarm* OR industry* OR wind-farm* OR park* OR development* OR facilit*). References
94 reporting collision mortality were identified. Population-level impacts such as mortality rates were
95 rarely available; instead most studies presented the numbers of collisions per species per turbine or
96 per megawatt (MW). The following data were extracted: study reference, wind farm name,
97 geographical location, species’ identity, number of deaths, study duration, wind farm and turbine
98 quantity, turbine size and study quality information (see below). In total, 133 studies for birds and
99 101 for bats reported collision rates. Of these, 88 bird and 87 bat studies were suitable for inclusion,
100 and contained information from 93 and 134 onshore wind farm sites (electronic supplementary
101 material appendix A1, Fig. S1), respectively. Dominant land cover within a 5 km buffer of the
102 centre point coordinate of wind farms was identified from GLC2000 [17]. References and further
103 information on traits are given in electronic supplementary file S1 and data collection files S2.

104 **(b) Study quality and site-specific information**

105 The detectability of collision victims is affected by many factors, including frequency of mortality
106 surveys, scavenger removal, observer skill and variation in encounter probability (detectability)
107 between species [18-20], ground and habitat types and ecosystems. Studies varied in the extent to
108 which they corrected for these factors, and did not provide sufficient information to produce a
109 standardised collision-rate metric [21,22]. Instead, we categorised studies based on quality as
110 follows: (1) ‘very low’: no corrections; (2) ‘low’: correction for aspects of scavenger removal and

111 observer skill, but detectability constant across species; (3) ‘medium’: as with (2) but with multiple
112 corrections for detectability for species’ groupings e.g. ‘small bird’ or ‘large bird’; (4) ‘high’:
113 species-specific corrections for main sources of error (electronic supplementary material appendix
114 A2). For bats, no distinctions were made for species groups, therefore a three-level variable was
115 used, combining low and medium categories. Corrections for bat scavenger removal were
116 sometimes based on proxy bird species, which might potentially introduce bias.

117 The search area around turbines (hereafter, ‘buffer area’) may influence discovery of
118 collision victims and so was included as a covariate (birds: mean \pm 1SD, 2.1 \pm 1.4 ha, range 0.1-8.6
119 ha; bats: 1.2 \pm 1.1 ha, 0.1-8.1 ha). We included ‘year’ (birds: 1.8 \pm 1.6 years, 1-10 years; bats: 1.4 \pm 0.9
120 years, 1-5 years), and ‘number of days’ (birds, 281.7 \pm 106.4 days, bats 238.7 \pm 110.1 days, range 42-
121 365 days) as covariates to control for study duration. A binary factor separated peer- and non-peer
122 reviewed literature. As studies varied in the number of wind farms monitored, this was added as an
123 additional covariate. Turbine size was included as a linear predictor, given its potential impact on
124 mortality rate [12], here assessed as turbine megawatt (MW) output [9] (birds: 1.3 \pm 0.7 MW, 0.2-
125 2.5; bats: 1.6 \pm 0.6 MW, 0.5-3.0 MW).

126 **(c) Species traits**

127 Traits for bird species were taken from the Birdlife International World Biodiversity Database [23]
128 except wing morphology, which was measured directly from museum skins [24] (electronic
129 supplementary material appendix A3). Flightless species were excluded. Habitat, foraging strata and
130 diet were specified using binary factors for each factor level. Migratory status and breeding
131 dispersal distance, body size, clutch size, generation length and Kipp’s distance (a measure of wing
132 morphology related to manoeuvrability [25]) were also obtained.

133 To account for species potentially present, but not recorded in collision, we used spatial
134 distribution polygons based on entire breeding ranges for birds [23] and bats [26] to generate
135 species lists of ‘pseudo-absences’. Although this approach may produce omission errors due to
136 coarse data resolution [27], it allowed potential species presences to be modelled. The frequency of

137 collision may depend on local abundance, but such information was inconsistently reported.
138 Therefore, we included global population size as a proxy, which is likely related to gross variation
139 in density, and is treated as a cautionary assumption.

140 Bat trait data were extracted from the PanTHERIA database [28] but consideration of all
141 traits simultaneously was not possible as data were available for subsets of species per trait. We
142 therefore tested: (1) Population group size [28]; (2) forearm length; (3) body mass; (4) litter size; (5)
143 age of sexual maturity and (6) gestation length. Body mass and forearm length were correlated ($R =$
144 0.92), so forearm length was excluded. As 96% of species were insectivorous [29], diet was not
145 included. Dispersal distance (7), use of tree roost sites (8) and hibernation behaviour (9) were
146 obtained through field guides [e.g. 30] and data portals [26,31,32]. For bats, current knowledge gaps
147 and terminology differences between studies prevented migration from being separated from
148 dispersal [32]. Maximum dispersal distance was defined as ‘sedentary’ <10 km, ‘regional’ 10-100
149 km, and ‘long-distance’ 100+ km, the latter likely equating to long-distance migration [32]. Binary
150 variables were specified for tree roost site and hibernation. Traits 1, 5 and 6 were only available for
151 a smaller proportion of species ($n = 36$), and were not significant ($P > 0.05$) when considered
152 alongside the remaining traits. Therefore, we present models for traits 3, 4 and 7-10 for 67 species
153 (see electronic supplementary material appendices A3-A5).

154 **(d) Phylogeny**

155 To account for potential phylogenetic non-independence of data, we used bootstrapped estimates of
156 phylogenetic relationships from the BirdTree database [33]. We generated 1,000 random trees,
157 reduced further into a single minimum consensus tree using a Python algorithm, taking a minimum
158 of 50% support for branching events [34]. Seven different methods for generating trees were
159 available for birds [33], providing seven alternative models. For bats, we used a phylogenetic tree
160 within the R package ‘ape’ [35]. This tree had no bootstrapped estimates available, but species with
161 available trait data were well represented (> 95%).

162 **(e) Statistical analysis**

163 Bayesian Markov Chain Monte Carlo (MCMC) generalized linear mixed models were used to
164 model the variation in collision rates, using the R package MCMCglmm [36,37]. Models were
165 specified using a zero-adjusted Poisson error structure and a response of collisions per turbine,
166 including the logarithm of the number of turbines surveyed as an offset; an R script for birds is
167 provided in electronic supplementary data collection files S2. Fixed effects were specified for
168 species traits, study quality and site-specific information (electronic supplementary material Table
169 S1). To assess the effect of inserting pseudo-absences, we repeated our analysis based on recorded
170 collisions, which produced similar results (electronic supplementary material appendix A5). We
171 therefore present results for models including pseudo-absences. Phylogenetic signals were included
172 by specifying the ‘tip label’ of species names from the minimum consensus tree as a random effect
173 [38], alongside a matrix inversely proportional to the covariance structure of ‘tip label’ [37].
174 Phylogenetic models were better fitting than those excluding phylogeny in all cases ($dDIC < -2.0$).
175 Study ID was included as a random effect to account for repeated measurements of collisions per
176 species and study. Uninformative priors were specified except for $\log(\text{turbine})$ included as an
177 informative prior to represent an offset. We specified 105,000 Monte Carlo iterations with a burn-in
178 of 5,000 and thinning of 100, to leave 1,000 samples from the posterior distributions. The
179 proportion of variance explained by fixed and random effects was examined [39] to generate
180 conditional (fixed plus random effects) and marginal (fixed effects only) R^2 values. Significance of
181 fixed effects was determined by whether 95% lower and upper credible intervals (‘LCL’, ‘UCL’)
182 drawn from the posterior distribution overlapped zero. For birds, model-averaged coefficients were
183 computed across all seven phylogenetic models with equal weighting.

184 For birds, predicted numbers of collisions/turbine/year were generated from full models for
185 9,568 species worldwide based on trait relationships. Predictions were generated marginal to the
186 random effect of study ID, and were made at highest data quality level for a 365-day duration,
187 equating to rates of collision per annum. Estimates for each species were treated as a final collision
188 vulnerability index. For bats, full trait data were available for the 67 species modelled. To maximise

189 the global generally of our predictions, we based predictions on phylogenetic correlation only (for
190 888 species) from a model including only study and site fixed effects ('no-traits' model). All
191 modelling was conducted in R version 3.3.1 [40]. Full predictions are given in electronic
192 supplementary files S3 and S4.

193 For an independent check of correspondence, predicted vulnerability values were compared
194 to a previous expert assessment of species vulnerability to the threat of 'renewable energy' in the
195 IUCN Red List (Threats Classification Scheme Version 3.2 [26]). Modelled predictions were
196 summarised in 5% percentiles, and presented for those threatened species identified in the IUCN
197 Red List. To assess whether species may be more at risk of collisions than other species, we used a
198 Generalised Linear Model to test whether collision rates varied by Red List category (Least
199 Concern, Near Threatened and 'Threatened', i.e. Vulnerable, Endangered or Critically Endangered)
200 in interaction with taxon (bird vs bat), weighted by the reciprocal of collision rate error.

201 **(f) Turbine capacity effects on bird and bat mortality**

202 We generated predictions of mean collisions/turbine/year across all species for increasing turbine
203 capacity, for the range of turbine sizes included in this review (0.1 MW to 2.5 MW). The number of
204 turbines required to meet a hypothetical 10 MW energy demand were then multiplied by these
205 estimates to investigate the mean number of predicted deaths/year across species for birds and bats
206 with increasing turbine capacity.

207 **(g) Spatial variation in vulnerability to wind energy**

208 Spatial variation in the potential impact of turbines on collision rates was mapped globally, based
209 on the predicted occurrence of species within a grid (resolution, 5x5 km), derived from overlaps
210 with species range maps [23]. For birds and bats, the MCMC posterior predictions for each species
211 were extracted. The predicted collision rates for each species that occurred in a 5 km cell (v_i) were
212 summed across all species ($v_1+v_2+v_3\dots v_j$), up to the total number j occurring in that cell. A mean
213 cumulative value, with 95% credible intervals, was then generated and mapped as a 'vulnerability'

214 surface for birds and bats. Spatial data processing was undertaken in SAS 9.3 (SAS Institute Inc.)
215 and ArcMap 9.3.

216

217 **3. Results**

218 **(a) Data summary**

219 A total of 362 bird and 31 bat species were recorded as collision victims with 407 and 41 further
220 bird and bat species included as pseudo-absences. Data were obtained from 16 countries for birds
221 and 12 countries for bats. The dataset was spatially-biased to North America (birds, 64.0%, bats
222 48.6%) and Europe (birds, 31.0%, bats 50.6%), although South Africa, Japan, Australia and New
223 Zealand were represented (electronic supplementary material appendix A1, Fig. S1). In total, 36%
224 studies were in forests and 29% were in agricultural areas (e.g. artificial landscapes) with fewer in
225 shrub (9%) and grassland (14%) landscapes. Agricultural land cover, was over-represented in the
226 review in comparison to global land cover (17%), whereas shrub (21%) and grassland (26%) were
227 under-represented and forest was sampled approximately in proportion (37%) - electronic
228 supplementary material appendix A4.

229 **(b) Study quality and site-specific variables**

230 Studies that had not corrected for carcass detection probability (birds ‘very low’; bats ‘low’) or the
231 size of birds (‘low’), significantly underestimated the number of collisions compared to studies that
232 had made such corrections ($P < 0.001$ in all cases, Fig. 1; see also electronic supplementary material
233 Tables S3 and S4). By contrast, ‘high’ and ‘medium’ quality levels were not significantly different
234 from the average (Fig. 1, $P > 0.05$). There was no residual variation explained by peer and non-peer
235 review studies, buffer area, number of wind farms and study duration in days or years, after
236 accounting for overall study-level variation using random effects ($P > 0.05$). There was, however, a
237 strong positive correlation between turbine capacity (MW) and collisions per turbine (Fig. 1, $P <$
238 0.01 in all models).

239 **(c) Species’ traits**

240 For birds, habitat association was an important predictor of collision rates (Fig. 1a, electronic
241 supplementary material Tables S3 and S4). Species using artificial (such as farmland and urban
242 areas) and grassland habitats had significantly higher collision rates than species not using these
243 habitats ($P < 0.01$ in all cases). Species using marine habitats had significantly lower collision rates
244 than species not using marine environments, likely influenced by a paucity of data for offshore wind
245 farms. Species feeding on fruit and nectar had lower collision rates compared with species with
246 other diets. Diet and foraging strata had smaller effects than habitat, with coefficients being mostly
247 non-significant (Fig. 1a). Migrants exhibited higher estimated collision rates than non-migrants
248 (Fig. 1). One model gave significant support to migratory status (electronic supplementary material
249 appendix A5), and the direction of the effect was consistent across all models, but the mean effect
250 size across models just overlapped zero. Species with median dispersal rates of 25-49 km or 50-99
251 km had significantly higher estimated collision rates from some models than those dispersing
252 smallest (<25 km) or longest distances (>100 km).

253 For bats, species dispersing furthest had significantly greater collision rates than sedentary
254 species (Fig. 1), but roost site and hibernation were not significant predictors (Fig. 1). When fitted
255 without dispersal, however, tree-roosting species had significantly higher collision rates than other
256 species (electronic supplementary material appendix A5).

257 **(d) Model fit**

258 The marginal R^2 explained by fixed effects was 0.46 for birds, and for bats was 0.30 for the trait-
259 based model, and 0.19 for the no-traits model (Table 1). For birds, the phylogenetic models
260 produced similar beta-coefficients (Fig. 1, electronic supplementary material appendices A4 and
261 A5, Tables S2 and S4). Phylogeny explained a high proportion of variance in all models (Table 1).
262 Effective sample sizes of >200 and diagnostic plots indicated that autocorrelation within MCMC
263 chains was appropriately accounted for.

264 **(e) Model predictions**

265 For birds, 957 species had collision rates of more than 0.046 collisions/turbine/year (90% quartile),
266 of which 175 species were Accipitriformes (Fig. 2), 57% species in that Order. Accipitriformes had

267 the highest predicted collision rates of any taxonomic order (0.073 ± 0.064 SD
268 collisions/turbine/year, mean LCI < 0.001 , mean UCI, 0.288). Mean predictions were also high for
269 Bucerotiformes, Ciconiformes and Charadriiformes, whereas Galbuliformes and Coraciiformes
270 were among the lowest, and waterbirds such as Anseriformes and Galliformes and Passeriformes
271 songbirds also had smaller than average predictions (Fig. 2).

272 For bats, the most vulnerable families containing > 10 species/family included Molossidae
273 and Hipposideridae, whilst Rhinolophidae were amongst the least vulnerable (Fig. 3). The largest
274 family, Vespertilionidae, had high collision rates (0.718 ± 0.586 SD, 294 species) and included the
275 five bat species most vulnerable to collision (electronic supplementary material appendix A6).

276 In total, 55 bird species (including 31 Acciptriformes) were identified as threatened by
277 ‘renewable energy’ [26], of which 43 species (78%) above the 75% percentile of our collision
278 predictions (electronic supplementary material Table S6). Of the 31 Acciptriformes, all were above
279 the 75% percentile and 26 (84%) were ranked above the 90% percentile. After accounting for a
280 significantly greater collision rate for bats than birds ($\chi^2 = 510.30$, $P < 0.001$), there was no residual
281 variation explained by IUCN Red List category ($\chi^2 = 0.63$ $P = 0.73$), or among categories
282 comprising the broader ‘threatened’ category (Vulnerable, Endangered or Critically Endangered)
283 ($\chi^2 = 0.19$ $P = 0.91$, electronic supplementary material appendix A7).

284 **(f) Relationships between turbine size and mortality**

285 For birds and bats, larger turbines were associated with increased collision rates (Fig. 1). A greater
286 number of small turbines, however, resulted in higher predicted mortality rates (Fig. 4) than a
287 smaller number of large turbines per wind farm unit energy output. Using 1000, 0.01 MW turbines
288 resulted in the largest estimated number of bird and bat fatalities; thereafter the numbers decreased
289 exponentially up to *ca.* 1.2 MW, where the relationship for birds continued to decline up to 2.5 MW
290 turbines (posterior means, LCL-UCL 0.8, 0.5-1.1). By contrast, the mortality for bats increased
291 again from 14 (8-21) bats with 1.2 MW turbines, to 24 (12-40) bats with 2.5 MW turbines (Fig. 4),
292 although with overlapping credible intervals.

293 **(g) Spatial variation in vulnerability to wind energy**

294 For birds, the greatest numbers of vulnerable species occurred along coastal and migratory
295 pathways in the eastern and south-western USA, the central American isthmus from Mexico to
296 Panama, northern Andes, Rift valley of east Africa and the Himalayas. For bats, the greatest number
297 of collisions was predicted in North America (Fig. 5).

298

299 **4. Discussion**

300 Previous studies into the collision risk of birds with terrestrial wind farms have documented a high
301 risk for Accipitriformes (raptors and birds of prey) [41,42]. Further studies have suggested that
302 raptors, migratory soaring birds and waterbirds may be particularly vulnerable [9,43-45]. Similarly,
303 our study showed that Accipitriformes had the highest rates of collision. Among other orders,
304 Bucerotiformes (hornbills and hoopoes), Ciconiformes (storks and herons) and some
305 Charadriiformes (shorebirds) were also vulnerable, but notably many waterbirds (e.g.
306 Anseriformes) were not.

307 Although there was less variation in predicted mortality between bat families (Fig. 3), a
308 small number of Vespertilionidae species were associated with relatively high rates of collision, as
309 also found in a recent review [8]. Our models predicted higher collision rates for bats than birds, as
310 reported elsewhere [15] and adds to the literature emphasising the risk that wind farms pose to bat
311 populations [7,8,14].

312 For birds, vulnerability to collision was related to habitat, migratory status and dispersal
313 distance. High collision rates for species associated with agricultural habitats may reflect the
314 disproportionate number of wind farms from agricultural landscapes in our sample. Species
315 associated with these human-modified habitats, however, may be less likely to avoid wind farms
316 than those occupying natural landscapes [46], while our results suggest that grassland species may
317 also be more vulnerable to collision.

318 Migratory species are often suggested as being vulnerable to collision with wind farms [44],
319 for which our results are supportive. Previous work has suggested high rates of collision with wind
320 turbines at avian migratory bottlenecks [9,41,42], and for migratory bats in North America [8,47],
321 suggesting, migration may outweigh the greater exposure time of residents to wind turbines [41].

322 Wind farms may have significant meta-population level impacts [45], for example on
323 species with large home-ranges and moderate rates of dispersal [12]. The link, however, between
324 dispersal distance and collision rate across multiple species has not previously been identified, and
325 demonstrates that bird species dispersing short or very long distances may have reduced
326 vulnerability to collision than species dispersing intermediate distances. Those species dispersing
327 furthest may exhibit unmeasured traits of flight behaviour, such as flight height rendering them less
328 susceptible to collision, but the large uncertainty in the effect emphasises further study is needed.
329 For bats, long-distance dispersers had the highest collision rates, but certainty of behaviour for
330 many species tempers our ability to draw firm conclusions. Tree-roosting bat species were
331 frequently recorded in collision, potentially through attraction mechanisms [48], although this effect
332 was weaker than dispersal. Overall, these findings emphasise the need to consider cumulative
333 impacts of wind farms on populations, particularly for migrants and wide-ranging species.

334 Our vulnerability estimates may not reflect population-level impacts, to understand which
335 requires further consideration of population demography and other impact metrics [22,45].
336 However, our findings may be problematic in terms of species conservation, as the species groups
337 with the greatest rate of collision tended to be *k*-selected species with low fecundity and late ages of
338 maturity, and most sensitive to impacts of additional mortality [49,50], such as Accipitriformes,
339 Bucerotiformes Ciconiformes and Charadriiformes for birds, and a range of bat species. Avoiding
340 placement of wind farms in areas with populations or high concentrations of such species, such as
341 coastal areas migratory flyways (Fig. 5), would reduce potential impacts of wind farms on
342 biodiversity. Although some passerine families (e.g. Motacillidae) and species (e.g. European
343 Starling *Sturnus vulgaris*) had high predicted rates of collision, their *r*-selected life-histories and

344 relatively high abundances make it less likely that large population-level effects would arise, as
345 population growth rate is less sensitive to reductions in adult survival [49].

346 Although as comprehensive as possible, our study has some limitations. First, data were
347 largely from well-studied parts of Europe and North America. While our results can be used to infer
348 potential collision risk for species in other parts of the world, uncertainty arises when extrapolating
349 to under-studied regions and taxa. This was particularly the case for bats, where studies were
350 exclusively from temperate northern latitudes with low species diversity. More geographically
351 widespread studies, from the tropics and from countries with rapidly growing wind industries (such
352 as India and China), are required to feed into meta-analyses like ours. In the absence of such
353 studies, our estimated collision rates should help indicate vulnerable species in these areas. Second,
354 collision rate data were not available from offshore wind farms. Only 5% of studies recorded
355 collisions with marine species at coastal wind farms, and further work is needed to estimate their
356 vulnerability to offshore wind turbines [51]. Third, trait information for bats was less
357 comprehensive than for birds, meaning it was not possible to extrapolate from a trait-based model
358 globally in the same manner. We also note the strong geographical variation in predicted bat
359 mortality rates between North America and Europe (Fig. 5), and suggest further work is required to
360 test whether this effect is real. Fourth, although we corrected for data quality, inevitably some
361 variation will not be captured by our classification, for example, correction for unsearchable portions
362 of the survey area were not always reported. Fifth, our study metric focused on a measured impact
363 after collision with turbines, reflecting both initial sensitivity and current exposure. Our study,
364 however, did not include future potential to habituate (adaptability), necessitating caution when
365 translating our findings more broadly. Finally, our list of species putatively present at a wind farm
366 were derived from broad-scale distribution polygons, and so may have included false negatives
367 [27].

368 Given the recent dramatic increases in wind-energy generating capacity in parts of the world
369 where wind farms have not previously been deployed [52], and likely continued increases to meet

370 climate change mitigation targets, wind farms pose an increasing threat to bird and bat species
371 worldwide. Our study can be used to mitigate this risk in two ways. First, although uncertain, our
372 species-level predictions of collision rates provide a useful starting point for scoping potential
373 impacts of wind farms on species where collision risk has not been studied. New wind
374 developments should preferably be in areas with low concentrations of species vulnerable to
375 collision. Our results can help identify locations based on the distribution of vulnerable species,
376 which alongside habitat restrictions on wind farm development, such as in forested areas, can be
377 used to minimise the risk of negative biodiversity impact. Although country and regional maps
378 [53,54] should be developed to help identify local hotspots, our global vulnerability maps (Fig. 5)
379 are a useful starting point, suggesting key areas and migratory pathways where collision may occur.
380 The agreement between our predictions and species classified by the IUCN Red List as being
381 threatened by ‘renewable energy’ suggests an emerging consensus for key taxa.

382 Second, there was a strong positive relationship between wind turbine capacity and collision
383 rate per turbine. The strength of this relationship, however, was insufficient to offset the reduced
384 number of turbines required per unit energy generation with larger turbines, at least for birds.
385 Therefore, to minimise bird collisions, wind farm electricity generation capacity should be met
386 through deploying fewer, large turbines, rather than many smaller ones, supporting suggestions for
387 marine birds [16]. For bats, an optimum turbine size of *ca.* 1.25 MW may minimise collision risk,
388 with the largest turbines associated with a disproportionately high collision rate, but we again
389 caution that model certainty for bats was low for the reasons outlined. More research is required to
390 understand the relationship between collision risk and turbine size for larger (and more efficient)
391 turbines, and how this may vary between habitats.

392 **5. Conclusion**

393 This study is the first global quantitative assessment from the published literature of the relative
394 vulnerability of different species groups to wind farms. Wind farms have the potential to benefit
395 biodiversity through their contribution to climate change mitigation, but our results emphasise the

396 global nature of the potential risks to biodiversity involved, which needs to be accounted for
397 through appropriate wind turbine design and planning, if those risks are to be minimised.

398

399 **Data accessibility.** Supporting data are available on the Dryad Digital Repository:

400 <http://dx.doi.org/>.

401 **Authors' contributions.** CBT, JWP-H, GMB, JC, SHMB, TN and REG conceived and designed
402 the study. CBT conducted the literature review and carried out the meta-analysis. JC, SHMB and
403 TAT extracted and provided data for analysis and GMB produced mapped outputs from statistical
404 models. CBT and JWP-H drafted the manuscript, and conceived appropriate testing and statistical
405 procedures, under the guidance of all authors, and an independent project advisory group, including
406 WBF and SO. All authors edited the manuscript and gave final approval for publication.

407 **Competing interests.** All authors have no competing interests.

408 **Funding.** This research was funded by the Cambridge Conservation Initiative

409 (<http://www.conservation.cam.ac.uk/>), a strategic collaboration between the University of

410 Cambridge, UK and nine leading conservation organisations, thanks to the generosity of the
411 Arcadia Fund.

412 **Acknowledgements.** We are grateful to the project advisory group (including Colin Galbraith, Aida
413 Kowalska, James Watson and Mark Wright) for their advice and support through the project.

414 Thanks also to Nadia Thornton for help with the bat literature review, and to Tina Sommarstorm for
415 help with processing the Pantheria trait data.

416

417 **References**

- 418 1. IPCC 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II*
419 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*
420 [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151
421 pp.
- 422 2. UNFCCC. 2015 Adoption of the Paris Agreement. FCCC/CP/2015/10/Add.1.
- 423 3. Schleussner C-F, Rogelj J, Schaeffer M, Lissner T, Licker R, Fischer EM, Kutti R,
424 Levermann A, Frieler K, Hare W. 2016 Science and policy characteristics of the Paris
425 Agreement temperature goal. *Nat. Clim. Chang.* **6**, 827–835.
- 426 4. Kumar Y, Ringenber J, Depuru SS, Devabhaktuni VK, Lee JW, Nikolaidis E, Andersen B,
427 Afjeh, A. 2016 Wind energy: trends and enabling technologies. *Renew. Sustainable Energy*
428 *Rev.* **53**, 209–224.
- 429 5. Schuster E, Bulling L, Köppel J. 2015 Consolidating the State of Knowledge: A Synoptical
430 Review of Wind Energy’s Wildlife Effects. *Environ. Manage.* **56**, 300–331.
- 431 6. Drewitt A, Langston RHW. 2006 Assessing the impacts of wind farms on birds. *Ibis* **148**, 29–
432 42.
- 433 7. Hayes MA. 2013 Bats killed in large numbers at United States wind energy facilities.
434 *BioScience* **63**, 975–979.
- 435 8. Zimmerling JR, Francis CM. 2016 Bat mortality due to wind turbines in Canada. *J. Wildl.*
436 *Manage.* (doi: 10.1002/jwmg.21128)
- 437 9. Pearce-Higgins JW, Green RE. 2014 *Birds and Climate Change: Impacts and Conservation*
438 *Responses*. Cambridge University Press, UK. www.cambridge.org/bacc.
- 439 10. Frick WF, Baerwald EF, Pollock JF, Barclay RMR, Szymanski JA, Weller TJ, Russell AL,
440 Loeb SC, Medellin RA, McGuire LP. 2017 Fatalities at wind turbines may threaten
441 population viability of a migratory bat. *Biol. Conserv.* **209**, 172–177.

- 442 11. Martin GR, Portugal SJ, Murn CP. 2012 Visual fields, foraging and collision vulnerability
443 in *Gyps* vultures. *Ibis* **154**, 626-631.
- 444 12. Carrete M, Sanchez-Zapata JA, Benitez JR, Lobon M, Donazar JA. 2009 Large scale risk-
445 assessment of wind-farms on population viability of a globally endangered long-lived raptor.
446 *Biol. Conserv.* **142**, 2954–2961.
- 447 13. Dahl EL, Bevanger K, Nygard T, Roskaft E, Stokke BG. 2012 Reduced breeding success in
448 white-tailed eagles at Smola windfarm, western Norway, is caused by mortality and
449 displacement. *Biol. Conserv.* **145**, 79–85.
- 450 14. Voigt CC, Popa-Lisseanu AG, Niermann I, Kramer-Schadt S. 2012 The catchment area of
451 wind farms for European bats: a plea for international regulations. *Biol. Conserv.* **153**, 80–86.
452 (doi:10.1016/j.biocon.2012.04.027)
- 453 15. Barclay RMR, Baerwald EF, Gruver JC. 2007 Variation in bat and bird fatalities at wind
454 energy facilities: assessing the effects of rotor size and tower height. *Can. J. Zool.* **85**, 381–
455 387
- 456 16. Johnston A, Cook ASCP, Wright LJ, Humphreys EM, Burton NHK. 2014 Modelling flight
457 heights of marine birds to more accurately assess collision risk with offshore wind turbines. *J.*
458 *Appl. Ecol.* **51**, 31–41.
- 459 17. Bartholomé E, Belward AS. 2005 GLC2000: a new approach to global land cover mapping
460 from Earth observation data. *Int. J. Remote Sens.* **26**, 1959–1977.
461 (dx.doi.org/10.1080/01431160412331291297)
- 462 18. Smallwood KS. 2013 Comparing Bird and Bat Fatality-Rate Estimates Among North
463 American Wind-Energy Projects. *Wildl. Soc. Bull.* **37**, 19–33.
- 464 19. Huso MMP, Dalthorp D. 2014 Accounting for unsearched areas in estimating wind turbine-
465 caused fatality. *J. Wildl. Manage.* **78**, 347–358.
- 466 20. Loss SR, Will T, Marra PP. 2013 Estimates of bird collision mortality at wind facilities in the
467 contiguous United States. *Biol. Conserv.* **168**, 201–209.

- 468 21. Smallwood KS. 2017. Long search intervals underestimate bird and bat fatalities caused by
469 wind turbines. *J. Wildl. Manage.* 41: 224-230.
- 470 22. Erickson WP, Wolfe MM, Bay KJ, Johnson DH, Gehring JL. 2014 A Comprehensive
471 Analysis of Small-Passerine Fatalities from Collision with Turbines at Wind Energy
472 Facilities. *PLoS ONE* 9(9): e107491. (doi:10.1371/journal.pone.0107491)
- 473 23. Birdlife International. 2016a Birdlife datazone. <http://www.birdlife.org/datazone>. (accessed
474 19/10/2016)
- 475 24. Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, Barlow J,
476 Tobias JA. 2016 Using avian functional traits to quantify the impact of land-cover change on
477 ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. Lond. B* **283**,
478 20161289.
- 479 25. Baldwin MW, Winkler H, Organ CL, Helm B. 2010 Wing pointedness associated with
480 migratory distance in common garden and comparative studies of stonechats (*Saxicola*
481 *torquata*). *J. Evol. Biol.* **23**, 1050–1063.
- 482 26. IUCN. 2016 The IUCN Red List of Threatened Species, 2016-2. ISSN 2307-8235.
483 <http://www.iucnredlist.org/>. (last accessed 20/10/2016)
- 484 27. Beresford AE, Buchanan GM, Donald PF, Butchart SHM, Fishpool LDC, Rondinini C. 2011
485 Poor overlap between the distribution of Protected Areas and globally threatened birds in
486 Africa. *Anim. Conserv.* **14**, 99–107.
- 487 28. Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, David C, Orme L, Safi K, Sechrest W,
488 Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA,
489 Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM,
490 Purvis A. 2009 PanTHERIA: a species-level database of life history, ecology, and geography
491 of extant and recently extinct mammals. *Ecology* **90**, 2648.
- 492 29. Kissling WD, Dalby L, Fløjgaard C, Lenoir J, Sandel B, Sandom C, Trøjelsgaard K, Svenning
493 J-C. 2014 Establishing macroecological trait datasets: digitalization, extrapolation, and

- 494 validation of diet preferences in terrestrial mammals worldwide. *Ecol. Evol.* **4**, 2913–2930.
495 (<http://dx.doi.org/10.1002/ece3.1136>)
- 496 30. Dietz C, Kiefer A. 2016 Bats of Britain and Europe. Bloomsbury Publishing, London.
- 497 31. Animal Diversity Web. 2017 The Animal Diversity Web (ADW), Musuem of Zoology,
498 university of Michigan. <http://animaldiversity.org/> [last accessed 06/07/2017]
- 499 32. Barova S. & Streit A. 2016 Action Plan for the Conservation of Bat Species in the European
500 Union - 2016 – 2021: DRAFT. Inf.EUROBATS.AC21.5. European Commission & UNEP
501 Eurobats.
- 502 33. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in
503 space and time. *Nature* **491**, 444–448. (<http://birdtree.org>)
- 504 34. Rubolini D, Liker A, Garamszegi LZ, Møller AP, Saino N. 2015 Using the BirdTree.org
505 website to obtain robust phylogenies for avian comparative studies: A primer. *Curr. Zool.* **61**,
506 959–965.
- 507 35. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R
508 language. *Bioinformatics* **20**, 289–290.
- 509 36. Hadfield JD. 2010 MCMC Methods for Multi-Response Generalized Linear Mixed Models:
510 The MCMCglmm R Package. *J. Stat. Soft.* **33**, 1–22.
- 511 37. Hadfield JD. 2016 Package ‘MCMCglmm’, Version 2.22.1. [https://cran.r-](https://cran.r-project.org/web/packages/MCMCglmm/MCMCglmm.pdf)
512 [project.org/web/packages/MCMCglmm/MCMCglmm.pdf](https://cran.r-project.org/web/packages/MCMCglmm/MCMCglmm.pdf). (last accessed 12/12/2016)
- 513 38. Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life history and
514 sexual selection on male and female plumage colouration. *Nat. Res. Lett.*
515 (doi:10.1038/nature15509)
- 516 39. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining *R* from
517 generalized linear mixed-effects models. *Methods Ecol. Evol.* **4** 133–142.
518 (doi: 10.1111/j.2041-210x.2012.00261.x)

- 519 40. R Core Team. 2016. R: A Language and Environment for Statistical Computing. R
520 Foundation for Statistical Computing, Vienna, Austria.
- 521 41. Barrios L, Rodriguez A. 2004 Behavioural and environmental correlates of soaring-bird
522 mortality at on-shore wind turbines. *J. Appl. Ecol.* **41**, 72–81.
- 523 42. Smallwood KS, Thelander C. 2008 Bird mortality in the Altamont Pass Wind Resource Area,
524 California. *J. Wildl. Manage.* **72**, 215–223.
- 525 43. Steward GB, Pullin AS Coles CF. 2007 Poor evidence-base for assessment of windfarm
526 impacts on birds. *Environ. Conserv.* **34**, 1–11.
- 527 44. Desholm M. 2009 Avian sensitivity to mortality: Prioritising migratory species for assessment
528 at proposed wind farms. *Journal of Environmental Management* 90: 2672-2679.
- 529 45. Beston JA, Diffendorfer J, Loss SR, Johnson DH. 2016 Prioritizing avian species for their risk
530 of population level consequences from wind energy development. *PLoS ONE* 11:e0150813.
- 531 46. Pearce-Higgins JW, Stephen L, Langston RHW, Bainbridge IP, Bullman R. 2009 The
532 distribution of breeding birds around upland wind farms. *J. Appl. Ecol.* **46**, 1323–1331.
- 533 47. Voigt CC, Lehnert, LS, Petersons G, Adorf F, Bach L. 2015 Wildlife and renewable energy:
534 German politics cross migratory bats. *Eur. J. Wildl. Res.* **61**, 213. (dx.doi:10.1007/s10344-
535 015-0903-y)
- 536 48. Cryan PM, Gorresen PM, Hein CD, Schirmacher MR, Diehl RH, Huso MM, Hayman DTS,
537 Fricker PD, Bonaccorso FJ, Johnson DH, Heist K, Dalton DC. 2014 Behavior of bats at wind
538 turbines. *PNAS* **111**, 15126-15131.
- 539 49. Sæther B-E, Bakke Ø. 2000 Avian Life History Variation and Contribution of Demographic
540 Traits to the Population Growth Rate. *Ecology* **81**, 642–653.
- 541 50. Niel C, Lebreton J-D. 2005 Using demographic invariants to detect overharvested bird
542 populations from incomplete data. *Conserv. Biol.* **19** 826–835. (doi: 10.1111/j.1523-
543 1739.2005.00310.x)

- 544 51. Newton I, Little B. 2009 Assessment of wind-farm and other bird casualties from carcasses
545 found on a Northumbrian beach over an 11-year period. *Bird Study* **56**, 158–167.
- 546 52. Ahmed S, Mahmood A, Hasan A, Sidhu GAS, Butt MFU. 2016 A comparative review of
547 China, India and Pakistan renewable energy sectors and sharing opportunities. *Renew.*
548 *Sustainable Energy Rev.* **57**, 216–225.
- 549 53. Bright JA, Langston RHW, Bullman R, Evans RJ, Gardner S, Pearce-Higgins JW, Wilson E.
550 2008 Map of bird sensitivities to wind farms in Scotland: a tool to aid planning and
551 conservation. *Biol. Conserv.* **141**, 2342–2356.
- 552 54. BirdLife International. 2016b Soaring bird sensitivity mapping tool. Available at
553 <https://maps.birdlife.org/MSBtool/>. (accessed 15/12/2016)

554

555

556

557

558

559

560

561 **Table 1.** Summary of MCMCglmm model fits, assessed using pseudo-R² values, for birds (model-
 562 average across seven phylogenetic models, electronic supplementary material Table S2) and bats.

Taxa	Model type	Marginal: fixed effects		Conditional: Random ID + Phylo		Conditional: Random ID	
		Mean	Posterior mode (95% CI)	Mean	Posterior mode (95% CI)	Mean	Posterior mode (95% CI)
Birds	Traits model	0.46	0.45 (0.35-0.56)	0.85	0.85 (0.82-0.88)	0.66	0.65 (0.57-0.72)
Bats	Traits model	0.30	0.30 (0.11-0.50)	0.84	0.83 (0.77-0.92)	0.58	0.64 (0.37-0.75)
Bats	No-traits model	0.19	0.08 (0.04-0.42)	0.88	0.87 (0.81-0.95)	0.39	0.39 (0.16-0.62)

563
 564

565 **Figure Legends**

566 **Figure 1.** Coefficients from MCMCglmm models for (a) birds, and (b) bats. For birds, model
567 averaged coefficients are presented from seven models using alternative phylogenetic
568 reconstruction methods, presenting: (1) mean posterior predictions averaged, (2) range of mean
569 estimates, (3) posterior standard deviations averaged, (4) mean 95% credible intervals (CIs) and (5)
570 maximum 95% credible intervals. For bats, the posterior mean estimate, and lower and upper 95%
571 credible intervals, are given from the single trait-based model; the significance of each term (“Sig”)
572 is presented using the maximum level of significance attained ($P < 0.01$; $*P < 0.05$, $** P < 0.01$;
573 $*** P < 0.001$).

574 **Figure 2.** Predictions of mean collisions per turbine (per year) (\pm SD) for bird orders (9,568 species)
575 from the posterior distributions of MCMCglmm models, ordered by mean predictions; numbers of
576 species per Order are shown by black dots.

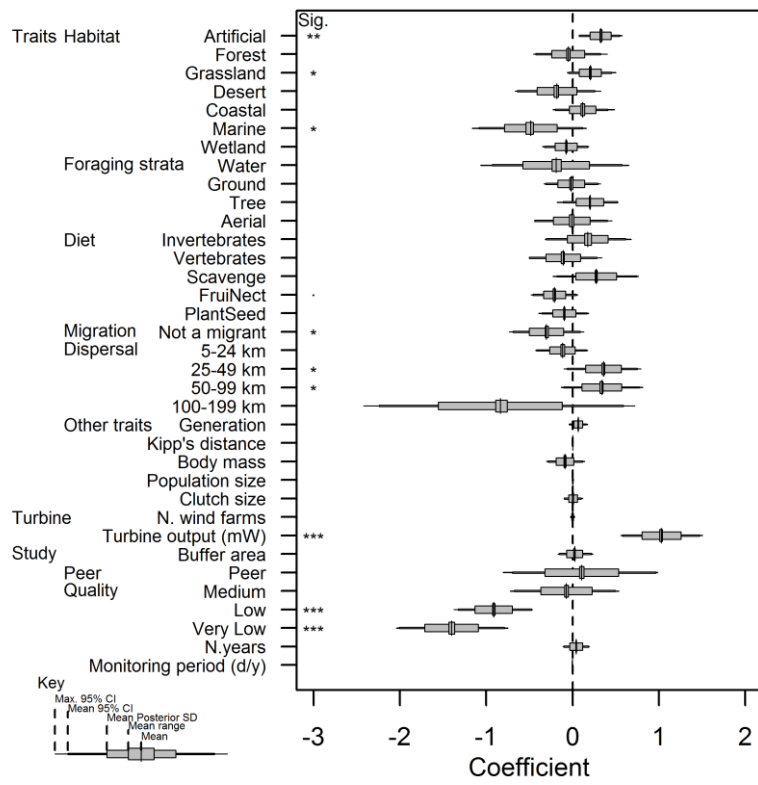
577 **Figure 3.** Predictions of mean collisions per turbine (per year) (\pm SD) for bat families (888 species)
578 from the posterior distributions of MCMCglmm models, ordered by mean predictions; numbers of
579 species per family are shown by black dots.

580 **Figure 4.** The mean total mortality rate across species for a hypothetical 10 MW wind farm, shown
581 in relation to individual turbine capacities (which in turn require different numbers of wind turbines
582 to meet the same capacity). Lines represent posterior means and 95% upper and lower credible
583 intervals.

584 **Figure 5.** Worldwide distribution of bird species’ vulnerability to wind farm collisions, based on
585 summing vulnerability of each species that occurs at each point, according to species range maps
586 for (a) mean across species, and lower and upper (b and c) credible intervals from MCMCglmm
587 models (for details of data manipulation and calculations behind these maps, see methods).

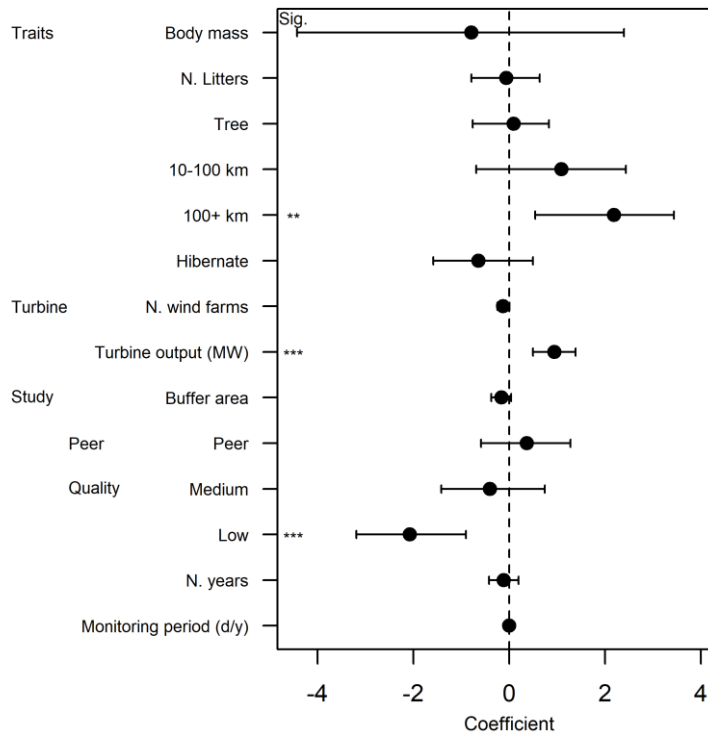
588

589 Fig. 1 (a)



590

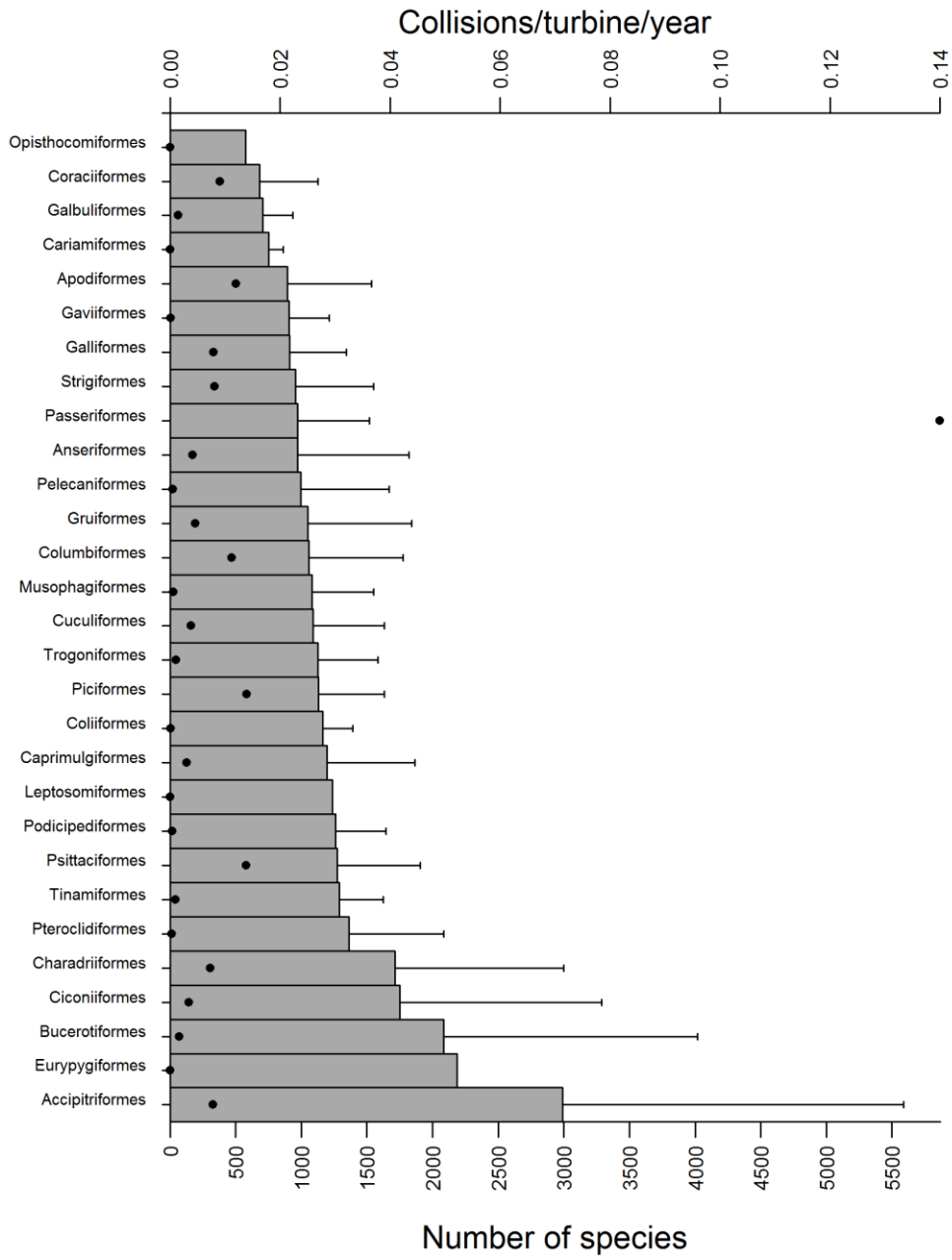
591 (b)

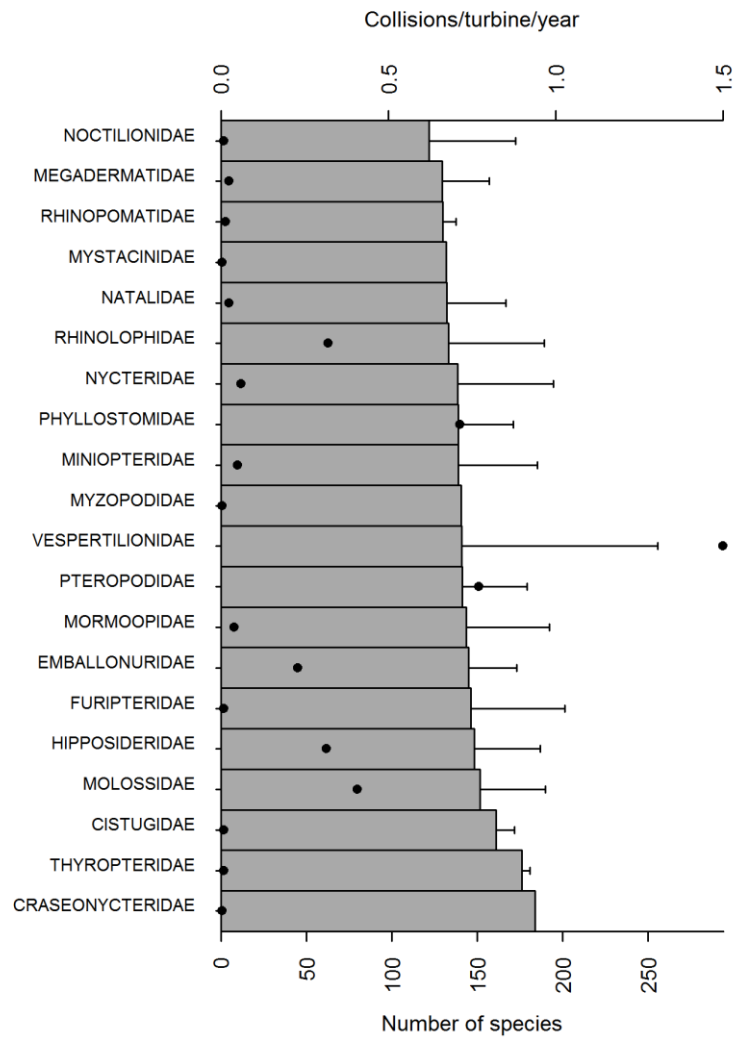


592

593

594



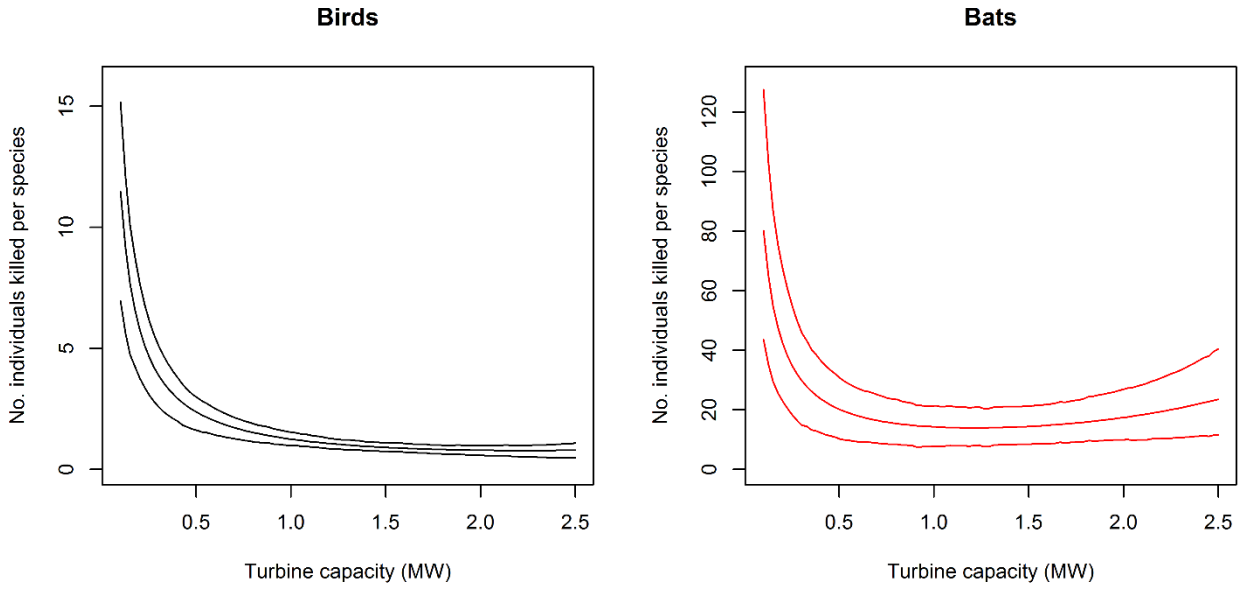


599

600

601

602 Fig. 4



603

604

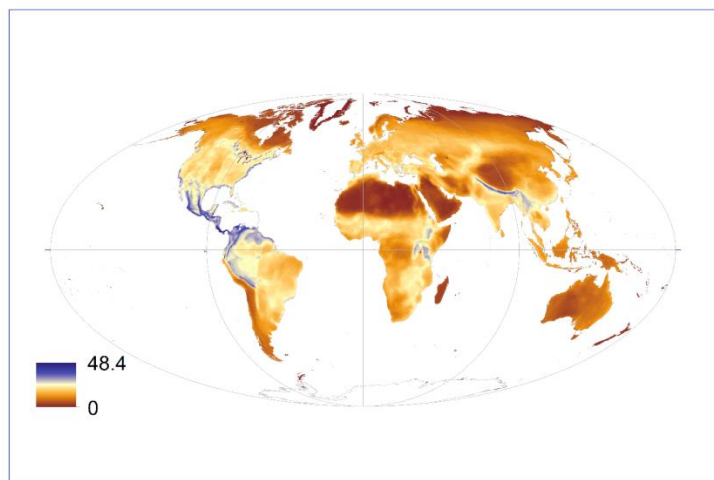
605

606

607

608 Fig. 5

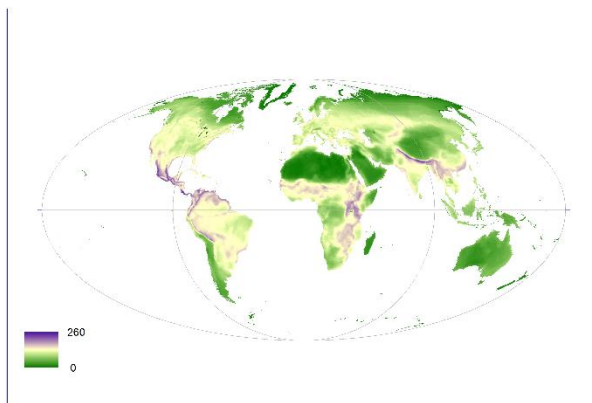
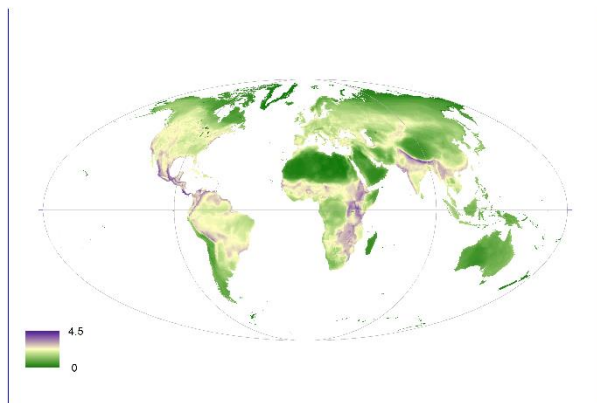
609 (a) mean



610

611 (b) lower credible interval

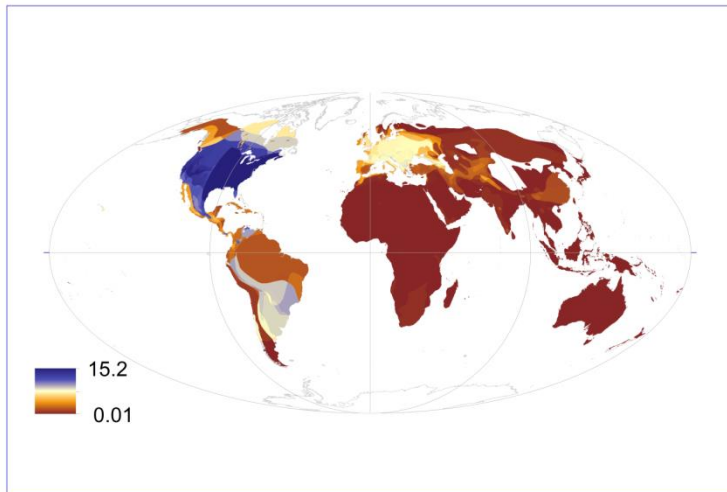
(c) upper credible interval



612

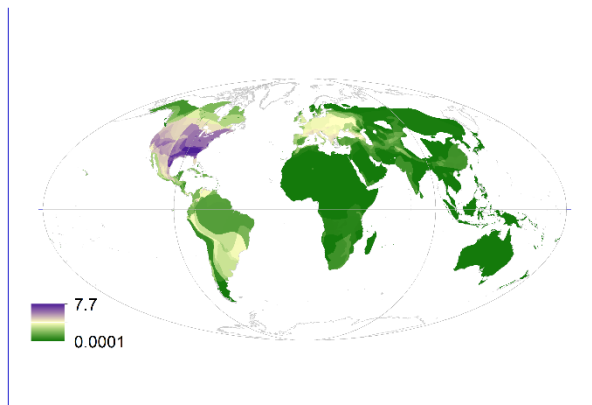
613

614 (a) mean

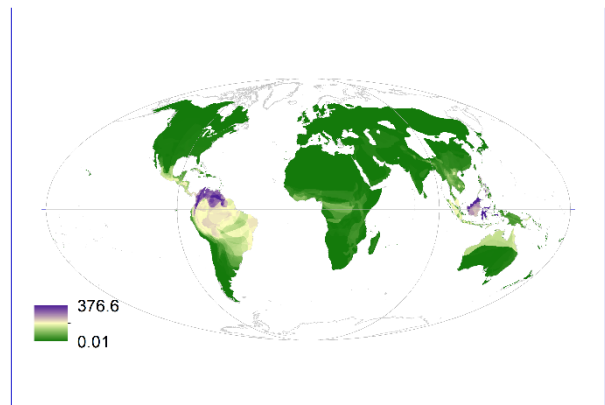


615

616 (b) lower credible interval



(c) upper credible interval



617

618

619

620

621