1	The effect of climate change on the distribution of Canidae
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3	Prediction of current and future distribution of canids.
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17 ABSTRACT

18 Land use by humans and climate change have been seriously affecting the distribution of 19 species resulting in a quarter of all known mammals currently threatened with extinction. 20 Here, we modeled the present and future potential distributions of all 36 extant Canidae 21 species to evaluate their response to future climate scenarios. In addition, we tested if canids 22 were likely to experience evolutionary rescue, which could allow some species to adapt to 23 climate change. Our results suggest that global warming will cause most species to lose or 24 maintain their ranges, while a few will have the potential to benefit from future conditions and 25 considerably expand their geographic distributions. Some canids have the potential to 26 experience evolutionary rescue, but Atelocynus microtis and Chrysocyon brachyurus are two 27 concerning cases that do not show this capacity to adapt given the current pace of climate 28 change. We also reveal that most Canidae hotspot regions are outside protected areas, which 29 may be useful for the identification of key areas for conservation.

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KEYWORDS: adaptation, ecological niche models, environmental change, geographical
 ranges, Haldanes.

33

34 **1 INTRODUCTION**

35 The pace of climate change induced by humans is much faster than predicted previously 36 (Pimm et al., 2014). Ceballos et al. (2015) showed that the rate of vertebrate species loss over 37 the last century is up to 100 times higher than the background extinction rate. This anthropogenic pressure causes habitat loss and increased competition from invasive 38 39 organisms (Butchart et al., 2010), which leads to species extinction (Ceballos et al., 2015; 40 May & Lawton, 1995), and thus has serious impacts on global biodiversity. Over the last 41 decades, several studies have shown how human impacts affect the structure of ecosystems 42 and how these changes can backfire and affect humans negatively with floods, fires, air 43 pollution, heat waves, and vector-borne diseases (Bellard et al., 2012; Cardinale et al., 2012; 44 Goberna et al., 2014; Kortsch et al., 2015; Nadeau et al., 2017; Parmesan & Yohe, 2003; Pecl et al., 2017; Woodward et al., 2010). Some species are more susceptible to extinction than 45 46 others due to their traits, including: reproductive rate, habitat specialization, body size, and 47 geographic range (Davidson et al., 2009; Fritz & Purvis, 2010). Therefore, understanding how 48 species are going to respond in future scenarios of climate change is necessary to predict the 49 impact of the loss of certain species on ecosystems, and it will be useful for conservation of 50 biodiversity.

51 Until recently, evolution was thought to play no substantial role in a population's 52 resilience when facing a rapid environmental change (Ferrière et al., 2004). The common idea 53 was that a population in decline, exposed to a deteriorating environment, would become extinct. However, Gonzalez et al. (2012) and Bell (2013) coined and matured the idea of 54 evolutionary rescue (ER). In an ER scenario, adaptive processes could be triggered in some 55 resistant individuals of the population under environmental stress, allowing them to rapidly 56 57 proliferate and counter the rate of decline of the population, thereby changing our perspective 58 on communities with populations that are threatened with extinction (van Eldijk et al., 2020).

The most used tools to evaluate how species are dealing with climate change are ecological niche models (ENMs) (Araújo & New, 2007; Ehrlén & Morris, 2015; Elith et al., 2010; Guisan & Thuiller, 2005). ENMs use mathematical modelling of a species' relationship with environmental variables, and predict habitat suitability for that species based on known occurrence data (Araújo et al., 2011; Guisan & Thuiller, 2005). ENMs based on climate data have proven extremely useful in assessing the effectiveness of the distribution of protected areas (Catullo et al., 2008), assessing species vulnerability to local land-use changes (Santos

et al., 2013), predicting distributions of rare species (Marino et al., 2011; Rheingantz et al.,

67 2014), and predicting possible responses to climate change by species and ecosystems (Moor

68 et al., 2015; Sobral-Souza et al., 2018).

However, the use of ENMs with climatic variables alone has been debated in several studies (Diniz-Filho et al., 2019; Elith et al., 2010; Synes & Osborne, 2011), mainly because ENMs do not incorporate intrinsic characteristics of the populations, relying on the idea that all the mechanisms that affect species` distributions are captured by the environmental data (Diniz-Filho et al., 2019). However, niche models that use traits (morphological and physiological) or genetic data are complex and do not work well when the niches of several species are modeled simultaneously (Norberg et al., 2012).

The attempt to predict responses of species to climate change is further limited by uncertainties surrounding climatic predictions - with slight differences existing between different general circulation models (GCM) - and by uncertainties about the possibilities of measuring evolutionary rescue.

80 Recently, Diniz-Filho et al. (2019) applied a macroecological framework to estimate 81 responses to evolutionary change and the likelihood of evolutionary rescue; they proposed the 82 H value (Haldanes) to estimate the evolutionary change required by species to maintain their 83 populations in future environmental scenarios, giving a biological and evolutionary meaning 84 to temperature variations that species will experience. According to the framework proposed by Diniz-Filho et al. (2019), the greater the variation in temperature between present and 85 86 future, the greater the H value, and consequently, the more difficult it is for the species to experience an ER scenario. Likewise, the fewer generations the species can have until the 87 88 future, the higher the H. In short, the smaller the temperature difference and the larger the 89 number of generations, the more likely it is for evolutionary rescue to happen, and for a 90 species to persist in the face of climate change.

91 WWF (2018) showed an average 60% decrease in vertebrate populations, and a 92 quarter of all known mammals are currently threatened with extinction (IUCN, 2020). Within 93 this group, the canids (family Canidae) is an excellent group to test the impacts of climate 94 changes on future distributions, as they are distributed in all continents, except Antarctica 95 (Sillero-Zubiri et al., 2004; Wang & Tedford, 2008), and because as medium-large mammals 96 they are more prone to extinction than smaller species (Rija et al., 2020). Like other species, 97 canids are affected by the consequences of urbanization and climate change: coyotes (Canis 98 *latrans*) and red foxes (Vulpes Vulpes) have been observed in urban areas in North-America 99 (Lombardi et al., 2017; Mueller et al., 2018; Poessel et al., 2013, 2017), while the red fox has

invaded a habitat in northern Europe that was previously occupied only by the arctic fox
 (*Vulpes lagopus*) (WWF, 2018). Understanding how canids are affected by changes in the
 landscape, and being able to predict their future distributions is essential to outline
 conservation strategies for different species.

Here we use climate-based ENMs to: 1) model the distribution of all canids under present climate conditions, 2) predict possible changes in Canidae distribution under climate change in the next 54 years (2075), and identify species at risk of losing some or all of their current range, but also assess if some species could enlarge it; and 3) identify which species are most likely to adapt to changing climatic conditions and therefore avoid the negative effects of temperature change.

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111 2 MATERIALS AND METHODS

112 **2.1 Occurrence and environmental data**

113 Species occurrence data for all canids were taken from VertNet (Constable et al., 2010) and 114 the Global Biodiversity Information Facility (GBIF, 2020) online databases. The number of 115 occurrence points is shown in Tables S1, and cover all the known distribution of the 36 116 species used here (which correspond to 100% of the living Canidae species). We spatially filtered the data using SDMToolbox 2.0 (Brown et al., 2017), in ArcGis 10.3.1 117 118 (Environmental Systems Resource Institute, 2019), to remove duplicate occurrence points. As 119 there are different classifications for the Canidae family in relation to the number of species 120 (Bardeleben et al., 2005; Perini et al., 2010; Zrzavy & Ricánková, 2004), here we use the 121 most recent canid phylogeny proposed by Porto et al. (2019) to define which species of 122 Canidae (n = 36 - Table S1) would be considered here to model their potential distributions.

123 For environmental variables, we downloaded a digital elevation model (DEM) (IUCN, 124 2019) and the standard 19 Worldclim bioclimatic variables for the present and future (2075) 125 (Hijmans et al., 2005). In addition, we used the distance to freshwater as a variable, which we 126 measured using the Natural Earth River and lake maps, and the Euclidean distance tool in 127 ArcGis. To clarify the environmental data we masked the variables and imported them into R 128 4.0-2 (R Development Core Team, 2020) and tested for multicollinearity using variance 129 inflation factor (VIF) tests with the package regclass 1.6 (Petrie, 2020) and pairwise plots. 130 Highly correlated variables (VIF score > 10 or Pearson correlation > 0.7 respectively) were 131 eliminated one at a time, starting with the variable(s) deemed to possess the least ecological 132 relevance based on the VIF tests.

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134 **2.2 Ecological niche modelling**

135 ENMs for the present were performed using the R package SDM 1.0-89 (Naimi & Araújo, 136 2016). To model species' niches for the present, we generated 10.000 random background 137 points within a mask equivalent to the species' known IUCN ranges, buffered to 220 km (or approximately two decimal degrees), producing a presence-absence matrix of species within 138 defined grids cells (pixels). We built ensembles (objects with a weighted averaging over all 139 predictions from several fitted models) of four different models: Maxent, Support Vector 140 141 Machine (SVM), Random Forest (RF), and Boosted Regression Tree (BRT). For all models, 142 we used 90% as training data and 10% were retained as test points. Models were only 143 accepted if they had acceptable True Skill Statistic (TSS - calculated as the sum of specificity 144 + sensitivity - 1) and Area Under the Curve (AUC) values (0.7 being the minimum accepted 145 AUC, 0.6 the minimum TSS (Allouche et al., 2006)). We used both TSS and AUC to evaluate 146 the models because they assign different weights depending on the sample size of the data 147 used (Guisan et al., 2017), and hence we believe our results to be more robust if both criteria 148 are met.

In order to verify whether the ENMs and IUCN polygons agree, we compared the current distribution maps of all species of canids available at IUCN against the maps created here through ENMs. IUCN maps were generated by minimum convex polygons, which represent the realized niche of the species, while the ENMs here bring a more detailed notion of their fundamental niche.

154 We modelled the future distribution of species based on the most pessimistic climate scenario for the year 2075 (RCP 8.5 - Representative Concentration Pathway) from IPCC 155 (2007). We chose this scenario because it seems to have become the most realistic one over 156 157 the last years, and can even be under-estimating future concentrations of atmospheric carbon 158 (Christensen et al. (2018). RCP 8.5 assumes high global CO₂ concentration, a high rate of 159 human population growth, and an increased use of energy and land. We used an ensemble of 160 three General Circulation Models (GCMs): Access1.0 (exhibits a high skill score with regard to historical climate), HadGEM2 (has a good representation of extreme El Niño events), and 161 162 MIROC5 (also has a good representation of extreme El Niño events, and represents all RCPs 163 scenarios well). Maps of suitability (present/future) are shown on a continuous scale to better 164 visualize the potential distribution of species.

166 **2.3 Evolutionary rescue calculations**

167 H values were calculated for each of the 36 canids to predict whether they can adapt to 168 climate change and prevent the loss of their habitat. We assumed that temperature is a 169 representation of the species' niche (tolerance) most closely reflecting climate change. For 170 each species, changes in maximum temperature of the warmest month (Bio05) across the 171 entire range were estimated, and the temperature change in each cell was calculated as the 172 average of the future temperature (in the warmest month) minus the average of the present temperature (in the warmest month). Following Diniz-Filho et al. (2019), H values were 173 174 calculated using:

$$H = \frac{\frac{Y_0 - Y_t}{Y_{sd}}}{g}$$

175 where Y_0 is the mean temperature at the present, Y_t is the mean temperature at time t in the 176 future, Y_{sd} is the standard deviation of the present temperature tolerance (assuming a constant 177 variance between generations), and g is the number of generations between present and future. 178 The generation lengths for all canid species was compiled from the Animal Diversity Web 179 (ADW - Myers et al., 2018) and PanTHERIA (Jones et al., 2009) (Table S1). The higher the 180 value of H, the greater the rate of evolutionary change needed for a species to experience ER, 181 and consequently, the more difficult it is to maintain its population facing a climatic change 182 scenario.

For the evolutionary rescue analyses, we used the threshold maps (binary) for each species, produced with the suitability maps because they show presence/absence values based on the specificity and sensitivity of the model (Liu et al., 2015).

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187 **3 RESULTS**

188 **3.1 Ecological niche modelling**

All ENMs produced acceptable accuracy values for TSS and AUC. After testing highly correlated variables, only five were not excluded and were used to model canid niches, they are: distance to freshwater (DIST), the maximum temperature in the warmest month (Bio05), precipitation in the driest month (Bio14), elevation (DEM).

To check the reliability of the ENMs we compared their predictions on the present
distributions with the actual current distributions according to IUCN polygons (realized niche)
(Appendix - Figure S1 – S36). With the exception of a single species, *Canis lupus*, the

196 distribution polygons fall within the areas that the ENMs demonstrate to be suitable for the 197 species to occupy (fundamental niche). Species richness maps for the present generated by 198 ENMs (Figure 1) and by polygons (Figure S37) show very similar patterns of species overlap, 199 generally maintaining the same hotspot locations in the Middle East + Northeast Africa region 200 and western part of the USA. However, there is an exception: the richness map based on 201 polygons shows the presence of Canis lupus in the Middle East region towards India, but this 202 is not predicted by the ENMs (see Discussion). Because of the high similarity our ENM 203 predictions seem highly reliable, and we therefore compare our future ENM predictions with 204 ENM predictions for the present, as they are better comparable (both describe the 205 fundamental niche).

Our models indicated that 27 species were predicted to experience range contractions under climate change, while 9 were predicted to expand in range overall (Table S2). In all three Canidae clades (wolves, foxes, and South-American canids), we find that most species will contract their ranges, and a few will expand their ranges (Figure S38A-S38C). We discuss them now in more detail.

211 The South-American canids (Figure S38C), Atelocynus microtis, Lycalopex fulvipes, 212 and Lycalopex sechurae are predicted to see future climate suitability fall below their 213 modelled threshold across their entire ranges (Table S2), losing a large part of their 214 geographical distributions (Appendix - Figures S39, S40, and S41). In contrast, Cerdocyon 215 thous is the only South-American canid that was predicted to have a considerable expansion 216 in its geographical area under future conditions; moreover, the ENM predicts that C. thous 217 will occupy areas within the Amazon Forest not inhabited before (Table S2, and also see 218 Appendix - Figure S38C and Figure S42).

In the clade of wolves, *Canis latrans* and *Canis rufus* are probably going to lose a large part of their ranges in North America, while *Canis anthus* and *Canis lupus* are expected to increase their distributions, mainly in desert areas such as the Middle East, for both species, and the deserts in the USA for *C. lupus* (Table S2, and also see Appendix - Figure S38A, Figure S43, and Figure S44).

Some of the fox species are predicted to suffer severe losses in their ranges (Table S2 and Figure S38B). Among them, *Urocyon littoralis* stands out: even though it is considered an endangered species at the moment, the ENMs predicted that *U. littoralis* will lose 28.6% of its (small) current distribution (Table S2). *Vulpes chama, Vulpes bengalensis,* and *Vulpes velox* also were predicted to have a considerable decrease in their geographical ranges. By contrast, *Vulpes corsac, Vulpes vulpes, Otocyon megalotis,* and *Urocyon cinereoargenteus* will

probably experience range expansions under future climatic conditions. In fact, the ENM
predicted that *V. vulpes* will increase 5.7% of its distribution, inhabiting new areas such as the
Middle East, Northern Canada, and Greenland (Appendix - Figure S45).

233 The richness map of the present (Figure 1) shows that the overlap of different species 234 is very low around the planet. The map also points to two hotspot areas for canid diversity, 235 one in the western part of the USA (Figure 1A), and another in the Middle East + Northeast 236 Africa region (Figure 1B). The richness map for the future (Figure 2) shows that patterns of 237 richness are predicted to change under future climatic conditions, where the main changes 238 will be in the hotspot areas. The USA hotspot is predicted to reduce its area considerably due 239 to the low species overlap in the future. By contrast, The Middle East + Northeast Africa 240 hotspot is predicted to increase in size.

241 The ENMs indicated species that do not overlap currently will start to overlap in their 242 distributions, and even those that overlap in only small parts of their distributions will suffer 243 considerable increases in their overlap areas. In South America, C. thous is predicted to 244 invade areas where only A. microtis and Speothos venaticus live, inside the Amazon rainforest 245 (Appendix - Figures S39, S42, and S46). With the great expansion of V. vulpes' geographical 246 distribution, this species is expected to overlap its area with V. bengalensis, Vulpes rueppellii, 247 and Vulpes zerda (Appendix - Figures S45, S47, S48, and S49). In addition, C. lupus will 248 probably overlap in areas occupied before only by V. bengalensis, V. rueppellii, V. zerda, and 249 Canis aureus (Appendix - Figures S44, S47, S48, S49, and S50).

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251 **3.2 Evolutionary rescue**

Most of canids presented evolutionary rates around 0.01 Haldanes (Table S2). The highest H value was found for *A. microtis* (H = 0.047 Haldanes), and the lowest value was from *Lycalopex griseus* (H = 0.004 Haldanes) (Table S2).

We found a significant weak negative correlation between change in range size and evolutionary potential: species that are predicted to undergo more habitat loss according to the ENMs have a lower potential for ER, according to the *H* values (Figure 3).

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4 DISCUSSION

We applied models of evolutionary rescue, using temperature and generation cycle as intrinsic characteristics of canids, together with ENMs to understand the magnitude of the effects of climate change on Canidae distribution. Predictions for the future by ENMs, derived from the

263 IPCC worst climate change scenario, suggested that climate change will affect canids in 264 distinct ways, where some species will expand or maintain their distributions, while most will 265 suffer a large reduction in their suitable areas. Furthermore, the calculated Haldanes suggest 266 that for some species it will be more difficult to keep up with the pace of temperature changes 267 than others. We detected a weak negative correlation between habitat loss and potential for 268 evolutionary rescue, indicating that the species with higher potential to evolutionary rescue 269 are the ones that gain area or lose only a small part of their future distributions, while the ones 270 which are going to lose a large part of their future distribution will need a higher evolutionary 271 change to maintain their populations. Atelocynus microtis, for example, is predicted to lose 272 about half of its potential distribution and has the highest H value among canids (H = 0.047273 Haldanes). This negative correlation is to be expected because larger differences between 274 present and future temperatures will increase H and will also make it more likely that range 275 sizes will change.

276 Our results suggest that global warming will be devastating to the Canidae family as a 277 whole. However, even in this pessimistic scenario, some species have the potential to benefit 278 from future conditions and considerably expand their geographic distributions. In general, 279 several taxa, including mammals, birds, amphibians, and reptiles, are expected to experience 280 drastic range reductions (Araújo & New, 2007; Diniz-filho et al., 2009; Hidasi-neto et al., 281 2019; Lawler et al., 2009; Maiorano et al., 2011; Peterson et al., 2002). In a scenario such as 282 this, several communities will probably lose phylogenetic and functional diversity (Davis et 283 al., 1998; Hidasi-neto et al., 2019), and considering the number of interactions that will be lost 284 within these areas, the ecological impacts due to indirect effects may be stronger than the 285 direct effects of climate change on species' distributions (Davis et al., 1998; Peterson et al., 286 2002). Carnivores, through population regulation, can promote the coexistence of several 287 species by reducing interspecific competition (Paine, 1966). Because canids, being carnivores, 288 hunt distinct animals, they end up regulating the population dynamics of their prey, which is 289 an important factor for maintaining biodiversity (Sanders et al., 2013; Sanders & van Veen, 290 2012).

In South-America, there is a very concerning situation, where *A. microtis* will probably contract its range substantially and undergo fragmentation of its distribution within the Amazon Forest, while *C. thous* will expand. *A. microtis* is ecologically restricted to very specific resources and conditions (Sillero-Zubiri et al., 2004; Wilson & Mittermeier, 2009). By contrast, *C. thous* is a generalist species with a large distribution across South-America (Sillero-Zubiri et al., 2004). Currently, the status of *A. microtis* is "Near Threatened" (IUCN,

2019), but considering the climate change effects shown here, and the fact that the Amazon 2019), but considering with wildfires and an intense deforestation process over the last 2019 decades (Exbrayat et al., 2017; INPE, 2019), *A. microtis* is probably experiencing a 300 substantial habitat loss followed by a very likely increase in the number of direct encounters 301 with another competitor. Thus, we suggest that its "Near Threatened" status must change, at 302 least, to "Vulnerable".

303 A similar situation applies to V. vulpes and V. lagopus. The first one has a wide 304 distribution over the northern hemisphere, while the second is restricted to areas covered by 305 snow around The North Pole, but both species overlap in the Tundra of North America and 306 Eurasia (Hersteinsson & Macdonald, 1992; Sillero-Zubiri et al., 2004). Over the past few 307 years there has been an increase in the number of encounters between the two species due to the warming temperatures that are gradually melting the Arctic ice cap, reducing the available 308 309 area for V. lagopus, but making it possible for V. vulpes to expand its distribution to the north 310 into arctic tundra in Eurasia and North America (Gallant et al., 2012). This reality is even 311 more aggravating in the future scenario shown here, considering the large area loss by V. 312 lagopus to V. vulpes (Figure S51). However, Gallant et al. (2012) suggested that food scarcity 313 in these areas seems to explain the dynamics of the geographical overlap of both two species 314 better than climate warming. Nevertheless, the effects of area loss must still be taken into 315 account to outline conservation strategies for V. lagopus.

The loss of species has severe impacts on the functioning of ecosystems (Cardinale et 316 al., 2012; Kennedy et al., 2002; Lyons & Schwartz, 2001; Pimm et al., 2014). In general, 317 318 reductions in the number of species (functional groups) decrease the efficiency of 319 communities to capture resources, and convert these into biomass (Balvanera et al., 2006; 320 Cardinale et al., 2012; Quijas et al., 2010). Our niche models detected two major richness 321 hotspots for Canidae: one in the Middle East + North East Africa and one in North America. 322 The former is predicted to undergo a small expansion, mainly due to the range expansion of 323 C. lupus, C. anthus, and V. vulpes over these areas, and the capacity of C. lupus and V. vulpes 324 to live around urban areas (Sillero-Zubiri et al., 2004; Wang & Tedford, 2008; Wilson & 325 Mittermeier, 2009). This capacity can also explain the wide distribution of both species 326 around the world. The other hotspot area, in North America, is expected to experience a 327 considerable area reduction. This can be explained by the small portion of this hotspot that is 328 within protected areas in the USA, according to Brum et al. (2017).

Here, the ENMs for all canids (appendix) agreed well with the current distribution of canids, suggesting that the methodology we applied is reliable to assess the impacts of climate

331 change on Canidae, taking into account their main niche dimensions. *Canis lupus* is the only 332 species for which the ENMs for the present did not encompass the entire distribution 333 presented by its polygon, because it is not predicted to occur in the Middle East. This might 334 be explained by the presence of a single population found in that region, which results in the 335 distribution of the species to be extended to areas that are not suitable. The IUCN distribution 336 maps are widely used in several studies for different purposes (Kyne et al., 2020; Porto et al., 337 2021; Shier, 2015; Zhang et al., 2019), and are defined as the area within the outermost limits 338 of known occurrence for a species, but this area is not an estimate of the extent of occupied 339 habitat, it only measures the general extension of the localities in which the species is found 340 (Gaston & Fuller, 2009). Thus, polygons are highly susceptible to sampling biases. 341 Nevertheless, it is important to point out that ENMs for the future suggest that *Canis lupus* will expand its distribution to the Middle East, which could be an indication that this region is 342 343 already becoming suitable for the species.

344 Our methods assumed that the prey of the Canidae will respond to environmental 345 changes at the same rate as their (apex or medium-level) predators. Indeed, climate change 346 has already been observed to have wide-ranging trophic effects (Gilman et al., 2010), and 347 physiological and behavioral effects in other species (Parmesan, 2006). Modelling the effect 348 of climate change on species' communities and trophic interactions has proven extremely 349 difficult, but these interactions can have serious impacts on species distributions (Sanders et 350 al., 2013; Sanders & van Veen, 2012). These trophic interactions may be further disrupted by 351 invasive species, the spread of which could be accelerated by climate change (Hellmann et al., 352 2008).

353 Looking at the H values, two cases are very concerning. Atelocynus microtis and 354 *Chrysocyon brachyurus* present higher H values compared to other canids (0.047 and 0.027, 355 respectively), and based on Diniz-Filho et al. (2019), these species have a lower potential for 356 evolutionary rescue. Although H values and ENMs try to elucidate the future of species, they 357 have distinct points of view about the effects of climate change on canids, and therefore 358 should not be compared. However, these two approaches can shed light on Canidae responses 359 to the future of the planet. H values suggest that some species have less potential than others 360 to adapt fast enough to temperature changes, but ENMs indicate that some of them may 361 increase their range, because more suitable habitats will become available for them due to 362 climate change. Thus, in these cases ecological processes seem to prevail over evolutionary 363 ones.

364 Unfortunately, very little is known about ER in nature to compare with our findings, 365 mostly because the idea that evolution may influence the persistence of a population facing a 366 rapid environmental change is very recent. Nevertheless, Diniz-Filho et al. (2019) already 367 suggested that the use of the ER approach for wider geographical areas might not be that 368 simple. They suggested that in order to obtain a standard temperature deviation, the real 369 temperature tolerances must be known. However, no lab values were available for any wild 370 canid, meaning that only values obtained from range estimations and ENMs could be used. 371 Nonetheless, both may underestimate a species' true temperature tolerance. For example, 372 while we have extracted values of mean Bio05 (maximum temperature in the warmest 373 month), sometimes these values are well below the highest value seen within a species range.

The biogeographic patterns observed in this study may provide useful information for assessing how canids are distributed in the present over the planet, being an alternative to the distribution polygons provided by IUCN (2020). Climate change is projected to play an essential role in the geographical distribution of canids, so our predictions can be used to identify key areas for conservation strategies. This should receive special attention because as we showed, most of the Canidae hotspot regions are not located within protected areas.

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381 DECLARATION SECTION

382 Ethics approval and consent to participate 383 Not applicable. 384 385 **Consent for publication** 386 Not applicable. 387 388 Availability of data and material 389 All data generated or analyzed during this study are included in this article and in the supplementary files. 390 391 **Competing interests** 392 We have no competing interests. 393 394 Funding 395 L.M.V.P. is supported by CAPES and by the University of Groningen. R. M. is supported by UFRGS, 396 FAPERGS, and CNPq (406497/2018-4). 397

398 Authors' contributions

- 399 L.M.V.P. and D.B. conceived and designed the study and analyses. L.M.V.P. and D.B. performed the analyses.
- 400 L.M.V.P. and D. B. wrote the first draft of the manuscript. R.S.E. and R.M. commented on the methods and
- 401 contributed to substantial revisions on the draft.
- 402

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633 FIGURE LIST

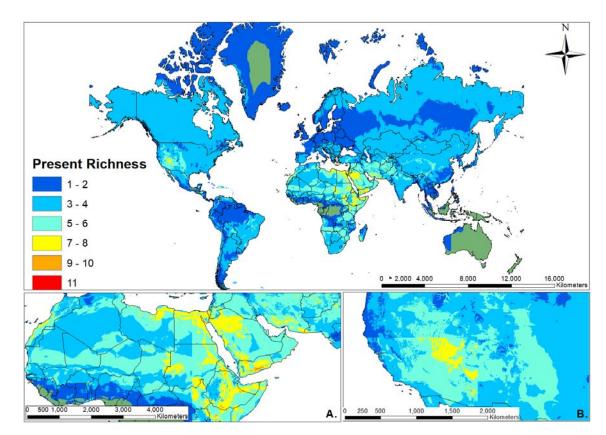


FIGURE 1 Species richness map of Canidae for the present produced by ENM. The richest
areas (hotspots) were identified in the Middle East + Northeast Africa region (A) and western
part of the USA (B). The legend on the left shows the number of overlapping species.

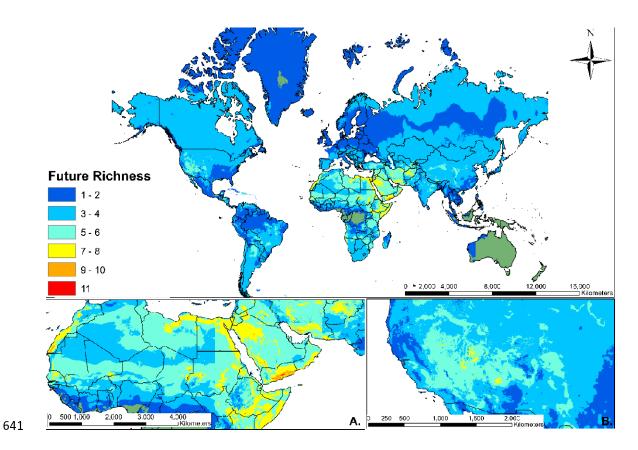


FIGURE 2 Species richness map of Canidae under future climate conditions produced by
ENM. The richest areas (hotspots) were identified in the Middle East + Northeast Africa
region (A) and western part of the USA (B). The legend on the left shows the number of
overlapping species.



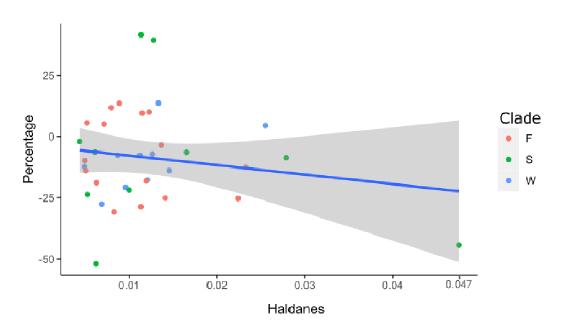




FIGURE 3 Plot representing the relationship between the percentage of area gained or lost by canids in relation to *H* values. The higher the *H* value, the lower the likelihood of evolutionary rescue. Red, green, and blue dots are species from the clades of foxes, South-American canids, and wolves, respectively. $R^2 = -0.187$ (*P* < 0.05).

664 SUPPLEMENTARY TEXT: TABLE LIST

665 TABLE S1 List of the 36 species of Canidae included in our study. Age of sexual maturity of

- 666 females (years), the number of generations until 2075, the number of occurrence points for each
- species, and the source of the original description are indicated here.

Species	Sexual maturity of females	Number of generations	Number of occurrence points	Descriptor
Canis adustus	0.75	100	1.028	Sundevall, 1847
Canis aureus	1	75	2.769	Linnaeus, 1758
Canis anthus	1	75	1.536	Cuvier, 1820
Canis lupus	2.5	25	8.490	Linnaeus, 1758
Canis latrans	0.84	89.3	2.402	Say, 1823
Canis mesomelas	0.84	89.3	645	Schreber, 1775
Canis rufus	1	75	30	Audubon & Bachman, 1851
Canis simensis	2	37.5	12	Rüppell, 1840
Cuon alpinus	1	75	507	Pallas, 1811
Lycaon pictus	1.23	60.4	281	Temminck, 1820
Nyctereutes procyonoides	0.82	91.5	846	Gray, 1834
Vulpes bengalensis	1.5	50	327	Shaw, 1800
Vulpes cana	0.82	91.5	396	Blanford, 1877
Vulpes chama	0.75	100	229	A. Smith, 1833
Vulpes corsac	1.38	54.3	1.193	Linnaeus, 1768
Vulpes ferrilata	1.15	65.2	264	Hodgson, 1842
Vulpes macrotis	0.82	91.5	229	Merriam, 1888
Vulpes pallida	1	75	406	Cretzschmar, 1826
Vulpes rueppellii	1	75	1.299	Schinz, 1825
Vulpes velox	1	75	88	Say, 1823
Vulpes vulpes	0.83	90.4	9.457	Linnaeus, 1758
Vulpes zerda	0.49	153.1	850	Zimmermann, 1780
Vulpes lagopus	0.83	90.4	3.468	Linnaeus, 1758
Urocyon cinereoargenteus	0.95	78.7	1.089	Schreber, 1775
Urocyon littoralis	1	75	30	Baird, 1857
Otocyon megalotis	0.61	122.6	515	Desmarest, 1822
Atelocynus microtis	1	75	238	Sclater, 1883
Cerdocyon thous	0.76	98.7	864	Linnaeus, 1766
Chrysocyon brachyurus	2	37.5	457	Illiger, 1815
Lycalopex culpaeus	1	75	345	Molina, 1782
Lycalopex fulvipes	1	75	8	Martin, 1837
Lycalopex griseus	1	75	255	Gray, 1837
Lycalopex gymnocercus	1	75	312	G. Fischer, 1814
Lycalopex sechurae	1	75	24	Thomas, 1900
Lycalopex vetulus	1	75	183	Lund, 1842
Speothos venaticus	0.83	90.4	1.076	Lund, 1842

668

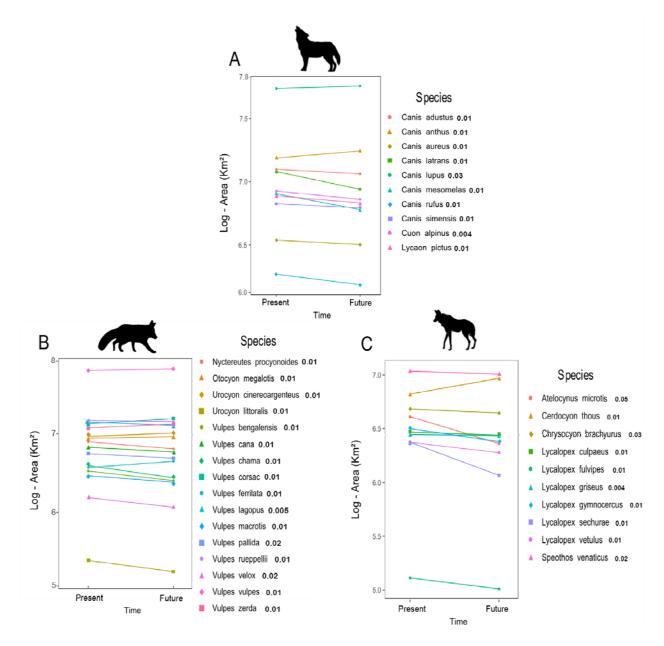
- 669 TABLE S2 Area difference in species distributions for present and future, showing expansion
- 670 or retraction of canids' geographical distributions. *H* values are also indicated.

Species	Present area (Km ²)	Future area (Km ²)	H
Atelocynus microtis	4.379.627	2.438.970	0,047520
Canis anthus	15.472.384	17.583.018	0,013342
Canis aureus	3.448.559	3.187.594	0,008698
Canis latrans	12.065.866	8.749.988	0,006891
Canis lupus	55.058.863	57.577.546	0,02551
Canis mesomelas	7.840.423	6.214.900	0,009592
Canis rufus	1.858.413	1.529.932	0,012079
Canis simensis	6.707.343	6.227.124	0,012671
Canis adustus	12.577.073	11.623.101	0,011225
Cerdocyon thous	7.224.726	10.225.538	0,011357
Chrysocyon brachyurus	5.202.737	4.755.462	0,027895
Cuon alpinus	7.757.856	6.803.830	0,004926
Lycalopex culpaeus	3.121.231	2.923.795	0,006086
Lycalopex fulvipes	126.236	98.762	0,009984
Lycalopex vetulus	2.539.881	2.040.550	0,012808
Lycalopex griseus	2.961.540	2.903.216	0,004344
Lycalopex gymnocercus	3.354.884	2.561.320	0,005269
Lycalopex sechurae	2.514.432	1.209.669	0,006207
Lycaon pictus	8.445.869	7.276.908	0,014579
Nyctereutes procyonoides	7.413.459	6.018.161	0,006262
Otocyon megalotis	8.251.366	8.676.914	0,007170
Speothos venaticus	11.953.879	11.185.765	0,016549
Urocyon cinereoargenteus	8.757.468	9.595.434	0,011490
Urocyon littoralis	200.615	143.194	0,011346
Vulpes bengalensis	3.053.463	2.287.423	0,014108
Vulpes cana	6.315.447	5.439.834	0,005072
Vulpes chama	3.594.029	2.487.370	0,008272
Vulpes corsac	13.114.501	14.423.740	0,012275
Vulpes ferrilata	3.502.426	3.977.712	0,008895
Vulpes lagopus	13.405.437	12.101.093	0,004969
Vulpes macrotis	2.651.764	2.171.680	0,011933
Vulpes pallida	5.164.447	4.518.576	0,023281
Vulpes velox	1.360.294	1.016.829	0,022411
Vulpes vulpes	64.415.599	68.080.936	0,005214
Vulpes zerda	11.242.325	12.574.885	0,007949
Vulpes rueppellii	14.074.266	13.588.853	0,013633

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674 SUPPLEMENTARY TEXT: FIGURE LIST

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FIGURE S38 Plot representation, on logarithmic scale, of range expansion or contraction
over time for the clades of wolves (A), foxes (B), and South American canids (C). *H* values
for each species are indicated next to each species name.

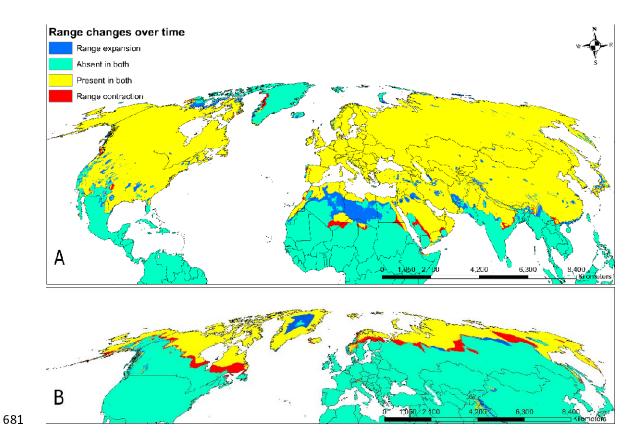


FIGURE S51 Comparison of present and future suitable areas of *Vulpes vulpes* (A) and *Vulpes lagopus* (B). The image shows regions where loss is expected to occur (red) and
regions where the species will increase their distributions (blue).