Imperial College London

# Impacts of climate change on the structure and function of global bird diversity

*Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy*

**Alexandre Jean Claude Rabeau**

Supervision: Professor Joseph Tobias, Professor Alex Pigot

**Imperial College London**

**Department of Life Sciences**

**November 2024**

## Declaration of Originality

I confirm that the research I present in this thesis is my own, conducted under the supervision of Professor Joseph Tobias and Professor Alex Pigot. Any material which could be construed as other people's work has been referenced and cited appropriately.

## Copyright Declaration

The copyright of this thesis rests with the author. Unless otherwise indicated, its contents are licensed under a Creative Commons Attribution-Non Commercial 4.0International Licence (CC BY-NC). Under this licence, you may copy and redistribute the material in any medium or format. You may also create and distribute modified versions of the work. This is on the condition that: you credit the author and do not use it, or any derivative works, for a commercial purpose. When reusing or sharing this work, ensure you make the licence terms clear to others by naming the licence and linking to the licence text. Where a work has been adapted, you should indicate that the work has been changed and describe those changes. Please seek permission from the copyright holder for uses of this work that are not included in this licence or permitted under UK Copyright Law.

## Funding

This PhD work was predominantly self-funded and supported by a Deutscher Akademischer Austauschdienst (DAAD) doctoral grant (Grant number: 57588369).

# Acknowledgments

As anyone who has undertaken a PhD will testify, the journey is pretty arduous. I have loved this PhD process but of course there have been many challenges along the way. And without the people I mention below, I would certainly not have come remotely close to completing this doctorate. So I want to take this opportunity to thank them properly.

First and foremost I would like to thank my supervisors whose support and guidance over the last three years has been instrumental in shaping the work presented throughout this thesis. I would like to thank Joe Tobias for initially agreeing to take me on as a self-funded student in his lab. I am sure this gave you a couple headaches at various points along the process so thank you for being understanding and supportive. It has been quite the adventure and you are a core contributor to that being the case so thank you. I would like to thank Alex Pigot, who in many ways opened the door for me into academia. When agreeing to undertake a research project together back in April 2021, I had no idea it would lead to such an enjoyable and fruitful collaboration. I have truly enjoyed working together these past three years and have always found our meetings incredibly insightful and fascinating. I would also like to express enormous gratitude to Matthias Schleuning for accommodating me in his lab in Frankfurt in the second year of my PhD. Thank you for being so flexible towards my unpredictable living arrangements and for hosting and collaborating on such a rewarding research stay.

Many thanks to all my fellow lab mates, with special thanks of course going to the “bird boiz” - Rob Barber, Pat Walkden and Tom Weeks - for taking me under their wing (pun very much intended). Thank you for the numerous occasions you helped me with coding issues and for the many discussions over a pint at the union bar. My PhD would have been a much less enjoyable experience without you guys.

To my amazing friends and family, thank you for putting up with me as a financial burden these past three years. Turning a blind eye at cheaper restaurant suggestions, skipped rounds at the pub and un-reciprocated present giving at holidays and

birthdays. Thank you all for distracting me, supporting me, just all in all making my life richer and more full of joy. Special thanks has to go to Mia, Ed, Oli, Daniel, Jonah, George, Flossie, Becca and Will. I'm also especially grateful to Morella, for quite literally sustaining me with her amazing cooking and for being such a lovely listener to my morning rants, whether PhD-related or otherwise, over breakfast while you were undoubtedly wishing you could get on with other things.

To my brother Jean, despite being the "younger" brother you are a constant source of inspiration to me. Thank you for your humour and your support, even as you were immersed in your own intense medical studies. To my parents, I am so enormously grateful for the sacrifices you have both made to provide me with such an outstanding upbringing and education. To Dad, thank you for supporting me, inspiring me, challenging me and gifting me a quantitative brain. To Mum, thank you for instilling a belief in me that anything is possible and for gifting me your optimistic lens - an invaluable asset, particularly over the past three years of researching climate change.

I count myself enormously fortunate to have this many wonderful people in my life. The work laid out across this thesis is dedicated to all of you.

# Abstract

Climate change poses a major threat to global biodiversity, disrupting ecosystems that human societies depend on. Predicting its impacts requires accurate estimates of species' climate niches—the range of climatic conditions a species can tolerate. In this PhD project, I developed a global dataset of avian climate niches and assessed how different methods affect niche estimates. I found that approaches using range maps versus point localities, and variations in spatial and temporal resolution, produced significantly different results. Temporal resolution—whether climate data were averaged monthly, seasonally, or annually—was especially influential. I then examined how well climate niches and local environmental variables predict recent bird population trends. Local factors, such as climate variability and change rates, were more predictive than species-level niche estimates, suggesting that species may respond to environmental shifts before reaching climatic thresholds. To understand broader ecological impacts, I constructed frugivory interaction networks using bird and plant trait data across the Americas and projected their responses to future climate change. Simulations indicated a likely decline in the average number of bird-plant interactions per species, but also showed potential for "interaction rewiring"—particularly in tropical regions with high trait diversity—buffering some negative effects. The findings presented in this thesis contribute significantly to the fields of macroecology and global change biology, offering new insights into species responses to climate change and the complex dynamics of ecological networks under future climatic conditions.

# Thesis outline of contents, contributions and publications

## Chapter 1: General introduction

In this chapter, I provide the background and motivation for the thesis, identifying key research gaps and outlining the approaches taken to address them. I am the sole contributor to this chapter.

## Chapter 2: Testing and implementing spatial and temporal refinements in global climate niche estimates for birds

I generate a global climate niche dataset with climate niche estimates derived from polygon range map and point locality data. I then test the influence of distinct niche quantification methods on climate niche estimates. Additionally, I test the independent effects of extracting climate at different spatiotemporal grain sizes and extents on niche position and volume. Analyses conducted throughout this chapter were dependent on several published datasets, namely polygon range map data from BirdLife International, point locality data from eBird and climate data from CHELSA. Eliot Miller from the Cornell Lab of Ornithology provided technical assistance in accessing eBird occurrence data. This chapter was conceived and developed by myself, Prof. Joseph Tobias and Prof. Alex Pigot. All the data analysis, data visualization and writing was conducted by myself with input from Prof. Joseph Tobias and Prof. Alex Pigot.

## Chapter 3: Properties of the local environment are more widely predictive of avian population trends compared to species climate niche features

I investigate the relative predictive capacity of species climate niche features compared to local environment features towards avian population trends. To inform population trends, I collated avian population time series from the Living Planet and the BioTIME databases. Other environmental datasets used throughout this chapter include climate data from CHELSA and land use data from LUH2. Louise McRae provided some guidance

with regards to accessing and using population time series data from the Living Planet Database. This chapter was conceived and developed by myself, Prof. Joseph Tobias and Prof. Alex Pigot. All the data analysis, data visualization and writing was conducted by myself with input from Prof. Alex Pigot.

## Chapter 4: Projected impacts of climate change on plant-frugivore interactions across the Americas

I constructed ecoregion level frugivory networks across the Americas by matching plant and bird functional trait data using a trait-based interaction model. I then simulated network level response to future climate change using a climate suitability method underpinned by climate niche estimates. Lastly, I re-ran these analyses integrating several interaction rewiring scenarios, namely allowing for avian diet flexibility and dispersal into ecoregion assemblages. Functional trait data was collated from various published datasets including McFadden et al., (2022), Dehling et al., (2016), Kissling et al., (2019) and Sinnott-Armstrong et al., (2018). Species distribution data was collated from BirdLife International and the BIEN database. Isabel Donoso, Larissa Nowak and Alke Voskamp provided input on the analyses implemented throughout this chapter. This chapter was conceived and developed by myself, Prof. Joseph Tobias, Prof. Alex Pigot and Dr. Matthias Schleuning. All the data analysis, data visualization and writing was conducted by myself with input from Prof. Joseph Tobias, Prof. Alex Pigot and Dr. Matthias Schleuning.

In August 2024, an adapted version of this chapter was submitted for review in *Global Ecology and Biogeography*. First decision (invited resubmission) was received in November 2024.

## Chapter 5: General discussion

I synthesize the key findings of this thesis and contextualise their contributions to the field. I acknowledge important limitations associated with this work and propose future avenues of research. I am the sole contributor to this chapter.

# Contents

1 | General Introduction ..... 11
1.1 Climate change ..... 12
1.2 Predicting biodiversity response to climate change ..... 14
1.3 Birds ..... 20
1.4 Thesis outline ..... 21
2| Testing and implementing spatial and temporal refinements in global climate niche estimates for birds ..... 24
2.1 Introduction ..... 25
2.2 Methods ..... 28
2.3 Results ..... 33
2.4 Discussion ..... 37
3| Properties of the local environment are more widely predictive of avian population trends compared to species climate niche ..... 43
3.1 Introduction ..... 43
3.2 Methods ..... 46
3.3 Results ..... 56
3.4 Discussion ..... 58
4| Projected impacts of climate change on interactions between plants and avian frugivores across the Americas ..... 65
4.1 Introduction ..... 66
4.2 Methods ..... 68
4.3 Results ..... 76
4.4 Discussion ..... 82
5| General Discussion ..... 88
5.1 Key findings ..... 88
5.2 Limitations ..... 93
5.3 Future work and conclusions ..... 96
Bibliography ..... 98
Appendices ..... 117
A1 – Supplementary materials for Chapter 2 ..... 119
A2 – Supplementary materials for Chapter 3 ..... 137
A3 - Supplementary materials for Chapter 4 ..... 173

# List of Figures and Tables

Figure 2.1| Conceptual figure outlining two different approaches to climatic niche estimation. 27
Figure 2.2| Extracting climate at different spatiotemporal grain sizes and extents.....33
Figure 2.3| The effects of different niche quantification methods on avian climate niche estimates.....34
Figure 2.4| Climate niche estimates vary across different spatiotemporal resolutions.....36
Figure 3.1| Map of study populations.....48
Figure 3.2| Environmental predictors.....49
Table 3.1| A summary table of the variables included in the core analysis.....53
Figure 3.3| Predictors of avian population trends.....57
Figure 3.4| Variable class analysis.....58
Figure 4.1| Projecting climate change impacts on plant-frugivore interactions.....69
Figure 4.2| Latitudinal patterns in fruit length and avian gape width across the Americas.....77
Figure 4.3| Latitudinal pattern in potential plant-frugivore interaction diversity across the Americas.....78
Figure 4.4| Projected impacts of climate change on plant-frugivore interactions.....80
Figure 4.5| Effects of interaction rewiring on projected future plant-frugivore interactions. .....82
Table A1.1| Method comparison t-test results.....123
Table A1.2| Spatial grain size comparison t-test results.....124
Table A1.3| Temporal grain size comparison t-test results.....125
Table A1.4| Temporal extent comparison t-test results.....126
Figure A1.1| Comparison of niche quantification methods between a migrant and resident species.....127
Figure A1.2| Point locality sampling effort across avian families.....128
Figure A1.3| Point locality sampling effort.....129
Figure A1.4| Niche metrics across different spatial grain sizes.....130
Figure A1.5| Niche metrics across different temporal grain sizes.....131
Figure A1.6| Niche metrics across different temporal extents.....132
Figure A1.7| Polygon range map global climate niche dataset.....133
Figure A1.8| Point locality global climate niche dataset.....134
Figure A1.9| Niche hypervolume stability test results.....135
Figure A1.10| The effect of using extreme climate layers on climate niche estimates.....136
Table A2.1| Core analysis model averaged results.....140
Table A2.2| Variable class analysis results.....141
Table A2.3| Core and sensitivity variables.....146
Table A2.4| Core analysis variable selection.....147
Table A2.5| Climate maximum sensitivity analysis model averaged results.....148

Table A2.6| Climate minimum sensitivity analysis model averaged results ..... 149
Table A2.7| Centroid direction sensitivity analysis model averaged results..... 150
Table A2.8| Annual rates of climate change sensitivity analysis model averaged results..... 151
Table A2.9| Standardized rates of climate change sensitivity analysis model averaged results 152
Table A2.10| Annual standardized rates of climate change sensitivity analysis ..... 153
Table A2.11| Variable abbreviation table ..... 154
Figure A2.1| Temporal distribution of population trend data ..... 155
Figure A2.2| Spatial distribution of population trend data ..... 156
Figure A2.3| Spatial variogram analysis results..... 157
Figure A2.4| Environmental predictor variable distributions ..... 162
Figure A2.5| Environmental predictor collinearity analysis..... 163
Figure A2.6| Relationship between mean rate of avian population change and environmental predictors in decreasing populations ..... 164
Figure A2.7| Relationship between mean rate of avian population change and environmental predictors in increasing populations ..... 165
Figure A2.8| $R^2$ of full and variable class models ..... 166
Figure A2.9| Climate maximum sensitivity analysis..... 167
Figure A2.10| Climate minimum sensitivity analysis..... 168
Figure A2.11| Centroid direction sensitivity analysis..... 169
Figure A2.12| Annual rates of climate change sensitivity analysis ..... 170
Figure A2.13| Standardized rates of climate change sensitivity analysis ..... 171
Figure A2.14| Annual standardized rates of climate change sensitivity analysis..... 172
Figure A3.1| Median avian range sizes across the Americas. ..... 173
Figure A3.2| Validation of the trait-based interaction model..... 174
Figure A3.3| Overlap threshold sensitivity analysis. ..... 175
Figure A3.4| Opportunistic frugivore interaction diversity across the Americas. ..... 176
Figure A3.5| Projected impacts of climate change on opportunistic frugivore networks. ..... 177
Figure A3.6| Effects of interaction rewiring on projected future opportunistic frugivore networks. ..... 178

# 1 | General Introduction

For the first time in Earth's history, humans have distinguished themselves from all other species through their ability to modify the natural world at a planetary scale. Human activity has caused such extensive disruption to global systems, that many experts argue we have entered a new geological epoch: the Anthropocene (Crutzen, 2002; Lewis & Maslin, 2015). Approximately 75% of the Earth's terrestrial surface area has been degraded through human activity with tropical dry forests and temperate grasslands the most impacted biomes (Jacobson et al., 2019; Luyssaert et al., 2014). Furthermore, greenhouse gas emissions into the Earth's atmosphere have already led to 1.1°C of warming compared to pre-industrial levels, with the Intergovernmental Panel on Climate Change projecting up to 2.7°C of warming by 2100 under a mid-range emissions scenario (Calvin et al., 2023). This magnitude of environmental change has had widespread consequences across the biosphere with modern species extinction rates estimated to be up to 1000 times higher than pre-human levels (De Vos et al., 2015). Biodiversity loss has occurred at such an unprecedented scale and pace, that many researchers believe we are entering a 6$^{th}$ mass extinction event (Barnosky et al., 2011). Evidently, nations of the world have struggled to meet the demands of a rapidly growing human population in an ecologically sustainable way.

As highlighted by the Nature Contributions to People (NCPs) framework devised by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem (IPBES), the natural world provides a wide range of cultural and economic benefits to human physical and emotional well-being (Díaz et al., 2018). Billions of people are dependent on nature for food and fuel (Isbell et al., 2017) with the most vulnerable communities in developing nations most exposed to the negative effects of biodiversity loss (Cardinale et al., 2012; Díaz et al., 2006, 2018). In addition, biodiversity loss threatens fundamental systems for maintaining the quality of air, soil and water (Mace et al., 2018). The deterioration of key ecosystem services will have severe economic consequences with one study estimating a 9.2% reduction in global wealth by 2100 with the overwhelming majority of these damages to be experienced by the poorest 50% of countries (Bastien-Olvera et al., 2024). Lastly, biodiversity also offers key avenues for combatting climate change through nature-based solutions (Seddon et al., 2021) and carbon sequestration

(Calvin et al., 2023). The restoration and improvement of land management alone is estimated to provide 37% of the carbon storage required to generate a 66% chance of restricting warming to 2°C (Griscom et al., 2017).

The severe consequences of biodiversity loss have begun to be recognised internationally. In December 2022, world governments convened at COP15 in Montreal, Canada, to agree upon a post-2020 Global Biodiversity Framework, which set forth the ambitious goal of halting and reversing biodiversity loss by 2030 (Hughes, 2023). A key target outlined in the framework involves conserving 30% of the world's land and oceans by 2030. While this agreement represents a significant step forward, its effectiveness will ultimately depend on targeted efforts and the strategic allocation of resources to curb biodiversity loss. To support this, it is essential to enhance our understanding of the regions and taxa most vulnerable to future climate change by improving predictive models of climate impacts on biodiversity.

## 1.1 Climate change

Climate change refers to long term shifts in the planet's climate primarily driven by increased greenhouse gas emissions from anthropogenic activity. Since the end of the 18$^{th}$ century, with society's transition into the industrial age, fossil fuel consumption and agricultural expansion has increased rapidly. As a result, greenhouse gas levels in the atmosphere have risen steadily, with concentrations of carbon dioxide ($CO_2$) having increased by 47% and methane ($CH_4$) by 156% relative to pre-industrial levels (Calvin et al., 2023). Atmospheric $CO_2$ and $CH_4$ levels are now higher than they have been at any point in the last 800,000 years (Brook, 2008). These elevated levels of greenhouse gases enhance the Earth's capacity to retain heat, leading to a corresponding rise in global surface temperatures (Kweku et al., 2018).

The effects of climate change are already evident with further disruptions expected to increase in intensity throughout the remainder of the century. The global water cycle will continue to be heavily disrupted, with precipitation levels expected to increase and become highly variable particularly in high latitude and equatorial regions (Pendergrass et al., 2017). The frequency of extreme weather events such as heatwaves, cyclones and

drought is projected to increase (Myhre et al., 2019). Additionally, as atmospheric $CO_2$ concentrations rise, a substantial portion is absorbed by the oceans, driving ocean acidification. By 2100, ocean pH could decrease by as much as 0.4 units (Findlay & Turley, 2021), a trend that is already contributing to widespread coral bleaching and die-offs (Anthony et al., 2008). Even if global warming is limited to 1.5°C, as proposed by the Paris Climate Agreement, we risk triggering several major "tipping point" thresholds, including the collapse of the Greenland and West Antarctic ice sheets and widespread thawing of the permafrost (Armstrong McKay et al., 2022). Due to positive feedback mechanisms across the Earth's systems, once these thresholds are crossed, a lot of the disruption caused by climate change may be irreversible (Armstrong McKay et al., 2022).

Several studies estimate that climate change will overtake land use change as the dominant threat towards biodiversity (Di Marco et al., 2019; Newbold, 2018). Climate conditions are projected to surpass historical levels previously experienced by species (Advani, 2023), with the rate of change increasing beyond the adaptive capacity of organisms (Radchuk et al., 2019; Steffen et al., 2004). Certain models estimate between 15-37% of species could be 'committed to extinction' by 2050 under an intermediate climate change scenario (Thomas et al., 2004), with endemic and island dwelling species being particularly sensitive (Manes et al., 2021; Veron et al., 2019). In addition, many species are expected to shift their ranges to track suitable conditions, with 35% of mammals and 29% of birds projected to have most of their future suitable range in regions they do not occupy currently (Parmesan & Yohe, 2003; Titley et al., 2021). Climate and biodiversity are undeniably linked, with some of the largest past alterations of the biosphere having been climate driven - notably the major mass extinctions in the Phanerozoic era (Song et al., 2021). However, while it is generally accepted that climate change will have extensive impacts on biodiversity across geographic regions and ecological guilds (Omann et al., 2009; Urban, 2015), there remains extensive uncertainty around the magnitude and spatial variability of effects. Given this complexity, improving predictive models of climate change impacts on biodiversity is essential to limiting the likelihood of severe biodiversity loss.

## 1.2 Predicting biodiversity response to climate change

### 1.2.1 Climate niche

A critical aspect of analysing species' responses to climate change is an accurate estimate of the range of climatic conditions a species can persist under - this is referred to as its climate niche (Blonder et al., 2014; Lu et al., 2021). Each species possesses a specific thermal tolerance range bounded by critical minimum and maximum temperatures, beyond which cellular and systemic functions fail (Miller & Stillman, 2012). These thresholds reflect the temperature sensitivity of enzymatic, protein, and membrane function, which collectively underpins metabolic performance (Pörtner, 2002; Pörtner et al., 2006). Water availability can also physiologically constrain species by limiting their capacity to maintain internal hydric balance, which is essential for survival (Miller & Stillman, 2012). In hot or arid environments, evaporative water loss can surpass an organism's ability to absorb or conserve water, leading to dehydration, cellular dysfunction, and ultimately death. This constraint is especially pronounced in water-dependent taxa such as amphibians, which rely on moist skin for cutaneous respiration, and in plants, where water deficits impair turgor pressure and photosynthesis (Hanley et al., 2021; Miller et al., 2018). Beyond direct physiological mechanisms, climate influences the timing of life-history events underpinning the reproductive success of many species, such as migration (Visser et al., 2004; Visser & Both, 2005). Climate change may also impact resource availability and disrupt habitat features, consequently influencing species survival and fitness (Mayor et al., 2017; Stirling & Derocher, 2012). Species distributions are therefore constrained by a specific climate niche and an accurate estimate of the climate range in which species tolerate presently can be informative towards future species response to climate.

The concept of an ecological niche, of which the climate niche is one dimension, was first introduced by Grinnell (1917), who defined it as the sum of all factors that constitute a species' habitat. The Grinellian concept of niche also introduced the idea that species occupy distinct roles within their environment (Grinnell, 1917). Elton (1927) further developed this by highlighting the importance of biotic interactions, such as predation and competition, in shaping a species' ecological role. A major advancement in ecological niche theory was proposed by Hutchinson (1957), who formalized the niche as an n-dimensional hypervolume defined by multiple

environmental axes. This framework has since become foundational to modern ecological niche theory. Hutchinson (1957) also differentiated between a species' fundamental niche - the broadest range of conditions a species could theoretically persist under - and its realised niche - the actual range of conditions within which the species exists (Soberón & Arroyo-Peña, 2017; Soberón & Peterson, 2005). The realised niche represents a subset of the fundamental niche as species' distributions are constrained by additional factors such as competition, dispersal limitation, and habitat availability (Bovo et al., 2018;Boyce et al., 2019; Pigot & Tobias, 2013, 2015). However, the gap between fundamental and realised niches remains ambiguous and difficult to quantify. Furthermore, early niche concepts typically assume that species are in equilibrium with their environment, overlooking the potential for dispersal lags and anthropogenic disruptions. A further limitation is the assumption that a species' niche is static, which fails to account for niche evolution or plasticity.

Various methodologies have been developed to quantify species' climatic niche. Experimental approaches, often conducted in laboratory settings, have measured population growth rates along a gradient of environmental conditions (e.g. temperature, humidity, pH, Ca2+ concentrations) to determine species' tolerance limits (Birch, 1953; Hooper et al., 2008). Additionally, some methods integrate species physiological tolerance data with spatial data to offer a more mechanistically informed method of niche modelling (Kearney & Porter, 2009). These methods provide a more accurate measurement of species fundamental niche by better capturing environmental tolerances and therefore represent a powerful tool in modelling species response to environmental change (Kearney & Porter, 2009). However these methods tend to be impractical for macroscale studies as they require detailed physiological data, are labour and computationally intensive and involve difficulties in integrating multiple niche dimensions (Holt, 2009).

More commonly, correlative approaches, such as ecological niche modelling, are implemented in which environmental variables are extracted across the established distribution of a species (A. T. Peterson, 2001, 2006; Thuiller, 2024). It is then possible to summarize the environmental conditions experienced by a species as occupied regions of a multidimensional niche space – otherwise known as "hypervolumes"

(Blonder et al., 2014; Lu et al., 2021). Therefore, climate niche estimates derived from methods that assume correlation between species distribution and tolerable climate offer estimates of realised niche and can likely be considered underestimates of fundamental niche (Soberón & Arroyo-Peña, 2017; Soberon & Peterson, 2005). These methods are incredibly powerful and have been widely deployed to model species response to environmental change (Thomas et al., 2004; Thuiller, Lavorel, Araújo, et al., 2005). However, it is unclear how different aspects of ecological niche modelling methods may influence niche estimates and subsequent analyses underpinned by climatic niches.

### 1.2.2 Modelling species response to climate change

Building on the concepts of ecological niche theory, species distribution models (SDMs) have emerged as a powerful tool for predicting biodiversity responses to climate change (Elith & Leathwick, 2009). Fundamentally, these models estimate species' potential distributions by correlating known occurrences with environmental variables, assuming that current distributions reflect ecological tolerances. The foundation of SDMs stems from early work by MacArthur and Wilson (1967), who emphasized the role of geography and environment in shaping species distributions. Advancements in geographic information systems (GIS) and spatial data analysis enabled the integration of species occurrences with environmental variables, facilitating the development of SDMs. BIOCLIM was among the first models to use climatic niche estimates for predicting suitable habitats (Booth et al., 2014), followed by various approaches including envelope-based (e.g. DOMAIN, LIVES) and regression-based models (e.g. GLMs, GAMs) (Araújo & Guisan, 2006; Guisan & Thuiller, 2005). More recently, MaxEnt has gained popularity for its effectiveness with presence-only data and strong predictive performance (Phillips et al., 2006).

Despite SDMs being highly scalable across a wide range of geographic regions and taxonomic groups, several limitations constrain their reliability under climate change scenarios. These models assume that species occurrence informs ecological tolerances, however the methods implemented to derive ecological niche from species distribution datasets have rarely been investigated. Specifically, key assumptions are made regarding distribution data type, environmental variable choice, as well as the spatial

and temporal scales at which said variables are summarized across. The influence of these methodological choices on model interpretations are potentially highly consequential, however remain largely unknown. Furthermore, many models assume species' niche conservatism - i.e. niche limits remain consistent across individuals and populations belonging to a species (Smith et al., 2019). Consequently, many SDMs may offer inaccurate outcomes below the species level.

Beyond issues of spatial, temporal and ecological scale, SDMs have often been criticised for offering too correlative an approach that neglects underlying ecological mechanisms relevant towards species response to climate change (Howard et al., 2023). Most SDMs emphasize abiotic factors such as temperature and precipitation, yet overlook biotic interactions - such as competition, predation, and mutualism - that critically shape species distributions (Guisan & Thuiller, 2005). Additionally, many models ignore dispersal constraints, assuming species can occupy all climatically suitable areas failing to account for the accessibility of these regions (Soberón & Arroyo-Peña, 2017). By focusing narrowly on individual species, SDMs often fail to capture community-level dynamics or cascading effects across ecosystems (Guisan & Thuiller, 2005). As climate change disrupts not only where species occur but also how they interact, there is growing recognition that biodiversity forecasts must incorporate species interaction networks to better reflect ecological complexity and predict system-level outcomes. Adopting a more community-oriented approach enables a deeper understanding of how climate change affects ecosystem services that arise from species interactions, including pollination, seed dispersal, and pest control. Given the widespread use of SDMs in both scientific research and ecological policy, it is crucial to critically evaluate their underlying methodologies and address key limitations to enhance their predictive power and the reliability of their interpretations.

### 1.2.3 Functional ecology

Ecological research is increasingly shifting from species-level assessments of anthropogenic impacts toward ecosystem-level metrics that more directly reflect the ecosystem functioning and services upon which human societies depend (Mason et al., 2005). Functional responses to climate change, in particular, offer a more mechanistic and ecologically relevant understanding of how ecosystems are likely to respond to

environmental stressors (Mason et al., 2005). For example, species turnover in response to climate change may leave traditional alpha diversity measures, such as species richness, relatively unchanged, while concealing profound shifts in functional composition and ecosystem processes (Cadotte et al., 2011). As a result, and increasingly supported by the publication of comprehensive functional trait databases (Kattge et al., 2020; Tobias et al., 2022) and advances in trait-based methods (Schleuning et al., 2020), the field of functional ecology has expanded rapidly in recent years, offering powerful tools to assess climate impacts on biodiversity from a functional perspective.

Functional ecology is based on the idea that species fulfil specific roles, or "functions," within ecosystems (Calow, 1987). Grounded in Darwinian evolutionary theory, the traits that enable an organism to perform these functions - known as "functional traits" - are expected to be well-adapted to their roles, and thus closely linked to ecosystem processes and trophic niches (Cadotte et al., 2011; Pigot et al., 2020). Trait-based ecology was pioneered by Tilman et al (1997), who demonstrated that specific traits could predict grass species' survival (Tilman et al., 1997). Further advancements were initially limited by the availability of comprehensive functional trait datasets (Eviner & Chapin, 2003; McGill et al., 2006), particularly for mammals and birds where data was largely restricted to body mass and categorical traits (Jones et al., 2009; Wilman et al., 2014). While, the TRY database provides continuous trait data for over 279,000 plant taxa, it still lacks complete taxonomic coverage (Kattge et al., 2020), which can introduce taxonomic biases in macroecological analyses (Etard et al., 2020; Kohli & Jarzyna, 2021; Naeem et al., 2016). The AVONET database represents a critical breakthrough, offering comprehensive, continuous ecological and morphological trait data for nearly all bird species, unlocking new potential for global functional ecology research (Tobias et al., 2022). Therefore, whilst the conceptual framework of functional ecology has existed for several decades, only recently has it become possible to explore it quantitatively, enabling a more mechanistic understanding of ecosystems (Tobias et al., 2022). Through the correct implementation, these novel functional trait datasets could facilitate investigations into ecosystem responses to climate change at a level of accuracy and scale not previously accessible (Cernansky, 2017; Tilman et al., 2014).

### 1.2.4 Functional response to climate change

Historically, studies investigated future climate change impacts on coarse metrics of ecosystem function such as NDVI and dietary categories (Giannini et al., 2017; Miranda et al., 2019; Pettorelli et al., 2012) or intrinsic traits such as body mass and life history properties (Pacifici et al., 2017). Several studies have capitalized on the emergence of more advanced functional trait datasets and methodological frameworks (Petchey et al., 2004) and implemented more informative trait-based metrics such as functional diversity to describe functional response to climate change (Albrecht et al., 2018; Bender et al., 2019; Stewart et al., 2020). Functional diversity refers to the diversity of functional traits observed across a given community and can be broken down into three core components related to the total volume of functional trait space occupied (functional richness) and the distribution of occupied trait space (functional evenness, functional divergence) (Cadotte et al., 2011; Mason et al., 2005).

When using functional metrics to model ecosystem function under future climate scenarios, large shifts in functional diversity occur suggesting that in addition to shifts in species compositions, ecological assemblages may adopt entirely new functional profiles in response to climate change (Stewart et al., 2020). Magnitudes of change in functional diversity varied geographically and between trophic guilds, with higher latitude regions tending to increase in functional diversity and disproportionately high losses in functional diversity experienced by frugivore assemblages (Stewart et al., 2020). However, despite species shifting their ranges in response to climate change, in certain scenarios, functional diversity is maintained (Bender et al., 2019). This is due to species which occupy similar regions of functional trait space moving into regions vacated by emigrating species and therefore compensating for declines in functional diversity (Bender et al., 2019). The use of functional metrics therefore highlights potential buffering avenues against future climate impacts on ecosystem function. Furthermore, these metrics allow for easier integration of ecology into policy as well as improved transferability of methods between taxonomic groups and geographic regions (Bregman et al., 2015, 2016; Pettorelli et al., 2021).

However, whilst functional diversity offers a coarse assessment on whether a species assemblage occupies a broad range of ecosystem functions (Cadotte et al., 2011), detail on which specific interactions are likely occurring is not determined using these metrics (Kissling & Schleuning, 2015). Given key ecosystem services such as pollination, seed dispersal and pest control, are the product of interacting species, it is essential to consider interaction networks when investigating the effects of climate change on ecosystem function (Bellard et al., 2012; Gilman et al., 2010; Walther, 2010). Furthermore, interaction networks may offer buffering effects against future climate impacts through interaction rewiring mechanisms (Schleuning et al., 2020). Many studies have therefore aimed to better incorporate the complexity of ecological networks and their subsequent contribution towards ecosystem function by modelling species interaction networks (Dehling et al., 2016; Nowak et al., 2019). These studies have tended to derive species interactions by comparing trends in species richness between groups of species whilst other studies have leveraged datasets of observed interaction networks (Kissling & Schleuning, 2015). Species richness analyses have received criticism for offering too correlative an approach whilst observed interaction networks have been criticised for containing high levels of site specific biases (Kissling & Schleuning, 2015). Therefore, accurate modelling of species interaction networks, potentially by incorporating increasingly available functional trait data of prospective interacting species, is a key feature of understanding ecosystem function response to climate change that requires further research.

## 1.3 Birds

Birds represent an ideal clade for investigating macroecological patterns and broad scale response to climate change. Given their relatively high dispersal capacity, they are distributed across all terrestrial biomes and many marine ecosystems globally (Gregory & Strien, 2010; Tobias et al., 2022; Whelan et al., 2008). Additionally, birds have evolved a broad diversity of morphological features, namely highly specialized beak morphologies, allowing this clade to occupy a wide range of trophic guilds (Tobias et al., 2022). Consequently, birds contribute enormously towards various key ecosystem services such as pollination, seed dispersal and pest control, occupying significant roles within ecosystems and increasing the need to better understand the response of this

clade to future change (Díaz-Siefer et al., 2022; Godínez-Alvarez et al., 2020; Gosper et al., 2005). Lastly, given their sensitivity to anthropogenic pressure and trophic positions, birds represent optimal indicator species of ecosystem health (Drever et al., 2008; Gregory et al., 2005; Mekonen, 2017).

Given a historical fascination with birds, this clade has become one of the most studied animal groups. As a result, one of the most attractive aspects of studying birds is the vast amount of data that is available for this clade (Gregory et al., 2005). Comprehensive data on avian taxonomy, life history, and ecological roles enhances the suitability of birds for large-scale ecological studies (Gregory et al., 2005). Furthermore, global datasets, such as the BirdLife database, exist detailing the distribution of all birds through expert range map data (BirdLife International and Handbook of the Birds of the World, 2021). Additionally, eBird contains 65.8 million complete point occurrence checklists covering 10,624 avian species (Sullivan et al., 2009), making it the world's largest citizen science project. This dataset has shown high levels of survey completeness and global coverage (La Sorte & Somveille, 2020) and has established protocols for the implementation of its data into distribution modelling techniques further facilitating its implementation in macroecological studies (Coxen et al., 2017; Johnston et al., 2021).

## 1.4 Thesis outline

This PhD thesis is situated at a pivotal moment in the global effort to combat climate change. In order to meet the targets set by the Paris Climate Agreement - specifically to keep global warming well below 2°C, with aspirations to limit the increase to 1.5°C above pre-industrial levels - greenhouse gas emissions must peak by 2025 and decrease by 43% by 2030 (UNFCCC, 2015). Beyond 1.5°C of warming, a number of key "tipping points" will likely be triggered, drastically increasing the severity of expected climate change impacts (Armstrong McKay et al., 2022). To reflect the urgency of the situation, in November 2024, nations of the world are preparing to meet at the 29$^{th}$ session of the Conference of the Parties to the United Nations Framework Convention on Climate Change (COP29) in Baku, Azerbaijan to re-establish commitments to global climate targets. This PhD thesis aims to enhance our ability to predict climate change impacts

on biodiversity, thereby informing climate policy and contributing to mitigation strategies.

Whilst climate niche estimates are an essential feature in analyses investigating species response to climate change, the influence of different niche quantification methodologies on climate niche estimates has not been extensively tested. Therefore, in Chapter 2, I look to address this gap by first generating a global dataset of accurate climatic niche estimates, with near full coverage across all bird species. I then test the influence of different climate niche quantification methodologies, particularly around summarizing climate across different spatiotemporal grain sizes and extents, on niche estimates. By demonstrating how niche position and volume vary with methodological approaches, particularly across the temporal dimension of niche quantification, this chapter aims to refine interpretations of analyses incorporating climate niche data.

Beyond the spatial and temporal scales used to derive climate niche estimates, there remains uncertainty around the scale at which climate niche limits are put under pressure (Smith et al., 2019). In Chapter 3, I therefore look to better understand which class of environmental features is most predictive of global avian population trends between species climate niche features and properties of the local environment. I first compile population trend data from the Living Planet and BioTIME databases (Collen et al., 2009; Dornelas et al., 2018). I then construct Bayesian mixed models between environmental predictors – namely species climate niche features, local climate features, local rates of environmental change and features comparing local climate to species niche – and rates of avian population change. I find that local environment features are consistently more predictive of avian population trends compared to species climate niche, suggesting response to climate change below species-level climate niche limits. The aim of this chapter is to improve our understanding of past population trends to better inform sensitivity to future change.

In Chapter 4, I move beyond investigating species level sensitivity to climate change and investigate impacts on ecological networks as well as potential mitigative avenues against future climate impacts offered through species interactions. Specifically, frugivory networks are investigated as despite the importance of this trophic guild,

particularly in forest biomes, the impacts of climate change on plant-frugivore networks are still largely unknown at a macroscale (Jordano et al., 2011; Neuschulz et al., 2016). I therefore address this knowledge gap by investigating how plant-frugivore networks are influenced under different climate change scenarios in my study system of the Americas. I first leverage large comprehensive functional trait datasets for both plants and birds to construct ecoregion-level plant-frugivore networks as derived from a trait-based interaction model (Donoso et al., 2017). I then investigate the impact of climate change on plants, as mediated by avian interaction partners, by comparing avian climate niche estimates from Chapter 2 with future climate scenarios. In this chapter I therefore model indirect climate impacts on plant species as determined by the effects on ecological dependencies. To understand whether interaction rewiring can potentially buffer against future climate impacts I re-run analyses allowing for avian dispersal between networks and increased dietary flexibility (Schleuning et al., 2020). I find that future climate change greatly damages the integrity of ecological communities as I project widespread reductions in species interactions across the majority of ecoregions, particularly in tropical and subtropical regions. However, interaction rewiring showed great potential to buffer against future climate impacts, particularly in the Neotropics.

This PhD project aims to take advantage of advancements in macroecology and functional ecology, predominantly in the form of novel datasets (Karger et al., 2017; Kissling et al., 2019; Sullivan et al., 2009; Tobias et al., 2022), to develop methods and identify macroscale patterns in biodiversity response to climate change. In Chapter 5, I synthesize the key findings from the previous chapters, discuss limitations, and propose future research directions. Throughout this thesis, I conduct analyses across different ecological resolutions, by first generating a species level dataset in Chapter 2 to then investigating macroecological trends at population and network levels in Chapters 3 and 4. All analyses are conducted at either a global or continental scale to offer an insight into macroscale ecological patterns which can ideally promote targeted regional strategies. Furthering our understanding of the complex mechanisms in which biodiversity responds to a changing climate is an essential step in developing strategies to minimise drastic impacts of climate change.

# 2| Testing and implementing spatial and temporal refinements in global climate niche estimates for birds

**Keywords:** climate niche, polygon range map, point locality, spatiotemporal grain size

## Abstract

Species climate niches have played a foundational role in global change biology, underpinning geographical range shift models and a rapidly growing number of studies investigating or predicting the response of biodiversity to climate change. However, climatic niches are inherently multi-dimensional and their quantification is subject to numerous potential biases depending on the spatial or temporal scale of analyses. Here I test the effects of implementing two widely used methods, which extract climate from polygon range map and point locality datasets, on climate niche estimates for all birds (polygon range map: 9892, point locality: 9935 species). I subsequently test the independent effects of extracting climate across distinct spatiotemporal grain sizes and extents on niche estimates. I find that niche estimates derived from polygon range map methods tend to occupy lower temperature and higher precipitation centroid positions. This is likely due to climate outside of the range experienced by species being captured when using polygon range map data, and subsequently being reflected as shifted niche centroid positions. Furthermore, niche volume tends to expand under point locality methods, likely due to the homogenisation effect of averaging climate at coarse spatiotemporal resolutions when using polygon range map data. These findings highlight the importance of considering different methodological approaches for climate niche estimation. Therefore, previous analyses underpinned by climate niche estimates should be interpreted accordingly. I hope studies of this nature can promote a more informed application of niche quantification methods.

## 2.1 Introduction

Species climate niches represent an important tool for understanding and predicting the response of biodiversity to future climate change. Climate niche estimates have been implemented across various ecological fields including macroevolution (Cooney et al., 2016; Lavergne et al., 2013), macroecology (Hawkins et al., 2007; Strubbe et al., 2013) and global change biology (Grinder & Wiens, 2023; Jetz et al., 2007; Thomas et al., 2004). Furthermore, species climate niche estimates underpin various species distribution modelling techniques which are widely used to forecast species response to future environmental change (Elith & Leathwick, 2009; A. T. Peterson, 2001). Despite the implementation of distinct niche quantification methods across these studies, it remains unclear the effect of different methods on shaping climate niche estimates, particularly at wider taxonomic and geographic scales. Therefore, interpretations of analyses based on climatic niches will potentially be influenced by the approach used to quantify niche estimates.

Niche quantification methods typically rely on extracting climate across the estimated distribution of a species (A. T. Peterson, 2001; Thuiller, 2024). There are therefore several methodological aspects to consider which are known to vary between studies, particularly regarding the species distribution data type (Figure 2.1) and the spatial and temporal grain size and extent climate is extracted at (Figure 2.2). A widely used method for quantifying climate niche involves extracting annual climate across the breeding range of a species using expert derived polygon range map data (Cooney et al., 2016; Hawkins et al., 2007; Lavergne et al., 2013; Strubbe et al., 2013; Zurell et al., 2018). The advantage of using expert range maps to describe species distributions is that this data type is particularly effective at describing broad regions where a species is likely to occur, particularly for widespread common species (Hurlbert & Jetz, 2007). However, these methods tend to overestimate climatic niche by extracting climate as annual mean values across a species' breeding range (Merow et al., 2017). This method fails to address temporal variability in species distributions, such as during seasonal migration (Marsh et al., 2022; Ozsanlav-Harris et al., 2023). Therefore, winter climate may be included as part of the climate niche estimate when the species does not in fact experience these conditions. The implication of this is that a broader niche estimate more adapted towards cooler conditions may be attributed to a given species,

potentially influencing assumptions about the species' resilience to future climate change (Ralston et al., 2016).

Given the disadvantages of polygon range map methods for niche quantification, many studies have begun leveraging point locality datasets instead to infer species distributions and subsequent climate niche estimates (Seeholzer et al., 2017; Zhao et al., 2023). Point locality data significantly reduces the spatial grain size at which climate is extracted perhaps better describing the niche of narrow ranged species or species occupying climatically variable regions such as steep elevation gradients (Merow et al., 2017). Furthermore, given more temporal detail provided in these datasets, it is possible to refine climate niche estimates by excluding climate known to not be experienced by species across their ranges (Eyres et al., 2017). Given the finer spatial and temporal consideration, I can assume climate niche estimates derived from these methods are likely more accurate for migratory and mobile species (Figure A1.1). Additionally, with growing data availability through longstanding regional surveys and citizen science projects it is increasingly possible to quantify species climate niches using point locality data (Barnagaud et al., 2012; Delgado et al., 2011; Jiguet et al., 2010; La Sorte & Jetz, 2012). Point locality datasets are however known to contain significant levels of sampling bias (Fourcade, 2016; Meyer et al., 2015). Additionally, due to potential sampling gaps, climate niche estimates generated through these methods may represent an underestimate for many species (La Sorte & Somveille, 2020), which consequently may inaccurately suggest said species are more sensitive to future climate change (Jiguet et al., 2006, 2007). A global synthesis, trying to understand how these different approaches give rise to different climate niche estimates does not yet exist, likely because of previously insufficient accurate point sampling of species worldwide.

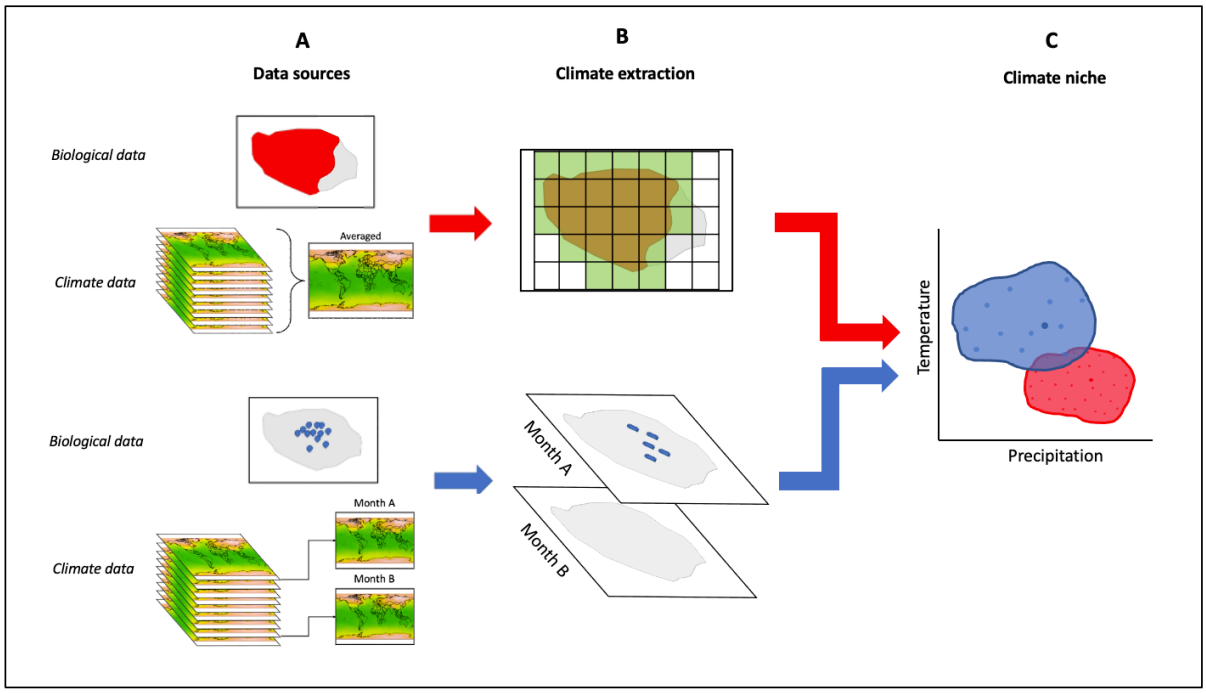



**Figure 2.1| Conceptual figure outlining two different approaches to climatic niche estimation.** In this study, I compare two widely used methods for quantifying species climate niche which implement polygon range map (A: red) and point locality data (A: blue). Under the polygon range map method, mean annual climate layers (1981 – 2010) are averaged across the species' breeding range (B: red). Specifically, a 50 km grid is overlayed across the breeding range polygon and climate is averaged across intersecting grid cells (B: red). Under the point locality method, climate is extracted at each occurrence data point at a 1km grain size, for the precise month and year the occurrence took place (B: blue). Niche hypervolumes summarizing extracted climate are subsequently generated in both methods (C). Different niche quantification methods can potentially generate drastically different climate niche estimates.

In this study, I assess the effects of distinct niche quantification methods, namely polygon range map and point locality derived methods (Figure 2.1), on climate niche estimates at a broad taxonomic and geographic scale. I capitalise on worldwide occurrence sampling of almost all bird species in the form of the eBird database, which contains over 1.5 billion occurrence records across more than 11,000 species, constituting the largest citizen science project globally (Sullivan et al., 2009). Specifically, I compare niche position and volume between estimates derived from polygon range map datasets and point locality data. I then investigate the independent effects of spatial grain size (1km, 25km, 50km) and temporal grain size (monthly, seasonal, annual) on niche position and volume (Figure 2.2). Beyond temporal grain

size, another consideration is the temporal extent across which climate conditions are averaged. Many studies use climate conditions averaged across multiple years, and therefore fail to account for sources of interannual climate variation, such as El Niño and La Niña events (Hallett et al., 2004; Stenseth et al., 2003). Therefore, I also investigate the effects of different strategies for capturing temporal extent on climate niche estimates.

Birds represent an ideal group to test these approaches as they are highly mobile, thus exhibiting more spatially and temporally sensitive distributions (Gregory & Strien, 2010; Tobias et al., 2022). Furthermore, comprehensive high quality occurrence datasets exist for this group, facilitating this investigation at a global scale (Sullivan et al., 2009). Lastly, a wide range of macroecological and macroevolution studies have used avian climate niche estimates further increasing the need to better understand how these analyses may have been influenced by different methodological approaches (Cooney et al., 2016; Jetz et al., 2007).

The goal of this study is to test the influence of different methodological approaches on species climate niche to promote better interpretations of analyses underpinned by niche estimates. As part of this I generate a global dataset of climate niche estimates derived using polygon range map and point locality data with near full coverage across all bird species. I hope that this dataset of avian climatic niches can facilitate further analyses into future climate impacts on ecosystems.

## 2.2 Methods

### 2.2.1 Quantifying species climatic niche

*Polygon range map method*

I generated a dataset of species climate niche estimates implementing polygon range map data to describe species distributions. Polygon range map data for nearly all avian species was sourced from BirdLife International (BirdLife International and Handbook of the Birds of the World, 2021). The BirdLife Species Range map database contains species distribution estimates for >11,000 bird species, in the form of expert delineated polygons (BirdLife International and Handbook of the Birds of the World, 2021). I

filtered and combined range map data to only include the breeding and resident species range. Only extant, native and re-introduced distributions were included. For a given species, mean annual temperature (°C) and precipitation (mm/month), with a temporal extent of 1981 – 2010, was extracted across the species range, using climate layers sourced from CHELSA (Karger et al., 2017). Specifically, a 50km grain size grid was overlayed across the species range and climate was averaged across each intersecting grid cell. Precipitation was log transformed to correct for data skewness driven by regions with disproportionately high levels of precipitation. Temperature and precipitation were selected as climate variables to inform niche estimates due to their known influence on avian distributions (Pigot et al., 2010) and the availability of high-resolution spatiotemporal data (Karger et al., 2017). Furthermore, given species can tolerate conditions outside their climatic niches for short periods (Pollock et al., 2021), mean climate layers were used to best approximate the conditions most relevant to niche adaptation. However, to assess the potential effects of alternative metrics, we conducted a supplementary analysis on a subset of species (n = 875), comparing niche centroid and volume estimates derived from mean, maximum, and minimum climate values (Figure. A1.10). For species with above 30 climate data points, niche hypervolumes (Blonder et al., 2014) were then generated from extracted climate data under the convex hull method, using the "hit and run" random sampling algorithm. The threshold of 30 occurrence points was derived from literature (Lu et al., 2021) and represents a recognised lower stochastic limit below which the instability of hypervolume estimates increases drastically. All niche hypervolume functions were conducted using the *hypervolume* R package (Blonder et al., 2023).

*Point locality method*

In addition to range map derived climate niche estimates I generated niche estimates using point locality data to describe species distributions. I first extracted point locality data for each avian species from the eBird Raw Database (EBD) (Sullivan et al., 2009) (Figure A1.2). I limited the protocol type to either "Stationary" or "Travelling" and only included point localities that took place after 1979 to filter against unreliable historical data points. To correct for spatial outliers, I superimposed BirdLife range map data for each species with a given point locality dataset and only included data points that occurred within a 500km buffer distance from the range map boundary (A1 - Additional

Methods). To address spatial biases identified in eBird point locality data (La Sorte & Somveille, 2020), I implemented a thinning step weighted by sampling effort on each species' point locality dataset (A1 - Additional Methods). I first generated a global raster layer of sampling effort as derived from eBird checklist data (Figure A1.3). For a given species' point locality dataset, the global raster of sampling effort was rescaled and cropped to the maximum extent of point localities. The species' point localities were subsequently intersected with the sampling effort raster, with the inverse sampling effort value assigned to a given intersecting point locality to then inform the weighted thinning process.

For each data point in a given species' processed point locality dataset, I extracted mean monthly temperature (°C) and mean monthly precipitation (mm/month), using high resolution CHELSA V2.1 climatology layers, for the precise month and year that the point locality took place (Karger et al., 2017). Precipitation was log transformed to correct for data skewness. I extracted climate to a 1km grain size. For species with above 30 climate data points after processing, niche hypervolumes (Blonder et al., 2014) were generated from extracted climate data under the convex hull method, using the "hit and run" random sampling algorithm (Quintero et al., 2022).

### 2.2.2 Testing climate niche methodologies

I investigated the effects of distinct niche quantification methods on climate niche estimates. Specifically, I assessed shifts in niche position and volume between polygon range map derived niche estimates and point locality derived niche estimates. Niche centroid and volume values were therefore extracted from climate niche estimates and compared between both groups (Blonder et al., 2014). In the case of point locality niche estimates, for species with above 30 point localities, I estimate niche position and volume as hypervolume centroid and volume whereas for species that fall under this threshold, these estimates are derived as median and range estimates. I ran pairwise t-tests to assess whether any differences in niche position or volume were statistically significant from one another. Additionally, I mapped centroid and niche volume values to visualise geographic variation in differences between quantification methods.

It is important to note that the time period we held climate data for differed between the polygon range map method (1981 – 2010) and the point locality method (1979 – 2018) due to data availability constraints across temporally coarse climate layers. Future work could look to supplement the climate data used in the polygon range map method by averaging climate layers from finer temporal resolutions to match. It is important to note that the climate data time periods differed between the polygon range map method (1981–2010) and the point locality method (1979–2018), reflecting limitations in the extents of temporally coarse climate layers. Future studies could address this discrepancy by aggregating higher-resolution climate data to ensure temporal consistency across both approaches. Lastly, a crosswalk between BirdLife and eBird taxonomies was used to compare species across taxonomies (Tobias et al., 2022).

The two commonly used approaches for climate niche estimation detailed differ primarily in the spatiotemporal resolution at which climate is extracted. To further evaluate how these differences influence niche estimates in more detail, I subsequently tested the independent effects of spatial grain size and temporal resolution on niche position and volume. I therefore modified aspects of the method used to derive point locality niche estimates as these datasets had fine enough spatial and temporal detail to facilitate tests across a range of grain sizes and extents. To individually assess the effect of spatial grain size on niche position and volume I generated niche estimates extracting annual mean climate at a grain size of 1km, 25km and 50km for all species (n = 9,935 species). Monthly climatology layers (1km grain size) were stacked and averaged to create mean annual climate layers. To produce mean annual climate layers for the remaining two spatial grain sizes I aimed to test (25km, 50km), I aggregated and averaged the original mean annual climate layer (1km grain size) across 25km and 50km grid cells. For a given species, I extracted climate across their point localities from either a 1km, 25km or 50km climate layer to generate climate niche estimates across all three spatial grain sizes.

To assess the independent effects of temporal grain size on niche position and volume I extracted climate across three distinct temporal grain sizes: (1) mean monthly, (2) mean seasonal and (3) mean annual across all species (n = 9,935 species). I kept spatial grain size consistent at 1km. To inform monthly estimates, I simply used climatic niche

estimates from the global point locality niche dataset. To inform seasonal estimates, monthly climatology layers were stacked and averaged across winter months (October – March), and across summer months (April – September) - as defined by equinox dates - to produce winter and summer climate layers for a given year. To inform annual estimates, monthly climatology layers were stacked and averaged to create mean annual climate layers for a given year. Climate was extracted at processed point localities from either monthly, seasonal or annual climate layers - as informed by the date of a given point locality - to generate climate niche estimates across all three temporal grain sizes.

Lastly, to assess the effect of temporal extent on niche position and volume I generated niche estimates using (1) specific month and year, (2) monthly averaged across 1981-2010 and (3) multi-year averaged across 1981 – 2010. I did this at a spatial grain size of 1km for all species (n = 9,935 species). To inform month and year estimates, I simply used climatic niche estimates from the global point locality niche dataset. To inform monthly (1981 – 2010) estimates, for a given month, all climatology layers between 1981 – 2010 were stacked and averaged. For instance, to generate a January (1981 – 2010) layer, climatology layers for January 1981, January 1982, January 1983 and so on up until January 2010 were stacked and averaged. Lastly, to inform multi-year averaged estimates, all annual climatology layers were simply stacked and averaged. For a given species, climate was extracted at processed point localities from either monthly, monthly (1981 – 2010) or multi-year averaged (1981 – 2010) climate layers - as informed by the date of a given point locality - to generate climate niche estimates across all three temporal extents.

Across all climate datasets extracted at distinct spatiotemporal grain sizes and extents, niche hypervolumes were generated for species with above 30 climate data points (Blonder et al., 2014). For a given analysis – i.e. spatial grain size, temporal grain size, temporal extent - niche centroid and volume values were extracted from climate niche estimates and compared between groups. All niche hypervolume functions were conducted using the *hypervolume* R package (Blonder et al., 2023).

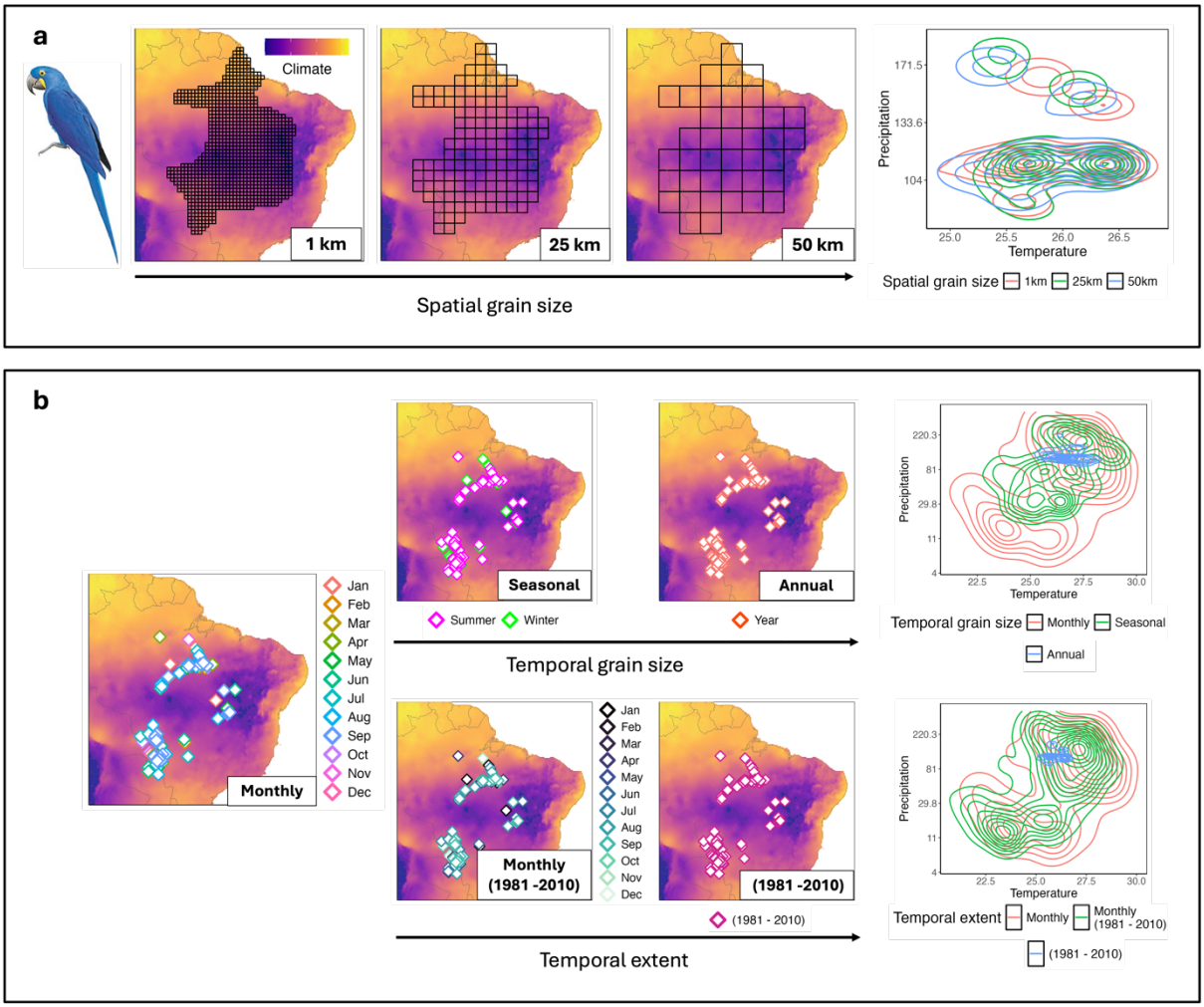



**Figure 2.2| Extracting climate at different spatiotemporal grain sizes and extents.** Shown are the independent effects of extracting climate at different spatiotemporal grain sizes and extents on the climate niche estimate of an example species (Hyacinth Macaw - *Anodorhynchus hyacinthinus*). Panel (a) shows the distinct spatial grain sizes (1km, 25km, 50km) investigated. Panel (b) shows the range of temporal grain sizes (monthly, seasonal, annual) and extents (monthly, monthly (1981 – 2010), annual (1981 – 2010)) investigated.

## 2.3 Results

I found clear differences between climate niche estimates derived from either the polygon range map method or point locality method. Specifically, polygon range map derived climate niches occupied lower temperature and higher precipitation centroid positions compared to point locality niche estimates (Figure 2.3). Furthermore, polygon range map derived niches tended to have narrower niche volumes. Differences in niche

centroid positions and volume between methods were shown to have statistical significance under a pairwise t-test analysis (Table A1.1).

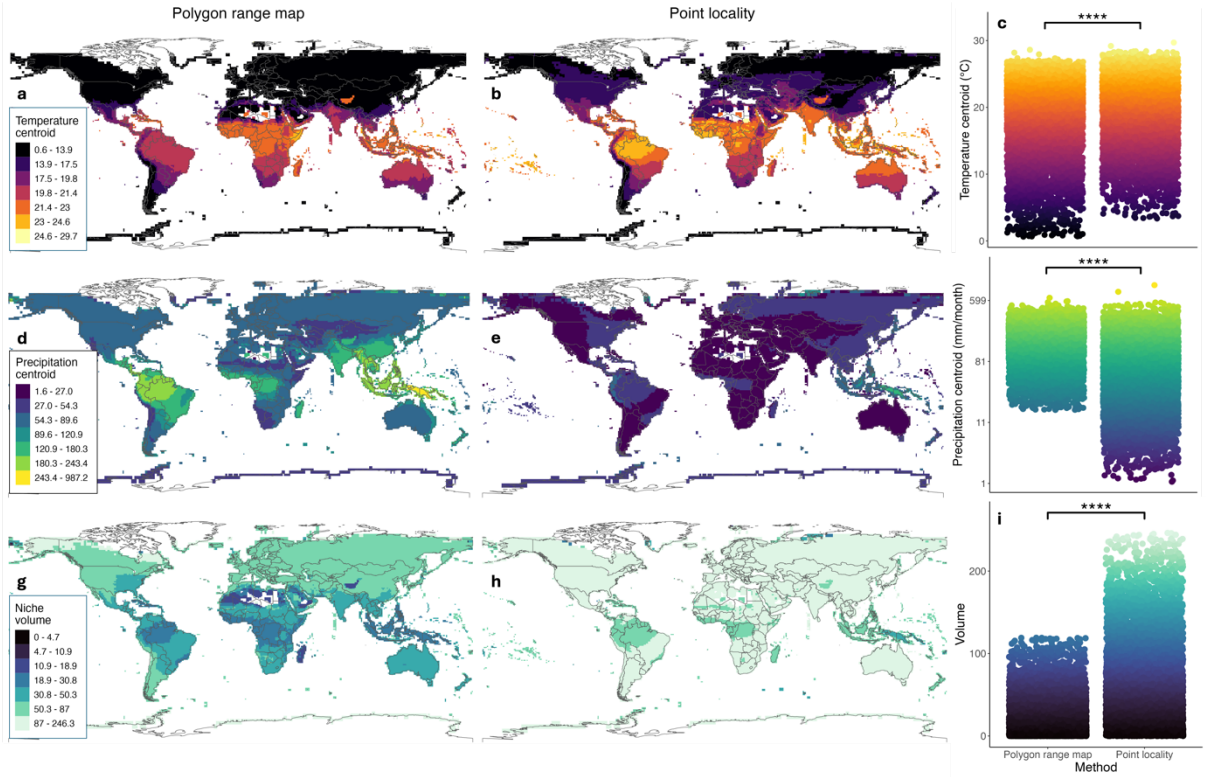



**Figure 2.3| The effects of different niche quantification methods on avian climate niche estimates.** Shown here are maps and accompanying plots of different niche metrics derived from the polygon range map and point locality niche quantification methods. The effects of different methods on temperature centroid (a - c), precipitation centroid (d - f) and niche volume (g - i) are exhibited. Maps summarize species climate niche features across 100 km grid cell communities. Climate niche estimates for almost all birds are exhibited (polygon range map; n = 9892 species, point locality; n = 9,935 species). Additional maps of niche centroid and volume across other methodological comparisons such as a spatial grain size (Figure A1.4), temporal grain size (Figure A1.5), temporal extent (Figure A1.6) are included in the Appendices.

Focusing on the effect of different spatial grain sizes on niche estimates, temperature centroid is shown to shift towards lower temperatures when extracting climate at finer spatial grain sizes (Figure 2.4). Precipitation centroid is shown to be minimally influenced by different spatial grain sizes (Figure 2.4). Lastly, niche volume is shown to expand as I extract climate at finer spatial grain sizes (Figure 2.4). All results, except trends in precipitation centroid position, were shown to have statistical significance under a pairwise t-test analysis (Table A1.2). With regards to the effects of different

temporal grain sizes on niche estimates, temperature niche position is shown to not be significantly influenced by different temporal grain sizes (Figure 2.4). Precipitation centroid is shown to clearly shift towards a lower niche position as climate is extracted at a finer temporal grain size (Figure 2.4). Niche volume is shown to expand as climate is extracted at finer grain sizes (Figure 2.4). All results, except trends in temperature centroid position, were shown to have statistical significance under a pairwise t-test analysis (Table A1.3). In addition to testing the effects of temporal grain size, I investigated how niche estimates differed when extracting climate across distinct temporal extents. I found that temperature niche position is shown to shift towards warmer temperatures at finer temporal extents (Figure 2.4). Precipitation centroid is shown to shift towards a lower niche position at finer temporal extents (Figure 2.4). Lastly, niche volume is shown to expand as climate is extracted at finer temporal extents (Figure 2.4). All results were shown to have statistical significance under a pairwise t-test analysis (Table A1.4).

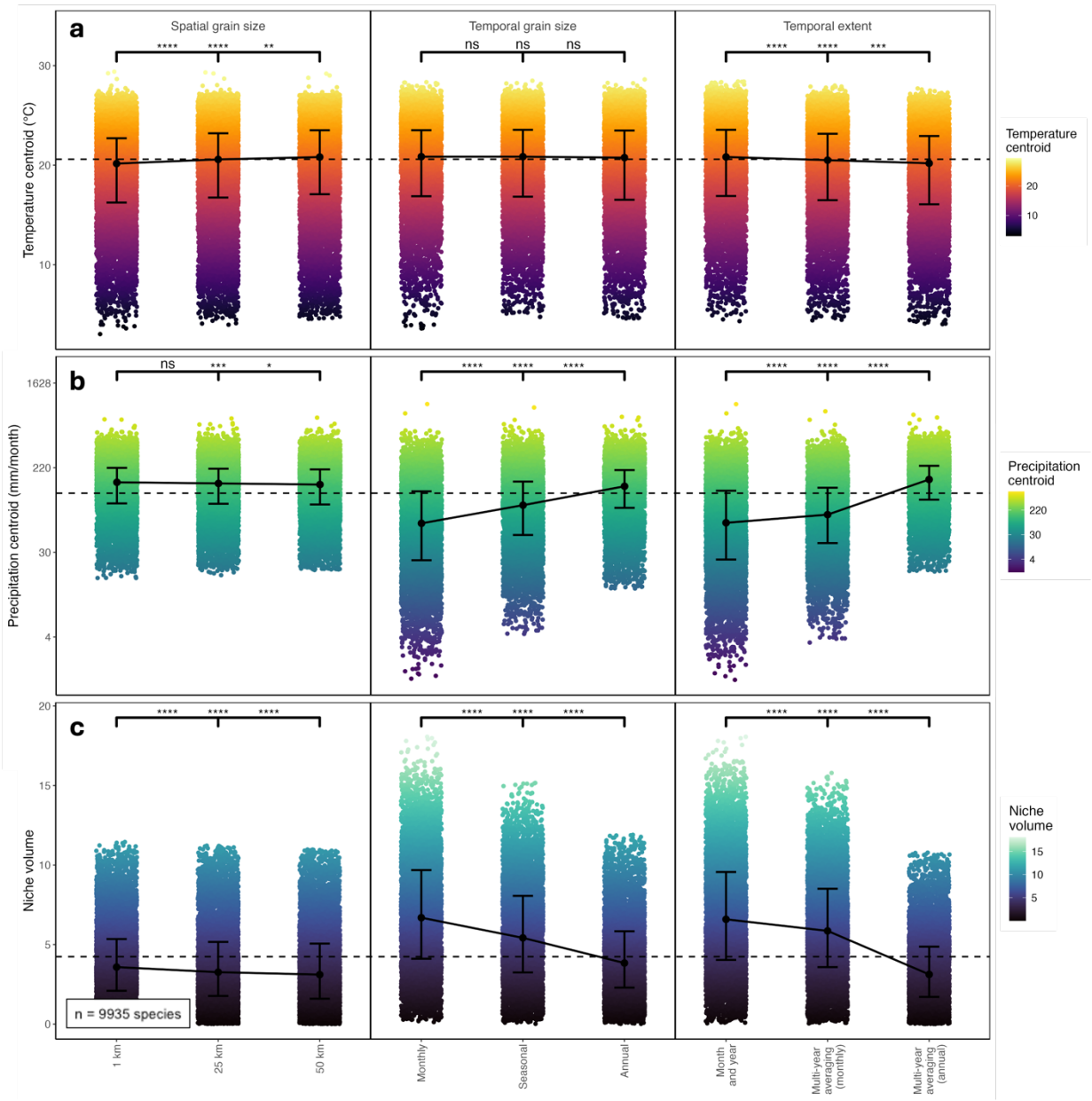



**Figure 2.4| Climate niche estimates vary across different spatiotemporal resolutions.** Plots show the effects of extracting climate at different spatial grain sizes (1km, 25km, 50km), temporal grain sizes (monthly, seasonal, annual) and temporal extents (monthly, multi-month averaged, multi-annual averaged) on climate niche estimates for almost all birds (n = 9,935 species). Specifically the effects on temperature centroid (a), precipitation centroid (b) and niche volume (c) are exhibited. Due to high data skewness, niche volume values were square root-transformed to improve interpretability of underlying effects. Statistically significant differences between comparisons, as determined through pairwise t-test analyses, are shown using asterisks.

## 2.4 Discussion

My global analysis of species climate niche quantification methods reveals significant differences in niche position and volume between niche quantification methods (Figure 2.3). Notably, the temporal dimension of niche quantification is shown to be particularly important in explaining variation in centroid position and volume between methods (Figure 2.4). These findings provide important insights that can better inform interpretations of past and future studies underpinned by climate niche estimates.

Climate niche estimates derived from polygon range map data generally occupied cooler and wetter centroid positions compared to point locality niche estimates (Figure 2.3). Furthermore, whilst these methods predominantly differ in the spatial and temporal resolution of climate data, it is clear that the temporal dimension is particularly influential towards climate niche estimates (Figure 2.4), indicating high temporal variability in many avian species' distributions. Many birds shift their geographic distributions seasonally during migration - often moving towards warmer regions during the winter period to access more favourable climatic conditions, increase resource availability and improve breeding prospects (Chesser & Levey, 1998; Ozsanlav-Harris et al., 2023). Therefore many migratory species will not experience the colder climatic conditions exhibited across their breeding range (Lehikoinen et al., 2021; Visser et al., 2009). More temporally sensitive niche estimates - such as those derived from point locality datasets - are therefore more likely to occupy warmer niche centroid positions (Eyres et al., 2017), reflecting the actual environmental conditions experienced by these migratory species. Conversely, range map-based niche estimates typically summarize annual mean climate across a species range (Lavergne et al., 2013; Strubbe et al., 2013; Zurell et al., 2018). These estimates therefore incorporate winter conditions not experienced by species, resulting in niche centroids that are systematically cooler relative to those derived from point locality data.

Moreover, because range map niche estimates often exclude non-breeding distributions, due to data limitations or uncertainty regarding wintering ranges (Cooney et al., 2016), they may omit substantial portions of the realised climatic niche. Empirical evidence indicates that many species occupy distinct regions of climatic niche space during different migratory phases (Cohen & Jetz, 2023). Therefore, niche estimates based

solely on breeding ranges can systematically underrepresent the full range of environmental conditions experienced throughout the year, further driving differences between the two methods.

The temporal sensitivity of climate niche estimates demonstrated in this study is expected to be particularly pronounced in migratory species (Figure A.1.1), where the temporal variability in the climate conditions species experience is most evident. Other avian guilds are also likely to exhibit heightened sensitivity to the temporal resolution implemented in niche quantification, particularly species reliant on seasonally variable resources such as frugivorous and nectarivorous species (Bennett et al., 2014; Quitián et al., 2019). For example, the Hawaiian nectarivorous honeycreeper *Himatione sanguinea* exhibits seasonal distributional shifts in response to blooming patterns of nectar sources (Smetzer et al., 2021). Additionally, larger-bodied species, which typically exhibit broader geographic ranges and higher dispersal capacities, are more likely to encounter a wider spectrum of climatic conditions (Sheard et al., 2020). Consequently, any movements within their ranges may result in greater variability in the climatic space they occupy across space and time.

In addition to temporal considerations, species occupancy is spatially non-random; individuals are often concentrated in specific biodiversity hotspots within their broader geographic ranges (Liang et al., 2017; Pang et al., 2023). Point locality datasets are better suited to capture this heterogeneity in distribution density, whereas polygon range maps typically assume uniform occupancy across a species' range, potentially contributing to discrepancies in climate niche estimates derived from each method. However, point locality data are themselves subject to sampling bias (Figure A1.3), often reflecting higher sampling intensity in areas with greater human population density and accessibility (La Sorte & Somveille, 2020). Consequently, regions characterized by more extreme climatic conditions are frequently underrepresented in such datasets. This bias may lead to climate niche centroids that are skewed toward more moderate climates when estimated from point locality records.

With regards to the independent effect of spatial grain size on niche estimates, at finer spatial resolutions, climate niche estimates tend to occupy cooler centroid positions

(Figure 2.4). There are several contexts whereby extracting climate at large spatial grain sizes would inaccurately overestimate species occupancy and subsequently their climate niche (Lu & Jetz, 2023). For instance, in the case of narrow-ranged species or species occurring at high elevations, extracting climate across the species range at coarse spatial grain sizes will inaccurately contribute warmer lowland or surrounding climate towards the climate niche estimate (Ellis-Soto et al., 2021; Lu & Jetz, 2023). Therefore, under these circumstances, extracting climate at finer spatial grain sizes offers a more refined and accurate niche estimate – likely occupying a cooler centroid position.

Niche volume is shown to narrow as climate is extracted using polygon range map data compared to point locality methods (Figure 4c). Beyond distribution data type and spatiotemporal resolutions, another key difference between niche quantification methods is the averaging of climate across grid cells intersecting a species range under range map methods (Lavergne et al., 2013; Strubbe et al., 2013). In general, averaging climate across coarser spatiotemporal grain sizes will drive a reduction in niche volume (Lu & Jetz, 2023). Climate niches derived from range map methods are still likely informed by a broader range of climate that may represent an overestimate of climate niche for many species. However, due to averaging across the species range, this broader range of climate is homogenized as a narrower climate niche estimate compared to methods that don't implement climate averaging. The difference in climate range exhibited between both methods is still reflected in shifted niche positions. In addition to capturing narrower climate ranges, niche estimates derived from averaged climate data will likely exhibit smoother shapes in climate space, as the averaging process dampens the influence of outlier microclimatic conditions (Suggitt et al., 2011). Conversely, niche estimates based on point locality data encompass a broader range of climatic conditions and typically display more irregular or rugged niche boundaries, reflecting the fine-scale environmental heterogeneity captured by individual occurrence records.

### 2.4.1 Limitations and future directions

There are several limitations to the method of climatic niche estimation used in this study that I acknowledge here. As mentioned previously, species distribution datasets

used to quantify climate niche throughout this study have associated weaknesses. Specifically, polygon range map data is known to often overestimates species range whilst due to sampling gaps point locality data will often underestimate the distribution of species (La Sorte & Somveille, 2020; Marsh et al., 2022). Furthermore, despite efforts to mitigate this through weighted thinning, point locality datasets remain subject to significant sampling bias (Fourcade, 2016; Johnston et al., 2019). In particular, occurrence records are often clustered in areas with greater human accessibility or higher population density. As a potential extension of this work, future analyses could aim to quantify the influence of this bias by comparing observed niche estimates to those generated from a null model comprising occurrence points exclusively drawn from highly sampled regions. Additionally, due to data availability constraints, the dimensionality of the climate niche estimates developed and implemented throughout this study was restricted to temperature and precipitation (Karger et al., 2017). Whilst there is suitable evidence to suggest that these environmental variables generally influence species distributions (Pigot et al., 2010), other climatic variables may be ecologically relevant. Furthermore, which climatic variables influence species distributions and therefore summarize species niche may vary between species. As high-resolution climate data becomes increasingly available, future studies should aim to enhance the methods presented here by estimating climate niches to a higher degree of dimensionality.

Previous studies have suggested strengths and weaknesses of different niche quantification methods (Merow et al., 2017). For instance, range map derived methods would likely be more accurate at describing occupancy and climate niche for widespread resident species whereas point locality methods would likely be more suitable for mobile or migrant species as well as narrow ranged species (Fourcade, 2016; Zhao et al., 2023). Therefore, future work investigating the influence of distinct niche quantification methods could focus on more extensive testing of the suitability of different methods across different ecological and geographic contexts. In addition, further work could be invested towards generating climate niche estimates that benefit from the advantages of both range map and point locality methods. For instance, a paper by Merow et al (2017), developed a method that combined features of both range maps and point locality dataset to improve upon species range predictions, specifically

by constraining the output of point locality informed species distribution models with expert range map delineations (Merow et al., 2017). Another possible improvement upon conventional methods, as wintering range map data becomes more reliable, could be seasonally sensitivity range map climate niches. Under this method, instead of extracting annual climate across the breeding range of species, winter and summer climate could be extracted across wintering and breeding ranges respectively.

### 2.4.2 Global climate niche dataset

As part of this study I generated a global dataset of climate niche estimates with near full coverage across all birds. I provide climate niche estimates derived from a polygon range map method for 9892 bird species, representing 90% of birds using the BirdLife taxonomy, with supporting niche hypervolumes for 8539 species (Figure A1.7). Specifically, to generate these niche estimates I extracted mean annual (1981 – 2010) temperature and precipitation across a 50 km grain size grid overlaying the breeding and resident ranges of species. These estimates would likely represent particularly accurate climate niches for widespread resident species (Fourcade, 2016). Additionally, I generated climate niche estimates from point locality data for 9,935 bird species, which represents 93% of all bird species using the eBird taxonomy (Figure A1.8). I also generated supporting niche hypervolumes for 8389 species. To inform these niche estimates, climate was extracted using point locality data at fine spatiotemporal grain sizes and extent. Specifically, temperature and precipitation was extracted at a 1km grain size and at the specific month and year a point locality took place. These estimates would likely be particularly accurate for narrow ranged, mobile and migratory species (Ellis-Soto et al., 2021).

I hope, a global climate niche dataset of this nature can facilitate advancements across various ecological fields. For instance, ecogeographic theories can be tested across all taxonomic groups and regions given this dataset's global and comprehensive taxonomic coverage. Secondly, in combination with phylogenetic methods, more in depth studies investigating evolutionary dynamics of climatic niche can be undertaken and subsequently adaptability to climate change can be inferred (Cooney et al., 2016). Lastly, these refined climatic niche estimates can inform climate suitability models to forecast species response to future climate change.

### 2.4.3 Conclusion

In this study I have identified that different niche quantification methods can generate drastically different climate niche estimates. The results of this study clearly confirm the importance of considering temporal sensitivity in species distributions as this dimension significantly contributed towards variation in niche estimates between methods (Eyres et al., 2017). These findings are particularly significant as the temporal dimension of niche estimation has been largely excluded from many studies estimating climatic niche (Pearman et al., 2010; Ralston et al., 2016; Strubbe et al., 2013). In addition, I provide a global climatic niche dataset, with near full coverage across an entire animal clade. I hope this niche dataset, along with a better understanding of the underlying methodologies, can promote the correct application of climate niche estimates to better understand biodiversity response to future climate change.

# 3| Properties of the local environment are more widely predictive of avian population trends compared to species climate niche

**Keywords: climate niche, local environment, population ecology, birds**

## Abstract

Determining accurate predictors of past population trends is essential to understanding how populations will respond to future environmental change. However, the extent to which species-level climatic niche characteristics reliably predict population trends, particularly in comparison to local environmental conditions, remains unclear. In this study, I fit Bayesian mixed effect models between a range of environmental variables and avian population trend data (3132 populations, 972 species) sourced from the Living Planet and BioTIME databases. Specifically, I construct models fitting mean rate of avian population change against properties of species climate niches, local environment as well as metrics comparing the position of local climate within its species niche. I consistently find properties of the local environment to have a higher predictive capacity of avian population trends, suggesting populations may respond to climate change before conditions reach their respective species-level niche limits. Therefore, analyses into future climate impacts on biodiversity underpinned by species climate niche estimates potentially offer overly optimistic outcomes, as these may have overestimated the true range of conditions populations will persist under.

## 3.1 Introduction

Biodiversity is responding to environmental change in complex ways. As per the latest Living Planet Report, wildlife populations have declined in relative abundance by an average of 69% since 1970 (Almond et al., 2022). Biodiversity decline can have severe cascading effects across ecosystems and result in the degradation of essential ecosystem services such as pollination, pest control and seed dispersal (Díaz et al., 2018). Beyond the known detrimental impacts of land use change (Newbold et al., 2019; Semenchuk et

al., 2022), climate change is predicted to become the primary driver of biodiversity loss by the year 2070 (Newbold, 2018). It is estimated that under a mid-range climate warming scenario, between 15-37% of species will be 'committed to extinction' by the year 2050 in response to climate change (Thomas et al., 2004). It is therefore increasingly important to enhance our understanding of species' responses to climate change, as well as the general drivers influencing biodiversity trends.

The climate niche of a species is defined as the range of climate conditions under which the species is able to tolerate (Blonder et al., 2014; Lu et al., 2021). Consequently, as climate regimes increasingly shift in relation to the conditions summarized by species climate niches, we would expect this to be predictive of biodiversity trends (Hollenbeck & Sax, 2024; Ralston et al., 2016). Previous research has identified significant associations between climatic niche breadth and historical population trends in avian species (Jiguet et al., 2006, 2007, 2010). Furthermore, empirical studies have demonstrated that local deviations from a species' climatic niche are strong predictors of population dynamics (Williams et al., 2022). The assumption that individuals can tolerate the full range of conditions described by the species' climatic niche underpins many important analyses projecting future climate impacts on biodiversity - namely species distribution modelling methods (Jetz et al., 2007; Thuiller, Lavorel, & Araújo, 2005).

However, some studies have shown that properties of a population's environment - particularly local climate conditions, can be significant predictors of population trends (Evans et al., 2024; Morrison et al., 2016). For instance, several studies have shown that local rates of climate change are predictive of population trends (Spooner et al., 2018; Williams et al., 2022). If local environment is widely more predictive of population trends relative to the broader species-level niche, climate niches may in fact overestimate the true range of conditions a population will persist under. Consequently, projections based on species climatic niches may be overly optimistic - particularly for widely distributed species assumed to possess broad environmental tolerances. Previous research has tended to focus on either the predictive capacity of local environmental conditions or that of species-level climate niches in isolation, leaving their relative importance unclear. To date, no comprehensive analysis has

systematically compared the predictive power of local environmental variables versus species climatic niches across any geographic or taxonomic scale, let alone at a global level. Therefore, amongst evidence suggesting both sets of variables can predict biodiversity trends, the key goal of this chapter is to disentangle their relative importance and identify which is more strongly predictive of population dynamics.

Niche volume and centroid metrics effectively summarize a species' climate niche and are expected to predict population trends, with broader and more centrally positioned niches generally associated with positive population trajectories (Jiguet et al., 2006, 2007, 2010). Additionally, niche evolutionary rates are likely to be a key determinant of adaptive capacity, reflecting a species' potential to respond to changing climatic conditions (Cooney et al., 2016). We can therefore expect higher rates of niche evolution to be positively associated with population trends. With respect to local environmental properties, environmental change can be summarized as both the magnitude of change experienced spatially as well as the temporal rate of change. Both dimensions are expected to predict population trends, with greater magnitudes and more rapid rates of change likely to drive a negative population response as local conditions depart the suitable range (Mattila et al., 2024; Radchuk et al., 2019). Furthermore, the position of local climate compared to the wider species-level niche is also critical to informing population trends as a larger divergence will likely negatively influence population trends, assuming species climate niches are conserved across populations (Antão et al., 2022; Manthey et al., 2015).

With the continual growth of population trend datasets, including the Living Planet Index (LPI) and BioTIME databases, it is now possible to conduct empirical analyses investigating the drivers of population trends at a global scale (Almond et al., 2022; Dornelas et al., 2018). Furthermore, comprehensive environmental datasets, including high resolution climatology layers (Karger et al., 2017) and land use change maps (Hurtt et al., 2019), allow us to map environmental predictors to a much higher degree of accuracy. Birds are a suitable study system for any analyses into species response to environmental change given the global distribution of this group, comprehensive data coverage and sensitivity of this group to environmental change (Sullivan et al., 2009; Tobias et al., 2022). Lastly, previous studies have tended to investigate the influence of

environmental variables of overall population trends, aggregating both increases and decreases (Martay et al., 2017; Ralston et al., 2016). Whilst drivers of population decreases may cause an increase in populations at a different site, as occurs during range shifts (Brooker et al., 2007; Williams & Blois, 2018), characteristics predictive of population declines may not be similarly predictive of population increases (Daskalova et al., 2020). It is therefore important to investigate predictors of population increases and decreases independently.

In this study, I conduct a global analysis investigating the predictors of avian population trends. Specifically, I construct Bayesian mixed effect models by fitting rates of avian population change against various environmental predictors summarizing species climate niche and local environment, such as climate niche volume, position and local rates of change. I also include metrics comparing the position of local climate and species climate niche. The aim of this study is to identify the most important environmental predictors of avian population trends between species climate niche and properties of a population's local environment. Improving our knowledge of the characteristics that are predictive of species sensitivity to environmental change allows for better identification of vulnerable ecological communities and the mitigation against damage to biodiversity.

## 3.2 Methods

### 3.2.1 Avian population trends

To inform avian population trends, I first sourced population time series data from both the Living Planet (LPD) and BioTIME databases. Populations were defined as independent groups of organisms belonging to the same species occupying a site within the wider species range. The LPD contains population trend data for 38,427 populations across 5268 vertebrate species (Almond et al., 2022). LPD data is sourced primarily from surveys, peer reviewed journal articles and government reports. The BioTIME database contains population trend data for 547,161 populations across 44,000 plant and animal species (Dornelas et al., 2018). BioTIME data has been sourced and curated mainly from literature and other large biodiversity databases. For Living Planet data, I only included avian time series affiliated with a specific location (e.g. lakes or national

parks), and filtered out regionally aggregated time series whereby site coordinates represent the midpoint of a large area (e.g. countries or regions). All BioTIME avian population time series included were affiliated with specific locations, such as sampling transects with less than 25km grain size intervals, instead of representing regionally aggregated statistics. The mean time series length was 13 years with a clear bias towards shorter time series across the dataset (Figure A2.1).

Different population time series used different metrics to describe population abundance such as total number of individuals counted, population density and encounter rate. Therefore all population abundance values across the dataset were $\log_{10}$ transformed to ensure more consistent scaling between time series. In addition, all population abundance values of 0 were converted to 1% of the mean population value for that time series, as per previous protocols (Collen et al., 2009), to avoid downstream issues during data transformations. Following methods implemented in previous studies (Collen et al., 2009), to derive rates of population change from the avian population time series data, I fitted regression models between population value and time (years). For time series with a length of over 6 records (n = 2864 populations), a generalized additive model (GAM) was fitted with the smoothing parameter set as half the time series length (Collen et al., 2009). For time series with a length of 6 records or less (n = 3330 populations), a linear model was fitted instead given higher levels of uncertainty around the variation in population abundance for shorter time series (Collen et al., 2009). For longer time series, GAM models were favoured as these models have greater flexibility and can therefore better derive a signal describing population change from longer non-linear time series data. Lastly, for a given population, the response variable of mean avian population change ($\bar{\lambda}$) (Figure 3.1) was calculated from the following equation:

$$\bar{\lambda} = \frac{1}{Y}\sum log_{10}\left(\frac{v_n}{v_{n-1}}\right)$$

$Y$ is the time series length, $v_n$ is the estimated population value for a given year and $v_{n-1}$ refers to the estimated population value of the preceding year. At this stage I removed populations with outlier mean lambda values (defined as +/- 3 standard deviations from the mean) (n = 710 populations) to avoid issues of high leverage in the response variable. Through implementing a spatial variogram analysis of mean lambda – whereby variance between mean population change values is compared with distance between population sites - low levels of spatial autocorrelation were described for the response variable (Figures A2.2 - A2.3).

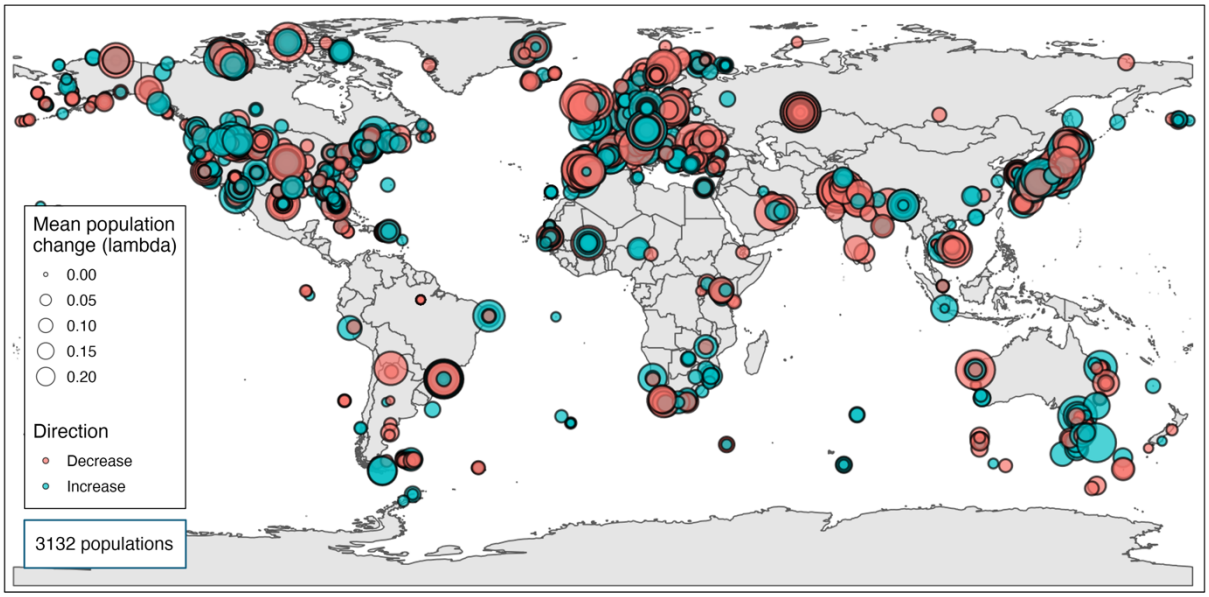



**Figure 3.1| Map of study populations.** All population sites investigated in my analyses with associated mean rates of avian population change. The final dataset, once all processing steps were implemented, contained 3132 avian populations across 972 species. Populations were split into either increasing (green circle) if mean population change ($\bar{\lambda}$) was more than 0 or decreasing (red circle) if mean population change ($\bar{\lambda}$) was less than 0. The size of each circle corresponds to the magnitude of the mean population change at a given population site, with larger circles indicating a larger mean population change.

### 3.2.2 Environmental predictors

*Species climatic niche*

To summarize species climate niche, average monthly temperature (°C) and precipitation (log 10kg/m$^2$) was extracted at processed eBird occurrence records at a 1 km resolution and at the month and year of the occurrence (Karger et al., 2017; Sullivan

et al., 2009). Following previous studies (Lu & Jetz, 2023), temperature and precipitation were selected as climate niche axes as these variables have previously been shown to influence avian distributions (Pigot et al., 2010). Furthermore, given data availability constraints, implementing temperature and precipitation niche axes allowed for the quantification of climate niche at much finer spatiotemporal resolutions. A multidimensional hypervolume was then generated from extracted climate data under the box kernel density method, using the Silverman bandwidth estimator to provide an appropriate bandwidth (Blonder et al., 2014). To summarise different climatic niche properties, I extracted niche volume and niche centroid. A larger niche volume would indicate that a given species has experienced a wide range of climate across its range (Figure 3.2). whereas centroid position corresponds to the average climatic conditions experienced across the species range.

Additionally, to summarize niche evolutionary rate, I extracted family level niche volume which corresponds to the total niche volume occupied by the taxonomic family a species belonged to (Figure 3.2). A larger family-level niche volume would indicate broader niche expansion over time and thus a more rapid niche evolutionary rate. All niche hypervolume and feature estimation was conducted using the *hypervolume* R package (Blonder et al., 2023).

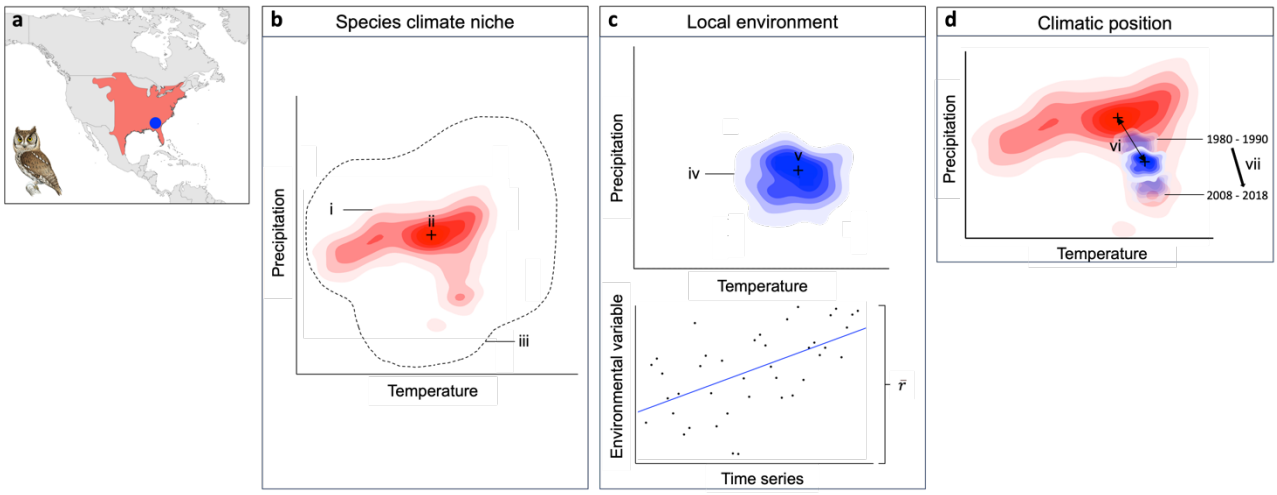



**Figure 3.2| Environmental predictors.** Concept figure summarizing the different environmental predictor variables included in my analyses. (a) The presented environmental variables are generated for an example species; Eastern screech owl, *Megascops asio* (photo

source: (Ritchison et al., 2020)). (b) Species-level climate niche metrics are derived from the climate across the entire range of the species (red) and include niche volume [i], niche centroid [ii] and a measure of family niche volume [iii]. (c) Spatial metrics summarizing the local environment are derived from the climate within a 10km buffer of the population location (blue dot) and include local climate volume [iv], local climate centroids [v]. Temporal metrics, namely local rates of environmental change at population locations, were calculated by fitting linear models along a time series of each respective environmental variable and then calculating mean rate of change across said timeseries ($\bar{r}$) –including local rates of temperature, precipitation and land use change. (d) Variables comparing species climate niche with local climate are included, specifically the distance between local climate centroid and species climate niche centroid [vi] and the extent local climate has moved towards or away from species climate niche centroid between 1980 – 2018 [vii]. All climate variables were generated using mean monthly climate layers.

*Local environment*

I wished to include variables that summarized spatial variation in the climatic conditions surrounding a population location. Therefore for a given avian population, I first generated a 10 km buffer around the population coordinates. A 10 km buffer was implemented to summarize climate surrounding a population site coordinate, to compensate for slight levels of uncertainty associated with population time series locations, whilst remaining computationally feasible (Almond et al., 2022; Dornelas et al., 2018). Then I extracted mean monthly climate (temperature, precipitation) included within the buffer region around a given population coordinate at a 1km grain size from January 1980 to December 2018 – which corresponded to the maximum period I had climate data for (n = 456 layers). As with species climate niche, a hypervolume was then generated from the extracted climate under the box kernel density method, using the Silverman bandwidth estimator to provide an appropriate bandwidth (Blonder et al., 2014). I subsequently extracted niche volume and niche centroid metrics to summarize the climatic conditions experienced at the population's location (Figure 3.2).

Beyond spatial variables, I wished to include variables that described rates of change of time. Therefore, to include measures of local rate of climate change (Figure 3.2), I first averaged climate included within the respective 10 km buffer region for a given population to generate a single temperature and precipitation data point for a given

month and year combination. I then truncated the time period of the extracted climate data series to match the time period of a given population time series. I subsequently fit linear regression models between climate and time and extracted the slope value as mean local rate of climate change across the time series. Climate data was not truncated below a 15 year time period as below this threshold model fit drastically deteriorated. Local rate of precipitation change was inverted (i.e. multiplied values by -1) to correspond to the local rate of drying.

Given the known impact of land use change on population trends (Newbold, 2018; Williams et al., 2022), I included a measure of local rates of land use change in my analyses (Figure 3.2). To estimate local rate of land use change at each population site, I first sourced historic global land use data from the Land-Use Harmonization Database (LUH2). LUH2 provides historic and future global land use data at a 0.25° x 0.25° resolution. Historic land use maps are generated using data from the History of Global Environment database (HYDE), which combines historical population estimates with land use per capita estimations and present day land use satellite data. Land use categories I considered to be anthropogenic included urban land, cropland (C3, C4, nitrogen fixing, perennial and annual) and managed pastureland. I combined all anthropogenic land use layers so that each 0.25° x 0.25° grid cell would have a percentage value of anthropogenic land use. At a given population site, I then extracted the level of anthropogenic land use for each year between 1977-2015 to keep the time period as consistent as possible between environmental variables. Lastly, from extracted land use data, I calculated the mean local rate of land use change by fitting a GAM model between percentage of anthropogenic land use change and time and then extracting mean rate of change across the time series. Across all variables describing local rates of environmental change, a larger value corresponds to a more rapid rate of change.

*Climatic position*

I wished to include metrics comparing the position of local climate within species climate niche. I therefore quantified the magnitude of difference between local climate and species climate niche by taking the Euclidean distance between the local climate centroid and the species climate niche centroid (Figure 3.2). Therefore a larger distance

would correspond to a greater difference between local climatic conditions and the species wide niche. In addition, I quantified the degree to which local climate had moved towards or away from their corresponding species niche centroid across the time span of the climate dataset (1980 – 2018) (Figure 3.2). For each population I therefore generated separate hypervolumes summarizing local climate in the first decade I have climate data for (1980 – 1990) and for the last decade I have climate data for (2008 – 2018). For a given population, I therefore stacked mean monthly 1km climate layers (temperature, precipitation) for the two periods respectively (1980 – 1990, 2008 – 2018) and extracted climate included within a 10km buffer region around a given population coordinate. Once niche hypervolumes were generated for both periods, the Euclidean distance was calculated between the first decade climate centroid and the species niche centroid and then between the last decade climate centroid and the species niche centroid. The difference between the two Euclidean distance measurements was then calculated – with a more negative value indicating that the local climate has moved away from the species niche centroid between the first and last decade time periods. Conversely, a positive value for this metric would indicate that local climate has moved towards the species niche across the investigated time period. Lastly, a value of 0 for this metric would indicate that local climate has remained stable across the investigated time period.

### 3.2.3 Data processing

In summary, I generated 12 environmental predictor variables to include in my analyses and 1 response variable; the mean rate of population change ($\bar{\lambda}$) (Table 3.1) (Figure A2.4). In addition to the effects of core environmental variables on the response variable investigated here, I conducted additional analyses with replicate variables to test the sensitivity of the results when altering aspects of the methods for generating the environmental predictors (A2 - Additional Methods). Prior to fitting Bayesian mixed effect models, I ran several processing tasks across the dataset. Given the start year for climate data was 1980, I excluded any populations with an end year before 1985 (n = 412 populations), so that the minimum number of climate data points informing models deriving local rates of climate change never fell below six. This threshold ensured better model fit (Collen et al., 2009) whilst not removing a sizeable number of populations from the final dataset. In addition, populations with a time series length of two or less data

points were also excluded (n = 1160 populations) from the final dataset as I assumed these to not reliably inform population trends (Collen et al., 2009). I removed outliers (n = 780 populations) - defined as +/- 3 standard deviations from the mean for a given variable – to reduce issues of high leverage in the final models. To correct for inherent sources of skewness that may exist across environmental datasets I transformed several variables. Specifically, in the case of variables which exhibited left sided skewness I inverted the variable based on the maximum value, ran a square root transformation and then re-inverted based on the maximum value. In the case of variables which exhibited right sided skewness, if the value was positive, I simply ran a square root transformation, whereas if the value was negative, I first converted it to positive, ran a square root transformation then re-converted it to negative. To allow for comparison between model effect sizes, I rescaled all variables. To avoid the inclusion of collinear variables within the same model, I assessed collinearity across all variables using the *corrplot* R package (Figure A2.5). I subsequently ensured that any pair of variables that exhibited Pearson correlation coefficient values of over 0.4 were not included in the same model.

**Table 3.1| A summary table of the variables included in the core analysis.** Variables included in my analysis summarize different properties of species climate niche, the local environment surrounding population locations and the position of local climate compared to species climate niche (Figure A2.4). All climate variables are generated from mean monthly temperature and mean monthly precipitation climate layers. The time period associated with climate data is 1980 – 2018. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

| **Variable name** | **Variable description** |
|---|---|
| Species climate niche volume | The total volume occupied by a hypervolume summarizing species climate niche, with temperature and precipitation as niche axes. |
| Species temperature centroid | The centroid position along the temperature axis of a hypervolume summarizing species climate niche, corresponding to the mean temperature experienced across a species range |
| Species precipitation centroid | The centroid position along the precipitation axis of a hypervolume summarizing species climate niche, corresponding to the mean precipitation experienced across a species range |
| Family climate niche volume | The total volume occupied by a hypervolume summarizing the combined climate niche of all species belonging to a given family, with temperature and precipitation as niche axes |
| Centroid distance | Euclidean distance between species niche and local climate centroids |
| Centroid direction | The extent to which local climate is moving towards/away from species niche centroid |

| | |
|---|---|
| Local climate volume | The total volume occupied by a hypervolume summarizing climate experienced within a 10km buffer of a given population location, with temperature and precipitation as niche axes |
| Local temperature centroid | The centroid position along the temperature axis of a hypervolume summarizing climate experienced within a 10km buffer of a given population location, corresponding to the mean temperature experienced across a population location |
| Local precipitation centroid | The centroid position along the precipitation axis of a hypervolume summarizing climate experienced within a 10km buffer of a given population location, corresponding to the mean precipitation experienced across a population location |
| Local rate of warming (monthly) | The mean rate of change in temperature at a population location across the time period population data is sampled for |
| Local rate of drying (monthly) | The mean rate of change in precipitation at a population location across the time period population data is sampled for |
| Local rate of land use change | The mean rate of change in percentage of anthropogenic land use at a population location |
| Mean rate of population change | The mean rate of change in population abundance at a given location |

To determine whether environmental variables were predictive of population decreases or increases I split population trend data into increasing populations (mean lambda > 0) and decreasing populations (mean lambda < 0) and ran separate mixed models on both datasets (Figures A2.6 – A2.7). To ensure a gaussian distribution and avoid large skews in the response variable through splitting the dataset, I transformed mean lambda. Specifically, for positive values (i.e. increasing populations), I took the fifth root value and for negative values (i.e. decreasing populations) I first inverted the value, then took the fifth root and subsequently re-inverted. Lastly, to have a consistent range as the response variable, I scaled mean lambda by subtracting the mean and dividing by the standard deviation. The final dataset, after implementing all data processing steps, consisted of 3132 avian populations, across 972 species, with associated environmental variables - including properties of species climatic niche metrics, local environment and metrics comparing species climate niche to local climate.

### 3.2.4 Mixed effect modelling

For both increasing and decreasing populations, I constructed Bayesian linear mixed effect models between mean rate of population change ($\bar{\lambda}$) and every possible combination of environmental predictor variables. The modelling stage of the analysis was conducted using the *MCMCglmm* R package. To correct for spatial and phylogenetic non-independence across the response variable, every model included random effects for

taxonomic family, site location and the biogeographic realm a population was located in. Given the distribution of the variables (Figure A2.4), I set the distribution family as "gaussian". In the absence of strong prior knowledge about variance structure, I applied weakly informative inverse-Wishart priors to random effects (V=1, ν=0.002), providing minimal constraint while supporting model regularization (Gelman, 2006). Fixed effects were assigned default flat (non-informative) priors, allowing the data to primarily inform their posterior estimates. Furthermore, I included a measurement error variable reflecting uncertainty in mean lambda measurements. Specifically, this corresponded to the residual error values from the fitted GAM and linear regression models used to calculate mean rate of population change.

To effectively parameterize the models whilst retaining computational feasibility, I set the total number of iterations to 6000, with a warm-up phase set at 2000 iterations and no thinning (Gelman, 2006). To reduce model uncertainty, I first ranked all models by AIC score and selected all top ranking models within a delta AIC of 6 as the final models. I then ran model averaging based on Akaike weights on top ranked models (Burnham & Anderson, 2002; Dormann et al., 2018). The model selection stage of the analysis was conducted using the *MuMIn* R package.

In addition to investigating the predictive capacity of each individual environmental variable on avian population trends, I investigated the average model fit across different variable classes (i.e. species climate niche, local environment, climatic position). Following the above protocol, for both decreasing and increasing populations, I fitted a set of models for each respective variable class made up solely of all possible combinations of variables belonging to a given class. Therefore 15 models were constructed for the species climate niche class, 64 models for the local environment class and 3 models for the climatic position class. I then re-ran model selection on each group of models. For better interpretation of results, I inverted model fit values by multiplying AIC scores by -1, so that a more positive value would correspond to a better model fit. I then compared each group's distribution of model fit scores to understand overall which class of variables best described avian population trends.

## 3.3 Results

### 3.3.1 Predictors of avian population trends

Species climate niche metrics had no significant effect on either decreasing or increasing avian population trends in my models (Figure 3.3). With regards to local environment, larger local climate volumes were significantly associated with larger population decreases (effect size: -0.093, p-val: 0.025) and larger population increases (effect size: 0.186, p-val: 5e-04) (Table A2.1). Additionally, higher local precipitation centroid positions were significantly associated with larger population decreases (effect size: -0.123, p-val: 0.003) and larger population increases (effect size: 0.089, p-val: 0.054) (Table A2.1). Local rates of environmental change were consistently predictive of avian population trends in both increasing and decreasing populations (Figure 3.3). Specifically, larger local rates of warming (monthly) were significantly associated with larger population decreases (effect size: -0.18, p-val: 5e-04) and larger population increases (effect size: 0.142, p-val: 5e-04) (Table A2.1). Lastly, larger local rates of drying (monthly) were significantly associated with larger population decreases (effect size: -0.07, p-val: 0.038) (Table A2.1). In summary, local environment metrics were consistently more predictive of avian population trends compared to species climate niche metrics in both increasing and decreasing populations (Figure 3.3). Climatic position metrics had no significant effects on decreasing populations trends (Figure 3.3). However, in the case of increasing populations, a larger distance between species climate niche centroid and local climate centroid is significantly associated with larger population increases (effect size: 0.068, p-val: 0.042) (Table A2.1).

Regarding sensitivity analyses results (Additional Results), when describing niche position using niche limits instead of centroid metrics, local maximum temperature position is now predictive of larger population decreases (effect size: -0.106, p-val: 0.01) (Table A2.5) (Figure A2.9) and local precipitation position is no longer predictive of larger population increases (effect size: 0, p-val: 0) (Table A2.5) (Figure A2.9). When using rates of climate change derived from annual climate data and standardizing rates of climate change for local climate variability, effects of local rates of climate change on mean avian population change tend to weaken or lose significance (Figure A2.12 – A2.14) (Table A2.8 – A2.10).

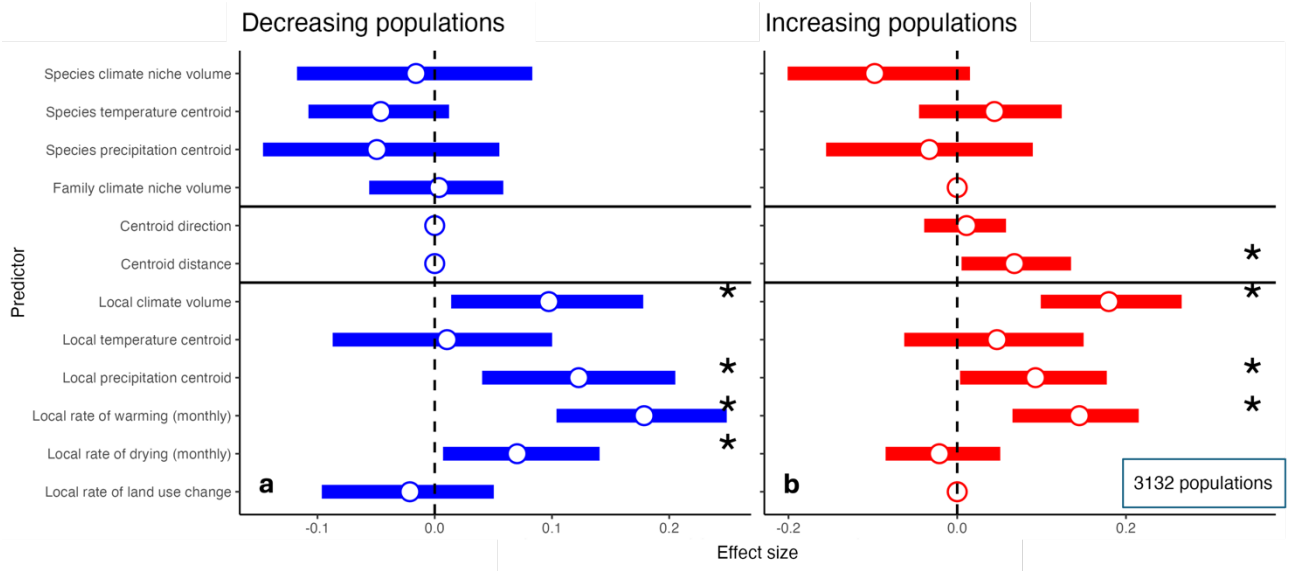



**Figure 3.3| Predictors of avian population trends.** Results shown represent the output from Bayesian linear mixed effect models fit between set combinations of environmental predictors and mean rate of population change. Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.4). (a) Decreasing population effect sizes are shown in blue. Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. (b) Increasing population effect sizes are shown in red. Error bars represent a 95% confidence interval for each respective model averaged effect size. Centroid direction – i.e. the extent to which local climate centroid is moving towards or away from species climate niche centroid - is calculated as a distance based metric in the analysis of decreasing populations, and as a ratio in the analysis of increasing populations as per the breakdown of core and replicate variables (Appendices). Black asterisks represent a significant effect size (p value < 0.05). This figure represents the analysis undertaken with the set of determined core variables – results from replicate sensitivity analyses implementing additional variables are shown in the Appendices (Table A2.5 – A2.10) (Figures A2.9 – A2.14).

### 3.3.2 Variable class analysis

In the case of decreasing populations, species climate niche and climatic position model classes generally had similar model fit scores in comparison (Figure 3.4). Models belonging to the local environment class tended to exhibit better model fit scores (Figure 3.4). For decreasing populations, model fit scores ranged from -2291 - -2229 for species climate niche models, -2281 - -2192 for local environment models and -2274 – -2257 for climatic position models (Table A2.2). In the case of increasing populations, all

three variable classes tended to exhibit similar model fit scores (Figure 3.4). For increasing populations, model fit scores ranged from -2241 – -2211 for species climate niche models, -2370 - -2204 for local environment models and -2256 – -2234 for climatic position models (Table A2.2).

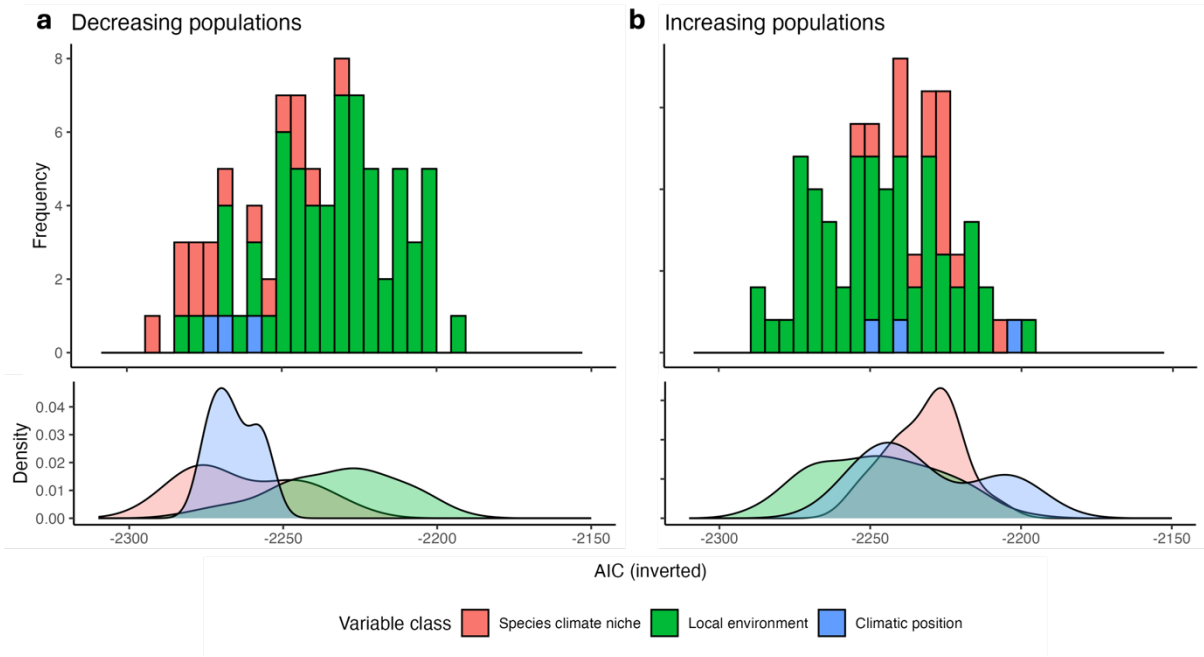



**Figure 3.4| Variable class analysis.** The distribution of model fit scores for sets of models only made up of metrics from a specific variable class (species climate niche: n = 15 models, climatic position group: n = 3 models, local environment: n = 64 models) between (a) decreasing populations and (b) increasing populations. Model fit scores are derived by inverting model AIC scores – therefore the higher the score, the better the model fit. The species climate niche class is shown in red, local environment class is shown in green and climatic position class is shown in blue.

## 3.4 Discussion

This study highlights the complexity of avian population dynamics by identifying key predictors of population trends at a macroscale. Specifically, I found that properties of a population's local environment tended to be more predictive of avian population trends compared to species climate niche and climatic position. Populations may therefore respond to climate change before their respective climate niche limits are tested. Consequently, projections of biodiversity responses to climate change that rely heavily

on species-level niche estimates may overestimate species resilience and should be interpreted with caution.

### 3.4.1 Predictors of avian population trends

As hypothesized, both the rate and magnitude of local climate change were associated with stronger population declines. These findings are consistent with previous analyses (Spooner et al., 2018; Williams et al., 2022). The faster the rate of local climate change, the less time populations have to respond to novel conditions—whether through evolutionary adaptation, phenotypic plasticity, or dispersal—increasing their vulnerability to decline (Radchuk et al., 2019). Compounding this, large local climate volumes - the total magnitude of climatic change experienced at a site - can push environmental conditions beyond the range species can persist under, leading to population decline (Parmesan et al., 1999). Topography will mediate species response to future climate owing to different "climate velocities" - i.e. the projected velocity of climate change across the Earth's surface (Loarie et al., 2009). For instance, mountainous regions have low climate velocities and therefore potentially allow for slower rates of species response compared to flooded grasslands and deserts with high climate velocities (Loarie et al., 2009). The concern of this finding of climate change having already driven population decreases is that these factors are only predicted to increase well into the future (Calvin et al., 2023). Interestingly, when I correct for local seasonality the effect of local rate of climate change on avian population trends is weakened and even loses significance in most cases (Figure A2.13 – A2.14). This suggests that populations in more seasonal environments may be more resilient to change due to historical exposure to greater climatic variability (Grinder & Wiens, 2023).

Broadly, the same climatic variables that predicted larger population decreases also tended to predict larger increases. One potential explanation is that as conditions become unsuitable in some locations, they simultaneously become more favourable elsewhere, facilitating range shifts as species track their climatic niches (Antão et al., 2022; Parmesan et al., 1999). For instance, regions at higher latitudes or elevations have become increasingly suitable for certain species, as evidenced by observed range expansions into these areas (Lehikoinen et al., 2021; Parmesan et al., 1999). This effect

is likely accentuated in migratory species – i.e. species that have a high dispersal capacity and can therefore respond rapidly to changes in climate (Parmesan et al., 1999; Virkkala & Lehikoinen, 2017). Additionally, species co-occurring at a given site may occupy different positions along their climatic niches—some near the lower limits, others near the upper—potentially leading to simultaneous population increases and declines in response to climate change. As climate becomes more suitable for certain populations, this may explain why local climate volume and rates of warming are also significantly associated with population increases. This result is further confirmed by the significant positive effect of centroid distance – i.e. populations that occupy conditions further away from the species niche centroid are more prone to population increases potentially due to conditions becoming more suitable.

Local precipitation centroid emerged as a significant predictor of population decreases, suggesting that populations occurring in wetter regions may be more susceptible to decline. This finding is consistent with previous research showing that species occupying tropical and sub-tropical regions are especially vulnerable to climate change due to narrower climatic tolerances (Bender et al., 2019; Read et al., 2018) and typically occupying the edge of their climatic niche (Grinder & Wiens, 2023). An alternative explanation is that regions with high precipitation levels are also subject to elevated rates of ecological disturbance, such as deforestation and agricultural expansion, which may exacerbate population declines (Jacobson et al., 2019). Interestingly, local precipitation centroid also significantly predicted population increases, potentially reflecting enhanced productivity in certain locations due to recent shifts in precipitation regimes (Li et al., 2021). However, more analysis of background levels of precipitation is required to distinguish between areas experiencing novel precipitation changes and those characterized by historically stable precipitation regimes.

Several variables unexpectedly exhibited insignificant effects on avian populations trends. Notably no significant associations were identified between species climate niche properties and avian population trends which contradicts my hypotheses and previous research (Jiguet et al., 2006, 2010). However, these studies have tended to estimate species climate niche at coarse spatial resolutions without considering temporal variability in species distributions, for instance through migratory behaviour.

Therefore, for many species these temporally non-sensitive estimates may offer inaccurate estimates of the true range of tolerable conditions as important regions of niche space are omitted (Cohen & Jetz, 2023; Eyres et al., 2017). Moreover, prior research has typically focused on particular regions or taxonomic groups that may have been disproportionately exposed to climate change, in contrast to the global trends investigated in this study (Jiguet et al., 2006, 2010). It is also possible that, at a global scale, the magnitude of climate change experienced by many populations has not yet been sufficient to approach the limits of their climatic niches. Climate niche estimates tend to represent the realised niche and can therefore be considered an underestimate of the true range of tolerable conditions – the fundamental niche (Soberón & Arroyo-Peña, 2017). Under this assumption, we would in fact expect species to tolerate an even broader range of conditions perhaps explaining why realised niche estimates are not informative towards population trends.

For the most part, climatic position metrics were not significantly predictive of avian populations – a finding that is inconsistent with previous literature (Williams et al., 2022). This may further support the limited utility of species-level climatic niche characteristics in explaining population dynamics. However, unlike in previous studies, instead of niche limits, I compare the centroid positions between species climate niche and local climate which may not be as informative of population trends (Figure A2.9 – A2.10). Two populations could occupy the same niche centroid position but have very different tolerable ranges of conditions - differences that would be more effectively detected using niche limit metrics. Lastly, my findings are inconsistent with previous studies that have identified land use change as having widespread detrimental effects towards biodiversity (Newbold, 2018; Semenchuk et al., 2022). Previous studies that have investigated land use change effects on avian population trends have also failed to detect strong associations (Spooner et al., 2018). Population trend datasets are predominantly made up of generalist species that are more resilient to anthropogenic land use change, and in many cases even benefit from agricultural expansion (Karp et al., 2018; Spooner et al., 2018). Another potential explanation is that the many sample locations tend to be in geographic regions where the majority of land use change has occurred historically, such as Europe and North America, and is therefore potentially not informative of more recent population trends (Figure 3.1) (Winkler et al., 2021).

### 3.4.2 Variable class analysis

I investigated the average model fit of models across three variable classes – i.e. models made up solely of either species climate niche, local environment or climatic position variables. I find that local environment metrics have the best fitting models, particularly in decreasing populations, thus further confirming my finding of the predictive capacity of local environment properties relative to species climate and climatic position properties.

One potential explanation for the higher predictive capacity of local environment metrics, is that populations have become adapted to local environmental conditions. Through local adaptation, novel population level climate niches evolve that represent a subset of the species climate niche (Benito Garzón et al., 2019; Smith et al., 2019). Empirical evidence supports the occurrence of distinct niche evolution below the species level (Morrison et al., 2016). For instance, a study by Morrison et al. (2016) investigated annual growth population rate response to distinct levels of winter severity across different populations of winter wren (*Troglodytes troglodytes*). Population growth rate was consistently negatively associated with winter severity, however the point at which growth rate reached stability varied between populations - indicating local adaptation and distinct climate niches at the population level (Morrison et al., 2016). Enhanced adaptation to local conditions is expected to be particularly pronounced in stationary and isolated populations, which would further drive the evolution of distinct population-level climate niches (Smith et al., 2019). With regards to future climate change, some studies have estimated that rates of climatic niche evolution would have to be over 10,000 times faster than previously observed rates across most clades to match projected climate change by 2100 (Quintero & Wiens, 2013).

Another possible explanation for the importance of local environment properties in predicting population trends is that resources a given population depend on may be constrained by local environmental conditions (Williams & de la Fuente, 2021). Habitat suitability may also be influenced by climate and influence population dynamics (Stirling & Derocher, 2012). For instance, the climate niche of a polar bear may be

broad, however as climate changes, sea ice that makes up the primary habitat of polar bears begins to melt, thus having a detrimental impact on polar bear populations (Stirling & Derocher, 2012). Additionally, climate changing locally may influence key phenological events that animal populations depend on and negatively impact populations without necessarily testing climate niche limits. One such example, is the climate driven mistiming between the arrival of migratory birds at their breeding grounds and the peaking of resource availability thus negatively impacting species populations (Mayor et al., 2017). Lastly, novel climatic conditions may facilitate the spread of pathogens or increase the abundance and range of predators, both of which can further exacerbate population declines (Bastille-Rousseau et al., 2018; Pounds et al., 2006).

### 3.4.3 Limitations

Several limitations of my analyses must be acknowledged. Inherently, quantifying species climate niche may be more complicated compared to capturing local environmental conditions, predominantly due to uncertainty in species distribution datasets. Therefore, species climate niche estimates implemented in these analyses may not capture the true range of conditions tolerable to a species potentially partly explaining weaker effect sizes exhibited in my models. Furthermore, there are known taxonomic, spatial and temporal biases exhibited in the population time series data (Cardinale et al., 2018). Firstly, common and widespread species tend to be sampled more compared to rare and sensitive species, potentially better informing increasing populations compared to population declines (Kuczynski et al., 2023). Secondly, regarding regions sampled, there is disproportionately high levels of sampling in regions such as Europe, United States and Japan (Figure 3.1). Geographic regions that are projected to experience the most intense impacts of future climate change are under sampled in these datasets (Calvin et al., 2023; Collen et al., 2009). In addition, particularly vulnerable biomes such as tropical landscapes and alpine areas are also under sampled (Calvin et al., 2023; Collen et al., 2009). Lastly, there is a clear bias towards the inclusion of shorter time series, obscuring the study of long term population trends (Figure A2.1).

### 3.4.4 Future work and conclusions

A key finding of this study is the higher predictive capacity of local environment towards avian population trends compared to species climate niche. Possible explanations for this include local adaptation at the population level and dependence on climatically constrained resources and habitats. Additional factors may involve mistimed phenological events, as well as altered predator-prey and disease dynamics. More explicit testing of these various hypotheses could better unpick the mechanisms behind why local environment influences population trends. For instance, one potential approach would be to run these analyses on subset niche estimates derived at finer taxonomic or geographic resolutions such as subspecies or individual populations (Smith et al., 2019). Environmental factors are known to influence populations in combination (Williams et al., 2022), therefore future analyses could look to include interaction terms between predictors in their models. Lastly, due to computational intensity, I corrected for phylogeny in my models by including taxonomic family as a random effect. However, future analyses could improve upon this by integrating more sophisticated phylogenetic datasets and methods.

This study aimed to identify key predictors of avian population trends across species climate niche features and local environment properties. Given that local environment is particularly important in predicting population declines, a key implication of this finding relates to the modelling of vulnerability to future climate change. Many investigations into future climate impacts on species implement species distribution modelling techniques and therefore assume that a given population can tolerate the range of conditions experienced across the species range (Johnston et al., 2021; Pearson & Dawson, 2003). However, these results suggest that population declines may occur before local conditions exceed species-level climatic niche limits. This indicates that current projections of species responses to climate change may be overly optimistic. While population dynamics and species responses to environmental stressors are inherently complex, studies such as this contribute to a more nuanced understanding of the drivers of population change and can help refine predictions of biodiversity responses to future climate change.

# 4| Projected impacts of climate change on interactions between plants and avian frugivores across the Americas

**Keywords:** Birds, climate change, dispersal, ecological assemblages, frugivory, functional traits, interaction rewiring

## Abstract

Frugivorous birds provide crucial seed-dispersal functions in terrestrial ecosystems. However, the impact of climate change on plant-avian frugivore interactions remains unclear. This study maps these interactions across the Americas and then projects potential changes in their interaction diversity under future climate change scenarios. Based on a trait-matching framework, I estimated interaction probabilities between frugivorous birds (n = 629 species) and fleshy-fruited plants (n = 3283 species) at an ecoregion level. To estimate climate impacts, I weighted interaction probabilities by the overlap between avian climate niches and current and future ecoregion climates. Based on these interaction probabilities, I calculated plant-frugivore interaction diversity as the effective number of avian interaction partners for a given plant species in an ecoregion. Lastly, I used simulations to examine how avian dietary flexibility, and dispersal may buffer the future diversity of plant-frugivore interactions. Under future climate scenarios, my models projected a decline in interaction diversity across most ecoregions, especially in tropical and subtropical ecoregions and biomes. In addition, simulations indicated that interaction rewiring through dietary flexibility and dispersal had the potential to mitigate future losses of interaction diversity, particularly in tropical forests. The results suggest that plant-frugivore interactions are at risk of losing diversity under continued rapid climate change, which may undermine their stability and resilience. However, projected losses of interactions depend on the capacity of frugivorous bird species to modify their ranges or dietary preferences in future. As it is unknown to what extent these factors can buffer the stability of species interactions, the maintenance of high plant-frugivore interaction diversity in the current assemblages is crucial to buffer ecosystems against future climatic changes, especially in the tropics.

## 4.1 Introduction

The composition of ecological assemblages, and thus the potential for interactions among coexisting species, is changing rapidly in response to climate change (Scheffers et al., 2016). Some species are declining as conditions change, leading to local or global extinction (Román-Palacios & Wiens, 2020; Pecl et al., 2017). Other species survive by moving across landscapes as they track their climatic niche, leading to reshuffled species assemblages and novel interactions (Gallagher et al., 2013; Nolan et al., 2018). Given that a wide range of mutualistic and antagonistic interactions between species play a fundamental role in ecological processes, such as predation, pollination and seed dispersal, it is clear that climate change may have serious consequences for the resilience of ecosystem functions and services derived from these interactions (Díaz et al., 2018). Nonetheless, the impacts of future climate change on species interactions are largely unknown at macroecological scales.

The interactions between fleshy-fruited plants and frugivorous animals are essential to many ecosystems (Lim et al., 2020; Howe & Smallwood, 1982), particularly in the tropics with 60-80% of all plant species dependent on frugivores (Jordano et al., 2011). Animal-mediated seed dispersal underpins forest regeneration, fostering plant functional connectivity and resilience to habitat degradation (McConkey et al., 2012; Mueller et al., 2014). Additionally, frugivory by mobile animals provides a key avenue for plant responses to climate change as the dispersal of seeds across the landscape helps plants to track their climatic niche (Sales et al., 2021), which can require movements of up to 10km/year (González-Varo et al., 2017). Despite the importance of frugivory and the sensitivity of plant-frugivore interactions to environmental change (Neuschulz et al., 2016), climate change impacts on plant-frugivore interactions are less known than that of other mutualistic interactions such as pollination (Teixido et al., 2022). It is therefore essential to investigate how plant-frugivore interactions are likely to respond to projected climate change.

Studies that have investigated climate change impacts on plant-frugivore interactions have generally been restricted to small taxonomic (Mackay & Gross, 2019; Sales et al., 2021) and geographic scales (Bender et al., 2019; Dehling et al., 2016). Previous large-

scale studies have mostly compared patterns in species richness between specific groups of prospective interaction partners (Kissling et al., 2007; Mota et al., 2022). Another widely used method is the construction of interaction networks from observed interaction data (Maglianesi et al., 2014; Quitián et al., 2019). Whilst this method is powerful to locally describe species interactions for specific ecological assemblages, site specific biases and constraints in data availability make it difficult to utilise such empirical data at large scales (Kissling & Schleuning, 2015). To overcome such limitations, previous studies have developed trait-based models to estimate interaction probabilities between plants and birds at macroecological scales (Donoso et al., 2017; Nowak et al., 2022). These models build on the matching between plant and bird morphology, especially between fruit size and avian gape width (Dehling et al., 2016; Wheelwright, 1985). I combine this method with climate niche estimates for frugivorous bird species to investigate potential impacts of climate change on plant-frugivore interactions at geographic and taxonomic scales previously not accessible.

The interactions between plants and birds are dynamic and are likely to change in response to environmental change (Tylianakis & Morris, 2017). First, species have shown a great capacity to adapt their diet and interact with a wider or different range of resources if resource availability changes (Bender et al., 2017). Second, many species are expected to shift their ranges in response to climate change to track their climatic niche (Schleuning et al., 2020). Both these mechanisms can lead to "interaction rewiring" – the formation of novel interactions between species – either because presently co-occurring species form new interactions or because novel interactions form with immigrating species (CaraDonna et al., 2017; Schleuning et al., 2020). Integrating such mechanisms of interaction rewiring into simulations is important to assess the potential resilience of plant-frugivore interactions to future climate change.

In this study, I use a trait-based approach (Figure 4.1) to assess projected impacts of climate change on plant-frugivore interactions at a macroecological scale across North and South America. My aim is to first derive patterns in plant-frugivore interaction diversity – the effective number of avian interaction partners for a given plant species in an ecoregion – across the Americas. Given historical climate patterns driving evolutionary radiations in vascular plant and subsequent frugivore diversity, I

hypothesize plant-frugivore interaction diversity to increase towards the tropics (Kissling et al., 2009). Second, I aim to determine the exposure of fleshy-fruited plants to climate change by assessing the suitability of future climate to their avian interaction partners (Figure 4.1). At lower latitudes, I hypothesize plant-frugivore interaction diversity to decrease in response to climate change, as I expect future climate to be less suitable for frugivorous birds than current climate, especially as bird species inhabiting these regions may have narrow dietary breadths and climatic niches (Cadena et al., 2012; Dalsgaard et al., 2017; Mota et al., 2022). Conversely, at higher latitudes, I expect potential increases in interaction diversity as climatic conditions become more suitable for avian frugivore partners (Martins et al., 2024). Clearly, any such future projection is complicated by the fact that losses in interaction diversity can potentially be compensated by the emergence of novel interactions due to avian dietary flexibility and/or dispersal (CaraDonna et al., 2017; Schleuning et al., 2020). Therefore, I also aim to understand the extent to which interaction rewiring may influence projections of plant-frugivore interactions under future climate scenarios (Figure 4.1). The direction of such effects is difficult to predict because, on one hand, avian dietary flexibility and dispersal ability peak at high latitudes (Morelli et al., 2021; Sheard et al., 2020), potentially increasing the number of species able to buffer any local losses in interaction diversity, whereas, on the other hand, the number of potential replacement species and dietary options are much higher in the tropics (Kissling et al., 2009; Schleuning et al., 2012). I attempt to disentangle these two possible mechanisms by accounting for dispersal ability and diet breadth in my projection models.

## 4.2 Methods

To assess the effects of climate change on plant-frugivore interactions, I projected current and potential future patterns in plant-frugivore interaction diversity – the effective number of avian interaction partners for a given plant species in an ecoregion - by using a simulation model with three consecutive steps (Figure 4.1). First, I estimated plant-frugivore interactions at an ecoregion-level using a trait-based interaction model informed by functional trait data of co-occurring plant and frugivorous bird species. Second, I determined the indirect exposure of plant species to climate change by comparing the climatic niche of their respective avian interaction partners with current

and future climate. Third, I quantified how interaction rewiring via increased avian dietary flexibility and dispersal into ecoregions may modify projected future patterns in plant-frugivore interaction diversity.

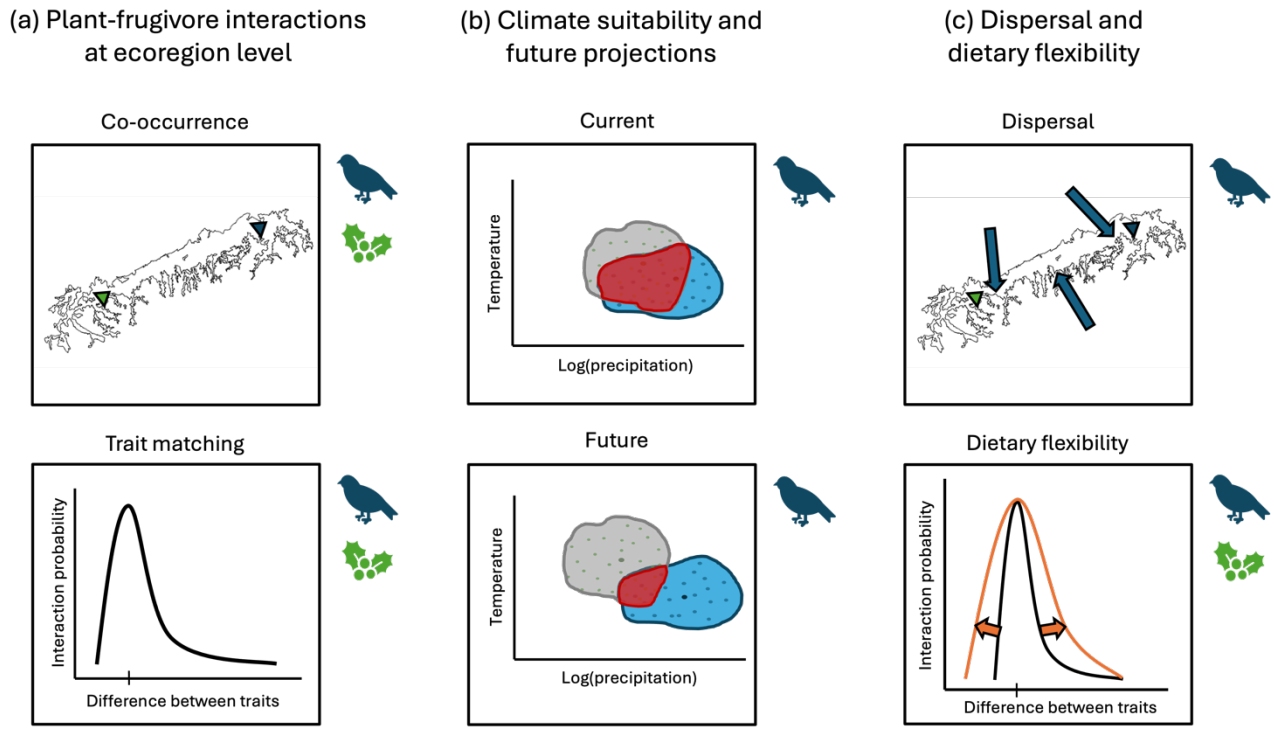



**Figure 4.1| Projecting climate change impacts on plant-frugivore interactions.** (a) I estimated interaction probabilities between species pairs by first establishing co-occurrence between plant and bird species in an ecoregion (top). Co-occurrence is established if a given bird (blue triangle) or plant (green triangle) species both occur within the same ecoregion. Interaction probabilities between prospective interaction partners are then calculated from a trait-based interaction model (bottom). As shown, interaction probability increases as the difference between fruit and gape size approaches 0. (b) Climatic suitability of an ecoregion for avian frugivores was estimated by calculating the level of overlap (red) between the avian climatic niche hypervolume (blue) and the ecoregion climate hypervolume (grey) under current and future climatic conditions. If the Sorensen's overlap was below 0.4, the bird species was dropped out of the assemblage in this ecoregion. (c) I accounted for potential positive effects of avian dispersal (top) and dietary flexibility (bottom) in future projections of plant-frugivore interactions. To integrate dispersal, I allowed species from surrounding ecoregions to immigrate into ecoregions if their source ecoregions were projected to become climatically unsuitable. To integrate dietary flexibility, I modified the trait matching parameter from a tighter relationship (black) to a looser relationship (orange) between fruit size and gape width.

The main analysis included obligate avian frugivore species with at least 50% of fruit in their diet (Wilman et al., 2014), corresponding to the group of avian frugivores that are the main seed dispersers in seed-dispersal networks (Schleuning et al., 2014). In an additional analysis, I lowered this threshold to 25% (Wilman et al., 2014) to include opportunistic avian frugivores which only occasionally feed on fruits and can be important seed dispersers, especially in marginal habitats and/or at higher latitudes (Dalsgaard et al., 2017; Schleuning et al., 2011). Hence, I ran all analyses once for obligate avian frugivores with >50% of fruit diet (n = 629 species) and once for obligate and opportunistic avian frugivores with >25% of fruit diet (n = 903 species).

### 4.2.1 Distribution data

To establish plant and bird species distributions, I used comprehensive range map datasets for the two groups. For fleshy-fruited plants, I extracted range map data from the BIEN database (Maitner et al., 2018). The BIEN database is composed of range map estimates for over 98,000 New World Plants, generated primarily through the implementation of Maximum Entropy distribution modelling informed by over 81 million georeferenced occurrence records (Maitner et al., 2018). In the case of birds, I extracted expert range maps from BirdLife (BirdLife International and Handbook of the Birds of the World, 2021). The Birdlife Species Range map database contains range map estimates for >11,000 bird species globally, derived by experts from over 5.6 million georeferenced occurrence records (BirdLife International and Handbook of the Birds of the World, 2021). I subset this dataset to only include resident, wintering and breeding ranges of birds. Range map datasets are particularly effective at describing broad regions where a species is likely to occur, particularly for widespread species (Merow et al., 2017). However, a key limitation is that these datasets tend to overestimate species occupancy (Merow et al., 2017).

### 4.2.2 Trait data

I compiled functional trait data for plants and birds, focusing on traits providing information about their interactions, particularly fruit and beak dimensions. For fleshy-fruited plants, I compiled a dataset from several sources providing data on fruit dimensions for 3,283 plant species that occur across the Americas (Dehling et al., 2016;

Kissling et al., 2019; Sinnott-Armstrong et al., 2018). I included plant species primarily dependent on birds for seed dispersal by filtering for plants with contrastive fruit colour syndromes (Sinnott-Armstrong et al., 2021). Fruit length (mm) was the plant functional trait with the highest coverage and is closely correlated with other fruit dimensions (McFadden et al., 2022). To inform the trait-based interaction model, I used fruit length rather than other plant functional traits such as seed size as fruit length has been shown to correlate strongly with avian gape width and would therefore more accurately determine interaction probability (Bender et al., 2018; Dehling et al., 2014). Given that most frugivorous birds consume the whole fruit, a key trait constraining or predicting plant-bird interactions is gape size (Wheelwright, 1985). I extracted gape-size (mm) for 629 frugivorous bird species from McFadden et al. (2022) and Tobias et al. (2022), which was measured as the horizontal distance between the points where the lower and upper mandibles connect.

### 4.2.3. Determining bird and plant co-occurrence at ecoregion level

I established co-occurrences between fleshy-fruited plant and frugivorous bird species to understand which pairs of species could potentially come into contact based on their current distributions. To do so, I first divided the study system into terrestrial ecoregions (n = 277) (Olson et al., 2001). Ecoregions have been shown to be a strong delineation for interacting plant-frugivore assemblages (Martins et al., 2022). I constructed co-occurrence matrices by intersecting each plant and bird species' range map with that of a given ecoregion. These assemblages thus represent the pool of plant and bird species that could potentially interact at the ecoregion level. For each ecoregion-level assemblage, I mapped the median and variance of fruit length, gape width and range size across all plant and bird species, respectively (Figure 4.2a-d) (Figure A3.1).

### 4.2.4 Climate data

To describe the range of climatic conditions tolerable by each frugivorous bird species, I generated climatic niche hypervolumes based on average monthly precipitation ($10g/m^2$) and temperature (°C) for processed eBird occurrence records at a 1 km resolution and at the month and year of the occurrence (Karger et al., 2017; Sullivan et al., 2009). Temperature and precipitation (log transformed) were selected as climate

variables to inform niche estimates as they have previously been shown to strongly shape avian distributions (Pigot et al., 2010). Niche hypervolumes were generated using the box kernel density method, with the Silverman bandwidth estimator used to provide an appropriate bandwidth (Blonder et al., 2014). I used a consistent method to summarize present and future climatic conditions for a given ecoregion. For current climate, average monthly temperature and precipitation layers (1 km resolution, 1980 – 2010) were extracted using the ecoregion polygon boundaries (Karger et al., 2017) and used to generate hypervolumes summarizing the multivariate range of climates within each given ecoregion (Blonder et al., 2014). This method thus used an identical spatial and temporal resolution of climate data used in estimating avian climate niches. For projected future climate (2070–2100), the same method was implemented across four climate models (GFDL-ESM4, IPSL-CM6A, MPI-ESM1, MRI-ESM2) under an RCP 7.0 emissions scenario which corresponds closest to ongoing rapid temperature increase (Pachauri & Meyer, 2014).

### 4.2.5 Trait-based interaction model

To determine plant-frugivore interaction diversity across the Americas, I estimated interaction probabilities at the ecoregion level using a trait-based model. With this model, it was possible to derive an interaction probability between a bird and plant species depending on the level of trait correspondence – determined as fruit size (mm) subtracted from gape width (mm) (Figure 4.1). The relationship between trait correspondence and interaction probability followed a theoretically determined right-skewed shape as birds with larger beaks are able to interact with smaller fruit, while small birds are unlikely to access larger fruits (Nowak et al., 2022; Donoso et al., 2017; Wheelwright, 1985).

In the model, the degree of interaction specificity was adjusted through a trait matching parameter ($s$) (Donoso et al., 2017). Modifying this parameter either widens or tightens the range of resources a bird can interact with. To represent a realistic degree of specificity comparable to empirical plant-frugivore networks, I set this parameter to $s$ = 1.5 to construct the ecoregion-level assemblages under current conditions (Nowak et al., 2022). This $s$ value corresponded to a mean complementary specialization of $H_2'$ = 0.43 ± 0.11 in the ecoregion-level assemblages (Schleuning et al., 2012). A high $H_2'$ value

determines a high level of specialization within an interaction network – i.e., most interactions are exclusive and occur between specific interaction partners - whereas a low $H_2$' number is indicative of more generalised and less exclusive interactions within a network (Blüthgen et al., 2006).

To empirically validate the trait-based interaction model, I compared the predicted ecoregion-level interactions with a global dataset comprising 173,639 observed interactions from 410 local frugivory networks (Fricke et al., 2022). I restricted the empirical dataset to interactions occurring in the Americas and involving avian frugivores. Further filtering excluded interactions involving plant or bird species absent from the study, yielding a final empirical dataset of 14,285 interactions from 103 local networks. I then evaluated the overlap between the observed interactions from these local networks and those predicted by my model from the corresponding ecoregion assemblages. An interaction was classified as a true positive if the model predicted an interaction probability >0 for a species pair also observed empirically. Model performance was assessed by calculating the true positive rate (TPR) as the proportion of true positives among all observed interactions. The overall TPR across the 103 local networks was 70.9%. I observed strong variation in TPRs among networks (71.6% ± 25.4%), most likely due to differences in the accuracy of the locally observed networks (Figure A3.2).

### 4.2.6 Current and future climatic suitability

To determine the impact of projected climate change on plant-frugivore interactions, I assessed the climatic suitability of current and projected future ecoregion climate for avian frugivores. For a given ecoregion, the climatic niche of each avian frugivore was compared to the ecoregion climate. Subsequently, every interaction probability between a given plant and bird species in an ecoregion was weighted by the climatic suitability of the respective ecoregion. The climatic weighting was calculated as the Sorensen's overlap (range: 0-1) between the hypervolumes of the avian climatic niche and the current and future ecoregion climate, respectively. A high overlap between the avian niche hypervolume and the ecoregion climate hypervolume indicates the ecoregion is climatically suitable resulting in a higher interaction probability between a bird and its plant partners. In contrast, a low overlap between the avian niche

hypervolume and the ecoregion climate hypervolume indicates the ecoregion is climatically less suitable and will result in a lower interaction probability, for instance due to low abundance, local extinction or emigration of the bird species from that ecoregion (Thomas et al., 2006). I excluded bird species from the ecoregion assemblage if only a fraction of the respective avian niche hypervolume overlapped with the ecoregion niche hypervolume. I assume here that a bird species is unlikely to occur in ecologically relevant numbers in an ecoregion that is mostly climatically unsuitable as the species would either go locally extinct or emigrate. For the main analyses, I set this overlap threshold to 0.4 – below which the respective bird species is excluded from the ecoregion assemblage; however, I also tested different thresholds (Figure A3.3). By applying the climatic suitability weighting method according to both current and future climate conditions, I used this approach to quantify projected impacts of changing climatic conditions on plant-frugivore interactions.

### 4.2.7 Projections of interaction diversity

To determine projected changes in plant-frugivore interactions, I first calculated the interaction diversity for each plant species in an ecoregion. Specifically, this metric is calculated as the exponential of the Shannon diversity of weighted pair-wise interaction probabilities between a given plant species and its co-occurring avian species (Dormann et al., 2009). Interaction diversity can be interpreted as the effective number of avian interaction partners for a given plant species in an ecoregion. I calculated interaction diversity prior to climate weighting (Figure 4.3) and accounting for both current and projected future climatic conditions, averaging it across all plant species within each ecoregion. Therefore, an ecoregion's interaction diversity value of 10 would indicate that on average a plant species occurring within the respective ecoregion would have an effective number of 10 avian interaction partners. To compare current and projected future interaction diversity, I calculated the proportional decrease or increase in the effective number of avian partners per plant species averaged both across all plant species in a given ecoregion and all four climate models. For instance, if the number of effective avian interaction partners for a given plant species doubles, this would be reflected as a 100% increase in interaction diversity. Conversely, a 100% decrease would determine that a plant species has lost all its avian interaction partners. Additionally, given the importance of frugivory in forests (Côrtes & Uriarte, 2013), I

compared the proportional changes in interaction diversity for ecoregions within the different forest biomes (Olson et al., 2001).

### 4.2.8 Interaction rewiring

I investigated the effects of interaction rewiring on future plant-bird interaction diversity by varying avian frugivore dietary flexibility and allowing for avian dispersal into an ecoregion. First, to reflect the capacity of species to adapt their diet as resource availability changes, I allowed avian interaction partners to adapt to a more generalist fruit choice by varying the specialization parameter ($s$) in the trait matching model (Bender et al., 2017; Donoso et al., 2020). I therefore modified the $s$ parameter of the trait-based interaction models from moderate ($s$ = 1.5) to generalized ($s$ = 0.5) trait matching (Nowak et al., 2022), resulting in a more generalized scenario corresponding to a mean complementary specialization of $H_2' = 0.25 \pm 0.05$ at the ecoregion level. A lower specialization parameter allows frugivorous birds to form new interactions with other fleshy-fruited plants, due to a relaxed trait matching between fruit size and gape width.

Second, I simulated the dispersal of bird species into ecoregions, potentially offering compensation through interaction rewiring with immigrating species (CaraDonna et al., 2017; Schleuning et al., 2020). I calculated maximum dispersal distances for each bird species using a method adapted from Stewart et al. (2020). This involved fitting a linear mixed effects model between avian functional traits and empirical maximum natal dispersal distances for a subset of the bird species (n = 285 species) and then using the fitted model to predict maximum dispersal distances for the species used in this study (Stewart et al., 2020). All possible combinations of linear and quadratic effects for hand-wing index, wing length, generation length, body mass and range size were fitted against maximum dispersal distance (Stewart et al., 2020). The model with the lowest AIC score was a function of the linear effects of wing length, hand-wing index, geographical range size and a quadratic effect of hand-wing index (marginal $R^2 = 0.43$, random terms = bird order/family). A dispersal buffer zone was then derived for each bird species by multiplying the predicted maximum dispersal distance by the number of generations that could occur between the midpoint of current (1995) and future climate periods (2085) (Bird et al., 2020). The established ecoregion assemblages were then

supplemented with those species where the minimum distance between the source and destination ecoregion borders was less than the dispersal buffer. That is, each bird species in a given ecoregion assemblage was compared with all other ecoregions and only allowed to immigrate into ecoregions it would be able to reach. Additionally, only bird species whose climatic suitability in the source ecoregion fell below the designated threshold (Sorensen's overlap index = 0.4) – i.e. the ecoregion became unsuitable under projected future conditions - were allowed to disperse to new ecoregions. While this would allow species to immigrate into climatically unsuitable ecoregions, I accounted for this by down-weighting interaction probabilities and excluding bird species from ecoregions with unsuitable climates according to the same threshold. Given established ecological barriers between biogeographic realms, species were only allowed to enter other ecoregions if both source and destination ecoregions belonged to the same realm (Stewart et al., 2020). For instance, a bird species originating from a Nearctic ecoregion could enter another Nearctic ecoregion but would not be able to enter any Neotropical ecoregions. However, birds were allowed to disperse to neighbouring biomes in or simulations. To quantify the effects of increased dietary flexibility and dispersal on projected future plant-frugivore interactions, I reran the analyses using scenarios with and without relaxed trait matching and dispersal.

## 4.3 Results

### 4.3.1 Current patterns in trait diversity and plant-frugivore interaction diversity

I found trait-specific latitudinal patterns in fruit size and gape width across the Americas. Median fruit length was highest across the Neotropical realm and in a few ecoregions on the west coast of North America (Figure 4.2a). The most diverse ecoregions, with regards to the variance in fruit length, were located around Patagonia and western North America (Figure 4.2c). Median gape width of obligate avian frugivores was highest at lower latitudes across Central America and Amazonia. Variance in gape width was highest in the Neotropics, with particularly high diversity of gape width in Eastern and Northern Amazonia (Figure 4.2d).

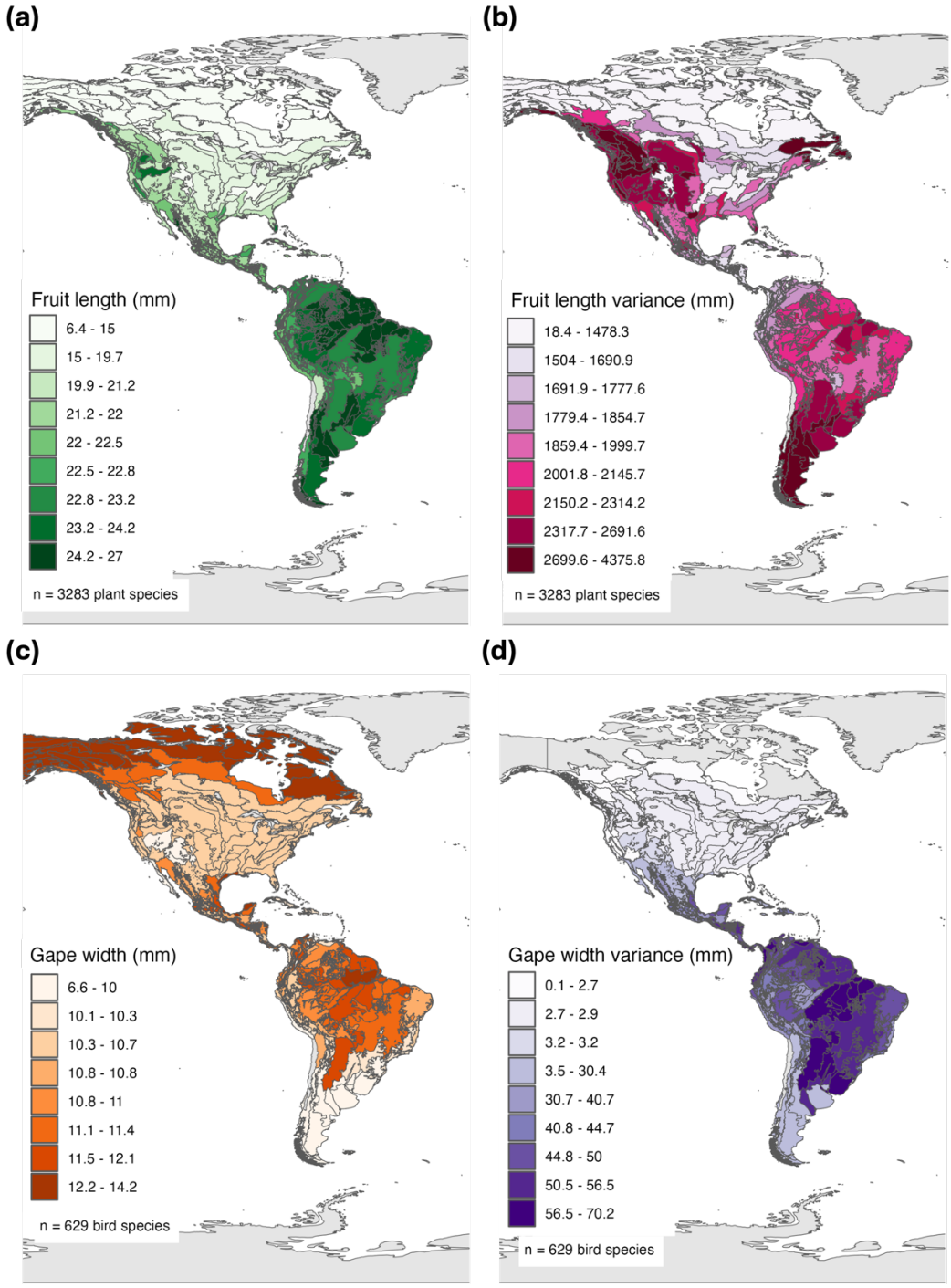



**Figure 4.2| Latitudinal patterns in fruit length and avian gape width across the Americas.** (a) Map of median fruit length across the Americas. Regions shaded in darker green are occupied by plant assemblages with high median fruit length. (b) Map of fruit length variance across the Americas. Regions shaded in darker pink are occupied by plant assemblages with a high variance in fruit length. (c) Map of median gape width of obligate avian frugivores across the Americas. Regions shaded in darker orange are occupied by bird assemblages with high median gape width. (d) Map of gape width variance of obligate avian frugivores across the

Americas. Regions shaded in darker purple are occupied by bird assemblages with a high variance in gape width.

As expected, I found a strong latitudinal gradient in plant-frugivore interaction diversity and an increase in the mean number of avian interaction partners available to plants towards the tropics (Figure 4.3). For instance, the mean number of obligate avian frugivores potentially available to plant species was 38 species in the Southwest Amazon moist forests. Conversely, plant species occupying ecoregions at higher latitudes had much fewer potential avian interaction partners. For instance, in the Low Arctic Tundra, the average number of obligate avian frugivores per plant species was only two species. In the analysis including obligate and opportunistic avian frugivores, the latitudinal patterns remained qualitatively similar, but plant species at high latitudes had a higher number of potential avian interaction partners (Figure A3.4).

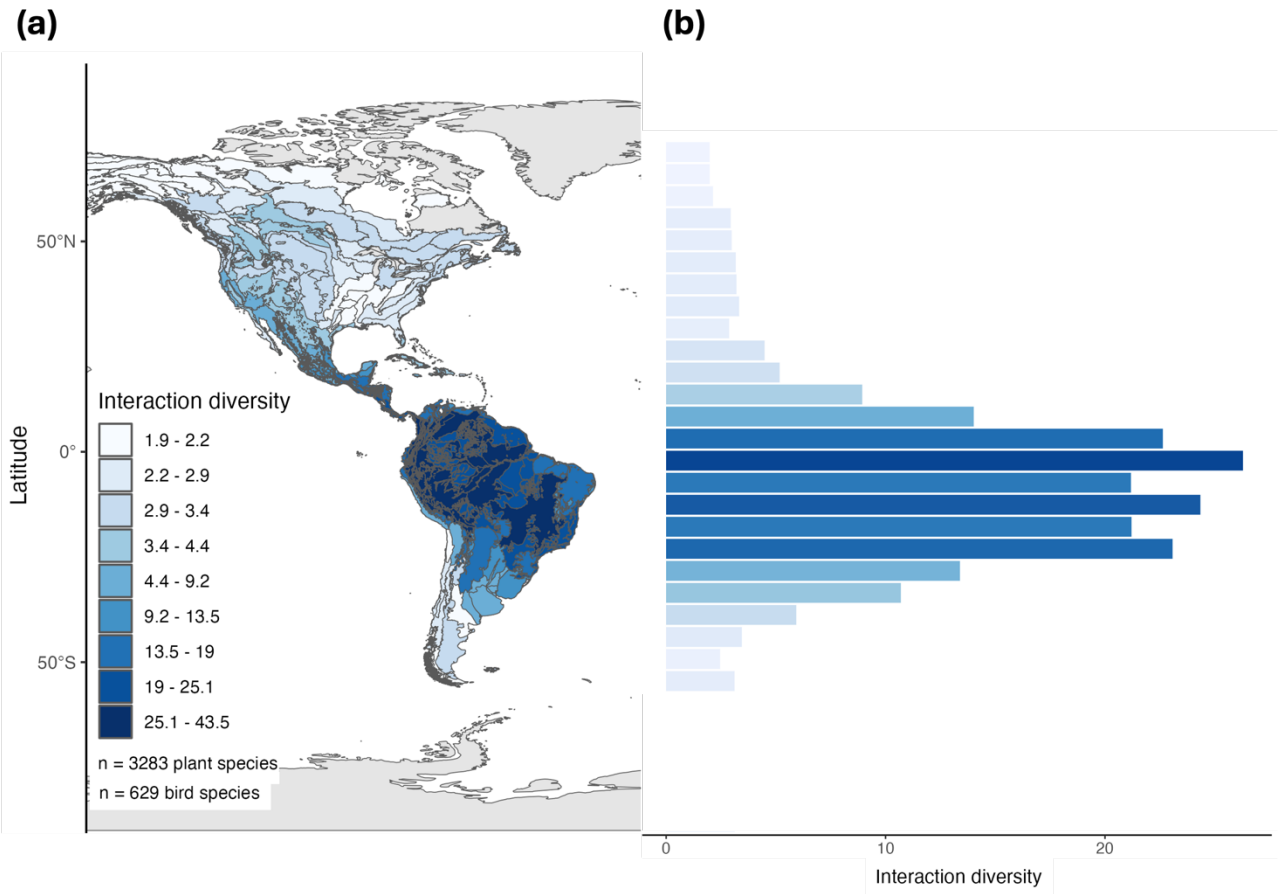



**Figure 4.3| Latitudinal pattern in potential plant-frugivore interaction diversity across the Americas.** Map of mean interaction diversity within an ecoregion (a) and across 5° latitudinal bands (b). Interaction diversity is defined as the effective number of avian interaction

partners for a given plant species (unweighted by climatic suitability). Darker blue ecoregions are occupied by plant species that, on average, are able to interact with many more frugivorous birds compared to plant species that occupy lighter blue ecoregions. Projections including both obligate and opportunistic avian frugivores are shown in Figures S3.

### 4.3.2 Projected future changes in plant-frugivore interaction diversity

Future climate projections revealed widespread declines in the number of potential avian interaction partners across most of the Americas, both in the analysis of obligate avian frugivores (Figure 4a) and that including obligate and opportunistic avian frugivores (Figure A3.5a). For obligate avian frugivores, the model projected a decline in future interaction diversity for 51% of the 277 ecoregions. The highest declines in plant-frugivore interaction diversity were concentrated across Central Amazonia (projected decrease in interaction diversity: 80%), as well as the eastern United States (projected decrease: 71%).

For a subset of ecoregions (n = 112), mostly those occupying high latitudes, the simulations of obligate avian frugivores projected a slight increase in the effective number of avian interaction partners as in these ecoregions climatic conditions largely became more suitable for avian species. Across all tropical and subtropical forest biomes where avian seed dispersal is particularly relevant, I found a consistent decline in projected plant-frugivore interaction diversity under projected future climate (Figure 4b, Figure A3.5b). For obligate avian frugivores, the highest declines in interaction diversity occurred in Mangroves (mean projected decrease: 28%). The analysis including both obligate and opportunistic avian frugivores showed qualitatively similar trends and a decline in projected interaction diversity across most of the ecoregions in tropical forest biomes (Figure A3.5b).

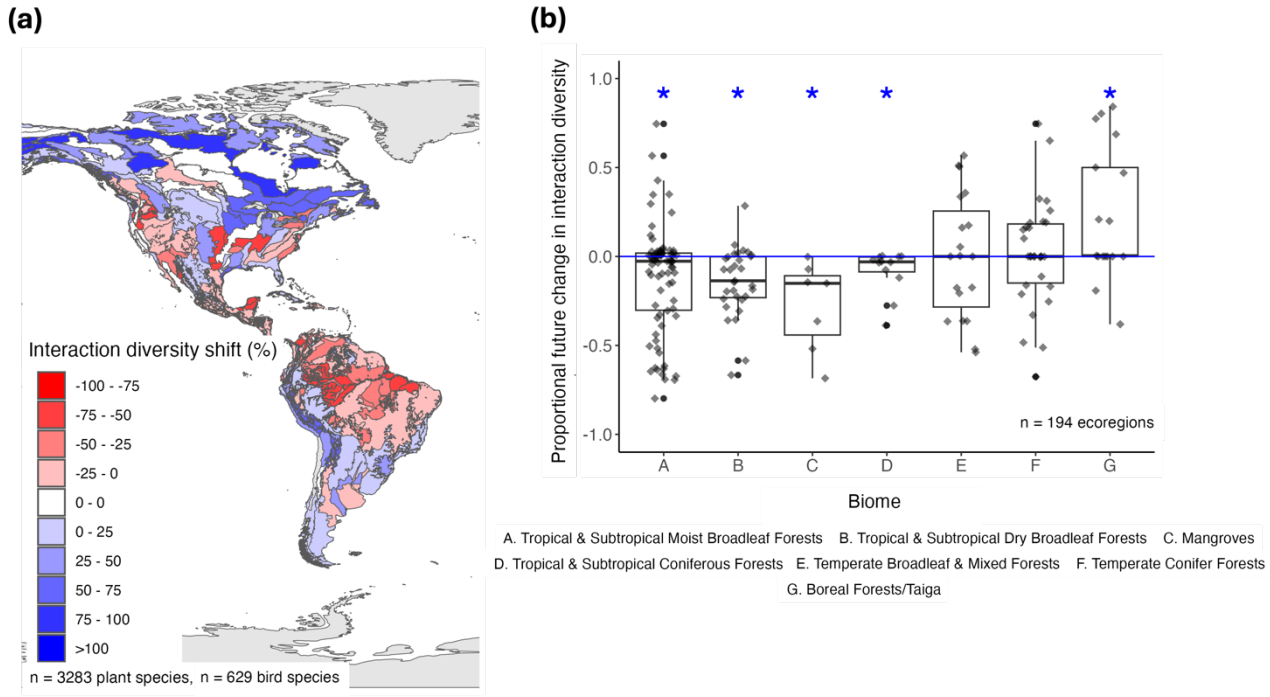



**Figure 4.4| Projected impacts of climate change on plant-frugivore interactions.** (a) Map of future climate impacts on plant-frugivore interactions. (b) Boxplot of future climate impacts on plant-frugivore interactions. Interaction diversity shift was calculated as the proportional difference in the effective number of avian frugivores per plant species averaged across all plant species in a given ecoregion. For instance, if the effective number of avian interaction partners for a given plant species doubles, this would be reflected as a 100% increase in interaction diversity. Asterisks above each boxplot indicates significant differences from 0 based on one-sample t-tests. Shown are simulation results from the projections including only obligate avian frugivores. Projections including both obligate and opportunistic avian frugivores are shown in Figure A3.5.

### 4.3.3 Effects of interaction rewiring on projected future plant-frugivore interaction diversity

Simulations of obligate avian frugivores that allowed for increased avian frugivore dietary flexibility and dispersal into ecoregions showed widespread positive effects on plant-frugivore interaction diversity. In the simulations allowing for increased dietary flexibility, 70% of the 277 ecoregions exhibited an increase in the interaction diversity, particularly around Western Amazonia (Figure 4.5a). In simulations allowing for dispersal, 76% of the 277 ecoregions exhibited an increase in projected plant-frugivore interaction diversity, with the strongest positive responses across Central and South

American ecoregions (Figure 4.5b). Once I combined the effects of increased dietary flexibility and dispersal, a positive effect was exhibited in 81% of the 277 ecoregions, indicating a widespread increase in projected interaction diversity, especially across Neotropical ecoregions (Figure 4.5c). Increased dietary flexibility and dispersal resulted in a consistent increase in projected interaction diversity in all tropical forest biomes (Figure 4.5), which all had projected negative trends without interaction rewiring (Figure 4.4). Simulations of obligate and opportunistic avian frugivores that allowed for increased dietary flexibility and/or dispersal showed positive effects on interaction diversity across both North and South America (Figure A3.6). In the scenario allowing for both increased dietary flexibility and dispersal, 82% of the ecoregions showed an increase in the projected number of obligate and opportunistic avian frugivores under future conditions.

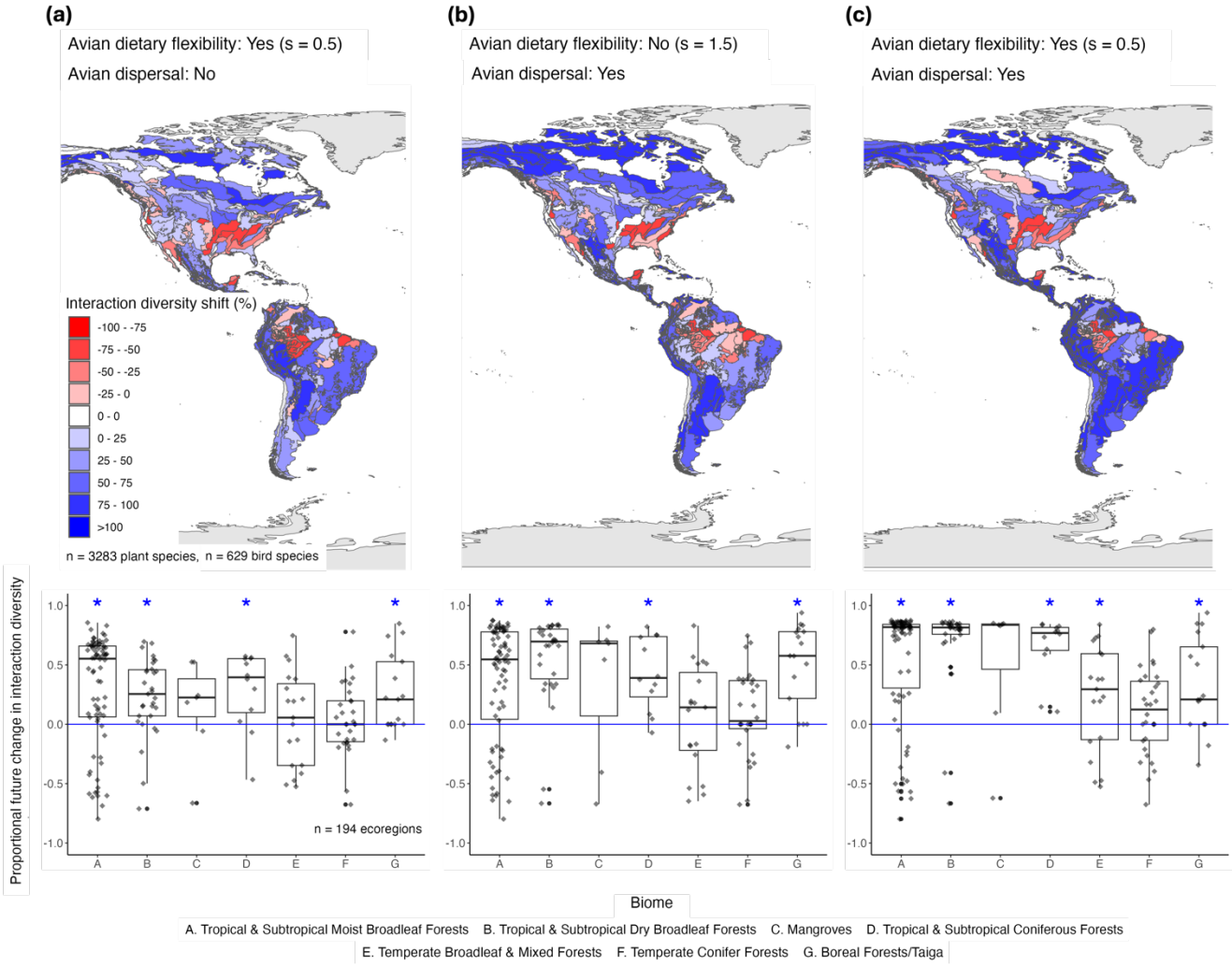


**Figure 4.5| Effects of interaction rewiring on projected future plant-frugivore interactions.** Map and boxplot of future climate impacts on plant-frugivore interactions allowing for (a) avian dietary flexibility (i.e., trait matching parameter *s* set to 0.5), (b) avian dispersal (i.e., immigration of species from surrounding ecoregions) and (c) both avian dietary flexibility and dispersal. Interaction diversity shift was calculated as the proportional difference in the effective number of avian frugivores per plant species averaged across all plant species in a given ecoregion. For instance, if the effective number of potential avian interaction partners for a given plant species double, this would be reflected as a 100% increase in interaction diversity. Asterisks above each boxplot indicates significant differences from 0 based on one-sample t-tests. Shown are simulation results from the projections including only obligate avian frugivores. Projections including both obligate and opportunistic avian frugivores are shown in Figure A3.6.

## 4.4 Discussion

I used a trait-based interaction model based on functional trait and range data of co-occurring fleshy-fruited plants and frugivorous birds to project plant-frugivore interaction diversity - the effective number of avian interaction partners for a plant species in an ecoregion - across the Americas. Under projected future climate, my simulations suggest widespread declines in plant-frugivore interaction diversity across most ecoregions, especially in tropical forest biomes. However, both increased avian dietary flexibility and dispersal had the potential to increase plant-frugivore interaction diversity and buffer the projected declines.

### 4.4.1 Current patterns in trait diversity and plant-frugivore interaction diversity

My models predicted geographic patterns in trait and interaction diversity that are consistent with empirical studies (Chen et al., 2017; Moles et al., 2007). Increased diversity of both fleshy-fruited plants and frugivorous birds at lower latitudes may be driven by the enhanced productivity in these ecosystems (Kreft & Jetz, 2007; Ting et al., 2008). Furthermore, major radiations in fleshy-fruited plant diversity in South and Central America may explain subsequent increases in frugivorous bird richness and trait diversity, particularly in the Passeriformes (Kissling et al., 2009). My predictions are also in line with previous macroecological studies that have identified the Neotropics as the most significant hotspot with regards to plant-frugivore interaction

diversity (Kissling et al., 2009). This latitudinal pattern in avian frugivore diversity was most pronounced for obligate avian frugivores whereas the diversity of obligate and opportunistic avian frugivores declined less steeply from Neotropical to Nearctic ecoregions (Kissling et al., 2009). The trait-based interaction model therefore accurately captures the current biogeographic patterns in plant-frugivore interactions.

### 4.4.2 Projected future changes in plant-frugivore interaction diversity

My simulations projected widespread reductions in plant-frugivore interaction diversity under future climate, especially in tropical and subtropical ecoregions and biomes. A widespread decline in interaction diversity in the tropics and subtropics was also found in simulations including both obligate and opportunistic avian frugivores (Figure A3.5). In line with previous work, Neotropical species are sensitive to future climate change given their high degree of niche specialization and narrow climatic niches (Miranda et al., 2019). Many tropical species are also likely to occupy the warm edge of their climatic niche and will therefore be sensitive to future warming (Huey et al., 2009). My findings are consistent with previous studies proposing that temperate bird species have a comparatively higher resilience because they experience a wider range of climate conditions across their larger geographic ranges (McCloy et al., 2022) (Figure A3.1).

My model projected declines in plant-frugivore interaction diversity across almost all major forest biomes. Declines in plant-frugivore interaction diversity were particularly pronounced in tropical and subtropical forest biomes, whereas the response of plant-frugivore interactions in temperate biomes was more variable. The projected declines in plant-frugivore interaction diversity will likely reduce seed-dispersal functions in forest ecosystems, especially in the tropics, and can lead to the co-extinction of dependent plant species through the disruption of their life cycles, especially in many tropical plant species reliant on animals for seed dispersal (Jordano et al., 2011). Reduced interaction diversity between plants and avian frugivores can lead to lowered seed-dispersal distances in these assemblages (Donoso et al., 2020). The consequences of such effects are expected to be particularly accentuated in landscapes that have already suffered habitat degradation and whose functional connectivity is reliant on long-distance seed dispersal (Mueller et al., 2014). Forests will be particularly susceptible to such effects given the high proportion of plant species dependent on animal mediated seed dispersal

in these ecosystems (Côrtes & Uriarte, 2013). The projected declines in plant-frugivore interaction diversity could therefore lead to a disruption of tropical and subtropical forest regeneration, driving cascading effects on other ecosystem functions and services such as carbon sequestration (Waring et al., 2020).

### 4.4.3 Potential effects of interaction rewiring on interaction diversity

Integrating mechanisms of interaction rewiring between plants and birds compensated for projected future losses in interaction diversity and led to increases in projected interaction diversity. Both mechanisms of dispersal and increased dietary flexibility would allow for new interactions to form between plants and avian frugivores (CaraDonna et al., 2017; Schleuning et al., 2020), either with species already present or with new bird species entering an assemblage. The simulations therefore suggest that these mechanisms can potentially buffer the projected negative impacts on plant-frugivore interaction diversity.

In simulations restricted to obligate avian frugivores, increased avian dietary flexibility and dispersal generated widespread positive effects on plant-frugivore interaction diversity**,** particularly across the Neotropics and in tropical and subtropical forest biomes that are likely to experience declining interaction diversity in the future without interaction rewiring (Figure 4.4). According to these findings, Neotropical assemblages would have a large potential for interaction rewiring because bird species from neighbouring assemblages could enter the assemblages and/or persisting species may be able to establish interactions to new plant partners. This pattern is likely driven by the large diversity of obligate frugivorous birds in the Neotropics. This diversity may facilitate the immigration of species into neighbouring ecoregions. Furthermore, the high trait diversity of Neotropical avian frugivores is likely to favour the formation of new interactions as especially large-gaped avian frugivores are able to interact with many different plant species (McFadden et al., 2022) and can potentially adapt their fruit diet under future conditions. These simulations suggest that both mechanisms of interaction rewiring are additive because simulations incorporating both mechanisms together resulted in the largest increases in interaction diversity, especially in the Neotropical forest biomes. For example, large-bodied avian frugivores, such as the red-ruffed fruitcrow (*Pyroderus scutatus)* or the white-throated toucan (*Ramphastos*

*tucanus)*, have a high dispersal capacity and therefore can reach a high number of other ecoregions, thus contributing to an increased interaction rewiring potential. Additionally, many such species have a large gape width and are therefore likely to have a high dietary flexibility in their prospective future assemblages (Bender et al., 2017).

According to these simulations of obligate avian frugivores, both interaction rewiring mechanisms had weaker positive effects on the Nearctic assemblages, likely due to the small species pool (Kissling et al., 2009) and the low diversity of obligate avian frugivores in these ecoregions (Dalsgaard et al., 2017; McFadden et al., 2022). The core of seed-dispersal networks composed by obligate avian frugivores is therefore likely to erode in such ecoregions under future climates. Many frugivorous birds in temperate forest biomes have a generalist diet and are opportunistic avian frugivores (Dalsgaard et al., 2017; Schleuning et al., 2012; Belmaker et al., 2012). This explains why simulations including both obligate and opportunistic avian frugivores showed a more widespread buffering effect of interaction rewiring across both the Nearctic and Neotropics. The seed-dispersal functions of opportunistic avian frugivores may be crucial to buffer climatic effects on plant-frugivore interaction diversity especially in Nearctic ecoregions and in temperate forest biomes. However, because many opportunistic species frequently switch between a fruit-based and an invertebrate diet (Carnicer et al., 2008), it is unknown to what extent these species may actually provide reliable seed-dispersal functions under future conditions.

A key innovative element of this study was the incorporation of interaction rewiring through increased avian dietary flexibility and dispersal, both of which would have the potential to buffer the projected losses in interaction diversity under future conditions. As there is very little empirical evidence of how interaction rewiring may reorganize ecological assemblages (Kissling & Schleuning, 2015), it is difficult to judge the ecological realism of these projections. Because I employed trait-based approaches to model both dietary flexibility and dispersal, I am confident that this approach presents the best possible practice and goes beyond more simplistic approaches used in other studies (Schleuning et al., 2016; Richardson et al., 2000). Nevertheless, I acknowledge these results are optimistic as these rewiring scenarios do not consider competition between avian frugivores which would likely reduce future interaction diversity (Lamb

et al., 2017). I therefore stress that a careful interpretation of these scenarios is needed as they were focused on the potential beneficial and stabilizing effects of rewiring on interaction diversity, and it is unknown whether plant species will indeed experience widespread positive effects through interaction rewiring in future assemblages.

### 4.4.4 Limitations of the simulations

I have generated macroscale projections of interaction diversity by deploying a trait-based interaction model, informed by species-level functional trait and distribution data, coupled with climatic niche estimates. This approach did not aim to predict local networks under future conditions, which has been done previously (Fricke et al., 2022), but I aimed to project interaction diversity at the ecoregion level. I therefore did not account for mechanisms of trait matching at the local scale, such as phenological matching or local co-occurrence (Blanchet et al., 2020). My predictions at ecoregion level may therefore overestimate the interaction diversity that is locally realised (Blanchet et al., 2020). I also focused entirely on avian seed dispersal although frugivorous mammals are also important seed dispersers (Lim et al., 2020), especially for large-sized seeds (Wright et al., 2020). Mammals may therefore help to buffer seed-dispersal functions in the future (Lim et al., 2020). Other limitations of this study include spatiotemporal biases in the underlying bird occurrence data used to generate the avian climate niche estimates (Johnston et al., 2019). Climatic niche estimates used in this study represent realised niche estimates which may underestimate fundamental tolerances. Additionally, the method does not control for potential species' adaptations to new climatic conditions, and my simulations assumed that the avian climatic niches were constant under future conditions. It is therefore possible that adaptations of avian frugivores to novel climatic conditions could pose an additional buffer to maintaining plant-frugivore interaction diversity under future conditions. Furthermore, while for birds there is comprehensive data on their geographic distributions and functional traits, these datasets are less complete for plants. In my simulations, I kept plant assemblages static although fleshy-fruited plants may be able to move and immigrate into new ecoregions through avian seed dispersal (Neilson et al., 2005). Because plant responses to climate change may often be delayed (Nowak et al., 2022), this is a conservative assumption of how these assemblages may adapt to climate change.

### 4.4.5 Conclusions

Using species traits to infer potential changes in plant-frugivore interactions, my simulations suggest a widespread vulnerability of plant-frugivore interactions to future climate change, especially in tropical and subtropical ecoregions and biomes. According to my analyses of interaction rewiring, the large diversity of traits and plant-frugivore interactions in Neotropical ecoregions may increase the resilience of tropical plant-frugivore interactions to these future changes. Maintaining this diversity is therefore key to maintain seed-dispersal functions and tropical biodiversity in the future. Large-scale studies such as ours can identify how the composition of ecological assemblages may influence how plant-animal interactions respond to climate change, improving our knowledge on essential ecological processes and functions in the most vulnerable ecosystems and biomes.

# 5| General Discussion

Climate change is widely regarded as the threat to biodiversity that will dominate the 21st century (Calvin et al., 2023). It is therefore crucial to develop better forecasting of species response to climate change. With the arrival of powerful new environmental datasets, analyses can be undertaken to understand the effects of future climate on species to a degree of accuracy not previously accessible (Sullivan et al., 2009; Tobias et al., 2022). As part of this PhD thesis, I have generated and tested a global climate niche dataset. Specifically, I investigated the effects of different spatiotemporal resolutions on climate niche estimates. In combination with other environmental variables, I then investigated the relationship between these climate niche features and avian population trends to identify predictive characteristics of vulnerability to environmental change at different ecological scales. Additionally, I leveraged plant and bird functional trait data to build ecological networks at a macroscale, and subsequently simulated network-level response to future climate change. In this chapter I expand upon the major findings from this PhD work and detail the implications these may have on the wider field of ecology. This PhD project has aimed to facilitate and implement more accurate modelling of biodiversity response to future climate change to hopefully inform better mitigation strategies against increasingly inevitable drastic impacts.

## 5.1 Key findings

This PhD thesis looks to address key gaps in the methods currently deployed to predict biodiversity response to climate change. Namely these relate to issues of spatial, temporal and ecological scale and overlooking the role of biotic interactions in influencing and mitigating climate change impacts. The three major findings presented here are: (i) The temporal dimension of climate niche quantification contributes significantly to differences in niche estimates between methods. (ii) Local climate is more predictive of avian population trends compared to species climate niche. (iii) Increased trait diversity offers resilience to future climate change through interaction rewiring. The results presented across this PhD thesis contribute significantly to the fields of global change biology, macroecology, and functional ecology.

### 5.1.1 The temporal dimension of climate niche quantification contributes significantly to differences in niche estimates between methods

Accurate estimation of climatic niches is fundamental to analyses assessing species' potential responses to climate change. Most methods for quantifying climate niches involve extracting climate across a species' estimated distribution (Thuiller, 2024). There are therefore several methodological decisions to be made around quantifying climate niche that may subsequently influence niche estimates. In Chapter 2, I conduct the first global assessment of the effect of different niche quantification methods, using polygon range map and point locality data respectively, on climate niche position and volume. Distinct niche quantification methods are shown to generate significantly different climate niche estimates with the temporal resolution of climate niche quantification contributing importantly towards variation between methods. Hopefully, insights gained from this chapter can improve interpretations of past analyses and better inform future studies underpinned by climate niche estimates.

The temporal resolution of climate data used to derive niche estimates contributed significantly to differences in climate niches between methods. Given the temporal variability in avian species distributions, for instance, during seasonal migration (Eyres et al., 2017), this temporal sensitivity in climate niche estimation is logical. Previous studies conducted at smaller spatial and taxonomic scales similarly demonstrated that changing the temporal resolution of climatic data can lead to markedly different niche estimates and model interpretations (Eyres et al., 2017; Perez-Navarro et al., 2021). Despite temporal variability in species distributions, the majority of studies using climate niche estimates have tended to extract climate at coarse temporal resolutions – such as mean annual climate or multi-year averages (Cooney et al., 2016; Lavergne et al., 2013; Strubbe et al., 2013). This trend is likely due to the widespread use of polygon range map datasets which offer limited temporal granularity. However, the increasing availability of high-resolution, temporally explicit global occurrence datasets now enables more precise tracking of species' climatic associations through (La Sorte & Somveille, 2020; Sullivan et al., 2009)le, 2020; Sullivan et al., 2009).

My findings may have implications across past analyses underpinned by climate niche estimates. These include studies that have investigated the relationship between climate experienced by species and morphology as the basis for widely established ecogeographic rules, namely Allen and Bergmann's rules. Both rules are based on the idea that thermoregulation will drive geographical trends in animal shape and size (Allen, 1877; Bergman, 1847). Specifically at higher latitudes, Allen's rule dictates that animals will have shorter appendages and Bergmann's rule states animals will have larger body sizes to prevent heat dissipation (Allen, 1877; Bergman, 1847). The unifying theory behind Allen and Bergmann's rules is that morphological patterns are driven by adaptation to different temperatures along a latitudinal gradient (Symonds & Tattersall, 2010). This hypothesis dictates that in colder climates animals have adapted shorter appendages and larger bodies to retain more heat through a reduced relative surface area and conversely, in warmer climates, animals have adapted longer appendages and smaller bodies allowing for increased heat loss (Symonds & Tattersall, 2010). Although these theories are quite widely supported by empirical studies in birds (Friedman et al., 2017; Fröhlich et al., 2023; Symonds & Tattersall, 2010), all previous analyses extract climate across polygon range maps without temporal precision. Based on my findings, these methods would overestimate species occupancy and subsequently climate niches and inaccurately infer that species have been exposed to colder temperatures than they directly experience in reality. Therefore, the use of point locality data and temporal refinements is required to re-examine these hypotheses and to reconsider latitudinal gradients in phenotype in the context of alternative hypotheses including roles for predation and starvation risk as well as foraging ecology (McNamara et al., 2016; McQueen et al., 2022).

Beyond providing a better understanding of niche quantification methodologies, the work presented in Chapter 2 also provides a global climate niche dataset with near full coverage across all birds - which represents a significant contribution to various ecological fields. Specifically, the dataset constitutes niche estimates derived from both polygon range map and point locality methods - providing climate niches suitable for a wide range of ecological and geographical contexts. As species track their climate niche in response to climate change, a dataset of this nature can facilitate macroscale scale studies monitoring these trends to a higher degree of accuracy thus better informing

future species distributions (Stewart et al., 2020). By integrating climatic niche data with morphological trait information, this resource also facilitates robust testing of ecogeographic theories at broad spatial scales (McQueen et al., 2022). Furthermore, it enhances the feasibility of quantifying rates of climatic niche evolution and assessing the role of niche dynamics in speciation, thereby offering deeper insights into historical evolutionary trajectories (Cooney et al., 2016). Such a dataset can also aid in identifying climatic refugia—areas that may offer resilience against future climatic shifts (Duarte et al., 2019). Finally, it provides a valuable tool for assessing climate compatibility, allowing for improved identification of regions vulnerable to biological invasions and the establishment of pest species (A. Peterson & Vieglais, 2001).

### 5.1.2 Local climate is more predictive of avian population trends compared to species climate niche

Whether species climate niches are truly informative towards population trends remains unclear. Therefore, in Chapter 3, I investigate the relative predictive capacity of species climate niche features compared to properties of the local environment in explaining recent avian population trends. The analysis reveals that local environmental conditions are substantially more predictive of population trends than species-level climatic niche features. A key implication of this finding is that populations may respond to climate change well before reaching the limits of their climatic niches.

Many studies that predict biodiversity response to climate change assume climate niche limits represent the tolerable range of conditions across a given species (Jetz et al., 2007; Stewart et al., 2020). For instance, a seminal paper by Thomas et al (2004), deployed species distribution models, underpinned by species climate niche estimates, to project extinction risk from climate change across 20% of the Earth's terrestrial surface (Thomas et al., 2004). The outcome of this analysis is that 15 – 37% of sample species will likely go extinct by 2050 under mid-climate scenarios (Thomas et al., 2004). Another paper by Thuiller et al (2005), similarly projected the distribution of 1,350 plant species under future climate scenarios, using species climate niche estimates, and determined species loss of up to 42% by 2080 under severe emissions scenarios (Thuiller, Lavorel, Araújo, et al., 2005). Notably, both studies assumed uniform species-level responses and did not account for intraspecific variation in vulnerability to climate

change. Therefore, based on my findings, it is possible these studies have overestimated the range of conditions populations will actually persist under and that outcomes will in fact be far more pessimistic. Identifying vulnerability to climate change before species reach the limits of their climatic niches represents a significant contribution to ecology, particularly given the widespread reliance on species-level niche estimates to infer environmental tolerance limits. Future work should focus on identifying the mechanisms driving this trend.

Lastly, my analyses focused on birds, which represent a particularly mobile animal group. Birds are capable of considerably shifting their ranges in response to climate change – offering a higher adaptive capacity relative to other clades (Sheard et al., 2020). We can therefore expect vulnerability to future climate change to be even higher in more sessile groups. In such cases we could perhaps expect an even larger gap between species climate niche limits and the true range of conditions populations will persist under (Thompson & Fronhofer, 2019).

### 5.1.3 Increased trait diversity offers resilience to future climate change through interaction rewiring

Frugivory represents a particularly important group of ecological interactions, especially in tropical landscapes where 60 – 80% of plant species are dependent on animal mediated seed dispersal (Jordano et al., 2011). However, the macroscale impacts of future climate change on frugivorous interaction networks have not been modelled before. In Chapter 4, I therefore leverage plant and bird functional trait datasets to construct ecoregion-level frugivory interaction networks across the Americas, and subsequently assess projected climate impacts on said networks as mediated by avian interaction partners.

Beyond finding widespread disruption to ecological networks under future climate change, I find a high buffering potential against future climate impacts in the Neotropics through interaction rewiring. Specifically, regions with higher levels of trait and species diversity, namely the tropics, were shown to have a higher potential of forming novel interactions between plant species and either already occurring or newly immigrated avian species. A key implication of this finding is that through the direct conservation of

these landscapes – for instance through the reduction of deforestation and other forms of land use change - ecological assemblages are likely better protected against future climate change. Tropical landscapes represent some of the most ecologically diverse parts of the world however they are also the most exploited (Luyssaert et al., 2014). Therefore, in addition to losing ecosystem integrity, for instance through increased habitat fragmentation and reduced habitat quality (Fahrig, 2003), these biomes are losing resilience to climate change. Promoting the intactness and supporting the diversity of such ecosystems will reduce vulnerability to future climate change.

Beyond my findings related to future climate impacts on frugivory networks and the buffering potential of interaction rewiring, another novel aspect of this analysis is the method implemented to construct ecological networks weighted by climate suitability. Whilst the fundamental trait-based interaction model was developed as part of other studies (Donoso et al., 2017), previous to this analysis, it had not been deployed to summarize macroscale interaction network diversity and response to future environmental change. When validating this method against known interactions and patterns of frugivory across the Americas, this method of network construction is accurate at predicting interactions (Kissling et al., 2009). Furthermore, this method is much more scalable and less labour intensive compared to other methods of network construction such as DNA metabarcoding or observed interaction datasets (Dehling et al., 2016; Pornon et al., 2017). As functional trait datasets improve in coverage across other plant and animal groups, the method of investigating network response to future climate implemented in Chapter 4 can be expanded across other ecosystem services.

Most macroscale analyses on impacts of future climate change on biodiversity describe how individual species or populations may respond. However, essential ecosystem services - such as pest control, seed dispersal and pollination – are the product of species interactions. Therefore, I hope studies such as this promote further investigation into network level response to future climate change at a macroscale.

## 5.2 Limitations

### 5.2.1 Limitations of niche quantification

Throughout this thesis, climatic niche estimates have been employed under the assumption that species' climatic niches remain static over space and time. Whilst empirical evidence exists which supports the concept of niche conservatism – the tendency of species climate niches to remain unchanged in space and time (Peterson et al., 1999; Tingley et al., 2009; Wiens & Graham, 2005) - it is increasingly clear that climate niches can be dynamic (Antão et al., 2022; La Sorte & Jetz, 2012). Another assumption implemented throughout this thesis is that species are in equilibrium with their environment and therefore their distributions are accurate and can infer climate niche estimates. Several studies have identified however that species are often in flux and in the process of "filling" their possible niche (Soberón & Arroyo-Peña, 2017) – i.e. a species distribution has not yet settled at an equilibrium (Guisan & Thuiller, 2005). One study investigating tree range expansion across Europe since the last glacial period estimated that 36/55 studies species were still in the process of reaching their maximum potential range limits and were likely strongly constrained by dispersal capacity (Svenning & Skov, 2004).

Reconciling the difference between fundamental and realised niche remains a key challenge in any analysis using correlative climatic niche models. The estimates presented in this thesis underestimate species' fundamental niches, and therefore analyses implementing these niches will potentially result in more pessimistic projections of biodiversity responses to climate change. However, when forecasting species response to future change, knowledge of fundamental niche is perhaps less important than previously considered. The biotic and abiotic constraints on climate niches may still be relevant into the future and potentially mediate species response to climate change (Soberón & Arroyo-Peña, 2017). For instance, a species' broad climatic tolerance is irrelevant if its key resources are lost under climate change. As much attention should therefore be dedicated to classifying and modelling these factors as towards understanding fundamental niche. Therefore, an additional aim of this PhD work was to test concepts of species being constrained before reaching their niche limits by investigating the predictive capacity of local climate factors in Chapter 3 and modelling the response of ecological dependencies – in the form of avian interaction partners - to future climate change in Chapter 4.

### 5.2.2 Limitations of macroscale analyses

Macroscale ecological studies offer valuable insights into broad spatial and temporal patterns, enabling the identification of large-scale processes such as biogeographical distributions and climate-driven biodiversity shifts (Wiens, 1989; Zizka et al., 2022). Generalizing findings across extensive spatial scales can be particularly important when investigating global phenomena – such as climate change (Zizka et al., 2022). However, such studies often overlook context-specific ecological and environmental factors, which can limit the applicability of their findings to understanding local-scale patterns.

One key limitation is the use of coarse data resolutions which may obscure local heterogeneity critical to ecosystem function. For instance, in Chapter 2, climate data was extracted at a resolution of 1 km and monthly temporal grain, which, while relatively fine for macroscale studies, may overlook important microclimatic variation (Maclean et al., 2015). Microclimate refugia, shaped by topographic or habitat heterogeneity, can allow species to persist locally even where broader-scale climates exceed their niche limits (García et al., 2020). As a result, niche estimates derived from occurrence data at this scale may overestimate the climatic conditions under which species can persist, particularly in complex terrains where climate varies sharply over short distances. Similarly, in Chapter 4, the exclusion of microclimates may lead to overly pessimistic projections of network-level responses to climate change, as microrefugia can buffer against broader climatic shifts (Maclean et al., 2015; Suggitt et al., 2018). Conversely, if microclimates foster niche specialization due to historically stable conditions, their omission could lead to overly optimistic outcomes (Trew et al., 2024). These contrasting possibilities highlight a key limitation of macroscale approaches: the inability to capture fine-scale variability in species–climate relationships.

Furthermore, macroecological studies tend to offer overly simplistic extrapolations that ignore finer scale ecological mechanisms. For instance, in Chapter 4, co-occurrence at the ecoregion level does not necessarily ensure bird and plant species would in fact come into contact (Blanchet et al., 2020). Especially, in habitats with high heterogeneity such as tropical rainforests with complex canopy structures – a key biome investigated in this chapter – it has been shown that many species do not come into contact through

occupying different layers of canopy (Blanchet et al., 2020). While macro-level understanding of ecological patterns is essential—particularly for forecasting global climate change impacts—it is equally important to account for context-specific factors when informing local conservation policy and management.

## 5.3 Future work and conclusions

Across the majority of the datasets used throughout this thesis, the animal clade with the dominant level of coverage has always been birds, therefore driving a focus on avian patterns. Different responses to future climate change across other animal groups can be expected and so findings presented across this thesis must not be extrapolated beyond birds. For instance, in Chapter 3, distinct animal groups would likely have different levels of sensitivity to climate change (Ma et al., 2024). Ectothermic groups - such as reptiles, amphibians and fish – have typically shown a narrower range of thermal tolerance, higher likelihood of range shifts and higher vulnerability to extreme heat events (Deutsch et al., 2008; Verheyen & Stoks, 2019). Furthermore, more sessile animal groups - such as reptiles and amphibians – have also exhibited increased vulnerability to future climate change due to a reduced dispersal capacity (Thompson & Fronhofer, 2019). Lastly, when assessing impacts of future climate on frugivory networks in Chapter 4, seed dispersal by mammals is excluded in my analyses despite this animal group significantly contributing to this ecosystem function, particularly in tropical systems (Jordano et al., 2011; Lim et al., 2020a). As data availability improves, future work could look to further expand upon methods and analyses presented in this thesis, across other animal groups.

Ecological data rarely offers a fully accurate and comprehensive picture and should therefore be considered as a non-random sample with the associated level of bias. Throughout this thesis I have tried to acknowledge sampling biases in the various datasets used. More effort however should be dedicated towards quantifying bias across important ecological datasets, to better identify the direction and magnitude of biases and their potential influence on ecological interpretations. While this thesis has focused primarily on climate change, it is important to recognize that multiple other factors are currently driving biodiversity loss and are projected to continue well into the future

(Jaureguiberry et al., 2022). Furthermore, interactions among these drivers are likely to compound their impacts; for instance, species' responses to climate change may be intensified when populations have already experienced extensive land-use change (J. J. Williams et al., 2022). Future work could expand upon the analyses presented in this thesis by incorporating additional drivers of biodiversity loss and further investigating the synergistic interactions among them.

The aim of this thesis was to significantly contribute to knowledge gaps in how species response to future climate change is modelled and interpreted. I generated and tested a global climate niche dataset intended to support future research on climate change impacts on ecosystems. Local climate features were shown to be strongly predictive of past avian population trends, potentially identifying vulnerability to climate change below the species-level climate niche. Additionally, I found that future climate change is likely to cause widespread disruption of frugivory networks at the macroscale, although regions with high trait diversity may exhibit greater resilience through interaction rewiring. Across this PhD thesis, I have undertaken analyses investigating past empirical trends and also run future simulations of climate impacts. Analyses have been undertaken at a species, population and network level, to offer a wide range of ecological resolutions. The continued loss of global biodiversity will have profound and far-reaching consequences for humanity. However, through advancing our understanding of biodiversity responses to climate change, this work contributes to informing more effective conservation strategies and policy interventions aimed at mitigating these escalating threats to the natural world.

# Bibliography


Advani, N. K. (2023). Assessing species vulnerability to climate change, and implementing practical solutions. *Biological Conservation*, *286*, 110284. https://doi.org/10.1016/j.biocon.2023.110284

Albrecht, J., Classen, A., Vollstädt, M. G. R., Mayr, A., Mollel, N. P., Schellenberger Costa, D., Dulle, H. I., Fischer, M., Hemp, A., Howell, K. M., Kleyer, M., Nauss, T., Peters, M. K., Tschapka, M., Steffan-Dewenter, I., Böhning-Gaese, K., & Schleuning, M. (2018). Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. *Nature Communications*, *9*(1), 3177. https://doi.org/10.1038/s41467-018-05610-w

Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review*, *1*, 108–140.

Almond, R. E. A., Grooten, M., Juffe Bignoli, D., & Peterson, T. (2022). *Living Planet Report 2022 – Building a nature positive society.* .

Antão, L. H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, Ø. H., Heliölä, J., Henttonen, H., Huitu, O., Korpimäki, E., Kuussaari, M., Lehikoinen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., … Laine, A.-L. (2022). Climate change reshuffles northern species within their niches. *Nature Climate Change*, *12*(6), 587–592. https://doi.org/10.1038/s41558-022-01381-x

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., & Hoegh-Guldberg, O. (2008). Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences*, *105*(45), 17442–17446. https://doi.org/10.1073/pnas.0804478105

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*(10), 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611). https://doi.org/10.1126/science.abn7950

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Bastien-Olvera, B. A., Conte, M. N., Dong, X., Briceno, T., Batker, D., Emmerling, J., Tavoni, M., Granella, F., & Moore, F. C. (2024). Unequal climate impacts on global values of natural capital. *Nature*, *625*(7996), 722–727. https://doi.org/10.1038/s41586-023-06769-z

Bastille-Rousseau, G., Schaefer, J. A., Peers, M. J. L., Ellington, E. H., Mumma, M. A., Rayl, N. D., Mahoney, S. P., & Murray, D. L. (2018). Climate change can alter predator–prey dynamics and population viability of prey. *Oecologia*, *186*(1), 141–150. https://doi.org/10.1007/s00442-017-4017-y

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bender, I. M. A., Kissling, W. D., Böhning-Gaese, K., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T., Dehling, D. M., & Schleuning, M. (2019). Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. *Scientific Reports*, *9*(1), 17708. https://doi.org/10.1038/s41598-019-53409-6

Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). Trait SDMs: species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, *222*(4), 1757–1765. https://doi.org/10.1111/nph.15716

Bennett, J. M., Clarke, R. H., Thomson, J. R., & Mac Nally, R. (2014). Variation in abundance of nectarivorous birds: does a competitive despot interfere with flower tracking? *Journal of Animal Ecology*, *83*(6), 1531–1541. https://doi.org/10.1111/1365-2656.12245

Bergman, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, *1*, 595–708.

Birch, L. C. (1953). Experimental background to the study of the distribution and abundance of insects. *Evolution*, *7*(2), 136–144. https://doi.org/10.1111/j.1558-5646.1953.tb00072.x

BirdLife International and Handbook of the Birds of the World. (2021). *Birdlife species distribution maps of the world*. http://datazone.birdlife.org/species/requestdis

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*(7), 1050–1063. https://doi.org/10.1111/ele.13525

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, *23*(5), 595–609. https://doi.org/10.1111/geb.12146

Blonder, B., Morrow, C. B., Brown, S., Butruille, G., Chen, D., Laini, A., & Harris, D. J. (2023). *hypervolume: High Dimensional Geometry, Set Operations, Projection, and Inference Using Kernel Density Estimation, Support Vector Machines, and Convex Hulls* (3.1.3).

Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). BIOCLIM : the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, *20*(1), 1–9. https://doi.org/10.1111/ddi.12144

Bovo, A. A. A., Ferraz, K. M. P. M. B., Magioli, M., Alexandrino, E. R., Hasui, É., Ribeiro, M. C., & Tobias, J. A. (2018). Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest. *Perspectives in Ecology and Conservation*, *16*(2), 90–96. https://doi.org/10.1016/j.pecon.2018.03.004

Boyce, A. J., Shakya, S., Sheldon, F. H., Moyle, R. G., & Martin, T. E. (2019). Biotic interactions are the dominant drivers of phylogenetic and functional structure in bird communities along a tropical elevational gradient. *The Auk*, *136*(4), 1–14. https://doi.org/10.1093/auk/ukz054

Bregman, T. P., Lees, A. C., MacGregor, H. E. A., Darski, B., de Moura, N. G., Aleixo, A., Barlow, J., & Tobias, J. A. (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844). https://doi.org/10.1098/rspb.2016.1289

Bregman, T. P., Lees, A. C., Seddon, N., Macgregor, H. E. A., Darski, B., Aleixo, A., Bonsall, M. B., & Tobias, J. A. (2015). Species interactions regulate the collapse of

biodiversity and ecosystem function in tropical forest fragments. In *Ecology* (Vol. 96, Issue 10).
Brook, E. (2008). Windows on the greenhouse. *Nature*, *453*(7193), 291–292. https://doi.org/10.1038/453291a
Brooker, R. W., Travis, J. M. J., Clark, E. J., & Dytham, C. (2007). Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, *245*(1), 59–65. https://doi.org/10.1016/j.jtbi.2006.09.033
Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*(1), 8–22. https://doi.org/10.1111/jbi.12228
Burnham, K., & Anderson, D. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer.
Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. In *Journal of Applied Ecology* (Vol. 48, Issue 5, pp. 1079–1087). https://doi.org/10.1111/j.1365-2664.2011.02048.x
Calow, P. (1987). Towards a Definition of Functional Ecology. *Functional Ecology*, *1*(1), 57. https://doi.org/10.2307/2389358
Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P. W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W. W. L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., … Ha, M. (2023). *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.* https://doi.org/10.59327/IPCC/AR6-9789291691647
Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., MacE, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. In *Nature* (Vol. 486, Issue 7401, pp. 59–67). Nature Publishing Group. https://doi.org/10.1038/nature11148
Cardinale, B. J., Gonzalez, A., Allington, G. R. H., & Loreau, M. (2018). Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biological Conservation*, *219*, 175–183. https://doi.org/10.1016/j.biocon.2017.12.021
Cernansky, R. (2017). *The biodiversity revolution*. *546*.
Chesser, R. T., & Levey, D. J. (1998). Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. *The American Naturalist*, *152*(2), 311–319.
Cohen, J., & Jetz, W. (2023). Diverse strategies for tracking seasonal environmental niches at hemispheric scale. *Global Ecology and Biogeography*, *32*(9), 1549–1560. https://doi.org/10.1111/geb.13722
Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R., & Baillie, J. E. M. (2009). Monitoring Change in Vertebrate Abundance: the Living Planet Index. *Conservation Biology*, *23*(2), 317–327. https://doi.org/10.1111/j.1523-1739.2008.01117.x
Cooney, C. R., Seddon, N., & Tobias, J. A. (2016). Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology*, *85*(4), 869–878. https://doi.org/10.1111/1365-2656.12530
Coxen, C. L., Frey, J. K., Carleton, S. A., & Collins, D. P. (2017). Species distribution models for a migratory bird based on citizen science and satellite tracking data. *Global*

*Ecology and Conservation*, *11*, 298–311. https://doi.org/10.1016/j.gecco.2017.08.001
Crutzen, P. J. (2002). Geology of mankind. *Nature*, *415*(6867), 23–23. https://doi.org/10.1038/415023a
Daskalova, G. N., Myers-Smith, I. H., & Godlee, J. L. (2020). Rare and common vertebrates span a wide spectrum of population trends. *Nature Communications*, *11*(1), 4394. https://doi.org/10.1038/s41467-020-17779-0
De Vos, J. M., Joppa, L. N., Gittleman, J. L., Stephens, P. R., & Pimm, S. L. (2015). Estimating the normal background rate of species extinction. *Conservation Biology*, *29*(2), 452–462. https://doi.org/10.1111/cobi.12380
Dehling, D. M., Jordano, P., Schaefer, H. M., Böhning-Gaese, K., & Schleuning, M. (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1823), 20152444. https://doi.org/10.1098/rspb.2015.2444
Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105
Di Marco, M., Harwood, T. D., Hoskins, A. J., Ware, C., Hill, S. L. L., & Ferrier, S. (2019). Projecting impacts of global climate and land-use scenarios on plant biodiversity using compositional-turnover modelling. *Global Change Biology*, *25*(8), 2763–2778. https://doi.org/10.1111/gcb.14663
Díaz, S., Fargione, J., Chapin, F. S., & Tilman, D. (2006). Biodiversity Loss Threatens Human Well-Being. *PLoS Biology*, *4*(8), e277. https://doi.org/10.1371/journal.pbio.0040277
Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaat, F., Schröter, M., Lavorel, S., … Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, *359*(6373), 270–272. https://doi.org/10.1126/science.aap8826
Díaz-Siefer, P., Olmos-Moya, N., Fontúrbel, F. E., Lavandero, B., Pozo, R. A., & Celis-Diez, J. L. (2022). Bird-mediated effects of pest control services on crop productivity: a global synthesis. In *Journal of Pest Science* (Vol. 95, Issue 2, pp. 567–576). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s10340-021-01438-4
Donoso, I., Schleuning, M., García, D., & Fründ, J. (2017). Defaunation effects on plant recruitment depend on size matching and size trade-offs in seed-dispersal networks. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855), 1–10. https://doi.org/10.1098/rspb.2016.2664
Dormann, C. F., Calabrese, J. M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K., Beale, C. M., Ciuti, S., Elith, J., Gerstner, K., Guelat, J., Keil, P., Lahoz-Monfort, J. J., Pollock, L. J., Reineking, B., Roberts, D. R., Schröder, B., Thuiller, W., Warton, D. I., … Hartig, F. (2018). Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs*, *88*(4), 485–504. https://doi.org/10.1002/ecm.1309
Dornelas, M., Antão, L. H., Moyes, F., Bates, A. E., Magurran, A. E., Adam, D., Akhmetzhanova, A. A., Appeltans, W., Arcos, J. M., Arnold, H., Ayyappan, N., Badihi, G., Baird, A. H., Barbosa, M., Barreto, T. E., Bässler, C., Bellgrove, A., Belmaker, J., Benedetti-Cecchi, L., … Zettler, M. L. (2018). BioTIME: A database of biodiversity

time series for the Anthropocene. *Global Ecology and Biogeography*, *27*(7), 760–786. https://doi.org/10.1111/geb.12729
Drever, M. C., Aitken, K. E. H., Norris, A. R., & Martin, K. (2008). Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biological Conservation*, *141*(3), 624–634. https://doi.org/10.1016/j.biocon.2007.12.004
Duarte, M., Guerrero, P. C., Arroyo, M. T. K., & Bustamante, R. O. (2019). Niches and climate-change refugia in hundreds of species from one of the most arid places on Earth. *PeerJ*, *7*, e7409. https://doi.org/10.7717/peerj.7409
Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159
Ellis-Soto, D., Merow, C., Amatulli, G., Parra, J. L., & Jetz, W. (2021). Continental-scale 1 km hummingbird diversity derived from fusing point records with lateral and elevational expert information. *Ecography*, *44*(4), 640–652. https://doi.org/10.1111/ecog.05119
Elton, C. (1927). *Animal Ecology*. The University of Chicago Press.
Etard, A., Morrill, S., & Newbold, T. (2020). Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography*, *29*(12), 2143–2158. https://doi.org/10.1111/geb.13184
Evans, M. E. K., Dey, S. M. N., Heilman, K. A., Tipton, J. R., DeRose, R. J., Klesse, S., Schultz, E. L., & Shaw, J. D. (2024). Tree rings reveal the transient risk of extinction hidden inside climate envelope forecasts. *Proceedings of the National Academy of Sciences*, *121*(24). https://doi.org/10.1073/pnas.2315700121
Eviner, V. T., & Chapin, F. S. (2003). Functional Matrix: A Conceptual Framework for Predicting Multiple Plant Effects on Ecosystem Processes. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 34, pp. 455–485). Annual Reviews Inc. https://doi.org/10.1146/annurev.ecolsys.34.011802.132342
Eyres, A., Böhning-Gaese, K., & Fritz, S. A. (2017). Quantification of climatic niches in birds: adding the temporal dimension. *Journal of Avian Biology*, *48*(12), 1517–1531. https://doi.org/10.1111/jav.01308
Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
Findlay, H. S., & Turley, C. (2021). Ocean acidification and climate change. In *Climate Change* (pp. 251–279). Elsevier. https://doi.org/10.1016/B978-0-12-821575-3.00013-X
Fourcade, Y. (2016). Comparing species distributions modelled from occurrence data and from expert-based range maps. Implication for predicting range shifts with climate change. *Ecological Informatics*, *36*, 8–14. https://doi.org/10.1016/j.ecoinf.2016.09.002
Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, *375*, 210–214. https://doi.org/10.1126/science.abk3510
Friedman, N. R., Harmáčková, L., Economo, E. P., & Remeš, V. (2017). Smaller beaks for colder winters: thermoregulation drives beak size evolution in Australasian songbirds. *Evolution*, *71*(8), 2120–2129. https://doi.org/10.1111/evo.13274
Fröhlich, A., Kotowska, D., Martyka, R., & Symonds, M. R. E. (2023). Allometry reveals trade-offs between Bergmann's and Allen's rules, and different avian adaptive

strategies for thermoregulation. *Nature Communications*, *14*(1), 1–13. https://doi.org/10.1038/s41467-023-36676-w
García, M. B., Domingo, D., Pizarro, M., Font, X., Gómez, D., & Ehrlén, J. (2020). Rocky habitats as microclimatic refuges for biodiversity. A close-up thermal approach. *Environmental and Experimental Botany*, *170*, 103886. https://doi.org/10.1016/j.envexpbot.2019.103886
Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis*, *1*(3). https://doi.org/10.1214/06-BA117A
Giannini, T. C., Costa, W. F., Cordeiro, G. D., Imperatriz-Fonseca, V. L., Saraiva, A. M., Biesmeijer, J., & Garibaldi, L. A. (2017). Projected climate change threatens pollinators and crop production in Brazil. *PLoS ONE*, *12*(8). https://doi.org/10.1371/journal.pone.0182274
Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002
Godínez-Alvarez, H., Ríos-Casanova, L., & Peco, B. (2020). Are large frugivorous birds better seed dispersers than medium- and small-sized ones? Effect of body mass on seed dispersal effectiveness. In *Ecology and Evolution* (Vol. 10, Issue 12, pp. 6136–6143). John Wiley and Sons Ltd. https://doi.org/10.1002/ece3.6285
Gonçalves, G. R., Santos, M. P. D., Cerqueira, P. V., Juen, L., & Bispo, A. Â. (2017). The relationship between bird distribution patterns and environmental factors in an ecotone area of northeast Brazil. *Journal of Arid Environments*, *140*, 6–13. https://doi.org/10.1016/j.jaridenv.2017.01.004
Gosper, C. R., Stansbury, C. D., & Vivian-Smith, G. (2005). Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. In *Diversity and Distributions* (Vol. 11, Issue 6, pp. 549–558). https://doi.org/10.1111/j.1366-9516.2005.00195.x
Gregory, R. D., & Strien, A. van. (2010). Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science*, *9*(1), 3–22. https://doi.org/10.2326/osj.9.3
Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1454), 269–288. https://doi.org/10.1098/rstb.2004.1602
Grinder, R. M., & Wiens, J. J. (2023). Niche width predicts extinction from climate change and vulnerability of tropical species. *Global Change Biology*, *29*(3), 618–630. https://doi.org/10.1111/gcb.16486
Grinnell, J. (1917). *The Niche-Relationships of the California Thrasher* (Vol. 34, Issue 4). https://www.jstor.org/stable/4072271
Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences*, *114*(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114
Guisan, A., & Thuiller, W. (2005a). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., & Thuiller, W. (2005b). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Grenfell, B. T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, *430*(6995), 71–75. https://doi.org/10.1038/nature02708

Hanley, P. A., Arndt, S. K., Livesley, S. J., & Szota, C. (2021). Relating the climate envelopes of urban tree species to their drought and thermal tolerance. *Science of The Total Environment*, *753*, 142012. https://doi.org/10.1016/j.scitotenv.2020.142012

Hawkins, B. A., Diniz-Filho, J. A. F., Jaramillo, C. A., & Soeller, S. A. (2007). Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, *170*(2), 16–27. https://doi.org/10.1086/519009

Hollenbeck, E. C., & Sax, D. F. (2024). Experimental evidence of climate change extinction risk in Neotropical montane epiphytes. *Nature Communications*, *15*(1), 6045. https://doi.org/10.1038/s41467-024-49181-5

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *PNAS*, *106*, 19659–19665.

Hooper, H. L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S. J., Hutchinson, T. H., & Sibly, R. M. (2008). The ecological niche of Daphnia Magnia characterized by population growth rate. *Ecology*, *89*(4), 1015–1022. https://doi.org/10.1890/07-0559.1

Howard, C., Marjakangas, E.-L., Morán-Ordóñez, A., Milanesi, P., Abuladze, A., Aghababyan, K., Ajder, V., Arkumarev, V., Balmer, D. E., Bauer, H.-G., Beale, C. M., Bino, T., Boyla, K. A., Burfield, I. J., Burke, B., Caffrey, B., Chodkiewicz, T., Del Moral, J. C., Mazal, V. D., … Willis, S. G. (2023). Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. *Nature Communications*, *14*(1), 4304. https://doi.org/10.1038/s41467-023-39093-1

Hughes, A. C. (2023). The Post-2020 Global Biodiversity Framework: How did we get here, and where do we go next? *Integrative Conservation*, *2*(1), 1–9. https://doi.org/10.1002/inc3.16

Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, *104*(33), 13384–13389. https://doi.org/10.1073/pnas.0704469104

Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., Doelman, J., Fisk, J., Fujimori, S., Goldewijk, K. K., Hasegawa, T., Havlik, P., Heinimann, A., Humpenöder, F., Jungclaus, J., Kaplan, J., Krisztin, T., Lawrence, D., Lawrence, P., … Zhang, X. (2019). Harmonization of Global Land Use Change and Management for the Period 850-2015. *Earth System Grid Federation*.

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., MacE, G. M., Wardle, D. A., O'Connor, M. I., Duffy, J. E., Turnbull, L. A., Thompson, P. L., & Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. In *Nature* (Vol. 546, Issue 7656, pp. 65–72). Nature Publishing Group. https://doi.org/10.1038/nature22899

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions.

*Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19685–19692. https://doi.org/10.1073/pnas.0901644106
Jacobson, A. P., Riggio, J., M. Tait, A., & E. M. Baillie, J. (2019). Global areas of low human impact ('Low Impact Areas') and fragmentation of the natural world. *Scientific Reports*, *9*(1), 14179. https://doi.org/10.1038/s41598-019-50558-6
Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45). https://doi.org/10.1126/sciadv.abm9982
Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631
Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*(6), 1211–1219. https://doi.org/10.1371/journal.pbio.0050157
Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S. E., & Couvet, D. (2007). Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology*, *13*(8), 1672–1684. https://doi.org/10.1111/j.1365-2486.2007.01386.x
Jiguet, F., Gregory, R. D., Devictor, V., Green, R. E., Vorísek, P., Van Strien, A., & Couvet, D. (2010). Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, *16*(2), 497–505. https://doi.org/10.1111/j.1365-2486.2009.01963.x
Jiguet, F., Julliard, R., Thomas, C. D., Dehorter, O., Newson, S. E., & Couvet, D. (2006). Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters*, *9*(12), 1321–1330. https://doi.org/10.1111/j.1461-0248.2006.00986.x
Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Gutierrez, V. R., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S. T., & Fink, D. (2019). Best practices for making reliable inferences from citizen science data: Case study using eBird to estimate species distributions. *BioRxiv*. https://doi.org/10.1101/574392
Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Ruiz Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S. T., & Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*, *27*(7), 1265–1277. https://doi.org/10.1111/ddi.13271
Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., … Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*(9), 2648–2648. https://doi.org/10.1890/08-1494.1
Jordano, P., Forget, P. M., Lambert, J. E., Böhning-Gaese, K., Traveset, A., & Wright, S. J. (2011). Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, *7*(3), 321–323. https://doi.org/10.1098/rsbl.2010.0986
Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1–20. https://doi.org/10.1038/sdata.2017.122

Karp, D. S., Frishkoff, L. O., Echeverri, A., Zook, J., Juárez, P., & Chan, K. M. A. (2018). Agriculture erases climate-driven β-diversity in Neotropical bird communities. *Global Change Biology*, *24*(1), 338–349. https://doi.org/10.1111/gcb.13821

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Göldel, B., Lim, J. Y., Onstein, R. E., & Svenning, J.-C. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data*, *6*(1), 178. https://doi.org/10.1038/s41597-019-0189-0

Kissling, W. D., Böhning-Gaese, K., & Jetz, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography*, *18*(2), 150–162. https://doi.org/10.1111/j.1466-8238.2008.00431.x

Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic levels at macroscales: retrospective and future directions. *Ecography*, *38*(4), 346–357. https://doi.org/10.1111/ecog.00819

Kohli, B. A., & Jarzyna, M. A. (2021). Pitfalls of ignoring trait resolution when drawing conclusions about ecological processes. *Global Ecology and Biogeography*, *30*(5), 1139–1152. https://doi.org/10.1111/geb.13275

Kuczynski, L., Ontiveros, V. J., & Hillebrand, H. (2023). Biodiversity time series are biased towards increasing species richness in changing environments. *Nature Ecology & Evolution*, *7*(7), 994–1001. https://doi.org/10.1038/s41559-023-02078-w

Kweku, D., Bismark, O., Maxwell, A., Desmond, K., Danso, K., Oti-Mensah, E., Quachie, A., & Adormaa, B. (2018). Greenhouse Effect: Greenhouse Gases and Their Impact on Global Warming. *Journal of Scientific Research and Reports*, *17*(6), 1–9. https://doi.org/10.9734/JSRR/2017/39630

La Sorte, F. A., & Jetz, W. (2012). Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, *81*(4), 914–925. https://doi.org/10.1111/j.1365-2656.2012.01958.x

La Sorte, F. A., & Somveille, M. (2020). Survey completeness of a global citizen-science database of bird occurrence. *Ecography*, *43*(1), 34–43.

Lavergne, S., Evans, M. E. K., Burfield, I. J., Jiguet, F., & Thuiller, W. (2013). Are species' responses to global change predicted by past niche evolution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1610), 1–11. https://doi.org/10.1098/rstb.2012.0091

Lehikoinen, A., Lindström, Å., Santangeli, A., Sirkiä, P. M., Brotons, L., Devictor, V., Elts, J., Foppen, R. P. B., Heldbjerg, H., Herrando, S., Herremans, M., Hudson, M. R., Jiguet, F., Johnston, A., Lorrilliere, R., Marjakangas, E., Michel, N. L., Moshøj, C. M., Nellis, R., … van Turnhout, C. (2021). Wintering bird communities are tracking climate change faster than breeding communities. *Journal of Animal Ecology*, *90*(5), 1085–1095. https://doi.org/10.1111/1365-2656.13433

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*(7542), 171–180. https://doi.org/10.1038/nature14258

Li, C., Zhou, M., Dou, T., Zhu, T., Yin, H., & Liu, L. (2021). Convergence of global hydrothermal pattern leads to an increase in vegetation net primary productivity. *Ecological Indicators*, *132*, 108282. https://doi.org/10.1016/j.ecolind.2021.108282

Liang, J., Ding, Z., Zhang, C., Hu, H., Duo, H., & Tang, H. (2017). Bird diversity spatial distribution patterns and hotspots in Maixiu Area of Sanjiangyuan National Nature Reserve, Qinghai Province. *Biodiversity Science*, *25*(3), 294–303. https://doi.org/10.17520/biods.2016252

Lim, J. Y., Svenning, J. C., Göldel, B., Faurby, S., & Kissling, W. D. (2020a). Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nature Communications*, *11*(1), 4904. https://doi.org/10.1038/s41467-020-18530-5

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Lu, M., & Jetz, W. (2023). Scale-sensitivity in the measurement and interpretation of environmental niches. *Trends in Ecology and Evolution*, *38*(6), 554–567. https://doi.org/10.1016/j.tree.2023.01.003

Lu, M., Winner, K., & Jetz, W. (2021). A unifying framework for quantifying and comparing n-dimensional hypervolumes. *Methods in Ecology and Evolution*, *12*(10), 1953–1968. https://doi.org/10.1111/2041-210X.13665

Luyssaert, S., Jammet, M., Stoy, P. C., Estel, S., Pongratz, J., Ceschia, E., Churkina, G., Don, A., Erb, K., Ferlicoq, M., Gielen, B., Grünwald, T., Houghton, R. A., Klumpp, K., Knohl, A., Kolb, T., Kuemmerle, T., Laurila, T., Lohila, A., … Dolman, A. J. (2014). Land management and land-cover change have impacts of similar magnitude on surface temperature. *Nature Climate Change*, *4*(5), 389–393. https://doi.org/10.1038/nclimate2196

Ma, X., Dong, R., Hughes, A., Corlett, R. T., Svenning, J.-C., & Feng, G. (2024). Population trends are more strongly linked to environmental change and species traits in birds than mammals. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2033). https://doi.org/10.1098/rspb.2024.1395

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press.

Mace, G. M., Barrett, M., Burgess, N. D., Cornell, S. E., Freeman, R., Grooten, M., & Purvis, A. (2018). Aiming higher to bend the curve of biodiversity loss. In *Nature Sustainability* (Vol. 1, Issue 9, pp. 448–451). Nature Publishing Group. https://doi.org/10.1038/s41893-018-0130-0

Maclean, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R., & Wilson, R. J. (2015). Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, *24*(11), 1340–1350. https://doi.org/10.1111/geb.12359

Manes, S., Costello, M. J., Beckett, H., Debnath, A., Devenish-Nelson, E., Grey, K.-A., Jenkins, R., Khan, T. M., Kiessling, W., Krause, C., Maharaj, S. S., Midgley, G. F., Price, J., Talukdar, G., & Vale, M. M. (2021). Endemism increases species' climate change risk in areas of global biodiversity importance. *Biological Conservation*, *257*, 109070. https://doi.org/10.1016/j.biocon.2021.109070

Manthey, J., Campbell, L., Saupe, E., Soberón, J., Hensz, C., Myers, C., Owens, H., Ingenloff, K., Peterson, A., Barve, N., Lira-Noriega, A., & Barve, V. (2015). A test of niche centrality as a determinant of population trends and conservation status in

threatened and endangered North American birds. *Endangered Species Research*, *26*(3), 201–208. https://doi.org/10.3354/esr00646

Marsh, C. J., Sica, Y. V., Burgin, C. J., Dorman, W. A., Anderson, R. C., del Toro Mijares, I., Vigneron, J. G., Barve, V., Dombrowik, V. L., Duong, M., Guralnick, R., Hart, J. A., Maypole, J. K., McCall, K., Ranipeta, A., Schuerkmann, A., Torselli, M. A., Lacher, T., Mittermeier, R. A., … Jetz, W. (2022). Expert range maps of global mammal distributions harmonised to three taxonomic authorities. *Journal of Biogeography*, *49*(5), 979–992. https://doi.org/10.1111/jbi.14330

Mason, N. W., Mouillot, D., Lee, W. G., Bastow Wilson Mason, J., H Mason, N. W., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, *111*.

Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., Barlow, K. E., Botham, M. S., & Pearce-Higgins, J. W. (2017). Impacts of climate change on national biodiversity population trends. *Ecography*, *40*(10), 1139–1151. https://doi.org/10.1111/ecog.02411

Martins, P. M., Anderson, M. J., Sweatman, W. L., & Punnett, A. J. (2024). Significant shifts in latitudinal optima of North American birds. *Proceedings of the National Academy of Sciences*, *121*(15). https://doi.org/10.1073/pnas.2307525121

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mattila, A. L. K., Opedal, Ø. H., Hällfors, M. H., Pietikäinen, L., Koivusaari, S. H. M., & Hyvärinen, M.-T. (2024). The potential for evolutionary rescue in an Arctic seashore plant threatened by climate change. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2032). https://doi.org/10.1098/rspb.2024.1351

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *7*(1), 1902. https://doi.org/10.1038/s41598-017-02045-z

McFadden, I. R., Fritz, S. A., Zimmermann, N. E., Pellissier, L., Kissling, W. D., Tobias, J. A., Schleuning, M., & Graham, C. H. (2022). Global plant-frugivore trait matching is shaped by climate and biogeographic history. *Ecology Letters*, *25*(3), 686–696. https://doi.org/10.1111/ele.13890

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McNamara, J. M., Higginson, A. D., & Verhulst, S. (2016). The influence of the starvation–predation trade-off on the relationship between ambient temperature and body size among endotherms. *Journal of Biogeography*, *43*(4), 809–819. https://doi.org/10.1111/jbi.12695

McQueen, A., Klaassen, M., Tattersall, G. J., Atkinson, R., Jessop, R., Hassell, C. J., Christie, M., & Symonds, M. R. E. (2022). Thermal adaptation best explains Bergmann's and Allen's Rules across ecologically diverse shorebirds. *Nature Communications*, *13*(1), 1–12. https://doi.org/10.1038/s41467-022-32108-3

Mekonen, S. (2017). Birds as Biodiversity and Environmental Indicator. In *Journal of Natural Sciences Research www.iiste.org ISSN* (Vol. 7, Issue 21). Online. www.iiste.org

Merow, C., Wilson, A. M., & Jetz, W. (2017). Integrating occurrence data and expert maps for improved species range predictions. *Global Ecology and Biogeography*, *26*(2), 243–258. https://doi.org/10.1111/geb.12539

Meyer, C., Kreft, H., Guralnick, R., & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nature Communications*, *6*, 1. https://doi.org/10.1038/ncomms9221

Miller, D. A. W., Grant, E. H. C., Muths, E., Amburgey, S. M., Adams, M. J., Joseph, M. B., Waddle, J. H., Johnson, P. T. J., Ryan, M. E., Schmidt, B. R., Calhoun, D. L., Davis, C. L., Fisher, R. N., Green, D. M., Hossack, B. R., Rittenhouse, T. A. G., Walls, S. C., Bailey, L. L., Cruickshank, S. S., … Sigafus, B. H. (2018). Quantifying climate sensitivity and climate-driven change in North American amphibian communities. *Nature Communications*, *9*(1), 3926. https://doi.org/10.1038/s41467-018-06157-6

Miller, N. A., & Stillman, J. H. (2012). Physiological Optima and Critical Limits. *Nature Education Knowledge*, *3*(10), 1.

Miranda, L. S., Imperatriz-Fonseca, V. L., & Giannini, T. C. (2019). Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. *PLoS ONE*, *14*(4). https://doi.org/10.1371/journal.pone.0215229

Morrison, C. A., Robinson, R. A., & Pearce-Higgins, J. W. (2016). Winter wren populations show adaptation to local climate. *Royal Society Open Science*, *3*(6), 160250. https://doi.org/10.1098/rsos.160250

Myhre, G., Alterskjær, K., Stjern, C. W., Hodnebrog, Ø., Marelle, L., Samset, B. H., Sillmann, J., Schaller, N., Fischer, E., Schulz, M., & Stohl, A. (2019). Frequency of extreme precipitation increases extensively with event rareness under global warming. *Scientific Reports*, *9*(1), 16063. https://doi.org/10.1038/s41598-019-52277-4

Naeem, S., Prager, C., Weeks, B., Varga, A., Flynn, D. F. B., Griffin, K., Muscarella, R., Palmer, M., Wood, S., & Schuster, W. (2016). Biodiversity as a multidimensional construct: a review, framework and case study of herbivory's impact on plant biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20153005. https://doi.org/10.1098/rspb.2015.3005

Neilson, R. P., Pitelka, L. F., Solomon, A. M., Nathan, R., Midgley, G. F., Fragoso, J. M., Lischke, H., & Thompson, K. (2005). Forecasting regional to global plant migration in response to climate change. *Bioscience*, *55*(9), 749–759.

Neuschulz, E. L., Mueller, T., Schleuning, M., & Böhning-Gaese, K. (2016). Pollination and seed dispersal are the most threatened processes of plant regeneration. *Scientific Reports*, *6*. https://doi.org/10.1038/srep29839

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), 20180792. https://doi.org/10.1098/rspb.2018.0792

Newbold, T., Adams, G. L., Albaladejo Robles, G., Boakes, E. H., Braga Ferreira, G., Chapman, A. S. A., Etard, A., Gibb, R., Millard, J., Outhwaite, C. L., & Williams, J. J. (2019). Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerging Topics in Life Sciences*, *3*(2), 207–219. https://doi.org/10.1042/ETLS20180135

Nowak, L., Kissling, W. D., Bender, I. M. A., Dehling, D. M., Töpfer, T., Böhning-Gaese, K., & Schleuning, M. (2019). Projecting consequences of global warming for the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient. *Diversity and Distributions*, *25*(9), 1362–1374. https://doi.org/10.1111/ddi.12946

Nowak, L., Schleuning, M., Bender, I. M. A., Böhning-Gaese, K., Dehling, D. M., Fritz, S. A., Kissling, W. D., Mueller, T., Neuschulz, E. L., Pigot, A. L., Sorensen, M. C., & Donoso, I. (2022). Avian seed dispersal may be insufficient for plants to track future temperature change on tropical mountains. *Global Ecology and Biogeography*, *31*(5), 848–860. https://doi.org/10.1111/geb.13456

Omann, I., Stocker, A., & Jäger, J. (2009). Climate change as a threat to biodiversity: An application of the DPSIR approach. *Ecological Economics*, *69*(1), 24–31. https://doi.org/10.1016/j.ecolecon.2009.01.003

Ozsanlav-Harris, L., Burgess, M. D., Hilton, G. M., & Bearhop, S. (2023). Changes in the spatial patterns of avian migrations: evidence, mechanisms and causes. *Diversity and Distributions*, *29*(12), 1527–1545. https://doi.org/10.1111/ddi.13785

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, *7*(3), 205–208. https://doi.org/10.1038/nclimate3223

Pang, S. E. H., Slik, J. W. F., Zurell, D., & Webb, E. L. (2023). The clustering of spatially associated species unravels patterns in tropical tree species distributions. *Ecosphere*, *14*(6). https://doi.org/10.1002/ecs2.4589

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579–583. https://doi.org/10.1038/21181

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*(5), 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports*, *7*(1), 17966. https://doi.org/10.1038/s41598-017-17966-y

Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Moya-Perez, J. M., Carreño, M. F., Guisan, A., & Lloret, F. (2021). Temporal variability is key to modelling the climatic niche. *Diversity and Distributions*, *27*(3), 473–484. https://doi.org/10.1111/ddi.13207

Petchey, O. L., Hector, A., & Gaston, K. J. (2004). How do different measures of funtional diversity perform? *Ecology*, *85*(3), 847–857. https://doi.org/10.1890/03-0226

Peterson, A. T. (2001). Predicting species' geographic distributions based on ecological niche modelling. *The Condor*, *103*(3), 599–605. https://doi.org/10.1093/condor/103.3.599

Peterson, A. T. (2006). Uses and Requirements of Ecological Niche Models and Related Distributional Models. *Biodiversity Informatics*, *3*(0). https://doi.org/10.17161/bi.v3i0.29

Peterson, A. T., Soberón, J., & Sánchez-Cordero, V. (1999). Conservatism of Ecological Niches in Evolutionary Time. *Science*, *285*(5431), 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Peterson, A., & Vieglais, D. (2001). Predicting species invasions using ecological niche modeling. *BioScience*, *51*(5), 363–371.

Pettorelli, N., Chauvenet, A. L. M., Duffy, J. P., Cornforth, W. A., Meillere, A., & Baillie, J. E. M. (2012). Tracking the effect of climate change on ecosystem functioning using protected areas: Africa as a case study. *Ecological Indicators*, *20*, 269–276. https://doi.org/10.1016/j.ecolind.2012.02.014

Pettorelli, N., Graham, N. A. J., Seddon, N., Maria da Cunha Bustamante, M., Lowton, M. J., Sutherland, W. J., Koldewey, H. J., Prentice, H. C., & Barlow, J. (2021). Time to integrate global climate change and biodiversity science-policy agendas. *Journal of Applied Ecology*, *58*(11), 2384–2393. https://doi.org/10.1111/1365-2664.13985

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pigot, A. L., Owens, I. P. F., & Orme, C. D. L. (2010). The environmental limits to geographic range expansion in birds. *Ecology Letters*, *13*(6), 705–715. https://doi.org/10.1111/j.1461-0248.2010.01462.x

Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., Seddon, N., Trisos, C. H., Weeks, B. C., & Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology and Evolution*, *4*(2), 230–239. https://doi.org/10.1038/s41559-019-1070-4

Pigot, A. L., & Tobias, J. A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, *16*(3), 330–338. https://doi.org/10.1111/ele.12043

Pigot, A. L., & Tobias, J. A. (2015). Dispersal and the transition to sympatry in vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1799), 1–8. https://doi.org/10.1098/rspb.2014.1929

Pollock, H. S., Brawn, J. D., & Cheviron, Z. A. (2021). Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. *Functional Ecology*, *35*(1), 93–104. https://doi.org/10.1111/1365-2435.13693

Pornon, A., Andalo, C., Burrus, M., & Escaravage, N. (2017). DNA metabarcoding data unveils invisible pollination networks. *Scientific Reports*, *7*(1), 16828. https://doi.org/10.1038/s41598-017-16785-5

Pörtner, H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *132*(4), 739–761. https://doi.org/10.1016/S1095-6433(02)00045-4

Pörtner, H. O., Bennett, A. F., Bozinovic, F., Clarke, A., Lardies, M. A., Lucassen, M., Pelster, B., Schiemer, F., & Stillman, J. H. (2006). Trade-Offs in Thermal Adaptation: The Need for a Molecular to Ecological Integration. *Physiological and Biochemical Zoology*, *79*(2), 295–313. https://doi.org/10.1086/499986

Pounds, A. J., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sánchez-Azofeifa, G. A., Still, C. J., & Young, B. E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, *439*(7073), 161–167. https://doi.org/10.1038/nature04246

Quintero, I., Suchard, M. A., & Jetz, W. (2022). Macroevolutionary dynamics of climatic niche space. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1975), 1–10. https://doi.org/10.1098/rspb.2022.0091

Quintero, I., & Wiens, J. J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters*, *16*(8), 1095–1103. https://doi.org/10.1111/ele.12144

Quitián, M., Santillán, V., Bender, I. M. A., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., & Lena Neuschulz, E. (2019). Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests. *Functional Ecology*, *33*(3), 399–410. https://doi.org/10.1111/1365-2435.13255

Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M. P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K. S., Borras, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A. A., … Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, *10*(1), 3109. https://doi.org/10.1038/s41467-019-10924-4

Ralston, J., DeLuca, W. V., Feldman, R. E., & King, D. I. (2016). Realized climate niche breadth varies with population trend and distribution in North American birds. *Global Ecology and Biogeography*, *25*(10), 1173–1180. https://doi.org/10.1111/geb.12490

Read, Q. D., Baiser, B., Grady, J. M., Zarnetske, P. L., Record, S., & Belmaker, J. (2018). Tropical bird species have less variable body sizes. *Biology Letters*, *14*(1), 20170453. https://doi.org/10.1098/rsbl.2017.0453

Ritchison, G., Gehlbach, F. R., Pyle, P., & Patten, M. A. (2020). Eastern Screech-Owl (Megascops asio). In P. G. Rodewald (Ed.), *Birds of the World*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.easowl1.01

Schleuning, M., Neuschulz, E. L., Albrecht, J., Bender, I. M. A., Bowler, D. E., Dehling, D. M., Fritz, S. A., Hof, C., Mueller, T., Nowak, L., Sorensen, M. C., Böhning-Gaese, K., & Kissling, W. D. (2020). Trait-based assessments of climate-change impacts on interacting species. *Trends in Ecology and Evolution*, *35*(4), 319–328. https://doi.org/10.1016/j.tree.2019.12.010

Seddon, N., Smith, A., Smith, P., Key, I., Chausson, A., Girardin, C., House, J., Srivastava, S., & Turner, B. (2021). Getting the message right on nature-based solutions to climate change. *Global Change Biology*, *27*(8), 1518–1546. https://doi.org/10.1111/gcb.15513

Seeholzer, G. F., Claramunt, S., & Brumfield, R. T. (2017). Niche evolution and diversification in a Neotropical radiation of birds (Aves: Furnariidae). *Evolution*, *71*(3), 702–715. https://doi.org/10.1111/evo.13177

Semenchuk, P., Plutzar, C., Kastner, T., Matej, S., Bidoglio, G., Erb, K.-H., Essl, F., Haberl, H., Wessely, J., Krausmann, F., & Dullinger, S. (2022). Relative effects of land conversion and land-use intensity on terrestrial vertebrate diversity. *Nature Communications*, *13*(1), 615. https://doi.org/10.1038/s41467-022-28245-4

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-16313-6

Sinnott-Armstrong, M. A., Downie, A. E., Federman, S., Valido, A., Jordano, P., & Donoghue, M. J. (2018). Global geographic patterns in the colours and sizes of animal-dispersed fruits. *Global Ecology and Biogeography*, *27*(11), 1339–1351. https://doi.org/10.1111/geb.12801

Smetzer, J. R., Paxton, K. L., & Paxton, E. H. (2021). Individual and seasonal variation in the movement behaviour of two tropical nectarivorous birds. *Movement Ecology*, *9*(1), 1–15. https://doi.org/10.1186/s40462-021-00275-5

Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.-H., & Warren, D. (2019). Niche Estimation Above and Below the Species Level. *Trends in Ecology & Evolution*, *34*(3), 260–273. https://doi.org/10.1016/j.tree.2018.10.012

Soberón, J., & Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLOS ONE*, *12*(4), 1–14. https://doi.org/10.1371/journal.pone.0175138

Soberon, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10. https://doi.org/10.17161/bi.v2i0.4

Song, H., Kemp, D. B., Tian, L., Chu, D., Song, H., & Dai, X. (2021). Thresholds of temperature change for mass extinctions. *Nature Communications*, *12*(1), 4694. https://doi.org/10.1038/s41467-021-25019-2

Spooner, F. E. B., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*, *24*(10), 4521–4531. https://doi.org/10.1111/gcb.14361

Steffen, W., Sanderson, A., Tyson, P., Jager, J., Matson, P., Moore, B., Oldfield, F., Richardson, K., Schellnhuber, J. H., Turner, B. L., & Wasson, R. J. (2004). *Global Change and the Earth System: A Planet Under Pressure* (1st ed.). Springer.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., Yoccoz, N. G., & Ådlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1529), 2087–2096. https://doi.org/10.1098/rspb.2003.2415

Stewart, P. S., Voskamp, A., Biber, M. F., Hof, C., Willis, S. G., & Tobias, J. A. (2020). Global impacts of climate change on avian functional diversity. *Ecology Letters*, *25*(3), 673–685. https://doi.org/10.1101/2020.06.01.127779

Stirling, I., & Derocher, A. E. (2012). Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology*, *18*(9), 2694–2706. https://doi.org/10.1111/j.1365-2486.2012.02753.x

Strubbe, D., Broennimann, O., Chiron, F., & Matthysen, E. (2013). Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, *22*(8), 962–970. https://doi.org/10.1111/geb.12050

Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., & Thomas, C. D. (2011). Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, *120*(1), 1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), 713–717. https://doi.org/10.1038/s41558-018-0231-9

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation*, *142*, 2282–2292.

Svenning, J., & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecology Letters*, *7*(7), 565–573. https://doi.org/10.1111/j.1461-0248.2004.00614.x

Symonds, M. R. E., & Tattersall, G. J. (2010). Geographical variation in bill size across bird species provides evidence for Allen's rule. *The American Naturalist*, *176*(2), 188–197. https://doi.org/10.1086/653666

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). *Extinction risk from climate change*. *427*, 145–148. www.nature.com/nature

Thompson, P. L., & Fronhofer, E. A. (2019). The conflict between adaptation and dispersal for maintaining biodiversity in changing environments. *Proceedings of the National Academy of Sciences*, *116*(42), 21061–21067. https://doi.org/10.1073/pnas.1911796116

Thuiller, W. (2024). Ecological niche modelling. *Current Biology*, *34*(6), 225–229. https://doi.org/10.1016/j.cub.2024.02.018

Thuiller, W., Lavorel, S., & Araújo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, *14*(4), 347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *102*(23), 8245–8250. https://doi.org/10.1073/pnas.0409902102

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). *The Influence of Functional Diversity and Composition on Ecosystem Processes*. https://www.science.org

Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19637–19643. https://doi.org/10.1073/pnas.0901562106

Titley, M. A., Butchart, S. H. M., Jones, V. R., Whittingham, M. J., & Willis, S. G. (2021). Global inequities and political borders challenge nature conservation under climate change. *Proceedings of the National Academy of Sciences*, *118*(7). https://doi.org/10.1073/pnas.2011204118

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898

Trew, B. T., Edwards, D. P., Lees, A. C., Klinges, D. H., Early, R., Svátek, M., Plichta, R., Matula, R., Okello, J., Niessner, A., Barthel, M., Six, J., Maeda, E. E., Barlow, J., do Nascimento, R. O., Berenguer, E., Ferreira, J., Sallo-Bravo, J., & Maclean, I. M. D. (2024). Novel temperatures are already widespread beneath the world's tropical forest canopies. *Nature Climate Change*, *14*(7), 753–759. https://doi.org/10.1038/s41558-024-02031-0

UNFCCC. (2015). *Paris Climate Change Conference*.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571–573. https://doi.org/10.1126/science.aaa4984
Verheyen, J., & Stoks, R. (2019). Temperature variation makes an ectotherm more sensitive to global warming unless thermal evolution occurs. *Journal of Animal Ecology*, *88*(4), 624–636. https://doi.org/10.1111/1365-2656.12946
Veron, S., Mouchet, M., Govaerts, R., Haevermans, T., & Pellens, R. (2019). Vulnerability to climate change of islands worldwide and its impact on the tree of life. *Scientific Reports*, *9*(1), 14471. https://doi.org/10.1038/s41598-019-51107-x
Virkkala, R., & Lehikoinen, A. (2017). Birds on the move in the face of climate change: High species turnover in northern Europe. *Ecology and Evolution*, *7*(20), 8201–8209. https://doi.org/10.1002/ece3.3328
Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 272, Issue 1581, pp. 2561–2569). Royal Society. https://doi.org/10.1098/rspb.2005.3356
Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global Climate Change Leads to Mistimed Avian Reproduction. In *Advances in Ecological Research* (Vol. 35, pp. 89–110). Academic Press Inc. https://doi.org/10.1016/S0065-2504(04)35005-1
Visser, M. E., Perdeck, A. C., Van Balen, J. H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. *Global Change Biology*, *15*(8), 1859–1865. https://doi.org/10.1111/j.1365-2486.2009.01865.x
Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021
Whelan, C. J., Wenny, D. G., & Marquis, R. J. (2008). Ecosystem Services Provided by Birds. *Annals of the New York Academy of Sciences*, *1134*(1), 25–60. https://doi.org/10.1196/annals.1439.003
Wiens, J. A. (1989). Spatial Scaling in Ecology. *Functional Ecology*, *3*(4), 385. https://doi.org/10.2307/2389612
Wiens, J. J., & Graham, C. H. (2005). Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431
Williams, J. E., & Blois, J. L. (2018). Range shifts in response to past and future climate change: Can climate velocities and species' dispersal capabilities explain variation in mammalian range shifts? *Journal of Biogeography*, *45*(9), 2175–2189. https://doi.org/10.1111/jbi.13395
Williams, J. J., Freeman, R., Spooner, F., & Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology*, *28*(3), 797–815. https://doi.org/10.1111/gcb.15978
Williams, S. E., & de la Fuente, A. (2021). Long-term changes in populations of rainforest birds in the Australia Wet Tropics bioregion: A climate-driven biodiversity emergency. *PLOS ONE*, *16*(12), e0254307. https://doi.org/10.1371/journal.pone.0254307
Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027–2027. https://doi.org/10.1890/13-1917.1

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. (2021). Global land use changes are four times greater than previously estimated. *Nature Communications*, *12*(1), 2501. https://doi.org/10.1038/s41467-021-22702-2

Wright, S. J., Heurich, M., Buchmann, C. M., Böcker, R., & Schurr, F. M. (2020). The importance of individual movement and feeding behaviour for long-distance seed dispersal by red deer: a data-driven model. *Movement Ecology*, *8*(1), 44. https://doi.org/10.1186/s40462-020-00227-5

Zhao, Y., O'Neill, G. A., & Wang, T. (2023). Predicting fundamental climate niches of forest trees based on species occurrence data. *Ecological Indicators*, *148*, 1–13. https://doi.org/10.1016/j.ecolind.2023.110072

Zizka, A., Barratt, C. D., Ritter, C. D., Joerger-Hickfang, T., & Zizka, V. M. A. (2022). Existing approaches and future directions to link macroecology, macroevolution and conservation prioritization. *Ecography*, *2022*(6). https://doi.org/10.1111/ecog.05557

Zurell, D., Gallien, L., Graham, C. H., & Zimmermann, N. E. (2018). Do long-distance migratory birds track their niche through seasons? *Journal of Biogeography*, *45*(7), 1459–1468. https://doi.org/10.1111/jbi.13351

# Appendices

## Additional methods

*Taxonomic reconciliation*

Several datasets used throughout this PhD work were mapped to different avian taxonomies. Therefore, when integrating these datasets at various points throughout analyses, published crosswalks were implemented to treat taxonomic discrepancies between datasets (Tobias et al., 2022). Specifically, in Chapter 2, polygon range maps were used to identify and exclude spatial outliers from point locality datasets. Furthermore, when comparing niche estimates between niche quantification methods, the two methods for estimating climatic niches described species occupancy using polygon range map data and point locality data respectively. The polygon range map datasets used in this chapter were mapped to the BirdLife taxonomy whereas the point locality datasets were mapped to the eBird taxonomy (BirdLife International and Handbook of the Birds of the World, 2021; Sullivan et al., 2009). Therefore, all datasets were aligned to the eBird taxonomy using the crosswalk.

In Chapter 3, population data was mapped to the BirdLife taxonomy whereas species climate niche data was mapped to eBird taxonomy (BirdLife International and Handbook of the Birds of the World, 2021; Sullivan et al., 2009). All datasets were therefore aligned to the BirdLife taxonomy using the crosswalk. Lastly, in Chapter 4, to determine whether a given bird species occurred in an ecoregion, BirdLife range maps were intersected with ecoregion polygons. As a result, ecoregion communities were mapped to the BirdLife taxonomy (BirdLife International and Handbook of the Birds of the World, 2021). However, avian climate niche data used to determine climatic suitability under future climate scenarios was mapped to the eBird taxonomy and avian functional trait data used in the trait matching stage was mapped to the BirdTree taxonomy (Jetz et al., 2012; Sullivan et al., 2009). All datasets were therefore aligned to the BirdLife taxonomy using the crosswalk.

*Climate data pre-processing*

Climate data used throughout this PhD thesis was sourced from CHELSA (Karger et al., 2017). Specifically, mean monthly temperature and precipitation layers with a spatial resolution of 1km were used. Climate layers were used to derive climate niche estimates in Chapter 2 which were subsequently implemented in Chapters 3 and 4. Secondly, these climate layers were used to determine local climate properties, including rates of climate change, in Chapter 3. Lastly, these climate layers were used to inform current and future ecoregion climate in Chapter 4. To ensure more interpretable scales, climate data units were transformed. Specifically, temperature layers were transformed from K/10 to °C and precipitation layers were log transformed and therefore had units of log(10kg $m^2$/month). Given precipitation was log transformed, an additional pre-processing step implemented across all precipitation data layers was handling of data values of 0. Specifically, values of 0 were converted to the next minimum precipitation value in a given dataset.

# A1 – Supplementary materials for Chapter 2

## A1.1 Global climate niche dataset

Available at:
https://www.icloud.com/iclouddrive/03aaZi6Di1RY_6m4QM14daN3g#GlobalClimNicheDataset

Sheet 1: Metadata – definitions for all variables included throughout the dataset.

Sheet 2: Climate niche estimates derived from polygon range map data (n = 9892 species)

Sheet 3: Climate niche estimates derived from point locality data (n = 9935 species)

## A1.2 Additional methods

*Point locality method:*

For large occurrence datasets belonging to common species, I randomly sampled 10,000 occurrence points to avoid computationally intensive loads (Figure A1.2). Range maps used for spatial outlier correction were sourced from BirdLife International (BirdLife International and Handbook of the Birds of the World, 2021). BirdLife range maps were filtered on presence (1: extant, 2: probably extant, 3: possibly extant), origin (1: native, 2: reintroduced, 3: introduced) and seasonality (1: resident, 2: breeding season, 3: non-breeding season). Given slight discrepancies between BirdLife and eBird taxonomies I are forced to implement slightly different strategies during the outlier removal stage. For species that have the same name between taxonomies or a 1 eBird to 1 BirdLife species name match I simply use the BirdLife name to source the relevant range map polygon to use for outlier removal. For species with many BirdLife name to 1 eBird name, I combine the BirdLife polygons to use for outlier removal. Lastly, for species with many eBird to 1 BirdLife name I simply use the 1 BirdLife range map to remove outliers for all corresponding eBird species.

To generate a global raster layer of sampling effort as derived from eBird checklist data (Figure A1.3), the frequency of sampling events was first calculated per coordinate. Data was rescaled and then a kernel-density estimate was calculated to provide a continuous matrix of sampling density as derived from checklist frequency. A raster was subsequently generated from this sampling density matrix. To correct for right sided skewness, a cube root transformation was implemented on raster values. For a given species' occurrence point dataset, the purpose of rescaling the range of local raster values between 0 and 1 was to avoid obscuring local differences in sampling effort when maintaining the global range of values. Each occurrence data point was then assigned the inverse of the sampling effort pixel value it intersected with. The entire species' occurrence dataset was subsequently sampled as weighted by the inverse sampling effort values. The result of this method is that data points that occur in regions with high sampling effort are thinned out more whereas data points occurring in regions with low sampling effort are thinned out less. The number of points to be included in the final thinned dataset is determined by how many points would be included when simply thinning the dataset at a 1km resolution. If it was not possible to generate this

number, then the sample number was taken as 15.7% of the original number of occurrence points – which represents the average amount datasets were thinned by. For species with either a low number of occurrence points (< 150) or small ranges (< 5000 $km^2$), occurrence datasets were simply thinned at a 1km resolution.

During climate extraction, a 'running mean' method is implemented here whereby for a given occurrence point taking place in a given month and year, an average final value is extracted across a +/- 5-year range either side of the time point – allowing for a buffer against anomalous climate years such as El Niño and La Niña events (Stenseth et al., 2003). Additionally, I avoid extracting modern day climate values for occurrence points that have occurred several years prior to the occurrence date – thus considering the interannual variability in species movement.

I aimed to ensure the stability of my climatic niche estimates. I therefore tested the effect of sampling effort on niche volume across both climate variables for a subset of species (n = 9 species) (Figure A1.9). If the rate of volume expansion begins to decelerate as I increase sampling effort, I determine this to mean the realised niche boundary has been reached, as increasing the number of climate data points beyond this level contributes decreasingly to the overall niche breadth. For a given species' extracted climate data, I randomly sampled the data at different levels of sampling effort and determined volume.

*Testing climate niche methodologies*

In certain cases, it was necessary to transform niche position and volume data before comparing across different spatiotemporal resolutions. This was to remove any skewness that may arise for instance from a disproportionate number of species occurring towards the tropics (Brown, 2014). Additionally, given I wanted to integrate statistical tests to confirm whether the difference between groups was significant, a normal distribution was required. Therefore, for both spatial and temporal comparisons, a square root transformation was implemented on volume values, and for niche position values it was necessary to take the square root of the inverse values and then inverse back. Transformations were not required for other comparisons as histograms confirmed normally distributed data in these cases.

In addition to investigating the effects of different spatiotemporal resolutions on niche position and breadth I wished to understand the effects of using mean, maximum and minimum climate layers and therefore compared niche estimates derived from these three layers (Figure A1.10). These extreme climate layers were generated by stacking monthly 1981-2010 climate layers and taking the maximum/minimum climate value for a given pixel respectively. For a random sample of 875 species, I extracted climate across their occurrence data points from either a mean, maximum or minimum climate layer to generate climate niche estimates across all three layer types. Niche volume and centroid position was then compared between the three layer types (Figure A1.10).

### A.1.3 Supplementary tables

**Table A1.1| Method comparison t-test results.** Results presented are derived from t-tests assessing the statistical significance of differences in niche metrics across different niche quantification methods. Under a polygon range map method, mean annual climate (temperature, precipitation) was extracted at a 50 km grain size from the breeding range of a species. Under a point locality method, mean monthly climate was extracted at a 1km grain size at occurrence points for a given species. Niche centroid and volume metrics were then compared between both groups using pairwise t-test analyses.

| Metric | Group 1 | Group 2 | p-value |
|---|---|---|---|
| Temperature centroid | Point locality | Polygon range map | 5.73E-31 |
| Precipitation centroid | Point locality | Polygon range map | 0 |
| Volume | Point locality | Polygon range map | 0 |

**Table A1.2| Spatial grain size comparison t-test results.** Results presented are derived from t-tests assessing the statistical significance of differences in niche metrics across varying spatial grain sizes. To test the independent effect of spatial grain size on climate niche, niche estimates were generated by extracting mean annual climate (temperature, precipitation) from point locality data at 1km, 25km and 50km spatial grain sizes. Niche centroid and volume metrics were then compared between groups using pairwise t-test analyses.

| Metric | Group 1 | Group 2 | p-value |
|---|---|---|---|
| Temperature centroid | 1km | 25km | 1.72E-04 |
| | 1km | 50km | 3.18E-10 |
| | 25km | 50km | 1.19E-02 |
| Precipitation centroid | 1km | 25km | 0.429 |
| | 1km | 50km | 0.0276 |
| | 25km | 50km | 0.155 |
| Volume | 1km | 25km | 0.00127 |
| | 1km | 50km | 7.7E-08 |
| | 25km | 50km | 0.0332 |

**Table A1.3| Temporal grain size comparison t-test results.** Results presented are derived from t-tests assessing the statistical significance of differences in niche metrics across varying temporal grain sizes. To test the independent effect of temporal grain size on climate niche, niche estimates were generated by extracting mean monthly, seasonal and annual climate (temperature, precipitation) from point locality data at a 1km spatial grain size. Niche centroid and volume metrics were then compared between groups using pairwise t-test analyses.

| Metric | Group 1 | Group 2 | p-value |
|---|---|---|---|
| Temperature centroid | Monthly | Seasonal | 0.844 |
| | Monthly | Annual | 0.0814 |
| | Seasonal | Annual | 0.123 |
| Precipitation centroid | Monthly | Seasonal | 9.38E-103 |
| | Monthly | Annual | 0 |
| | Seasonal | Annual | 1.20E-157 |
| Volume | Monthly | Seasonal | 5.79E-95 |
| | Monthly | Annual | 0 |
| | Seasonal | Annual | 5.02E-193 |

**Table A1.4| Temporal extent comparison t-test results.** Results presented are derived from t-tests assessing the statistical significance of differences in niche metrics across varying temporal extents. To test the independent effect of temporal extent on climate niche, niche estimates were generated by extracting mean monthly climate (temperature, precipitation) as well as monthly and annual climate averaged across 1981 – 2010 from point locality data at a 1km spatial grain size. Niche centroid and volume metrics were then compared between groups using pairwise t-test analyses.

| Metric | Group 1 | Group 2 | p-value |
|---|---|---|---|
| Temperature centroid | Monthly | Monthly (1981-2010) | 8.93E-06 |
| | Monthly | Annual (1981-2010) | 3.56E-15 |
| | Monthly (1981-2010) | Annual (1981-2010) | 5.47E-04 |
| Precipitation centroid | Monthly | Monthly (1981-2010) | 1.28E-42 |
| | Monthly | Annual (1981-2010) | 0 |
| | Monthly (1981-2010) | Annual (1981-2010) | 0 |
| Volume | Monthly | Monthly (1981-2010) | 1.99E-46 |
| | Monthly | Annual (1981-2010) | 0 |
| | Monthly (1981-2010) | Annual (1981-2010) | 0 |

## A1.4 Supplementary figures

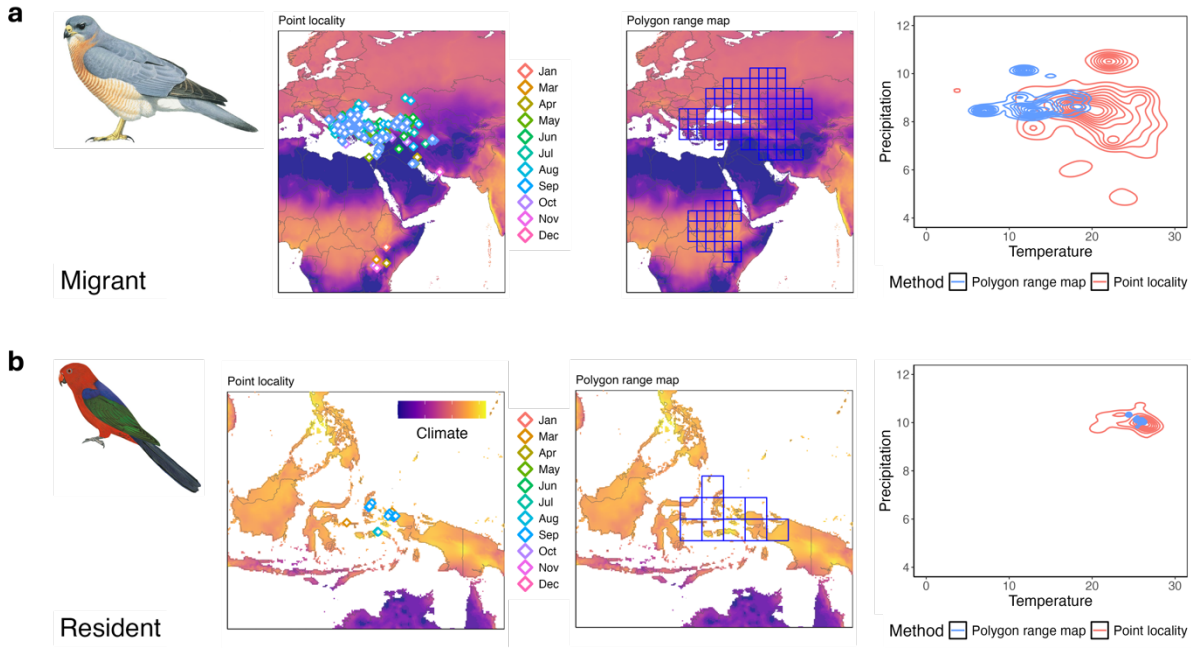



**Figure A1.1| Comparison of niche quantification methods between a migrant and resident species.** Climate niche estimates derived from both the polygon range map and point locality methods for (a) a migrant species (Levant Sparrowhawk, *Accipiter brevipes*) and (b) a resident species (Moluccan king parrot, *Alisterus amboinensis*). Hypervolumes summarising niche estimates derived from the polygon range map method (blue) and the point locality method (blue) are shown (right). Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

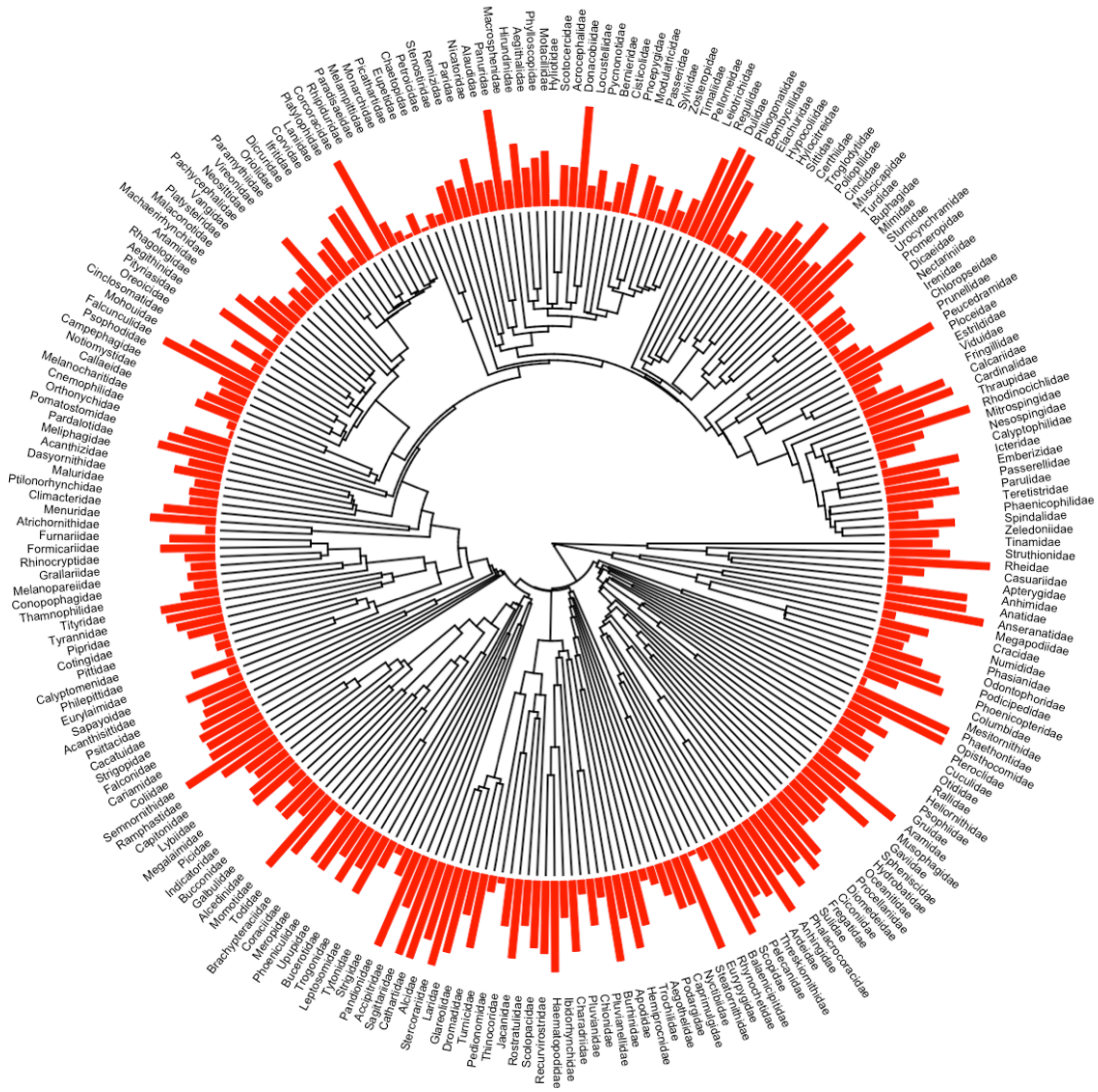


**Figure A1.2| Point locality sampling effort across avian families.** Mean eBird occurrence data coverage across all 249 bird families. The raw eBird database contains over 1.5 billion occurrence records with coverage across almost all bird species globally. Data is primarily collected through citizen science surveys. External bars (red) represent the average number of occurrence records for a given avian family, with a maximum value of 10,000 data points.

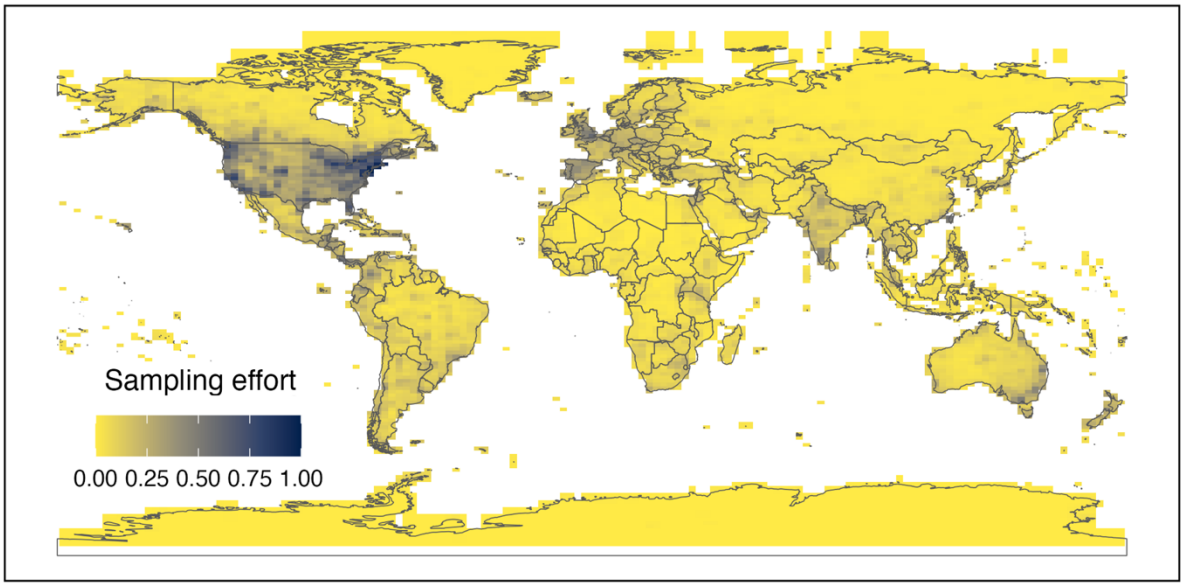



**Figure A1.3| Point locality sampling effort.** Map of global eBird sampling effort used to correct for sampling bias across point locality datasets. Point locality data was thinned proportionally against sampling effort. Specifically, occurrence points that were located in low sampled regions were thinned out less. The raster was generated from eBird checklist data.

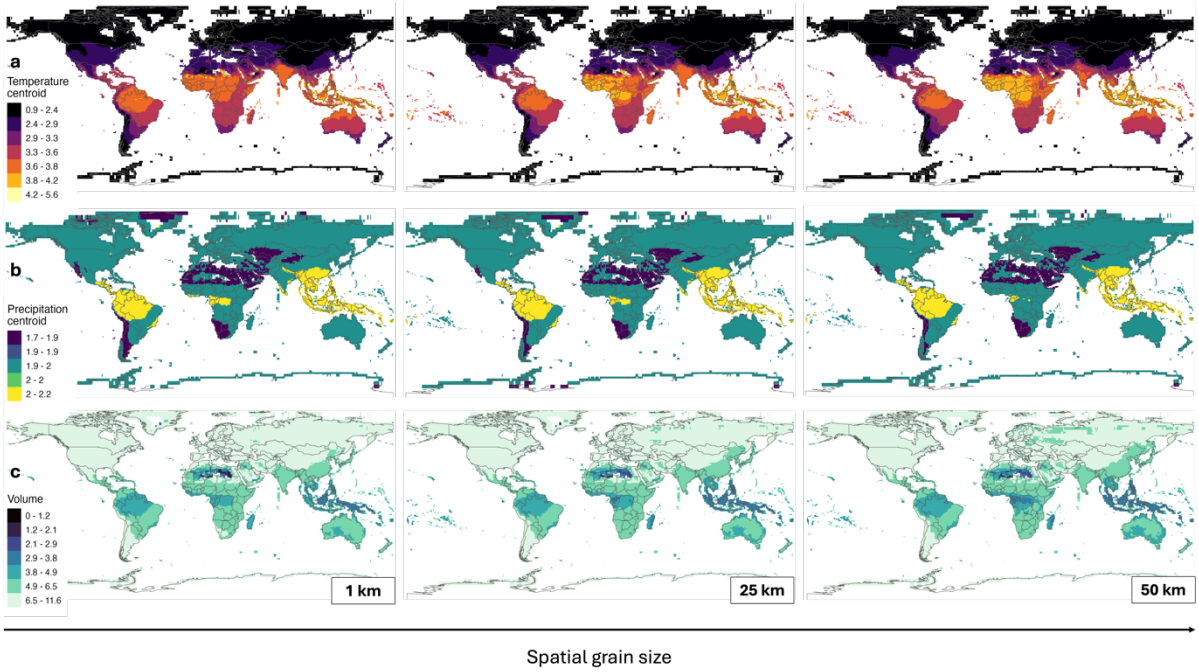



**Figure A1.4| Niche metrics across different spatial grain sizes.** Maps of (a) temperature centroid, (b) precipitation centroid and (c) niche volume across different spatial grain sizes (1km, 25km, 50km), averaged across 100km grid cell communities. To test the independent effect of spatial grain size on climate niche, niche estimates were generated by extracting mean annual climate (temperature, precipitation) from point locality data at 1km, 25km and 50km spatial grain sizes. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

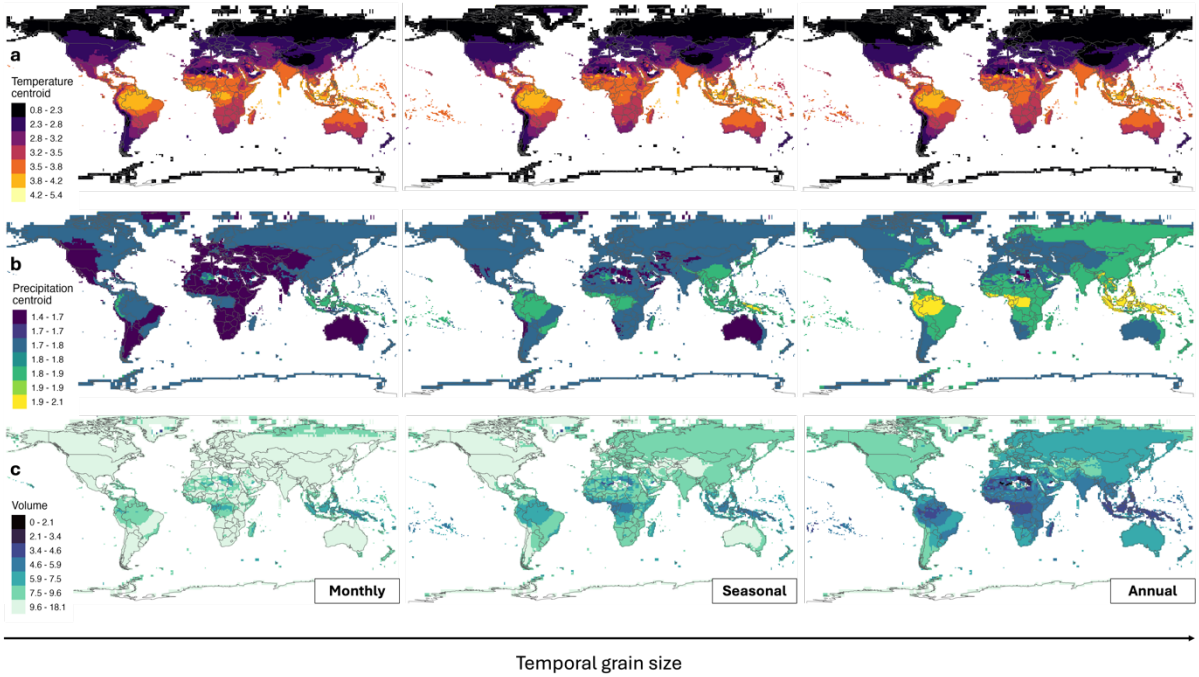



**Figure A1.5| Niche metrics across different temporal grain sizes.** Maps of (a) temperature centroid, (b) precipitation centroid and (c) niche volume across different temporal grain sizes (monthly, seasonal, annual), averaged across 100km grid cell communities. To test the independent effect of temporal grain size on climate niche, niche estimates were generated by extracting mean monthly, seasonal and annual climate (temperature, precipitation) from point locality data at a 1km spatial grain size. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

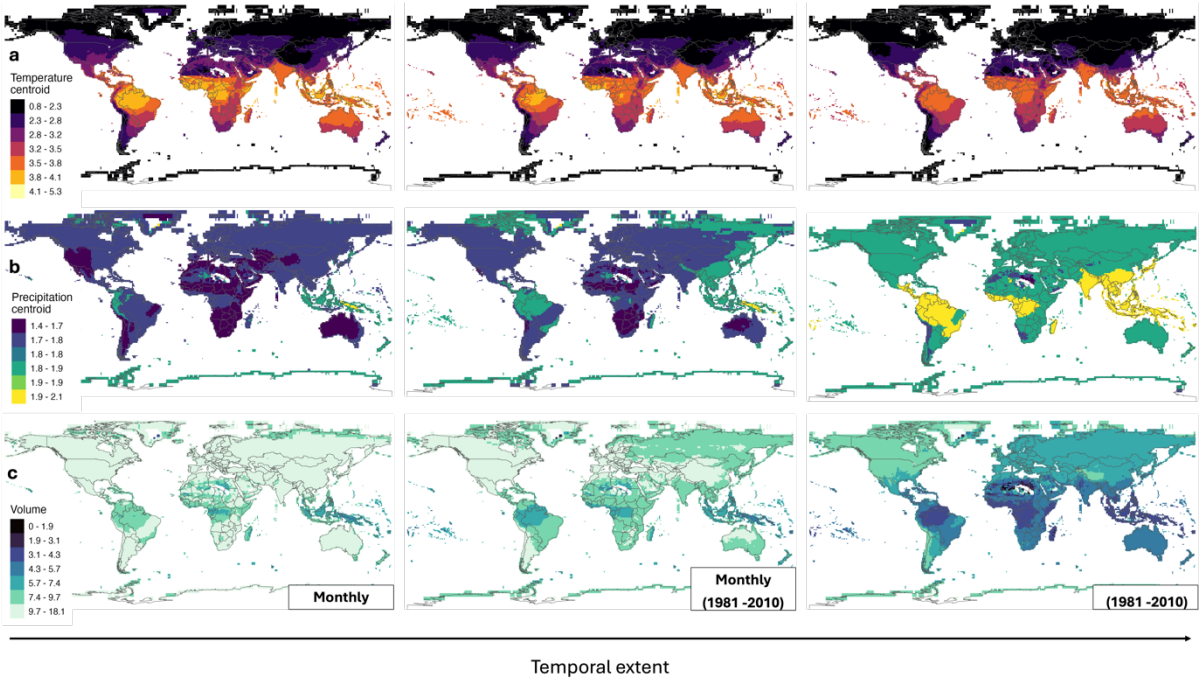



**Figure A1.6| Niche metrics across different temporal extents.** Maps of (a) temperature centroid, (b) precipitation centroid and (c) niche volume across different temporal extents (monthly, multi-year averaging (monthly), multi-year averaging (annual)), averaged across 100km grid cell communities. To test the independent effect of temporal extent on climate niche, niche estimates were generated by extracting mean monthly climate (temperature, precipitation) as well as monthly and annual climate averaged across 1981 – 2010 from point locality data at a 1km spatial grain size. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

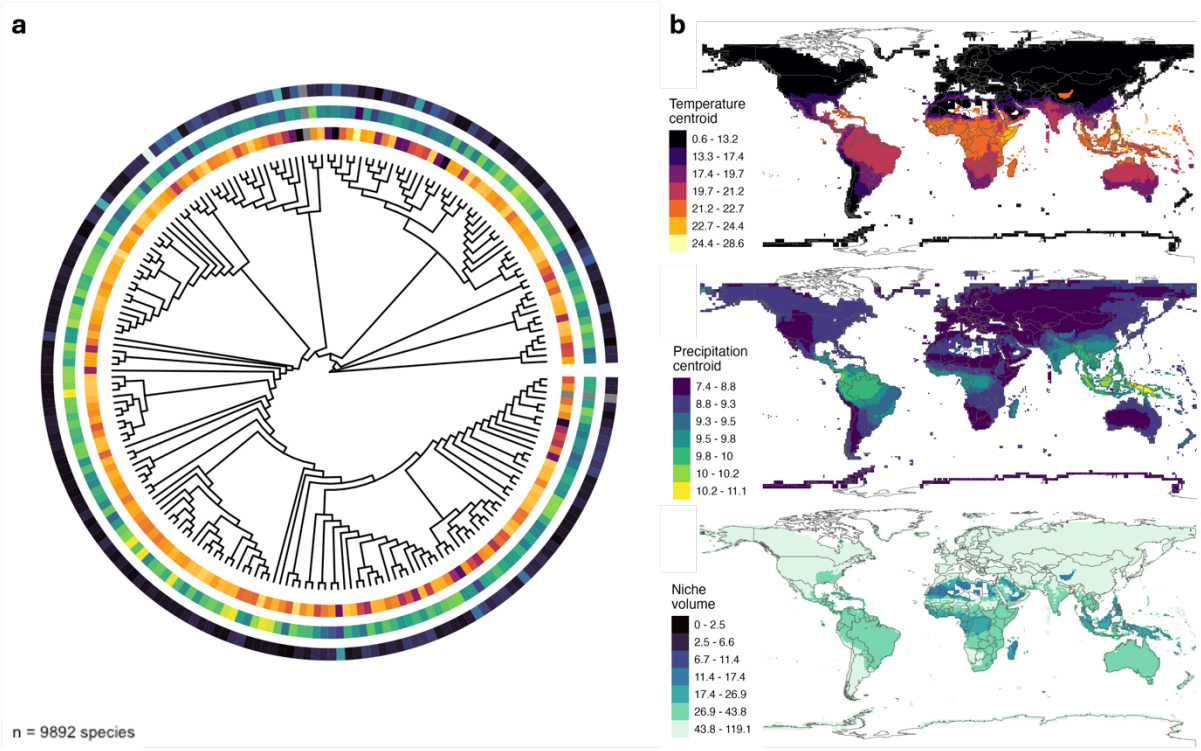



**Figure A1.7| Polygon range map global climate niche dataset.** A global dataset of climate niche estimates derived using polygon range map data (n = 9892 species). Under a polygon range map method, mean annual climate (temperature, precipitation) is extracted at a 50 km grain size from the breeding range of a species. (a) Niche centroid and volume metrics averaged across all 249 avian families. (b) Maps of niche centroid and volume metrics averaged across 100km grid cell communities. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

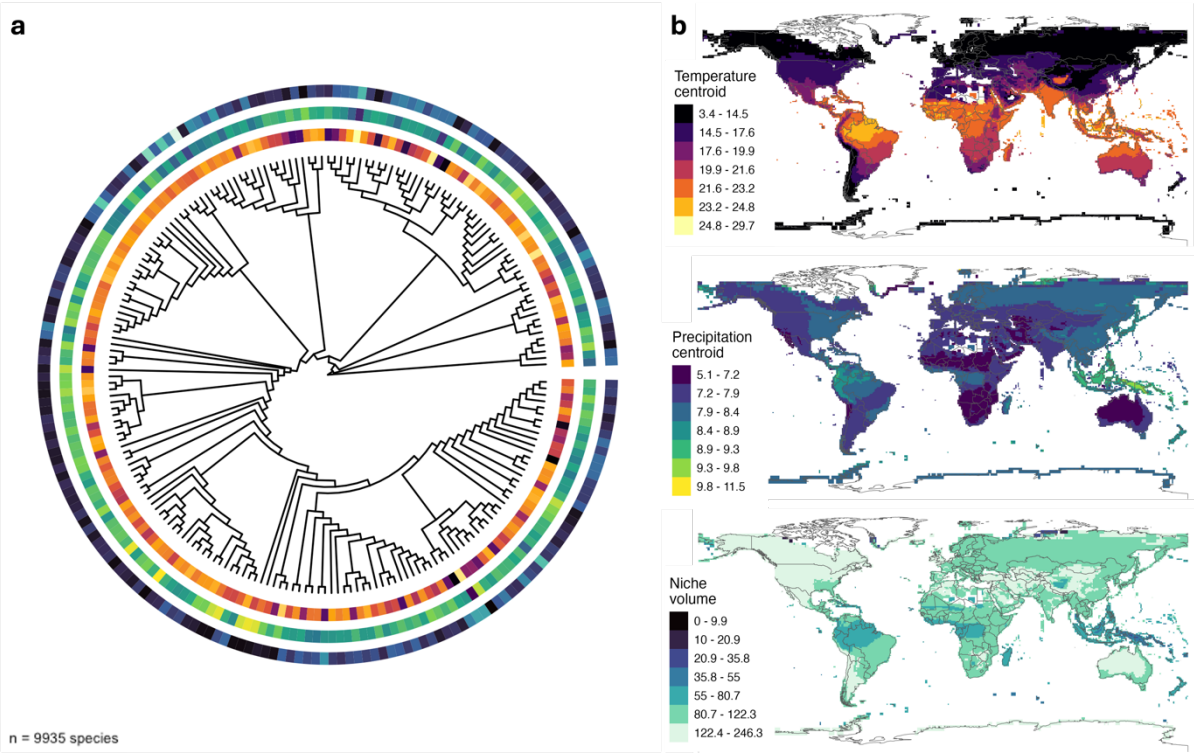



**Figure A1.8| Point locality global climate niche dataset.** A global dataset of climate niche estimates derived using point locality data (n = 9935 species). Under a point locality method, mean monthly climate is extracted at a 1km grain size at occurrence points for a given species. (a) Niche centroid and volume metrics averaged across all 249 avian families. (b) Maps of niche centroid and volume metrics averaged across 100km grid cell communities. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

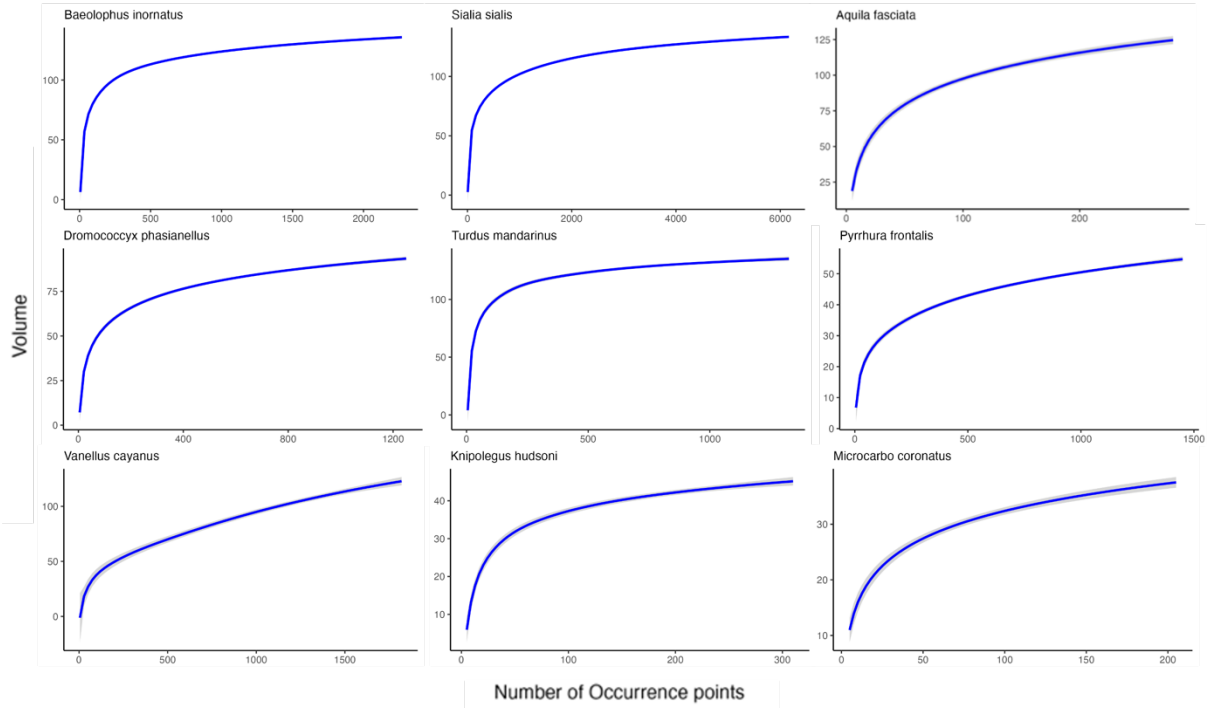



**Figure A1.9| Niche hypervolume stability test results.** Test results for a random sample of 9 species showing how climatic niche volume is influenced by increasing sampling effort. From my sample of species shown above I can see that as I increase sampling effort niche volume converges to a natural point indicating that a stable estimate of realised niche is reached for a given species.

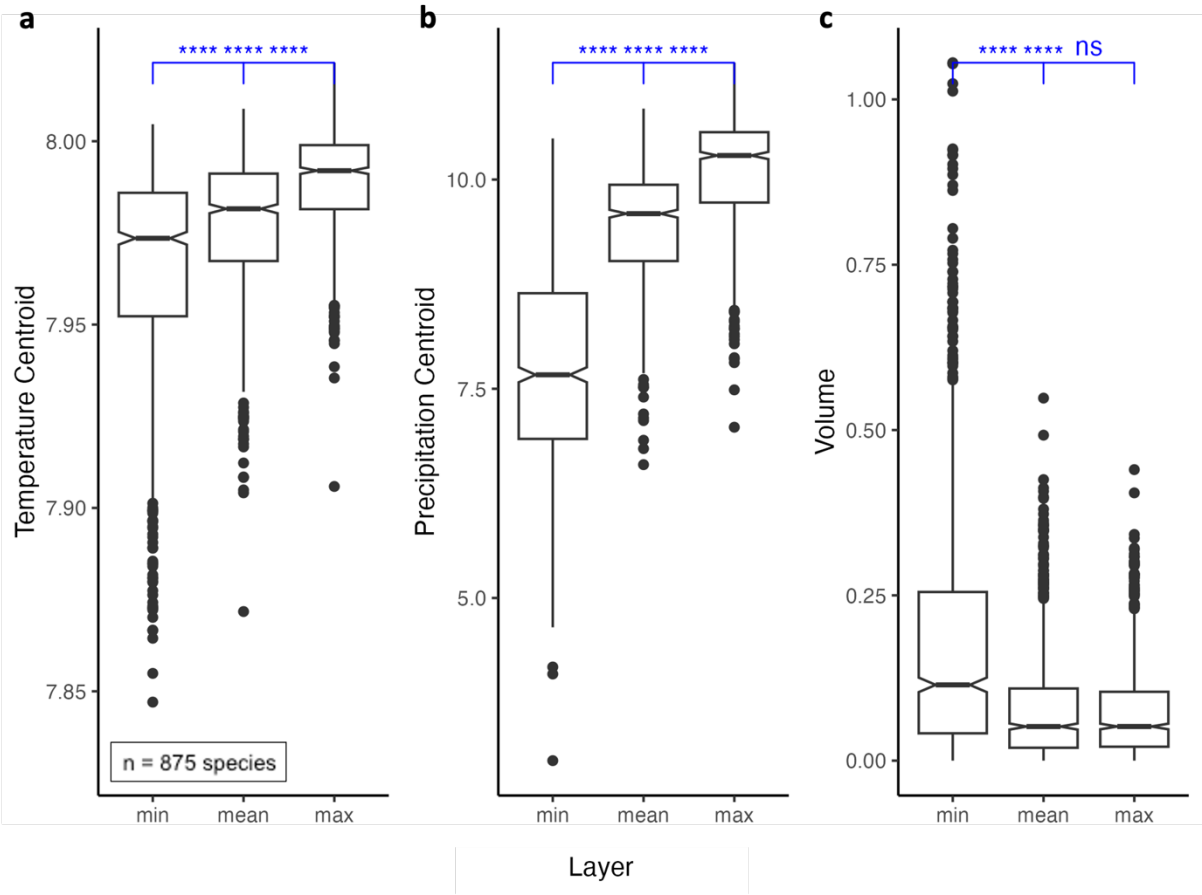



**Figure A1.10| The effect of using extreme climate layers on climate niche estimates.** Boxplots comparing (a) temperature centroid, (b) precipitation centroid and (c) niche volume when using mean, maximum and minimum climate layers for a random sample of 875 species. Maximum and minimum climate layers were generated by stacking monthly 1981-2010 climate layers and taking the largest/lowest climate value for a given pixel. Extracting maximum climate during niche quantification clearly results in climate niche estimates occupying higher niche positions. Niche volume is shown to expand when extracting minimum climate. Blue asterisks indicates the difference between a given pair of groups is statistically significant as per pairwise t-test analyses. Temperature units = °C. Precipitation units = log(10kg $m^2$/month).

# A2 – Supplementary materials for Chapter 3

## A2.1 Additional methods

*Model $R^2$ values*

I wished to understand the proportion of variance in my response variable explained by each variable class for both increasing and decreasing populations. I therefore fit linear mixed effect models between my response variable (mean rate of avian population change) and all core variables as well as distinct variable classes (species climate niche features, climatic position features, local environment features) with taxonomic family, site location and biogeographic realm set as random effects. I then assessed the conditional and marginal $R^2$ values of each model (Figure A2.8).

*Sensitivity replicates*

I investigated whether predictor effects on mean rate of avian population change were influenced by differing methodologies for extracting respective features. I determined which variables would be classified as core variables and sensitivity replicates (Table A2.3), by fitting different mixed effect models between my response variable (avian population change) and variables generated through different methodologies. I then ran model selection based on AIC score and the variables making up the best fitting model would be included in the core analysis and the other set of variables would be included in the sensitivity analyses (Table A2.4). Firstly, in my core analysis I use niche centroid to determine niche position, whereas here I investigate the effects of using niche maximum and minimum positions instead. Due to having an atypical distribution that wasn't possible to correct for I had to remove local precipitation minimum limit as a feature in the analysis.

Second, I generated a variable summarising the trending direction of local climate as a ratio by dividing early distance value by the late distance value instead. In my core analysis to determine niche directionality I use a distance based metric for decreasing populations and a distance ratio metric for increasing populations, whereas this is inverted here. This is due to the respective features performing differently between increasing and decreasing populations in the models used to classify core and sensitivity variables (Table A2.4).

Lastly, in my core analysis, rates of climate change are derived using monthly data climate data points however as a sensitivity replicate, I also included annual-derived rates of climate change. Additionally, I included rates of climate change variables weighted by the degree of seasonality at each population site. I calculated seasonality at a given population location, by subtracting the minimum monthly climate value from the maximum monthly climate value for a given year (1980 – 2018). I then averaged the yearly seasonality values to generate a mean seasonality score for a given population location. For a given population, I then divided local rates of climate change by the mean seasonality score to apply the weighting. The assumption here is that rate of climate change in a highly climatically variable location would be less impactful compared to the same rate of climate change in a climatically stable location (Jackson et al., 2009).

## A2.2 Additional results

*Model $R^2$ values*

I find that fixed effects in the full model explain 4.9% of the total variance in my response variable for decreasing populations and 7% for increasing populations (Figure A2.8). Local environment features seemingly contribute the most to the overall marginal $R^2$ of the full model as these variables explain 4.1% of the variance in my response variable for decreasing populations and 6.9% for increasing populations (Figure A2.8). Species climate and climatic position features only explain 0.5% and 0.2% of the variance respectively in decreasing populations as well as 0.7% and 0.5% respectively in increasing populations (Figure A2.8).

*Sensitivity replicates*

When using climate niche maximum limits as a measure of niche position, precipitation niche position still has a negative effect on decreasing populations – i.e. predictive of larger decreases (Table A2.5) (Figure A2.9). However, local temperature position now has a negative effect on decreasing populations (Table A2.5) (Figure A2.9) and local precipitation position no longer has a positive effect on increasing populations (Table A2.5) (Figure A2.9). When using climate niche minimum limits as a measure of niche

position, temperature niche position still has no significant effect on decreasing or increasing populations (Table A2.6) (Figure A2.10).

When using centroid direction ratio and centroid direction as a measure of niche directionality in decreasing populations and increasing populations respectively, there is still no significant effect of niche directionality on population trends (Table A2.7) (Figure A2.11). However, centroid distance no longer has a positive effect on increasing populations (Table A2.7) (Figure A2.11). When using rates of climate change derived from annual climate data, rate of warming no longer has a negative effect on decreasing populations or positive effect on increasing populations (Table A2.8) (Figure A2.12). When standardizing rates of climate change for local climate variability, monthly derived rate of precipitation and warming no longer have a positive effect on decreasing populations and increasing populations respectively (Table A2.9) (Figure A2.13). Standardized rates of climate change derived from annual climate data have no significant effects on population trends (Table A2.10) (Figure A2.14).

## A2.3 Supplementary tables

**Table A2.1| Core analysis model averaged results.** Results presented here represent the model averaged (ΔAIC <6) output from the core analysis investigating predictors of avian population trends. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| sp_vol | 0.01427361 | -0.0798526 | 0.1189119 | 0.782 | decreasing |
| sp_pcent | 0.04908355 | -0.0543022 | 0.15059905 | 0.34111095 | decreasing |
| pop_tcent | -0.0133746 | -0.1021334 | 0.07845441 | 0.61727734 | decreasing |
| pop_pcent | -0.1231658 | -0.2037795 | -0.0403268 | 0.00310002 | decreasing |
| t_meanl_intra | -0.1797919 | -0.2549934 | -0.106559 | 5.00E-04 | decreasing |
| p_meanl_intra | -0.07055314 | 0.00349928 | 0.13441191 | 0.03770682 | decreasing |
| clad_vol | -0.0047372 | -0.0612725 | 0.0520253 | 0.88727646 | decreasing |
| luc_meanl | 0.0197381 | -0.0584033 | 0.09200519 | 0.60763812 | decreasing |
| sp_tcent | 0.04748455 | -0.0120637 | 0.11281061 | 0.23348419 | decreasing |
| pop_vol | -0.0932383 | -0.1678154 | -0.0082968 | 0.025 | decreasing |
| cent_exp | 0 | 0 | 0 | 0 | decreasing |
| cent_dir | 0 | 0 | 0 | 0 | decreasing |
| sp_vol | -0.0945971 | -0.2086291 | 0.00633952 | 0.10964427 | increasing |
| sp_pcent | -0.0255662 | -0.1416511 | 0.09907276 | 0.51774085 | increasing |
| pop_vol | 0.1856651 | 0.10248143 | 0.272867 | 5.00E-04 | increasing |
| pop_tcent | 0.04314242 | -0.0664281 | 0.13853163 | 0.27982904 | increasing |
| pop_pcent | 0.0893495 | 0.00342149 | 0.17811533 | 0.054 | increasing |
| cent_exp | 0.06832176 | 0.00372843 | 0.13513836 | 0.04176305 | increasing |
| t_meanl_intra | 0.14231262 | 0.06780965 | 0.21747198 | 5.00E-04 | increasing |
| sp_tcent | 0.04597379 | -0.0329367 | 0.13520509 | 0.299 | increasing |
| cent_dir_r | 0.00989067 | -0.0373658 | 0.05723017 | 0.684 | increasing |
| p_meanl_intra | -0.0204041 | 0.04934355 | -0.0923436 | 0.577 | increasing |
| clad_vol | 0 | 0 | 0 | 0 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.2| Variable class analysis results.** Summary table of model fit scores for each model belonging to a specific class of variables (species climate niche, local environment, climatic position) for both decreasing and increasing populations. To determine which variable class was most predictive of avian population trends, models fitted solely with variables belonging to one variable class (species climate niche, local environment, climatic position) were grouped together. Model fit scores were subsequently compared between variable classes.

| Model number | AIC (inverted) | Weight | Variable class | Trend direction |
|---|---|---|---|---|
| 14 | -2228.98 | 0.99 | Species climate niche | decreasing |
| 11 | -2237.93 | 0.01 | Species climate niche | decreasing |
| 9 | -2244.03 | 0.00 | Species climate niche | decreasing |
| 8 | -2244.25 | 0.00 | Species climate niche | decreasing |
| 6 | -2248.54 | 5.58E-05 | Species climate niche | decreasing |
| 15 | -2253.58 | 4.49E-06 | Species climate niche | decreasing |
| 3 | -2261.18 | 1.01E-07 | Species climate niche | decreasing |
| 4 | -2267.96 | 3.38E-09 | Species climate niche | decreasing |
| 5 | -2273.40 | 2.23E-10 | Species climate niche | decreasing |
| 13 | -2273.47 | 2.15E-10 | Species climate niche | decreasing |
| 12 | -2277.65 | 2.66E-11 | Species climate niche | decreasing |
| 2 | -2278.07 | 2.16E-11 | Species climate niche | decreasing |
| 7 | -2281.36 | 4.17E-12 | Species climate niche | decreasing |
| 1 | -2282.05 | 2.95E-12 | Species climate niche | decreasing |
| 10 | -2290.55 | 4.20E-14 | Species climate niche | decreasing |
| 27 | -2192.43 | 0.97 | Local environment | decreasing |
| 56 | -2201.18 | 0.01 | Local environment | decreasing |
| 48 | -2203.29 | 0.00 | Local environment | decreasing |
| 61 | -2203.44 | 0.00 | Local environment | decreasing |
| 47 | -2203.52 | 0.00 | Local environment | decreasing |
| 51 | -2204.59 | 0.00 | Local environment | decreasing |
| 62 | -2204.84 | 0.00 | Local environment | decreasing |
| 63 | -2208.28 | 0.00 | Local environment | decreasing |
| 35 | -2209.25 | 0.00 | Local environment | decreasing |
| 31 | -2211.93 | 5.66E-05 | Local environment | decreasing |
| 60 | -2212.10 | 5.20E-05 | Local environment | decreasing |
| 59 | -2212.97 | 3.37E-05 | Local environment | decreasing |
| 38 | -2213.08 | 3.18E-05 | Local environment | decreasing |
| 14 | -2213.18 | 3.03E-05 | Local environment | decreasing |

| | | | | |
|---|---|---|---|---|
| 17 | -2216.40 | 6.06E-06 | Local environment | decreasing |
| 41 | -2217.36 | 3.75E-06 | Local environment | decreasing |
| 40 | -2219.35 | 1.38E-06 | Local environment | decreasing |
| 55 | -2221.22 | 5.45E-07 | Local environment | decreasing |
| 54 | -2221.27 | 5.30E-07 | Local environment | decreasing |
| 53 | -2221.51 | 4.70E-07 | Local environment | decreasing |
| 57 | -2221.73 | 4.22E-07 | Local environment | decreasing |
| 10 | -2223.55 | 1.70E-07 | Local environment | decreasing |
| 19 | -2223.82 | 1.48E-07 | Local environment | decreasing |
| 5 | -2223.84 | 1.47E-07 | Local environment | decreasing |
| 9 | -2224.60 | 1.01E-07 | Local environment | decreasing |
| 43 | -2226.01 | 4.97E-08 | Local environment | decreasing |
| 8 | -2226.35 | 4.20E-08 | Local environment | decreasing |
| 49 | -2226.68 | 3.55E-08 | Local environment | decreasing |
| 13 | -2229.34 | 9.39E-09 | Local environment | decreasing |
| 37 | -2230.47 | 5.33E-09 | Local environment | decreasing |
| 42 | -2230.67 | 4.84E-09 | Local environment | decreasing |
| 45 | -2231.14 | 3.81E-09 | Local environment | decreasing |
| 12 | -2231.26 | 3.59E-09 | Local environment | decreasing |
| 52 | -2232.01 | 2.48E-09 | Local environment | decreasing |
| 36 | -2232.82 | 1.65E-09 | Local environment | decreasing |
| 58 | -2233.37 | 1.25E-09 | Local environment | decreasing |
| 33 | -2233.50 | 1.17E-09 | Local environment | decreasing |
| 29 | -2235.98 | 3.39E-10 | Local environment | decreasing |
| 50 | -2236.30 | 2.89E-10 | Local environment | decreasing |
| 30 | -2237.93 | 1.28E-10 | Local environment | decreasing |
| 23 | -2240.92 | 2.87E-11 | Local environment | decreasing |
| 26 | -2241.67 | 1.97E-11 | Local environment | decreasing |
| 3 | -2242.08 | 1.61E-11 | Local environment | decreasing |
| 24 | -2244.40 | 5.04E-12 | Local environment | decreasing |
| 39 | -2246.50 | 1.76E-12 | Local environment | decreasing |
| 16 | -2246.85 | 1.48E-12 | Local environment | decreasing |
| 46 | -2246.86 | 1.47E-12 | Local environment | decreasing |
| 32 | -2246.96 | 1.40E-12 | Local environment | decreasing |
| 21 | -2247.08 | 1.32E-12 | Local environment | decreasing |
| 11 | -2247.33 | 1.17E-12 | Local environment | decreasing |
| 28 | -2248.35 | 7.00E-13 | Local environment | decreasing |
| 4 | -2251.44 | 1.49E-13 | Local environment | decreasing |
| 25 | -2251.51 | 1.44E-13 | Local environment | decreasing |

| | | | | |
|---|---|---|---|---|
| 44 | -2251.67 | 1.33E-13 | Local environment | decreasing |
| 15 | -2252.71 | 7.91E-14 | Local environment | decreasing |
| 2 | -2258.12 | 5.29E-15 | Local environment | decreasing |
| 20 | -2259.91 | 2.16E-15 | Local environment | decreasing |
| 22 | -2264.85 | 1.83E-16 | Local environment | decreasing |
| 7 | -2266.87 | 6.66E-17 | Local environment | decreasing |
| 6 | -2269.29 | 1.99E-17 | Local environment | decreasing |
| 18 | -2269.68 | 1.63E-17 | Local environment | decreasing |
| 34 | -2276.30 | 5.96E-19 | Local environment | decreasing |
| 1 | -2281.72 | 3.96E-20 | Local environment | decreasing |
| 2 | -2257.26 | 0.99 | Climatic position | decreasing |
| 1 | -2267.09 | 0.01 | Climatic position | decreasing |
| 3 | -2273.53 | 0.00 | Climatic position | decreasing |
| 12 | -2210.87 | 0.87 | Species climate niche | increasing |
| 5 | -2215.15 | 0.10 | Species climate niche | increasing |
| 14 | -2219.61 | 0.01 | Species climate niche | increasing |
| 6 | -2220.32 | 0.01 | Species climate niche | increasing |
| 13 | -2220.76 | 0.01 | Species climate niche | increasing |
| 1 | -2224.03 | 0.00 | Species climate niche | increasing |
| 10 | -2224.90 | 0.00 | Species climate niche | increasing |
| 2 | -2225.24 | 0.00 | Species climate niche | increasing |
| 15 | -2228.13 | 0.00 | Species climate niche | increasing |
| 7 | -2229.60 | 7.44E-05 | Species climate niche | increasing |
| 8 | -2230.84 | 4.00E-05 | Species climate niche | increasing |
| 9 | -2233.69 | 9.63E-06 | Species climate niche | increasing |
| 4 | -2238.17 | 1.02E-06 | Species climate niche | increasing |
| 3 | -2240.95 | 2.56E-07 | Species climate niche | increasing |
| 11 | -2241.15 | 2.31E-07 | Species climate niche | increasing |
| 7 | -2203.76 | 0.46 | Local environment | increasing |
| 57 | -2205.50 | 0.19 | Local environment | increasing |
| 32 | -2206.74 | 0.10 | Local environment | increasing |
| 26 | -2206.76 | 0.10 | Local environment | increasing |
| 52 | -2208.06 | 0.05 | Local environment | increasing |
| 27 | -2208.76 | 0.04 | Local environment | increasing |
| 22 | -2209.22 | 0.03 | Local environment | increasing |
| 42 | -2212.27 | 0.01 | Local environment | increasing |
| 10 | -2214.57 | 0.00 | Local environment | increasing |
| 48 | -2215.71 | 0.00 | Local environment | increasing |
| 43 | -2216.93 | 0.00 | Local environment | increasing |

| | | | | |
|---|---|---|---|---|
| 45 | -2216.98 | 0.00 | Local environment | increasing |
| 1 | -2221.39 | 6.89E-05 | Local environment | increasing |
| 14 | -2222.59 | 3.78E-05 | Local environment | increasing |
| 29 | -2222.75 | 3.48E-05 | Local environment | increasing |
| 38 | -2223.98 | 1.88E-05 | Local environment | increasing |
| 24 | -2227.04 | 4.08E-06 | Local environment | increasing |
| 35 | -2228.87 | 1.63E-06 | Local environment | increasing |
| 4 | -2229.09 | 1.46E-06 | Local environment | increasing |
| 28 | -2231.61 | 4.15E-07 | Local environment | increasing |
| 3 | -2231.99 | 3.44E-07 | Local environment | increasing |
| 9 | -2232.34 | 2.89E-07 | Local environment | increasing |
| 47 | -2235.35 | 6.39E-08 | Local environment | increasing |
| 25 | -2236.37 | 3.84E-08 | Local environment | increasing |
| 49 | -2237.00 | 2.81E-08 | Local environment | increasing |
| 8 | -2237.13 | 2.63E-08 | Local environment | increasing |
| 2 | -2237.85 | 1.84E-08 | Local environment | increasing |
| 19 | -2238.14 | 1.59E-08 | Local environment | increasing |
| 16 | -2239.58 | 7.71E-09 | Local environment | increasing |
| 59 | -2240.23 | 5.59E-09 | Local environment | increasing |
| 13 | -2241.05 | 3.71E-09 | Local environment | increasing |
| 11 | -2241.76 | 2.60E-09 | Local environment | increasing |
| 17 | -2242.14 | 2.15E-09 | Local environment | increasing |
| 44 | -2242.28 | 2.00E-09 | Local environment | increasing |
| 23 | -2243.67 | 9.99E-10 | Local environment | increasing |
| 61 | -2246.83 | 2.06E-10 | Local environment | increasing |
| 12 | -2246.84 | 2.05E-10 | Local environment | increasing |
| 18 | -2250.77 | 2.87E-11 | Local environment | increasing |
| 40 | -2251.60 | 1.90E-11 | Local environment | increasing |
| 56 | -2252.84 | 1.02E-11 | Local environment | increasing |
| 30 | -2253.45 | 7.52E-12 | Local environment | increasing |
| 5 | -2254.29 | 4.93E-12 | Local environment | increasing |
| 54 | -2256.27 | 1.84E-12 | Local environment | increasing |
| 31 | -2257.86 | 8.29E-13 | Local environment | increasing |
| 33 | -2258.68 | 5.49E-13 | Local environment | increasing |
| 39 | -2258.75 | 5.31E-13 | Local environment | increasing |
| 51 | -2258.83 | 5.11E-13 | Local environment | increasing |
| 6 | -2259.02 | 4.65E-13 | Local environment | increasing |
| 34 | -2261.26 | 1.52E-13 | Local environment | increasing |
| 50 | -2261.56 | 1.30E-13 | Local environment | increasing |

| | | | | |
|---|---|---|---|---|
| 53 | -2262.87 | 6.78E-14 | Local environment | increasing |
| 58 | -2264.37 | 3.20E-14 | Local environment | increasing |
| 55 | -2265.43 | 1.88E-14 | Local environment | increasing |
| 63 | -2266.27 | 1.24E-14 | Local environment | increasing |
| 46 | -2270.62 | 1.41E-15 | Local environment | increasing |
| 15 | -2273.09 | 4.09E-16 | Local environment | increasing |
| 36 | -2276.22 | 8.54E-17 | Local environment | increasing |
| 20 | -2277.00 | 5.78E-17 | Local environment | increasing |
| 62 | -2278.41 | 2.85E-17 | Local environment | increasing |
| 21 | -2280.44 | 1.04E-17 | Local environment | increasing |
| 37 | -2286.61 | 4.75E-19 | Local environment | increasing |
| 60 | -2311.29 | 2.07E-24 | Local environment | increasing |
| 41 | -2369.79 | 4.11E-37 | Local environment | increasing |
| 1 | -2234.06 | 1.00 | Climatic position | increasing |
| 2 | -2246.62 | 0.00 | Climatic position | increasing |
| 3 | -2255.88 | 1.82E-05 | Climatic position | increasing |

**Table A2.3| Core and sensitivity variables.** Summary table of which environmental predictors are included in the core analysis and which are included in the sensitivity replicate analyses to replace the respective core variable.

| | | | | |
|---|---|---|---|---|
| | **1. Climatic niche features** | | | |
| | *Core* | *Sensitivity replicate 1* | *Sensitivity replicate 2* | |
| | population precipitation centroid | population maximum precipitation | population minimum precipitation | |
| | population temperature centroid | population maximum temperature | population minimum temperature | |
| | population volume | | | |
| | species precipitation centroid | species maximum precipitation | species minimum precipitation | |
| | species temperature centroid | species maximum temperature | species minimum temperature | |
| | species volume | | | |
| | clade volume | | | |
| | **2. Climate position features** | | | |
| | *Core* | *Sensitivity replicate 1* | | |
| *decreasing:* | centroid direction | centroid direction ratio | | |
| *increasing:* | centroid direction ratio | centroid direction | | |
| | centroid distance | | | |
| | **3. Rates of environmental change** | | | |
| | *Core* | *Sensitivity replicate 1* | *Sensitivity replicate 2* | *Sensitivity replicate 3* |
| | rate of temperature change (monthly) | rate of temperature change (annual) | rate of temperature change (monthly, standardized) | rate of temperature change (annual, standardized) |
| | rate of precipitation change (monthly) | rate of precipitation change (annual) | rate of precipitation change (monthly, standardized) | rate of precipitation change (annual, standardized) |
| | rate of land use change | | | |

**Table A2.4| Core analysis variable selection.** Results presented here represent the model selection output of models to determine core variables between increasing and decreasing populations. I included different variables summarizing climate niche position, centroid direction and rates of climate change features. Specifically, I summarized climate niche position as niche centroid as well as maximum and minimum niche limits. Centroid direction was summarized as both a distance based metric and as a ratio. Lastly, rates of climate change were derived from either mean monthly or annual climate as well as standardized by local seasonality. Model selection based on AIC was run for each group of models and the constituent variables making up the best fitting model were included in the core analysis. All variables are exhibited here as abbreviations (Table A2.11).

| Formula | AIC | Delta(AIC) | Weight | DF | Trend direction |
|---|---|---|---|---|---|
| mean_l ~ sp_vol + sp_tcent + sp_pcent + pop_vol + pop_tcent + pop_pcent | 2228.19 | 0.00 | 1.00 | 12 | decreasing |
| mean_l ~ sp_vol + sp_tmin + sp_pmin + pop_vol+ pop_tmin | 2243.21 | 15.02 | 0.00 | 11 | decreasing |
| mean_l ~ sp_vol + sp_tmax + sp_pmax + pop_vol + pop_tmax + pop_pmax | 2245.79 | 17.61 | 0.00 | 12 | decreasing |
| mean_l ~ cent_exp + cent_dir | 2271.97 | 0.00 | 0.91 | 8 | decreasing |
| mean_l ~ cent_exp + cent_dir_r | 2276.64 | 4.68 | 0.09 | 8 | decreasing |
| mean_l ~ t_meanl_intra + p_meanl_intra + luc_meanl | 2223.08 | 0.00 | 0.81 | 9 | decreasing |
| mean_l ~ t_meanlw_intra + p_meanlw_intra + luc_meanl | 2226.64 | 3.55 | 0.14 | 9 | decreasing |
| mean_l ~ t_meanlw_inter + p_meanlw_inter + luc_meanl | 2228.70 | 5.62 | 0.05 | 9 | decreasing |
| mean_l ~ t_meanl_inter + p_meanl_inter + luc_meanl | 2244.50 | 21.42 | 0.00 | 9 | decreasing |
| mean_l ~ sp_vol + sp_tcent + sp_pcent + pop_vol + pop_tcent + pop_pcent | 2161.04 | 0.00 | 0.87 | 12 | increasing |
| mean_l ~ sp_vol + sp_tmin + sp_pmin + pop_vol+ pop_tmin | 2164.85 | 3.81 | 0.13 | 11 | increasing |
| mean_l ~ sp_vol + sp_tmax + sp_pmax + pop_vol + pop_tmax + pop_pmax | 2190.56 | 29.52 | 0.00 | 12 | increasing |
| mean_l ~ cent_exp + cent_dir_r | 2237.06 | 0.00 | 0.97 | 8 | increasing |
| mean_l ~ cent_exp + cent_dir | 2244.21 | 7.15 | 0.03 | 8 | increasing |
| mean_l ~ t_meanl_intra + p_meanl_intra + luc_meanl | 2256.92 | 0.00 | 1.00 | 9 | increasing |
| mean_l ~ t_meanlw_intra + p_meanlw_intra + luc_meanl | 2269.58 | 12.66 | 0.00 | 9 | increasing |
| mean_l ~ t_meanl_inter + p_meanl_inter + luc_meanl | 2271.36 | 14.43 | 0.00 | 9 | increasing |
| mean_l ~ t_meanlw_inter + p_meanlw_inter + luc_meanl | 2276.97 | 20.05 | 0.00 | 9 | increasing |

**Table A2.5| Climate maximum sensitivity analysis model averaged results**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using climate niche maximum as a measure of niche position instead of niche centroid position. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| sp_vol | -0.0139926 | -0.0787579 | 0.0495964 | 0.69 | decreasing |
| sp_pmax | 0.03023364 | -0.0275231 | 0.09156975 | 0.32175043 | decreasing |
| pop_vol | -0.0391037 | -0.122218 | 0.04180831 | 0.343 | decreasing |
| pop_tmax | -0.105516 | -0.1873743 | -0.0338411 | 0.01 | decreasing |
| cent_exp | -0.0142149 | -0.0688729 | 0.05340581 | 0.668 | decreasing |
| cent_dir | 0.01522425 | -0.0321661 | 0.06484824 | 0.557 | decreasing |
| t_meanl_intra | -0.1778832 | -0.2509589 | -0.1088842 | 5.00E-04 | decreasing |
| p_meanl_intra | 0.05851163 | -0.0044288 | 0.12524949 | 0.07355279 | decreasing |
| pop_pmax | -0.1215341 | -0.1963228 | -0.0522019 | 5.00E-04 | decreasing |
| luc_meanl | 0.02492574 | -0.0512281 | 0.09810762 | 0.504 | decreasing |
| sp_tmax | 0 | 0 | 0 | 0 | decreasing |
| clad_vol | 0 | 0 | 0 | 0 | decreasing |
| sp_vol | -0.1024033 | -0.1764631 | -0.0269118 | 0.00736645 | increasing |
| sp_pmax | 0.02752662 | -0.0337775 | 0.0873464 | 0.359 | increasing |
| pop_vol | 0.20566425 | 0.12394911 | 0.28809873 | 5.00E-04 | increasing |
| clad_vol | -0.008494 | -0.075136 | 0.0625179 | 0.79215894 | increasing |
| p_meanl_intra | -0.024933 | 0.04617483 | -0.0926766 | 0.48500626 | increasing |
| sp_tmax | 0.06338553 | -0.0257876 | 0.15207285 | 0.1546727 | increasing |
| pop_tmax | -0.0089571 | -0.0981667 | 0.07378621 | 0.84715738 | increasing |
| cent_dir_r | 0.01335832 | -0.0327963 | 0.06205426 | 0.599 | increasing |
| pop_pmax | 0 | 0 | 0 | 0 | increasing |
| cent_exp | 0 | 0 | 0 | 0 | increasing |
| t_meanl_intra | 0 | 0 | 0 | 0 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.6| Climate minimum sensitivity analysis model averaged results**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using climate niche minimum as a measure of niche position instead of niche centroid position. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Minimum precipitation had to be removed as a variable due to having an erroneous distribution. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| pop_vol | -0.0769554 | -0.1601607 | 0.0003157 | 0.06429884 | decreasing |
| clad_vol | 0.00780703 | -0.0499247 | 0.0616096 | 0.77579991 | decreasing |
| cent_exp | 0.01168214 | -0.0478396 | 0.07336678 | 0.72410521 | decreasing |
| t_meanl_intra | -0.1654181 | -0.2406242 | -0.091204 | 0.00058074 | decreasing |
| p_meanl_intra | 0.05846699 | -0.0060984 | 0.12417409 | 0.07669608 | decreasing |
| sp_vol | -0.0136483 | -0.0909605 | 0.05835718 | 0.67484832 | decreasing |
| sp_tmin | 0.03869692 | -0.0195052 | 0.09744021 | 0.20445025 | decreasing |
| pop_tmin | 0.06116179 | -0.0468534 | 0.1796805 | 0.29841555 | decreasing |
| sp_pmin | -0.0375614 | -0.154723 | 0.07680437 | 0.513 | decreasing |
| cent_dir | 0.01645099 | -0.0347697 | 0.06565461 | 0.53781973 | decreasing |
| luc_meanl | 0.01968973 | -0.0617821 | 0.08870541 | 0.637 | decreasing |
| sp_vol | -0.0652159 | -0.1370428 | 0.00701924 | 0.17850754 | increasing |
| pop_vol | 0.18669322 | 0.10153477 | 0.26789446 | 5.00E-04 | increasing |
| cent_exp | 0.08066717 | 0.01957301 | 0.13824072 | 0.01098865 | increasing |
| cent_dir_r | 0.01478083 | -0.0306358 | 0.06129742 | 0.54026746 | increasing |
| p_meanl_intra | -0.0207399 | 0.04398364 | -0.0919947 | 0.55705442 | increasing |
| sp_pmin | 0.04834867 | -0.0623227 | 0.15942391 | 0.403 | increasing |
| t_meanl_intra | 0.12945581 | 0.05532073 | 0.20708646 | 0.001 | increasing |
| sp_tmin | 0 | 0 | 0 | 0 | increasing |
| pop_tmin | 0 | 0 | 0 | 0 | increasing |
| clad_vol | 0 | 0 | 0 | 0 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.7| Centroid direction sensitivity analysis model averaged results**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using different metrics for centroid direction (decreasing populations: ratio, increasing populations: distance-based metric). I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| sp_tcent | 0.04226257 | -0.017393 | 0.10547799 | 0.27889705 | decreasing |
| pop_vol | -0.0957102 | -0.1772151 | -0.0149556 | 0.02347047 | decreasing |
| pop_pcent | -0.1222758 | -0.1989331 | -0.0421677 | 0.00253673 | decreasing |
| clad_vol | 0.01154148 | -0.0446509 | 0.06253379 | 0.67745263 | decreasing |
| cent_exp | 0.00397871 | -0.0510752 | 0.06295092 | 0.88946313 | decreasing |
| t_meanl_intra | -0.1711505 | -0.2450212 | -0.1015306 | 5.00E-04 | decreasing |
| p_meanl_intra | 0.06561362 | -0.0001378 | 0.13066389 | 0.04986164 | decreasing |
| luc_meanl | 0.00754342 | -0.0700988 | 0.07997612 | 0.826 | decreasing |
| sp_vol | 0.0392562 | -0.0569204 | 0.12534938 | 0.22116896 | decreasing |
| sp_pcent | 0.1238819 | 0.00827384 | 0.2400042 | 0.04298365 | decreasing |
| pop_tcent | 0 | 0 | 0 | 0 | decreasing |
| cent_dir_r | 0 | 0 | 0 | 0 | decreasing |
| sp_vol | -0.0734107 | -0.1271191 | -0.0172616 | 0.0076997 | increasing |
| pop_vol | 0.18706624 | 0.09650594 | 0.26649493 | 5.00E-04 | increasing |
| pop_tcent | 0.02087413 | -0.0853585 | 0.12570873 | 0.45292567 | increasing |
| pop_pcent | 0.07051213 | -0.0108938 | 0.15344421 | 0.11095541 | increasing |
| cent_exp | 0.07311308 | 0.00806224 | 0.13730741 | 0.02664331 | increasing |
| t_meanl_intra | 0.14371214 | 0.06796111 | 0.21380887 | 5.00E-04 | increasing |
| sp_tcent | 0.05699517 | -0.0223014 | 0.12859574 | 0.15345821 | increasing |
| sp_pcent | 0.08305434 | 0.02081247 | 0.15278083 | 0.02266489 | increasing |
| cent_dir | 0.01021283 | -0.0409485 | 0.0568936 | 0.67988377 | increasing |
| clad_vol | 0 | 0 | 0 | 0 | increasing |
| p_meanl_intra | 0 | 0 | 0 | 0 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.8| Annual rates of climate change sensitivity analysis model averaged results**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using rates of climate change metrics derived from mean annual climate data instead of mean monthly data. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| pop_vol | -0.1148032 | -0.1998598 | -0.0311626 | 0.00857983 | decreasing |
| pop_tcent | 0.0373225 | -0.0553415 | 0.12771598 | 0.43407492 | decreasing |
| pop_pcent | -0.1089103 | -0.1912984 | -0.0300868 | 0.01136243 | decreasing |
| cent_dir | 0.01115432 | -0.0401437 | 0.05814197 | 0.66511971 | decreasing |
| p_meanl_inter | 0.08447526 | 0.02047384 | 0.15221358 | 0.01338808 | decreasing |
| sp_vol | 0.05850757 | -0.054647 | 0.1656496 | 0.34964719 | decreasing |
| sp_tcent | 0.06060699 | -0.007485 | 0.12864216 | 0.12634674 | decreasing |
| sp_pcent | 0.09227414 | -0.0197851 | 0.20228595 | 0.16986637 | decreasing |
| clad_vol | 0.00738719 | -0.0507339 | 0.06472241 | 0.7595436 | decreasing |
| t_meanl_inter | -0.0560675 | -0.1198685 | 0.00346921 | 0.07877768 | decreasing |
| cent_exp | -0.0188801 | -0.0831087 | 0.03916446 | 0.531 | decreasing |
| luc_meanl | 0.03548927 | -0.0408756 | 0.11205816 | 0.374 | decreasing |
| sp_vol | -0.0866716 | -0.1859773 | 0.00966012 | 0.08163156 | increasing |
| sp_tcent | 0.05525981 | -0.020401 | 0.13440407 | 0.1773103 | increasing |
| sp_pcent | 0.02614924 | -0.0764228 | 0.12484286 | 0.3193387 | increasing |
| pop_vol | 0.19231681 | 0.11150104 | 0.27734174 | 5.00E-04 | increasing |
| pop_pcent | 0.07660996 | -0.0055463 | 0.15742975 | 0.07882867 | increasing |
| cent_dir_r | 0.01203081 | -0.0358935 | 0.05870166 | 0.64135093 | increasing |
| t_meanl_inter | 0.05270509 | -0.0121515 | 0.11662083 | 0.11618677 | increasing |
| pop_tcent | -0.008582 | -0.1167513 | 0.10382152 | 0.88274203 | increasing |
| cent_exp | 0.07114272 | 0.00231866 | 0.13651412 | 0.03968663 | increasing |
| p_meanl_inter | -0.0010844 | 0.0684405 | -0.0671578 | 0.96343455 | increasing |
| clad_vol | -0.0105218 | -0.0810012 | 0.05979271 | 0.753 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.9| Standardized rates of climate change sensitivity analysis model averaged results**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using rates of climate change metrics standardized by local seasonality levels. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| sp_vol | 0.083782 | -0.029853 | 0.200227 | 0.134 | decreasing |
| sp_tcent | 0.073292 | -0.005375 | 0.152189 | 0.068 | decreasing |
| sp_pcent | 0.142059 | 0.016985 | 0.286021 | 0.037 | decreasing |
| pop_vol | -0.140707 | -0.224708 | -0.054224 | 0.004 | decreasing |
| pop_tcent | 0.016892 | -0.088817 | 0.115353 | 0.742 | decreasing |
| pop_pcent | -0.12646 | -0.210143 | -0.040354 | 0.004 | decreasing |
| clad_vol | 0.010896 | -0.049728 | 0.065719 | 0.718 | decreasing |
| cent_dir | 0.011592 | -0.033978 | 0.063471 | 0.665 | decreasing |
| t_meanlw_intra | -0.07624 | -0.146833 | -0.009163 | 0.032 | decreasing |
| p_meanlw_intra | 0.045661 | -0.021334 | 0.104361 | 0.174 | decreasing |
| cent_exp | 0 | 0 | 0 | 0 | decreasing |
| luc_meanl | 0 | 0 | 0 | 0 | decreasing |
| sp_vol | -0.079304 | -0.135399 | -0.025399 | 0.008 | increasing |
| sp_tcent | 0.031427 | -0.028482 | 0.100148 | 0.356 | increasing |
| pop_vol | 0.199672 | 0.115919 | 0.284803 | 5.00E-04 | increasing |
| pop_pcent | 0.069925 | -0.010348 | 0.144707 | 0.097 | increasing |
| cent_exp | 0.07771 | 0.018446 | 0.138344 | 0.014 | increasing |
| cent_dir_r | 0.013439 | -0.031932 | 0.059679 | 0.578 | increasing |
| sp_pcent | 0 | 0 | 0 | 0 | increasing |
| pop_tcent | 0 | 0 | 0 | 0 | increasing |
| clad_vol | 0 | 0 | 0 | 0 | increasing |
| t_meanlw_intra | 0 | 0 | 0 | 0 | increasing |
| p_meanlw_intra | 0 | 0 | 0 | 0 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.10| Annual standardized rates of climate change sensitivity analysis**. Results presented here represent the model averaged (ΔAIC <6) output from a sensitivity analysis testing the effects of using rates of climate change metrics standardized by local seasonality levels and derived using mean annual climate data. I fit Bayesian mixed effect models between environmental predictors and mean rate of avian population change, with population site location, biogeographic realm and taxonomic family set as random effects. Values of 0 indicate that the respective variables were not present in any top ranking model. All variables are exhibited here as abbreviations (Table A2.11).

| Variable | Effect size | Lower CI (95%) | Upper CI (95%) | p-value | Trend direction |
|---|---|---|---|---|---|
| sp_tcent | 0.02772191 | -0.0275102 | 0.08785932 | 0.356 | decreasing |
| pop_vol | -0.119679 | -0.1983291 | -0.0347421 | 0.003 | decreasing |
| pop_pcent | -0.0932723 | -0.1742812 | -0.010804 | 0.038 | decreasing |
| p_meanlw_inter | 0.06286559 | -0.0002612 | 0.1287526 | 0.057 | decreasing |
| luc_meanl | 0.02053314 | -0.0540889 | 0.09329922 | 0.61 | decreasing |
| sp_vol | 0 | 0 | 0 | 0 | decreasing |
| sp_pcent | 0 | 0 | 0 | 0 | decreasing |
| pop_tcent | 0 | 0 | 0 | 0 | decreasing |
| clad_vol | 0 | 0 | 0 | 0 | decreasing |
| cent_exp | 0 | 0 | 0 | 0 | decreasing |
| cent_dir | 0 | 0 | 0 | 0 | decreasing |
| t_meanlw_inter | 0 | 0 | 0 | 0 | decreasing |
| sp_vol | -0.0780703 | -0.1747802 | 0.02501071 | 0.1592367 | increasing |
| sp_tcent | 0.03876911 | -0.0455809 | 0.11822001 | 0.36941282 | increasing |
| sp_pcent | -0.0011398 | -0.1320929 | 0.1265772 | 0.74958009 | increasing |
| pop_vol | 0.2022086 | 0.11932616 | 0.28498761 | 5.00E-04 | increasing |
| pop_tcent | -0.0071324 | -0.1181828 | 0.09712628 | 0.77073879 | increasing |
| pop_pcent | 0.07107156 | -0.0112605 | 0.15401145 | 0.10056778 | increasing |
| clad_vol | -0.0025595 | -0.072924 | 0.07318432 | 0.93621268 | increasing |
| cent_exp | 0.07708202 | 0.01338294 | 0.14341265 | 0.02638602 | increasing |
| t_meanlw_inter | 0.04352484 | -0.0218862 | 0.11184037 | 0.2013705 | increasing |
| p_meanlw_inter | 0.00642149 | 0.07114558 | -0.0622417 | 0.847 | increasing |
| cent_dir_r | 0.01640805 | -0.0287887 | 0.06449984 | 0.509 | increasing |
| luc_meanl | 0 | 0 | 0 | 0 | increasing |

**Table A2.11| Variable abbreviation table.** A table summarizing the abbreviations of all predictor variables I included in my core and sensitivity analyses.

| Variable abbreviation | Variable name |
|---|---|
| sp_vol | Species climate niche volume |
| sp_tcent | Species temperature centroid |
| sp_pcent | Species precipitation centroid |
| sp_tmax | Species temperature maximum limit |
| sp_tmin | Species temperature minimum limit |
| sp_pmax | Species precipitation maximum limit |
| sp_pmin | Species precipitation minimum limit |
| clad_vol | Family climate niche volume |
| pop_vol | Local climate volume |
| pop_tcent | Local temperature centroid |
| pop_pcent | Local precipitation centroid |
| pop_tmax | Local temperature maximum limit |
| pop_tmin | Local temperature minimum limit |
| pop_pmax | Local precipitation maximum limit |
| pop_pmin | Local precipitation minimum limit |
| cent_exp | Centroid distance |
| cent_dir | Centroid direction |
| cent_dir_r | Centroid direction ratio |
| t_meanl_inter | Local rate of warming (annual) |
| t_meanl_intra | Local rate of warming (monthly) |
| p_meanl_inter | Local rate of drying (annual) |
| p_meanl_intra | Local rate of drying (monthly) |
| t_meanlw_inter | Local rate of warming (annual, standardized) |
| t_meanlw_intra | Local rate of warming (monthly, standardized) |
| p_meanlw_inter | Local rate of drying (annual, standardized) |
| p_meanlw_intra | Local rate of drying (monthly, standardized) |
| luc_meanl | Local rate of land use change |
| mean_l | Mean rate of population change |

## A2.4 Supplementary figures

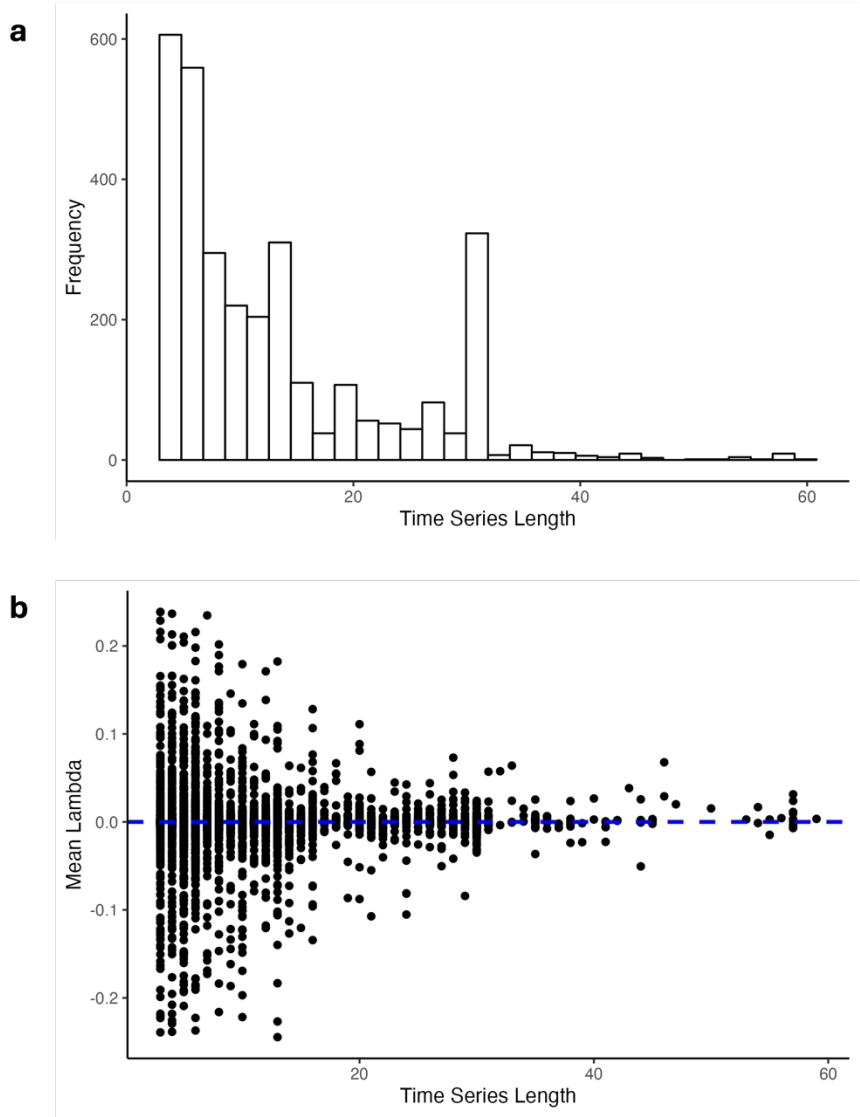



**Figure A2.1| Temporal distribution of population trend data**. (a) Histogram of time series lengths across my population trends dataset. The mean time series length is 13 years. Median time series length is 10 years. (b) Scatter plot of mean lambda against time series length.

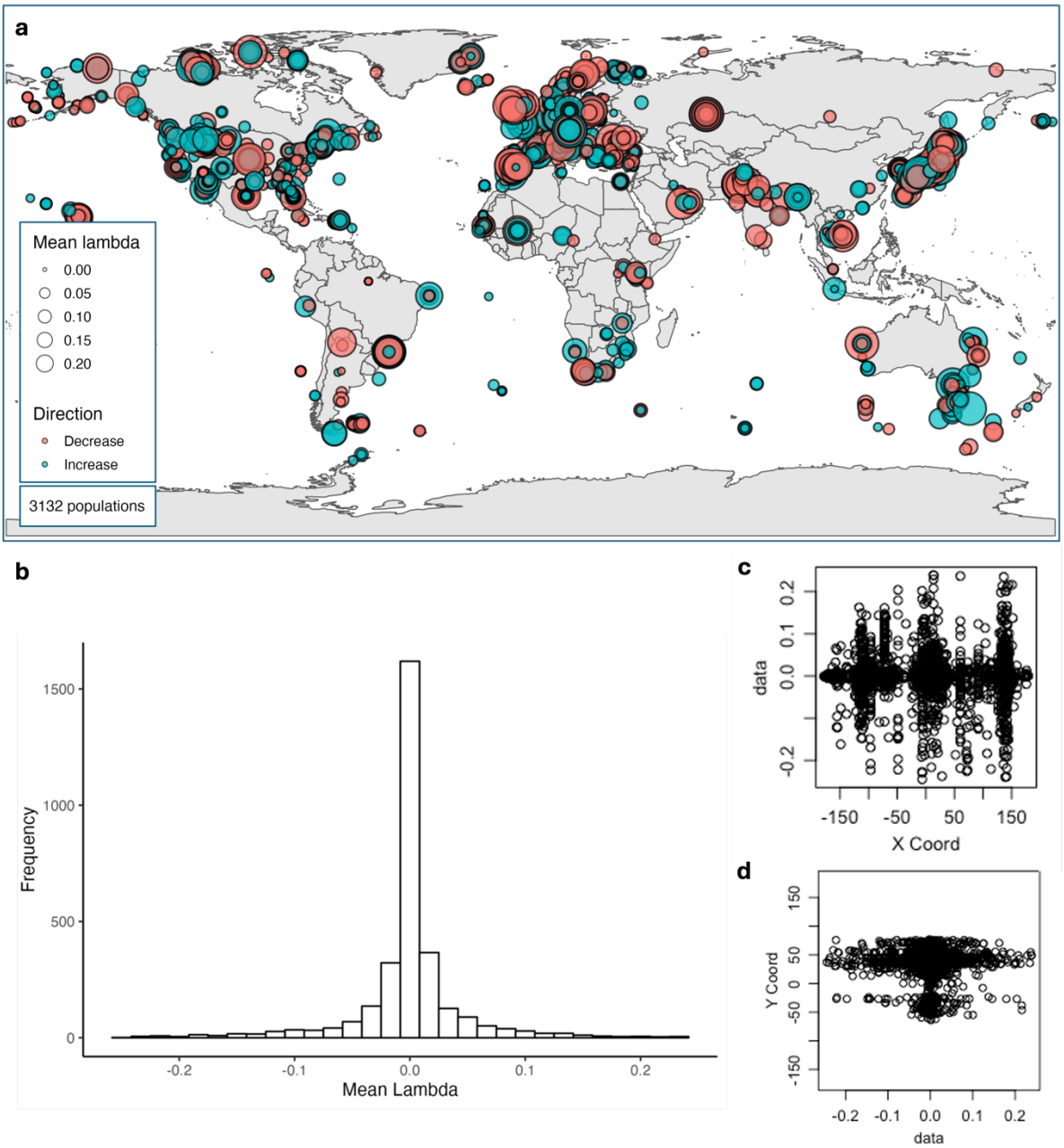



**Figure A2.2| Spatial distribution of population trend data.** (a) Map of mean rate of avian population change (lambda). Populations were split into either increasing (green circle) if mean population change ($\bar{\lambda}$) was more than 0 or decreasing (red circle) if mean population change ($\bar{\lambda}$) was less than 0. The size of each circle corresponds to the magnitude of the mean population change at a given population site, with larger circles indicating a larger mean population change. (b) A histogram showing the distribution of mean rate of avian population change (lambda) – the response variable used throughout this chapter. (c) The distribution of mean rate of avian population change (lambda) against longitude. (d) The distribution of mean rate of avian population change (lambda) against latitude.

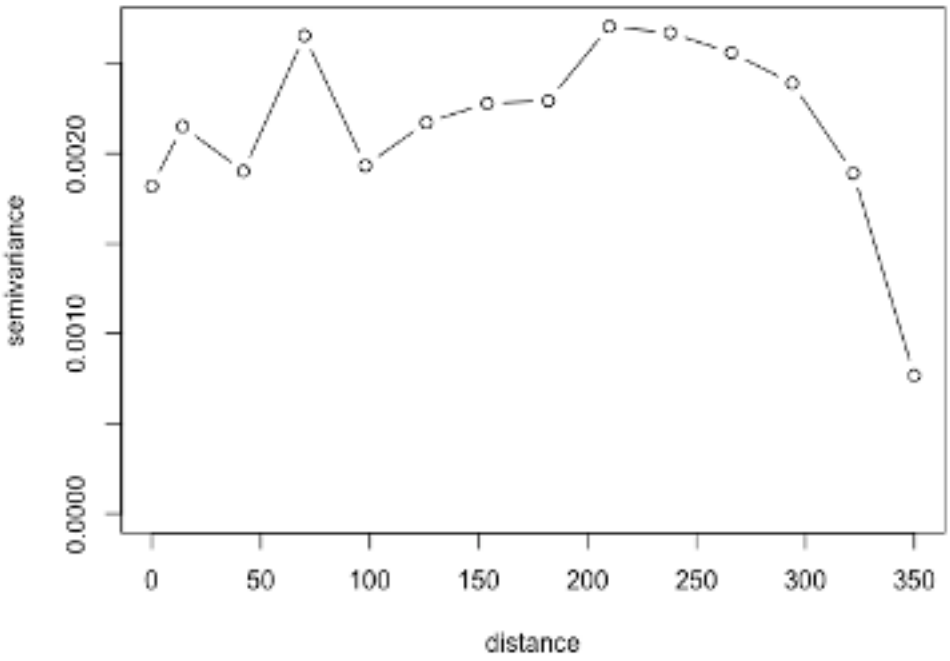
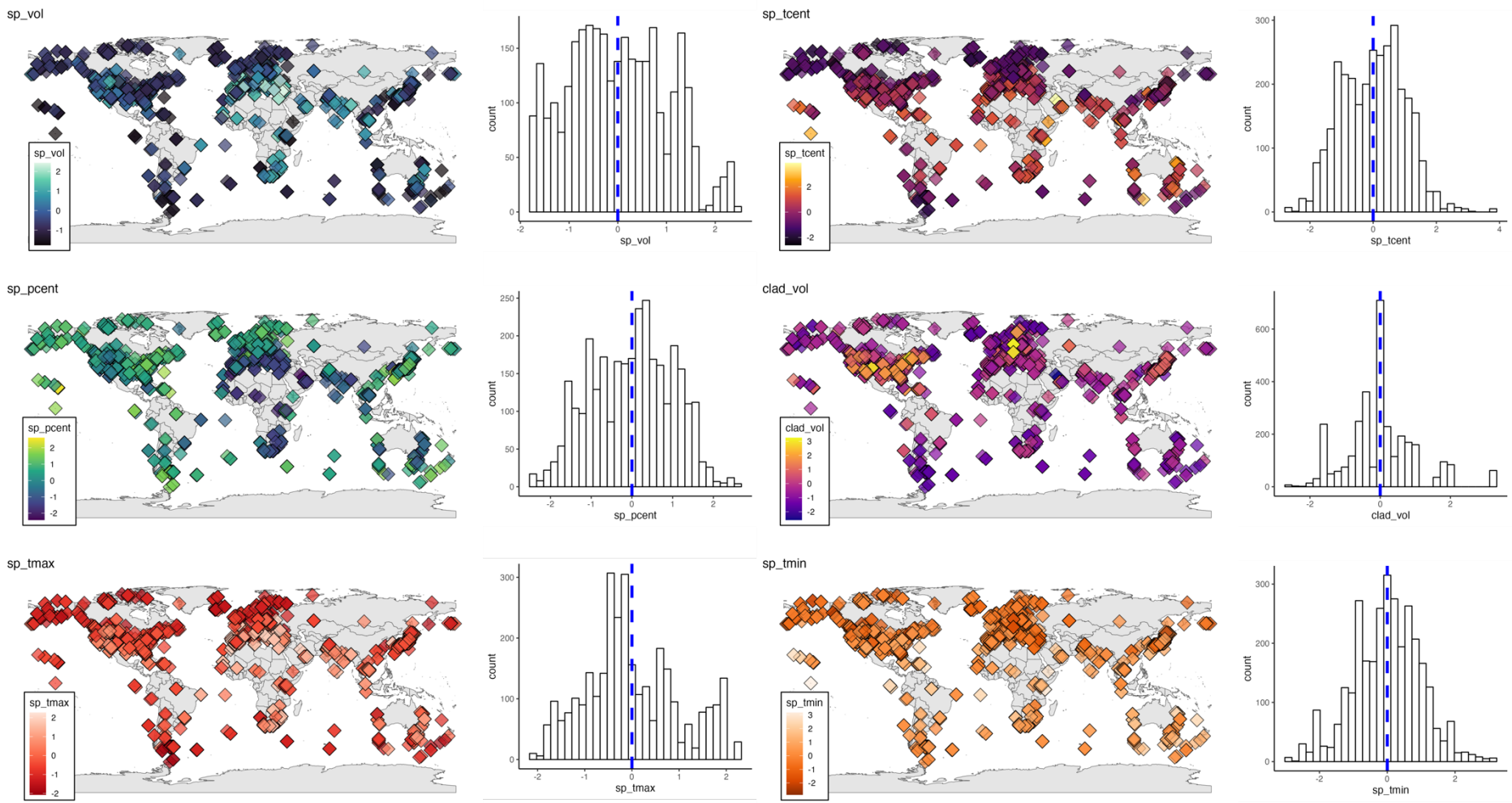
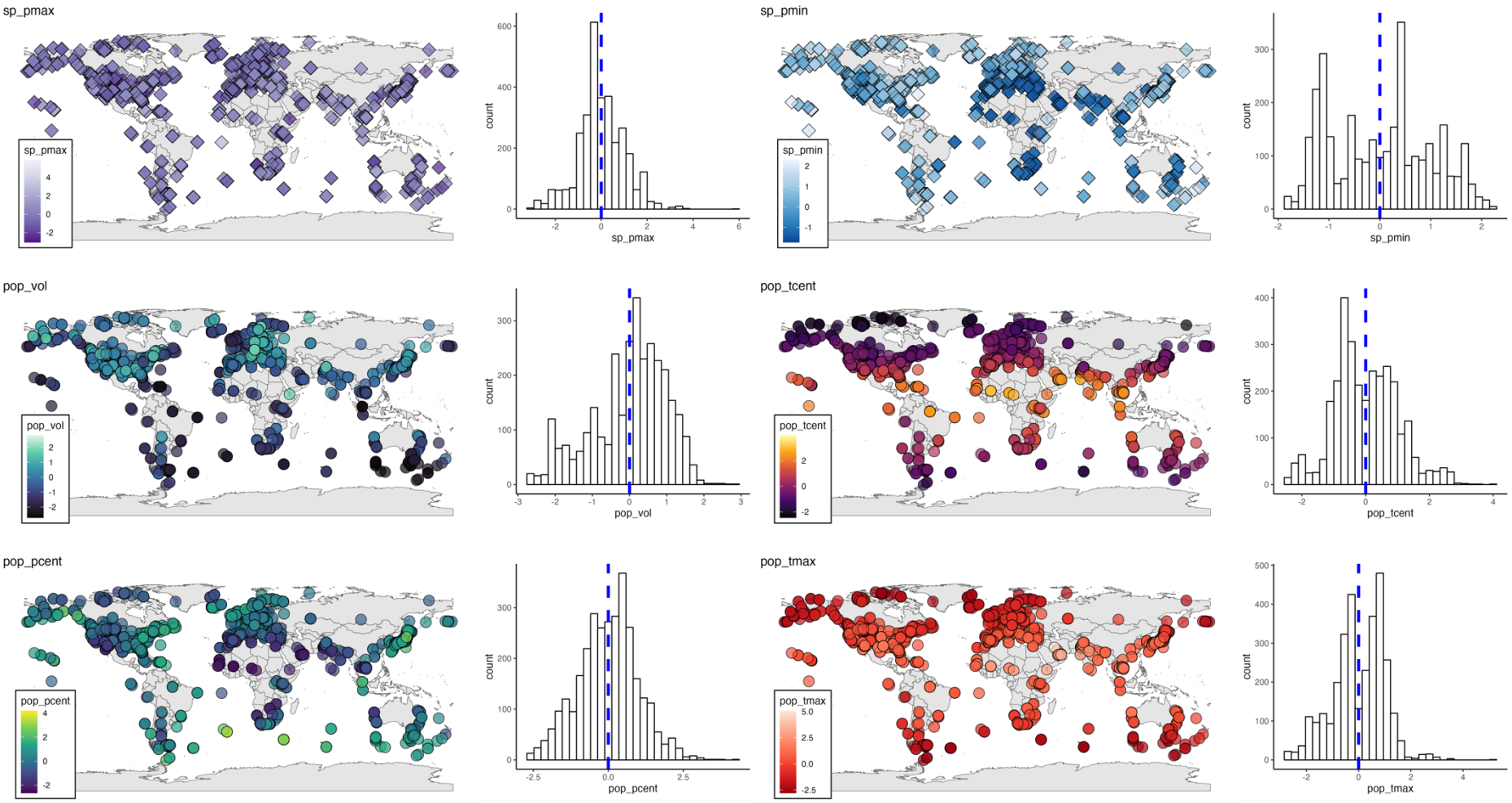
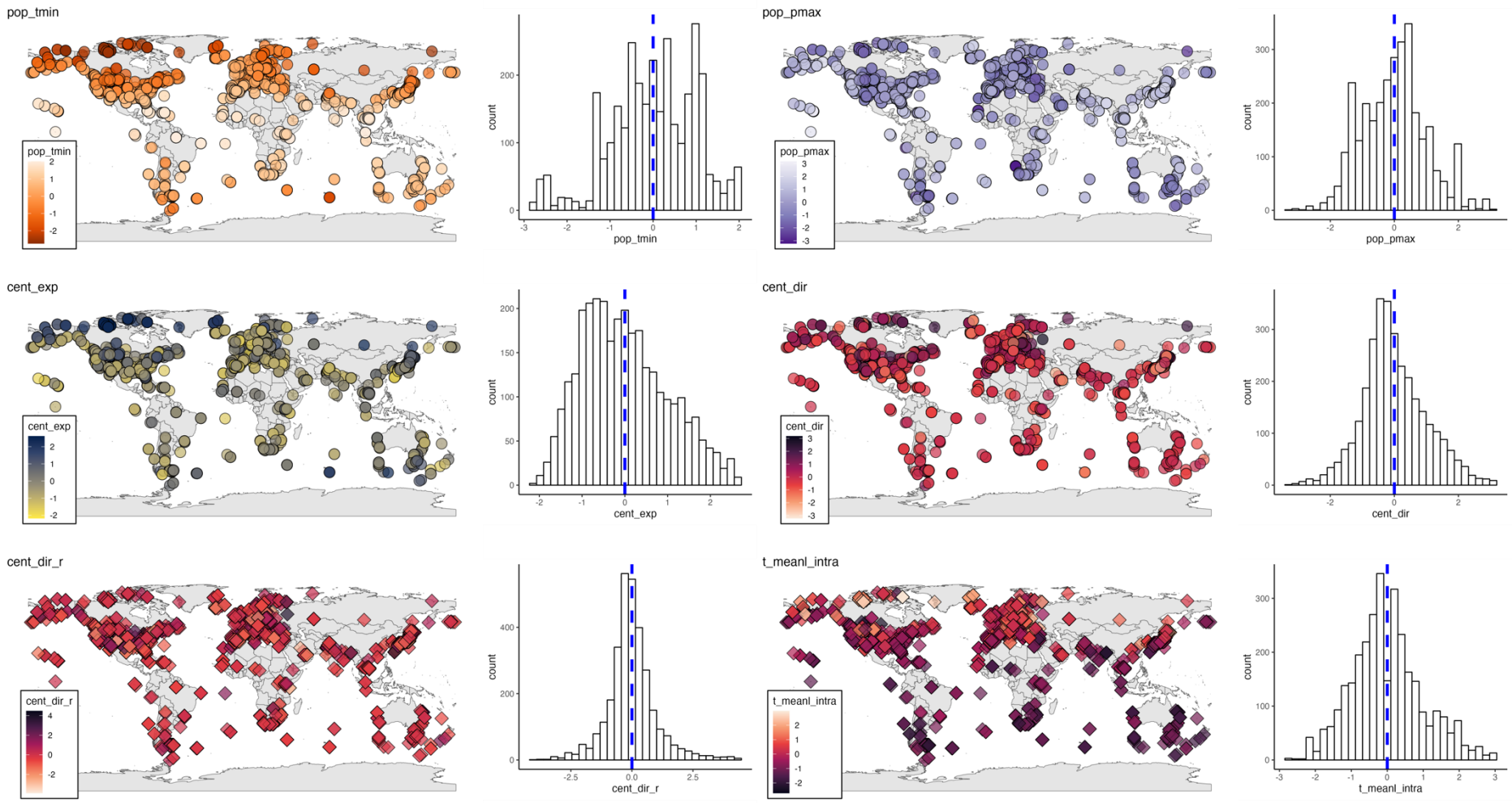
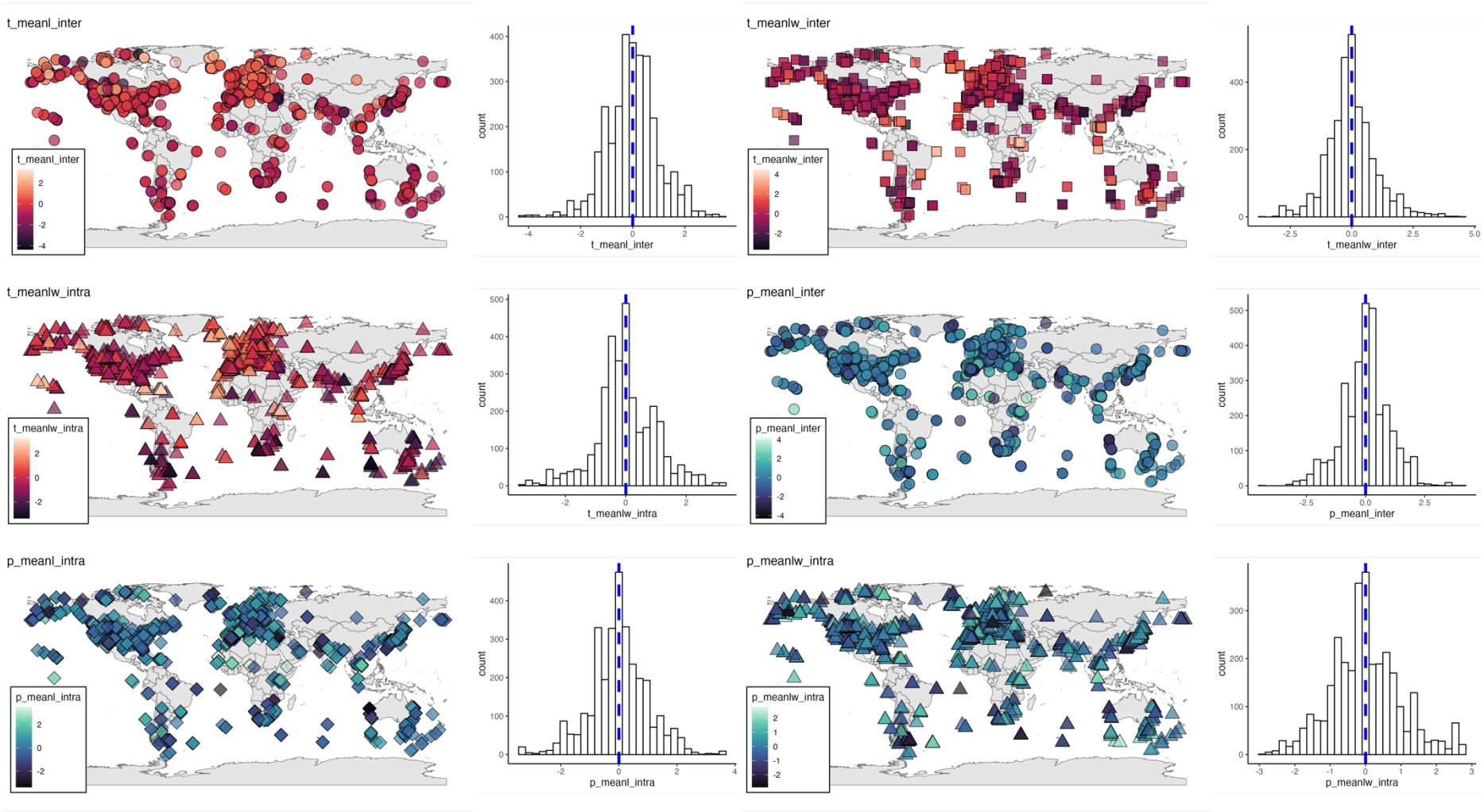



**Figure A2.3| Spatial variogram analysis results.** The results of a spatial variogram analysis aimed at understanding the level of spatial autocorrelation across my response variable (mean rate of avian population change). Semivariance (half the variance) between values of my response variable is plotted on the y-axis and distance between population sites is plotted on the x-axis. I find that there is seemingly low levels of spatial autocorrelation between mean rate of avian population change – i.e. response variable values are not more similar if they occur spatially proximal to each other - as there is no increasing slope of semivariance as distance between population sites increases. The spatial variogram analysis described here was conducted using the *geoR* R package.


sp_vol
sp_vol
count
sp_vol
sp_tcent
sp_tcent
count
sp_tcent
sp_pcent
sp_pcent
count
sp_pcent
clad_vol
clad_vol
count
clad_vol
sp_tmax
sp_tmax
count
sp_tmax
sp_tmin
sp_tmin
count
sp_tmin


sp_pmax
sp_pmax
count
sp_pmax
sp_pmin
sp_pmin
count
sp_pmin
pop_vol
pop_vol
count
pop_vol
pop_tcent
pop_tcent
count
pop_tcent
pop_pcent
pop_pcent
count
pop_pcent
pop_tmax
pop_tmax
count
pop_tmax


pop_tmin
pop_tmin
count
pop_tmin
pop_pmax
pop_pmax
count
pop_pmax
cent_exp
cent_exp
count
cent_exp
cent_dir
cent_dir
count
cent_dir
cent_dir_r
cent_dir_r
count
cent_dir_r
t_meanl_intra
t_meanl_intra
count
t_meanl_intra


t_meanl_inter
t_meanl_inter
count
t_meanl_inter
t_meanlw_inter
t_meanlw_inter
count
t_meanlw_inter
t_meanlw_intra
t_meanlw_intra
count
t_meanlw_intra
p_meanl_inter
p_meanl_inter
count
p_meanl_inter
p_meanl_intra
p_meanl_intra
count
p_meanl_intra
p_meanlw_intra
p_meanlw_intra
count
p_meanlw_intra

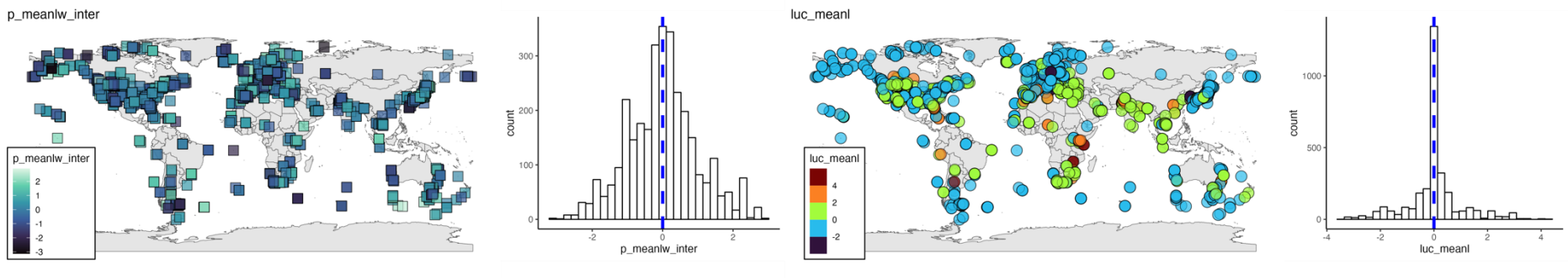



**Figure A2.4| Environmental predictor variable distributions.** Maps and histograms of all environmental predictors included in both core and sensitivity analyses. The colour of each population site corresponds to the value of a given predictor variable. My final dataset, once all processing steps were implemented, contained 3132 avian populations across 972 species. Histograms exhibit the distribution of each predictor post-processing – i.e. outlier values removed, data transformations and scaling implemented. In the case of climate niche features and local climate, temperature units = °C and precipitation units = log(10kg $m^2$/month). For rates of climate change derived from monthly climate data, units = °C per month and = log(10kg $m^2$/month) per month respectively. For rates of climate change derived from annual climate data, units = °C per year and = log(10kg $m^2$/month) per year respectively. For rate of land use change, units = percentage of anthropogenic land use activity per year. All variable names are exhibited here as abbreviations (Table A2.11).

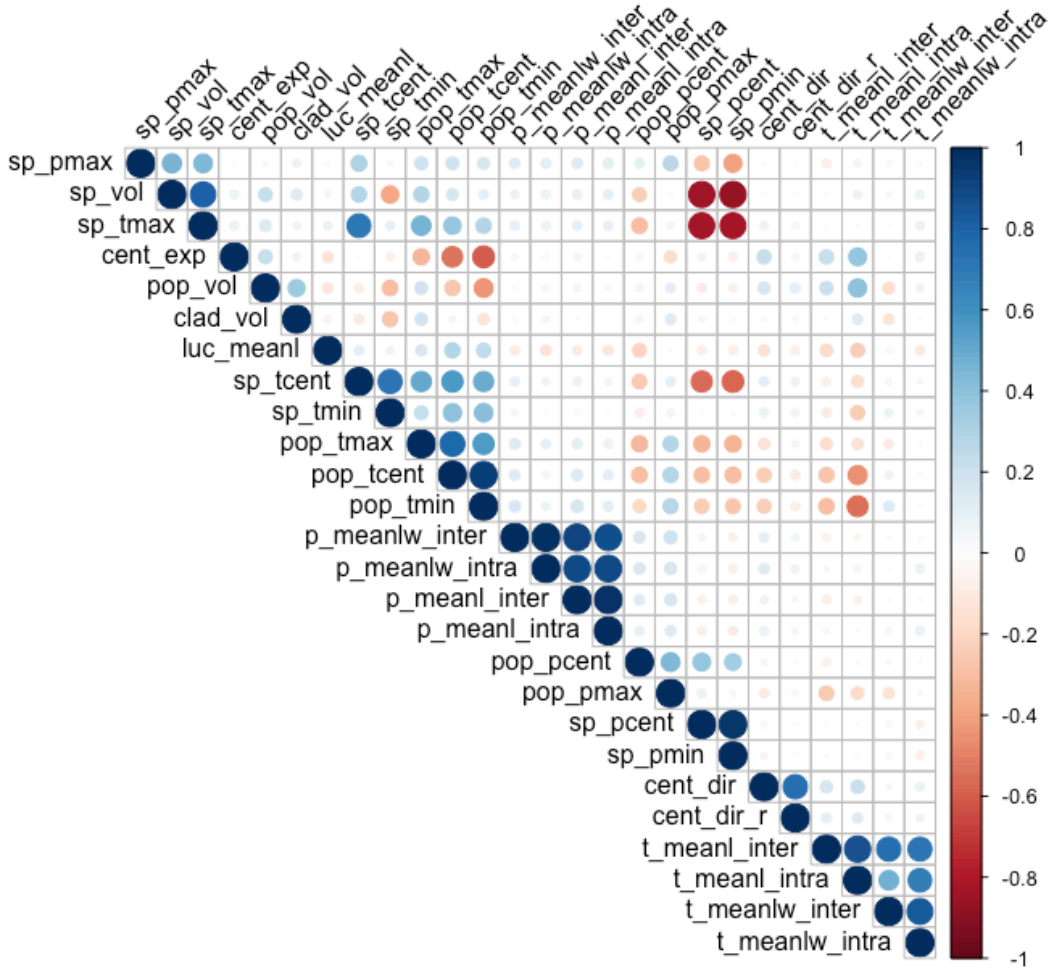



**Figure A2.5| Environmental predictor collinearity analysis.** Correlation matrix between all environmental predictors included in my analyses exhibiting the level of collinearity (Pearson correlation coefficient) between pairs of predictors. Any pair of variables that exhibited Pearson correlation coefficient values of over 0.4 were not included in the same model. The R package *corrplot* was used to generate this plot. All variable names are exhibited here as abbreviations (Table A2.11).

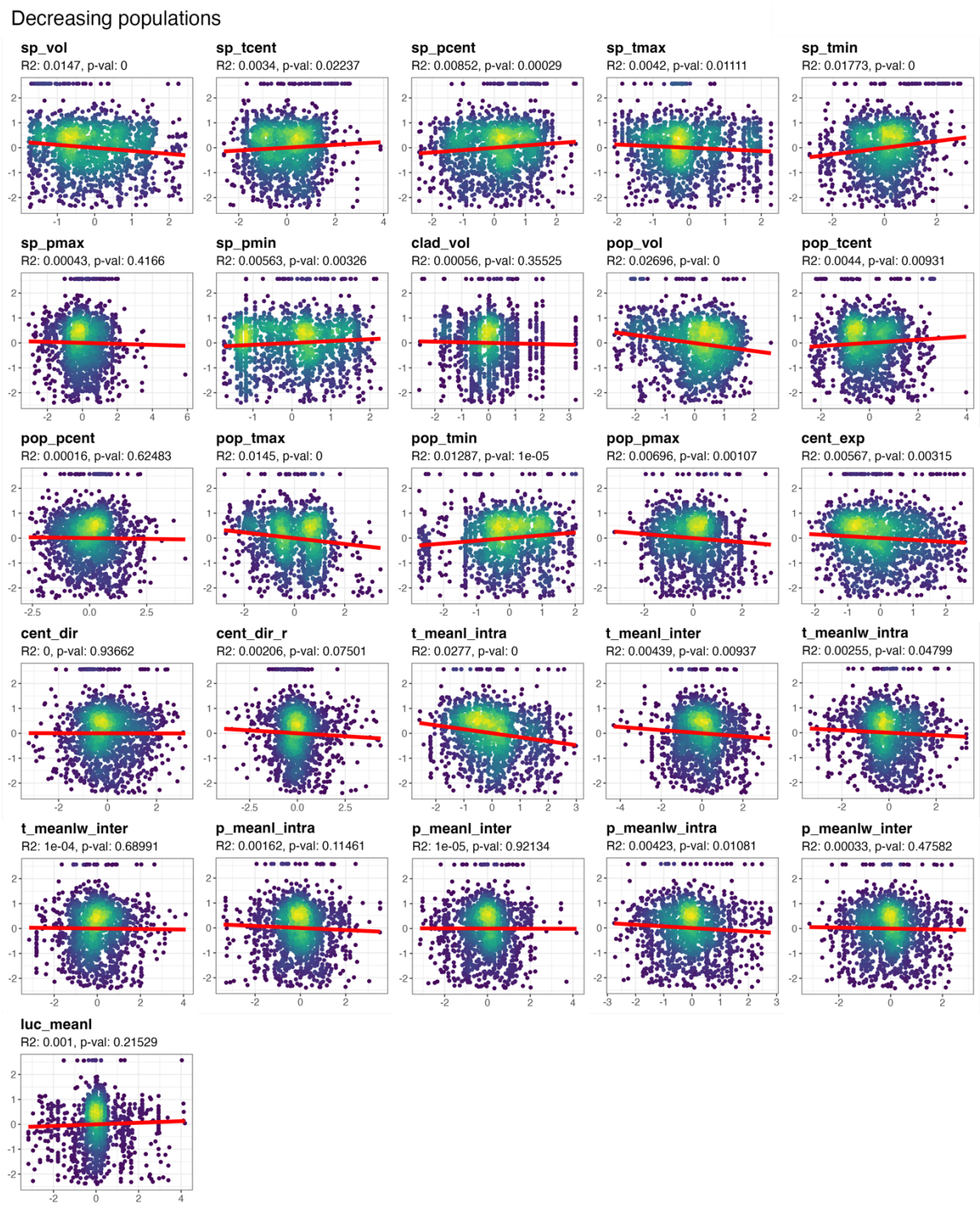



**Figure A2.6| Relationship between mean rate of avian population change and environmental predictors in decreasing populations.** Scatter plots exhibiting the relationship between each environmental predictor (x axis) and my response variable, mean rate of population change (y axis), for decreasing populations. $R^2$ and p-values are provided, summarizing the relationship between a given predictor variable and mean rate of avian population change as derived by univariate linear regression models. All variable names are exhibited here as abbreviations (Table A2.11).

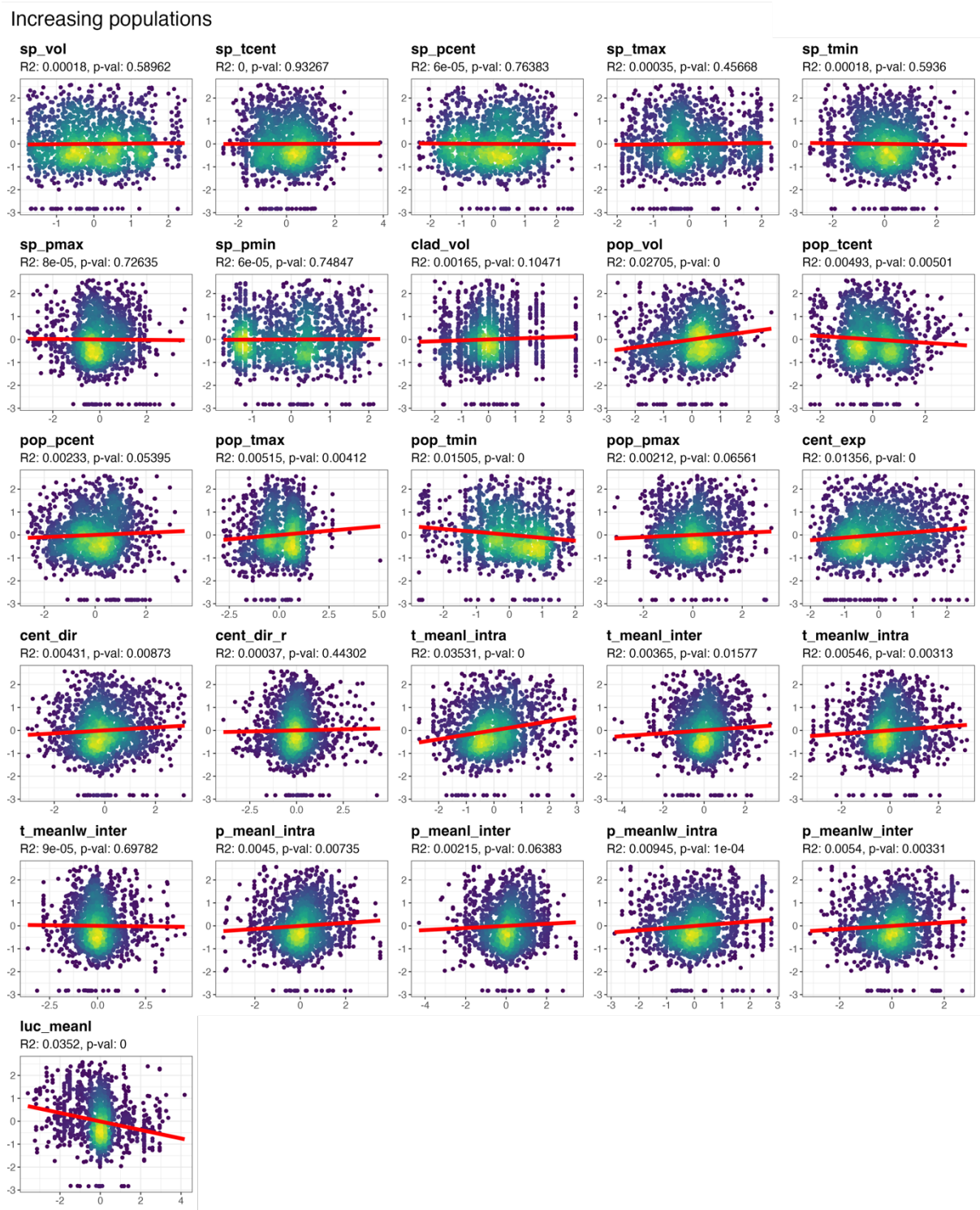



**Figure A2.7| Relationship between mean rate of avian population change and environmental predictors in increasing populations.** Scatter plots exhibiting the relationship between each environmental predictor (x axis) and my response variable, mean rate of population change (y axis), for increasing populations. $R^2$ and p-values are provided, summarizing the relationship between a given predictor variable and mean rate of avian population change as derived by univariate linear regression models. All variable names are exhibited here as abbreviations (Table A2.11).

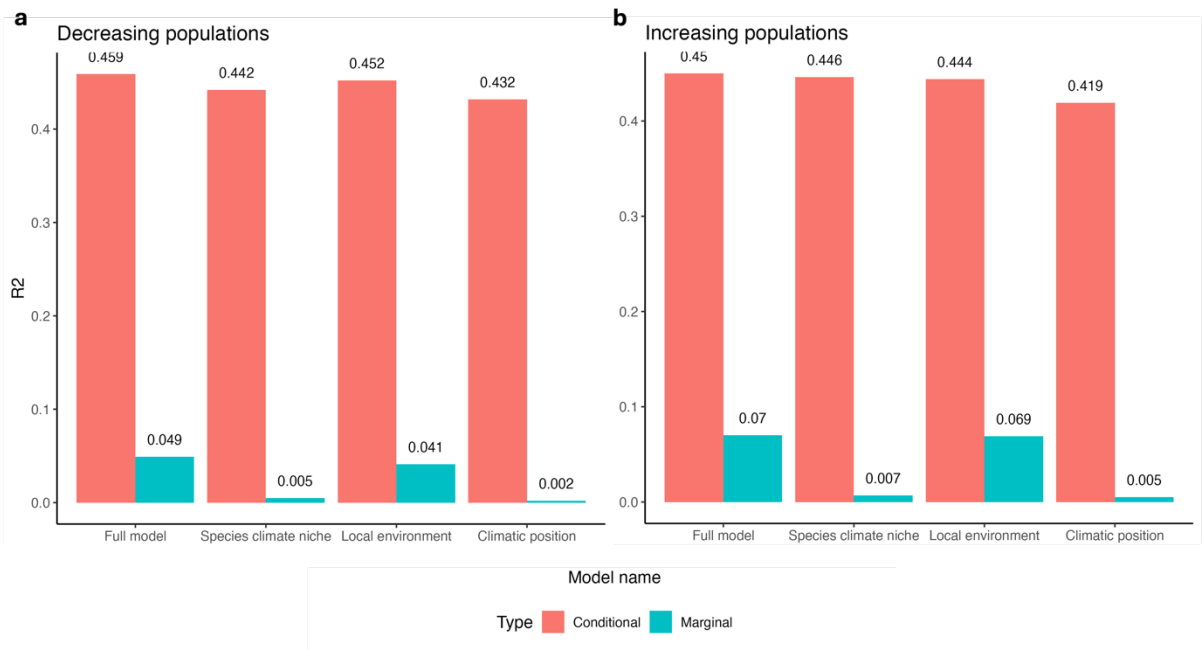



**Figure A2.8| $R^2$ of full and variable class models.** The conditional (red) and marginal (blue) $R^2$ values for linear mixed effects models fitted between my response variable (mean rate of avian population change) and all core variables (full model) and distinct variable classes (species climate niche, climatic position, local environment) across both (a) decreasing populations and (b) increasing populations.

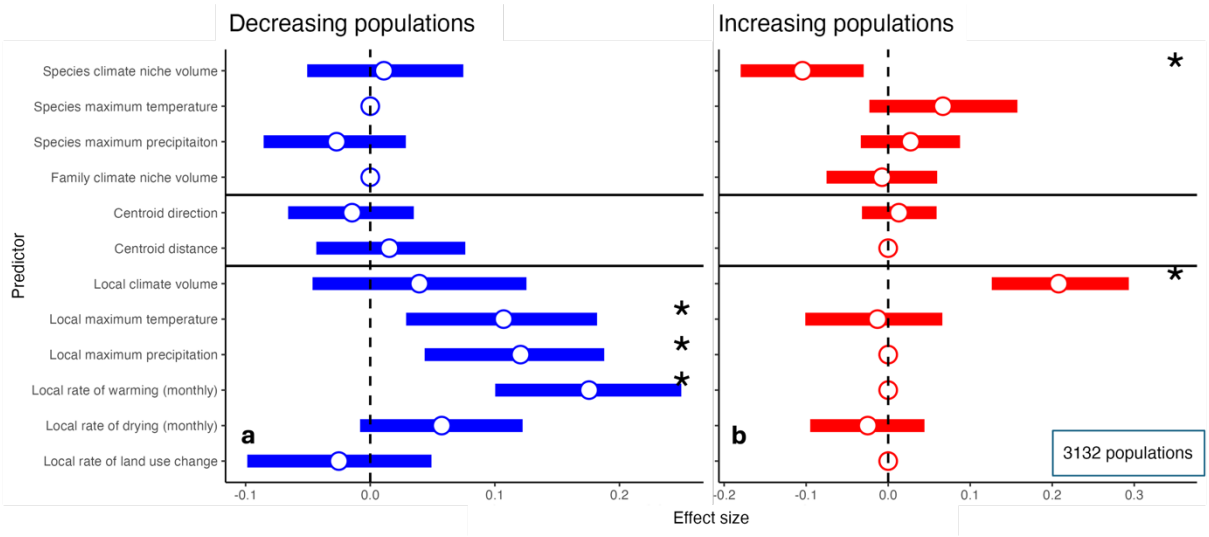



**Figure A2.9| Climate maximum sensitivity analysis.** Sensitivity test results investigating the effects of using climate niche maximums as a measure of niche position in (a) decreasing populations (blue) and (b) increasing populations (red). Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.5). Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

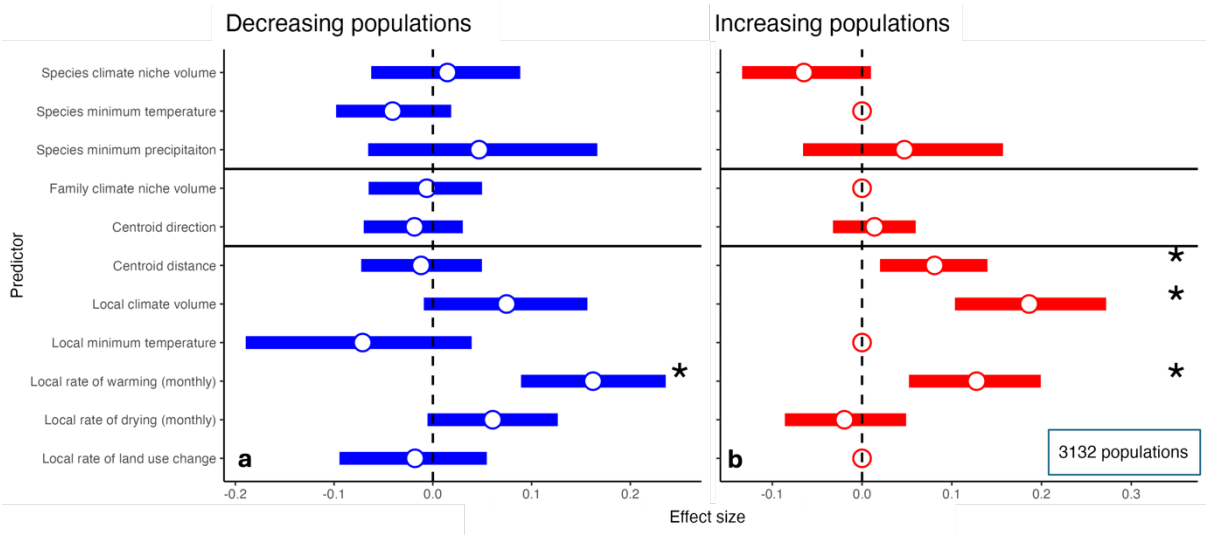



**Figure A2.10| Climate minimum sensitivity analysis.** Sensitivity test results investigating the effects of using climate niche minimums as a measure of niche position in (a) decreasing populations (blue) and (b) increasing populations (red). Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.6). Minimum precipitation had to be removed as a variable due to having an erroneous distribution. Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

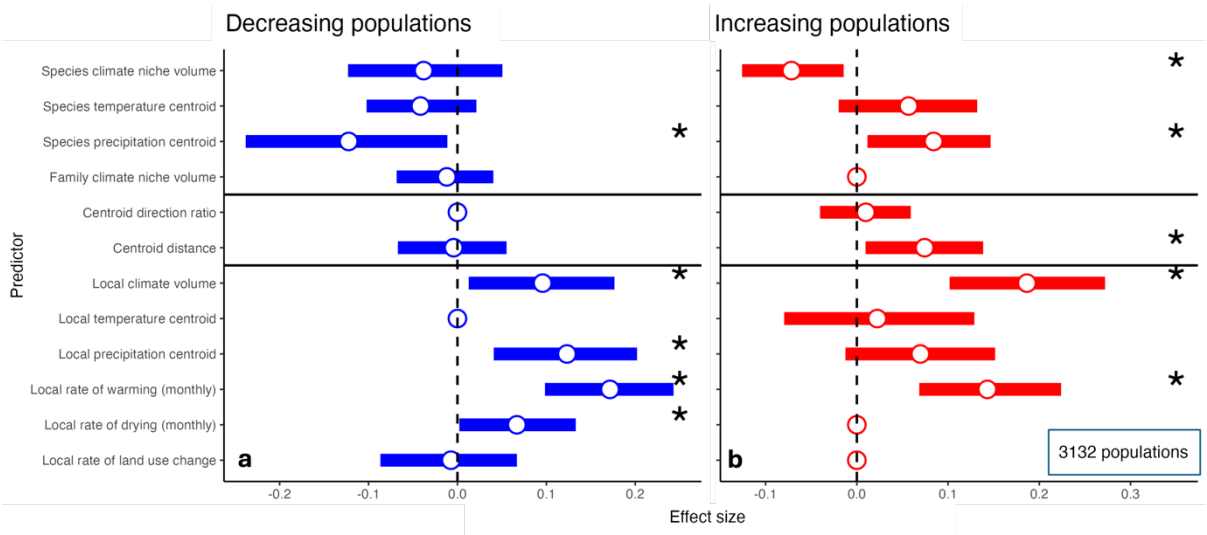



**Figure A2.11| Centroid direction sensitivity analysis.** Sensitivity test results testing the effects of using centroid direction ratio for (a) decreasing populations (blue) and centroid direction for (b) increasing populations (red) as a measure of niche directionality. Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.7). Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

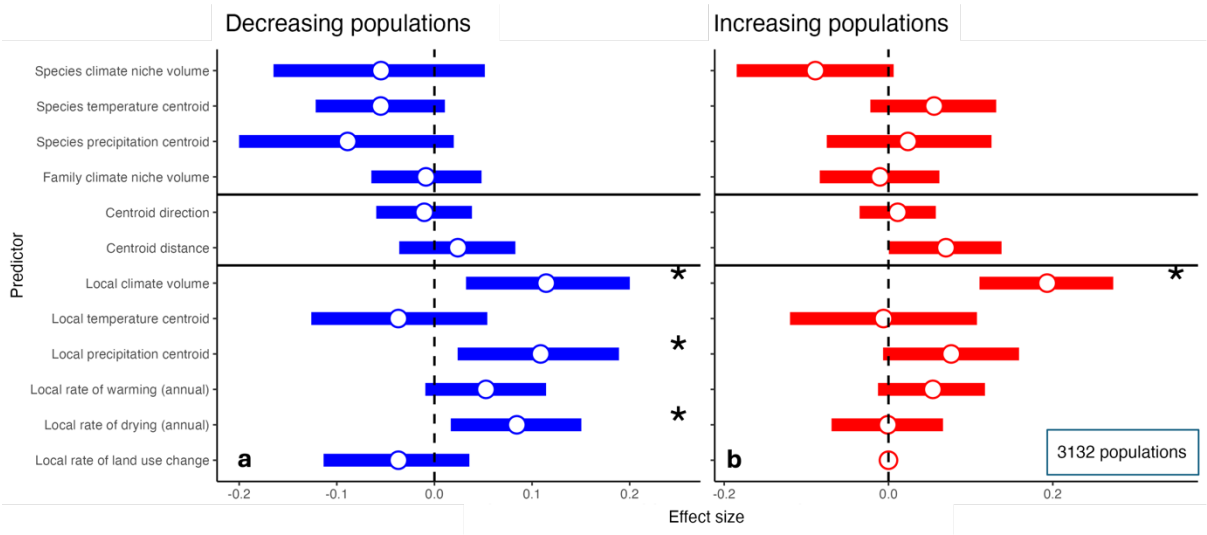



**Figure A2.12| Annual rates of climate change sensitivity analysis.** Sensitivity test results testing the effects of using rates of climate change derived from annual climate data (a) decreasing populations (blue) and (b) increasing populations (red). Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.8). Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

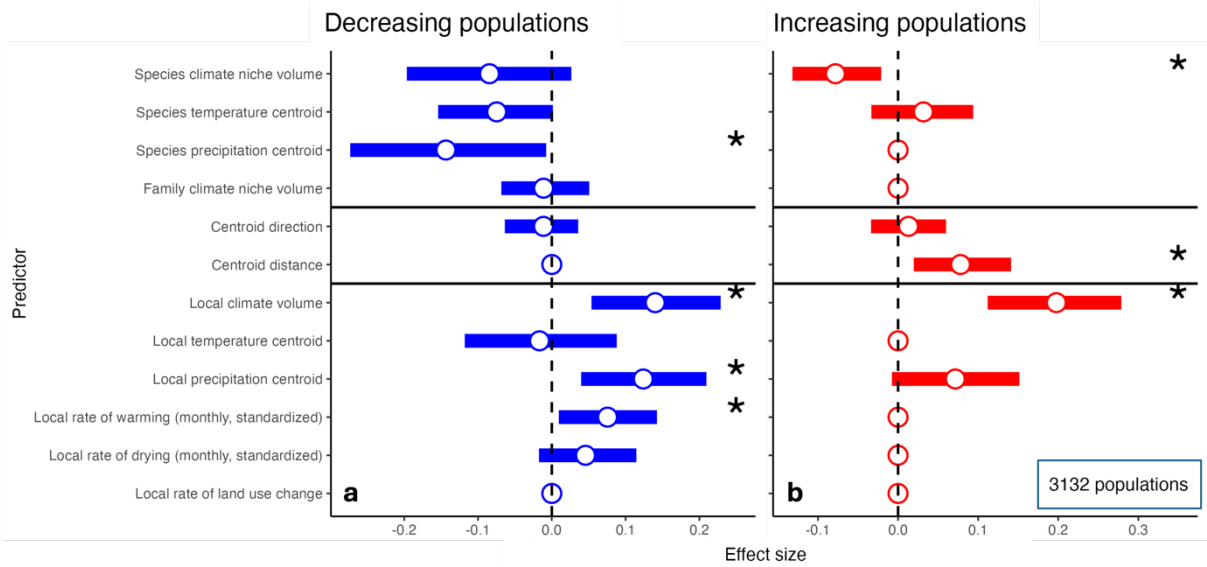



**Figure A2.13| Standardized rates of climate change sensitivity analysis.** Sensitivity test results testing the effects of using rates of climate change derived from monthly climate data and standardized for local seasonality in (a) decreasing populations (blue) and (b) increasing populations (red). Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.9). Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

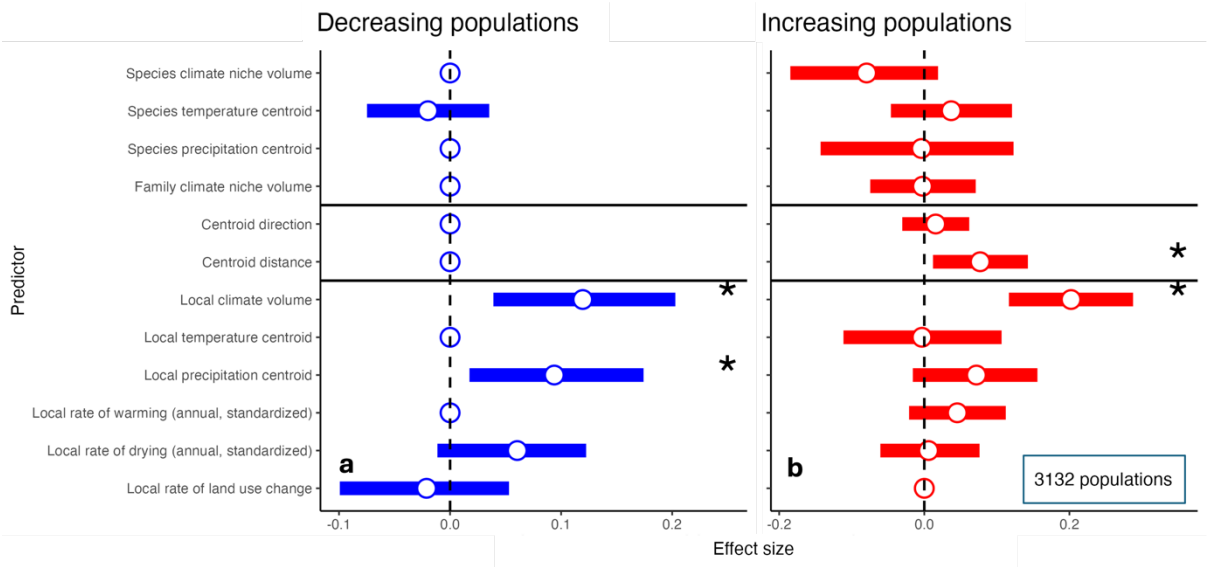



**Figure A2.14| Annual standardized rates of climate change sensitivity analysis.** Sensitivity test results testing the effects of using rates of climate change derived from annual climate data and standardized for local seasonality in (a) decreasing populations (blue) and (b) increasing populations (red). Top ranking models (ΔAIC <6) were averaged based on Akaike weights and the resultant averaged effect sizes are shown (Table A2.10). Decreasing population effect sizes have been inverted for easier comparison with increasing population effects sizes – i.e. a positive effect size represents larger population decreases and large population increases. Error bars represent a 95% confidence interval for each respective model averaged effect size. Black asterisks represent a significant effect size (p value < 0.05).

# A3 - Supplementary materials for Chapter 4

## A3.1 Data and code

All data and code for this chapter are deposited on Dryad: https://datadryad.org/stash/share/2j5QzuT14XjerbGUK-mKTBqhgUKYADPkeyPsRllkW3U.

## A3.2 Supplementary figures

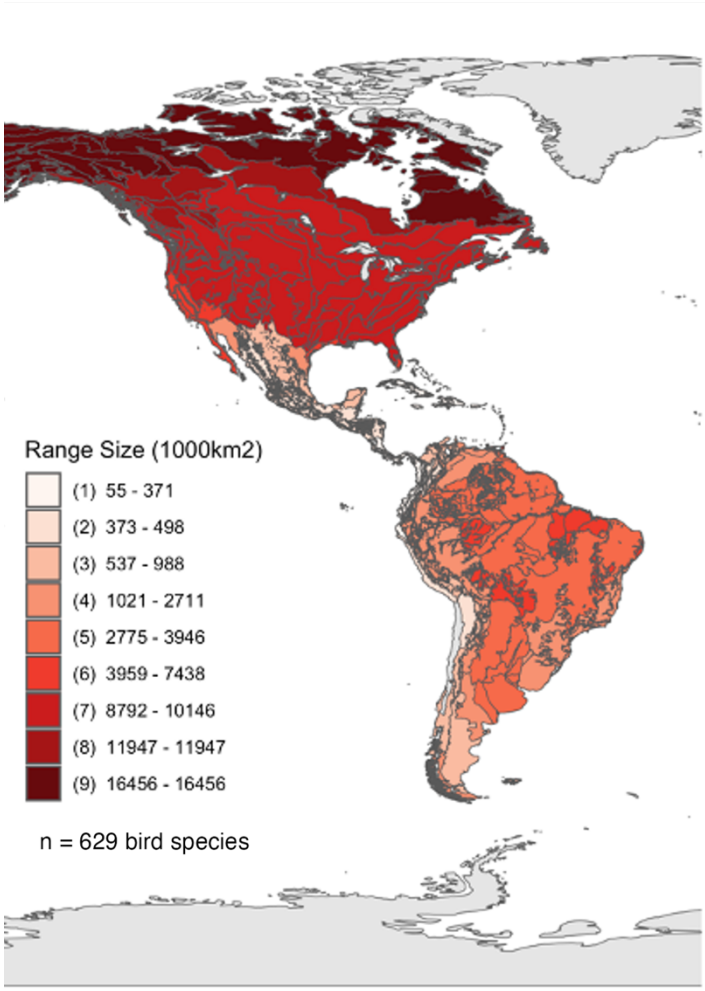
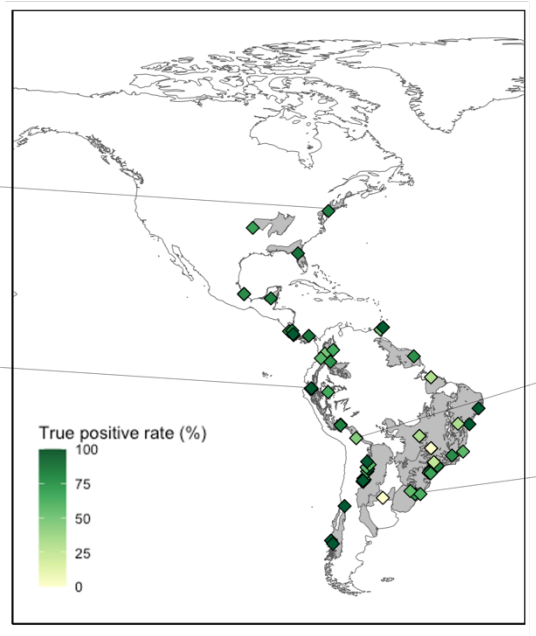



**Figure A3.1| Median avian range sizes across the Americas.** Map of median range size across bird species within an ecoregion. Darker red ecoregions are occupied by bird species that generally have larger ranges. Range size estimates of each bird species were extracted from the AVONET database and averaged across ecoregions.

| Plant species | Bird species |
|---|---|
| *C. orbiculatus* | *B. cedrorum* |
| *C. orbiculatus* | *M. polyglottos* |
| *C. orbiculatus* | *T. migratorius* |
| *C. florida* | *M. polyglottos* |
| *C. florida* | *T. migratorius* |
| *L. benzoin* | *T. migratorius* |
| *S. rotundifolia* | *M. polyglottos* |

| Plant species | Bird species |
|---|---|
| *C. bracteata* | *I. jelskii* |
| *C. elliptica* | *A. coeruleicinctis* |
| *D. chrysostachya* | *A. igniventris* |
| *D. chrysostachya* | *T. vassorii* |
| *G. bracteata* | *I. jelskii* |
| *G. buxifolia* | *A. igniventris* |
| *M. pubescens* | *A. igniventris* |
| *M. pubescens* | *T.fuscater* |
| *P. oleifolius* | *A. igniventris* |
| *P. oleifolius* | *B. montana* |
| *P. oleifolius* | *P. montagnii* |
| *P. oleifolius* | *P. arcuata* |
| *P. oleifolius* | *P. intermedia* |
| *P. integrifolia* | *A. hypoglauca* |
| *P. integrifolia* | *B. montana* |
| *P. integrifolia* | *P. arcuata* |
| *P. integrifolia* | *T. serranus* |
| *T. crenulata* | *A. rubrocristatus* |
| *T. crenulata* | *T. fuscater* |
| *V. seemenii* | *P. arcuata* |




| Plant species | Bird species |
|---|---|
| *A. distichantha* | *E. cyanocephala* |
| *A. distichantha* | *T. rufiventris* |
| *B. salicifolius* | *E. cyanocephala* |
| *B. salicifolius* | *T. rufiventris* |
| *C. iguanaea* | *T. rufiventris* |
| *C. lorentzianum* | *T. rufiventris* |
| *C. strigillatum* | *T. rufiventris* |
| *C. striata* | *T. rufiventris* |
| *C. vernalis* | *T. rufiventris* |
| *D. serratifolia* | *T. rufiventris* |
| *E. uniflora* | *E. cyanocephala* |
| *E. uniflora* | *T. rufiventris* |
| *M. pungens* | *T. rufiventris* |
| *M. laetevirens* | *T. rufiventris* |
| *P. tucumanum* | *T. rufiventris* |
| *P. carthagenensis* | *E. cyanocephala* |
| *P. carthagenensis* | *T. rufiventris* |
| *S. riparium* | *T. rufiventris* |
| *U. baccifera* | *T. rufiventris* |
| *Z. coco* | *T. rufiventris* |

| Plant species | Bird species |
|---|---|
| *C. microcarpa* | *R. dicolorus* |
| *C. microcarpa* | *T. desmaresti* |
| *C. microcarpa* | *T. rufiventris* |
| *M. cinnamomifolia* | *C. caudata* |
| *M. cinnamomifolia* | *C. cyanea* |
| *M. cinnamomifolia* | *E. mesoleuca* |
| *M. cinnamomifolia* | *P. plumbea* |
| *M. cinnamomifolia* | *P. bailloni* |
| *M. cinnamomifolia* | *R. dicolorus* |
| *M. cinnamomifolia* | *T. desmaresti* |
| *M. cinnamomifolia* | *T. viridis* |
| *M. cinnamomifolia* | *T. rufiventris* |

**Figure A3.2| Validation of the trait-based interaction model.** The mean true positive rate across all networks was 71.6% ± 25.4%. Interaction probabilities predicted by the trait-based model were validated against locally observed interactions within the respective ecoregion (n = 14,285 interactions from 103 local networks). True positive rates (TPR) quantify the overlap between the predicted interactions within ecoregion assemblages (grey) and the observed interactions in the local networks (green). Darker green indicates higher correspondence between model predictions and empirical data. That is, a true positive rate of 100% indicates that all observed interactions were correctly predicted by the model. Four example network matrices illustrate model performance. In these matrices, interactions between bird and plant species are shaded green when accurately predicted, and red when missed in the predictions.

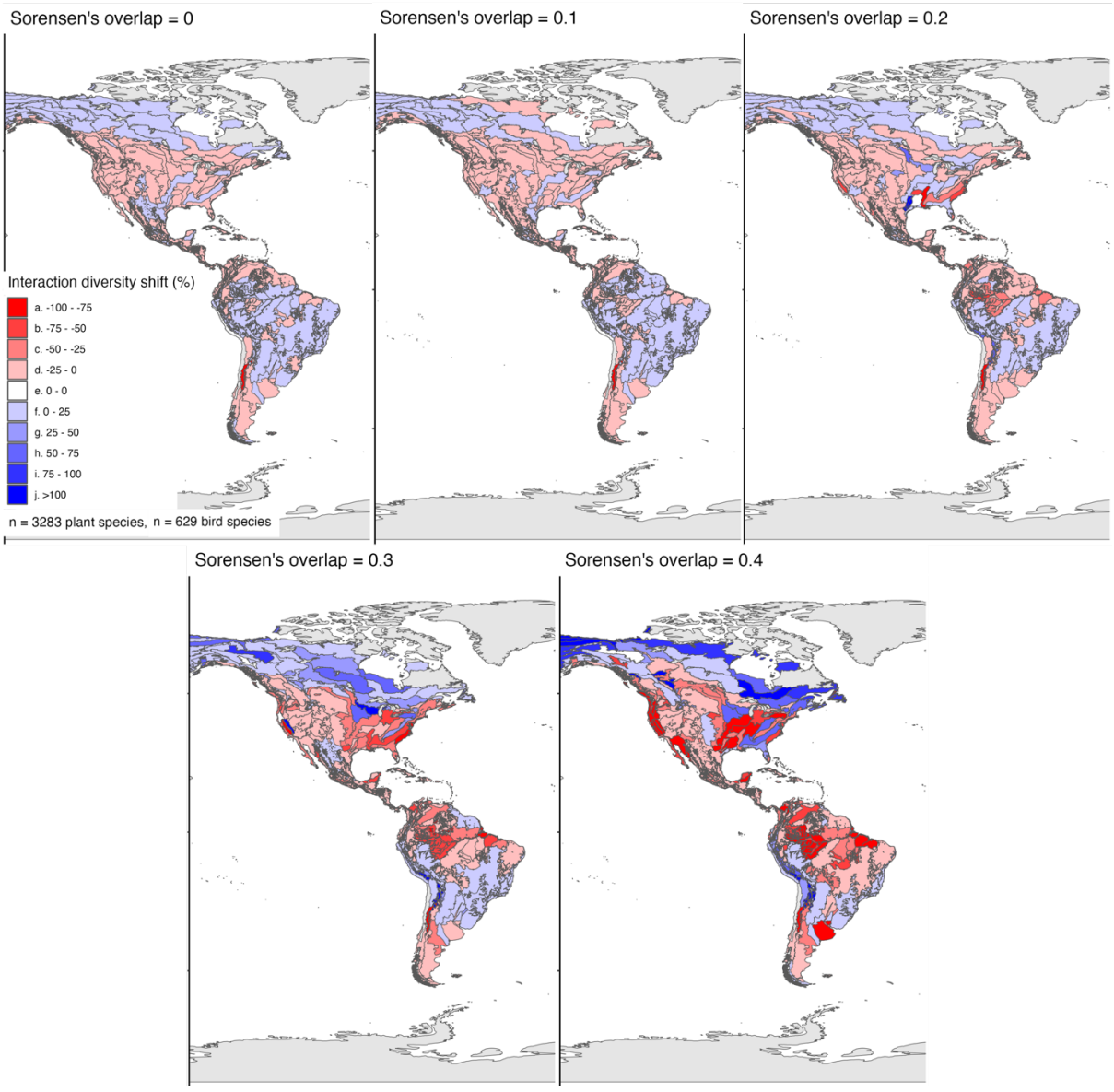



**Figure A3.3| Overlap threshold sensitivity analysis.** Maps of future climate impacts on plant-frugivore interactions under different Sorensen's overlap threshold scenarios (Sorensen's overlap: 0, 0.1, 0.2, 0.3, 0.4). Thresholds define the minimum overlap between a bird species' climatic niche and the climate of an ecoregion, below which the climate is considered unsuitable and the species is excluded from the ecoregion's assemblage. Effect sizes increase with an increase in the overlap threshold, but geographic patterns of changes in interaction diversity are qualitatively identical.

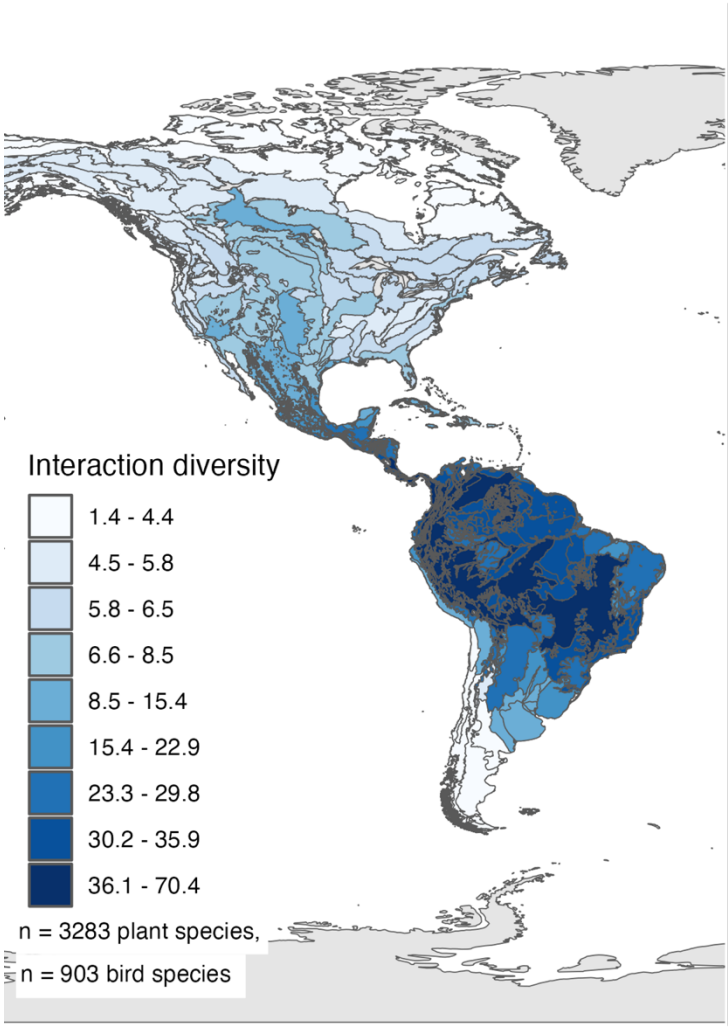



**Figure A3.4| Opportunistic frugivore interaction diversity across the Americas.** Map of mean interaction diversity across ecoregions including both obligate and opportunistic avian frugivores. Interaction diversity is defined as the effective number of avian interaction partners for a given plant species in an ecoregion. Darker blue ecoregions are occupied by plant species that, on average, are able to interact with many more frugivorous birds compared to plant species that occupy lighter blue ecoregions. Plant interaction diversity shown here is not weighted by the climatic suitability of the respective ecoregions.

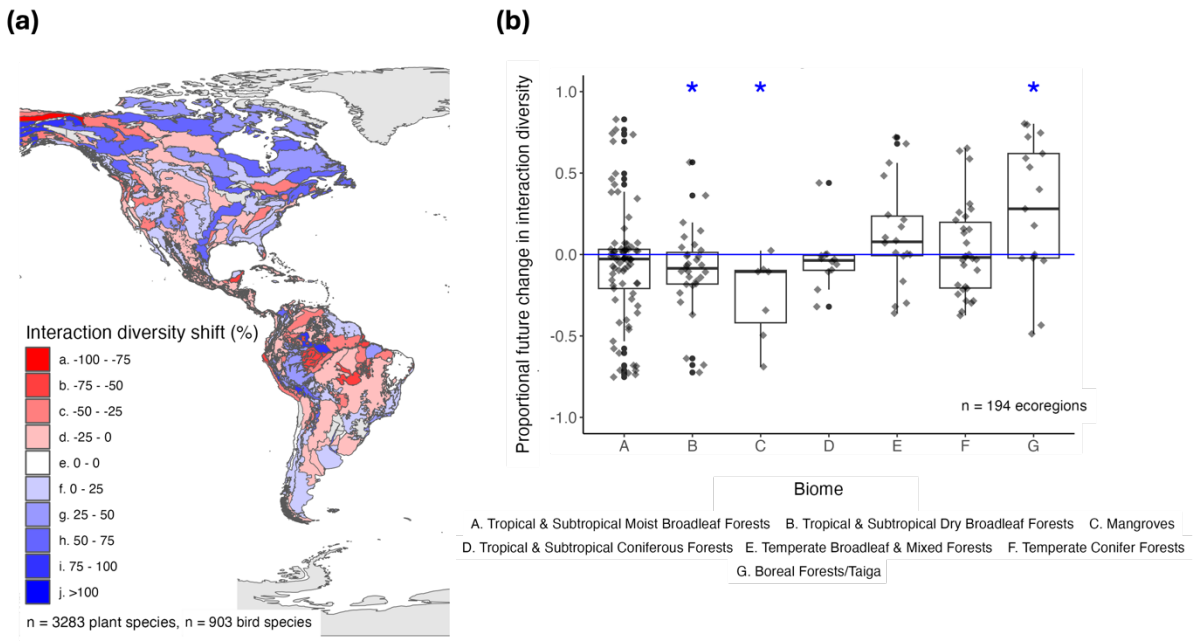



**Figure A3.5| Projected impacts of climate change on opportunistic frugivore networks.** Climate change impacts on plant-frugivore interactions including both obligate frugivores (>50% frugivory in their diet) and opportunistic (>25% frugivory in their diet). (a) Map of future climate impacts on plant-frugivore interactions. (b) Boxplot of future climate impacts on plant-frugivore interactions. Interaction diversity shift was calculated as the proportional decrease or increase in the effective number of avian partners per plant species averaged across all plant species in a given ecoregion. For instance, if the number of avian interaction partners for a given plant species doubles, this would be reflected as a 100% increase in interaction diversity. Asterisks above each boxplot indicates significant differences from 0 based on one-sample t-tests.

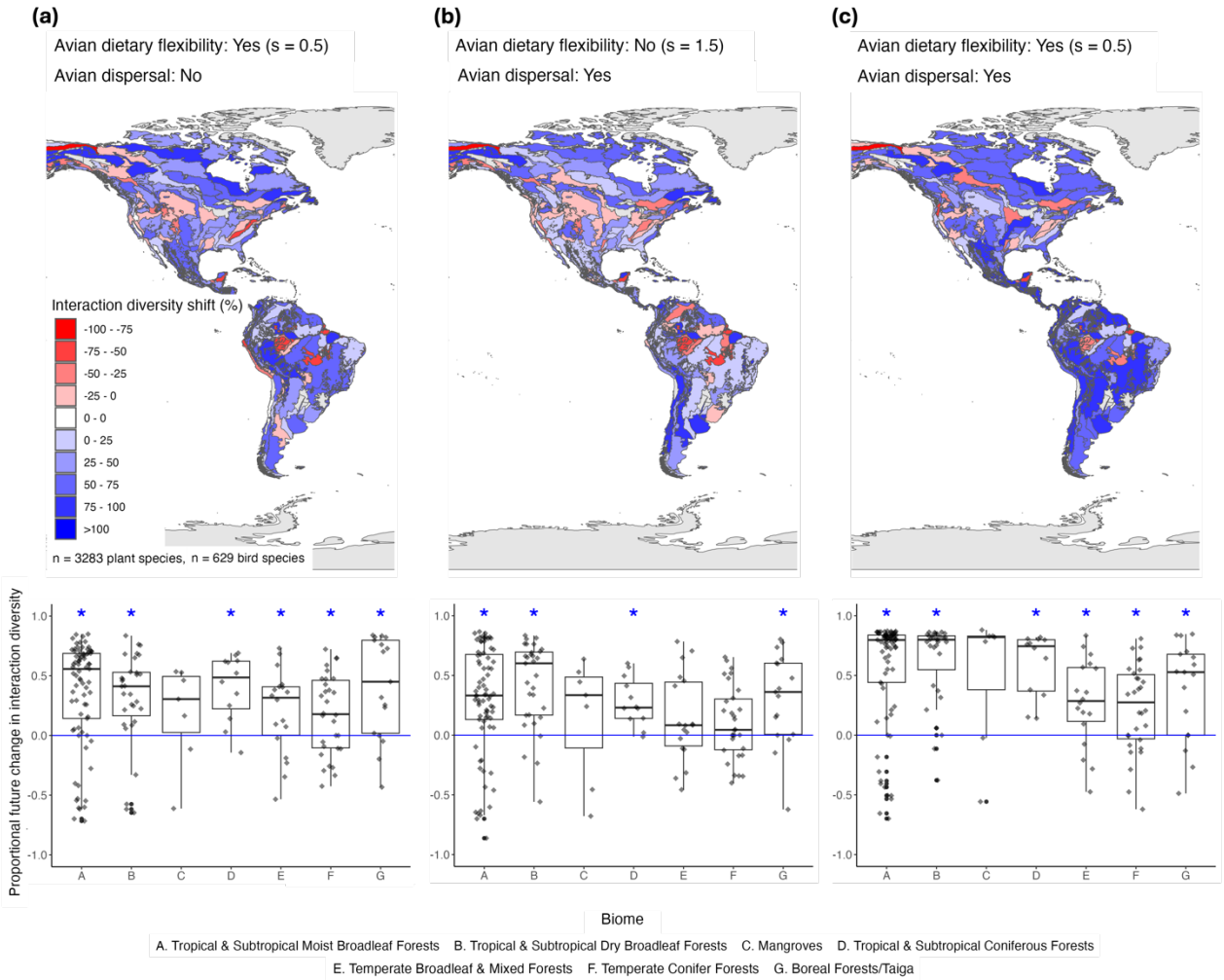



**Figure A3.6| Effects of interaction rewiring on projected future opportunistic frugivore networks.** Climate change impacts on plant-frugivore interactions including both obligate frugivores (>50% frugivory in their diet) and opportunistic (>25% frugivory in their diet) under different interaction rewiring scenarios. Map and boxplot of future climate impacts on plant-frugivore interactions allowing for (a) avian dietary flexibility (i.e., trait matching parameter *s* set to 0.5), (b) avian dispersal (i.e., immigration of species from surrounding ecoregions) and (c) both avian dietary flexibility and dispersal. Interaction diversity shift was calculated as the proportional decrease or increase in the effective number of avian partners per plant species averaged across all plant species in a given ecoregion. For instance, if the number of avian interaction partners for a given plant species doubles, this would be reflected as a 100% increase in interaction diversity. Asterisks above each boxplot indicates significant differences from 0 based on one-sample t-tests.

# Appendices bibliography


BirdLife International and Handbook of the Birds of the World. (2021). *Birdlife species distribution maps of the world*. http://datazone.birdlife.org/species/requestdis

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*(1), 8–22. https://doi.org/10.1111/jbi.12228

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19685–19692. https://doi.org/10.1073/pnas.0901644106

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1–20. https://doi.org/10.1038/sdata.2017.122

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., Yoccoz, N. G., & Ådlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1529), 2087–2096. https://doi.org/10.1098/rspb.2003.2415

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation*, *142*, 2282–2292.

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898