

The impacts of extreme climate change on mammals differ among functional groups at regional scale: The case of Iranian terrestrial mammals

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Abstract

Aim: The negative impacts of climate change on mammals have been largely based on assessments of total species' assemblages or individual species at broad scales. Here, we evaluate how the predicted magnitude and velocity of climate change in the arid region of southwest Asia might affect regional functional groups of terrestrial mammals.

Location: Iran.

Methods: We gathered data from 186 species to map diversity hotspots of 12 functional groups, threatened species richness and total species richness. We mapped areas with high risk of exposure to extreme drying and warming events and calculated the velocity of climate change by using precipitation and temperature data from current and future periods. We then quantified the exposure of these hotspots to extreme changes in magnitude and velocity.

Results: Hotspots of functional groups, threatened species and species richness were most exposed to precipitation decline in current and future scenarios (average of 17.9% and 29.9% respectively), compared to temperature rise. While most hotspots are found in mountains, hotspots located in lowlands were more exposed to extreme drying, particularly for carnivore, desert and large-bodied functional groups, as well as threatened species. These patterns remained intact when we considered only hotspots covered by existing protected areas. The impacts of velocity also varied significantly among functional groups, with highest levels for carnivore, large-bodied and specialist groups and threatened species.

Main conclusions: We show that climate change does not equally impact all species within a community and that vulnerability to these changes differed between functional groups. We found that the areas with the highest risk of exposure to extreme climates are located in lowlands and not in mountains. We found that extreme drying, rather than warming, is the major threat to regional mammal diversity in this arid region, particularly for large-bodied and threatened species.

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KEYWORDS

arid region, climate change velocity, drought, functional traits, large mammals, southwest Asia, species richness, upper critical temperature

1 | INTRODUCTION

Climate is predicted to drive marked increase in temperature and pronounced changes in precipitation patterns worldwide (IPCC, 2018). Although species may be able to survive in situ or adapt to the new conditions (Vaughan et al., 2015), these changes are expected to greatly impact the distribution patterns of many species globally (Thomas et al., 2006; Lenoir and Svenning, 2015). Projected temperature increases and precipitation decreases impact species through direct effects from thermal heat stress and dehydration and indirectly via impacts on primary productivity (Hoffmann et al., 2013; Ward, 2016). The magnitude of these changes is not the only challenge, as the ability of species to cope with climate change is also linked to the velocity of climate change: species may face greater risk if climatic conditions change too fast (e.g., higher velocities) (Loarie et al., 2009; Garcia et al., 2014). These trends are likely to be amplified in arid regions, where both magnitude and velocity of climate change are predicted to be higher, thus exposing species to extreme drying and warming events (Heffelfinger et al., 2018; Loarie et al., 2009).

Accumulating evidence suggests that the species' responses to climate change, besides the level of exposure, are largely related to their biological and ecological traits (e.g., Pacifici et al., 2017; Pearson et al., 2014). Considering that species assemblages with different functional traits and resource use strategies may have spatially heterogeneous richness patterns (González-Maya et al., 2017; Vidan et al., 2019 and references therein), dividing the total species assemblage into distinct ecological or functional groups may improve our understanding of specific problems for the associated groups (Newbold et al., 2020). This approach avoids the generation of highly variable predictions for total species' assemblage or highly specific predictions for individual species (Newbold et al., 2020). Nevertheless, previous studies of climate change impacts have focused mostly on changes in potential climate suitability at species level by constructing individual species distribution models under present and future conditions (Pacifici et al., 2015). Yet, few attempts have been made to forecast the exposure of species to future climate changes (but see Morrison et al., 2018; Pacifici et al., 2018), particularly by using a generalized approach suitable to deal with a comprehensive set of species grouped by their ecological roles or resource use (i.e., ecological or functional groups).

Within mammals, a variety of morphological (body size), ecological (diet or feeding guild) and behavioural (climate and habitat use and locomotion type) traits have been suggested to affect species responses to climate change, and functional or ecological groups defined based on these traits will be differently affected by the magnitude and velocity of climate changes (Vale & Brito, 2015; Mason-Romo et al., 2017). Mammal body size, for example, has been suggested to strongly relate with responses to climate change,

and significant differences have been observed between large and small mammals in this regard (McCain & King, 2014). Another study (Pacifici et al., 2017) found that diet specialization increases mammal vulnerability to climate change. As such, a better understanding of the impacts of climate change requires considering species traits and the individual assessment of groups that may respond similarly to the same set of environmental conditions (Newbold et al., 2020). This approach is particularly useful for conservation purposes (Foden & Young, 2016; Pacifici et al., 2018), because the results are easy to interpret and can be used by conservation practitioners when understanding the risks that climate change places on species.

Current models of global climate change have indicated that Southwest Asia (or Middle East) has a high risk of exposure to extreme climatic events (Evans, 2009; Lelieveld et al., 2012). Warming in this region is projected to exceed the thresholds of human tolerance and adaptability (Pal & Eltahir, 2015; Schär, 2016), and aridity is expected to increase across the entire region during the coming decades (Chenoweth et al., 2011). The region has high species diversity, resulting from its crossroad location at the intersection of three biogeographical realms (Palearctic, Saharo-Arabian and Oriental), but the potential impacts of climate change on its biodiversity remain largely unknown. Within Southwest Asia, Iran is very rich in fauna and flora, particularly in mammal diversity, accumulating 192 species of terrestrial mammals with a variety of lifestyles (Yusefi, Faizolah, Darvish, Safi, & Brito, 2019). The country constitutes the last stronghold for severely threatened mammals, such as the Asiatic cheetah (*Acinonyx jubatus venaticus*), Persian fallow deer (*Dama mesopotamica*) and Onager (*Equus hemionus onager*), and is also home to the largest remaining populations of some other large mammals (e.g. many ungulates and carnivores) in the southwest Asia region (Firouz, 2005). Most of these species have experienced severe reductions in their range and population numbers during the last decades (Yusefi, Faizolah, et al., 2019).

Here, we evaluate how the predicted magnitude and velocity of climate change might affect regional mammal diversity in an already hot and arid region. To achieve this, we analyse distributional data for 186 mammal species inhabiting Iran. We address the following questions: (i) How are the richness hotspots of functional groups, threatened species and total species distributed? (ii) Where are the areas with high risk of exposure to extreme climate change? (iii) To what extent will richness hotspots be exposed to these potential risk areas? (iv) Which functional groups are most likely to be exposed to high magnitude and velocity of climate change? and (v) How effective is the current network of protected areas (PAs) in preserving richness hotspots in a changing climate? This research represents a regional scale study that explores the links between functional traits and vulnerability to climate change, a topic which remains largely understudied when compared to large spatial scales (e.g., Morrison et al., 2018; Pacifici et al., 2018), despite the fact that practical

conservation actions take place at regional scales, usually within the boundaries of individual countries (Smith et al., 2009).

2 | METHODS

2.1 | Study area

Iran covers 1,648,195 km², with elevations ranging from -60 up to 5,671 m. Major terrestrial ecosystems are the Hyrcanian dense forest, high mountains of Alborz and Zagros, Kopet-Dag mountains, Caucasus region, Central Basin, Persian Gulf and Oman Sea coastal areas, and Mesopotamian lowlands (Figure 1). The Central

Basin covers most of the country and has high physiographic complexity, including several mountains and large hyper-arid deserts (Firouz, 2005). A large section of the country is covered by Caucasus and Irano-Anatolian hotspots, that are two of the seven global biodiversity hotspots recognized in Asia. Iran's climate is highly heterogeneous with eight climate regions recognized (Yusefi, Safi, & Brito, 2019).

2.2 | Distribution data

We used distribution data of terrestrial mammalian species from a database of 14,251 georeferenced occurrence records, representing all of Iran's



FIGURE 1 The map of the study area, main toponymies mentioned in text and geographic location of Iran within global context (small inset)

mammal species ($n = 186$) distributed across 7 orders and 33 families (Yusefi, Faizolah, et al., 2019). Six introduced species were excluded (see species list in Table S1). This comprehensive dataset on Iranian mammal fauna was built from extensive literature reviews, online occurrence records, presence records from 459 areas under protection, unpublished observations and our own surveys. We used a grid of 25 km \times 25 km spatial resolution (2,240 square grid cells) and intersected it with the species distribution data to generate a database of species presence/absence by cell. We opted to use species' occurrence data (or area of occupancy) because it tends to be more precise than the extent of occurrence (Graham & Hijmans, 2006; Kreft & Jetz, 2010), as the latter usually overestimate species distributions and species richness (Lawler et al., 2009 and references therein) thus overestimating the degree of exposure to climate change (Ameca y Juárez et al., 2013). ArcGIS ver. 10.4.1 (ESRI, 2016) was used to process all data and to perform all following analyses, unless otherwise stated.

2.3 | Functional groups

We selected functional traits relating to the biology and ecology of mammals and representing multiple aspects of resource use, including feeding habit, climate and habitat use and the type of locomotion (following Chillo & Ojeda, 2012; González-Maya et al., 2017). Traits included (1) body size (mean adult body mass); (2) feeding guild; (3) climate breadth (number of climate regions in which a species has been recorded); (4) habitat use (e.g. type of habitats used by each species); and (5) locomotion type (see details of traits definitions and thresholds in Table S2). These traits have been commonly used to cluster species from different taxonomic groups into functional groups (e.g., García-Llamas et al., 2019; Hector et al., 1999; Newbold et al., 2020; Tilman et al., 1997) and are representative of many of the ecological roles that are played by species in ecosystems (e.g., body size and diet reflect the amount and type of resources that species consume, while locomotion influences mobility and thus ability to track suitable climates). Additionally, these traits have been found to influence overall climate risk for species (Pacifi et al., 2017, 2018), and presumably associated groups respond similarly to the same set of environmental conditions (Newbold et al., 2020). Accordingly, our mammal assemblage of 186 species was classified into 12 functional groups, including small-bodied, large-bodied, carnivores, herbivores, insectivores, climate generalists, climate specialists, desert species, forest species, mountain species, non-volant species and volant species (Table S2). We also considered threatened species, including those categorized as Critically Endangered, Endangered or Vulnerable (Yusefi, Faizolah, et al., 2019), and total species richness (additional details can be found in Table S2).

2.4 | Climate variables and thresholds

Mean annual temperature (BIO01; °C) and total annual precipitation (BIO12; mm) were obtained from the WorldClim database

(<https://worldclim.org>) at 10 arc-minutes resolution, for the current time period (average for 1970–2000) and for 2070 (average for 2061–2080) under two Representative Concentration Pathway (RCP) scenarios (RCP4.5 and RCP8.5). These moderate (RCP4.5) and extreme (RCP8.5) scenarios are implemented by 19 and 17 global climate models (GCMs) (respectively). All variables were projected to the study area and upscaled to 25 km \times 25 km resolution. We then calculated the mean and upper and lower predictions of mean annual temperature and total annual precipitation in 2070s for the RCP4.5 and RCP8.5 as the mean \pm standard deviation (SD) of the 19 and 17 GCMs, respectively (Appendix S1 for additional details).

To identify areas where temperature may be extreme, the upper critical temperature (UCT) of the thermoneutral zone was used (Khaliq et al., 2014). The UCT is the threshold value of air temperature above which endotherms must increase metabolic rate to maintain body temperatures, which can drive fitness declines or can be detrimental to survival (Hoffmann et al., 2013; Vaughan et al., 2015). We calculated average and standard deviation (SD) of UCT following previous studies (Araújo et al., 2013; Vale & Brito, 2015) for the mammal species occurring in Iran based on the largest sets of endotherms UCT data available (Bennett et al., 2018; Khaliq et al., 2014). The average + SD UCT among 46 species was 29.6°C. We considered temperature values in a cell as "extreme" when it exceeded the UCT (average + SD) threshold. Note, following similar analyses (Araújo et al., 2013; Vale & Brito, 2015), this UTC value was based on yearly averages, not maximum temperatures. To identify potential further drylands, a 200 mm/year precipitation threshold was used (Maestre et al., 2012; Ward, 2016). This threshold has been associated with significant changes in species composition and richness (Ward, 2016), and precipitation reduction may strongly affect species survival and increase vulnerability levels (Pacifi et al., 2017).

2.5 | Hotspot mapping

We used the species' occurrence data (area of occupancy) to calculate a species richness map for each species separately (25 km spatial resolution). From the database of species presence/absence, we calculated species richness as the number of species present in each cell. Hotspots were defined as cells accumulating >50% of the highest number of species found in any one cell (following Brito et al., 2016). We mapped the location of hotspots for each functional group, as well as threatened and total species.

2.6 | Areas at high risk of exposure to climate extremes

To map areas most likely to be at risk from extreme climate, we calculated differences between the predicted (2070, for scenarios RCP4.5 and RCP8.5) and current mean annual temperature and total annual precipitation. For current conditions and for each climate scenario (RCP4.5 and

RCP8.5), we produced binary maps with the location of areas with temperatures above the UCT threshold (29.6°C) and areas with precipitation values below the dryland threshold (200 mm/year). Lastly, we quantified the relationship between dryness and warming by intersecting the areas with temperatures above the UCT threshold with the areas with precipitation values below the threshold for dryland classification.

2.7 | Exposure to high magnitude climate change

To map areas where hotspots of each functional group as well as threatened and total species are likely to be at risk from climate change, we tested the degree of overlap between hotspot distributions and areas with temperatures above UCT and precipitation below dryland threshold. We did this both for current conditions and for the most extreme scenario (RCP8.5). Exposure was defined as the degree to which the spatial extent of extreme climate changes overlaps the geographic area within which a hotspot of a functional group occurs (i.e., number of grid cells overlapping).

2.8 | Exposure to velocity of climate change

We calculated the velocity of climate change for mean annual temperature (°C) and annual precipitation (mm) as the ratio of the temporal gradient of change to the spatial gradient (Loarie et al., 2009). To measure the temporal gradient, we have used three time points (present, 2050 and 2070) to fit a linear model of climate in respect to time and extracted the slope as the rate of change. To calculate the spatial gradient, we calculated from the current climate maps the rate of change from each cell to its neighbouring cells using the average maximum technique in ArcGIS. We calculated the velocity of climate

change for two pathways (RCPs 4.5 and 8.5) and three time periods (including current conditions, 2050 and 2070) and for the 19 separate GCMs and summarized into the mean velocity of climate change. We plotted the histograms of the velocity of climate change for each functional group extent of occupancy and compared with the mean velocity of climate change of each group (Appendix S1 for detailed analyses). Calculations were implemented in R programming environment (R Development Core Team, 2018), using the “raster” package (Hijmans et al., 2018) and a custom script (Appendix S2).

2.9 | Protected areas, hotspots and exposure to climate extremes

The range of 12 functional groups as well as threatened and total species were intercepted (at 25 km side cells) with the current network of protected areas (PAs), to quantify the level of representation of hotspots within PAs and then to identify areas above UCT and below dryland thresholds to quantify the level of exposure of protected hotspots (i.e. hotspots already included in PAs or protected hotspots) to extreme climate change (i.e. number of grid cells overlapping). We included 248 areas under protection of the Department of the Environment of Iran (DoE-GIS, 2016), which consist of National Parks ($n = 31$), Wildlife Refuges ($n = 49$) and Protected Areas ($n = 166$).

3 | RESULTS

3.1 | Hotspot mapping

Overall, hotspots of the 12 functional groups as well as of threatened and total species tended to follow a similar pattern: richness

	Current	BIO01—Temperature		BIO12—Precipitation	
	N (% PA)	N PA (%) <UCT	N PA (%) >UCT	N PA (%) >200 mm	N PA (%) <200 mm
TOTAL	156 (26.3)	39 (95.1)	2 (4.9)	30 (73.2)	11 (26.8)
Threatened	174 (40.8)	71 (100.0)	0 (0.0)	28 (39.4)	43 (60.6)
Volant	14 (28.6)	4 (100.0)	0 (0.0)	4 (100.0)	6 (0.0)
Non-volant	217 (26.3)	55 (96.5)	2 (3.5)	37 (64.9)	20 (35.1)
Carnivore	219 (39.7)	84 (96.6)	3 (3.4)	44 (50.6)	43 (49.4)
Herbivore	146 (22.6)	31 (93.9)	2 (6.1)	25 (75.8)	8 (24.2)
Insectivore	23 (26.1)	6 (100.0)	0 (0.0)	6 (100.0)	0 (0.0)
Large	320 (37.2)	112 (94.1)	7 (5.9)	52 (43.7.0)	67 (56.3)
Small	66 (16.7)	11 (100.0)	0 (0.0)	1 (100.0)	0 (0.0)
Specialist	20 (5.0)	1 (100.0)	0 (0.0)	1 (100.0)	0 (0.0)
Generalist	194 (27.8)	52 (96.3)	2 (3.7)	39 (72.2)	15 (27.8)
Mountain	157 (24.8)	37 (94.9)	2 (5.1)	34 (87.2)	5 (12.8)
Forest	58 (25.9)	14 (93.3)	1 (6.7)	15 (100.0)	0 (0.0)
Desert	84 (22.6)	17 (89.5)	2 (10.5)	8 (42.1)	11 (57.9)

TABLE 1 Summary of the number of cells classified as hotspots (N) and percentage covered by protected areas (%PA) based on the current distribution range (Current) of 12 functional groups, threatened species and total Iranian terrestrial mammals and their predicted levels of exposure to changes in temperature (BIO01) and precipitation (BIO12) in 2070 according to RCP8.5 scenario. BIO01: number of hotspot cells (%) currently included in protected areas not exposed to future extreme temperatures (<UCT) or exposed (>UCT). BIO12: number of hotspot cells (%) currently included in protected areas that are not exposed to future reductions in precipitation (>200 mm) or exposed (<200 mm) (and the percentage covered by protected areas)

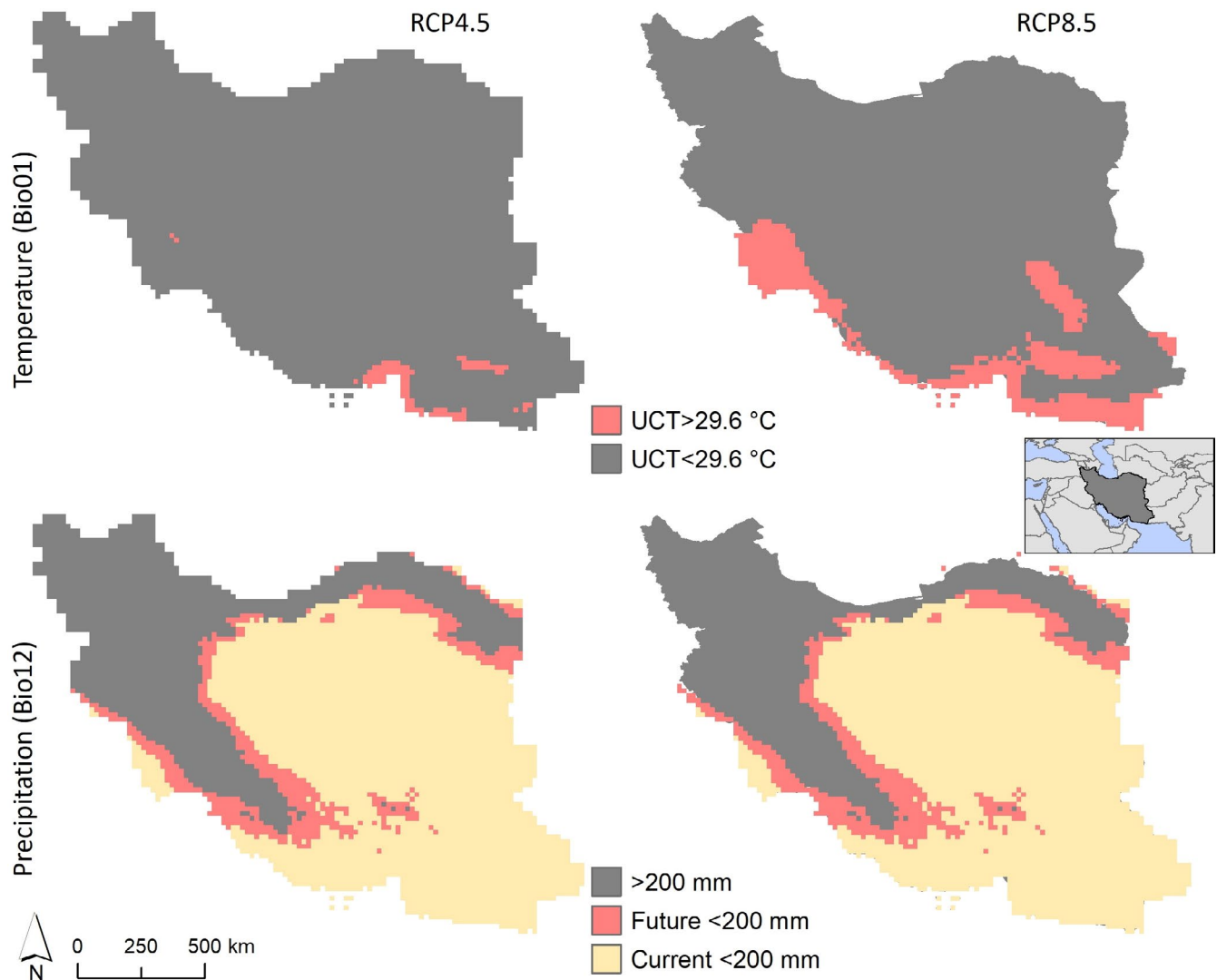


FIGURE 2 Areas with high risk of exposure to extreme climate change in Iran predicted for 2070 according to scenarios RCP4.5 and RCP8.5. Top: Areas experiencing mean annual temperature above the upper critical temperature threshold (mean UCT + sd: 29.6°C). Bottom: Areas experiencing total annual precipitation below the dryland threshold (<200 mm), distinguishing the current and future predicted expanding drylands. Inset: Location of Iran within global context

was concentrated in mountains, particularly in the Alborz and Zagros (Figure S1). The area (number of cells) of hotspots varied widely among functional groups: carnivore, generalist, large-bodied and non-volant functional groups had the largest areas, whereas specialist and volant functional groups were relatively restricted (Table 1).

3.2 | Areas at high risk of exposure to climate extremes

Under both scenarios (RCP4.5 and RCP8.5), almost the entirety of Iran is expected to experience an increase in temperature from 3 to 7°C (Figure S2). Under RCP4.5, the Zagros is expected to experience the highest increases (4–5°C) in temperature, whereas under RCP8.5, the entire country (except coastal areas of Caspian and Oman Seas) is predicted to experience temperature increases from 5 to 7°C. Decreases in precipitation by 50 to 250 mm were predicted

for the entire country in both scenarios, with highest decreases for Zagros and Hyrcanian regions.

Currently, no part of Iran has mean annual temperatures above the UCT threshold (29.6°C). However, 1.6% to 11.4% of the country will be exposed to extreme temperatures under RCP4.5 and RCP8.5 (Figure 2). Temperature change will most significantly affect the Mesopotamian region, Persian Gulf and Oman Sea coastal areas, as well as the south-eastern Central Basin (Dasht-e Lut or Lut desert). Currently, about 57.2% of Iran is classified as dryland (<200 mm/year). This proportion is projected to increase up to 67.1%–67.8% according to RCP4.5 and RCP8.5 scenarios. The entire Central Basin, Mesopotamian region, and the Persian Gulf and Oman Sea coastal areas are currently drylands, and future precipitation reduction (expanding drylands) will likely affect the southern slopes of Alborz and eastern and western slopes of Zagros (Figure 2).

Concerning the relationship between dryness and warming, a relatively small portion of the areas above the UCT threshold (2.7%)

will likely be exposed to annual precipitation below the dryland thresholds under the RCP4.5, whereas this percentage will increase to 15.4% in the RCP8.5 scenario. No single areas above the UCT threshold will be exposed to expanding drylands under RCP4.5, while this will increase about 13.6% under the RCP8.5 scenario (Figure S3).

3.3 | Hotspot exposure to magnitude of climate change

As expected, no single hotspot (for 12 functional groups, threatened and total species) is currently exposed to areas above the UCT threshold (Figures 3, 4 and Figure S4). However, by 2070, about 3.2% to 16.7% (average 4.2%) of these groups' hotspots will likely be exposed to extreme temperatures (Figure S4). The desert functional

group will be the one most exposed (16.7% of total hotspot area) to extreme temperatures (Figure 4 and Figure S4). The only hotspots not expected to be exposed are of insectivores, small-bodied, specialists and volant functional groups. The Mesopotamian region and scattered areas along the Persian Gulf and Oman Sea coasts have the highest incidence of exposure across functional groups (Figure S4).

Currently, about 3.0% to 35.9% (average 17.9%) of the hotspot areas of 10 functional groups (except insectivore and volant) as well as threatened and total species are already in drylands <200 mm/year (Figure 4 and Figure S5). This percentage is predicted to increase by 2070 (by 10.3% for RCP4.5 and by 53.6% for RCP8.5; average 29.9%), which would affect all groups analysed here (Figures 3 and 4). The carnivore, desert and large-bodied functional groups (43.8%, 53.6% and 49.1% of hotspot areas, respectively) and threatened species (47.7%) will be most exposed to reductions in precipitation

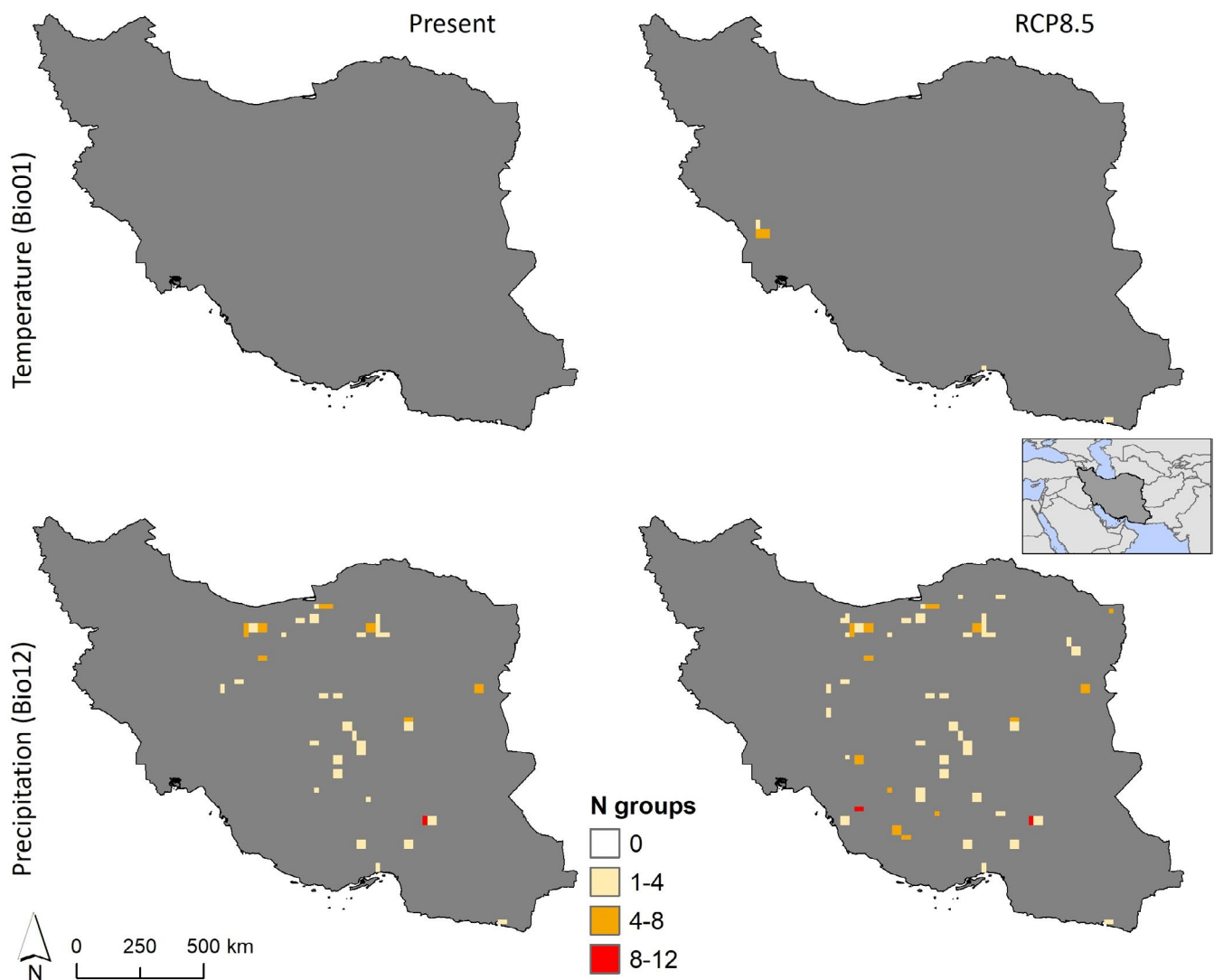


FIGURE 3 Geographic exposure of mammal richness hotspots of Iran to extreme climate change. Top: Distribution of functional group richness in the areas with mean annual temperature above the upper critical temperature threshold (mean UCT + sd: 29.6°C) in current time (left) and predicted in 2070 according to scenario RCP8.5 (right). Bottom: Distribution of functional group richness in the areas with total annual precipitation below the dryland threshold (200 mm/year) in current time (left) and predicted in 2070 according to scenario RCP8.5 (right)

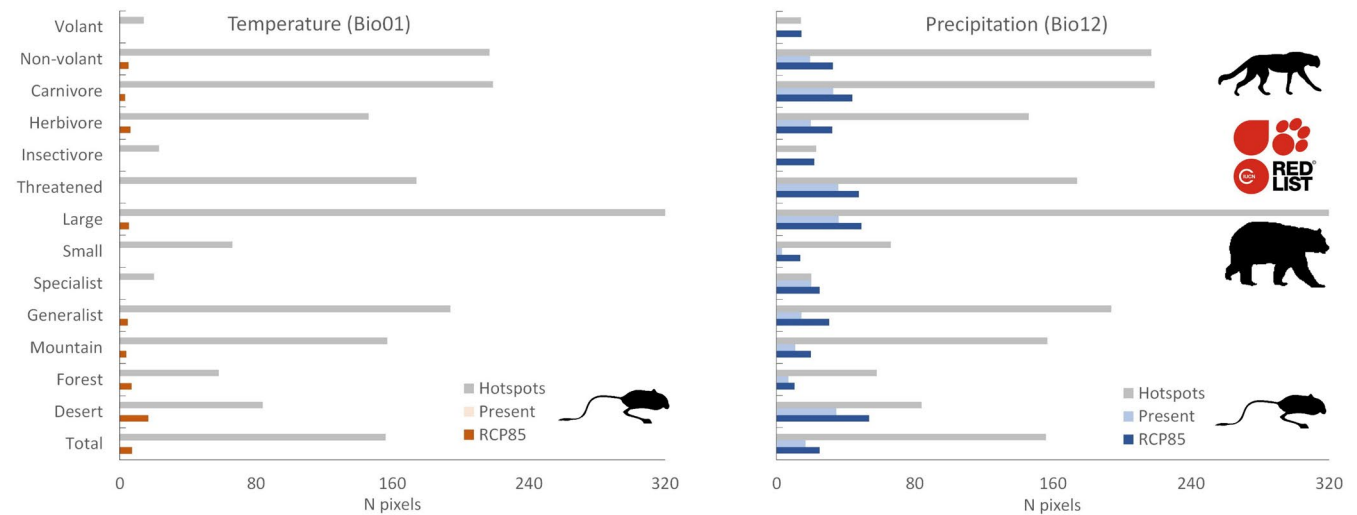


FIGURE 4 Quantitative exposure of mammal richness hotspots of Iran to extreme climate change. Left: Number of cells (pixels) of hotspots of 12 functional groups and threatened and total species (grey bar) and respective number of cells that are exposed to mean annual temperatures above the upper critical temperature threshold (mean UCT +sd: 29.6°C) in current time and predicted in 2070 according to scenario RCP8.5. Right: Number of cells of hotspots exposed to total annual precipitation below the dryland threshold (200 mm) in current time and predicted in 2070 according to scenario RCP8.5

(Figure 4 and Figure S5). The Central Basin contains the highest incidence of exposure across functional groups (Figure 3).

3.4 | Hotspot exposure to velocity of climate change

Climate change velocities strongly overlapped all diversity hotspots (functional groups, threatened species and total species). However, climate change velocity is projected to most strongly affect carnivores, large-bodied, specialist functional groups and threatened species under both RCP4.5 and RCP8.5 scenarios (Figure 5 and Figure S6). Functional groups were more exposed to areas with higher velocities of change in temperature relative to precipitation velocity.

3.5 | Protected areas, hotspots and exposure to climate extremes

In the present time, no single PA is exposed to temperatures above the UCT threshold (29.6°C), while for 2070, about 10.9% of the area of PAs will be. Currently, 65.6% of the area of PAs is located in drylands and 8.8% will be further exposed to expanding drylands (Figure S7). On average, 26.5% of the hotspot areas of the 12 functional groups and threatened and total species were represented in established PAs (Table 1). The specialist group is poorly represented in PAs (5.0%), while the carnivore and large-bodied groups and threatened species are better represented (all above 37.2%). By 2070, <10% of all the hotspots represented in PAs will experience temperatures above the UCT threshold. However, the desert functional group is predicted to be most exposed, with 10.5% of their threatened cells exposed to extreme temperature (Table 1). By 2070, large portions

(>50%) of currently protected hotspots of desert, carnivores and large-bodied functional groups will be exposed to reduced precipitation. Threatened species will be particularly exposed, with over 60% of the currently protected hotspots located in areas predicted to become arid (<200 mm/year precipitation) (Table 1).

4 | DISCUSSION

By using a generalized approach which aims at analysing the majority of species communities, we were able to identify the functional groups likely to be exposed to climate extremes in a highly vulnerable region. Exposure to climate change varied by functional group, with denizens of lowland areas more exposed to future climate change than mountain-dwelling functional groups.

4.1 | Exposure of functional groups to climate extremes

We found that the magnitude and velocity of the impacts significantly varied among functional groups, with highest exposure for carnivore, desert, large-bodied, specialist groups and threatened species. We found that the desert functional group will likely be the most exposed to the most extreme temperatures, in comparison with other functional groups. This is important and has been largely unrecognized. Desert species often occur at the limits of their thermal tolerance (Hetem et al., 2014), and the predicted climate changes may induce levels of thermal stress that could reduce their fitness and chance of survival (Moses et al., 2012). While groups' hotspots were most exposed to areas with higher velocities of temperature change, they were still projected to be

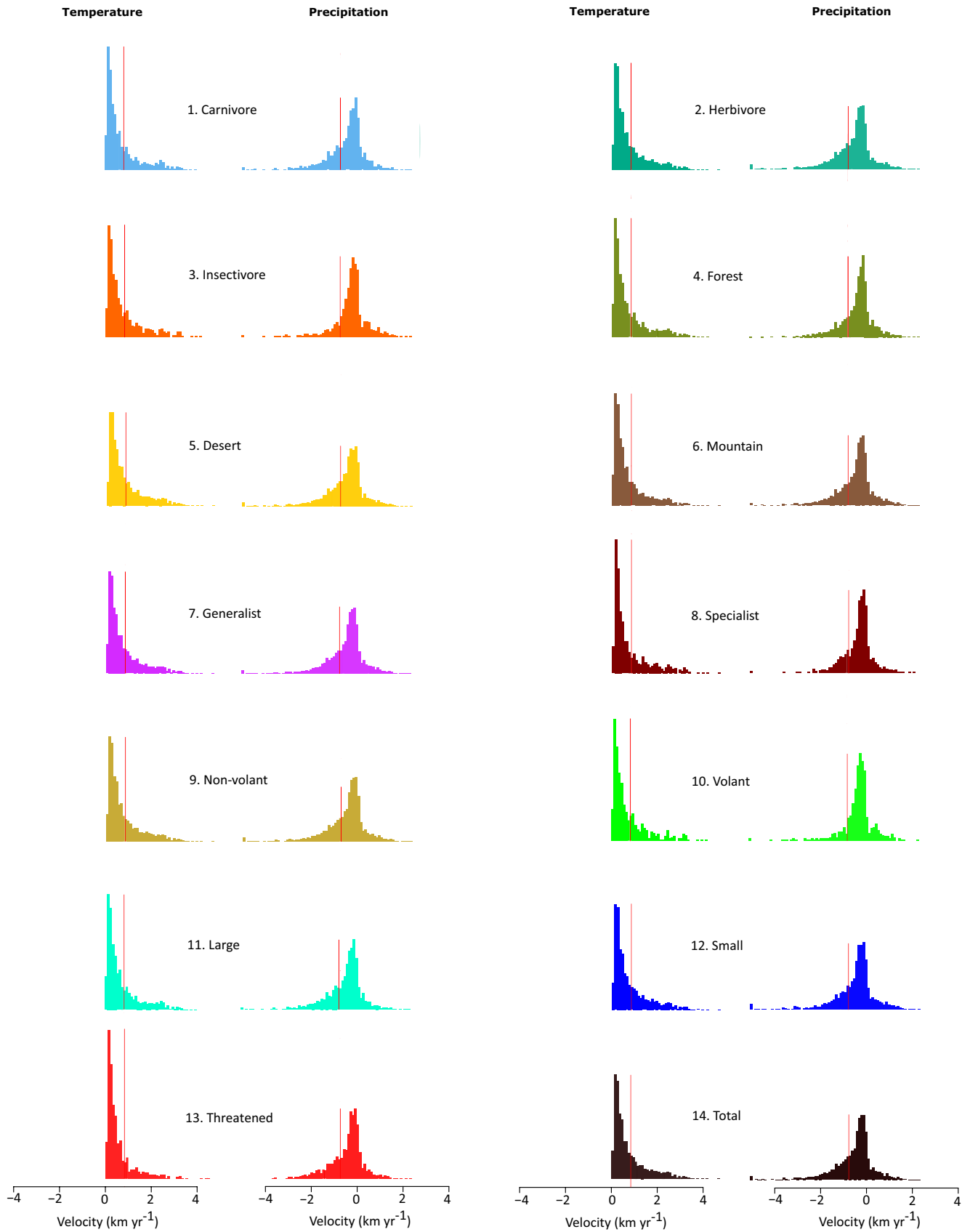


FIGURE 5 Predicted velocity of climate change in mean annual temperature (temperature) and mean total annual precipitation (precipitation) within the area of occupancy of each functional group, threatened species and total species according to RCP8.5 scenario. Histograms are averages of the velocity for RCP8.5 with respect to 19 global climate models. Vertical bars indicate the mean velocity for each group

exposed to extreme precipitation decline. Reduced precipitation already affects hotspots of carnivore, desert, large-bodied functional groups and threatened species, and projected future declines (from 40% in current range to 50% in 2070) may challenge species physiology via hydric stress (Chesson et al., 2004). Furthermore, climate change will probably impact indirectly desert species through declines in primary productivity (Chesson et al., 2004; Ward, 2016).

Large-bodied and threatened mammals are at the highest risk from predicted climate change. These two groups of species already strongly overlap, as 41% of large-bodied species are already threatened (Yusefi, Faizolahi, et al., 2019). The high risk for large mammals in Iran is in contrast with results from climate change projections in North Africa (Vale & Brito, 2015; Soutlan, Wikelski, & Safi, 2019), where small mammals were identified as the most vulnerable ones. In general, large body size has been identified as a key determinant of vulnerability to extinction (Verde Arregoitia, 2016). Large mammals may face additional challenges because of their intrinsic biological traits (Fuller et al., 2016) and because of their difficulties in sheltering from excessive heat and surviving extreme climate events (McCain & King, 2014). Furthermore, globally large mammals have faced dramatic range contractions and population declines over the last decades (Ripple et al., 2015), which make them a special case of conservation concern and emphasizes the importance of preserving remaining populations (Rondinini & Visconti, 2015).

We found that the levels of exposure of threatened species to precipitation decline were much higher (47.7%) in comparison with non-threatened ones (13.6%), the latter mostly represented by small-bodied functional group that included the vast majority (94%) of the species in this category. Contrasting results were found at the global scale, where exposure to precipitation decline was similar between threatened and non-threatened mammals (Ameca y Juárez et al., 2013). The distinct pattern here may be partly related to the location of the hotspots of threatened species, which range mostly in areas with precipitation levels already below dryland thresholds (Figure S5).

4.2 | Lowland species versus montane species

Most previous predictions of species vulnerability to climate change at large spatial scales (e.g. Maiorano et al., 2011, 2013; Pacifici et al., 2018) have shown that mountains where mammal species are more concentrated are likely to be at high extinction risk from climate change. This is mostly because there may be limited opportunities for upward movements in mountain-dwelling species. However, we found a strikingly opposite pattern and our estimates of exposure to climate change suggest more challenging climates for lowland areas than for mountains. Our results indicate that although the Alborz and Zagros mountain ranges hold more species and concentrate more hotspots of functional groups, the Central Basin lowlands will be at higher risk (Figure 2). Accordingly, the most exposed

functional groups to climate change are those inhabiting the low-elevation areas, especially the desert functional group. Despite the fact that the opposite pattern found here may relate with distinct methodology that we applied to determine climate risk areas (Maiorano et al., 2013 for instance, defined extreme as exceeding of average monthly temperature patterns from the mean of the 1961–1990 baseline period), our results emphasize the vulnerability of lowlands, which has been unreported from climate change impacts assessment conducted in arid regions (e.g. Soutlan et al., 2019).

Additionally, it must be noted that although the entire dry Central Basin is considered lowland in general, in fact it is topographically complex (with an elevational gradient over 4,000 m), which provides considerable climatic variation. Thus, low-laying topographically flat areas have a warm desert climate, while considerably colder and more humid climates can be found in higher elevations. This variability may provide refugia for local desert animals, buffering against the effects of climate change on their persistence (Ford et al., 2013). However, some species such as gazelles (*Gazella bennettii* and *G. subgutturosa*) are unlikely to move upwards in elevation given their adaptation to flat, open terrain. Conversely, climate refugia are likely unavailable for species living in disjunct mountain ranges across the Central Basin, including Pika (*Ochotona rufescens*), wild sheep (*Ovis gmelini* and *O. vignei*) and wild goat (*Capra aegagrus*), which already dwell in the upper elevational limits of available suitable habitat. In fact, a recent study (Malakoutikhah, Fakharan, Hemami, Tarkesh & Senn, 2020) using species distribution modelling showed that mountain species (wild sheep and wild goat) will lose more suitable habitats in future because of climate change (69% and 76%, respectively) than those located in lowlands (goitered gazelle will lose 55% of its suitable habitat by 2070). Yet, more studies are needed to better understand the capacity of both desert and montane species to respond climate change.

The findings of our study are alarming because the ability of mammals to track their preferred habitats and climatic niches in response to climate changes may be very limited (Morrison et al., 2018; Schloss et al., 2012) and have been identified as highly sensitive to climate-related environmental variations (Pacifici et al., 2017). Climate change velocity is predicted to be highest in arid lands (Loarie et al., 2009), with projections suggesting that 17% of the endemic mammals adapted to the warm deserts of the Afro-Arabian region will become extinct in 2050 due to climate change (Soutlan et al., 2019). Whether desert species have the capacity to colonize new habitats and survive under altered biotic conditions (e.g. prey availability) remains unknown.

4.3 | Implications for local conservation actions

Overall, these findings (3 to 7°C increase in mean annual temperature and 10% expansion in drylands) are alarming given that temperature increases of 2 to 3°C, for instance, have been predicted to cause massive species turnover (IPCC, 2018). A warming trend has already been observed over past decades across Iran (e.g. Tab ari

& Hosseinzadeh Talaei, 2011), but we are the first to report that the Zagros region is expected to experience the highest increases in temperature and decrease in precipitation. The southern slopes of Alborz and eastern-western slopes of Zagros (7.7% of the country) are also of special concern because local precipitation decrease could eliminate current humid conditions and become drylands. Southern Iran, particularly Mesopotamian region, is expected to experience temperatures above the UCT threshold in the future. Within the region, the critically endangered Persian fallow deer represent a major concern for conservation because the species is restricted only into two protected areas of Karkheh and Dez forest in this high-risk area (Yusefi, Faizolahi, et al., 2019). Since arid-adapted species are already near their thermal limits, even small increases in temperature may threaten them (Hetem et al., 2014; Khaliq et al., 2014 and references therein). Regionally, there are no suitable habitats left for species and increasing temperatures above the species tolerance will likely be detrimental for the species.

Although the largest precipitation decreases are not predicted in the Central Basin, but since the Central Basin average rainfall is already low (<200 mm/year), even a small decrease in precipitation could have catastrophic effects on its local biodiversity. Reductions in annual precipitation have caused decrease in abundance of large mammals (Ogutu & Owen-Smith, 2005) especially in arid regions (Heffelfinger et al., 2018). Central basin is home to many of Iran's most emblematic species, including cheetahs, leopards (*Panthera pardus*), bears (*Ursus arctos* and *U. thibetanus*), Onager, gazelles, wild sheep's and wild goats, which are at the same time threatened with extinction due to poaching, persecuting, habitat loss etc. (Yusefi, Faizolahi, et al., 2019). Management actions are needed to mitigate the effects of human threats, and to monitor population trends, particularly for the Asiatic cheetah and Onager, two species that have already lost most of their range and population (Rosenbom et al., 2015; Khalatbari et al., 2018).

The representation of hotspots within PAs is relatively high for most functional groups (26% in average), which suggests an alignment with the Aichi Targets (17% of terrestrial land protected; <https://www.cbd.int/sp/targets/>). Still, the hotspots of small-bodied species are underrepresented, probably resulting from the historically definition of PAs in Iran considering the protection of large-bodied and hunted mammals (Firouz, 2005). Since the highest concentration of functional groups' hotspots including highly exposed group of threatened species is found in the Alborz and Zagros mountains, establishment of additional PAs in these areas should be considered to alleviate the effects of climate change, especially given the overall low levels of protection of mountains worldwide (Elsen et al., 2018). Overall, these estimates of climate change impacts on this rich regional mammal diversity are obviously a major concern and we hope that our findings facilitate proactive conservation efforts.

4.4 | Methodological limitations and considerations

In this study, we applied an approach that allowed us to quantify the exposure of areas (and species assemblages occurring there) to

different dimensions of climate change. This approach was convenient as it allowed us to analyse the impacts of climate change without the need for complex ecological models or large datasets on species presence, and it was applicable to all species (Foden & Young, 2016; Garcia et al., 2014), which make it suitable to use in regions with limited distribution data, such as our case. However, due to the limitations of the approach adopted, our results should be considered carefully. First, the occurrence data used is based only on the current known species' ranges, which may be underestimated compared with potential ranges that can be identified by ecological models. Accordingly, identified ranges and richness hotspots (or species-rich areas) both in current time and in future might be smaller and different (Levinsky et al., 2007), which may affect the level of biodiversity hotspots impacted by climate change. Still, we have tried to avoid underestimation of species' ranges inherent in occurrence data by increasing the spatial scale to a resolution of 25 km × 25 km (Graham and Hijmans, 2006). Second, a strong input of uncertainty derives from future climate predictions and the need to address multiple pathways of climate evolution, as GCMs exhibit considerable variation among models, which can affect the accuracy of climate change assessments (Buisson et al., 2010). With that in mind, we have applied a multi-model ensemble average forecast technique (Loarie et al., 2009) and summarized uncertainty by mapping the upper and lower values of changes in the magnitude of climate change. Further, we calculated a mean of the velocity of climate change and its standard deviation of each GCM and pathway (results not shown), to account for their differences. Third, our approach is based merely on climate data, but impact analyses need to consider also other factors, such as land use change, biotic and abiotic factors and dispersal ability. Although climate variables are widely used as predictive variables in distribution modelling, there are many other factors contributing to species distributions (Bradie & Leung, 2017).

The assignment of species to pre-defined and arbitrary functional groups may represent a simplistic approach. First, it ignores all possible differences between species belonging to a single group (so it can influence the obtained results), and second, the exposure risk may be dependent on the number and type of functional traits and also on the number of functional groups (Petchev et al., 2004; Legras et al., 2018). The rationale for our approach grounds on the fact that predicting the impacts of climate change on simply defined groups (e.g. large mammals or carnivores) other than complex statistically derived groups is easier to interpret and use by conservation practitioners and may have more direct feedback (Foden & Young, 2016).

The estimation of the UCT was based on a limited dataset of 46 species with available data, which limits accurate UCT estimations (Khaliq et al., 2014). Lack of data on precise vulnerability thresholds associated with each trait is widely seen as a main drawback of trait-based vulnerability assessment approaches in climate change analyses (Pacifi et al., 2015). Still, our dataset included representatives of all mammalian orders within the study and thus the available data cover a substantial portion of the heat tolerances within the full dataset of studied taxa. Here, we collected the UCTs from the species level or from the closest member of the same species group

or sister species of the same genus. If data were only available for another species in the same genus, we used that to characterize a certain species with missing data. If data were available for more than one species in a genus, we used the data from those species that live in more similar habitats to characterize the missing species.

4.5 | Concluding remarks

The extreme changes in climate expected to occur in the coming decades will affect many species and regions particularly arid regions such as southwest Asia. This study provided the first quantification of the potential exposure of a large mammal assemblage in one of the most globally vulnerable regions to predicted change in climate extremes. Our results suggest more challenging climates for lowland species than for montane ones and considerable variation of potential vulnerability among functional groups, with highest risk levels for large and threatened species. We found that drought, rather than warming, is the factor that most likely will affect regional biodiversity in arid regions. Although our study is focused on Iran, the methodological approach followed is broadly applicable to other species and regions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The dataset needed to replicate the distribution models and statistical analyses is provided at <https://doi.org/10.5061/dryad.1c59zw3vj>. The dataset is embargoed until 05/05/2022.

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BIOSKETCH

Gholam Hosein Yusefi has a PhD from the University of Porto. This study is part of his PhD thesis (2014–2019) focused on the diversity and distribution of Iranian mammals. His main research interests include mammal's biogeography, systematics, ecology and conservation.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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