

1 **Title:** A framework for the identification of hotspots of climate  
2 change risk for mammals

3 **Running head:** Hotspots of climate change risk for mammals

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17 mammals, vulnerability

18

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20 **Abstract**

21 As rates of global warming increase rapidly, identifying species at risk of decline due to  
22 climate impacts and the factors affecting this risk have become key challenges in ecology and  
23 conservation biology. Here we present a framework for assessing three components of  
24 climate-related risk for species: vulnerability, exposure and hazard. We used the relationship  
25 between the observed response of species to climate change and a set of intrinsic traits (e.g.,  
26 weaning age) and extrinsic factors (e.g., precipitation seasonality within a species geographic  
27 range) to predict, respectively, the vulnerability and exposure of all data-sufficient terrestrial  
28 non-volant mammals (3953 species). Combining this information with hazard (the magnitude  
29 of projected climate change within a species geographic range) we identified global hotspots  
30 of species at risk from climate change that includes the western Amazon basin, south-western  
31 Kenya, north-eastern Tanzania, north-eastern South Africa, Yunnan province in China, and  
32 mountain chains in Papua-New Guinea. Our framework identifies priority areas for  
33 monitoring climate change effects on species and directing climate mitigation actions for  
34 biodiversity.

35

## 36 **Introduction**

37           Global mean temperature is projected to rise in excess of 2°C by 2050 relative to  
38 preindustrial levels, which is expected to severely impact ecosystems, and cause an extensive  
39 loss of ecosystem functions and services (IPCC, 2014). Climate change is expected to impact  
40 severely on animal populations and to drive massive extinction of species in the future (Isaac,  
41 2009), but its effects are also already documented for several taxa. For example, marine  
42 species have shifted the poleward edge of their range by 72 km per decade and terrestrial  
43 species by 6 km per decade (Scheffers *et al.*, 2016), while both mammal and bird species have  
44 been negatively affected in terms of reductions in population and range size, survival and  
45 reproductive rates (Pacifiçi *et al.*, 2017).

46           Not all species are expected to respond to climate change alike. Life-history traits, and  
47 to a lesser extent taxonomy and geographic distribution, mediate species responses to climate  
48 change (Pacifiçi *et al.*, 2017). Different mammal species, in particular, have shown variable  
49 responses to recent climate change according to their life-history traits and the breadth of  
50 environmental and climatic conditions they experience (Boutin & Lane, 2014; Santini *et al.*  
51 2016; Pacifiçi *et al.*, 2017). The above evidence is the basis for the identification of species at  
52 higher risk of decline due to climate impacts, and of the factors affecting this risk. This is  
53 done through a family of methods collectively named climate change vulnerability  
54 assessments (CCVA; Foden & Young, 2016). CCVA methods include correlative approaches  
55 (which project species niches into the future based on forecasts of climate change),  
56 mechanistic approaches (that model individual behaviour in response to climate change), and  
57 trait-based analyses. Trait-based CCVAs use species-specific intrinsic life-history traits (e.g.,  
58 body mass, habitat and diet specialization, reproductive rates) to estimate species  
59 vulnerability to climate change (Pacifiçi *et al.*, 2015a).

60 Existing CCVA techniques have drawbacks (Pacifci *et al.*, 2015a). The vast majority  
61 of correlative CCVAs (e.g., Hughes *et al.*, 2012; Songer *et al.*, 2012; Baker *et al.*, 2015) use  
62 the relationship between the observed geographic distribution of a species and the current  
63 climate to infer potential climatically suitable areas for a given species in the future, without  
64 considering the intrinsic characteristics of a species that make it more or less predisposed to  
65 be impacted by changing climatic conditions (but see Pearson *et al.*, 2014; Visconti *et al.*,  
66 2015). Trait-based CCVAs use a deductive (expert-based) approach rather than an inductive  
67 (evidence-based) approach to infer which traits are more important in determining species  
68 vulnerability. This introduces an unquantifiable error in the process (Pacifci *et al.*, 2015a).  
69 Most trait-based CCVAs also lack a spatial component to identify the areas in which the  
70 climatic hazard will be more severe (Laidre *et al.*, 2008; Moyle *et al.*, 2013). Consensus is  
71 growing over the benefits of combining different CCVA approaches to overcome some of  
72 these limitations outlined above (Pacifci *et al.*, 2015a; Willis *et al.*, 2015; Foden & Young,  
73 2016).

74 Here we propose a framework that combines elements of several CCVA approaches  
75 under one single statistical model, to assess the overall likelihood of adverse effects of climate  
76 change on species based on observed impacts on animal populations. Our framework  
77 represents a biodiversity-relevant interpretation of the IPCC general framework for climate  
78 impact assessment (IPCC, 2014). The IPCC framework uses the interaction of climate-related  
79 hazards, vulnerability (the predisposition to be adversely affected) and exposure (the  
80 probability to experience the hazard) to derive an overall risk of climate-related impacts to  
81 human and natural systems. Here we operationalize the IPCC framework for species as  
82 follows: i) vulnerability is the intrinsic predisposition of a species to be adversely affected by  
83 climate change (given its life-history traits); ii) exposure is the likelihood that climatic refugia  
84 exist for the species (related to the span of geographic and climatic variables currently

85 experienced by the species within its natural geographic range); and iii) hazard is the  
86 magnitude of projected climate change within the species geographic range.

87 We applied our framework to 3953 species of data-sufficient terrestrial non-volant  
88 mammals, using the multinomial logistic model recently developed by Pacifici *et al.* (2017).  
89 Mammals are an ideal taxonomic group for our analysis since they include relatively few  
90 species and abundant information is available on their life-history traits (e.g., Jones *et al.*,  
91 2009; Tacutu *et al.*, 2013). While Pacifici *et al.* (2017) found species that could have been  
92 already negatively impacted by climate change, here for the first time we identified areas with  
93 the highest numbers of mammals likely to be at risk in the near future (hotspots of climate  
94 risk). Our predictions for the future are based on observed impacts of climate change on  
95 mammals, which has never been done before at a global scale. In addition, our framework  
96 quantifies the relationship between life-history traits and selected spatial variables and the  
97 response of species to climate change, in order to identify hotspots of species likely to be at  
98 risk, thus overcoming some of the important limitations associated with trait-based and  
99 correlative approaches outlined above. Finally, we propose a set of actions that can be applied  
100 according to the risk element/s analysed. This work can be the basis for planning ad hoc  
101 conservation actions for those species and areas likely to be more impacted by future climatic  
102 changes.

103

## 104 **Materials and methods**

### 105 *Hazard*

106 Hazard is usually calculated using climatic scenarios. We used climate predictions  
107 from 11 GCMs (global circulation models) and 3 representative concentration pathway (RCP)  
108 scenarios (RCP2.6, RCP6.0 and RCP8.5) from the WorldClim database at 10 km resolution

109 (<http://www.worldclim.org>), to compute the difference between the current and the future  
110 (2050) mean annual temperature in each grid cell. These greenhouse gas concentration  
111 scenarios display different trends in radiative forcing during the 21<sup>st</sup> century and high human  
112 population growth energy consumption, from the most optimistic scenario (RCP2.6) to the  
113 most severe one (RCP8.5). We then averaged these values across the entire species range  
114 provided by the IUCN, in order to obtain a mean value of temperature change in the areas  
115 where the species is currently distributed.

116

### 117 *Hotspots of climate risk*

118 For our analysis, we adopted the database and multinomial logistic model used by  
119 Pacifici *et al.* (2017), in which species response to recent climate change (negative, positive,  
120 unchanged or mixed) was used as dependent categorical variable. The negative response was  
121 assigned to a species if >50% of its populations were reported to have undergone declines in  
122 the extent of the geographic range, population size, survival or reproductive rates, and body  
123 mass. On the contrary, the positive response was assigned if the majority of the populations of  
124 a species experienced expansions in the above mentioned metrics. The unchanged response  
125 was attributed if no response was observed despite the recorded change in climate. Finally,  
126 the mixed response was attributed to species that exhibited a combination of positive and  
127 negative impacts (see Pacifici *et al.* 2017 for further details). We used as independent  
128 variables those identified as most important for determining an overall climate risk for the  
129 species in Pacifici *et al.* 2017, i.e. non-fossorial behaviour, restricted dietary breadth, reduced  
130 precipitation seasonality and high minimum altitude, the latter two computed within the  
131 current species range (Table 1). In Pacifici *et al.* (2017), large differences in temperature  
132 between the present and the past were also important determinant of negative responses. Since

133 the expected increase in temperatures is likely to be 3-4 times higher than that of the past 100  
 134 years, we included the difference in mean annual temperature between the present and the  
 135 future as predictor representing the hazard component. In addition, we considered taxonomy  
 136 as a fixed effect, in order to control for the non-independence of observed responses across  
 137 species (Table 1).

138

Variable	Description	Main data sources	Climate risk component
Dietary breadth	Number of categories of food items eaten by a species. In order to identify the species with the highest dietary specialization, the categories of food items were defined as fruit, flowers/nectar/pollen, wood/bark/stems, leaves, seeds/grains/nuts, roots/tubers, sap or other plant fluids, bryophytes, fungi, mammals, birds, reptiles, amphibians, fishes, molluscs, aquatic crustaceans, insects, terrestrial non-insect arthropods, terrestrial worms	Nowak (1999); Wilson & Reeder (2005); IUCN (2016)	Vulnerability
Fossoriality	YES or NO, referred to mammal species adapted/non-adapted to digging and life underground	Wilson & Reeder (2005)	Vulnerability
Order	Taxonomic order to which the species belongs	IUCN (2016)	Vulnerability
Precipitation seasonality	(mm), represents the difference in mean precipitation between the wettest and the driest quarters within a species current distributional range	<a href="http://www.worldclim.org/">http://www.worldclim.org/</a>	Exposure
Minimum altitude	(meters), is the minimum altitude at which a species currently lives	Jarvis <i>et al.</i> , (2008)	Exposure
$\Delta$ temperature	Mean difference between the current (mean 1980-2009) and the future (2050) temperature within a species range	<a href="http://www.cru.uea.ac.uk/data">http://www.cru.uea.ac.uk/data</a>	Hazard

139 **Table 1** Description of the independent variables used in the model.

140

141 By using the function *predict* in R, we predicted the likely response of all species  
142 (3953) to projected scenarios of climate change (climate risk). In order to account for the  
143 uncertainty in our models, we first predicted the probabilities associated with each of the four  
144 options of the response variable, and then we sampled the response category assigned to each  
145 species from the multinomial distribution 100 times to derive the mean and standard deviation  
146 of the richness of species with a negative response. We then produced richness maps for each  
147 climatic scenario to find hotspots of species that are likely to be at greatest risk from climate  
148 change in 2050, defined as those species having a higher probability of showing a negative  
149 response in the future, according to model predictions. In addition, to determine which areas  
150 will be more severely affected in terms of potential loss of the overall local mammalian  
151 biodiversity, we divided the number of species at risk in each grid cell by the total number of  
152 species in the cell, to obtain a map of the areas hosting the highest proportion of species at  
153 greatest risk from climate change.

154

### 155 *Vulnerability and exposure*

156 In order to consider the three components of climate risk both together and  
157 independently, we also identified the areas with the highest concentration of vulnerable and  
158 exposed species. To do that, we ran two different models by using the predictors of the  
159 multinomial logistic model for climate risk, but held the variables related to vulnerability (i.e.,  
160 dietary breadth and fossoriality) and exposure (i.e., precipitation seasonality and minimum  
161 altitude recorded within the current geographic range), respectively, constant at their mean  
162 (numeric variables) or mode (nominal variables), calculated among all 3953 species  
163 considered. In both the vulnerability and exposure models, in order to control for the latent

164 variables that may affect the responses to climate change that are phylogenetically conserved,  
165 we did not change the values for taxonomic order. For example, in order to look at the effect  
166 of intrinsic life-history traits, we held the mean difference in temperature, minimum altitude  
167 within a species range, and precipitation seasonality constant, while we used species-specific  
168 values for dietary breadth, fossoriality and taxonomic order. We then stacked the distribution  
169 ranges of these species obtained from the IUCN database ([www.iucn.org](http://www.iucn.org)) to derive a richness  
170 map of global vulnerability. We applied the same procedure to identify the areas hosting the  
171 highest numbers of species likely to be exposed to climate change, but holding constant only  
172 the predictors not related to exposure.

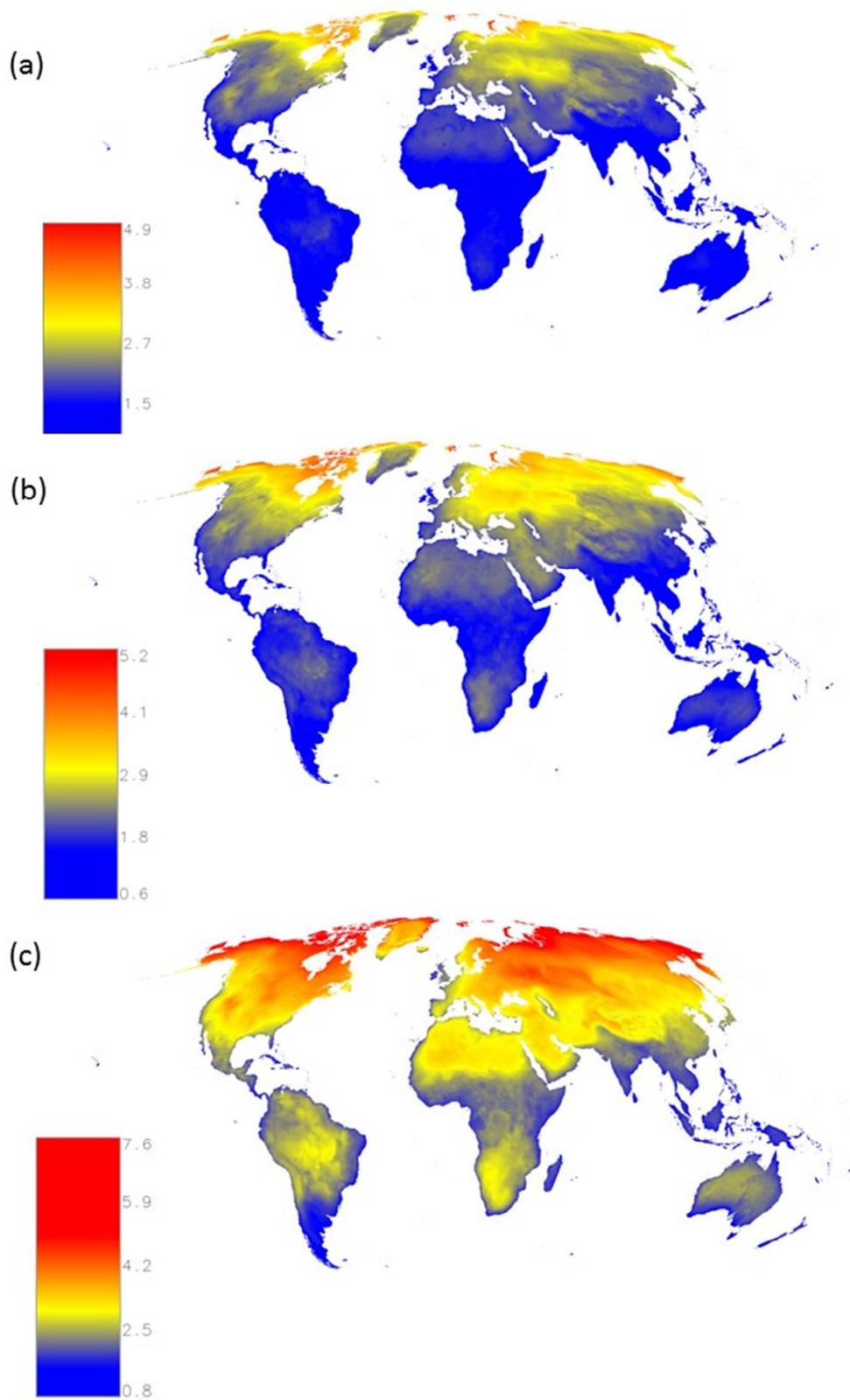
173

## 174 **Results**

### 175 *Areas experiencing the greatest changes in temperature*

176 In all the three RCP scenarios considered, the minimum change in mean temperature  
177 between the present and the future in a grid cell is  $\geq 0.4^{\circ}\text{C}$  ( $0.4^{\circ}\text{C}$  in RCP2.6,  $0.6^{\circ}\text{C}$  in RCP6.0  
178 and  $0.8^{\circ}\text{C}$  in RCP8.5; Fig. 1). As expected, the most severe changes in climate is projected  
179 under the RCP8.5 scenario (mean global temperature increase of  $2.97^{\circ}\text{C}$ ), followed by the  
180 RCP6.0 ( $2.16^{\circ}\text{C}$ ) and RCP2.6 ( $1.89^{\circ}\text{C}$ ). Despite the great differences in the magnitude of  
181 climate change between the three scenarios, all the three converge in identifying areas that  
182 would experience the highest changes in temperatures. These correspond to the northern polar  
183 region (Fig. 1), where the predicted increase in temperature is always  $>1.7^{\circ}\text{C}$  (RCP2.6: min  
184  $+1.7^{\circ}\text{C}$ , mean  $+3.06^{\circ}\text{C}$ , max  $+4.9^{\circ}\text{C}$ ; RCP6.0: min  $+1.8^{\circ}\text{C}$ , mean  $+3.3^{\circ}\text{C}$ , max  $+5.2^{\circ}\text{C}$ ;  
185 RCP8.5: min  $+2.8^{\circ}\text{C}$ , mean  $+4.7^{\circ}\text{C}$ , max  $+7.5^{\circ}\text{C}$ ). In the RCP8.5 scenario, 87.5% of the  
186 world will experience an increase in mean annual temperature  $>2^{\circ}\text{C}$  by 2050 (while in  
187 RCP6.0 and RCP2.6 these percentages stand at 50% and 37.5%, respectively), and additional

188 areas that are likely to be considerably affected by these changes are the Kamchatka Peninsula  
189 in Russia, the Himalayas, West Russia, the territories on the border between Russia and  
190 Kazakhstan, and the mountain chains in North America. From Fig. 1 it is evident that, in  
191 general, the Northern Hemisphere is likely to be more subject to global climate change than  
192 the Southern Hemisphere, in particular in the RCP2.6 and RCP6.0 scenarios.



193

194 **Figure 1** Mean annual temperature difference between the present and the future in 2050 in the a)

195 RCP2.6, b) RCP6.0 and c) RCP8.5 scenarios.

196 *Species most at risk under projected climate change*

197         Our predictions of species responses to projected climate change were very similar  
198 among the three different scenarios, with only 195 species out of 3953 (4.9%) showing  
199 differing results. As expected, the number of species showing no response to climate change  
200 decreased as the changes in mean annual temperatures became more intense, with 1.34% of  
201 the species classified as ‘unchanged’ in the RCP2.6 scenario, 0.46% in the RCP6.0 and 0  
202 species in the RCP8.5. The taxonomic orders having >85% of the species with a likely future  
203 negative response in all scenarios were Proboscidea, Dasyuromorphia, Primates,  
204 Diprotodontia, Cetartiodactyla, Perissodactyla and Lagomorpha (Tables S1, S2, S3).

205         Surprisingly, considering only the set of species having different responses in the  
206 different scenarios, the majority of them were likely to benefit from increases in mean annual  
207 temperatures (133 species out of 195 had a negative or unchanged response in the RCP2.6  
208 scenario and a positive one in the RCP8.5 scenario, Tables S1, S3). These species mostly  
209 included small mammals (belonging to the Rodentia and Eulipotyphla taxonomic orders). On  
210 the contrary, only 24 and 37 species changed their responses to negative and mixed,  
211 respectively, in the RCP8.5 scenario.

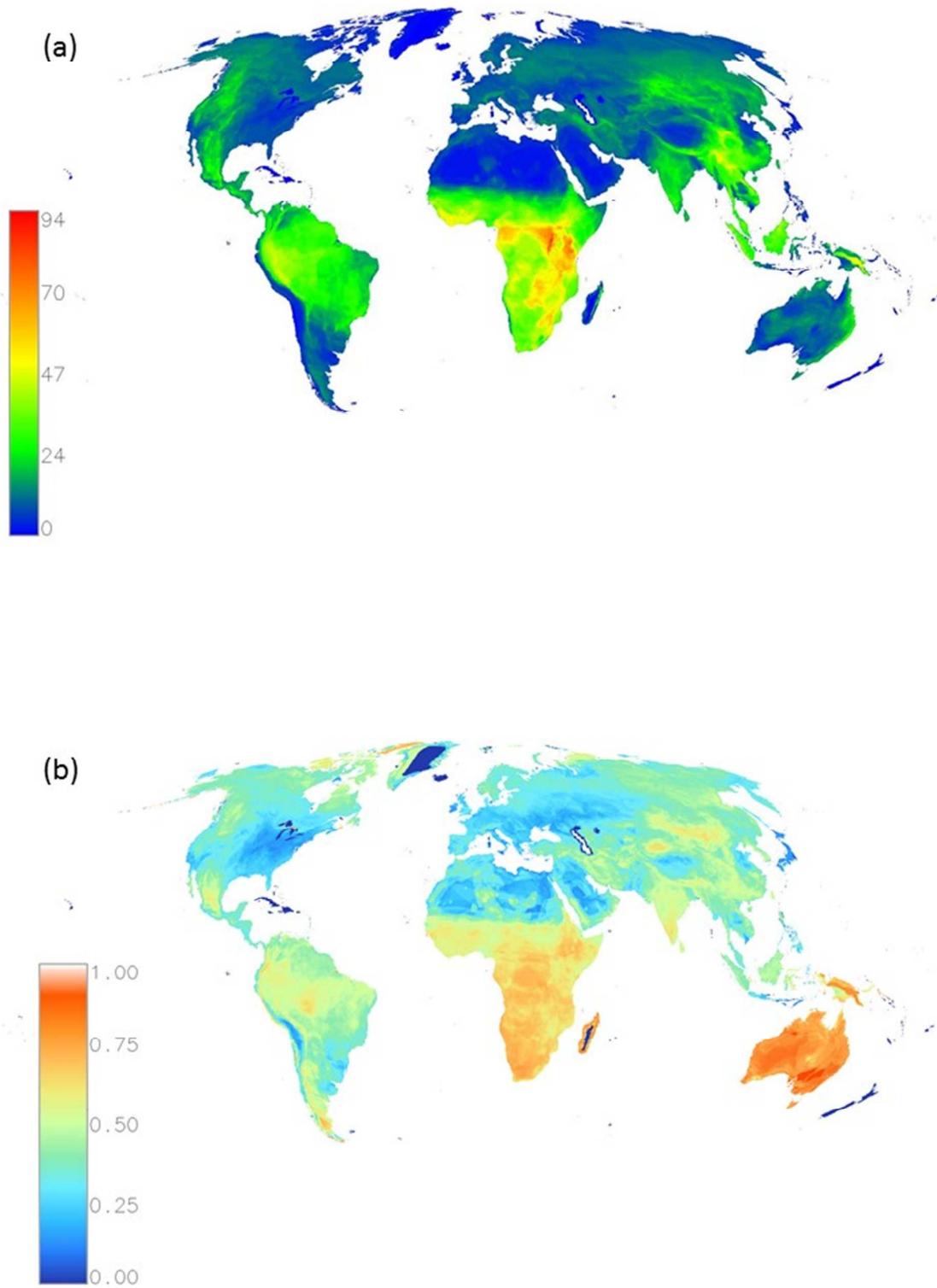
212

213 *Identifying hotspots of species at climate risk*

214         In general, we found the highest concentration of mammals most likely to be at risk  
215 from climate change in mountainous areas. In particular, hotspots of species richness are  
216 concentrated in the western Amazon River basin, south-western Kenya, north-eastern  
217 Tanzania, north-eastern South Africa, Yunnan province in China, and mountain chains in  
218 Papua-New Guinea (Figs. 2a & S1). It is interesting to note that they rarely overlap with areas  
219 identified as having the highest probability of experiencing significant changes in mean

220 annual temperatures. In fact, while most of the hotspots are found in the Southern  
221 Hemisphere, the differences between mean annual temperature in the RCP scenarios between  
222 2050 and the present show that the Northern Hemisphere will experience the greatest changes.

223         When we consider the number of species likely to be negatively impacted by climate  
224 change in the future, with respect to the total number of species present in a grid cell, the  
225 areas with the highest proportions of species at risk are found in northern Greenland, Tierra  
226 del Fuego, lower altitudes of Madagascar, north-west Russia, Mongolia, north-western China,  
227 Tibetan Plateau, Papua-New Guinea, Western Australia and New South Wales (Figs. 2b &  
228 S2). These areas only partly overlap with the hotspots of species richness in central Africa.



229

230 **Figure 2** Maps of projected negatively impacted species by grid cell in the RCP8.5 scenario. a)

231 Richness and b) proportion of species with a negative predicted response.

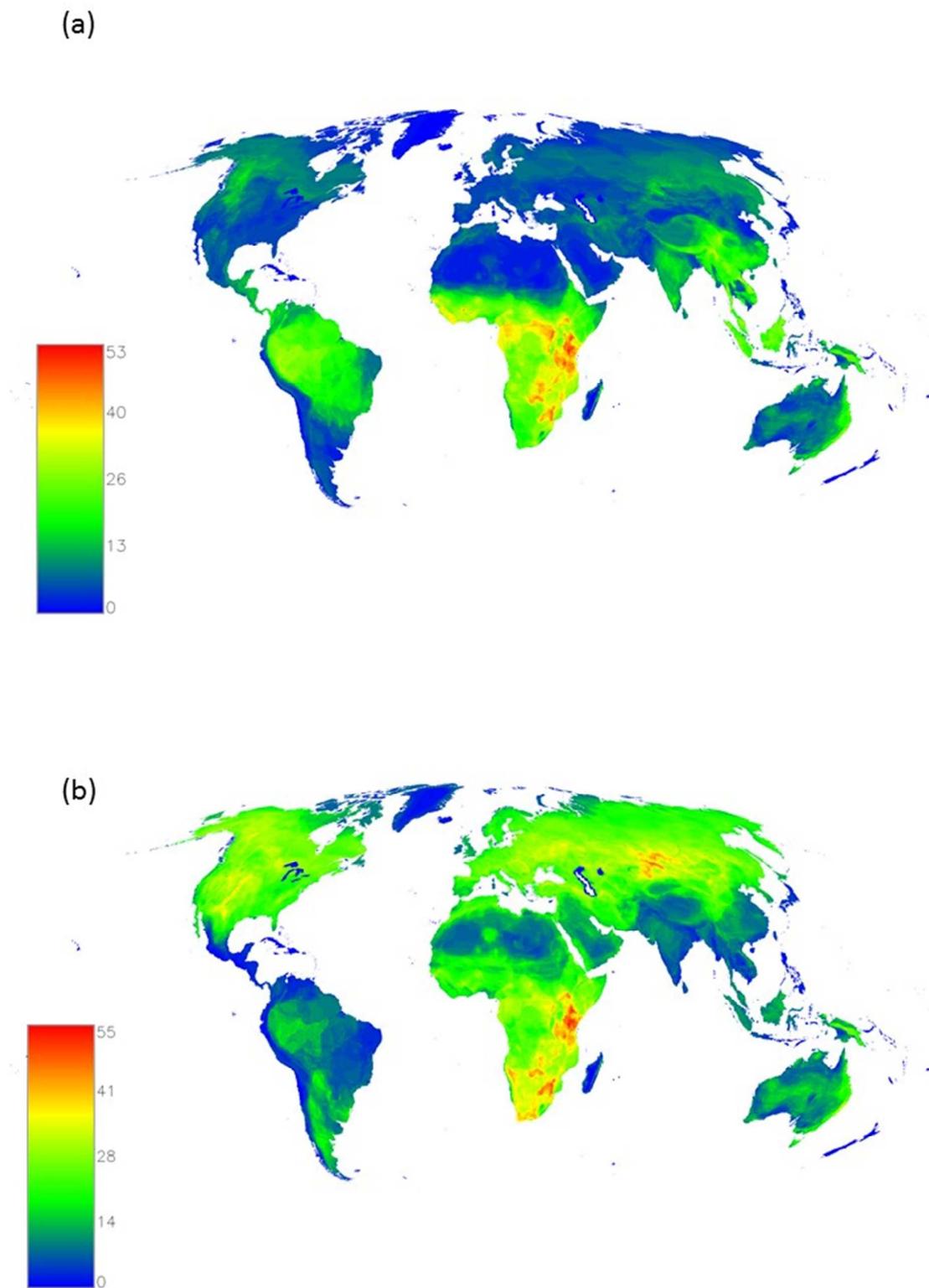
232 *Hotspots of vulnerable-only species*

233           According to our models, the areas hosting large numbers of vulnerable species are  
234 mostly concentrated in eastern Sub-Saharan Africa (Fig. 3a), specifically in the eastern side of  
235 the Democratic Republic of Congo, southern South Sudan and Ethiopia, Kenya, Tanzania,  
236 Zambia and north-eastern regions in South Africa.

237

238 *Hotspots of exposed-only species*

239           The areas hosting high numbers of exposed species include almost all the hotspots of  
240 vulnerable-only species, as well as the Rocky mountains side of Colorado and New Mexico in  
241 the United States, central Namibia, the Cape province in South Africa, and the Altai  
242 Mountains, a mountain system in central Asia extending through China, Russia, Mongolia  
243 and Kazakhstan (Fig. 3b).



244

245 **Figure 3** Relative richness of a) vulnerable and b) exposed species according to multinomial logistic

246 models.

247 **Discussion**

248           The Northern Hemisphere has outpaced the Southern Hemisphere in terms of  
249 temperature increase since about 1980. This is mostly due to the fact that the Northern  
250 Hemisphere has more land and less ocean than the Southern Hemisphere, and the general rate  
251 of warming of the oceans is relatively slow (Friedman *et al.*, 2013). The strong loss of Arctic  
252 sea ice and global ocean currents are another possible factor contributing to the Northern  
253 Hemisphere greater warming. These currents transport heat away from southern oceans and  
254 into the northern waters, helping to further warm nearby land areas in the north (Feulner *et*  
255 *al.*, 2013).

256           Physiographic factors such as slope, elevation and topographic convergence influence  
257 meteorological elements including precipitation, air temperature, wind, solar insolation, snow  
258 accumulation and melt (Dobrowski, 2011). Microtopography can cause large temperature  
259 differences within a short distance, conditions that would otherwise be observed only over  
260 large altitudinal or latitudinal gradients. This suggests that for species living at high altitudes,  
261 which are often limited by dispersal, it is not always necessary to migrate several hundred  
262 meters upslope to avoid warmer conditions (Patsiou *et al.*, 2014). Microrefugia can be found  
263 in sites that are consistently decoupled from regional patterns because they are more likely to  
264 support relict climates. In order to favour species persistence in areas that are likely to  
265 experience the greatest changes in climate, identifying potential microclimate refugia at local  
266 scale would be fundamental for species that have limited ability to move elsewhere.

267           Despite the fact that the northern territories are warming faster than the southern ones,  
268 and that this trend is likely to exacerbate in the coming decades, we found that most species  
269 threatened by climate change mainly occur south of the Equator. Oceania is home to the vast  
270 majority of marsupials at risk from climate change. Specifically, the tropical montane forests

271 have undergone major declines due to increasing land conversion in the last decades, and  
272 global warming has already allowed changes in agricultural practices, such as a continuing  
273 use of the same land with the same crop, with a reduced shortfall period (Brown, 2013). More  
274 than 2/3 of the above mentioned species are currently listed in a threat category on the IUCN  
275 Red List (IUCN, 2016). An important hotspot of species at risk is Papua-New Guinea.  
276 Marsupials are very diversified in this island and are among the species with the larger body  
277 mass. As demonstrated by McNab (1994), resource limitation on continental shelf islands  
278 impacts larger-bodied mammals, often resulting in extinction. In the face of increasing global  
279 warming, island species are unlikely to be able to track the change in climate and move into  
280 new suitable climate space. Therefore, in addition to unrestricted logging and hunting (the  
281 current most serious threats to marsupials in these areas; Grzimek *et al.*, 2004), the very high  
282 rates of temperature change that these mammals are likely to experience in the next decades  
283 will probably have deleterious consequences for their survival, possibly leading to the  
284 disruption and disaggregation of extant communities (Williams *et al.*, 2007).

285         The second and largest hotspot of species at climate risk includes most of the central  
286 and eastern Sub-Saharan Africa. Savannas and forests are home to many of Africa's most  
287 prized species belonging to different taxonomic groups, including cheetahs, elephants, lions,  
288 black and white rhinos, leopards, eastern gorillas and chimpanzees. Almost all these species  
289 are currently threatened with extinction, predominantly due to hunting, habitat loss and  
290 overexploitation (Schipper *et al.*, 2008). Vegetation dynamic models predict that large  
291 portions (>45%) of today's savannas will be replaced by deciduous woodlands under elevated  
292 temperature and CO<sub>2</sub> concentrations (Scheiter & Higgins, 2009), with a consequent further  
293 reduction of the species suitable habitat and geographic ranges, and increases in their risk of  
294 extinction. In southern Africa, the east-west aridity gradient will probably induce to a  
295 westward shift of the geographic ranges of species towards the moister and cooler areas at

296 higher elevations (Erasmus *et al.*, 2002; Thuiller *et al.*, 2006). Studies have shown that some  
297 species of ungulates (e.g., roan antelope (*Hippotragus equinus*), tsessebe (*Damaliscus*  
298 *lunatus*), and kudu (*Tragelaphus strepsiceros*) among the antelopes) have suffered reductions  
299 in abundance with decreases in mean annual precipitation in South African national parks  
300 (Ogutu & Owen-Smith, 2003; Ogutu & Owen-smith, 2005), and this trend is likely to become  
301 more severe when projecting increases in aridity conditions (Pacifci *et al.*, 2015b).

302         The third hotspot, which is also a crucial site for primates, is the western portion of the  
303 Amazon river, on the border of the Andes between Peru and Ecuador. This area is considered  
304 one of the most biodiverse of the planet, and hosts more than 20 species of primates (Jenkins  
305 *et al.*, 2013; Gouveia *et al.*, 2014) in large portions of intact tropical moist forest (Killeen *et*  
306 *al.*, 2007). Despite assumptions on future climatic stability (Finer *et al.*, 2008), we found that  
307 relatively small changes in temperatures could have major impacts on the species living in the  
308 western Amazon. This is probably due to the fact that these areas have been climatically  
309 stable over time (Killeen *et al.*, 2007), therefore it is unlikely that the species inhabiting this  
310 region will be able to adapt soon to these changes. Additional threats to these species are  
311 linked to oil and gas extraction, which had a boom in the 1970s (Finer *et al.*, 2008). The  
312 intensification of these activities has already led to both direct and indirect impacts on species  
313 including deforestation for access roads, increased logging and hunting, and contamination  
314 from oil spills and wastewater discharges (Finer *et al.*, 2008), and it is likely to exacerbate  
315 when acting in combination with climate change.

316         We found that the majority of species benefitting from an increase in severity of  
317 climate change (i.e., different responses in the different scenarios, changing from  
318 negative/unchanged in RCP2.6 to positive in RCP8.5) belong to the orders Rodentia and  
319 Eulipotyphla. All these species with a negative response in the RCP2.6 scenario are not  
320 adapted to living underground and exploit a relatively restricted number of dietary items.

321 However, small mammals, in particular rodents, are typically associated with reduced  
322 vulnerability and high capacity of adjusting to environmental changes due to the fact that they  
323 usually produce high numbers of offspring that need limited parental care, and that they are  
324 often habitat generalists (Capizzi *et al.*, 2014). Most of the small mammals with different  
325 responses in our sample live in tropical areas (Figure S3) and are already adapted to living at  
326 high temperatures. In this case, factors other than the life-history traits considered in our  
327 analysis are probably more important in determining the response of species to climate  
328 change. In addition, despite the general perception that climate change mitigation improves  
329 water condition, it has been shown that increased demand for irrigation water for bioenergy  
330 crops in mitigation scenarios might result in increased water stress (Hejazi *et al.*, 2015). We  
331 can therefore hypothesize that mitigation strategies, as those planned in the RCP2.6 scenario,  
332 might be worse than climate change if not designed with careful attention to water resources.  
333 This will be particularly important for some of the species of carnivores listed in Table S4,  
334 because water is a key element that has both direct (drinking water) and indirect (prey often  
335 concentrate around water points) effects on their persistence.

336         It is interesting to note that high richness of impacted species and the highest  
337 proportion of species at climate risk overlap only in part of central Africa and Papua-New  
338 Guinea (Fig. 2). In contrast to what we found for the hotspots, these areas are generally found  
339 in less inhabited regions (Doxsey-Whitfield *et al.*, 2015), usually characterized by extreme  
340 environments and climate, e.g., Greenland, deserts of the southern Hemisphere and Tierra del  
341 Fuego. Species living in these zones have probably been less subject to human threats like  
342 hunting and land-use changes because in such extreme places human occupation may have  
343 been intermittent (Johnson, 2002), but in the face of continuing climate change, the high  
344 degrees of specialization that these species exhibit is likely to place them at great risk of  
345 extinction. More importantly, in areas hosting high proportions of species at risk but low

346 absolute numbers of taxa, if all species decline or go extinct there will be no ecological  
347 replacement, and there is a high probability of losing the ecosystem services and functions  
348 these species provide.

349         One of the areas with a high proportion of species at climate risk is the Tibetan  
350 Plateau. Since 1978 the Tibetan Plateau has warmed  $>0.04$  °C/year, the greatest value for the  
351 whole China and East Asia. These changes in climatic conditions have been attributed to a  
352 positive feedback between the increase in grazing pressure, with consequent degradation of  
353 pastures, and that of potential evapotranspiration (Du *et al.*, 2004). Analyses of  
354 meteorological stations, combined with projections of climate models, reveal that the  
355 prominent warming and the thawing of permafrost at higher elevations are likely to continue  
356 in the next decades (Liu *et al.*, 2009), thus leading to a possible reduction of several biomes,  
357 such as the temperate desert, alpine steppe, and ice/polar desert (Ni, 2000). These areas are  
358 currently inhabited by several species of lagomorphs (pikas and hares), which are restricted to  
359 mountainous habitats and cold climates, and by large threatened mammals. Some of these  
360 large threatened species are currently recovering thanks to habitat protection, like the Tibetan  
361 antelope (*Pantholops hodgsonii*; IUCN SSC Antelope Specialist Group 2016), while many  
362 others are already declining due to habitat destruction and overexploitation, for example the  
363 leopard (*Panthera pardus*; Stein *et al.* 2016) and the white-lipped deer (*Cervus albirostris*;  
364 Harris, 2015). The Tibetan Plateau also hosts relatively large numbers of primates belonging  
365 to the genus *Macaca*; here climate change is likely to further worsen the conservation status  
366 of these species acting in concomitance with hunting, habitat loss and human disturbance,  
367 which are currently considered the major threats to the species (Boonratana *et al.*, 2008).

368         When considering only the intrinsic component of climate risk, we found that areas  
369 hosting large numbers of vulnerable species overlap well with the sites of high mammalian  
370 diversity and endemism, in particular of Cetartiodactyla and Carnivores (Pimm *et al.*, 2014),

371 in central Africa. Here, human population size is expected to increase steeply by 2050, from a  
372 minimum of 16% in South Africa, up to 117% in the Democratic Republic of Congo and  
373 127% in Zambia (United Nations, 2015). This projected increase in human population,  
374 associated with expected increases per-capita consumption, are likely to cause an acceleration  
375 in the conversion of remaining forest habitats into human-dominated settlements and  
376 agricultural areas (Barrie *et al.*, 2007). This, in turn, is expected to endanger several mammal  
377 species in Sub-Saharan Africa, with similar trends in insular Southeast Asia and the Amazon  
378 rainforest (Visconti *et al.*, 2015). In the areas inhabited by large numbers of vulnerable  
379 species, priority actions should be aimed at mitigating the effects of other threats that may act  
380 concurrently with climate change. Temperature has clear effects on the behaviour of most  
381 animal species, and this might translate in changes in the interactions between predators and  
382 their preys (Creel *et al.*, 2016), thus indirectly leading to possible increases in conflicts  
383 between humans and wildlife.

384 As already observed in previous studies on other taxa (e.g. birds; Goodenough & Hart,  
385 2013), hotspots of species under high climate threat exposure include areas with the highest  
386 concentration of species with limited or no availability of climatic refugia. These obviously  
387 include mountainous areas, where species are likely to be unable to move upslope to cope  
388 with climate change. For example, in our study we found that the Rocky Mountains of  
389 Colorado and New Mexico in the United States and the Altai Mountains in central Asia are  
390 important centres for exposed species. The latter are home to several species of threatened  
391 large mammals, like the snow leopard (*Panthera uncia*), the Asiatic Wild Dog (*Cuon alpinus*)  
392 and the Siberian Musk Deer (*Moschus moschiferus*). For these species, translocations or  
393 assisted colonization actions could be necessary in the coming decades if changes in climatic  
394 conditions exacerbate. The Siberian Musk Deer is already successfully bred in captivity at

395 musk deer farms in Russia and China (Nyambayar *et al.*, 2015), and these captive herds might  
396 be used for future movements to wild populations.

397 *Importance of combining intrinsic and extrinsic factors to identify species at high risk from*  
398 *climate change*

399         This work brings together information from life-history traits, distribution patterns and  
400 predicted future levels of climate change to create a unique assessment of climate risk. Our  
401 framework enables the first predictive assessment of the mammal species most at risk from  
402 climate change, on the basis of empiric data and considering all the three components of risk.  
403 With this work we have demonstrated that considering only the intrinsic characteristics that  
404 make a species more vulnerable to climate change is not enough to predict its real climate  
405 induced risk. Species displaying similar life-history traits may be differently affected by  
406 global warming simply because they live in areas experiencing different rates of climate  
407 change. In our analyses, we found that >55% of the species of terrestrial non-volant mammals  
408 may potentially be negatively impacted by climate change, depending on the climatic  
409 scenario. In the Fourth IPCC Report a projected increase of 2-3°C was expected to lead to  
410 high risk of extinction approximately 20 to 30% of the species assessed so far (IPCC, 2007).  
411 However, in the Fifth and most recent Report (IPCC, 2014), it has been estimated that the  
412 expected increase in temperatures is likely to exceed the threshold of 4°C by 2100. This  
413 translates into increased threats for species. Accounting for both the life-history traits that  
414 make a species more vulnerable and the environmental conditions of its geographic range,  
415 could in many cases help prioritization actions and make the difference between species  
416 extinction or survival. However, due to the paucity of life-history trait data for numerous  
417 species, it is often difficult to provide a rapid assessment of their vulnerability to climate  
418 change. Although mammals are among the best-known taxa, the number of new recognised  
419 species is still increasing. For instance, newly described mammals have been found mostly in

420 Madagascar and the Amazon, while the Congo basin still remains scarcely explored (Schipper  
421 *et al.*, 2008). These new species are usually poorly known and severely threatened, in part due  
422 to their restricted geographic range, and may therefore become rapidly extinct. These new  
423 data-deficient species are generally found in tropical forests (Schipper *et al.*, 2008), that well  
424 overlap with the hotspots of species at risk from climate change.

425         Changes in the distribution or phenology of species are often detected via long-term  
426 surveys. Establishing or expanding systematic monitoring of abundance and distribution of  
427 species is a very high priority in order to validate species assessments and monitor  
428 effectiveness of adaptation. For species identified as most vulnerable, exposed, and that live  
429 in places where impacts are likely to occur sooner, intensive monitoring is essential to  
430 increase our understanding of the ongoing process of climate change, and possibly respond to  
431 it. This is not only true for species living in the hotspots, but also for those occupying areas  
432 we identified as having the highest rates of mammals at risk. Although these areas often host  
433 a reduced number of species, it is essential to monitor their status in order to avoid the loss of  
434 entire mammalian communities characterized by peculiar specializations.

435         Life-history traits have been often used in conservation biology to identify the most  
436 vulnerable species to environmental changes. The identification of traits specifically related to  
437 climatic risk will further strengthen species risk assessments, thus helping to plan appropriate  
438 conservation actions in the differently exposed areas and prioritize intervention targets. This  
439 is particularly important for many species of mammals living in climatic hotspots, which are  
440 almost unknown, to draw attention to them and begin fill some knowledge gaps.

441

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444 **Supporting Information captions**

445 **Table S2** Percentage of predicted species responses by taxonomic group for the RCP2.6  
446 scenario

447 **Table S2** Percentage of predicted species responses by taxonomic group for the RCP6.0  
448 scenario

449 **Table S3** Percentage of predicted species responses by taxonomic group for the RCP8.5  
450 scenario

451 **Table S4** Species showing a change from an “Unchanged”/ “Negative” response in the  
452 scenario RCP2.6 to a “Negative” response in the scenario RCP8.5

453 **Figure S1** Richness of species with a negative predicted response by grid cell in the a)  
454 RCP2.6 and b) RCP6.0 scenarios..

455 **Figure S2** Proportion of species with a negative predicted response by grid cell in the a)  
456 RCP2.6 and b) RCP6.0 scenarios.

457 **Figure S3** Richness of species showing a change from an “Unchanged”/ “Negative” response  
458 in the scenario RCP2.6 to a “Negative” response in the scenario RCP8.5.

459

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