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# The effect of past defaunation on ranges, niches, and future biodiversity forecasts

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## Abstract

Humans have reshaped the distribution of biodiversity across the globe, extirpating species from regions otherwise suitable and restricting populations to a subset of their original ranges. Here, we ask if anthropogenic range contractions since the Late Pleistocene led to an under-representation of the realized niches for megafauna, an emblematic group of taxa often targeted for restoration actions. Using reconstructions of past geographic distributions (i.e., *natural ranges*) for 146 extant terrestrial large-bodied (>44 kg) mammals, we estimate their climatic niches as if they had retained their original distributions and evaluate their observed niche dynamics. We found that range contractions led to a sizeable under-representation of the realized niches of several species (i.e., *niche unfilling*). For 29 species, more than 10% of the environmental space once seen in their natural ranges has been lost due to anthropogenic activity, with at least 12 species undergoing reductions of more than 50% of their realized niches. Eighteen species may now be confined to low-suitability locations, where fitness and abundance are likely diminished; we consider these taxa *'climatic refugees'*. For those species, conservation strategies supported by current ranges risk being misguided if current, suboptimal habitats are considered baseline for future restoration actions. Because most climate-based biodiversity forecasts rely exclusively on current occurrence records, we went on to test the effect of neglecting historical information on estimates of species' potential distribution – as a proxy of sensitivity to climate change. We found that niche unfilling driven by past range contraction leads to an overestimation of sensitivity to future climatic change, resulting in 50% higher rates of global extinction, and underestimating the potential for megafauna conservation and restoration under future climate change. In conclusion, range contractions since the Late Pleistocene have also left imprints on megafauna realized climatic niches. Therefore, niche truncation driven by defaunation can directly affect climate and habitat-based conservation strategies.

KEYWORDS

biodiversity conservation, defaunation, ecological niche models, refugee species, shifting baselines

## 1 | INTRODUCTION

Humans have directly or indirectly altered the geographic ranges of numerous species—either by local extirpation or introduction into non-native ranges (Andermann et al., 2020; Bartlett et al., 2016; LeFebvre et al., 2019; Sandom et al., 2014). From hunting and overexploitation to pollution and land-use change, humans have reshaped the distribution of countless species across the globe. Today's distribution of biodiversity is, thus, an altered and truncated version of what it would be without human impact (Andermann et al., 2020; Faurby & Svenning, 2015).

Those human activities still drive changes to life on Earth at unprecedented rates. Being able to predict how biodiversity responds to such changes will be key for planning and implementing effective conservation and restoration actions to counteract biodiversity loss (Pollock et al., 2020). However, global scientific assessments demonstrate the need to further improve the predictive ability of biodiversity forecasts (Bongaarts, 2019), particularly those model-based conservation strategies that rely on observations of current biological parameters, such as species' habitat and environmental preferences across space (Peterson et al., 2018; Soberón & Peterson, 2005). Some of the most widely used methods to predict distribution changes—correlative distribution models (Guisan & Thuiller, 2005)—assume that the current distribution of a species reflects and is at equilibrium with its ecological and physiological thermal limits (Peterson, 2011) and, thus, treat current conditions as conservation baselines (Monsarrat et al., 2019; Rodrigues et al., 2019).

It is, however, unlikely that current geographic ranges reflect the full set of suitable climates that a species would be able to inhabit under current climates and landscapes, but without human interference (Martínez-Freiría et al., 2016; Nüchel et al., 2018; Silliman et al., 2018). Should there be favorable environmental conditions in areas where species have been extirpated due to non-climatic processes, only a subset of their suitable environments, that is, *realized climatic niches* (Soberón & Peterson, 2005), will be occupied in geographic space (Peterson et al., 2018). In that case, parts of the species' niches are said to be *unfilled* (*sensu* Guisan et al., 2014) as a consequence of reductions in their geographical distributions (Martínez-Freiría et al., 2016). This sub-representation of geographical distributions limits our understanding of the environmental constraints of numerous species (Martínez-Freiría et al., 2016; Nüchel et al., 2018; Silliman et al., 2018; Walder et al., 2021) and may bias conservation strategies based exclusively on current distributional patterns (Monsarrat et al., 2019; Rodrigues et al., 2019). Moreover, in cases where the unfilling of niches was caused by the extirpation of populations in optimal environments, remaining populations may now occupy regions of marginal suitability and be at higher risk from subsequent stressors (Bocherens et al., 2015; Kuemmerle et al., 2012; Nüchel et al., 2018). Understanding how current geographical distributions and observed climatic associations differ from what they could be in the absence of human impact may, therefore, improve habitat-based conservation strategies and prediction of vulnerability to climate change (Martínez-Freiría et al., 2016).

To explore how human interference may have truncated species distributions and impacted current estimates of environmental preferences, we consider an emblematic group of species: the mammalian megafauna, here defined as terrestrial species >44 kg (Martin & Klein, 1984). Megafaunal mammals have been particularly affected by humans, with several documented events of extinction linked directly or indirectly to human pressures, from the Late Pleistocene to recent history (Andermann et al., 2020; Bartlett et al., 2016; Sandom et al., 2014). Outside the mainland of Afro-Eurasia, the timing of megafaunal extinctions followed a highly distinctive landmass-by-landmass pattern that closely parallels the migration events of modern humans (Andermann et al., 2020; Bartlett et al., 2016; Sandom et al., 2014). Human activities have also led to extirpations and massive range contractions of several large mammals throughout the Holocene (Crees & Turvey, 2014; Prevosti et al., 2015). In addition to hunting (Bar-Oz et al., 2011), anthropogenic land-use change may have limited migration and recolonization that would otherwise have allowed megafaunal species to cope with changing environments (Németh et al., 2017). Continued poaching and environmental disturbance, associated with cultural filtering, have led to additional megafaunal extinctions in the recent past (Teng et al., 2020), increasing the risk of further extinctions in the future.

Regardless of whether megafaunal extinctions are unequivocally tied or not to human expansion and direct exploitation, the range contractions of mammalian megafauna in the recent past challenge the assumption that species' occurrences are at equilibrium with the current environmental conditions across their ranges (Early & Sax, 2014). In this work, we test the hypothesis that niche unfilling due to range contractions leads to an incomplete representation of species' climate niches and affects the outcome of climate-based distributional forecasts. To do so, we focus on extant large mammals and reconstructions of their past geographical distributions, which depict the ranges they would hold today had they never experienced anthropogenic stressors (*present-natural ranges* from Faurby et al., 2020; hereafter just *natural ranges*). First, we estimate species' environmental envelopes derived from natural ranges and from current distribution to test if the observed changes in geographic distributions have led to significant changes in their inferred realized niches. Then, we ask if these range contractions occurred toward locations of high or low suitability by comparing the realized climatic niches associated with natural versus current geographic distributions. Finally, we investigate the potential impact of this incomplete characterization of the realized niche (i.e., *niche unfilling*) on species' estimated vulnerability to future climate change. Besides showing that range contractions often lead to the loss of representation of the diversity of suitable environments, we further demonstrate that such niche truncation undermines the reliability of climate-based forecasts as conservation tools. By doing so, we also provide the most comprehensive assessment so far of the expected effects of future climate change on all extant large mammals.

## 2 | METHODS

### 2.1 | Megafauna distribution data

We assessed the changes on the realized climate niches of 146 extant megafaunal mammal species, that is, those whose body mass exceeds 44 kg (Martin & Klein, 1984). The median weight of species in our dataset was 99.97 kg, where the smallest species (*Priodontes maximus*) weights ca. 45 kg, whereas the largest species (*Loxodonta africana*) has an average body mass close to 4400 kg (Table S1) (data from Faurby et al., 2020). Nine mammal orders are represented in the data set, namely Carnivora (16 species), Artiodactyla (104 species), Cingulata (1 species), Diprotodontia (1 species), Perissodactyla (16 species), Primates (4 species), Proboscidea (2 species), Rodentia (1 species), and Tubilidentata (1 species). The most well-represented threat category was *Least Concern* (LC) according to the International Union for Conservation of Nature (IUCN, 2020) conservation status; however, all IUCN categories were represented (*Critically Endangered* CR = 15; *Endangered* EN = 27; LC = 54; *Near Threatened* NT = 16; *Vulnerable* VU = 34). Species from across the globe, except Antarctica, were included, with Africa exhibiting the highest current diversity of megafauna mammals (with up to 26 species per cell), followed by Asia, North and South America, Europe, and Australia (with 14, 11, 9, 5, and 1 species per cell, respectively).

We compared the environments that those species currently occupy against those that they would be presumably occupying today had anthropogenic range contraction not occurred. To characterize the latter, we used maps of present-natural ranges from The Phylogenetic Atlas of Mammal Macroecology (PHYLACINE—Faurby et al., 2018), version 1.2.1. The PHYLACINE 1.2.1 is a taxonomically integrated platform that provides data on phylogenies, range maps, trait data, and conservation statuses for all known mammal species from the Late Quaternary (Late Pleistocene and Holocene). Natural range maps were estimated by Faurby and Svenning (2015) with a combination of climate suitability modeling and biotic restrictions on historical and paleoecological occurrence records—some of which based on fossil co-occurrence—to the current ranges of species whose local extinction is mainly attributed to human pressures (Faurby et al., 2018; Faurby & Svenning, 2015).

Natural range maps are not, therefore, restricted to a specific timeframe, encompassing data from 120k years ago to more recent local extinctions in the post-industrial era, but are a representation of the distribution that each species would likely occupy today (i.e., under current climates) if their distributions had never been affected by *Homo sapiens*(Faurby et al., 2018). Thus, the environmental niche space inferred from natural ranges represents the set of environmental conditions a species would be able to occur in the present based on climatic suitability inferred from past and current distribution. For a detailed explanation of natural range calculations, please append to the Supporting Information from Faurby and Svenning (2015).

The current range maps for extant species, which were also obtained from this database, are based on the IUCN Red List extent of occurrences. In the present work, we downscaled raster files to a resolution of 9.63 km² but maintained the same projection as in PHYLACINE 1.2.1 (i.e., Behrmann cylindrical equal-area). Extinct species were not included in this work.

### 2.2 | Past to present

#### 2.2.1 | Niche overlap tests

To test whether the observed range shifts of megafaunal species have affected their realized climatic niches, we extracted climatic information associated with each species' distributions under their current and natural ranges. Climate information was obtained at WorldClim's version 2 (http://worldclim.org/version2), in the form of spatial raster files of bioclimatic predictors (Fick & Hijmans, 2017; details given as Supporting Information section *"Climate data"*). Our goal here was not to estimate the climatic niche species would have had in past climate conditions but to estimate how large the climatic niche of extant megafaunal species would be if those species had retained their natural distributions until the present. To do so, we intersected those ranges to the climatic variables and adapted Broennimann et al.'s (2012) protocols to 1) calculate the frequency of climatic conditions along the main environmental axes of a multivariate ordination; 2) measure niche overlap along the gradients of this multivariate ordination; 3) test the statistical significance of niche equivalence and similarity; and 4) decompose niche changes into main drivers, here focusing on the *unfilling* component (Guisan et al., 2014). This method also allowed us to separate the effect of changes in range size, from changes on the realized niche per se.

To compare the environmental space occupied by each species' current versus natural range, we used the values of $z_{ij}$ to calculate niche overlap, using the Schoener's *D* index, described as

$$D = 1 - \frac{1}{2}\left(\sum_{ij} |Z_{1ij} - Z_{2ij}|\right)$$

where $z_{1ij}$ is the occupancy of climatic conditions from natural ranges and $z_{2ij}$ is the current range environmental occupancy (Broennimann et al., 2012). Niche overlap, therefore, varied between 0 (no overlap) and 1 (complete overlap).

Observed niche overlap was, then, confronted to random expectations using equivalence and similarity tests (Warren et al., 2008). The *equivalence* test assesses if the environmental conditions within two geographical ranges are equivalent by evaluating whether the observed niche overlap resists random reallocations of environmental conditions among them. In this test, environmental conditions are pooled and randomly divided into two datasets, maintaining the number of cells as in the original datasets. Then, the niche overlap statistic *D* is calculated for each permutation. To ensure that the null hypothesis of niche equivalence can be rejected with confidence, this procedure is repeated 100 times to obtain a null distribution and if the observed *D* value falls within the distribution of 95% of simulated values, the null hypothesis cannot be rejected. The *similarity* test, on the other hand, determines if the observed niche overlap is different from that between environments within one range and environments selected randomly at the other range (Broennimann et al., 2012). In the similarity test, we randomly shuffle the frequency of environmental conditions in one range and calculate the overlap of this simulated niche with the observed niche at the other range. We also built the null distribution for the similarity test based on 100 repetitions.

Although satisfying in their ability to understand niche overlap from an environmental perspective, the tests of stability and equivalence do not address the causes of changes in niches. To explicitly explore whether realized niche changes were due to the loss of representation of environments occupied by megafauna species since the Late Pleistocene, we calculated the observed niche *unfilling* associated with range contraction while controlling for the availability of analog climates across the compared ranges (Guisan et al., 2014). Niche *unfilling* is detected when environmental conditions in the natural ranges are currently available and accessible to the species, but unoccupied (Figure S1). By representing the proportion of the present natural niche that is not filled based on the current distribution and the availability of current environments, niche unfilling can, thus, be considered a proxy of the loss of representativeness of suitable environments across species' ranges. We also registered whether the centroid of the niches moved when inferred based on current versus natural ranges. The centroid of the niche represents the set of climatic conditions a species is more likely to occupy based on the analyzed occurrences. We, thus, assume that the niche centroid estimated from the natural distribution represents climatic conditions of regions with the greatest suitability for that species. Therefore, the displacement of the most frequent conditions observed across species' ranges toward locations farther from the original centroid position can be interpreted as the movement of ranges toward regions of lower climatic suitability.

## 2.3 | Into the future

### 2.3.1 | Modeling framework

To evaluate the effect of shifted baselines on estimates of sensitivity to future climate change—measured in terms of potential distribution variation—we used ecological niche models based on different assumptions. The first scenario assumes that species' distributions are in equilibrium with the environmental conditions across their ranges today and uses climatic information solely from species' current ranges to calibrate ecological niche models, which we call *current-based* models. The second scenario relies on climatic information from species' natural ranges, that is, simulating a scenario where species have never experienced heavy anthropogenic stressors (Faurby & Svenning, 2015). The latter considers that fundamental niches tend to be conserved over time (Peterson, 2011) so that occurrence records from different periods should provide additional information on species' climatic tolerances from environments without contemporary counterparts (Faurby & Araújo, 2018; Lima-Ribeiro et al., 2017; Martínez-Freiría et al., 2016). We name this approach a *natural-based* model, to adhere to the terminology originally proposed by the authors of the PHYLACINE 1.2.1 dataset (Faurby et al., 2018).

For each species, we sampled random points within the species' current and natural ranges, proportionally to its range size (Table S2), and used ecological niche models to generate potential distribution maps. To do so, we used MaxEnt, a presence-background method in which the species' distribution is an unknown probability along with the full background points, that is, non-negative values that add up to one (Elith et al., 2011). MaxEnt is robust to the presence of a moderate level of locational error and still provides useful predictions of species' environmental preferences (Graham et al., 2008). The values of predictor variables at localities within natural and current ranges restrict the unknown distributions so that the average and variance values of environmental predictor should be, therefore, close to empirical values (Graham et al., 2008; Merow & Silander, 2014). However, the complexity of the fit to the observed values can be adjusted by transformations on the original predictor values ("feature classes") (Muscarella et al., 2014). In this work, we compared two combinations of feature classes: (1) MXS: Maxent Simple (only linear and quadratic features); (2) MXD: Maxent Default (linear, quadratic hinge, product, and threshold features, based on MaxNet package) (S. Phillips, 2017; S. J. Phillips et al., 2017). The combination of feature classes exhibiting the highest accuracy metric ($F_{pb}$, calculation explained in Supporting Information section *"Model accuracy assessment"*) was then selected for final projections.

Because the performance of ecological niche models is affected by the spatial distribution of background points (Barbet-Massin et al., 2012), we used a stepwise approach to select and partition our background data. First, we defined species-specific background extents and built a preliminary BIOCLIM (Busby, 1991) habitat suitability model to constrain our background data to regions considered less suitable, that is, suitability <0.3 (Engler et al., 2004). Then, we partitioned our presence-background data by the latitude and longitude lines that divide occurrence localities into blocks in a checkerboard-like fashion. Optimal band sizes were considered those that (i) exhibited smaller spatial autocorrelation, based on Moran's I, and (ii) minimized the difference in the number of records between blocks (Roberts et al., 2017; Velazco et al., 2019). Blocks were then alternatively used for fitting and evaluating the model, and evaluation metrics were summarized across iterations (Andrade et al., 2020; Muscarella et al., 2014). Continuous suitability surfaces (values ranging from 0 to 1) were then created to reflect the relationship between species' occurrences and their environment. Values closer to zero indicate lower predicted suitability, whereas values closer to 1 suggest high environmental suitability.

Because we used range maps as a source of environmental information, the outcome of our ecological niche models represents the environmental conditions most frequently observed across species' known distributional limits. Therefore, our results should not be interpreted in terms of probability of occurrence *per se*, nor can be directly translated into any abundance-related metric. Such broadly defined climate envelopes, however, are meant to provide an initial assessment of species climatic suitability at the continental scale and are useful to investigate macroecological relationships between biotas and environments (Sales et al., 2019, 2020a, 2020b). We stress that our results should not be explored at face value in conservation assessments at local spatial scales.

Climate information from current and natural ranges was, therefore, used as input in our ecological niche models and was compared in terms of future potential distribution areas, for each species (model details and parameterization are presented in the Supporting Information section *"Modeling framework")*. To do so, the ecological niches inferred from current-based and natural-based models were projected onto climate forecasts, dated to the year 2090 and based on the 6th Assessment Report of the International Panel of Climate Change (IPCC, 2021). Two representative concentration pathways were considered: an optimistic level of emission of greenhouse gases (*ssp126*), and a more extreme scenario (*ssp585*). While the first scenario represents the "best case" future from a sustainability perspective, with temperature increases of less than 2°C, the latter assumes "no climate policy" and predicts potential increases of almost 5°C in global mean temperature. Both forecasts, therefore, anticipate increases in temperature that are above the 1.5°C thresholds suggested to avoid the negative effects of climate change on global ecosystems and human well-being (IPCC, 2018).

Within each climate change scenario, we chose three distinct climate models to encompass uncertainty on future projections—namely BCC-CSM2-MR, CanESM5, and MIROC6—using a stepwise procedure aimed at minimizing similarity (Sanderson et al., 2015). The resulting projections of those three climate forecasts were combined to create a single consensus map of the potential future distribution for each species at each climate change scenario. Only cells that were predicted as suitable by all climate models were included in the final consensus map. Models were evaluated using methods that do not rely on true absence, namely the Jaccard's (1908) and the Sørensen's (1948) similarity indexes, in addition to the $F_{pb}$, a proxy of the F-measure based on presence-background data (Li & Guo, 2013), according to the equations in Table S3. To restrict our analysis to regions likely accessible to species, we further limited access to future suitable areas according to species-specific dispersal constraints (details in Supporting Information, sections *Model accuracy assessment* and *Spatial constraints*).

# 3 | RESULTS

## 3.1 | Range changes versus niche changes

Although nearly one-third of the analyzed species experienced no changes in distribution, most (90 out of 146) suffered range contractions with an average (± SD) loss of 31.6% (± 31.3%). Extreme cases lost up to 99% of their potential geographic distributions, such as the case of the Javan rhino *Rhinoceros sondaicus*. Comparing the realized niches inferred from natural and current ranges revealed that they are usually not equivalent but more similar than expected by chance (Appendix S1). Notably, 113 species exhibited truncation of their realized niches to a fraction of their historical volume ($unfilling_{mean} = 0.14 \pm 0.22$) (Figure 1, Table S4 and Appendix S2). Twenty-nine species, including the lion, *Panthera leo*, the African bush elephant *Loxodonta africana* and the American bison, *Bison bison*, have lost >10% of the area of niche space corresponding to the diversity of environments they would have occupied in the past. Furthermore, 12 species had a reduction of more than 50% in their realized niches, including the Sumatran orangutan, *Pongo abelii*, and the European bison, *Bison bonasus*. This is to say that the populations of those species are currently restricted to less than half of the environmental space they could potentially occupy, with large areas with suitable climatic conditions becoming unoccupied in the recent past.

## 3.2 | Centroid movement

After comparing natural versus current ranges and the associated niche dynamics in environmental space, we tested for changes in species' niche centroids. We found evidence that at least 18 species had their niche centroids relocated (Figure 1; Appendix S2 and Table S4). Those species' ranges have, therefore, been displaced from regions of presumably high suitability and are now restricted to locations of marginal suitability when compared to natural ranges. Interestingly, most of those species are listed in the IUCN Red List of Threatened species. Eight of those species are considered Critically Endangered (CR), such as the Javan rhino, *Rhinoceros sondaicos* (Figure 1), whereas four other species are considered Endangered (EN), and three are listed as Vulnerable (VU) (Tables S1 and S4). All those species whose centroid have moved have lost at least 14% of the diversity of the environments occupied ($unfilling_{mean} = 0.55 \pm 0.25$). Such movements away from niche core regions were, therefore, more frequent for species exhibiting higher values of niche unfilling (Table S4). However, another 27 species had their distributional changes directed toward the centroid of their realized niches (Figures S1 and S2, Table S4).

## 3.3 | Climate change forecasts

To understand the effect of past range contractions on biodiversity forecasts and future biogeographical patterns, we compared the expected outcome of models that account for past geographic ranges (*natural-based*), to those that solely consider current distribution information (*current-based* models) (Figure 2, lower panels; Table S4). Overall model accuracy was high for both types of modeling approaches (Table S5; Natural-based: $Jaccard_{mean} > 0.91$; $Sorensen_{mean} > 0.89$; $Fpb_{mean} > 1.82$; Current-based: $Jaccard_{mean} > 0.90$; $Sorensen_{mean} > 0.90$; $Fpb_{mean} > 1.79$). Models calibrated with natural ranges revealed vast areas that are

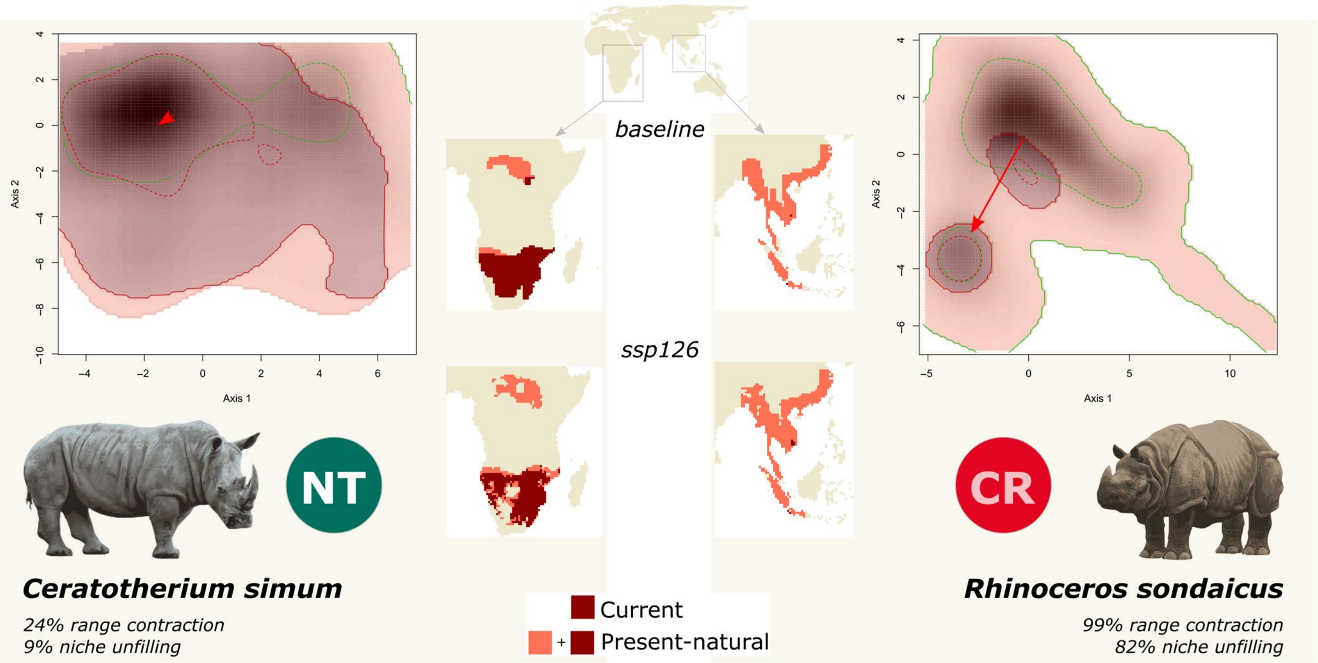

**FIGURE 1** Range and niche changes, plus the effect of niche truncation on climate-based forecasts, for two species subjected to severe anthropogenic defaunation. Hunting and poaching of the white rhinoceros *Ceratotherium simum* (left panel—IUCN category Near Threatened) and that of the Javan rhinoceros *Rhinoceros sondaicos* (right panel—Critically Endangered) have led to massive contraction on the geographic range of the species (upper-middle inset—baseline). Dark red cells indicate current ranges, while the coral color is for areas that have been lost from present-natural ranges. This distribution truncation affected the species' realized niche (larger panels), here projected onto two axes of an ordination analysis performed at climate variables. The red arrow indicates the movement of species' niche centroid in relation to high-suitability areas (darker shade in niche panels), where the size of the arrow is relative to the magnitude of change in niche centroid. The Javan can be considered a climatic refugee, in contrast to the white rhino. Distribution forecasts calibrated with natural versus current ranges lead to different expectations under climate change (lower middle panels)—those results refer to the optimistic scenario of climate change, *ssp126*

potentially suitable for some species and that could experience a future increase in the richness of megafauna species, such as Western Europe, the Middle East, several parts of Central-Southern Asia and the Great Plains of North America (Figure 2, panels c and e). In natural-based forecasts, richness increases were expected across most of the globe, except in central African countries such as Kenia, Tanzania, as well as in southern dry steppe and savanna regions of Zambia, Botswana and South Africa.

We also observed differences in biodiversity forecasts for contrasting expectations of greenhouse gas emission and climate change (Figure 3; Table S6 and Appendix S3). At a low emission scenario (Figure inset, dark yellow bars), both model types indicated that most megafauna species could expand their potential ranges (*Natural-based*$_{gain}$ = 13 ± 64, $n$ = 125; *Current-based*$_{gain}$ = 0.64 ± 0.90, $n$ = 114). Under this "optimistic" climate change scenario, expected losses were relatively small and less frequent (*Natural-based*$_{loss}$ = −0.13 ± 0.11, $n$ = 21; *Current-based*$_{loss}$ = −0.15 ± 0.18, $n$ = 32). However, we observed a shift in the expected signal of climate change, from positive to negative, as greenhouse gas emissions become more severe (Figure inset, dark purple bars). Although a relatively high number of species may still experience range expansions under a high emission scenario (*Natural-based*$_{gain}$ = 17 ± 59, $n$ = 64; *Current-based*$_{gain}$ = 0.56 ± 0.76, $n$ = 34), more species are expected to undergo range contractions (*Natural-based*$_{loss}$ = −0.43 ± 0.28, $n$ = 82; *Current-based*$_{loss}$ = −0.48 ± 0.28, $n$ = 112). Overall, models relying on current distribution patterns predicted smaller and less frequent range expansions, as well as greater and more frequent range reductions and local extinctions (Figure 3). Comparing natural-based and current-based models, predictions of global extinctions (the number of species predicted to have no future analog climates) increased from 0 to 1, under the *ssp126*, and from 2 to 4, under the *ssp585*, respectively (Table S6).

## 4 | DISCUSSION

Anthropogenic impacts on large-bodied animals have led to massive and ongoing range contractions across the globe (Ceballos et al., 2020; Dirzo et al., 2014; Faurby & Svenning, 2015). In addition to effects on demography and genetic diversity, these contractions may wipe out populations from climatically suitable locations that would otherwise be occupied. Here, we confronted the current and "natural" ranges (Faurby et al., 2020) of extant megafaunal mammals to understand how such range contractions map into reductions in species' realized niches. We found that the range contractions observed in some megafauna mammals led to the loss of the diversity of

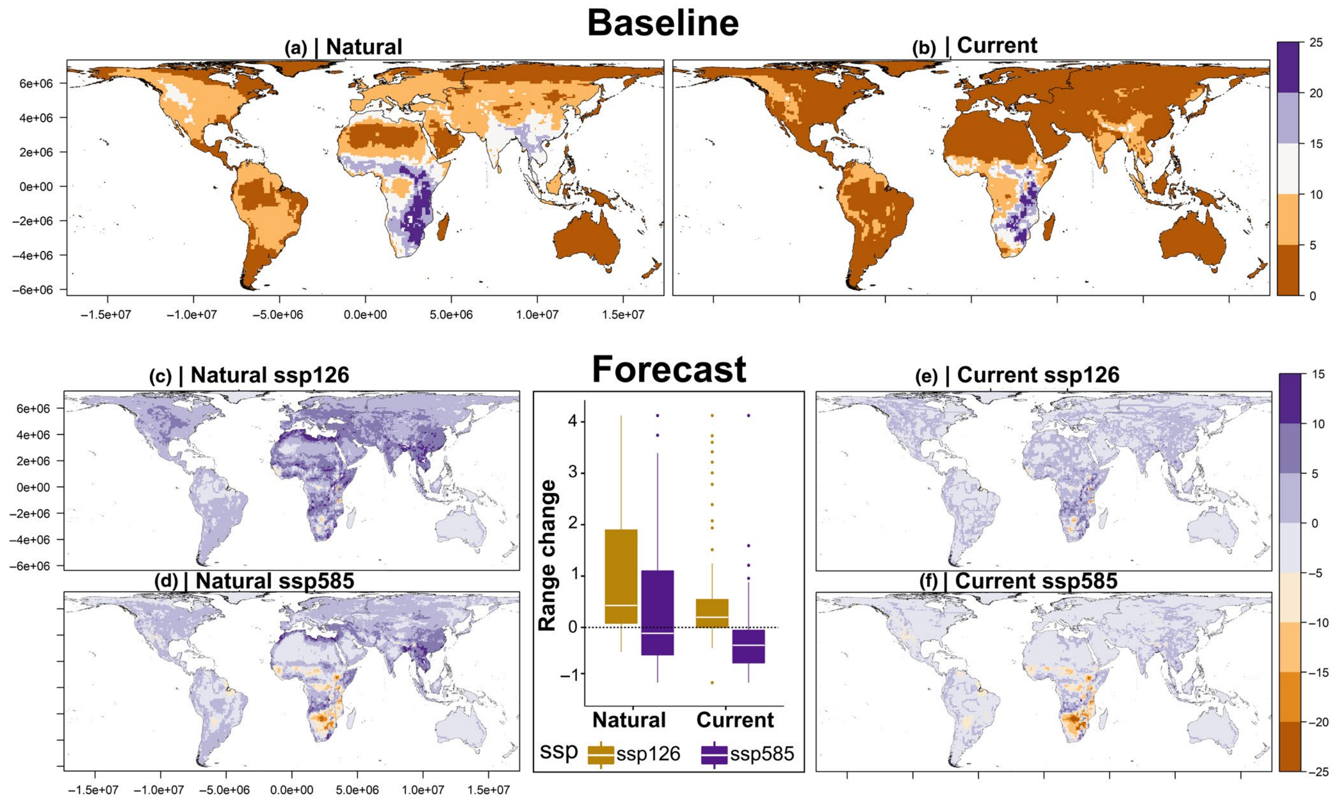

**FIGURE 2** Biogeographic patterns of species richness of extant megafauna (>44 kg) mammals. Upper panels contrast the expected richness patterns of living megafauna species had they not experienced past range contraction—natural conditions (panel a), from Faurby et al. (2020), and under current conditions (panel b). Such baseline richness maps were obtained by the superimposition of natural range maps and IUCN polygons of extent of occurrence, respectively. Lower panels indicate the effect of shifting baselines on biodiversity forecast models, measured as the difference from currently observed species richness. The acronyms *ssp126* and *ssp585* refer to climate change emission scenarios. The inset indicates the propotional range change for individual species as predicted by natural- and current-based models

occupied environments and the consequent sub-representation of the realized niches, i.e., *niche unfilling* (Guisan et al., 2014). For those species with only a subset of their natural realized niches currently occupied in geographic space, we show differences between climate-based forecast models that rely exclusively on current distributional patterns relative to models based on their natural ranges.

Our results indicate that several species have lost populations in areas with the most suitable climates across their ranges. Their remaining populations now occupy habitats of supposedly lower quality. These species may, therefore, be considered *climatic refugees* (Kerley et al., 2012; Kuemmerle et al., 2012), for they may no longer have access to optimal environmental conditions. If these species are indeed confined to suboptimal environments, where fitness and abundance are likely lower, these species could be facing higher extinction risks (Kerley et al., 2012). Due to the habitat and range limits forced on these species, the refugee status is, therefore, a cryptic signature, only revealed by the uncovering of historical distribution information (Kerley et al., 2012; Kuemmerle et al., 2012). In such cases, the misrepresentation of environmental niches can bias conservation assessments based on habitat availability and use. This truncation of realized niches may also explain, at least partially, the poor outcome of earlier conservation actions targeting megafauna species that have experienced past range contractions, such as the giant panda *Ailuropoda melanoleuca*(Han et al., 2019) and the snub-nosed monkeys of genus *Rhinopithecus* (Nüchel et al., 2018) – the so-called Protected Area Paradox (Kerley et al., 2020). For those species, conservation strategies based solely on current ranges may be misguided because the habitat currently occupied may not be optimal, but conservation assessments assume it as such (Monsarrat et al., 2019). Thus, in those cases, plans for reintroduction, management, translocation, and even the designation of protected areas may mostly encompass marginal environments that are not likely to sustain viable populations in the long term (Kerley et al., 2020; Kuemmerle et al., 2012).

We found that climate-based models aimed at predicting the distribution of megafauna species under future climate change were affected by the choice of the baseline distribution. Models that incorporate natural ranges predict larger suitable areas and, therefore, estimate fewer local extinctions due to climate change. Vast areas of Northern Africa, the Arabian Peninsula and most of Central and Southern Asia were identified as sites where megafauna species could expand their distribution in the future, a finding only revealed by the inclusion of the natural distribution information. Those locations are likely to offer suitable climates for several megafauna

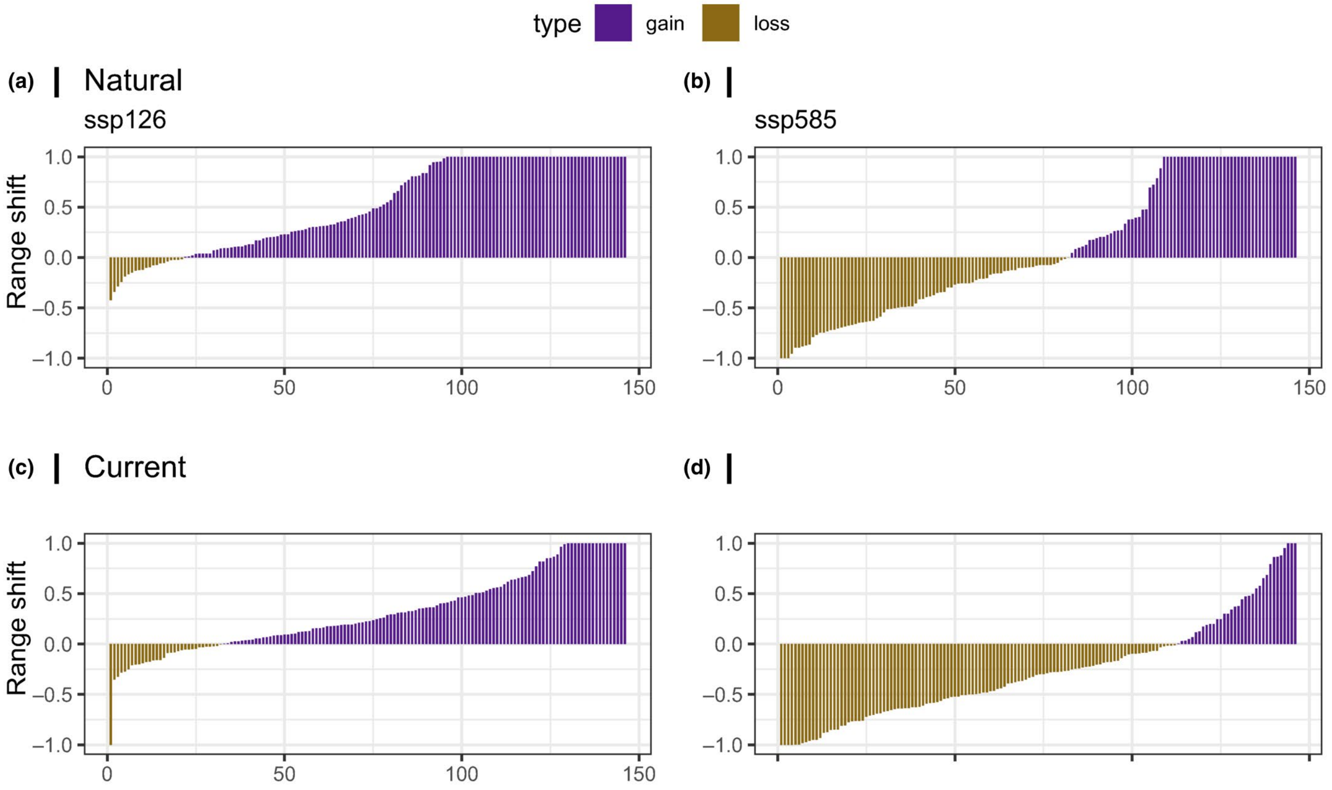

**FIGURE 3** Forecasted change in range size per species. Panels indicate the proportional variation in total suitable area, as predicted by models calibrated with different baselines (natural vs. current), under two distinct future climate change scenarios (*ssp126* and *ssp585*). Range expansion values are presented up to the limit of 100% increase, to enhance readability. For exact values, please refer to Table S3

species in the future and could, therefore, work as potential rewilding zones aimed at conservation planning under climate change (Jarvie & Svenning, 2018). We acknowledge that many of those regions, although climatically suitable, may not include enough habitat due to land-use changes or may be inaccessible due to landscape structure limiting dispersal (Sales et al., 2019). As such, recolonization will depend on active reintroduction programs that also consider the local socio-ecological context (Perino et al., 2019). For example, fertile flatlands in South America and elsewhere are known to have hosted a myriad of plants and animals before the anthropogenic conversion into agricultural lands (Tabarelli et al., 2010). Yet, correctly identifying the climatic suitability is an important step toward the restoration of degraded ecosystems (Strassburg et al., 2020). Our results show that the definition of the distribution baseline strongly impacts the predicted responses of species to climate change, which has several implications for the future preservation of biodiversity. Furthermore, our findings also support some optimistic expectations that the inclusion of environmental information from natural ranges in ecological niche models could reveal reduced potential impacts of climate change in large-bodied animals (Faurby & Araújo, 2018; Jarvie & Svenning, 2018; Lima-Ribeiro et al., 2017).

Our results have straightforward implications for the conservation of species that have been subjected to known range contractions in the past and biodiversity climate modeling in general. However, we caution that our methods are not without flaws. The very nature of our dataset on species' natural and current ranges (PHYLACINE's maps - Faurby et al., 2020) poses limitations to the scope of our conclusions. For example, Faurby et al. (2020) did not include regions classified as "non-native" by IUCN; yet some species, such as *Dama dama* and *Axis axis*, currently occupy large areas classified as such. Had those areas been considered "native," they would have been included in "current" maps, and range expansion would have been found in comparisons between natural and current ranges. Additionally, we acknowledge that an ideal representation of species' realized niches should rely on well-designed, comprehensive, and non-autocorrelated occurrence data sets (Araújo et al., 2019; Araújo & Guisan, 2006). Such data are, however, rarely available for large datasets that include species from undersampled regions, like most tropical regions. Nonetheless, we argue that the general patterns found here should be valid at the biogeographical scale, where the effect of macroecological processes should prevail over local idiosyncrasies and microhabitat selection (Soberón & Nakamura, 2009).

Estimating the range of environmental conditions that a species could possibly occupy in the absence of human impacts requires some information on its prehistorical or historical occurrence records. Therefore, this approach does not apply for species without known fossil records or historical descriptions and museum specimens that could help reconstructing past distributions (Monsarrat et al., 2019). Unfortunately, such information is limited for several taxa and is often unevenly available across the species' distribution. In those cases, expert opinion and traditional ecological knowledge may help inferring past distributions (e.g., Eckert et al., 2018). Even though estimating natural ranges may not be possible for all species, we consider that, when applicable, information other than current observed patterns should be used to obtain a more realistic depiction of range and niche dynamics, as well as distribution limits.

In conclusion, we demonstrate that the range contractions observed for several megafauna mammal species since the Late Pleistocene have left imprints not only on their geographical distributions but also on their realized climatic niches. Importantly, these range contractions were shown to also reduce the representation of suitable environments for these species, truncating the climatic preferences inferred from current distributions. Furthermore, 20% of the species that experienced range contractions have lost several or most populations in what could be their optimal habitats. For those species, here considered *climatic refugees*, remaining populations may now be restricted to low-suitability areas, which has serious implications for conservation assessments based on habitat use. We argue that management and conservation strategies that rely on distributional information should not neglect historic range dynamics when defining geographic calibration areas. If climate-based forecasts are to be used as conservation tools, they must also include assessments of species' environmental preferences and their realized niche dynamics that encompass multiple time spans to improve the reliability, and ultimately the usefulness, of the outcomes they aim to provide.

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## DATA AVAILABILITY STATEMENT

The climate data used in this work can be downloaded at http://worldclim.org/version2. Reconstructions of historic geographic ranges of megafauna mammals are available at https://megapast2future.github.io/PHYLACINE_1.2/. An example of the R codes used in this work is available as Supporting Information in the section *"Example R Code"*. Furthermore, all species-specific raster files are available at Dryad (https://doi.org/10.5061/dryad.280gb5mrq).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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