SAPIENZA
UNIVERSITÀ DI ROMA

Department of Environmental Biology

PhD in Environmental and Evolutionary Biology, XXXIV Cycle
PhD thesis

PROJECTED EFFECT OF GLOBAL CHANGE ON SPECIES' CHANGE IN EXTINCTION RISK

PhD candidate
Carmen Diana Soria

Supervisors
Dr. Carlo Rondinini
Dr. Michela Pacifici
Dr. Stuart Butchart

BirdLife
INTERNATIONAL

Inspire4Nature

Acknowledgments

To my supervisors, Carlo Rondinini, Michela Pacifici and Stu Butchart. I cannot thank you enough for trusting me with this project, supporting and accompanying me all the way. You have guided me and given me the freedom to explore. Thanks for listening and helping with all my questions and caring on a professional and personal level. Thanks to Ana Rodrigues for helping me be a better researcher and sharing her infectious passion for conservation.

During this project, I was incredibly lucky to be part of three amazing research groups, the GMA, BirdLife International, and Inspire4Nature. I made not only professional colleagues but also friends that I hope will accompany me for a long time. Thanks for making me feel at home and for sharing all the highs and lows. Even though we were apart during most of this thesis due to COVID, I still felt accompanied in the distance. I would like to especially thank Marta, Dario, Lisa, Dino, Andrea Cristiano, Valeria, Ivon, Cristina, Gonzalo, Matt, João, Kathrin, Joe, Konstantina, and Prabhat.

Maria, I do not know how to express how thankful I am for sharing this journey with you. Thanks for believing in me when I could not and for helping me with all the big and small things. Not only did we do a PhD together, but we also built a home along the way. Thanks for making me a better researcher and person.

Diego, thanks for accompanying me and for all the feedback, especially when discussing ideas, concepts and statistics. Thanks for sharing your stories, finding cosmic improbabilities between unseen stars is something I immensely cherish. Thanks to María Leo for helping me hugely throughout the PhD, as an amazing friend and researcher. We climbed mountains, resolved life crises, and tried to write coherent scientific sentences together.

Thanks to my family, especially to my mother and my uncle Gonzalo, for sparking my love for science and to my siblings for supporting me. Thanks to all my friends, thinking of all of you makes my heart full, I would not have made it here without you. This thesis is not my own but of all you that have accompanied me throughout the years.

This project was possible thanks to the economic support of the European Union’s Horizon 2020 research and innovation programme (Marie Skłodowska Curie grant agreement No 766417).

List of contents

Summary

Climate change has become one of the major drivers of biodiversity loss, its effects are not only already evident across all levels of biological organization (from genes to ecosystems) but are projected to increase in the coming decades. The probability of a species or population being negatively impacted by climate change (i.e., risk) is determined by the occurrence of adverse climatic events or trends (i.e., hazard), the occurrence of the species or population in areas that could be impacted (i.e., exposure), and their predisposition to be adversely affected, including their sensitivity or susceptibility and lack of capacity to cope or adapt (i.e., vulnerability). Species or populations can adapt to adverse climatic conditions by shifting their geographical distribution or adapting *in situ*, generally by changing their phenology, morphology or physiology.

Recent efforts to assess the impacts of climate change have predominantly relied on bioclimatic niche modeling, which predicts species' or populations' distributions by linking their geographical range and bioclimatic variables. However, these models assume that all species are affected and will respond to climate change similarly, and do not consider differences in vulnerability and exposure. Trait-based assessments have aimed to address this gap, identifying which traits influence risk, allowing assessing multiple species simultaneously in a simple way and serving as a useful tool for prioritizing conservation actions, especially in the absence of distribution data. However, their applicability can be limited as they are not spatially explicit, the relationship between traits and responses is still uncertain, there are gaps in trait data availability and the approach is generally implemented at the species level, ignoring intraspecific differences in exposure, vulnerability and hazard. The objective of this thesis is to overcome some of these limitations for birds and terrestrial non-volant mammals.

To overcome gaps in mammal trait data availability, I compiled in my first chapter *COMBINE: A Coalesced Mammal Database of Intrinsic and Extrinsic traits* data for 54 traits for 6,234 mammal species, using data from 14 different data sources. These traits covered aspects such as physiology, reproduction, behavior, longevity, diet, and dispersal. I further filled in gaps in the data through a phylogenetic multiple imputation procedure, providing a complete dataset for 21 traits. All data sources and imputed data were flagged, facilitating identifying the origin of the data. This dataset constitutes a useful tool for large-scale ecological and conservation analyses that use traits, including identifying species at risk from climate change.

In my second analytical chapter, *Relative latitude, temperature increase and breadth of climatic niche influence mammal populations' response to climate change*, I identified current terrestrial non-volant mammal responses to climate change and the intrinsic traits and environmental factors influencing risk. To achieve this, I first performed a literature review on responses to climate change and categorized them into changes in (a) distribution and abundance, (b) phenology, and (c) morphology. I also identified the direction of each type of response: expansion or contraction for distribution and abundance, advance or delay for phenology, increase or decrease for body size, and no change if no response was detected. To model the relationship between risk from climate change and intrinsic and environmental factors, I focused exclusively on distribution and abundance responses due to their direct relationship. I then selected and obtained data for a series of intrinsic traits and environmental factors previously associated with climate change risk. To account for intraspecific variability in environmental factors, I identified populations of the species that experience similar climatic conditions. As these populations were distributed across large geographical areas, I grouped the responses by species and country, reducing the number of instances of opposing or mixed responses (i.e., different studies for the same species and country reporting distribution and abundance contractions and expansions or phenological advances and delays) and allowing the inclusion of the location of the response within the population. I obtained 382 responses belonging to 130 species located in 30 countries. Most of these responses were distribution and abundance responses (80.6%) while phenological and morphological changes constituted 4.5% (17 responses) and 10.2% (39 responses) respectively. The remaining 4.7% did not fit into any of these categories. Regarding distribution and abundance responses, there were more than twice as many contractions (46.43%) as expansions (20.78%), while in 32.79% of cases there was no clear response. The results of our model indicated that contractions were more likely at the warm edge of the population, while expansions were more likely at the cold edge. Small litter size, hibernation, high temperature increase, low climate seasonality and low altitudinal breadth were also linked to an elevated risk of experiencing a negative response.

In my third analytical chapter, *Local environmental factors influence bird distribution and phenological responses to climate change*, I followed the same approach but focused on bird distribution and abundance and spring phenological responses to climate change. I also gathered data for nine intrinsic bird traits that have been previously hypothesized to be relevant in determining responses to climate change. This allowed me to identify which intrinsic traits and environmental

factors influence experiencing distribution contractions or expansions and spring phenological advances, delays or no changes. I obtained 3,012 responses for 918 species located in 32 countries, 60% of them were distribution and abundance responses and the remaining 40% were spring phenology responses. I found that environmental factors played an important role in determining both distribution and abundance and phenological responses to climate change. Maximum temperature, restricted climate seasonality, relative latitudinal position, and maximum longevity influenced the probability of experiencing contractions and a subsequent increase in risk. Similarly, maximum temperature, climate seasonality, relative latitudinal position, and temperature increase influenced the probability of experiencing advances in spring phenology.

The results presented in this thesis constitute an advance in current knowledge on the variables influencing responses to climate change locally and serve as a starting point for future research.

Chapter I

General Introduction

Biodiversity crisis in the Anthropocene Epoch

Humans have become the main driver of contemporary environmental change and have profoundly transformed the planet in a short length of time (Lewis & Maslin 2015), leading to the start of a new geological epoch named the Anthropocene (Crutzen 2002). The fingerprints of human activity on Earth are already evident at multiple levels, from major biogeochemical cycles to species' evolution (Lewis & Maslin 2015; Otto 2018), even marking the stratigraphic record, where they will probably last millions of years (Waters et al. 2016).

Nature has been substantially affected by human activities, and global indicators of species status and ecosystem health mostly indicate rapid declines (WWF 2018; Díaz et al. 2019). The current species' extinction rate is considerably greater than average background rates, with some authors suggesting that the sixth mass extinction in Earth's history has started (Pievani 2014; Ceballos et al. 2015; Cowie et al. 2022). Extinction constitutes an irreversible fate, resulting in the loss of not only species and populations, but also the wide range of characteristics associated with them, including genetic information, phenotypes, behaviors, and interactions with other species (Ceballos et al. 2020).

Recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), issued a report identifying the main drivers behind the loss of nature and quantifying their relative negative impact (Díaz et al. 2019). From largest to smallest impact, these drivers are changes in land and sea use, direct exploitation of organisms, climate change, pollution, and invasion of alien species. The impact of these drivers has accelerated during the past 50 years, causing a change in nature unprecedented in human history. Nature's contributions to people, such as resource provision, climate regulation, air and water quality maintenance, or plant pollination, are essential for human persistence and wellbeing. Therefore, avoiding further biodiversity loss is vital (Díaz et al. 2019).

Among these drivers of loss, climate change not only occupies the third position in order of impact when considered in isolation but also exacerbates and amplifies the effects of other drivers (Díaz et al. 2019; Schulte to Bühne et al. 2021). Climate change effects are projected to increase (IPCC 2021; Arneth et al. 2020; Nunez et al. 2019), potentially becoming the main driver of loss in the next decades (Newbold 2018). Identifying the mechanisms through which climate change is currently impacting biodiversity will help to predict future impacts more accurately and to design effective measures that will minimize negative outcomes for biodiversity.

Climate change: definition and effects

The Intergovernmental Panel on Climate Change (IPCC) is the principal international organization synthesizing and assessing current knowledge on human-induced climate change. It was established in 1988 by the World Meteorological Organization (WMO) and the United Nations Environmental Programme (UNEP). Its ultimate goal is to periodically provide policymakers with objective and comprehensive scientific information on the impacts and risks of climate change, as well as to suggest adaptation and mitigation solutions. The IPCC is currently undertaking its 6th Assessment, of which the Physical Science Basis section was recently published in 2021 (IPCC 2021), providing the most updated knowledge on climate change. Here, I summarize the key points of this report.

The IPCC defines climate change as ‘a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings such as modulations of the solar cycles, volcanic eruptions and persistent anthropogenic changes in the composition of the atmosphere or in land use’ (IPCC 2021). The concentration of greenhouse gases – especially CO_2 – present in the atmosphere has increased since 1750 as a product of human actions, leading to an increase in the temperature of the atmosphere and the ocean and land surface. The rate of warming we are currently experiencing is unprecedented in at least 2,000 years, and each of the last four decades has been increasingly warmer than the previous since 1850. Surface temperatures have increased on average 0.99ºC since 1850-1900, an increase that has been higher in terrestrial environments (1.59ºC) than in the ocean (0.88ºC). Global ice is melting as a consequence of temperature increase, causing the retreat of glaciers globally and spring snow cover in the Northern Hemisphere since 1950, and the decrease of Arctic sea ice between 1978-1988 and 2010-2019. Mean sea level has exponentially increased worldwide since the beginning of the 20th century, reaching 0.2 m in 2018, due to the additional water from melting ice sheets and glaciers and the expansion of seawater caused by temperature increase. Global average precipitation has also increased since 1950 due to increased evaporation, this increase becoming more marked since 1980.

Climate change has also affected weather and climate extremes, including heatwaves, heavy precipitation events, droughts, and tropical cyclones, amongst others. Heat extremes (e.g., droughts and heatwaves) and heavy precipitation events have become more intense and frequent, while cold events (e.g., cold spells) have gone in the opposite direction. Global major cyclones not only have increased over the past four decades, but the latitude of their intensity peak has also shifted northward in the western Northern Pacific. Compound extreme events (such as simultaneous heatwaves and droughts) have also increased their frequency since 1950.

Biodiversity responses to the effects of climate change

These changes in climate have deeply affected biodiversity, both directly and indirectly. The study of the effects of climate change and its subsequent response is an active field of current research, with an increasing number of studies (Parmesan 2006; Bellard et al. 2012; Scheffers et al. 2016). These studies are spread across taxonomic groups, although there are differences in the type of observed response (e.g., distributional responses are mostly documented for animals, while phenological responses are most frequently documented on plants; Parmesan 2006). Currently, the largest gaps in knowledge are at the geographic level, as studies have been predominantly carried out in North America, northern Europe, and Russia, while Africa and Asia have the least information, and studies in these areas are mostly concentrated in South Africa and Japan (Parmesan 2006; Scheffers et al. 2016). Most studies have been conducted at local scales, such as research stations or protected areas, although there are some at the country or region level (e.g., France or New South Wales). Very few are at a scale that encompasses the whole distribution of a species (i.e., continental scale for terrestrial species; Parmesan 2006). The effects of climate change have already been recorded at all levels of biological organization, from genes to communities and ecosystems (Parmesan 2006; Scheffers et al. 2016), but most studies are at the organism or species level.

Changes in climate may result in an organism or species no longer being adapted to the environmental conditions within its distribution. To survive, they can adapt through two types of mechanisms, micro-evolution and phenotypic plasticity (Bellard et al. 2012; Thurman et al. 2020). Micro-evolution consists of genetic adaptation through directional selection of existing genotypes or mutations (Salamin et al. 2010) and is heritable. On the other hand, phenotypic plasticity is the production of a different phenotype – with no changes to the genotype – caused by a change in the environmental conditions (Pigliucci et al. 2006), and generally only lasts the lifetime of the individual (Charmantier et al. 2008). Both mechanisms can result in changes in morphological, physiological or behavioral characteristics and can occur on different timescales (Bellard et al. 2012; Nogués-Bravo et al. 2018). Disentangling the relative role of each mechanism is challenging and infrequently studied, although recent analyses indicate that phenotypic plasticity is the predominant mechanism (Charmantier et al. 2008; Charmantier & Gienapp 2014; Merilä & Hendry 2014).

Responses to climate change have been observed along three distinct and non-exclusive axes, independently of the mechanism driving the response. These three axes, identified by Bellard et al. (2012), are spatial, temporal and 'self'. Spatial responses consist in tracking the appropriate climate conditions in space, predominantly through dispersion, but also local shifts at the habitat or microhabitat level. Temporal responses consist in shifting the timing of activities to keep up with other factors that cyclically vary and that have changed their timing due to climate change. Lastly, 'self' responses consist in adapting in situ to the new conditions, through physiological or behavioral modifications. Based on the adaptive capacity of the species or population, responses can also be classified into two non-exclusive axes, namely "persist in place" or "shift in space" (Thurman et al. 2020), depending on if the species or population is able to survive in situ or move to an area with suitable bioclimatic conditions.

Populations or species that fail to adapt along one or more of these axes when exposed to adverse climatic conditions may go extinct locally or globally. Relatively few species went extinct during recent ice ages, potentially indicating that the strategies to cope with climate change were sufficient (Botkin et al. 2007), providing a glimmer of hope in the present situation. Nonetheless, other studies indicate that current responses might not be enough, especially if global temperatures continue rising (Nunez et al. 2019; Radchuk et al. 2019).

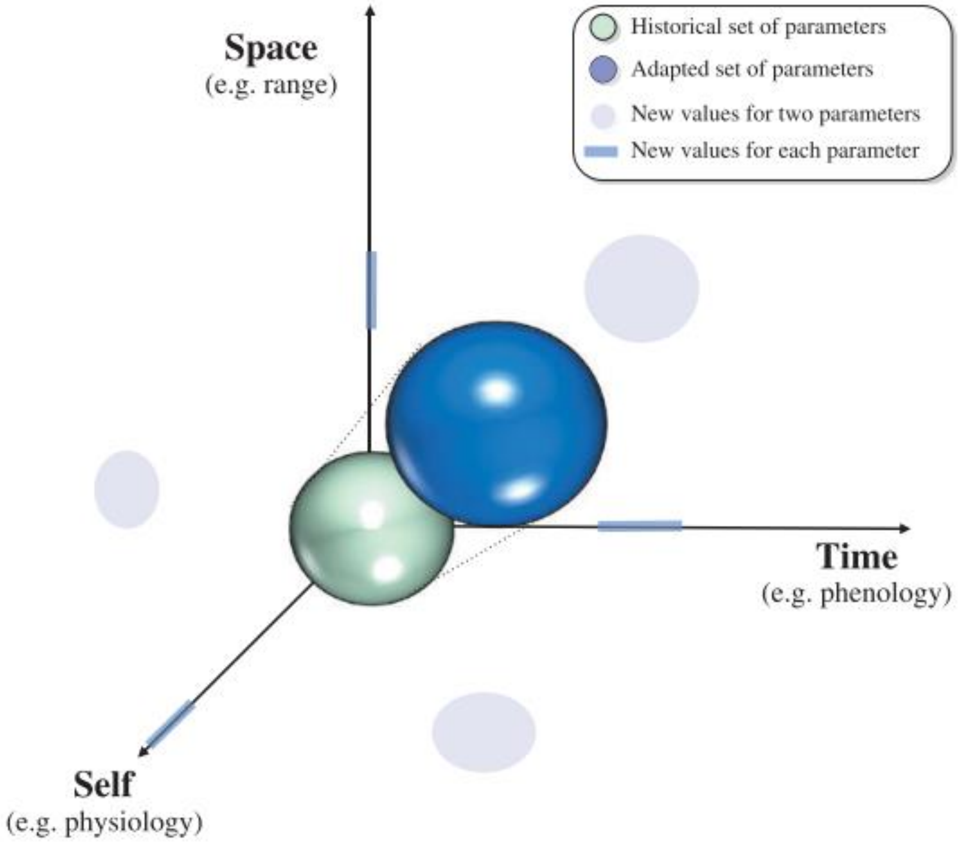


Figure 1.1: The three directions of responses to climate change through phenotypic plasticity or evolutionary process: space, time and 'self' (from Bellard et al. 2012).

Extinction risk from climate change

The Bramble Cay melomys (*Melomys rubicola*) was the first mammalian species whose extinction was uniquely attributed to climate change (Waller et al. 2017). Although currently no other extinctions have been exclusively attributed to climate change, we cannot assume that climate change has not been the main cause of other recent extinctions, especially of lesser-known and monitored species. Climate-induced extinctions will probably become more frequent in the future, although predictions of loss range widely (Thomas et al. 2004). A meta-analysis using 131 predictions of extinction risk, estimated that 7.9% of species will become extinct and the areas more impacted will be South America, Australia and New Zealand (Urban 2015). However, when considering both niche shifts and dispersal, that estimation increased to between 16% and 30% (Roman-Palacios & Wiens 2020).

The IPCC definition of climate change risk is not specific to biodiversity and covers other factors related to human societies, economy and wellbeing. I have therefore tailored these definitions to cover only biodiversity, the subject of this thesis, using as reference other studies that have done this with previous IPCC reports (Pacifici et al. 2015; Foden et al. 2018). Extinction risk due to climate change can be defined as the potential for adverse consequences caused by the potential impacts of climate change, as well as those derived from responses to climate change. Risks result from the dynamic interaction between climate-induced hazards and the exposure and vulnerability of the affected biological system (Reisinger et al. 2020).

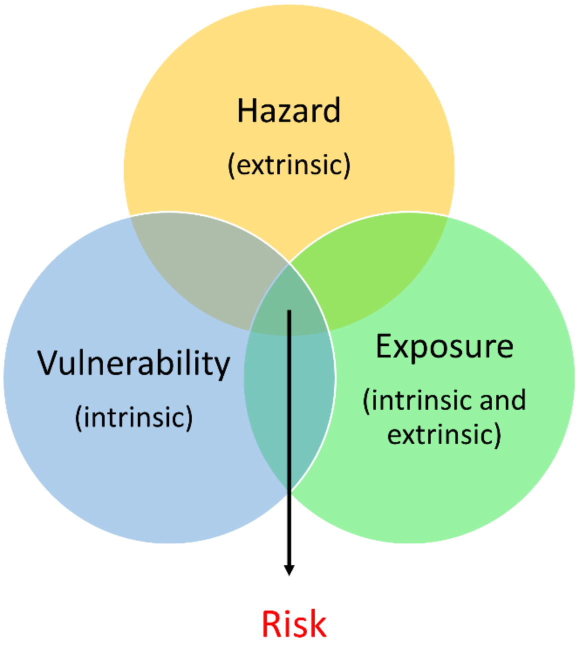


Figure 1.2: Components of risk from climate change (adapted from Foden et al. 2018).

Hazard is the potential occurrence of a natural or human-induced physical event that may cause impacts on species or populations (IPCC 2019). In the context of extinction risk, this refers to potentially adverse climatic conditions that may cause a species or population to fall outside its climatic niche, constituting an extrinsic factor to the biological unit considered. Exposure is the presence of organisms, populations or species in areas that could be adversely affected (IPCC 2019). This generally consists of being in areas that are experiencing the effects of climate change, but also the existence of physical structures (e.g., caves, microhabitats) or behaviors (e.g., hibernation, fossoriality) that could help avoid or mitigate the impact of hazardous events, constituting both an intrinsic and extrinsic factor. Vulnerability is the propensity or predisposition to be adversely impacted by climate change, including sensitivity or susceptibility (e.g., physiological thermal tolerance, dietary requirements) and lack of capacity to cope or adapt (e.g., dispersal capacity, behavioral flexibility, evolutionary potential) (IPCC 2019). Vulnerability is exclusively intrinsic to the organism, population or species and is determined by their traits.

Traits, extinction risk, and responses to climate change

Traits are well-defined, measurable properties of organisms, generally obtained at the individual level, and are often compared across species (McGill et al. 2006; Violle et al. 2007; Degen et al. 2018). They have been categorized in a multitude of ways, the most frequent being life-history traits, which influence the allocation of resources to growth, body maintenance and reproduction (e.g., age of reproduction, longevity or fecundity) and functional traits, which influence organismal performance (e.g., diet, habitat use or limb morphology). Traits are what ultimately mediate extinction risk and responses to climate change, as no two species present in the same area will be equally exposed or vulnerable. Previous studies support this, finding that species with certain traits are more prone to go extinct than others (Cardillo et al. 2008; Di Marco et al. 2014). In the context of climate change, such traits have generally been those associated with movement ability, ecological generalization, reproductive strategy, ability to endure adverse conditions and competitive ability (Estrada et al. 2016).

Study taxa

Mammals and birds are among the best-known and best-studied groups of species, with trait information readily available (e.g., Jones et al. 2009; Kissling et al. 2014; Wilman et al. 2014) and many studies published on the responses of these species to climate change (e.g., Pacifici et al. 2017; Usui et al. 2017; Freeman et al. 2018; McCain 2019). The latest versions of the International Union for Conservation of Nature (IUCN) Red List identified 5,968 mammal and 11,162 bird species (https://www.iucnredlist.org/) of which 1,333 (22%) and 1,445 (13%) have respectively been classified as threatened (i.e., Vulnerable, Endangered or Critically endangered). Both groups are largely distributed throughout the globe (Ceballos & Ehrlich 2006; Loiseau et al. 2020), play key roles in ecosystems as pollinators, seed dispersers, predators and pest regulators, and contribute to nutrient cycling and ecosystem engineering (Sekercioglu 2006; Whelan et al. 2008; Jones & Safi 2011; Michel et al. 2020). They also provide food, materials and cultural services to people (Moleón et al. 2014; Michel et al. 2020). Thus, losing mammal and bird diversity will potentially impact many other species, including humans. Birds are also considered good bioindicators of environmental change, potentially informing the fate of other lesser-known taxa under the effects of climate change (Pearson et al. 2005, BirdLife International 2013).

Mammals and birds have similar thermal physiologies, both groups being endotherms. Endotherms maintain a high and constant body temperature, which is largely decoupled from the direct influence of ambient conditions, providing a high degree of thermal independence (Khaliq et al. 2014). However, when the environmental temperature falls outside of the thermoneutral zone of the species, they need to make a high energy investment to control their body temperature and return to the thermoneutral zone (McNab 2008; Kingma et al. 2014). Thermal physiology has been identified as a crucial factor when determining the potential impacts of climate change on species (Huey et al. 2012), therefore mammals and birds will probably be affected by climate change through similar mechanisms. Based on their intrinsic traits and the environmental characteristics they experience throughout their range, Pacifici et al. (2017) estimated that 47% of terrestrial non-volant threatened mammals and 23% of threatened birds may have already been negatively impacted by climate change in at least part of their distribution. Therefore, bird and mammal conservation in the face of climate change may already be a pressing issue.

Scientific rationale of the thesis

Traits can be used as predictors of extinction risk from climate change (‘trait-based approaches’; Pacifici et al. 2015; Foden et al. 2018), allowing the identification of potentially threatened species or populations for which we lack empirical data. Traits can also be used as predictors of responses to climate change, such as temporal shifts in migration (Usui et al. 2017). However, there are several potential barriers to doing this: the relationship between traits and risk is still uncertain, there are gaps in the availability of trait data (Foden et al. 2018), and most trait data and studies are at the species level, overlooking intraspecific trait variation. Additionally, risk and responses to climate change are not only a product of traits (which influence vulnerability and exposure) but also the environmental conditions (i.e., climate and topography, influencing hazard and exposure). Considering different types of responses separately is also essential, as the relationship between risk and response may not be as clear in temporal and ‘self’ changes as in spatial responses (Maxwell et al. 2019). Therefore, to identify accurately which traits are associated with experiencing risk or showing specific responses to climate change, it is necessary to consider intraspecific variability in intrinsic traits and environmental factors. Doing so would facilitate the identification of populations that are or will be affected by climate change and the mechanisms behind their response.

Thesis structure and objectives

This thesis comprises three main analytical chapters (Chapters II to IV). Here, I briefly describe the objectives of each chapter in order of appearance:

Chapter II: Gather intrinsic trait data for mammals, combine them using a common and updated taxonomy, and fill information gaps.

To be able to identify the relationship between traits, responses, and risk from climate change, it is necessary to have good quality data on the wide range of traits that have been previously theorized to be relevant. Mammal trait data is distributed across many separate datasets, each with its taxonomy, data collection, and management. Here I created a trait database for mammals globally through the evaluation and combination of previously published datasets.

Chapter III: Review recent terrestrial non-volant mammal responses to climate change and identify which intrinsic traits and environmental factors influence risk at the local level.

Here I identify recent terrestrial non-volant mammal responses to climate change through a literature review and classify them into changes in distribution (spatial), phenology (temporal), and morphology ('self'). I then identify the species-level intrinsic traits (obtained in Chapter II) and population-level environmental factors that influence risk by analyzing their relationship with local changes in distribution.

Chapter IV: Review recent distributional and spring phenological responses of birds to climate change and identify which intrinsic traits and environmental factors influence their outcomes at the local level.

Here I identify recent distributional and spring phenological responses of birds to climate change through a literature review. I then gather species-level intrinsic trait data and population-level environmental factors and identify which of these are associated with local range contractions (and a subsequent increase in risk) and spring phenological advances.

Chapter II

COMBINE: A Coalesced Mammal Database of Intrinsic and Extrinsic traits

Carmen D. Soria[1,2]*, Michela Pacifici*[1]*, Moreno Di Marco*[3]*, Sarah M. Stephen*[3,4] *and Carlo Rondinini*[1,5]

1. Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy
2. BirdLife International, Cambridge, UK
3. Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy
4. Department of Conservation Biology, Centre for Nature Conservation, Georg-August-University Göttingen, Von-Slebold-Str. 2, 37075 Göttingen, Germany
5. Global Wildlife Conservation Center, College of Environmental Science and Forestry, State University of New York, Syracuse, USA

Abstract

The use of species' traits in macroecological analyses has gained popularity in the last decade, becoming an important tool to understand global biodiversity patterns. Currently, trait data can be found across a wide variety of data sets included in websites, articles, and books, each one with its own taxonomic classification, set of traits and data management methodology. Mammals, in particular, are among the most studied taxa, with large sources of trait information readily available. To facilitate the use of these data, we did an extensive review of published mammal trait data sources between 1999 and May 2020 and produced COMBINE: a COalesced Mammal dataBase of INtrinsic and Extrinsic traits. We aimed to create a taxonomically integrated database of mammal traits that maximized trait number and coverage without compromising data quality. COMBINE contains information on 54 traits

for 6,234 extant and recently extinct mammal species, including information on morphology, reproduction, diet, biogeography, life-habit, phenology, behavior, home range and density. Additionally, we calculated other relevant traits such as habitat and altitudinal breadths for all species and dispersal for terrestrial non-volant species. All data are compatible with the taxonomies of the IUCN Red List v. 2020-2 and PHYLACINE v. 1.2. Missing data were adequately flagged and imputed for non-biogeographical traits with 20% or more data available. We obtained full data sets for 21 traits such as female maturity, litter size, maximum longevity, trophic level, and dispersal, providing imputation performance statistics for all. This data set will be especially useful for those interested in including species' traits in large-scale ecological and conservation analyses.

Site description

Global trait data compilation for extant and recently extinct mammals from already published sources.

Data availability

All datasets mentioned in this chapter can be accessed through the publication "COMBINE: a coalesced mammal database of intrinsic and extrinsic traits" (Soria et al. 2021) available on https://doi.org/10.1002/ecy.3344.

Taxonomy

This database includes two different taxonomies at the species level: PHYLACINE v. 1.2 (Faurby et al. 2018; 5,831 species) and IUCN Red List (IUCN version 2020-2; 5,961 species). We included both taxonomies in our data set, as they can be used for different purposes. PHYLACINE v. 1.2 taxonomy covers species that have lived since the last interglacial period (around 130,000 years ago until present) and allows phylogenetic trait analyses. IUCN Red List taxonomy ensures compatibility with all IUCN Red List products such as current species' conservation status, range maps and information contained in species' assessments. COMBINE is also mostly compatible with other large-scale mammal data compilation initiatives such as the ASM Mammal Diversity database (https://www.mammaldiversity.org/), focused on taxonomy; and the VertLife initiative (http://vertlife.org/data/), focused on vertebrate phylogenetic data.

Research methods

We conducted a bibliographical search for mammal trait databases and data included in peer-reviewed articles published between 1999 and May 2020. We searched for relevant data combining keywords relevant to the target group ("vertebrate*", "mammal*"), the type of source ("database*", "dataset*", "data") and the target information ("trait*", "life-history trait*") in Web of Science and Google Scholar. In addition to the sources identified in the initial search, we included others discovered by snowball principle (i.e., papers and databases cited in the selected sources). We found and reviewed 43 of these data sources (trait_databases.csv). To maximize efficiency, we kept a subset of 14 sources that focused on all mammal species globally, and we selected traits that had over 10% data coverage. For sources that had raw data, we computed the mean value of the trait per species. For every species, the variable-specific source is referenced in a separate source data set (trait_data_sources.csv; variable information in Supplementary Material Appendix S2.2). To ensure compatibility between sources and avoid data loss, we aggregated all of them under a common taxonomy (IUCN 2020 version 2020-2). Nomenclatural mismatches were due to taxonomic changes, misspellings, and formatting inconsistencies. Mismatches were resolved following a two-step procedure. We first extracted synonyms from the IUCN Red List website (https://www.iucnredlist.org/) using the IUCN API in R environment (R Core Team 2020) and verified potential matches. Those that could not be resolved automatically were checked manually and assigned to the target nomenclatures. The following species were not recognized under IUCN (2020) or PHYLACINE v. 1.2 taxonomies and were not included in the analysis: *Brotomys contractus*, *Bubalus bubalis*, *Cavia porcellus*, *Cercopithecus albogularis*, *Cervalces scotti*, *Clidomys osborni*, *Elephas antiquus*, *Felis catus*, *Gazella erlangeri*, *Ictidomys parvidens*, *Melomys spechti*, *Natalus lanatus*, *Nesophontes longirostris*, *Nesophontes submicrus*, *Nesophontes superstes*, *Plagiodontia araeum*, *Pseudopotto martini*, *Pteronotus pristinus*, *Saiga borealis*, *Solenodon aredondoi*, *Spirocerus kiakhtensis*, *Vicugna pacos* and *Vombatus hacketti*. The nomenclature conversion table between the taxonomies of all data sources and IUCN v. 2020-2 can be found in taxonomic_crosswalk.csv. Nomenclatural and taxonomic changes fell into 4 categories, and we derived data for these species based on the description below:

A. Genus and/or specific epithet change: Data was kept unchanged.
B. New species discovered: No data.
C. Species to subspecies: For all species included in the databases, that have been recently moved to the subspecies level in the last IUCN Red List taxonomic revision or PHYLACYNE 1.2 classification, we took the mean value of continuous traits between these formerly considered species and assigned it to the new formal species (except maximum longevity, upper and lower elevation limits). For maximum longevity and maximum elevation limit we kept the maximum value, and for minimum elevation limit we kept the minimum, to reflect the maximum and minimum values. For categorical traits, we used the value that better captured the variation between subspecies (e.g. if one subspecies is herbivorous and the other omnivorous, we considered the species to be omnivorous).
D. Subspecies to species: Data were kept unchanged. If there were no trait data for the new species in any of the data sources, we used the data of the species from which it was split. These data are flagged in trait_data_sources.csv as “data split from (species name)”.

To select only species-specific reported data (i.e., those coming from direct observations) we did not consider calculated values (e.g., imputed, mean value of congenerics or confamilials) included in the data sources.

Many of our data sources take their information from the same 7 databases and data sets (Table 2.1). To avoid pseudoreplication bias, we decided to sequentially include trait values from one source rather than taking measures of central tendencies (e.g., mean or median) from all sources for that value. The order of data inclusion (Supplementary Material Appendix S2.2) was trait-specific and based on the relevance of the source to the considered trait, presence of data verification or data quality checks and time since publication. For instance, trophic level data is probably more accurate in MammalDIET2 (Kissling et al. 2014; Gainsbury et al. 2018), a diet focused source, than in PanTHERIA (Jones et al. 2009), a more general source

Common sources	Data sources included in COMBINE
Smith et al. (2003)	PanTHERIA, EltonTraits, PHYLACINE, Pacifici et al. (2013)
Nowak et al. (1999)	PanTHERIA, EltonTraits, AnAge, Pacifici et al. (2013), Turbill et al. (2011)
Ernest (2003)	AnAge, Amniotes (Myhrvold et al. 2015)
Hayssen et al. (1993)	PanTHERIA, AnAge, Amniotes
PanTHERIA (Jones et al. 2009)	EltonTraits, AnAge, (Pacifici et al. 2013), Heldstab et al. (2018), Botero et al. (2013)
EltonTraits (Wilman et al. 2014)	PHYLACINE, Heldstab et al. (2018), Buckley et al. (2018)
AnAge (De Magalhães & Costa 2009)	Pacifici et al. (2013), Amniotes

Table 2.1. Data sources used by two or more of the databases and data sets included in COMBINE

We assembled data on a wide variety of traits, including morphology, reproduction, diet, biogeography, life-habit, phenology, behavior, home range and density; creating a common repository of already published trait data. Most traits provide information on a wide variety of orders within the class Mammalia, except forearm length which is almost exclusive to order Chiroptera (99.6% of the data). We decided to keep two different diet classifications from PHYLACINE v. 1.2 and EltonTraits (coded with the prefix “dphy” and “det” in trait_data.csv, respectively). The first provides a proportional split of each species dietary preferences across plant, vertebrate, and invertebrate food items. The second gives more detailed information on the food item consumed: invertebrates, fish, reptiles and amphibians, mammals, and birds, general or unknown vertebrates, fruits, seeds, nectar and pollen, other plant materials or carrion.

Most traits were homogenous amongst sources and could be coalesced together with minimal or no transformations (changing measurement units). The following traits, that required more complex transformations, were combined from many other traits or were calculated:

A. Activity cycle: Defined as the time of the day in which the species carries out most of its activities. Data came from EltonTraits and PanTHERIA. PanTHERIA classified species as nocturnal only, diurnal only or mixed, while EltonTraits had a non-exclusive binary measure of diurnal, nocturnal and crepuscular. We decided to follow PanTHERIA's classification, considering EltonTraits species that were not strictly diurnal or nocturnal as mixed.

B. Life-habit method: Life-habit traits indicate whether a species can be considered terrestrial, marine, or freshwater. Data came from IUCN (2020) and PHYLACINE v. 1.2. Following PHYLACINE v. 1.2, we decided to separate data from IUCN terrestrial mammals into terrestrial volant (those capable of powered flight, belonging to order Chiroptera) and terrestrial non-volant (the rest of terrestrial mammals).

C. Brain mass: Defined as the weight of the adult brain in grams. Data came from Tsuboi et al. (2018) and Heldstab et al. (2018). We decided to use brain mass instead of volume, as it was the most used unit of measurement. We converted volume to mass using the known density of mammal brain tissue of 1.036 g/cm^3 (Blinkov and Glezer 1968).

D. Adult body length: Defined as the total length from the tip of the nose to the anus or base of the tail of an adult individual. Data came from Amniotes and PanTHERIA. Gaps were filled using information from male body length, female body length, female body length at maturity and undefined sex body length from Amniotes.

E. Sexual maturity: Defined as the age at which individuals start being physically capable of reproducing. Data came from PanTHERIA and missing data was completed using female maturity and male maturity from Amniotes and AnAge, and undefined sex maturity from Amniotes.

F. Age of first reproduction: Defined as the age at which females give birth for the first time. Data came from Pacifici et al. (2013) and PanTHERIA. To fill in data gaps, we estimated the age of first reproduction as the sum of gestation length and age at female sexual maturity (Pacifici et al. 2013).

G. Dietary breadth: Dietary breadth can be used as an indicator of the number of different food elements a species consumes. Estimated as the number of different EltonTraits categories that constitute ≥20% of a species' diet (Usui et al. 2017).

H. Habitat breadth: Habitat breadth can be used as an indicator of a species' environmental tolerance. Estimated as the number of distinct level 1 IUCN habitats suitable for the species.

I. Dispersal: Defined as the distance traveled by a species between the birth site and the breeding site. Estimated for terrestrial non-volant species (bats, cetaceans, pinnipeds and sirenids were not considered) following Santini et al. (2013), using species' body mass and trophic level.

J. Altitude breadth: Calculated as the difference between the upper and lower elevation limit of a species. Data came from IUCN assessments.

K. Hibernation and/or torpor (heterothermy): Hibernation and torpor constitute adaptations that enable species to survive during adverse periods (such as cold temperatures, food shortages and droughts) by lowering their body temperature and metabolism. Torpor lasts less than 24 hours, while hibernation is defined by bouts of inactivity lasting from some days to several weeks (Ruf and Geiser 2015). Data came from Buckley et al. (2018), Heldstab et al. (2018), Botero et al. (2013) and Turbill et al. (2011). We grouped together both types of adaptations, considering them as an indicator of avoidance of adverse environmental conditions. Fully aquatic species (sirenids and cetaceans) were considered unable to hibernate (Heldstab et al. 2018).

The data set containing only reported data can be found in trait_data_reported.csv (for variable information and completeness of the reported data, see Supplementary Material Appendix AS2.1).

Imputation of missing data

Each species and trait we analyzed were characterized by the presence of missing data. The percentage of missing data per trait ranged between 3.67% for body mass to 89.16% for teat number. To fill these data gaps, making the data set ready to use for analyses, missing values were imputed for a subset of 27 traits (Supplementary Material Appendix AS2.1) with the missForest algorithm in R (Nonparametric Missing Value Imputation using Random Forest; Stekhoven and Buhlmann, 2012). This algorithm allows the imputation of categorical and continuous variables and does not need tuning parameters or assumptions of the distribution of the data (Breiman, 2001). Our subset of traits was composed of those with more than 20% data completeness that could be adequately imputed phylogenetically (i.e., we did not include the following biogeographical traits: upper and lower elevation limits, island-dwelling, island endemicity, glaciation, dissected by mountains and biogeographical realm). For diet, we only used PHYLACINE’s classification (plant, invertebrate and vertebrate) as it can be accurately imputed phylogenetically (Faurby et al. 2018, Gainsbury et al. 2018). To include phylogenetic information, we randomly selected 10 phylogenies from PHYLACINE v. 1.2 (IDs: 1, 30, 83, 181, 209, 219, 729, 756, 825, 979), and extracted 10 eigenvectors for each phylogeny to be included as variables in the imputation routine. We thus obtained a total of 10 phylogeny-specific data sets. To select the optimum number of eigenvectors, we ran an imputation routine with 5, 10, 15 and 20 eigenvectors and selected the number of eigenvectors with the highest accuracy of imputation. We ran an imputation routine over each data set, with 10 iterations per imputation, obtaining 10 complete data sets (imputation_phylo archives), with imputed data filling in gaps in the observed data. To estimate the accuracy of the imputation, we used the out of bag (OOB) error provided by the algorithm to calculate the normalized root mean squared error (NRMSE; Oba et al 2003) and the proportion of falsely classified entries (PFC), for continuous and categorical variables respectively (found in imputation_error.csv). Both estimates range from 0 (highest accuracy) to 1 (lowest accuracy). We calculated the NRMSE and PFC for each phylogeny and the mean across all of them, which can be found in imputation_error.csv. We retained all variables for which the NRMSE or PFC values were < 0.4. Imputed values are flagged in the source table, to allow easy separation from observed values (trait_data_sources.csv). The methodology we used to calculate dispersal cannot be applied to marine or terrestrial volant mammals (Santini et al., 2013). We thus estimated dispersal missing values from a separate imputation routine, including only terrestrial non-volant species. We also produced a "combined" imputed data set, by calculating the mean of the imputation value across all ten imputed data sets (for continuous variables) or the most repeated imputed value (for categorical variables). If there was a tie between the most repeated imputed values, we assigned an NA. The data set containing reported and imputed data can be found in trait_data_imputed.csv (for variable information and completeness of the imputed data, see Supplementary Material Appendix AS2.1).

Even though adequate imputation methodologies are useful to temporarily fill in data gaps, we acknowledge that it is not ideal and want to remark the importance of the collection and digitization of primary natural history data.

Data quality control procedures

We developed a two-step data validation process to identify potentially erroneous data pre-imputation. We first checked for inconsistencies in mass and longevity-related traits. For each species, adult body mass had to be higher than weaning body mass and neonate body mass; and maximum longevity higher than maturity (female, male and combined), age at first reproduction, weaning age, gestation length and interbirth interval. Nineteen longevity-related values did not meet these criteria and were not included. To check the data quality, we calculated the standard deviation (SD) between the original value and those obtained from the jackknifed multiple imputation of 10 phylogenies (same IDs and methodology as in Class IV Section C) for continuous traits included in the imputation with an NRMSE < 0.4 (brain mass, adult body length, maximum longevity, litter size, litters per year, interbirth interval, gestation length, weaning age, female maturity, age of first reproduction, and generation length). These jackknifed imputations were done by sequentially extracting 5% of the trait data, obtaining 20 tables per trait. To avoid phylogenetic bias in the extraction, species were ordered randomly. Standard deviation values can be found in SD_validation.csv. Imputation NRMSE can be found in mean_error_validation.csv.

For estimations of global model parameters that account for uncertainty in data imputation (e.g., the estimate of body mass vs. gestation time relationship), we recommend repeating all analyses independently across the 10 data sets and calculating the mean parameter and the overall variance (Nakagawa and Freckleton, 2008). For global analyses not associated with the estimate of statistical parameters (e.g., global-scale mapping of functional diversity) the use of the combined (already averaged) data set might be sufficient to users' needs. For species and site-specific studies, we encourage using more specialized data sources. Despite our efforts in gathering as much good quality data, the scope of the project implies that there were uncertainties beyond our control and intraspecific variability is not represented.

Computer programs and data processing algorithms used

Trait data were assembled using the statistical language R, version 3.6.3 (R Core Team 2020) and the R packages 'missForest' (Stekhoven & Buehlmann 2012), 'PVR' (Santos 2018) and 'ape' (Paradis & Schliep 2019).

Chapter III

Relative latitude, temperature increase and breadth of climatic niche influence mammal populations' response to climate change

Carmen D. Soria[1,2]*, Michela Pacifici*[1]*, Stuart H. M. Butchart*[2,3]*, Carlo Rondinini*[1,4]

1. Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy
2. BirdLife International, Cambridge, UK
3. Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK
4. Global Wildlife Conservation Center, College of Environmental Science and Forestry, State University of New York, Syracuse, USA

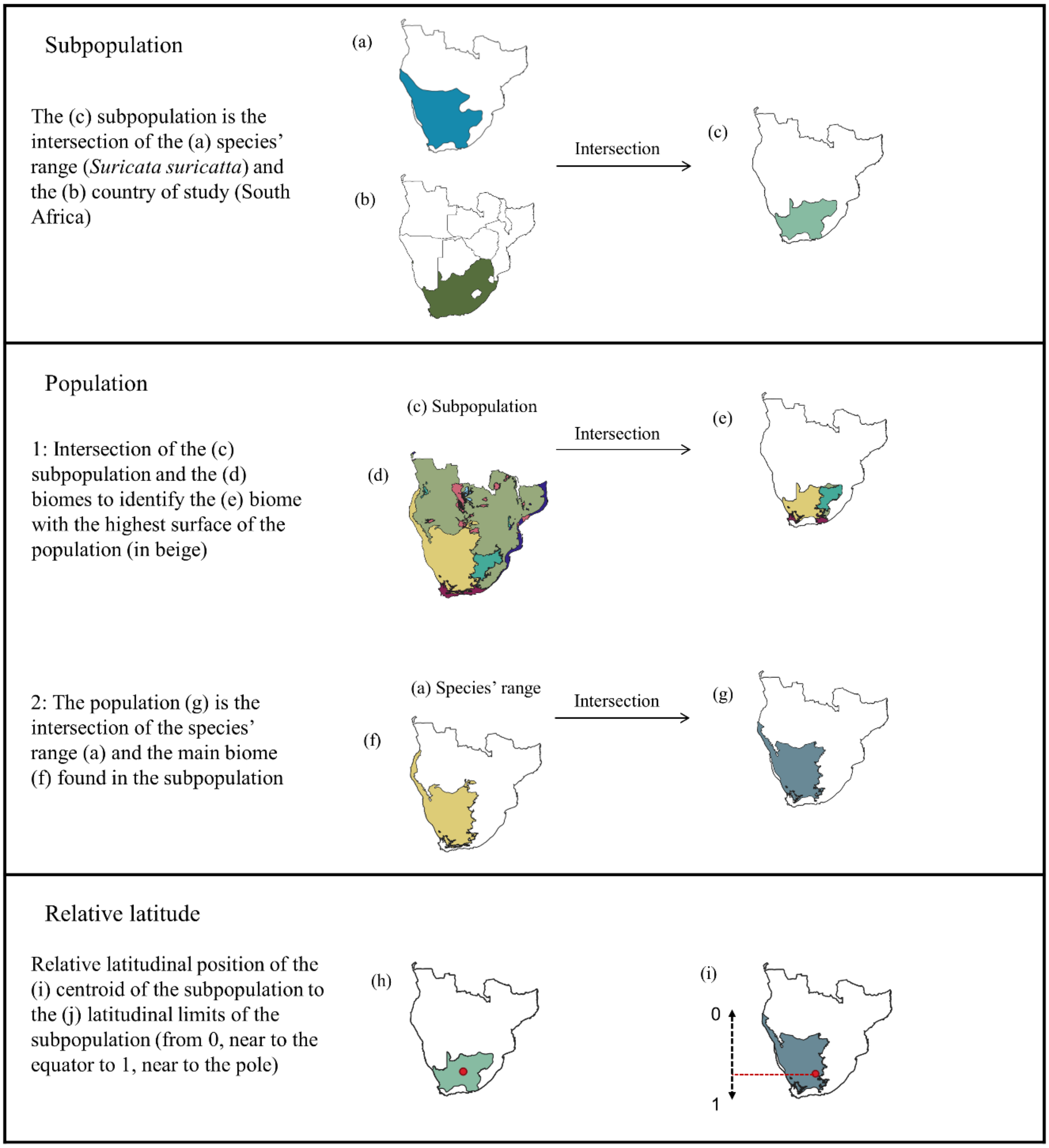
Identifying which traits and environmental factors influence risk from climate change is key to determining which populations may be under current or future threat. Previous studies have been mostly conducted at the species level, overlooking differences in climatic conditions and environmental tolerance. Through a literature review, we identified terrestrial non-volant mammal responses and modelled the relationship between changes in distribution and abundance and species-level traits and population-level environmental factors. There were more than twice as many negative responses (46.43%) as positive (20.78%), while 32.79% of cases showed no clear response. Negative responses were more likely at the warm edge of the population and positive responses at the warm edge. High temperature increase, low temperature and precipitation seasonality, low altitudinal and habitat breadth, small litter size and heterothermy were also associated with experiencing negative responses. Our results highlight the importance of location and environmental factors in determining climate change risk.

Climate change has become one of the main drivers of biodiversity loss (Parmesan & Yohe 2003; Díaz et al. 2019). Global land temperatures have increased by an average of 1.59ºC compared with the second half of the 19th century, and each of the last four decades has averaged warmer than the previous (IPCC 2021). Many species have responded to this change in climate by altering their distribution, abundance, phenology, morphology and/or physiology, experiencing local extirpations when unable to adapt to these new conditions (Bellard et al. 2012; Hetem et al. 2014). The probability of a species or population being negatively impacted by climate change (i.e. risk) is determined by the occurrence of adverse climatic events or trends (i.e. hazard), the occurrence of the species or population in areas that could be impacted (i.e. exposure), and their predisposition to be adversely affected, including sensitivity or susceptibility and lack of capacity to cope or adapt (i.e. vulnerability; IPCC 2019). Vulnerability to climate change has been previously linked to certain characteristics or traits of species (Isaac et al. 2009; Pacifici et al. 2015); for instance, ecological specialization and limited dispersal ability have been associated with increased sensitivity and low capacity to cope with climate change (Angert et al. 2011; Schloss et al. 2012; Estrada et al. 2016). Recent efforts to assess climate change risk have predominantly relied on bioclimatic niche modeling, which predicts species' or populations' distributions by linking their geographical range and bioclimatic variables (Pearson & Dawson 2003; Elith & Leathwick 2009; Pacifici et al. 2015). However, these models assume that all species are affected and will respond to climate change similarly, ignoring differences in vulnerability and exposure (Pacifici et al. 2015). Trait-based approaches have aimed to address this gap, identifying which traits influence risk, but have mostly been conducted at the species level and are not spatially explicit, assuming that all individuals of a species are exposed to the same degree of climate change and are adapted to the same conditions, irrespective of their location within the species' range (e.g., Foden et al. 2013; Böhm et al. 2016; but see Young et al. 2015 for examples of local assessments in the United States). There are already examples of particular species demonstrating contrasting responses to climate change in different parts of their distribution (Brodie & Post 2010; Gibson-Reinemer & Rahel 2015; Rowe et al. 2015; Pacifici et al. 2017; McCain 2019). Therefore, accounting for local variation in the effects of climate change and species' adaptation potential is essential in order to better understand likely impacts and to unravel the relationship between traits and risk.

This study aims to provide an overview of recently observed responses to climate change of terrestrial (i.e., excluding those species whose ranges are entirely or mostly marine such as pinnipeds) non-volant (i.e., excluding bats) mammals and to determine which traits and environmental factors influence the occurrence of negative local responses (high risk) compared with positive or no responses. Marine species and bats were not considered as data on the environmental factors that influence marine mammals are drastically different from terrestrial mammals (e.g., seawater acidity and temperature) and data on bat intrinsic traits are scarce (Pacifici et al. 2017).

Responses were obtained from a literature review of global mammal responses to climate change. To ensure that the observed response was a trend and not an exception, we only included studies that reported a change (or lack thereof) in one or more mammal species attributable to recent climate change and that spanned at least 10 years (Root et al. 2003). Of the 79 identified studies, we documented 382 responses by 130 species located in 30 countries. These responses were classified as changes in (a) distribution and abundance, (b) phenology or (c) body size (Daufresne et al. 2009; Gardner et al. 2011). Distribution and abundance responses were aggregated, as both are generally positively correlated, with larger ranges supporting larger populations (Brown 1984; Lawton 1993). We also identified the direction of each type of response: expansion or contraction for distribution and abundance, advance or delay for phenology, increase or decrease for body size, and no change if no response was detected. To model the relationship between traits and climate change risk, we focused exclusively on distribution and abundance responses. While changes in distribution size and abundance are directly linked to extinction risk (Purvis et al. 2000), the consequences of changes in phenology and body size can be more ambiguous and their association with risk is unclear (Maxwell et al. 2019). There were also insufficient cases to support robust analyses on phenological and body size responses.

Species' distributions can be spread across climatically diverse areas, so not all individuals are potentially able to endure the same climatic conditions nor experience the same degree of climate change. To represent these climatic differences, we defined as our 'population' unit the distribution of the target species within the biome in which the response was recorded (Figure 3.1). Biomes constitute areas with similar environmental conditions (Penone et al. 2016), so they can be used as potential proxies for differences in climate hazard or even adaptation. However, given biomes are extensive, responses were further aggregated by species and country (or highest administrative unit for countries larger than 2.2 million km^2) into units which, for the purposes of our analyses, we refer to as 'subpopulations', while recognizing that we have no data on actual population structure for each species (Figure 3.1). A subpopulation was considered to be expanding if it had experienced only expansions or a combination of expansions and no changes according to the studies we reviewed; a similar rationale was applied to contractions. If the subpopulation had experienced both expansions and contractions, the response was classified as mixed; if it did not show any response, it was classified as no change.



The (c) subpopulation is the intersection of the (a) species' range (*Suricata suricatta*) and the (b) country of study (South Africa)

1: Intersection of the (c) subpopulation and the (d) biomes to identify the (e) biome with the highest surface of the population (in beige)

2: The population (g) is the intersection of the species' range (a) and the main biome (f) found in the subpopulation

Relative latitudinal position of the (i) centroid of the subpopulation to the (j) latitudinal limits of the subpopulation (from 0, near to the equator to 1, near to the pole)

Figure 3.1. Designation of subpopulation, population and relative latitude. *The figure shows as an example the meerkat (Suricata suricatta) in South Africa. In the first panel, the (c) subpopulation is*

identified as the intersection of the (a) species' range and the (b) country of study. In the second panel, the population is identified by first identifying (e) biomes found in the subpopulation by intersecting the (c) subpopulation and the (d) biomes and determining the biome with the highest surface (in beige in map e). Then, the (f) biome with the highest surface in the subpopulation is intersected with the (a) species' range, producing the (g) population. Lastly, the (f) relative latitudinal position of the subpopulation results from projecting the (h) centroid of the subpopulation onto the (g) population and identifying its position relative to the (0) warm edge, closest to the equator and the (1) cold edge, closest to the pole.

We compiled a set of intrinsic traits and environmental factors (i.e., characteristics of the area, such as maximum temperature, temperature and precipitation seasonality, and altitudinal range) for each subpopulation, as well as its latitudinal position relative to the warm or cold edge of the population, and the magnitude of climate change experienced. Intrinsic traits such as body mass or dispersal distance were obtained at the species level, as comprehensive local data on these are currently unavailable. Environmental factors were obtained at the population level, and relative latitudinal position was calculated at the subpopulation level (Figure 3.1). All environmental factors were calculated as the mean value of the population (e.g., mean maximum temperature of the population). The magnitude of climate change experienced was represented by the mean difference between the present (1991-2018) and recent past (1941-1960) temperatures in the population, as major climate change started to become evident in the 1980s (Bonardi et al. 2017; Kharouba et al. 2018).

To identify which intrinsic traits and environmental factors were associated with a potential increase in extinction risk, we performed two contrasting binomial generalized linear mixed models (GLMMs), establishing contraction as the baseline response, and comparing it with expansion and no change. We could not include mixed responses as too few were documented (7 out of 185 subpopulation responses). For the first time, we were able to do this at the local level for terrestrial non-volant mammals worldwide, taking into consideration intraspecific differences in the degree of climate change experienced, location, and environmental factors. This also allowed testing hypotheses on the relationship between responses to climate change and traits at the species level and environmental factors at the intraspecific level.

Recent mammalian responses to climate change

Of the studies identified in our literature search, over half (52.5%) were conducted in North America (specifically in the United States of America and Canada) and over one-third (36.25%) in Europe. Other regions such as Africa, Asia and Oceania had little representation, with 6.25%, 2.5% and 2.5% of the studies respectively, while South America had no representation (Supplementary Material Appendix S3.6). Due to this geographical bias, the tropics were barely represented in our review, with the two most equatorial study areas located in Sichuan (China; latitude 31.46ºN) in the Northern Hemisphere and the Northern Territories (Australia; latitude 19.49ºS) in the Southern Hemisphere. This bias is also evident when comparing both hemispheres, with only 8.75% of the studies conducted in the Southern Hemisphere. Only one-third of the global landmass is located in the Southern Hemisphere, and its mainland does not expand poleward as far as in the Northern hemisphere (53.53ºS in Cape Froward (Chile) compared with 83.40ºN in Greenland). Seas and oceans constitute an effective barrier for terrestrial non-volant mammals, restricting their ability to disperse and expand into areas that become climatically suitable under climate change. This is confirmed by the studies of our review, in which out of the 16 population and abundance responses detected in the Southern Hemisphere, 11 were contractions, 4 were no changes and only 1 was an expansion.

Of the 382 recorded responses, the vast majority (80.6%, 308 responses) were distributional and abundance changes, while phenological and morphological changes constituted 4.5% (17 responses) and 10.2% (39 responses) respectively (Figure 3.2a). The remaining 4.7% (18 responses) responses did not fit into any of these categories, consisting of changes in diet, denning location, genes, adult sex ratio and color, as well as population fluctuations and habitat or longitudinal shifts (Figure 3.2a). This corroborates the findings of a previous review (Parmesan 2006), which identified that distribution changes are the most recorded type of response for animals, in contrast to plants, for which phenological responses have been predominantly recorded, although we note that shifts in bird phenology have been extensively studied (Usui et al. 2017; Radchuk et al. 2019). Hibernation and reproduction were the two seasonal behaviors represented in our review, although some mammals migrate seasonally (Fryxell & Sinclair 1988; Bischof et al. 2012). These behaviors might be more difficult to monitor as they do not happen throughout the year, which could explain why we did not find many studies on phenological changes. Additionally, bats (order Chiroptera) constitute one of the main orders of hibernating mammals, especially in temperate areas (Turbill & Geiser 2008), and including them in our literature search would potentially have yielded a higher proportion of phenological responses. The lack of body size responses is probably due to the difficulty of obtaining these data, as it requires access to live or preserved individuals or relevant body parts (e.g., skull in Balčiauskienė et al. 2018) spanning multiple generations.

Responses to climate change generally went in the expected direction (Figure 3.2a). Contractions were the most frequent distributional or abundance changes, representing 46.43% (143) of these responses, followed by no changes (32.79%, 101 responses) and expansions (20.78%, 64 responses) (Figure 3.2b). Phenological responses were primarily advances in phenology (70.58%, 12 responses), followed by delays (17.65%, 3 responses) and no changes (11.75%, 2 responses) (Figure 3.2d). Body size mainly decreased (43.59%, 17 responses), followed by no changes (33.33%, 13 responses), and increases (27.08%, 9 responses) (Figure 3.2c). However, it should be noted that even though a decrease in body size is the expected response (as a bigger body surface to volume ratio increases heat exchange with the environment), recent warming has caused an increase in body size in some populations (Eastman et al. 2012; Scheffers et al. 2016). There does not seem to be an apparent strong publication bias in distribution and abundance and body size responses, as the number of expected responses (contractions or body size decreases) and no or unexpected responses (expansions or body size increases) were similar. This is not the case for phenology, as the expected responses (advance in phenology) constituted the vast majority of the responses, although this might change if more studies were considered.

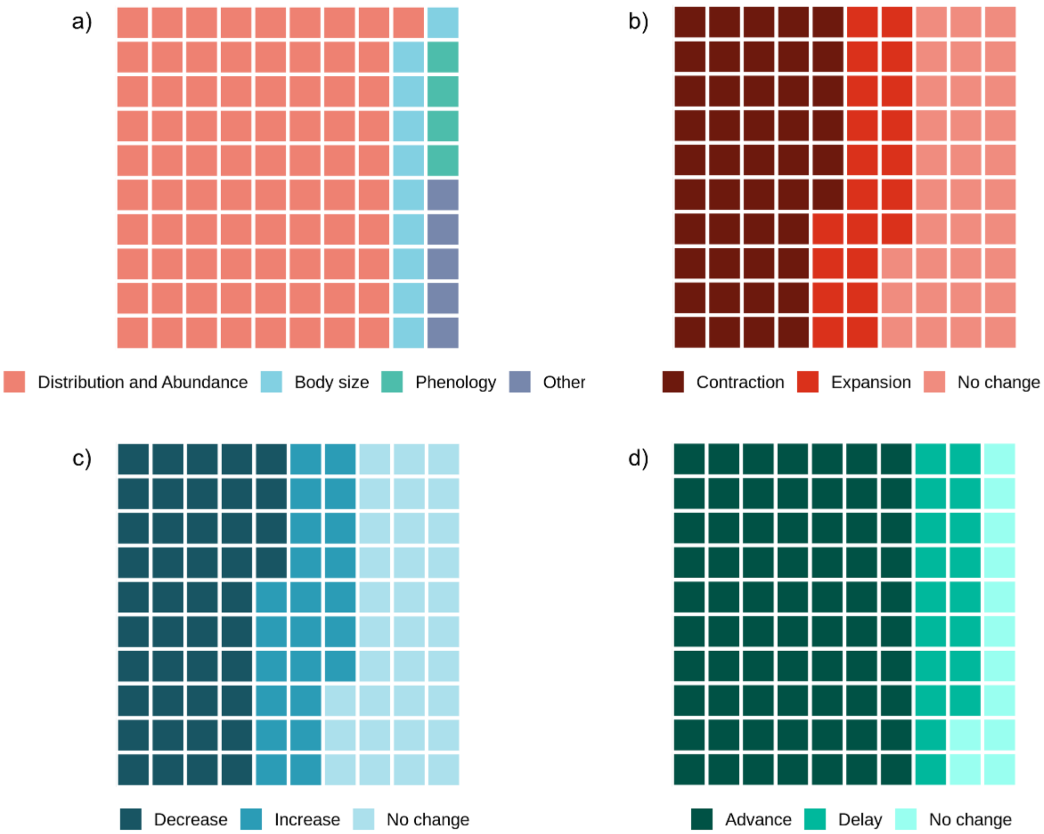


Figure 3.2. Proportion of the responses obtained from the literature review. a. *the proportion of all responses that were classified as changes in distribution and abundance (red), changes in body size (blue), changes in phenology (green) and other (purple).* ***b.*** *the proportion of distribution and abundance responses classified as contractions (dark red), expansions (medium red) and no changes (light red).* ***c.*** *the proportion of body size responses classified as decrease (dark blue), increase (medium blue) and no change (light blue).* ***d.*** *the proportion of phenological responses classified as advance (dark green), delay (medium green) and no change (light green).*

Traits and environmental factors associated with risk from climate change

We found that the latitudinal position of the subpopulation relative to the warm and cold edges of the distribution of its population was significantly associated with the observed response (Supplementary Material Appendix S3.3). Subpopulations located near the warm edge had a higher probability of experiencing contractions while those located near the cold edge had a higher probability of experiencing expansions or no changes. This pattern has already been observed when considering the average shift of taxonomic groups present in the same geographical region, with species moving away from the equator at a median rate of 16.9 km per decade (Chen et al. 2011). However, the direction of the range shift appears to be inconsistent for many species when comparing different areas of their distribution (Gibson-Reinemer & Rahel 2015). Our results indicate that poleward expansions and equatorial contractions are not occurring exclusively at the edges of the distribution of the species, but also at the edges of our climatic 'populations'. This potentially explains inconsistencies in the direction of the shift across the range, as climatically separate populations will have different edges of contraction and expansion. Contrary to our expectations, populations with a large latitudinal range had a higher probability of experiencing contractions compared with expansions and no changes (Supplementary Material Appendix S3.3 and S3.4). Populations spread across a large latitudinal range theoretically experience a wider range of climatic conditions, consequently having a higher tolerance to climate variability. However, almost all biomes with large latitudinal ranges are fully or partially located at high latitudes (i.e., Rock and Ice, and Temperate Broadleaf and Mixed Forests in both hemispheres, Tundra in the Northern Hemisphere and Temperate Grasslands, Savannas and Shrublands in the Southern Hemisphere) and most of the populations with the largest latitudinal ranges were located in these biomes, near or directly in contact with the polar edge of their respective landmass (see Supplementary Material Appendix S3.1 for Supplementary Methods of this chapter). This indicates that populations with large latitudinal ranges are also located in areas where they cannot expand towards higher latitudes, further stressing the importance of considering the location of each subpopulation.

Other environmental factors associated with contractions compared with expansions and no changes were restricted altitudinal range and high temperature increase (Supplementary Material Appendix S3.3 and S3.4). Low precipitation and temperature seasonality, restricted habitat breadth, and the intrinsic traits of small litter size and heterothermy were linked to experiencing contractions compared with no changes (Supplementary Material Appendix S3.4). Altitudinal range, as well as precipitation and temperature seasonality, were hypothesized to be indicators of the climatic conditions that the population is experiencing and to which it is potentially adapted, with higher values of these variables associated with a wider range of conditions that the population can endure. Contrary to the latitudinal range, all three of these variables followed this pattern, with higher values being associated with a lower probability of experiencing a negative response. Our expectations in relation to habitat breadth followed a similar rationale, with a wider habitat breadth indicating that the population has a higher ecological generalization and resource availability (Estrada et al. 2016), decreasing its climate change risk. Nonetheless, we note that our data on this trait were at the species level, and the results could differ if considered at the population level. Large litter size has been previously linked to greater colonization capacity, as such species tend to have a fast reproductive strategy, reaching high abundances quickly (Angert et al. 2011; Estrada et al. 2016). Although our results link this trait with experiencing no changes instead of expansions, this might be because these species tend to be small and have a lower dispersal capacity and the expansion might have gone undetected. Strikingly, heterothermy was related to higher risk due to climate change. Previous studies have identified heterothermy as an advantageous trait, allowing species to avoid adverse climatic conditions by lowering their body temperature and energy expenditure within the same day (torpor) or on multi-day bouts (hibernation) (Geiser & Turbill 2009; Liow et al. 2009). Although opportunistic (torpid) heterotherms may be better suited than homeotherms to face climate change, this might not be the case for hibernating species. An increase in seasonality may cause climate disruptions during winter dormancy, with potentially severe effects on species (Geiser 2013; Goldberg & Conway 2021). Warmer winters may also affect the conditions needed for the species to feed (e.g., reducing the length of the period in which the sea ice is sufficiently stable for polar bears to hunt; Williams et al. 2015). Out of the 27 heterothermic species included in our analysis, 23 of them undergo hibernation (or hibernation and torpor), while only 4 undergo torpor exclusively (Supplementary Material Appendix S3.5).

Conclusions

Local adaptation is a common phenomenon, with populations of the same species exhibiting trait differences across its geographic distribution, frequently matching the environmental gradient (Aitken

& Whitlock 2013; Moran et al. 2016). However, trait data are generally available only at the species level, and the majority of previous studies on the relationship between traits and risk have not been able to consider intraspecific variation (e.g., Mccain & King 2014; MacLean & Beissinger 2017; Pacifici et al. 2017; McCain 2019). By establishing as our unit of intraspecific variation the intersection of the species' distribution and the biome in which the response was recorded (population) and using data on the environmental conditions as an indicator of local adaptation (environmental factors), we were able to overcome this limitation. Furthermore, range and abundance responses to climate change are location-dependent, as range shifts towards higher latitudes and altitudes are driven by local expansions and contractions or extirpations. By considering the country in which the response was located (to define subpopulations), we greatly reduced the incidence of mixed responses (from roughly 15% in Pacifici et al. 2017, to below 4% in our study). We found that the location of the response within the population, temperature increase, climate seasonality, habitat breadth, litter size and heterothermy influenced risk from climate change. Even though not all of our variables were at the population level, our results indicate that some of the patterns that have been previously observed at the species level also occur locally, such as the degree of climate change experienced (temperature increase) and precipitation seasonality (Pacifici et al. 2017). However, we observed that traits linked to avoidance of adverse conditions, which had been previously found to be associated with a decreased extinction risk (i.e., flexible activity time in Mccain & King 2014 and fossoriality in Pacifici et al. 2017) were not significant or even associated with increased extinction risk in the case of heterothermy. The conditions experienced by populations (i.e., extrinsic factors) influenced their response to climate change in our study, although we currently do not know if it is through local adaptations from phenotypic plasticity or evolutionary change, or indirectly through species interactions. Regarding adaptation, few studies have currently been able to measure the relative roles of both phenotypic plasticity and evolutionary change (Réale et al. 2003; Boutin & Lane 2014; Edic et al. 2020), but the number is projected to increase as genetic data become increasingly available.

Recent studies reporting mammalian responses to climate change have focused on measuring distribution and abundance responses in Europe, the United States and Canada, while tropical areas remain poorly studied. Even though our results may not apply to tropical species due to the shortage of data, these species have been hypothesized to be more vulnerable to climate change as they inhabit regions with historically more stable environments (Hetem et al. 2014; Pacifici et al. 2017). Studying these regions and species must be a priority in order to effectively determine how climate change is influencing them, which will help identify which species might be at risk.

Our study constitutes one of the first efforts to consider intraspecific variation in the identification of intrinsic traits and environmental factors associated with a high risk from climate change. Even though our intraspecific-level data (i.e., environmental factors) were not recorded directly from the populations, but instead were extracted from their distribution, some of these variables did play a role in determining risk, potentially serving as surrogates of local adaptation until more directly relevant data become available. Future studies should also explore interactions between variables, as well as the influence of other drivers of biodiversity loss such as land-use change in combination with climate change (Williams et al. 2021) and the interaction between species located in the same area. Even though climate change is a global threat to biodiversity, species are impacted, and conservation actions are carried out locally; therefore, accounting for intraspecific variation is vital to effectively identify and conserve the populations that are most at risk.

Methods

To identify local responses to climate change by terrestrial non-volant mammals, we used, augmented, and updated the data collected by Pacifici et al. (2017), which identified mammal and bird responses reported in scientific articles between 1990 and 2014. We replicated their approach using the same search tool (ISI Web of Knowledge) and set of keywords (see Supplementary Material Appendix S3.1) to identify studies published between January 2015 and April 2020. For a study to be considered, it had to report a change in climate aligned with the effects of climate change in the study area in the past 150 years and indicate the response or lack thereof of the studied mammal species. We only included data belonging to wild populations that had not been subject to experimental manipulation, that had been monitored for a span of at least 10 years (Root et al. 2003), and for which the author or authors considered climate change to be the main driver of the observed response. Lastly, we only included studies that reported responses related to cyclical climatic events such as the Northern Atlantic Oscillation and El Niño (or Southern Oscillation) if there had been a disruption in the cycle attributable to climate change or if the cycle was not the main climatic factor behind the response (Root et al. 2003). All 63 studies on terrestrial non-volant mammal responses considered in Pacifici et al. (2017) were re-evaluated against these criteria, out of which 34 were included in our study.

Classifying responses to climate change

For each study, location and species, we classified all reported responses to climate change into the three main responses to warming (Daufresne et al. 2009; Gardner et al. 2011): (a) changes in distribution (Chen et al. 2011), (b) changes in phenology (Visser & Both 2005), and (c) changes in body size (Sheridan & Bickford 2011; although see Teplitsky & Millien 2014 and Siepielski et al. 2019). Changes in abundance were grouped with changes in distribution, as abundance and range size are generally positively correlated (Brown 1984; Lawton 1993). Responses that did not fit into the three categories were classified as "other". We assigned the direction for each type of response: expansion, contraction and no change for distribution and abundance; advance, delay and no change for phenology; and increase, decrease and no change for body size (for further information on response classification, see Supplementary Material Appendix S3.1).

To analyze the relationship between species' traits and responses to climate change, we focused exclusively on changes in distribution and abundance, as they were the most abundant and are directly associated with extinction risk (Purvis et al. 2000). To account for intraspecific variability in the environmental conditions, we defined our population unit as the intersection of the species' range and the main biome (defined as the biome with the largest area in the distribution of the species within the country of study; Figure 3.1). Biomes can be considered as areas with similar environmental conditions (Penone et al. 2016), potentially providing a better measure of climatic variability and adaptation than considering the whole species' range. Previous studies have identified that geographical location influences the direction of the response, with contractions occurring more frequently near the warm edge and expansions near the cold edge of the distribution (Parmesan 2006; Angert et al. 2011; Wiens 2016). Therefore, considering the location of the response is essential when interpreting responses to climate change. However, the area of study varied greatly across articles, from small sites (e.g., three 1-hectare sites in Santoro et al. 2017) to whole countries (e.g., Germany or Austria in Vetter et al. 2015). To account for location uncertainty, we defined country as the subpopulation unit, grouping all responses belonging to the same species in the same country. For very large countries (i.e., Russia, Canada, the United States and Australia, with a surface area higher than 3.5 million km^2), we used the Level 1 administrative division from the Database of Global Administrative Areas (GADM version 3.6, 2018; https://gadm.org/). Islands that were recognized in the Level 1 administrative division of the GADM (i.e., Greenland, Svalbard and Jan Mayen and Marion Island) were considered separate subpopulations. A response was considered as a contraction when, within the same subpopulation, only contractions or a combination of contractions and no changes were reported in the reviewed studies; the same rationale was applied when considering expansions. If there were a combination of expansions and contractions, the response was considered as mixed (regardless of their proportion) and if only no changes were reported, the response was considered as no change. Mixed responses were not included in our statistical analyses due to their small sample size (n = 7), although exploring the species and areas that showed these responses may help further understand the effects of climate change on biodiversity. We acknowledge that using administrative areas to define study units has its limitations, as species distributions do not follow political barriers. However, we wanted to highlight the relevance of location when identifying factors that influence responses to climate change, and country (or level 1 GADM administrative division when needed) constituted the best compromise.

Assigning species traits and environmental factors

We assigned a set of intrinsic traits and environmental factors to each subpopulation, as well as its relative latitudinal location (see Supplementary Material Appendix S3.1 for variable description and *a priori* hypotheses on the relationship between the selected variables and responses). Intrinsic trait data were obtained at the species level from the COMBINE database (Soria et al. 2021). Although we acknowledge intraspecific intrinsic trait variation and its influence in biodiversity responses to global change (González-Suárez et al. 2015; Moran et al. 2016), these data are not widely available for these traits (e.g., body mass, weaning age, or litter size) and could not be included. Environmental factors were obtained at the population level. Of these factors, the mean temperature difference between the present (1991 – 2018) and recent past (1941 – 1960) indicated the degree of climate change each population has experienced. The remaining environmental factors (i.e., maximum temperature of the warmest month, temperature and precipitation seasonality, minimum altitude and altitudinal and latitudinal range) indicated the conditions to which the population has been historically exposed, potentially serving as surrogates of environmental tolerances. Climatic environmental factors were calculated as the mean of the variable across the population (e.g., mean maximum temperature of the population). Relative latitude indicated the geographical position of the subpopulation within the population and was calculated as the position of the centroid of the subpopulation (intersection of species range and country) within the population (intersection of the species range and main biome) (Figure 3.1). This variable defined the location of the subpopulation relative to the warm and cold edges of the distribution of the population. Species' ranges were obtained from the IUCN version 2020-2 (IUCN, 2020), biome maps from the Ecoregions map (Dinerstein et al. 2017), climate data from WorldClim 2.1 (Fick & Hijmans 2017) at a resolution of 5 arc-minutes and CRU 4.05 (Climate Research Unit; Harris et al. 2020) at a resolution of 0.5 arc-degrees and elevation data from WorldClim 2.1 (Fick & Hijmans 2017) at a resolution of 5 arc-minutes and IUCN Red List (IUCN, 2020). All spatial operations were performed in the R software version 3.6.3 (R Core Team 2020) using the 'raster' (Hijmans 2021) and 'sf' (Pebesma 2018) R packages.

Statistical analyses

We modeled the relationship between mammal distribution and abundance responses to climate change and a set of intrinsic traits and environmental factors, as well as the location of the response, using generalized linear mixed models (GLMMs) with a binomial error structure and logit-link function with the 'lme4' R package (Bates et al. 2015). Binomial GLMMs allow modeling binary outcomes for non-independent data, such as our case, as individuals from the same species and/or in the same biome will share more similar traits than at random. To avoid variable collinearity, following Polidori et al. (2021), we first performed a hierarchical cluster analysis, resulting in a dissimilarity dendrogram (Dormann et al. 2007) using the Ward clustering method based on the Spearman correlation index (Harrell 2015) and established a distance threshold of 0.3 for variable selection (i.e., correlation equal to or less than 70%; Polidori et al. 2021). There were two clusters of correlated traits, the first composed of female maturity, litters per year and interbirth interval (hereafter reproductive speed), and the second composed of dispersal distance, weaning age, adult mass and generation length (hereafter spread capacity). We performed a Principal Component Analysis for each of these clusters and retrieved the value of the first principal component, which explained 84.26% and 83.77% of the variance of reproductive speed and spread capacity, respectively. We then calculated the variance inflation factor (VIF; Lin et al. 2011) of the variables and discarded those which overestimated the variance and contributed redundant information to the model (VIF > 10; Antonelli et al. 2018). Lastly, all continuous variables were standardized.

We fitted two contrasting binomial GLMMs establishing 'contraction' as the reference response (i.e., Contraction – Expansion and Contraction – No change) and the selected variables as the independent variables. For both these models, we initially considered species and biome as random factors.

However, in the Contraction – Expansion model, biome variance was 0; while in the Contraction – No change model, species variance was 0. To avoid model singularity, we excluded the pertinent random factor from each respective model, keeping species for Contraction – Expansion and biome for Contraction – No change. To ensure that phylogenetic non-independence was not influencing our results, we tested the existence of phylogenetic signal in the residuals of both models using Pagel's lambda calculated using the Phylacine version 1.2 (Faurby et al. 2018) consensus tree from Abraham et al. (2021) in the 'phytools' R package (Revell 2012). Lambda values range from 0 to 1 and represent the transformation of the phylogeny that best predicts the variation of traits across the phylogenetic tree. A lambda of 0 indicates that there is no phylogenetic signal, while a value of 1 indicates that there is a perfect correlation between the trait and the tree topology if it followed a Brownian model (i.e., phylogenetic signal). The probability that the observed lambda significantly differed from the null hypothesis of a lambda value equal to 0 (no phylogenetic signal) was calculated using a likelihood ratio test. For both models, we obtained a lambda of 0 and a p-value of the likelihood ratio test of 1, indicating an absence of a phylogenetic signal. Model residuals were checked using the simulateResiduals function from the 'DHARMa' R package (Hartig 2021), grouping by random factors as recommended in the vignette for Bernoulli binomial tests. All statistical analyses were performed in the R software version 3.6.3 (R Core Team 2020).

Chapter IV

Local environmental factors influence bird distribution and phenological responses to climate change

Carmen D. Soria[1,2], *Michela Pacifici*[1], *Stuart H. M. Butchart*[2,3], *Carlo Rondinini*[1,4]

1. Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy
2. BirdLife International, Cambridge, UK
3. Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK
4. Global Wildlife Conservation Center, College of Environmental Science and Forestry, State University of New York, Syracuse, USA

Abstract

Bird species have responded to recent climate change primarily by shifting their distributions and modifying their phenology. These changes allow them to track their appropriate conditions in space (changes in distribution) and time (changes in phenology). Although distributions have generally tended to shift polewards and spring events have tended to advance, responses have varied substantially within and among species. Intrinsic traits, as well as the environmental conditions and latitudinal position, potentially influence the outcome of these responses. Determining how responses are affected by which factors, while accounting for intraspecific differences in exposure and adaptation to climate, will help predict the consequences of climate change on species.

Here, we undertook a literature review of how bird species have modified their distributions and spring phenological responses to climate change in the last 150 years. We then model the relationship between these responses and species-level intrinsic traits, population-level environmental factors, and the latitudinal position of the location of the documented response within the population. To account for intraspecific differences in climate adaptation, we define populations as the intersection of species' distributions and areas with similar climatic conditions (biomes).

We found that environmental factors played an important role in determining responses to climate change. Populations with a low maximum temperature and a restricted climatic seasonality were more likely to experience contractions. Populations with a low maximum temperature and high climate seasonality were more prone to advance their phenology. Latitude also influenced responses, with distribution contractions and phenological advances more likely to be documented near the warm edge of the population. Maximum longevity was the only significant intrinsic trait, with longer-lived species being less susceptible to experiencing distribution contractions, although this might indicate a time-lag in response rather than greater resilience to climate change. Our findings highlight the importance of incorporating intraspecific variability and the potential use of environmental characteristics as indicators of tolerance when analyzing responses to climate change.

Introduction

Climate change has become a major threat to biodiversity, affecting all levels of biological organization, from genotypes to ecosystems (Parmesan & Yohe 2003; Scheffers et al. 2016; Díaz et al. 2019). During the past decades, species from a wide variety of taxa have been reported to respond and adapt to these novel conditions by modifying their distributions, phenology, and/or morphology (Parmesan 2006; Bellard et al. 2012). Among these responses, changes in distribution and spring phenology were the two most widespread and frequently reported (Parmesan 2006; Princé & Zuckerberg 2015). Species' distributions have tended to shift towards higher latitudes and altitudes as temperature has increased in the recent past (Chen et al. 2011; MacLean & Beissinger 2017). These shifts are characterized by local contractions along the warm boundary of the distribution (and thus an increased local risk from climate change) and/or expansions towards new climatically available areas along the cold boundary of the distribution (Gillings et al. 2015; Wiens 2016). The onset of spring has also advanced as a consequence of climate change, with springtime phenological events starting earlier for a wide variety of taxa (Root et al. 2003; Parmesan 2006; Visser et al. 2006; Cohen et al. 2018). Some examples of seasonal events that have been observed to advance in certain populations are the flowering of plants (Parmesan 2006), the emergence of insects (Forrest 2016), and the migration and breeding of birds (Charmantier et al. 2008; Usui et al. 2017).

Previous studies and meta-analyses on bird responses to climate change indicate that they are shifting their distributions towards higher latitudes and altitudes, tracking their thermal niche (Hitch & Leberg 2007; Forero-Medina et al. 2011; Gillings et al. 2015), and advancing their spring phenology, tracking changes in the availability of seasonal biotic resources (Visser & Both 2005; Usui et al. 2017; Radchuk et al. 2019). However, responses to climate change have been observed to vary within and among bird species, with different species in the same location (Michel et al. 2021) and different populations of the same species (Gibson-Reinemer & Rahel 2015) showing contrasting responses.

Life history and ecological traits have been hypothesized to be linked with specific distribution and phenological responses (MacLean & Beissinger 2017; Pacifici et al. 2017; Usui et al. 2017), although the influence of some of these traits has yet to be clarified. For instance, high dispersal potential, offspring number, and wide dietary and habitat breadths are expected to aid distribution expansions due to increased mobility, colonization pressure and resource availability (Angert et al. 2011; Estrada et al. 2016). However, a recent meta-analysis (MacLean & Beissinger 2017), found that while habitat breadth was associated with an increased ability to expand distributions, fecundity and dietary breadth did not influence distribution shifts. Species with restricted dietary and habitat breadths have also been hypothesized to advance their phenology more, due to experiencing a stronger selection pressure (Both et al. 2010). But some studies found that these traits did not influence phenological responses (Usui et al. 2017) or had the opposite effect, with generalist species advancing their phenology instead (Végvári et al. 2010). High body mass has been associated with a higher susceptibility to climate change in mammals (Mccain & King 2014) and greater advances in bird migration (Usui et al. 2017). Species with a longer generation time have a lower evolutionary potential, making them more likely to be negatively impacted by climate change (Vedder et al. 2013), but such impacts may occur over a longer period, making them harder to detect (Pearson et al. 2014; Pacifici et al. 2017). Migratory species have been reported to experience greater population declines than resident species, potentially due to a temporal mismatch between breeding and the peak of food availability (Both et al. 2006; Møller et al. 2008) or needing climatically favorable conditions in geographically separate areas across their life-cycle. Within migratory species, short-distance migrants have advanced their migration more than long-distance migrants (Lehikoinen et al. 2004; Usui et al. 2017), potentially helping avoid this mismatch.

Environmental factors have also been associated with distribution and phenological responses to climate change. The degree of climate change that a population has experienced (mainly measured as the increase in temperature), has been directly linked to the probability of experiencing population declines (Freeman et al. 2018; Riddell et al. 2019) and advancing spring phenology events such as migration (Usui et al. 2017) or breeding date (Halupka et al. 2008; Halupka & Halupka 2017). Populations residing exclusively at high altitudes have also been more impacted by climate change, as they are not able to move further upslope and have to compete with low-altitude species shifting their distributions (Şekercioğlu et al. 2008; Urban 2018). Additionally, populations with a restricted altitudinal breadth and located in areas with a restricted temperature and/or precipitation seasonality may also be at higher risk, as these factors can reflect the variety of climatic conditions that the species (or the species they depend upon) can endure (Bonebrake & Mastrandrea 2010). The latitudinal position of the population has also been observed to influence distributional responses, with populations located at high latitudes experiencing expansions and those located at low latitudes experiencing contractions (Wiens 2016). Contrastingly, the effect of latitude on phenology has been previously considered as weak (Parmesan 2007) or even non-existent (Usui et al. 2017), and shifts in phenology have been recorded at high, mid, and low latitudes (Chmura et al. 2019).

Previous studies on the influence of traits and environmental factors on responses to climate change have been mostly carried out considering these variables at the species level and have not considered the influence of location (MacLean & Beissinger 2017; Pacifici et al. 2017) or have done so but did not include environmental factors (Usui et al. 2017). In this study, we aimed to determine the influence of these variables on distribution and phenological responses at the local level, accounting for intraspecific differences in exposure and potential adaptation to climatic conditions. To achieve this, we identified observed distribution and spring phenological responses to climate change and compiled a set of intrinsic traits and environmental factors that have been previously associated with these responses. To account for intraspecific variability in environmental factors, we identified populations of the species that experience similar climatic conditions. As these populations were distributed across large geographical areas, we grouped the responses by species and country, reducing the number of instances of opposing or mixed responses (i.e., different studies for the same species and country reporting distribution and abundance contractions and expansions or phenological advances and delays) and allowing the inclusion of the location of the response within the population. Lastly, we performed generalized linear mixed models to identify the intrinsic traits and environmental factors that influenced the outcome of distributional (i.e., contractions vs. expansions) and phenological (i.e., advances vs. delays or no changes) changes in response to climate change.

Methods

Response identification, selection criteria and classification

To identify local responses to climate change, we used, augmented, and updated the data from the literature review performed by Pacifici et al. (2017) on bird and terrestrial non-volant mammal responses to climate change published between 1990 and 2014. For the purposes of this study, we focused exclusively on birds and covered the period between January 2015 and April 2020 (both included). To keep consistency between both reviews, we used the same search tool (ISI Web of Knowledge), keywords (keeping only those relevant for birds), and search structure. This search structure consisted of all possible combinations of (a) the effects of climate change (climate change*, global warming*, sea-level rise*, elevated CO2*, drought* cyclone*, extreme temperature*, el Niño event*, la Niña event*, severe weather*, NAO change*, sea ice extent*), (b) their effect or lack of effect (population reduction*, population decline*, increase in population size*, range change*, range shift*, range reduction*, turnover*, extinction risk*, extinction probability*, survival*, mortality*, fertility*, changes in phenology*, adaptation*, no change*, unchanged*, no effect*) on (c) avian species or populations (bird*, bird* of prey, penguin*, passeriformes*, non-flying*).

We only considered studies that reported bird distributional, abundance and/or phenological responses (or lack thereof) of wild populations that had not been subject to experimental manipulation in the last 150 years. To avoid including responses caused by other drivers such as land-use change, we only included studies in which the author or authors unequivocally considered climate change as the main driver of the reported response. Furthermore, to ensure that the observed response was a consistent trend and not a one-off or short-term exception, we also only considered studies that spanned at least 10 years (Root et al. 2003). Studies reporting the effects of cyclical climatic events such as the Northern

Atlantic Oscillation (NAO) and El Niño (or Southern Oscillation), were only considered if climate change had caused a disruption in the cycle or the cycle was not the main climatic factor behind the observed response (Root et al. 2003). All 66 studies included in Pacifici et al. (2017) on bird responses were re-evaluated against these criteria, and 33 were excluded as they did not meet them.

We classified the responses obtained from the review by species, location and focus of study (distribution and/or abundance responses vs spring phenological responses). Distribution and abundance responses were considered together as both are generally positively correlated, with larger areas supporting a higher number of individuals (Brown 1984; Lawton 1993). These responses included latitudinal and altitudinal range contractions, expansions and shifts, and changes in the number of individuals (i.e., abundance, density, population size, population trend, occupancy, survival, breeding success, number of clutches, clutch size, offspring growth rate and juvenile body mass). Responses that indicated a net increase in distribution size or number of individuals were considered as expansions, while net decreases were considered as contractions, and no responses were considered as no changes. Distribution shifts were assigned to contraction or expansion based on the information provided by the article. Shifts towards lower altitudes (i.e., decreases in upper limits and/or reductions in lower limits) were considered as expansions, while shifts towards higher altitudes (increases in upper limits and/or increases in lower limits) were considered as contractions. Spring phenological responses included changes in breeding phenology (i.e., changes in the date of nesting, breeding, laying, hatching, fledging, second clutch and juvenile capture) and breeding migration (i.e., the departure date from non-breeding grounds, passage date to breeding grounds and arrival and settling date in breeding grounds). These responses were classified into advances, delays and no changes based on their deviation from the past timing of the activity.

Species' distributions can be spread across climatically diverse areas; therefore, we cannot assume that all individuals will be able to endure the same climatic conditions nor experience the same degree of climate change. To account for intraspecific variability, we defined as our 'population' unit the distribution of the species within the main biome, defined as the biome with the largest area within the distribution of the species in the country of the study. Biomes constitute areas with similar environmental conditions (Penone et al. 2016), potentially serving as a better proxy of climate variability or even adaptation than considering the whole species' distribution. Biomes are extensive, so to account for the influence of the geographical location, we further grouped our responses by species and country into units we refer to as 'subpopulations' (recognizing that we do not have information on the actual population structure for each species). For countries larger than 2.5 million km2 (i.e., Russia, Canada, Australia, and the United States of America) we used the Level 1 administrative division from the Database of Global Administrative Areas (GADM version 3.6, 2018; https://gadm.org/). Islands that were recognized in the GADM Level 1 (i.e., Greenland, Svalbard and Jan Mayen and Martinique) were also considered as separate subpopulations. The area of study varied greatly across articles, from small sites (e.g., Heligoland Island (Germany) in Hüppop & Hüppop 2003) to whole countries (e.g., Czech Republic in Koleček et al. 2020), therefore, although we acknowledge that species' distributions do not follow political barriers, we believe that country (or GADM Level 1 when relevant) represented the best compromise. Species distributions were obtained from the IUCN Red List of Threatened Species version 2020-2 (IUCN 2020, BirdLife International 2020) and biomes from the Ecoregions map of Dinerstein et al. (2017).

Using the distribution and abundance responses extracted in our literature review, we considered subpopulations to be experiencing (a) an expansion if only expansions or a combination of expansions and no changes were reported, (b) a contraction if only contractions or a combination of contractions and no changes were reported, (c) no change if only no changes were reported and (d) a mixed response if there were a combination of expansions and contractions, regardless of their proportion. We applied the same principle for phenological responses, classifying them into advance, delay, no change and mixed.

Intrinsic traits, environmental factors and latitudinal position of the response

We compiled data on intrinsic traits and environmental factors that have been suggested to be associated with distribution, abundance and phenological responses to climate change. These traits consisted of adult body mass, clutch size, maximum longevity, generation length, dispersal distance, habitat and dietary breadth, dependency on seasonal food types and migration. Adult body mass was obtained from Dunning (1992) and Wilman et al. (2014), clutch size from Wilman et al. (2014), and maximum longevity from Bird et al. (2020). Generation length, defined as "the average age of parents of the current cohort" (IUCN 2019) came from Bird et al. (2020). Dispersal, or the maximum distance covered by young individuals between their birth and breeding site, came from Santini et al. (2019). Habitat breadth was calculated as the number of distinct Level 1 IUCN habitat types (IUCN 2012) and dietary breadth as the number of distinct EltonTraits food categories that comprised a substantial part

(≥20%) of the diet (Wilman et al. 2014; Usui et al. 2017). Dependence on seasonal food types was calculated by first identifying the main food type consumed by a species using the EltonTraits categorization and then classifying it into seasonal (i.e., Fruit/Nectar, Plant/Seed, Invertebrate) or non-seasonal (i.e., Omnivore and Fish/Vertebrate/Scavenge). We also classified species into migratory and non-migratory using the BirdLife migration classification (BirdLife International 2020). Full migrant and altitudinal migrant species were classified as migratory, and nomadic and non-migrant species were considered as non-migratory. Nomadic species were not considered as migratory as their movements are generally in response to sporadic resources, and do not follow any regular pattern. All intrinsic trait data were obtained at the species level, due to the lack of currently available intraspecific data.

The selected environmental factors consisted of a set of climate and geographical variables obtained at the population level. All climatic variables except temperature increase were obtained from WorldClim 2.1 (Fick & Hijmans 2017) at a 5 arc-minutes resolution. These variables included maximum temperature of the warmest month (bio5), temperature seasonality (bio7) and precipitation seasonality (difference in mean precipitation between the wettest (bio16) and driest (bio17) quarters). Mean temperature increase between the recent past (1941 – 1960) and the present (1991 – 2018) aimed to represent the degree of climate change experienced by the population and was obtained from the Climate Research Unit version 4.03 (Harris et al. 2020) at a resolution of 0.5 arc-degrees. Major changes in Earth’s temperature became evident in the early 1980s (Kharouba et al. 2018), therefore, we believe that the difference between both selected periods accurately represents temperature increase attributable to climate change. To account for species migration when obtaining temperature increase, we first identified if the population was mostly resident, breeding, non-breeding or passing through (i.e., passage) using the seasonality data of the distribution maps and calculated the increase only for the relevant period of the year. These periods were (a) the whole year for resident species, (b) from March to August for breeding populations in the Northern Hemisphere and non-breeding populations in the Southern Hemisphere, (c) from September to February for non-breeding populations in the Northern Hemisphere and breeding populations in the Southern Hemisphere, and (d) from September to February and from March to May for passage populations. Geographic variables consisted of latitudinal range (difference between the maximum and minimum latitude), minimum altitude, and altitudinal range (difference between the maximum and minimum altitude). Both altitudinal variables were obtained by adjusting the elevation at which the species can be found (BirdLife International

2020) to the altitudinal range available within the population obtained from the SRTM elevation data (accessed through WorldClim 2.1).

We accounted for the location of the response by including the relative latitudinal position of the response respective to the warm and cold edges of the distribution. This variable was calculated as the position of the centroid of the subpopulation (the distribution of the target species in the country) within the population (the distribution of the target species in the main biome). The value of the relative latitude ranged from 0 (edge of the population nearest to the equator) to 1 (edge of the population nearest to the respective pole). If the distribution of the population spanned over the two hemispheres, we considered the equator as 0 and calculated the relative latitudinal position within the hemisphere in which the response was identified.

All spatial operations were performed in the R software version 3.6.3 (R Core Team 2020) using the 'raster' (Hijmans 2021) and 'sf' (Pebesma 2018) R packages.

Statistical analyses

To identify which intrinsic traits and environmental factors were associated with experiencing a potential increase in risk from climate change and advances in breeding phenology, we performed binomial generalized mixed models (GLMMs) with a binary response distribution and a logit-link function using the 'lme4' R package (Bates et al. 2015). Binomial GLMMs allow modeling binary responses for non-independent data, such as our case, as subpopulations of the same species and/or biome will share a higher proportion of variables than at random.

To determine and avoid variable correlation, we performed a two-step correlation analysis (Polidori et al. 2021). First, we conducted a hierarchical cluster analysis using Ward's clustering method based on Spearman's correlation index (Harrell 2015). This analysis segregates the variables into clusters based on the Euclidean distance between their correlation indices, producing a dissimilarity dendrogram (Dormann et al. 2013), allowing the easy visualization of the correlation structure. We established 0.3 as the distance threshold for variable selection (i.e., keeping variables that are correlated equal to or less than 70%; Polidori et al. 2021). We then selected one variable per cluster prioritizing non-derived variables and calculated their variance inflation factor (VIF), discarding those that overestimated the variance and contributed the most redundant information to the model (VIF > 5; Miles, 2005).

Once we selected the final set of variables for our analyses, we fitted three binomial GLMMs. For distribution and abundance responses we fitted one GLMM considering only contractions and expansions. We did not consider no change or mixed responses as the objective of this analysis is to identify which variables influence experiencing negative or positive responses to climate change. Breeding phenological responses to climate change are characterized by a general advancement of phenological activities, therefore we fitted two binomial GLMMs, the first one using as responses advances and delays and the second one using advances and no change and mixed responses. This way we aimed to identify which variables influence experiencing advances instead of other responses. We included species and biome as random factors in all models and standardized all continuous variables. Once we identified the significant variables for all models (full models), we ran another set of GLMMs considering only significant ($P < 0.05$) and marginally significant ($P < 0.1$) variables (reduced models). We tested if phylogeny was influencing our results by calculating the value of Pagel's lambda of the residuals of all GLMMs. We used the BirdTree consensus tree (Jetz et al. 2014) obtained from Abraham et al. (2021) and the function 'phylosig' from the 'phytools' R package (Revell 2012). The strength of the phylogenetic signal (Pagel's lambda) ranges from 0 or no phylogenetic signal and 1 or strong phylogenetic signal. Using a likelihood ratio test, we calculated the probability of the observed lambda differing significantly from the null hypothesis of a lambda equal to 0. Model residuals were evaluated using the 'simulateResiduals' function from the 'DHARMa' R package (Hartig 2021), grouping by random factors (species and biome), as recommended for Bernoulli binomial GLMMs.

We did not include responses of species located in their invasive distributions (14 subpopulation level responses, 10 distributional and 4 phenological), as these areas do not necessarily reflect the conditions to which the species is adapted. We also did not include responses located in the Antarctic (22 subpopulation level responses, 14 distributional and 8 phenological), as the Climate Research Unit data (Harris et al. 2020) used to calculate temperature increase is not available for this area.

Results

Review data and bias

We obtained 3,012 local responses to climate change from the 143 studies that met our criteria (30 from Pacifici et al. 2017 plus 113 additions), belonging to 918 bird species located in 32 different countries. The vast majority of the studies were conducted either in Europe (60%) or in the United States or Canada (27%), while Central and South America (4.2%), Oceania (2.7%), Africa (2.7%), Antarctica (2.1%), Asia (0.7%) and Greenland (0.7%) were under-represented (Supplementary material Appendices S4.7 and S4.8). The mean duration of the studies was 32.5 years and ranged from 10 to 121 years.

Distribution and abundance responses were recorded for 763 species and constituted 59.4% (1,789) of the responses, of which 39.3% (703) were contractions, 35.8% (640) were expansions and 24.9% (446) were no changes. Spring phenological responses were recorded for 386 species and constituted the remaining 40.6% (1,223) of the responses, of which 50.8% (621) were advances, 6.1% (75) were delays and 43.1% (527) were no changes.

Variable selection and GLMMs

There were two clusters of correlated variables, the first composed of adult body mass and dispersal and the second composed by generation length and maximum longevity. We kept adult body mass and maximum longevity for the GLMMs, as both dispersal and generation length are derived variables from adult body mass and maximum longevity, respectively. Dispersal was calculated as a function of body mass, hand wing index and geographic range (Santini et al. 2019) and generation length as a function of adult body mass, maximum longevity and annual adult survival (Bird et al. 2020). Once these variables were excluded, none of the variables had a VIF higher than 5. Thus, the variables considered in the GLMMs were adult body mass, clutch size, maximum longevity, diet and habitat breadth, diet seasonality, migration, maximum temperature, temperature and precipitation seasonality, temperature increase between the recent past and the present, latitudinal and altitudinal range, minimum altitude and relative latitudinal position. We only considered migration in the distribution GLMM, as the advancement of migration itself constituted one of the main phenological responses.

Traits and environmental factors associated with distribution and phenological responses

We found that low values of maximum longevity, relative latitude of the subpopulation within the population, temperature and precipitation seasonality, and maximum temperature were significantly associated ($P < 0.05$) with contractions compared with expansions in both the full (Supplementary material Appendix S4.1) and reduced (Figure 4.1 Supplementary material Appendix S4.2) models. Having a high minimum altitude was marginally associated ($P < 0.1$) with experiencing contractions in both the full and reduced distribution models.

When analyzing phenological advances and delays, we found that large temperature increases, high temperature seasonality and low maximum temperatures were significantly associated ($P < 0.05$) with experiencing advances in both full (Supplementary material Appendix S4.3) and reduced (Figure 4.2 and Supplementary material Appendix S4.4) models. High maximum longevity was significantly associated with experiencing delays in the full model but was not significant in the reduced model. High precipitation seasonality was marginally associated ($P < 0.1$) with phenological advances in both models, while high relative latitude was marginally associated with advances in the full model but was not significant in the reduced model.

Finally, low relative latitude and high temperature increase were significantly associated ($P < 0.05$) with advances compared with no changes or mixed responses in both the full (Supplementary material Appendix S4.5) and reduced (Figure 4.3 and Supplementary material Appendix S4.6) model. Low precipitation seasonality was marginally associated with advances in the full model ($P<0.1$) and significantly ($P<0.05$) in the reduced model.

Phylogeny did not seem to influence our results, as all Pagel's lambda values were 0 and the likelihood ratio tests had a P-value of 1.

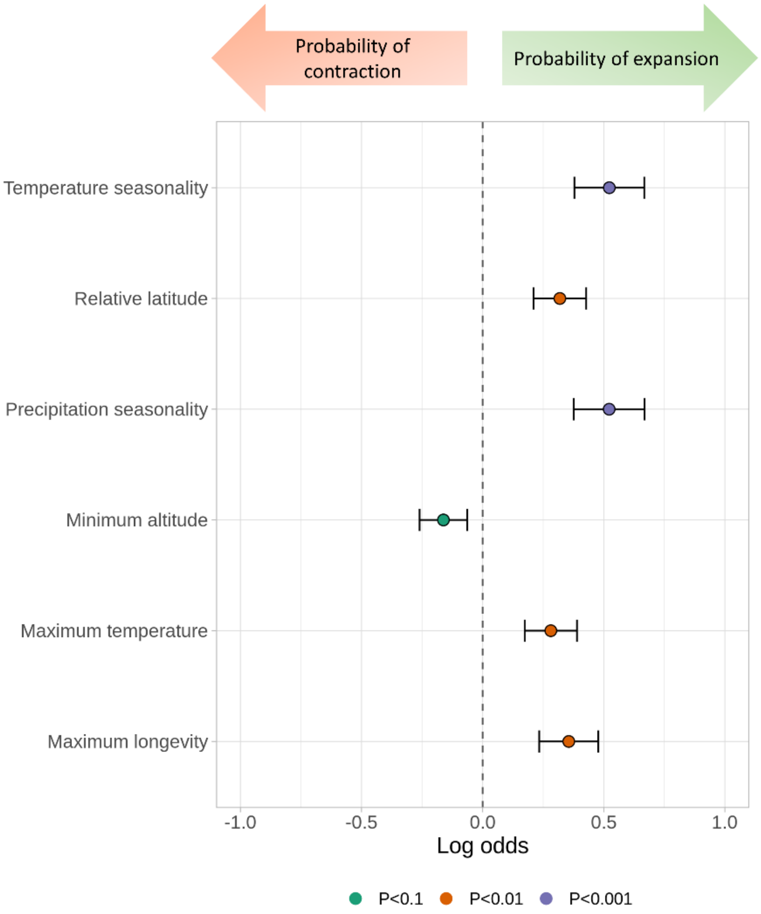


Figure 4.1 Influence of the intrinsic trait and the environmental factors on distribution responses included in the reduced GLMM. *The log-odds inform how the probability of a subpopulation experiencing a contraction or an expansion varies with an increase in the value of the selected variables. Negative log-odds (at the left of the dashed line) indicate that an increase in the variable is associated with an increase in the probability of experiencing a contraction. Positive log-odds (at the right of the dashed line) indicate that an increase in the variable is associated with an increase of the probability of experiencing an expansion. The statistical significance of each variable is indicated by the color of the dots and the horizontal bars represent the standard error.*

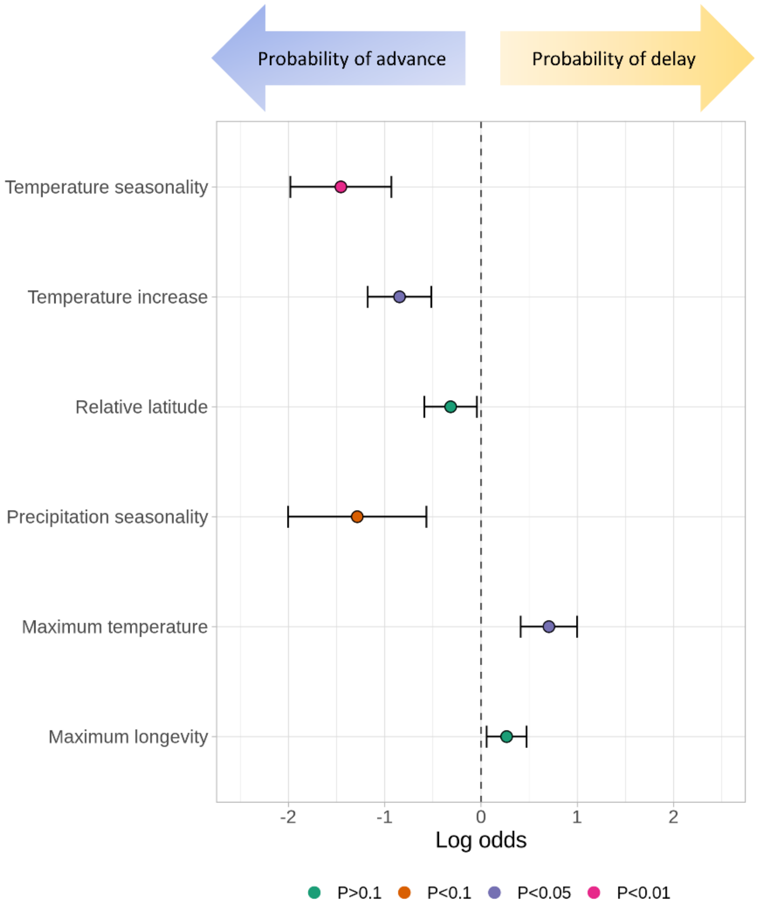


Figure 4.2 Influence of the environmental factors on phenological advances and delays included in the reduced GLMM. *The log-odds inform how the probability of a subpopulation experiencing an advance or delay varies with an increase in the value of the selected variables. Negative log-odds (at the left of the dashed line) indicate that an increase in the variable is associated with an increase in the probability of experiencing an advance in spring phenology. Positive log-odds (at the right of the dashed line) indicate that an increase in the variable is associated with an increase of experiencing a delay in spring phenology. The statistical significance of each variable is indicated by the color of the dots and the horizontal bars represent the standard error.*

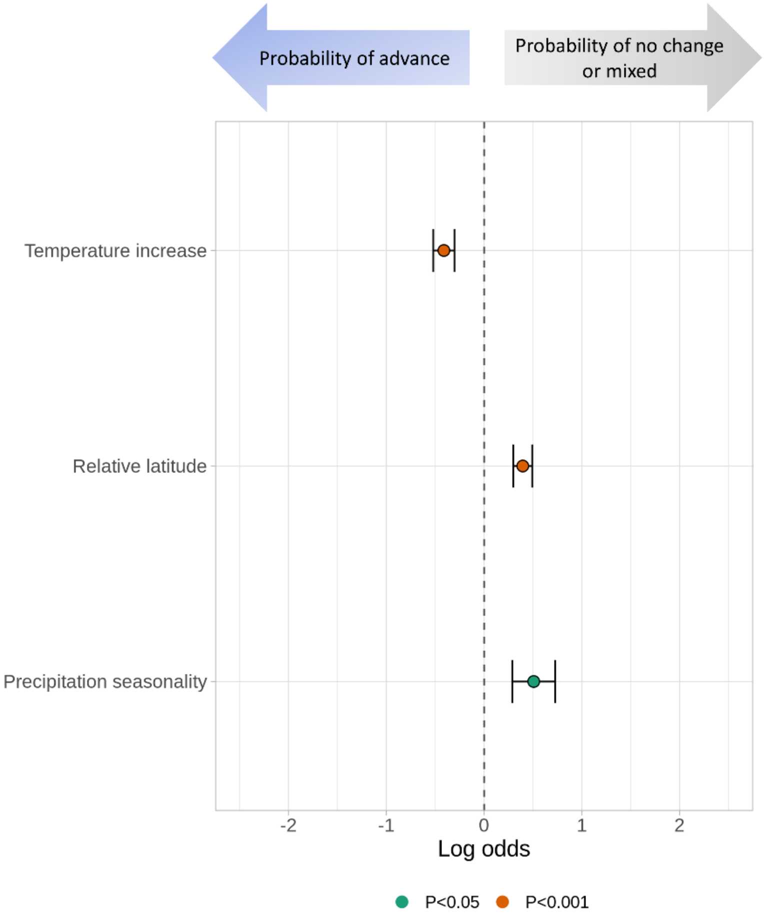


Figure 4.3 Influence of the environmental factors on phenological advances and no changes or mixed responses included in the reduced GLMM. *The log-odds inform how the probability of a subpopulation experiencing an advance or no change/mixed response varies with an increase in the value of the selected variables. Negative log-odds (at the left of the dashed line) indicate that an increase in the variable is associated with an increase in the probability of experiencing an advance in spring phenology. Positive log-odds (at the right of the dashed line) indicate that an increase in the variable is associated with an increase of experiencing a delay or a mixed spring phenology response. The statistical significance of each variable is indicated by the color of the dots and the horizontal bars represent the standard error.*

Discussion

In this study, we analyzed for the first time the influence of intrinsic traits, environmental factors, and latitudinal position on distributional and phenological responses of bird populations to climate change. We found that relative latitudinal position, population-level climate variables and maximum longevity, influenced the outcome of the response to climate change.

Latitude has been previously identified as one of the main factors influencing climate-driven changes in distribution (Chen et al. 2011; MacLean & Beissinger 2017) and phenology (Chmura et al. 2019). Our results indicate that contractions were more likely to occur in populations closer to the warm border of the population, while expansions were more likely closer to the cold border. Therefore, these changes in distribution are not exclusively happening at the borders of the distribution of the species but also at the borders of populations with similar climatic conditions. This might explain why, although a tendency to poleward shifts has typically been observed when considering multiple species in the same area (Chen et al. 2011; Wiens 2016), less consistent patterns have been found when comparing different areas of the distribution of the same species (Gibson-Reinemer & Rahel 2015). Spring phenological advances also had a higher probability of occurring near the warm border of the populations. This might be because temperatures have generally increased more at higher latitudes (IPCC 2013) and temperature increase has been directly linked with the rate of phenological advance (Usui et al. 2017; Chmura et al. 2019). Our results further support this hypothesis, as phenological advances were positively associated with the degree of temperature increase. However, contrary to our expectations, temperature increase did not influence the probability of experiencing expansions or contractions. This might be a consequence of considering the increase only for the period in which the species is present in the area of study. While this approach allowed us to determine the direct influence of temperature increase on the species, it also overlooked indirect effects derived from biological interactions, which have been shown to influence population trends (Visser et al. 2006).

Responses to climate change were also influenced by the environmental conditions to which the population has been exposed – and potentially acclimatized to – in the recent past. Subpopulations with a low temperature and precipitation seasonality were more likely to experience contractions, potentially because they are adapted to more stable climates and are less able to cope with an increase in seasonality caused by climate change (Bonebrake & Mastrandrea 2010). This has already been observed in the Australian tropical rainforest, where climate is generally stable and an increase in seasonality has caused decreases in bird abundance due to a resource bottleneck (i.e., insects, nectar and fruit) during the dry season (Williams & Middleton 2008). Low temperature seasonality has also been previously associated with a higher probability of negative responses in birds at the species level (Pacifici et al. 2017). However, we found that phenological advances (i.e., positive responses) were associated with high temperature seasonality. Areas with high temperature seasonality are generally located in temperate regions, where plants and insects have also generally advanced their phenology due to an increased sensitivity to climate change (Forrest 2016; Prevéy et al. 2017). Therefore, bird species in these areas will experience a stronger pressure to advance their phenology to keep up with their resources. Subpopulations located in areas with a high maximum temperature seemed to be less affected by climate change, potentially because they have a higher tolerance to high temperatures. Interestingly, Pacifici et al. (2017), found the opposite when considering the maximum temperature of the entire breeding distribution, potentially because this temperature may be closer to the actual thermal limit of the species. Species with higher maximum longevity were more likely to experience distribution expansions compared with contractions. Although this might indicate that these species have benefitted from climate change, this seems unlikely in the long run. Adaptation to climate change has been slower in longer-lived species such as seabirds (Sandvik & Einar Erikstad 2008); therefore, studies on changes in distribution may not have detected the ultimate impacts of current climate change on these species (Pacifici et al. 2017).

Most of the studies we considered were carried out in temperate areas, with only 7% of them conducted in tropical areas (i.e. between the tropics of Cancer and Capricorn). This limits the degree to which we can assume our results apply to tropical areas. Nonetheless, our findings imply that populations located in areas with a stable climate such as the tropics will be more susceptible to climate change, as they will have a higher probability of experiencing distribution contractions and a reduced capacity to advance their phenology, potentially increasing their risk owing to a mismatch with their resources (Gordo & Sanz 2005; Both et al. 2010). Notably, we found a similar proportion of reported contractions and expansions. While this might suggest that the impact of climate change on birds may not be severe, this result needs to be interpreted carefully. Populations shifting towards higher latitudes will eventually reach a dispersal barrier, especially in the Southern Hemisphere, where the mainland (except Antarctica) does not expand polewards as far as in the Northern Hemisphere. A similar effect has been previously identified in high altitude species residing near the elevation limit, popularly referred to as an “escalator to extinction” (Freeman et al. 2018; Urban 2018).

In contrast with spring phenology, the consequences of climate change on the timing of autumn events are not as well studied (Gallinat et al. 2015) and appear to be less consistent (Lehikoinen et al. 2004; Van Buskirk et al. 2009). While spring phenology in birds has generally tended to advance (Usui et al. 2017), the distance between non-breeding and breeding areas has been reported to determine changes in autumn departure dates, with long-distance migrants showing an advance in departure and short-distance migrants showing a delay (Jenni & Kéry 2003; Van Buskirk et al. 2009). The specific mechanisms behind these shifts are still largely unknown, although a recent study found that wind influenced the departure date for intra-European migrants while temperature and precipitation influenced trans-Saharan migrants (Haest et al. 2019). Applying the framework of this study to autumn phenological responses, including relevant variables such as migration distance and wind, might help clarify these responses.

Although most studies have focused exclusively on one type of response (i.e., distribution, phenology, or morphology), their interactions are likely complex (Zimova et al. 2021). For instance, Californian bird communities have compensated the increase in temperature during the breeding season by advancing their phenology, potentially reducing the need to change their distribution (Socolar et al. 2017). A study in the Czech Republic found that species advancing their arrival to a greater degree had more positive population trends (Koleček et al. 2020). These studies indicate that phenological changes may mediate distributional changes by mitigating the effects of temperature increases. Here, we analyzed the relationship between the same set of variables and changes in distribution and phenology. Although we cannot establish a direct link between both types of responses with our data, as most studies either focused on distribution or spring phenology, we did find that relative latitude, maximum temperature, and seasonality influenced both responses. The complementarity between types of responses to climate change and their consequences remain largely unknown and their study might shed some light on adaptation to climate change.

This study constitutes one of the first efforts to include intraspecific variation in the identification of variables influencing local distribution and phenological responses in birds. Although intraspecific-level data were only available for environmental factors, which were determined from the distribution of the population, many of them were relevant in determining responses to climate change and might serve as better proxies of intraspecific tolerance than species-level traits. Considering intraspecific variation in exposure and vulnerability to climate change will help determine which populations will likely be affected by climate change and facilitate the design and implementation of local conservation actions.

Chapter V
General discussion

Key findings

In the last section of the introduction, I defined the main objectives of each of the analytical chapters included in this thesis (Chapters II to IV). Here, I will briefly describe the main outcomes of each chapter:

Chapter II: Global mammal trait dataset

I identified 43 publicly available mammal trait data sources published in the last two decades. I selected 14 of them based on their geographic extent, traits included and data completeness, and combined them under two different taxonomies, IUCN version 2020-2 (IUCN 2020) and PHYLACINE version 1.2 (Faurby et al. 2018). I designed a trait-specific data-inclusion framework to reduce unnecessary pseudorreplication and to prioritize data sources based on their relevance, time since publication and presence of data verification or quality checks. This resulted in a dataset covering 54 different traits for 6,234 extant and recently extinct mammal species, including information on morphology, reproduction, diet, biogeography, life-habit, phenology behavior, home range, and density. I also calculated other relevant traits such as habitat and altitudinal breadth for all species and dispersal for terrestrial non-volant species (i.e., excluding cetaceans, pinnipeds, sirenids, and bats). Missing data were flagged and imputed for non-biogeographical traits with 20% or more data available, obtaining full datasets for 21 traits. This dataset will be especially useful for large-scale ecological and conservation analyses that use traits in their analyses.

Chapter III: Mammal responses to climate change and variables influencing risk

I collected data on recent terrestrial non-volant mammal responses to climate change through a literature review and categorized them into changes in (a) distribution and abundance, (b) phenology, and (c) morphology. I obtained 382 responses belonging to 130 species located in 30 countries. Most of these responses were distribution and abundance responses (80.6%) while phenological and morphological changes constituted 4.5% (17 responses) and 10.2% (39 responses) respectively. The remaining 4.7% did not fit into any of these categories. To identify the variables influencing risk from climate change, I modeled the relationship between the outcome of distribution and abundance responses (i.e., contraction, expansion, and no change) and species-level intrinsic traits (obtained in Chapter II) and population-level environmental factors. I found that relative latitude, temperature increase, climate seasonality, altitudinal breadth, litter size, and heterothermy influenced the probability of distribution and abundance contractions among mammal species and a subsequent increase in risk from climate change.

Chapter IV: Variables influencing bird distribution, abundance and spring phenological responses to climate change

Following a similar approach, I collected data on recent bird responses to climate change through a literature review, focusing exclusively on distribution and abundance and spring phenological responses. I obtained 3,012 responses for 918 species located in 32 countries, 60% of them were distribution and abundance responses and the remaining 40% were spring phenology responses. I compiled a dataset of nine intrinsic bird traits that have been previously hypothesized to be relevant in determining responses to climate change. I modeled separately the relationship between the outcomes of both types of responses and species-level intrinsic traits and population-level environmental factors. I found that environmental factors played an important role in determining both distribution and abundance and phenological responses to climate change. Maximum temperature, restricted climate seasonality, relative latitudinal position, and maximum longevity influenced the probability of experiencing contractions and a subsequent increase in risk. Similarly, maximum temperature, climate seasonality, relative latitudinal position, and temperature increase influenced the probability of experiencing advances in spring phenology.

Relevance of the results

Identifying which species and populations are or will be negatively impacted by climate change has become a key priority for conservation biology. The approaches that are currently used to achieve this can be categorized into three main groups: correlative, trait-based and mechanistic (Pacifici et al.

2015). Trait-based approaches use traits associated with vulnerability to climate change as predictors of extinction risk, sometimes in combination with data on exposure. This methodology allows assessing multiple species simultaneously in a simple way, serving as a useful tool for prioritizing conservation actions, especially in the absence of distribution data. However, its applicability can be limited as the approach is not spatially explicit, the relationship between traits and responses is still uncertain, there are gaps in trait data availability (Foden et al. 2018) and the approach is generally implemented at the species level, ignoring intraspecific differences in exposure, vulnerability and hazard. In this thesis, I attempted to overcome some of these limitations.

In Chapters II and IV, I compiled trait data for mammals and birds from multiple sources and unified them under a common taxonomy. For mammals, I also filled in gaps in the data through a phylogenetic multiple imputation procedure, providing a complete dataset for 21 traits, including sexual maturity, litter size, maximum longevity, tropic level, and dispersal. These datasets underpinned subsequent analyses in the thesis and will be useful in the future for other analyses. Trait datasets have become a fundamental tool for research in conservation, ecology and evolutionary biology. Besides being used to assess vulnerability to climate and land-use change, they are also being used to understand evolutionary processes, interspecific relationships and global patterns of species and functional diversity (Etard et al. 2020). Therefore, the availability of updated and complete trait datasets is of paramount importance.

In Chapters III and IV, I collected data on terrestrial non-volant mammal and bird responses to climate change. I found that most of the studies were carried out in Europe and North America, while studies in other regions were limited or non-existent, especially in tropical areas. Distributional responses constituted the most frequently reported group, comprising 80% of the mammal and 60% of the bird responses. While phenological responses were quite rare in mammals (around 5%), bird spring phenological responses were commonly documented (40%). This difference is probably because I excluded bats (which are one of the main orders of hibernating mammals) and because bird migration is an easily observable phenomenon with a high level of interest from professional ornithologists and citizen scientists (BirdLife International & National Audubon Society 2015; Usui et al. 2017).

To avoid the incidence of mixed responses (i.e., the same species showing opposing responses in different studies or areas), I grouped the responses by species and country. This helped clarify the relationship between the outcome of the responses and the considered variables and also allowed me to identify and include the latitudinal position of the response in our analyses. To account for intraspecific differences in exposure and vulnerability, I identified populations of the species exposed to the same climatic conditions using data on the species' distribution and biomes. This permitted obtaining population-level environmental factors, which represent the conditions that the population is experiencing and is potentially adapted to.

I found that distribution expansions predominantly occurred at the warm edge of the distributions of mammals and bird populations, and contractions predominantly occurred at the cold edge. Previous studies indicate that species are shifting their distributions polewards (Chen et al. 2011), but the direction of the shift is not always consistent when comparing different parts of the distribution of the species (Gibson-Reinemer & Rahel 2015). Our results indicate that poleward expansions and equatorial contractions are also occurring at the population scale, potentially explaining range shift inconsistencies when considering the entire distribution of the species. In the case of mammals, I also found that populations with large latitudinal ranges were more likely to have undergone range contractions. I hypothesized that this may be because most biomes with large latitudinal ranges are fully or partially located at high latitudes, near or directly in contact with the polar edge of their respective landmass. Populations that had experienced greater temperature increases had a higher probability of having undergone range contractions, further supporting the negative influence that climate change is having on species and populations.

Other population-level environmental factors such as temperature and precipitation seasonality (mammals and birds), maximum temperature (birds), and altitudinal breadth (mammals) also influenced risk from climate change. Even though these data were not measured at the population scale and do not represent population tolerances to environmental factors, they can be used as proxies of local adaptation and environmental tolerance until relevant data become available. In contrast, only three intrinsic species-level traits influenced risk from climate change. These traits were litter size and heterothermy for mammals and maximum longevity for birds. Furthermore, the direction of the effect of both heterothermy and maximum longevity was unexpected, probably due to the complex relationship between these traits and responses to climate change. In the case of heterothermy, I hypothesized that while opportunistically torpid species may be able to avoid adverse climate conditions when they emerge from torpor, obligate hibernators will suffer from a disruption in the timing of their life cycle caused by earlier springs and increased temperatures. In relation to maximum longevity, the observed results are probably a product of extinction debt masking the true impacts of climate change, which will become evident in the coming decades.

Both mammals and birds share similar thermal physiologies, maintaining a high and constant body temperature, which provides them with a high degree of thermal independence from the environment (Khaliq et al. 2014). In both cases, environmental factors influenced their risk from climate change in a similar direction, especially the degree of climate change experienced and climate seasonality. Therefore, it seems that the mechanisms through which mammals and birds are affected and respond to climate change are similar.

In Chapter IV, I found that only environmental factors influenced phenological advances. These advances were more prone to happen near the warm edge of the population and in populations that have experienced a greater temperature increase, in areas where contractions are also happening, based on the results of our previous models. Populations located in areas with a high seasonality tended to advance their phenology, probably due to their interactions with the species they depend upon. Although I could not establish a direct link between both types of responses, as most of them were not measured from the same population, I did find that relative latitude, maximum temperature, and seasonality influenced both responses.

Limitations and future research

In this thesis, I studied the relationship between local responses to climate change and intrinsic traits and environmental factors in both terrestrial non-volant mammals and birds. To achieve this, I compiled two datasets of intrinsic traits, and I conducted extensive literature reviews on mammal and bird responses to climate change. I developed a methodology to account for intraspecific variation in environmental factors by defining populations that have experienced - and are potentially adapted to - similar climatic conditions. However, there are some limitations that I discuss below, alongside future areas of research that can help solve these caveats and further develop the outcomes of this thesis.

In Chapters II and IV, I compiled trait datasets using data from many different data sources. Although I tried to control for errors in these data, some may nevertheless have occurred. Additionally, the methods used to obtain these data were not specified in most sources, and it is not clear how many individuals were measured or the geographical extent of the observations, making the representativeness of these data unclear. Frequent changes in taxonomy may also have affected data representativity. For instance, when a species was split in two, I used the trait data of the parent species, even though one or both of them may have different mean values. Therefore, datasets that include raw data such as TetraDENSITY (Santini et al. 2018) or Utheria (from which PanTHERIA (Jones et al. 2009) was derived, www.utheria.org) are especially valuable due to their transparency. Even though mammal and bird traits are well sampled (Etard et al. 2020), there were still data gaps in both datasets. In the case of mammals, I filled in data gaps using phylogenetic multiple imputation, which is not only a robust way to fill in gaps but also provides an estimation of uncertainty (Nakagawa & Freckleton 2008; Penone et al. 2014; Etard et al. 2020). Although robust imputation can temporarily solve the issue of missing data, it is no substitute for field sampling and efforts should be made towards obtaining these data, especially for unsampled areas and taxa.

In Chapters III and IV, I extracted data on terrestrial non-volant mammal and bird responses to climate change from studies that either provided statistical evidence of the relationship between the response and climate change or in which the author(s) unequivocally claimed that climate change was the driver behind the response. Drivers of biodiversity loss rarely act in isolation (Schulte to Bühne et al. 2021), therefore other drivers (such as land-use change or alien species) or mere chance may be behind the reported responses, especially in the articles in which I trusted the judgment of the authors. The analyses I performed on the relationship between intrinsic traits and environmental factors and responses to climate change cannot be considered as formal meta-analyses, as I did not extract or calculate effect sizes from the considered studies (Haddaway et al. 2020). I used a vote-counting methodology, assigning each observed response to a category, in order to identify which variables may influence specific response outcomes. As a consequence, I could not provide a measure of changes in distribution or phenology nor evaluate the strength of the relationships between responses and variables. Therefore, future efforts should focus on extracting data suitable for a meta-analysis, providing further insights on the variables influencing responses to climate change.

The effects and responses to extreme events were largely excluded from my analyses, as I only considered studies that spanned at least 10 years, while extreme events generally have a short duration (although some events can last decades, for example, drought in Brown & Brown 2014), and many studies reporting their effects cover less than one year (Maxwell et al. 2019). Studying the effects of extreme events on biodiversity constitutes an urgent line of research, as their frequency and intensity are projected to increase (IPCC 2021).

To identify the intrinsic traits and environmental factors influencing responses to climate change, I grouped all the responses by species and country into 'subpopulations' and used them as my unit of analysis. I did this to account for variation in the size of the area of study of each article and to include latitudinal position of the response. However, it must be acknowledged that species' distributions do not follow political limits and using administrative areas to group responses has its limitations.

I identified populations of species that are exposed to similar climatic conditions using the intersection of the species' distributions with terrestrial biomes. This allowed inclusion of intraspecific variation in environmental factors in a simple way that can be applied to all species with available distribution data. Even though biomes have been previously identified as areas with climatically similar conditions (Penone et al. 2016), this relationship still needs to be tested. Intrinsic trait data were included at the species level due to the lack of intraspecific-level data. This may have influenced my results and could potentially explain why a limited number of intrinsic traits were associated with local responses to climate change. However, obtaining this information in the near future is highly unlikely. Thus, exploring the use of intraspecific-level environmental factors as proxies might prove to be valuable.

Most of the studies on responses to climate change were carried out in Europe and North America, while the rest of the world remained largely understudied or unrepresented. Additionally, even though I collected data on a wide range of species (130 mammal species and 918 bird species), there will probably be combinations of intrinsic traits and environmental factors that are not represented in our analyses. Both these biases may limit the applicability of my results to lesser-known areas and species. The results of my models indicate that populations located in areas with stable climates will be more at risk from climate change. These areas tend to be located in the tropics, which constitute one of the least-studied areas. Therefore, studying and directing conservation actions in these areas is essential to ensure the persistence of tropical biodiversity.

Throughout this thesis, I considered risk from climate change as a function of distribution size and abundance. However, this relationship is complex and my results on these types of responses should be interpreted carefully. For instance, even though local range expansions could be classified as a positive response when considered in isolation, if it is accompanied by contractions at the opposite edge of the distribution (i.e. the population's distribution is shifting), the population will eventually reach a dispersal barrier and experience a local extirpation. Populations that have benefitted from climate change and expanded their distribution may also become native invaders, negatively impacting other species and populations (Carey et al. 2012; Scheffers et al. 2019). Furthermore, it cannot be assumed that the population will be able to persist in new areas it has expanded into. Changes in the distribution of populations have already altered the composition of ecological communities and ecosystem functioning, impacting both biological and human communities (Pecl et al. 2017).

Future avenues of research directly linked to this thesis would include the exploration of autumn phenological responses for birds, mammalian phenological responses and interaction between traits when influencing responses to climate change. The direction of body size responses remains unclear, therefore further exploring morphological responses to climate change might prove valuable to identify the effects of climate change on biodiversity. It would also be interesting to explore the relationship between different axes of responses to climate change, and the influence of traits and environmental conditions on the responses of marine, freshwater and ectotherm species.

Concluding remarks

With this thesis, I aimed to improve trait data availability and identify the relationship between intrinsic traits, environmental factors and local responses to climate change. The mammal trait database was developed to gather all currently available mammal trait data into a free and easily accessible repository that will serve as a fundamental tool in future trait analyses. Both literature reviews provided a snapshot of the current state of reported mammal and bird responses to climate change, highlighting which responses and areas are understudied. Analyzing the relationship between traits and environmental factors and distribution responses, allowed identifying which variables influence local risk. Similarly, analyzing this relationship for bird spring phenological responses, allowed identifying the characteristics of the populations advancing their phenology to keep up with climate change. The results of these analyses reinforced the importance of considering intraspecific variation in responses to climate change, as most of the significant traits were population-level environmental factors hypothesized to be associated with climate tolerance, as well as the latitudinal position of the response within the population. Therefore, using environmental factors as proxies of the climate tolerance of populations will help facilitate determining how populations are responding to climate change and which will be at risk. The results presented in this thesis constitute an advance in current knowledge on the variables influencing responses to climate change locally and serve as a starting point for future research.

Chapter VI

Research outputs and contributions

Key research outputs

Soria CD, Pacifici M, Di Marco M, Stephen SM, Rondinini C. 2021. COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. Ecology **102:**13028255.

Soria CD, Pacifici M, Butchart SHM, Rondinini C. Relative latitude, temperature increase and breadth of climatic niche influence mammal populations' response to climate change. (In preparation)

Soria CD, Pacifici M, Rondinini C, Butchart SHM. Local environmental factors influence bird distribution and phenological responses to climate change. (In preparation)

Collaborative research outputs

Lumbierres M., Dahal RP, **Soria CD**, Di Marco M, Butchart SHM, Donald FP, Rondinini C. Area of Habitat maps for the world's terrestrial birds and mammals. (Under review in Scientific Data)

Gil-Tapetado D, **Soria CD**, Gómez JF, Sesma JM, Cabrero-Sañudo JF. Aridity has driven the local extinction of a common and polyvoltine diurnal butterfly. (Under review in Insect Conservation and Diversity)

Soria CD, Serlupi-Crescenzi M, Rondinini, C. Future exposure of terrestrial mammals to extreme heatwaves and droughts under climate change scenarios. (In preparation)

Conference contributions

2019 29th International Congress for Conservation Biology. Kuala Lumpur, Malaysia, 21-25th July. Poster – Trait data quality and availability: a review of mammal trait databases.

2021 100th Annual Meeting of the American Society of Mammalogists. Online, 14-18th June. Symposium – Global trends in mammal distribution and threats, Oral presentation – How do species traits determine their responses to climate change?

2021 30th International Congress for Conservation Biology. Online, 12-16th December. Oral presentation – Do traits determine bird local responses to climate change?

2022 Student Conference on Conservation Science. Cambridge, UK, 29-31st March. Poster: The floor is lava: Mapping mammal exposure to extreme drought and warm spells.

References

Abraham AJ, Prys-Jones TO, De Cuyper A, Ridenour C, Hempson GP, Hocking T, Clauss M, Doughty CE. 2021. Improved estimation of gut passage time considerably affects trait-based dispersal models. Functional Ecology **35:**860–869.

Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics **44:**367–388.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters **14:**677–689.

Antonelli A et al. 2018. Geological and climatic influences on mountain biodiversity. Nature Geoscience **11:**718–725.

Balčiauskienė L, Balčiauskas L, Timm U. 2018. Changes in size of Baltic field voles over the last 50 years: are they really shrinking? Biologia (Poland) **73:**247–257.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using {lme4}. Journal of Statistical Software **67:**1–48.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters **15**:365–377.

Bird JP, Martin R, Akçakaya HR, Gilroy J, Burfield IJ, Garnett ST, Symes A, Taylor J, Şekercioğlu ÇH, Butchart SHM. 2020. Generation lengths of the world's birds and their implications for extinction risk. Conservation Biology **34:**1252–1261.

BirdLife International. 2013. Birds are very useful indicators for other kinds of biodiversity. Downloaded from http://www.birdlife.org on 26/01/2022.

BirdLife International, National Audubon Society. 2015. The messengers: what birds tell us about threats from climate change and solutions for nature and people. Cambridge, UK and New York, USA.

Bischof R, Loe LE, Meisingset EL, Zimmermann B, van Moorter B, Mysterud A. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? American Naturalist **180:**407–424.

Blinkov SM, Glezer IA. 1968. The Human Brain in Figures and Tables: A Quantitative Handbook. Basic Books, New York, USA.

Böhm M, Cook D, Ma H, Davidson AD, García A, Tapley B, Pearce-Kelly P, Carr J. 2016. Hot and bothered: Using trait-based approaches to assess climate change vulnerability in reptiles. Biological Conservation **204:**32–41.

Bonardi A, Corlatti L, Bragalanti N, Pedrotti L. 2017. The role of weather and density dependence on population dynamics of Alpine-dwelling red deer. Integrative Zoology **12**:61–76.

Bonebrake TC, Mastrandrea MD. 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. Proceedings of the National Academy of Sciences of the United States of America **107:**12581–12586.

Botero CA, Dor R, McCain CM, Safran RJ. 2013. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. Molecular Ecology **23:**259-268.

Both C, Bouwhuis S, Lessells CM, Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. Nature **441:**81–83.

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B: Biological Sciences **277:**1259–1266.

Botkin DB et al. 2007. Forecasting the effects of global warming on biodiversity. BioScience **57**:227–236.

Boutin S, Lane JE. 2014. Climate change and mammals: Evolutionary versus plastic responses. Evolutionary Applications **7**:29–41.

Brodie JF, Post E. 2010. Nonlinear responses of wolverine populations to declining winter snowpack. Population Ecology **52:**279–287.

Brown JH. 1984. On the Relationship between Abundance and Distribution of Species. The American Naturalist **124:**255–279.

Brown CR, Brown MB. 2014. Breeding time in a migratory songbird is predicted by drought severity and group size. Ecology **95**:2707–2714.

Breiman L. 2001. Random Forests. Machine Learning **45**:5–32.

Buckley LB, Khaliq I, Swanson DL, Hof C. 2018. Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? Ecology and Evolution **8**:12375–12385.

Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A. 2008. The predictability of extinction: Biological and external correlates of decline in mammals. Proceedings of the Royal Society B: Biological Sciences **275**:1441–1448.

Carey MP, Sanderson BL, Barnas KA, Olden JD. 2012. Native invaders - Challenges for science, management, policy, and society. Frontiers in Ecology and the Environment **10**:373–381.

Ceballos G, Ehrlich PR. 2006. Global mammal distributions, biodiversity hotspots, and conservation. Proceedings of the National Academy of Sciences of the United States of America **103**:19374–19379.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances **1:** e1400253.

Ceballos G, Ehrlich PR, Raven PH. 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proceedings of the National Academy of Sciences of the United States of America **117**:13596–13602.

Charmantier A, Gienapp P. 2014. Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. Evolutionary Applications **7**:15–28.

Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science **320**:800–803.

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333:**1024–1026.

Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH. 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. Ecological Monographs **89:** e01337.

Cohen JM, Lajeunesse MJ, Rohr JR. 2018. A global synthesis of animal phenological responses to climate change. Nature Climate Change **8:**224–228.

Cowie RH, Bouchet P, Fontaine B. 2022. The Sixth Mass Extinction: fact, fiction or speculation? Biological reviews Early View.

Crutzen PJ. 2002. Geology of mankind. Nature **415**:23.

Daufresne M, Lengfellner K, Sommer U. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences of the United States of America **106:**12788–12793.

Degen R et al. 2018. Trait-based approaches in rapidly changing ecosystems : A roadmap to the future polar oceans **91**:722–736.

De Magalhães JP, Costa J. 2009. A database of vertebrate longevity records and their relation to other life-history traits. Journal of Evolutionary Biology **22**:1770–1774.

Di Marco M, Buchanan GM, Szantoi Z, Holmgren M, Marasini GG, Gross D, Tranquilli S, Boitani L, Rondinini C. 2014. Drivers of extinction risk in african mammals: The interplay of distribution state, human pressure, conservation response and species biology. Philosophical Transactions of the Royal Society B: Biological Sciences **369**:20130198.

Díaz S et al. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem. Services. IPBES secretariat.

Dinerstein E et al. 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience **67:**534–545.

Dormann CF et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, **36:**27–46.

Dunning JB. 1992. Handbook of Avian Body Masses. CRC Press, Boca Raton, Florida, USA.

Eastman LM, Morelli TL, Rowe KC, Conroy CJ, Moritz C. 2012. Size increase in high elevation ground squirrels over the last century. Global Change Biology **18**:1499–1508.

Estrada A, Morales-Castilla I, Caplat P, Early R. 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends in Ecology and Evolution **31:**190–213.

Edic MN, Martin JGA, Blumstein DT. 2020. Heritable variation in the timing of emergence from hibernation. Evolutionary Ecology **34:**763–776.

Elith J, Leathwick JR. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics **40:**677–697.

Ernest SKM. 2003. Life history characteristics of placental nonvolant mammals. Ecology **84**:3402.

Estrada A, Morales-Castilla I, Caplat P, Early R. 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends in Ecology and Evolution **31**: 190–203.

Etard A, Morrill S, Newbold T. 2020. Global gaps in trait data for terrestrial vertebrates. Global Ecology and Biogeography **29**:2143–2158.

Faurby S, Davis M, Pedersen R, Schowanek SD, Antonelli A, Svenning JC. 2018. PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. Ecology **99**:2626.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology **37:**4302–4315.

Foden WB et al. 2018. Climate change vulnerability assessment of species. Wiley Interdisciplinary Reviews: Climate Change **10**:1–36.

Foden WB et al. 2013. Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. PLoS ONE **8:**6.

Forero-Medina G, Terborgh J, Socolar SJ, Pimm SL. 2011. Elevational Ranges of Birds on a Tropical Montane Gradient Lag behind Warming Temperatures. PLoS ONE **6:**1-5.

Forrest JR. 2016. Complex responses of insect phenology to climate change. Current Opinion in Insect Science **17:**49–54.

Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proceedings of the National Academy of Sciences **115**:11982-11987.

Fryxell JM, Sinclair ARE. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution **3:**237–241.

Gainsbury AM, Tallowin OJS, Meiri S. 2018. An updated global data set for diet preferences in terrestrial mammals: testing the validity of extrapolation. Mammal Review **48**:160–167.

Gallinat AS, Primack RB, Wagner DL. 2015. Autumn, the neglected season in climate change research. Trends in Ecology and Evolution **30:**169–176.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011. Declining body size: A third universal response to warming? Trends in Ecology and Evolution **26:**285–291.

Geiser F. 2013. Hibernation. Current Biology **23:**188–193.

Geiser F, Turbill C. 2009. Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften **96:**1235–1240.

Gibson-Reinemer DK, Rahel FJ. 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. PLoS ONE **10:**1–15.

Gillings S, Balmer DE, Fuller RJ. 2015. Directionality of recent bird distribution shifts and climate change in Great Britain. Global Change Biology **21:**2155–2168.

Goldberg AR, Conway CJ. 2021. Hibernation behavior of a federally threatened ground squirrel: Climate change and habitat selection implications. Journal of Mammalogy **102:**574–587.

González-Suárez M, Bacher S, Jeschke JM. 2015. Intraspecific trait variation is correlated with establishment success of alien mammals. American Naturalist **185:**737–746.

Gordo O, Sanz JJ. 2005. Phenology and climate change: A long-term study in a Mediterranean locality. Oecologia **146:**484–495.

Haddaway NR, Bethel A, Dicks L V., Koricheva J, Macura B, Petrokofsky G, Pullin AS, Savilaakso S, Stewart GB. 2020. Eight problems with literature reviews and how to fix them. Nature Ecology and Evolution **4**:1582–1589.

Haest B, Hüppop O, van de Pol M, Bairlein F. 2019. Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. Global Change Biology **25:**4064–4080.

Halupka L, Dyrcz A, Borowiec M. 2008. Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. Journal of Avian Biology **39:**95–100.

Halupka L, Halupka K. 2017. The effect of climate change on the duration of avian breeding seasons: a meta-analysis. Proceedings of the Royal Society B: Biological Sciences **284:**1867.

Harrell FE. 2015. Regression Modeling Strategies, 1st edition. Springer New York, New York, NY.

Harris I, Osborn TJ, Jones P, Lister D. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data **7:**1–18.

Hartig F. 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. Available from https://cran.r-project.org/package=DHARMa.

Hayssen V, Tienhoven AV. 1993. Asdell's Patterns of Mammalian Reproduction: A Compendium of Species-Specific Data. Cornell University Press, Ithaca, New York, USA.

Heldstab SA, Isler K, van Schaik CP. 2018. Hibernation constrains brain size evolution in mammals. Journal of Evolutionary Biology **31**:1582–1588.

Hetem RS, Fuller A, Maloney SK, Mitchell D. 2014. Responses of large mammals to climate change. Temperature **1:**115–127.

Hijmans RJ. 2021. raster: Geographic Data Analysis and Modeling. Available from https://cran.r-project.org/package=raster.

Hitch AT, Leberg PL. 2007. Breeding distributions of North American bird species moving north as a result of climate change. Conservation Biology **21:**534–539.

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences **367**:1665–1679.

Hüppop O, Hüppop K. 2003. North Atlantic Oscillation and timing of spring migration in birds. Proceedings of the Royal Society B: Biological Sciences **270:**233–240.

IPCC. 2019. Annex I: Glossary. Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)]. In press.

IPCC. 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen,. Cambridge University Press:3949.

IPCC. 2013. Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D.

Qin, G.- K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley Eds.). Cambridge University Press.

Isaac JL, Vanderwal J, Johnson CN, Williams SE. 2009. Resistance and resilience: Quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. Diversity and Distributions **15:**280–288.

IUCN. 2020. IUCN Red List of threatened species. Version 2020-2. http://www.iucnredlist.org.

IUCN Standards and Petitions Committee. 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. IUCN Standards and Petitions Committee. IUCN Red List **14:**1–60.

Jenni L, Kéry M. 2003. Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society B: Biological Sciences **270:**1467–1471.

Jetz W, Thomas GH, Joy JB, Redding DW, Hartmann K, Mooers AO. 2014. Global Distribution and Conservation of Evolutionary Distinctness in Birds. Current Biology **24:**919–930

Jones KE et al. 2009. PanTHERIA : a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology **90**:2648.

Jones KE, Safi K. 2011. Ecology and evolution of mammalian biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences **366**:2451–2461.

Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proceedings of the Royal Society B: Biological Sciences **281**: 20141097.

Kharouba HM, Ehrlén J, Gelman A, Bolmgren K, Allen JM, Travers SE, Wolkovich EM. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences **115:**201714511.

Kingma BRM, Frijns AJH, Schellen L, van Marken Lichtenbelt WD. 2014. Beyond the classic thermoneutral zone: Including thermal comfort. Temperature **1**:142–149.

Kissling WD, Dalby L, Fløjgaard C, Lenoir J, Sandel B, Sandom C, Trøjelsgaard K, Svenning JC. 2014. Establishing macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. Ecology and Evolution **4**:2913–2930.

Koleček J, Adamík P, Reif J. 2020. Shifts in migration phenology under climate change: temperature vs. abundance effects in birds. Climatic Change **159:**177–194.

Lawton JH. 1993. Range, population abundance and conservation. Trends in Ecology and Evolution **8:**409–413.

Lewis SL, Maslin MA. 2015. Defining the Anthropocene. Nature **519:**171–180. Nature Publishing Group.

Lehikoinen E, Sparks TH, Zalakevicius M. 2004. Arrival and Departure Dates. Advances in Ecological Research **35:**1–31.

Lin D, Foster DP, Ungar LH. 2011. VIF regression: A fast regression algorithm for large data. Journal of the American Statistical Association **106:**232–247.

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC. 2009. Lower extinction risk in sleep-or-hide mammals. American Naturalist **173:**264–272.

Loiseau N et al. 2020. Global distribution and conservation status of ecologically rare mammal and bird species. Nature Communications **11**:5071.

MacLean SA, Beissinger SR. 2017. Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. Global Change Biology **23:**4094–4105.

Maxwell SL, Butt N, Maron M, McAlpine CA, Chapman S, Ullmann A, Segan DB, Watson JEM. 2019. Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions **25**:613–625.

McCain CM. 2019. Assessing the risks to United States and Canadian mammals caused by climate change using a trait-mediated model. Journal of Mammalogy **100**:1808–1817.

McCain CM, King SRB. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology **20:**1760–1769.

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution **21**:178–185.

McNab BK. 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology **151**:5–28.

Merilä J, Hendry AP. 2014. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. Evolutionary Applications **7:**1–14.

Michel NL, Whelan CJ, Verutes GM. 2020. Ecosystem services provided by Neotropical birds. Condor **122**:1–21.

Michel NL, Hobson KA, Morrissey CA, Clark RG. 2021. Climate variability has idiosyncratic impacts on North American aerial insectivorous bird population trajectories. Biological Conservation **263:**109329.

Miles J. 2005. Tolerance and variance inflation factor. Encyclopedia of statistics in behavioural science. John Wiley and Sons. Chichester, United Kingdom.

Møller AP, Rubolini D, Lehikoinen E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences of the United States of America **105:**16195–16200.

Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donázar JA. 2014. Humans and scavengers: The evolution of interactions and ecosystem services. BioScience **64**:394–403.

Moran E V., Hartig F, Bell DM. 2016. Intraspecific trait variation across scales: Implications for understanding global change responses. Global Change Biology **22**:137–150.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology **96**:3109–000.

Nakagawa S, Freckleton RP. 2008. Missing inaction: the dangers of ignoring missing data. Trends in Ecology and Evolution **23**:592–596.

Newbold T. 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proceedings of the Royal Society B: Biological Sciences **285**:1881.

Nogués-Bravo D, Rodríguez-Sánchez F, Orsini L, de Boer E, Jansson R, Morlon H, Fordham DA, Jackson ST. 2018. Cracking the Code of Biodiversity Responses to Past Climate Change. Trends in Ecology and Evolution **33**:765–776.

Nowak RM. 1999. Walker's Mammals of the World. 6th edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Nunez S, Arets E, Alkemade R, Verwer C, Leemans R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 °C enough? Climatic Change **154**:351–365.

Oba S, Sato M, Takemasa I, Monden M, Matsubara K, Ishii S. 2003. A Bayesian missing value estimation method for gene expression profile data. Bioinformatics **19**:2088–2096.

Otto SP. 2018. Adaptation, speciation and extinction in the Anthropocene. Proceedings of the Royal Society B: Biological Sciences **285**:20182047.

Pacifici M et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change **5:**215–225.

Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017. Species' traits influenced their response to recent climate change. Nature Climate Change **7:**205–208.

Pacifici M, Santini L, Di Marco M, Baisero D, Francucci L, Grottolo Marasini G, Visconti P, Rondinini C. 2013. Generation length for mammals. Nature Conservation **5**:89–94.

Paradis E, Schliep K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in {R}. Bioinformatics **35**:526–528.

Parmesan C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics **37**:637–669.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421:**37–42.

Parmesan C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology **13:**1860–1872.

Pearson RG, Dawson TP. 2003. Predicting the impact of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography **12:**361–371.

Pearson RG et al. 2014. Life history and spatial traits predict extinction risk due to climate change. Nature Climate Change **4:**217–221.

Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal **10:**439–446.

Pecl GT et al. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science **355:**eaai9214.

Penone C, Weinstein BG, Graham CH, Brooks TM, Rondinini C, Hedges SB, Davidson AD, Costa GC. 2016. Global mammal beta diversity shows parallel assemblage structure in similar but isolated environments. Proceedings of the Royal Society B: Biological Sciences **283:**1837.

Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC. 2014. Imputation of missing data in life-history trait datasets: Which approach performs the best? Methods in Ecology and Evolution **5**:1–10.

Pievani T. 2014. The sixth mass extinction: Anthropocene and the human impact on biodiversity. Rendiconti Lincei **25**:85–93.

Pigliucci M, Murren CJ, Schlichting CD. 2006. Phenotypic plasticity and evolution by genetic assimilation. Journal of Experimental Biology **209**:2362–2367.

Prevéy J et al. 2017. Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. Global Change Biology **23:**2660–2671.

Princé K, Zuckerberg B. 2015. Climate change in our backyards: The reshuffling of North America's winter bird communities. Global Change Biology **21:**572–585.

Polidori C, García-Gila J, Blasco-Aróstegui J, Gil-Tapetado D. 2021. Urban areas are favouring the spread of an alien mud-dauber wasp into climatically non-optimal latitudes. Acta Oecologica **110:**103678.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences **267:**1947–1952.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria. Available from https://www.r-project.org/.

Radchuk V et al. 2019. Adaptive responses of animals to climate change are most likely insufficient. Nature Communications **10:**3109.

Réale D, McAdam AG, Boutin S, Berteaux D. 2003. Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society B: Biological Sciences **270:**591–596.

Reisinger A et al. 2020. The Concept of Risk in the IPCC Sixth Assessment Report: A Summary of Cross-Working Group Discussions. Intergovernmental Panel on Climate Change, Geneva, Switzerland. pp15.

Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution **3:**217–223.

Riddell EA, Iknayan KJ, Wolf BO, Sinervo B, Beissinger SR. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proceedings of the National Academy of Sciences of the United States of America **116:**21609–21615.

Román-Palacios C, Wiens JJ. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences of the United States of America **117**:4211–4217.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. Nature **421:**57–60.

Rowe KC, Rowe KMC, Tingley MW, Koo MS, Patton JL, Conroy CJ, Perrine JD, Beissinger SR, Moritz C. 2015. Spatially heterogeneous impact of climate change on small mammals of montane California. Proceedings of the Royal Society B: Biological Sciences **282:**20141857.

Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. Biological Reviews **90**:891–926.

Salamin N, Wüest RO, Lavergne S, Thuiller W, Pearman PB. 2010. Assessing rapid evolution in a changing environment. Trends in Ecology and Evolution **25**:692–698.

Sandvik H, Einar Erikstad K. 2008. Seabird life histories and climatic fluctuations: A phylogenetic-comparative time series analysis of North Atlantic seabirds. Ecography **31:**73–83.

Santini L, Di Marco M, Visconti P, Baisero D, Boitani L, Rondinini C. 2013. Ecological correlates of dispersal distance in terrestrial mammals. Hystrix **24**:181–186.

Santini L, Isaac NJB, Ficetola GF. TetraDENSITY: a database of population density estimates in terrestrial vertebrates. Global Ecology and Biogeography **27**:787-791.

Santini L, Butchart SHM, Rondinini C, Benítez-López A, Hilbers JP, Schipper AM, Cengic M, Tobias JA, Huijbregts MAJ. 2019. Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. Conservation Biology **33:**1084–1093.

Santoro S, Sanchez-Suarez C, Rouco C, Palomo LJ, Fernández MC, Kufner MB, Moreno S. 2017. Long-term data from a small mammal community reveal loss of diversity and potential effects of local climate change **63:**515–523.

Santos T. 2018. PVR: Phylogenetic Eigenvectors Regression and Phylogentic Signal-Representation Curve. Available from https://cran.r-project.org/package=PVR.

Scheffers BR et al. 2016. The broad footprint of climate change from genes to biomes to people. Science **354:**719.

Scheffers BR, Pecl G. 2019. Persecuting, protecting or ignoring biodiversity under climate change. Nature Climate Change **9:**581–586.

Schloss CA, Nuñez TA, Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America **109:**8606–8611.

Schulte to Bühne H, Tobias JA, Durant SM, Pettorelli N. 2021. Improving Predictions of Climate Change–Land Use Change Interactions. Trends in Ecology and Evolution **36**:29–38.

Sekercioglu CH. 2006. Increasing awareness of avian ecological function. Trends in Ecology and Evolution **21**:464–471.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR. 2008. Climate change, elevational range shifts, and bird extinctions. Conservation Biology **22:**140–150.

Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change **1:**401–406.

Schulte to Bühne H, Tobias JA, Durant SM, Pettorelli N. 2021. Improving Predictions of Climate Change–Land Use Change Interactions. Trends in Ecology and Evolution **36**:29–38.

Siepielski AM, Morrissey MB, Carlson SM, Francis CD, Kingsolver JG, Whitney KD, Kruuk LEB. 2019. No evidence that warmer temperatures are associated with selection for smaller body sizes. Proceedings of the Royal Society B: Biological Sciences **286:**1907.

Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP. 2003. Body mass of late quaternary mammals **84**:87131.

Socolar JB, Epanchin PN, Beissinger SR, Tingley MW. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. Proceedings of the National Academy of Sciences of the United States of America **114:**12976–12981.

Soria CD, Pacifici M, Di Marco M, Stephen SM, Rondinini C. 2021. COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. Ecology **102:**13028255.

Stekhoven DJ, Buehlmann P. 2012. MissForest - non-parametric missing value imputation for mixed-type data. Bioinformatics **28**:112–118. Oxford Univ Press.

Teplitsky C, Millien V. 2014. Climate warming and Bergmann's rule through time: Is there any evidence? Evolutionary Applications **7:**156–168.

Thomas CD et al. 2004. Extinction risk from climate change. Nature **427**:145–148.

Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proceedings of the Royal Society B: Biological Sciences **278**:3355–3363.

Turbill C, Geiser F. 2008. Hibernation by tree-roosting bats. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology **178:**597–605.

Usui T, Butchart SHM, Phillimore AB. 2017. Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. Journal of Animal Ecology **86**:250–261.

Urban M. 2015. Accelerating risk from climate change. Science **348**:571–573.

Urban MC. 2018. Escalator to extinction. Proceedings of the National Academy of Sciences **115:**201817416.

Van Buskirk J, Mulvihill RS, Leberman RC. 2009. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. Global Change Biology **15:**760–771.

Vedder O, Bouwhuis S, Sheldon BC. 2013. Quantitative Assessment of the Importance of Phenotypic Plasticity in Adaptation to Climate Change in Wild Bird Populations. PLoS Biology **11:**1–10.

Végvári Z, Bókony V, Barta Z, Kovács G. 2010. Life history predicts advancement of avian spring migration in response to climate change. Global Change Biology **16:**1–11.

Vetter SG, Ruf T, Bieber C, Arnold W. 2015. What is a mild winter? Regional differences in within-species responses to climate change. PLoS ONE **10:**1–17.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! Oikos **116**:882–892.

Visser ME, Both C. 2005. Shifts in phenology due to global climate change: The need for a yardstick. Proceedings of the Royal Society of London B: Biological Sciences **272:** 2561–2569.

Visser ME, Holleman LJM, Gienapp P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia **147:**164–172.

Waters CN et al. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science **351:**aad2622-1

Whelan CJ, Wenny DG, Marquis RJ. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences **1134**:25–60.

Wiens JJ. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLoS Biology **14:**1–18.

Wilman H, Belmaker J, Simpson J, de la Rosa C., Rivadeneira MM, Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology **95**:2027.

Williams CM, Henry HAL, Sinclair BJ. 2015. Cold truths: How winter drives responses of terrestrial organisms to climate change. Biological Reviews **90:**214–235.

Williams JJ, Freeman R, Spooner F, Newbold T. 2021. Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. Global Change Biology **00:**1–19.

Williams SE, Middleton J. 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: Implications for global climate change. Diversity and Distributions **14:**69–77

WWF. 2018. Living Planet Report - 2018: Aiming higher. Page Environmental Conservation. Available from https://www.wwf.eu/campaigns/living_planet_report_2018/.

Young B, Dubois N, Rowland E. 2015. Using the climate change vulnerability index to inform adaptation planning: Lessons, innovations, and next steps. Wildlife Society Bulletin **39:**174-181.

Zimova M, Willard DE, Winger BM, Weeks BC. 2021. Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. Journal of Animal Ecology **90:**2348–2361.

Supplementary Material

Supplementary Material Chapter II

Appendix S2.1. Variable information of the reported and imputed datasets.

order
Definition: Order name of the species
Data type: Character
Values: 29 order names
Completeness: 100%

family
Definition: Family name of the species
Data type: Character
Values: 175 family names
Completeness: 100%

genus
Definition: Genus name of the species
Data type: Character
Values: 1429 genus names
Completeness: 100%

species
Definition: Specific epithet name of the species
Data type: Character
Values: 4422 specific epithets
Completeness: 100%

iucn2020_binomial
Definition: IUCN v. 2020-2 binomial name
Data type: Character
Values: 5961 binomial names
Completeness: 100%

phylacine_binomial

Definition: PHYLACINE v. 1.2 binomial name
Data type: Character
Values: 5831 binomial names
Completeness: 100%

adult_mass_g

Definition: Body mass of an adult individual in grams
Data type: Numeric (float)
Values: Estimates range from 1.6 g to $1.49*10^8$ g
Completeness: 96.33%

brain_mass_g

Definition: Weight of the brain of an adult individual in grams
Data type: Numeric (float)
Values: Estimates range from 0.071 g to 7,818 g
Completeness: 29.30% (97.5% with imputed data)

adult_body_length_mm

Definition: Total length from tip of the nose to anus or base of the tail of an adult individual in millimeters
Data type: Numeric (float)
Values: Estimates range from 30.99 mm to 30,490 mm
Completeness: 66.66% (97.5% with imputed data)

adult_forearm_length_mm

Definition: Total length from elbow to wrist of an adult individual in millimeters, specific to order Chiroptera
Data type: Numeric (float)
Values: Estimates range from 26 mm to 246 mm
Completeness: 16.27%

max_longevity_d

Definition: Maximum reported age at death for the species in days
Data type: Numeric (float)
Values: Estimates range from 30.42 days to 77,015 days
Completeness: 44.10% (97.5% with imputed data)

maturity_d

Definition: The amount of time needed to reach sexual maturity in days
Data type: Numeric (float)
Values: Estimates range from 13.57 days to 6,041.21 days
Completeness: 34.40%

female_maturity_d

Definition: The amount of time needed for a female to reach sexual maturity in days
Data type: Numeric (float)
Values: Estimates range from 23.81 days to 6,391.56 days
Completeness: 34.10% (97.5% with imputed data)

male_maturity_d

Definition: The amount of time needed for a male to reach sexual maturity in days
Data type: Numeric (float)
Values: Estimates range from 36 days to 8,212 days
Completeness: 17.84%

age_first_reproduction_d

Definition: Age at which females give birth to their first litter or their young attach to teats in days
Data type: Numeric (float)
Values: Estimates range from 39 days to 8,599.95 days
Completeness: 33.77% (97.5% with imputed data)

gestation_length_d

Definition: Length of time of fetal growth in days
Data type: Numeric (float)
Values: Estimates range from 10 days to 669.68 days
Completeness: 37.96% (97.5% with imputed data)

teat_number_n

Definition: Total number of teats present in an individual of the species
Data type: Numeric (integer)
Values: Estimates range from 1 teat to 26 teats
Completeness: 10.84%

litter_size_n

Definition: Number of offspring born per litter per female
Data type: Numeric (float)
Values: Estimates range from 0.9 offspring to 16.87 offspring
Completeness: 60.17% (97.5% with imputed data)

litters_per_year_n

Definition: Number of litters per female per year
Data type: Numeric (float)
Values: Estimates range from 0.12 litters to 10 litters

Completeness: 36.81% (97.5% with imputed data)

interbirth_interval_d

Definition: Time between reproduction events in days
Data type: Numeric (float)
Values: Estimates range from 55.58 days to 231 days
Completeness: 21.51% (97.5% with imputed data)

neonate_mass_g

Definition: Weight of an individual at birth in grams
Data type: Numeric (float)
Values: Estimates range from 0.0043 g to 2,250,000 g
Completeness: 32.40%

weaning_age_d

Definition: Age at which primary nutritional dependency on the mother ends and independent foraging begins in days
Data type: Numeric (float)
Values: Estimates range from 1.94 days to 1,826.25 days
Completeness: 35.00% (97.5% with imputed data)

weaning_mass_g

Definition: Weight at weaning in grams
Data type: Numeric (float)
Values: Estimates range from 0.7 g to 17,000,000 g
Completeness: 18.11%

generation_length_d

Definition: Average age of parents of the current cohort in days
Data type: Numeric (float)
Values: Estimates range from 128.98 days to 18980 days
Completeness: 22.91% (97.5% with imputed data)

dispersal_km

Definition: The distance an animal travels between its place of birth to the place where it reproduces in kilometers
Data type: Numeric (float)
Values: Estimates range from 0.040 km to 109.14 km
Completeness: 69.62%

density_n_km2

Definition: Number of individuals of the species per squared kilometer
Data type: Numeric (float)

Values: Estimates range from 0.00026 ind/km^2 to 57,067.85 ind/km^2
Completeness: 20.15%

hibernation_torpor

Definition: Individuals of the species go through hibernation or torpor
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 49.46% (97.27% with imputed data)

fossoriality

Definition: The species is above ground dwelling or ground/fossorial dwelling
Data type: Binary
Values: Two levels:

- 1: fossorial and/or ground dwelling
- 2: above ground dwelling

Completeness: 46.20% (97.19% with imputed data)

home_range_km2

Definition: Size of the area within which everyday activities of individuals or groups of individuals are typically restricted in km^2
Data type: Numeric (float)
Values: Estimates range from 2.04x10-5 to 79244.75 km^2
Completeness: 12.78%

social_group_size_n

Definition: Number of individuals in a group that spends most of their daily time together
Data type: Numeric (float)
Values: Estimates range from 1 individual to 110 individuals
Completeness: 13.10%

dphy_invertebrate

Definition: Percentage of the diet composed of invertebrates
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 96.73% (97.5% with imputed data)

dphy_vertebrate

Definition: Percentage of the diet composed of vertebrates
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 96.73% (97.5% with imputed data)

dphy_plant

Definition: Percentage of the diet composed of plants and/or fungi
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 96.73% (97.5% with imputed data)

det_inv

Definition: Percentage of the diet composed of invertebrates
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_vend

Definition: Percentage of the diet composed of mammals, birds
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_vect

Definition: Percentage of the diet composed of reptiles, snakes, amphibians, salamanders
Data type: Numeric (float)
Values: Percentage values range from 0% to 60%
Completeness: 74.37%

det_vfish

Definition: Percentage of the diet composed of fish
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_vunk

Definition: Percentage of the diet composed of vertebrates – general or unknown
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_scav

Definition: Percentage of the diet composed of scavenge, garbage, offal, carcasses, trawlers, carrion
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%

Completeness: 74.37%

det_fruit
Definition: Percentage of the diet composed of fruit, drupes
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_nect
Definition: Percentage of the diet composed of nectar, pollen, plant exudates, gums
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_seed
Definition: Percentage of the diet composed of seed, maize, nuts, spores, wheat, grains
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_plantother
Definition: Percentage of the diet composed of other plant elements
Data type: Numeric (float)
Values: Percentage values range from 0% to 100%
Completeness: 74.37%

det_diet_breadth_n
Definition: Number of prevalent (≥ 20%) EltonTraits dietary categories consumed
Data type: Numeric (integer)
Values: Values range from 1 dietary category to 5 dietary categories
Completeness: 74.37% (97.5% with imputed data)

trophic_level
Definition: Trophic level of the species
Data type: Ordinal
Values: Three levels:
1: herbivore
2: omnivore
3: carnivore
Completeness: 91.28% (97.5% with imputed data)

foraging_stratum

Definition: Assignment to one of five foraging stratum categories
Data type: Ordinal
Values: Five levels:

- M: marine
- G: ground level, including aquatic foraging
- S: scansorial
- Ar: arboreal
- A: aerial

Completeness: 90.15% (97.6% with imputed data)

activity_cycle

Definition: Activity cycle of each species
Data type: Ordinal
Values: Three levels:
1: nocturnal only
2: nocturnal/crepuscular, cathemeral, crepuscular or diurnal/crepuscular
3: diurnal only
Completeness: 80.96% (97.4% with imputed data)

freshwater

Definition: The species spends a significant amount of time in freshwater bodies
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 96.68%

marine

Definition: The species spends a significant amount of time in oceans and/or seas
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 96.68%

terrestrial_non-volant

Definition: The species spends a significant amount of time on land
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 96.68%

terrestrial_volant

Definition: The species is capable of powered flight and spends a significant amount of time flying in the air
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 96.68%

upper_elevation_m

Definition: Upper elevation limit at which the species can be found in meters
Data type: Numeric (float)
Values: Estimates range from 0 m to 6,700 m
Completeness: 50.67%

lower_elevation_m

Definition: Lower elevation limit at which the species can be found in meters
Data type: Numeric (float)
Values: Estimates range from -100 m to 4,500 m
Completeness: 46.53%

altitude_breadth_m

Definition: Difference between the upper and lower elevation limits of a species in meters
Data type: Numeric (float)
Values: Estimates range from 0 to 6200 m
Completeness: 43.31%

island_dwelling

Definition: 20% or more of the breeding range occurs on an island
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 50.38%

island_endemicity

Definition: Score of island endemicity obtained from species' ranges and historical and fossil occurrence records
Data type: Ordinal
Values: Four levels:

- Exclusively marine
- Occurs on mainland
- Occurs on large land bridge islands: the species occurs on islands greater than 1,000 km2 that are separated from the mainland by water no more than 110 m deep. The islands would have been part of the mainland during the last glacial maximum.

- Occurs on small land bridge islands: the species occurs on islands smaller than 1,000 km2 that are separated from the mainland by water no more than 110 m deep. The islands would have been part of the mainland during the last glacial maximum.
- Occurs only on isolated islands: the species occurs on islands separated from the mainland by water deeper than 110 m.

Completeness: 93.10%

dissected_by_mountains

Definition: Range dissected by mountains (based on elevation gradients with slopes equal or higher than 5 degrees)
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 50.38%

glaciation

Definition: Historical exposure to glaciation, considered as more than 20% range overlap with areas glaciated in the last 21000 years
Data type: Binary
Values: 0 (no), 1 (yes)
Completeness: 50.38%

biogeographical_realm

Definition: Biogeographical realms in which the species can be encountered
Data type: Ordinal
Values: Eight biogeographical realms:

- Afrotropical
- Antarctic
- Australasian
- Indomalayan
- Nearctic
- Neotropical
- Oceanian
- Palearctic

Completeness: 95.66%

habitat_breadth_n

Definition: Number of distinct suitable level 1 IUCN habitats
Data type: Numeric (integer)
Values: Estimates range from 1 habitat to 9 habitats
Completeness: 90.30%

Appendix S2.2: Variable information of the used sources and data inclusion order

order

Definition: Order name source
Data type: Character
Values: 29 order names

family

Definition: Family name source
Data type: Character
Values: 175 family names

genus

Definition: Genus name source
Data type: Character
Values: 1429 genus names

species

Definition: Specific epithet name source
Data type: Character
Values: 4422 specific epithets

iucn2020_binomial

Definition: IUCN v. 2020-2 binomial name source
Data type: Character
Values: 5961 binomial names

phylacine_binomial

Definition: PHYLACINE v. 1.2 binomial name source
Data type: Character
Values: 5831 binomial names

adult_mass_g

Definition: Adult body mass source
Data type: Character
Values/inclusion order: Amniotes, Pacifici et al. (2013), Smith et al. (2003) (EltonTraits), AnAge, PHYLACINE, split from (species name)

brain_mass_g

Definition: Adult brain mass source
Data type: Character
Values/inclusion order: Tsuboi et al. (2018), Heldstab et al. (2018), split from (species name), imputed

adult_body_length_mm

Definition: Adult body length source

Data type: Character

Values/inclusion order: Amniotes, PanTHERIA, mean of female and female head body length (Amniotes), female head body length (Amniotes), undefined sex head body length (Amniotes), split from (species name), imputed

adult_forearm_length_mm

Definition: Adult forearm length source

Data type: Character

Values/inclusion order: PanTHERIA, split from (species name)

max_longevity_d

Definition: Maximum longevity source

Data type: Character

Values/inclusion order: Amniotes, Pacifici et al. (2013), AnAge, split from (species name), imputed

maturity_d

Definition: Maturity source

Data type: Character

Values/inclusion order: PanTHERIA, female maturity (Amniotes), mean of female (Amniotes) and male (AnAge), mean of female and male (AnAge), mean of female and undefined sex (Amniotes), mean of female, male and undefined sex (Amniotes), mean of female and male (Amniotes), mean of male and undefined (Amniotes), undefined sex maturity (Amniotes), split from (species name)

female_maturity_d

Definition: Female maturity source

Data type: Character

Values/inclusion order: Amniotes, AnAge, split from (species name), imputed

male_maturity_d

Definition: Male maturity source

Data type: Character

Values/inclusion order: Amniotes, AnAge, split from (species name)

age_first_reproduction_d

Definition: Age of first reproduction source
Data type: Character
Values/inclusion order: Pacifici et al. (2013), PanTHERIA, split from (species name), calculated, imputed

gestation_length_d

Definition: Gestation length source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name), imputed

teat_number_n

Definition: Teat number source
Data type: Character
Values/inclusion order: PanTHERIA, split from (species name)

litter_size_n

Definition: Litter size source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name), imputed

litters_per_year_n

Definition: Litters per year source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name), imputed

interbirth_interval_d

Definition: Interbirth interval source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name)

neonate_mass_g

Definition: Neonate mass source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name)

weaning_age_d

Definition: Weaning age source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name), imputed

weaning_mass_g

Definition: Weaning mass source
Data type: Character
Values/inclusion order: Amniotes, AnAge, PanTHERIA, split from (species name)

generation_length_d

Definition: Generation length source
Data type: Character
Values/inclusion order: Pacifici et al. (2013), IUCN, split from (species name), imputed

dispersal_km

Definition: Dispersal source
Data type: Character
Values/inclusion order: calculated, split from (species name), imputed

density_n_km2

Definition: Density source
Data type: Character
Values/inclusion order: TetraDENSITY, PanTHERIA, split from (species name)

hibernation_torpor

Definition: Hibernation and torpor source
Data type: Character
Values/inclusion order: Buckley et al. (2018), Heldstab et al. (2018), Botero et al. (2013), Turbill et al. (2011), marine, split from (species name), imputed

fossoriality

Definition: Fossoriality source
Data type: Character
Values/inclusion order: PanTHERIA, split from (species name), imputed

home_range_km2

Definition: Home range source

Data type: Character
Values/inclusion order: PanTHERIA, split from (species name)

social_group_size_n
Definition: Social group size source
Data type: Character
Values/inclusion order: PanTHERIA, split from (species name)

dphy_invertebrate
Definition: Diet invertebrate source
Data type: Character
Values/inclusion order: PHYLACINE, split from (species name), imputed

dphy_vertebrate
Definition: Diet vertebrate source
Data type: Character
Values/inclusion order: PHYLACINE, split from (species name), imputed

dphy_invertebrate
Definition: Diet plant source
Data type: Character
Values/inclusion order: PHYLACINE, split from (species name), imputed

det_inv
Definition: Diet inv source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_vend
Definition: Diet vend source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_vect
Definition: Diet vect source
Data type: Character

Values/inclusion order: EltonTraits, split from (species name)

det_vfish
Definition: Diet vfish source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_vunk
Definition: Diet vunk source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_scav
Definition: Diet scav source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_fruit
Definition: Diet fruit source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_nect
Definition: Diet nect source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_seed
Definition: Diet seed source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name)

det_plantother
Definition: Diet plantother source
Data type: Character

Values/inclusion order: EltonTraits, split from (species name)

det_diet_breadth_n

Definition: Diet breadth source
Data type: Character
Values/inclusion order: Calculated (EltonTraits), split from (species name), imputed

trophic_level

Definition: Trophic level source
Data type: Character
Values/inclusion order: MammalDIET2, PanTHERIA, split from (species name), imputed

foraging_stratum

Definition: Foraging stratum source
Data type: Character
Values/inclusion order: EltonTraits, split from (species name), imputed

activity_cycle

Definition: Activity cycle source
Data type: Character
Values/inclusion order: EltonTraits, PanTHERIA, split from (species name), imputed

freshwater

Definition: Freshwater source
Data type: Character
Values/inclusion order: IUCN, PHYLACINE, split from (species name)

marine

Definition: Marine source
Data type: Character
Values/inclusion order: IUCN, PHYLACINE, split from (species name)

terrestrial_non-volant

Definition: Terrestrial non-volant source
Data type: Character

Values/inclusion order: IUCN, PHYLACINE, split from (species name)

terrestrial_volant
Definition: Terrestrial volant source
Data type: Character
Values/inclusion order: IUCN, PHYLACINE, split from (species name)

upper_elevation_m
Definition: Upper elevation limit source
Data type: Character
Values/inclusion order: IUCN, split from (species name)

lower_elevation_m
Definition: Lower elevation limit source
Data type: Character
Values/inclusion order: IUCN, split from (species name)

altitude_breadth_m
Definition: Altitude breadth source
Data type: Character
Values/inclusion order: calculated, split from (species name)

island_dwelling
Definition: Island dwelling source
Data type: Character
Values/inclusion order: Botero et al. (2013)

island_endemicity
Definition: Island endemicity source
Data type: Character
Values/inclusion order: PHYLACINE

dissected_by_mountains
Definition: Dissected by mountains source
Data type: Character

Values/inclusion order: Botero et al. (2013)

glaciation

Definition: Glaciation source
Data type: Character
Source order: Botero et al. (2013)

biogeographical_realm

Definition: Biogeographical realm source
Data type: Character
Values/inclusion order: IUCN

habitat_breadth_n

Definition: Number of distinct suitable level 1 IUCN habitats
Data type: Character
Values/inclusion order: calculated, split from (species name)

Supplementary Material Chapter III

Appendix S3.1. Supplementary methods

Keywords

Literature reviews can be susceptible to publication bias, therefore taking preventive steps to avoid this is vital. Although we were not able to quantitatively measure publication bias (i.e., through funnel plots or Egger's test; Haddaway et al. 2020), previous formal meta-analyses on species' response to climate change did not find evidence of bias (Maclean & Wilson 2011; MacLean & Beissinger 2017; Nunez et al. 2019; Radchuk et al. 2019; Siepielski et al. 2019). For this study, we used a combination of keywords designed to reduce the publication bias and the ISI Web of Knowledge search tool (Pacifici et al. 2017). These keywords aimed to identify studies on climate change (climate change*, global warming*, sea-level rise*, elevated CO2*, drought*, cyclone*, CO2 concentration*, extreme temperature*, el Niño event*, la Niña event*, severe weather*, NAO change*, sea ice extent*); impacts or no impacts (population reduction*, population decline*, increase in population size*, range change*, range shift*, range reduction*, turnover*, extinction risk*, extinction probability*, survival*, mortality*, fertility*, changes in phenology*, advances in hibernation*, adaptation*, no change*, unchanged*, no effect*) on species or populations (mammal*, carnivore*, herbivore*, ungulate*, primate*, rodent*, marsupial*). We searched for all possible combinations of these three groups of keywords.

Response type and direction

We classified all the responses identified in the literature review into: (a) changes in distribution and abundance, (b) phenology and (c) changes in body size. Changes in distribution and abundance included range expansions, contractions or shifts (latitudinal and/or altitudinal), and changes in survival, fecundity, litter size, reproductive success, offspring survival, recruitment, population trends, female/male population growth, abundance, density, population or group size, physical condition, offspring growth rate, or juvenile body mass. Responses that indicated a net increase in range size or number of individuals were classified as expansions, while those that indicated a decrease were classified and contractions and those that indicated no changes were classified as no changes.

Responses classified as range shifts were assigned to contraction or expansion based on the information provided by the article. Shifts towards lower altitudes (net upper limit contraction and lower limit expansion) were considered as expansions, while shifts towards higher altitudes (net upper limit expansion and lower limit contraction) were considered as contractions.

Changes in phenology included changes in breeding date, birth date, weaning date, the start of hibernation, and the end of hibernation/denning. Responses that indicated an earlier start or end of seasonal events were classified as advances, while those that indicated a later start or end were classified as delays and those that indicated no temporal changes were classified as no changes.
Changes in body size included changes in adult body mass, body length, body size, and skull size. Responses that indicated an increase in body size were classified as increases, while those that indicated a decrease were considered as decreases and those that indicated that body size had remained unchanged were classified as no changes.

Responses that did not fit into any of these categories were classified as "other" and included changes in diet, fur color, denning place, adult sex ratio and genes, fluctuations in population size, longitudinal range shifts, and displacement towards inland areas.

Intrinsic trait data

We selected fifteen characteristics that influence mammal responses to climate change according to published literature (see Hypotheses for inclusion). These data were obtained at the species level from the COMBINE database(Soria et al. 2021), data sources for the underlying data can be found in Supplementary Material Appendix S3.2.

1) Adult body mass (grams): mean body mass of adult individuals.
2) Residual brain mass: residuals of the linear regression of the log10 of mean adult brain mass and the log10 of mean adult body mass (Estrada et al. 2015).
3) Generation length (days): average of the parents of the current cohort (Pacifici et al. 2013).
4) Female maturity (days): number of days needed for a female to reach sexual maturity.
5) Litter size: mean number of offspring per litter per female.
6) Litters per year: number of litters per female per year.

7) Interbirth interval (days): time between reproductive events.

8) Weaning age (days): age at which the primary nutritional dependency on the mother ends and independent foraging begins.

9) Dispersal distance (kilometers): maximum distance covered by young individuals between their birth and breeding site.

10) Heterothermy (1 or 0): individuals of the species go through hibernation or torpor (1) or not (0).

11) Fossoriality (1 or 0): the species is ground/fossorial dwelling (1) or over ground-dwelling (0).

12) Trophic level: the species primarily consumes meat (carnivore), plants (herbivore), or both (omnivore).

13) Activity cycle (1, 2 or 3): time of the day when the species perform most of their activities, classified as strictly nocturnal (1), flexible (2) or strictly diurnal (3).

14) Habitat breadth: number of IUCN level 1 in which the species can be found.

15) Dietary breadth: the number of food types that constitute a substantial (>= 20%) of the species' diet (Usui et al. 2017), dietary data came from the EltonTraits 1.0 database (Wilman et al. 2014).

Environmental traits and magnitude of climate change experienced

We selected seven environmental characteristics of the climatic populations each of our subpopulations were located in. These populations were the intersection of the species' distribution and the main biome. The main biome was identified as the biome with the highest area in the distribution of the species within the country of study. These characteristics provide information on the conditions the population has experienced in the recent past and, potentially, are acclimatized to and the degree of climate change (temperature increase) it has experienced. These characteristics are:

1) Maximum temperature of the warmest month experienced by the population (ºC).

2) Temperature seasonality (ºC), calculated as the difference between the maximum and the minimum temperature experienced by the population.

3) Precipitation seasonality (ºC), calculated as the difference in mean precipitation between the wettest and driest quarters experienced by the population.

4) Minimum altitude (meters), minimum altitude in which the species is located adjusted by the altitudinal range available within the population.

5) Altitudinal range (meters), the difference between the maximum and minimum altitudes at which the species is located (IUCN) adjusted by the altitudinal range available within the population.

6) Latitudinal range (degrees), calculated as the difference between the maximum and minimum latitude of the population.

7) Mean difference between the present (1991 – 2018) and recent past (1941 – 1960) temperature (ºC) within the population.

Environmental factors were obtained using the R software (R Core Team 2020) using the IUCN v. 2020-2 range maps (IUCN 2020), biomes from the Ecoregions maps (Dinerstein et al. 2017), climatic data from the WorldClim 2.1 database at a 5 arc-minutes resolution (Fick & Hijmans 2017) and from the Climate Research Unit 4.03 at a 0.5 arc-degrees resolution (Harris et al. 2020) and elevation from the SRTM accessed through WorldClim 2.1 at a 5 arc-minutes resolution (Fick & Hijmans 2017).

Geographic location of the response

We identified the latitudinal location of each of our subpopulations relative to the latitudinal range of the populations. This allowed us to identify if the subpopulation was located nearer to the warm or cold edge of the distribution. Relative latitude is the relative position of the centroid of the intersection of the species' range and the country of study in the distribution of the species within the main biome. Values range from 0 to 1, those closer to 1 indicate proximity to the cold border or poles, and values nearer to 0 indicate proximity to the warm border or equator. If the population crossed the equator, spanning the two hemispheres, we considered the equator as the warm edge of the population and calculated the relative latitudinal location within the hemisphere in which the response was identified.

Variable correlation and Principal Component Analyses

When testing for variable collinearity, some of the intrinsic traits were distributed into two clusters. We performed a Principal Component Analysis for each cluster, obtaining two composite traits, used in the models. These traits were:

A) Reproductive speed: composed by female maturity (negative), litters per year (positive) and interbirth interval (negative).

B) Spread capacity: composed by weaning age (negative), generation length (negative), dispersal (negative) and adult body mass (negative).

Hypotheses between the selected traits and responses to climate change

We used generalized linear mixed models (GLMMs) to test a series of hypotheses on the relationship between mammal distribution and abundance responses to recent climate change and the set of intrinsic and environmental variables, as well as the geographical position, described above:

- Species with low female maturity age, small interbirth interval, high number of litters per year and large litter size, have a fast reproductive strategy, producing many offspring per year. This allows reaching high abundances quickly, which increases colonization success under favorable conditions (Purvis et al. 2000; Angert et al. 2011; Estrada et al. 2016; Morrison et al. 2018).
- Species with a higher generation length and/or weaning age will respond more slowly to new climatic conditions, having an increased risk of being negatively impacted (Pearson et al. 2014).
- Species with generalist characteristics such as omnivory and large habitat, dietary and altitudinal breadths, will have a wider range of available resources and be less prone to experience contractions (Angert et al. 2011; Pacifici et al. 2017; Morrison et al. 2018).
- Species with smaller body size and/or presenting behaviors such as nocturnality (or flexible activity times), burrowing or heterothermy will be less affected by climate change, as they are able to avoid adverse climatic conditions (Liow et al. 2009; Mccain & King 2014).
- Species with a higher brain mass relative to their body mass will have higher behavioral flexibility and competitive ability, increasing their survival under novel conditions (Sol et al. 2008; Estrada et al. 2016; Morrison et al. 2018).

- Species with a high dispersal capacity will likely have an increased ability to move to suitable areas, facilitating their ability to expand or shift their distribution (Angert et al. 2011; Schloss et al. 2012).
- Subpopulations located near the warm edge of the population will potentially be nearer to their physiological limits and will probably experience contractions, while those located near the cold edge will experience expansions as new areas become available under the new climatic conditions (Beever et al. 2011; Mccain & King 2014).
- Populations located in higher elevations are near the limit of their altitudinal distributions and cannot move further upslope, being more susceptible to experience contractions (Urban 2018).
- Populations that live in areas with a restricted temperature range and a low precipitation seasonality, are more habituated to stable temperatures and precipitations and will be more negatively impacted by climate change and its associated increase in temperature and precipitation variability (Williams & Middleton 2008; Bonebrake & Mastrandrea 2010). Similarly, populations that are spread over a bigger latitudinal range, will be acclimatized to a wider range of conditions and will potentially be less affected by climate change.

Biome location and latitudinal range

To ensure that biomes with a large latitudinal range are located towards the poles, we performed a nonparametric Siegel regression (Siegel 1982) establishing the latitudinal range of the biome as the independent variable and the edge of the biome with the highest absolute latitudinal value as the independent variable. This analysis is robust for estimating the true slope in a simple linear regression and is not sensitive to outliers, which were present in our data due to the low number of observations ($n = 15$). The relationship between latitudinal range and highest absolute latitudinal value was significant (Siegel linear regression: Estimate = 1.7561, MAD = 0.4038, $V = 112$, $P = 0.00153$). The analysis was performed using the function mblm from the ‘mblm’ R package (Komsta 2019). Latitudinal range and highest absolute latitudinal value were calculated using Dinerstein’s biome map (Dinerstein et al. 2017) and the ‘sf’ R package (Pebesma 2018).

Appendix S3.2. Selected traits and main data sources

Intrinsic trait	**Data sources**	**Environmental trait**	**Data sources**
Body mass	Pacifici et al. 2013 Myhrvold et al. 2015	Maximum temperature	http://www.worldclim.org/
Brain mass	Heldstab et al. 2018 Tsuboi et al. 2018 Soria et al. 2021	Temperature seasonality	http://www.worldclim.org/
Generation length	Pacifici et al. 2013 Soria et al. 2021	Precipitation seasonality	http://www.worldclim.org/
Litter size	Myhrvold et al. 2015 Soria et al. 2021	Mean T difference	http://www.cru.uea.ac.uk/data
Litters per year	Myhrvold et al. 2015 Soria et al. 2021	Latitudinal range	https://ecoregions.appspot.com/ www.iucn.org
Interbirth interval	Myhrvold et al. 2015 Soria et al. 2021	Relative latitude	https://ecoregions.appspot.com/ www.iucn.org
Weaning age	Myhrvold et al. 2015 Soria et al. 2021	Altitudinal range	http://www.worldclim.org/ www.iucn.org
Dispersal	Santini et al. 2013		
Hibernation	Turbill et al. 2011 Botero et al. 2013 Buckley et al. 2018 Heldstab et al. 2018 Soria et al. 2021		
Fossoriality	Jones et al. 2009 Soria et al. 2021		
Activity cycle	Wilman et al. 2014 Soria et al. 2021		
Trophic level	Kissling et al. 2014 Gainsbury et al. 2018		
Habitat breadth	www.iucn.org		
Dietary breadth	Wilman et al. 2014 Soria et al. 2021		

Appendix S3.3 Summary of the Contraction – Expansion GLMM.

Coefficient estimates, standard error, z value and Pr(>|z|) of the Contraction – Expansion GLMM. Positive estimate values indicate an association with expansions and negative values indicate an association with contractions. Significant values are marked in bold.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.67571	0.90371	-0.74771	0.454635
s_PC1_reproductive_speed	-0.24538	0.631116	-0.38881	0.697418
s_PC1_spread_capacity	-0.05679	0.789781	-0.07191	0.942672
s_litter_size_n	0.912492	0.592817	1.539248	0.123744
s_brain_residuals	-0.37723	0.391512	-0.96351	0.335291
s_relative_lat	1.189638	0.439288	2.708107	**0.006767**
s_lat_range	-1.84525	0.653228	-2.82482	**0.004731**
s_max_temp	-0.18911	0.400533	-0.47215	0.636818
s_alt_range	1.213771	0.492074	2.466641	**0.013639**
s_min_alt	-0.82132	0.451707	-1.81826	0.069024
s_temperature_seasonality	0.358113	0.508557	0.704175	0.481324
s_precipitation_seasonality	0.328791	0.409646	0.802622	0.422193
s_temp_increase	-1.35041	0.557151	-2.42377	**0.01536**
hibernation_torpor1	-1.57985	1.02398	-1.54285	0.122867
fossoriality2	0.41068	0.924178	0.444374	0.656772
trophic_level2	0.474319	0.834681	0.568264	0.569856
trophic_level3	0.400538	1.262789	0.317185	0.751103
activity_cycle2	-0.40382	0.872623	-0.46277	0.643531
activity_cycle3	-0.54409	1.192693	-0.45618	0.648258
s_habitat_breadth_n	0.497627	0.456425	1.09027	0.275594
s_diet_breadth_n	0.33362	0.454611	0.733858	0.463035

Appendix S3.4 Summary of the Contraction – No Change GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the Contraction – No change GLMM. Positive estimate values indicate an association with expansions and negative values indicate an association with no changes. Significant values are marked in bold.

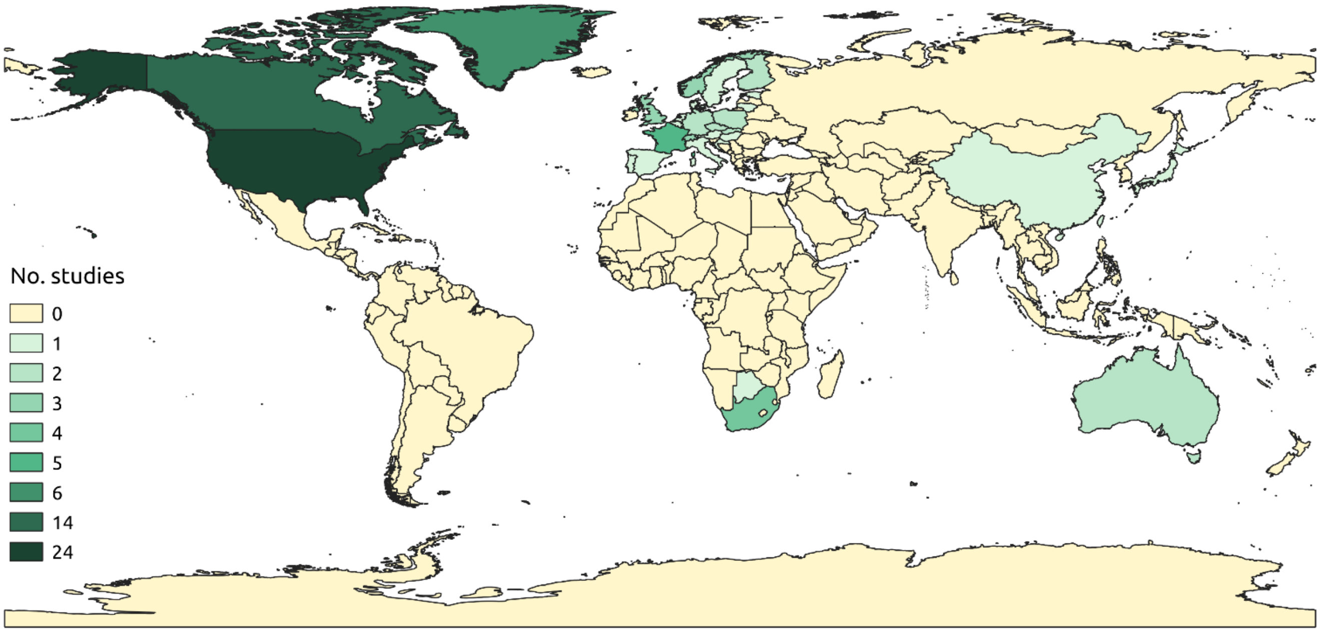
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-0.7361	1.021354	-0.72071	0.47109
s_PC1_reproductive_speed	-0.53498	0.728364	-0.7345	0.462646
s_PC1_spread_capacity	-0.4736	0.774518	-0.61147	0.540886
s_litter_size_n	1.519952	0.728666	2.085938	**0.036984**
s_brain_residuals	-0.18431	0.446617	-0.41268	0.679838
s_relative_lat	1.395773	0.53731	2.597706	**0.009385**
s_lat_range	-2.55766	0.829981	-3.08159	**0.002059**
s_max_temp	0.479522	0.655525	0.731508	0.464469
s_alt_range	1.435261	0.6597	2.175627	**0.029583**
s_min_alt	-0.23891	0.385092	-0.6204	0.534997
s_temperature_seasonality	1.654706	0.83824	1.974025	**0.048379**
s_precipitation_seasonality	1.012721	0.48553	2.085805	**0.036996**
s_temp_increase	-2.10131	0.625875	-3.3574	**0.000787**
hibernation_torpor1	-2.15667	0.978202	-2.20472	**0.027473**
fossoriality2	0.480854	1.000321	0.480699	0.63073
trophic_level2	-0.5292	0.748485	-0.70703	0.479547
trophic_level3	1.241903	1.307247	0.950014	0.342105
activity_cycle2	-0.80038	0.940493	-0.85102	0.394756
activity_cycle3	0.697384	1.144801	0.609175	0.542409
s_habitat_breadth_n	1.496827	0.529352	2.827657	**0.004689**
s_diet_breadth_n	-0.57568	0.465323	-1.23717	0.216026

Appendix S3.5 List of heterothermic mammals

List of mammals that go into heterothermy included in the study, indicating if they enter hibernation or torpor.

Scientific name	**Family**	**Hibernation / Torpor**
Callospermophilus lateralis	Sciuridae	Hibernation
Crocidura russula	Soricidae	Torpor
Eliomys quercinus	Gliridae	Hibernation
Glis glis	Gliridae	Hibernation
Marmota flaviventris	Sciuridae	Hibernation
Marmota marmota	Sciuridae	Hibernation
Marmota monax	Sciuridae	Hibernation
Napaeozapus insignis	Dipodidae	Hibernation
Neotamias alpinus	Sciuridae	Hibernation
Neotamias merriami	Sciuridae	Torpor or hibernation at high altitudes
Neotamias minimus	Sciuridae	Hibernation
Neotamias quadrimaculatus	Sciuridae	Hibernation
Neotamias senex	Sciuridae	Hibernation
Neotamias speciosus	Sciuridae	Hibernation
Neotamias umbrinus	Sciuridae	Hibernation
Otospermophilus beecheyi	Sciuridae	Hibernation
Peromyscus leucopus	Cricetidae	Torpor
Peromyscus maniculatus	Cricetidae	Torpor
Poliocitellus franklinii	Sciuridae	Hibernation
Reithrodontomys megalotis	Cricetidae	Torpor
Tamias striatus	Sciuridae	Hibernation
Urocitellus beldingi	Sciuridae	Hibernation
Urocitellus colombianus	Sciuridae	Hibernation
Ursus arctos	Ursidae	Hibernation
Ursus maritimus	Ursidae	Hibernation
Zapus hudsonius	Dipodidae	Hibernation
Zapus princeps	Dipodidae	Hibernation

Appendix S3.6 Map of number of studies per country



Supplementary material Chapter IV

Appendix S4.1 Summary of the full Contraction – Expansion GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the full Contraction – Expansion GLMM. Positive estimate values indicate an association with expansions and negative values indicate an association with contractions. Significant values are marked in bold.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.120234	0.243043	0.494703	0.62081
Adult mass	0.208239	0.198392	1.049632	0.293887
Clutch size	-0.0539	0.139453	-0.38649	0.699133
Maximum longevity	0.283287	0.151818	1.865962	**0.062047**
Diet breadth	0.033893	0.116113	0.291894	0.770368
Altitude breadth	-0.18836	0.118517	-1.58931	0.11199
Minimum altitude	-0.19349	0.100607	-1.92321	**0.054454**
Relative latitude	0.317692	0.108991	2.914851	**0.003559**
Latitudinal range	-0.08854	0.144167	-0.61412	0.539134
Maximum temperature	0.406935	0.13275	3.065422	**0.002174**
Temperature seasonality	0.622837	0.188585	3.302687	**0.000958**
Precipitation seasonality	0.544212	0.154752	3.516678	**0.000437**
Temperature increase	-0.08724	0.150058	-0.58136	0.560999
Seasonal diet (Seasonal)	-0.02339	0.269039	-0.08693	0.930731
Habitat breadth	-0.01737	0.125629	-0.13829	0.890012
Migratory (Not a migrant)	-0.14357	0.291341	-0.49279	0.62216

Appendix S4.2 Summary of the reduced Contraction – Expansion GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the reduced Contraction – Expansion GLMM. Positive estimate values indicate an association with expansions and negative values indicate an association with contractions. Significant values are marked in bold.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.036128	0.109873	0.328814	0.742296
Maximum longevity	0.355607	0.121928	2.916544	**0.003539**
Minimum altitude	-0.16186	0.098372	-1.64537	0.099893
Relative latitude	0.318793	0.108744	2.931604	**0.003372**
Maximum temperature	0.281548	0.107947	2.608202	**0.009102**
Temperature seasonality	0.522963	0.144202	3.626607	**0.000287**
Precipitation seasonality	0.522321	0.146398	3.567802	**0.00036**

Appendix S4.3 Summary of the full Advance – Delay GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the full Advance – Delay GLMM. Positive estimate values indicate an association with spring phenology advances and negative values indicate an association with spring phenology delays. Significant values are marked in bold.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-3.22928	0.806093	-4.00609	**6.17E-05**
Adult mass	-0.91142	0.683349	-1.33375	0.182284
Clutch size	0.178278	0.268821	0.663187	0.507211
Maximum longevity	0.576823	0.284228	2.02944	**0.042413**
Diet breadth	-0.01197	0.233718	-0.05121	0.959159
Altitude breadth	0.137637	0.271944	0.506121	0.612771
Minimum altitude	0.118711	0.235238	0.504641	0.613811
Relative latitude	-0.54632	0.310636	-1.75871	**0.078627**
Latitudinal range	0.234805	0.21511	1.091559	0.275027
Maximum temperature	0.683905	0.308984	2.213403	**0.02687**
Temperature seasonality	-1.66795	0.601058	-2.77502	**0.00552**
Precipitation seasonality	-1.43058	0.789527	-1.81194	**0.069995**
Temperature increase	-0.96126	0.368244	-2.6104	**0.009044**
Seasonal diet (Seasonal)	0.296199	0.548713	0.539807	0.58933
Habitat breadth	-0.23292	0.250899	-0.92834	0.35323
Migratory (Not a migrant)	-1.31919	1.114788	-1.18336	0.236668

Appendix S4.4 Summary of the reduced Advance – Delay GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the reduced Advance – Delay GLMM. Positive estimate values indicate an association with spring phenology advances and negative values indicate an association with spring phenology delays. Significant values are marked in bold.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	3.092462	0.679206	4.553057	**0.000005**
Maximum longevity	0.266381	0.207415	1.284290	0.199040
Relative latitude	0.315098	0.273216	1.153290	0.248791
Maximum temperature	0.705130	0.292598	2.409896	**0.015957**
Temperature seasonality	1.455027	0.525042	2.771268	**0.005584**
Precipitation seasonality	1.284939	0.718685	1.788650	0.073671
Temperature increase	0.846702	0.329885	2.568388	**0.010322**

Appendix S4.5 Summary of the full Advance – No change/Mixed GLMM

Coefficient estimates, standard error, z value and Pr(>|z|) of the full Advance – No change/Mixed GLMM. Positive estimate values indicate an association with spring phenology advances and negative values indicate an association with spring phenology no change or mixed response. Significant values are marked in bold.

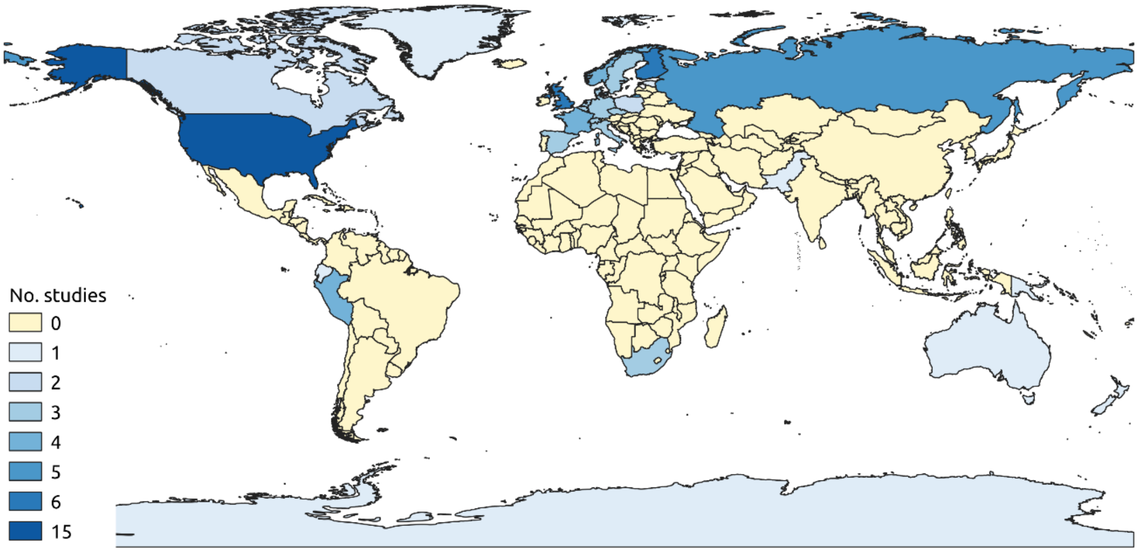
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.436145	0.323612	1.347738	0.177743
Adult mass	-0.05952	0.083008	-0.71705	0.47334
Clutch size	-0.16853	0.104493	-1.61285	0.106777
Maximum longevity	0.101044	0.105867	0.954448	0.339857
Diet breadth	-0.13369	0.096426	-1.38644	0.165614
Altitude breadth	0.026233	0.118392	0.221577	0.824643
Minimum altitude	0.016577	0.108039	0.153431	0.878058
Relative latitude	0.37583	0.105468	3.563449	**0.000366**
Latitudinal range	-0.0339	0.08942	-0.37906	0.704645
Maximum temperature	-0.04752	0.146775	-0.32374	0.746137
Temperature seasonality	-0.30842	0.197081	-1.56495	0.117594
Precipitation seasonality	0.416063	0.246889	1.685225	**0.091945**
Temperature increase	-0.40965	0.134346	-3.04919	**0.002295**
Seasonal diet (Seasonal)	-0.19924	0.229521	-0.86807	0.385354
Habitat breadth	-0.03049	0.096314	-0.31655	0.751583
Migratory (Not a migrant)	-0.09039	0.383191	-0.23588	0.813529

Appendix S4.6 Summary of the reduced Advance – No change/Mixed GLMM

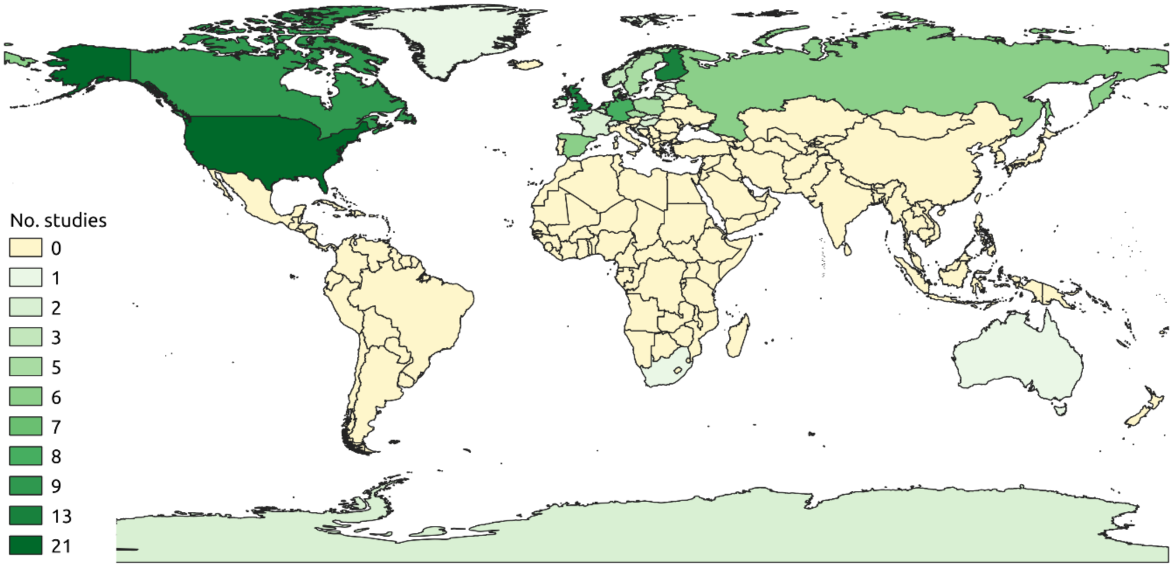
Coefficient estimates, standard error, z value and Pr(>|z|) of the reduced Advance – No change/Mixed GLMM. Positive estimate values indicate an association with spring phenology advances and negative values indicate an association with spring phenology no change or mixed response. Significant values are marked in bold.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.219064	0.212744	1.029709	0.303147
Relative latitude	0.394982	0.096709	4.084247	**0.000044**
Precipitation seasonality	0.507083	0.219187	2.313468	**0.020697**
Temperature increase	-0.41172	0.108171	-3.80614	**0.000141**

Appendix S4.7 Map of number of distribution and abundance studies per country



Appendix S4.8 Map of number of spring phenological studies per country



Supplementary references

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters **14:**677–689.

Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW. 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biology **17:**2054–2070.

Bonebrake TC, Mastrandrea MD. 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. Proceedings of the National Academy of Sciences of the United States of America **107:**12581–12586.

Botero CA, Dor R, McCain CM, Safran RJ. 2013. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. Molecular Ecology **23:**259–268.

Buckley LB, Khaliq I, Swanson DL, Hof C. 2018. Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? Ecology and Evolution **8:**12375–12385.

Dinerstein E et al. 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience **67:**534–545.

Estrada A, Meireles C, Morales-castilla I, Poschlod P, Vieites D, Araújo MB, Early R. 2015. Species' intrinsic traits inform their range limitations and vulnerability under environmental change. Global Ecology and Biogeography **24:**849–858.

Estrada A, Morales-Castilla I, Caplat P, Early R. 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends in Ecology and Evolution **31:**190–203.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology **37:**4302–4315.

Gainsbury AM, Tallowin OJS, Meiri S. 2018. An updated global data set for diet preferences in terrestrial mammals: testing the validity of extrapolation. Mammal Review **48:**160–167.

Haddaway NR, Bethel A, Dicks L V., Koricheva J, Macura B, Petrokofsky G, Pullin AS, Savilaakso S, Stewart GB. 2020. Eight problems with literature reviews and how to fix them. Nature Ecology and Evolution **4:**1582–1589.

Harris I, Osborn TJ, Jones P, Lister D. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data **7:**1–18.

Heldstab SA, Isler K, van Schaik CP. 2018. Hibernation constrains brain size evolution in mammals. Journal of Evolutionary Biology 3**1:**1582–1588.

IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020-2.

Jones KE et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology **90:**2648.

Kissling WD, Dalby L, Fløjgaard C, Lenoir J, Sandel B, Sandom C, Trøjelsgaard K, Svenning JC. 2014. Establishing macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. Ecology and Evolution **4:**2913–2930.

Komsta L. 2019. mblm: Median-Based Linear Models. Available from https://cran.r-project.org/package=mblm.

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC. 2009. Lower extinction risk in sleep-or-hide mammals. American Naturalist **173:**264–272.

Maclean IMD, Wilson RJ. 2011. Recent ecological responses to climate change support predictions of high extinction risk. Proceedings of the National Academy of Sciences of the United States of America **108:**12337–12342.

MacLean SA, Beissinger SR. 2017. Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. Global Change Biology **23:**4094–4105.

Mccain CM, King SRB. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology **20:**1760–1769.

Morrison L, Estrada A, Early R. 2018. Species traits suggest European mammals facing the greatest climate change are also least able to colonize new locations. Diversity and Distributions **24:**1321–1332.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology **96:**3109–000.

Nunez S, Arets E, Alkemade R, Verwer C, Leemans R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 °C enough? Climatic Change **154:**351–365.

Pacifici M, Santini L, Di Marco M, Baisero D, Francucci L, Grottolo Marasini G, Visconti P, Rondinini C. 2013. Generation length for mammals. Nature Conservation **5:**89–94.

Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017. Species' traits influenced their response to recent climate change. Nature Climate Change **7:**205–208.

Pearson RG et al. 2014. Life history and spatial traits predict extinction risk due to climate change. Nature Climate Change **4:**217–221.

Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal **10:**439–446.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences **267:**1947–1952.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria. Available from https://www.r-project.org/.

Radchuk V et al. 2019. Adaptive responses of animals to climate change are most likely insufficient. Nature Communications **10:**3109.

Santini L, Di Marco M, Visconti P, Baisero D, Boitani L, Rondinini C. 2013. Ecological correlates of dispersal distance in terrestrial mammals. Hystrix **24:**181–186.

Schloss CA, Nuñez TA, Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America **109:**8606–8611.

Siegel AF. 1982. Robust regression using repeated medians. Biometrika **69:**242–244.

Siepielski AM, Morrissey MB, Carlson SM, Francis CD, Kingsolver JG, Whitney KD, Kruuk LEB. 2019. No evidence that warmer temperatures are associated with selection for smaller body sizes. Proceedings of the Royal Society B: Biological Sciences **286**.

Sol D, Bacher S, Reader SM, Lefebvre L. 2008. Brain size predicts the success of mammal species introduced into novel environments. American Naturalist **172:**63–71.

Soria CD, Pacifici M, Di Marco M, Stephen SM, Rondinini C. 2021. COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. Ecology **102:**13028255.

Tsuboi M, van der Bijl W, Kopperud BT, Erritzøe J, Voje KL, Kotrschal A, Yopak KE, Collin SP, Iwaniuk AN, Kolm N. 2018. Breakdown of brain–body allometry and the encephalization of birds and mammals. Nature Ecology and Evolution **2:**1492–1500.

Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proceedings of the Royal Society B: Biological Sciences **278:**3355–3363.

Urban MC. 2018. Escalator to extinction. Proceedings of the National Academy of Sciences **115:**201817416.

Usui T, Butchart SHM, Phillimore AB. 2017. Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. Journal of Animal Ecology **86:**250–261.

Williams SE, Middleton J. 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: Implications for global climate change. Diversity and Distributions **14:**69–77.

Wilman H, Belmaker J, Jennifer S, de la Rosa C, Rivadeneira MM, Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world' s birds and mammals. Ecology **95:**2027.