Climatic Drivers of Biodiversity: Influence on Ecophylogenetics and Specialization Across Spatial Scales

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Abstract

Climatic Drivers of Biodiversity: Influence on Ecophylogenetics and Specialization Across Spatial Scales

Pedro Henrique Pereira Braga, MSc. in Ecology and Evolution, Ph.D. Candidate in Biology

Concordia University, 2024

Climate plays a critical role in shaping the diversity, structure, and evolutionary history of ecological communities across spatial and temporal scales. In my thesis, I investigate how three dimensions of climate—average, variability, and frequency across space—determine the phylogenetic structure and climatic specialization of biological communities worldwide, first focusing on bats and then on tetrapods more broadly. In the first chapter, I explore how historical and contemporary processes, such as palaeoclimatic stability, geographical isolation, and local diversification rates, influence the global phylogenetic structure of bat communities. The findings reveal that stable climates since the Last Glacial Maximum have promoted phylogenetic clustering, while geographical isolation and varying diversification rates further shape community structure across different scales. In the second chapter, I examine the underexplored role of the spatial frequency of climate—how often specific climatic conditions occur across space—on specialization within ecological communities. Through a combination of global empirical analyses of tetrapod distributions and theoretical simulations, I demonstrate that rare climates limit specialization, favouring the coexistence of generalists and specialists, whereas common climates promote specialization in tetrapod communities. Finally, in the third chapter, I investigate how climatic commonness and rarity influence the phylogenetic structure and suitability of tetrapod communities. Rare climates are less supportive of closely related species, with recent ecological dynamics playing a more significant role than deep evolutionary constraints. Overall, my thesis provides a comprehensive understanding of the multifaceted role of climate in shaping biodiversity, offering valuable insights into biodiversity responses to climatic variation, including ongoing rapid climate change.

Keywords: scale-dependence, phylogenetic structure, community assembly, climate variability, climatic specialisation, climatic frequency, geographical isolation, phylogenetic scales, spatial scales, paleoclimate, comparative methods, Chiroptera, Tetrapoda

Résumé

Effets climatiques sur la biodiversité : L'influence sur l'écophylogénétique et la spécialisation à travers des échelles spatiales

Pedro Henrique Pereira Braga, MSc. en Écologie et Évolution, Candidat au Ph.D. en Biologie

Université Concordia, 2024

Le climat joue un rôle crucial dans le façonnement de la biodiversité, la structure et l'histoire évolutive des communautés écologiques à différentes échelles spatiales et temporelles. Dans ma thèse, j'étudie comment trois dimensions du climat—la moyenne, la variabilité et la fréquence spatiale des conditions climatiques—déterminent la structure phylogénétique et la spécialisation climatique des communautés biologiques à l'échelle mondiale, en me concentrant sur les chauves-souris et les tétrapodes. Dans le premier chapitre, j'explore l'influence des processus historiques et contemporains, tels que la stabilité paléoclimatique, l'isolement géographique et des taux de diversification locale, sur la structure phylogénétique globale des communautés de chauves-souris. Les résultats montrent que les climats stables depuis le dernier maximum glaciaire favorisent le regroupement phylogénétique, tandis que l'isolement géographique et les taux de diversification variables modulent la structure des communautés à différentes échelles. Dans le deuxième chapitre, j'examine le rôle sous-estimé de la fréquence spatiale du climat—c'est-à-dire la récurrence de certaines conditions climatiques dans l'espace—sur la spécialisation au sein des communautés biologiques. Grâce à une combinaison d'analyses globales des tétrapodes et de simulations théoriques, je démontre que les climats rares limitent la spécialisation, favorisant la coexistence d'espèces généralistes et spécialistes, tandis que les climats communs favorisent la spécialisation. Enfin, dans le dernier chapitre, j'étudie comment la fréquence et la rareté climatiques influencent la structure phylogénétique et l'aptitude écologique des communautés de tétrapodes. Je constate que les climats rares sont moins favorables aux espèces étroitement apparentées, les dynamiques écologiques récentes jouant un rôle plus déterminant que les contraintes évolutives. Ma thèse approfondit notre compréhension du rôle complexe du climat dans la formation de la biodiversité, apportant des perspectives précieuses sur les réponses de la biodiversité aux variations climatiques, y compris le changement climatique en cours.

Mots-clés : structure phylogénétique, assemblage communautaire, variabilité climatique, spécialisation climatique, fréquence climatique, isolement géographique, échelles phylogénétiques, échelles spatiales, paléoclimat, méthodes comparatives, Chiroptera, Tetrapoda

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Dedication

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Preface

This thesis follows the manuscript-based format as per Concordia University's Thesis Office regulations. It consists of three chapters, each of which I am the primary author. The general introduction and conclusion sections provide a comprehensive overview of the research conducted and summarize the main findings. Each chapter is a standalone manuscript, either submitted or in preparation for submission to peer-reviewed journals. The style of each chapter aligns with the specific requirements of its target journal, and the content has been adapted to fit the overall thesis structure.

Authored contributions

Pedro Peres-Neto and Steven Kembel contributed to the conception, planning, editing and reviewing of my thesis chapters.

Chapter 2: Historical and contemporary processes drive global phylogenetic structure across geographical scales: Insights from bat communities

Pedro Henrique Pereira Braga led the conceptualization, data curation, analysis, software development, investigation, and visualization of the study, and wrote the main versions of the manuscript.

Pedro Peres-Neto assisted with methodological and analytical solutions, performed validations, and gave extensive feedback on manuscript drafts.

Steven Kembel contributed with critical feedback on manuscript drafts.

All authors provided valuable feedback throughout the research process and contributed to refining the manuscript.

Chapter 3: Climatic frequency across space drives climatic specialisation in biological communities: evidence from simulations and tetrapods worldwide

Pedro Henrique Pereira Braga led the conceptualization, formal analysis, software development, investigation, computations, data curation, and visualization, and wrote the original draft of the manuscript.

Pedro Peres-Neto contributed to methodological development, and gave substantial feedback in the study development and in the manuscript.

Chapter 4: The commonness and rarity of contemporary climates drives phylogenetic structure and climatic suitability in tetrapod communities

Pedro Henrique Pereira Braga led the conceptualization, data curation, formal analysis, and investigation of the study, developed the methodology, performed visualization, and was responsible for writing the original draft of the manuscript.

Pedro Peres-Neto provided feedback, methodological guidance, analytical solutions, and reviewed manuscript drafts.

Steven Kembel provided feedback and reviewed manuscript drafts.

Additional contributions

Alongside my supervisors, Pedro Peres-Neto and Steven Kembel, Jean-Philippe Lessard and Jonathan Davies participated as committee members of the qualifying exam and project proposal for this thesis, and contributed with recommendations on the planning, scientific approaches, and discussions that helped improve the outcome of the research presented in this thesis.

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Table of Contents

List of Figures

List of Tables

Glossary

Community An assemblage of species found together in a specific area or a habitat at a given time, usually interacting with each other.

Evolutionary rates The rate at which genetic changes accumulate in a population or species over time, reflecting adaptations to environmental pressures or neutral evolutionary changes.

As in: Pagel (1997)

Geographical ranges The spatial extent or distribution of a species, encompassing all the areas where it is found.

***In situ* diversification** Species diversification occurring within a specific geographical area without external immigration, driven by local ecological and evolutionary processes.

Net diversification rates The net outcome of speciation and extinction rates within a clade or community over a given period.

As in: Ricklefs (2007); Rabosky (2014)

Palaeoclimatic stability The extent to which climate has remained stable over geological time periods, affecting species distributions and community structure.

Niche breadth The range of environmental conditions or resources that a population or species can utilize; similar to ‘niche tolerance’.

As in: Hutchinson (1957); Macarthur & Levins (1967); also see Devictor *et al.* (2010)

Niche marginality The position of a species’ realized niche in relation to the centroid of the environmental conditions available in its habitat.

As in: Doledec *et al.* (2000); Hurlbert (1978)

Niche overlap The extent to which two or more species share the same resources or environmental conditions, potentially leading to competition.

As in: Macarthur & Levins (1967)

Niche tolerance The ability of a species to endure environmental conditions outside its optimal range.; similar to ‘niche breadth’.

As in: Doledec *et al.* (2000); Hurlbert (1978)

Metacommunities A set of multiple local communities in an area or region, linked by the dispersal of several interacting species from those local communities.

As in: Leibold *et al.* (2004)

Phylogenetic clustering The tendency for closely related species to co-occur within a community.

As in: Webb (2000); Webb *et al.* (2002); Cavender-Bares *et al.* (2009)

Phylogenetic extent The total range of phylogenetic diversity included in an analysis, encompassing varied evolutionary histories and lineage diversities.

As in: Graham *et al.* (2018)

Phylogenetic grain The resolution at which phylogenetic differences among taxa are examined, capturing fine evolutionary distinctions within a specific phylogenetic extent.

As in: Graham *et al.* (2018)

Phylogenetic overdispersion The pattern in which species within a community are more distantly related to each other than expected by chance.

As in: Webb (2000); Webb *et al.* (2002); Cavender-Bares *et al.* (2009)

Phylogenetic scale The spatial or temporal scale over which phylogenetic relationships among taxa are analyzed, integrating aspects of phylogenetic grain and extent.

As in: Graham *et al.* (2018)

Phylogenetic signal The tendency of closely related species to exhibit similar traits, consistent with expectations from an evolutionary model.

As in: Blomberg & Garland Jr (2002); Losos (2008); Pagel (1997); Crisp & Cook (2012)

Phylogenetic structure The arrangement and distribution of species' phylogenetic relationships within a community.

As in: Webb (2000); Webb *et al.* (2002); Cavender-Bares *et al.* (2009)

Realm Also, "biogeographical realm". A large-scale biogeographical division of the Earth's surface, characterized by distinct sets of flora, fauna, and ecological processes that have evolved over time due to geological, climatic, and evolutionary histories. Realms are often delineated based on major barriers to species dispersal, such as oceans, mountain ranges, or deserts

As in: Udvardy (1975); Wallace (1876); Holt *et al.* (2013)

Scale dependence The phenomenon where ecological or evolutionary processes and patterns vary depending on the spatial, temporal, or phylogenetic scale at which they are studied.

As in: Levin (1992); Chave (2013)

Spatial extent The total area or size over which ecological data are collected or ecological processes are studied, representing the broadest dimension of spatial scale.

As in: Levin (1992); Chave (2013)

Spatial frequency of climate The commonness or rarity of specific climatic conditions across a geographical area.

Spatial grain The resolution used in a spatial analysis, determining the level of detail of the data.

As in: Wiens (1989); Levin (1992); Chave (2013)

Spatial scale The scale at which ecological or geographical data are analyzed or interpreted, encompassing both spatial extent (the area covered) and spatial grain (the resolution of the data). It ranges from narrow (local) to broad (global) scales.

As in: Wiens (1989); Levin (1992); Chave (2013)

Trait conservatism The tendency of certain traits to remain unchanged over evolutionary time.

As in: Wiens & Graham (2005)

Trait divergence The evolution of differences in traits among populations or species, typically in response to divergent selection pressures or ecological niches.

As in: Wiens & Graham (2005)

Trait evolution The changes in species' traits over time, driven by natural selection, genetic drift, and other evolutionary forces.

As in: Pagel (1997); Blomberg & Garland Jr (2002); Crisp & Cook (2012)

List of Abbreviations and Acronyms

ANOVA Analysis of Variance

BAMM Bayesian Analyses for Macroevolutionary Mixtures

CI Confidence Interval

Clim. Climatic, Climate

CWM Community Weighted Mean

Dist. Distance

GAM Generalized Additive Model

Geog. Geographical

GLM Generalized Linear Model

LGM Last Glacial Maximum

MAP Mean Annual Precipitation

MAT Mean Annual Temperature

MCMC Monte-Carlo Markov-Chain

MNTD Mean Nearest Taxon Distance

MPD Mean Phylogenetic Distances

NRI Net Relatedness Index

NTI Nearest Taxon Index

OMI Outlying Mean Index

PC, RS Principal Component

Pr, P Probability

Prox. Proximity

Q Quantile

Raref. Rarefaction

SES Standardized Effect Size

Tol Tolerance

$\beta_{\mathbf{Sor}}$ Sørensen’s dissimilarity between sites (beta diversity)

λ Speciation Rate

μ Extinction Rate

Chapter 1

General Introduction

1.1 The study of climate-biodiversity interactions appeals to pluralism

> "In this great chain of causes and effects, no single fact can be considered in isolation."
> — Alexander von Humboldt, *Cosmos: A Sketch of the Physical Description of the Universe*, Volume 1, 1845.

The intricate relationship between climate and biodiversity has long fascinated naturalists and scientists. Early pioneers such as Alexander von Humboldt and Alfred Russel Wallace laid the foundation for understanding these interactions. Humboldt's influential work, *Cosmos* (Humboldt 1845), emphasized the interconnectedness of nature, documenting plant distributions in relation to climate. His observations in the Andes, where he recorded altitudinal zonation, highlighted how temperature and moisture gradients influenced vegetation patterns (Wulf 2015; Pausas & Bond 2019). A few years later, Wallace's travels in the Malay Archipelago led to the formulation of the Wallace Line, a significant biogeographical demarcation that underscores the role of geographical barriers and climate in species distribution (Wallace 1869).

These early works were not merely descriptive but carried substantial philosophical weight, urging the scientific community to view Earth as a dynamic system where climate plays a pivotal role in shaping life. Humboldt's holistic approach, considering factors from geology to human activity, was an early precursor to modern interdisciplinary studies. His assertion that "everything is interconnected" resonates with today's integrative models, which incorporate climate data to analyze biodiversity patterns (see Wulf 2015). Wallace's contributions further underscored the complexity of biogeographical patterns, emphasizing the role of climate in evolutionary processes and species distribution (see Hortal *et al.* 2023).

The transition from descriptive natural history to analytical biogeography marked a significant paradigm shift in understanding biodiversity. This shift was driven by the development of theories and methods to quantify relationships between the environment and species distributions. Key theoretical advancements include Arrhenius' (1921) species-area relationship, Mayr's (1942) mechanisms of allopatric speciation, Hutchinson's (1957) niche theory, MacArthur and Wilson's (1963) equilibrium theory of island biogeography, and Levins' (1966, 1969) metapopulation theory. These theories fundamentally changed how ecologists and biogeographers approached the study of species diversity, laying the foundation for mechanistic thinking in macroecology (see McGill *et al.* 2019).

Technological advancements in recent decades, such as Geographic Information Systems (GIS), molecular phylogenetics, big data, and other computational tools, have further transformed biogeography and biodiversity and climate research. These innovations have enabled spatial analysis at unprecedented scales and the reconstruction of phylogenetic trees, providing deeper insights into speciation and extinction dynamics within clades and across space (Heads 2009; see Millington *et al.* 2013; Farley *et al.* 2018; Oyston *et al.* 2022, and references therein). Such tools have fostered a more holistic and interdisciplinary approach, allowing researchers to synthesize data across various scientific domains.

Despite these technological strides, the study of climate-biodiversity dynamics is often characterized by underdetermination, implying empirical data alone cannot conclusively determine theoretical explanations due to the complex interplay of multiple factors and plausible theories[1]. For instance, observed patterns in species' distributions may be concurrently explained by present climatic conditions (*e.g.*, Salces-Castellano *et al.* 2019; Harrison *et al.* 2020), historical climatic events (*e.g.,* Antão *et al.* 2022; Braga *et al.* 2023b), and biotic interactions (*e.g.,* Martorell & Freckleton 2014; Brazeau & Schamp 2019), each underpinned by substantial empirical support. Addressing these epistemic challenges necessitates a pluralistic approach in ecological research, advocating for the simultaneous exploration and refinement of multiple hypotheses and models to develop a comprehensive understanding of natural systems (see Diniz-Filho *et al.* 2023). For example, combining present climatic conditions (such as averages across space) with their variability can offer insights into how climatic stability and fluctuations influence community assembly processes and species coexistence (*e.g.*, Delgado-Baquerizo *et al.* 2017, 2018; Saladin *et al.* 2020; Qian *et al.* 2024). Integrating this approach with phylogenetic data can further elucidate how historical and evolutionary processes contribute to current biodiversity patterns, offering a more comprehensive understanding of these complex dynamics (Mouquet *et al.* 2012; Davies 2021).

The integration of diverse methodological approaches is crucial for developing robust explanations that account for the multifaceted nature of climate-biodiversity interactions. Throughout this thesis, I address these complexities by employing pluralistic and integrative frameworks to elucidate selected questions addressing geological, environmental, and climatic controls on biodiversity patterns. These frameworks use empirical data, theoretical models, comparative phylogenetic methods, and consider several taxa and climatic components to answer questions on climate-biodiversity dynamics. By acknowledging the inherent uncertainty and complexity in ecological research, these approaches advocate for a comprehensive and nuanced understanding of natural systems. Through this work, I aim to contribute to the broader scientific discourse on climate-biodiversity interactions, providing insights that are both theoretically rigorous and empirically grounded.

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[1] Underdetermination highlights the challenge of attributing observed patterns to specific causal mechanisms when multiple theories can explain the same data. There are different types of underdetermination: (1) Transient underdetermination occurs when current data supports multiple theories, but future data might resolve the ambiguity (Stanford 2001). (2) Permanent underdetermination implies that no amount of data can decisively favour one theory over another (Laudan & Leplin 1991). (3) Holistic underdetermination suggests that theories are evaluated within a broader network of assumptions and hypotheses, making it difficult to isolate individual theories (Quine 1951; Duhem 1954).

In the following sections, I set the stage by providing a comprehensive overview of the role of climatic components in shaping ecological communities, drawing on both classical theories and modern empirical studies. I then further discuss potential frameworks using phylogenetic information for understanding the evolutionary and ecological processes governing species distributions and community structures. Then, I delve into the implications of these processes for understanding the historical and contemporary patterns of biodiversity. By integrating these dimensions, I propose a holistic view of climate's role in driving ecological and evolutionary dynamics across different spatial and temporal scales.

1.2 Climate as a driver of biodiversity patterns

1.2.1 The role of averages and variability in climate

Climate—the long-term patterns of temperature, precipitation, and other meteorological variables—profoundly influences the distribution, abundance, and diversity of life on Earth (Humboldt 1893; Hutchinson 1957). The interaction between climate and species-specific adaptations dictates where and when species thrive, influencing their phenology, population dynamics, and interactions with other species (Gaston 2009b; Sexton *et al.* 2009), ultimately shaping the structure and dynamics of biological communities (Currie & Paquin 1987; Rohde 1992).

Historically, studies on climate-biodiversity relationships have focused on how the climatic conditions themselves (usually, in the form of averages across specific extents) and their variability influence ecological patterns, in both temporal and spatial scales.

Climatic conditions primarily set environmental spaces within which species operate, contributing to their fundamental and realized climatic niches (Hutchinson 1957; Pulliam 2000; Soberón 2007). These conditions determine the availability of resources such as light, water, and nutrients, setting the baseline for primary productivity and energy flow within ecosystems (Brown *et al.* 2004). Areas with climatic conditions that support higher primary productivity and are favourable for a wide range of species generally provide greater resource availability, often resulting in increased biodiversity (Hawkins *et al.* 2003; Field *et al.* 2009). While some species may thrive in specific climatic regimes where their physiological processes such as growth, reproduction, and metabolism are optimized (Angilletta 2009), others may face constraints that limit their fitness in the same conditions. Regions where climatic conditions align closely to the physiological optima of the resident species may foster higher fitness and competitive abilities leading to denser populations and more persistent communities (Chesson 2000b).

Climatic variability, encompassing both spatial and temporal fluctuations in climatic conditions, also structures ecological communities (Fagre *et al.* 2003; Jackson *et al.* 2009; Vázquez *et al.* 2017; Terry *et al.* 2022). Spatially heterogeneous climatic conditions provide diverse habitats and microclimates, accommodating different species' requirements. This leads to increased opportunities for niche differentiation and reduced interspecific competition, enabling the coexistence of more species (Kerr & Packer 1997; Chesson 2000b; Rahbek & Graves 2001). Conversely, spatially homogeneous climates may promote competitive exclusion, where few well-adapted species dominate (Connell 1978)[2].

Variability in climatic conditions manifests across diverse temporal scales and spatial extents (Mitchell Jr 1976; see Franzke *et al.* 2020; Stuecker 2023), driving significant changes in regional and local biodiversity. Climatic events such as abrupt shifts (*e.g.*, the Younger Dryas cold interval[3], the Paleocene–Eocene thermal maximum), gradual orbitally driven climate changes (*e.g.*, glacial-interglacial cycles), the current rapid human-induced climate change, along with intra- and inter-annual fluctuations (*e.g.*, seasonal variations, the El Niño-Southern Oscillation), all prompting transient or enduring shifts in diversity patterns (*e.g.*, Svenning & Skov 2007; Kissling *et al.* 2012; Burrows *et al.* 2014; Zhang *et al.* 2018; Xu *et al.* 2020; Khattar *et al.* 2021; Antão *et al.* 2022). Climatic variability inherently leads to extreme events, such as heatwaves, droughts, and storms (van der Wiel & Bintanja 2021), which can cause abrupt shifts in ecosystem structure and function, leading to rapid species turnover, local extinctions, and altered community compositions (Ma *et al.* 2015; Rammig & Mahecha 2015; see Buckley & Huey 2016; De Boeck *et al.* 2018; Latimer & Zuckerberg 2019).

Conversely, decreased variability in climatic conditions over time is often associated with environmental stability, which favours specialized adaptations that maximize resource use efficiency and optimize interactions within communities (Futuyma & Moreno 1988; Leigh 1990; also see Terry *et al.* 2022). This stability can foster niche differentiation and species packing within ecosystems, enhancing biodiversity by reducing niche overlap and minimizing competitive exclusion (Tilman 1982; Chesson 2000b).

Together, the average and variability of climatic conditions jointly drive both the spatial and temporal dynamics of biodiversity. However, the influence of climate on biodiversity dynamics extends beyond these determinant factors.

1.2.2 The frequency of climate across space: an overlooked, but important component

The frequency of climatic conditions across space, a less studied component, also plays a significant role in shaping biodiversity dynamics. Climatic conditions can range from rare (also referred to as "scarce," "less frequent," or "marginal") to common (equally referred to as "abundant" or "more frequent"). Similar to climatic averages and variability, climatic frequency should influence biological communities. The frequency of a particular climatic condition across space could influence species distribution and community composition by affecting the availability and predictability of

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[2] This relationship assumes that niche differentiation outweighs fitness dominance within specific environment-trait relationships. If fitness dominance prevails, competitive exclusion could still occur in heterogeneous environments, complicating the interpretation of community patterns. For a detailed discussion on this issue, see Cadotte and Tucker (2017).

[3] The Younger Dryas (~12,870 years before present) was one of the most abrupt climatic events in recent history, lasting approximately 1,300 years. A series of events leading to slowdowns and shifts in ocean circulation caused a reduction in northward heat transport, which reversed the course of the global warming that had been ending the last Ice Age (Pearce *et al.* 2013). At the termination of the Younger Dryas cold event, between one-third and one-half of the 10,000-year deglacial warming in Greenland occurred in less than 15 years (Severinghaus *et al.* 1998). This rapid shift to cooler and drier conditions during the Younger Dryas is closely associated with a significant decline in both plant and animal diversity (see Seersholm *et al.* 2020).

suitable habitats. Rare climates, by definition, occur in limited geographic areas, and thus species occupying them may face significant trade-offs. While rare climates can offer unique selective pressures, they may also impose substantial costs on species attempting to specialize in such conditions (van Tienderen 1997). Specialization to rare climates often requires highly specific adaptations, which can be energetically expensive to maintain and may reduce a species' ability to adapt to changes or exploit alternative resources (Kassen 2002). As a result, species in rare climates might be more prone to extinction if these climates shift or disappear because of environmental changes. Consequently, rather than leading to high specialization, rare climates may support more generalist species that can tolerate a broader range of conditions, or species with flexible phenotypes that can survive in fluctuating environments (see Fournier *et al.* 2020).

High variability in climatic conditions, whether spatial or temporal, can amplify the challenges associated with rare climates. In highly variable environments, the predictability of climatic conditions can be reduced (Boer 2009), limiting the success of specialized species (Moldenke 1975; Tonkin *et al.* 2017; Riotte-Lambert & Matthiopoulos 2020). This increased variability might favour traits that enhance ecological flexibility, such as broader physiological tolerance or phenotypic plasticity, over traits that promote narrow specialization (see Moldenke 1975). For species inhabiting rare climates, this variability may further exacerbate the costs associated with specialization, potentially leading to a greater reliance on generalist strategies or adaptive behaviours that allow them to cope with a wider range of conditions.

Conversely, in regions characterized by frequent and stable climates, species may have more opportunities to specialize, as both the predictability of conditions and decreased frequency of extreme climatic events reduce the risks associated with narrow ecological adaptation (Tonkin *et al.* 2017). Such environments are likely to support higher niche differentiation, where species can fine-tune their interactions with both the environment and other species within a more stable climate framework (Chesson 2000b; see Terry *et al.* 2022). Even in these frequent and stable climates, some degree of climatic variability can mitigate competitive exclusion and promote temporal niche partitioning, thereby sustaining species coexistence (Chesson 2000b).

The interaction between climatic frequency and variability can then be expected to shape the complex mosaic of ecological strategies across landscapes. In regions with frequent and stable climates, communities may be structured by intense competitive interactions and fine-scale niche partitioning, resulting in high local diversity and beta diversity across the landscape (Tilman 1982; see Leibold *et al.* 2004). In contrast, regions with rare and highly variable climates may support communities that are characterized by more generalized strategies, where species must balance the trade-offs between specialization and adaptability. These areas could function either as ecological refugia or as regions of high species turnover (*e.g.*, Ordonez & Svenning 2015), depending on the interplay between climatic stability and variability.

Despite playing a crucial role in biodiversity dynamics, the study of climate frequency across space has been surprisingly rare, particularly in biogeographical contexts (but see Meyer & Pie 2018; Fournier *et al.* 2020; Cutts *et al.* 2023). My thesis explores this gap by providing insights into how these three dimensions of climate—the conditions themselves, their variability, and frequency—influence the structure of biological communities.

1.3 Using phylogenetic information to link evolutionary processes to community patterns

The study of biodiversity responses to climate has evolved considerably beyond the traditional metrics of taxonomic diversity. Contemporary approaches integrate methods that capture the outcomes of other processes, including the interplay of ecological interactions, evolutionary histories, and environmental factors within communities. One such approach comes through the integration of phylogenetic information into community ecology, which has revolutionized our understanding of the evolutionary relationships among species and their interactions within ecological communities. By analyzing the evolutionary relationships among species within a community, community phylogenetics allows for the inference of historical biogeographical patterns, ecological interactions, and adaptive evolution that collectively shape current biodiversity patterns (Cadotte *et al.* 2010; Davies & Cadotte 2011; Tucker *et al.* 2017). This approach offers a robust framework for examining how historical processes, such as vicariance and dispersal, interact with contemporary ecological processes, such as competition and environmental filtering, to drive community assembly (Webb 2000; Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Kembel 2009).

Traditional expectations about the phylogenetic structure of communities have centred on three key mechanisms: habitat filtering, competitive exclusion, and neutrality. Habitat filtering posits that abiotic factors select for species with similar ecological niches, leading to phylogenetically clustered assemblages (Webb 2000; Ackerly & Renner 2004; Cavender-Bares *et al.* 2004b). Competitive exclusion, conversely, suggests that closely related species are less likely to coexist due to overlapping niches, resulting in phylogenetically overdispersed assemblages (Hardin 1960; Roughgarden 1983; Tilman 1994). Lastly, the neutrality model assumes that species are ecologically equivalent, leading to randomly structured communities (MacArthur & Wilson 1963, 2001; Hubbell 2001; Kembel & Hubbell 2006).

Nevertheless, these traditional expectations are built upon assumptions that have been continuously challenged, as demonstrated by accumulating evidence (Mouquet *et al.* 2012; Godoy *et al.* 2014; Pastore & Scherer 2016; Wilcox *et al.* 2018). For instance, the anticipation that closely related species are more likely to exclude each other has been refuted in numerous taxa, where it has been argued that shared traits among close relatives may enhance their fitness by balancing competitive abilities, thereby facilitating coexistence (Grime 2006; Mayfield & Levine 2010; Godoy *et al.* 2014; see opinion from Wilcox *et al.* 2018). Additionally, community phylogenetic clustering driven by environmental selection is predicated on the assumption that species retain niche requirements across evolutionary time and geographical space, a concept known as ‘phylogenetic niche conservatism’ (Webb *et al.* 2002; Cavender-Bares & Wilczek 2003). However, Webb et al. (2002) and Cavender-Bares and Wilczek (2003) have shown that environmental selection within clades that have experienced convergent niche evolution can lead to phylogenetically overdispersed assemblages. Convergent evolution may not only affect niche requirements but also influence competitive abilities, leading to scenarios where distantly related species are less likely to coexist than closely related species with similar competitive traits (Mayfield & Levine 2010; Kunstler *et al.* 2012; Weber & Strauss 2016; Germain *et al.* 2019; but see Anderson *et al.* 2011).

Beyond environmental filtering, species interactions and neutral effects, other processes influence the phylogenetic structure of communities (see Note 1), including—but not limited to—variation in net diversification rates (Cardillo 2011), time since divergence (Cavender-Bares *et al.* 2006), local and regional saturation in richness (Machac *et al.* 2013; Machac & Graham 2016; but see Stohlgren *et al.* 2008; Szava-Kovats *et al.* 2013), vicariant events and their historical context (Brooks *et al.* 1991), secondary contact following vicariance (Johnson & Stinchcombe 2007), adaptive radiation and dispersal limitation (Horner-Devine & Bohannan 2006). Even where communities appear randomly structured, phylogenetic relatedness can vary along with environmental gradients, underscoring the dynamic interplay of historical and ecological factors in shaping biodiversity (Liang *et al.* 2017). Additionally, abrupt and strong climatic shifts during past geological periods have left lasting imprints on community phylogenetic structure, away from the patterns expected for given contemporary conditions (*e.g.*, Hortal *et al.* 2011; Kissling *et al.* 2012; Svenning *et al.* 2015).

Note 1: The phylogenetic structure of communities can be determined by processes and mechanisms different than competitive exclusion, habitat filtering and neutrality

Phylogenetic structure within assemblages can be influenced by processes beyond competitive exclusion and habitat filtering (see Emerson & Gillespie 2008). For instance, increased speciation rates or decreased extinction rates (i.e., higher net diversification rates) can lead to a higher proportion of closely related species within regional assemblages (Cardillo 2011). However, as clades and regional assemblages become species rich, saturation may occur, potentially leading to a decline in diversification rates (Rabosky 2009, 2013, 2014; see Graham *et al.* 2018). This saturation can subsequently increase extinction rates, resulting in longer apparent branches in the phylogeny and promoting phylogenetic overdispersion.

The formation and disappearance of dispersal barriers, along with the timing of these events, can also shape phylogenetic community structure. For example, distantly related species are less likely to co-occur in regions where speciation has been driven by ancient vicariance, such as continental separation. Conversely, speciation driven by the isolation of islands during interglacial periods can result in negative co-occurrence among close relatives, due to insufficient time for competitive pressure to drive ecological divergence (see Emerson & Gillespie 2008). Alternatively, vicariant speciation may lead to greater co-occurrence among close relatives if these species inhabit different communities or regions (Anacker & Strauss 2014). However, intense recolonization (e.g., following island reconnection during periods of low sea level) may disrupt this pattern, leading to either positive or negative co-occurrence among distantly related species (Emerson & Oromi 2005).

Phylogenetic community structure may also vary across ecological (environmental and spatial) gradients, even if random structure is observed within regions (Cavender-Bares *et al.* 2009). For instance, increased environmental heterogeneity within a region may allow the persistence and co-occurrence of distantly related species (Keddy 1992; Urban *et al.* 2008). Regions with cold, arid, and seasonal climates are expected to exert stronger selective pressures on species, resulting in phylogenetic community structures more influenced by climatic gradients. Moreover, significant changes in past climatic and habitat conditions can drive phylogenetic structure away from patterns expected under stable conditions (Hortal *et al.* 2011; Kissling *et al.* 2012; see Svenning *et al.* 2015).

Finally, the dynamics of phylogenetic community structure are scale-dependent, both spatially and temporally (Kembel & Hubbell 2006; Swenson *et al.* 2006, 2007; Kraft & Ackerly 2010). Different ecological and historical-evolutionary processes influence community assembly at different scales (Ricklefs & Schluter 1993; McPeek 1996; Ricklefs 2007; Jenkins & Ricklefs 2011; Ricklefs & Jenkins 2011). For example, at larger scales, historical and evolutionary processes are expected to determine diversity structure through speciation and biota exchange. In contrast, at smaller scales, ecological processes may limit species diversity through mechanisms such as predation and competition (Ricklefs & Schluter 1993). Evolutionary processes not only generate diversity but also influence ecological processes by restricting phenotypes (*e.g.*, through conservatism in adaptive traits), thereby affecting species' abilities to integrate into ecological interactions (Ricklefs & Schluter 1993; Ackerly 2003). Ecological processes may simultaneously lead to phylogenetic clustering at larger spatial and taxonomic scales, while promoting overdispersion within more recent clades at smaller scales (*e.g.*, Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Swenson *et al.* 2006) or clustering species pairs with significant ecological differentiation (*e.g.*, Parmentier & Hardy 2009).

Alongside the assessment of phylogenetic relatedness within communities, the processes driving biodiversity across geographical and environmental gradients can be further elucidated with evolutionary models and estimates of evolutionary rates. These include species diversification rates, which reflect the balance between speciation and extinction (Ricklefs 2006; Mittelbach *et al.* 2007), and shifts in traits across diversification events (Ackerly *et al.* 2006; Kraft *et al.* 2007; Vamosi *et al.* 2009; Title & Rabosky 2019). These rates provide insights into how species and clades emerge, persist, and adapt to their environments, thereby complementing our understanding of the processes underlying biodiversity patterns.

For instance, high diversification rates, when coupled with evidence for stable or slowly evolving traits (*i.e.*, phylogenetic niche conservatism), suggest that certain lineages have successfully exploited broad ecological opportunities, maintaining resilience across varying climates (Wiens & Graham 2005; Fine & Ree 2006). This resilience may lead to phylogenetic clustering within communities, where ancestral traits confer broad adaptability, allowing related species to persist across diverse environments (Webb *et al.* 2002; Helmus *et al.* 2010). Conversely, lower diversification rates may coincide with rapid ecological and trait differentiation during speciation, reflecting the evolution of lineages to specific niches over extended periods, often in response to newly available ecological opportunities or changing environments (Rundell & Price 2009; Weiss-Lehman *et al.* 2017).

These complexities in mapping ecological mechanisms onto phylogenetic patterns underscore the necessity of integrating multiple methods and biodiversity into ecological studies to infer underlying ecological and evolutionary processes (Davies 2021). Throughout this thesis, I rely on this perspective to investigate how climatic frequency, variability, and extremes influence the assembly, persistence, and diversification of biological communities. By integrating diversification rates, trait evolution, and phylogenetic structure, I aim to provide a comprehensive understanding of how communities are assembled and maintained over time, particularly in response to varying climatic components and geological and historical contexts.

1.4 Scale dependencies in ecological and evolutionary processes

Over 40 years ago, MacArthur (1984) recognized the hierarchical nature of habitats and introduced the concept of "scale" as a critical lens through which to understand ecological phenomena. His insights laid the groundwork for a deeper examination of how ecological processes operate across different spatial scales, influencing not just the structure of ecological communities but also the evolutionary processes that shape biodiversity. Two decades later, Levin (1992) profoundly influenced the field by emphasizing the interdisciplinary nature of scale, pattern, and ecology, urging ecologists to consider the implications of scale more rigorously.

Since then, an increasing number of studies have bridged different spatial scales, leading to rich discussions on some of the most central issues in ecology. These studies have explored how scale influences both ecological patterns and evolutionary processes, yielding insights from species diversity to ecosystem function (Morris 1987; Ricklefs & Schluter 1993; Whittaker *et al.* 2001; Diffenbaugh *et al.* 2005; McGill 2010; Chase 2014; Cohen *et al.* 2016; *e.g.*, Chase *et al.* 2018; Guisan *et al.* 2019; Colwell 2021; Fletcher Jr. *et al.* 2023; Lu & Jetz 2023; Zelnik *et al.* 2024). The traditional view that ecological processes act over much smaller timescales than evolutionary ones has evolved to recognize that ecosystems are not only shaped by but also shape their environments through evolutionary processes. This perspective emphasizes the intertwined nature of historical, temporal, and spatial components in ecosystem dynamics (Chave 2013). Despite advances, the relative importance of ecological and evolutionary processes across scales remains underexplored, particularly in studies that integrate phylogenetic methods (Cavender-Bares *et al.* 2009; Lessard *et al.* 2012).

Ecological and evolutionary processes generate species diversity at local and regional scales (Ricklefs & Schluter 1993; McPeek & Miller 1996; Ricklefs 2007). Locally, negative interspecific interactions (*e.g.*, predation, competition) and deterministic environmental factors are expected to be the main constraints to diversity. Regionally, diversity increases through speciation, long-distance dispersal, and historical events that enrich local assemblages (Ricklefs & Schluter 1993; McPeek & Miller 1996; Willis & Whittaker 2002). These processes do not operate in isolation; their interplay across scales determines community structure, with no community shaped solely by local or regional processes (Loreau 2000; Zelnik *et al.* 2024).

Importantly, numerous patterns in ecology and evolution depend on the phylogenetic scale at which they are examined. Large phylogenetic grains (*e.g.*, orders or families) often highlight the role of deterministic abiotic processes, such as environmental filtering, which tend to dominate at broader evolutionary extents (Cavender-Bares *et al.* 2009). Conversely, smaller phylogenetic grains (*e.g.*, genera or species) may reveal the influence of biotic interactions, including competition and mutualism, that operate more strongly at finer scales. Additionally, different phylogenetic extents—spanning clades with varying life-history traits and strategies—can uncover distinct responses to environmental factors, potentially leading to contrasting interpretations of ecological and evolutionary processes depending on the scale of analysis (Chalmandrier *et al.* 2013). This variability across scales underscores the importance of carefully considering phylogenetic scale in studies of biodiversity, as the processes shaping community assembly and diversification may differ significantly across phylogenetic grains and extents, reflecting the interplay of multiple ecological and evolutionary mechanisms (see Graham *et al.* 2018).

These insights underscore the critical importance of considering both spatial and phylogenetic scales when studying ecological and evolutionary processes. By integrating these concepts, we can infer the complex interplay between historical legacies, environmental conditions, and biotic interactions. As the following chapters will demonstrate, this multi-scale approach provides a robust framework for elucidating the relationships between climate and evolutionary dynamics and their outcomes in biodiversity patterns.

1.5 Aims and scope

Scientific disciplines often oscillate between phases of empirical research and theoretical development, as well as between reductionist and holistic approaches[4]. This thesis navigates both empirical and theoretical terrains, employing a variety of approaches and spanning multiple geographical scales.

The overall aim of this thesis is to investigate how three dimensions of climate—average, variability, and frequency across space—influence community assembly through changes in phylogenetic structure and climatic specialization.

In the first research chapter, Chapter 2, I investigated the phylogenetic structure of bat communities worldwide, focusing on the role of historical and contemporary processes in shaping their current configurations. By estimating phylogenetic relatedness across multiple geographical extents—from global scales to ecoregions—I assess the influence of palaeoclimatic stability, local diversification rates, and geographical barriers. This chapter reveals that the phylogenetic structure of bat communities varies strongly with geographical scale, highlighting the scale-dependent nature of dispersal barriers, historical climate stability, and *in situ* diversification as key drivers of community assembly. These findings provide novel insights into how historical processes have left lasting imprints on the evolutionary dynamics of highly mobile taxa like bats, suggesting that both past and present climatic conditions must be considered when evaluating contemporary biodiversity patterns.

In Chapter 3, I shift the focus from bats to a broader taxonomic scope, examining how the spatial frequency of climatic conditions affects climatic specialization in biological communities of tetrapods. Using a combination of global empirical data on over 25,000 species of tetrapods (including amphibians, birds, mammals, and reptiles) and theoretical simulations, I examine how the spatial frequency of climatic conditions affects the distribution and dominance of specialist and generalist species within communities. In both empirical analyses and theoretical simulations, I find that rare environments tend to limit specialization by favouring generalist species that can thrive across a range of conditions. Conversely, in more common climates, specialist species often

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[4] Scientific progress is often driven by the integration of empirical discoveries and theoretical frameworks, where basic principles and idealized models provide generalized insights across various domains. While reductionist research unravels the underlying components and processes at limited extents and scales, it is through holistic approaches that we understand how these elements coalesce to form and sustain complex systems at higher levels of organization. Typically, these theoretical and empirical, reductionist and holistic investigations are undertaken by different researchers, each motivated by distinct questions and methodological preferences. Nevertheless, both approaches are indispensable for advancing our scientific understanding and creating a cohesive body of knowledge.

outcompete generalists due to their adaptations. This chapter offers a novel perspective on how the spatial distribution of climatic conditions drives ecological strategies and community assembly.

The final research chapter, Chapter 4, addresses how the spatial frequency of climatic conditions influences the phylogenetic structure of tetrapod communities across geographical scales. Building on the findings of the previous chapters, I test the hypothesis that communities in rare climates exhibit less phylogenetic clustering than those in more common climates. By integrating phylogenetic data with climatic and geographical variables, this chapter reveals that the rarity of certain climates disrupts typical patterns of phylogenetic relatedness across phylogenetic and geographical scales, suggesting that species co-occurrence in these environments is more shaped by recent ecological dynamics than by deep evolutionary histories.

Recognizing the persistent challenge of underdetermination in biogeography, I have undertaken a critical examination of underlying assumptions through both the theoretical frameworks and empirical analyses presented herein. Collectively, these chapters advance our understanding of how climate shapes biodiversity through both direct and indirect mechanisms. By integrating empirical data, phylogenetic analyses, and theoretical models, these chapters provide a comprehensive framework for examining the multifaceted effects of climate on species distributions, community structures, and evolutionary processes. Moreover, they highlight the significance of historical climatic legacies, the variability and frequency of climatic conditions across spatial scales, and the evolutionary strategies at play in these dynamics.

Chapter 2

Historical and contemporary processes drive global phylogenetic structure across geographical scales: Insights from bat communities

2.1 Abstract

Aim

Patterns of evolutionary relatedness among co-occurring species are driven by scale-dependent contemporary and historical processes. Yet, we still lack a detailed understanding of how these drivers impact the phylogenetic structure of biological communities. Here, we focused on bats (one of the most species-rich and vagile groups of mammals) and tested the predictions of three general biogeographical hypotheses that are particularly relevant to understanding how palaeoclimatic stability, local diversification rates and geographical scales shaped their present-day phylogenetic community structure.[1]

Location

World-wide, across restrictive geographical extents: global, east–west hemispheres, biogeographical realms, tectonic plates, biomes and ecoregions.

Time period

Last Glacial Maximum (~22,000 years ago) to the present.

Major taxa studied

Bats (Chiroptera).

Methods

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[1] This study has been published in *Global Ecology and Biogeography as:*
Braga, P. H. P., Kembel, S., & Peres-Neto, P. (2023). Historical and contemporary processes drive global phylogenetic structure across geographical scales: Insights from bat communities. *Global Ecology and Biogeography*, 32, 747–765.

We estimated bat phylogenetic community structure across restrictive geographical extents and modelled it as a function of palaeoclimatic stability and *in situ* net diversification rates.

Results

Limiting geographical extents from larger to smaller scales greatly changed the phylogenetic structure of bat communities. The magnitude of these effects is less noticeable in the western hemisphere, where frequent among-realm biota interchange could have been maintained through the adaptive traits of bats. Bat communities with high phylogenetic relatedness are generally more common in regions that have changed less in climate since the Last Glacial Maximum, supporting the expectation that stable climates allow for increased phylogenetic clustering. Finally, increased *in situ* net diversification rates are associated with greater phylogenetic clustering in bat communities.

Main conclusions

We show that the world-wide phylogenetic structure of bat assemblages varies as a function of geographical extents, dispersal barriers, palaeoclimatic stability and *in situ* diversification. The integrative framework used in our study, which can be applied to other taxonomic groups, has not only proved useful to explain the evolutionary dynamics of community assembly, but could also help to tackle questions related to scale dependence in community ecology and biogeography.

2.2 Introduction

One of the most striking patterns in ecology is the non-random distribution of species across space. This unevenness in species compositions is determined by the interplay of spatial, temporal and historical processes (Ricklefs 1987). In the past decades, our understanding about how species assemblages are structured and maintained through space and time has advanced significantly owing to the field of "community phylogenetics" (Webb 2000; Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Kembel 2009; Peres-Neto *et al.* 2012; Davies 2021). The core basis of this field is to quantify the phylogenetic relatedness of co-occurring species (*i.e.*, the community phylogenetic structure) to infer ecological patterns and associated mechanisms of species assembly (Webb 2000; Ackerly & Renner 2004; Cavender-Bares *et al.* 2004a; Emerson & Gillespie 2008; Kembel 2009; for a recent review, see Davies 2021). Notwithstanding, we still have fragmented knowledge about how history itself, including palaeoclimatic legacies, spatial scale dependence and local diversification rates, influenced the contemporary phylogenetic structure of communities (Kissling *et al.* 2012; but see Calatayud *et al.* 2019), despite their potential role increasingly being highlighted (Kembel & Hubbell 2006; Swenson *et al.* 2006; Kraft & Ackerly 2010; Graham *et al.* 2018). Considering the fingerprints of historical and contemporary processes together should improve our ability to understand the complexities underlying the structure of species assemblages. For instance, the spatial structure of historical climatic gradients can vary within and across geographical scales, which, in turn, can affect how species interact and are sorted into species assemblages at smaller geographical extents (Peres-Neto *et al.* 2012). Here, we set out to quantify the legacies of different historical and contemporary processes globe-wise on the present-day phylogenetic community structure of bats (Chiroptera), which are one of the most successful and geographically widespread groups of mammals.

Variation in phylogenetic community structure across large geographical extents is driven by ecological and evolutionary processes linking immigration, species interactions, speciation and extinction (Lomolino *et al.* 2017 and references therein). Given that species abilities to adapt and/or to disperse in response to environmental variation are often phylogenetically conserved, strong turnover of lineages across geographical and environmental gradients is observed (Harvey & Pagel 1991). Historical climatic fluctuations, such as glacial—interglacial oscillations, are thus expected to drive patterns of phylogenetic community structure and niche differences via changes to species dispersal routes, speciation and extinction dynamics. This arises not only directly from clade-dependent responses to the environment (*i.e.*, through common ancestry), but also from increased speciation rates driven by allopatry in species fragmented ranges and increased extinction rates associated with extensive disturbances in deep time (Wiens & Donoghue 2004; Hortal *et al.* 2011; Svenning *et al.* 2015; Saladin *et al.* 2020). Furthermore, post-disturbance periods have not always been associated with immediate and/or extensive regional recolonization by previously excluded lineages, especially if those were poor dispersers and stress intolerant (Svenning & Skov 2004; Normand *et al.* 2011; Kissling *et al.* 2012; Rebelo *et al.* 2012). As such, the phylogenetic structure of contemporary biological communities should exhibit the accumulated imprints of the strength and stability of past climatic changes (Kissling *et al.* 2012; Delgado-Baquerizo *et al.* 2017).

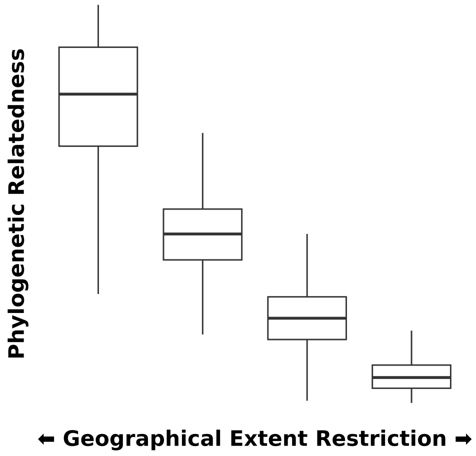
The phylogenetic structure of communities can also be determined strongly by the maintenance of geographical isolation (mediated by geological barriers to dispersal), both through clade-specific responses to these geographical processes and through dramatic changes in net diversification rates (*e.g.*, Hortal *et al.* 2011; Kissling *et al.* 2012; see Svenning *et al.* 2015). Speciation driven by early geographical separation and isolation of regions during interglacial periods can promote negative co-occurrence among closely related species (see review by Emerson & Gillespie 2008). In contrast, less phylogenetically related species should co-occur less where speciation has been driven by more ancient vicariance (*e.g.*, separation between continents and realms) because closely related species might establish across different communities and regions (Anacker & Strauss 2014). Nevertheless, intense subsequent regional recolonization and lower *in situ* speciation might produce regionally similar communities independent of their phylogenetic associations (see Emerson & Oromi 2005).

Finally, the ecological and evolutionary processes underlying species assembly in communities are commonly scale dependent in space (Wiens 1989; Levin 1992; Kembel & Hubbell 2006; Swenson *et al.* 2006; Chave 2013; Chase *et al.* 2018; Graham *et al.* 2018). The nature of community phylogenetic patterns in space often varies as a function of the species pool and geographical extents used to quantify metrics of interest, because different species pools reflect different underlying ecological and evolutionary processes (Peres-Neto *et al.* 2001). Larger geographical scales contribute with species pools having a greater potential number of species assumed to be able potentially to colonize and successfully establish in small-scale (local) species assemblages (Lessard *et al.* 2012; Carstensen *et al.* 2013). Species composition at broader geographical scales is often defined by major geological and historical events that could have influenced clade dispersal and diversification, such as orogenesis, land-mass separation through tectonics, island isolation and palaeoclimatic changes favouring the expansion or contraction of biomes (Cornell & Harrison 2014; Fukami 2015). As such, communities can appear phylogenetically clustered at larger spatial scales owing to limited dispersal and isolation of their species pools and local radiation mediated by biogeographical processes (Pennington *et al.* 2006). Alternatively, species composition at local spatial scales is expected to be more associated with local biotic processes and abiotic differences across communities (Wiens 1989; Levin 1992; McGill 2010). Taken together, an explicit consideration of different geographical scales in the phylogenetic structuring of communities should assist in revealing the relative importance of finer- and broader-scale ecological and evolutionary processes that have contributed to form present-day species assemblages (Graham *et al.* 2018).

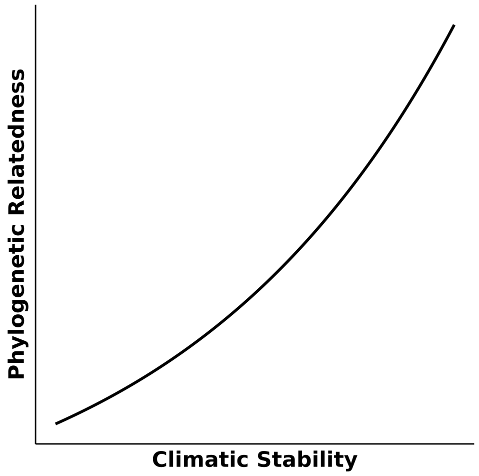
Here, we quantify the phylogenetic relatedness of bat communities world-wide across multiple spatial scales (here, in the form of hierarchically nested geographical extents) as a function of multiple potential historical influences. Bats (Chiroptera) are a good model system because their geographical distributions are known to have been influenced by multiple historical drivers (Jones *et al.* 2005; Teeling *et al.* 2005; Carstens *et al.* 2018; López-Aguirre *et al.* 2018). They are the only mammals with real flight capability, which, along with their echolocation ability, has allowed them to occupy most of the globe (Simmons 2005). Phylogenetically structured bat communities have been found across different ecosystems and associated with environmental variation (Grimshaw & Higgins 2017), seasonal changes (Presley *et al.* 2018), geological context and diversification regimes (López-Aguirre *et al.* 2018), and species pools (Patrick & Stevens 2014). Diversification rates in bats are known not to be constant across clades, a finding that has been linked to innovations in adaptive traits (Monteiro & Nogueira 2011; Rojas *et al.* 2012; Santana *et al.* 2012), vicariance and migration events (Rojas *et al.* 2016), and diversity-dependent diversification events (Shi & Rabosky 2015; Upham *et al.* 2020).

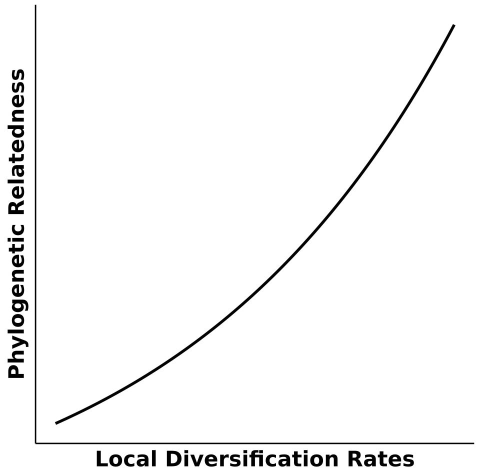
To focus on a subset of a potentially extensive set of results, we selected three key biogeographical hypotheses and related predictions underlying the phylogenetic structure of bat communities globally (Table 2.1). First, because long-term isolation mediated by strong dispersal barriers between biogeographical realms leads to dispersal limitations and within-realm diversification [hypothesis H_1; Cavender-Bares *et al.* (2009); Crisp *et al.* (2011); Kissling *et al.* (2012)], we predict that bat communities should become less phylogenetically clustered when restricting the geographical extent of the regions containing species that could have colonized these communities historically (*e.g.*, from global to east-west hemispheres, from east-west hemispheres to realms). However, because of the greater vagility of bats owing to their capacity for flight, we predict that biogeographical realms that have been isolated recently or that are connected through islands should be more similar in their phylogenetic structure owing to more frequent biota exchange (MacArthur & Wilson 2001; see Peixoto *et al.* 2014), and thus vary less as geographical extents become restricted. Second, regions with a history of climatic instability should have constrained the dispersal and colonization dynamics of climate-sensitive species [hypothesis H_2; Eiserhardt *et al.* (2015); Hortal *et al.* (2011); Normand *et al.* (2011); Svenning *et al.* (2015)]. Given this process, we predicted an increase in phylogenetic clustering in regions where climate has remained more stable during recent geological times [*i.e.*, the regions where the climate remained stable in relationship to the Last Glacial Maximum (LGM)]. Given that climatic legacies are thought to drive and leave signatures in community assembly and composition patterns from large to small geographical scales (Ricklefs 1987; Warren *et al.* 2014; Pollock *et al.* 2015; Delgado-Baquerizo *et al.* 2018), we expected to observe these effects on community phylogenetic relatedness across varying geographical scales. Finally, because variation in regional historical, geographical and environmental conditions influences community assembly through changes in both *in situ* speciation and extinction rates [hypothesis H_3; Cardillo *et al.* (2008); Emerson & Gillespie (2008)], we predicted that increased *in situ* net diversification rates should foster communities with greater phylogenetic clustering independent of geographical extent (or geographical scale) restriction.

Table 2.1: **Biogeographical hypotheses and related predictions for the phylogenetic structure of bat communities across geographical extents (spatial scales).**

Spatial scale	Hypothesis	Predictions	References	Representation
Broader to local	H_1: Strong dispersal barriers between regions limit dispersal and lead to within-region diversification	1.1 Co-occurring species in bat communities should be more phylogenetically related at broader geographical scales (e.g., hemispheric extent vs. realm extent). These communities should become less phylogenetically structured when restricting the geographical extent of the regions encompassing species that could have colonized these communities historically	Kissling et al. (2012), Crisp et al. (2012), Peixoto et al. (2014)	

Spatial scale	Hypothesis	Predictions	References	Representation
		1.2 Owing to the high vagility of bats, biogeographical realms that have been isolated recently or that are connected through islands should have fewer striking differences in their phylogenetic structure, and thus be less sensitive to variation in geographical extent		

Spatial scale	Hypothesis	Predictions	References	Representation
Broader to local	H_2: Climatic disturbances during glaciation cycles exclude species and limit the dispersal and the colonization dynamics of clades	2.1 Bat communities located in climatically stable regions (here, the difference between the contemporary period and the Last Glacial Maximum) should be more phylogenetically related than in regions that underwent large fluctuations in the climate during geological epochs across geographical scales	Svenning et al. (2015), Eiserhardt et al. (2015), Kissling et al. (2012) Normand et al. (2011)	

Spatial scale	Hypothesis	Predictions	References	Representation
Broader to local	H_3: Historical, geographical and environmental factors drive community assembly through changes in diversification rates	3.1 Increased *in situ* diversification rates create clusters of closely related species, leading to high levels of phylogenetic clustering independent of geographical scale	Emerson and Gillespie (2008)	

To test these hypotheses, we devised a framework that explicitly integrates phylogenetic community relatedness across a hierarchically restrictive gradient of geographical extents based on biogeographically relevant regional separations. We then quantified rates of palaeoclimatic stability and local net diversification and estimated the effects of long-term isolation, relating these to the present-day phylogenetic structure of bat communities across geographical extents. This approach can be extended to tackle more specific hypotheses about the historical legacies on current patterns (phylogenetic or not) of species assemblages. Our results provide strong evidence for the predictions underlying these three hypotheses, highlighting strong effects of scale dependence, geographical extent and isolation, recent glacial-interglacial climatic oscillations and diversification in the phylogenetic structure of contemporary bat communities.

2.3 Methods

2.3.1 Study area: Restricting geographical extents from larger to smaller scales

To estimate the influence of spatial scale dependence in the phylogenetic structure of bat communities, we applied a framework that computed and compared the phylogenetic relatedness of ecological communities relative to a gradient of hierarchically restrictive geographical extents (or spatial extents): global, east–west hemispherical (New World and Old World), biogeographical realms [Palaearctic, Indo-Malaya, Afrotropics, Australasia, Nearctic and Neotropics; Olson *et al.* (2001)], tectonic plates [14 large plates; Bird (2003)], within-realm biomes [14 biomes; Olson & Dinerstein (1998)] and within-realm terrestrial ecoregional scales [867 ecoregions; Olson *et al.* (2001)].

We used the species found within each geographical extent for estimating standardized effect sizes of phylogenetic relatedness within any given local community in relationship to that in the region delimited in that extent. The geographical extents we adopted have often been used while studying the causes underlying spatial scale dependence in the structure of ecological communities (*e.g.*, Kissling *et al.* 2012; Thuiller *et al.* 2020). Each of these discrete separations is known to be related to eco-evolutionary mechanisms that regionalize flora and fauna and underlie their diversity patterns (Ricklefs & Latham 1992; Jenkins & Ricklefs 2011; Mazel *et al.* 2017; Smith *et al.* 2018, 2020). Moreover, the hierarchical nature of this set of biogeographical separations allows inference concerning the ecological and evolutionary mechanisms driving the phylogenetic structure of bat communities across geographical scales. These mechanisms and their effects range from clade origin and species responses to long-term dispersal barriers (such as tectonics and realm or continental isolation). They also include changes to regional colonization and diversification dynamics owing to climate change, and biotic regionalization that biomes and their nested ecoregions promote through their geographically segregated climatic domains and vegetational types, all contributing to variation in the geographical distribution of species and clades (*e.g.*, Cox 2000; Peixoto *et al.* 2014; Descombes *et al.* 2017; Mazel *et al.* 2017; Smith *et al.* 2018, 2020) (see Table 2.1).

2.3.2 Species geographical ranges

We compiled species distributional data of bat assemblages from expert-drawn maps of the International Union for Conservation of Nature (IUCN) database (IUCN 2019). We overlaid these species distributions on a spatial polygon equal-area projection grid of 50 km × 50 km cells (*c.* 0.5° × 0.5° along the Equator line) and converted them into site-per-species incidence matrices.z As in other studies, we referred to the species within these cells as "local communities". Species ranges had to cover ≥50% of a given cell to be considered present. The spatial grain (2500 km^2) we chose has been shown to distinguish between local communities and to be sensitive to the scale of biodiversity patterns emerging from bionomic and biogeographical determinants relevant to our study (Whittaker *et al.* 2001; Ricklefs 2004; Barton *et al.* 2013; Loiseau *et al.* 2020).

2.3.3 Phylogenetic relationships and divergence time data

We used the recent time-calibrated phylogenetic hypothesis for all 5020 extant and late Quaternary extinct mammals by Faurby and Svenning (2015) to extract bat evolutionary relationships. To avoid polytomies and negative branch lengths, we computed an ultrametric maximum clade credibility (MCC) tree from the 1000 posterior distributions of the mammal trees. We then pruned the phylogenetic tree to match our species distributions dataset, ending up with 954 bat species.

To account for phylogenetic uncertainty, we repeated the analyses of our study on 100 randomly sampled trees from the posterior distribution of phylogenetic trees from Faurby and Svenning (2015) and compared the results with the ones obtained from the MCC tree. These comparisons yielded very similar results, supporting the robustness of our inferences to the uncertainty of phylogenetic trees (Supporting Information in Section 2.10, Figure 2.14, Figure 2.15, Figure 2.16, Figure 2.17).

2.3.4 Phylogenetic community structure

We quantified the phylogenetic community structure of bat communities by calculating the net relatedness index (NRI) and the nearest taxon index (NTI) for each community across each geographical extent (Webb 2000; Webb *et al.* 2002). The NRI represents the overall phylogenetic structure of communities using mean pairwise phylogenetic distances (MPDs) among all taxa persisting in each community, whereas the NTI is based on the mean nearest-taxon distances (MNTDs) among co-occurring taxa. Given that the latter is more sensitive to the community structure driven by phylogenetic tips [*i.e.*, reflecting more recent processes; Webb *et al.* (2002)], the combined use of NRI and NTI can inform about community structuring mechanisms working across different phylogenetic scales (Cavender-Bares *et al.* 2009; Graham *et al.* 2018). To assess how phylogenetic community structure changed as a function of geographical extent restriction, we applied null models to estimate standardized effect sizes for both metrics ($\mathrm{MPD_{SES}}$ and $\mathrm{MNTD_{SES}}$, respectively) (Kembel *et al.* 2010). Each null model simulated random assemblages by permuting species names across the phylogeny tips 999 times within each geographical extent (*i.e.*, the spatial extent from which species were sampled to compose random assemblages): global (all species in the phylogeny); east-west hemispherical (also referred as Old World and New World); biogeographical realms; tectonic plates; within-realm biomes; and within-realm terrestrial ecoregion scales. The NRI and NTI were obtained by multiplying $\mathrm{MPD_{SES}}$ and $\mathrm{MNTD_{SES}}$, respectively, by minus one. Larger values of NTI and NRI indicate that $\mathrm{MPD_{SES}}$ and $\mathrm{MNTD_{SES}}$ are lower than expected for its spatial extent, hence that local communities are composed of species more phylogenetically similar (or clustered) than what would be expected from random assemblages. Conversely, negative NTI and NRI values indicate phylogenetic evenness.

The magnitude of standardized effect sizes of indices for phylogenetic community structure can increase artificially as a function of the geographical or phylogenetic extents (because of the greater number of species in larger biogeographical regions) used to estimate the null distributions underlying community phylogenetic metrics (Sandel 2018). We assessed whether our results held after adjusting for this potential bias by repeated random subsampling (rarefying) of any given local community matrix to have the same number of species as the immediately inferior nested geographical extent. Community phylogenetic indices for any given local community were then estimated as the average indices across subsamples. We reproduced all figures (with the exception of Figure 2.1) and analyses from our study using the rarefied NRI and NTI indices (Supporting Information in Section 2.8, Figure 2.7, Figure 2.8, Figure 2.9, Figure 2.10), and they all had patterns similar to those depicted in the figures using the original (unrarefied) values (Figure 2.2, Figure 2.3, Figure 2.4, Figure 2.5). For the purposes of simplification and to avoid any small but potential loss of information introduced by the rarefaction procedure, we use the original values for NRI and NTI in the main study.

2.3.5 Measurement of historical climatic stability

To represent the effects of climatic legacies on the phylogenetic community structure of bats, we compiled global bioclimatic variables for temperature and precipitation from the contemporary period [yearly averages between 1960 and 1990; Karger *et al.* (2017)] and the LGM period [*i.e.*, *c.* 22,000 years ago; PaleoClim; Brown *et al.* (2018)]. These bioclimatic variables were projected and aggregated (by calculating the average of all pixels occurring in each cell) to fit the 50 km × 50 km equal-area grid cells.

To assess the influence of historical changes in climate on the present-day phylogenetic assemblage structure of bats, we calculated two indices of climatic stability, based on temperature and precipitation, by subtracting values for mean annual temperature (MAT) and mean annual precipitation (MAP) in the contemporary period from those of the LGM for each site (*i.e.*, $\mathrm{MAT}_{\mathrm{contemporary}} - \mathrm{MAT}_{\mathrm{LGM}}$ and $\mathrm{MAP}_{\mathrm{contemporary}} - \mathrm{MAP}_{\mathrm{LGM}}$), respectively. Our approach to measurement of climatic stability is based on the differences in two temporally distant snapshots and could potentially not directly represent the climatic variability in between the LGM and the contemporary period. Nevertheless, although climatic anomalies (such as rapid cooling or rapid warming events) happened across varying temporal and spatial scales (*e.g.*, Goslar *et al.* 2000; Hemming 2004), climatic changes during the last ~20,000 years have been demonstrated to have a coarsely linear unidirectional nature, and our approach for measuring historical climatic stability has been shown to be correlated strongly with the rates of change in climate at time-scales of thousands of years (see Delgado-Baquerizo *et al.* 2017).

To provide an additional metric for historical climatic stability, we also calculated gradient-based change velocities in temperature and in precipitation from the LGM to the contemporary period and assessed how they influenced the phylogenetic relatedness of bat communities across geographical scales (Supporting Information in Section 2.9).

2.3.6 Average community-weighted estimates of diversification rates

To assess the relationship between community phylogenetic structure and local net diversification rates, we estimated speciation and extinction rates using Bayesian analyses of macroevolutionary mixtures [BAMM; Rabosky (2014); Rabosky *et al.* (2013)], which accommodates heterogeneous mixtures of evolutionary speciation and extinction rates. BAMM has been demonstrated to provide more robust, less biased estimates for net diversification rates under incomplete taxon sampling (Sun *et al.* 2020) and offers an advantage over constant-rate models by allowing extinction to be higher than speciation, allowing for complex patterns of discrete shifts and among-clade variation in speciation and extinction rates (Rabosky 2014).

Combining the estimated species-level speciation and extinction rates and the community species occurrence matrix, we computed community-weighted means on the weighted, standardized speciation and extinction tip rates (as in the study by Peres-Neto *et al.* 2017). Weights were computed with respect to both species richness per community and the total number of occurrences per species. As such, we restricted the contribution of both geographically widespread taxa and diverse sites when estimating community means. Finally, we calculated local net diversification rates for each bat community by subtracting both community-weighted speciation and extinction means (for further details, see Supporting Information in Section 2.6).

2.3.7 Statistical analyses

When performing the statistical analyses for our study, we started by applying general and generalized linear and linear mixed-effects models to test our predictions and hypotheses and inspected their residuals and the data for violations of any underlying parametric assumption (on both raw and ln-transformed data). Whenever these assumptions were violated, we tested our hypothesis using alternative non-parametric and robust statistical methods, which are specified below.

2.3.7.1 Effects of spatial extent restriction on phylogenetic community structure (H_1)

To test the effects of geographical extent restriction on bat phylogenetic community structure (H_1), we performed separate robust heteroscedastic repeated-measurement ANOVAs based on 20% trimmed means (Wilcox 2012b). This non-parametric method is designed to handle violations of the assumption of sphericity (as found in the parametric versions using standard repeated measures) associated with standard parametric tests (Wilcox 1993; Wilcox *et al.* 2000; Wilcox 2012a). To account for regional effects when testing the predictions of this hypothesis, we repeated our tests for each biogeographical realm. For each realm, we estimated whether the NRI and NTI (response variables, in separate analyses) of bat communities (block levels; random effects) differed across our discrete gradient of geographical extents (group levels; fixed effects). Finally, we performed post-hoc comparisons using Hochberg's approach to control for family-wise type I error (Hochberg 1988; Wilcox 2012b) (see Supporting Information in Section 2.7, Table 2.6).

We also supplemented the analyses for the prediction that broader geographical extents are associated with phylogenetically related bat communities (H_1) with combined probability tests. For this, to focus on the evidence of phylogenetically clustered communities, we first replaced the *p*-

values for the indices of phylogenetic relatedness in phylogenetically overdispersed communities (NRI and NTI less than zero) by their complement (*i.e.*, subtracting the *p*-value from one). Then, separately for NRI and NTI and for each biogeographical realm, we applied Stouffer's probability combination tests (Stouffer *et al.* 1949), whereby we subset the *p*-values of the independent null models performed at each geographical extent and divided them by the square root of the number of null models we performed (communities). Among other probability combination approaches, Stouffer's meta-analytical method has been shown to have high power, precision and type I error control rates (Rice 1990; Whitlock 2005). The resulting combined probabilities that were <.05 were then used as evidence for phylogenetic clustering in bat communities to that geographical extent (see Figure 2.2; Supporting Information in Section 2.7, Table 2.3).

2.3.7.2 Effects of historical climatic stability and *in situ* diversification rates on phylogenetic community structure (H_2 and H_3)

We used two complementary approaches (one descriptive and the other inferential) to assess the predictions that phylogenetically clustered communities are more frequent in historically climatically stable regions (H_2) and that increased *in situ* diversification rates generate regional clusters of closely related species (H_3).

To describe how phylogenetic relatedness of bat communities (for both NRI and NTI) changed as a function of historical change in temperature, historical change in precipitation and *in situ* net diversification rates, we plotted the mean phylogenetic relatedness of bat communities (for both NRI and NTI) across each percentile (100 quantiles) of the predictor variables of interest (*i.e.*, historical change in temperature, historical change in precipitation and *in situ* net diversification rates; see Figure 2.3, Figure 2.4). This representation allowed us to describe how phylogenetic structure varies as a response to the predictors of interest.

To test hypotheses H_2 and H_3 inferentially, we tested explicitly how changes in historical climatic stability and *in situ* diversification rates independently increased (or decreased) the likelihood of a community being composed of species with a high degree of phylogenetic relatedness. For this, we used two upper conditional proportional percentiles of community phylogenetic relatedness, the 90th and the 75th percentiles, as thresholds to consider whether a community exhibited a high degree of phylogenetic relatedness. These values were chosen somewhat arbitrarily; however, selection of these percentiles allowed us to focus on the effects of historical climatic stability and local net diversification affecting long-term persistence of species, and thus influencing communities exhibiting a high degree of phylogenetic relatedness. We started by attributing a value of one to a community if its phylogenetic structure (either NRI or NTI) was greater than its upper conditional quantile (either the 90th or the 75th percentile) across all communities. If smaller, a value of zero was assigned instead. Based on this classification (of whether the community exhibited a high degree of phylogenetic relatedness or not), we then applied conditionally unbiased, bounded influence robust logistic regressions [*i.e.*, robust to reduce the influence of potential outliers; see Kunsch *et al.* (1989)], in which the response variable was the vector of binary outcomes (ones and zeros) representing relatively high or low phylogenetic structure (separately for NRI and NTI) and the predictors were *z*-score standardized values (*i.e.*, to have a mean of zero and variance of one) of historical change in temperature, historical change in precipitation and *in situ* net diversification rates. As such, we were able to estimate the relative importance of each predictor. To estimate confidence intervals for each predictor, we took a bootstrap approach based on 1000 resamples of 2500 random communities each. These logistic regressions allowed us to describe how changes in historical climatic stability and *in situ* diversification rates independently affected the log-odds (the logistic response) of a community exhibiting a high degree of phylogenetic relatedness.

We repeated these analyses for each geographical extent to assess whether the influence of historical changes in temperature and precipitation and *in situ* net diversification rates on the phylogenetic structure of bat communities was consistent across spatial scales. For simplicity, we report the figures containing the bootstrapping partial coefficients for the 90th percentile (*i.e.*, communities with bat species exhibiting a high degree of phylogenetic relatedness) in the main manuscript (see Figure 2.5; Table 2.2) and include the results from the 75th percentile in the Supporting Information (Section 2.12, Figure 2.19; Table 2.9). We also applied the same analyses when assessing the robustness of our results across the size of spatial extents (Supporting Information in Section 2.8)), to phylogenetic uncertainty (Supporting Information in Section 2.10) and when assessing the effects of temperature and precipitation change velocities since the LGM on the phylogenetic relatedness of bat communities (Supporting Information in Section 2.9).

2.3.8 Computational tools

All data manipulation and analyses were performed in R and RStudio (R Core Team 2021; RStudio Team 2021). The data and code necessary to reproduce the analyses and figures, BAMM set-up files and information on tools used in this manuscript are available in the Supporting Information (Tools) and within the Open Science Framework (accessible at osf.io/amvp5) and the Dryad (accessible at 10.5061/dryad.rjdfn2zgj) repositories for this study.

2.4 Results

2.4.1 Geographical extent restriction determines bat phylogenetic community structure (H_1)

Limiting the geographical extent from larger to smaller scales (in a hierarchical fashion) significantly affected the phylogenetic structure of bat communities, at different extents, for both NRI and NTI (Figure 2.1, Figure 2.2; Supporting Information in Section 2.7), Table 2.3, Table 2.4; Figure 2.6 and Figure 2.18). The NRI decreased with the restriction of geographical extents in the Neotropical, Nearctic and Australasian regions, and NTI consistently decreased with the geographical extent across all biogeographical realms, revealing distinctions between deep time and more recent effects of spatial and environmental isolation and within-region diversification on the phylogenetic community structure of bats (hypothesis H_1). The Afrotropical, Indomalayan and Palaearctic realms had local assemblages with an overall phylogenetic structure (NRI) independent of the size of the geographical extent but had their tip-level phylogenetic structure (NTI) decreasing with geographical extent restriction (Figure 2.2; Section 2.7, Table 2.4; Figure 2.6 and Figure 2.18). A contrasting pattern to the invariance or to the decrease in phylogenetic relatedness with geographical extent appeared in the Nearctic realm, where NRI values increased when restricting the geographical scale from the hemispheric to the realm extent (Figure 2.2).

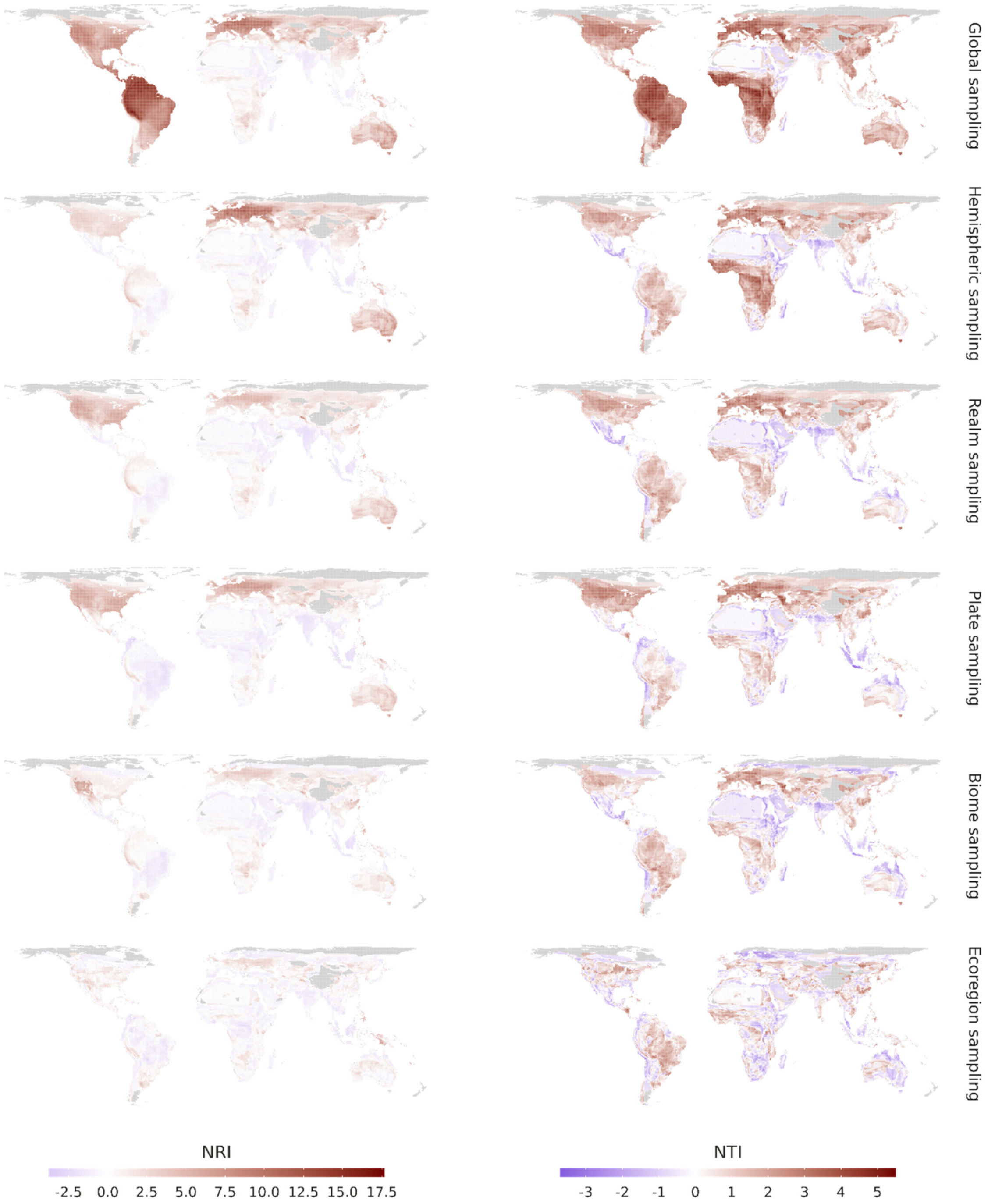


Figure 2.1: **The geographical distribution of the phylogenetic structure of bat assemblages, measured through the net relatedness index (NRI; left) and the nearest taxon index (NTI; right), across a gradient of geographical (or spatial) extent restrictions (see Methods)**. Geographical extents were restricted for (from top to bottom) the global, east–west hemispheric, biogeographical realm, tectonic plate, within-realm biome and ecoregional extents. Bat communities with positive values of NRI and NTI (red) indicate that co-occurring species in these communities are more phylogenetically related in relationship to a given geographical extent. On the contrary, negative values of NRI and NTI (in blue) indicate that bat communities are composed mainly of less phylogenetically related species in relationship to that given geographical extent.

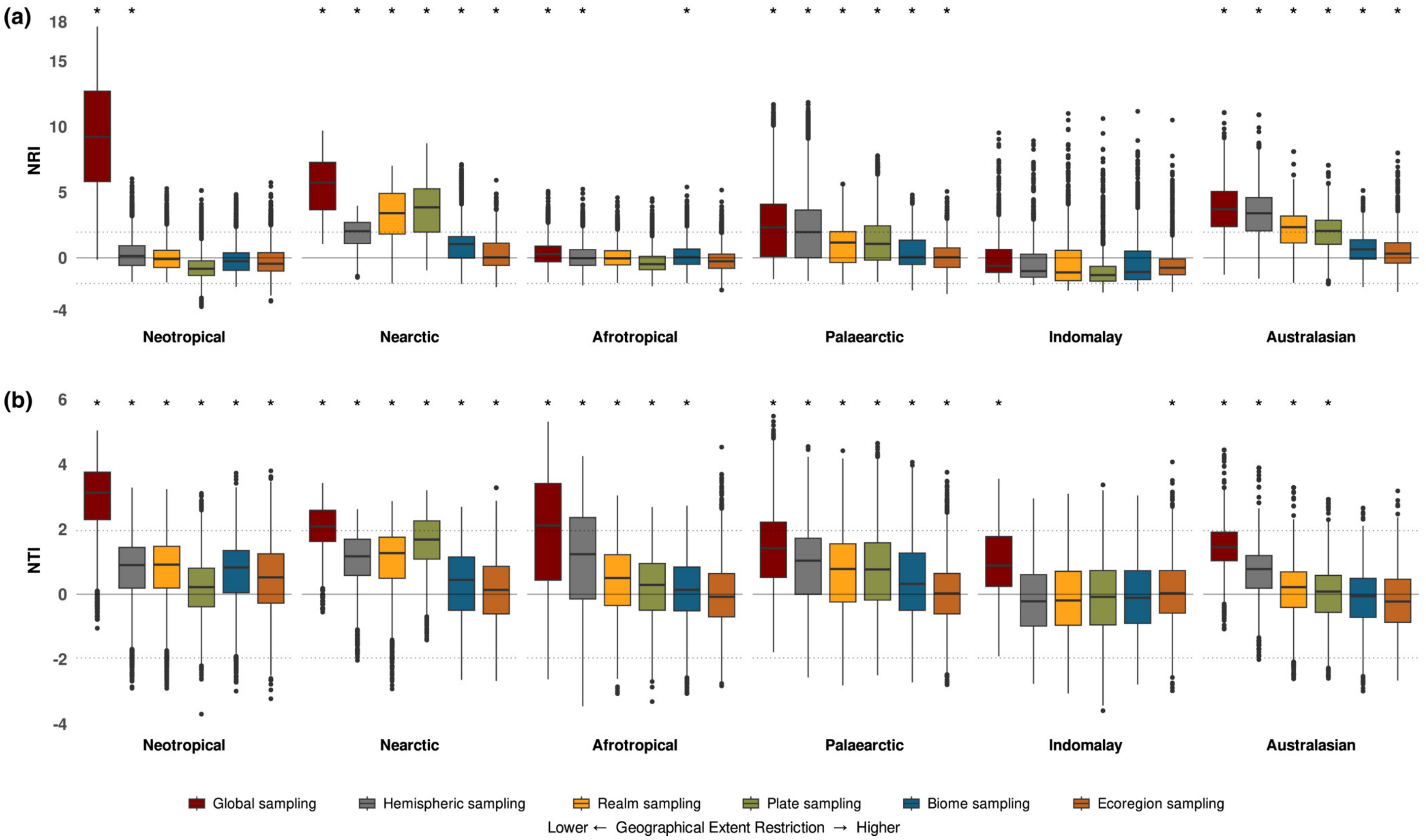


Figure 2.2: **Realm comparison of the phylogenetic structure of bat assemblages, measured through (a) the net relatedness index (NRI) and (b) the nearest taxon index (NTI), across a gradient of geographical extent restrictions (see Methods)**. Geographical extents were restricted for the global, east–west hemispheres (New World versus Old World), biogeographical realms, tectonic plates, within-realm biomes and ecoregions. Positive values of NRI and NTI indicate that co-occurring species in bat communities are phylogenetically related in relationship to a given geographical extent, whereas negative values of NRI and NTI are indicative of phylogenetic evenness in relationship to that geographical extent. Boxes represent interquartile ranges, with the upper edge representing the 75th percentile, the middle line the median, and the lower edge the 25th percentile. Upper and lower whiskers represent values 1.5 times above and below the interquartile range, respectively. Black-filled circles represent outliers. Dotted horizontal lines represent the confidence interval (at 95% or ±1.96 units) for community phylogenetic structure. Within-realm geographical extents found to be significantly composed of phylogeneti-

2.4.2 Strong palaeoclimatic legacies restrict bat phylogenetic community structure across geographical extents (H_2)

Historical changes in both temperature and precipitation had strong and independent influences on the phylogenetic structure of bat communities (see Figure 2.3, Figure 2.4, Figure 2.5; Table 2.2). The relationship between historical change in climate (in temperature and in precipitation) and the phylogenetic relatedness of bat communities was highly nonlinear and spatial scale dependent (*i.e.*, it varied across geographical extents).

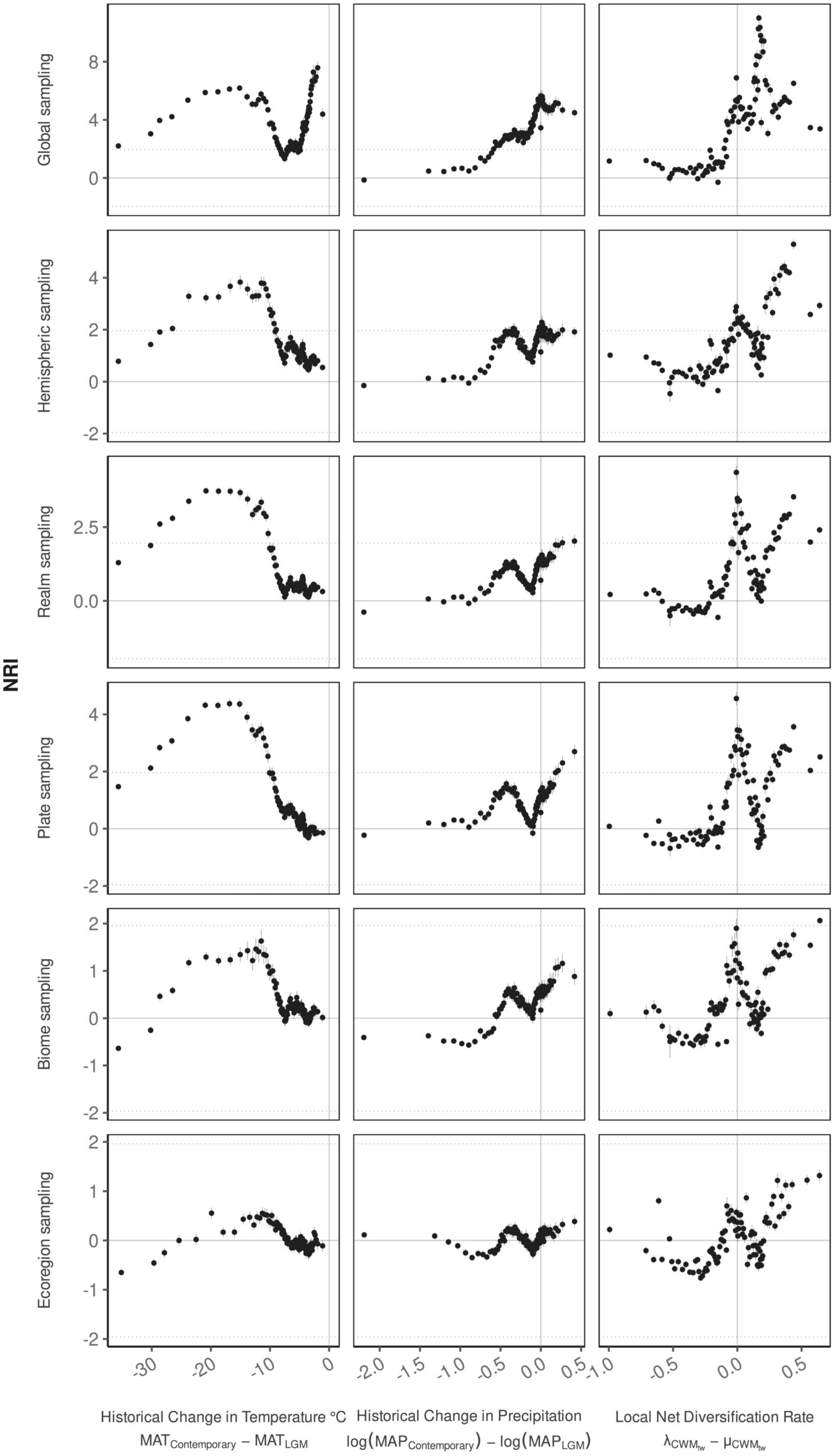
Historical stability in precipitation was consistently associated with increased phylogenetic relatedness in bat communities across all geographical extents, for both shallow (NTI) and overall (NRI) phylogenetic structures (Figure 2.3, Figure 2.4, Figure 2.5). The probability of a local community being composed of species with relatively high phylogenetic relatedness (*i.e.*, those belonging to the 90th percentile of phylogenetic relatedness) increased with historical precipitation (Figure 2.5; Table 2.2), regardless of geographical extent.

The effects of historical stability in temperature on bat community phylogenetic relatedness varied strongly across geographical extents. At the global extent, bat communities located in regions that were much colder in relationship to the contemporary period showed a general lack of phylogenetic clustering (Figure 2.3, Figure 2.4). At this geographical extent, the probability of a local community being composed of species with relatively high phylogenetic relatedness increased with historical precipitation (see Figure 2.5; Table 2.2). However, in all other geographical extents, phylogenetic structure weakened as a function of historical stability in temperature (see Figure 2.5; Table 2.2). Climate change velocities had, in general, qualitatively similar effects to their corresponding measures of historical change in climate on the phylogenetic relatedness of bat communities across geographical scales (Supporting Information in Section 2.9, Figure 2.11, Figure 2.12, Figure 2.13; Table 2.7).

These strong effects of palaeoclimatic legacies on the phylogenetic relatedness of bat communities support our prediction that regional communities located in palaeoclimatically stable regions contain more phylogenetically clustered assemblages than regions that underwent large fluctuations in climate between geological periods (hypothesis H_2), but the magnitude of effects depended on the variable and on the geographical scale.

2.4.3 *In situ* net diversification increases phylogenetic clustering in bat communities (H_3)

In situ net diversification strongly drove the contemporary phylogenetic structure of world-wide bat communities across all geographical extents (Figure 2.3, Figure 2.4, Figure 2.5; Table 2.2). The average values of NRI and NTI generally increased across the percentiles of community-weighted means of local net diversification rates in bat communities (Figure 2.3, Figure 2.4). In bat communities exhibiting high phylogenetic relatedness (at the 90th percentile), increases in community-weighted means of local net diversification rates were always associated with increases in NRI and NTI, independently from historical changes in temperature and in precipitation (Figure 2.5; Table 2.2). Taken together, these results corroborate the expectation that increased local diversification rates lead to more phylogenetically clustered communities (hypothesis H_3).



NRI
Global sampling
Hemispheric sampling
Realm sampling
Plate sampling
Biome sampling
Ecoregion sampling
8
4
0
-2
2
2.5
0.0
1
-1
-30
-20
-10
0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
-1.0
-0.5
0.0
0.5
Historical Change in Temperature °C
$MAT_{Contemporary} - MAT_{LGM}$
Historical Change in Precipitation
$\log(MAP_{Contemporary}) - \log(MAP_{LGM})$
Local Net Diversification Rate
$\lambda_{CWM_{tw}} - \mu_{CWM_{tw}}$

Figure 2.3 *(preceding page)*: **Average net relatedness index (NRI) of bat communities across percentiles of historical change in temperature, historical change in precipitation and in situ net diversification rates across geographical extents**. In situ net diversification rates were obtained from the differences between community-weighted means weight standardized for speciation (λ) and extinction (μ) rates. Palaeoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago. Vertical bars on points represent the mean ± 1.96 times the SE for the percentile of NRI. Dotted horizontal lines represent the confidence interval (at 95% or ±1.96 units) of NRI.

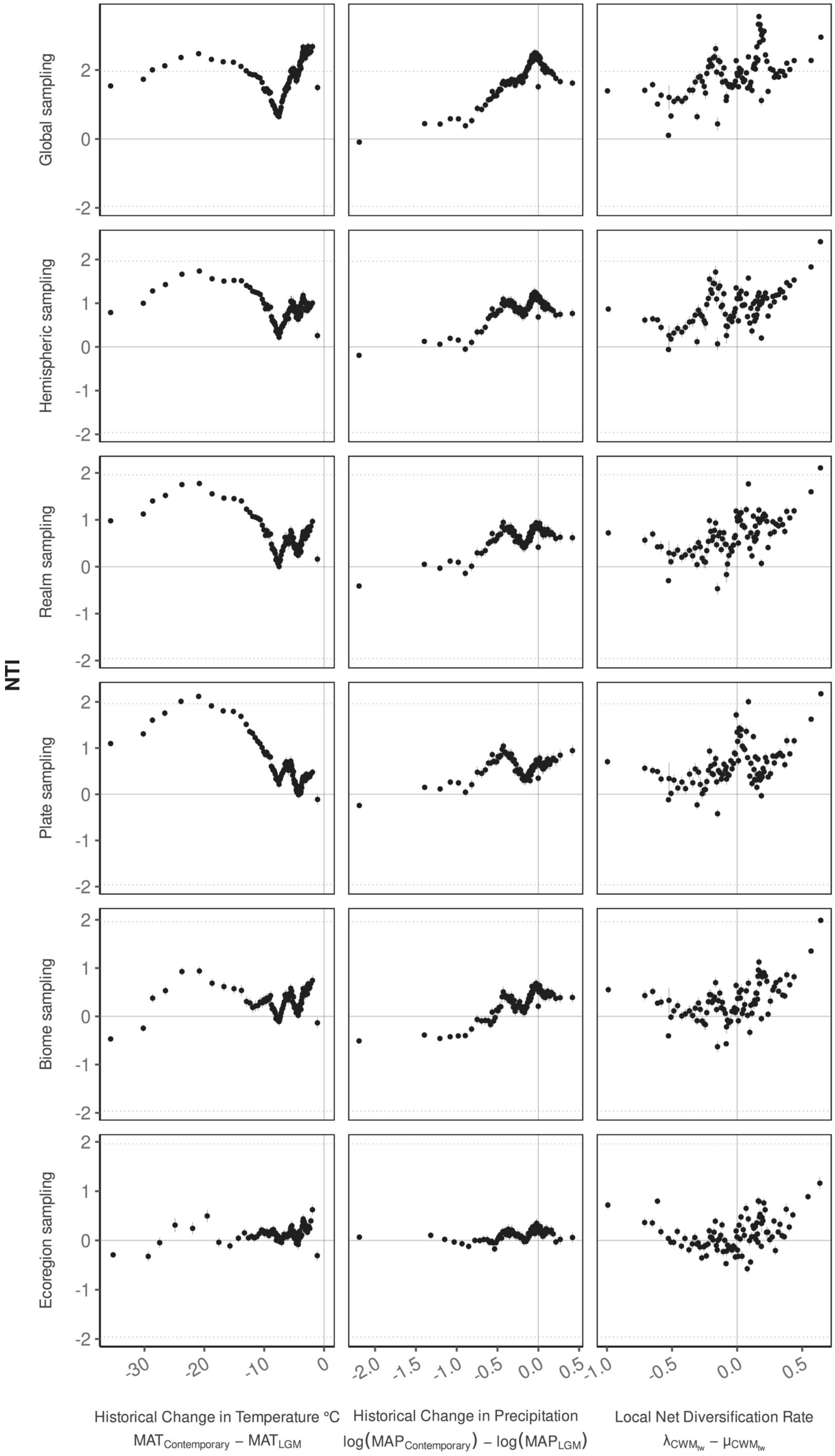

NTI
Global sampling
Hemispheric sampling
Realm sampling
Plate sampling
Biome sampling
Ecoregion sampling
2
1
0
-1
-2
-30
-20
-10
0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
-1.0
-0.5
0.0
0.5
Historical Change in Temperature °C
$MAT_{Contemporary} - MAT_{LGM}$
Historical Change in Precipitation
$\log(MAP_{Contemporary}) - \log(MAP_{LGM})$
Local Net Diversification Rate
$\lambda_{CWM_{tw}} - \mu_{CWM_{tw}}$

Figure 2.4 *(preceding page)*: **Average nearest taxon index (NTI) of bat communities across the percentiles of historical change in temperature, historical change in precipitation and in situ net diversification rates across geographical extents.** *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight standardized for speciation (λ) and extinction (μ) rates. Palaeoclimatic legacies for each bat community were obtained as the historical change in climate since the Last Glacial Maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago. Vertical bars on points represent the mean ± 1.96 times the SE for the percentile of NTI. Dotted horizontal lines represent the confidence interval (at 95% or ±1.96 units) of NTI.

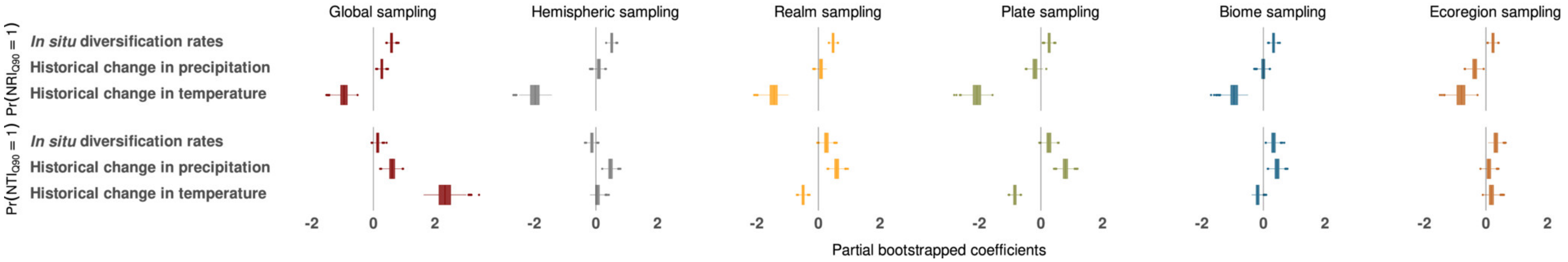


Figure 2.5: **Influence of historical legacies on phylogenetic structure of bats across different geographical extents.** Distributions represent boxplots of bootstrapped logistic regression coefficients using binary outcomes (at the 90th percentile) for the indices of phylogenetic community relatedness [Pr(NRIQ90=1) and Pr(NTIQ90=1)] as response variables (in separate models) and the z-score standardized (with values transformed to have a mean of zero and one-unit variance) historical change in temperature, historical change in precipitation and in situ net diversification rates as predictive variables. The phylogenetic structure of bat communities was measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. In situ net diversification rates were obtained by subtracting the difference between community-weighted means weight standardized for speciation and extinction rates. Palaeoclimatic legacies for each bat community were obtained as the historical change in climate since the Last Glacial Maximum (LGM); specifically, the mean annual temperature or logarithm of the mean annual precipitation from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago.

2.5 Discussion

Our results provide evidence that geographical scales, palaeoclimatic legacies and variation in the *in situ* diversification rates contributed differently to the phylogenetic structure of bat communities world-wide. The framework we present here should be useful while studying any taxa, regardless of their geographical distribution and not only for the case of the widely distributed bats.

2.5.1 Effects of geographical extent restriction on phylogenetic community structure (H_1)

The general tendency for co-occurring bats in local assemblages to be less evolutionarily related when restricting geographical extents revealed the existence of strong effects of long-term spatial and environmental isolation and within-region diversification in the assembly of bat communities (hypothesis H_1). How phylogenetic community structure responded to the gradient in geographical extent restriction varied between both metrics (NRI and NTI) and across different realms (Figure 2.1 and Figure 2.2; Supporting Information in Section 2.7, Table 2.3). As discussed next, this variation suggests that realms vary historically either in the challenges and opportunities they provided for immigration or in the lack of time for dispersal to overcome historically challenging geographical and environmental barriers (Losos & Glor 2003; Svenning & Skov 2004).

The incongruency in the phylogenetic structuring patterns among the New World and Old World adjacent realms (Figure 2.2) indicates the role of distinctive historical evolutionary processes in the regional formation of assemblages. Primarily, the separation between the Old World and New World is a strong longitudinal barrier for dispersal in many taxa [including bats; Procheş (2006)] and has been associated with differences in biogeographical histories and contemporary diversity patterns (Davies & Buckley 2012; Peixoto *et al.* 2014). Moreover, despite the existence of geological and historical climatic barriers between the adjacent Old World realms [*i.e.*, the Himalayan chain, and the African and Arabian deserts; Edgell (2006); Matthews *et al.* (2016); Zhang *et al.* (2014)], the increased vagility to overcome barriers through flight probably allowed for continuous historical dispersal and establishment of major bat lineages among these regions, contributing to the decreased and less differentiated broader phylogenetic structure of bat communities (Procheş & Ramdhani 2013; see Gerhold *et al.* 2015).

Nearctic bat assemblages are more phylogenetically clustered in relationship to the hemispheric, realm and plate spatial extents. However, this was not the case for Neotropical bat communities (Figure 2.2). The absence of phylogenetically structured Neotropical bat assemblages (in relationship to the New World geographical scale) is aligned with the lack of dispersal limitation, whereas the predominance of phylogenetically structured Nearctic bat assemblages highlights the existence of distinct biogeographical mechanisms allowing for more structured assemblages in relationship to the Neotropics. The existence of long-term geological barriers for southward (or even bidirectional) cross-realm sustained dispersal of New World bat clades has been disputed (Arita *et al.* 2014; Rojas *et al.* 2016; Alroy 2019). First, Palaeogene fossils of noctilionoid, molossid and emballonurid bats found in the Nearctic support the case that bats were not greatly affected by the historical isolation between North and South America before the rise of the isthmus of Panama (*c.* 3 Ma) and the Great American Biotic Interchange (Procheş 2006; López-Aguirre *et al.* 2018). Second, Nearctic and Neotropical bat species pools present low phylogenetic turnover rates (Peixoto *et al.* 2014). The distinctive phylogenetic structure patterns of Nearctic bat communities could be explained by the combination of the following factors: (1) the predominance of basal lineages in the Nearctic realm and more derived bat lineages in the Neotropics (Ramos Pereira & Palmeirim 2013); (2) multiple diversification events in the bat evolutionary history across both realms (Arita *et al.* 2014); and (3) the evolutionary conservatism of climatic preferences among bat clades occurring in the Nearctic (Peixoto *et al.* 2017).

2.5.2 Palaeoclimatic stability shapes phylogenetic community structure (H_2)

Palaeoclimatic changes driven by glacial–interglacial transitions from warm to cold phases are expected to decrease the phylogenetic relatedness of biological communities through changes in colonization and diversification dynamics (*e.g.*, Dynesius & Jansson 2000; Normand *et al.* 2011; Kissling *et al.* 2012; Eiserhardt *et al.* 2015; Xu *et al.* 2020). Palaeoclimatically stable regions, on the contrary, are thought to enable the long-term persistence and accumulation of species and thus allow for increased phylogenetic relatedness (Svenning & Skov 2007). We show that since the LGM, historical stability in both temperature and precipitation has had strong and independent influences on the present-day phylogenetic structure of bat communities. Importantly, our study reveals that these effects of palaeoclimatic stability on bat communities can exhibit high spatial scale dependence.

On the one hand, historical stability in precipitation had the clearest and most consistent effects on the phylogenetic relatedness of bat communities, whereby it strongly favoured phylogenetic clustering (especially in the gradient of the most phylogenetically related communities), regardless of geographical extent (Figure 2.3, Figure 2.4, Figure 2.5; Table 2.2). The strong effect of precipitation stability is consistent with previous observations for higher intraspecific genetic diversity, phylogenetic diversity, taxonomic diversity and phylogenetic relatedness across spatial scales and spatial extents in a broad range of taxa, such as plants, terrestrial mammals and bats (*e.g.*, Rowan *et al.* 2020; Theodoridis *et al.* 2020). Bats are sensitive to precipitation levels, with drought causing direct water balance stress and physiological stress and changing their energy costs and phenology (Adams 2010; Frick *et al.* 2012; Geipel *et al.* 2019; Piccioli Cappelli *et al.* 2021). Indirectly, drought can also modulate bat feeding resources [*i.e.*, by changing the abundance or flight activity of insects or the distribution of angiosperms, and thus their availability to bats; Anthony *et al.* (1981); Bush *et al.* (2004)], and therefore, presumably, cause variation in trophic guilds to adapt to changing conditions (Voigt *et al.* 2011; Stevens 2013; Pettit & O'Keefe 2017).

On the other hand, temperature stability since the LGM was associated with strong increases in phylogenetic relatedness, but only at the broadest, global geographical extent. These effects we observed in bats coincide with similar effects of recent climatic cooling found in many taxa, including beetles (Calatayud *et al.* 2019), vascular plants (Mienna *et al.* 2020) and angiosperms (Ma *et al.* 2016). Interestingly, at the more restrictive geographical extents, historical stability in temperature was even associated with marginal decreases in the phylogenetic relatedness of bat communities. Multiple factors can explain the decreased phylogenetic clustering in bats observed in regions with a historically stable climate, and at the more restrictive geographical scales, such as with the presence of old lineages, lags in niche filling and recolonization dynamics, recent diversification pulses sustained by the long-term stability, within-clade competition and increased regional extinction rates (Gerhold *et al.* 2015; Svenning *et al.* 2015). For instance, at the global geographical scale, clades could have been selected in relationship to historical temperature changes, but at more restrictive, smaller geographical scales, community-wide adaptive responses to palaeoclimate change could have been more phylogenetically widespread, favouring the long-term establishment and diversification of well-adapted related taxa (Maguire *et al.* 2016; Carstens *et al.* 2018; Williams & Blois 2018). Moreover, these effects could also have been buffered by the adaptation of bats to other feeding resources, glacial refugia and postglacial colonization dynamics and/or hindered by relatively increased influence of historical changes in temperature in the phylogenetic structuring of bat assemblages.

Table 2.2: **Influence of climatic legacies and *in situ* diversification rates on the phylogenetic structure of bat communities across different geographical extents**

Response	**Predictor**	**Global sampling**	**Hemispheric sampling**	**Realm sampling**	**Plate sampling**	**Biome sampling**	**Ecoregion sampling**
Pr(NRI(Q90) = 1)	Intercept	-3.45 (-3.69; -3.20)	-2.63 (-2.83; -2.43)	-3.60 (-3.89; -3.32)	-3.34 (-3.60; -3.09)	-2.67 (-2.87; -2.46)	-2.56 (-2.75; -2.37)
	Historical change in temperature	1.05 (0.56; 1.55)	-0.40 (-0.51; -0.30)	-1.61 (-1.85; -1.37)	-1.57 (-1.80; -1.33)	-0.63 (-0.75; -0.52)	-0.33 (-0.45; -0.21)
	Historical change in precipitation	1.10 (0.80; 1.40)	0.76 (0.53; 0.99)	2.48 (2.13; 2.83)	2.28 (1.93; 2.63)	1.12 (0.86; 1.37)	0.39 (0.14; 0.64)
	In situ diversification rates	1.33 (1.19; 1.46)	0.93 (0.73; 1.13)	0.97 (0.75; 1.19)	0.65 (0.50; 0.81)	0.73 (0.51; 0.96)	0.92 (0.72; 1.12)
Pr(NTI(Q90) = 1)	Intercept	-4.20 (-4.60; -3.80)	-2.48 (-2.66; -2.30)	-2.52 (-2.69; -2.34)	-2.70 (-2.87; -2.52)	-2.42 (-2.58; -2.26)	-2.29 (-2.43; -2.14)
	Historical change in temperature	2.72 (2.00; 3.44)	-0.02 (-0.18; 0.14)	-0.61 (-0.72; -0.49)	-0.95 (-1.12; -0.78)	-0.49 (-0.60; -0.37)	-0.07 (-0.21; 0.07)
	Historical change in precipitation	0.90 (0.55; 1.25)	0.89 (0.69; 1.09)	1.10 (0.85; 1.34)	1.48 (1.20; 1.77)	1.07 (0.87; 1.27)	0.54 (0.36; 0.72)
	In situ diversification rates	1.30 (1.16; 1.44)	0.44 (0.27; 0.60)	0.29 (0.13; 0.45)	0.21 (0.06; 0.36)	0.11 (-0.03; 0.25)	0.20 (0.02; 0.38)

Overall, the patterns we observed support our prediction that climatically stable regions should harbour more phylogenetically clustered assemblages than regions that have undergone large climatic fluctuations during geological times (hypothesis H_2). These findings are consistent with the increasing evidence of glacial extinction dynamics and postglacial colonization lags in bats and in the main woodland taxa that provide them with foraging and roosting habitats [McLachlan *et al.* (2005); Rebelo *et al.* (2012). However, the importance of climatic legacies to the phylogenetic structure of bat assemblages was not uniform and varied across spatial scales, being in accordance with previous research affirming the role of large-scale palaeoclimatic legacies in driving both local-scale community patterns and assembly processes (see Svenning *et al.* 2015).

2.5.3 Influence of *in situ* net diversification rates on phylogenetic community structure (H_3)

The increase in both deep (NRI) and shallow (NTI) scales of phylogenetic relatedness in bat assemblages with increasing quantiles of local net diversification rates (Figure 2.3, Figure 2.4, Figure 2.5), regardless of spatial extent, is consistent with the expectation that biogeographical patterns of phylogenetic clustering are driven by spatial variation in net diversification rates (hypothesis H_3). This corroborates the well-known expectation that *in situ* net diversification is a fundamental component of the phylogenetic structuring of biological communities (Emerson & Gillespie 2008). Although support for this expectation is often inferred from heuristic associations between physical and bioclimatic geographical characteristics and phylogenetic community structure metrics (Webb *et al.* 2002), the direct association between *in situ* diversification rates and phylogenetic community structure has rarely been addressed explicitly (but see Eme *et al.* 2020), especially in a scale-dependent perspective. The extension of our reconstruction of net bat diversification rates across a geographical context provides a way to disentangle their contribution to the formation of phylogenetic patterns in their communities, while avoiding the potential caveat with failing to estimate variation in diversification rates from latent biogeographical drivers of speciation and extinction rates alone.

2.5.4 General implications

There is broad interest in assessing the phylogenetic structure of ecological communities from local to regional spatial scales and from ecological to evolutionary temporal scales (Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009). In line with a more integrative approach, we related the modern-day phylogenetic structure of bat assemblages to processes and mechanisms acting across geographical and historical scales, as explained by geological barriers and the tectonic arrangement of biogeographical regions, historical climatic stability and local diversification rates. We showed widespread effects of geographical extents in driving the phylogenetic assembly of ecological communities. However, the magnitude of these effects varied across different biogeographical realms and evolutionary scales, invoking a complicated historically and geographically contingent explanation for the assembly of bat communities. Future studies should investigate the extent to which these spatial scale-dependent patterns could be associated with the different functional, ecological adaptations and life-history strategies that bat clades possess. We add that during the post-glaciation period, colonization from refugia to colonizing regions might have been a major driving force shaping the phylogenetic structure of communities in relationship to *in situ* diversification. This highlights the role of recent historical events (such as the Quaternary ice age) rather than only deep-time evolutionary processes in leaving strong imprints in the evolutionary structure of biological communities. Further research should focus on estimating the time and location of ancestral ranges across bat communities and the contribution of environmental constraints and of the conservatism of environmental requirements to elucidate their contribution to the spatial structuring of bat lineages during glacial–interglacial cycles. Finally, we also showed that local diversification rates play a strong role in shaping assemblage structure. The integrative framework built in the present study, which can be applied to other taxonomic groups, has proved useful not only to further our knowledge about the evolutionary dynamics of species assemblages, but also to reveal the effects of historical dispersal limitations and thus, potentially, solve well-known problems related to scale dependence in community ecology and biogeography.

2.6 Supporting Information 1

2.6.1 Extended methods

2.6.1.1 Estimating species speciation and extinction rates and computing community-weighted means to obtain *in situ* net diversification rates

The Bayesian analyses for macroevolutionary mixtures (BAMM) were performed on the time-calibrated phylogenetic hypothesis containing the 953 bat-species available for this study. We performed BAMM runs for 50 million generations using default Metropolis-coupled Markov-chain Monte Carlo operators and relevant shift, speciation and extinction rates priors estimated under a pure birth model (Rabosky *et al.* 2014). Because BAMM has been criticized to be overly sensitive to the prior on the number of shifts (Moore *et al.* 2016), we evaluated the effect of different priors (1, 5 and 10) on the posterior distribution of the shifts, and ultimately did not find meaningful differences on the final results. We kept 1 prior expected shifts to facilitate model convergence (Mitchell & Rabosky 2017). Because incomplete taxon sampling can bias estimations of diversification rates (Pybus & Harvey 2000; Cusimano & Renner 2010), we accounted for missing taxa by incorporating genus-specific sampling fractions in the estimations (Table S2.3). We discarded the first 10% of each run as ‘burn-in’ and tested the distribution for convergence by computing the effective sample size in the number of evolutionary rate regimes. We then computed the mean of the marginal posterior distribution of speciation and extinction rates for each tip in the phylogeny across all sampled rate shift configurations, which were used to obtain community-weighted extinction and speciation means (see Methods).

2.6.1.2 Tools

All data manipulation and analyses were performed in R and RStudio (R Core Team 2021; RStudio Team 2021). Parallelized computations were done using `snowfall` and `doSNOW` (Knaus 2015; Corporation & Weston 2022). Geospatial manipulation was done using the `sf`, `raster`, `terra`, and `exactextractr` packages (Pebesma 2018; Hijmans 2021, 2022). Velocity of climate change, local spatial and long-term climatic gradients were calculated using the `VoCC` package (García Molinos *et al.* 2019). Phylogenetic manipulation and analyses were done using the packages `ape`, `picante`, `PhyloMeasures` and `phangorn` (Kembel *et al.* 2010; Schliep 2011; Tsirogiannis & Sandel 2016, 2017; Paradis & Schliep 2019). Diversification rate estimation and posterior manipulation were done using BAMM 2.5.0 and the `BAMMtools` package (Rabosky *et al.* 2014). Effective sizes and diagnostics for MCMC chains were performed using the `coda` package (Plummer *et al.* 2006). Robust analyses of variance for repeated measurements were performed using the `WRS2` package (Mair & Wilcox 2020). Robust generalized linear models were performed with the `robust` package (Wang *et al.* 2022). Quantile regressions were performed using the `quantreg` package (Koenker 2021). General data manipulation was done with the `tidyverse` package suite (Wickham *et al.* 2019). Figures were generated using the `ggplot2` package (Wickham 2016).

2.7 Supporting Information 2

Table 2.3: **Per realm averages for net relatedness index [NRI_{mean} (± NRI_{SD})] and nearest taxon index [NTI_{mean} (± NTI_{SD})] of bat communities for each spatial extent and geographical extent**. Within-realm geographical extents found to be significantly composed of phylogenetically related bat communities (with $p < 0.01$ in Stouffer's combined probability tests; see Methods in the main manuscript) are annotated with asterisks.

Spatial extent	Sampling Pool	Phylogenetic relatedness	
		NTI_{mean} (± NTI_{SD})	**NRI_{mean} (± NRI_{SD})**
Global	Global	1.79 (±1.36)*	3.54 (±3.99)*
Neotropical	Global	2.84 (±1.22)*	9.06 (±4.13)*
	Hemispheric	0.74 (±0.97)*	0.27 (±1.06)*
	Realm	0.75 (±0.99)*	0.02 (±0.97)
	Plate	0.21 (±0.88)*	-0.65 (±1.03)
	Biome	0.68 (±0.99)*	-0.17 (±1.02)
	Ecoregion	0.48 (±1.05)*	-0.24 (±1.08)
Nearctic	Global	2 (±0.74)*	5.38 (±2.38)*
	Hemispheric	1.11 (±0.81)*	1.83 (±1.09)*
	Realm	1.1 (±0.96)*	3.34 (±1.95)*
	Plate	1.59 (±0.86)*	3.66 (±1.89)*
	Biome	0.38 (±0.95)*	1.18 (±1.77)*
	Ecoregion	0.2 (±0.98)*	0.36 (±1.13)*
Afrotropical	Global	1.94 (±1.71)*	0.34 (±0.97)*
	Hemispheric	1.09 (±1.48)*	0.09 (±0.94)*
	Realm	0.43 (±1.02)*	0.06 (±0.85)
	Plate	0.23 (±0.94)*	-0.33 (±0.82)
	Biome	0.13 (±0.95)*	0.14 (±0.92)*
	Ecoregion	0.01 (±0.97)	-0.18 (±0.89)

Spatial extent	Sampling Pool	Phylogenetic relatedness	
Palearctic	Global	1.39 (±1.21)*	2.75 (±2.86)*
	Hemispheric	0.98 (±1.04)*	2.58 (±2.89)*
	Realm	0.79 (±1.12)*	1.08 (±1.55)*
	Plate	0.86 (±1.1)*	1.49 (±2)*
	Biome	0.36 (±1.16)*	0.45 (±1.36)*
	Ecoregion	0.06 (±0.95)*	0.15 (±1.08)*
Indomalay	Global	1 (±1.04)*	-0.1 (±1.44)
	Hemispheric	-0.15 (±1.05)	-0.46 (±1.44)
	Realm	-0.09 (±1.11)	-0.41 (±1.82)
	Plate	-0.1 (±1.19)	-1.03 (±1.23)
	Biome	-0.06 (±1.09)	-0.38 (±1.81)
	Ecoregion	0.14 (±1.03)*	-0.56 (±1.14)
Australasian	Global	1.44 (±0.7)*	3.69 (±2.08)*
	Hemispheric	0.67 (±0.79)*	3.26 (±1.99)*
	Realm	0.13 (±0.83)*	2.09 (±1.55)*
	Plate	0.02 (±0.85)*	1.9 (±1.41)*
	Biome	-0.11 (±0.88)	0.65 (±1.09)*
	Ecoregion	-0.17 (±0.92)	0.49 (±1.3)*

Table 2.4: **Summary statistics for per-realm tests on whether the net relatedness index or the nearest taxon index (response variables, in separate tests) of bat communities (dependent groups) differed across the discrete sampling pool restriction gradient (group-levels)**. Results reflect independent robust heteroscedastic repeated measurement analyses of variance based on 20% trimmed means and post-hoc comparisons using Hochberg's approach to control for family-wise error.

				NRI						**NTI**					
Realm	**Comparison**			$\widehat{\Psi}$	**CI$_{lower}$**	**CI$_{upper}$**	***P***	**P$_{crit}$**		$\widehat{\Psi}$	**CI$_{lower}$**	**CI$_{upper}$**	***P***	**P$_{crit}$**	
Neotropical	Global sampling	*vs.*	Hemispheric sampling	9.879	9.726	10.032	< 0.001	0.025	***	1.891	1.866	1.916	< 0.001	0.017	***
		vs.	Realm sampling	10.115	9.956	10.274	< 0.001	0.017	***	1.883	1.858	1.907	< 0.001	0.013	***
		vs.	Plate sampling	10.834	10.641	11.027	< 0.001	0.013	***	2.496	2.456	2.536	< 0.001	0.010	***
		vs.	Biome sampling	10.387	10.225	10.550	< 0.001	0.010	***	1.984	1.962	2.007	< 0.001	0.009	***
		vs.	Ecoregion sampling	10.277	10.081	10.473	< 0.001	0.009	***	2.406	2.364	2.447	< 0.001	0.007	***
	Hemispheric sampling	*vs.*	Realm sampling	0.241	0.235	0.247	< 0.001	0.007	***	0.004	0.002	0.006	< 0.001	0.025	***
		vs.	Plate sampling	1.089	1.063	1.116	< 0.001	0.006	***	0.684	0.671	0.698	< 0.001	0.006	***
		vs.	Biome sampling	0.550	0.540	0.559	< 0.001	0.006	***	0.060	0.050	0.069	< 0.001	0.006	***

				NRI						**NTI**					
		vs.	Ecoregion sampling	0.561	0.521	0.600	< 0.001	0.005	***	0.616	0.592	0.640	< 0.001	0.005	***
	Realm sampling	*vs.*	Plate sampling	0.856	0.836	0.876	< 0.001	0.005	***	0.693	0.678	0.708	< 0.001	0.005	***
		vs.	Biome sampling	0.264	0.259	0.269	< 0.001	0.004	***	0.060	0.050	0.069	< 0.001	0.004	***
		vs.	Ecoregion sampling	0.330	0.295	0.365	< 0.001	0.004	***	0.610	0.586	0.634	< 0.001	0.004	***
	Plate sampling	*vs.*	Biome sampling	-0.572	-0.592	-0.553	< 0.001	0.004	***	-0.515	-0.538	-0.492	< 0.001	0.004	***
		vs.	Ecoregion sampling	-0.428	-0.455	-0.400	< 0.001	0.003	***	0.003	-0.020	0.025	0.729	0.050	
	Biome sampling	*vs.*	Ecoregion sampling	0.076	0.044	0.108	< 0.001	0.050	***	0.429	0.399	0.460	< 0.001	0.003	***
Nearctic	Global sampling	*vs.*	Hemispheric sampling	3.563	3.478	3.648	< 0.001	0.050	***	0.812	0.804	0.820	< 0.001	0.050	***
		vs.	Realm sampling	1.826	1.784	1.868	< 0.001	0.025	***	0.822	0.805	0.840	< 0.001	0.025	***
		vs.	Plate sampling	1.614	1.574	1.654	< 0.001	0.017	***	0.428	0.420	0.436	< 0.001	0.017	***

			NRI							NTI					
	vs.	Biome sampling	4.118	4.031	4.205	< 0.001	0.013	***		1.479	1.460	1.498	< 0.001	0.013	***
	vs.	Ecoregion sampling	5.145	5.060	5.229	< 0.001	0.010	***		1.699	1.669	1.730	< 0.001	0.010	***
Hemispheric sampling	*vs.*	Realm sampling	-1.479	-1.524	-1.435	< 0.001	0.009	***		0.042	0.031	0.054	< 0.001	0.009	***
	vs.	Plate sampling	-1.677	-1.723	-1.632	< 0.001	0.007	***		-0.389	-0.391	-0.386	< 0.001	0.007	***
	vs.	Biome sampling	1.140	1.089	1.190	< 0.001	0.006	***		0.630	0.611	0.650	< 0.001	0.006	***
	vs.	Ecoregion sampling	1.731	1.685	1.778	< 0.001	0.006	***		0.868	0.831	0.905	< 0.001	0.006	***
Realm sampling	*vs.*	Plate sampling	-0.182	-0.194	-0.170	< 0.001	0.005	***		-0.435	-0.446	-0.424	< 0.001	0.005	***
	vs.	Biome sampling	2.270	2.178	2.361	< 0.001	0.005	***		0.617	0.590	0.644	< 0.001	0.005	***
	vs.	Ecoregion sampling	3.168	3.081	3.255	< 0.001	0.004	***		0.856	0.813	0.900	< 0.001	0.004	***
Plate sampling	*vs.*	Biome sampling	2.458	2.373	2.543	< 0.001	0.004	***		1.031	1.012	1.050	< 0.001	0.004	***

				NRI						NTI					
		vs.	Ecoregion sampling	3.351	3.264	3.438	< 0.001	0.004	***	1.255	1.219	1.291	< 0.001	0.004	***
	Biome sampling	*vs.*	Ecoregion sampling	0.620	0.572	0.668	< 0.001	0.003	***	0.159	0.126	0.191	< 0.001	0.003	***
Afrotropical	Global sampling	*vs.*	Hemispheric sampling	-0.149	-0.152	-0.145	< 0.001	0.050	***	0.049	0.047	0.051	< 0.001	0.050	***
		vs.	Realm sampling	0.158	0.153	0.162	< 0.001	0.025	***	1.138	1.109	1.166	< 0.001	0.025	***
		vs.	Plate sampling	0.540	0.519	0.561	< 0.001	0.017	***	1.271	1.237	1.306	< 0.001	0.017	***
		vs.	Biome sampling	0.063	0.059	0.068	< 0.001	0.013	***	1.462	1.422	1.503	< 0.001	0.013	***
		vs.	Ecoregion sampling	0.401	0.375	0.428	< 0.001	0.010	***	1.646	1.590	1.702	< 0.001	0.010	***
	Hemispheric sampling	*vs.*	Realm sampling	0.322	0.315	0.329	< 0.001	0.009	***	1.087	1.058	1.115	< 0.001	0.009	***
		vs.	Plate sampling	0.692	0.669	0.715	< 0.001	0.007	***	1.216	1.182	1.251	< 0.001	0.007	***
		vs.	Biome sampling	0.226	0.221	0.232	< 0.001	0.006	***	1.413	1.372	1.453	< 0.001	0.006	***

				NRI						NTI					
		vs.	Ecoregion sampling	0.560	0.531	0.589	< 0.001	0.006	***	1.593	1.537	1.649	< 0.001	0.006	***
	Realm sampling	*vs.*	Plate sampling	0.403	0.386	0.421	< 0.001	0.005	***	0.169	0.162	0.176	< 0.001	0.005	***
		vs.	Biome sampling	-0.071	-0.075	-0.066	< 0.001	0.005	***	0.321	0.310	0.332	< 0.001	0.005	***
		vs.	Ecoregion sampling	0.257	0.234	0.279	< 0.001	0.004	***	0.506	0.477	0.536	< 0.001	0.004	***
	Plate sampling	*vs.*	Biome sampling	-0.449	-0.468	-0.429	< 0.001	0.004	***	0.158	0.149	0.166	< 0.001	0.004	***
		vs.	Ecoregion sampling	-0.103	-0.120	-0.087	< 0.001	0.004	***	0.361	0.336	0.386	< 0.001	0.004	***
	Biome sampling	*vs.*	Ecoregion sampling	0.331	0.306	0.355	< 0.001	0.003	***	0.197	0.175	0.219	< 0.001	0.003	***
Palearctic	Global sampling	*vs.*	Hemispheric sampling	-0.079	-0.083	-0.076	< 0.001	0.050	***	0.010	0.009	0.012	< 0.001	0.050	***
		vs.	Realm sampling	1.463	1.423	1.503	< 0.001	0.025	***	0.774	0.767	0.782	< 0.001	0.025	***
		vs.	Plate sampling	1.193	1.154	1.232	< 0.001	0.017	***	0.696	0.680	0.711	< 0.001	0.017	***

			NRI						NTI					
	vs.	Biome sampling	2.033	1.975	2.091	< 0.001	0.013	***	1.040	1.025	1.055	< 0.001	0.013	***
	vs.	Ecoregion sampling	2.268	2.192	2.345	< 0.001	0.010	***	1.313	1.275	1.352	< 0.001	0.010	***
Hemispheric sampling	*vs.*	Realm sampling	1.531	1.490	1.573	< 0.001	0.009	***	0.774	0.767	0.781	< 0.001	0.009	***
	vs.	Plate sampling	1.272	1.230	1.314	< 0.001	0.007	***	0.685	0.670	0.700	< 0.001	0.007	***
	vs.	Biome sampling	2.102	2.042	2.162	< 0.001	0.006	***	1.023	1.008	1.037	< 0.001	0.006	***
	vs.	Ecoregion sampling	2.333	2.254	2.412	< 0.001	0.006	***	1.311	1.273	1.349	< 0.001	0.006	***
Realm sampling	*vs.*	Plate sampling	-0.356	-0.367	-0.346	< 0.001	0.005	***	-0.094	-0.098	-0.089	< 0.001	0.005	***
	vs.	Biome sampling	0.434	0.418	0.451	< 0.001	0.005	***	0.214	0.207	0.220	< 0.001	0.005	***
	vs.	Ecoregion sampling	0.783	0.741	0.825	< 0.001	0.004	***	0.542	0.511	0.574	< 0.001	0.004	***
Plate sampling	*vs.*	Biome sampling	0.789	0.760	0.818	< 0.001	0.004	***	0.323	0.315	0.330	< 0.001	0.004	***

				NRI						NTI					
		vs.	Ecoregion sampling	0.954	0.907	1.001	< 0.001	0.004	***	0.549	0.522	0.576	< 0.001	0.004	***
	Biome sampling	*vs.*	Ecoregion sampling	0.135	0.107	0.162	< 0.001	0.003	***	0.102	0.076	0.128	< 0.001	0.003	***
Indomalaya	Global sampling	*vs.*	Hemispheric sampling	-0.099	-0.102	-0.095	< 0.001	0.017	***	0.068	0.064	0.072	< 0.001	0.025	***
		vs.	Realm sampling	0.496	0.474	0.518	< 0.001	0.013	***	1.635	1.613	1.658	< 0.001	0.017	***
		vs.	Plate sampling	0.888	0.831	0.946	< 0.001	0.010	***	1.407	1.347	1.466	< 0.001	0.013	***
		vs.	Biome sampling	0.493	0.468	0.518	< 0.001	0.009	***	1.712	1.682	1.743	< 0.001	0.010	***
		vs.	Ecoregion sampling	0.479	0.425	0.532	< 0.001	0.007	***	1.330	1.258	1.403	< 0.001	0.009	***
	Hemispheric sampling	*vs.*	Realm sampling	0.578	0.554	0.601	< 0.001	0.006	***	1.563	1.541	1.584	< 0.001	0.007	***
		vs.	Plate sampling	1.000	0.941	1.058	< 0.001	0.006	***	1.334	1.274	1.393	< 0.001	0.006	***
		vs.	Biome sampling	0.579	0.552	0.606	< 0.001	0.005	***	1.643	1.614	1.672	< 0.001	0.006	***

				NRI						**NTI**					
		vs.	Ecoregion sampling	0.585	0.529	0.641	< 0.001	0.005	***	1.257	1.186	1.328	< 0.001	0.005	***
	Realm sampling	*vs.*	Plate sampling	0.223	0.158	0.288	< 0.001	0.004	***	-0.131	-0.171	-0.090	< 0.001	0.005	***
		vs.	Biome sampling	-0.015	-0.019	-0.011	< 0.001	0.004	***	0.104	0.096	0.112	< 0.001	0.004	***
		vs.	Ecoregion sampling	-0.135	-0.193	-0.077	< 0.001	0.050	***	-0.268	-0.320	-0.217	< 0.001	0.004	***
	Plate sampling	*vs.*	Biome sampling	-0.207	-0.265	-0.149	< 0.001	0.004	***	0.038	-0.002	0.077	0.006	0.050	**
		vs.	Ecoregion sampling	-0.452	-0.476	-0.428	< 0.001	0.003	***	-0.163	-0.194	-0.132	< 0.001	0.004	***
	Biome sampling	*vs.*	Ecoregion sampling	-0.138	-0.190	-0.087	< 0.001	0.025	***	-0.203	-0.249	-0.157	< 0.001	0.003	***
Australasia	Global sampling	*vs.*	Hemispheric sampling	-0.232	-0.246	-0.219	< 0.001	0.050	***	0.085	0.082	0.088	< 0.001	0.013	***
		vs.	Realm sampling	1.364	1.340	1.387	< 0.001	0.025	***	1.399	1.382	1.415	< 0.001	0.010	***
		vs.	Plate sampling	1.502	1.475	1.529	< 0.001	0.017	***	1.551	1.528	1.574	< 0.001	0.009	***

			NRI							NTI					
	vs.	Biome sampling	2.530	2.463	2.597	< 0.001	0.013	***		1.614	1.588	1.640	< 0.001	0.007	***
	vs.	Ecoregion sampling	3.081	2.977	3.184	< 0.001	0.010	***		1.774	1.732	1.816	< 0.001	0.006	***
Hemispheric sampling	*vs.*	Realm sampling	1.590	1.564	1.616	< 0.001	0.009	***		1.318	1.301	1.335	< 0.001	0.006	***
	vs.	Plate sampling	1.745	1.713	1.778	< 0.001	0.007	***		1.472	1.448	1.496	< 0.001	0.005	***
	vs.	Biome sampling	2.804	2.734	2.875	< 0.001	0.006	***		1.532	1.504	1.561	< 0.001	0.005	***
	vs.	Ecoregion sampling	3.329	3.223	3.436	< 0.001	0.006	***		1.694	1.653	1.734	< 0.001	0.004	***
Realm sampling	*vs.*	Plate sampling	0.139	0.128	0.149	< 0.001	0.005	***		0.169	0.162	0.176	< 0.001	0.004	***
	vs.	Biome sampling	1.146	1.090	1.201	< 0.001	0.005	***		0.170	0.152	0.187	< 0.001	0.004	***
	vs.	Ecoregion sampling	1.747	1.662	1.833	< 0.001	0.004	***		0.293	0.253	0.333	< 0.001	0.003	***
Plate sampling	*vs.*	Biome sampling	1.074	1.015	1.132	< 0.001	0.004	***		0.010	0.000	0.020	0.005	0.050	**

				NRI						NTI					
		vs.	Ecoregion sampling	1.649	1.570	1.728	< 0.001	0.004	***	0.116	0.074	0.158	< 0.001	0.017	***
	Biome sampling	*vs.*	Ecoregion sampling	0.286	0.235	0.336	< 0.001	0.003	***	0.044	0.003	0.086	0.002	0.025	**
*p < 0.05; **p < 0.01; ***p < 0.001															

Table 2.5: **Sampling proportions at the genus-level used to account for missing taxa when estimating speciation and extinction rates in BAMM**. The sampling fraction for each genus was calculated by dividing the number of species included in the final phylogeny used in this study by the number of species available within the American Society of Mammalogists (ASM) Mammal Diversity Database (Burgin *et al.*, 2018; Mammal Diversity Database, 2021).

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Acerodon	4	5	80.00 %
Aethalops	2	2	100.00 %
Alionycteris	1	1	100.00 %
Ametrida	1	1	100.00 %
A morphochilus	1	1	100.00 %
Anoura	6	10	60.00 %
Anthops	1	1	100.00 %
Antrozous	1	1	100.00 %
Arielulus	3	5	60.00 %
Ariteus	1	1	100.00 %
Artibeus	10	11	90.91 %
Asellia	2	4	50.00 %
Aselliscus	2	3	66.67 %
Austronomus	2	2	100.00 %
Balantiopteryx	3	3	100.00 %
Balionycteris	1	1	100.00 %
Barbastella	2	5	40.00 %
Bauerus	1	1	100.00 %
Brachyphylla	2	2	100.00 %
Cardioderma	1	1	100.00 %
Carollia	6	9	66.67 %
Casinycteris	1	3	33.33 %
Centronycteris	2	2	100.00 %
Centurio	1	1	100.00 %
Chaerephon	15	21	71.43 %
Chalinolobus	7	7	100.00 %
Cheiromeles	2	2	100.00 %
Chilonatalus	2	3	66.67 %
Chiroderma	4	6	66.67 %
Chironax	1	1	100.00 %
Choeroniscus	3	3	100.00 %
Choeronycteris	1	1	100.00 %
Chrotopterus	1	1	100.00 %
Cloeotis	1	1	100.00 %

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Coelops	2	2	100.00 %
Coleura	1	3	33.33 %
Cormura	1	1	100.00 %
Corynorhinus	3	3	100.00 %
Craseonycteris	1	1	100.00 %
Cynomops	5	6	83.33 %
Cynopterus	7	7	100.00 %
Cyttarops	1	1	100.00 %
Dermanura	9	12	75.00 %
Desmodus	1	2	50.00 %
Diaemus	1	1	100.00 %
Diclidurus	3	4	75.00 %
Diphylla	1	1	100.00 %
Dobsonia	10	13	76.92 %
Dyacopterus	2	3	66.67 %
Ectophylla	1	1	100.00 %
Eidolon	2	2	100.00 %
Emballonura	7	8	87.50 %
Enchisthenes	1	1	100.00 %
Eonycteris	3	3	100.00 %
Epomophorus	7	10	70.00 %
Epomops	3	2	100.00 %
Eptesicus	17	28	60.71 %
Erophylla	2	2	100.00 %
Euderma	1	1	100.00 %
Eumops	10	17	58.82 %
Falsistrellus	5	5	100.00 %
Furipterus	1	1	100.00 %
Glauconycteris	8	11	72.73 %
Glischropus	1	4	25.00 %
Glossophaga	5	5	100.00 %
Glyphonycteris	3	3	100.00 %
Haplonycteris	1	1	100.00 %
Harpiocephalus	1	1	100.00 %
Harpiola	1	2	50.00 %
Harpyionycteris	2	2	100.00 %
Hesperoptenus	4	5	80.00 %
Hipposideros	58	80	72.50 %
Histiotus	7	8	87.50 %
Hylonycteris	1	1	100.00 %
Hypsignathus	1	1	100.00 %

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Ia	1	1	100.00 %
Idionycteris	1	1	100.00 %
Kerivoula	19	24	79.17 %
Laephotis	4	4	100.00 %
Lampronycteris	1	1	100.00 %
Lasionycteris	1	1	100.00 %
Lasiurus	15	19	78.95 %
Latidens	1	1	100.00 %
Lavia	1	1	100.00 %
Leptonycteris	3	3	100.00 %
Lichonycteris	1	1	100.00 %
Lionycteris	1	1	100.00 %
Lissonycteris	1	4	25.00 %
Lonchophylla	7	16	43.75 %
Lonchorhina	5	6	83.33 %
Lophostoma	5	7	71.43 %
Macroderma	1	1	100.00 %
Macroglossus	2	2	100.00 %
Macrophyllum	1	1	100.00 %
Macrotus	2	2	100.00 %
Megaderma	2	2	100.00 %
Megaerops	4	4	100.00 %
Megaloglossus	1	2	50.00 %
Melonycteris	3	3	100.00 %
Mesophylla	1	1	100.00 %
Micronycteris	8	11	72.73 %
Micropteropus	2	2	100.00 %
Mimetillus	1	1	100.00 %
Mimon	4	4	100.00 %
Molossops	4	4	100.00 %
Molossus	7	10	70.00 %
Monophyllus	1	2	50.00 %
Mops	15	17	88.24 %
Mormoops	2	2	100.00 %
Mormopterus	7	18	38.89 %
Mosia	1	1	100.00 %
Murina	12	38	31.58 %
Musonycteris	1	1	100.00 %
Myonycteris	2	5	40.00 %
Myopterus	2	2	100.00 %
Myotis	85	139	61.15 %

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Mystacina	1	2	50.00 %
Myzopoda	2	2	100.00 %
Nanonycteris	1	1	100.00 %
Natalus	5	8	62.50 %
Neonycteris	1	1	100.00 %
Neopteryx	1	1	100.00 %
Neoromicia	13	18	72.22 %
Noctilio	2	2	100.00 %
Notopteris	2	2	100.00 %
Nyctalus	7	8	87.50 %
Nycteris	14	16	87.50 %
Nycticeinops	1	1	100.00 %
Nycticeius	2	3	66.67 %
Nyctiellus	1	1	100.00 %
Nyctimene	14	15	93.33 %
Nyctinomops	4	4	100.00 %
Nyctophilus	7	16	43.75 %
Otomops	2	8	25.00 %
Otonycteris	1	2	50.00 %
Otopteropus	1	1	100.00 %
Paratriaenops	2	3	66.67 %
Paremballonura	2	2	100.00 %
Penthetor	1	1	100.00 %
Peropteryx	4	5	80.00 %
Philetor	1	1	100.00 %
Phoniscus	3	4	75.00 %
Phylloderma	1	1	100.00 %
Phyllonycteris	1	2	50.00 %
Phyllops	1	1	100.00 %
Phyllostomus	4	4	100.00 %
Pipistrellus	38	54	70.37 %
Platalina	1	1	100.00 %
Platymops	1	1	100.00 %
Platyrrhinus	15	21	71.43 %
Plecotus	10	19	52.63 %
Plerotes	1	1	100.00 %
Promops	2	3	66.67 %
Ptenochirus	2	2	100.00 %
Pteralopex	3	6	50.00 %
Pteronotus	6	15	40.00 %
Pteropus	36	66	54.55 %

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Pygoderma	1	1	100.00 %
Rhinolophus	66	103	64.08 %
Rhinonicteris	1	1	100.00 %
Rhinophylla	3	3	100.00 %
Rhinopoma	3	6	50.00 %
Rhogeessa	8	13	61.54 %
Rhynchonycteris	1	1	100.00 %
Rousettus	8	9	88.89 %
Saccolaimus	4	4	100.00 %
Saccopteryx	5	5	100.00 %
Sauromys	1	1	100.00 %
Scleronycteris	1	1	100.00 %
Scoteanax	1	1	100.00 %
Scotoecus	3	5	60.00 %
Scotomanes	1	1	100.00 %
Scotonycteris	2	3	66.67 %
Scotophilus	13	21	61.90 %
Scotorepens	4	4	100.00 %
Scotozous	1	1	100.00 %
Sphaerias	1	1	100.00 %
Sphaeronycteris	1	1	100.00 %
Stenoderma	1	1	100.00 %
Sturnira	12	23	52.17 %
Styloctenium	1	2	50.00 %
Syconycteris	2	3	66.67 %
Tadarida	8	8	100.00 %
Taphozous	14	14	100.00 %
Thoopterus	1	2	50.00 %
Thyroptera	4	5	80.00 %
Tomopeas	1	1	100.00 %
Tonatia	2	2	100.00 %
Trachops	1	1	100.00 %
Triaenops	2	4	50.00 %
Trinycteris	1	1	100.00 %
Tylonycteris	2	6	33.33 %
Uroderma	2	5	40.00 %
Vampyressa	3	5	60.00 %
Vampyriscus	3	3	100.00 %
Vampyrodes	1	2	50.00 %
Vampyrum	1	1	100.00 %
Vespadelus	9	9	100.00 %

Clade (Genus)	Species kept from Faurby & Svenning (2015)	Species within ASM	Sampling fraction
Vespertilio	2	2	100.00 %
Xeronycteris	1	1	100.00 %

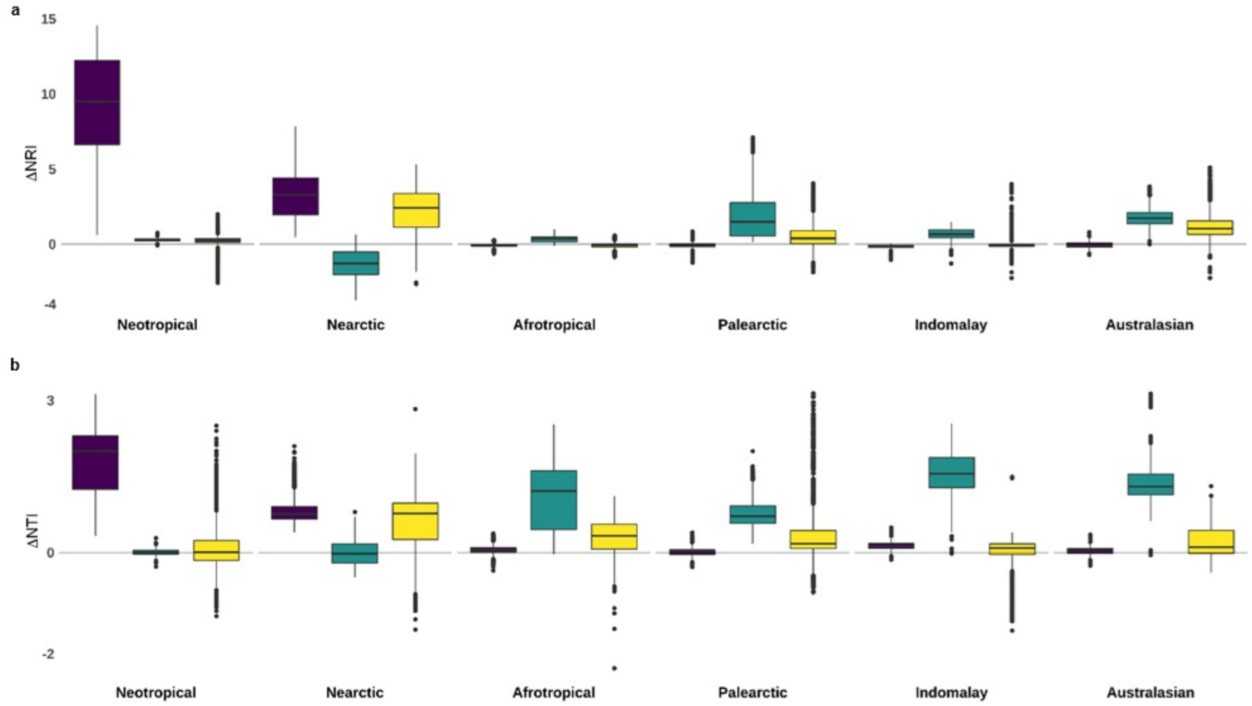


Figure 2.6: **Effects of species pool scaling on (a) NRI and (b) NTI within biogeographic realms**. Each bar represents the change in phylogenetic structure between the immediately restricted sampling and the broader sampling pools (*e.g.*, $\text{NRI}_{\text{global}} - \text{NRI}_{\text{hemispheric}}$). Values above 0 indicate stronger phylogenetic clustering with the geographically more extensive sampling pool.

2.8 Supporting Information 3

2.8.1 Adjusting for the artificial influence of geographical extent size on indices of community phylogenetic relatedness through rarefactions

The magnitude of standardized effect sizes of indices for phylogenetic community structure can artificially increase as a function of the geographical or phylogenetic extents (because of greater number of species in larger biogeographical regions) used to compute the null models pertinent to these metrics (Sandel 2018). This bias requires that studies comparing standardized effect sizes of phylogenetic relatedness between biological communities to assess whether these comparisons hold after adjusting for this problem. One possible approach to adjust for this potential bias is to repeatedly randomly subsample (*i.e.* rarefy) the community composition matrix to smaller geographical extent sizes, and then to calculate the average indices for phylogenetic community structure [here, the net relatedness index (NRI) and the nearest taxon index (NTI); see Methods] across the rarefied subset (see Sandel 2018). The resulting index from this procedure should show a negligible relationship with the size of the geographical extent or the phylogeny. Because the original size of the geographical extent is decreased, this correction comes at the expense of losing power intrinsic to the rarefaction procedure (Sandel 2018). The information from geographical extents that have less species than the size chosen for the subsampling procedure is also lost.

2.8.1.1 Implementation

We assessed whether our results held after adjusting for this potential bias by: (i) randomly subsampling (rarefying) the community presence-absence matrix to the lowest species richness of the geographical extent of the subsequently nested region (up to a minimum of 10 species); (ii) calculating the indices for phylogenetic community structure at this subsampled data; (iii) repeating the previous procedures 1,000 times and calculating the average rarefied net relatedness index and nearest taxon indices ($\mathsf{NRI}_{\mathsf{raref}}$ and $\mathsf{NTI}_{\mathsf{raref}}$) across the rarefied data sets; and, (iv) reproducing the figures describing the patterns underlying our predictions.

The interpretation of the rarefied indices follow the same ones for NRI and NTI [see Methods in the main document; Webb (2000)].

2.8.1.2 Results

As expected, the rarefied net relatedness index ($\mathsf{NRI}_{\mathsf{raref}}$) and nearest taxon index ($\mathsf{NTI}_{\mathsf{raref}}$) for bat communities were closer to zero, but highly correlated with their respective unrarefied indices for phylogenetic relatedness (Pearson's r of 0.83, and Pearson's r 0.69, respectively).

All figures we reproduced with the rarefied NRI and NTI indices (Figure 2.7, Figure 2.8, Figure 2.9, Figure 2.10) had similar patterns to those we observed in the figures from the main study (Figure 2.2, Figure 2.3, Figure 2.4, Figure 2.5).

For the purposes of simplification and to avoid the loss of information introduced by the rarefaction procedure, we use the unrarefied values for NRI and NTI in the main manuscript.

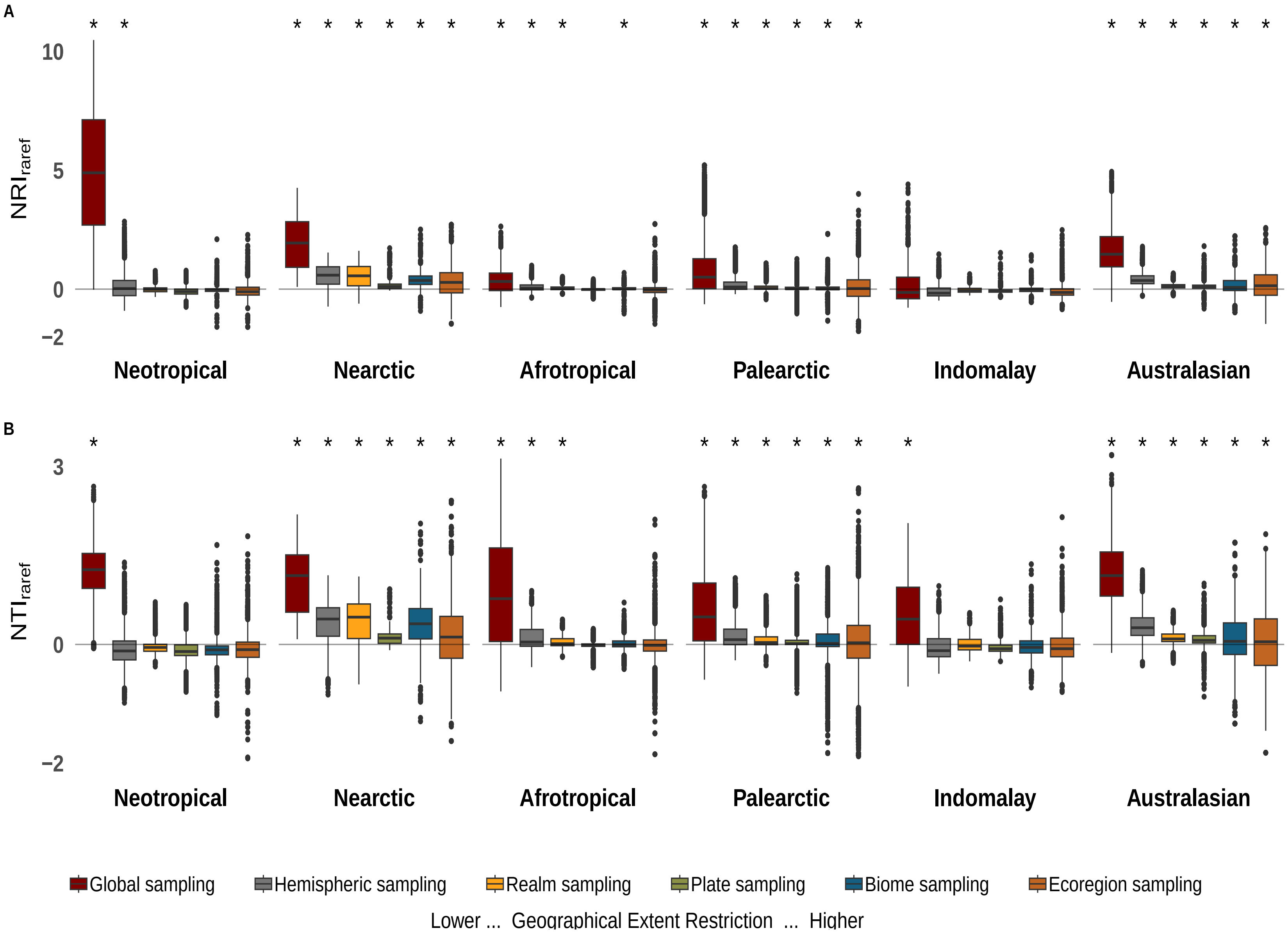
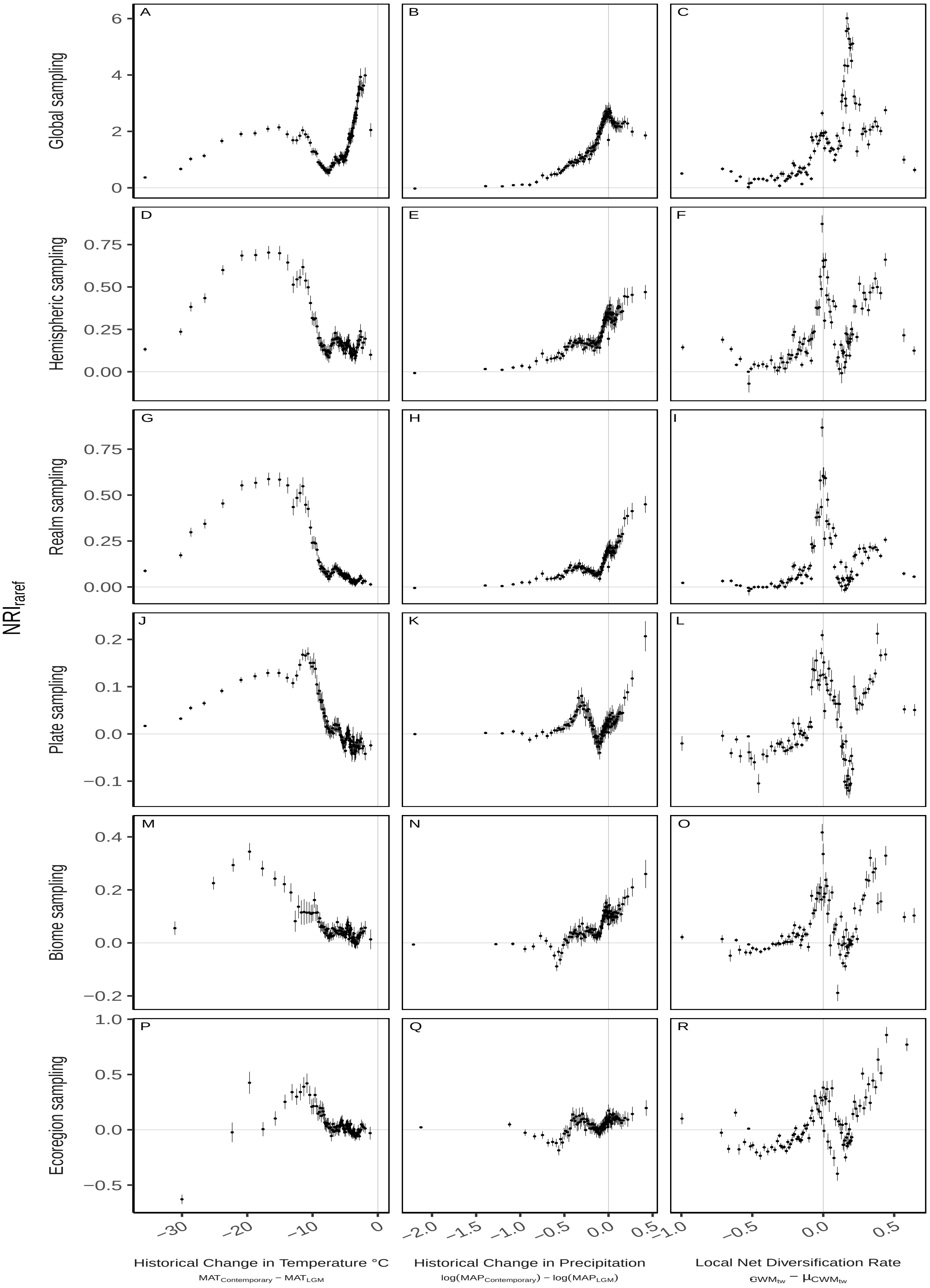


Figure 2.7: **Realm-comparison of the geographical extent size bias-corrected phylogenetic structure of bat assemblages – measured through the (A) rarefied net relatedness index (NTI$_{\text{raref}}$) and (B) nearest taxon index (NRI$_{\text{raref}}$) – across a gradient of geographical extent restrictions (see Methods)**. Geographical extents were restricted for the (i) global, (ii) east-west hemispheric (New World *versus* Old World), (iii) biogeographical realm, (iv) tectonic plate, (v) within-realm biome, and (vi) ecoregional extents. Bat communities with positive values of NRI$_{\text{raref}}$ and NTI$_{\text{raref}}$ indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NRI and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Hemispheric sampling
Realm sampling
Plate sampling
Biome sampling
Ecoregion sampling
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−0.2
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0.2
0.4
−0.5
0.0
0.5
1.0
−30
−20
−10
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−2.0
−1.5
−1.0
−0.5
0.0
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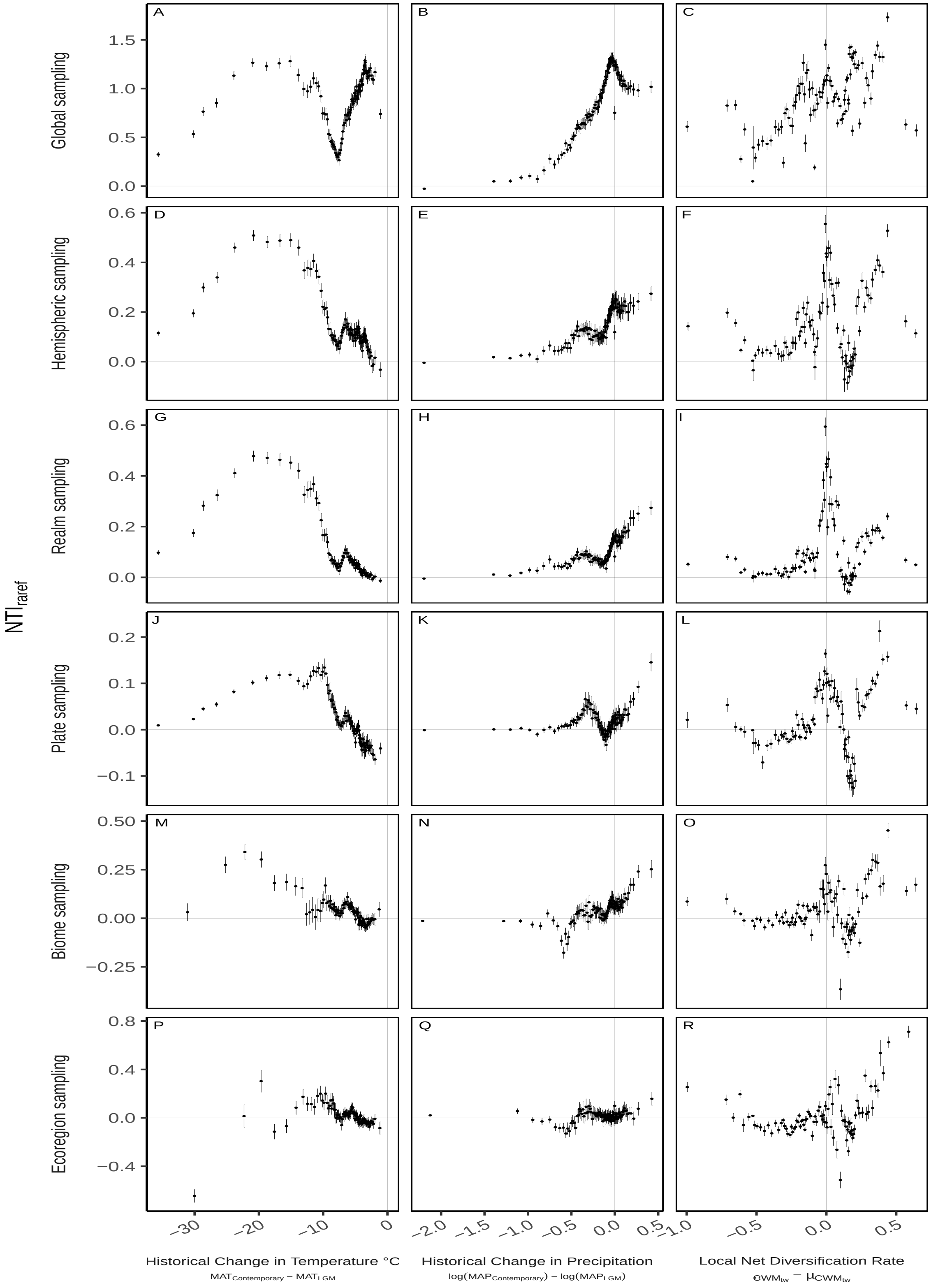
−1.0
−0.5
0.0
0.5
Historical Change in Temperature °C
$MAT_{Contemporary} - MAT_{LGM}$
Historical Change in Precipitation
$\log(MAP_{Contemporary}) - \log(MAP_{LGM})$
Local Net Diversification Rate
$\epsilon WM_{tw} - \mu_{CWM_{tw}}$

Figure 2.8 *(preceding page)*: **Average bias-corrected rarefied net relatedness index (NRI_{raref}) of worldwide bat communities across the percentiles of historical change in temperature, historical change in precipitation and in situ net diversification rates across geographical extents**. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). NRI_{raref} was measured at the (A, B and C) global, (D, E and F) east-west hemispheric (New World vs. Old World), (G, H and I) biogeographical realm, (K, L and M) tectonic plate, (N, O and P) within-realm biome, and (Q, R and S) ecoregional geographical extents. Bat communities with positive values of NRI_{raref} indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NRI indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent. Vertical lines represent the mean plus or minus 1.96 times the standard error for the percentile of NRI.


NTI$_{raref}$
Global sampling
Hemispheric sampling
Realm sampling
Plate sampling
Biome sampling
Ecoregion sampling
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0.1
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0
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0.5
−1.0
−0.5
0.0
0.5
Historical Change in Temperature °C
$MAT_{Contemporary} - MAT_{LGM}$
Historical Change in Precipitation
$\log(MAP_{Contemporary}) - \log(MAP_{LGM})$
Local Net Diversification Rate
$\epsilon WM_{tw} - \mu_{CWM_{tw}}$

Figure 2.9 *(preceding page)*: **Average bias-corrected rarefied nearest taxon index ($\mathrm{NTI}_{\mathrm{raref}}$) of worldwide bat communities across the percentiles of historical change in temperature, historical change in precipitation and *in situ* net diversification rates across geographical extents**. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). $\mathrm{NTI}_{\mathrm{raref}}$ was measured at the (A, B and C) global, (D, E and F) east-west hemispheric (New World vs. Old World), (G, H and I) biogeographical realm, (K, L and M) tectonic plate, (N, O and P) within-realm biome, and (Q, R and S) ecoregional geographical extents. Bat communities with positive values of $\mathrm{NTI}_{\mathrm{raref}}$ indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NTI indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent.

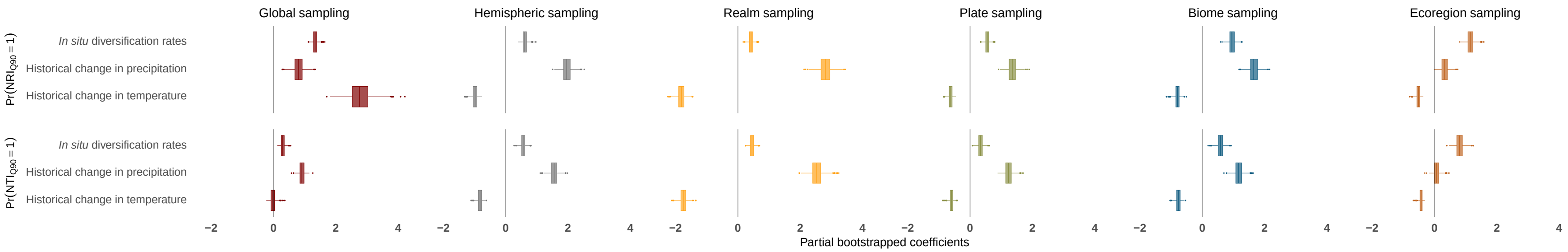


Figure 2.10: **Partial bootstrapped coefficients for the effects of paleoclimatic legacies and *in situ* diversification rates in the phylogenetic structure of bat communities across spatial geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature or logarithm of the mean annual precipitation from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). Bootstrapped partial coefficients were extracted from robust logistic generalized linear models using binary outcomes (at the 90-th percentile) for the indices for phylogenetic community relatedness ($Pr(\mathsf{NRI}_{\mathsf{raref-Q90}} = 1)$) and $Pr(\mathsf{NTI}_{\mathsf{raref-Q90}} = 1)$) as response variables (in separate models) and the z-score standardized historical change in temperature, historical change in precipitation and *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Table 2.6: **Model-averaged bootstrapped coefficients for the effects of historical change in temperature and in precipitation and *in situ* diversification rates in the rarefied phylogenetic structure of bat communities across geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Bootstrapped partial coefficients (and their 95% confidence intervals) were extracted from robust logistic generalized linear models using binary outcomes (at the 90th percentile) for the indices for phylogenetic community relatedness (NRI_{raref} and NTI_{raref}) as response variables (in separate models) and the z-score standardized historical change in temperature, historical change in precipitation and *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Characteristic	**Global sampling**, N = 1,000[1]	**Hemispheric sampling**, N = 1,000[1]	**Realm sampling**, N = 1,000[1]	**Plate sampling**, N = 1,000[1]	**Biome sampling**, N = 1,000[1]	**Ecoregion sampling**, N = 1,000[1]
NRI						
Intercept	-4.21 (-4.61; -3.80)	-3.04 (-3.27; -2.81)	-3.60 (-3.88; -3.31)	-2.67 (-2.86; -2.48)	-3.12 (-3.37; -2.88)	-2.75 (-2.98; -2.52)
Historical change in temperature	2.78 (2.06; 3.50)	-0.99 (-1.16; -0.81)	-1.81 (-2.07; -1.56)	-0.62 (-0.75; -0.49)	-0.80 (-0.96; -0.63)	-0.52 (-0.65; -0.39)
Historical change in precipitation	0.81 (0.46; 1.15)	1.97 (1.66; 2.28)	2.81 (2.41; 3.21)	1.36 (1.07; 1.65)	1.66 (1.35; 1.97)	0.33 (0.08; 0.58)
In situ diversification rates	1.34 (1.18; 1.49)	0.61 (0.45; 0.77)	0.42 (0.27; 0.57)	0.55 (0.41; 0.69)	0.95 (0.75; 1.16)	1.15 (0.92; 1.39)
NTI						
Intercept	-2.44 (-2.59; -2.29)	-2.83 (-3.03; -2.63)	-3.47 (-3.76; -3.19)	-2.54 (-2.72; -2.35)	-2.77 (-2.99; -2.56)	-2.49 (-2.69; -2.28)
Historical change in temperature	-0.02 (-0.19; 0.15)	-0.82 (-0.98; -0.67)	-1.75 (-1.99; -1.52)	-0.59 (-0.71; -0.48)	-0.77 (-0.92; -0.61)	-0.43 (-0.53; -0.33)
Historical change in precipitation	0.92 (0.73; 1.10)	1.55 (1.28; 1.83)	2.53 (2.14; 2.92)	1.23 (0.97; 1.49)	1.17 (0.91; 1.44)	0.07 (-0.14; 0.28)
In situ diversification rates	0.30 (0.17; 0.43)	0.56 (0.40; 0.72)	0.45 (0.30; 0.61)	0.34 (0.17; 0.50)	0.58 (0.37; 0.80)	0.81 (0.54; 1.07)

[1] Mean (Lower CI; Upper CI)

2.9 Supporting Information 4

2.9.1 Assessing the effects of climate change velocity on the phylogenetic relatedness of bat communities

2.9.1.1 Implementation

The approach we used for calculating climatic historical stability comes with several assumptions. An important one is that changes in climate between the last glacial maximum (LGM) and the contemporary period are constant, so that the differences between climate estimates between both periods are informative. Delgado-Baquerizo *et al.* (2017) have shown that climatic changes during the last 21,000 years were indeed largely unidirectional and often linear at the resolution of hundreds of years, supporting that calculating differences between the climate from the last glacial maximum and the contemporary period can account for the largest changes in temperature and precipitation over the last 21,000 years.

To further support our approach, we assessed if the patterns we observed for the effects of climatic historical stability (measured as the difference between the snapshots of climate estimates for the last glacial maximum (LGM) and climate observations for the contemporary period; see Methods) on the phylogenetic community structure of bats would be congruent to those expected using an alternative metric for climatic stability, the index for velocity of climate change proposed by Loarie *et al.* (2009). This index combines spatial and temporal gradients of change in climate to provide information on how much local climate changes in space across time periods (see examples of its usage in Sandel *et al.* (2011).

We started by downloading high-resolution rasters containing worldwide bioclimatic variables for mean annual temperature and mean annual precipitation for every 500 years before present (BP) until the LGM from the CHELSA-TraCE21k paleoclimatic data base (Karger *et al.* 2021). CHELSA-TraCE21k provides downscaled averages from global monthly climatologies for temperature and precipitation at the resolution of 30 arc-seconds in 100-year time steps for the last 21,000 years (Karger *et al.* 2021).

We projected and aggregated each raster (by calculating the average of all pixels occurring in each cell, weighted by the coverage overlapping area of cells) to the 50 km × 50 km equal-area cell-grid we used in this study (see Methods). Our final data set consisted of 45 geographical raster layers for each climatic variable, with each layer containing the climatic data estimated at every 500-year step, from the 2,000s to the 21,000 years BP. We log-transformed precipitation values to decrease its skewness and to improve the resolution of dry and very dry climates.

We then computed gradient-based change velocities in temperature and in precipitation following Loarie *et al.* (2009) and Burrows *et al.* (2011). For each cell, we: (i) calculated the long-term temporal trend in climate by extracting the coefficients of simple linear regressions performed between each climatic variable and the time period; (ii) calculated the local spatial gradient in climate for each cell by determining the magnitude of the differences in each climatic variable over its surrounding neighbouring cells (3 × 3); and, then (iii) obtaining the climate change velocity for each variable by dividing its temporal trend by its spatial gradient.

This climate change velocity index derived from both spatial and temporal gradients informs how much climate change in space across time, *i.e.* here, in metres (m) per year. Attractively, this index can be both negative and positive, as the temporal trend provides the direction for the magnitude of climate change velocity.

To make the interpretation congruent to our initial measure of historical change in climate using differences between the climate from the contemporary period and the LGM, we multiplied the climate change velocity index by minus one. With this, large negative values of temperature change velocity represents an accelerated increase in temperature since the LGM, while large positive temperature change velocities indicate accelerated decreases in temperature since the LGM. Similarly, low negative values of precipitation change velocity represent an slow increase in precipitation since the LGM, while low positive precipitation change velocities indicate slow decreases in precipitation since the LGM.

Finally, we applied the same approaches used to test the predictions that phylogenetically clustered communities are more frequent in historically climatically stable regions (H_2) and that increased *in situ* diversification rates generate regional clusters of closely-related species (H_3) (see Methods).

We independently represented the average phylogenetic relatedness of bat communities [*i.e.* for both the net relatedness index (NRI) and the nearest taxon index (NTI)] across each one of the 100-quantiles (percentiles) of temperature change velocity, precipitation change velocity and *in situ* net diversification rates (see Figure 2.11, Figure 2.12).

We also applied bootstrapping robust logistic generalized linear models using binary outcomes for the indices for phylogenetic community relatedness as response variables (NRI and NTI; in separate models; at the 90% percentile cut-off), and the z-score standardized temperature change velocity, precipitation change velocity and *in situ* net diversification rates as predictive variables (*i.e.*, NRI or NTI ~ temperature change velocity + precipitation change velocity + community-weighted net diversification rates means) (see Figure 2.13).

2.9.1.2 Results

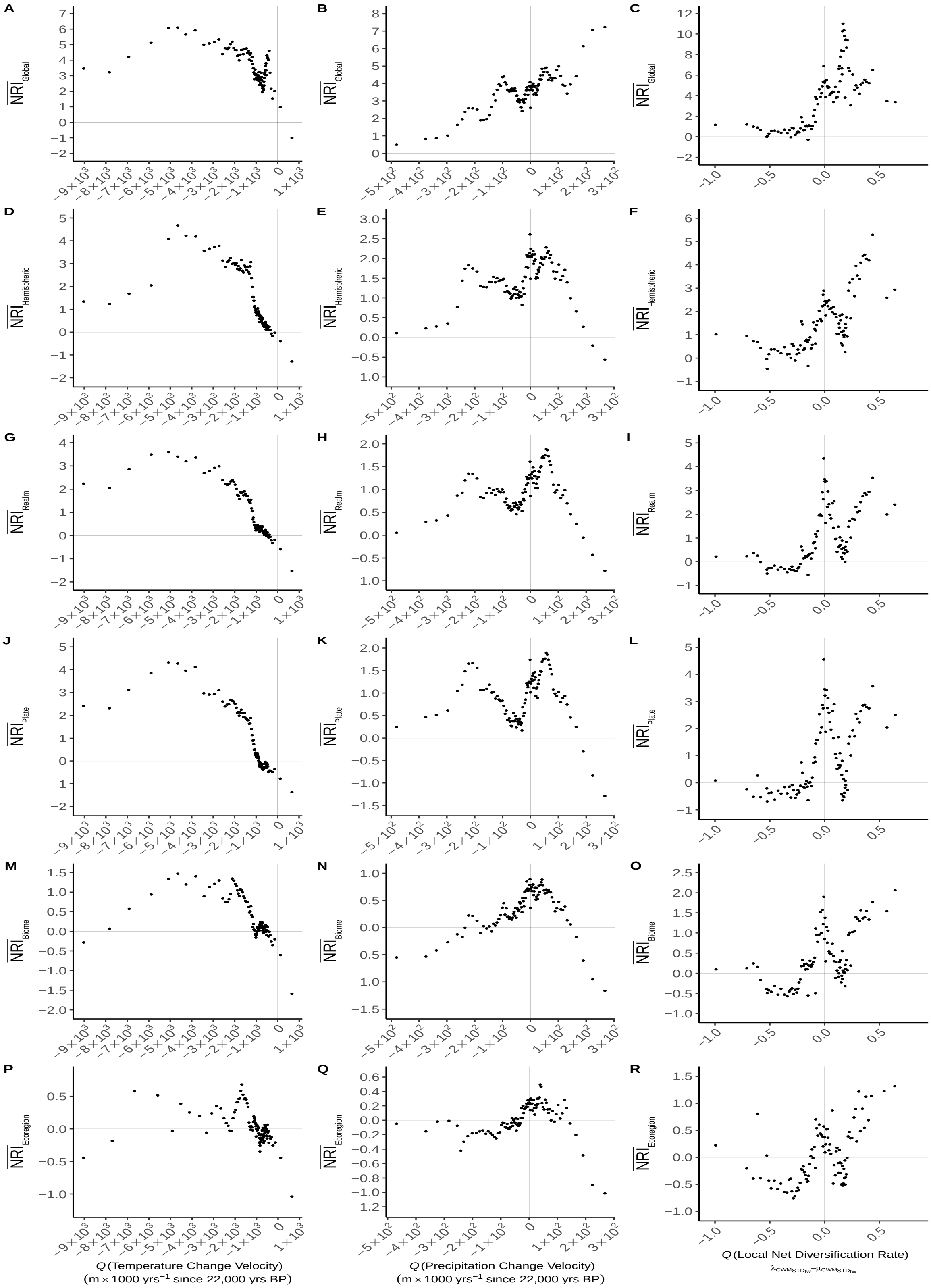
Temperature change velocity was highly correlated with the measure of historical climatic stability in temperature we used in our study (Pearson's r of 0.86), while precipitation change velocity was marginally correlated with the measure of historical change in precipitation (Pearson's r of 0.24).

Both velocities of change in temperature and in precipitation drove the phylogenetic relatedness of bat communities at both overall phylogenetic structure (net relatedness index; NRI) and tip-level phylogenetic structure (nearest taxon index; NTI) of bat communities. Departures in precipitation change velocity from stability (*i.e.* slow or zero velocity of change in climate) generally caused NRI and NTI values to decrease. Nevertheless, the effects of increases in temperature change velocity towards stability in NRI and NTI was less uniform and varied across the gradient of velocity of change and across spatial scales (see Figure 2.11, Figure 2.12, Figure 2.13).

At the global scale, increases in temperature change velocity towards climatic stability (*i.e.* towards no or zero velocity of change in temperature) were associated with increases in the odds of highly phylogenetically related bat communities. At the more restricted geographical extents, increases in temperature change velocity towards stability were associated with decreases in the odds of highly phylogenetically related bat communities (see Figure 2.13).

Increases in precipitation change velocity consistently increased the odds of highly phylogenetically related communities (those belonging to the 90th-percentile of both NRI and NTI); except at the global geographical extent, where it was associated with marginal decreases in the odds of NRI (see Figure 2.13).

The effects of velocities of climate change generally coincided with the ones we observed using historical climatic change.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$\overline{\mathrm{NRI}}_{\mathrm{Global}}$
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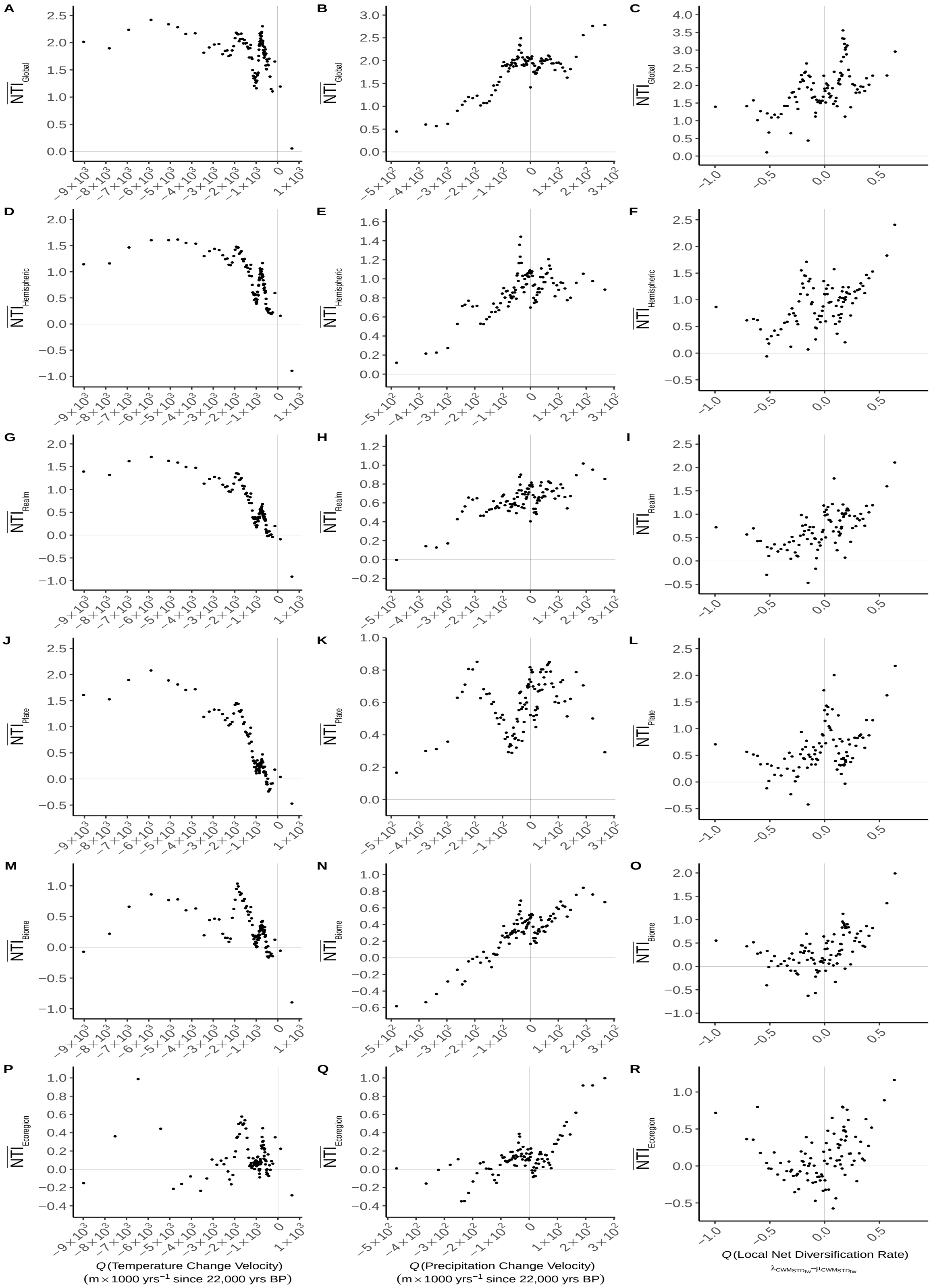
$\overline{\mathrm{NRI}}_{\mathrm{Realm}}$
$\overline{\mathrm{NRI}}_{\mathrm{Plate}}$
$\overline{\mathrm{NRI}}_{\mathrm{Biome}}$
$\overline{\mathrm{NRI}}_{\mathrm{Ecoregion}}$
-9×10^3 -8×10^3 -7×10^3 -6×10^3 -5×10^3 -4×10^3 -3×10^3 -2×10^3 -1×10^3 0 1×10^3
-5×10^2 -4×10^2 -3×10^2 -2×10^2 -1×10^2 0 1×10^2 2×10^2 3×10^2
−1.0 −0.5 0.0 0.5
Q (Temperature Change Velocity)
(m × 1000 yrs^{-1} since 22,000 yrs BP)
Q (Precipitation Change Velocity)
(m × 1000 yrs^{-1} since 22,000 yrs BP)
Q (Local Net Diversification Rate)
$\lambda_{\mathrm{CWM}_{\mathrm{STD}_{\mathrm{tw}}}}-\mu_{\mathrm{CWM}_{\mathrm{STD}_{\mathrm{tw}}}}$

Figure 2.11 *(preceding page)*: **Average net relatedness index (NRI) of bat communities across the percentiles of temperature change velocity, precipitation change velocity and *in situ* net diversification rates across geographical extents**. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Climate change velocities were derived from spatial gradients rates of climate change over time from the contemporary period until 21,000 years before present (BP).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$\overline{\mathrm{NTI}}_{\mathrm{Realm}}$
$\overline{\mathrm{NTI}}_{\mathrm{Plate}}$
$\overline{\mathrm{NTI}}_{\mathrm{Biome}}$
$\overline{\mathrm{NTI}}_{\mathrm{Ecoregion}}$
-9×10^3 -8×10^3 -7×10^3 -6×10^3 -5×10^3 -4×10^3 -3×10^3 -2×10^3 -1×10^3 0 1×10^3
-5×10^2 -4×10^2 -3×10^2 -2×10^2 -1×10^2 0 1×10^2 2×10^2 3×10^2
−1.0 −0.5 0.0 0.5
Q (Temperature Change Velocity)
(m × 1000 yrs^{-1} since 22,000 yrs BP)
Q (Precipitation Change Velocity)
(m × 1000 yrs^{-1} since 22,000 yrs BP)
Q (Local Net Diversification Rate)
$\lambda_{\mathrm{CWM}_{\mathrm{STD}_{\mathrm{tw}}}}-\mu_{\mathrm{CWM}_{\mathrm{STD}_{\mathrm{tw}}}}$

Figure 2.12 *(preceding page)*: **Average net relatedness index (NTI) of bat communities across the percentiles of temperature change velocity, precipitation change velocity and *in situ* net diversification rates across geographical extents**. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Climate change velocities were derived from spatial gradients rates of climate change over time from the contemporary period until 21,000 years before present (BP).

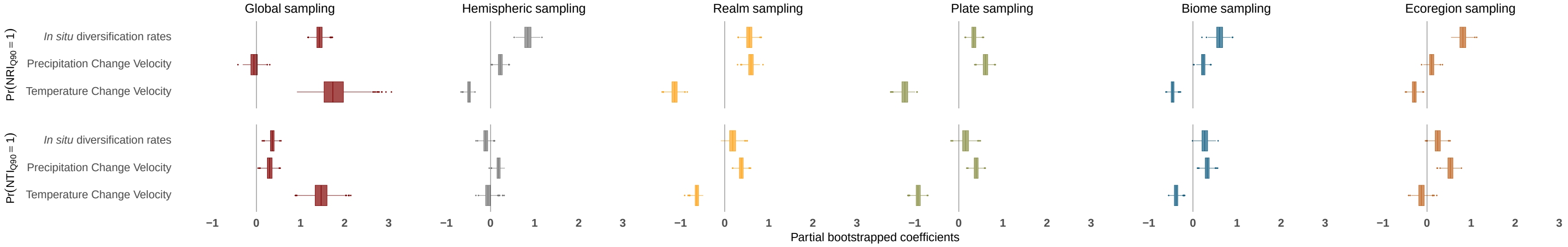


Figure 2.13: **Influence of paleoclimatic legacies and *in situ* diversification rates in the phylogenetic structure of bat communities across spatial geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Climate change velocities were derived from spatial gradients rates of climate change over time from the contemporary period until 21,000 years before present (BP) (see Methods). Bootstrapped partial coefficients were extracted from robust logistic generalized linear models using binary outcomes (at the 90th percentile) for the indices for phylogenetic community relatedness ($Pr(NRI_{Q90} = 1)$) and $Pr(NTI_{Q90} = 1)$) as response variables (in separate models) and the z-score standardized velocity of change in temperature, velocity of change in precipitation and *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Table 2.7: **Model-averaged coefficients for the influence of velocities of change in temperature and in precipitation and *in situ* diversification rates in the phylogenetic structure of bat communities across geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Bootstrapped partial coefficients were extracted from robust logistic generalized linear models using binary outcomes (at the 90th percentile) for the indices for phylogenetic community relatedness ($Pr(NRI_{Q90} = 1)$) and Pr($NTI_{Q90} = 1$)) as response variables (in separate models) and the z-score standardized velocity of change in temperature, velocity of change in precipitation and *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Characteristic	**Global sampling**, N = 1,000[1]	**Hemispheric sampling**, N = 1,000[1]	**Realm sampling**, N = 1,000[1]	**Plate sampling**, N = 1,000[1]	**Biome sampling**, N = 1,000[1]	**Ecoregion sampling**, N = 1,000[1]
NRI						
Intercept	-3.25 (-3.59; -2.91)	-2.50 (-2.68; -2.32)	-2.69 (-2.87; -2.51)	-2.61 (-2.78; -2.44)	-2.36 (-2.53; -2.20)	-2.46 (-2.64; -2.28)
Temperature change velocity	1.76 (1.11; 2.42)	-0.49 (-0.58; -0.40)	-1.14 (-1.31; -0.96)	-1.23 (-1.42; -1.03)	-0.46 (-0.56; -0.36)	-0.29 (-0.41; -0.16)
Precipitation change velocity	-0.05 (-0.27; 0.16)	0.22 (0.09; 0.35)	0.60 (0.45; 0.75)	0.61 (0.45; 0.76)	0.23 (0.12; 0.35)	0.11 (-0.03; 0.25)
In situ diversification rates	1.43 (1.25; 1.61)	0.85 (0.65; 1.05)	0.56 (0.39; 0.73)	0.34 (0.21; 0.47)	0.61 (0.41; 0.80)	0.82 (0.63; 1.00)
NTI						
Intercept	-2.68 (-2.88; -2.48)	-2.20 (-2.34; -2.06)	-2.35 (-2.50; -2.20)	-2.45 (-2.61; -2.30)	-2.26 (-2.41; -2.12)	-2.35 (-2.51; -2.20)
Temperature change velocity	1.47 (1.08; 1.86)	-0.05 (-0.22; 0.11)	-0.63 (-0.75; -0.52)	-0.92 (-1.07; -0.78)	-0.38 (-0.50; -0.27)	-0.13 (-0.31; 0.06)
Precipitation change velocity	0.30 (0.14; 0.46)	0.18 (0.08; 0.29)	0.38 (0.25; 0.50)	0.39 (0.26; 0.53)	0.32 (0.19; 0.46)	0.53 (0.36; 0.70)
In situ diversification rates	0.36 (0.24; 0.48)	-0.11 (-0.24; 0.02)	0.18 (-0.01; 0.38)	0.15 (-0.05; 0.35)	0.27 (0.09; 0.45)	0.24 (0.07; 0.42)

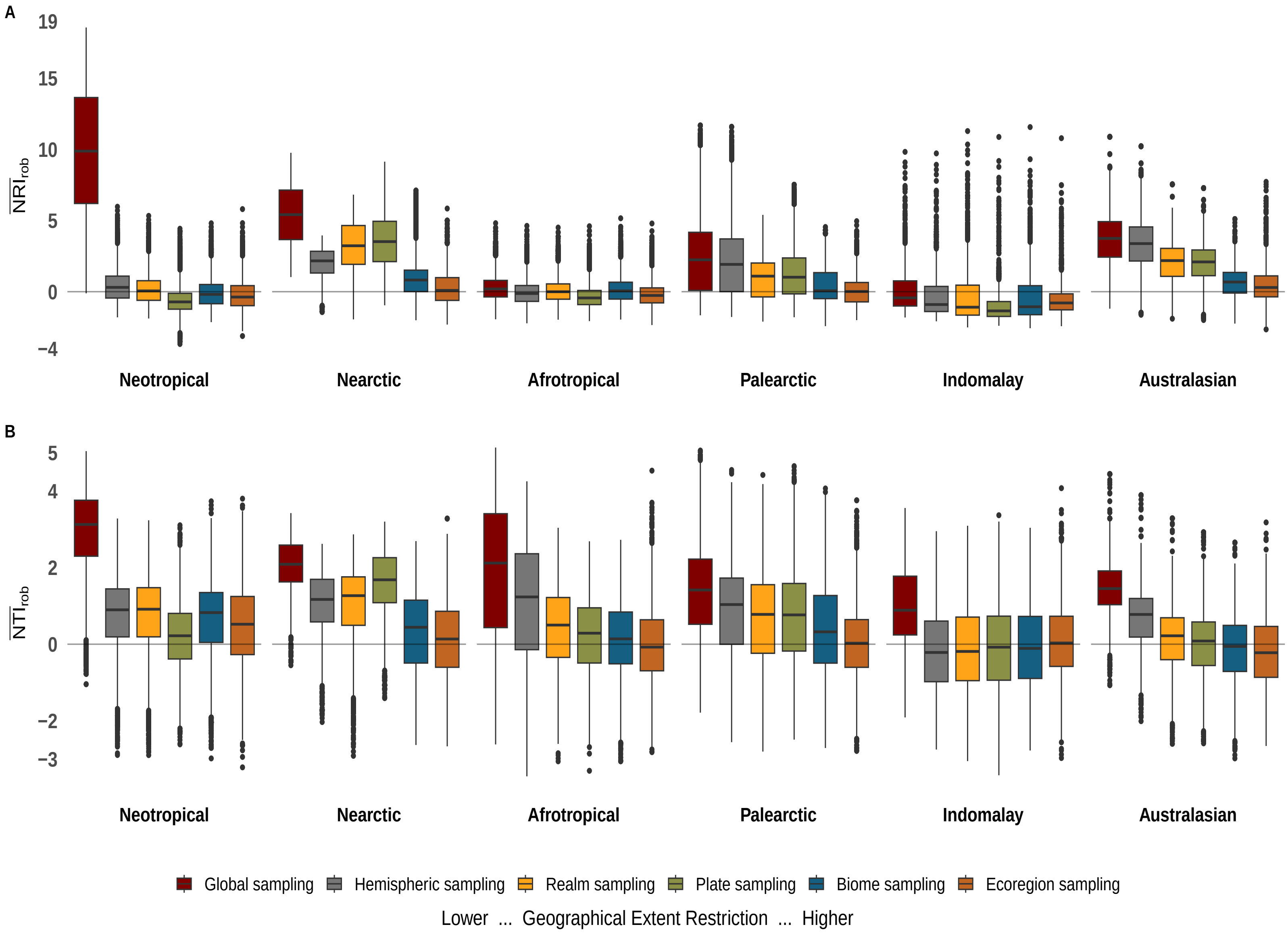
[1] Mean (Odds Ratio)

2.10 Supporting Information 5

2.10.1 Robustness to phylogenetic uncertainty

To account for phylogenetic uncertainty, we recalculated the phylogenetic relatedness and the *in situ* diversification rates of bat communities on a subset of randomly sampled trees from the posterior distribution of phylogenetic trees from Faurby and Svenning (2015) (see Donoghue & Ackerly 1996). The phylogenetic relatedness of bat communities was calculated across 50 randomly sampled phylogenetic trees, while diversification rates were estimated on 100 randomly sampled phylogenetic trees. We were limited from including higher sample sizes because of restrictions in computational resources. We then computed the average net relatedness index, average nearest taxon index and average community-weighted net diversification rates across the calculations done with the sampled phylogenetic trees and used these averages to reproduce the figures testing each hypothesis from our study.

These results were qualitatively similar to the ones computed on the maximum credibility clade phylogenetic tree (see Figure 2.2, Figure 2.3, Figure 2.4, Figure 2.5, and Figures S5.1, S5.2, S5.3 and S5.4), providing evidence that our inferences are robust the uncertainty of phylogenetic hypotheses from the posterior distribution of the phylogenetic relationships we used in our study.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Nearctic
Afrotropical
Palearctic
Indomalay
Australasian
Global sampling
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Realm sampling
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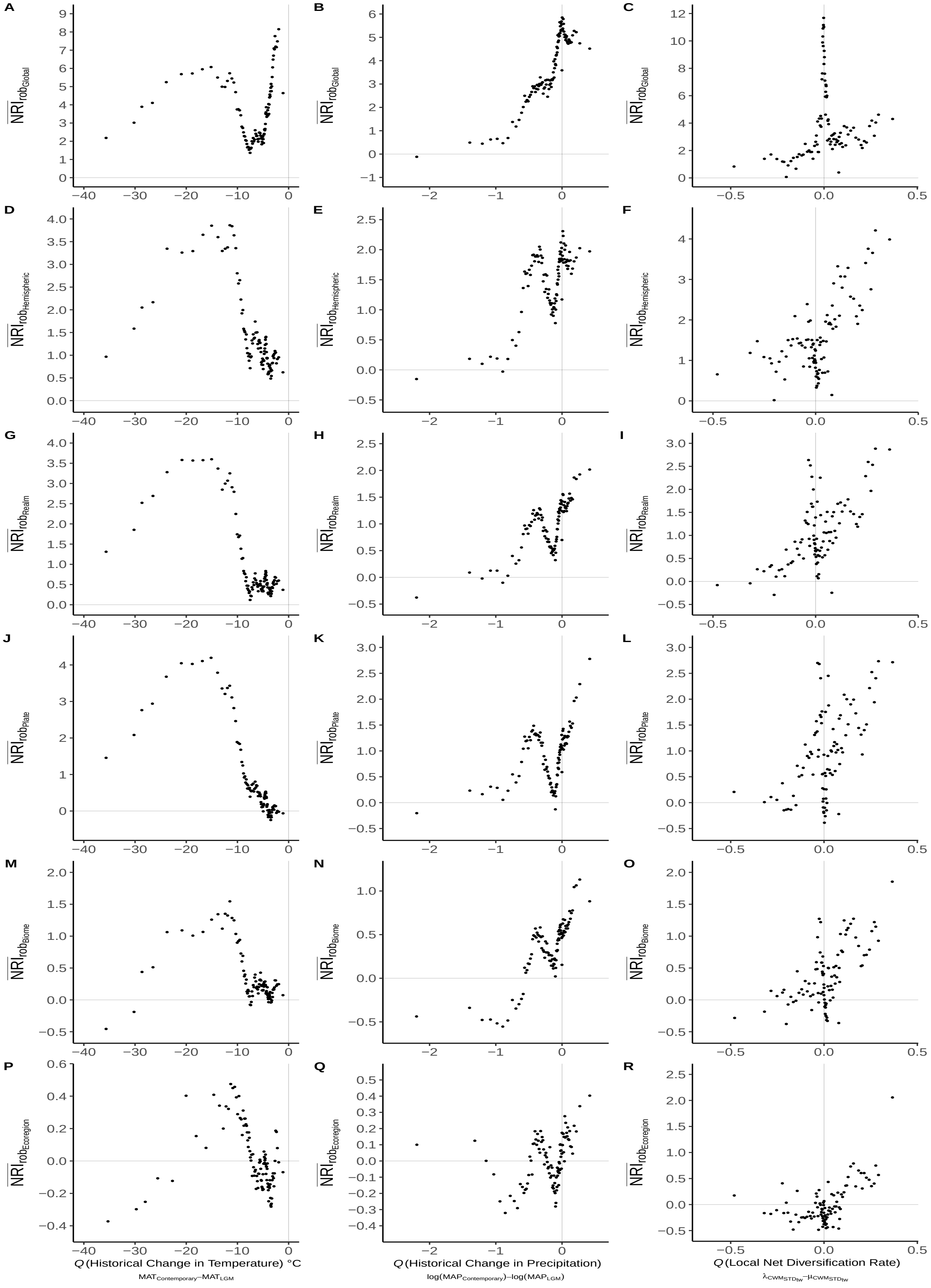
Biome sampling
Ecoregion sampling
Lower ... Geographical Extent Restriction ... Higher

Figure 2.14 *(preceding page)*: **Realm-comparison of the phylogenetic structure of bat assemblages – measured through the averages of (A) net relatedness index ($\textbf{NRI}_{\textbf{rob}}$) and (B) nearest taxon index ($\textbf{NTI}_{\textbf{rob}}$) across computations on a subset of 50 phylogenetic trees sampled from the posterior distribution of phylogenetic trees available in Faurby and Svenning (2015) – across a gradient of geographical extent restrictions (see Methods)**. Spatial extents were restricted for the (i) global, (ii) east-west hemispheric (New World vs. Old World), (iii) biogeographical realm, (iv) tectonic plate, (v) within-realm biome, and (vi) ecoregional extents. Bat communities with positive values of NRI and NTI indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. On the other hand, negative values of NRI and NTI indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent. Boxes represent interquartile ranges, with the upper hinge being the 75th percentile, the middle the median, and the lower hinge, the 25th percentile. Upper and lower whiskers represent values 1.5 times above and below the interquartile range, respectively. Black-filled circles represent outliers.



A
B
C
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Global}}$
0
1
2
3
4
5
6
7
8
9
−1
10
12
D
E
F
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Hemispheric}}$
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
−0.5
G
H
I
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Realm}}$
J
K
L
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Plate}}$
M
N
O
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Biome}}$
P
Q
R
$\overline{\mathrm{NRI}}\mathrm{rob}_{\mathrm{Ecoregion}}$
−0.4
−0.3
−0.2
−0.1
0.1
0.2
0.3
0.4
0.6
−40
−30
−20
−10
0
−2
−1
0
−0.5
0.0
0.5
Q (Historical Change in Temperature) °C
$\mathrm{MAT}_{\mathrm{Contemporary}} - \mathrm{MAT}_{\mathrm{LGM}}$
Q (Historical Change in Precipitation)
$\log(\mathrm{MAP}_{\mathrm{Contemporary}}) - \log(\mathrm{MAP}_{\mathrm{LGM}})$
Q (Local Net Diversification Rate)
$\lambda_{\mathrm{CWM}_{\mathrm{STD_{tw}}}} - \mu_{\mathrm{CWM}_{\mathrm{STD_{tw}}}}$

Figure 2.15 *(preceding page)*: **Average net relatedness index (NRI_{rob}) of worldwide bat communities across the percentiles of historical change in temperature, historical change in precipitation and average *in situ* net diversification rates across geographical extents**. Average *in situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). NRI_{rob} was measured at the (A, B and C) global, (D, E and F) east-west hemispheric (New World vs. Old World), (G, H and I) biogeographical realm, (K, L and M) tectonic plate, (N, O and P) within-realm biome, and (Q, R and S) ecoregional geographical extents. Bat communities with positive values of NRI_{rob} indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NRI_{rob} indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent.

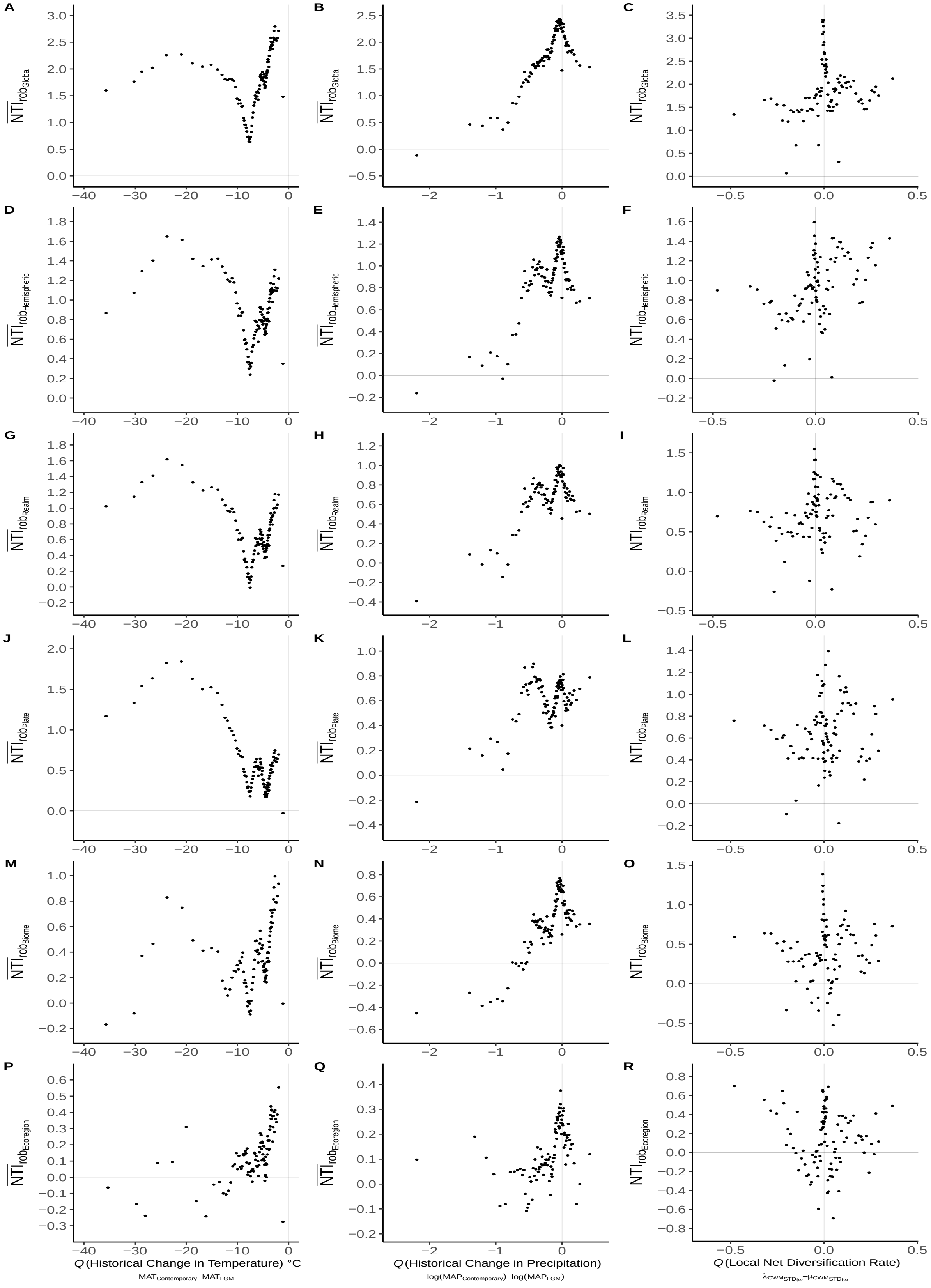

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
$\overline{NTI}rob_{Global}$
$\overline{NTI}rob_{Hemispheric}$
$\overline{NTI}rob_{Realm}$
$\overline{NTI}rob_{Plate}$
$\overline{NTI}rob_{Biome}$
$\overline{NTI}rob_{Ecoregion}$
−40
−30
−20
−10
0
−2
−1
0
−0.5
0.0
0.5
Q (Historical Change in Temperature) °C
$MAT_{Contemporary} - MAT_{LGM}$
Q (Historical Change in Precipitation)
$\log(MAP_{Contemporary}) - \log(MAP_{LGM})$
Q (Local Net Diversification Rate)
$\lambda_{CWM_{STDtw}} - \mu_{CWM_{STDtw}}$

Figure 2.16 *(preceding page)*: **Average bias-corrected rarefied nearest taxon index (NTI_{rob}) of worldwide bat communities across the percentiles of historical change in temperature, historical change in precipitation and *in situ* net diversification rates across geographical extents**. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature (MAT) or logarithm of the mean annual precipitation (MAP) from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). NTI_{rob} was measured at the (A, B and C) global, (D, E and F) east-west hemispheric (New World vs. Old World), (G, H and I) biogeographical realm, (K, L and M) tectonic plate, (N, O and P) within-realm biome, and (Q, R and S) ecoregional geographical extents. Bat communities with positive values of NTI_{rob} indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NTI indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent.

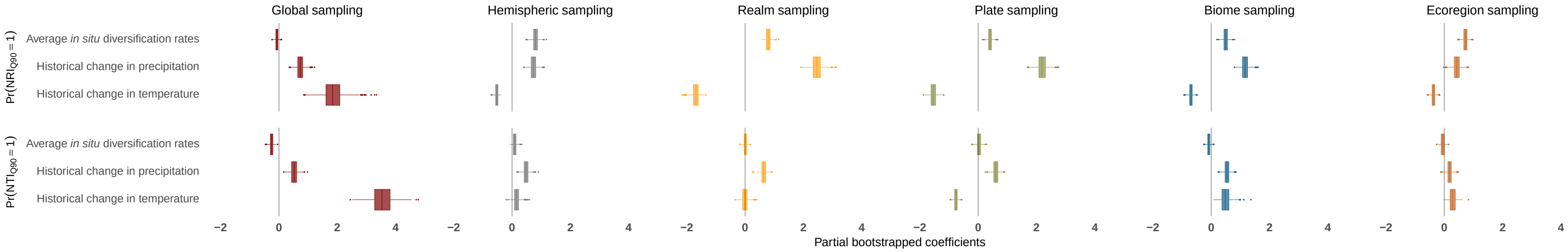


Figure 2.17: **Partial bootstrapped coefficients for the effects of paleoclimatic legacies and *in situ* diversification rates in the phylogenetic structure of bat communities across spatial geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature or logarithm of the mean annual precipitation from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago (see Methods). Bootstrapped partial coefficients were extracted from robust logistic generalized linear models using binary outcomes (at the 90-th percentile) for the indices for phylogenetic community relatedness (NRI_{rob} and NTI_{rob}) as response variables (in separate models) and the z-score standardized historical change in temperature, historical change in precipitation and average *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Table 2.8: **Model-averaged bootstrapped coefficients for the effects of historical change in temperature and in precipitation and *in situ* diversification rates in the rarefied phylogenetic structure of bat communities across geographical extents**. The phylogenetic structure of bat communities is measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Bootstrapped partial coefficients (and their 95% confidence intervals) were extracted from robust logistic generalized linear models using binary outcomes (at the 90th percentile) for the indices for phylogenetic community relatedness (NRI_{rob} and NTI_{rob}) as response variables (in separate models) and the z-score standardized historical change in temperature, historical change in precipitation and *in situ* net diversification rates as predictive variables (with 2,500 random samples drawn with replacement for 1,000 repetitions).

Characteristic	**Global sampling**, N = 1,000[1]	**Hemispheric sampling**, N = 1,000[1]	**Realm sampling**, N = 1,000[1]	**Plate sampling**, N = 1,000[1]	**Biome sampling**, N = 1,000[1]	**Ecoregion sampling**, N = 1,000[1]
NRI						
Intercept	-3.08 (-3.44; -2.73)	-2.55 (-2.74; -2.35)	-3.48 (-3.75; -3.20)	-3.17 (-3.41; -2.93)	-2.58 (-2.77; -2.39)	-2.45 (-2.62; -2.28)
Historical change in temperature	1.86 (1.14; 2.59)	-0.52 (-0.63; -0.41)	-1.69 (-1.93; -1.46)	-1.54 (-1.76; -1.31)	-0.70 (-0.82; -0.57)	-0.37 (-0.50; -0.24)
Historical change in precipitation	0.73 (0.48; 0.98)	0.74 (0.51; 0.96)	2.46 (2.09; 2.82)	2.20 (1.86; 2.54)	1.16 (0.90; 1.41)	0.42 (0.17; 0.68)
In situ diversification rates	-0.07 (-0.17; 0.03)	0.80 (0.62; 0.99)	0.79 (0.61; 0.98)	0.40 (0.26; 0.55)	0.50 (0.33; 0.67)	0.72 (0.57; 0.88)
NTI						
Intercept	-3.88 (-4.30; -3.45)	-2.30 (-2.44; -2.15)	-2.36 (-2.51; -2.22)	-2.42 (-2.59; -2.26)	-2.40 (-2.57; -2.23)	-2.30 (-2.45; -2.15)
Historical change in temperature	3.55 (2.80; 4.29)	0.15 (-0.06; 0.37)	-0.01 (-0.23; 0.21)	-0.76 (-0.89; -0.63)	0.49 (0.16; 0.83)	0.29 (0.04; 0.54)
Historical change in precipitation	0.52 (0.28; 0.77)	0.48 (0.29; 0.67)	0.64 (0.45; 0.83)	0.60 (0.40; 0.81)	0.54 (0.35; 0.73)	0.18 (0.01; 0.35)
In situ diversification rates	-0.25 (-0.37; -0.13)	0.09 (-0.03; 0.21)	0.01 (-0.10; 0.12)	0.03 (-0.13; 0.18)	-0.08 (-0.20; 0.03)	-0.06 (-0.19; 0.08)

[1] Mean (Lower CI; Upper CI)

2.11 Supporting Information 6

2.11.1 Raw data representation

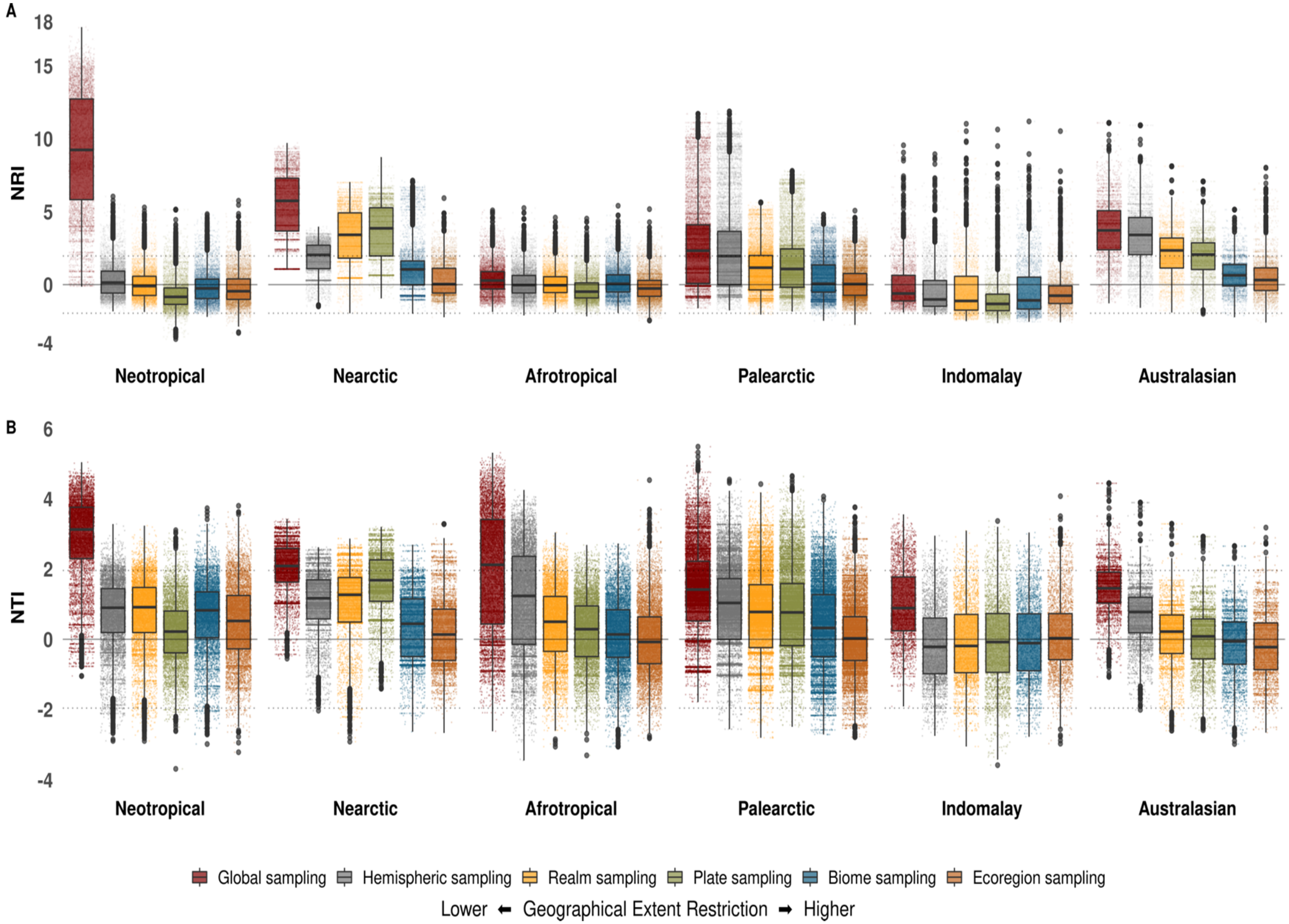

A
18
15
10
5
0
-4
NRI
Neotropical
Nearctic
Afrotropical
Palearctic
Indomalay
Australasian
B
6
4
2
0
-2
-4
NTI
Neotropical
Nearctic
Afrotropical
Palearctic
Indomalay
Australasian
Global sampling
Hemispheric sampling
Realm sampling
Plate sampling
Biome sampling
Ecoregion sampling
Lower ⬅ Geographical Extent Restriction ➡ Higher

Figure 2.18 *(preceding page)*: **Realm-comparison of the geographical extent size bias-corrected phylogenetic structure of bat assemblages – measured through the (A) rarefied net relatedness index (NRI) and (B) nearest taxon index (NTI) – across a gradient of geographical extent restrictions (see Methods)**. Geographical extents were restricted for the (i) global, (ii) east-west hemispheric (New World versus Old World), (iii) biogeographical realm, (iv) tectonic plate, (v) within-realm biome, and (vi) ecoregional extents. Bat communities with positive values of NRI and NTI indicate that co-occurring species in these communities are phylogenetically related in relation to a given geographical extent. Conversely, negative values of NRI and NTI indicate that bat communities are mainly composed of distantly-related species in relation to that given geographical extent. Boxplots overlay raw data values with added horizontal jitter for visibility. Dotted lines represent the confidence interval (at 95% or ±1.96 units) of the indices for phylogenetic community structure.

2.12 Supporting Information 7

2.12.1 Effects of historical climatic stability and *in situ* diversification rates in the odds of phylogenetic community structure from the upper quartile

When testing hypotheses H_2 and H_3 inferentially, we also used the upper unconditional quartile (*i.e.*, the 75th percentile) to obtain the binary outcomes for the phylogenetic structure (either NRI or NTI) in each community (see Methods). With this, a value of one was assigned to a given community if it belonged to the 75th percentile of phylogenetic relatedness, otherwise a value of zero was assigned to them. We then applied conditionally unbiased bounded influence robust logistic regressions in which the response variable was the vector of binary outcomes (ones and zeros) representing relatively high or low phylogenetic structure (separately for NRI and NTI) and the predictors were z-score standardized values (*i.e.*, to have mean zero and variance one) of historical change in temperature, historical change in precipitation and *in situ* net diversification rates. With this, we could estimate the relative importance of each predictor within a single model. To estimate confidence intervals for each predictor, we used a bootstrap approach based on 1,000 resamples of 2,500 random communities each. This approach allowed us to explicitly test how changes in historical climatic stability and *in situ* diversification rates independently increased (or decreased) the log-odds (the logistic response) of a community being composed of highly phylogenetically related species (in relation to the 75th percentile).

These results were highly qualitatively similar to the ones using the 90th percentile of phylogenetic relatedness as cut-off, with the exception for the effects of historical change in temperature at the global sampling geographical extent (see Figure 2.5 and Figure 2.19, and Tables 2 and Table 2.9). This highlights the variation in importance of temperature stability across different portions of the gradient of phylogenetic relatedness in biological communities.

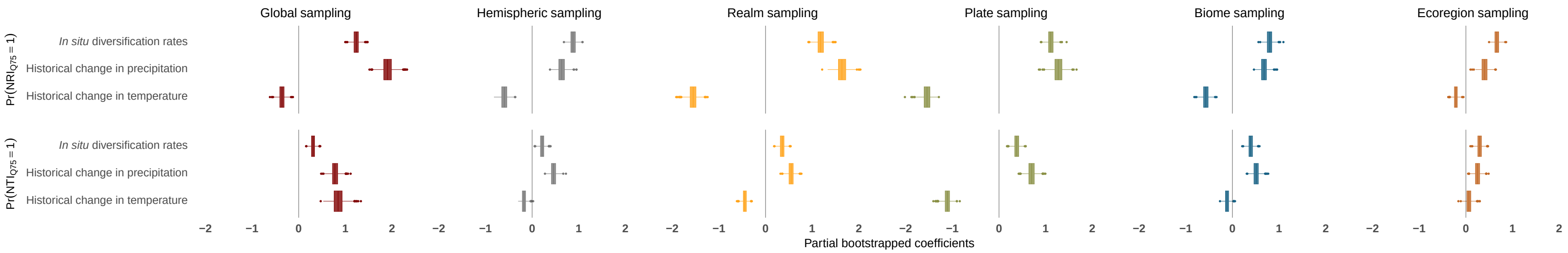


Figure 2.19: **Influence of historical legacies on phylogenetic structure of bats across different geographical extents**. Distributions represent boxplot of bootstrapped logistic regression coefficients using binary outcomes (at the 90th percentile) for the indices of phylogenetic community relatedness ($Pr(\mathsf{NRI}_{\mathsf{Q75}} = 1)$) and $Pr(\mathsf{NTI}_{\mathsf{Q75}} = 1)$) as response variables (in separate models) and the z-score standardized (with values transformed to have mean zero and one-unit variance) historical change in temperature, historical change in precipitation and in situ net diversification rates as predictive variables. Phylogenetic structure of bat communities was measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. In situ net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Paleoclimatic legacies for each bat community were obtained as the historical change in climate since the last glacial maximum (LGM); specifically, the mean annual temperature or logarithm of the mean annual precipitation from the contemporary period minus the estimated mean annual temperature or logarithm of the mean annual precipitation from 22,000 years ago.

Table 2.9: **Influence of climatic legacies and *in situ* diversification rates on the phylogenetic structure of bat communities across different geographical extents**. Regression coefficients (and ± 95% bootstrap-based confidence intervals) for the robust logistic generalized linear models using binary outcomes (at the 90th percentile) for the indices of phylogenetic community relatedness ($Pr(\mathsf{NRI}_{\mathsf{Q975}} = 1)$) and $Pr(\mathsf{NTI}_{\mathsf{Q75}} = 1)$) as response variables (in separate models) and the standardized (mean zero and variance one) historical change in temperature, historical change in precipitation and *in situ* net diversification rates as predictive variables. The phylogenetic structure of bat communities was measured through the net relatedness index (NRI) and the nearest taxon index (NTI) at each geographical extent. *In situ* net diversification rates were obtained by subtracting the difference between community-weighted means weight-standardized for speciation and extinction rates. Historical change in climate for each bat community was obtained as the difference between the contemporary climate (either temperature or the logarithm of precipitation) from the estimated climate from the last glacial maximum (22,000 years ago).

Characteristic	**Global sampling**, N = 1,000[1]	**Hemispheric sampling**, N = 1,000[1]	**Realm sampling**, N = 1,000[1]	**Plate sampling**, N = 1,000[1]	**Biome sampling**, N = 1,000[1]	**Ecoregion sampling**, N = 1,000[1]
NRI						
Intercept	-1.94 (-2.10; -1.79)	-1.34 (-1.46; -1.21)	-1.79 (-1.96; -1.62)	-1.65 (-1.80; -1.50)	-1.33 (-1.45; -1.21)	-1.24 (-1.35; -1.14)
Historical change in temperature	-0.36 (-0.49; -0.23)	-0.60 (-0.75; -0.44)	-1.56 (-1.75; -1.36)	-1.54 (-1.73; -1.36)	-0.57 (-0.71; -0.43)	-0.22 (-0.31; -0.12)
Historical change in precipitation	1.91 (1.65; 2.16)	0.63 (0.46; 0.81)	1.64 (1.41; 1.87)	1.28 (1.05; 1.50)	0.68 (0.52; 0.84)	0.40 (0.24; 0.56)
In situ diversification rates	1.23 (1.10; 1.37)	0.88 (0.74; 1.01)	1.18 (1.00; 1.36)	1.11 (0.97; 1.26)	0.80 (0.66; 0.94)	0.66 (0.55; 0.78)
NTI						
Intercept	-1.50 (-1.63; -1.36)	-1.15 (-1.24; -1.06)	-1.21 (-1.32; -1.11)	-1.26 (-1.38; -1.14)	-1.20 (-1.30; -1.09)	-1.16 (-1.26; -1.07)
Historical change in temperature	0.85 (0.59; 1.11)	-0.17 (-0.28; -0.07)	-0.45 (-0.54; -0.35)	-1.11 (-1.26; -0.96)	-0.11 (-0.22; -0.01)	0.06 (-0.06; 0.19)
Historical change in precipitation	0.78 (0.61; 0.95)	0.46 (0.34; 0.59)	0.55 (0.41; 0.68)	0.70 (0.52; 0.88)	0.51 (0.37; 0.65)	0.25 (0.12; 0.38)
In situ diversification rates	0.31 (0.21; 0.40)	0.21 (0.11; 0.32)	0.36 (0.24; 0.47)	0.38 (0.25; 0.50)	0.39 (0.28; 0.51)	0.29 (0.18; 0.41)

[1] Mean (Lower CI; Upper CI)

Chapter 3

Climatic frequency drives specialisation in biological communities: insights from simulations and tetrapods worldwide

3.1 Abstract

Climate profoundly shapes biological communities, dictating their diversity, structure, and function. Although spatial heterogeneity in climatic conditions is often associated with more generalist species, the role of climatic frequency has been largely ignored. We identify that a critical, yet underexplored dimension of this relationship, the spatial frequency in climate—how often certain climatic conditions recur across space—strongly affects climatic specialisation in biological communities. We first analyzed global climatic conditions and the geographical distributions of more than 30,000 species belonging to four major taxa of tetrapods: amphibians, birds, mammals, and reptiles. We then used an array of theoretical simulations, we demonstrate that rare environments can limit the specialisation within communities regardless of the characteristics of the environment itself. Our findings reveal that common environments put generalist species at a competitive disadvantage as they are outcompeted by specialists. Conversely, rare environments hinder specialization, facilitating the prevalence of generalists. Our conclusions demonstrate that beyond within-community environmental averages and variation, the frequency of a given set of environmental conditions also affects how specialist and generalist species are selected to inhabit local communities.

3.2 Introduction

Climate—the long-term trends of temperature, precipitation and other meteorological variables—profoundly shapes ecosystem structure and dynamics (Currie & Paquin 1987; Parmesan 2006; Fine 2015; Rammig & Mahecha 2015). Through its interaction with species-specific adaptations, which confer varying tolerances to specific conditions (Hutchinson 1957), climate determines the spatial and temporal success of individuals and populations (Holt 2009). Consequently, climate delineates geographical boundaries of species distributions (Sexton *et al.* 2009), regulates their population abundances (Gaston 2009b), influences their phenological timing (Forrest & Miller-Rushing 2010;

Lamers *et al.* 2023), and shapes their interactions with other species (Englund *et al.* 2011). These factors collectively contribute to the unique composition of biological communities (Zhang *et al.* 2018; Oita *et al.* 2021; Terry *et al.* 2022), underpinning global biodiversity patterns (Hawkins *et al.* 2003; Wang *et al.* 2009; Vázquez-Rivera & Currie 2015).

The consensus that rapid anthropogenic climate change is profoundly altering Earth's ecosystems (IPCC 2014; Cook *et al.* 2016; Pecl *et al.* 2017; Díaz *et al.* 2019) has catalysed extensive research into the ecological responses to climate. Most studies have focused on the effects of average conditions, and to a lesser extent, variability and extremes, in climate on biodiversity (*e.g.*, Easterling *et al.* 2000; Craine *et al.* 2012; Solow 2017; Zhang *et al.* 2018; Terry *et al.* 2022). However, few have recognized how spatially common and rare climates influence patterns of biodiversity (but see Parmesan 2006; Meyer & Pie 2018; Fournier *et al.* 2020; Coelho *et al.* 2023; Cutts *et al.* 2023).

In this study, we established the spatial frequency of climatic conditions as a critical, yet overlooked, driver of species occurrence and assembly patterns. By analyzing empirical data from over 26,000 species of tetrapods (four-limbed vertebrates) and using theoretical models of ecological dynamics, we demonstrated that the frequency of climate across space significantly influences species distributions and coexistence based on their climatic specializations. These effects are beyond direct climatic controls on climatic specialisation along the specialisation gradient. Our findings not only highlight an essential factor in community assembly, but also have significant implications for understanding ecological responses to climate change. Alterations to spatially rare climatic conditions, such as contraction or disappearance, across geographical scales have the potential to profoundly alter biological communities (Saxon *et al.* 2005; Williams *et al.* 2007).

Every species has a realized ecological niche, representing the set of environmental conditions that allow its persistence, as conceptualized by Hutchinson (1957). The breadth of the niche describes the range of habitats or resources a species utilizes. Species with narrow niche breadths are termed 'specialists', and are specialized on (or constrained to) exploiting reduced sets of environmental conditions (Smith 1982; Brown 1984). Conversely, species with wide niche breadth are termed 'generalists' and are adapted to exploit a broader spectrum of environments, often at the cost of reduced efficiency in any particular niche dimension or component (Wilson & Yoshimura 1994; see McPeek 1996; Morris 1996; Chase & Leibold 2003).

Climate, in terms of both spatial average and variability (*e.g.*, within patches, combinations of patches, or regions), not only imposes physiological constraints that filter specialists from regions with non-optimal conditions but also influences the strength and outcomes of species interactions (Pither 2003; Fauteux *et al.* 2021; Antão *et al.* 2022). While generalists can persist across broader climatic gradients, it is widely assumed they may be outcompeted by specialists within their optimal conditions (MacArthur & Levins 1964; Morris 1996). This dynamic suggests a potential for competitive exclusion of generalists, where antagonistic interactions among overlapping niches preclude stable coexistence (Hardin 1960). However, empirical evidence often contradicts this simplistic expectation (*e.g.*, Wilson & Yoshimura 1994; Morris 1996; Abrams 2006; Bar-Massada 2015; Brazeau & Schamp 2019). Sustained coexistence between generalists and specialists is known to be possible due to temporal variation and spatial heterogeneity in environmental conditions (Kassen 2002; Nagelkerke & Menken 2013), resource partitioning (Schoener 1974; Chase & Leibold 2003), colonization-extinction trade-offs (Wilson & Yoshimura 1994; Egas *et al.* 2004), mutualistic interactions (Bastolla *et al.* 2009), fitness variation (Chesson 2000b), dispersal limitation (Büchi &

Vuilleumier 2014), evolutionary rescue (Bono *et al.* 2015), all of which act to mitigate competition and promote community diversity.

The spatial frequency of climate, reflecting the commonness or rarity of climatic conditions over spatial extents, may significantly influence species distributions and their co-occurrences, particularly based on their specialization strategies. Specialization on scarce resources is typically infrequent (Kassen 2002). Rare climates, which are often spatially fragmented and more unstable, may favour generalist species because of their resilience to edge effects and environmental instability (Holway 2005; Magura *et al.* 2017). Specialists, on the other hand, may be especially susceptible to environmental and demographic fluctuations and face restricted movements in rare, unstable, or highly variable climates (Lotterhos *et al.* 2021). Conversely, common climates could enable the dominance of specialist species if they outperform generalists under stable environmental conditions (Futuyma & Moreno 1988; Kassen 2002).

It is therefore intuitive to expect that extensive climatic specialisation is uncommon in rare climates. However, this assumption has been challenged by findings of increased variability in specialisation strategies with climatic rarity in angiosperm communities across the contiguous United States (see Fournier *et al.* 2020). The mechanisms proposed to underlie these effects—namely, dispersal limitation, environmental heterogeneity, and source-sink dynamics—provide a compelling explanation for increased coexistence among generalist and specialists in rare climates. Despite the few studies on the isolated effects of climatic frequency on diversity patterns across ecological communities (*e.g.*, Fournier *et al.* 2020; Coelho *et al.* 2023), a comprehensive empirical and theoretical approach that integrates these mechanisms is still missing.

We investigate how the spatial frequency of environmental conditions drives environmental specialisation through both empirical and theoretical lenses. First, we analyze global climatic conditions alongside the geographical distribution of tetrapods, assessing how the climatic niche breadth of amphibians, birds, mammals, and reptiles is influenced by the commonness of climatic conditions across space. Second, leveraging the theory of metacommunities—where communities are spatially linked by the dispersal of multiple potentially interacting species (Hanski 1999; Leibold *et al.* 2004)—, we conduct mechanistic simulations of minimal population dynamics under explicit spatial and environmental structure. Metacommunity simulations, which are well-established for reproducing and elucidating the mechanisms that maintain biodiversity patterns across spatialized landscapes (Thompson *et al.* 2020), provided us a controlled framework to understand how the spatial frequency of environmental conditions, environmental heterogeneity, disturbance, and dispersal influence species distributions and coexistence dynamics along specialisation gradients. The combined theoretical and empirical allowed us to test predictions that rare environments (here, 'climates') constrain specialization while enabling the coexistence of both generalists and specialists. We found that climatic frequency strongly regulated species distributions and coexistence along the specialisation gradient, consistently across taxonomic groups, geographical scales, and simulated communities. Our empirical observations from tetrapod communities globally align with our theoretical models, suggesting a generalizable pattern governing ecological specialization and community assembly through environmental frequencies across space.

3.3 Results

3.3.1 The distribution of climatic frequency worldwide

We first investigated the distribution of climatic frequency across terrestrial regions worldwide and its impact on the specialization of tetrapods and their communities.

We began with overlaying Earth's terrestrial landscapes onto a hexagonal tessellation, with each hexagon representing an ecological community. This tessellation, superior to square-grid cells (Birch *et al.* 2007), formed the basis of our analyses of climatic conditions and species distributions (see Methods). Recognizing the scale-dependence of climatic and ecological processes (Levin 1992; Ricklefs & Schluter 1993; Chase 2014; Chase *et al.* 2018), we calculated the spatial frequency of climatic conditions across three hierarchical geographical scales: global, hemispherical, and biome. These scales, commonly used in studying spatial scale-dependence in community ecology, are closely linked to eco-evolutionary mechanisms shaping regional biodiversity (Ricklefs & Latham 1992; *e.g.*, Jenkins & Ricklefs 2011; Mucina 2019). For simplicity, we present findings at the global scale in the main manuscript and provide detailed analyses for the other scales within the Supporting Information (see Supporting Information at Section 3.8 and Section 3.10).

We first extracted contemporary climatic conditions for each hexagon from a set of high-resolution eight bioclimatic variables derived from monthly temperature and precipitation (Fick & Hijmans 2017). These bioclimatic variables are often associated with species' physiological limits, and constrain their distributions and ecosystem dynamics (*e.g.*, Garcia-Porta *et al.* 2019). To condense climate data while preserving covariance among climatic variables, we applied a principal component analysis, selecting the first principal components that cumulatively accounted for more variation in climate than expected by a broken-stick model (see Jackson (1993); see Table 3.1).

Next, we described the spatial commonness of climate by computing multivariate binned kernel density estimates on the selected climatic principal components (Duong & Hazelton 2003). Multivariate approaches are preferred over simpler univariate analyses of climatic conditions because it integrates the interplay among multiple climatic factors and their spatial heterogeneity (Zscheischler & Seneviratne 2017; Abatzoglou *et al.* 2020). This analysis yielded estimates of the spatial frequency distribution of climatic conditions, ranging from exceedingly rare to very common, across terrestrial communities worldwide (excluding Antarctica; see Figure 3.1, Figure 3.5).

We revealed that abrupt transitions from common to infrequent climates typically occur near major mountain ranges, such as the Andes, the Alaska and Saint Elias ranges, the Himalayas, and the Caucasus chains (see Figure 3.1, Figure 3.5). Arid deserts and polar climates emerged as the rarest climates, whereas tropical savannas, rain forests, and monsoon climates were the most common (see Table 4.1, and Figure 3.6).

The predominance of rare climates in mid- to high-elevation and coastal regions aligns with previous studies on climatic frequency across various geographical extents (*e.g.*, Batllori *et al.* 2014; Wang *et al.* 2018; Fournier *et al.* 2020; Cutts *et al.* 2023). Our analysis also revealed that rare climates have higher densities at broader geographical scales compared to narrower ones (details in Figure 3.5, and Figure 3.6). Because environmental (climate) isolation and fragmentation can lead to reduced dispersal, increased vulnerability to local extinctions, and limited gene flow among

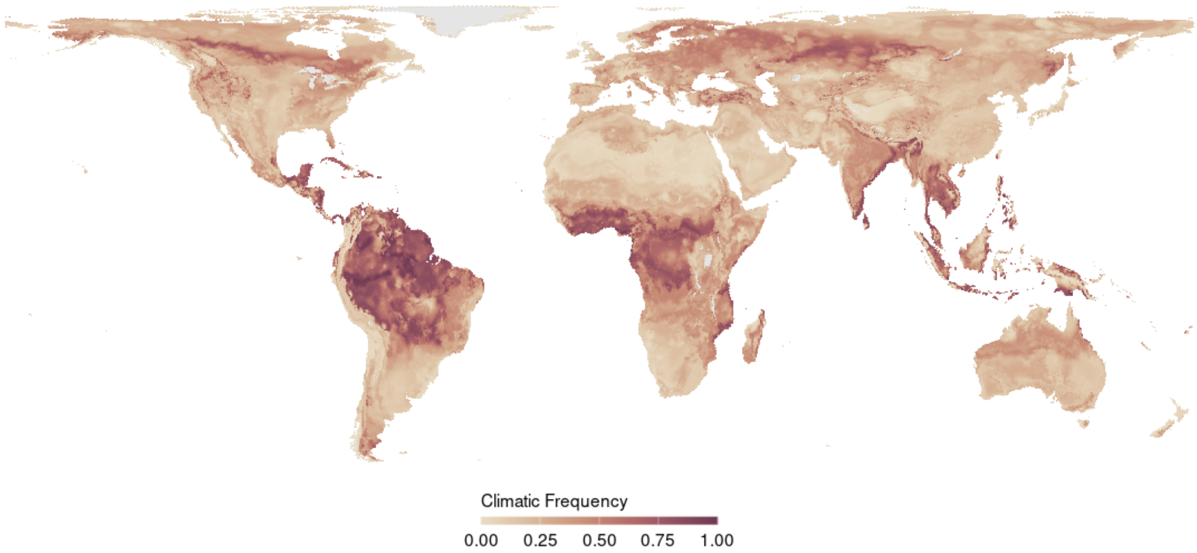


Figure 3.1: **The distribution of global-scale climatic frequency across space.** Climatic frequency was calculated via multivariate kernel density estimates on the principal components of eight bioclimatic variables representing precipitation and temperature.

populations (Quinn & Harrison 1988; Tilman *et al.* 1994; Fahrig 2003), which affect community structure and specialisation dynamics (see Gamboa *et al.* 2024), we also investigated the extent to which common climatic conditions are better geographically connected and widespread in relation to rare climates. By computing the average climatic distances weighted by geographical distances of each geographical cell (*i.e.*, ecological community) in relation to all others, and contrasting these with the frequency of climate across space, we observed that communities withing rare climates are climatically distinct and isolated, while communities withing common climates are better connected and exhibit more similar climatic conditions (see Figure 3.2, Figure 3.10; Section 3.9). This pattern suggests that common climates promote higher connectivity and stability within ecological communities, while rare climates contribute to fragmentation and ecological isolation.

3.3.2 Climatic frequency restricts specialisation in tetrapod communities globally

Using geographical distribution data of 26,971 terrestrial four-limbed vertebrate species — including 4,409 amphibians, 10,384 birds, 4,994 mammals, and 7,184 reptiles — we investigated the effects of climatic frequency on climatic specialization. Our analysis considered both the climatic conditions themselves and the heterogeneity of climate within each community (geographical cell).

We measured climatic specialization for each species by calculating their climatic tolerances (*i.e.*, climatic niche breadth) using the outlying mean index (Dolédec *et al.* 2000), which describes the hypervolumetric space of a species' niche across environmental variables (*sensu* Hurlbert 1978; also see Thuiller *et al.* 2005). Here, the climatic niche breadth of each species was computed based on the same principal components from our prior analyses to estimate the spatial frequency

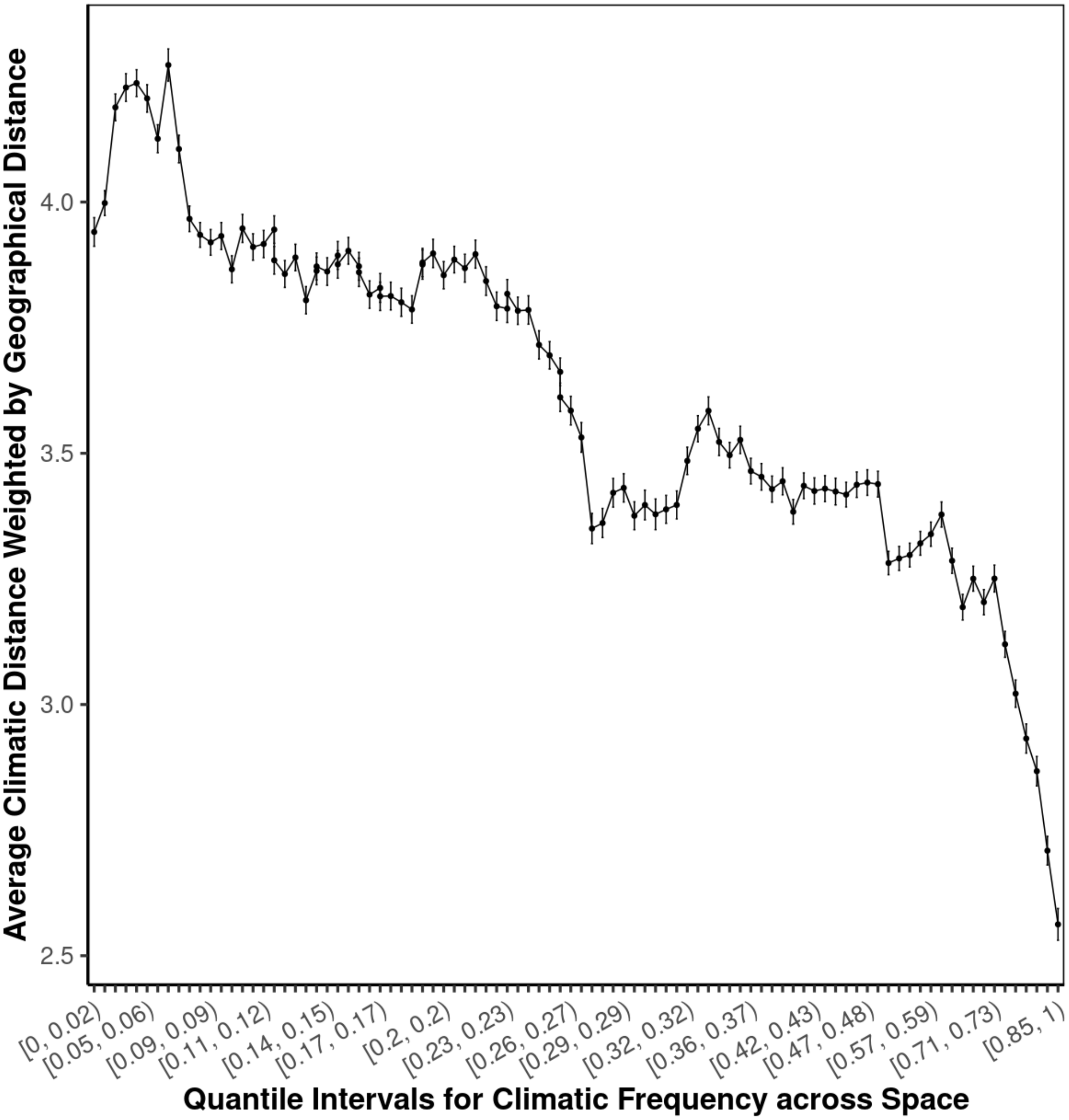


Figure 3.2: **Rarer climates are more climatically distinct and geographically isolated than common climates globally.** The average climatic (Mahalanobis) distance was weighted by the average geographical distance between all geographical cells (hexagons) across percentiles of climatic frequency across global terrestrial landscapes (n = 2424 geographical cells per percentile; see Methods and Supporting Information in Section 3.9). Vertical bars represent 95% confidence intervals.

of climates (Figure 3.1, Figure 3.5).

To assess the effects of climatic frequency on climatic specialization across taxonomic groups and geographical scales in tetrapod communities, we performed a series of double generalized linear models [DGLMs; Smyth (1989); Smyth & Verbyla (1999)]. DGLMs extend the generalized linear model framework by simultaneously modelling the mean and dispersion (variance) of the response variable. This approach is particularly suitable when the variance in the response variable is not constant (Smyth 1989). By capturing both the effect of mean climatic frequency and its variability across ecological contexts, we can make inferences about the dynamics of co-occurrence and specialization within communities.

Our results provide strong evidence that climatic frequency significantly influences community specialization across all tetrapod taxa. On a global scale, we found that the spatial frequency of climatic conditions reduces the average niche breadth within tetrapod communities (see Figure 3.3, and Table 3.2). Communities in very common climates harbour mostly specialist species, while communities in rare climates harbour more generalist species (see Figure 3.3, Figure 3.7). We also observed that the variability in community mean niche breadth decreases with climatic frequency, suggesting that communities in rare climates favour the co-occurrence of specialist and generalist species while specialists dominate in common climates (see Figure 3.3). These models explained 29% of the variation in community average niche breadth in amphibians, 38% in birds, 44% in mammals, and 19% in reptiles (see Table 3.2).

The responses of climatic specialisation in tetrapods to climatic frequency were qualitatively consistent for climatic frequency measured across more geographically restricted extents (see Figure 3.8 and Figure 3.9). Interestingly, in amphibian and reptilian communities, higher climatic frequency was associated with reduced variability in specialisation across all scales, reflecting more specialized niche adaptations in response to frequent climatic conditions. In birds and mammals, while the global and hemispheric scales showed similar trends, the effect was less pronounced at the biome scale (see Table 3.2).

Climatic frequency continued to negatively influence climatic specialization in tetrapod communities in our statistical models accounting for the influence of climatic heterogeneity (see Table 3.3). When considering climatic heterogeneity along with climatic frequency within communities, our models explained 30% of the variation in average niche breath for amphibians, 40% for birds, 47% for mammals, and 32% for reptiles (see Table 3.3). Notably, the effect sizes for climatic frequency were often stronger than those of climatic heterogeneity, which is one of the strongest predictors of environmental generalisation in ecological communities (Levins 1968; Futuyma & Moreno 1988; Kassen 2002; Ackermann & Doebeli 2004). This pattern remains evident across hemispheric and biome scales, although the strength of the relationship varies among taxonomic groups (see Table 3.3).

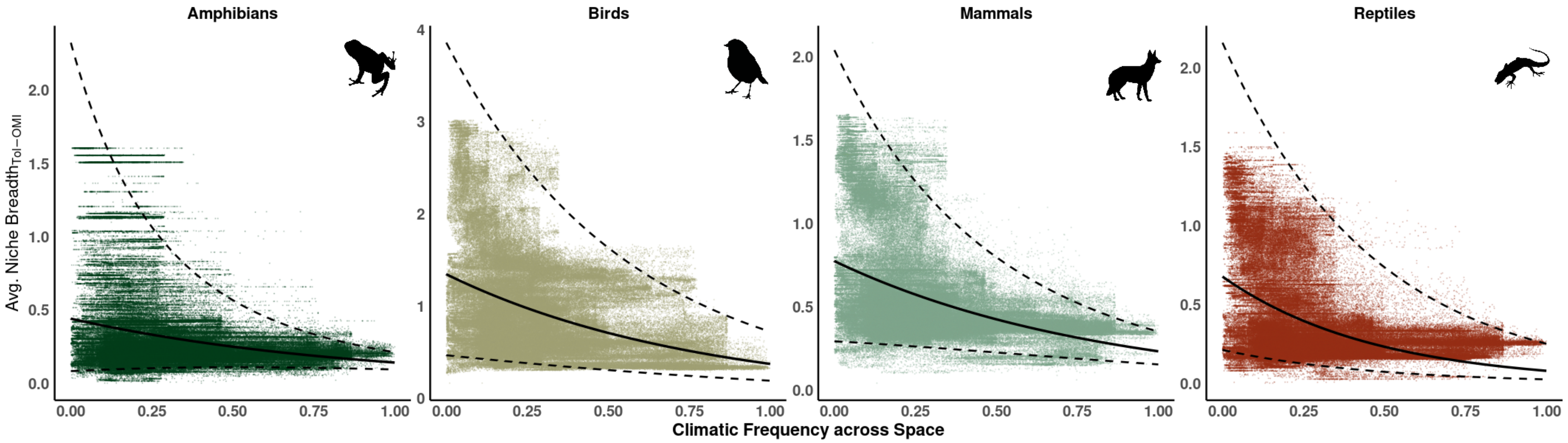


Figure 3.3: **The spatial frequency of climatic conditions strongly constrains specialisation in tetrapods worldwide.** The spatial frequency of climatic conditions negatively influenced the average of niche breadth in amphibian, bird, mammal, and reptilian communities. Each point represents a community (geographical cell). Across all four groups of tetrapods and their communities, common climates allow for increased variation in niche breadth while rare climates favour decreased niche breadth (*i.e.*, specialisation). The calculation of climatic frequency for each community at the global scale was based on contemporary climatic conditions across the globe. The continuous and dashed lines respectively represent mean and dispersion fits for effects of climatic frequency on community weighted average niche breadth using double generalized additive model with Gamma log-link functions (see Methods). We credit the animal silhouette icons to PhyloPic (phylopic.org).

3.3.3 Simulations of ecological dynamics demonstrate that environmental frequency influences ecological specialization

To elucidate the ecological mechanisms and dynamics behind through which climatic frequency mediates and shape large-scale ecological dynamics, we employed a theoretical simulation approach that allows for a controlled exploration of ecological processes (Huston *et al.* 1988; see Levin 1992). We used a process-based metacommunity framework to simulate population dynamics across a spatially explicit landscape (detailed in Methods). This model, which integrates both deterministic and stochastic elements, encompassed metacommunities undergoing reproduction, competition, dispersal among patches (hereafter "internal dispersal"), and dispersal from the regional pool (hereafter "external dispersal"), population limit regulation, and disturbance. Our model draws heavily from well-established studies (Büchi & Vuilleumier 2014; *e.g.*, Thompson *et al.* 2020).

Each metacommunity in our simulation consisted of a network of patches, or local communities, situated along a spatially autocorrelated, normally distributed and temporally static environmental gradient, such as temperature or precipitation (*sensu* Hanski 1999). We initiated communities with individuals randomly sourced from a regional pool, where species varied among themselves in terms of environmental niche breadth and optima.

Our simulations explored three ecological scenarios that cumulatively incorporated more complexity in the responses of populations to environmental conditions during reproduction and competition (see Methods). This design enabled us to assess the extent to which the modulation of spatial frequency of climate on specialisation arises from different environmental controls on population dynamics and species coexistence.

The first and most basic ecological scenario, the "equal competition" scenario, relates population growth rates to environmental suitability. Here, the closer species and populations were to their preferred environmental conditions (*i.e.*, the overlap of their niche breadth and proximity to their niche optima), the higher was their population growth (Hutchinson 1957). This scenario disregarded the direct effects of environmental conditions on species' competitive performances and the intensity of interspecific competition, thereby assuming that individuals of all species competed equally. Here, coexistence was unstable and primarily driven by stochastic processes (Hubbell 2001).

The second and third scenarios progressively incorporated environmental influences into competitive interactions. In the "niche overlap competition" scenario, species whose environmental optima were closer to the patch's condition had superior competitive performance (Tilman 1982, 1994). In the more complex "niche overlap and environmental proximity" scenario, in addition to varying competitive effectiveness based on proximity to optimal environmental conditions, species with overlapping environmental niches faced more intense competition (Chesson 2000b, a). These dynamics ensured that competition coefficients dynamically adjusted in response to environmental suitability and species' specialisation strategies (see Amarasekare 2003 and references therein).

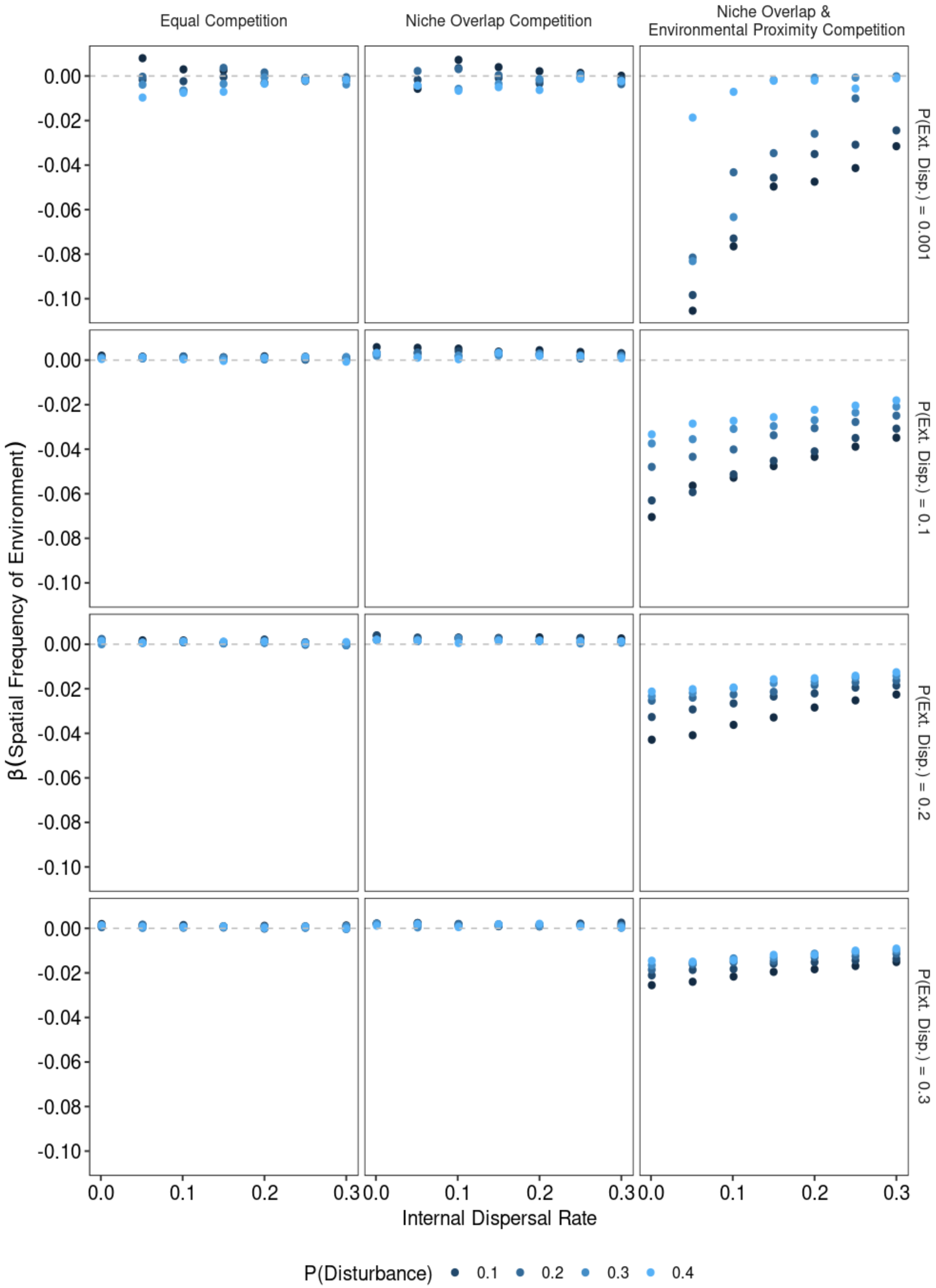
Alongside deterministic environmental controls on population dynamics, dispersal and disturbance significantly impact community composition by altering immigration, extinction, and growth rates of individuals and species across patches (Vellend 2016). Dispersal can counteract the effects of local environmental selection and competitive exclusion on population dynamics, thereby promoting local species diversity and community homogenization through the influx of individuals that might otherwise face extinction in a metacommunity (Leibold *et al.* 2004). Conversely, stochastic disturbances reshape community assembly at both local and regional scales by driving extinction-colonization dynamics, mass effects, and dispersal, thereby introducing variability into community composition (Altermatt *et al.* 2011; Vanschoenwinkel *et al.* 2013; Ojima & Jiang 2017).

To further examine the mechanisms behind effects of climatic frequency on specialisation, we simulated scenarios with varying rates of internal (among-patch) and external (from the regional pool) dispersal, alongside stochastic disturbances (see Fukami 2005). If our prediction holds that specialization in rare environments is infrequent, then under decreased disturbance and internal and external dispersal rates, specialists should outperform their co-occurring generalists and thus dominate spatially common environments. Conversely, when disturbance and dispersal rates increase, generalists—assumed to be more resilient, better colonizers, and prolific dispersers (Futuyma & Moreno 1988; Devictor *et al.* 2008; Verberk *et al.* 2010; Büchi & Vuilleumier 2016)—would thrive alongside or potentially outperform specialists in their optimal environments.

We ran each simulation for 1,400 steps, which provided sufficient variation in community dynamics to establish equilibrium states. At the conclusion of our simulations, we computed the spatial frequency of environmental conditions using a univariate kernel density estimation approach (Duong & Hazelton 2003; see Chacón & Duong 2018), and investigated how it influenced ecological specialisation in the simulated metacommunities.

Across scenarios, we fitted ordinary least square regressions, with response variables describing niche breadth and predictive variables for the spatial frequency in environmental conditions across communities. This was done separately for each combination of internal dispersal, external dispersal, disturbance, and ecological competition scenarios.

The spatial frequency of environmental conditions was strongly associated with specialization within the communities we simulated (see Figure 3.4). How strongly species and communities responded to environmental frequency varied with the regimes of dispersal, disturbance and competition we implemented.


Equal Competition
Niche Overlap Competition
Niche Overlap & Environmental Proximity Competition
P(Ext. Disp.) = 0.001
P(Ext. Disp.) = 0.1
P(Ext. Disp.) = 0.2
P(Ext. Disp.) = 0.3
β(Spatial Frequency of Environment)
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
0.0
0.1
0.2
0.3
Internal Dispersal Rate
P(Disturbance)
● 0.1
● 0.2
● 0.3
● 0.4

The abundance-weighted average of niche breadth across communities strongly decreased with the spatial frequency of environmental conditions when species competitive performance and the intensity of competition were mediated by the environment (*i.e.*, through niche overlap and environmental matching) (see Figure 3.4). These effects were especially stronger under decreased disturbance, internal and external dispersal rates (see Figure 3.4).

the responses of community niche breadth to the spatial frequency of environmental conditions (Figure 3.4). Importantly, the tendency for niche breadth to decrease with spatial frequency of the environment was less evident in scenarios with decreased or absent environmental controls on competition (equal competition and niche overlap competition scenarios; Figure 3.4). Increasing internal dispersal (or between-patch dispersal) and disturbance also homogenized environmental frequency, but their effects were lower than the ones of external dispersal.

We assessed the robustness of these findings through simulations of metacommunity dynamics spanning a broad range of parameters to reflect a diverse array of ecological scenarios see 3.4. Varying the number of patches, the diversities of the local community and of the species pool, and the intensity of the dispersal decay for internal dispersal produced qualitatively similar negative influence of climatic frequency across space on specialisation see Supporting Information in 3.13, Figure 3.12.

Taken together, these results suggest that environmental specialisation increases with the spatial frequency of environmental conditions in simulated metacommunities. They demonstrate the tendency of communities in rarer climates to favour increased co-occurrence of generalists and specialists, aligning with the observations from our empirical analyses. This pattern suggests that the rarity of environmental conditions creates a niche space where both generalists and specialists can find suitable conditions to thrive, potentially because of reduced competitive pressures for specialists.

3.4 Discussion

Our study demonstrates that the spatial frequency of climatic conditions significantly influences ecological communities. By analysing results from mechanistic simulations and empirical data on tetrapods within global climates, we identified consistent patterns showing that common envi-

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Figure 3.4 *(preceding page)*: **Community-level environmental specialisation responses to the spatial frequency of environmental conditions in simulated metacommunities under different ecological competition scenarios, and varying rates of disturbance, external dispersal and internal dispersal.** Each point represents a different simulation under a combination of ecological scenarios, with varying rates of disturbance, external dispersal, internal dispersal, and environmental mediation in competition. Here, β denotes the ordinary least square regression coefficient of the spatial frequency of the environment in each community on the community's abundance-weighted average of environmental niche breadth.

ronments promote specialization. In contrast, rare environments support the coexistence of both specialists and generalists. These findings have important implications for understanding community assembly and species distribution patterns in response to varying climatic conditions.

Ecological theory posits that environmental specialization is driven by the availability and distribution of suitable habitats, mediated by competition, dispersal, and disturbance dynamics (Hutchinson 1957; Chesson 2000b; Leibold *et al.* 2004; Büchi & Vuilleumier 2014). Our findings indicate that these dynamics are significantly influenced by the spatial frequency of climatic conditions. Our theoretical simulations revealed that the impacts of environmental frequency on specialization are most pronounced when both the intensity of competition and competitive performance are environmentally driven. Specifically, in scenarios where niche overlap and environmental suitability govern competitive interactions, communities in common environments exhibit higher levels of specialization compared to those in rare environments. This pattern supports the competitive exclusion of generalists by specialists in stable, common climates and suggests that niche differentiation mechanisms are at play in these frequent environments (MacArthur & Levins 1964; Tilman 1982). Consequently, species in common environments should show greater differences in their niche optima compared to species in rare climates, resulting in reduced niche overlap and increased specialization (Chesson 2000b).

Decreased external dispersal (immigration or invasion from the species pool) and internal dispersal (between-patch dispersal), along with reduced disturbance, amplified the effects of climatic frequency on specialization in our simulations. Reduced dispersal and disturbance rate led to stronger negative correlations between niche breadth and climatic frequency. This is because limited immigration restricts the influx of generalist species that might otherwise persist through mass effects, while decreased disturbance minimizes the opportunities for competitive release, allowing specialists to dominate in common climates (Hanski 1999; Chesson 2000a; Büchi & Vuilleumier 2014). Conversely, increased dispersal and disturbance rates buffer the specialization-promoting effects of climatic frequency. Higher external dispersal rates facilitate the continuous influx of species with varying niche breadths, promoting species diversity and reducing the dominance of specialists (see Vellend 2016 and references therein). Similarly, frequent disturbances create opportunities for generalists to recolonize and persist, thereby mitigating competitive exclusion and promoting coexistence (Altermatt *et al.* 2011).

Our empirical findings closely align with the predictions of our theoretical simulations, providing a mechanistic demonstration of the influence of climatic frequency on the selection of species to form local communities on the basis of their ecological specialization. Specifically, the mechanisms we identified can explain the observed patterns in tetrapods globally. Common climates tend to favour specialists among tetrapods due to increased environmental stability, allowing these specialists to exploit their niche optimally and out-compete generalists, who are less efficient in any specific niche (Chesson 2000b).

In common climates, where similar climatic conditions are spatially widespread (*i.e.*, better connected and more homogeneous), communities are often composed of species with narrow niche breadths (*i.e.*, specialists) that minimize niche overlap (Chesson 2000b). This high level of niche segregation is suggestive of competitive exclusion, where specialists, through effective resource partitioning and competitive superiority, dominate their preferred environments and exclude generalist species (Tilman 1994). Such niche segregation in common climates is further supported by the high beta diversity of their communities relative to their geographical proximity, indicating increased spatial turnover among communities with different species composition (see Supporting Information in Section 3.10; see Figure 3.11).

In contrast, rare climates, characterized by their spatial fragmentation and environmental variability, diminish the competitive advantage of specialists. Increased geographical and climatic isolation in rare climates (Figure 3.2, Figure 3.10) limits the dispersal opportunities for species, further influencing specialization patterns. Reduced internal dispersal hinders the spread of both specialists and generalists between communities (Leibold *et al.* 2004), leading to unique local community compositions and high beta diversity weighted by geographical distance (see Figure 3.11). These patterns are consistent across different spatial scales, emphasizing the broad applicability of our findings and the importance of spatial climatic frequency in shaping biodiversity patterns.

Our study also sheds light on how biodiversity might respond to climate change. As climatic conditions shift (Easterling *et al.* 2000; see IPCC 2014), the spatial frequency of environments changes, potentially leading to the contraction or disappearance of rare climates. These changes can alter the balance between specialists and generalists in ecosystems, affecting the coexistence among these groups, and driving the homogenization of communities towards specialization, impacting biodiversity (Saxon *et al.* 2005; Williams *et al.* 2007). Conversely, the emergence of new, rare climates (Radeloff *et al.* 2015) might create opportunities for generalists to thrive, likely shifting diversity patterns in communities.

We acknowledge the simplicity of our model framework and recognize that incorporating factors, such as evolutionary adaptation and temporal variations in environmental conditions, could add further complexities to these dynamics. Despite this, our study provides a solid foundation for understanding how climatic frequency influences community assembly across spatial scales. By linking our theoretical model to empirical patterns, we highlighted the importance of including spatial climatic frequency as a driver in ecological and biodiversity research. This approach should also deepen our understanding of species and community responses to climate change and aid in forecasting the impacts of shifting climatic conditions on biodiversity.

3.5 Methods

3.5.1 Empirical assessment

3.5.1.1 Study area

To spatially aggregate all biodiversity and climate data for our study, we established an equal-area flat-topped hexagonal tessellation covering Earth's terrestrial lands, compiled from Natural Earth (naturalearthdata.com) and projected to a Behrmann cylindrical equal-area projection. We opted for a hexagonal tessellation instead of a traditional square cell grid, because hexagons provide equidistant connections to neighbouring geographical cells. This feature ensures a more accurate representation of local movements and connectivity in ecological studies(Birch *et al.* 2007; White & Kiester 2008). Each hexagon covered an area of 541.3 km^2 with a short-diagonal length of 25 km. After eliminating hexagons with less than 50% terrestrial land coverage, we retained 248,139 hexagons (globally) for analysis.

3.5.1.2 Species data

We gathered geographical distributions for amphibians, birds, mammals, and reptiles from the IUCN Red List of Threatened Species database (IUCN 2022). We created presence-absence matrices for each tetrapod group by intersecting species ranges with our hexagonal tessellation, ensuring all data were aligned to the same equal-area projection. A species was considered present in a hexagon if it occupied at least half of its area.

3.5.1.3 Climate data

We compiled nineteen bioclimatic variables from WorldClim version 2.1 (Fick & Hijmans 2017), which are derived from monthly temperature and precipitation data averaged between 1970 and 2000. These variables underline the impact of temperature, precipitation, and energy constraints on species distributions. We projected and aggregated these variables from their original resolution of 30 arc-seconds resolution to our equal-area hexagonal tessellation by computing the mean values of the pixels contained within each hexagon. We then log-transformed non-symmetrically distributed variables, primarily precipitation-related, to minimize data heteroscedasticity. Subsequently, we identified and removed highly correlated bioclimatic variables using the variance inflation factor, determined from iterations of 10,000 randomly selected hexagons.

Our refined dataset included eight bioclimatic variables: mean annual temperature (BIO 1), mean diurnal range (BIO 2), temperature seasonality (BIO 4), mean temperature of the wettest quarter (BIO 8), logarithm of 1 plus annual precipitation) (BIO 12), precipitation seasonality (BIO 15), logarithm of 1 plus precipitation of the warmest quarter (BIO 18), and logarithm of 1 plus precipitation of the coldest quarter) (BIO 19).

3.5.1.4 Spatial climatic frequency

We characterized the spatial frequency of climatic conditions across communities using a probability density estimation approach.

We first reduced the dimensionality of the climatic dataset through principal component analysis (as in Graham 2003). We retained the principal components that captured a significant portion of the climatic variation as determined by comparison of eigenvalues against the broken-stick distribution (see Jackson 1993). These orthogonal principal components summarised 89.78% of the global variation in climate (see Table 3.1), and were then used to calculate indices of spatial climatic frequency and spatial climatic heterogeneity.

The probability density estimation approach was based on a multivariate kernel density applied to the retained principal components, using a multivariate generalisation plug-in for bandwidth matrix selection (see Jones 1994; Duong & Hazelton 2003; Chacón & Duong 2018).

To facilitate the interpretation of the density distribution, we scaled values to a range of zero and one. These scaled values correspond to the frequency (or commonness) of climatic conditions across the geographical space. Communities inhabiting geographical cells with lower climatic frequency values experience rarer combinations of climates, while those with higher encounter more common climatic conditions.

3.5.1.5 Species climatic niche breadth, average community climatic niche breadth

We estimated climatic niche breadth for each species with the outlying mean index ordination method [OMI; Doledec *et al.* (2000)]. OMI derives species niche position, breadth, and inertia within a hypervolumetric space defined by a set of environmental variables [*sensu* the Hutchinsonian multidimensional niche; Hutchinson (1957)]. This method provides equal weight to species-rich and species-poor sites. Within the OMI framework, species tolerances are derived by measuring the dispersion of each species across their realized niches (*sensu* Hurlbert 1978). Here, we used the same principal components retained from the earlier principal component analysis on climatic variation. Species with high tolerance values are considered generalists, occurring across a range of wide climates, while those with low tolerance values are specialists, restricted to a narrower range of climatic conditions. We used the average of climatic niche breadth within a geographical cell as a measure of community specialisation.

3.5.1.6 Statistical analyses

To evaluate the impact of climatic frequency (predictor) on community mean climatic niche breadth (response), we performed a series of double generalized linear models (DGLMs) (Smyth 1989; Smyth & Verbyla 1999), across taxonomic groups and geographical scales in tetrapod communities. DGLMs extend the generalized linear model framework by jointly modeling the mean and dispersion of the response variable, making them particularly suitable when the variance is not constant (Smyth 1989). By capturing the direct effects of climatic frequency on average community specialisation and the dispersion of niche specialization within communities, we could assess how climatic frequency lead to specialisation, as well as whether rarer conditions lead varying niche breadths, *i.e.*, a mix of specialists and generalists. We specified the models with a Gamma family distribution and a log-link function to account for the non-normal distribution of community mean climatic niche breadth.

3.5.2 Theoretical simulations and model specifications

3.5.2.1 Landscape construction

To simulate the heterogeneity observed in natural landscapes, we constructed a spatial environment composed of 400 discrete, equally spaced square cells. This structure enabled our process-based metacommunity simulation of large-scale population dynamics and captures ecological dynamics with manageable complexity (Weinstein & Shugart 1983; see Bowers & Harris 1994).

To mitigate boundary-induced anomalies (*i.e.*, edge effects) typical in spatial simulations, we applied a toroidal structure to our landscape, wrapping the space around both horizontal and vertical axes. This procedure allows for spatial dynamics (*e.g.* migration) to cross over from the edges to their opposing sides of the landscape (see Supporting Information in Section 3.11).

A single variable of environmental conditions (e_x) characterized all patches, and ranged between 0 and 1, with mean and variance of 0.5, following a normal distribution, as it is relevant for representing a broad range of ecological scenarios (Macarthur & Levins 1967; Chesson 2000b).

We conditioned environmental conditions to be positively auto-correlated so that neighbouring cells are more environmentally similar, a common feature in real environments (see Supporting Information in Section 3.11).

3.5.2.2 Regional pool and local populations

We created a regional species pool consisting of 1,000 species, each characterized by a randomly assigned environmental niche optimum, ranging from 0.05 to 0.95, which represents the ideal environmental condition for each species. Additionally, each species was given an environmental niche breadth, ranging from 0.01 to 0.5. These attributes facilitate examining species' responses to varying environmental conditions (Hutchinson 1957; Chesson 2000b). From this regional pool, we sampled 200 species along with their corresponding environmental niche optima and breadths and distributed them across the landscape. Mirroring natural systems where species are introduced sequentially and at low abundances, we placed a random number of individuals, up to a maximum of 250, on 10 randomly chosen patches for each selected patch. These parameters were chosen to strike a balance between computational efficiency and ecological realism.

3.5.2.3 Model dynamics

Our model simulates species population dynamics across the landscape over generations, incorporating the following phases: (1) reproduction and competition, (2) internal dispersal between patches and external dispersal from the regional pool, (3) population regulation and (4) disturbance. Throughout these phases, populations changes within each patch are driven by stochastic and deterministic events that influence the relative fitness of taxa.

We incorporated demographic stochasticity into all phases to reflect the unpredictability of natural ecosystems, consistent with previous demographical models used in studying competitive communities and metacommunities (Vellend 2016; Levins & Culver 1971; *e.g.*, Fournier *et al.* 2017; Shoemaker *et al.* 2020; Thompson *et al.* 2020; Khattar *et al.* 2021; Khattar *et al.* 2024).

3.5.2.3.1 Reproduction and competition phases

To simulate reproduction and interspecific competition dynamics within patches, we integrated the Beverton-Holt discrete time population growth with generalized Lotka-Volterra, which are spatially explicit for competition and dispersal. The Beverton-Holt model captures population reproduction dynamics (Beverton & Holt 1957), while the generalized Lotka-Volterra framework elucidates the mathematical conditions under which competing species either coexist or exclude one another based on competition intensity (Lotka 1925; Volterra 1926). These models are widely recognized for their ability to simplify the complex dynamics of ecological interactions (Shoemaker *et al.* 2020; *e.g.*, Thompson *et al.* 2020; Guzman *et al.* 2022; Khattar & Peres-Neto 2023).

The population N_{t+1} of species i at time $t+1$ in any given patch x, prior to dispersal is determined by:

$$N_{i,t+1} = \frac{r_{i,t} \times N_{i,t}}{1 + \sum_j \alpha_{ij} \times N_{j,t}},$$

where the numerator represents the population growth for N_t, while the denominator accounts for the effects of interspecific competition from all species present in that patch on N_t. In the numerator, $r_{i,t}$ denotes the effective (or intrinsic) growth rate of species i at time t, and in the denominator, α_{ij}, the competition coefficient, quantifies the impact of species j on species i (see Shoemaker *et al.* 2020).

The final population of each patch x in any given time step as a positive number drawn from a Poisson distribution ranging from 0 to N_{t+1}.

Intrinsic growth mediated by environmental niche matching-mismatching

We modelled population growth across patches as a function of species-specific niche preferences—namely, their environmental optima and breadth, which strongly influence species reproductive success across different habitats (see Holt & Gaines 1992) and the environmental conditions of each patch, incorporating stochasticity. To ensure that reproductive fitness is influenced by environmental conditions, we adjusted species intrinsic growth rates based on the environmental conditions of the patch, the species' environmental optima, and species' niche breadth using:

$$r_{i,t} = r_{max} \times e^{-\frac{(u_i - e_x)^2}{2 \times s_i^2}},$$

where, r_{max} represents the maximum potential growth rate of species, u_i denotes the species' niche optimum, which is the environmental condition at which the species achieves maximum growth rate, r_{max}, e_x the environmental condition of patch x, and s_i is the species' niche breadth, with larger values reflecting a broader environmental tolerance.

This equation, derived from the Gaussian function (*sensu* Macarthur & Levins 1967), models the species' response to the environmental gradient, determining that the growth rate of a species declines as the environmental conditions move away from the species' niche optimum Thompson *et al.* (2020).

Regulating density-dependent competition by environmental niche matching-mismatching and by environmental niche overlap

To investigate how spatial climate frequency and variability influences specialization, population dynamics, and species coexistence, we incorporated three ecological scenarios, progressively adding complexity to the population responses to environmental conditions during competitive interactions:

1. The "equal competition" scenario represents the most basic scenario, where reproductive rates are tied to environmental suitability. In this scenario, a species' reproductive success is proportional to its proximity to preferred environmental conditions, determined by the

overlap of its niche breadth with other species and closeness to its niche optima (Hutchinson 1957). Importantly, this scenario disregards the direct impact of environmental conditions on interspecific competition and competitive performance, assuming equal competition among all species. As a result, coexistence is unstable and primarily driven by stochastic processes (Hubbell 2001);

2. The second scenario, the “niche overlap competition” scenario, incorporates the influence of environmental optima on competitive performance (Tilman 1982, 1994). Here, species that are more closely aligned with a patch’s environmental conditions become stronger competitors;
3. The third and most complex scenario, the “niche overlap and environmental proximity” scenario, further considers both the proximity to environmental optima and the intensity of competition among species with overlapping niches. In this scenario, species with environmental niches closer to the patch’s environment not only have higher competitive performance but also experience more intense competition (Chesson 2000a). These dynamics ensure that competition coefficients dynamically adjust in response to environmental suitability and species’ specialization strategies (see Amarasekare 2003 and references therein).

These dynamics ensured that competition coefficients dynamically adjusted in response to environmental suitability and species’ specialisation strategies (see Amarasekare 2003; Chase & Leibold 2003).

To implement these different ecological scenarios, we allowed the competition coefficient of species pairs, α_{ij}, to be defined by two factors θ_{ij}, which define environmental niche matching (or mismatching), and β_{ij} , which represents the environmental niche overlap between species i and j, as detailed below.

Regulating density-dependent competition by environmental niche matching-mismatching

Considering that species are more competitive when they are closer to their optimal environments (Hutchinson 1957; Macarthur & Levins 1967), we define θ_{ij} as:

$$\theta_{ij} = e^{\frac{-(d_i+d_j)^2}{2\times(s_i^2+s_j^2)}},$$

where d_i and d_j denote the difference between the environmental value e of the patch x and the species’ optimal environment u_i and u_j, respectively. Species pairs whose environmental optima are closer to the patch’s environmental conditions should exhibit higher θ_{ij}, and, consequently, greater competitive ability.

This adjustment implies that species i will be a stronger competitor when within its environmental preferences, particularly against any given species j whose environmental preferences do not align with the local conditions.

Regulating density-dependent competition by environmental niche overlap

Because species with similar niches compete more against each other (Hardin 1960), we also modulated α by:

$$\beta_{ij} = e^{\frac{-(u_i - u_j)^2}{2 \times (s_i^2 + s_j^2)}}.$$

3.5.2.3.2 Internal dispersal phase

We assumed that the probability of individuals, P_m, moving from one patch to another decreases exponentially with the spatial distance between patches, as follows:

$$P_m = e^{-\alpha \times d_{t,s}},$$

where d_{ts} is the Euclidean spatial distance between the target patch t and the source patch s, while α is a decay parameter that adjusts the sensitivity (or strength) of dispersal to distance. This decay function, based on empirical observations, reflects the tendency of organisms to migrate more readily to nearby patches than those far away (Ovaskainen & Hanski 2001).

3.5.2.3.3 Population limit regulation phase

Population sizes can temporarily exceed their respective carrying capacities because of environmental variability and species interactions (see Chapman & Byron 2018). Our model incorporates density-dependent regulation by setting the carrying capacity K at 500 individuals per species. The population size for species i in patch j at time $t + 1$, N_{ij}^{t+1}, is calculated as:

$$N_{ij}^{t+1} = \begin{cases} N_{ij} & \text{if } N_{ij} \leq K \\ K & \text{otherwise} \end{cases}$$

3.5.2.3.4 External dispersal phase

Each species j_r in the regional pool has a probability ρ to immigrate to the local landscape. To prevent complete extinction across any given landscape, we allowed for non-zero probabilities that individuals of any species in the regional pool arriving to the landscape.

Given a species' environmental response, characterized by its environmental niche optimum u_{j_r} and niche breadth s_{j_r} (which can originate from either the local landscape u_i, s_i or the regional pool $u_{i_{\text{regional}}}, s_{i_{\text{regional}}}$), the likelihood that species establishing in a new patch depends on both the regional immigration rate and stochastic events.

The immigration of species j_r from the regional pool was implemented as:

$$I_{j_r}(\rho) = \begin{cases} 1, & \text{if a randomly drawn number} < \rho \\ 0, & \text{otherwise} \end{cases}$$

If $I_{j_r}(\rho) = 1$ and species j_r is not already present in the local landscape, it is then added to the local population (and its species pool):

$$j \leftarrow j \cup j_r$$

After this, irrespective of whether species j_r is newly introduced or was already present, a random subset of patches I_j is selected for this species to settle in. The populations' matrix N is updated for species j in patches I_j:

$$N_{I_j,j} \leftarrow N_{I_j,j} + \text{random integer between 1 to 5}$$

Simultaneously, the environmental niche optima u_i and niche breadth s_i in the local landscape species list are updated:

$$u_i \leftarrow u_i \cup \{u_{i_{\text{regional}}}[j_r]\}$$

$$s_i \leftarrow s_i \cup \{s_{i_{\text{regional}}}[j_r]\}$$

3.5.2.3.5 Disturbance phase

Since disturbances rarely affect all patches in a landscape uniformly (Turner *et al.* 1989), we defined P_d as the probability that any patch i will experience a disturbance event at any given time step in our simulation.

When a patch is marked for disturbance, the resident species undergo a population decline proportional to the disturbance intensity I_d, which represents the proportion of species populations reduced in affected patches, as below:

$$N_{ij}^{t+1} = \text{floor}\left(N_{ij}^{t} \times (1 - I_d)\right)$$

We defined $I_d = 0.9$, consistent with evidence showing that severe disturbances, such as wildfires or catastrophic habitat destruction, can drastically reduce population size (Hughes 1994; *e.g.*, Dale *et al.* 2001; Dornelas 2010; Cunillera-Montcusí *et al.* 2021).

3.5.2.4 Simulation runs

We ran our simulations for 1,400 time steps (generations), which were sufficient to establish dynamic equilibrium states in species distributions and abundances.

Our models contained a combination 1,209 different models (see Table 3.4 for a detailed description of the parameters used in the simulations), each with 10 replicates, resulting in a total of 12,090 simulations.

3.5.2.5 Statistical analysis

We fitted ordinary linear regressions to determine how environmental specialisation changed as a function of the spatial frequency in environmental conditions (computed using the same kernel density estimation approach as used with the empirical dataset; see Section 3.5.1.4) across the different ecological scenarios (parameters) implemented in our simulation models.

3.5.3 Computational tools

All data manipulations and analyses were performed in R and RStudio (Posit Team 2023; R Core Team 2023). Extended information on software and hardware used is available within the Supporting Information in Section 3.7.

3.6 Data Availability and Reproducibility Statement

All code and data necessary to reproduce the analyses and figures from this study are respectively available within the Open Science Framework (accessible at osf.io/zcedg) repository for this study.

3.7 Supporting Information 1

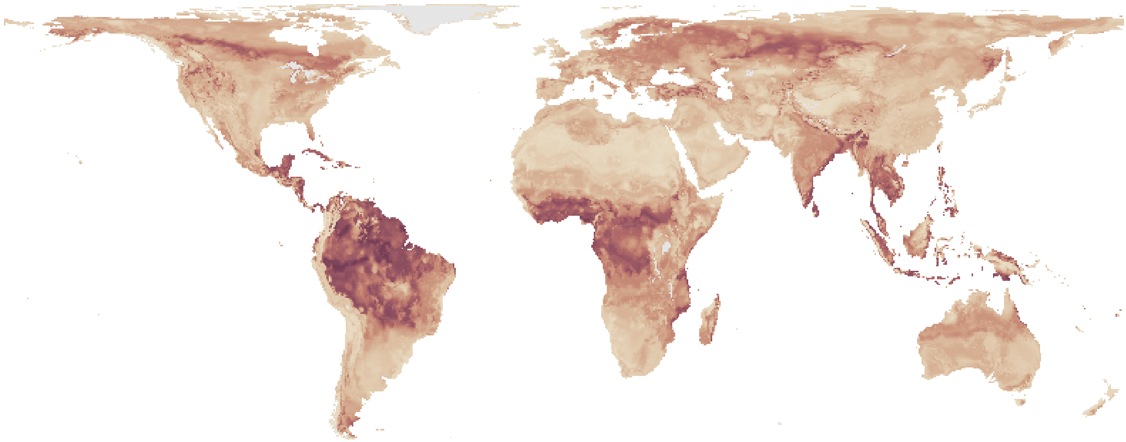
3.7.1 Computational resources and tools

All data manipulation and analyses were performed in R (versions 4.0.4 and 4.3.0) and RStudio Server (versions between 2022.07.2 and 2024.10.0) (Posit Team 2023; R Core Team 2023) on an Ubuntu Bionic server with Intel(R) Xeon(R) Platinum 8168 CPU @ 2.70GHz, with 192 cores and 1.62 TB of RAM. While the meta-community simulations of ecological dynamics require few computational resources and can be executed on an ordinary last-gen personal computer, the dimensions of the empirical data are large (*e.g.*, 248,139 rows, and up to 10,384 columns for the bird dataset, making 2,576,675,376 elements), and its analysis and manipulation require large availability of RAM (> 650 GB) and disk storage space (> 2 TB).

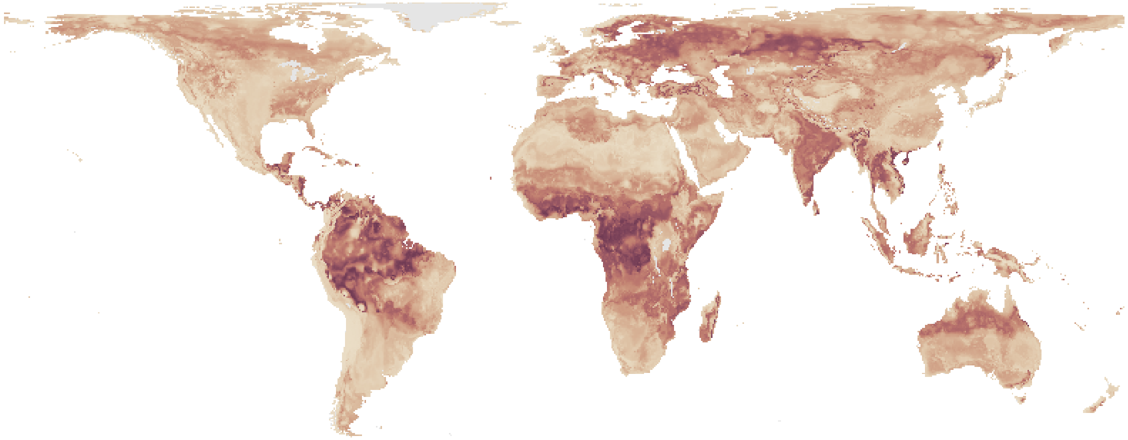
Parallelized computations were done using `snowfall` and `doSNOW` (Knaus 2015; Corporation & Weston 2022). Geospatial manipulation was done using the `sf`, `raster`, `terra`, and `exactextractr` packages (Pebesma 2018; Hijmans 2022, 2023). Kernel density estimations were performed using the `ks` package (Duong 2007, 2022). Multivariate niche analysis and decomposition was performed using the `ade4` package (Dray & Dufour 2007). Robust generalized linear models were performed with the `robust` package (Wang *et al.* 2022). Quantile regressions were performed using the `quantreg` package (Koenker 2021). Double generalized models were performed and diagnosed with the `dglm` package (Smyth *et al.* 2023). General data manipulation was done with the `tidyverse` package suite (Wickham *et al.* 2019). Figures were generated using the `ggplot2`, `ggpubr`, and `patchwork` packages (Wickham 2016; Pedersen 2022; Kassambara 2023). Tables were generated using the `flextable` package (Gohel & Skintzos 2024).

3.8 Supporting Information 2

a. Global



b. East-West Hemisphere



c. Biome

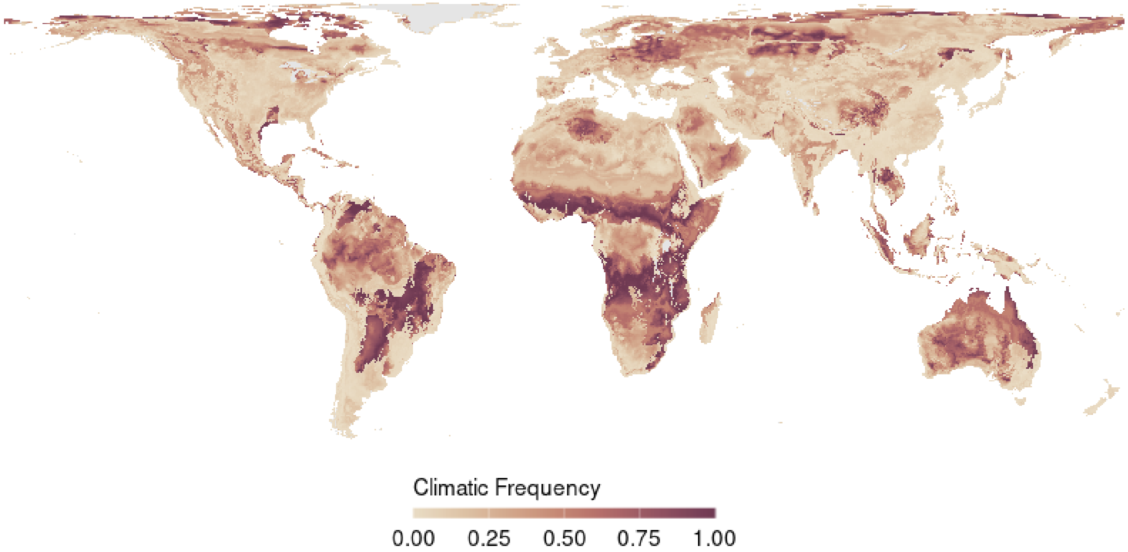


Figure 3.5 *(preceding page)*: **Global distribution of climatic frequencies across geographical scales.** Three geographical scales are depicted: (a) global, (b) east-west hemispheric, and (c) biomes. Climatic frequencies were calculated using probability density estimation methods based on the principal components derived from eight bioclimatic variables representing precipitation and temperature (see Methods).

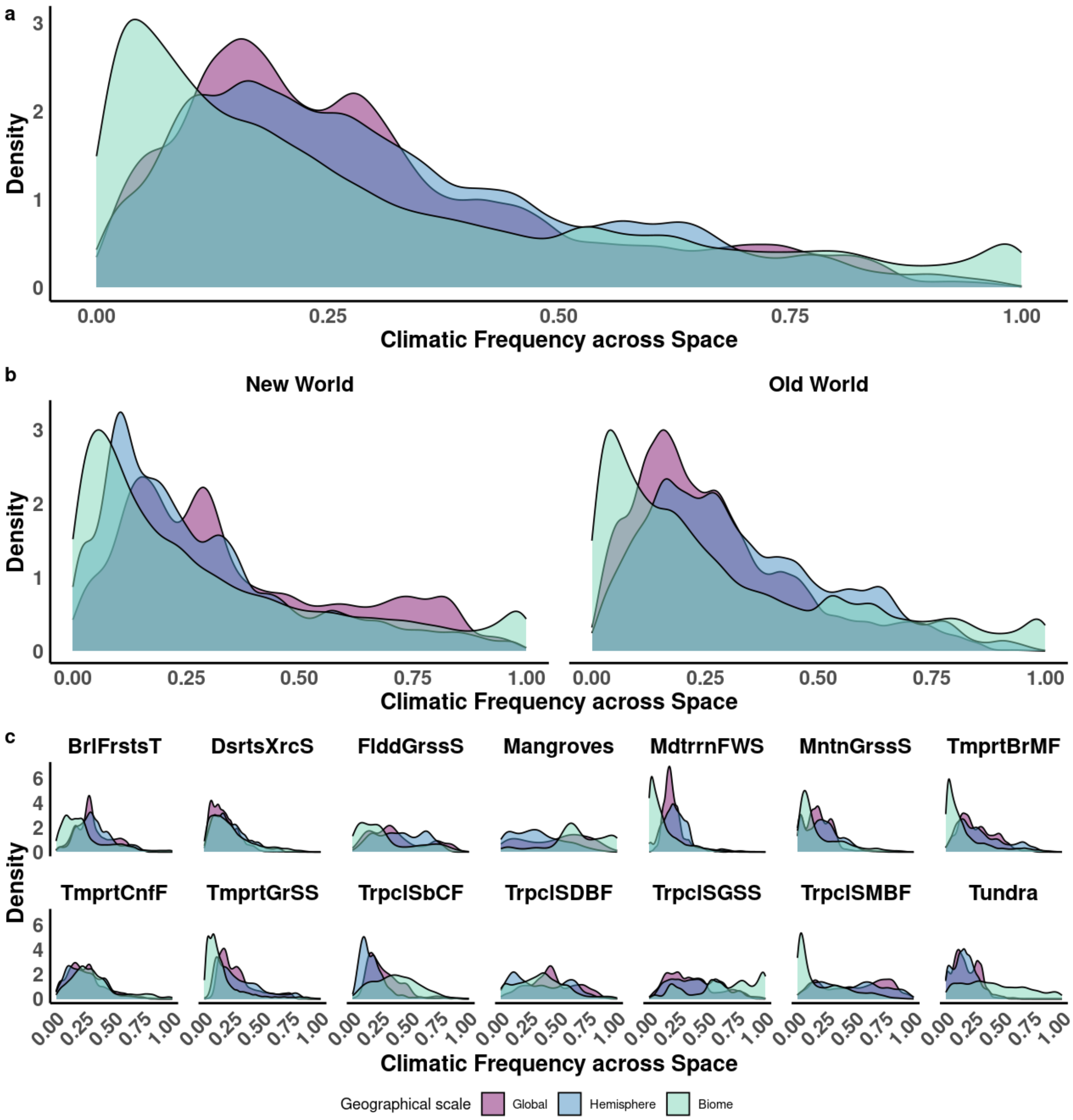


Figure 3.6: **Density distributions of climatic frequencies computed across geographical scales for the (a) global, (b) hemispheric, and (c) biome scales.** The shaded colour of the curves denotes the hierarchical geographical extent from which climatic conditions were subset and then used to compute climatic frequencies, being them: global (rose), east-west hemispheric (blue), and biome (green), extents (see Methods). Acronyms denominate worldwide biomes, and signify as follows: TmprtBrMF = Temperate Broadleaf & Mixed Forests; Tundra = Tundra; TmprtGrSS = Temperate Grasslands, Savannas & Shrublands; MntnGrssS = Montane Grasslands & Shrublands; MdtrrnFWS = Mediterranean Forests, Woodlands & Scrub; TrpclSGSS = Tropical & Subtropical Grasslands, Savannas & Shrublands; FlddGrssS = Flooded Grasslands & Savannas; TrpclSMBF = Tropical & Subtropical Moist Broadleaf Forests; DsrtsXrcS = Deserts & Xeric Shrublands; Mangroves = Mangroves; TrpclSDBF = Tropical & Subtropical Dry Broadleaf Forests; TrpclSbCF = Tropical & Subtropical Coniferous Forests; TmprtCnfF = Temperate Conifer Forests; BrlFrstsT = Boreal Forests/Taiga.

Table 3.1: **Explained variation and correlations between bioclimatic variables and principal components.** Correlations between each bioclimatic variable and the first eight principal components (PC1 to PC8), alongside the explained variation (%) and the cumulative explained variation (%) for each principal component. The bioclimatic variables correspond to: annual mean temperature (BIO1), mean diurnal range (BIO2), temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), annual precipitation (log-transformed) (log(1+BIO12)), precipitation seasonality (BIO15), precipitation of warmest quarter (log-transformed) (log(1+BIO18)), and precipitation of coldest quarter (log-transformed) (log(1+BIO19)). The table also includes the .

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
BIO1: Annual Mean Temperature	0.545	-0.765	0.306	-0.034	-0.029	0.044	0.090	0.107
BIO2: Mean Diurnal Range (Mean of monthly (max temp - min temp))	0.781	0.053	-0.014	0.486	0.383	-0.061	-0.009	-0.010
BIO4: Temperature Seasonality (standard deviation * 100)	-0.210	0.847	-0.261	0.266	-0.154	0.260	0.078	0.053
BIO8: Mean Temperature of Wettest Quarter	0.546	-0.667	-0.064	0.239	-0.412	0.148	-0.034	-0.062

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
log(1+BIO12): Annual Precipitation (log-transformed)	-0.627	-0.678	-0.275	0.028	0.191	0.069	0.161	-0.054
BIO15: Precipitation Seasonality (Coefficient of Variation)	0.688	-0.141	-0.566	-0.312	0.190	0.222	-0.058	0.013
log(1+BIO18): Precipitation of Warmest Quarter (log-transformed)	-0.595	-0.519	-0.532	0.200	-0.075	-0.193	-0.078	0.066
log(1+BIO19): Precipitation of Coldest Quarter (log-transformed)	-0.771	-0.363	0.356	0.110	0.190	0.294	-0.113	0.012
Explained Variance (%)	38.31	32.88	12.15	6.45	5.69	3.41	0.79	0.32
Cumulative Explained Variance (%)	38.31	71.19	83.34	89.79	95.48	98.89	99.68	100

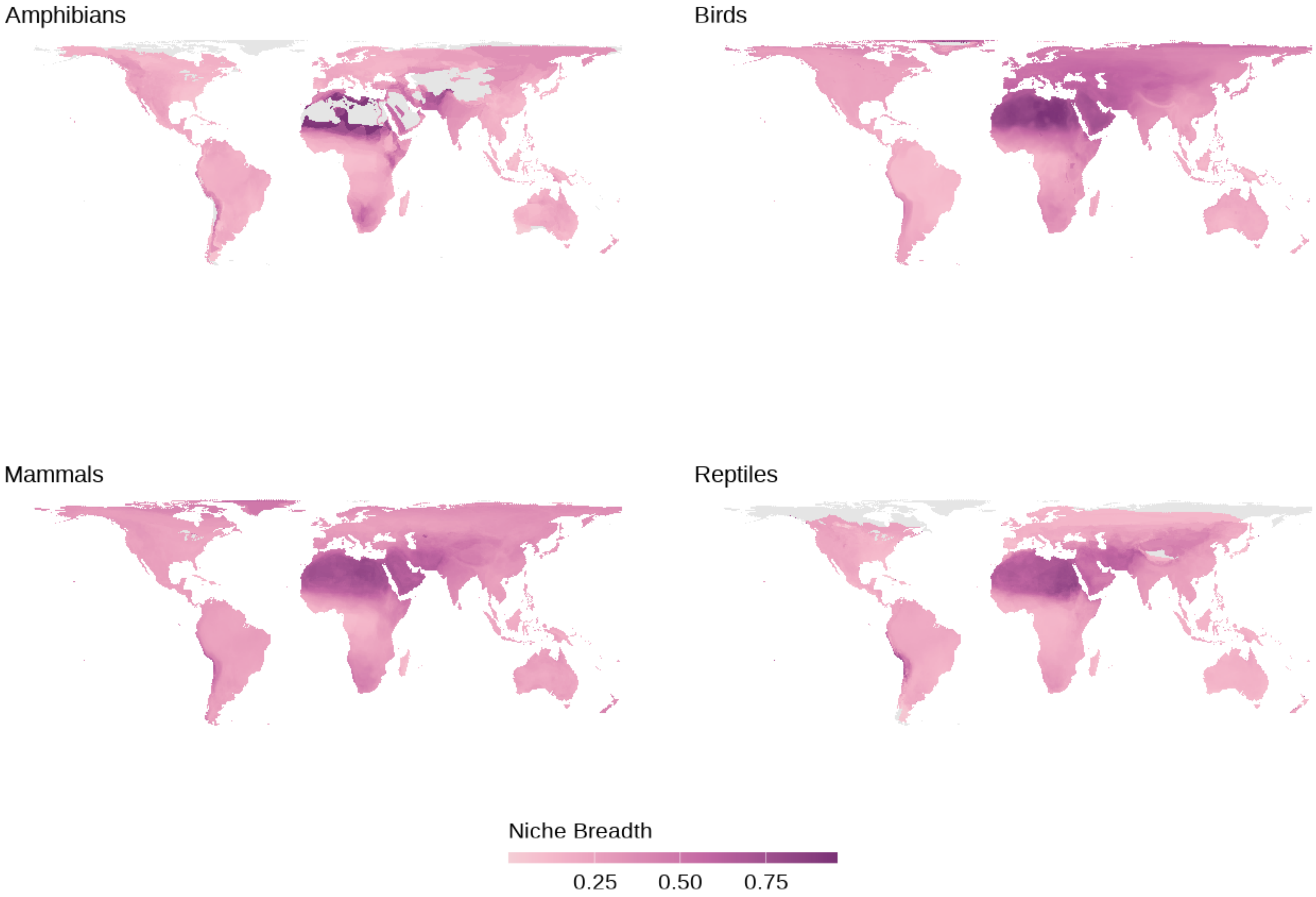


Figure 3.7: **Global distribution of average climatic niche breadth in tetrapod communities.**

Table 3.2: **Model coefficients for the effects of climatic frequency on niche breadth across tetrapod communities at multiple geographical scales.** The table presents mean and dispersion model coefficients from double generalized linear models (DGLMs) fitted separately for amphibians, birds, mammals, and reptiles. Climatic frequency is calculated as the spatial frequency of climatic conditions, while climatic heterogeneity is based on environmental variability within geographical cells. Nagelkerke's R^2 values indicate the proportion of explained variation for each model, and p-values less than 0.05 are highlighted in bold. Models were fitted using the Gamma distribution with log-link functions for both the mean and dispersion structures. Coefficients are presented for three spatial scales: global, hemispheric, and biome.

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
Amphibians	206,616	Global	0.295	267,494	217,782	Mean	(Intercept)	-0.818	0.003	-291.282	**0.000**
							Clim. Frequency	-1.134	0.007	-168.293	**0.000**
						Dispersion	(Intercept)	-0.331	0.008	-40.107	**0.000**
							Clim. Frequency	-2.827	0.022	-130.051	**0.000**
		Hemisphere	0.157	243,039	219,362	Mean	(Intercept)	-0.919	0.003	-283.381	**0.000**
							Clim. Frequency	-0.727	0.008	-96.174	**0.000**
						Dispersion	(Intercept)	-0.384	0.009	-43.393	**0.000**
							Clim. Frequency	-1.979	0.022	-88.439	**0.000**
		Biome	0.117	236,897	219,672	Mean	(Intercept)	-1.015	0.003	-374.767	**0.000**
							Clim. Frequency	-0.481	0.006	-82.995	**0.000**
						Dispersion	(Intercept)	-0.542	0.008	-71.796	**0.000**
							Clim. Frequency	-1.615	0.019	-85.907	**0.000**
						Mean	(Intercept)	0.299	0.002	170.594	**0.000**
							Clim. Frequency	-1.273	0.006	-216.388	**0.000**
							(Intercept)	-1.247	0.007	-190.274	**0.000**

Birds	242,359	Global	0.380	332,048	251,214

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
						Dispersion	Clim. Frequency	-0.944	0.018	-52.322	**0.000**
		Hemisphere	0.106	270,843	252,864	Mean	(Intercept)	0.130	0.002	65.331	**0.000**
							Clim. Frequency	-0.593	0.006	-106.800	**0.000**
						Dispersion	(Intercept)	-1.141	0.006	-181.183	**0.000**
							Clim. Frequency	-0.655	0.017	-39.538	**0.000**
	242,375	Biome	0.061	263,101	253,143	Mean	(Intercept)	0.048	0.002	28.259	**0.000**
							Clim. Frequency	-0.342	0.005	-76.044	**0.000**
						Dispersion	(Intercept)	-1.228	0.006	-211.268	**0.000**
							Clim. Frequency	-0.299	0.014	-20.750	**0.000**
	242,055	Global	0.443	348,108	248,224	Mean	(Intercept)	-0.255	0.002	-166.862	**0.000**
							Clim. Frequency	-1.195	0.005	-262.739	**0.000**
						Dispersion	(Intercept)	-1.412	0.007	-203.145	**0.000**
							Clim. Frequency	-1.729	0.019	-90.233	**0.000**
		Hemisphere	0.295	307,008	249,346	Mean	(Intercept)	-0.340	0.002	-194.219	**0.000**
							Clim. Frequency	-0.816	0.005	-177.680	**0.000**
						Dispersion	(Intercept)	-1.252	0.008	-162.165	**0.000**
							Clim. Frequency	-1.589	0.020	-78.010	**0.000**
						Mean	(Intercept)	-0.473	0.002	-299.131	**0.000**
							Clim. Frequency	-0.387	0.004	-103.694	**0.000**
							(Intercept)	-1.331	0.006	-213.007	**0.000**

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
	242,070	Biome	0.116	269,746	250,148	Dispersion	Clim. Frequency	-1.020	0.016	-65.416	**0.000**
Reptiles	213,723	Global	0.194	257,230	225,974	Mean	(Intercept)	-0.390	0.002	-167.325	**0.000**
							Clim. Frequency	-2.139	0.010	-210.025	**0.000**
						Dispersion	(Intercept)	-1.048	0.007	-153.615	**0.000**
							Clim. Frequency	-0.023	0.018	-1.300	0.194
		Hemisphere	0.287	275,960	226,043	Mean	(Intercept)	-0.633	0.003	-243.734	**0.000**
							Clim. Frequency	-1.040	0.006	-165.473	**0.000**
						Dispersion	(Intercept)	-0.365	0.007	-54.989	**0.000**
							Clim. Frequency	-2.406	0.017	-140.585	**0.000**
		Biome	0.184	256,204	226,832	Mean	(Intercept)	-0.777	0.002	-340.073	**0.000**
							Clim. Frequency	-0.632	0.005	-115.738	**0.000**
						Dispersion	(Intercept)	-0.621	0.006	-107.937	**0.000**
							Clim. Frequency	-1.427	0.015	-98.062	**0.000**

3.8.1 Accounting for the influence of climatic heterogeneity in the relationship between climatic frequency and climatic specialisation

We performed double generalized linear models (DGLMs) to account for the effects of climatic heterogeneity (as a covariate) in the relationship between climatic frequency and niche breadth in tetrapod communities. These models were fitted using a Gamma distribution with a log-link function to account for the positively skewed nature of the niche breadth data. The mean structure of the model captured the central tendency of niche breadth, while the dispersion structure modelled its variability.

Climatic frequency, defined as the spatial frequency of climatic conditions (see Methods for details on the calculations), and climatic heterogeneity, defined as the mean Euclidean distance of climatic conditions within geographical cells, were standardized across taxonomic groups and spatial scales (global, hemispheric, and biome). Separate models were run for each taxonomic group (amphibians, birds, mammals, and reptiles) to examine the effects across scales.

The negative relationship between climatic frequency and community mean niche breadth (for both mean and dispersion) was still strong after controlling for the effects of climatic heterogeneity (see Figure 3.8, Figure 3.9, and Table 3.3).

Table 3.3: **Model coefficients for the partial effects of climatic frequency and climatic heterogeneity on niche breadth across tetrapod communities at multiple geographical scales.** The table presents mean and dispersion model coefficients from double generalized linear models (DGLMs) fitted separately for amphibians, birds, mammals, and reptiles. Climatic frequency is calculated as the spatial frequency of climatic conditions, while climatic heterogeneity is based on environmental variability within geographical cells. Nagelkerke's R^2 values indicate the proportion of explained variation for each model, and p-values less than 0.05 are highlighted in bold. Models were fitted using the Gamma distribution with log-link functions for both the mean and dispersion structures. Coefficients are presented for three spatial scales: global, hemispheric, and biome.

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
		Global	0.293	267,061	217,721	Mean	(Intercept)	-1.190	0.001	-794.496	**0.000**
							Clim. Frequency	-0.235	0.001	-164.415	**0.000**
							Clim. Heterogeneity	-0.049	0.001	-34.371	**0.000**
						Dispersion	(Intercept)	-1.256	0.004	-279.718	**0.000**
							Clim. Frequency	-0.577	0.005	-126.184	**0.000**
							Clim. Heterogeneity	-0.028	0.004	-6.319	**0.000**
		Hemisphere	0.160	243,518	219,246	Mean	(Intercept)	-1.168	0.002	-689.113	**0.000**
							Clim. Frequency	-0.149	0.002	-91.306	**0.000**
							Clim. Heterogeneity	-0.062	0.002	-38.237	**0.000**
						Dispersion	(Intercept)	-1.065	0.005	-223.733	**0.000**
							Clim. Frequency	-0.411	0.005	-84.979	**0.000**
							Clim. Heterogeneity	-0.059	0.005	-12.529	**0.000**
						Mean	(Intercept)	-1.165	0.002	-674.905	**0.000**
							Clim. Frequency	-0.130	0.002	-83.188	**0.000**
							Clim. Heterogeneity	-0.077	0.002	-46.530	**0.000**

		Biome	0.139	240,233	219,517

Taxonomic Group	N	Scale	Nagelkerke’s R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
						Dispersion	(Intercept)	-1.061	0.005	-209.808	**0.000**
							Clim. Frequency	-0.458	0.005	-89.109	**0.000**
							Clim. Heterogeneity	-0.108	0.005	-21.521	**0.000**
		Global	0.400	337,826	251,015	Mean	(Intercept)	-0.089	0.001	-82.028	**0.000**
							Clim. Frequency	-0.251	0.001	-203.589	**0.000**
							Clim. Heterogeneity	-0.088	0.001	-131.755	**0.000**
						Dispersion	(Intercept)	-1.549	0.004	-405.338	**0.000**
							Clim. Frequency	-0.169	0.004	-43.527	**0.000**
							Clim. Heterogeneity	0.027	0.004	6.997	**0.000**
		Hemisphere	0.152	279,010	252,504	Mean	(Intercept)	-0.065	0.001	-58.215	**0.000**
							Clim. Frequency	-0.108	0.001	-91.854	**0.000**
							Clim. Heterogeneity	-0.106	0.001	-142.038	**0.000**
						Dispersion	(Intercept)	-1.381	0.004	-384.836	**0.000**
							Clim. Frequency	-0.107	0.004	-29.425	**0.000**
							Clim. Heterogeneity	0.003	0.004	0.705	0.481
						Mean	(Intercept)	-0.063	0.001	-55.454	**0.000**
							Clim. Frequency	-0.084	0.001	-71.317	**0.000**
							Clim. Heterogeneity	-0.117	0.001	-152.475	**0.000**
							(Intercept)	-1.367	0.004	-359.664	**0.000**
							Clim. Frequency	-0.074	0.004	-19.269	**0.000**

Dispersion

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
							Clim. Heterogeneity	-0.022	0.004	-5.678	**0.000**
Mammals	242,054	Global	0.471	357,392	248,035	Mean	(Intercept)	-0.619	0.001	-696.847	**0.000**
							Clim. Frequency	-0.239	0.001	-249.472	**0.000**
							Clim. Heterogeneity	-0.083	0.001	-132.023	**0.000**
						Dispersion	(Intercept)	-1.954	0.004	-481.465	**0.000**
							Clim. Frequency	-0.331	0.004	-80.059	**0.000**
							Clim. Heterogeneity	0.017	0.004	4.196	**0.000**
		Hemisphere	0.321	313,212	249,059	Mean	(Intercept)	-0.604	0.001	-629.651	**0.000**
							Clim. Frequency	-0.158	0.001	-161.514	**0.000**
							Clim. Heterogeneity	-0.094	0.001	-127.024	**0.000**
						Dispersion	(Intercept)	-1.790	0.004	-403.101	**0.000**
							Clim. Frequency	-0.301	0.005	-66.591	**0.000**
							Clim. Heterogeneity	-0.023	0.004	-5.069	**0.000**
		Biome	0.193	284,206	249,650	Mean	(Intercept)	-0.597	0.001	-591.155	**0.000**
							Clim. Frequency	-0.098	0.001	-101.391	**0.000**
							Clim. Heterogeneity	-0.113	0.001	-144.006	**0.000**
						Dispersion	(Intercept)	-1.705	0.004	-384.789	**0.000**
							Clim. Frequency	-0.283	0.004	-63.276	**0.000**
							Clim. Heterogeneity	-0.067	0.004	-15.292	**0.000**
							(Intercept)	-1.039	0.002	-630.153	**0.000**

Taxonomic Group	N	Scale	Nagelkerke's R2	Null Deviance	Residual Deviance	Model Type	Parameter	Estimate	Std. Error	t Value	P-value
Reptiles	213,723	Global	0.318	281,700	224,946	Mean					
							Clim. Frequency	-0.396	0.002	-206.504	**0.000**
							Clim. Heterogeneity	-0.098	0.001	-155.427	**0.000**
						Dispersion	(Intercept)	-1.154	0.004	-300.514	**0.000**
							Clim. Frequency	-0.118	0.004	-30.255	**0.000**
							Clim. Heterogeneity	0.086	0.004	22.095	**0.000**
		Hemisphere	0.325	283,911	225,555	Mean	(Intercept)	-0.985	0.001	-701.069	**0.000**
							Clim. Frequency	-0.212	0.001	-154.775	**0.000**
							Clim. Heterogeneity	-0.119	0.001	-138.886	**0.000**
						Dispersion	(Intercept)	-1.190	0.004	-302.914	**0.000**
							Clim. Frequency	-0.489	0.004	-121.848	**0.000**
							Clim. Heterogeneity	0.028	0.004	6.976	**0.000**
		Biome	0.264	270,956	226,089	Mean	(Intercept)	-0.978	0.001	-656.010	**0.000**
							Clim. Frequency	-0.161	0.001	-113.469	**0.000**
							Clim. Heterogeneity	-0.144	0.001	-155.165	**0.000**
						Dispersion	(Intercept)	-1.113	0.004	-269.998	**0.000**
							Clim. Frequency	-0.397	0.004	-94.645	**0.000**
							Clim. Heterogeneity	-0.044	0.004	-10.827	**0.000**

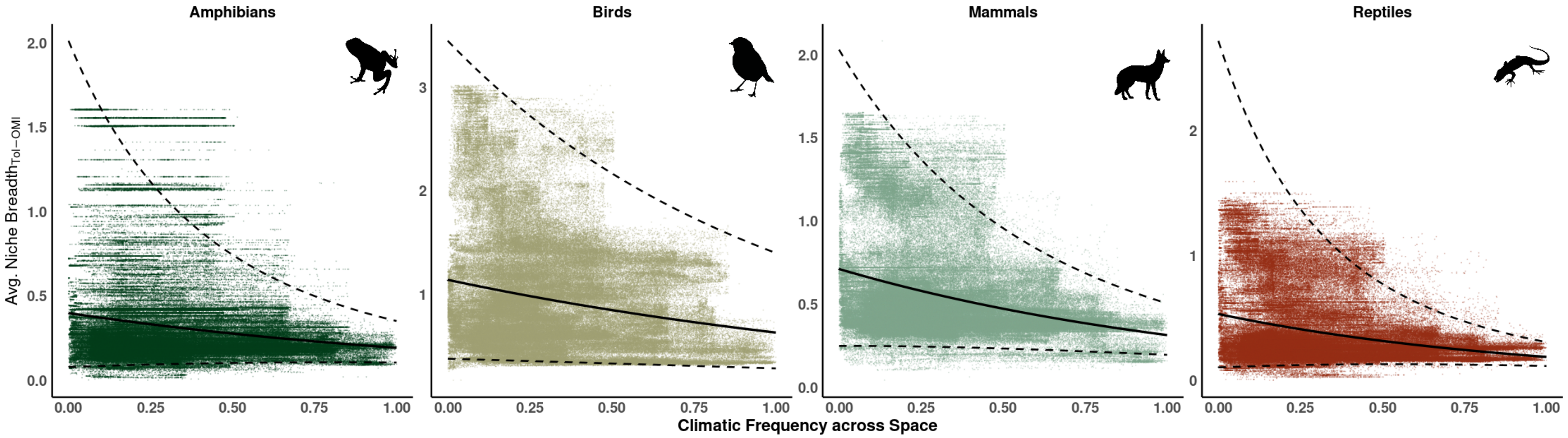


Figure 3.8: **The spatial frequency of climatic conditions measured at the east-west hemisphere scale constrains specialisation in tetrapods worldwide.** The spatial frequency of climatic conditions negatively predicted the average of niche breadth in amphibian, bird, mammal, and reptilian communities. Each point represents a community. Across all four groups of tetrapods and their communities, common climates allow for increased variation in niche breadth while rare climates favour decreased niche breadth (*i.e.*, specialisation). The calculation of climatic frequency derived from contemporary climatic conditions was done for each hemisphere. The continuous and dashed lines respectively represent mean and dispersion fits for effects of climatic frequency on community average niche breadth using double generalized additive model with Gamma log-link functions (see Methods). We credit the animal silhouette icons to PhyloPic (phylopic.org).

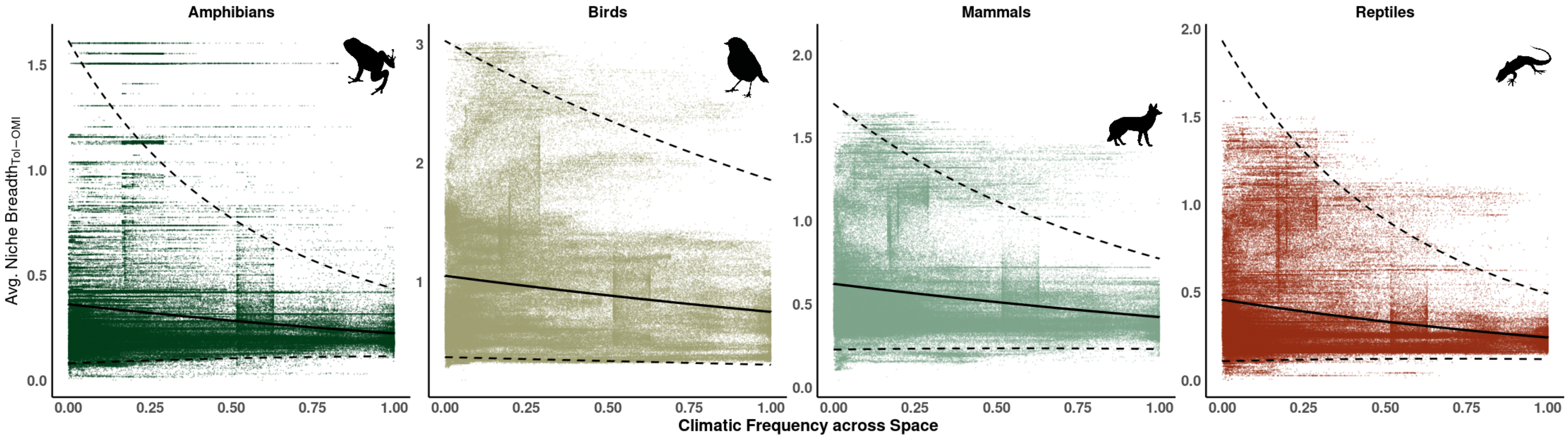


Figure 3.9: **The spatial frequency of climatic conditions measured at the biome scale constrains specialisation in tetrapods worldwide.** The spatial frequency of climatic conditions negatively predicted the average of niche breadth in amphibian, bird, mammal, and reptilian communities. Each point represents a community. Across all four groups of tetrapods and their communities, common climates allow for increased variation in niche breadth while rare climates favour decreased niche breadth (i.e., specialisation). The calculation of climatic frequency derived from contemporary climatic conditions was done for each biome. The continuous and dashed lines respectively represent mean and dispersion fits for effects of climatic frequency on community average niche breadth using double generalized additive model with Gamma log-link functions (see Methods). We credit the animal silhouette icons to PhyloPic (phylopic.org).

3.9 Supporting Information 3

3.9.1 Geographical distance-weighted average climatic distance across climatic frequency gradients

We investigated whether frequent climatic conditions are better connected and widespread compared to rare climates.

To begin, we described how communities differ from each other because of climatic conditions by computing the pairwise Mahalanobis distances (Mahalanobis 2018) between all communities worldwide. This computation was based on the eight standardized climatic variables used in our study, which allowed us to account for correlations between variables and the different scales of measurements.

Next, we computed the Vincenty geodetic distance (Vincenty 1975) to describe the geographical distance among all communities.

For each community, we computed the average climatic distance from all other communities, weighted by the geographical distances from all other communities. This approach ensures that closer sites have a greater influence on the average climatic distance, capturing the influence of geographical proximity on climatic connectivity. Communities with high geographical distance-weighted average climatic distances are more climatically isolated, indicating that they are surrounded by communities experiencing significantly different climatic conditions. In contrast, communities with low values are more climatically integrated, suggesting that communities experiencing similar climatic conditions surround them, reflecting better connectivity and widespread distribution of those climatic conditions.

To represent how climatic conditions of different spatial frequencies are geographically interconnected, we plotted the geographical distance-weighted average climatic distances against the climatic frequency across space divided into percentiles (*i.e.*,each containing a similar number of communities; see Figure 3.2), and against climatic frequency divided into 100 equally spaced intervals (Figure 3.10). Both figures demonstrate that climatic conditions with higher spatial frequencies are more geographically connected and widespread compared to rare climatic conditions.

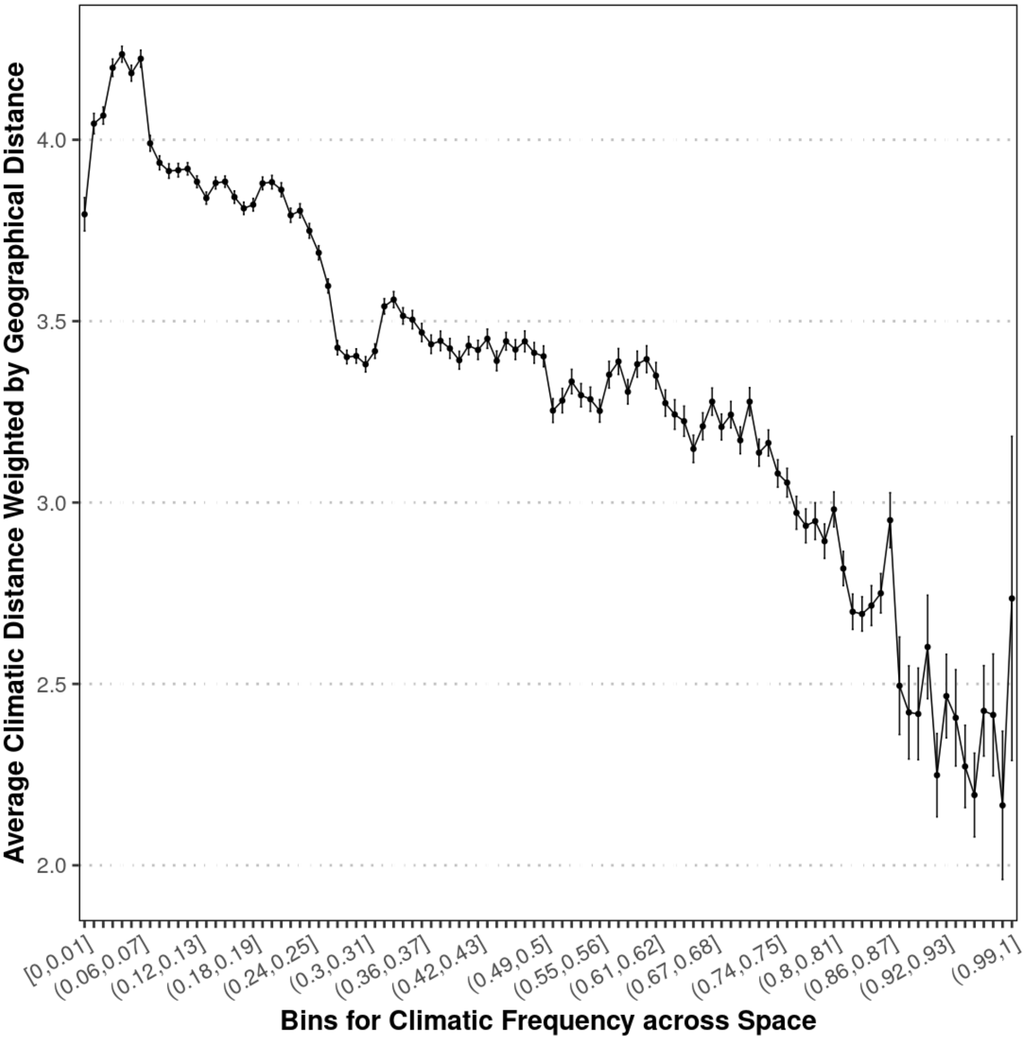


Figure 3.10: **Distribution of climatic distances weighted by geographical distances across equally spaced intervals of climatic frequency across space measured across the globe.** The average climatic Mahalanobis distance was weighted by the average geographical distance between all hexagons into across 100 intervals of climatic frequency across global terrestrial landscapes (see Methods and Supporting Information 6). Vertical bars represent 95% confidence intervals.

3.10 Supporting Information 4

3.10.1 Geographical distance-weighted average beta diversity across climatic frequency gradients

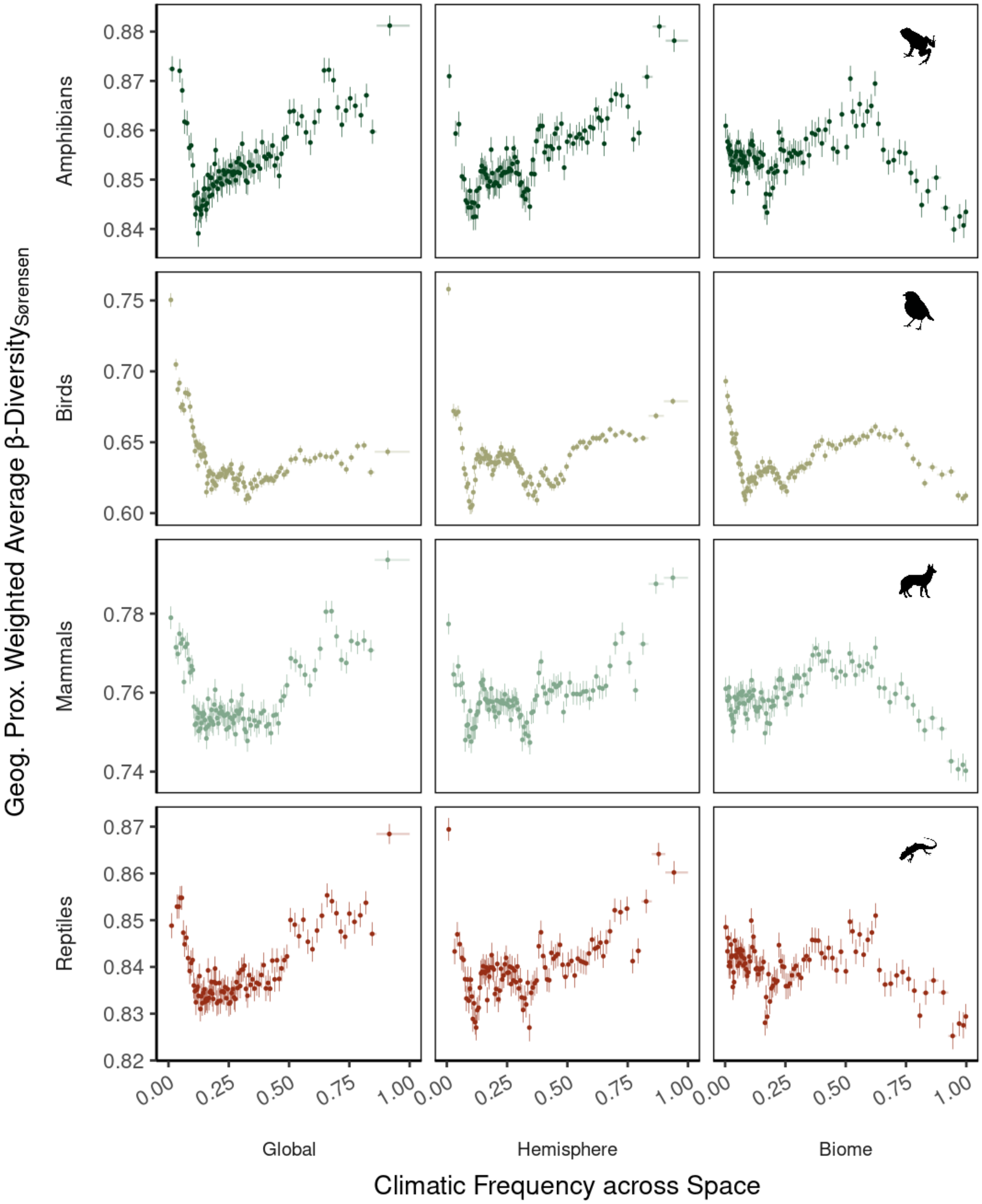
To demonstrate how sites are varying in composition across the climatic frequency gradient, we computed the average beta diversity weighted by the geographical distances of these sites so that closer sites have a greater influence on the average dissimilarity measure. By adjusting our metric to the geographical proximity of sites, we acknowledge the influence of more similar environmental conditions and biotic interactions because of geographical proximity alone, more accurately representing local beta diversity patterns (Nekola & White 1999; Soininen *et al.* 2007).

Given $\beta_{Sor_{ij}}$ is the Sørensen's dissimilarity between sites i and j (Sørensen 1948), and G_{ij} is the Vincenty's geodetic geographical distance between sites i and j (Vincenty 1975), we computed the geographical distance-weighted average beta diversity $\overline{\beta}_{Sor_{GW}}$ for each site i as:

$$\overline{\beta}_{Sor_{GW_i}} = \frac{\sum\limits_{j \neq i} \beta_{Sor_{ij}} \cdot w_{ij}}{\sum\limits_{j \neq i} w_{ij}},$$

where the weight w_{ij} is defined by the exponential decay function $e^{-G_{ij}}$, gradually capturing the influence of medium-distance interactions that might be overlooked with a steeper decay function (see Soininen *et al.* 2007).

We then plotted the average beta diversity weighted by geographical distances separately for amphibians, birds, mammals, and reptiles against each percentile (100 quantiles) of the climatic frequency gradient, separately for each geographical scale (see Figure 3.11).


Geog. Prox. Weighted Average β-Diversity$_{\text{Sørensen}}$
Amphibians
Birds
Mammals
Reptiles
0.88
0.87
0.86
0.85
0.84
0.75
0.70
0.65
0.60
0.78
0.76
0.74
0.87
0.86
0.85
0.84
0.83
0.82
0.00
0.25
0.50
0.75
1.00
Global
Hemisphere
Biome
Climatic Frequency across Space

3.11 Supporting Information 5

3.11.1 Simulating a Spatially Auto-Correlated Environment

Upon defining the gridded landscape for the simulations, we introduced a spatial autocorrelation structure to the environmental values, E', generated from one of three frequency distributions: normal, uniform, or mixed. To maintain spatial continuity, we computed toroidal distances among patches in our landscape using the following equation:

$$d_{torus} = \sqrt{\min(|x_1 - x_2|, L_x - |x_1 - x_2|)^2 + \min(|y_1 - y_2|, L_y - |y_1 - y_2|)^2}$$

where x_1 and x_2 are the positions of the patches along the x-axis, y_1 and y_2 are the positions along the y-axis, and L_x and L_y are the dimensions of the landscape, typically the square root of the total number of patches N.

We then obtained a spatial correlation matrix for all patches by taking the negative exponent of the multiplication of the toroidal distance matrix D_{torus} by a spatial autocorrelation coefficient θ:

$$W = e^{-\theta \times D_{torus}}$$

This ensures higher correlations for patches that are closer together. Finally, we multiplied the spatial correlation matrix with the environmental values, yielding a vector of spatially correlated environmental values:

$$E = W \times E'$$

This simulation of environmental conditions that exhibit realistic spatial autocorrelation is crucial for understanding how organisms respond to spatially structured environments in our simulations.

Figure 3.11 *(preceding page)*: **Community-average beta diversity weighted by geographical proximity separately for amphibians, birds, mammals, and reptiles across each percentile (100 quantiles) of climatic frequency across space measured across different geographical scales**. Error bars describe confidence intervals computed from standard errors for each quantile.

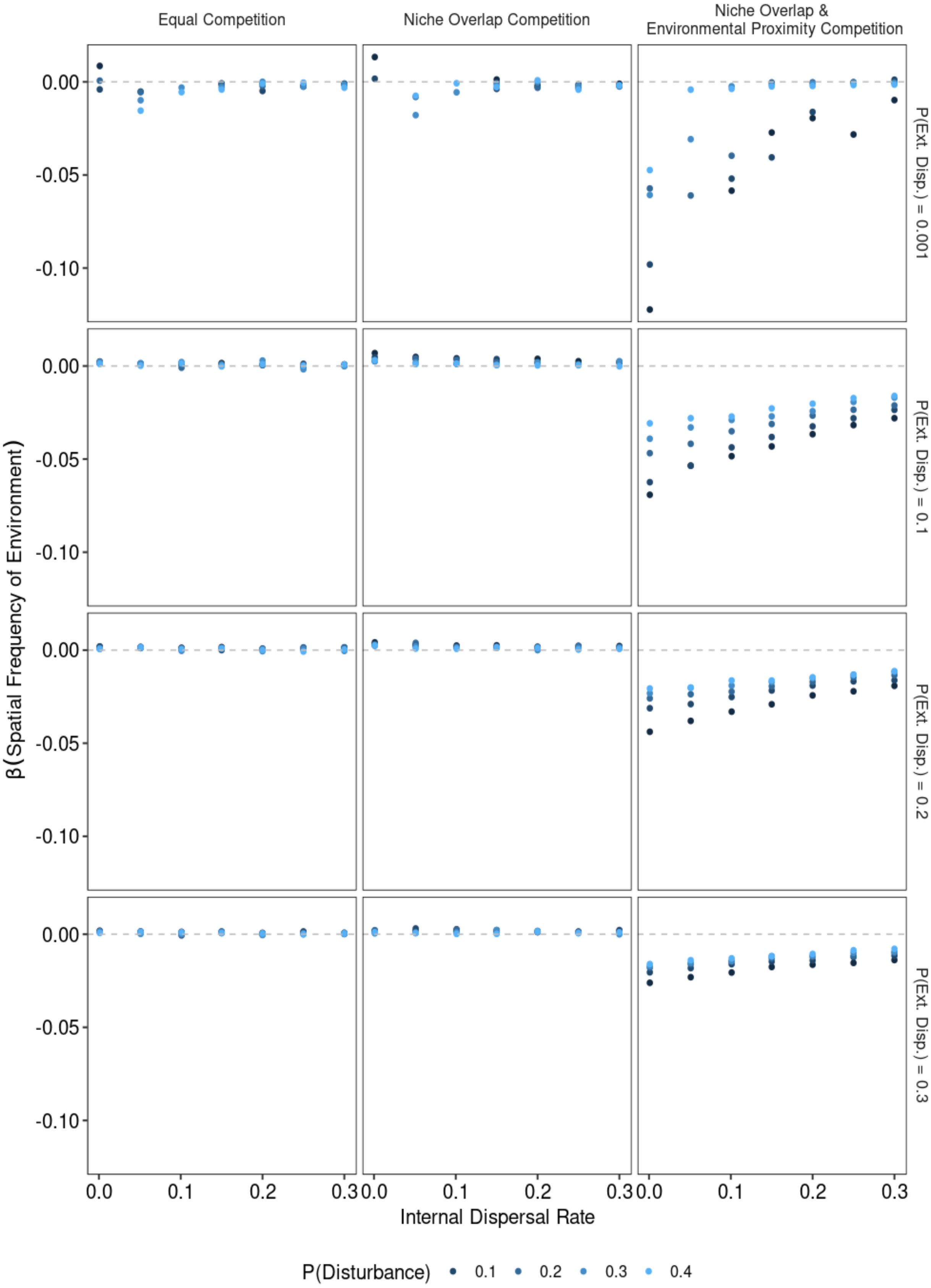
3.12 Supporting Information 6

Table 3.4: **Parameters used in the metacommunity simulations**. They include the number of patches, carrying capacity, richness levels, dispersal probabilities, and disturbance regimes. The parameters are categorized into ecological and environmental settings, dispersal dynamics, disturbance scenarios, and different types environmental-dependent interspecific competition scenarios. The values are presented as unique combinations (totalling 1,209 different combinations) to represent the different simulation settings explored.

Parameter	**Values**
Number of patches	400
Carrying capacity (K)	500
Richness in the metacommunity (S)	200
Number of generations	1500
Richness in the regional pool	1000
Distribution type for the environment	Spatial autocorrelation, Normal
Maximum number of offspring	10
Disturbance probability	0.00, 0.10, 0.20, 0.30, 0.40
Disturbance intensity	0.90
Strength of exponential distance decay during dispersal	0.50, 1.00, 1.50
Internal dispersal probability	0.00, 0.05, 0.10, 0.15, 0.20, 0.25, 0.30
Max. dispersal distance	10
External dispersal probability	0.00, 0.10, 0.20, 0.30
Number of patches receiving immigrant populations	10
Max. number of immigrants	10
Simulation scenario	Equal competition
	Niche overlap competition
	Niche overlap and environmental proximity competition

3.13 Supporting Information 7

3.13.1 Robustness of parameters within the metacommunity simulations


Equal Competition
Niche Overlap Competition
Niche Overlap & Environmental Proximity Competition
P(Ext. Disp.) = 0.001
P(Ext. Disp.) = 0.1
P(Ext. Disp.) = 0.2
P(Ext. Disp.) = 0.3
β(Spatial Frequency of Environment)
0.00
-0.05
-0.10
0.0
0.1
0.2
0.3
Internal Dispersal Rate
P(Disturbance)
0.1
0.2
0.3
0.4

3.13.2 Accounting for the influence of environmental conditions in the relationship between environmental frequency and community weighted niche breadth

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Figure 3.12 *(preceding page)*: **Community-level environmental specialisation responses to the spatial frequency of environmental conditions in simulated metacommunities under different ecological competition scenarios, and varying rates of disturbance, external dispersal and internal dispersal**. Each point represents a different simulation under a combination of ecological scenarios, with varying rates of disturbance, external dispersal, internal dispersal, and environmental mediation in competition, and with the exponential decay parameter, α, of 0.5. β denotes the ordinary least square regression coefficient of the spatial frequency of the environment in each community on the community's average of environmental niche breadth.

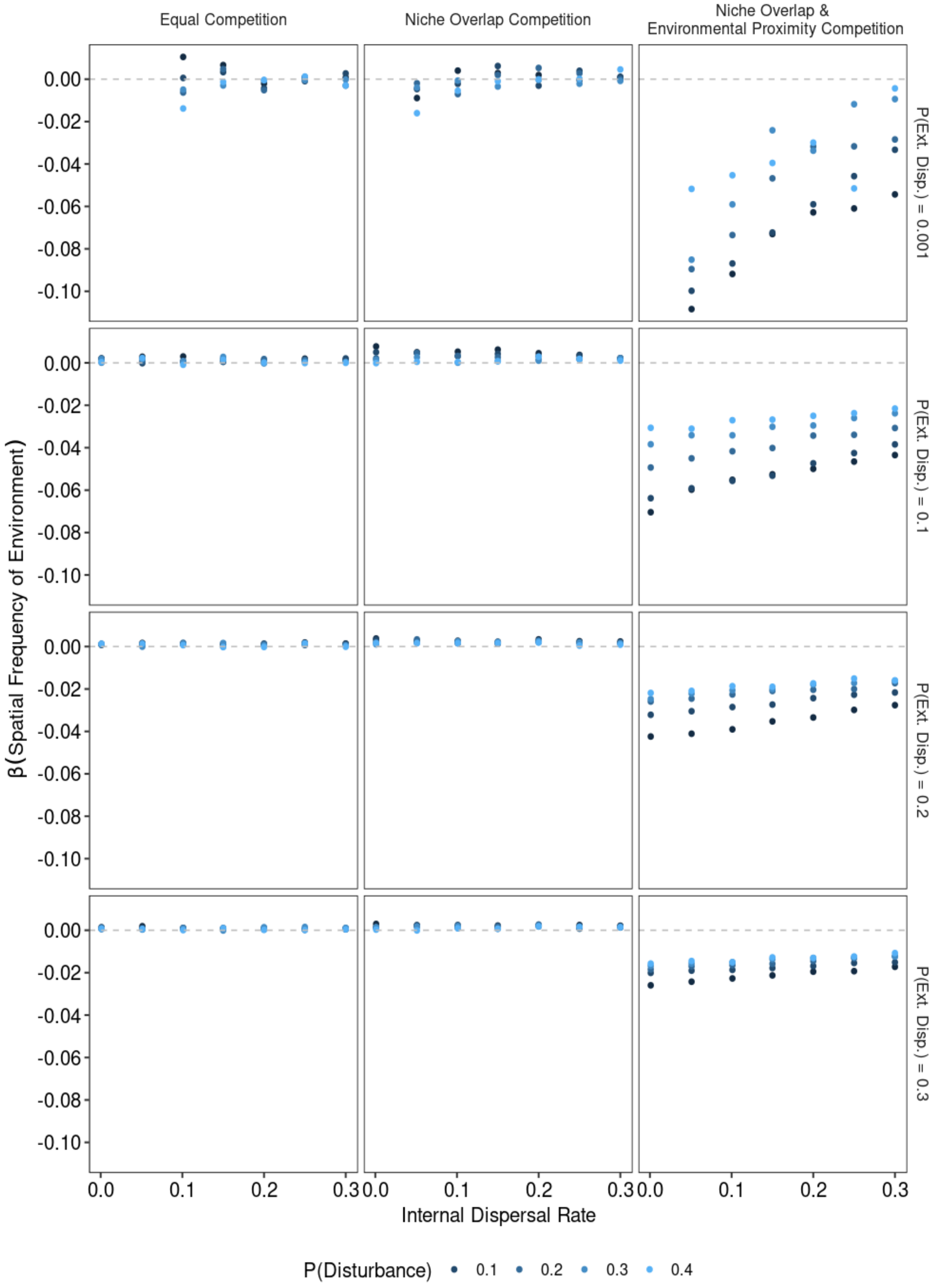
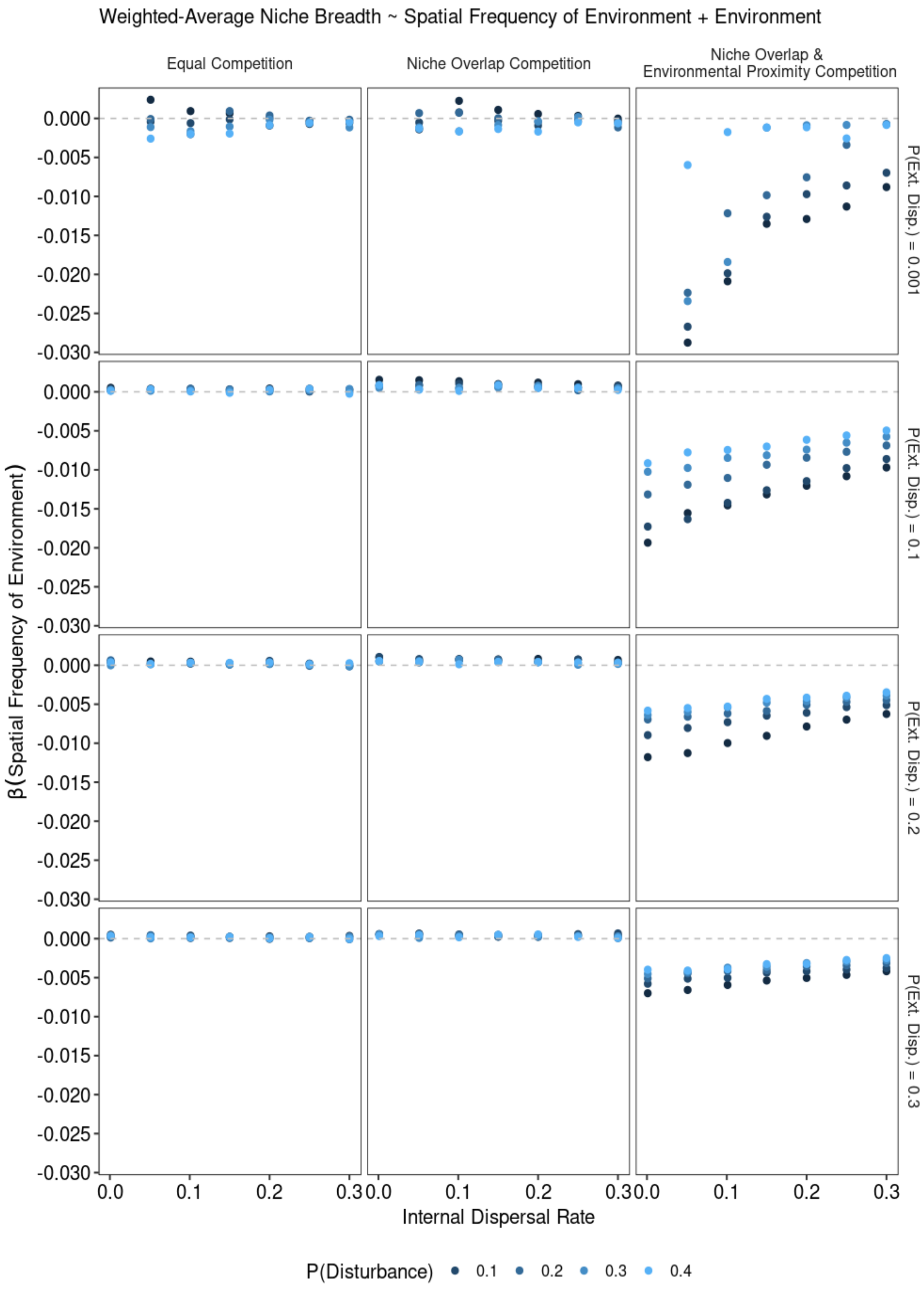

Equal Competition
Niche Overlap Competition
Niche Overlap &
Environmental Proximity Competition
P(Ext. Disp.) = 0.001
P(Ext. Disp.) = 0.1
P(Ext. Disp.) = 0.2
P(Ext. Disp.) = 0.3
β(Spatial Frequency of Environment)
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
0.0
0.1
0.2
0.3
Internal Dispersal Rate
P(Disturbance)
0.1
0.2
0.3
0.4

Figure 3.13 *(preceding page)*: **Community-level environmental specialisation responses to the spatial frequency of environmental conditions in simulated metacommunities under different ecological competition scenarios, and varying rates of disturbance, external dispersal and internal dispersal**. Each point represents a different simulation under a combination of ecological scenarios, with varying rates of disturbance, external dispersal, internal dispersal, and environmental mediation in competition, and with the exponential decay parameter, α, of 1.5. Here, β denotes the ordinary least square regression coefficient of the spatial frequency of the environment in each community on the community's abundance-weighted average of environmental niche breadth.



Weighted-Average Niche Breadth ~ Spatial Frequency of Environment + Environment
Equal Competition
Niche Overlap Competition
Niche Overlap & Environmental Proximity Competition
P(Ext. Disp.) = 0.001
P(Ext. Disp.) = 0.1
P(Ext. Disp.) = 0.2
P(Ext. Disp.) = 0.3
β(Spatial Frequency of Environment)
0.000
-0.005
-0.010
-0.015
-0.020
-0.025
-0.030
0.0
0.1
0.2
0.3
Internal Dispersal Rate
P(Disturbance)
● 0.1
● 0.2
● 0.3
● 0.4

Figure 3.14 *(preceding page)*: **Partial coefficients from the models containing the environmental conditions besides environmental frequency.** Each point represents a different simulation under a combination of ecological scenarios, with varying rates of disturbance, external dispersal, internal dispersal, and environmental mediation in competition, and with the exponential decay parameter. Here, β denotes the ordinary least square regression partial coefficient of the spatial frequency of the environment after controlling for environmental conditions in each community on the community's abundance-weighted average of environmental niche breadth.

Chapter 4

Climatic commonness and rarity shape phylogenetic structure and suitability in tetrapod communities

4.1 Abstract

Climate shapes ecological communities across space and time. It sets physiological limits for organisms, driving population dynamics, species distributions, community assembly and ultimately, biodiversity patterns. Among the various aspects of climate, an underexplored dimension is its frequency distribution—how common or rare climatic conditions are across space. To uncover the mechanisms driving community-level responses to climatic frequency, we addressed three key questions: Does climatic frequency influence the phylogenetic structure of ecological communities across geographical scales? Are rare climates less suitable for supporting the diversity of closely related species than common climates? Do species with relatively recent ancestors exhibit similar preferences for climatic frequencies? We analyzed global data on climate, geographical distributions, and phylogenetic relationships of extant terrestrial tetrapods – amphibians, birds, mammals, and squamate reptiles. Globally, we found that ecological communities are less phylogenetically clustered in rare climates. Our results reveal that communities in rare climates exhibit lower phylogenetic clustering, reflecting greater phylogenetic diversity. Additionally, species co-occurring in both exceedingly rare and highly common climates tend to depart from their climatic optima. Our findings suggest that climate frequency plays a more influential role in recent ecological dynamics and evolutionary adaptations than deep ancestral constraints in shaping these communities.[1]

4.2 Introduction

Every species experiences environmental variation across space and time. Such fluctuations create conditions that either facilitate or impede the survival, persistence, and reproductive success of individuals and populations, ultimately shaping the biodiversity patterns observed today (von

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[1] This study is under peer-review, and a preprint is available in *Authorea as:*
Braga, P. H. P., Kembel, S., & Peres-Neto, P. (2024). Climatic commonness and rarity shape phylogenetic structure and suitability in tetrapod communities. *Authorea*, October 31, 2024.

Humboldt 1849; Hutchinson 1957; Soberón 2007; Soberón & Nakamura 2009). Among a myriad environmental factors, climate —the long-term patterns of weather—emerges as a predominant factor underlying species distributions. Its influence extends to the composition and structure of ecological communities, significantly affecting ecological and evolutionary dynamics (*e.g.,* Lieth 1975; Currie 1991; Rohde 1992; Currie *et al.* 2004; Araújo & Pearson 2005; Svenning & Skov 2007; Rakotoarinivo *et al.* 2013; Eiserhardt *et al.* 2015; Vázquez-Rivera & Currie 2015; Barreto *et al.* 2021). As such, understanding the ecological effects of climate has long been an attractive area of study, now receiving much increased attention due to the challenges posed by ongoing contemporary climate change.

In the study of biodiversity patterns, both average climate conditions and their spatial variability (heterogeneity) have been extensively explored. Differences in mean climate across localities and regions drive variation in species compositions and abundance through direct physiological and metabolic constrains (*e.g.*, Easterling *et al.* 2000; Sunday *et al.* 2012; Buckley & Huey 2016), influencing population phenology, behaviour, and ecological optima (*e.g.,* González 1974; Magnuson *et al.* 1979; Sunday *et al.* 2012; Sunday *et al.* 2014). At the same time, spatial variability in climatic conditions promotes species coexistence by facilitating niche partitioning (Kerr & Packer 1997; Chesson 2000a; Currie 2001). However, beyond spatial differences, the availability of climate conditions across localities and regions is uneven (Fournier *et al.* 2020), and their ecological effects on biodiversity remain poorly understood.

Climatic conditions vary from rare (also ‘marginal’ or ‘scarce’) to common. As with average conditions and spatial heterogeneity, the frequency of climatic conditions is expected to shape biodiversity. Rare climates may favour climatic generalists (Fournier *et al.* 2020) because specialisation and adaptation to rare resources can be excessively costly (Kassen 2002). These climates are also less predictability, often spatially disjunct or fragmented (Fournier *et al.* 2017), limiting dispersal and population fitness (Kawecki *et al.* 1997; see Hoffmann 2005), further constraining the establishment of climatic specialists. In contrast, generalists, with their broader climatic tolerances, are more likely to thrive in rare climates. Nonetheless, there is evidence of specialization through evolutionary radiation in rare environments, where species exploit vacant niches (Gaston 1994), as observed in endemic taxa on islands and at higher elevations (*e.g.*, Steinbauer *et al.* 2013; Fernández-Palacios *et al.* 2021).

Climatic frequency is expected to shape species co-occurrences patterns within communities. Species co-distributions are often influenced by geographical and historical variations in interactions, habitat preferences, dispersal, and speciation processes (*e.g.,* Peres-Neto 2004; Kembel 2009; Svenning *et al.* 2015; Braga *et al.* 2023b). Ecologically similar species are expected to compete more intensely when they rely on overlapping resources, limiting their co-occurrence (Darwin 1859; Macarthur & Levins 1967; Szabó *et al.* 2006). Rare climatic conditions may generate unique ecological niches that favour specialized species or facilitate coexistence among generalists. However, the scarcity of rare climates may constrain opportunities for specialists to co-occur and establish stable populations, potentially promoting the dominance of generalist species in more rare climates. Conversely, species with similar niche requirements may accumulate in common environments, leading to either positive or negative co-occurrence patterns among specialists.

Our study employs an ecophylogenetics framework (see Davies 2021) to investigate how climatic frequency shapes community structure across global scales, revealing patterns beyond species composition by accounting for the evolutionary diversity of communities, even when they share no species in common. From an evolutionary perspective, species with similar traits and niches are expected to respond similarly to environmental variation across speciation events—a process known as 'phylogenetic niche conservatism' (see Harvey & Pagel 1991). As a result, the phylogenetic relatedness within communities vary strongly across geographical climatic gradients (*e.g.*, Webb 2000; Cavender-Bares *et al.* 2009; Kembel 2009; Stevens *et al.* 2012). Harsh or stressful climatic conditions, such as cold or arid environments, as well as rare environments, may promote the coexistence of closely related species that share stress-tolerant traits, leading to phylogenetic clustering (Wiens & Donoghue 2004; Qian & Sandel 2017).

Disentangling the effects of climate frequency, averages, and heterogeneity on ecological communities is challenging, as these factors may not operate in isolation. Climatic heterogeneity, for example, can increase ecological opportunities by offering diverse environments and resources, promoting species and lineage coexistence (MacArthur & MacArthur 1961; Stevens *et al.* 2012). At the same time, it can constrain species ranges and elevate extinction risks, followed by recolonization by newly diversified taxa (*e.g.*, Colville *et al.* 2020). Since both climate heterogeneity and frequency can shape species composition during community assembly and influence evolutionary trajectories, studies of climatic frequency must also consider the role of climatic heterogeneity (*i.e.*, changes in average conditions across regions). Moreover, the impact of climatic frequency on phylogenetic community structure is further complicated by spatial and phylogenetic scale dependencies, reflecting the interplay of ecological and evolutionary processes across multiple (Wiens 1989; Levin 1992; Whittaker *et al.* 2001; Chave 2013; Graham *et al.* 2018).

To investigate how climatic frequency shapes the phylogenetic structure and ecological suitability of ecological communities, we addressed three complementary questions, each grounded in specific hypotheses:

Q_1. Does climatic frequency influence the phylogenetic structure of biological communities across geographical scales? Assuming that specialization in rare climatic conditions is detrimental to population performance and persistence (Kawecki *et al.* 1997), co-occurring species should belong to clades capable of tolerating both rare and common climates. In contrast, communities in common climates are expected to consist of well-adapted specialist species, resulting in a higher degree of phylogenetic relatedness among them than among species found in rare climates.

Q_2. Are rare climates less suitable for ecological communities than common climates? Populations generally thrive in habitats where they are well-adapted. If long-term adaptation to rarer climates is less likely than to common ones (Kawecki *et al.* 1997), making colonization more challenging, species in communities within rare climates are expected to deviate further from their climatic optima, becoming ecologically marginal.

Q_3. Do closely related species exhibit similar climatic frequencies? If climatic frequency shapes phylogenetic community structure through long-term evolutionary processes, we would expect strong similarity in the climatic frequencies of species' distributional ranges, indicating a phylogenetic signal. Phylogenetic clustering along the climatic frequency gradient (from rare to common) would suggest phylogenetic conservatism in climatic frequency (*sensu* Keddy 1992; Kraft *et al.* 2007; Cavender-Bares *et al.* 2018). Conversely, the absence of phylogenetic signal in climatic frequencies across taxa might indicate that species assembly in communities occurs through stochastic processes such as genetic drift or divergence, phenotypic plasticity or coexistence mechanisms (see Crisp & Cook 2012).

We adressed these questions by analyzing global data on the distributions and phylogenetic relationships of 22,125 species across four major four-limbed terrestrial vertebrates (Tetrapoda)—amphibians, birds, mammals, and squamate reptiles—in relation to global cliomate. Using eight high-resolution bioclimatic variables representing temperature and precipitation, we calculated climatic frequencies at found geographical scales: global, hemispheric (east-west), realm, and biome. We evaluated the phylogenetic structure of communities by computing the standardized effect sizes of mean phylogenetic distances and mean nearest-taxon distances. We also quantified climatic marginality as the extent to which co-occurring species deviate from their preferred climatic conditions. Next, we used statistical models to assess how climatic frequency influences phylogenetic community structure (Q_1) and climatic marginality (Q_2), accounting for climatic heterogeneity and average climatic conditions. Finally, we examined phylogenetic signals in species-specific climatic frequencies using evolutionary models (Q_3). Our results demonstrate that climatic frequency plays a critical role in shaping tetrapod community structure across diverse geographical scales and phylogenetic levels.

4.3 Methods

4.3.1 Study area and geographical scales

We created an equal-area flat-topped hexagonal tessellation that covered Earth's terrestrial lands, which we compiled from Natural Earth (naturalearthdata.com; projected to the Behrmann cylindrical equal-area projection). We used hexagonal tessellation for aggregating all biodiversity and climate data used in our study, which better represents local connectivity factors that are relevant for ecological studies (Carr *et al.* 1992; Birch *et al.* 2007; White & Kiester 2008). The hexagons we used had an area of 541.3 km^2 with a short-diagonal length of 25 km. After eliminating hexagons that covered less than 50% of their terrestrial land area, we were left with 248,139 hexagons.

To determine whether scale dependencies in climatic spatial frequency influence patterns of phylogenetic relatedness and the average deviation of species in a community from their climatic optima (hereafter also referred to as "climatic marginality") in ecological communities, we applied a framework for identifying, regionalizing and computing climatic frequencies for three hierarchical geographical scales: (i) global, (ii) east-west hemispherical (New World and Old World), (iii) biogeographical realms [Palaearctic, Indo-Malaya, Afrotropics, Australasia, Nearctic and Neotropics; Olson *et al.* (2001)], and (iv) biomes (Olson & Dinerstein 1998; Mucina 2019). We selected these geographical scales for calculating climatic frequencies based on several considerations. Climate regimes are known to vary with spatial scales (Franzke *et al.* 2020), exhibiting differences between the Eastern and Western hemispheres. The Eastern hemisphere contains more climate zones, and while the Western hemisphere experiences steeper temperature gradients (*e.g.*, Latonin *et al.* 2022). Sensible heat transport dominates the Western hemisphere, whereas latent heat transport systems dominating the Eastern hemisphere – which contribute to heat excess and moist patterns. In addition to these distinctions in east-west meridional atmospheric internal energy transport systems, North

Atlantic and El-Niño-Southern oscillations contribute to climate in the Western hemisphere, while Asian monsoon systems influence the Eastern hemisphere, contributing to the observed east-west climate asymmetries (see Latonin *et al.* 2022). Biogeographical realms represent large regions with ecosystems sharing similar biotic histories shaped by geological, climate, and evolutionary processes (Udvardy 1975; Lomolino *et al.* 2017). Lastly, biomes are distinct climatic and vegetation domains (Whittaker 1975; Colin Prentice *et al.* 1992; Mucina 2019). These geographical extents have also been used to study the causes underlying spatial scale dependence in community structure (*e.g.*, Kissling *et al.* 2012; Thuiller *et al.* 2020; Braga *et al.* 2023b).

4.3.2 Species distributions

We obtained species presence-absence records for amphibians, birds, mammals, and reptilian squamates from distributional range maps available within the International Union for Conservation of Nature Red List of Threatened Species database (IUCN 2022).

We projected each species' range onto a Behrmann cylindrical equal-area projection and overlaid it onto the hexagonal tessellation.

A species was considered present in a hexagon only if it occupied a minimum of 50% of its area. To minimize false occurrences, we only retained species that were present in at least two hexagons.

4.3.3 Species phylogenetic relationships and divergence time data

We obtained dated evolutionary relationships from phylogenetic hypotheses for amphibians [Jetz & Pyron (2018); 7,406 species], birds [Jetz *et al.* (2012); built on the backbone phylogeny from Ericson *et al.* (2006); 9,993 species], mammals [Upham *et al.* (2020); 5,991 species], and squamate reptiles [Tonini *et al.* (2016); 9,754 species] from the Vert Life database (vertlife.org). These datasets collectively included 33,144 extant and recently extinct species.

To ensure there were no polytomies and no negative branch-lengths, we computed ultrametric maximum clade credibility trees for each of the four tetrapod groups from a random subset of 100 posterior distributions trees.

Next, we pruned the resulting phylogenetic trees to match the species distribution data, resulting in dated phylogenetic trees that included 3,627 amphibians, 7,498 birds, 4,565 mammals, and 6,435 squamate reptiles.

To account for the uncertainty associated with phylogenetic relationships, we conducted identical analyses on 30 trees randomly selected trees from the posterior distributions of the phylogenetic hypotheses. The comparisons of these results with those obtained using the maximum clade credibility trees yielded very similar outcomes, supporting the robustness of our findings to the uncertainty in phylogenetic hypotheses (see Supporting Information 3).

4.3.4 Phylogenetic community structure

For each tetrapod group, we quantified the degree of relatedness among co-occurring species within their communities (*i.e.*, co-occurring species within each hexagon) using two complementary indices of community phylogenetic structure: the mean phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD) (Webb 2000; Webb *et al.* 2002).

MPD provides an overall estimate of community phylogenetic structure, whereas MNTD is more sensitive to the community structure driven by phylogenetic tips [*i.e.*, reflecting more recent processes; Webb *et al.* (2002)]. The use of both MPD and MNTD allows one to gain insights into the mechanisms underlying community structure across phylogenetic scales (Cavender-Bares *et al.* 2009; Graham *et al.* 2018).

To make phylogenetic community structure comparable among communities, we applied null models to estimate standardized effect sizes for both metrics ($\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$, respectively) (Webb *et al.* 2002; Kembel 2009). We simulated random assemblages by permuting species' names across the phylogenetic tips 999 times in relation to the worldwide communities for that taxonomic group. Note that the observed value (MPD or MNTD) was considered as one possible value within the null distribution, resulting in 1,000 random values, as is common in null model applications. Lower values of $\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$ indicate that the phylogenetic relatedness of co-occurring species is greater than expected for a given geographical extent, suggesting that local communities are composed of species that are more phylogenetically similar than what would be expected from random assemblages. Conversely, positive $\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$ values indicate phylogenetic evenness, meaning that species are more distantly related than expected by random chance.

4.3.5 Climate

We compiled nineteen bioclimatic variables derived from monthly temperature and precipitation data (averaging between 1970 and 2000) from the WorldClim (version 2.1) database (Fick & Hijmans 2017). These variables, at a resolution of 30 arc-seconds—equivalent to nearly 1 km × 1 km at the Equator—, are known to reflect ecosystem processes, imposing physiological constraints, and influencing species survival (Title & Bemmels 2018).

To align the climatic data with our spatial analysis framework, we projected it onto the same resolution and projection as the hexagonal tessellation. We also applied a log transformation to non-symmetrical variables, primarily precipitation variables, to reduce heteroskedasticity.

Given the potential for biased results due to collinearity among bioclimatic variables, we iteratively computed variance inflation factors [VIF; following Marquardt (1970); Chatterjee & Hadi (1977)] on 10,000 randomly-drawn observation units (hexagons) to identify and remove highly colinear variables from our dataset. Variables with a VIF exceeding 15, indicative of substantial collinearity, were sequentially removed from the dataset until no further variables met this threshold.

The final set of bioclimatic variables, which were then used in further analyses, included mean annual temperature (BIO 1), mean diurnal range (BIO 2), temperature seasonality (BIO 4), mean temperature of the wettest quarter (BIO 8), $\log_e(1+$ annual precipitation) (BIO 12), precipitation seasonality (BIO 15), $\log_e$(1+ precipitation of the warmest quarter) (BIO 18), and $\log_e$(1+ precipitation of the coldest quarter) (BIO 19).

4.3.6 Spatial climatic frequency

We characterized the spatial frequency of climatic conditions across communities using a probability density estimation approach.

To calculate climatic frequency across all communities, we started by decreasing the dimensionality of the climatic dataset using a principal component analysis based on a correlation matrix (standardized to have mean zero and standard deviation one). We retained the principal components that captured the variation in climate better than expected by chance [*i.e.*, based on the broken-stick rule; see Jackson (1993) for an explanation on the rule]. These orthogonal principal components were then used to calculate indices of spatial climatic frequency and spatial climatic heterogeneity.

We computed the multivariate kernel density on the retained climate principal components using a multivariate generalisation plug-in for bandwidth matrix selection (see Jones 1994; Chacón & Duong 2018; and Duong & Hazelton 2003).

To facilitate the interpretation of the density distribution, we normalized the frequency values by scaling them to range between zero (rarest) and one (most frequent). These resulting values correspond to the frequency (or commonness) of climatic conditions across the geographical space. Communities located within less frequent climates experience rarer combinations of contemporary climates and communities with larger climatic frequency have common climatic conditions.

Because climatic frequencies are relative to the geographical extent of climatic conditions, we computed climatic frequency across four different geographical scales (extents): global, east-west hemispheres (also referred to as Old World and New World), biogeographical realms, and biomes, and performed separate analyses for each of these scales.

4.3.7 Spatial climatic heterogeneity

To quantify climatic heterogeneity within each community (hexagon), we used the eight selected bioclimatic variables (see above) in their original, high resolution of 30 arc-seconds. First, we standardized these variables to zero mean and unit variance. We then projected the standardized data to the same principal component space used to compute climatic frequencies, ensuring the framework was comparable and consistent. We then recalculated the standardization for these principal component scores to maintain normalization across scales, we further standardized the high-resolution climatic principal components. Using these principal component scores, we estimated climatic heterogeneity within each community by averaging the pairwise Euclidean distances between all scores within each community. This measure reflects the extent of climatic variation, with higher values indicating greater variability in climatic conditions within the community.

4.3.8 Spatial climatic marginality

To characterize how far species occurring in a community are from their preferred climate, we began by calculating the climatic optimum of each species. This involved computing the average of each standardized climate principal component value across all communities where each species occurs. Then, we used the resulting climatic optima of each species to compute the weighted average marginality (*i.e.*, the deviation from their climatic optima) of each community, separately for each tetrapod group.

High climatic marginality values in a community suggest that co-occurring species of that taxonomic group are, on average, located far from their preferred climate. Conversely, low values indicate species in that community are generally closer to their climatic optima.

4.3.9 Statistical analyses

We assessed the effects of climatic frequency on community phylogenetic structure (Q_1) and on community climatic marginality (Q2) using a series of generalized additive models (GAMs). GAMs are advantageous for their flexible semi-parametric capability to model both linear and non-linear relationships between response and explanatory variables (Hastie & Tibshirani 1987; Hastie & Tibshirani 1990). Smoothing parameters were estimated using restricted maximum likelihood, and we inspected all resulting models for assumption violations and selected smoothing basis dimensions that were less restrictive (*sensu* Wood 2004).

Although our primary objective was to explore how climatic frequency influenced tetrapod communities, our analyses also addressed the influence of climatic heterogeneity in community phylogenetic structure. Consequently, we present additional analyses that consider the effects of both climatic heterogeneity and average climatic conditions (in the form of the selected principal components representing climate) in the relationships we explored (Supporting Information 2). Finally, to aid the interpretation of results, we also partition the linear from the non-linear effects of climatic frequency on community phylogenetic structure (Supporting Information 2).

4.3.9.1 Effects of climatic frequency on community phylogenetic structure (Q_1)

To assess the effects of climatic frequency on the phylogenetic structure of tetrapod communities (Q_1), we employed separate GAMs with MPD_{SES} and $MNTD_{SES}$, respectively, as response variables and penalized thin-plate splines for climatic frequency and climatic heterogeneity, separately for each geographical scale and each taxonomic group combination.

4.3.9.2 Effects of climatic frequency on community climatic marginality (Q_2)

To test whether climatic frequency modulates community climatic marginality (Q_2), we also performed GAMs with climatic marginality as a response variable and penalized thin-plate splines of climatic frequency and climatic heterogeneity, separately for each geographical scale and each taxonomic group combination.

4.3.9.3 Phylogenetic signal in climatic frequency (Q_3)

To determine if closely related species exhibit similar climatic frequencies (Q_3), we assessed the degree to which species' evolutionary relatedness correlated with ecological similarity. This involved assessing the strength of the phylogenetic signal in the average climatic frequency across the distributional range of each species, for each geographical scale and each tetrapod group.

Because evolutionary differences in traits structuring species co-occurrence do not consistently correlate with phylogenetic distances (see Cadotte *et al.* 2017), it is important to compare alternative models of trait evolution to ensure accurate ecophylogenetic interpretations.

We applied four maximum-likelihood-based phylogenetic comparative models to assess phylogenetic signals in climatic frequency. The first three were Pagel's λ (lambda), Pagel's δ (delta), and Blomberg's K (Pagel 1997, 1999; Blomberg & Garland Jr 2002), and are based on a Brownian motion model of evolution, where differences in trait values along branches of a phylogeny are drawn from a normal distribution with a mean equal to the ancestral state and variance proportional to a constant rate of change and time (Cavalli-Sforza & Edwards 1967; Felsenstein 1973). The fourth model, the stationary-peak model, focuses on the average duration required for a trait value to reach halfway toward an optimal trait value. It assumes an Ornstein–Uhlenbeck (OU) model of evolution, which accounts for the strength of attraction of a trait toward an optimum trait value (Lande 1976; Hansen 1997).

Because within-species trait variation can bias the estimation of phylogenetic signals, we used the standard error in climatic frequency across the geographical distribution of each species to account for uncertainty in the models we performed (see Ives *et al.* 2007; Silvestro *et al.* 2015).

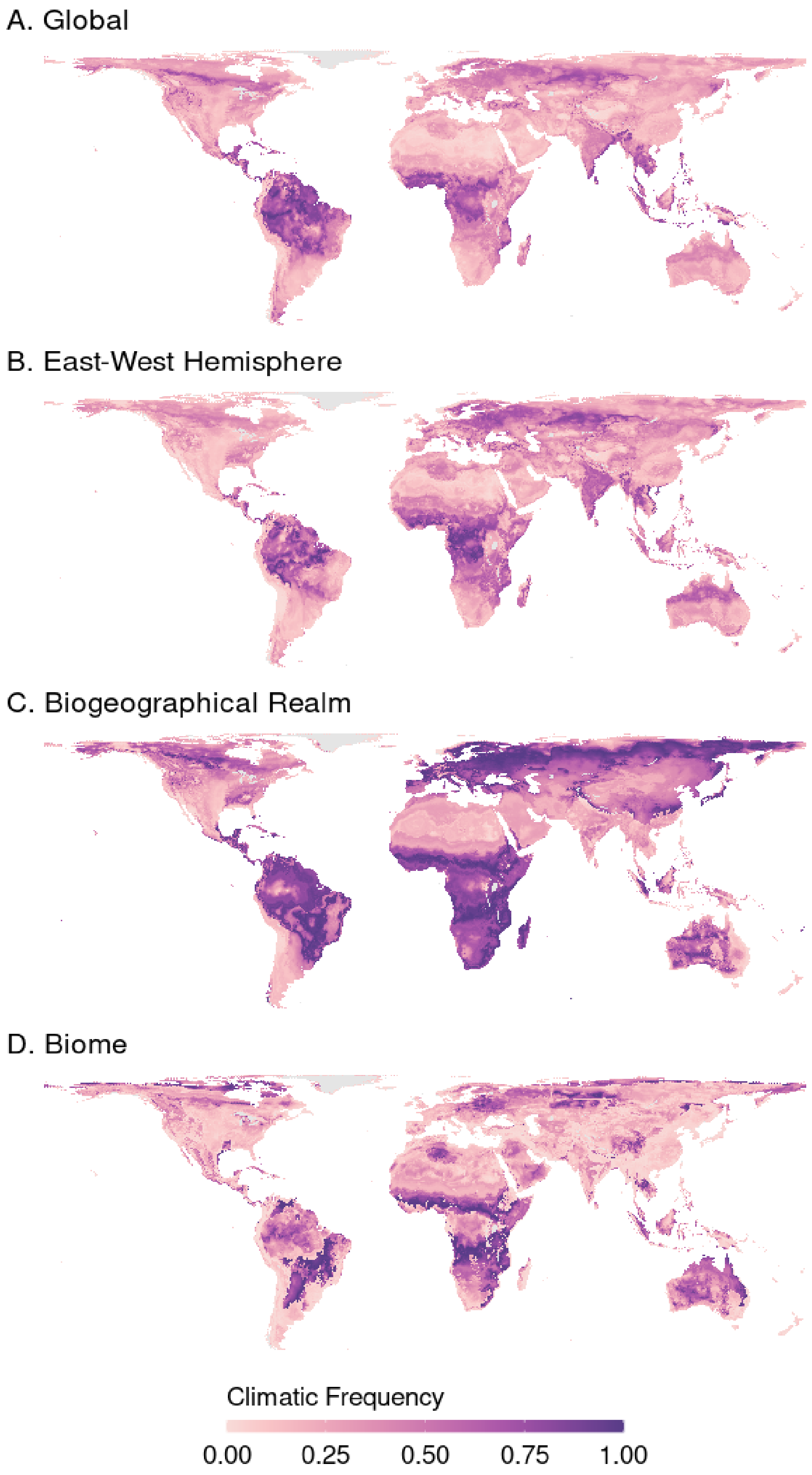
4.3.10 Computational tools

All data manipulation and analyses were performed in R and RStudio (Posit Team 2023; R Core Team 2023). The description of R libraries and software versions we used, and the necessary code and data to fully reproduce the analyses and figures from this study are respectively available within the Supporting Information 1 and the Open Science Framework (https://osf.io/3hkn7/) repository.

4.4 Results

4.4.1 The worldwide distribution of frequent climates

Climatic frequency varies considerably worldwide, ranging from broader, global scales, to more localized, biome scales (see Figure 4.1, and Figure 4.5). Across scales, abrupt transitions from common to rarer climates are particularly marked by mountain ranges. Arid desert and polar climates were the rarest across scales, while tropical savannas, rainforest, and monsoon climates were the most common climates (see Table 4.1). This concentration of rare climates near mid- and high-elevational, and coastal regions is aligns with previous depictions of climatic frequency across different geographical extents (*e.g.*, Batllori *et al.* 2014; Wang *et al.* 2018; Fournier *et al.* 2020). The density of rare climatic conditions is higher at broader scales compared to narrower geographical scales (Figure 4.1, and Figure 4.5).


A. Global
B. East-West Hemisphere
C. Biogeographical Realm
D. Biome
Climatic Frequency
0.00
0.25
0.50
0.75
1.00

4.4.2 Climatic frequency as a driver of phylogenetic community structure (Q_1)

After accounting for climatic heterogeneity, we observed that tetrapod communities were increasingly phylogenetically clustered as climatic conditions become more common. This trend is particularly notable at the global, east-west hemispheric, and biome scales (see Figure 4.2; Table 4.2 and Table 4.3). These effects are more pronounced for $\mathrm{MNTD}_{\mathrm{SES}}$ compared to $\mathrm{MPD}_{\mathrm{SES}}$, underscoring differences between deep time and more recent effects of climatic frequency on phylogenetic community structure (see Figure 4.2; Table 4.2 and Table 4.3). Despite being less pronounced at certain geographical scales, the negative relationship between climatic frequency and phylogenetic community structure remained evident after controlling for the effects of climatic conditions and climatic heterogeneity using residualization (see Supporting Information 2; Figure 4.6, Table 4.6 and Table 4.7).

The relationship between climatic frequency and phylogenetic community structure also varied across taxonomic groups as well as geographical scales. Generally, climatic frequency had stronger influence on the community phylogenetic relatedness more strongly within amphibian and squamate communities, compared to those of birds and mammals (see Figure 4.2, Figure 4.6, Table 4.2 and Table 4.3).

4.4.3 Community-level species climatic marginality is lower in very common and in very rare climates (Q_2)

Climatic frequency significantly influenced climatic marginality in tetrapod communities. Across geographical scales, co-occurring species tend to be farther from their optima in exceedingly rare or exceedingly common climates (see Figure 4.3; Table 4.4). These patterns were remarkably consistent across the major tetrapod lineages we investigated.

Figure 4.1 *(preceding page)*: **Global distribution of climatic frequencies across geographical scales.** It depicts climatic frequency related to four geographical scales: (a) global, (b) east-west hemispheric, (c) biogeographical realm, and (d) biomes. Climatic frequencies were calculated using a probability density estimation methods based on the principal components derived from eight bioclimatic variables representing precipitation and temperature (see Methods).

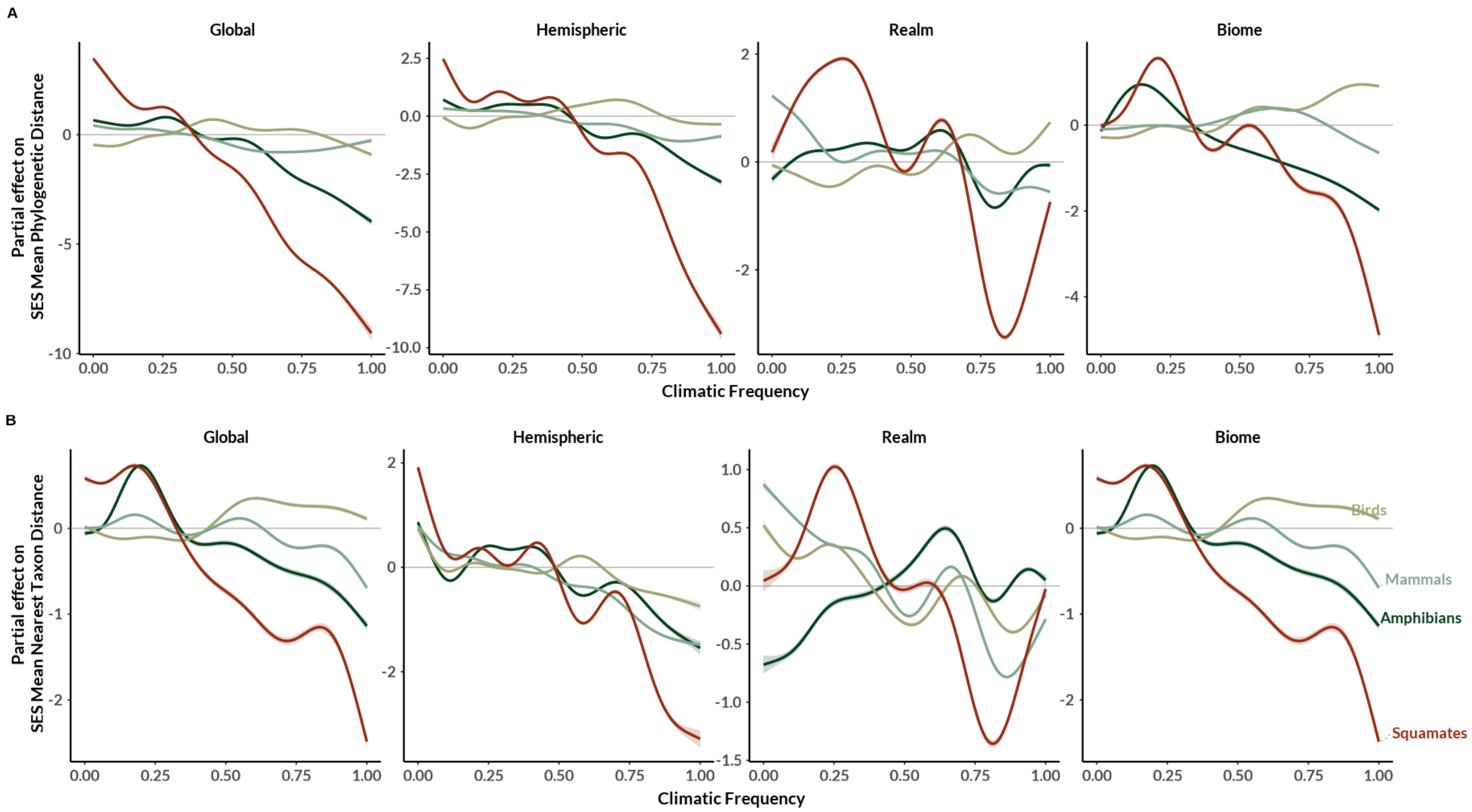


Figure 4.2: **Partial effect plots depicting the influence of climatic frequency on the phylogenetic structure of worldwide communities (248,139 geographical hexagons, in total) of four tetrapod groups: amphibians (3,627 species), mammals (4,565 species), birds (7,495 species), and reptilian squamates (6,435 species).** Phylogenetic community structure was assessed using standardized effect sizes of (A) mean phylogenetic distances and (B) mean nearest taxon distances for each tetrapod group. Climatic frequency was calculated for each community at four geographical scales (global, hemispheric, realm, and biome), and was based on contemporary climatic conditions across the globe (see Methods). The lines represent thin-plate spline smooths estimated for the partial effects of climatic frequency from GAMs with both climatic frequency and climatic heterogeneity as predictors of standardized effect sizes of mean phylogenetic distances and mean nearest taxon distances (in separate models). The shaded region around the curves denotes the 95% confidence intervals.

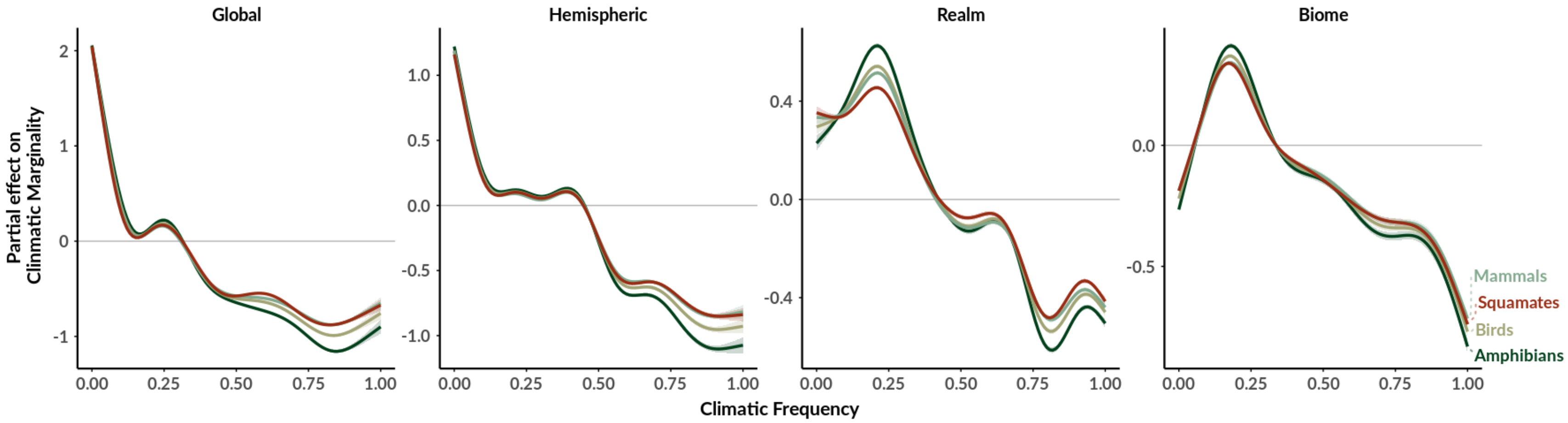


Figure 4.3: **Partial effect plots of climatic frequency on average climatic marginality in worldwide tetrapod communities.** Lines represent thin-plate regression spline smooths estimated for the effects of climatic frequency from GAMs, with both climatic frequency and climatic heterogeneity as predictors of climatic marginality for each tetrapod taxa (amphibians, birds, mammals, and squamate reptiles) and each geographical scale. Climatic marginality was measured as the average departure of each co-occurring species from their average preferred climatic conditions. Climatic frequency was estimated in each community for each one of four geographical scales (global, hemispheric, realm, and biome), and was based on contemporary climatic conditions across the globe. Shaded regions around the curves indicate 95% confidence intervals and describe uncertainty in model predictions (see Methods).

4.4.4 Lack of phylogenetic similarities in average climatic frequency (Q_3)

Overall, there were no to weak phylogenetic similarities in climatic frequency across tetrapods, irrespective of geographical extent from which climatic frequency was calculated (see Figure 4.4, and Table 4.5).

Blomberg's *K* estimates for climatic frequency being closer to zero for all taxa across geographical scales suggest no tendency in climatic frequency similarities among closely-related species. Pagel's λ estimates approached one, indicating that phylogenetic resemblance in climatic frequency across taxa does not strongly deviate from evolutionary expectation under Brownian motion. Pagel's δ values were much greater than one, suggesting high variation in climatic frequency nearing the tips of the phylogenies. Ornstein-Uhlenbeck stationary α values remained close to zero, indicating there is no tendency for climatic frequencies to converge towards an optimal value among clades.

These findings suggest that associations between the average climatic frequency across tetrapod communities were evolutionary labile across geographical scales.

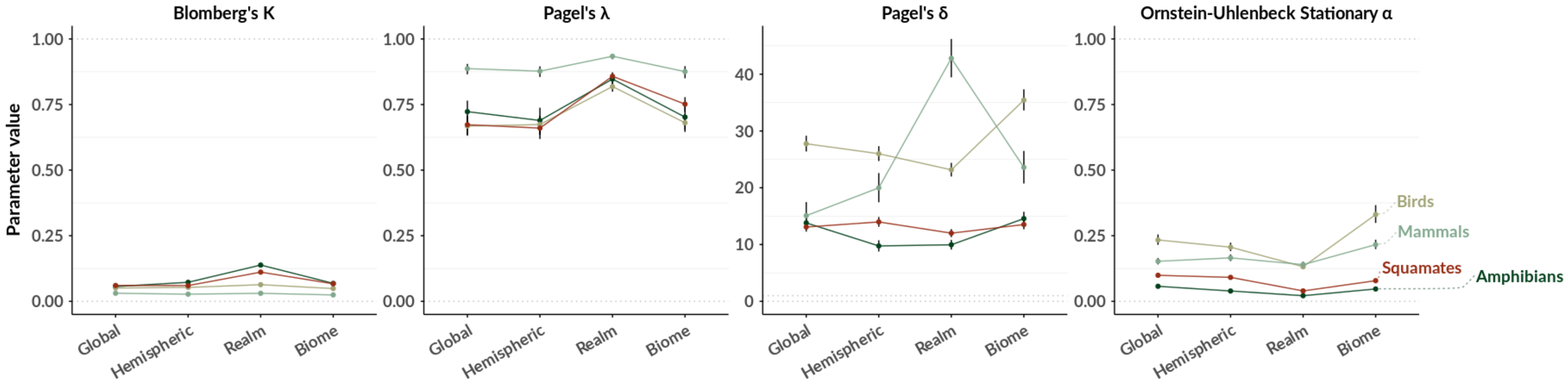


Figure 4.4: **Phylogenetic signals for species-specific average climatic frequencies computed across geographical scales using different evolutionary models.** Parameters were estimated with maximum-likelihood evaluation using phylogenetically independent contrasts and included species-specific standard errors in climatic frequency to account for within-species variation. Vertical lines denote lower and upper limits of maximum-likelihood 95% confidence intervals for parameter estimates. Blomberg's *K* values nearing zero indicate that closely related species are not more similar in climatic frequency than distant relatives. *K* values closer to one suggest that the distribution of climatic frequency across the phylogenetic tree resembles what would be expected by a Brownian motion model of evolution, while *K* values above one indicate that close relatives retain similar climatic frequencies. Pagel's λ values nearing zero demonstrate minimal phylogenetic signal, while values approaching one suggest that traits evolved in accordance with a Brownian motion model or random genetic drift. Pagel's δ values between zero and one indicates that trait values slowly changed in the recent past, while δ values greater than one indicate rapid trait variation nearing the tips of phylogeny. Ornstein-Uhlenbeck stationary α nearing zero indicates no adaptation towards an optimum trait, while large values of α indicate that climatic frequency is strongly pulled towards an optimal value along the phylogeny (see Methods).

4.5 Discussion

Our study revealed global patterns in the distribution of climatic frequencies across geographical scales and examined their ecological and evolutionary impacts on biological communities of four major terrestrial vertebrate groups. Firstly, we elaborate on the pervasive relationship between climatic frequency and community phylogenetic structure. We observed that species co-occurring in rarer climates are less phylogenetically related, whereas tetrapod communities in common climates accumulated greater evolutionary history. We then discuss how co-occurring species tend to be further from their climatic optima in both exceptionally rare and exceptionally common climates. Additionally, we discuss the lack of phylogenetic similarities in climatic frequency across tetrapod clades.

4.5.1 Climatic frequency as a driver of phylogenetic community structure

Consistent with the hypothesis that adaptation to rare environments is costly and less common (Kawecki *et al.* 1997) (Q_1), we observed that tetrapod communities in rare climates tended to be less phylogenetically clustered (Figure 4.2). This pattern held true irrespective of local heterogeneity and average climatic conditions (see Figure 4.6).

Marginal environmental conditions are often linked to increased vulnerability for environmental fluctuations and disturbances, which are known to influence co-occurrence patterns (*e.g.*, Verdú & Pausas 2007; Cavender-Bares & Reich 2012). Therefore, spatially rare climates are expected to be more susceptible to disturbance (including from paleoclimatic change), making them potential hot spots for the extinction of local populations of climate specialists (see Ohlemüller *et al.* 2008; also see Fournier *et al.* 2020). Unlike stable ecosystems, environments characterized by rapid changes, frequent disturbances, and regular local extinctions tend to lead to either phylogenetically random or phylogenetically overdispersed communities (*e.g.*, Dinnage 2009; Braga *et al.* 2023b; but see Helmus *et al.* 2010). Our observation of decreased phylogenetic clustering in communities within rare climates aligns with this perspective (see Figure 4.2).

The influence of climatic frequency on phylogenetic community structure varies in strength across tetrapod taxa. Amphibians and reptiles exhibited a stronger response in their phylogenetic structure to climatic frequency than birds and mammals (see Figure 4.2). We attribute the differences among tetrapod groups in how climatic frequency drives their community phylogenetic structure to a few interrelated factors. First, ectotherms (amphibians and squamate reptiles) are more sensitive to climate variations than endotherms (birds and mammals) due to the influence of environmental temperatures on their basic physiological functions, such as locomotion, growth, metabolism, and reproduction (*e.g.*, Paaijmans *et al.* 2013; see McNab 2002). The ability of endotherms to regulate their own body temperature enables them to be more active across a wider range of climatic conditions (Angilletta 2009). Second, birds and mammals are known be better dispersers than amphibians and reptiles (Carrier 1987; McNab 2002; Dingle 2014). Increased dispersal abilities may have allowed endothermic tetrapods to effectively occupy both rare and common environments, contributing to the homogenization of community phylogenetic relatedness along the climatic frequency gradient (see Olden & Rooney 2006; Cavender-Bares *et al.* 2009). While climatic frequency had similar weak effects on the deep-scale phylogenetic structure (MPD_{SES}) of bird and mammal communities, it had stronger effects on the shallow-scale phylogenetic structure in mammal communities, along with squamate and amphibian communities (MNTD_{SES}; see Figure 4.2). These variations in the effects of climatic frequency across phylogenetic scales of community structure suggest that climatic frequency have played a pronounced role in recent times.

4.5.2 Deviation from climatic optima in the extremes of climatic frequency

Our findings indicate that co-occurring species in rare climates are, on average, further from their climatic optima (see Figure 4.3, Table 4.4), supporting our expectation that local adaptation to climatic rarity is both costly and infrequent (Q_2). Populations on the fringes of their species' environmental tolerances face greater risks of fragmentation and decline (*e.g.*, Perez-Navarro *et al.* 2022), largely due to increased abiotic stress, both temporarily and spatially, and increased interspecific competition (Aitken *et al.* 2008), which can ultimately result in population decline, reduced relative fecundity, and local extinctions (Soulé 1973; Lawton 1993; *e.g.*, Case & Taper 2000; Thomas *et al.* 2004; Nicastro *et al.* 2013).

Additionally, we found that tetrapods in communities located in both extremely rare and very common climates deviated from their optimal (or preferred) climate (see Figure 4.3, Table 4.4). This trend is especially evident in communities in common climates, characterized by increased phylogenetic relatedness and greater phylogenetic diversity (see Figure 4.2).

Intense competition for similar resources may force populations to inhabit sub-optimal conditions Chesson (2000b). At evolutionary scales, phylogenetically closely-related species with similar ecological requirements may undergo competition-induced differentiation in their characteristics, including climatic preferences, as a way to stabilize coexistence by decreasing niche overlap and competition intensity, and thus leading them to occupy regions more marginal to their climatic optima (Brown & Wilson 1956; Dayan & Simberloff 2005). Furthermore, ecological character displacement can drive the evolution of specialization among competitor species (Egas *et al.* 2004), suggesting that rare climates favour climatic generalists, while specialists are more likely to establish in common climates (Fournier *et al.* 2020).

4.5.3 Lack of strong phylogenetic similarities in climatic frequencies

The finding that rare climates limit community phylogenetic relatedness contrasts with the lack of strong phylogenetic similarity in climatic frequency among tetrapod groups (Q_3) (see Figure 4.4, Table 4.5). While phylogenetic clustering in ecological communities along environmental gradients has been linked to species sharing similar key fitness traits (Cavender-Bares *et al.* 2009; Mayfield & Levine 2010), the lack of strong phylogenetic signals in climatic frequency across tetrapods and geographical scales suggests factors other than shared ancestry in climatic frequency also contribute to the formation of less phylogenetically related communities in rare climates.

The role of niche mechanisms may depend on the phylogenetic signal in traits that contribute to community assembly (Webb 2000; Cavender-Bares *et al.* 2009). The absence of phylogenetic similarities in climatic frequency suggests the possibility that rare climates might act as "filters" of species with labile functional traits rather than through shared ancestry. This could allow for the possibility of distantly-related species with convergent functional traits coexisting in rare climates, resulting in the less phylogenetically related communities we observed. This might indicate a prevalence of generalist species from different clades in rare climates. Fournier *et al.* (2020) observed decreased functional diversity in rare climates over a large geographical extent, while Cutts *et al.* (2023) found no functional trait distinctiveness between species in rarer *versus* common climates in oceanic islands. Moreover, the colonization of rare climates could occur as new niche spaces become available, allowing species to occupy available niches without strong environmental filtering or evolutionary innovations. However, it is worth acknowledging that adaptation to rare climates is not implausible. Species radiating into vacant niches might specialize in geographically scarce (rare) habitats (Gaston 1994).

The lack of phylogenetic similarities in climatic frequency remained consistent across all studied geographical scales. However, it is plausible that a mosaic of microclimates, at much finer geographical scales than those explored, within a given macroclimate, could facilitate multiple evolutionary pathways towards similar preferences for the spatial frequency of climate. This could lead to convergence in these preferences among distantly related species (Losos 2011). In this scenario, rare climates might be used by species that are less phylogenetically related, owing to the availability of diverse niches within these climates.

4.5.4 Synthesis, limitations, and concluding remarks

Frequency, or rarity, has long intrigued ecologists, yet most studies have focused on the frequency of species and organisms instead of the diversity of their environmental conditions. While the macroecological and macroevolutionary biodiversity patterns related to climate frequency we identified are robust, our study assumes a deterministic nature of ecological and evolutionary processes. However, rarer climates often correspond to smaller, fragmented habitats, which may disproportionately expose species to stochastic processes such as genetic drift, demographic fluctuations, and local extinctions (see Lande 1993; Adler & Drake 2008; Ord *et al.* 2017). These microevolutionary dynamics, driven by smaller effective population sizes, can amplify ecological instability and decouple community assembly from deterministic forces, potentially driving shifts in community composition (*e.g.*, opportunistic or generalist species over specialists). If the spatial frequency of climates shifts rapidly with climate change, such stochasticity could exacerbate community reassembly dynamics, with species sorting mechanisms dominating over long-term evolutionary forces (see Parmesan 2006). Given the significant past changes in climate and predictions that certain contemporary climates will disappear in the next seventy years (Saxon *et al.* 2005; Williams *et al.* 2007; Ackerly *et al.* 2010), future research incorporating temporal trends in climatic frequency and its interplay with stochastic forces will offer deeper insights into its effects on community assembly and persistence.

Interpreting ecological and evolutionary dynamics from community phylogenetic structure is challenging, as multiple processes can lead to similar patterns (see Münkemüller *et al.* 2020). Our framework is based on an 'ecophylogenetics redux' approach (see Davies 2021) and moves beyond simple extrapolations of ecological and evolutionary mechanisms from community phylogenetic structure (*i.e.*, competitive exclusion *versus* environmental filtering) or phylogenetic signals in traits (*i.e.*, trait conservatism *versus* trait convergence). By focusing on phylogenetic community structure, deviations from species climatic optima across communities, and contrasting evolutionary models in climatic frequencies, we provide a novel framework to shed light on the dynamics of climate, including its heterogeneity and frequency, as key drivers of the phylogenetic structure in biological communities.

4.6 Supporting Information 1

4.6.1 Computational tools

All data manipulation and analyses were performed in R and RStudio (R Core Team 2019; Posit Team 2023). Parallelized computations were done using `snowfall`, `doSNOW`, and `future` (Bengtsson 2021; Corporation & Weston 2022; Knaus 2022). Geospatial manipulation was done using the `sf` , `raster`, `terra`, and `exactextractr` packages (Pebesma 2018; Hijmans 2022, 2023). Phylogenetic manipulation and phylogenetic comparative analyses were done using the packages `ape`, `picante`, `PhyloMeasures`, `motmot`, `phytools`, and `phangorn` (Kembel *et al.* 2010; Schliep 2011; Revell 2012; Tsirogiannis & Sandel 2016, 2017; Paradis & Schliep 2019; Puttick *et al.* 2020). Kernel density estimations were performed using the `ks` package (Duong 2007, 2022). Generalized additive models were performed and diagnosed with the `mgcv` and `gratia` packages (Wood 2003, 2004; Wood 2017; Simpson 2023). General data manipulation was done with the `tidyverse` package suite (Wickham *et al.* 2019). Figures were generated using the `ggplot2`, `ggpubr`, and `patchwork` packages (Wickham 2016; Pedersen 2022; Kassambara 2023). Tables were generated using the `flextable` package (Gohel & Skintzos 2024).

4.6.2 Figures and Tables

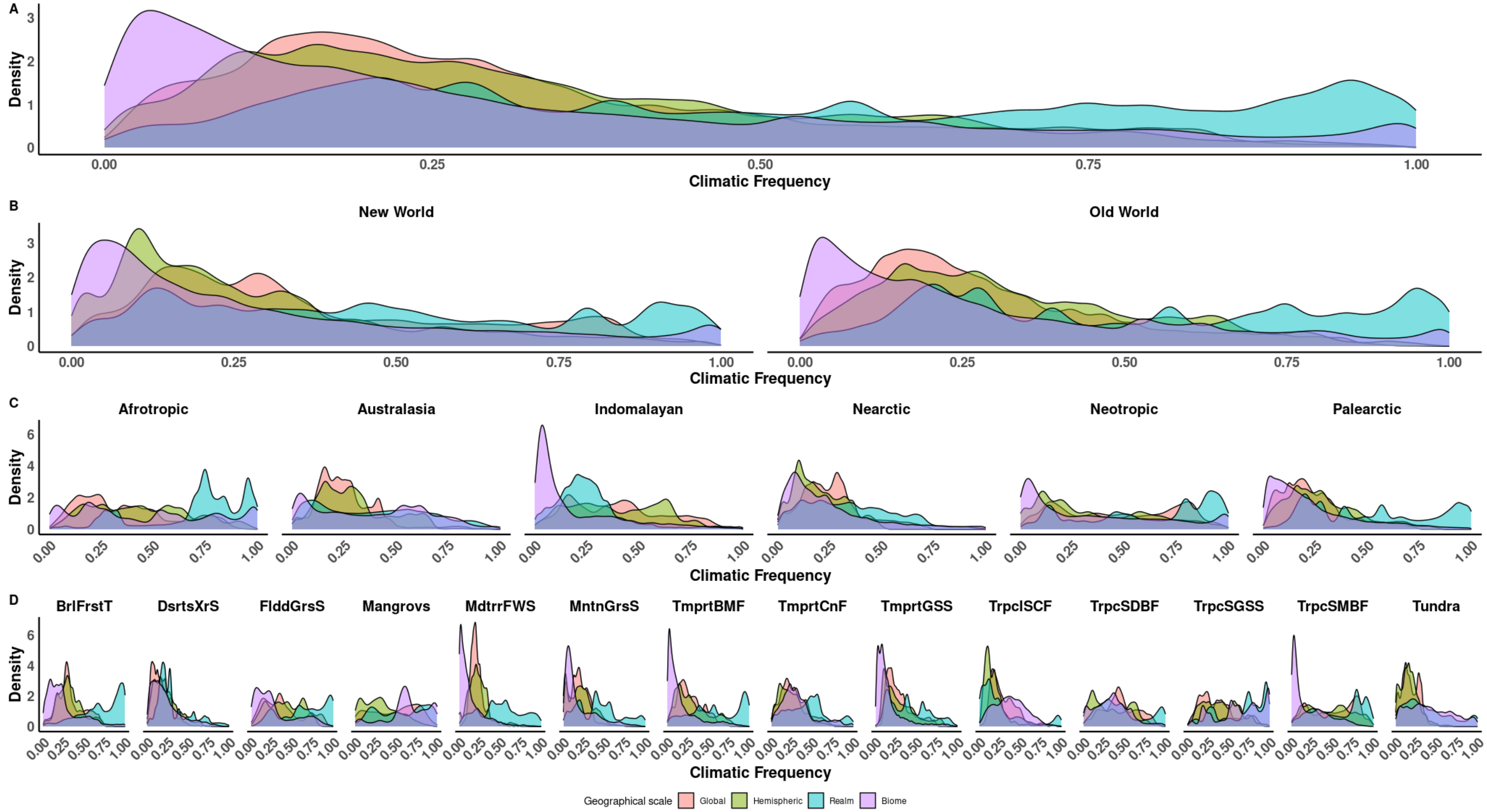


Figure 4.5: **Density distributions of climatic frequencies computed across geographical scales for the (A) global, (B) hemispheric, (C) biogeographical realm, and (D) biome scales**. The shaded colour of the curves denotes the hierarchical geographical extent from which climatic conditions were subset and then used to compute climatic frequencies, being them: global (rose), east-west hemispheric (green), realm (blue), and biome (purple) extents (see Methods). Acronyms denominate worldwide biomes, and signify as follows: TmprtBMF = Temperate Broadleaf & Mixed Forests; Tundra = Tundra; TmprtGSS = Temperate Grasslands, Savannas & Shrublands; MntnGrsS = Montane Grasslands & Shrublands; MdtrrFWS = Mediterranean Forests, Woodlands & Scrub; TrpcSGSS = Tropical & Subtropical Grasslands, Savannas & Shrublands; FlddGrsS = Flooded Grasslands & Savannas; DsrtsXrS = Deserts & Xeric Shrublands; Mangrovs = Mangroves; TrpcSDBF = Tropical & Subtropical Dry Broadleaf Forests; TrpclSCF = Tropical & Subtropical Coniferous Forests; TmprtCnF = Temperate Conifer Forests; TmprtCnF = Temperate Conifer Forests; and, BrlFrstT = Boreal Forests/Taiga.

Table 4.1: **Distribution of average spatial climatic frequencies across contemporary Köppen-Geiger climate classes and subtypes.** Climatic frequency was measured across three geographical scales: global, east-west hemisphere, and biogeographical realm extents (see Methods). The Köppen-Geiger system classifies contemporary climate (from 1980 to 2016) into five main classes and 30 sub-types, based on threshold values and seasonality of monthly air temperature and precipitation. For each scale of climatic frequency, we calculated the average climatic frequency across the Köppen-Geiger system (obtained from Beck *et al.* 2018), and ordered the values in ascending order to reveal the most common and the rarest climates across the world's climatic system.

Geographical scale	**Köppen-Geiger climate classification**	**Average climatic frequency**
	Polar frost	0.024
	Temperate, no dry season, cold summer	0.059
	Arid desert, hot	0.157
	Temperate, no dry season, warm summer	0.160
	Polar tundra	0.177
	Temperate, no dry season, hot summer	0.178
	Arid desert, cold	0.185
	Cold dry winter, very cold winter	0.188
	Cold dry winter, hot summer	0.195
	Temperate, dry summer, warm summer	0.202
	Cold, no dry season, very cold winter	0.210
	Temperate, dry winter, warm summer	0.213
	Temperate, dry summer, hot summer	0.217
	Cold, no dry season, hot summer	0.252
	Temperate, dry winter, cold summer	0.253
	Arid steppe cold	0.259
	Cold dry winter warm summer	0.260
	Cold dry winter cold summer	0.265
	Arid steppe hot	0.271
	Cold dry summer, cold summer	0.282
	Cold dry summer, very cold winter	0.284

Geographical scale	Köppen-Geiger climate classification	Average climatic frequency
	Cold dry summer, hot summer	0.305
	Temperate, dry summer, cold summer	0.332
	Cold, no dry season, cold summer	0.332
	Temperate, dry winter, hot summer	0.347
	Cold dry summer warm summer	0.392
	Cold, no dry season, warm summer	0.399
	Tropical Savannah	0.525
	Tropical Rainforest	0.554
	Tropical Monsoon	0.624
	Polar frost	0.035
	Temperate, no dry season, cold summer	0.068
	Temperate, dry winter, cold summer	0.082
	Temperate, dry summer, warm summer	0.180
	Cold dry winter, hot summer	0.184
	Polar tundra	0.184
	Temperate, no dry season, warm summer	0.189
	Temperate, no dry season, hot summer	0.200
	Temperate, dry winter, warm summer	0.200
	Cold, no dry season, hot summer	0.210
	Arid desert, cold	0.215
	Arid desert, hot	0.223
	Cold dry summer, cold summer	0.237
	Temperate, dry summer, hot summer	0.243
	Temperate, dry summer, cold summer	0.247
	Cold, no dry season, very cold winter	0.264
	Cold dry winter, very cold winter	0.271
	Arid steppe cold	0.273
	Cold dry winter warm summer	0.279

Geographical scale	Köppen-Geiger climate classification	Average climatic frequency
	Cold, no dry season, cold summer	0.314
	Cold dry summer, very cold winter	0.315
	Arid steppe hot	0.329
	Cold dry winter cold summer	0.348
	Cold dry summer warm summer	0.348
	Cold dry summer, hot summer	0.377
	Temperate, dry winter, hot summer	0.397
	Cold, no dry season, warm summer	0.415
	Tropical Rainforest	0.475
	Tropical Savannah	0.487
	Tropical Monsoon	0.563
	Polar frost	0.074
	Temperate, dry summer, cold summer	0.134
	Temperate, dry winter, cold summer	0.166
	Temperate, no dry season, cold summer	0.221
	Arid desert, hot	0.310
	Arid desert, cold	0.314
	Polar tundra	0.370
	Temperate, dry summer, warm summer	0.401
	Arid steppe cold	0.417
	Cold, no dry season, hot summer	0.421
	Cold dry winter, hot summer	0.472
	Temperate, no dry season, hot summer	0.473
	Temperate, dry winter, hot summer	0.485
	Arid steppe hot	0.487
	Cold dry summer, hot summer	0.495
	Temperate, no dry season, warm summer	0.501
	Cold dry summer, cold summer	0.510

Geographical scale	Köppen-Geiger climate classification	Average climatic frequency
	Temperate, dry summer, hot summer	0.513
	Cold dry winter warm summer	0.527
	Tropical Rainforest	0.561
	Cold dry summer warm summer	0.574
	Cold dry winter cold summer	0.590
	Temperate, dry winter, warm summer	0.597
	Cold, no dry season, cold summer	0.654
	Cold, no dry season, warm summer	0.703
	Tropical Savannah	0.718
	Tropical Monsoon	0.721
	Cold dry summer, very cold winter	0.767
	Cold, no dry season, very cold winter	0.902
	Cold dry winter, very cold winter	0.922
	Temperate, dry summer, cold summer	0.022
	Cold dry summer, hot summer	0.050
	Temperate, no dry season, cold summer	0.064
	Cold dry winter, hot summer	0.069
	Temperate, dry summer, hot summer	0.081
	Temperate, dry winter, cold summer	0.086
	Temperate, dry summer, warm summer	0.093
	Temperate, no dry season, warm summer	0.096
	Cold dry winter warm summer	0.112
	Polar frost	0.112
	Cold dry winter, very cold winter	0.120
	Cold dry summer, very cold winter	0.124
	Cold, no dry season, very cold winter	0.135
	Arid desert, cold	0.138
	Cold, no dry season, hot summer	0.151

Geographical scale	Köppen-Geiger climate classification	Average climatic frequency
	Arid steppe cold	0.171
	Cold dry summer warm summer	0.172
	Temperate, no dry season, hot summer	0.182
	Cold dry winter cold summer	0.185
	Arid desert, hot	0.275
	Cold dry summer, cold summer	0.290
	Tropical Monsoon	0.304
	Temperate, dry winter, hot summer	0.305
	Cold, no dry season, warm summer	0.316
	Cold, no dry season, cold summer	0.318
	Temperate, dry winter, warm summer	0.339
	Polar tundra	0.345
	Tropical Rainforest	0.358
	Arid steppe hot	0.406
	Tropical Savannah	0.546

Table 4.2: **Parameter estimates and model summaries from thin-plate regression smooth splines for the effects of climatic frequency and climatic heterogeneity on mean phylogenetic distances of tetrapod communities.** Climatic frequency was measured across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. Mean phylogenetic distances (MPD) denote how closely-related co-occurring taxa are in a given community, and was estimate for each tetrapod group separately, being them: amphibians, birds, mammals, and squamate reptiles. Effective estimated degrees of freedom (edf) are taken as number of data minus model degrees of freedom (df) (see Methods).

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Global	Amphibians	0.175	0.039	s(Climatic Frequency)	8.947	8.999	4,036.315	**0.001** ***
				s(Climatic Heterogeneity)	8.245	8.848	69.791	**0.001** ***
	Birds	0.077	0.038	s(Climatic Frequency)	8.944	8.999	1,759.881	**0.001** ***
				s(Climatic Heterogeneity)	8.043	8.764	262.706	**0.001** ***
	Mammals	0.053	0.007	s(Climatic Frequency)	8.597	8.954	1,443.429	**0.001** ***
				s(Climatic Heterogeneity)	6.910	8.030	194.454	**0.001** ***
	Squamates	0.295	0.017	s(Climatic Frequency)	8.961	9.000	8,955.419	**0.001** ***
				s(Climatic Heterogeneity)	8.599	8.955	92.035	**0.001** ***
Hemispheric	Amphibians	0.098	0.026	s(Climatic Frequency)	8.966	9.000	2,002.689	**0.001** ***
				s(Climatic Heterogeneity)	8.310	8.872	74.588	**0.001** ***
	Birds	0.079	0.031	s(Climatic Frequency)	8.984	9.000	1,780.030	**0.001** ***
				s(Climatic Heterogeneity)	8.231	8.844	322.540	**0.001** ***
	Mammals	0.045	0.007	s(Climatic Frequency)	8.903	8.997	1,165.528	**0.001** ***
				s(Climatic Heterogeneity)	6.864	7.992	200.430	**0.001** ***
	Squamates	0.154	0.036	s(Climatic Frequency)	8.974	9.000	3,622.233	**0.001** ***
				s(Climatic Heterogeneity)	8.691	8.973	223.319	**0.001** ***

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Realm	Amphibians	0.037	0.025	s(Climatic Frequency)	8.959	9.000	622.826	**0.001** ***
				s(Climatic Heterogeneity)	8.437	8.913	123.845	**0.001** ***
	Birds	0.076	0.018	s(Climatic Frequency)	8.971	9.000	1,695.439	**0.001** ***
				s(Climatic Heterogeneity)	8.176	8.822	301.777	**0.001** ***
	Mammals	0.065	0.017	s(Climatic Frequency)	8.945	8.999	1,757.596	**0.001** ***
				s(Climatic Heterogeneity)	6.583	7.754	203.782	**0.001** ***
	Squamates	0.148	0.035	s(Climatic Frequency)	8.978	9.000	3,445.816	**0.001** ***
				s(Climatic Heterogeneity)	8.726	8.979	222.048	**0.001** ***
Biome	Amphibians	0.132	0.027	s(Climatic Frequency)	8.882	8.996	2,850.339	**0.001** ***
				s(Climatic Heterogeneity)	8.390	8.899	108.262	**0.001** ***
	Birds	0.074	0.008	s(Climatic Frequency)	8.928	8.998	1,616.335	**0.001** ***
				s(Climatic Heterogeneity)	8.180	8.824	449.583	**0.001** ***
	Mammals	0.016	0.015	s(Climatic Frequency)	8.449	8.914	343.438	**0.001** ***
				s(Climatic Heterogeneity)	6.679	7.836	98.364	**0.001** ***
	Squamates	0.089	0.031	s(Climatic Frequency)	8.944	8.999	1,751.096	**0.001** ***
				s(Climatic Heterogeneity)	8.721	8.978	340.924	**0.001** ***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < '' < 1

Thin-plate regression splines with formula: MPD ~ s(Clim. Frequency) + s(Clim. Heterogeneity)

Table 4.3: **Parameter estimates and model summaries from thin-plate regression smooth splines for the effects of climatic frequency and climatic heterogeneity on mean nearest taxon distances of tetrapod communities.** Climatic frequency was measured across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. Mean phylogenetic distances denote how closely-related co-occurring taxa are in a given community, and was estimate for each tetrapod group separately, being them: amphibians, birds, mammals, and squamate reptiles. Effective estimated degrees of freedom (edf) are taken as number of data minus model degrees of freedom (see Methods)

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Global	Amphibians	0.092	0.028	s(Climatic Frequency)	8.956	8.999	1,877.661	**0.001** ***
				s(Climatic Heterogeneity)	8.035	8.758	75.015	**0.001** ***
	Birds	0.056	0.027	s(Climatic Frequency)	8.980	9.000	1,481.468	**0.001** ***
				s(Climatic Heterogeneity)	8.197	8.830	120.784	**0.001** ***
	Mammals	0.213	0.011	s(Climatic Frequency)	8.884	8.996	6,994.934	**0.001** ***
				s(Climatic Heterogeneity)	6.905	8.026	53.070	**0.001** ***
	Squamates	0.184	0.020	s(Climatic Frequency)	8.952	8.999	4,468.980	**0.001** ***
				s(Climatic Heterogeneity)	8.535	8.941	242.997	**0.001** ***
Hemispheric	Amphibians	0.048	0.030	s(Climatic Frequency)	8.968	9.000	859.482	**0.001** ***
				s(Climatic Heterogeneity)	8.132	8.802	87.548	**0.001** ***
	Birds	0.018	0.018	s(Climatic Frequency)	8.973	9.000	373.810	**0.001** ***
				s(Climatic Heterogeneity)	8.228	8.843	135.750	**0.001** ***
	Mammals	0.088	0.008	s(Climatic Frequency)	8.909	8.998	2,358.529	**0.001** ***
				s(Climatic Heterogeneity)	7.097	8.176	93.736	**0.001** ***
	Squamates	0.102	0.027	s(Climatic Frequency)	8.984	9.000	1,979.527	**0.001** ***
				s(Climatic Heterogeneity)	8.613	8.958	329.233	**0.001** ***

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Realm	Amphibians	0.025	0.014	s(Climatic Frequency)	8.904	8.997	378.791	**0.001** ***
				s(Climatic Heterogeneity)	8.230	8.842	136.506	**0.001** ***
	Birds	0.023		s(Climatic Frequency)	8.945	8.999	489.101	**0.001** ***
				s(Climatic Heterogeneity)	8.158	8.815	121.093	**0.001** ***
	Mammals	0.116	0.018	s(Climatic Frequency)	8.980	9.000	3,259.549	**0.001** ***
				s(Climatic Heterogeneity)	6.760	7.905	56.320	**0.001** ***
	Squamates	0.101	0.034	s(Climatic Frequency)	8.949	8.999	1,943.195	**0.001** ***
				s(Climatic Heterogeneity)	8.652	8.966	412.492	**0.001** ***
Biome	Amphibians	0.057	0.026	s(Climatic Frequency)	8.922	8.998	1,058.645	**0.001** ***
				s(Climatic Heterogeneity)	8.205	8.832	108.491	**0.001** ***
	Birds	0.017	0.010	s(Climatic Frequency)	8.677	8.969	343.803	**0.001** ***
				s(Climatic Heterogeneity)	8.250	8.851	140.465	**0.001** ***
	Mammals	0.022	0.008	s(Climatic Frequency)	8.886	8.996	366.640	**0.001** ***
				s(Climatic Heterogeneity)	7.244	8.284	224.391	**0.001** ***
	Squamates	0.127	0.011	s(Climatic Frequency)	8.884	8.996	2,665.944	**0.001** ***
				s(Climatic Heterogeneity)	8.604	8.956	423.392	**0.001** ***

Signif. codes: 0 <= ’***’ < 0.001 < ’**’ < 0.01 < ’*’ < 0.05 < ’.’ < 0.1 < ” < 1

Thin-plate regression splines with formula: MNTD ~ s(Clim. Frequency) + s(Clim. Heterogeneity)

Table 4.4: **Parameter estimates and model summaries from thin-plate regression smooth splines for the effects of climatic frequency and climatic heterogeneity on the climatic marginality of tetrapod communities.** Climatic frequency was measured across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. Mean phylogenetic distances denote how closely-related co-occurring taxa are in a given community, and was estimate for each tetrapod group separately, being them: amphibians, birds, mammals, and squamate reptiles. Effective estimated degrees of freedom (edf) are taken as number of data minus model degrees of freedom (see Methods).

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Global	Amphibians	0.380	0.073	s(Climatic Frequency)	8.989	9.000	13,220.192	**0.001** ***
				s(Climatic Heterogeneity)	8.766	8.985	1,227.888	**0.001** ***
	Birds	0.381	0.085	s(Climatic Frequency)	8.991	9.000	13,262.339	**0.001** ***
				s(Climatic Heterogeneity)	8.760	8.984	1,202.376	**0.001** ***
	Mammals	0.383	0.094	s(Climatic Frequency)	8.991	9.000	13,266.189	**0.001** ***
				s(Climatic Heterogeneity)	8.757	8.983	1,233.913	**0.001** ***
	Squamates	0.377		s(Climatic Frequency)	8.993	9.000	13,070.463	**0.001** ***
				s(Climatic Heterogeneity)	8.752	8.983	1,097.237	**0.001** ***
Hemispheric	Amphibians	0.227	0.044	s(Climatic Frequency)	8.979	9.000	5,146.282	**0.001** ***
				s(Climatic Heterogeneity)	8.801	8.989	1,768.875	**0.001** ***
	Birds	0.229	0.047	s(Climatic Frequency)	8.981	9.000	5,199.751	**0.001** ***
				s(Climatic Heterogeneity)	8.797	8.988	1,773.925	**0.001** ***
	Mammals	0.228	0.049	s(Climatic Frequency)	8.981	9.000	5,091.717	**0.001** ***
				s(Climatic Heterogeneity)	8.796	8.988	1,836.850	**0.001** ***
	Squamates		0.048	s(Climatic Frequency)	8.983	9.000	5,296.446	**0.001** ***
				s(Climatic Heterogeneity)	8.790	8.987	1,675.270	**0.001** ***

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
Realm	Amphibians	0.229	0.036	s(Climatic Frequency)	8.973	9.000	5,242.163	**0.001** ***
				s(Climatic Heterogeneity)	8.792	8.988	1,677.314	**0.001** ***
	Birds	0.222	0.032	s(Climatic Frequency)	8.968	9.000	4,907.986	**0.001** ***
				s(Climatic Heterogeneity)	8.790	8.987	1,695.548	**0.001** ***
	Mammals	0.224		s(Climatic Frequency)	8.965	9.000	4,934.855	**0.001** ***
				s(Climatic Heterogeneity)	8.786	8.987	1,760.222	**0.001** ***
	Squamates	0.204	0.027	s(Climatic Frequency)	8.966	9.000	4,290.490	**0.001** ***
				s(Climatic Heterogeneity)	8.785	8.987	1,622.787	**0.001** ***
Biome	Amphibians	0.152	0.058	s(Climatic Frequency)	8.930	8.999	2,304.424	**0.001** ***
				s(Climatic Heterogeneity)	8.774	8.986	2,246.410	**0.001** ***
	Birds		0.055	s(Climatic Frequency)	8.927	8.998	2,288.517	**0.001** ***
				s(Climatic Heterogeneity)	8.772	8.985	2,265.904	**0.001** ***
	Mammals	0.150	0.053	s(Climatic Frequency)	8.926	8.998	2,158.814	**0.001** ***
				s(Climatic Heterogeneity)	8.767	8.985	2,345.851	**0.001** ***
	Squamates		0.052	s(Climatic Frequency)	8.924	8.998	2,339.256	**0.001** ***
				s(Climatic Heterogeneity)	8.768	8.985	2,166.906	**0.001** ***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < '' < 1

Thin-plate regression splines with formula: Clim. Marginality ~ s(Clim. Frequency) + s(Clim. Heterogeneity)

Table 4.5: **Parameter estimates and model summaries from maximum-likelihood-based phylogenetic comparative models assessing the phylogenetic signal in climatic frequency across geographical scales for tetrapod communities.** The analysis was conducted across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. The table includes parameter estimates for Pagel's λ (lambda), Pagel's δ (delta), Blomberg's K, and the Ornstein-Uhlenbeck (OU) stationary-peak model (α). These parameters were evaluated to determine how evolutionary relatedness correlates with ecological similarity in climatic frequency. The table also provides the effective degrees of freedom (edf), Brownian variance, root-state estimates, and model fit statistics, including AIC and AICc, for each tetrapod group (amphibians, birds, mammals, and squamate reptiles) at different geographical scales. Uncertainty in parameter estimates is accounted for by incorporating the standard error of climatic frequency across species distributions.

Taxonomic group	**Geographical scale**	**Evolutionary parameter type**	**Parameter estimate**	**Lower 95% CI**	**Upper 95% CI**	**Brownian variance**	**Root-state estimate**	**Likelihood**	**Type**	**AIC**	**AICc**	**N**
	Global	Pagel's λ	0.723	0.675	0.765	0.000	0.323	1,002.688	Maximum-Likelihood	-1,999.376	-1,999.369	3,627
		Ornstein-Uhlenbeck Stationary α	0.057	0.052	0.063	0.005	0.341	30.375	Maximum-Likelihood	-54.751	-54.744	3,627
		Pagel's δ	13.806	12.665	14.973	0.000	0.350	-427.642	Maximum-Likelihood	861.284	861.290	3,627
		Blomberg's K	0.056			0.003	0.326	-718.094	Log-likelihood	1,440.189	1,440.192	3,627
	Hemispheric	Pagel's λ	0.689	0.634	0.738	0.000	0.286	1,504.929	Maximum-Likelihood	-3,003.858	-3,003.852	3,626
		Ornstein-Uhlenbeck Stationary α	0.039	0.036	0.043	0.003	0.307	716.169	Maximum-Likelihood	-1,426.337	-1,426.331	3,626
		Pagel's δ	9.754	8.776	10.746	0.000	0.310	358.658	Maximum-Likelihood	-711.315	-711.309	3,626
		Blomberg's K	0.072			0.002	0.288	187.319	Log-likelihood	-370.639	-370.636	3,626
	Realm	Pagel's λ	0.847	0.824	0.868	0.000	0.525	1,074.790	Maximum-Likelihood	-2,143.581	-2,143.574	3,626
		Ornstein-Uhlenbeck Stationary α	0.021	0.020	0.023	0.003	0.546	377.323	Maximum-Likelihood	-748.646	-748.640	3,626
		Pagel's δ	9.961	9.110	10.821	0.000	0.548	253.746	Maximum-Likelihood	-501.492	-501.485	3,626
		Blomberg's K	0.138			0.002	0.530	34.755	Log-likelihood	-65.510	-65.507	3,626
		Pagel's λ	0.702	0.653	0.746	0.000	0.190	1,131.832	Maximum-Likelihood	-2,257.664	-2,257.657	3,626
		Ornstein-Uhlenbeck Stationary α	0.047	0.043	0.051	0.004	0.206	444.036	Maximum-Likelihood	-882.072	-882.066	3,626

Biome

Taxonomic group	Geographical scale	Evolutionary parameter type	Parameter estimate	Lower 95% CI	Upper 95% CI	Brownian variance	Root-state estimate	Likelihood	Type	AIC	AICc	N
		Pagel’s δ	14.568	13.395	15.772	0.000	0.218	102.403	Maximum-Likelihood	-198.807	-198.800	3,626
		Blomberg’s K	0.068			0.002	0.188	-215.871	Log-likelihood	435.742	435.745	3,626
Birds	Global	Pagel’s λ	0.668	0.631	0.702	0.001	0.363	2,803.015	Maximum-Likelihood	-5,600.031	-5,600.028	7,495
		Ornstein-Uhlenbeck Stationary α	0.234	0.215	0.255	0.016	0.355	1,729.665	Maximum-Likelihood	-3,453.331	-3,453.328	7,495
		Pagel’s δ	27.749	26.391	29.156	0.000	0.354	1,170.613	Maximum-Likelihood	-2,335.227	-2,335.224	7,495
		Blomberg’s K	0.051			0.007	0.363	-343.843	Log-likelihood	691.686	691.688	7,495
	Hemispheric	Pagel’s λ	0.674	0.637	0.707	0.000	0.315	3,738.709	Maximum-Likelihood	-7,471.417	-7,471.414	7,473
		Ornstein-Uhlenbeck Stationary α	0.206	0.191	0.223	0.011	0.323	2,665.600	Maximum-Likelihood	-5,325.199	-5,325.196	7,473
		Pagel’s δ	25.994	24.704	27.330	0.000	0.326	2,146.139	Maximum-Likelihood	-4,286.277	-4,286.274	7,473
		Blomberg’s K	0.053			0.005	0.316	736.608	Log-likelihood	-1,469.216	-1,469.215	7,473
	Realm	Pagel’s λ	0.819	0.799	0.837	0.001	0.493	1,450.483	Maximum-Likelihood	-2,894.965	-2,894.962	7,479
		Ornstein-Uhlenbeck Stationary α	0.132	0.124	0.140	0.018	0.508	-64.723	Maximum-Likelihood	135.445	135.448	7,479
		Pagel’s δ	23.157	21.986	24.378	0.000	0.505	-346.391	Maximum-Likelihood	698.781	698.784	7,479
		Blomberg’s K	0.063			0.010	0.494	-1,692.649	Log-likelihood	3,389.297	3,389.299	7,479
	Biome	Pagel’s λ	0.680	0.646	0.712	0.001	0.295	2,632.242	Maximum-Likelihood	-5,258.484	-5,258.481	7,478
		Ornstein-Uhlenbeck Stationary α	0.331	0.299	0.367	0.023	0.258	1,601.866	Maximum-Likelihood	-3,197.732	-3,197.729	7,478
		Pagel’s δ	35.434	33.620	37.338	0.000	0.262	1,113.931	Maximum-Likelihood	-2,221.862	-2,221.859	7,478
		Blomberg’s K	0.049			0.008	0.309	-723.649	Log-likelihood	1,451.298	1,451.299	7,478
		Pagel’s λ	0.887	0.865	0.905	0.001	0.293	1,931.512	Maximum-Likelihood	-3,857.025	-3,857.020	4,565
		Ornstein-Uhlenbeck Stationary α	0.153	0.141	0.165	0.010	0.349	1,219.509	Maximum-Likelihood	-2,433.018	-2,433.012	4,565

Mammals Global

Taxonomic group	Geographical scale	Evolutionary parameter type	Parameter estimate	Lower 95% CI	Upper 95% CI	Brownian variance	Root-state estimate	Likelihood	Type	AIC	AICc	N
		Pagel’s δ	15.080	12.735	17.477	0.000	0.339	635.249	Maximum-Likelihood	-1,264.498	-1,264.492	4,565
		Blomberg’s K	0.031			0.007	0.289	553.677	Log-likelihood	-1,103.353	-1,103.351	4,565
	Hemispheric	Pagel’s λ	0.877	0.855	0.896	0.000	0.288	2,284.096	Maximum-Likelihood	-4,562.192	-4,562.187	4,564
		Ornstein-Uhlenbeck Stationary α	0.166	0.153	0.179	0.009	0.321	1,473.677	Maximum-Likelihood	-2,941.354	-2,941.349	4,564
		Pagel’s δ	19.991	17.447	22.588	0.000	0.321	894.660	Maximum-Likelihood	-1,783.321	-1,783.315	4,564
		Blomberg’s K	0.027			0.006	0.290	768.606	Log-likelihood	-1,533.213	-1,533.210	4,564
	Realm	Pagel’s λ	0.934	0.923	0.943	0.002	0.463	765.974	Maximum-Likelihood	-1,525.949	-1,525.944	4,564
		Ornstein-Uhlenbeck Stationary α	0.140	0.130	0.151	0.020	0.514	22.460	Maximum-Likelihood	-38.919	-38.914	4,564
		Pagel’s δ	42.789	39.447	46.211	0.000	0.516	-249.562	Maximum-Likelihood	505.123	505.128	4,564
		Blomberg’s K	0.031			0.013	0.467	-637.556	Log-likelihood	1,279.111	1,279.114	4,564
	Biome	Pagel’s λ	0.876	0.850	0.896	0.001	0.244	1,280.653	Maximum-Likelihood	-2,555.306	-2,555.301	4,564
		Ornstein-Uhlenbeck Stationary α	0.216	0.199	0.234	0.016	0.256	808.181	Maximum-Likelihood	-1,610.361	-1,610.356	4,564
		Pagel’s δ	23.585	20.754	26.484	0.000	0.255	134.915	Maximum-Likelihood	-263.830	-263.825	4,564
		Blomberg’s K	0.024			0.009	0.252	-15.480	Log-likelihood	34.960	34.963	4,564
	Global	Pagel’s λ	0.673	0.635	0.708	0.000	0.340	2,391.801	Maximum-Likelihood	-4,777.603	-4,777.599	6,435
		Ornstein-Uhlenbeck Stationary α	0.099	0.092	0.107	0.007	0.324	1,190.790	Maximum-Likelihood	-2,375.580	-2,375.576	6,435
		Pagel’s δ	13.087	12.274	13.919	0.000	0.330	446.840	Maximum-Likelihood	-887.680	-887.676	6,435
		Blomberg’s K	0.060			0.004	0.331	-90.932	Log-likelihood	185.863	185.865	6,435
		Pagel’s λ	0.660	0.619	0.698	0.000	0.296	3,011.459	Maximum-Likelihood	-6,016.918	-6,016.915	6,421
		Ornstein-Uhlenbeck Stationary α	0.091	0.085	0.098	0.005	0.299	1,878.246	Maximum-Likelihood	-3,750.491	-3,750.488	6,421

Hemispheric

Taxonomic group	Geographical scale	Evolutionary parameter type	Parameter estimate	Lower 95% CI	Upper 95% CI	Brownian variance	Root-state estimate	Likelihood	Type	AIC	AICc	N
		Pagel’s δ	13.980	13.128	14.849	0.000	0.298	1,174.202	Maximum-Likelihood	-2,342.404	-2,342.400	6,421
		Blomberg’s K	0.060			0.003	0.291	604.702	Log-likelihood	-1,205.404	-1,205.402	6,421
	Realm	Pagel’s λ	0.858	0.841	0.873	0.001	0.452	1,713.016	Maximum-Likelihood	-3,420.032	-3,420.028	6,421
		Ornstein-Uhlenbeck Stationary α	0.040	0.037	0.042	0.006	0.505	554.754	Maximum-Likelihood	-1,103.509	-1,103.505	6,421
		Pagel’s δ	12.003	11.308	12.715	0.000	0.504	378.522	Maximum-Likelihood	-751.044	-751.040	6,421
		Blomberg’s K	0.111			0.004	0.444	-195.514	Log-likelihood	395.027	395.029	6,421
	Biome	Pagel’s λ	0.751	0.722	0.778	0.000	0.245	1,843.397	Maximum-Likelihood	-3,680.795	-3,680.791	6,421
		Ornstein-Uhlenbeck Stationary α	0.079	0.074	0.084	0.007	0.246	736.134	Maximum-Likelihood	-1,466.269	-1,466.265	6,421
		Pagel’s δ	13.522	12.690	14.372	0.000	0.243	121.088	Maximum-Likelihood	-236.176	-236.172	6,421
		Blomberg’s K	0.067			0.004	0.242	-434.211	Log-likelihood	872.421	872.423	6,421

4.7 Supporting Information 2

4.7.1 Accounting for the influence of average climatic conditions in the relationship between climatic frequency and community phylogenetic relatedness

In addition to climatic heterogeneity, the association between climatic frequency and community phylogenetic relatedness can be confounded by the effects of the climatic conditions in a region themselves. This is because areas characterized by rare climates may also be underpinned by unique average climatic conditions, which can strongly influence the evolutionary trajectories of species and, in turn, community structure. For instance, areas with rare climatic conditions but stable mean temperatures might foster different adaptive strategies compared to those with common climates and fluctuating average conditions. Such conditions can modulate the influence of climatic rarity on community assembly, as species' evolutionary responses to rare climate may be tempered by the prevailing climates from where they occur (Gaston 2003).

To account for this, we performed generalized additive models (GAMs) incorporating the climatic principal components as covariates alongside climatic heterogeneity (see Methods for information on how these variables have been calculated). These models were fitted using penalized thin-plate splines for the partial effects of climatic frequency, climatic heterogeneity, and climatic principal components on the community phylogenetic metrics ($\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$), in separate models for each taxa and geographical scale.

Despite being less strong at certain geographical scales, the negative relationship between climatic frequency and phylogenetic community structure (for both $\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$), remained evident after controlling for the effects of climatic conditions and climatic heterogeneity (see Supporting Information 2; Figure 4.6, Table 4.6 and Table 4.7).

4.7.2 Figures and Tables

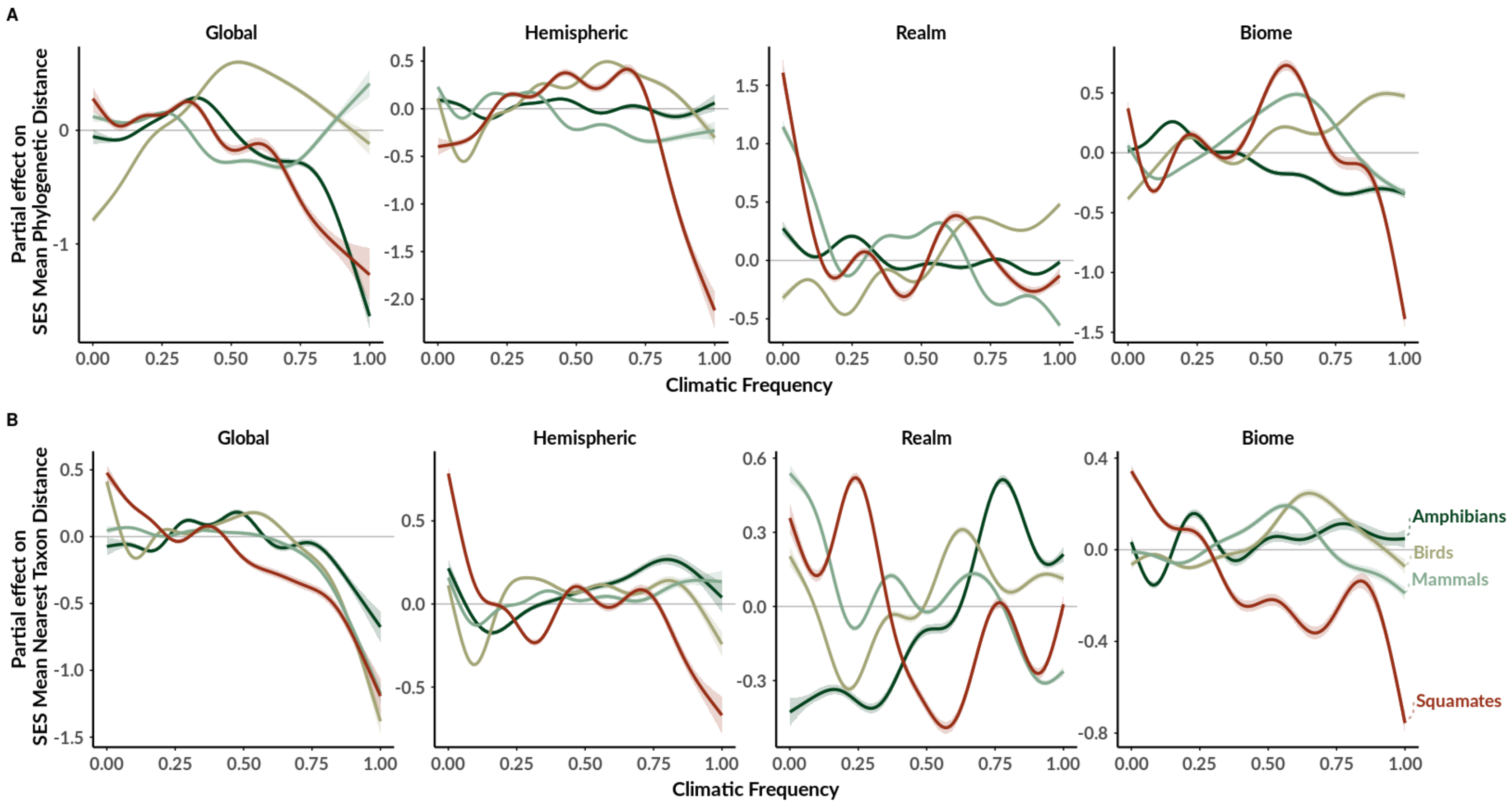


Figure 4.6: **Partial effects of climatic frequency on the phylogenetic structure of worldwide communities (248,139, in total) of four tetrapod groups: amphibians (3,627 species), mammals (4,565 species), birds (7,495 species), and reptilian squamates (6,435 species)**. Phylogenetic community structure was measured as standardized effect sizes of (A) mean phylogenetic distances and (B) mean nearest taxon distances for each tetrapod group. Climatic frequency was estimated in each community for each one of four geographical scales (global, hemispheric, realm, and biome), and was based on the first four principal components representing contemporary climatic conditions across the globe (see Methods).

Table 4.6: **Parameter estimates and model summaries from thin-plate regression smooth splines for the effects of climatic frequency, climatic heterogeneity, and principal components from average climatic conditions on mean phylogenetic distances of tetrapod communities.** Climatic frequency was measured across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. Mean phylogenetic distances denote how closely-related co-occurring taxa are in a given community, and was estimate for each tetrapod group separately, being them: amphibians, birds, mammals, and squamate reptiles. Effective estimated degrees of freedom (edf) are taken as number of data minus model degrees of freedom (see Methods).

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
	Amphibians	0.650	0.079	s(Climatic Frequency)	8.781	8.986	347.212	**0.001** ***
				s(Climatic Heterogeneity)	6.154	7.364	44.407	**0.001** ***
				s(RS1)	8.899	8.997	1,086.237	**0.001** ***
				s(RS2)	8.987	9.000	16,176.614	**0.001** ***
				s(RS3)	8.976	9.000	595.288	**0.001** ***
				s(RS4)	8.885	8.996	563.482	**0.001** ***
	Birds	0.267	0.174	s(Climatic Frequency)	8.643	8.964	1,264.550	**0.001** ***
				s(Climatic Heterogeneity)	7.594	8.521	91.653	**0.001** ***
				s(RS1)	8.972	9.000	884.010	**0.001** ***
				s(RS2)	8.974	9.000	2,515.547	**0.001** ***
				s(RS3)	8.990	9.000	2,071.478	**0.001** ***
				s(RS4)	8.917	8.998	634.621	**0.001** ***
	Mammals	0.223	0.145	s(Climatic Frequency)	8.719	8.978	215.609	**0.001** ***
				s(Climatic Heterogeneity)	6.110	7.320	124.145	**0.001** ***
				s(RS1)	8.976	9.000	786.291	**0.001** ***
				s(RS2)	8.894	8.997	996.144	**0.001** ***
				s(RS3)	8.975	9.000	1,213.409	**0.001** ***
				s(RS4)	8.963	9.000	2,788.312	**0.001** ***
				s(Climatic Frequency)	8.637	8.963	112.840	**0.001** ***
				s(Climatic Heterogeneity)	8.310	8.873	7.148	**0.001** ***
				s(RS1)	8.969	9.000	1,840.880	**0.001** ***
				s(RS2)	8.925	8.998	15,380.145	**0.001** ***

	Squamates	0.636	0.104

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(RS3)	8.972	9.000	292.566	**0.001** ***
				s(RS4)	8.865	8.995	566.524	**0.001** ***
Hemispheric	Amphibians	0.645	0.074	s(Climatic Frequency)	8.734	8.980	39.881	**0.001** ***
				s(Climatic Heterogeneity)	6.381	7.576	50.141	**0.001** ***
				s(RS1)	8.924	8.998	1,067.090	**0.001** ***
				s(RS2)	8.989	9.000	19,183.278	**0.001** ***
				s(RS3)	8.974	9.000	603.141	**0.001** ***
				s(RS4)	8.887	8.996	521.173	**0.001** ***
	Birds	0.272	0.178	s(Climatic Frequency)	8.979	9.000	1,259.033	**0.001** ***
				s(Climatic Heterogeneity)	7.789	8.635	76.352	**0.001** ***
				s(RS1)	8.957	8.999	491.959	**0.001** ***
				s(RS2)	8.980	9.000	2,447.730	**0.001** ***
				s(RS3)	8.989	9.000	2,000.049	**0.001** ***
				s(RS4)	8.915	8.998	660.720	**0.001** ***
	Mammals	0.225	0.140	s(Climatic Frequency)	8.932	8.999	259.987	**0.001** ***
				s(Climatic Heterogeneity)	6.126	7.335	132.394	**0.001** ***
				s(RS1)	8.977	9.000	841.137	**0.001** ***
				s(RS2)	8.895	8.997	1,200.270	**0.001** ***
				s(RS3)	8.973	9.000	1,253.597	**0.001** ***
				s(RS4)	8.958	9.000	2,700.404	**0.001** ***
	Squamates	0.641	0.106	s(Climatic Frequency)	8.839	8.992	277.893	**0.001** ***
				s(Climatic Heterogeneity)	2.915	3.708	3.660	0.007 **
				s(RS1)	8.971	9.000	2,174.102	**0.001** ***
				s(RS2)	8.933	8.999	19,245.736	**0.001** ***
				s(RS3)	8.965	9.000	254.003	**0.001** ***
				s(RS4)	8.839	8.993	466.643	**0.001** ***
				s(Climatic Frequency)	8.854	8.994	74.733	**0.001** ***
				s(Climatic Heterogeneity)	6.367	7.563	46.713	**0.001** ***
				s(RS1)	8.925	8.998	1,072.822	**0.001** ***

Realm	Amphibians	0.646	0.075

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(RS2)	8.988	9.000	20,081.093	**0.001** ***
				s(RS3)	8.973	9.000	656.075	**0.001** ***
				s(RS4)	8.890	8.997	467.278	**0.001** ***
	Birds	0.268	0.175	s(Climatic Frequency)	8.963	9.000	1,112.978	**0.001** ***
				s(Climatic Heterogeneity)	7.780	8.630	98.403	**0.001** ***
				s(RS1)	8.927	8.998	850.960	**0.001** ***
				s(RS2)	8.979	9.000	2,124.966	**0.001** ***
				s(RS3)	8.989	9.000	1,871.674	**0.001** ***
				s(RS4)	8.922	8.998	621.336	**0.001** ***
	Mammals	0.252	0.167	s(Climatic Frequency)	8.963	9.000	1,225.531	**0.001** ***
				s(Climatic Heterogeneity)	5.854	7.069	166.762	**0.001** ***
				s(RS1)	8.977	9.000	725.379	**0.001** ***
				s(RS2)	8.915	8.998	1,416.190	**0.001** ***
				s(RS3)	8.975	9.000	1,281.275	**0.001** ***
				s(RS4)	8.961	9.000	2,748.331	**0.001** ***
	Squamates	0.640	0.105	s(Climatic Frequency)	8.901	8.997	193.976	**0.001** ***
				s(Climatic Heterogeneity)	8.389	8.899	8.369	**0.001** ***
				s(RS1)	8.976	9.000	1,931.234	**0.001** ***
				s(RS2)	8.935	8.999	20,322.281	**0.001** ***
				s(RS3)	8.969	9.000	289.340	**0.001** ***
				s(RS4)	8.869	8.995	565.167	**0.001** ***
	Amphibians	0.650	0.078	s(Climatic Frequency)	8.805	8.989	274.543	**0.001** ***
				s(Climatic Heterogeneity)	6.552	7.728	45.189	**0.001** ***
				s(RS1)	8.917	8.998	939.544	**0.001** ***
				s(RS2)	8.989	9.000	19,054.364	**0.001** ***
				s(RS3)	8.974	9.000	653.999	**0.001** ***
				s(RS4)	8.882	8.996	463.493	**0.001** ***
				s(Climatic Frequency)	8.880	8.996	713.661	**0.001** ***
				s(Climatic Heterogeneity)	7.753	8.615	96.761	**0.001** ***

	Birds	0.257	0.164					

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(RS1)	8.814	8.990	340.521	**0.001** ***
				s(RS2)	8.981	9.000	2,149.787	**0.001** ***
				s(RS3)	8.991	9.000	1,950.619	**0.001** ***
				s(RS4)	8.923	8.998	680.642	**0.001** ***
	Mammals	0.233	0.148	s(Climatic Frequency)	8.757	8.983	545.937	**0.001** ***
				s(Climatic Heterogeneity)	5.928	7.142	103.716	**0.001** ***
				s(RS1)	8.976	9.000	886.856	**0.001** ***
				s(RS2)	8.922	8.998	1,467.973	**0.001** ***
				s(RS3)	8.971	9.000	1,345.575	**0.001** ***
				s(RS4)	8.959	9.000	2,927.398	**0.001** ***
	Squamates	0.642	0.107	s(Climatic Frequency)	8.930	8.999	316.802	**0.001** ***
				s(Climatic Heterogeneity)	8.394	8.901	5.853	**0.001** ***
				s(RS1)	8.974	9.000	2,093.046	**0.001** ***
				s(RS2)	8.941	8.999	19,975.092	**0.001** ***
				s(RS3)	8.962	8.999	248.495	**0.001** ***
				s(RS4)	8.867	8.995	518.618	**0.001** ***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < '' < 1

Thin-plate regression splines with formula: MPD ~ s(Clim. Freq.) + s(Clim. Het.) + s(Clim. RS1) + s(Clim. RS2) + s(Clim. RS3) + s(Clim. RS4)

Table 4.7: **Parameter estimates and model summaries from thin-plate regression smooth splines for the effects of climatic frequency, climatic heterogeneity, and principal components from average climatic conditions on mean phylogenetic distances of tetrapod communities.** Climatic frequency was measured across four geographical scales: global, east-west hemisphere, biogeographical realm, and biome extents. Mean phylogenetic distances denote how closely-related co-occurring taxa are in a given community, and was estimate for each tetrapod group separately, being them: amphibians, birds, mammals, and squamate reptiles. Effective estimated degrees of freedom (edf) are taken as number of data minus model degrees of freedom (see Methods).

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(Climatic Frequency)	8.823	8.991	106.420	**0.001***
				s(Climatic Heterogeneity)	5.966	7.182	84.051	**0.001***

Global	Amphibians	0.505	0.051					

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(RS1)	8.975	9.000	775.086	**0.001*****
				s(RS2)	8.971	9.000	11,417.103	**0.001*****
				s(RS3)	8.822	8.991	253.535	**0.001*****
				s(RS4)	8.773	8.986	741.251	**0.001*****
	Birds	0.358	0.133	s(Climatic Frequency)	8.951	8.999	359.690	**0.001*****
				s(Climatic Heterogeneity)	7.040	8.134	71.279	**0.001*****
				s(RS1)	8.961	9.000	4,535.819	**0.001*****
				s(RS2)	8.985	9.000	2,640.269	**0.001*****
				s(RS3)	8.976	9.000	1,260.804	**0.001*****
				s(RS4)	8.947	8.999	705.456	**0.001*****
	Mammals	0.433	0.181	s(Climatic Frequency)	8.560	8.946	230.480	**0.001*****
				s(Climatic Heterogeneity)	6.626	7.793	28.303	**0.001*****
				s(RS1)	8.921	8.998	1,158.004	**0.001*****
				s(RS2)	8.985	9.000	4,787.775	**0.001*****
				s(RS3)	8.960	9.000	768.429	**0.001*****
				s(RS4)	8.983	9.000	1,162.573	**0.001*****
	Squamates	0.617	0.068	s(Climatic Frequency)	8.677	8.971	207.967	**0.001*****
				s(Climatic Heterogeneity)	6.844	7.976	123.418	**0.001*****
				s(RS1)	8.977	9.000	1,525.088	**0.001*****
				s(RS2)	8.881	8.996	18,756.475	**0.001*****
				s(RS3)	8.932	8.998	1,316.387	**0.001*****
				s(RS4)	8.923	8.998	2,922.284	**0.001*****
	Amphibians	0.507	0.049	s(Climatic Frequency)	8.454	8.917	124.303	**0.001*****
				s(Climatic Heterogeneity)	5.967	7.185	93.003	**0.001*****
				s(RS1)	8.978	9.000	764.903	**0.001*****
				s(RS2)	8.973	9.000	12,699.506	**0.001*****
				s(RS3)	8.819	8.991	242.392	**0.001*****
				s(RS4)	8.769	8.985	689.913	**0.001*****
				s(Climatic Frequency)	8.964	9.000	530.370	**0.001*****

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
		0.361	0.132	s(Climatic Heterogeneity)	7.084	8.167	67.871	**0.001*****
				s(RS1)	8.963	9.000	5,192.928	**0.001*****
				s(RS2)	8.990	9.000	2,868.556	**0.001*****
				s(RS3)	8.972	9.000	1,243.180	**0.001*****
				s(RS4)	8.943	8.999	594.503	**0.001*****
	Mammals	0.428	0.224	s(Climatic Frequency)	8.882	8.996	97.272	**0.001*****
				s(Climatic Heterogeneity)	6.687	7.845	25.036	**0.001*****
				s(RS1)	8.922	8.998	1,497.005	**0.001*****
				s(RS2)	8.985	9.000	7,150.056	**0.001*****
				s(RS3)	8.966	9.000	833.062	**0.001*****
				s(RS4)	8.981	9.000	1,088.207	**0.001*****
	Squamates	0.619	0.075	s(Climatic Frequency)	8.899	8.997	242.207	**0.001*****
				s(Climatic Heterogeneity)	7.140	8.209	119.638	**0.001*****
				s(RS1)	8.982	9.000	1,546.427	**0.001*****
				s(RS2)	8.895	8.996	22,672.997	**0.001*****
				s(RS3)	8.946	8.999	1,254.856	**0.001*****
				s(RS4)	8.913	8.998	2,843.412	**0.001*****
	Amphibians	0.524	0.057	s(Climatic Frequency)	8.901	8.997	822.715	**0.001*****
				s(Climatic Heterogeneity)	5.644	6.863	95.422	**0.001*****
				s(RS1)	8.983	9.000	1,075.159	**0.001*****
				s(RS2)	8.963	9.000	12,904.093	**0.001*****
				s(RS3)	8.824	8.991	172.505	**0.001*****
				s(RS4)	8.712	8.977	578.899	**0.001*****
	Birds	0.361	0.132	s(Climatic Frequency)	8.946	8.999	510.049	**0.001*****
				s(Climatic Heterogeneity)	6.907	8.028	75.767	**0.001*****
				s(RS1)	8.959	9.000	5,394.628	**0.001*****
				s(RS2)	8.989	9.000	2,394.769	**0.001*****
				s(RS3)	8.971	9.000	1,245.745	**0.001*****
				s(RS4)	8.946	8.999	579.921	**0.001*****

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
	Mammals	0.443	0.234	s(Climatic Frequency)	8.961	9.000	832.690	**0.001*****
				s(Climatic Heterogeneity)	6.432	7.620	48.392	**0.001*****
				s(RS1)	8.916	8.998	1,115.405	**0.001*****
				s(RS2)	8.986	9.000	7,554.797	**0.001*****
				s(RS3)	8.972	9.000	779.436	**0.001*****
				s(RS4)	8.980	9.000	990.439	**0.001*****
	Squamates	0.624	0.078	s(Climatic Frequency)	8.954	8.999	584.800	**0.001*****
				s(Climatic Heterogeneity)	6.892	8.015	123.125	**0.001*****
				s(RS1)	8.984	9.000	1,751.255	**0.001*****
				s(RS2)	8.932	8.998	23,737.453	**0.001*****
				s(RS3)	8.904	8.997	1,513.751	**0.001*****
				s(RS4)	8.906	8.998	2,751.700	**0.001*****
	Amphibians	0.506	0.050	s(Climatic Frequency)	8.866	8.995	82.510	**0.001*****
				s(Climatic Heterogeneity)	5.972	7.190	83.443	**0.001*****
				s(RS1)	8.977	9.000	758.711	**0.001*****
				s(RS2)	8.967	9.000	12,639.573	**0.001*****
				s(RS3)	8.791	8.988	242.927	**0.001*****
				s(RS4)	8.745	8.982	716.324	**0.001*****
	Birds	0.352	0.122	s(Climatic Frequency)	8.493	8.927	148.033	**0.001*****
				s(Climatic Heterogeneity)	6.915	8.034	72.716	**0.001*****
				s(RS1)	8.936	8.999	4,796.526	**0.001*****
				s(RS2)	8.990	9.000	2,390.925	**0.001*****
				s(RS3)	8.973	9.000	1,166.562	**0.001*****
				s(RS4)	8.949	8.999	641.749	**0.001*****
				s(Climatic Frequency)	8.532	8.937	154.384	**0.001*****
				s(Climatic Heterogeneity)	6.703	7.859	24.268	**0.001*****
				s(RS1)	8.919	8.998	1,510.962	**0.001*****
				s(RS2)	8.986	9.000	7,646.496	**0.001*****
				s(RS3)	8.966	9.000	814.765	**0.001*****

Geographical Scale	Taxon	Total Adj. R2	Non-linear Adj. R2	Predictor	edf	df	F	p-value
				s(RS4)	8.981	9.000	1,106.012	**0.001*****
	Squamates	0.622	0.070	s(Climatic Frequency)	8.810	8.989	439.377	**0.001*****
				s(Climatic Heterogeneity)	6.925	8.042	118.993	**0.001*****
				s(RS1)	8.980	9.000	1,441.758	**0.001*****
				s(RS2)	8.909	8.997	21,670.412	**0.001*****
				s(RS3)	8.937	8.999	1,294.279	**0.001*****
				s(RS4)	8.923	8.998	2,721.551	**0.001*****

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < '' < 1

Thin-plate regression splines with formula: MNTD ~ s(Clim. Freq.) + s(Clim. Het.) + s(Clim. RS1) + s(Clim. RS2) + s(Clim. RS3) + s(Clim. RS4)

4.8 Supporting Information 3

4.8.1 Robustness of phylogenetic uncertainty

To account for phylogenetic uncertainty, we recalculated the phylogenetic relatedness of tetrapod communities and the phylogenetic signals on climatic frequencies on subsets of 30 randomly sampled trees from the posterior distribution of phylogenetic trees for each one of the tetrapod groups: amphibians (Jetz & Pyron 2018), birds (Jetz & Fine 2012), mammals (Upham *et al.* 2020), and squamate reptiles (Tonini *et al.* 2016) (see Donoghue & Ackerly 1996). We were limited from including higher sample sizes due to limitations on computational resources. For each tetrapod group, we then computed the average standardized effect sizes of mean phylogenetic distances and mean nearest taxon distances for each community as well as the comparative phylogenetic analyses on the evolution of climatic frequencies across the calculations done with the sampled phylogenetic trees, and used these averages to reproduce the figures and analyses from our study.

We observed qualitatively similar results to the ones computed using the maximum credibility clade phylogenetic trees (see Figure 4.2, Figure 4.4), providing evidence that our inferences are robust to the uncertainty of phylogenetic hypotheses from the posterior distribution of the phylogenetic relationships we used in our study.

Chapter 5

Synthesis, conclusions, and future directions

In this thesis, I investigated how climate—through its averages, variability, and frequency across space—drives patterns in biological communities. By adopting a pluralistic and integrative approach, I bridged historical perspectives, theoretical advancements, empirical data, and modern computational methods to provide a nuanced understanding of climate-biodiversity interactions. Each chapter contributes to this overarching framework, elucidating the distinct roles that different climatic components play in driving ecological strategies, community assembly, and evolutionary trajectories. This conclusion synthesizes the findings from the chapters, reflects on their broader implications, and discusses how this thesis advances ecological research by refining theoretical frameworks, challenging existing paradigms, and proposing new directions for future studies.

Together, the chapters in this thesis illustrate that a comprehensive understanding of climate-biodiversity dynamics requires an integrative approach that encompasses multiple dimensions of climate and their interactions across different spatial and phylogenetic scales. The findings demonstrattWe how climatic averages, variability, frequency, paleoclimatic stability, and diversification rates shape community structure and ecological specialisation.

5.1 Climate drives ecophylogenetics and specialisation

Chapter 2 underscores the profound influence of historical climatic legacies on contemporary biodiversity patterns. By examining the phylogenetic structures of bat communities across multiple geographical extents, this chapter highlights paleoclimatic stability as a critical determinant of community assembly processes. Historical shifts in temperature and precipitation since the last glacial maximum have left enduring imprints on these communities' phylogenetic structures, revealing patterns of relatedness shaped by the stability and change in climatic conditions over millennia. Regions with more stable climates since the last glacial maximum harbour more phylogenetically clustered communities, reflecting the persistence of lineages adapted to specific environmental conditions. In contrast, regions that have undergone significant climatic shifts show less phylogenetic clustering, suggesting that recent ecological dynamics, such as dispersal and colonization, have a more prominent role than deep evolutionary histories.

These findings resonate with ongoing discussions on how glacial-interglacial cycles have left discernible imprints on community composition and structure, influencing contemporary biodiversity patterns (e.g., Kissling *et al.* 2012; Svenning *et al.* 2015; Delgado-Baquerizo *et al.* 2017). The evidence supports established ecological theories, such as the "time-stability" (Fine & Ree 2006) and "climatic-stability" hypotheses (Wiens & Graham 2005), which posit that stable environments over evolutionary timescales foster phylogenetically clustered communities. However, this chapter also challenges these hypotheses by demonstrating that phylogenetic clustering is not a uniform outcome; it varies significantly across geographical and phylogenetic scales. The diversity patterns resulting from climatic legacies are contingent upon the interplay between historical stability and contemporary ecological dynamics. This nuanced perspective emphasizes that community assembly is shaped by the interaction of both long-term climatic legacies and recent processes, reflecting a more complex narrative than is typically assumed.

Chapters 3 and 4 then extend the exploration of climatic drivers by investigating the role of climatic frequencies in shaping community specialisation and phylogenetic structure.

Chapter 3 reveals that communities in rare climatic conditions tend to exhibit increased climatic niche breadths, with generalist species more likely to occur in less common environments. In contrast, species in more common climates are more likely to be climatic specialists. These results align with the outcomes from the process-based metacommunity simulations, which show similar patterns where rare environments tend to support the co-occurrence between both generalists and specialists, while specialists dominate in common environments.

The mechanisms through which climatic frequency influences specialisation within communities are complex. In common climates, relative environmental stability allows specialists to thrive by optimizing their niche use, out-competing species with broader niches who are less efficient in any particular environment. Conversely, rare climates, marked by greater spatial fragmentation and environmental variability, diminish the competitive edge of specialists because of limited opportunities for dispersal and colonization. Reduced internal dispersal in rare climates further hinders both specialists and generalists from dispersing between communities, thus affecting local community composition. In more connected and common climates, specialists dominate by successfully colonizing and persisting within their preferred environments.

In many ways, Chapter 4 complements Chapter 3. Chapter 4 further explores the influence of climatic frequency on the phylogenetic structure of communities across different scales. The findings demonstrate that regions with rare climatic conditions exhibit reduced phylogenetic clustering, suggesting that these areas are shaped more by recent colonization and adaptation events than by deep evolutionary histories. These findings add nuance to the traditional understanding of how climate shapes community assembly by highlighting the distinct ecological and evolutionary dynamics in regions characterized by rare climatic conditions. At finer scales, localized evolutionary radiations or adaptive responses to unique selective pressures can lead to significant phylogenetic clustering, even in rare environments. This suggests that while climatic rarity tends to promote the co-occurrence of species with varying evolutionary backgrounds, under specific conditions, it may also foster specialisation and local adaptation, leading to clustered phylogenetic patterns. These scale-dependent findings reinforce the importance of context in determining community assembly processes and suggest that different ecological and evolutionary mechanisms may be at play depending on the spatial scale.

These two last chapters emphasize that ecological specialisation and community structure are not dictated only by climatic averages or variability. This approach provides a novel perspective that moves beyond traditional metrics and opens new avenues for understanding climate-biodiversity interactions.

5.2 Scale-dependence matters

A unifying thread across all chapters of this thesis is the recognition of scale dependency in ecological research. This emphasis stems from the understanding that ecological and evolutionary processes operate at different spatial and temporal scales and that their effects can vary depending on the scale of analysis (Levin 1992; Ricklefs & Schluter 1993; Chave 2013).

Scale-dependent nuances appeared in all research chapters. For instance, in Chapter 2, the analysis of bat communities across different geographical scales revealed that the phylogenetic structure of these communities is not uniform but shifts significantly depending on the spatial extent considered. At broader scales, the dominance of historical biogeographical processes becomes apparent, leading to patterns of phylogenetic clustering driven by long-term climatic stability and large-scale dispersal barriers. Conversely, at more localized scales, the reduced phylogenetic clustering observed suggests that more recent diversification events, local adaptation, and ecological interactions play a more prominent role in shaping community structure.

Similarly, Chapters 3 and 4 reveal that the influence of climatic frequency on community structure and specialisation varies with spatial scale. On the global scale, the general trend is that rare climates promote generalists, while common climates encourage specialisation. However, when at finer scales, such as within specific biomes, these patterns can become more complex and context dependent. This complexity underscores the importance of considering multiple spatial scales in ecological research to clarify the diverse mechanisms driving community assembly and biodiversity patterns.

Beyond spatial scale dependencies, this thesis also underscores the importance of phylogenetic scales in ecological research. Different taxonomic and phylogenetic groups—such as ectothermic reptiles and amphibians versus endothermic mammals and birds—responded differently to climatic frequency and variability, likely due to distinct physiological and ecological traits, which influence their sensitivity to climatic variation (Chapter 4). Furthermore, the response of community phylogenetic structure to climatic drivers was shown to depend on the sensitivity to phylogenetic distances of the metrics used. Metrics that emphasized deeper evolutionary distances (e.g., mean phylogenetic distances) revealed different patterns of community phylogenetic relatedness compared to those focusing on more recent evolutionary divergences (e.g., mean nearest taxon distances) (Chapters 2 and 4). These findings highlight the importance of considering phylogenetic scales when analyzing community assembly processes, as different phylogenetic grains and extents can reveal varying degrees of influence from historical legacies, ecological interactions, and evolutionary dynamics.

5.3 Assumptions and limitations

This thesis is based on several key assumptions that underpin the analyses and interpretations of climate–biodiversity interactions. While these assumptions are grounded in well-established theory and empirical evidence, it is essential to acknowledge their potential limitations. By critically evaluating these points, I aim to clarify the scope of our inferences and highlight possible directions for future refinement. Nevertheless, the robustness of our conclusions is reinforced by comprehensive empirical analyses across multiple taxa and scales, and the corroboration of empirical findings through theoretical simulations.

5.3.0.1 Species' occupied environments reflect their climatic niches and optima

Our analyses assume that the climatic conditions experienced by species at their occupied sites reliably approximate their physiological and ecological climate optima. This assumption implies that species' realized niches closely approach their fundamental climatic niches and that environmental filtering by climate is a dominant mechanism structuring their geographic distributions (Soberón & Nakamura 2009). Under this view, species are considered to be in equilibrium with current macroclimatic gradients, and climate is posited as the principal environmental driver over other factors such as habitat heterogeneity, soil properties, dispersal barriers, or biotic interactions.

However, species distributions arise from the interplay of myriad abiotic and biotic constraints. Factors such as topographic complexity, microclimatic refugia, land-use patterns, dispersal limitations, phylogenetic history, and interactions such as competition, predation, and mutualism can restrict species to subsets of their potential climatic space (Hutchinson 1957; Ricklefs 1987, 2004; Pearson & Dawson 2003; Soberón 2007; Gaston 2009a; Holt & Barfield 2009; Thakur *et al.* 2022). Additionally, coarse-scale macroclimatic variables may fail to capture local thermal heterogeneity or fine-grained environmental conditions that determine physiological performance [Currie & Paquin (1987); Hawkins *et al.* (2003); Harrison *et al.* (2020); Sears *et al.* (2011); Buckley & Huey (2016); Pincebourde *et al.* (2016); Pateman *et al.* (2016); Scheffers et al. 2014]. If local microclimates and other unmeasured environmental factors strongly shape species' realized niches, then our characterization of species as climatic "specialists" or "generalists" may be incomplete or, in some cases, misleading.

Nevertheless, several aspects reinforce the robustness of our conclusions. First, our analyses encompass over 26,000 tetrapod species worldwide, including amphibians, birds, mammals, and reptiles, spanning diverse phylogenetic, environmental, and geographical realms. This taxonomic and spatial breadth dilutes the influence of idiosyncratic species-level anomalies and highlights patterns that are unlikely to be driven solely by local, rare, or lineage-specific constraints. Second, climate is widely recognized as a primary determinant of broad-scale biodiversity patterns. By employing multivariate climatic indices and principal component analyses, we reduce the risk that any single climatic variable or collinearity among them biases our inferences (Graham 2003). Third, theoretical simulations, structured to isolate the role of environmental frequency in driving specialisation, confirm that climatic patterns alone can generate observed macroecological gradients, bolstering our empirical conclusions even in the absence of additional environmental complexities.

5.3.0.2 Climatic niches are static and do not shift over time

We also assume that species' climatic niches remain relatively stable over the temporal scales of interest, implying that their current distributions and niche characteristics are a reliable representation of their longstanding ecological preferences. While niche conservatism has strong empirical and theoretical underpinnings (Wiens & Graham 2005), evolutionary processes can shift niches over time (Quintero & Wiens 2013). It is possible that such evolutionary niche shifts have been extensive, so that the contemporary patterns we document likely do not capture the full dynamics of past climatic adaptations.

Our analysis targets present-day conditions and current species distributions, which mitigates potential substantial distortions from historical niche evolution toward our conclusions. With this, the consistent patterns observed across a wide array of taxa and biogeographical contexts suggest that niche shifts have not fundamentally altered the relationship between climatic frequency and species specialisation we observed. Parallel outcomes from theoretical simulations, which assume temporally stable environmental and niche parameters, further substantiate that environmental frequency can independently shape specialisation patterns, even if evolutionary adjustments occur over longer timescales.

5.3.0.3 Climatic data as a proxy for environmental conditions

A further assumption is that climate can serve as a robust proxy for the environmental conditions that govern species distributions and community assembly. While climate is indisputably critical at macroecological scales, other environmental axes—including disturbance regimes, substrate type, and land-use intensity—also exert significant pressures (Pearson & Dawson 2003). Because we focus primarily on climatic gradients, we may underrepresent the importance of these non-climatic factors. If overlooked variables strongly modulate species' realized niches, our attribution of specialisation patterns to climatic frequency could be incomplete.

Multiple lines of evidences support the validity of our approach. The strong and consistent macroecological patterns observed across multiple vertebrate classes and broad spatial extents attest to a pervasive climatic influence. By complementing the empirical analyses with theoretical models that incorporate only a single varying environmental dimension, we confirm that variability in climate frequency alone can induce specialisation patterns that mirror those seen in nature. Thus, while our framework does not exclude additional environmental gradients, it demonstrates that climate, as a first-order driver, exerts a significant and independent influence on broad-scale biotic patterns.

5.3.0.4 Phylogenetic relatedness may not reflect ecological similarity

Finally, our use of phylogenetic metrics to interpret community assembly is founded on the expectation that phylogenetically related species share traits and thus exhibit ecological resemblance (Losos 2008). However, convergence in ecological function can arise among distantly related taxa, and rapid adaptive divergence may occur among close relatives (Blomberg *et al.* 2003; Cavender-Bares *et al.* 2009). In such cases, phylogenetic structure may be a weak indicator of ecological similarity, potentially confounding inferences drawn from patterns of relatedness.

Our study mitigates this concern by centering analyses on direct measures of species' climatic niches, rather than relying solely on phylogenetic relationships. Using metrics such as the outlying mean index to quantify niche breadth ensures that the observed patterns are closely tied to measured environmental tolerances rather than inferred ecological traits. The cross-taxon consistency of our results suggests that the association between climatic frequency and specialisation is not contingent on specific phylogenetic assumptions, further underscoring the robustness of our broader findings.

5.4 Future directions

This thesis opens several avenues for future research, particularly in the integration of climatic frequency and variability with ecological and evolutionary theories. One promising direction is to refine the integrative framework developed in this thesis by incorporating temporal dynamics of climatic conditions and their variability. As climate change progresses, shifts in spatial climatic frequencies are expected to alter community assembly processes, potentially leading to novel configurations of ecological communities. Elucidating how rare climatic conditions may promote or hinder species adaptation and diversification could be achieved through high-resolution paleoclimatic reconstructions and future climatic projections combined with advanced modelling approaches. These models could aid in inferring the evolutionary trajectories of communities under varying climatic scenarios, contributing to a clearer understanding of how species respond to changes in climatic conditions.

Moreover, future research could expand the scope by examining trait-based and phylogenetic approaches in more detail. Although this thesis has highlighted the role of phylogenetic structure in understanding community assembly, there is an opportunity to further investigate the specific traits that mediate species' responses to climatic variability and frequency. Which functional traits are most predictive of species' success in rare versus common climates, and how do these traits vary across different phylogenetic lineages? Answering these questions could involve combining trait-based ecology with phylogenetic methods to identify key traits that govern ecological and evolutionary dynamics under changing climates.

The findings of this thesis suggest that a more holistic and integrative approach is essential for understanding climate-biodiversity interactions, moving beyond reductionist models that focus on singular climatic factors or scales. By embracing complexity, acknowledging the underdetermination of ecological theories by data, and recognizing the context-dependency of processes across spatial and temporal scales, this work aligns with a pluralistic framework in ecological research—one that incorporates multiple, sometimes competing, explanations to account for the intricate interplay between climatic components, historical legacies, and biodiversity patterns. The scale-dependent and context-specific insights presented here challenge the idea that ecological and evolutionary dynamics can be fully explained by a single model, underscoring the need for flexible methodologies and theories that accommodate diverse ecological and evolutionary processes. This perspective encourages future research to develop more comprehensive models that integrate multiple scales and contexts to better capture the complexity of climate-biodiversity dynamics.

Finally, in conducting my research, I made a deliberate effort to uphold an open and reproducible workflow, recognizing the importance of transparency and collaboration in advancing scientific knowledge (see Perkel 2020; Gomes *et al.* 2022; Braga *et al.* 2023a). I leveraged online platforms such as GitHub and Open Science Framework to ensure my data, code, and protocols were documented and available for review, replication, and further development by others. I hope that this approach to conducting research openly inspires other researchers to embrace similar practices, leveraging these tools to foster a culture of collaboration and reproducibility in their own projects.

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Figure 5.1: **Art by Roger Winkler (2019).** This is a partial representation from the artwork, created by Roger Winkler as part of the 2019 Creative Reactions and Pint of Science events in Montréal, draws inspiration from the research presented in the Chapter 2 of this thesis. In the Creative Reactions project, scientists were paired with local artists who interpreted their scientific work through art. These artistic interpretations were then showcased in a vernissage.