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Research

Drivers of change in the realised climatic niche of terrestrial mammals

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The breadth of a species' climatic niche is an important ecological trait that allows adaptation to climate change, but human activities often reduce realised niche breadth by impacting species distributions. Some life-history traits, such as dispersal ability and reproductive speed, allow species to cope with both human impact and climate change. But how do these traits interact with human pressure to determine niche change? Here we investigate the patterns and drivers of change in the realised climatic niche of 258 terrestrial mammal species. Our goal is to disentangle the impacts of human land use, climate change and life history. We quantified the past and present climatic niches of each species by considering past climatic conditions (Mid Holocene) within their pre-human impact distributions, and current climatic conditions within the current distributions. Depending on the difference between past and current niche, we defined four categories of change: 'shrink', 'shift', 'stable' and 'expand'. We found over half of the species in our sample have undergone niche shrink, while only one in six retained a stable niche. Climate change and distribution change were the strongest correlates of species niche change, followed by biogeography, anthropogenic land use and life-history traits. Factors that increased the probability of niche shrink included: overall climatic instability, reduction in distribution range, historical land use, large body mass and long weaning age. Species with these characteristics might require interventions that facilitate natural dispersal or assisted colonisation to survive rapidly changing climates.

Keywords: climate change, extinction risk, human pressure, life-history traits, mammals

Introduction

A species' niche – the set of environmental conditions in which the species can persist (Peterson et al. 2011) – represents the essential ecological characteristics of a species, and niche breadth – the 'distance through' a niche along particular lines in the niche space (Colwell and Futuyma 1971) – is an important trait that allows adaptation to environmental change (Thuiller et al. 2005, Pacifici et al. 2015, Ficetola et al. 2020). Niche breadth is considered a key correlate of species sensitivity to habitat change

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(Swihart et al. 2003) and climate change (Thuiller et al. 2005, Chown et al. 2010). Yet, the fundamental niche of a species (which would be observed in the absence of limiting factors) is often unknown, and niche breadth is usually assessed by relating the observed occurrences of species to their current and past habitat characteristics; this implies looking at species' realised niches, rather than their fundamental ones (Peterson et al. 2011). While alteration of a species' realised niche does not necessarily imply alteration of the fundamental niche, the loss of realised niche breadth can be associated with a loss in local adaptation capacity and was shown to predict extinction risk (Saupe et al. 2015). Exposure to environmental conditions beyond those historically experienced by a species might lead to population decline and overall ecological disruption (Trisos et al. 2020), and reducing the variability of the species realised niche can result in reduced adaptation capacity if local adaptations are lost alongside niche variability (Hanson et al. 2020). Analysing realised niches is a well-established technique to identify differences in species' ecology (Olalla-Tárraga et al. 2011, Mahon et al. 2016), predict the potential spread of invasive species (Liu et al. 2017) and project past and future changes in species distributions (Maiorano et al. 2013, Visconti et al. 2016).

The role of human threats as drivers of species decline and extinction has been often demonstrated (Johnson et al. 2017, Di Marco et al. 2018, Pacifici et al. 2020), but their role as drivers of realised niche erosion has proven more difficult to quantify (Pearman et al. 2008). Threats such as overexploitation, habitat loss and fragmentation, and invasive species have been recognised as global drivers of species decline in recent centuries (Hoffmann et al. 2010, Maxwell et al. 2016). More recently, substantial attention has been devoted to the emerging threat of climate change, with effects that might become soon predominant over those of already established threats (Newbold 2018, Di Marco et al. 2019). Climate change is recognised as having potential magnifying effects on biodiversity decline in the absence of adaptation and coping mechanisms (Bellard et al. 2012, Mantyka-Pringle et al. 2015, Visconti et al. 2016). Yet, species might also be able to tolerate changing climates, depending on their characteristics (Adrian et al. 2006, Jiguet et al. 2007, Urban et al. 2014, Santini et al. 2016, Pacifici et al. 2017). Life-history traits, such as dispersal ability and reproductive speed for example, have been hypothesized to play a central role in determining the sensitivity of species to climate change and their ability to cope with it (Dawson et al. 2011). Evolutionary adaptation through genetic change or phenotypic plasticity might also allow species to survive changing climates (Diniz-Filho et al. 2019), including mechanisms such as change in reproductive strategies or body mass (Hoffmann and Sgró 2011). However, it is unclear whether these mechanisms are compatible with the pace of current climate change for most species (Loarie et al. 2009). In addition, how do these mechanisms act in combination with human pressure to determine change in species realised climatic niches?

Here we investigate the patterns and drivers of change in the realised climatic niche of terrestrial mammals. In defining realised climatic niches we only focus on scenopoetic variables (temperature and precipitation) sensu Hutchinson (Peterson et al. 2011). We defined the past and present realised climatic niches of each species by considering the past climatic conditions within their historical range and the current conditions in the current range. We then predicted niche change as a function of overall climatic stability for each species, past and present levels of human land use to which they have been exposed, and life-history traits. Our goal is to disentangle the impacts of humans, climate change and life-history variables on the observed change in species' niches. Separating intrinsic and extrinsic vulnerability of species to niche change, as well as the role of direct and indirect human pressure, is essential to understand which species are most likely to suffer from environmental change.

Methods

Species distribution

We focused our analyses on 258 terrestrial mammal species worldwide (Supporting information), representing all species which are known to have changed their geographic distribution in response to human pressure (Faurby and Svenning 2015), have not gone extinct in prehistorical times, have been assessed in the Red List of the International Union for Conservation of Nature (IUCN), and have suitable information on their historical distribution (below). Selecting these species allowed us to disentangle the relative impact of climate change (within species' historical ranges) from that of direct human influence on species' distributions in determining change in realized niche. We used species distributions referring to the present day, and those assumed to represent species' historical ranges (i.e. before modern human impact modified them). We retrieved present distributions from the IUCN Red List (IUCN 2018) and historical distributions from the 'present natural ranges' of the PHYLACINE dataset ver. 1.2 (Faurby and Svenning 2015, Faurby et al. 2018). Our use of present natural ranges as proxies for 'historical' distributions is similar to that of Belote et al. (2020) and Lim et al. (2020), but we employed a selection filter based on how these ranges were derived. In fact, present natural ranges represent species potential distributions in the absence of human modification, and they have been derived using a variety of techniques to estimate pre-impact distributions of each species. Such techniques include merging disjunct portions of the ranges, expanding the range to cover environmentally suitable areas, expanding the ranges to cover entire islands, etc. (Faurby and Svenning 2015). We decided to only retain species for which no consideration of climatic suitability were employed to define present natural ranges, to avoid any potential risk of circularity in our modelling of realised climatic niches: i.e. we only considered range modification categories 1, 2, 4 and 8 from Faurby and Svenning (2015). All ranges were considered at a spatial resolution of 1 arc-degree (roughly 110 km-wide at the equator), which is the native resolution in the PHYLACINE database.

Species characteristics and human pressure

For each species, we collected variables that are potentially correlated to changes in their realised climatic niches. First, we considered external forcing factors within which niche change has occurred for each species. We included the species biogeographic realms (Olson et al. 2001), the climatic change each species has experienced (see below 'Representing realised climatic niches'), and the overall human-induced change in species distribution (Faurby et al. 2018). These variables represent the broad regional context to which each species has been exposed.

Second, we retrieved life-history traits (Soria et al. 2021) known to influence species response to climate change. We included diet specialisation, which was recognised as an important factor influencing species' ability to adapt to new environments under climate change (Pacifici et al. 2017); we considered the percentage of vertebrate-based, invertebrate-based and plant-based diet (Faurby et al. 2018). We then included body mass (Faurby et al. 2018), which is a general proxy of species' decline and extinction risk in mammals (Cardillo et al. 2005); body mass represents species spatial requirements, including both sensitivity to habitat fragmentation and ability to disperse (Swihart et al. 2003), and also their sensitivity to human pressure. We included reproductive strategy, which is an important factor allowing species to rapidly establish in new areas under climate change (Angert et al. 2011); we selected two traits able to represent mammal species position along the fast-slow continuum of reproductive strategies (Bielby et al. 2007): gestation length, a proxy of reproductive output and weaning age, a proxy of reproductive timing. These latter two traits had missing data which were imputed from other life-history traits and phylogeny (Soria et al. 2021), using the R package 'missForest' (Stekhoven and Bühlmann 2012) as in Penone et al. (2014). During imputation process, species phylogeny was represented by extracting phylogenetic eigenvectors (Diniz-Filho et al. 1998) from the PHYLACINE dataset (Faurby et al. 2018). That phylogeny was derived using a hierarchical Bayesian approach with a posterior distribution of 1000 trees, which represent uncertainties in topology and branch lengths. Ten imputed datasets were produced, each based on a different tree from the phylogeny, allowing us to test the sensitivity of our results to imputation uncertainty. We decided to only use the average trait values across imputations, after verifying the effect of phylogenetic uncertainty on data imputation was negligible in terms of predicted niche class (the class with the highest probability from the multinomial model did not change when using traits imputed from alternative phylogenies). We also tested whether directly including phylogenetic relationships improved the performance of our niche prediction models, see below, and verified this was not the case as phylogenetic eigenvectors did not lead to an overall significant improvement in the AIC of our models (Supporting information).

Third, we accounted for the level of human land-use to which species were exposed through time, as anthropogenic driver of change in niches We measured human land use as the proportional amount of agricultural land within each species' historical range for the years 4000 BC and 2017 AD. The former year corresponds to the Mid-Holocene (MID) climatic period from Worldclim (Hijmans et al. 2005), which we used for representing past realised niches (below). Land-use change has been recognised as the key driver of species decline globally (Newbold et al. 2016), and it is expected to act synergistically with climate change (Mantyka-Pringle et al. 2015). We used the HYDE dataset to derive current agricultural coverage (Goldewijk et al. 2017) and the KK10 dataset to derive historical coverage, as this was demonstrated to better represent past land use compared to HYDE (Kaplan et al. 2011). We acknowledge that human colonisation was globally asynchronous, and human impact on species has started at different periods in different continents. But we selected a period when significant levels of human impact were present in each continent, and agricultural practice had started to intensify in at least some areas worldwide. In order to derive the best estimate of human land use, we measured the quartiles of the distribution of this pressures within species past ranges, to then select the value leading to highest predictive performance of the variables (see below 'Modelling change in realised climatic niche').

Representing realised climatic niches

We defined the past and present realised climatic niches of each species by considering the past climatic conditions within their historical range and the current conditions in the current range using the Worldclim dataset. We considered past climatic conditions in the MID period (ca year 4000 BC) as obtained by the IPSL-CM5A-LR and the MPI-ESM-P general circulation models (GCMs). These GCMs were chosen due to their differences, in order to represent the uncertainty of climatic model prediction (Knutti et al. 2013). We averaged the results based on those two GCMs to account for uncertainty in past climatic projections. In addition, given uncertainty around reconstruction of historical ranges, we also considered conditions at an earlier period, the Latest Interglacial (LIG; ca 130 000 years ago) to represent a different 'past climate' for comparison. We then considered present climate as that referring to the period 1960–1990 (Hijmans et al. 2005). For each time period, a set of 10 bioclimatic variables were extracted from the Worldclim dataset (Hijmans et al. 2005, Otto-Bliesner et al. 2006, Braconnot et al. 2007), previously identified for their ability to model mammal species' climatic preferences (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. We extracted climatic conditions within the pre-impact and current distribution range of each species at a resolution of 30 arc-seconds (approximately 1 km at the equator), which is the common resolution available across the various climatic datasets we analysed. We represented climatic conditions throughout each species' range by sampling the centroid of each 2.5 arc-minutes grid cell (approximately 5 × 5 km at the equator) within the coarse species ranges, as a compromise between spatial coverage and computational feasibility.

The delineation of realised niches was done using the open source platform R (<www.r-project.org>) and the package 'ecospat' (Di Cola et al. 2017). We treated the pre-impact and current species distributions in a similar way to how native and non-native distributions are treated when investigating niche change for invasive species. We followed Broennimann et al. (2012) in defining a gridded niche space for each species, delimited by the two major axes of a principal component analysis (PCA) built on the above-listed bioclimatic variables. We verified that the first two component of the PCA represented between 69.4% and 88.8% (under the IPSL-CM5A-LR GCM) or between 73.9% and 88.7% (under the MPI-ESM-P GCM) of the inertia for the species analysed. We defined such environmental space by using past and present climate within each species' biogeographic domain as the reference (i.e. background) climatic regions, and the climate registered within pre-impact and current species distribution as proxy of realised climatic niches. This implies each species is assigned to a 'study region' that represents its biogeographical realm (or realms). We projected the PCA scores of the past and current climate experienced by the species onto the gridded ecological space, to define smoothed density of 'occurrences' (in this case pixels within the range) using a kernel density function. We represented the past and current niches of species, separately, as the polygons encompassing the species 'occurrences' in the gridded ecological space (as defined by the PCA bivariate plot). In doing so, we only retained those grid cells that were part of the top 95% highest density values of grid occurrences.

We classified categories of change in the realised climatic niches of terrestrial mammal species by considering the relative size and position of the niche polygons in the gridded environmental space (Fig. 1). In particular, we defined four categories of niche change: 'shrink', when a species' niche has reduced over time; 'shift', when a niche has changed position without substantial reduction in its variability; 'stable', when a niche has not substantially reduced or shifted; 'expand', when a niche has increased in size over time.

We defined thresholds of tolerance below which niche changes were considered minimal, and the species classified as 'stable'; this prevented the model from being over-sensitive to data uncertainty (e.g. in terms of past climate and species distributions). We tested incremental tolerance thresholds of 5, 10 and 20% to separate niche stability from niche change, both in terms of shifts in niche position (stable versus shift) and niche size (stable versus shrink/expansion).

We also measured the overall climatic stability by comparing the current and past climate within the historical range of each species. By measuring the proportion of past climatic space that is retained in the present, we were able to represent the effect of regional climate change for each species. We used this metric of overall climate stability as one of the predictors in our model.

Modelling change in realised climatic niche

To select the variables better able to represent intrinsic and extrinsic drivers of niche change, we run a Random Forest model using the R package 'randomForest' (Liaw and Wiener 2002). Random Forest is a non-parametric machine-learning technique, which measures variable importance by looking at the decrease in model's classification accuracy if the values of a predictor variable are randomly permuted. We used the estimate of variable importance to select the most appropriate variables to be used in the subsequent step of multinomial model. Using the selected variables, we ran multinomial logistic regression models to predict the probability of species to be assigned to a given class of niche change, using the R package 'nnet' (Venables and Ripley 2002). The same model structure was repeated under different past climate scenarios (in terms of GCM and time period), after verifying that the selected variables are not correlated with each other (Pearson's $r < 0.7$). All continuous variables were scaled to improve comparability of model's coefficients.

As the dataset was largely imbalanced towards species in the 'shrink' category (under all climatic scenarios considered), we employed a subsampling approach where we selected a number of species in the 'shrink' category equal to the number of species in the second most-numerous category. This way, we reduced the risk of favouring the correct prediction of shrink species against that of species in other (less represented) categories. We repeated this sampling approach 100 times, generating 100 'reduced' datasets that were each analysed independently. The results of the 100 model runs were then aggregated for subsequent analyses.

We measured the models fit using *Nagelkerke's* pseudo-R^2 (Nagelkerke 1991), and evaluated the models performance using a leave-one-out validation approach. The validation routine was performed by iteratively excluding one species at a time, and then using the model calibrated on all other species to predict the probability that the left-out species belongs to any of the four classes of niche change. We compared the predicted class probabilities with the original (observed) class of each species. We measured the model's classification accuracy in a binary way, and in a continuous way. First, we defined a 'predicted class' for each species, as the class with the highest assigned probability by the model; comparing such class with that observed for the species allowed us to estimate the percent correctly classified (PCC) species. We estimated both the overall classification accuracy, across all species and the accuracy for species in each separate category of niche change. Second, we reported the predicted probability of species in each observed category of niche change to belong to each of the four categories; in this case the expectation is that the observed class would have a higher probability than any other classes.

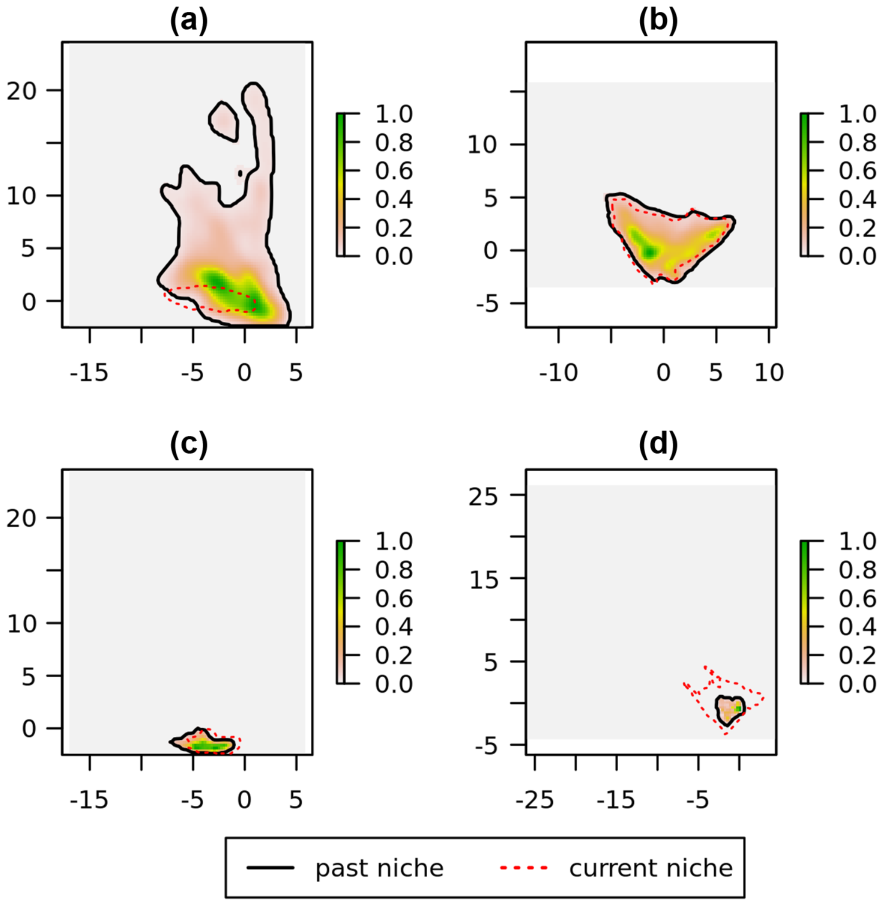

Figure 1. Categories of change in the realised climatic niches of terrestrial mammal species, derived by comparison of past climate in historical distribution (black solid line) and current climate in current distribution (red dashed line). Each plot represents niches into a two-dimension principal component analysis space. The density of species distribution within the past niche is represented as an orange-to-green gradient. The four panels represent: (a) an example of niche 'shrink', the Ethiopian wolf *Canis simensis*; (b) an example of niche 'stability', the spectacled bear *Tremarctos ornatus*; (c) an example of niche 'shift', the mountain zebra *Equus zebra*; (d) an example of niche 'expansion', the coyote *Canis latrans*.

We estimated the model coefficients and represented the relationship between key predictors in our model and the probability of species being in a given category of niche change. To represent the latter relationships, we produced partial effect plots that represent the effect of one variable (e.g. body mass) on the response (e.g. probability of the species to belong to the category 'stable niche') while holding all other variables constant.

Table 1. Performance of multinomial models for predicting categories of climatic niche change, using a tolerance of 20% to separate niche change from niche stability under alternative past climates: mid-Holocene under global circulation model IPSL-CM5A-LR (MID/IP); mid-Holocene under global circulation model MPI-ESM-P (MID/ME); last interglacial (LIG). For each climate scenarios, 100 models were run on randomly reduced datasets, where the 'shrink' category was made as numerous as the second most numerous class. The following stats are reported as mean (and SD in parenthesis) across the 100 runs: Nagelkerke pseudo-R^2, overall percentage of correctly classified species (PCC), class-averaged percentage of correctly classified species.

	Pseudo-R^2	PCC (overall)	PCC (class)
MID/IP	0.65 (0.032)	0.46 (0.036)	0.42 (0.028)
MID/ME	0.57 (0.029)	0.45 (0.023)	0.36 (0.018)
LIG	0.71 (0.021)	0.52 (0.038)	0.48 (0.032)

Results

Model's ability to classify change in realised niches

We run a Random Forest model on the full dataset (Supporting information), and retained the following variables as the most important ones to represent our chosen predictors of niche change: climatic stability, change in distribution, realm, 25th percentile of present land use, 25th percentile of past land use, gestation length, body mass, weaning age, percentage invertebrate diet.. The multinomial model built on these variable, and based on the full dataset, led to imbalanced performance, higher for the shrink class than other classes, due to the imbalance in class numerosity (Supporting information). Under any climatic scenario, using higher tolerance thresholds to separate stability from change

(20%) led to an increase in the variance explained by the model, a decrease in the overall prediction accuracy (across all species), and an increase in the class-averaged prediction accuracy. A threshold of 20% to separate niche stability from niche change led to the best overall performances, under all climate scenarios. The LIG climate resulted in higher model performance compared to MID climate.

When running 100 iterations of the multinomial model across reduced datasets, each with equal representation of different niche classes, we obtained more balanced model's performance compared to the full-data model iteration (Table 1). Models run on the reduced datasets had good variance explained, and moderate overall prediction accuracy under a 20% tolerance threshold (Table 1). Good balance in these models' predictions was reflected in class-level prediction accuracy, where observed species classes were predicted to have the highest probability for most species (Fig. 2). This latter performance was much less balanced if based on the full dataset (Supporting information). There was an exception for species in the 'niche expansion' category, the least numerous class (representing just 4–9% of species), which were typically misclassified as shift. Once again, the LIG climate resulted in slightly higher model performance compared to MID climate.

Drivers of change in realised climatic niche

After merging the result of the multinomial models based on the two GCMs for the MID climate, and across 100 runs on reduced datasets, we found that different niche categories were best predicted by different sets of variables (Supporting information). As expected, overall climatic stability was a strong discriminant of stable versus shrinking niche, with a less strong effect on the prediction of other classes. Past land use was a relatively strong predictor of stable niche, while current land use was a predictor of niche shift versus shrink together with gestation time and, to a lesser extent, weaning age. Body mass and invertebrate diets were predictors of niche expansion.

When looking at partial plots of the relationship between model predictors and the probability of being in a given class

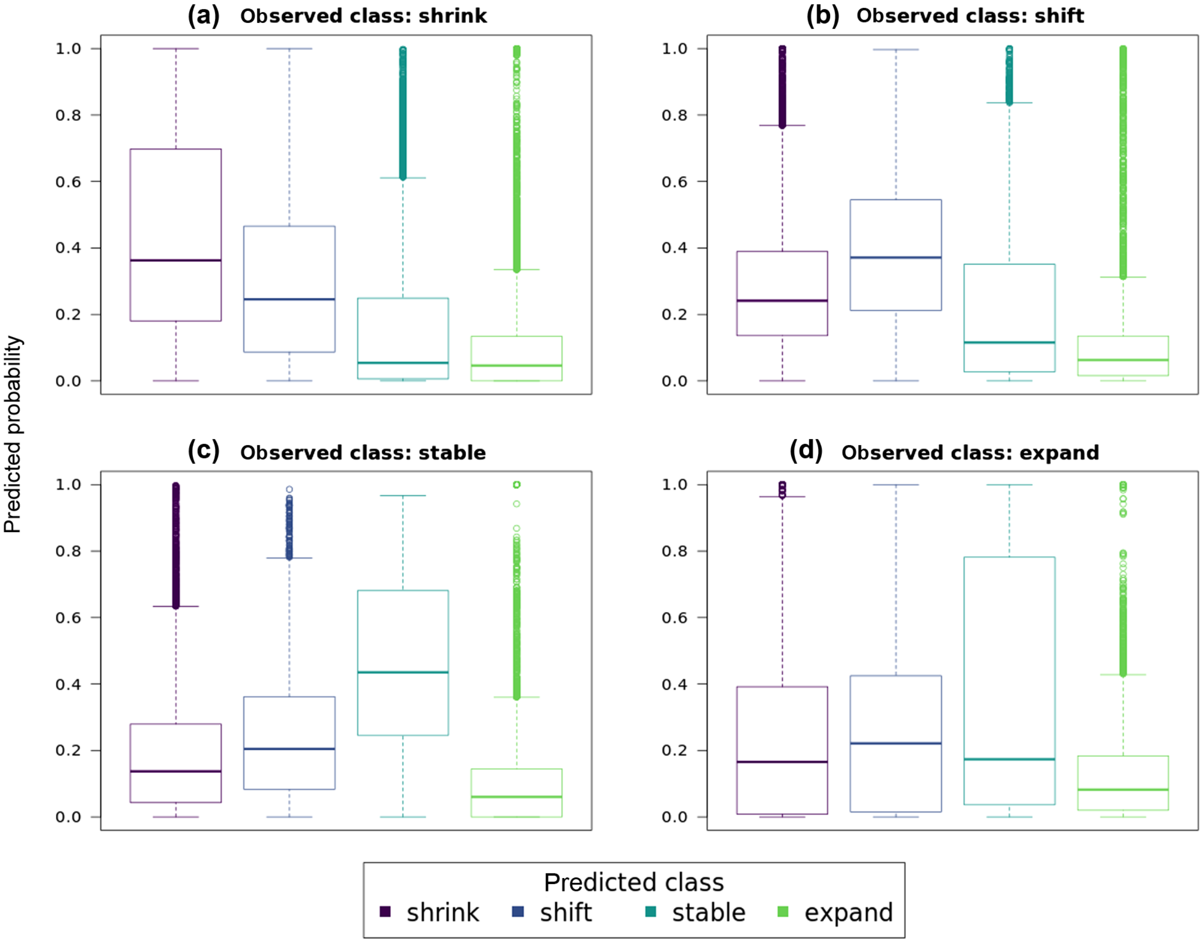

Figure 2. Probability to belong to different categories of niche change, for species in different observed categories, as predicted by a multinomial model based on Mid-Holocene climate (under two global circulation models) and a tolerance of 20% to separate niche change from niche stability. Each set of boxplots reports the probability of species within an observed niche category (reported in the plot title) to belong to any of the four categories. The data derive from 100 models run on randomly reduced datasets, where the 'shrink' category was made as numerous as the second most numerous class.

of niche change, we found that moving from low climatic stability to medium-high stability reduces the probability of niche shrink and increases the probability of having niche shift; moving towards very high climatic stability rapidly increases the probability of having a stable niche (Fig. 3a). The probability of undergoing niche shrink dropped very rapidly as climate stability became high – i.e. when ca 70–75% of the original climatic space was preserved depending on the climate model (corresponding to a value of ca 0 on the averaged scaled axis in Fig. 3a). Substantial reduction in the size of distribution range between the past and the present instead led to rapid increase in the probability of niche shrink, with rapid decline in the chances of niche stability (Fig. 3b).

When considering diet, we found species consuming higher percentage of invertebrate food had a higher probability of niche expansion (Fig. 4). When considering life-history traits instead, we found species were more likely to undergo niche shrink as their body mass increases, with the exception of very large species (i.e. pachyderms) which were less likely to undergo niche shrink; in fact the curve shows an inflection point at ca 3.5 (Fig. 3b), which correspond to the scaled body size value of the Indian rhinoceros *Rhinoceros unicornis*. Larger species were also much more likely to expand their niche, and less likely to show niche shift or stability. Species with longer gestation times were much more likely to undergo niche shift and less likely to face niche shrink or stability. Species with longer weaning age instead were more likely to face niche shrink, and less likely to have niche stability or expansion (Fig. 4).

When looking at agricultural land use, we found the level of past land use increased the probability of niche shrink while the level of current land use increased the probability of niche shift. Both past and current land use decreased the probability of stable niche (Fig. 5).

Discussion

We focussed our analyses on terrestrial mammals, given the availability of distribution data for all species both at present (IUCN 2018) and before substantial human impact occurred (Faurby and Svenning 2015). Terrestrial mammals make fundamental contributions to key ecological processes such as predation, herbivory and seed dispersal, but are facing high risk of extinction (Fragoso et al. 2003, Soulé and Estes 2003, Pringle et al. 2007, Hoffmann et al. 2011). Yet, their ability to adapt to rapidly changing climate (or lack thereof) is an essential element to consider when forecasting future extinction rates and defining appropriate conservation measures (Pacifici et al. 2017). We found over half of the species analysed (i.e. species that underwent anthropogenic range alteration) faced a shrink in their realised climatic niche, while only ca 15% retained a stable niche. This result emerged despite using a conservative threshold of 20% to separate niche stability from niche change. Such conservative threshold minimised the risk of identifying changes that were an artefact of data uncertainty (especially for past climate and species distributions), and at the same time resulted in the best performing model (in terms of validation) compared to less conservative thresholds.

From the random forest model, climatic factors were the strongest correlates of niche change, followed by anthropogenic range modification and biogeography; land-use change was the next important factor, followed by species' life history. At intermediate or low levels of climatic stability – i.e. when less than 70–75% of the original climatic space was maintained within a species' historical distribution – species were more likely to undergo niche shrink than any other category of niche change, irrespective of other variables (life history and anthropogenic pressure). Unsurprisingly, at high

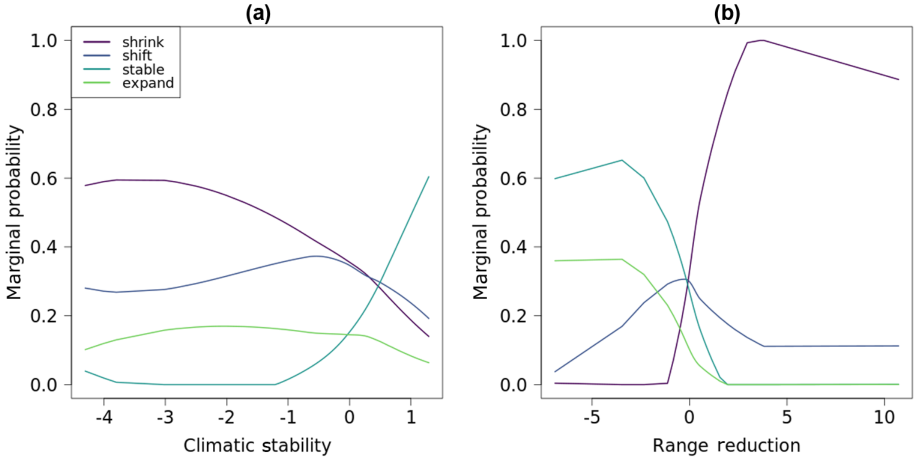

Figure 3. Averaged partial effect plot of the relationship between climatic and distribution factors and the probability of species to be assigned to one of four categories of niche change (shrink, stable, shift, expand), using Mid Holocene as the reference past climate and two alternative global circulation models. Panel (a) represents the effect of climatic stability (percentage original climatic space maintained), panel (b) represents the reduction in size between past versus present species distribution. The data derive from 100 models run on randomly reduced datasets, where the 'shrink' category was made as numerous as the second most numerous class. All values were scaled from their original units, for use in the multinomial model.

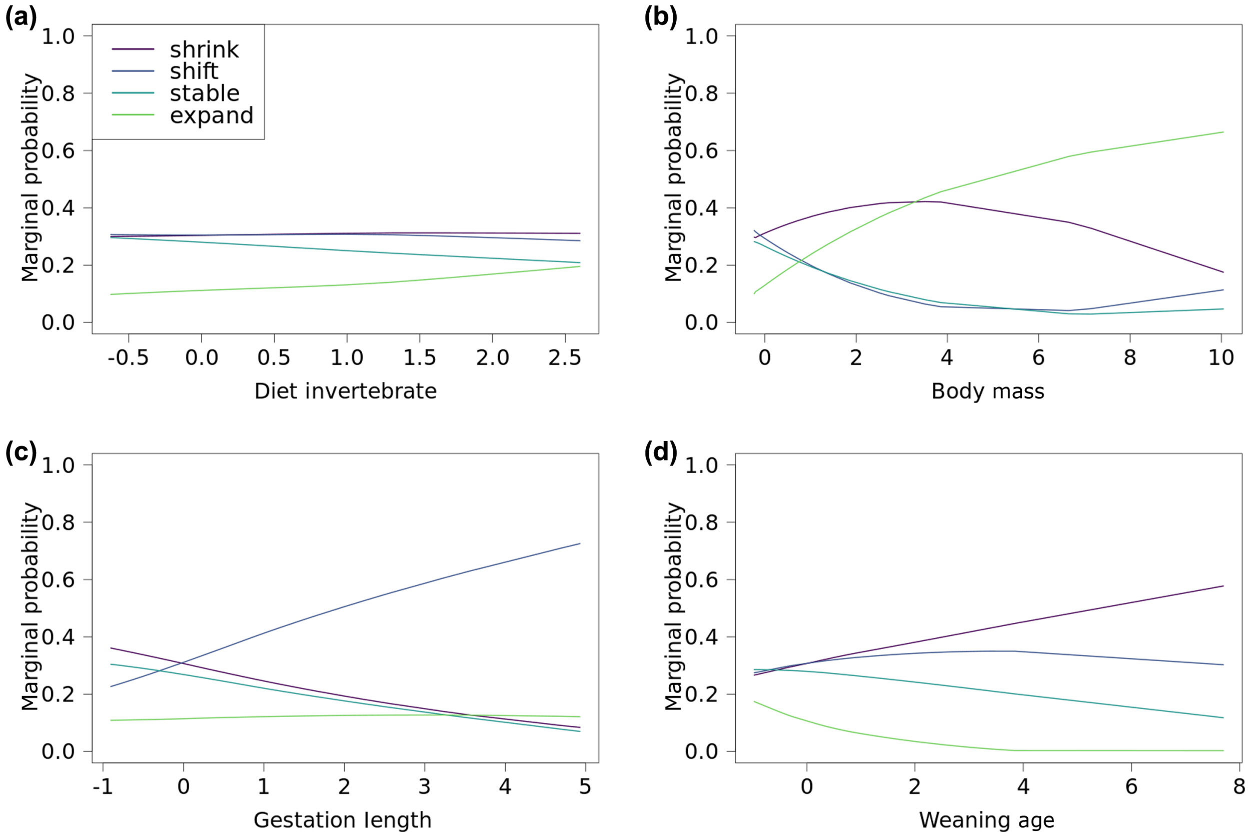

Figure 4. Average partial effect plots of the relationship between species intrinsic characteristics and probability of species to be assigned to one of four categories of niche change (shrink, stable, shift, expand), using Mid Holocene as the reference past climate and two alternative global circulation models. Panels represent: (a) species diets, as percentage of invertebrate food consumed; (b) species' body mass (grams); (c) gestation length (days); (d) weaning age (days). The data derive from 100 models run on randomly reduced datasets, where the 'shrink' category was made as numerous as the second most numerous class. All values were scaled from their original units, for use in the multinomial model.

levels of climatic stability species were instead very likely to have a stable niche. The probability of having an expanding niche was also higher as climatic stability increased, while the probability of species to undergo niche shrink was very low. Low levels of climatic change increased the chances of species shifting their niches (i.e. without any substantial reduction or expansion), which was less the case under both highly unstable and highly stable climates. This result points towards the ability of species to cope with (or even take advantage of) low levels of climatic change, through small readjustments in their realised climatic niche. These readjustments might still be within species' fundamental niche limits, even if some level of change might allow for evolutionary adaptation over the time frame considered in our study (Hoffmann and Sgró 2011), which would imply a more direct correlation between realised and fundamental niche dynamics.

The clear dominance of the niche shrink category when climate stability was not high might imply that species will be unable to cope with the current velocity of climate change, in case local adaptations are lost with portions of the realised niche. This level of niche conservatism under a 6000 year time frame raises concern about future biodiversity scenarios, given the current acceleration in the pace of climate change (Loarie et al. 2009, van Vuuren et al. 2011). Both plasticity and evolutionary changes have proven to occur rapidly in a number of taxa (Hendry et al. 2008, Urban et al. 2014), including in species that have invaded new territories and in native species that face biological invasions (Carroll 2008). But evolutionary adaptation to projected climatic changes in the next decades would require rates of evolution that are largely unprecedented (Quintero and Wiens 2013), which jeopardizes the persistence of species if they are unable to track suitable climate by natural dispersal or human-mediated translocation.

We found species with certain biological characteristics are more likely to undergo niche shrink. Large-bodied species for example were more likely to undergo niche shrink compared to smaller species, and less likely to show niche shift or stability. There was an exception however for pachyderms, which might be due to some difficulties in the model to predict these (few) species. A correlation between niche shrink and large body mass might depend on the large mammals' vulnerability to human impact, which determines low resistance to niche erosion. In fact high body mass is also

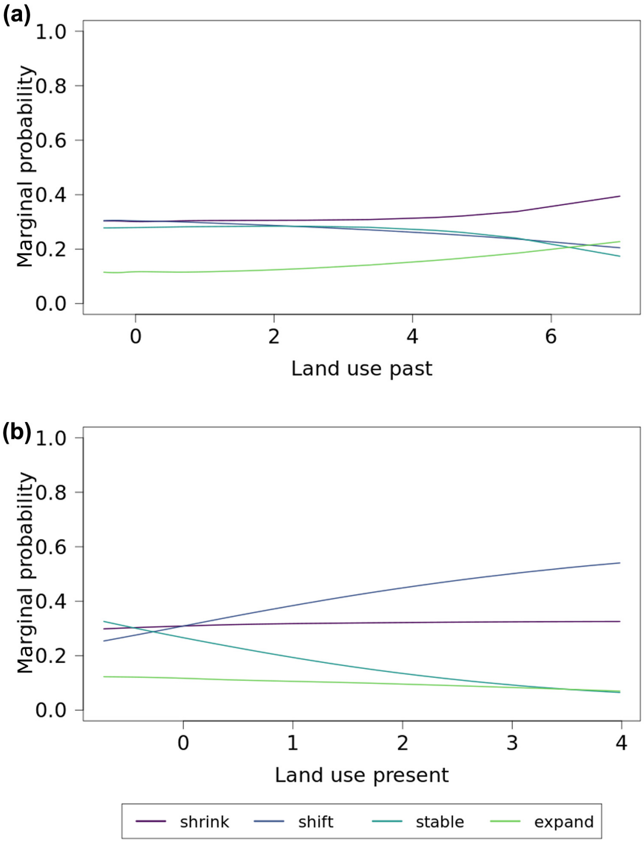

Figure 5. Average partial effect plot of the relationship between human pressure and probability of species to be assigned to one of four categories of niche change (shrink, stable, shift, expand), using Mid Holocene as the reference past climate and two alternative global circulation models. Panel (a) represents historic proportional agricultural land coverage within species range, while panel (b) represents current coverage. The data derive from 100 models run on randomly reduced datasets, where the 'shrink' category was made as numerous as the second most numerous class. All values were scaled from their original units, for use in the multinomial model.

a correlate of geographic range contraction (Pacifici et al. 2020). Larger species have higher potential to extend their distribution range via long-distance dispersal (Santini et al. 2013), but are also typically characterised by slower life histories compared to smaller species (Bielby et al. 2007) and are more sensitive to human impact (Cardillo et al. 2005). In fact, this result is reflected when looking at weaning age, a proxy of reproductive timing (Bielby et al. 2007), with longer values associated with higher probability of niche shrink. This complements previous works on population trends showing that species with late weaning age have a higher probability of decline (González-Suárez and Revilla 2013), thus providing key information on the role of intrinsic traits as a buffering mechanism against extinction. Instead we found gestation time, a proxy of reproductive output (Bielby et al. 2007), was positively associated with niche shift and negatively associated with niche shrink or stability. We found the main effect of diet was determined by invertebrate food items, with higher percentage of invertebrate diet leading to lower probability of niche stability and higher probability of expansion. This might imply highly insectivorous species have higher potential to exploit new climates, also considering most highly insectivorous species are small-bodied and fast-reproducing (Pineda-Munoz et al. 2016).

Human pressure is known to alter species climatic niches, even if comprehensive information is still lacking due to uncertainty in past information on species distribution, climatic conditions and human presence (Walther et al. 2005). In fact some evidence of how humans have altered species' realised niche is already available, for example analyses on the giraffe *Giraffa camelopardalis* and African elephant *Loxodonta africana* in the last 150 years show a reduction in their climatic niche as a consequence of poaching, fragmentation and conflicts (Martínez-Freiría et al. 2016). We found species responded to past and current levels of agricultural land use in slightly different ways. Higher levels of land-use change within a species' historical distribution determined higher probability of niche shrink. Current land use was instead associated with higher probability of niche shift. This result might have emerged because part of the current human influence occurs over portions of the natural species distributions which have been lost. Species might be able to adapt to human pressure inside their present-day distributions, which already resisted to some level of historical pressure. When low levels of climate change affect these core distribution areas, species might show some adaptation capacity via niche shift mechanisms. Interestingly the probability of niche expansion increased with past land use intensity. This result might represent a possible facilitation of human–wildlife coexistence in those areas when human colonization started earlier (Carter and Linnell 2016), but we are cautious in this interpretation because our model had poor performance in predicting niche expansion.

Our model has demonstrated poor performance in predicting the 'niche expand' category due to the very limited number of species which showed a substantial increase in their niche breadth over time. This implies our understanding of the mechanisms of niche expansion is still limited, until additional species examples are identified. A promising field of research in this case is represented by invasive species (Broennimann et al. 2012). Invasive species might maintain their original realised climatic niche in the invaded region (Petitpierre et al. 2012), or exploit a wider variety of climatic conditions and shift or expand their niche (Lauzeral et al. 2011). Understanding more of the dynamics and drivers of niche change for these species can shed light on the past dynamics of niche change for native species.

We identified the conditions under which species are unlikely to maintain a varied niche, potentially losing their climate adaptive potential. Our results showed that even intermediate levels of climatic instability lead to high risk of shrink in niches, while holding other factors constant. This means areas which will experience substantially different climates in the future should be given special attention to understand whether threatened and restricted-range species might undergo rapid decline. Interventions that facilitate natural dispersal, or assisted colonisation, should be carefully evaluated for these species, as part of international strategies to combat the effects of climate change on biodiversity such as the Convention on Biological Diversity and the United Nation Framework Convention on Climate Change.

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Author contributions

MDM framed the study with support from CR, LM, MP. MDM carried out the analyses. MDM, MP, LM and CR discussed and interpreted the results. MDM wrote the manuscript with support from MP, LM and CR.

Data availability statement

Climatic, biological and human-pressure variables measured for each species, under each climate scenario, are available from Dryad at: <https://doi.org/10.5061/dryad.5x69p8d2q>.

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