

1 **Drivers of change in the realised climatic niche of terrestrial mammal species**

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14 **Abstract**

15 The breadth of a species' climatic niche is an important ecological trait that allows adaptation
16 to climate change, but human activities drive niche erosion. Life-history traits, such as
17 dispersal ability and reproductive speed, instead allow species to cope with climate change.
18 But how do these characteristics act in combination with human pressure to determine niche
19 change? Here we investigate the patterns and drivers of change in the realised climatic niche
20 of 589 terrestrial mammal species. Our goal is to disentangle the impacts of humans, climate
21 change, and life history. We calibrated the past and present climatic niches of each species by
22 considering past climatic conditions (Mid Holocene) within their pre-human impact
23 distributions, and current climatic conditions within the current distributions. Depending on
24 the relationship between past and current niche, we defined four categories of change:
25 "shrink", "shift", "stable", and "expand". We found over half of the species in our sample
26 have undergone niche shrink, while only 15-18% of species retained a stable niche. After
27 controlling for biogeography, climatic factors were the strongest correlates of species niche
28 change, followed by anthropogenic pressure and species' life history. Factors that increased
29 the probability of niche shrink include: overall climatic instability in the area (both
30 intermediate or high), large body mass, long gestation time, highly carnivorous or
31 herbivorous diets, historical land-use change, and current human population density. We
32 identified the conditions under which species are less likely to maintain their niche breadth,
33 potentially losing adaptation capacity under climate change. Species with these
34 characteristics require interventions that facilitate natural dispersal or assisted colonisation, to
35 survive to rapidly changing climates.

36

37 **Introduction**

38 The breadth of a species' niche - the set of environmental conditions in which the species can
39 persist (Peterson et al. 2011) - is an important ecological trait that allows adaptation to
40 environmental change (Thuiller et al. 2005; Pacifici et al. 2015). Niche breadth is a key
41 correlate of species sensitivity to future climate change (Swihart et al. 2003; Thuiller et al.
42 2005; Chown et al. 2010), and is usually assessed by relating the observed occurrences of
43 species to their respective climate. This implies looking at species' realised niches, rather
44 than their fundamental ones (Peterson et al. 2011). In fact, analysing realised niches is a well-
45 established technique to identify differences in species' ecology (Olalla-Tárraga et al. 2011;
46 Mahon et al. 2016), predict the potential spread of invasive species (Liu et al. 2017), and
47 project past and future changes in species distributions (Maiorano et al. 2013; Visconti et al.
48 2016).

49 While the roles of human threats as drivers of species decline and extinction have been often
50 demonstrated (Johnson et al. 2017; Pacifici et al. 2017; Di Marco et al. 2018), their role as
51 drivers of niche erosion has proven more difficult to quantify (Pearman et al. 2008). Yet this
52 is a critical element to consider, because disregarding the effect of human modifications of
53 species realized niches might result in biased estimates of the future impact of climate change
54 (Faurby & Araújo 2018). Some evidence of how humans have altered species niche is already
55 available, despite uncertainty in past information on species distribution, climatic conditions,
56 and human pressure (Walther et al. 2005). For example, analyses on the distribution range of
57 the giraffe (*Giraffa Camelopardalis*) and African elephant (*Loxodonta Africana*) in the last
58 150 years show a reduction in their climatic niche as a consequence of poaching,
59 fragmentation, and conflicts (Martínez-Freiría et al. 2015).

60 Threats such as overexploitation, habitat loss and fragmentation, or invasive species have
61 been recognised as global drivers of species decline in recent centuries (Hoffmann et al.

2010; Maxwell et al. 2016). More recently, substantial attention has been devoted to the emerging threat of climate change, with effects that might become soon predominant over those of already established threats (Newbold 2018; Di Marco et al. 2019). Climate change is recognised to have potential magnifying effects on biodiversity decline in the absence of adaptation and coping mechanisms (Bellard et al. 2012; Mantyka-Pringle et al. 2015; Visconti et al. 2016). Yet species might be able to tolerate changing climates to some extent, depending on their characteristics (Adrian et al. 2006; Jiguet et al. 2007; Urban et al. 2014; Santini et al. 2016; Pacifici et al. 2017). Life-history traits, such as dispersal ability and reproductive speed for example, have been hypothesized to play a central role in determining the sensitivity of species to climate change and their ability to cope with it (Dawson 2011). Evolutionary adaptation might also allow species to cope with changing climate (Hoffmann & Sgró 2011), even if it is unclear whether this mechanism is compatible with the pace of current climate change (Loarie et al. 2009). But how do these mechanisms act in combination with human pressure to determine change in species climatic niches?

Here we investigate the patterns and drivers of change in the realised climatic niche of terrestrial mammals. Our goal is to disentangle the impacts of humans, climate change, and life history on species climatic niches. Separating intrinsic and extrinsic vulnerability of species to niche change, as well as the role of direct and indirect human pressure, is essential to understand which species are unlikely to adapt to future climatic conditions. We focus our analysis on terrestrial mammals, a data-rich group compared to other taxa, given the availability of distribution data for all species, both at present (IUCN 2018) and before human impact took place (Faurby & Svenning 2015). Terrestrial mammals make fundamental contributions to key ecological processes such as predation, herbivory, and seed dispersal, but are facing high risk of extinction (Fragoso et al. 2003; Soulé & Estes 2003; Pringle et al. 2007; Hoffmann et al. 2011). Their ability to adapt to rapidly changing climate (or lack

87 thereof) is an essential element to consider when forecasting future extinction rates and
88 defining appropriate conservation measures (Pacifci et al. 2017).

89

90

91 **Methods**

92 **Species data**

93 We focused our analyses on 589 terrestrial mammal species (Table S1), representing all
94 species which are known to have changed their geographic distribution in response to human
95 pressure, and have been assessed in the Red List of the International Union for Conservation
96 of Nature (IUCN). Selecting these species allowed us to disentangle the relative impact of
97 climate change (within species' natural ranges) from that of direct human influence on
98 species' distributions (Faurby & Svenning 2015). We used species distributions referring to
99 the present day, and those assumed to represent species' natural ranges (i.e. before human
100 impact modified them). We retrieved present distributions from the IUCN Red List (IUCN
101 2018) and pre-impact distributions from the PHYLACINE dataset (Faurby & Svenning 2015;
102 Faurby et al. 2018). All ranges were considered at a spatial resolution of 1 degree (roughly
103 110 km x 110 km at the equator), which is the native resolution in the PHYLACINE
104 database.

105 We collected life-history and ecological traits of species that are potentially correlated to
106 change in their realised climatic niches. We considered the following variables: species
107 biogeographic domains (Olson et al. 2001), percentage of vertebrate/invertebrate/plat diet
108 (Faurby et al. 2018), body mass (Faurby et al. 2018), gestation length (Jones et al. 2009;
109 Tacutu et al. 2013), and interbirth interval (Jones et al. 2009; Tacutu et al. 2013). Missing
110 data for gestation length and interbirth interval were imputed from other life-history traits and

111 phylogeny, using the R package “missForest” (Stekhoven & Bühlmann 2012) and following
112 the procedure of Penone et al. (2014). During imputation process, we represented species
113 phylogeny by extracting phylogenetic eigenvectors (Diniz-Filho et al. 1998) from the
114 PHYLACINE dataset (Faurby et al. 2018). That phylogeny was derived using a hierarchical
115 Bayesian approach with a posterior distribution of 1,000 trees, which represent uncertainties
116 in topology and branch lengths. We extracted 10 random trees from the phylogeny and re-ran
117 our data imputation process using each of the trees, to test the sensitivity of our imputation to
118 phylogenetic uncertainty. We also verified whether directly including phylogenetic
119 relationships improved the performance of our niche models, using phylogenetic eigenvectors
120 as model predictors (see below).

121 We also included anthropogenic drivers of change in species niches. We quantified the levels
122 of human pressure to which species were exposed through time, by accounting for past and
123 current levels of human encroachment within species’ natural ranges (pre-impact
124 distributions). We measured both human population density and the amount of agricultural
125 land within each species’ range. We derived population densities and land-use data for the
126 years 4,000 BC and 2017 AD, from the HYDE dataset at their original 5 arc-minutes
127 resolution (Goldewijk et al. 2017). This corresponds to the Mid Holocene climatic period
128 from Worldclim (Hijmans et al. 2005), which we used for representing past species niches
129 (see below). We measured different percentiles of the distribution of these pressures within
130 species ranges, and selected the percentile leading to highest predictive importance of the
131 variables (Di Marco et al. 2015): 95% for past land use, 50% for current land use, 75% for
132 past human density, and 25% for current human density.

133

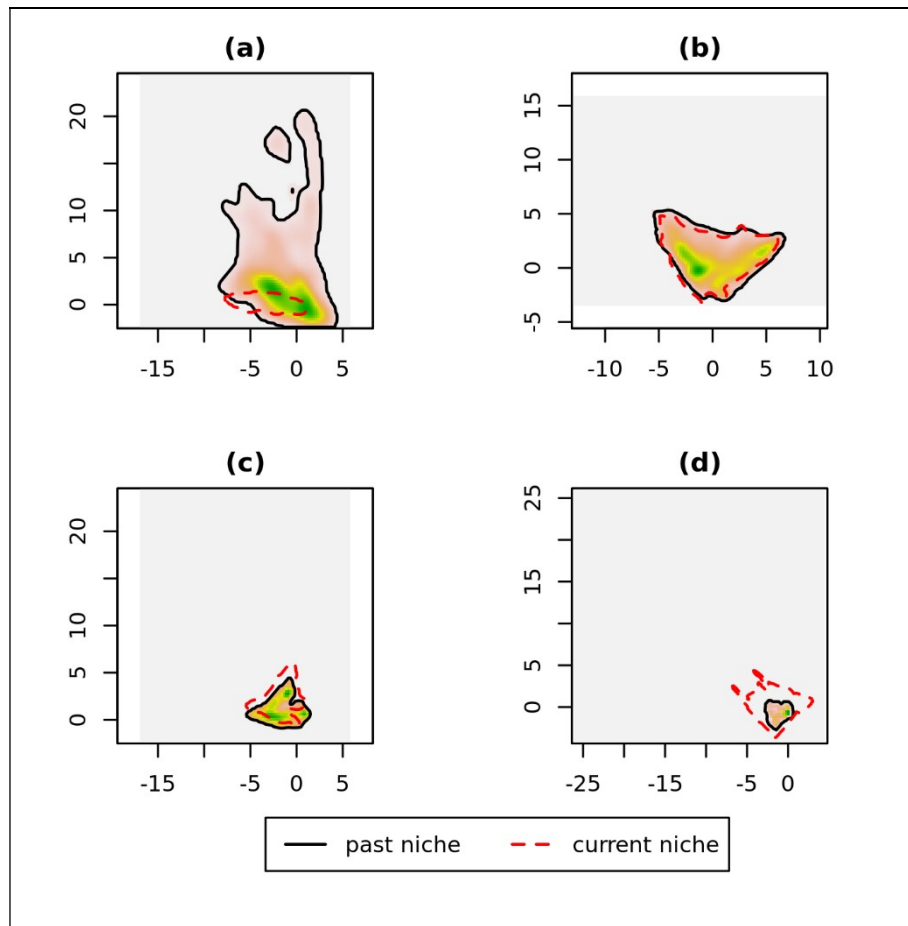
134 **Representing species climatic niches**

135 We calibrated the past and present climatic niches of each species by considering the past
136 climatic conditions within their pre-impact range and the current conditions in the current
137 range. We considered past climatic conditions in the Mid Holocene (MID; ca. year 4,000 BC)
138 as obtained by the IPSL-CM5A-LR and the MPI-ESM-P general circulation models (GCMs).
139 We averaged the results based on those two GCMs to account for uncertainty in past climatic
140 projections. We also considered conditions at an earlier period, the Last Inter-Glacial (LIG;
141 ca. 130,000 years ago) as a sensitivity test. A set of 10 bioclimatic variables were extracted
142 from the Worldclim dataset (Hijmans et al. 2005), previously identified for their ability to
143 model mammal species' climatic preferences (Visconti et al. 2016): Annual Mean
144 Temperature, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter,
145 Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Annual
146 Precipitation, Precipitation of Wettest Quarter, Precipitation of Driest Quarter, Precipitation
147 of Warmest Quarter, Precipitation of Coldest Quarter. We extracted climatic conditions
148 within the pre-impact and current distribution range of each species at a resolution of 30 arc-
149 seconds (approximately 1 km at the equator), which is the common resolution among the
150 various climatic datasets we analysed. We represented fine-scale climatic conditions
151 throughout each species' range, by sampling the centroid of each 2.5 arc-minutes grid cell
152 (approximately 5 km x 5 km at the equator) within the coarse species ranges, as a
153 compromise between spatial coverage and computational feasibility. We extracted the
154 climatic characteristics for all sampled pixels and analysed them using a principal component
155 analysis (PCA) approach. This way we represented the combination of relatively fine-scaled
156 climatic conditions that a species experienced within its broad distribution range through
157 time.

158 The delineation of species niches was done using the software R (R Core Team 2018) and the
159 package “ecospat” (Di Cola et al. 2017). We treated the pre-impact and current species
160 distributions in a similar way to how native and non-native distributions are treated when
161 investigating niche change for invasive species. We followed Broennimann et al. (2012) in
162 defining a gridded ecological niche space for each species, delimited by the two major axes
163 of a PCA built on the above-listed bioclimatic variables. We defined such environmental
164 space by using past and present climate within each species’ biogeographic domain as the
165 reference climatic regions, and the climate registered within pre-impact and current species
166 distribution as proxy of species realised niches. This implies each species is associated to a
167 “study region” that represents its biogeographical domain. We projected the PCA scores of
168 the past and current climate experienced by the species onto the gridded ecological space, to
169 define smoothed density of occurrences using a kernel density function.

170 We represented the past and current niches as the polygons encompassing 95% of the gridded
171 occurrences, respectively around the pre-impact occurrences and the current occurrences. We
172 classified categories of change in the realised climatic niches of terrestrial mammal species
173 by considering the relative size and position of the niche polygons in the gridded
174 environmental space (Fig. 1). In particular, we defined four categories of niche change:
175 “shrink”, when a species’ niche has reduced over time; “shift”, when a species niche has
176 changed position without substantial reduction in its variability; “stable”, when a species
177 niche has not substantially reduced or shifted; “expand”, when a species’ niche has increased
178 in size over time.

179



180

181 **Figure 1** Categories of change in the realised climatic niches of terrestrial mammal species,
182 derived by comparison of past climate in pre-human impact distribution (black solid line)
183 and current climate in current distribution (red dashed line). The density of species
184 distribution within the past niche is represented as an orange-to-green gradient. The four
185 panels represent: a) an example of niche “shrink”, the Ethiopian wolf (*Canis simensis*); b)
186 an example of niche “stability”, the Spectacled Bear (*Tremarctos ornatus*); c) an example of
187 niche “shift”, the Eastern Red Forest Rat (*Nesomys rufus*); d) an example of niche
188 “expansion”, the Coyote (*Canis latrans*).

189

190 We defined thresholds of tolerance below which niche changes were considered minimal, and
191 the species classified as “stable”; this way we prevented the model from being over-sensitive
192 to data uncertainty (e.g., in terms of past climate and species distributions). We tested
193 tolerance thresholds of 5%, 10%, and 20% to separate niche stability from niche change, both
194 in terms of position shift and in terms of shrink/expansion, and to separate niche shift from
195 niche expansions and shrinks.

196

197 **Modelling change in species climatic niche**

198 We run multinomial logistic regression models to predict the probability of species to be
199 assigned to a given class of niche change, using the R package ‘nnet’ (Venables & Ripley
200 2002). The same model structure was repeated under different past climate scenarios (in
201 terms of GCM and time period). We used the class “shrink” as the reference level in the
202 models. We included all the above-described intrinsic and extrinsic variables as model
203 predictors, after verifying that these are not collinear with each other (Pearson’s $r < 0.7$). All
204 continuous variables were scaled to improve comparability of model’s coefficients. In order
205 to disentangle the effect of regional climate change from that of other drivers influencing the
206 dynamics of a species’ niche, we also measured the overall climatic stability within species
207 pre-impact ranges. We did so by measuring the proportion of past climatic space that is
208 retained in the present, within the same PCA gridded ecological space used to define species
209 niches. We used this metric of overall climate stability as one of the predictors in our model.
210 We measured the model’s fit using Nagelkerke pseudo- R^2 , and evaluated the model’s
211 performance using a leave-one-out validation approach. The validation routine was
212 performed by iteratively excluding one species at a time, and then using the model calibrated
213 on all other species to predict the probability that the left-out species belongs to each of the
214 four classes of niche change. We compared the predicted class probabilities with the original
215 (observed) class of each species. We measured the model’s classification accuracy with three
216 different metrics. First, we defined a “predicted class” for each species, as the class with the
217 highest assigned probability by the model. Second, for each species we ranked the predicted
218 niche classes from the most probable to the least probable, and measured the rank of the
219 observed class. Third, for each species we measured the difference between the predicted
220 probability of the observed category and that of the most probable category according to the

221 model (δ -prediction). This value would be zero if the observed class is also the one with the
222 highest predicted probability, and >0 otherwise; as an example, a species with a “stable”
223 niche for which the models assigns a 50% chance of niche “shift” and a 40% chance of niche
224 “stable” has a δ -prediction of 10%. We estimated both the overall classification accuracy,
225 across all species, and the accuracy for species in each separate category of niche change.
226 We estimated the models’ coefficients and their statistical significance, and we represented
227 the relationship between key predictors in our model and the probability of being in a given
228 class of niche change. To represent the latter relationships, we produced partial effect plots
229 that represent the effect of one variable (e.g. body mass) on the response (e.g probability of
230 the species to belong to the category “stable niche”) while holding all other variables
231 constant. Finally, we compared our results from the multinomial model to those obtained
232 with a Random Forest model (a non-parametric machine-learning technique), using the R
233 package ‘randomForest’ (Liaw & Wiener 2002).

234

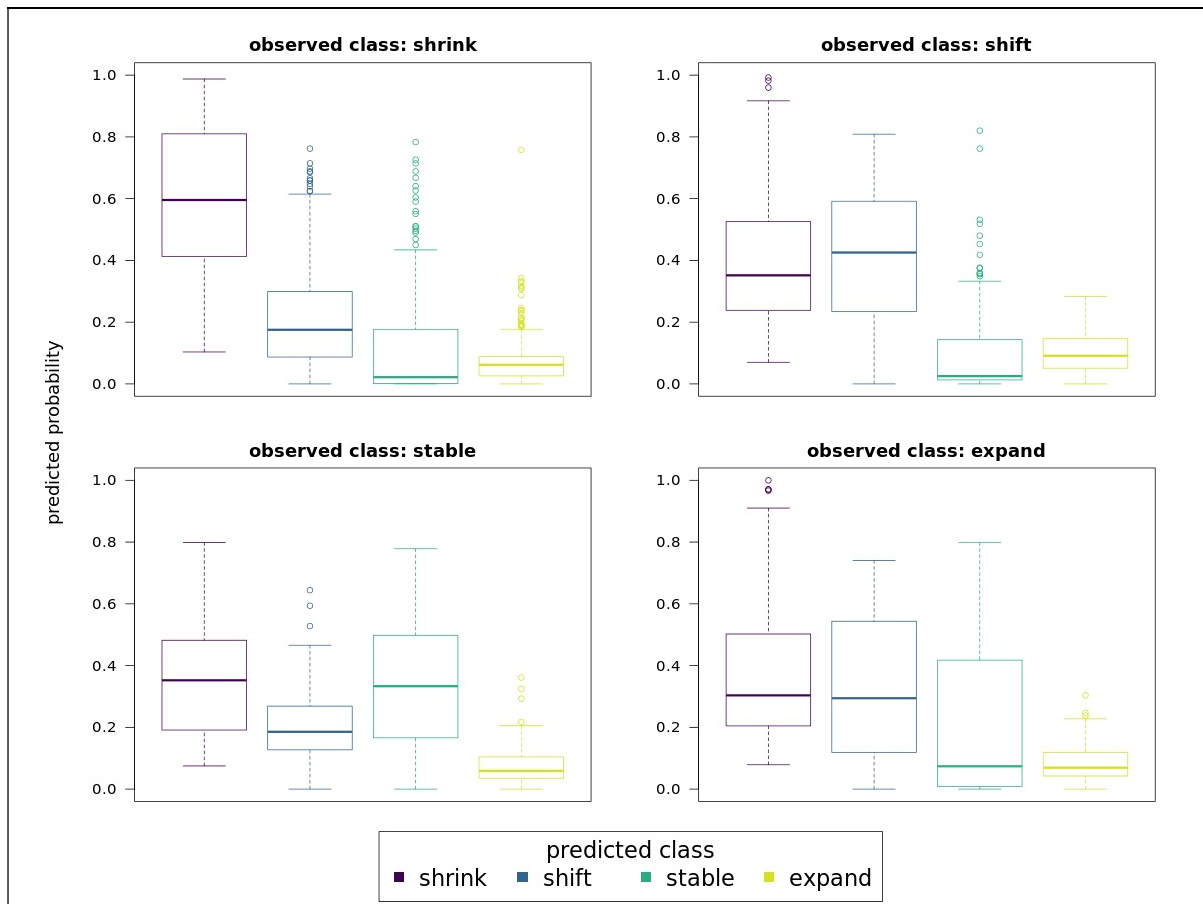
235 **Results**

236 **Model’s ability to classify change in species niche**

237 The combination of MID climate (under the IPSL-CM5A-LR General Circulation Model)
238 and 20% tolerance threshold, resulted in the best model’s performances (Table S2). Under
239 those settings, the model had good overall classification accuracy (59% species correctly
240 assigned to their observed niche classes) and a lower class-averaged accuracy (43%), which
241 was still the highest value across all model settings. In fact, under any climatic scenario,
242 using higher tolerance thresholds led to an increase in the variance explained by the model, a
243 decrease in the overall prediction accuracy (across all species), and an increase in the class-
244 averaged prediction accuracy. The mean prediction rank of the observed class was 1.64,

245 while the average δ -prediction value was 15% (Table S3). The most numerous class, niche
246 shrink, had very high validation performance, followed by the second most-numerous class,
247 niche shift (Fig. 2). Species in the “stable” class were often misclassified as shifts. The main
248 validation problem though occurred for species undergoing niche expansion, the least
249 numerous class (representing just 8% of species), which were typically misclassified. This
250 outcome is in part related to the level of tolerance of 20%, which does not classify niche
251 increases as expansions (or niche contractions as shrinks) unless these are substantial. In fact,
252 with a tolerance level of 5% there would be more than twice as many species classified as
253 niche expansions, and the model is slightly better able at classifying them (but much less able
254 at classifying shifting species).

255



256

257 **Figure 2** Probability to belong to different classes of niche change, for species in different
258 observed categories, as predicted by the model based on Mid Holocene climate (under global
259 circulation model IPSL-CM5A-LR) and a tolerance of 20% to separate niche change from
260 niche stability. Each set of boxplots reports the probability of species within an observed
261 niche category (reported in the plot title) to belong to any of the 4 categories.

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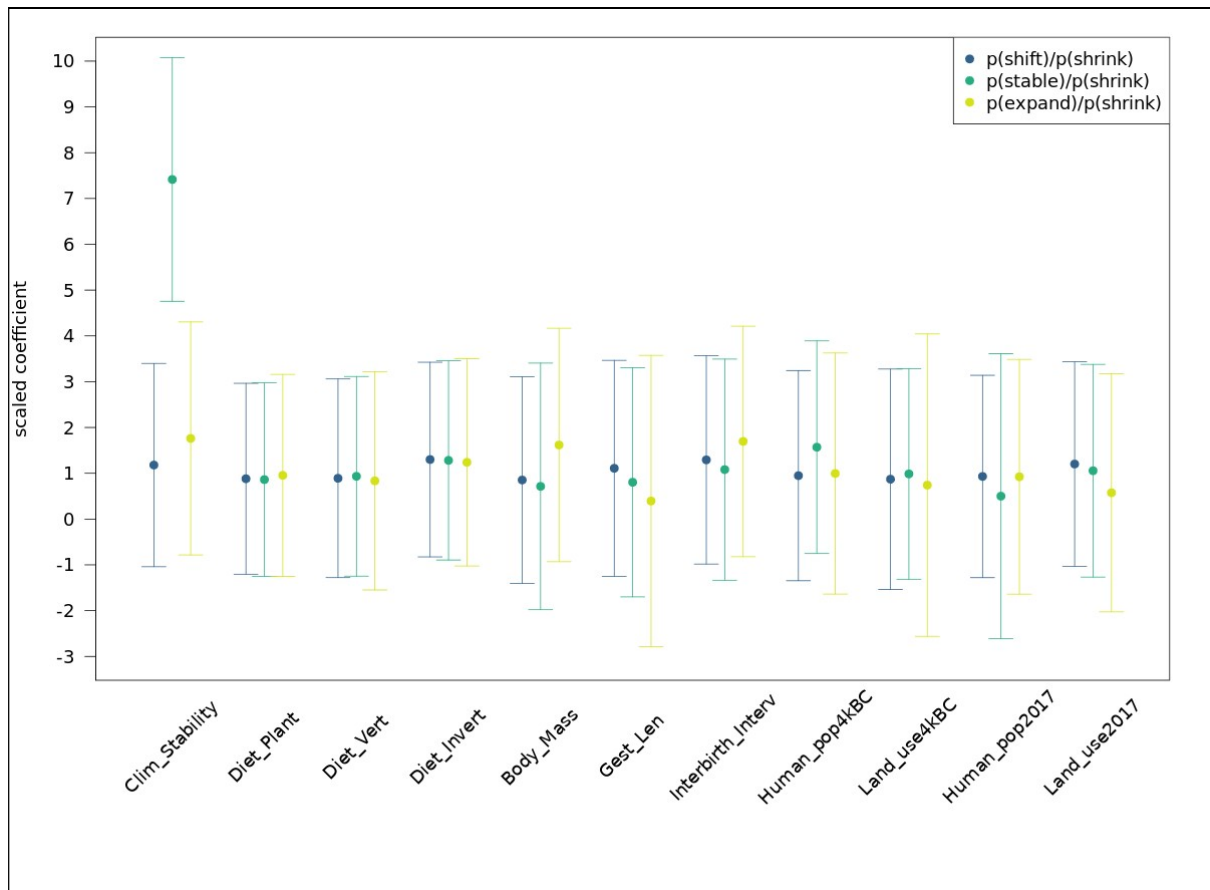
263 We did not use phylogenetic relationships as predictors in our final model, after verifying that
264 including phylogenetic eigenvectors did not improve the AIC of our best performing model
265 based on IPSL-CM5A-LR MID climate and a tolerance of 20% (Table S4). The two imputed
266 variables in our model, gestation length and inter-birth interval, had acceptable performances
267 during imputation, in terms of normalised root mean square error (NRMSE), with gestation
268 length (NRMSE = 0.22) performing better than inter-birth interval (NRMSE = 0.32). We
269 only used one imputation (out of ten imputations run), as the effect of phylogenetic
270 uncertainty on data imputation was negligible when predicting species niche classes. In fact,

271 for 98% of the species the predicted class (i.e. the one with the highest probability from the
272 multinomial model) did not change when using intrinsic traits imputed from 10 alternative
273 phylogenies (Table S5).

274

275 **Drivers of change in species climatic niches**

276 After averaging the result of niche predictions based on the two GCMs for the MID climate,
277 we found that different niche categories were best predicted by different sets of variables
278 (Fig. 3). As expected, we found overall climatic stability was a strong discriminant of stable
279 vs shrinking niche, with a less strong effect on the prediction of other classes (Fig. 3, Table
280 S6). Invertebrate diet and current land use are relatively strong predictors of niche shift,
281 together with body mass and interbirth interval. These latter two variables are also relatively
282 important predictor of niche expansion. Past human population density and current land-use
283 are relatively important predictors of niche stability and shift, respectively. Variable
284 importance measured in a random forest model for classification reflected the overall patterns
285 of the multinomial model, with the most important variables being climatic stability,
286 biogeographic realm, past human population, current land-use, and body mass (Fig. S1).



287

288 **Figure 3** Averaged model's coefficients for the prediction of species niche change categories,
289 using Mid Holocene as the reference past climate and two alternative GCMs. For each
290 quantitative predictor variable used in the multinomial models, the scaled coefficient is
291 reported representing the odds of being in the categories "shift", "stable", or "expand"
292 rather than the class "shrink" (used as a reference).

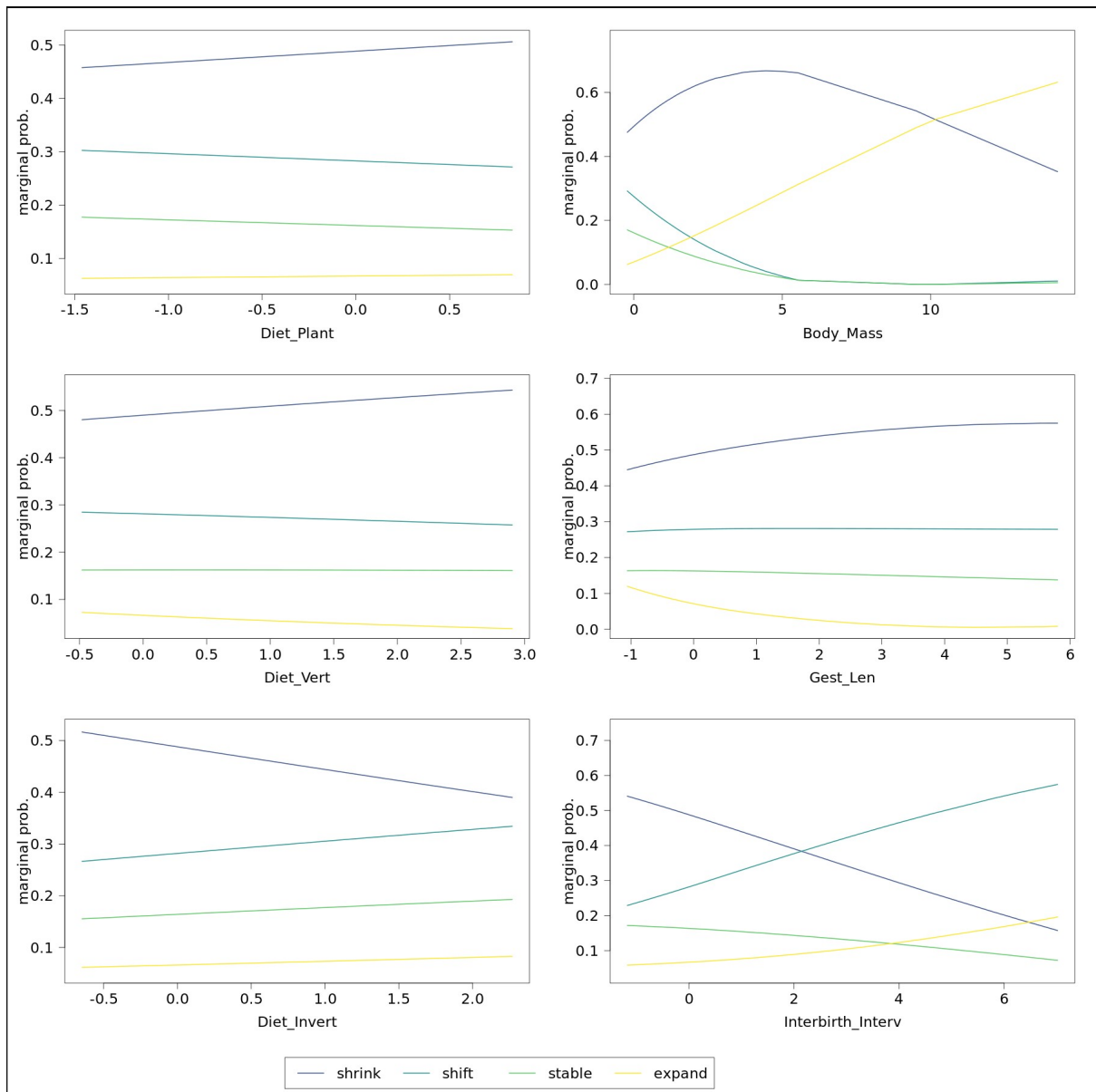
293

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295 When considering diet, we found species consuming higher percentage of invertebrate food
296 had a lower probability of undergoing niche shrink and higher probability of niche expansion
297 or shift (Fig. 4a,c,e). Species consuming more vertebrate or plant food showed the opposite
298 pattern. When considering life-history traits instead, we found species were more likely to
299 undergo niche shrink as their body mass increases, with the exception of very large species
300 (pachyderms) which are less likely to undergo niche shrink (Fig. 4b). Larger species were
301 also much more likely to expand their niche, and less likely to show niche shift or stability.

302 Species with longer gestation time – i.e. low reproductive output, *sensu* Bielby et al. (2007) -
303 were much more likely to undergo niche shrink and less likely to belong to any other class of
304 niche change (Fig. 5d). Species with longer interbirth intervals - slow reproductive timing,
305 *sensu* Bielby et al. (2007) - instead were less likely to have a shrink or stable niche, but more
306 likely to shift their climatic niche (Fig. 4f). This same pattern was observed when replacing
307 interbirth interval with other variables representing reproductive timing, such as weaning age
308 or age at sexual maturity (Fig. S2). However these variables had even lower performance
309 during data imputation routine (NRMSE was 0.42 and 0.36 respectively).

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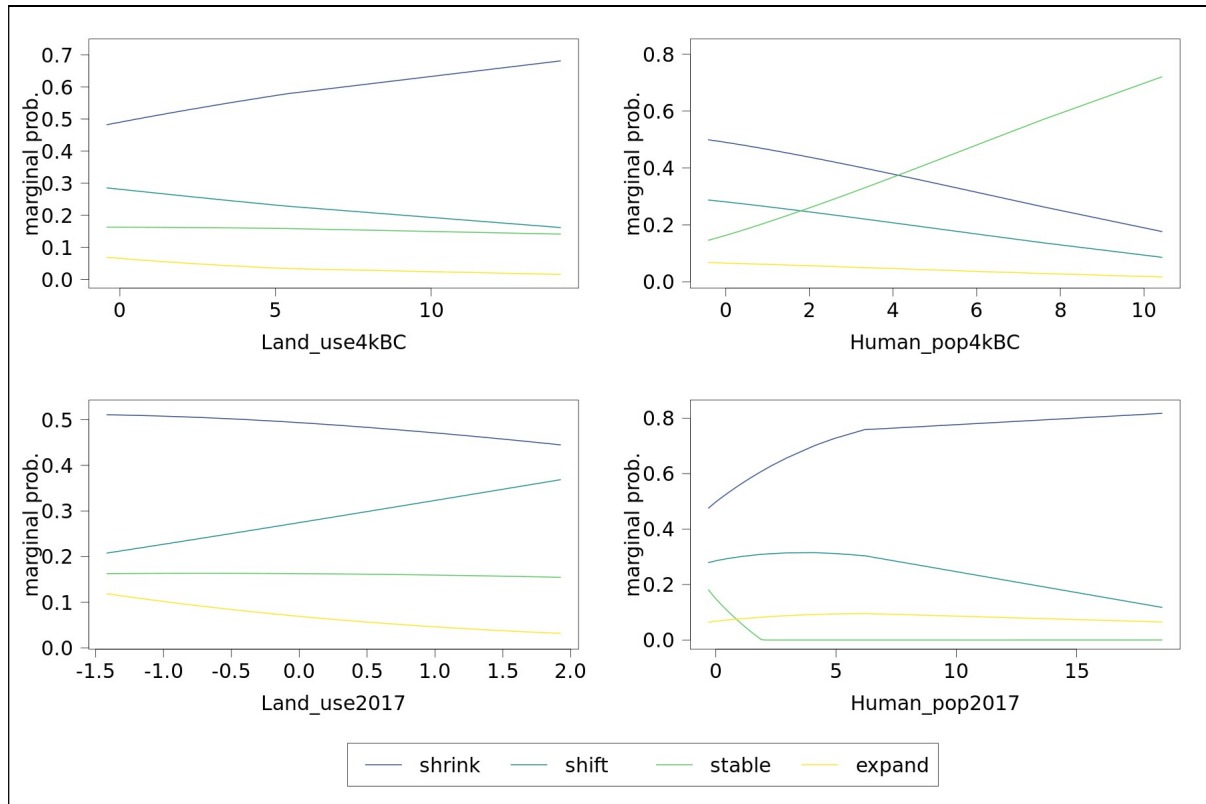
312 **Figure 4** Average partial effect plots of the relationship between species intrinsic
 313 characteristics (scaled for the multinomial model) and probability of species to be assigned
 314 to one of four categories of niche change (shrink, stable, shift, expand), using Mid Holocene
 315 as the reference past climate and two alternative GCMs. Panels a,c,e represents species diets
 316 as proportion of plant, vertebrate, and invertebrate food consumed. Panels b,d,f represents
 317 species' body mass, gestation length, and inter-birth interval.

318

319 When looking at human pressure, we found past and current variables have somewhat
 320 different relationships with niche class probabilities (Fig. 5). Higher probability of niche
 321 shrink is associated with past agricultural land-use, while current land-use is associated with
 322 higher probability of niche shift. Human population density instead shows different patterns,

323 as past density is associated with higher probability of niche stability and current density is
324 associated with higher probability of niche shrink.

325



326

327 **Figure 5** Average partial effect plot of the relationship between human pressure (scaled for
328 the multinomial model) and probability of species to be assigned to one of four categories of
329 niche change (shrink, stable, shift, expand), using Mid Holocene as the reference past climate
330 and two alternative GCMs. Panels a,c represents historic and current human land use,
331 panels b,d represents historic and current human population.

332

333

334

335 Discussion

336 Overall, half of the species we analysed have faced a shrinkage in their realised climatic
337 niche of more than 20%, in response to human alteration of their distribution, global climatic
338 change, and life history traits. At the same time, only 15-18% of species retained a stable or

339 nearly stable niche. We used 20% as a threshold to separate stability from change, both in
340 terms of change in niche position and change in overall niche variability. This is a quite
341 conservative threshold, which was chosen for practical and statistical reasons. Practically,
342 given the coarse resolution of past species distribution data, choosing a relatively high
343 threshold minimised the risk of identifying changes that were an artefact of data uncertainty.
344 Statistically, this choice resulted in the best performance of the model, which was higher with
345 threshold of 20% especially when looking at category-level classification accuracy.

346 We found species with certain biological characteristics were more likely to undergo niche
347 shrink. Large-bodied species for example were more likely to undergo niche shrink compared
348 to smaller species, and less likely to show niche shift or stability. There was an exception
349 however for very large species, i.e. pachyderms, which might be due to the large conservation
350 attention that some of these species receive nowadays. A correlation between niche shrink
351 and large body mass might depend on the large mammals' vulnerability to human impact,
352 which determines low resistance to niche erosion. Larger species have the biological potential
353 to extend their distribution range via dispersal mechanisms (Santini et al. 2013), but are also
354 typically characterised by slower life histories compared to smaller species (Bielby et al.
355 2007) and are more sensitive to human impact (Cardillo et al. 2005). In fact, this result is
356 reflected when looking at gestation length, a proxy of reproductive output (Bielby et al.
357 2007), with longer values associated with higher probability of niche shrinkage. Instead
358 interbirth interval, a proxy of reproductive timing (Bielby et al. 2007), was positively
359 associated with niche shift and negatively associated with niche shrink. However there was
360 limited available data on this trait (and other reproductive timing traits), and the data
361 imputation procedure had lower performance for this variable compared to gestation length.
362 Improved information would be needed before drawing conclusions on this variable.

363 Species' diet was not an overall dominant driver of niche change in our model, but showed
364 fairly clear relationship with niche categories. We found the main effect was determined by
365 invertebrate food items, with higher percentage of invertebrate diet leading to lower
366 probability of niche shrink and higher probability of expansion. This might imply highly
367 insectivorous species have higher adaptability compared to both highly carnivorous and
368 highly herbivorous ones, similar to omnivores.

369 We found species responded to past and current levels of human pressure in different ways.
370 Higher levels of historical land-use change within a species' natural distribution determined
371 higher probability of niche shrink. Current levels of land-use change instead determined
372 higher probability of shift. This result might have emerged because part of the current human
373 influence is realized over portions of the natural species distributions which have been lost.

374 Species might be able to adapt to human pressure inside their present-day distributions, which
375 already resisted to some level of historical pressure. When low levels of climate change affect
376 these core distribution areas, species might show some adaptation capacity via niche shift
377 mechanisms. The relationship with human population density showed the opposite pattern
378 instead, with past density positively correlated with the probability of stable niche and
379 negatively correlated with the probability of shrinking niche. This scenario of past co-
380 existence between human and other mammal species might be a reflection of both human and
381 animal communities settling in productive natural environments, but also a possible
382 facilitation of human-wildlife coexistence in those areas when human colonization started
383 earlier (Carter & Linnell 2016). This result however is also in part dependent on the threshold
384 of 20% that was used to distinguish between niche stability and niche change. In fact, we
385 verified that a lower threshold of 5% would result in a positive correlation between past
386 human density and probability of niche shrink; this means past human density resulted in
387 either niche stability or very low levels of niche shrink. Instead we found current human

388 population density within natural species distributions was positively associated with niche
389 shrink, regardless of the threshold. This shows the risk faced by species living in highly
390 anthropogenic areas (Di Marco et al. 2018), which might become more vulnerable to the
391 additive effect of climate change (Mantyka-Pringle et al. 2012, 2015).

392 Our model has demonstrated good overall performance during validation, except for the
393 ‘expand’ category. This is due to the limited number of species which showed a substantial
394 (>20%) increase in their niche breadth over time. This implies our understanding of the
395 mechanisms of niche expansion is still limited, until additional species examples are
396 identified. A promising field of research in this case is represented by invasive species
397 (Broennimann et al. 2012). Invasive species might maintain their original climatic niche in
398 the invaded region (Petitpierre et al. 2012), or exploit a wider variety of climatic conditions
399 and shift or expand their realised niche (Lauzeral et al. 2011). Understanding more of the
400 dynamics and drivers of niche change for these species can shed light on the past dynamics of
401 niche change.

402 We identified the conditions under which species are unlikely to maintain a varied climatic
403 niche, potentially losing their climate adaptive potential. Areas which will experience
404 substantially different climates in the future should be given special attention to prevent
405 threatened and restricted-range species from rapid decline. Interventions that facilitate natural
406 dispersal, or assisted colonisation, should be carefully evaluated for these species, as part of
407 international strategies to combat the effects of climate change on biodiversity such as the
408 Convention on Biological Diversity and the United Nation Framework Convention on
409 Climate Change.

410

411

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416 **References**

417 Adrian R, Wilhelm S, Gerten D. 2006. Life-history traits of lake plankton species may govern
418 their phenological response to climate warming. *Global Change Biology* 12:652–661.

419 Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate
420 change on the future of biodiversity. *Ecology Letters* 15:365–377.

421 Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CDL,
422 Purvis A. 2007. The fast-slow continuum in mammalian life history: an empirical
423 reevaluation. *The American Naturalist* 169:748–757.

424 Broennimann O et al. 2012. Measuring ecological niche overlap from occurrence and spatial
425 environmental data. *Global Ecology and Biogeography* 21:481–497.

426 Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL,
427 Purvis A. 2005. Multiple causes of high extinction risk in large mammal species.
428 *Science* 309:1239–1241.

429 Carroll SP. 2008. Facing change: Forms and foundations of contemporary adaptation to biotic
430 invasions. *Molecular Ecology* 17:361–372.

431 Carter NH, Linnell JDC. 2016. Co-Adaptation Is Key to Coexisting with Large Carnivores.
432 *Trends in Ecology and Evolution* 31:575–578.

433 Chown SL, Hoffmann A a., Kristensen TN, Angilletta MJ, Stenseth NC, Pertoldi C. 2010.
434 Adapting to climate change: A perspective from evolutionary physiology. *Climate*
435 *Research* 43:3–15.

436 Dawson TP. 2011. Beyond predictions: Biodiversity conservation in a changing climate.
437 *Science* 332:664.

- 438 Di Cola V et al. 2017. ecospat: an R package to support spatial analyses and modeling of
439 species niches and distributions. *Ecography* 40:774–787.
- 440 Di Marco M, Collen B, Rondinini C, Mace G. 2015. Historical drivers of extinction risk:
441 using past evidence to direct future monitoring. *Proceedings of the Royal Society B*
442 282:20150928.
- 443 Di Marco M, Harwood TD, Hoskins AJ, Ware C, Hill SLL, Ferrier S. 2019. Projecting
444 impacts of global climate and land-use scenarios on plant biodiversity using
445 compositional-turnover modelling. *Global Change Biology* 25:2763–2778.
- 446 Di Marco M, Venter O, Possingham HP, Watson JEM. 2018. Changes in human footprint
447 drive changes in species extinction risk. *Nature Communications* 9:4621.
- 448 Diniz-Filho JAF, de Sant’Ana CER, Bini LM. 1998. An Eigenvector Method for Estimating
449 Phylogenetic Inertia. *Evolution* 52:1247–1262.
- 450 Faurby S, Araújo MB. 2018. Anthropogenic range contractions bias species climate change
451 forecasts. *Nature Climate Change* 8:252–256.
- 452 Faurby S, Davis M, Pedersen R, Schowanek SD, Antonelli A, Svenning JC. 2018.
453 PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*
454 99:2626.
- 455 Faurby S, Svenning J-C. 2015. Historic and prehistoric human-driven extinctions have
456 reshaped global mammal diversity patterns. *Diversity and Distributions* 21:1155–1166.
- 457 Fragoso J, Silvius K, Correa J. 2003. Long-distance seed dispersal by tapirs increases seed
458 survival and aggregates tropical trees. *Ecology* 84:1998–2006.
- 459 Goldewijk KK, Beusen A, Doelman J, Stehfest E. 2017. Anthropogenic land use estimates
460 for the Holocene - HYDE 3.2. *Earth System Science Data* 9:927–953.

- 461 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution
462 interpolated climate surfaces for global land areas. *International Journal of Climatology*
463 25:1965–1978.
- 464 Hoffmann AA, Sgró CM. 2011. Climate change and evolutionary adaptation. *Nature*
465 470:479–485.
- 466 Hoffmann M et al. 2010. The impact of conservation on the status of the world’s vertebrates.
467 *Science* 330:1503–9.
- 468 Hoffmann M, Belant JL, Chanson JS, Cox N a., Lamoreux J, Rodrigues a. SL, Schipper J,
469 Stuart SN. 2011. The changing fates of the world’s mammals. *Philosophical*
470 *Transactions of the Royal Society B: Biological Sciences* 366:2598–2610.
- 471 IUCN. 2018. The IUCN Red List of Threatened Species. Version 2018-1. Available from
472 <http://www.iucnredlist.org> (accessed July 5, 2018).
- 473 Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D. 2007. Climate envelope, life history
474 traits and the resilience of birds facing global change. *Global Change Biology* 13:1672–
475 1684.
- 476 Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Guangchun L, Wilmshurst JM.
477 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science*
478 356:270–275.
- 479 Jones KE et al. 2009. PanTHERIA: a species-level database of life history, ecology, and
480 geography of extant and recently extinct mammals. *Ecology* 90:2648.
- 481 Lauzeral C, Leprieur F, Beauchard O, Duron Q, Oberdorff T, Brosse S. 2011. Identifying
482 climatic niche shifts using coarse-grained occurrence data: A test with non-native
483 freshwater fish. *Global Ecology and Biogeography* 20:407–414.

- 484 Liaw A, Wiener M. 2002. The randomforest package. *R News* 2:18–22.
- 485 Liu X, Petitpierre B, Broennimann O, Li X, Guisan A, Li Y. 2017. Realized climatic niches
486 are conserved along maximum temperatures among herpetofaunal invaders. *Journal of*
487 *Biogeography* 44:111–121.
- 488 Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of
489 climate change. *Nature* 462:1052–1055.
- 490 Mahon CL, Holloway G, Szymos P, Cumming SG, Bayne EM, Schmiegelow FK a, Song
491 SJ. 2016. Community structure and niche characteristics of upland and lowland western
492 boreal birds at multiple spatial scales. *Forest Ecology and Management* 361:99–116.
- 493 Maiorano L et al. 2013. Threats from climate change to terrestrial vertebrate hotspots in
494 Europe. *PloS one* 8:e74989.
- 495 Mantyka-Pringle CS, Martin TG, Rhodes JR. 2012. Interactions between climate and habitat
496 loss effects on biodiversity: a systematic review and meta-analysis. *Global Change*
497 *Biology* 18:1239–1252.
- 498 Mantyka-Pringle CS, Visconti P, Di Marco M, Martin TG, Rondinini C, Rhodes JR. 2015.
499 Climate change modifies risk of global biodiversity loss due to land-cover change.
500 *Biological Conservation* 187: 103-111.
- 501 Maxwell SL, Fuller R a., Brooks TM, Watson JEM. 2016. The ravages of guns, nets and
502 bulldozers. *Nature* 536:146–145.
- 503 Newbold T. 2018. Future effects of climate and land-use change on terrestrial vertebrate
504 community diversity under different scenarios. *Proceedings of the Royal Society B:*
505 *Biological Sciences* 285:20180792.
- 506 Olalla-Tárraga MÁ et al. 2011. Climatic niche conservatism and the evolutionary dynamics

- 507 in species range boundaries: Global congruence across mammals and amphibians.
508 *Journal of Biogeography* 38:2237–2247.
- 509 Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC,
510 D’Amico JA, Itoua I, Strand HE, Morrison JC. 2001. Terrestrial ecoregions of the
511 world: a new map of life on earth. *BioScience* 51:933–938.
- 512 Pacifici AM et al. 2015. Assessing species vulnerability to climate change. *Nature Climate*
513 *Change* 5:215–225.
- 514 Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017.
515 Species’ traits influenced their response to recent climate change. *Nature Climate*
516 *Change* 7: 205–208.
- 517 Pearman PB, Guisan A, Broennimann O, Randin CF. 2008. Niche dynamics in space and
518 time. *Trends in Ecology and Evolution* 23:149–158.
- 519 Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE,
520 Graham CH, Costa GC. 2014. Imputation of missing data in life-history traits datasets:
521 which approach performs the best? *Methods in Ecology and Evolution* 5:961–970.
- 522 Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Bastos
523 Araujo M. 2011. *Ecological niches and geographic distributions*. PRINCETON
524 UNIVERSITY PRESS, Princeton and Oxford.
- 525 Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. 2012. Climatic
526 Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science* 335:1344–1348.
- 527 Pringle RM, Young TP, Rubenstein DI, McCauley DJ. 2007. Herbivore-initiated interaction
528 cascades and their modulation by productivity in an African savanna. *Proceedings of the*
529 *National Academy of Sciences of the United States of America* 104:193–7.

- 530 R Core Team. 2018. R: A Language and Environment for Statistical Computing. Vienna,
531 Austria. Available from <https://www.r-project.org/>.
- 532 Santini L, Cornulier T, Bullock JM, Palmer SCF, White SM, Hodgson JA, Bocedi G, Travis
533 JMJ. 2016. A trait-based approach for predicting species responses to environmental
534 change from sparse data: how well might terrestrial mammals track climate change?
535 *Global Change Biology* 22:2415–2424.
- 536 Santini L, Di Marco M, Visconti P, Baisero D, Boitani L, Rondinini C. 2013. Ecological
537 correlates of dispersal distance in terrestrial mammals. *Hystrix* 24:181–186.
- 538 Soulé M, Estes J. 2003. Ecological effectiveness: conservation goals for interactive species.
539 *Conservation Biology* 17:1238–1250.
- 540 Stekhoven DJ, Bühlmann P. 2012. MissForest--non-parametric missing value imputation for
541 mixed-type data. *Bioinformatics* 28:112–8.
- 542 Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. 2003. Responses of “resistant”
543 vertebrates to habitat loss and fragmentation: The importance of niche breadth and range
544 boundaries. *Diversity and Distributions* 9:1–18.
- 545 Tacutu R, Craig T, Budovsky A. 2013. Human Ageing Genomic Resources: Integrated
546 databases and tools for the biology and genetics of ageing. *Nucleic acid research*
547 41:1027–1033.
- 548 Thuiller W, Lavorel S, Araújo MB. 2005. Niche properties and geographical extent as
549 predictors of species sensitivity to climate change. *Global Ecology and Biogeography*
550 14:347–357.
- 551 Urban MC, Richardson JL, Freidenfelds NA. 2014. Plasticity and genetic adaptation mediate
552 amphibian and reptile responses to climate change. *Evolutionary Applications* 7:88–103.

- 553 Venables WN, Ripley BD. 2002. Modern Applied Statistics with S Fourth. Springer, New
554 York. Available from <http://www.stats.ox.ac.uk/pub/MASS4>.
- 555 Visconti P et al. 2016. Projecting global biodiversity indicators under future development
556 scenarios. *Conservatio Letters* 9:5–13.
- 557 Walther GR, Berger S, Sykes MT. 2005. An ecological “footprint” of climate change.
558 *Proceedings of the Royal Society B: Biological Sciences* 272:1427–1432.
- 559