

TITLE: Species' traits influenced their response to recent climate change

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1 **TITLE: Species' traits influenced their response to recent climate change**

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3 **While it is widely accepted that future climatic change — if unabated — is likely to**
4 **have major impacts on biodiversity^{1,2}, few studies have attempted to quantify the number of**
5 **species whose populations have already been impacted by climate change^{3,4}. Using a**
6 **systematic review of published literature, we identified mammals and birds for which there is**
7 **evidence that they have already been impacted by climate change. We modelled the**
8 **relationships between observed responses and intrinsic (e.g., body mass) and spatial traits**
9 **(e.g., temperature seasonality within the geographic range). Using this model, we estimated**
10 **that 47% of terrestrial non-volant threatened mammals (out of 873 species) and 23.4% of**
11 **threatened birds (out of 1272 species) may have already been negatively impacted by climate**
12 **change in at least part of their distribution. Our results suggest that populations of large**
13 **numbers of threatened species are likely to be already affected by climate change, and that**
14 **conservation managers, planners and policy makers must take this into account in efforts to**
15 **safeguard the future of biodiversity.**

16 The rate of warming over the last 50 years ($0.13^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$ per decade) is nearly twice that
17 for the previous 50 years⁵, and the global temperature by 2100 is likely to be 5-12 standard
18 deviations above the Holocene mean⁶. The effects of climate change on some species are already
19 being witnessed, with changes documented in spatial distribution, abundance, demography,
20 phenology and morphology^{7,8}. However, to date, no quantification of the number of species for
21 which at least one population has been currently impacted by climate change, and the extent of
22 these impacts, has been conducted, even for the better-studied taxa such as birds and mammals. The
23 predominant focus of climate change assessments for species has been that of bioclimatic niche
24 modelling, which focuses on correlative analyses between species' geographic ranges and
25 bioclimatic variables^{9,10}, but these studies ignore observed changes in distribution, phenology and

26 abundance of species in response to contemporary climate change¹⁰. Species' life-history traits,
27 such as dispersal and generation length, have been hypothesised to be important in determining
28 species' sensitivity to climate change and their capacity to adapt to it¹¹, but only a limited number of
29 studies have so far provided evidence that animal species with certain traits are more likely than
30 others to be adversely affected by changes in climate¹²⁻¹⁵.

31 In this study we first aimed at performing a meta-analysis to identify the life-history traits
32 that confer vulnerability to climate change in birds and mammals (Supplementary Table 1). From a
33 literature search, we identified 70 studies covering 120 mammal species and 66 studies relating to
34 569 bird species whose populations had (or sought evidence for) a response to climate change in
35 recent decades. We divided this response into four categories: i) negative, if >50% of the
36 populations experienced reductions in one or more of the following parameters: population size,
37 geographic range size, reproductive rate, survival rate, body mass ii) positive, if the species
38 experienced increases in one or more of the parameters and/or adaptability to new climatic
39 conditions, iii) unchanged, if no response was observed despite the recorded change in climate, and
40 iv) mixed, if the species showed opposite responses of one or more of the parameters across its
41 geographic range (Supplementary Table 2; see Methods). For all mammals and birds covered by the
42 studies, we compiled data on selected intrinsic traits and spatial traits in order to assess
43 quantitatively which of these are associated with negative responses to climate change. To control
44 for the magnitude of climate change experienced, we also computed the mean difference in
45 temperature between the present and the recent past within the geographic range of each species,
46 treating breeding and non-breeding ranges separately for migratory birds.

47 By using information on the impacts of climate change in the study areas and life-history
48 traits, we were able to identify the species whose populations are more likely to have experienced
49 negative impacts in the regions affected by climatic changes as those described in the analysed
50 papers. We estimated the likelihood of a species' population to have exhibited any of the four

51 categories of responses to climate change with a multinomial regression model. This allowed us to
52 test our hypotheses about the relationship between intrinsic and spatial traits and the responses of
53 mammals and birds to climate change. Since we believe that these factors mediate the response to
54 climate change similarly worldwide, although future studies will be crucial to test this assumption,
55 we then predicted the likely past responses of all birds and terrestrial non-volant mammals listed as
56 threatened in the IUCN Red List of Threatened species¹⁶. By making predictions on the species for
57 which the levels of climatic hazard experienced are known, we provide the first quantification of the
58 number of taxa that may have already been impacted, although further data need to be collected to
59 say with certainty that there has been an effect on the whole species' persistence. We focused on
60 threatened species because the vast majority are known or inferred to have declined, therefore if
61 they are at risk from climate change there is a real chance that it has played a role in these declines,
62 even if it was not recorded in the assessments.

63 For the first time we identified a relationship between a set of several variables, both
64 intrinsic and spatial, and the response of mammals and birds to climate change, while previous
65 studies mostly focused on a few biological traits and their relation with the type of impact^{3,4,17,18}. In
66 addition, we were able to provide insights into the estimation of climate change threat for poorly-
67 studied species.

68

69 **Characteristics of observed and potentially impacted species**

70 The observed response to recent climate change was negative for 38.3% of mammals and
71 20.9% of birds in our dataset (Fig. 1a). Birds and mammals in Europe and North America were the
72 subjects of considerably more studies (54% and 38%, respectively) than were taxa in South
73 America (4%) and Oceania (2%), and less than 1% of species in our dataset were in Africa, Asia

74 and Antarctica (Fig. 2). This spatial bias implies that, for species with particular traits living in less
75 studied continents, our findings might be less generalizable.

76 Mammals most at risk from climate change are those not fossorial, that experienced large
77 changes in temperature in the last 60 years and have low precipitation seasonality within their
78 distributions (Supplementary Table 3). In areas with reduced precipitation and/or temperature
79 seasonality, it is likely that plant species may have narrower climatic tolerances, and therefore that
80 these areas may have already experienced vegetation changes with consequential loss of habitat for
81 animals living there¹⁹. A more specialized diet was also associated with greater probability of
82 negative responses in mammals. Our findings are in agreement with previous studies on the
83 predictors of general extinction risk²⁰, in which species with narrower diet breadths were associated
84 with lower ability to exploit resources and adapt to new environmental conditions and selective
85 pressures.

86 For birds, negative responses in both breeding and non-breeding areas were generally
87 observed in species that experienced large changes in temperatures in the last 60 years, live at high
88 altitudes, and have low temperature seasonality within their distributions. Negative impacts were
89 also associated with relatively high maximum temperature recorded within breeding areas, and low
90 dispersal distances, longer generation lengths, reduced precipitation seasonality and restricted
91 altitudinal ranges in non-breeding distributions (Supplementary Tables 4-5). Populations of species
92 living at high altitudes and in colder places have fewer opportunities to move toward cooler areas or
93 upslope to avoid increasing temperatures, and hence may have increased extinction risk. Modest
94 shifts to higher or lower altitudes are associated with large changes in ambient temperature²¹, thus
95 facilitating potential adaptive flexibility. In addition, temperature is an important determinant of
96 laying dates of birds because higher temperatures may induce earlier laying²², and so for animals
97 living in these environments the effects of temperature changes may have been exacerbated,
98 potentially leading to disruption in synchronisation between the timing of chick-feeding and peak

99 food availability²³. Interestingly, we found that birds with longer generation times have responded
100 less to warming. In long-lived species, the effects of climate change have probably been less
101 evident because adaptation and range shifts occur over a longer time span²⁴, therefore we would
102 need to monitor the populations of these species for an extended period in order to observe any
103 changes.

104 On average, it is likely that at least one population of 414 threatened mammals out of 873
105 species (47%), and 298 threatened birds out of 1272 (23.4%) has responded negatively to climate
106 change (Fig. 1; Supplementary Tables 6-7), because they have the same combinations of traits as
107 those species documented to have declined owing to climate change. This implies that, in the
108 presence of adverse environmental conditions, populations of these species had a high probability of
109 being negatively impacted by recent climatic changes.

110 Mammals had only 2 orders out of 11 (i.e. rodents and insectivores) that mostly benefited
111 from recent climatic changes. Both of these orders are generally characterized by fast reproductive
112 rates and low habitat specialization²⁵. Moreover, most of the species in these orders are fossorial,
113 and they may be less exposed to climate change owing to buffering of temperatures in burrows.
114 Primates, Proboscidea and marsupials are the mammals with the highest percentage of threatened
115 species predicted to have been negatively impacted by climate change (Table 1), and for which we
116 are more confident about our predictions (Supplementary Table 10). Primates and marsupials are
117 mostly concentrated in tropical areas²⁶, most of which have had climatically stable environments
118 during the Holocene. Therefore, many of these taxa have evolved to live within more restricted
119 environmental tolerances and are likely to be most affected by rapid changes and extreme events²⁷.
120 In addition, primates and elephants are characterized by very slow reproductive rates that reduce
121 their ability to adapt to rapid changes in environmental conditions¹³.

122 Birds showed the opposite trend, with only 3 orders out of 19 (i.e. Anseriformes,
123 Charadriiformes and Cuculiformes) having more species with a predicted negative impact than not

124 (Table 1). Most of the species included in the first two orders inhabit aquatic environments, which
125 are considered among the most vulnerable to temperature increase due to habitat loss and
126 fragmentation²⁸ and harmful algal bloom expansions²⁹. In addition, changes in climate in tropical
127 and subtropical forest areas, already exacerbated by habitat degradation², may threaten forest-
128 dependent species (e.g., Cuculiformes).

129

130 **Conclusions**

131 The vast majority of assessments of species' risk from climate change have focused on
132 future projections (e.g.,^{30,31}), while analyses of observed impacts to date have focused on detecting a
133 signal of climate change rather than quantifying the number of species whose populations are likely
134 to have been impacted. By undertaking a systematic review, we found evidence of observed
135 responses to recent changes in climate for almost 700 species of mammals and birds. We note that
136 only 7% of mammals and 4% of birds for which we found evidence of a negative response are
137 coded on the IUCN Red List of Threatened Species as threatened by 'climate change and severe
138 weather' under the 'threats classification scheme' (Supplementary Tables 8-9). While this can
139 partly be explained by the fact that species classified as 'Least Concern' on the Red List generally
140 have few or no threats coded, the figures we found were 11% and 31%, respectively for threatened
141 mammals and birds. This apparent mismatch is probably due to the severity of decline driven by
142 climate change being uncertain for most species. Reasons for this include: (a) information from
143 other parts of their distribution is not available; (b) other threats (e.g., habitat loss from agricultural
144 expansion, overexploitation etc.) may have had a greater impact, thus masking the effects of
145 climate; and/or (c) data on climatic trends at a local scale are difficult to obtain, making it difficult
146 to make inferences about the threat severity. Furthermore, threats to several species remain poorly
147 understood because the majority of threatened species live in tropical areas which are generally
148 poorly studied and monitored³².

149 Although our predictions for individual species may be subject to varying degrees of
150 uncertainty, depending on the taxonomic order and the spatial or intrinsic trait considered, the
151 confidence intervals around the number of species whose populations may have been negatively
152 impacted suggest that our extrapolation is robust, especially for mammals. Improved monitoring of
153 the abundance and distribution of those taxa identified as most vulnerable (Supplementary Figs. 1-
154 2-3-4-5-6), and targeting such monitoring in areas where the effects of climate change are likely to
155 occur soonest - particularly in the tropics - are crucial to increase empirical knowledge about
156 climate change impacts on species, and to validate and improve projections of future impacts.

157 Despite these uncertainties, our results suggest that the impact of climate change on
158 mammals and birds in the recent past is currently greatly underappreciated: large numbers of
159 threatened species have already been impacted in at least part of their range. Given that scientific
160 efforts in this field have largely focussed on predicting the impact of future climate change on
161 species and ecosystems³³, we recommend that research and conservation efforts give greater
162 attention to the ‘here and now’ of climate change impacts on life on earth. This also has significant
163 implications for intergovernmental policy fora such as the Convention on Biological Diversity and
164 the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services, and the
165 revision of the strategic plan of the United Nation Framework Convention on Climate Change.

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173

174 **Author contributions**

175 M.P., P.V., C.R., J.E.M.W. designed the framework for the meta-analysis. M.P. conducted the
176 analyses and collected the data for mammals. P.V. contributed to the analyses. S.H.M.B. provided
177 data and examined the results for birds. F.C. collected data for birds. All authors contributed to the
178 writing, discussed the results and commented on the manuscript.

179

180 **Competing financial interests**

181 The authors declare no competing financial interests.

182

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Table 1: Predicted responses of threatened species in different taxonomic orders to climate change.

Taxonomic order	Negative	Positive
Mammals		
CARNIVORA	18 (29.51%)	35 (57.38%)
CETARTIODACTYLA	56 (59.57%)	2 (2.13%)
DASYUROMORPHIA	12 (100%)	0
DIDELPHIMORPHIA	0	9 (100%)
DIPROTODONTIA	44 (100%)	0
EULIPOTYPHILA	0	4 (4.82%)
LAGOMORPHA	10 (55.56%)	0
PERISSODACTYLA	8 (61.54%)	0
PRIMATES	199 (100%)	0
PROBOSCIDEA	2 (100%)	0
RODENTIA	65 (19.23%)	44 (13.02%)
Birds		
ACCIPITRIFORMES	8 (16%)	34 (68%)
ANSERIFORMES	10 (40%)	8 (32%)
BUCEROTIFORMES	0	0
CAPRIMULGIFORMES	8 (13.11%)	21 (34.43%)
CHARADRIIFORMES	26 (57.78%)	3 (6.67%)
CICONIIFORMES	3 (50%)	3 (50%)
COLUMBIFORMES	16 (25%)	47 (73.44%)
CORACIIFORMES	0	17 (89.47%)
CUCULIFORMES	6 (66.67%)	2 (22.22%)
FALCONIFORMES	2 (33.33%)	0
GALLIFORMES	22 (29.33%)	3 (4%)
GRUIFORMES	13 (29.55%)	29 (65.91%)
PASSERIFORMES	171 (30%)	112 (19.65%)
PELECANIFORMES	6 (31.58%)	8 (42.11%)
PICIFORMES	5 (14.71%)	17 (50%)
PODICIPEDIFORMES	1 (25%)	1 (25%)
PROCELLARIIFORMES	0	8 (13.56%)
PSITTACIFORMES	0	103 (99.04%)
SPHENISCIFORMES	1 (10%)	0
STRIGIFORMES	0	6 (13.95%)
SULIFORMES	0	10 (100%)

273 Positive responses were assigned to species that benefited from recent climatic changes. Percentages indicate
274 the proportion of threatened species for each type of response.

275

276 **Figure legends**

277 **Figure 1 | Observed and predicted response of mammals and birds to climate change.** a) Red
278 bars show the percentage of species whose populations were documented to have had, or are
279 predicted to have had, a negative response to climate change in the study period (studies spanned
280 from 1858 to 2010); green bars represent the percentage of species with a positive response; blue
281 bars indicate the percentage of species with no response; orange bars show the percentage of
282 species with mixed responses. b) Bars with the number of species whose populations had an
283 observed response to climate change are coloured in white, while those used for predictions are
284 shown in black.

285

286 **Figure 2 | Map of the study sites.** Circle size represents the number of bird (blue circles) and
287 mammal (red circles) species in each site. Colour of countries represent the number of studies per
288 country.

289

290

291 **Methods**

292 Using ISI Web of Knowledge we conducted a systematic literature search of all relevant
293 articles – published between 1990 and 2015 - that i) reported an observed change in climate in the
294 study area, ii) indicated that birds and/or mammals have undergone a change (e.g., in distribution,
295 population size, phenology, behaviour, genotype, phenotype) attributable to climate in the past 100
296 years, and/or iii) suggested that populations of a species were not affected by recent climate change.
297 For each study and each species considered (70 studies and 120 species for mammals, 66 studies
298 and 569 species for birds), we identified the type of impact experienced.

299 A negative response was assigned to a species if all (at least one) or >50% of its populations
300 (if the species had both negative and no responses in different portions of its range) were reported to
301 have undergone declines in population size, geographic range size, survival or reproductive rate,
302 and body mass, thus reducing the risk of false attributions. These responses were confidently
303 attributable to recent climate change by the authors of the studies, for instance due to the fact that
304 the most significant change in environmental and biotic conditions reported in the area in which the
305 population of the species was impacted was related to climatic variables. Although we acknowledge
306 that some of the studies may have been more rigorous than others, with such variation in the
307 methods used and the effect size themselves it would have been difficult to adjudicate the level of
308 confidence around the claimed relationship, although we believe that evaluating the strength of
309 attribution is a priority for future work.

310 A positive response was assigned if the majority of the populations of a species experienced
311 geographic range expansions, increase in population size, survival rate and/or reproductive rate,
312 body mass, and/or changes in phenology. An unchanged response was attributed if no response was
313 observed despite the recorded change in climate. Finally, species that exhibited a combination of the
314 negative and positive (not necessarily in the same proportion) responses in different parts of their
315 range were classified as mixed.

316 **Statistical analysis**

317 To identify the relationships between the observed response of mammals and birds to
318 climate change and a set of intrinsic and spatial variables (see Supplementary Methods for
319 description of these predictors and *a priori* hypotheses), we performed a multinomial logistic
320 regression using the 'nnet' package in R. This model uses maximum likelihood estimation to
321 evaluate the probability of the different possible outcomes of a categorical dependent variable with
322 more than two classes. In order to reduce the overdispersion in models and avoid collinearity, we
323 performed Spearman's correlation tests between the predictors and removed those that were highly
324 correlated ($R^2 > 0.75$) and led to the minimum loss in model performance.

325 We included taxonomic order as fixed variable of our models, for a total of 11 orders of
326 mammals and 22 of birds. By including taxonomy as a fixed effect, we aimed to control for the non-
327 independence of observed responses across species, and for the latent variables that may affect the
328 responses to climate change that are phylogenetically conserved. We did not include taxonomic
329 family or genus because it resulted in strong underdispersion, as observed data on the response to
330 climate change (which we used as a base for our predictions on threatened species) were often only
331 available for the populations of one species per family/genus. Since we are not aware of frequentist
332 methods to implement phylogenetically corrected models with a multinomial distribution, and
333 concerned that phylogenetic non-independence in the species in our dataset could nevertheless be
334 important, we tested for the existence of phylogenetic signal in the residuals of our models. We
335 used phylogenetic trees for mammals and birds^{34,35} to estimate Pagel's lambda, assuming a star-
336 shaped phylogeny and the actual phylogeny (Brownian motion models). We tested whether the
337 value of lambda differed significantly from 0 (no phylogenetic signal) and 1 (trait distribution
338 matches a Brownian model of evolution), by computing the likelihood ratio, and then comparing it
339 to a Chi-squared distribution with one degree of freedom. If the test is significant there is
340 phylogenetic signal in the residuals. However, we found lambda values of 6.73e-05, 5.56e-04 and
341 2.68e-04, and p-values of 0.51, 0.47 and 0.62 for mammals, birds in breeding ranges and birds in

342 non-breeding ranges, respectively. Therefore we conclude that there is no phylogenetic signal in the
343 residuals of the models and a phylogenetically-informed model is not justified.

344 We performed a model selection using the AIC to find the set of predictors to include in the
345 final model that minimize the Kullback-Leibler distance between the model and the observed
346 values. We applied logarithmic and quadratic transformations to the predictors and included
347 variable interactions in the models, but most of them did not lead to a decrease in AIC or increase in
348 model performance calculated by using the Area Under the Curve (AUC). Finally, to test our
349 models for overdispersion, we calculated the sum of squared Pearson residuals and compared it to
350 the residual degrees of freedom by using a Chi-squared test. P-values close to 1 indicate that the
351 probability of the model being overdispersed approaches 0 (Supplementary Table 13).

352 On the basis of the relationship between the observed response of species and our
353 independent variables found with the best multinomial models, we predicted the probabilities of the
354 four classes of response to climate change by using the function *predict* in R. For predictions we
355 considered all threatened birds (1272 species, as listed on the 2014 IUCN Red List) and terrestrial
356 non-volant mammals (873 species) with available data. We excluded sea mammals from our
357 analysis because the environmental variables that influence the persistence of marine and terrestrial
358 species are different, and most of the variables important for marine species (e.g., sea temperature,
359 salinity) were not available for the study period. Chiroptera could not be considered in this study
360 because of the paucity of data available on their life history.

361 Our model is at the species level, but our data (observed responses to climate change) is at
362 the population level. Because the spatial extent of the study area was not available for the vast
363 majority of studies, we were forced to average the annual temperature change experienced by the
364 species across all of its range. However, the average climatic change might not be representative of
365 the change experienced by the populations we used to train the model, especially with species with
366 large range size. By resampling the response category assigned to each species from the

367 multinomial distribution 100 times and deriving coefficient intervals and mean values of the
368 richness of species with negative responses, we tried to reduce the uncertainty around our
369 predictions. In addition, to identify the taxonomic orders for which our predictions were most
370 reliable, we used a Kolmogorov–Smirnov nonparametric test which quantifies the distance between
371 the empirical continuous distribution functions of two samples, and the null hypothesis is that the
372 samples are drawn from the same distribution. By comparing the distribution of the same numeric
373 trait in both the observed and the predicted sample, if the p-value of the test is above the α
374 threshold, i.e. 0.05, we can assume that threatened species in the considered taxonomic order are
375 well represented in the sample of observed data. This means that, for this order, our predictions are
376 more robust.

377

378 **Data availability**

379 The authors declare that [the/all other] data supporting the findings of this study are available within
380 the article and its Supplementary Information files.

381 **Supplementary Table 1 | Selected potential correlates of extinction risk associated with**
382 **climate change.**

383 **Supplementary Table 2 | Negative observed impacts on species.**

384 **Supplementary Table 3 | Threatened mammal species identified from models as likely to have**
385 **already been negatively impacted by climate change.**

386 **Supplementary Table 4 | Threatened bird species identified from models as likely to have**
387 **already been negatively impacted by climate change.**

388 **Supplementary Table 5 | Coefficient estimates, standard errors and confidence intervals of the**
389 **most important predictors resulting from the best multinomial model in mammals.**

390 **Supplementary Table 6 | Coefficient estimates, standard errors and confidence intervals of the**
391 **most important predictors resulting from the best multinomial model in birds (breeding**
392 **range).**

393 **Supplementary Table 7 | Coefficient estimates, standard errors and confidence intervals of the**
394 **most important predictors resulting from the best multinomial model in birds (non-breeding**
395 **range).**

396 **Supplementary Table 8 | Response of mammals to climate change by taxonomic order.**

397 **Supplementary Table 9 | Response of birds to climate change by taxonomic order.**

398 **Supplementary Table 10 | Numeric predictor variables and orders for which our predictions**
399 **on threatened species are most reliable for mammals.**

400 **Supplementary Table 11 | Numeric intrinsic and climatic predictor variables and orders for**
401 **which our predictions on threatened species are most reliable for birds.**

402 **Supplementary Table 12 | Numeric spatial predictor variables and orders for which our**
403 **predictions on threatened species are most reliable for birds.**

404 **Supplementary Table 13 | Results of Chi-squared tests for overdispersion.**

405 **Supplementary Table 14 | Results of a binomial model having "negative" and "non-negative"**
406 **classes for the response variable of mammals.**

407 **Supplementary Table 15 | Results of a binomial model having "negative" and "non-negative"**
408 **classes for the response variable of birds (breeding areas).**

409 **Supplementary Table 16 | Results of a binomial model having "negative" and "non-negative"**
410 **classes for the response variable of birds (non-breeding areas).**

411 **Supplementary Table 17 | Number of studies/populations per mammal species.**

412 **Supplementary Table 18 | Number of studies/populations per mammal species.**

413 **Supplementary Figure 1 | Richness map of impacted mammals.**

414 **Supplementary Figure 2 | Richness map of threatened mammals.**

415 **Supplementary Figure 3 | Richness map in breeding ranges of impacted birds.**

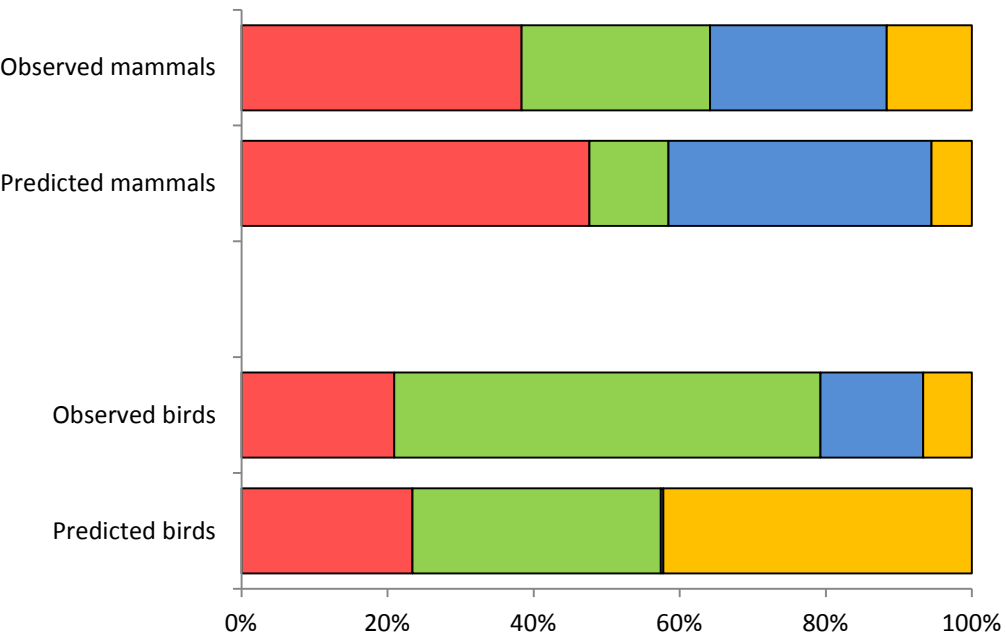
416 **Supplementary Figure 4 | Richness map in non-breeding ranges of migratory impacted birds.**

417 **Supplementary Figure 5 | Richness map in the breeding ranges of threatened birds.**

418 **Supplementary Figure 6 | Richness map in non-breeding ranges of threatened migratory**
419 **birds.**

420

a.



b.

