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The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis

Submission to *Journal of Animal Ecology* for consideration as *Review*

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Keywords

Climate vulnerability; temperature extremes; comparative demography; demographic rates; population growth rate

Abstract

1. Approximately 25% of mammals are currently threatened with extinction, a risk that is amplified under climate change. Species persistence under climate change is determined by the combined effects of climatic factors on multiple demographic rates (survival, development, reproduction), and hence, population dynamics. Thus, to quantify which species and regions on Earth are most vulnerable to climate-driven extinction, a global understanding of how different demographic rates respond to climate is urgently needed.

2. Here, we perform a systematic review of literature on demographic responses to climate, focusing on terrestrial mammals, for which extensive demographic data are available.
3. To assess the full spectrum of responses, we synthesize information from studies that quantitatively link climate to multiple demographic rates. We find only 106 such studies, corresponding to 87 mammal species. These 87 species constitute < 1% of all terrestrial mammals.
4. Our synthesis reveals a strong mismatch between the locations of demographic studies and the regions and taxa currently recognized as most vulnerable to climate change. Surprisingly, for most mammals and regions sensitive to climate change, holistic demographic responses to climate remain unknown. At the same time, we reveal that filling this knowledge gap is critical as the effects of climate change will operate via complex demographic mechanisms: a vast majority of mammal populations display projected increases in some demographic rates but declines in others, often depending on the specific environmental context, complicating simple projections of population fates.
5. Assessments of population viability under climate change are in critical need to gather data that account for multiple demographic responses, and coordinated actions to assess demography holistically should be prioritized for mammals and other taxa.

Introduction

The *ca*. 6,400 extant mammal species have colonized virtually all terrestrial and most aquatic habitats (Jenkins *et al.* 2013). This evolutionary success has been facilitated by the wide range of mammalian life history strategies (Healy *et al*. 2019), which enable them to cope with vastly different climates (Promislow *et al*. 1990). These strategies include extreme examples like male semelparity in some Australian marsupials, characterized by short, explosive mating seasons (Fisher *et al.* 2013), or high behavioral and demographic plasticity in long-lived primates that buffers populations from the negative effects of environmental variation (Campos *et al*. 2017). This

tremendous variation in life history strategies can be captured by differences among organisms in their rates and timing of survival, development, and reproduction (Stearns 1992). It is these demographic rates that determine population growth and thus species persistence (Morris & Doak 2002). Therefore, understanding the effects of climate drivers on the viability of natural mammal populations requires a simultaneous consideration of multiple demographic rates (Paniw *et al*. 2019).

Important efforts have been made in the last decade to increase the amount of comparative data to understand the variation in demographic rates across mammals (Conde *et al*. 2019). These data have resulted in the broader availability of open-access demographic information on populations of mammals and other taxa (Jones *et al*. 2009; Salguero-Gómez *et al*. 2016) and have produced key life-history knowledge, for instance on lifespan and mortality schedules (Conde *et al*. 2019; Jones *et al*. 2014). However, we still lack a holistic understanding of how climate drivers simultaneously affect survival, development, and reproduction in mammals worldwide. This gap is at odds with an emerging consensus that interactions among demographic rates and biotic and abiotic drivers hinder simplistic projections of persistence under climate change (Benton *et al*. 2006; Urban *et al*. 2016). For instance, a negative effect of climate on a specific demographic rate does not necessarily cause a population to go extinct, when another demographic rate responds positively to climate, or when population dynamics are mediated by interactions among climate drivers and density-dependent feedbacks (Reed *et al*. 2013; Paniw *et al*. 2019). Consequently, it is important to assess whether the complexity of demographic responses to climate is widespread among mammals and whether research quantifying such complexity is available for regions most vulnerable to climate change or for the most vulnerable species.

Here, we synthesize our understanding regarding where, which, and how mammal populations respond to climate. We searched for literature linking multiple demographic rates to climatic drivers, thus capturing the complexity of demographic responses, for 5,728 terrestrial mammal species (Myhrvold *et al*. 2015). We then performed a rigorous review of studies that matched our search

criteria and linked data from the review to information on ecoregion and species' vulnerability to climate change (Beaumont *et al*. 2011; IUCN 2019). Our review allows us to explore (i) whether mammal demographic studies are conducted in ecoregions that are most vulnerable to projected increases in temperature and precipitation extremes (Q1: *Where*?); (ii) whether potential future demographic responses to climate change reflect species' extinction risk as determined by the IUCN Red List status of mammals (Q2: *Which species*?); and (iii) through which demographic processes projected changes in climate may show negative and/or positive effects on populations (Q3: *How*?).

Methods

We obtained scientific names of 5,728 terrestrial mammal species from the Amniote database (Myhrvold *et al*. 2015). For each species, we searched SCOPUS for studies (published before January 2018) that quantified demographic-rate-climate relationships (for the full list of search terms, see Supporting information S1). We also confirmed, using a subset of species, that a search in Web of Science did not produce different results (Supporting information S1). From any study that matched our search terms, we extracted information on demographic-rate-climate relationships only if (i) the study linked at least two different demographic rates (*i.e.*, survival, development/growth, or reproduction) to a climatic driver (*i.e.*, any direct or indirect measure of temperature or precipitation); and (ii) the response of a demographic rate to a climatic driver was quantified using statistical methods (*i.e.*, excluding qualitative or descriptive studies). To standardize our search protocol and to assess potential global demographic consequences of climate change, we recorded local climatic factors such as winds or storms only when these factors were related to temperature and precipitation. In addition, we only considered studies on natural populations of terrestrial mammals, or partially terrestrial mammals (e.g., polar bears), because initial results showed that there were few climate-related population studies on fully aquatic mammals, which considered distinct climatic drivers that lack future projection information (e.g., ocean circulation indices).

From all studies meeting our criteria, we extracted the effects any climatic driver had on unstructured or age- or stage-specific demographic rates. We grouped these effects as positive (*i.e.,* increased rate), negative (*i.e.*, reduced rate), no effect, or context-dependent (e.g., increased rate at low population densities and no effect at high densities; see Supporting information S1 for details). We also recorded whether climate effects were measured at annual or seasonal scales and, when applicable, the factors that mediate these effects (e.g., density, biotic interactions). In studies that indicated future projections of drivers, we recorded whether drivers were projected to increase, decrease, or show context-dependent trends.

For the 68% of studies that did not report on climate projections (Figs. S1.4 & S1.5) but assessed demographic effects of direct temperature and precipitation measures, we approximated whether future averages and extremes in these drivers were likely to increase, decrease, or remain unchanged under global climate change (Supporting information S1). To do so, we obtained monthly average temperatures and precipitation data as well as maximum and minimum monthly temperatures from 1979-2013 for all relevant study locations using *climatologies at high resolution for the earth's land surface areas* (CHELSA; ca. 1 km^2 resolution) (Karger *et al*. 2017). The monthly scale corresponded to the finest scale used to aggregate climatic variables for demographic analyses in the reviewed studies. We also obtained projections of these variables for 2041-2060 assuming five diverging climate models (NorESM1-M; MPI-ESM-LR; GISS-E2-R; CMCC-CM; CESM1-BGC; Supporting information S1). We averaged historical and projected climate records for each month and each of the five climate models. We then calculated changes in each of the climate variables by subtracting the monthly average historical records from the projected values. We set the change to 0 if 95 % CI of the monthly averages across the five projection models crossed corresponding average historical values. Finally, we averaged these changes across all months to obtain a unique value of projected increase, decrease, or no change in total precipitation or average and extremes in temperature. We also calculated the standard deviation of the monthly averaged historical and projected climate records and assessed the changes in this deviation using the 95 %

163 CI as above, which gave us a unique value of increase, decrease, or no change in the variation of
164 the above variables.

165 To quantify potential demographic effects of global changes in temperature and precipitation, we
166 linked the changes in precipitation and temperature variables obtained from CHELSA to the
167 reviewed studies in the following way: If a study assessed seasonal/annual averages or deviations
168 in precipitation, mean temperature, or minimum/maximum temperature but did not project future
169 changes in these variables, we assigned future changes using our CHELSA climate data –
170 assuming that precipitation and temperature variables used in a given study would change in the
171 same direction as the CHELSA climatic data. From this information, we then determined whether
172 a demographic rate would potentially decrease (e.g., where a rate has a positive response to
173 maximum temperature and maximum temperature projected to decrease) or increase (e.g., where
174 a rate has a positive response to maximum temperature and maximum temperature projected to
175 increase). Unless explicitly stated otherwise in a study, we assumed that demographic rates that
176 were not affected by a climatic variable would not change in the future, and ones that showed
177 context-dependent responses would also likely show context-dependent responses in the future.

178 A full list of extracted studies and a more detailed description of the extraction protocol and climate
179 modelling can be found in Supporting information S1 and Table S1.1. We note that the multitude
180 of methodological approaches used to study demographic responses (e.g. correlation analyses,
181 structured demographic models, individual-based models) and the lack of a full statistical report in
182 some studies (Gerstner *et al*. 2017) render a full meta-analytical approach of climate-demography
183 relationships impractical.

184 We determined how well our studies provided knowledge in global ecoregions with high biodiversity
185 and high vulnerability to climate change (Q1, *Where?*) using two approaches. First, we built on the
186 results of Beaumont and colleagues (2011), which found that temperature, unlike precipitation, is
187 projected to become more extreme in all of the 132 terrestrial ecoregions of exceptional biodiversity
188 (i.e., in the "Global 200", Pimm *et al*. 2014). Specifically, the authors classified temperature

189 vulnerability of the G200 ecoregions using, among other measures, the weighted average minimum
190 monthly distance in temperatures (under the A2 climate model ensemble) from the mean of the
191 1961-1990 baseline. The higher the distance, the more vulnerable an ecoregion (Beaumont *et al*.
192 2011). We quantified the proportion of our studies that were conducted in these highly biodiverse
193 ecoregions, and the proportion of these studies that assess the demographic effects of temperature
194 increases. Further, we quantified and visualized whether demographic rates were reported to be
195 decreasing (-), not changing (0), or increasing (+) under increasing temperatures across ecoregion
196 temperature vulnerability scores.

197 Second, to assess how well our studies provided knowledge in areas projected to experience the
198 highest changes in temperature and precipitation, regardless of whether they have high
199 biodiversity, we obtained gridded global data on annual average surface air temperature and total
200 precipitation anomalies, the latter driven by seasonal variation (Collins et al. 2013), for the period
201 (2030-2049) compared to present day (1986-2005). Climatic anomalies were based on the
202 Representative greenhouse-gas Concentration Pathway scenario 6.0 (NCAR 2012), which is
203 similar to the previous SRES A2 climate model ensemble (Moss *et al*. 2008). We matched the
204 geographic locations of the studied mammal populations to the gridded global anomalies.

205 To assess whether demographic responses to projected changes in climate agree with the
206 International Union for Conservation of Nature and Natural Resources (IUCN) Red List status of
207 mammals (Q2: *Which species?*), we obtained IUCN assessments (including threats) for all species
208 identified in the literature review. We used the R package *rredlist* (Chamberlain 2020) to access
209 the IUCN Red List database and extract available information on whether the species are listed in
210 the database, and, if so, what status they are assigned to and whether climate change is listed as
211 an existing or potential threat. Lastly, for each IUCN threat category, we quantified the diversity of
212 projected positive (+), negative (-), and context-dependent (CD) climatic effects across different
213 demographic rates and life-cycle stages modelled for the mammal populations (Q3: *How?*).

Results

For most terrestrial mammals, we did not find studies on detailed demographic responses to climate. We extracted information on climate-demography relationships from 106 studies, for a total of 87 mammal species, that quantified simultaneous responses to climate in at least two different demographic rates. These studies span 12 biomes, with the exception of tropical and subtropical coniferous forests and mangroves (Fig. S1.1). Overall, more studies assess only the direct effects of precipitation (n = 42) than the direct effects of temperature (n = 11) (Fig. S1.2); and in eight of the 106 studies, only indirect effects are assessed via indices such as the North Atlantic Oscillation (NAO) or El Niño–Southern Oscillation (ENSO), while only seven studies assess the combined demographic effects of temperature, precipitation and climate indices (Fig. S1.2). A majority of studies (71%) only test demographic responses to seasonal (n = 40) or annual (n = 36) averages or sums in climate variables, while 16 % of studies assess responses to climate extremes (maxima, minima, or deviation from averages) as well as averages (Fig. S1.3). Few studies (10%) test how different climatic drivers interact with one another, approximately half (55%) test for the effects of density dependence on demographic rates, and an additional 27% test for effects of non-climatic drivers other than population density (e.g. predation, food availability). Studies that test for driver interactions typically find context-dependent climate effects in some demographic rates, with 15% of all reviewed studies reporting such effects.

In addressing "Q1: *Where*?", our synthesis reveals that few demographic studies are conducted in ecoregions that are both biodiverse and highly vulnerable to climate change (Olson and Dinerstein 2002). We find that 42 out of the 106 demographic studies were conducted in one of the G200 ecoregions (Fig. 1). However, only 13 of these studies assess the demographic effects of temperature increases. In addition, no study has examined the responses of different demographic rates in ecoregions with the highest vulnerability scores (e.g., the Central Congo Basin; darkest red in Fig. 1). Only one study, which included three primate species, assessed temperature effects in

241 a G200 ecoregion with relatively high vulnerability to climate change; and found no effects (Fig. 1
242 insert) likely due to the primates' behavioural and physiological flexibility before climate variation
243 (Campos *et al*. 2017). Similarly, our synthesis reveals that few demographic studies are conducted
244 in ecoregions projected to have the greatest anomalies in annual temperature and precipitation
245 (Fig. S1.6). Only one study (Hunter *et al*. 2010) assessed climate-demography relationships, of
246 polar bears (*Ursus maritimus*), in an arctic region with highest projected increases in average
247 temperature (> 2.5 ºC; Fig. S1.6a). Lastly, no study has examined demographic responses to
248 precipitation in ecoregions with highest projected decreases in precipitation. Only two studies
249 (Campos et al. 2017; Marshall *et al.* 2016), considering a banded mongoose and two primate
250 populations, examined demographic responses to precipitation in regions in East Africa, where
251 precipitation is projected to increase substantially (> 100 mm; Fig. S1.6).
252
253 In addition to an ecoregion bias, in answering "Q2: *Which species*?", we highlight that demographic
254 analyses suffer from a taxonomic bias too. Studies linking multiple demographic rates to climatic
255 drivers are primarily performed in regions with a relatively low mammal richness and on species
256 that are not currently vulnerable to climate change (Fig. 2), based on IUCN classifications. Indeed,
257 the IUCN has identified at least 17% of listed vertebrates to be sensitive to climate change, *i.e*.,
258 decreasing in numbers or losing habitat under changes in temperature and precipitation regimes
259 due to elevated atmospheric CO_2 levels (Marris 2008). Our synthesis reveals that only 4% of all
260 mammals assessed as climate sensitive by the IUCN have detailed studies linking demography to
261 climate (*i.e*., 13% of studies we assessed). Interestingly, the proportion of demographic rates per
262 study that may decline under global climate change (0.31, ± 0.10 S.E.) is highest for species that
263 have been flagged by the IUCN as climate sensitive. However, this proportion is followed closely
264 by species for which climate change is not considered a threat by the IUCN (Fig. 2 insert).
265
266 In addressing "Q3: *How*?", our synthesis reveals that complex demographic responses to climate
267 are prevalent. Only eight (7%) of the 106 studies report unidirectional (all positive) responses of

demographic rates to climatic drivers, while in 19 cases no effect of climate on any demographic rate is reported (Figs. S1.4 & S1.5). For the vast majority of species, effects of climate reported in the studies (79%) and projected under global change as presented in the studies or approximated in our analysis (75%) can be positive, negative or context-dependent depending on the population studied and the specific driver, demographic rate, and life-cycle stage considered (examples in Fig. 4). In addition, 13 studies assess the effects of climate on population growth rates in addition to underlying demographic rates (Fig. S1.4, Table S1.1). These examples show that population responses are not readily predictable from a single demographic rate when multiple climatic drivers and their interactions with biotic drivers affect demography. For instance, Lawler and co-authors (2009) show that survival, stage transitions, and reproduction all determine how the population growth rate of the long-lived Verreaux's sifakas (*Propithecus verreauxi verreauxi*) responds to annual rainfall.

Discussion

Our synthesis shows that gaining a global understanding of the mammals that are most vulnerable to climate-driven extinction will require filling important knowledge gaps. Studies on climate effects across the whole life cycle of populations are needed in regions that are highly susceptible to climate change, many of which are biodiversity hotspots (Beaumont *et al*. 2011). Many of these ecoregions are not only threatened by increases in climate extremes (Beaumont *et al*. 2011; Stott 2016) but also face strong pressures on biodiversity from direct human activities (Venter *et al*. 2016). A majority of studies linking demographic rates to climate in vulnerable ecoregions and elsewhere nevertheless focus on demographic responses to changes in average climate and do not account for interactions with non-climate drivers. It is possible that publication bias plays a part in our observations of these omissions, as authors may, for instance, explore interactions but not mention this in their published study due insignificant or inconclusive results (Jennions and Møller 2002). At the same time, population dynamics are typically driven by compound effects of interacting climatic and non-climatic drivers (Benton *et al*. 2006; Zarnetske *et al*. 2012), which are

295 projected to become more extreme under climate change (Zscheischler *et al*. 2018). A stronger
296 focus on extremes and driver interactions is therefore required to improve our estimates of
297 population viability.
298
299 Our analysis also reveals that studies assessing responses to climate across different demographic
300 rates are required for most mammals considered climate-sensitive by the IUCN. These results
301 support recent calls to gain a better understanding of the complex effects of climate on population
302 viability (e.g., Doak and Morris 2010; Cahill *et al*. 2013; Román-Palacios and Wiens 2020), allowing
303 this threat to be understood and potentially mitigated through conservation. On the other hand,
304 given that a large number of mammals not considered to be climate sensitive may actually show
305 negative demographic responses to climate change, our results support the need for current IUCN
306 efforts to re-evaluate the importance of climate as an extinction threat to mammals (Foden and
307 Young 2016). It is noteworthy that the majority of demographic studies on mammals do not project
308 demographic effects of climate change. Our simplified and broad approximation of climate change
309 for these studies allowed for global synthesis in this review, but we note that this approximation
310 does not match the spatiotemporal resolution of the climatic drivers assessed in the relevant
311 studies, averages over seasonal climatic patterns, and does not allow examination of interactions
312 with other important factors, which can exacerbate or dampen large-scale climate trends (van de
313 Pol *et al*. 2013). Thus, an important challenge for future studies is to project changes in local climatic
314 variables that have been considered important drivers of demographic rates (Snover *et al*. 2013).
315
316 By focusing on studies that have assessed several demographic responses to climate, we
317 necessarily limited the number of taxa in our review. In fact, we identified at least 111 more studies
318 on 68 additional species that only assessed climatic effects on single demographic rates. We stress
319 here that we do not question the validity of such studies when population dynamics can be
320 accurately predicted from the changes in one demographic rate with a uniquely high contribution
321 to the population growth rate. However, population responses to climate are typically determined

by the covariation among multiple demographic rates, which itself is often mediated by a myriad of interacting biotic and abiotic factors (e.g., Reed *et al*. 2013). For instance, impalas (*Aepyceros melampus*), which the IUCN characterizes as threatened by drought (Table S1.1), may show positive or negative responses in survival and reproductive success under rainfall scarcity depending on the seasonal patterning of rainfall and population density (Ogutu *et al*. 2012). Similarly, meerkats (*Suricata suricatta*), which currently face no threats according to the IUCN, show both positive and negative responses to precipitation across several critical demographic rates depending on social stage, group size, and temperature extremes (Ozgul *et al*. 2014; Paniw *et al*. 2019). Therefore, as a cooperative breeder, meerkats may be vulnerable to compound effects of increases in seasonal climatic extremes that decrease group densities (Paniw *et al*. 2019). Such complex demographic responses make it challenging to project species' fates under climate change because the future of populations cannot be accurately determined from single demographic rates (Urban *et al.* 2016).

As consistently negative demographic responses to climate change are only relatively common in species the IUCN flagged as climate sensitive, our results suggest that complexity of demographic responses may buffer populations from adverse climate effects (González-Suárez and Revilla 2013). One important aspect of such complexity is that different populations may show starkly different responses to climate, and less severe demographic effects in one population may compensate for climate-related losses of individuals in another population (Schindler *et al*. 2015; Villellas *et al*. 2015). In addition, dispersal can stabilize decreasing populations and allow mammals to track new suitable habitats, and may itself be strongly mediated by climate (Parmesan and Yohe 2003; Root 2003; Travis *et al*. 2013). However, these important spatial aspects of demographic complexity have thus far been rarely assessed, with only three of the 106 studies quantitatively linking dispersal (emigration or emigration), in addition to local survival or reproduction, to climate (Kreuzer and Huntly 2003; Ozgul et al. 2014; Wauters et al. 2004). Therefore, despite the challenges involved in collecting long-term demographic parameters, including dispersal, across

the entire life cycle (Foden and Young 2016), the mechanistic insights gained from such parameters will be invaluable to understand the drivers of biodiversity loss under climate change (Travis *et al*. 2013; Urban *et al*. 2016).

In conclusion, our current mechanistic knowledge on mammal responses to climate change would benefit from strategic studies that fill the knowledge gaps identified here. Our take-home message echoes recent calls for more integrative climate-demography studies in bird populations (Zurell 2017), along with numerous studies showing the benefits of such integrative research for evidence-based conservation (Møller *et al*. 2012). Other taxa, such as insects or amphibians, are far less well studied demographically than mammals or birds, but recent evidence suggests that demographic responses to climate change are complex and that understanding this complexity is key to conservation planning (Boggs 2016; Muths *et al*. 2017). Along with recent calls for a renewed global effort to collect natural-history information (Urban *et al*. 2016), we therefore advocate for a coordinated effort to collect and model multiple demographic responses to climate across various taxa.

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Data availability and archiving

The data that support the findings in this study are available in the Supporting information S1 and Table S1.1. The code that supports the findings in this study is available in the Supplementary Online Materials, `climate_change_analyses_mammal_review.R`. Upon acceptance, all data and code will be archived on *Dryad* and will be freely accessible.

Author Contributions

MP, TDJ, GR, and RS-G devised the overall manuscript. MP and TDJ designed the literature review protocol, which was then implemented by MP, TDJ, GR, CRA, SL, AM, JC, NSG, JMB, and AP. The climatic data were derived by AC. The first draft of the manuscript was written by MP and RS-G, and all co-authors contributed to the final manuscript. See Table S1.2 for further specifics regarding task contributions.

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509 **Supplementary Information** is available in the online version of the paper.

510

511 **Figure legends**

512

513 **Figure 1.** Global distribution of 106 mammal studies (grey points) that have assessed multiple
514 demographic responses to climate across the species' life cycles. Point size indicates number of
515 relationships between climatic drivers and age/stage-specific demographic rates (survival,

development, and/or reproduction). Red-scale map background indicates projected climate-change vulnerability for the most biodiverse (G200) ecoregions, with redder colours indicating higher increase in extreme temperatures. Left insert shows number of demographic rates decreasing (-), not changing (0), or increasing (+) under increasing temperatures as function of ecoregion vulnerability. Shading on insert indicates total number of demographic rates linked to temperature per ecoregion vulnerability level.

Figure 2. Global distribution of mammals (points) with available information on climate-demography relationships. Point and bar colours indicate levels of threat assessment by the IUCN (No IUCN - species not assessed; No T - species assessed and currently faces no threats; No CT - climate change not considered a threat; CT - climate change considered a threat). Darker background on the map indicates higher mammal richness (number of species). Bottom-left insert displays the mean proportion of demographic rates per mammal population ± S.E. (error bars) that may decrease under projected global climate change in different IUCN categories. Total number of populations with at least one decreasing rate per threat level are indicated above the bars. Species highlighted in Figure 4 are mapped here.

Figure 3. Summary potential demographic responses under projected global changes in temperature and precipitation across IUCN threat categories. Out of total number of populations reviewed per IUCN threat category (indicated next to bars), we show the proportion of populations where increasing or decreasing (+/-) responses to climate are projected for different ages/stages of the same demographic rate ("within"; e.g. pre-reproductive versus reproductive stage), or for different demographic rates ("among", e.g. survival versus reproduction). Categories include No IUCN - species not assessed; No T - species assessed and currently faces no threats; No CT - climate change is not considered a threat; CT - climate change is considered a threat.

Figure 4. Detailed potential demographic responses to climate change for 11 example species. Demographic rates include survival (S), probability of reproducing and reproductive output (R), and growth and development (G), which can show only positive (+), only negative (-), context-dependent (CD; both positive and negative, depending on interactions with other drivers), or no (0) responses in the future. The number of instances that responses are recorded include all stage-specific and climate driver-specific combinations. From top left to bottom right, the species include Soay sheep (*Ovis aries*), agile antechinus (*Antechinus agilis*), yellow-bellied marmot (*Marmota flaviventer*), meerkat (*Suricata suricatta*), pika (*Ochotona curzoniae*), long-tailed wattled bat (*Chalinolobus tuberculatus*), Milne-Edwards's sifaka (*Propithecus edwardsi*), northern muriqui (*Brachyteles hypoxanthus*), Saiga antelope (*Saiga tatarica*), impala (*Aepyceros melampus*), and black-flanked rock-wallaby (*Petrogale lateralis*).

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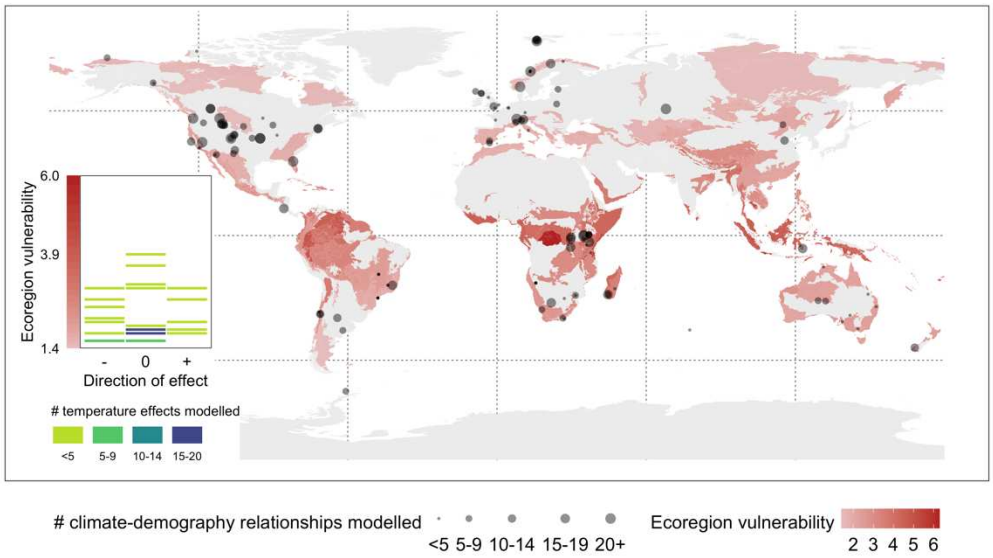
561 **Figure 1**



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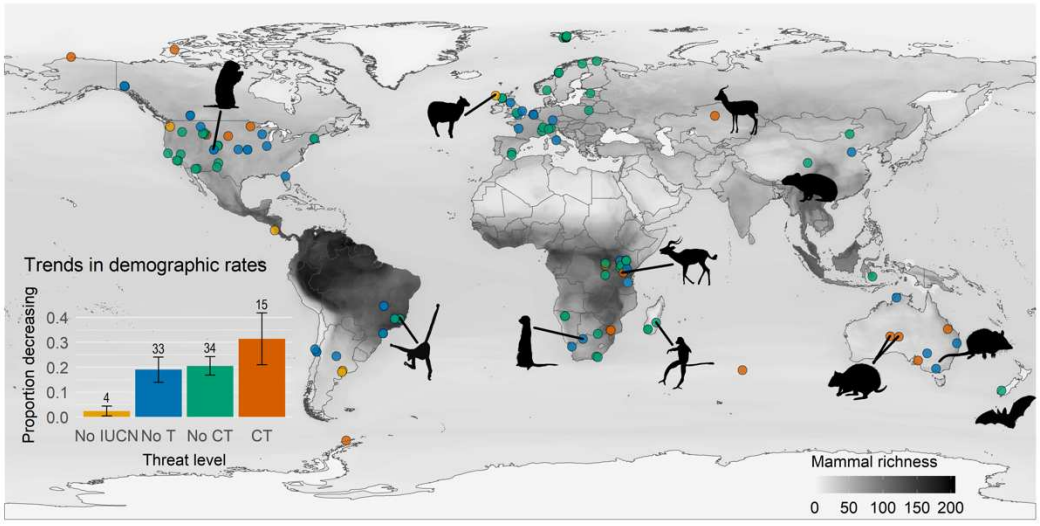
564 **Figure 2**



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568 **Figure 3**

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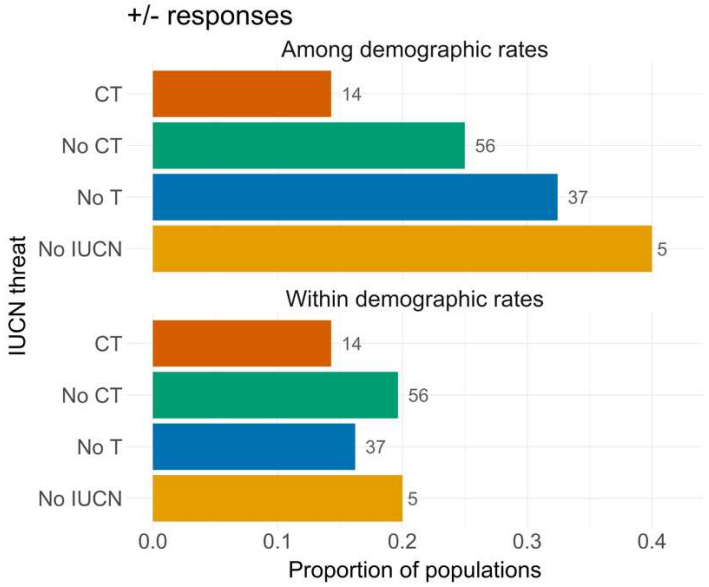

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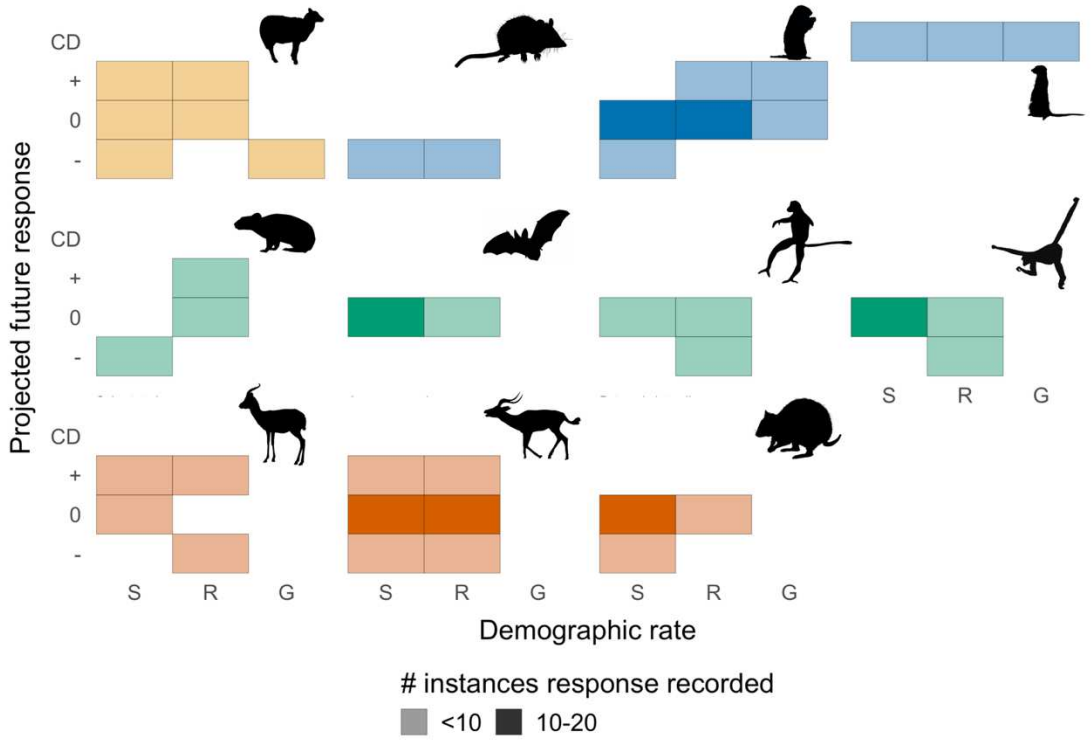
571 **Figure 4**



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