

Implications of exceeding the Paris Agreement for mammalian biodiversity

Valeria Y. Mendez Angarita  | Luigi Maiorano  | Chiara Dragonetti  |
Moreno Di Marco 

Department of Biology and
Biotechnologies "Charles Darwin",
Sapienza University of Rome, Italy

Correspondence

Valeria Y. Mendez Angarita and Moreno
Di Marco, Department of Biology and
Biotechnologies "Charles Darwin,"
Sapienza University of Rome, Italy.
Email: mendezvaleria.y@gmail.com and
moreno.dimarco@uniroma1.it

Abstract

The Paris Agreement settled to limit global warming to 2°C and possibly 1.5°C from pre-industrial times. However, little is known about the implications of such climatic goals for biodiversity once species' adaptability to new climatic conditions is accounted for. Here, we projected the bioclimatic space loss for mammalian communities across terrestrial biomes, under four alternative emission scenarios to year 2050, and evaluated the risk for taxonomic, phylogenetic, and functional biodiversity in each biome. The high-emission scenario (largely overshooting Paris limits) will lead to an average 34% bioclimatic space loss across biomes, surpassing critical levels in half of them (31 out of 63), including six biomes with high biodiversity content. Overall, these biomes account for an area at risk which is 10 times larger compared to that identified under low-emission scenarios. Under intermediate-emission scenario the loss is reduced to 28%, but two biomes with high biodiversity content will still be at risk. Achieving the 1.5°C target would reduce the average bioclimatic space loss to 19%, with only eight biomes facing critical levels of loss, none of which hosts high biodiversity content. These results highlight the biological risk of climate inaction and the consequences of exceeding Paris Agreement's climatic goals.

KEYWORDS

adaptation, biodiversity, biomes, climate change, conservation, emission scenarios, global change, mammals

1 | INTRODUCTION

Anthropogenic climate change is now affecting most of the biological and ecological processes on Earth (Scheffers et al., 2016) and its impact on terrestrial biodiversity is expected to surpass that of land-use change in the coming decades (Di Marco et al., 2019; Newbold, 2018; Pereira

et al., 2020). The response of the global community was laid out by the United Nations Framework Convention on Climate Change (UNFCCC) in the Paris Agreement, with the definition of a long-term goal "to hold the increase in the global average temperature to well below 2°C above pre-industrial levels and pursuing efforts to limit the temperature increase to 1.5°C" by the end of the century

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(United Nations, 2015). However, the world is still off track from reaching this goal, with the current climate policies leading towards a $+2.7^{\circ}\text{C}$ global warming by the end of the century (IPCC, 2021). While the Paris Agreement's goal has been delineated based on policy perspectives and the available scientific knowledge, little is still known about its implications for biodiversity (Hulme, 2016). A multi-taxa analysis has shown that achieving the 2°C target can reduce the number of species that will experience $>50\%$ change in their current bioclimatic space to one third compared to a business as usual emission scenario (Warren et al., 2018). The same analysis has shown that achieving a 1.5°C target can further halve that number. Yet, these measures of climate exposure do not account for species' sensitivity to climate change, i.e., their ability to persist (or not) in different climate conditions, and adaptive capacity, i.e., their ability to cope (or not) with the negative impacts of climate change (Foden et al., 2013).

Species can adapt to some degree of climate change via plasticity, adaptive and/or dispersal mechanisms (Cooper et al., 2015; Nogués-Bravo et al., 2018), but there are uncertainties around the degree of change that species are capable of tolerating (Pacifi et al., 2015). Moreover, it remains unclear whether the rate of current changes will be compatible with species adaptation capacity (Loarie et al., 2009; Trisos et al., 2020). In fact, assessing future climate impact on species is challenging for two main reasons. The first challenge consists in exploring future emission scenarios which are subject to inherent uncertainties (Riahi et al., 2017). The second challenge derives from estimating species response to climate change when adaptation capacity is unknown.

To deal with the first challenge, several socio-economic scenarios and General Circulation Models (GCMs) are typically considered, hopefully representing the full spectrum of uncertainty around future climate projections. The coupled Shared Socio-economic Pathways—Representative Concentration Pathways (SSP-RCPs) (O'Neill et al., 2014, 2017; van Vuuren, Edmonds, et al., 2011a) are used to represent different climatic outputs determined by alternative patterns of energy consumption, land use change, human population growth, technological innovation, governance and lifestyles (Hoegh-Guldberg et al., 2018). Furthermore, multiple GCMs have been developed to model spatially-explicit changes in climate from the past to the present, and to project changes into the future. These models are broadly used to represent future projections, derived as the climatic outputs of the emissions constraints delineated by the RCPs (Tokarska et al., 2020).

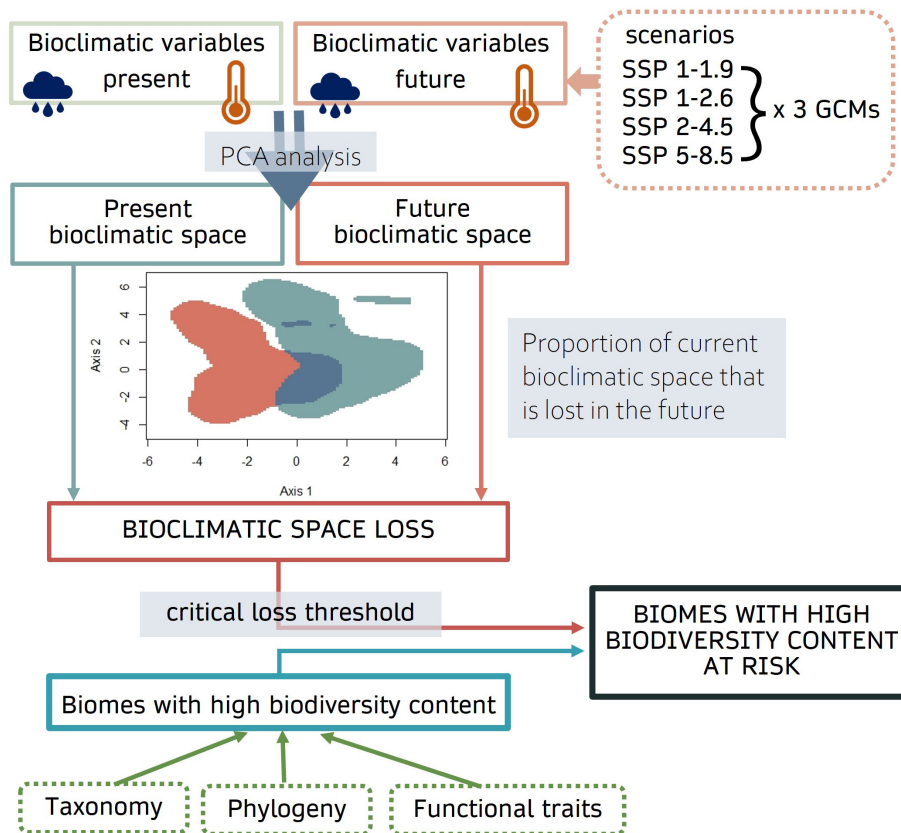
Overcoming the second challenge—estimating species response to climate change—is more difficult and cannot rely solely on correlative approaches, which often consider species as static, isolated entities (Araújo

et al., 2019). Species can adapt to some degree of climate change (Nogués-Bravo et al., 2018), but adaptation is reduced when multiple threats occur in synergy (Brook et al., 2008; Hoffmann & Sgró, 2011; Mantyka-pringle et al., 2012). Moreover, species responses to climate change can arise as a direct consequence of bioclimatic changes or as an indirect consequence of the complex interactions between climate, species' ecology, and their environment (Braga et al., 2019; Cooper et al., 2015; Pacifi et al., 2018; Parmesan, 2006). Many studies have investigated species exposure to future climate change (e.g., Newbold, 2018; Trisos et al., 2020; Warren et al., 2018), but species sensitivity to it (i.e., their ability to tolerate climatic variations) remains only partly understood (Foden et al., 2013; Pacifi et al., 2015). Assessing how species bioclimatic envelopes (the position and range of bioclimatic variables species live in) have responded to past climate change, is a promising way to measure species ability to cope with climate change (Di Marco et al., 2021; Maiorano et al., 2013). Species that were able to tolerate past change without facing a substantial reduction in their bioclimatic envelopes might be able to cope with future climate change, tolerating exposure to new conditions. Instead, species that have experienced a reduction of their bioclimatic envelope (i.e., bioclimatic space loss) under past climate change might be less able to adapt to new conditions. This is an important consideration to evaluate the full ecological implications of climate mitigation policies.

Here we aimed to better understand the impact of climate change on multiple aspects of mammalian biodiversity, comparing climate scenarios that meet the Paris Agreement to those that do not. Our goal is to investigate the relevance of different climate mitigation strategies for multiple aspects of biodiversity, not explicitly considered during the definition of such strategies, allowing to better understand the implications of climate mitigation policy at the ecosystem level.

We adopted a comprehensive approach to account for the impact of climate change on three dimensions of biodiversity: taxonomic (total and endemic), phylogenetic, and functional. While taxonomic diversity is a proxy of species richness, phylogenetic diversity reflects the degree of genetic divergence between species, being a proxy of evolutionary history, and functional diversity represents the ecological complexity of a given species assemblage, as defined by species functional traits (Safi et al., 2013; Thuiller et al., 2015; Zupan et al., 2014). In addition, endemic species in each region represents unique elements of biodiversity which might be globally lost if environmental conditions in the region change. We focused our analysis on terrestrial mammals as they are broadly distributed across all regions of the world (except for Antarctica), having colonized almost all the Earth's

FIGURE 1 Conceptual framework of the methodology adopted to measure bioclimatic space loss and its effect on biome biodiversity. First the bioclimatic variables are measured inside each biome and used to delineate current and future bioclimatic space (across four Shared Socio-economic Pathways and three Global Circulation Models) in the same PCA space. Second, a measure of bioclimatic space loss is derived as the difference between current and future bioclimatic space, separately for each biome/scenario. Third, for each biome, taxonomic, functional, and phylogenetic diversity are calculated considering the species occurring in the area. Finally, biomes with high biodiversity content at risk are identified.



habitats due to their great adaptation capacity. Furthermore, mammals play key ecological roles including predation, seed dispersal and grazing (Hoffmann et al., 2011), and provide important benefits for human livelihoods, having a long history of domestication and interrelation with human communities (Clutton-Brock, 2015). Mammal species also include many apex consumers, the role of which is essential for regulating ecosystem functions (Estes et al., 2011).

2 | METHODS

We focused our analysis on 63 terrestrial biome-realms of the globe (hereafter “biomes”; Olson et al., 2001), combining 14 biomes across 7 biogeographic realms, with the exclusion of Antarctica. We focused our analysis on biomes instead of individual species to evaluate how biogeographically distinct communities of mammals might be affected by climate change. We evaluated the impact of climate change on mammalian biodiversity in each biome, by assessing how much climate space will be lost under different emission scenarios, across different climatic models, in terms of the present-day bioclimatic space that is expected to be lost by 2050. For each biome, we measured the bioclimatic space lost by 2050 compared to the present-day conditions. We defined biomes at high climate risk as those facing a critical bioclimatic loss of

>30%, measured in terms of non-analogue climate, which was found to lead to high risk of bioclimatic niche loss for mammals in the past (Di Marco et al., 2021). This threshold comes from a partial effect plot of climatic stability and the probability of species to experience climate niche change and defines a limit of bioclimatic space loss, averaged across terrestrial mammals, beyond which species have a high probability of undergoing niche shrink. In other words, this parameter defines the magnitude of climate change beyond which species have not been able to adapt in the past, resulting in a reduction in their niche breadth. We then measured the biodiversity content of each biome, to evaluate areas of high biodiversity value that face high risk under different scenarios (Figure 1).

2.1 | Climate data

We delineated the bioclimatic space available for each biome using 10 variables which have previously been successfully used to project future climate risk for mammal species (Visconti et al., 2016): Annual Mean Temperature, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Annual Precipitation, Precipitation of Wettest

Quarter, Precipitation of Driest Quarter, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter.

For present-day climate, we used Worldclim 2.0 (Fick & Hijmans, 2017) data covering the period 1970–2000, while for future climate we used the data representing 2050 (mean for 2041–2060) from the same database. We considered four scenarios corresponding to different warming levels: SSP1-1.9*, SSP1-2.6, SSP2-4.5 and SSP5-8.5. The selected scenarios have been chosen to represent different possible pathways of future climate conditions associated with socio-economic strategies. Scenarios SSP1-1.9* and the SSP1-2.6, are meant to represent the warming limits proposed by the Paris Agreement (respectively, no more than 1.5 and 2°C above pre-industrial level; Tebaldi et al., 2020; van Vuuren, Edmonds, et al., 2011a, van Vuuren, Stehfest, et al., 2011b). As scenario SSP1-1.9 was not available in Worldclim, we approximated it by adopting the climatic conditions of the scenario SSP1-2.6 in year 2030. This projection, which we named “SSP1-1.9*,” represents a lower-warming scenario with lower GHG emission compared to the one represented by SSP1-2.6 in 2050. The two projections (SSP1-2.6 in year 2030 and year 2050), differs by around 0.5°C warming (Tebaldi et al., 2020), which reflects the difference in the outputs of the radiative forcing between RCP 1.9 and RCP 2.6 in year 2050 (O'Neill et al., 2016). Scenario SSP2-4.5 projects a warming of around 2.1–3.5°C above pre-industrial (IPCC, 2021; Thomson et al., 2011). The business-as-usual scenario SSP5-8.5 corresponds to the pathway with the highest greenhouse gas emissions, and temperature increase is projected to be between 3.3 and 5.7°C (IPCC, 2021; Riahi et al., 2011). For each scenario we used three different Global Circulation Models (GCMs), representing uncertainty behind future climatic predictions. We selected BCC-CSM2-MR (Wu et al., 2019), MIROC6 (Tatebe et al., 2019), and IPSL-CM6A-LR (Boucher et al., 2020), based on their high degree of independence (i.e., models created under different frameworks) in CMIP6 (Brunner et al., 2020; Knutti et al., 2013).

2.2 | Estimates of bioclimatic space loss under different emission scenarios

Following Iwamura et al. (2010) and Di Marco et al. (2021), we measured the bioclimatic space loss for each scenario as the proportion of current bioclimatic space that is lost in the future. For each biome, we considered all scenarios versus GCMs climate combinations and calculated the average bioclimatic space loss and its standard deviation under each scenario (averaging all GCMs). To represent the bioclimatic space of each biome we considered the first two axes of a Principal Component

Analysis (PCA) run over all the bioclimatic variables, current and future (separately for each emission scenario in each biome), projecting current and future variables in the same PCA space. We evaluated the performance of the PCA in terms of the cumulative variance explained by the two main components (Broennimann et al., 2012). The bioclimatic space of each biome was then defined using a kernel density function of 95% around occupied cells in the PCA space, which excluded climatic conditions only rarely observed. We divided the environmental space defined by the PCA axes into a grid of 100 × 100 cells (Broennimann et al., 2012), each cell representing PCA scores derived for a vector of bioclimatic conditions, and converted into two Principal Component axes. The overall bioclimatic space of projection for the PCA was derived from the current and future climate conditions registered within the biogeographical realm where a biome is located (separately for each emission scenario). This way we could determine the change in bioclimatic space of the biome within the biogeographical context of reference. All analyses relative to the bioclimatic space were done using the “Ecospat” package in the platform R (Di Cola et al., 2017; R Core Team, 2020).

Finally, we adopted a “critical loss threshold” of 30% to define biomes “at risk,” as this is the threshold beyond which mammal species in an area have faced high risk of undergoing niche shrink, based on the work of Di Marco et al. (2021) on the relation between bioclimatic space loss and changes in terrestrial mammals species' climate niche since mid-Holocene. Hence, such metric is not a species-specific indicator, rather a generalized parameter that reflects the past adaptation capacity of terrestrial mammals to climatic change.

2.3 | Measuring the biodiversity content of each biome

To represent patterns of biodiversity within each biome, we considered three dimensions of mammalian biodiversity: the taxonomic (both total and endemic), phylogenetic, and functional diversity. As a first step, we created a matrix of “biome by species,” representing the distribution of each species in each biome. We retrieved the distribution range maps of 5598 species of terrestrial mammals from the IUCN Red List (IUCN, 2019), and overlapped each map with the map of biomes (Olson et al., 2001) to estimate the proportional overlap of each species with each biome. We considered a species to be present in a biome when at least 5% of its range was included in it. In this way we excluded from a biome species whose presence was only marginal and more subject to uncertainty in underlying distribution data.

We represented taxonomic diversity as the total number of species within a biome (i.e., measuring regional species richness or “gamma diversity”). Additionally, we measured the number of endemic terrestrial mammal species in each biome. We considered a species to be endemic to a biome if its range overlapped by at least 95% with the biome's area (Table S1). We then represented phylogenetic diversity by performing a phylogenetic eigenvector analysis (Diniz-Filho et al., 1998), following Brum et al. (2017). We extracted 16 eigenvectors from a phylogenetic tree in the dataset PHYLACINE (Faurby et al., 2018), each representing orthogonal axes of the phylogenetic distance among species. To obtain a map of phylogenetic diversity in each biome, firstly, we split the eigenvectors into 5% quantiles, generating 20 groups of species for each eigenvector. Then we determined the number of “phylogenetic groups” in each biome, based on the species association with biomes and their position in separate “eigenvector groups.” The result is a unique set of values per each biome that represents its overall phylogenetic diversity.

We estimated the functional diversity of each biome following Brum et al. (2017), as the combination of 14 functional traits for each species: adult body mass, adult body length, maximum longevity, female maturity, age at first reproduction, gestation length, litter size, litter per year, weaning age, neonate body mass, diet breadth, trophic level, activity cycle and habitat breadth. Variables used to define the functional diversity represent species' resource use and life history traits and have been selected for having sufficient data coverage (Brum et al., 2017). Data were derived from the COMBINE database (Soria et al., 2021). We used the imputed version of the dataset, where missing data have been imputed using a machine learning technique accounting for biological and phylogenetic relationships among species. We verified that the imputation had no noticeable effect on our results (see Supporting Information materials S1). To assess the number of “functional groups” in each spatial unit, quantitative variables were processed following the same procedure used for phylogenetic eigenvectors, where values are split into 20 groups adopting a 5% quantiles approach. Groups for categorical variables, instead, were based on the individual category levels. Functional diversity for each biome was measured based on the number of functional groups represented by the species present in it, across all life-history traits. We measured the value of each biodiversity metric in each biome, and we also derived “weighted” measures of diversity, dividing each of the diversity values by the biomes' area (measured as $\log_{10} \text{ km}^2$, using an equal-area Sphere Mollweide projection) and scaled them such that the highest values equal one. This way, we accounted for both the absolute biodiversity content of each biome and the relative content, irrespective of area size. We identified biomes

with high biodiversity content as those in the top quartile according to one or more of the biodiversity metrics. We also performed a sensitivity analysis by defining biomes of high biodiversity content as those with above-median biodiversity values. Finally, we highlighted biomes in the top quartile of biodiversity value according to multiple metrics and facing high climate risk (i.e., biomes at risk) when considering the critical bioclimatic loss threshold.

3 | RESULTS

3.1 | The bioclimatic space loss of the terrestrial biomes

The first two axes of the PCA explained an average 81.9% of the bioclimatic variability of each biome, ranging from 74.2% to 89.4% across all scenarios. Bioclimatic space loss (i.e., the portion of bioclimatic space lost by 2050 in each biome) varied depending on the scenario, always increasing from scenario SSP1-1.9* to scenario SSP5-8.5, and it was substantial even under the lowest emission levels, with an average loss of 19% (range 7%–48%) under scenario SSP1-1.9*, and 24% (range 10%–61%), under scenario SSP1-2.6. Intermediate and high emission levels lead to high and very high loss of 28% (range 9%–67%) and 34% (range 17%–75%) under scenarios SSP2-4.5 and SSP5-8.5, respectively. Our results were not dependent on biome size, as Pearson's correlation between biome's area size and bioclimatic space loss was below 0.3 under all the projected scenarios (Table S2).

Despite differences in overall levels of risk, the geographical patterns of bioclimatic space loss were similar across scenarios (Figure 2), with the highest values found in North America, India, equatorial regions, and northern Australia. Areas of low relative loss across scenarios instead were in the Middle East, North Africa, and central Asia.

We also considered the uncertainty behind our estimates of bioclimatic space loss, as represented by the standard deviation of values derived from different GCMs (Figure S1) and found that the correlation between standard deviation and biome size is low and not significant under any of the projected scenarios (Table S3); this means that small and large biomes had similar uncertainty around climatic projections. We also found that higher standard deviation did not match high values of bioclimatic space loss, but there were a few exceptions in the Nearctic Tropical and subtropical dry broadleaf forest, the Indomalayan Flooded grasslands and savannas and the Indomalayan Mangroves. Therefore, our estimates of high bioclimatic space loss for these areas come with high uncertainty.

We observed that the bioclimatic space loss is lower for biomes characterized by seasonal variability and/or moist

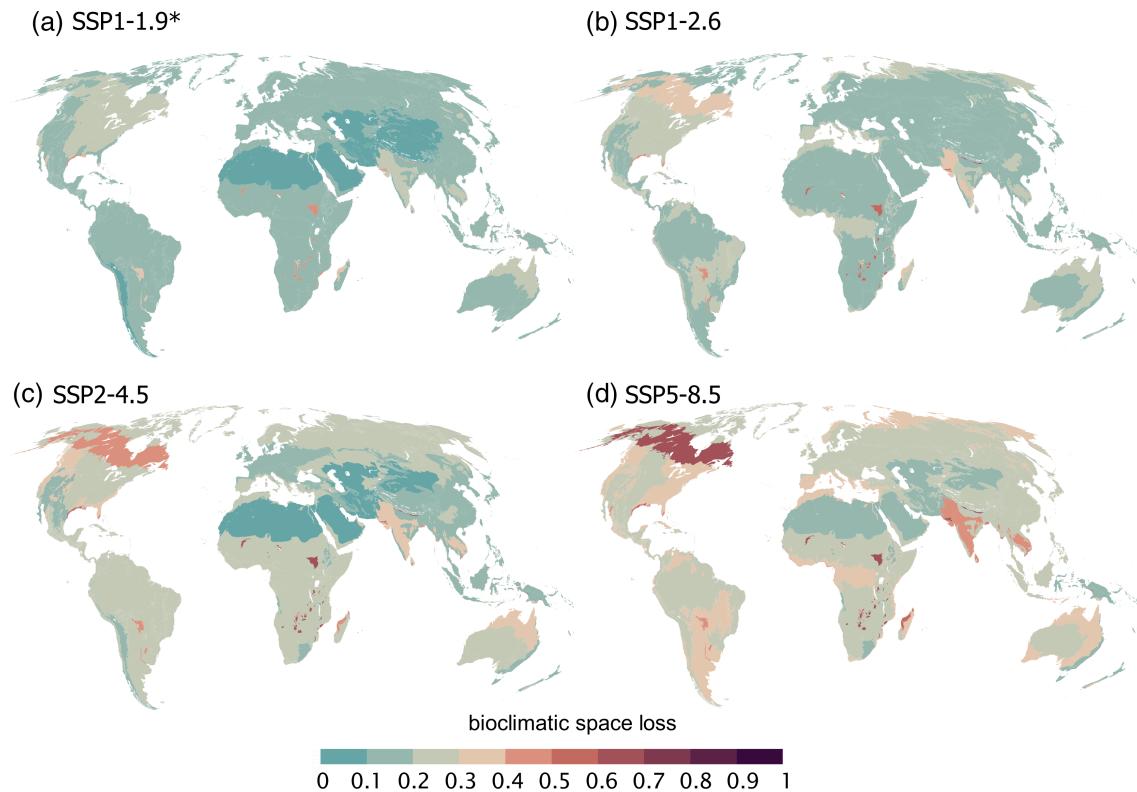


FIGURE 2 Maps of the bioclimatic space loss of the terrestrial biomes under four emission scenarios, projected for the year 2050 (compared to the reference period 1970–2000): (a) scenario SSP1-1.9*, (b) scenario SSP1-2.6, (c) scenario SSP2-4.5 and (d) scenario SSP5-8.5.

climate (i.e., Montane grasslands and shrublands, Temperate coniferous forest and Temperate broadleaf and mixed forest), while it is higher for biomes characterized by a dry climate and precipitation unevenly distributed during the year (rain season), for instance: Flooded grasslands and savannas, and Mangroves (Figure 3a). Flooded grasslands and savannas was the only biome type retaining very high bioclimatic space loss (on average > 35%) under all scenarios and in each realm. Instead, the Mediterranean forests, woodlands and shrublands were found to be highly sensitive to the projected scenario, with high bioclimatic space loss under scenarios SSP5-8.5 (on average 32%) and low loss under the SSP1-1.9* scenarios (on average 18%).

Indomalayan was the biogeographic realm with the highest average projected loss (22%–41% depending on the scenario), followed by the Afrotropic (loss between 22% and 38%) and the Nearctic (loss between 23% and 37%). The Palearctic and the Oceanian, respectively the largest and the smallest realms in terms of land area size, had the lowest average risk (Figure 3b).

3.2 | Climate risk for biomes with high biodiversity content

We found that 24 out of 63 biomes have high biodiversity content (i.e., having a diversity value in the top-quartile)

for at least one dimension of biodiversity (taxonomic, functional, or phylogenetic; Figure S2). These biomes cover 52.2% of the terrestrial globe (excluding Antarctica). While eight biomes (6.8% of the study area) were important for just one dimension, 10 biomes (39% of the study area) were important for two dimensions, and six biomes (6.5% of the study area) were important for all of them. Biomes where there is an overlap of high values for the three dimensions of biodiversity are mainly Afrotropical and Neotropical, with the only exception of the Palearctic Temperate coniferous forests.

We identified biomes facing high climate risk (i.e., biomes at risk), and found that about half of all biomes (31 out of 63) are at risk according to the most pessimistic scenario SSP5-8.5, while 17 remained at risk also under scenario SSP2-4.5. The biomes that were at risk under scenario SSP5-8.5 contain 3153 species (56% out of the 5598 mammalian species analyzed), and an average of 169 phylogenetic groups and 146 functional groups each (Table 1). The most optimistic scenarios, SSP1-2.6 and SSP1-1.9*, include 12 and 8 biomes at risk, respectively. In other words, the number of biomes projected to face threshold-levels bioclimatic space loss is 1.5 times higher under scenario SSP1-2.6 compared to SSP1-1.9*, and 4 times higher under scenario SSP5-8.5. Biomes at risk under scenario SSP1-1.9* represent less than 1% of the terrestrial globe (compared to 28% under

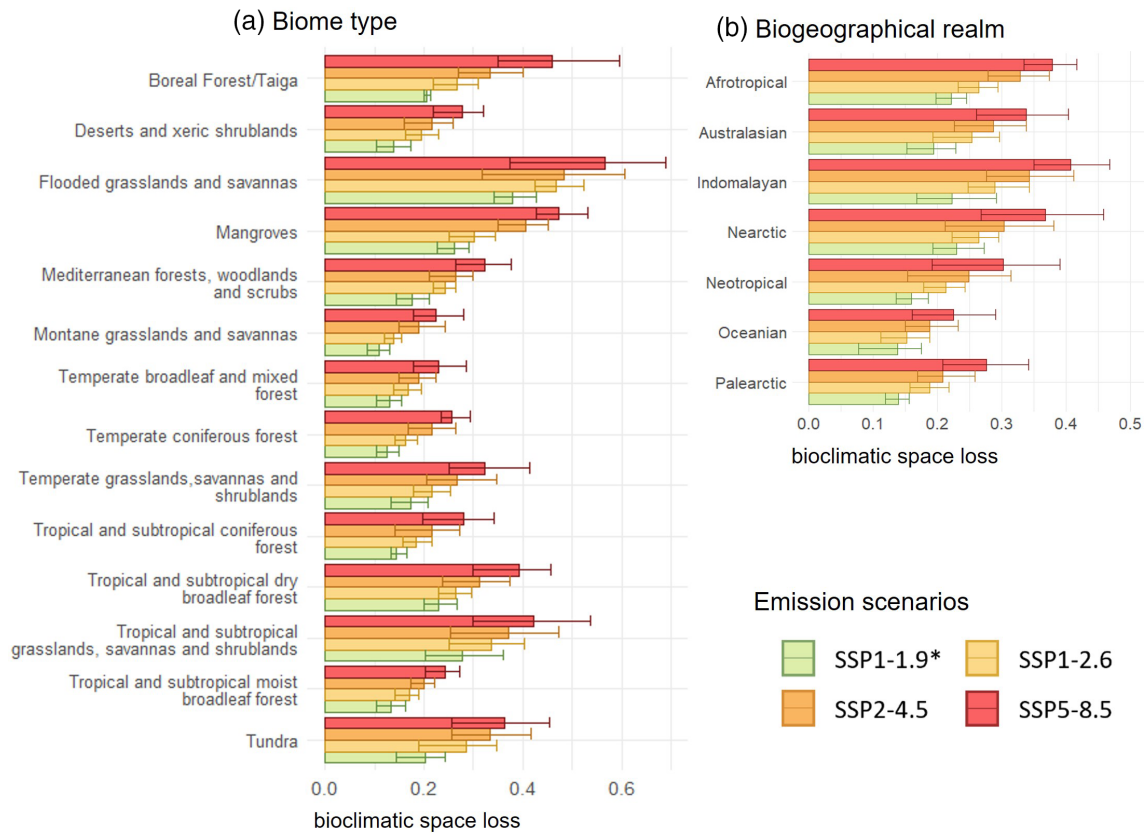


FIGURE 3 Bioclimatic space loss across (a) biome types and (b) biogeographical realms under four emission scenarios (SSP1-1.9*, SSP1-2.6, SSP2-4.5 and SSP5-8.5). Values represent the average bioclimatic space loss across biomes of the same type or belonging to the same realm.

TABLE 1 Total number of different mammalian species, average number of species, number of endemic species and average number of phylogenetic and functional groups in the biomes facing high climate risk under four emission scenarios (SSP1-1.9*, SSP1-2.6, SSP2-4.5 and SSP5-8.5).

	Number of species	Average number of species	Number of endemic species	Average number of phylogenetic groups	Average number of functional groups
SSP1-1.9*	251	31	22	125	116
SSP1-2.6	364	36	22	132	119
SSP2-4.5	989	67	83	146	133
SSP5-8.5	3153	128	434	169	157

scenario SSP5-8.5) and contain 251 different mammalian species (<5% of the total) with an average 125 phylogenetic groups and 116 functional groups. We found a relatively small overlap between the biodiversity content of the biomes and climate risk (Figure 4), even if, as expected, the overlap increased proportionally across scenarios. Specifically, of the 31 biomes facing high climate risk under scenario SSP5-8.5, only six were found to have high biodiversity content. Two of these biomes—the Afrotropical Tropical and subtropical moist broadleaf forest and the Neotropical Tropical and subtropical dry broadleaf forests—have top values for

all three dimensions of biodiversity, while one—the Indomalayan Tropical and subtropical dry broadleaf forests—has top values of phylogenetic and functional biodiversity.

Under scenario SSP2-4.5 the risk for biodiversity rich biomes is drastically reduced and just two biomes of high biodiversity content are projected to face high climate risk. The most optimistic scenarios, SSP1-2.6 and SSP1-1.9*, reduce the number of biomes of high biodiversity content at risk to one and zero biomes, respectively. These results demonstrate that overshooting the 1.5°C goal of the Paris agreement generates substantial risk

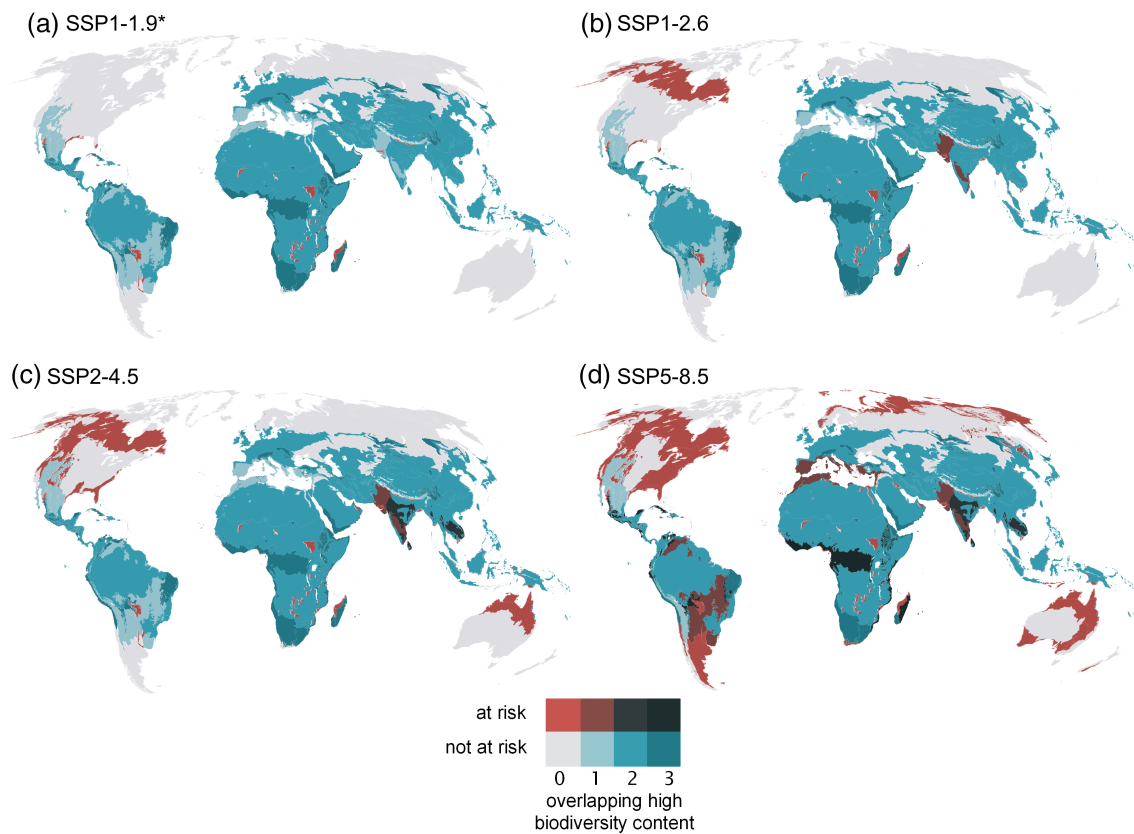


FIGURE 4 Bivariate map of biodiversity content of biomes and climate risk. Biomes' biodiversity content and their climate risk under four emission scenarios—(a) scenario SSP1-1.9*, (b) scenario SSP1-2.6, (c) scenario SSP2-4.5 and (d) scenario SSP5-8.5. Biomes are colored based on the overlap between high biodiversity content for one or more dimensions (taxonomic, phylogenetic and/or functional diversity are considered equal) and whether they are facing high climate risk (bioclimatic space loss above 30%).

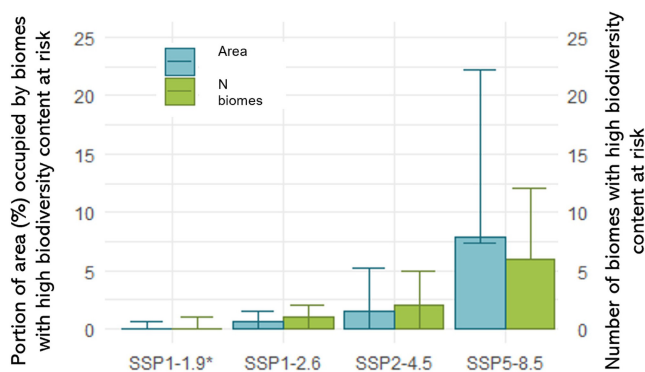


FIGURE 5 Number of biomes with high biodiversity content facing high climate risk, and their respective area. Number of biomes and their area, expressed in percentage, is represented across different emission scenarios (scenario SSP1-1.9*, SSP1-2.6, SSP2-4.5 and SSP5-8.5). Height of bars represent the mean number of biomes at risk (green), or their area (light blue), among three alternative Global Circulation Models. Error bars represent the minimum and maximum number of biomes at risk, or their area.

for biodiversity rich biomes. Moreover, even in the most optimistic Paris scenario, there is still some risk to biodiversity for example in the Afrotropical Tropical

and subtropical dry broadleaf forest, which contains 20 biome-restricted (endemic) species.

The increase in number of biomes at risk, among those hosting high biodiversity, corresponds to a 10-fold increase in the area at risk (Figure 5). In fact, while 0.7% of the total study area is both highly diverse and at risk under scenario SSP1-2.6, 7.9% become at risk under scenario SSP5-8.5. Interestingly, while the number of biomes with high biodiversity content at risk is doubled between scenario SSP1-2.6 and SSP2-4.5 (intermediate emission), and again doubled between scenario SSP2-4.5 and SSP5-8.5 (high emission), the area at risk gets five times larger each time. This same trend was observed even when biomes with high biodiversity content are selected as those in the top two quartiles, rather than just the first quartile (Figure S3).

4 | DISCUSSION

We evaluated the potential future impact of climate change on mammalian biodiversity across biogeographic assemblages, accounting for the level of bioclimatic space

loss that might trigger negative species response. Our results show that the impact of climate change on biomes increases consistently with higher emission scenarios, and so does the impact on areas of high biodiversity value. We found that terrestrial biomes will experience moderate to high change in their bioclimatic space in year 2050 under all emission scenarios, including the most optimistic one. However, our results highlight that there are substantial biological risks to exceeding warming limits set under the Paris Agreement. In fact, if global warming is kept below 1.5°C above pre-industrial levels, as represented by scenario SSP1-1.9*, the bioclimatic space loss is expected to halve compared to the highest emission scenario. This risk becomes higher if global warming reaches 2°C above pre-industrial levels by the end of the century (scenario SSP1-2.6); in this case, biomes are expected to lose 5% more of their bioclimatic space.

We measured the bioclimatic space loss of each biome as the overlap between their current and future bioclimatic space under the assumption that a biome's current bioclimatic space indirectly reflects the niche requirement of the species it hosts—in other words, we assumed that current species' realized climatic niche is not merely determined by species climatic tolerance but also by the effect that climate has on the ecological requirements of the species (for instance, seasonal resources availability). Additionally, we assumed that future changes in the bioclimatic variability inside a biome will affect species ecological requirements. In fact, biomes are frequently used to represent large-scale changes in biodiversity (Beyer et al., 2020; Iwamura et al., 2010; Loarie et al., 2009) and changes affecting a biome are expected to also affect the community of species that are adapted to its peculiar ecosystem characteristics. In this sense our results are not meant to assess which are the most threatened species, as species-specific responses to future climate are not predicted here. Instead, they describe biomes in which mammalian communities are more likely to undergo climatic niche shrink due to the magnitude of bioclimatic space loss.

Our results on geographical patterns of climate risk confirmed those from previous studies (Beyer & Manica, 2020; Iwamura et al., 2010; Loarie et al., 2009; Trisos et al., 2020), as we found biomes with low seasonal variability, such as the Tropical and subtropical dry broadleaf forest, are expected to experience major bioclimatic space loss. Instead, biomes with high seasonal variability, such as Temperate coniferous forests and Temperate broadleaf and mixed forests, tend to experience lower bioclimatic space loss. This explains why equatorial regions characterized by small temperature oscillations, both in time and space, are projected to face relatively high bioclimatic space loss, compared to temperate regions, despite lower magnitude of warming. This results in higher

potential climatic impact for tropical species, that also have narrower range size due to the narrow climate variability to which they are exposed (Stevens, 1989). These species occur close to their upper realized thermal limits throughout their geographic range (Trisos et al., 2020) and are considered to be particularly sensitive to future warming (Williams et al., 2007). On the other hand, our results show that biomes that occupy areas of large altitudinal gradients (high geographical variability), such as Montane grasslands and shrublands, are predicted to face lower bioclimatic space loss. However, even small bioclimatic space loss might determine a risk for species occupying these biomes, due to their limited geographic distribution and their isolation (Elsen & Tingley, 2015). Interestingly, biomes characterized by the succession of a dry and a wet season and precipitations unevenly distributed during the year have been found to have high bioclimatic space loss. This is the case of the Mangroves and the Flooded grasslands and savannas biomes, which have shown high climate risk even under the lowest emission scenarios. This finding is coherent with the fact that climate change is expected to increase the extent of arid zones in the future (Asadi Zarch et al., 2017).

At the same time, our results show some important differences with past works, for example for Tropical and subtropical coniferous forest and Tropical and subtropical moist broadleaf forest, which we found to face low climate risk. Iwamura et al. (2010) found mayor climate instability in the West of Amazon basin, Mora et al. (2013) found that the tropics will experience the earliest emergence of historically unprecedented climates, and Trisos et al. (2020) found that the Amazon is among the areas that will experience the greatest abruptness of exposure to climate change. We believe that these differences with our results derive, at least in part, from the different methodologies applied in our study compared to others. In fact, Iwamura et al. (2010) used smaller spatial units (i.e., ecoregions) and scenario projections compared to us, while Trisos et al. (2020) observed the maximum climate exposure after year 2060, a timeframe beyond that of our projections. Instead, Mora et al. (2013) investigated the climate departure dividing the locations in an equal-area grid, while we used biomes as spatial units (each having different size). There is increasing evidence that many biomes are already on a trajectory of extensive compositional and structural changes due to climate change (Dobrowski et al., 2021). Here we showed that the magnitude of such change might pose high risk to mammal species living in the biome, making them unable to adapt to abrupt shifts in climatic conditions.

Coherently with previous works, we found significant correlation across multiple biodiversity metrics (Brum et al., 2017), especially between phylogenetic and functional

diversity. In addition, the correlation across biodiversity metrics is weaker when looking at biomes with high biodiversity value, which typically exhibit low overlap across values for the three dimensions of biodiversity. This geographical divergence, observed also in other studies (Brum et al., 2017; Pollock et al., 2017; Sibarani et al., 2019), demonstrates the importance of considering multiple biodiversity facets. Overlooking phylogenetic and functional diversity neglects the role of the genetic pool of species assemblages on biodiversity conservation from one side (Pollock et al., 2017), and the ecological properties of the environment from the other (Mammola et al., 2021). Considering just taxonomic species richness could lead to overlooking areas of high evolutionary and/or ecological diversity which might be at risk from climate change, as it is the case of the Afrotropical Flooded grassland and savannas and the Neotropical Tropical and subtropical coniferous forest.

Among biomes of high biodiversity importance, we found that only a few faced high climate risk (10.5% of biomes, covering 8% of terrestrial globe, according to the highest emission scenario). This result is coherent with Iwamura et al. (2010), who found that the ecoregions of low bioclimatic space loss largely overlap with the areas known for their high biodiversity. However, even a few highly biodiverse biomes at high risk might represent a crucial challenge for global biodiversity conservation, for example, our results showed that even under a Paris-compliant scenario up to 22 endemic species are found in biomes at risk (hence facing risk of global extinction).

Importantly, we found that meeting the Paris goal of 2°C would reduce the number of biomes at risk by six-fold compared to the most pessimistic scenario, and the area at risk by 10 times. Additionally, meeting the Paris goal of 1.5°C would prevent any biome of high biodiversity importance from facing risk of high climate risk. Biomes with high biodiversity content that will benefit the most from climate mitigation policies are found in Indochina and India, the west coast of Madagascar, the Congo basin and central South America. It must be noted that these biomes are found in areas where major landscape changes, due to anthropogenic land use, have also been produced in the last few decades and are projected to increase under some of the scenarios we analyzed (SSP2 and SSP5), (Baisero et al., 2020; Newbold, 2018). Other studies have highlighted that the projected risk of warming is in general expected to be greater for most invertebrates, plants, amphibians, and reptiles than for mammals owing to the slower dispersal rates of the former groups (e.g., Beyer & Manica, 2020; Warren et al., 2018). Besides, it has been found that anthropogenic-induced climate change has a great potential to cause abrupt disruptions in ecological assemblages, which is not evident when focusing on individual temporal

snapshots (Trisos et al., 2020). This means that the impact of climate change is projected to be systemic and acute, rather than chronic and specific.

Here, we aimed at forecasting mammal biodiversity risk from climate change, based on the level of change to which species assemblages in each biome will be exposed, and the sensitivity of terrestrial mammals to past climate change. This was possible due to knowledge on the impact of past climate change on species niches. A key point in achieving these findings, has been the integration of empirical data on species sensitivity (i.e., their capacity to tolerate some degree of change) to past climate change to models projecting changes in the biomes' bioclimatic space. The 30% critical loss threshold, used here to define critical levels of bioclimatic space loss, represents the limit above which climate change has determined climatic niche shrink for species in the past, while controlling for the effect of other confounding factors such as land-use change (Di Marco et al., 2021). This threshold defines an empirical value above which terrestrial mammals showed negative responses and an inability to cope with changing climates during the Holocene. By operating directly on the empirical data of species' response to climate niche changes, and not being reliant on any particular statistical model or parameterization, the approach used here allows to extrapolate risk at a broader scale. Our results on projected patterns of climate risk, determined by biomes' bioclimatic space loss, spatially diverge from those of vertebrates climatic determined range loss which are higher in South Africa and Australia (Warren et al., 2018), while we found that biodiversity risk in these areas is low. This is likely related to our consideration of species' ability to tolerate some level of climate change, in evaluating vulnerability from future climate exposure.

In addition, we consider our results to reflect conservative projections of future climate change impact on biome's bioclimatic space. In fact, it must be stressed that the 30% critical loss threshold comes from a model calibrated over climate change taking place over 6000 years (between Mid-Holocene and present), (Di Marco et al., 2021), while our projections are based on predicted changes in climate during only 30 years. This implies that, even with some degree of uncertainty, biomes facing high climate risk reflect areas of rapid bioclimatic space loss and our projections are likely optimistic, as the loss comes in a much shorter time frame reducing species capability for adaptation.

Furthermore, the 30% critical loss threshold used in our framework indicates the level of change beyond which mammal species were typically unable to adapt to climate change, despite their ability to disperse (and consequently to modify their geographic range). This also implies that species might be less able to track change in suitable climate via dispersal, as these are much more

rapid than in the past. As mentioned above, our 30% threshold accounts for the confounding effect of variables such as land-use change. However, current rates of land-use change, poaching, and environmental degradation are accelerating compared to the past, and this increases the challenges to future terrestrial mammals' conservation.

Seven years have passed since the Paris Agreement was signed. These years have been marked by tough political negotiations, struggles to align to mitigation plans and an increasing societal demand to act against climate change. Yet, the only reduction in global emission levels since the beginning of the century has been determined by circumstances beyond direct political control: the 2008s global economic crisis and 2020s COVID-19 pandemic; and in both cases it was followed by a rapid rebound of emissions (Peters et al., 2012; Le Quéré et al., 2021). Even under COP26's Glasgow Climate Pact, the risk of surpassing the 1.5°C and even the 2°C threshold is concrete, as governments failed to define concrete measures to reach the Paris Agreement.

Under increasing concerns on whether achieving the 1.5°C and even the 2°C goals is still feasible (McKay et al., 2022), there is now mounting evidence on the biological risks of missing such goals. Here we show that exceeding the Paris Agreement goals (the 1.5°C and especially the 2°C) can have important effects on increasing climate risk for biomes with a high mammalian biodiversity content.

ACKNOWLEDGEMENTS

MDM was supported by the MUR Rita Levi Montalcini programme.

DATA AVAILABILITY STATEMENT

Data analyzed in this study are openly available at locations cited in the reference section. Processed data are available on request from the corresponding authors.

ORCID

Valeria Y. Mendez Angarita  <https://orcid.org/0000-0002-0117-5799>

Luigi Maiorano  <https://orcid.org/0000-0002-2957-8979>

Chiara Dragonetti  <https://orcid.org/0000-0002-9829-8970>

Moreno Di Marco  <https://orcid.org/0000-0002-8902-4193>

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SUPPORTING INFORMATION

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How to cite this article: Mendez Angarita, V. Y., Maiorano, L., Dragonetti, C., & Di Marco, M. (2023). Implications of exceeding the Paris Agreement for mammalian biodiversity. *Conservation Science and Practice*, 5(3), e12889. <https://doi.org/10.1111/csp2.12889>