Shifts in Climate Change and Their Influence on Deep-Time Fossil Composition Dynamics

Gabriel Munoz-Acevedo

JP Lessard

2024-09-27

Abstract

Novel environmental pressures influences community assembly dynamics and broad scale patterns in biodiversity composition. While modern community assembly theory offers insights into the effects of climate change on broad-scale biodiversity patterns, these are often based on short-term snapshots, limiting our understanding of long-term processes underlying patterns of species turnover across ecological communities. Morevoer, a critical gap remains in elucidating how deep-time climatic shifts have shaped historical community assembly, as represented by the fossil record. In this study, we aim to uncover the historical dynamics into the mechanisms that could shape present and future biodiversity patterns in response to ongoing climate change. We evaluate two hypotheses regarding the impact of paleo-climate change on shifts in fossil species composition between distinct sites within a broader region, also known as beta-diversity. The Severity of Climate Change hypothesis posits that species turnover increases with the magnitude of climate change, while the Climatic Instability hypothesis suggests that frequent climate fluctuations promote higher species turnover through dynamic niche shifts. We evaluate our hypothesis alongside the influences of contemporary niche and dispersal assembly processes, which are typically considered in current ecological studies. To test these, we integrate fossil and paleoclimatic data focusing on large-mammals in the Neogene, a time marked by major climatic shifts in Northern latitudes. We found that …

# Introduction

The impact of climate change on biodiversity patterns, particularly at broad spatial scales, has been a central focus in modern community assembly theory (Ackerly 2003; Kraft et al. 2015; Harrison, Spasojevic, and Li 2020). However, much of the current research remains limited by the temporal scope of available data. Ecologists critic community assembly studies on their relying on “one-time snapshots” of species distributions to infer long-term processes (Khattar et al. 2021; Harrison, Spasojevic, and Li 2020; Chang and HilleRisLambers 2016). Such approach als falls short in capturing how species turnover is shaped by climate dynamics over extended geological periods (Weiher et al. 2011; Fukami 2015; DiMichele et al. 2004). The result is a fragmented understanding of how long-term climate change dynamics has influenced species turnover across large spatial scales, especially over timescales relevant to both evolutionary and ecological community assembly processes (Erwin 2009; S. T. Jackson and Blois 2015; J. B. Jackson and Erwin 2006).

In addition to the typically evaluated contemporary niche and dispersal based processes, two hypotheses offer a framework to understand climate change’s impact on biodiversity distribution across several time periods. The severity of climate change hypothesis suggests that if the magnitude of climate change drives turnover, then the compositional differences between fossil assemblages in space and over time will increase with larger climatic magnitude deltas. This is because shifts in the average climate conditions of a region over multi-million years may encourage species origination through local adaptation or migration from neighboring regions, while also increasing global extinction and local extirpation rates (Davis and Shaw 2001; Davis, Shaw, and Etterson 2005; Fuente et al. 2022; Vasconcelos, O’Meara, and Beaulieu 2022). The Climatic Instability hypothesis posits that compositional differences between fossil assemblages in space to be associated with the degree of temporal change in a region’s climate spatial heterogeneity. This is because unstable climates can create new ecological niches within a region that offer opportunities for diversification and extinction, while stable climates lessen the pressures for adaptation, migration, and extinction (Vasconcelos, O’Meara, and Beaulieu 2022; Cavender-Bares et al. 2016; Sonne et al. 2022; Gerhold et al. 2018)

Along Earth’s history, broad scale climatic changes (Zachos et al. 2001) create novel pressures that influences species’ distributional ranges (Erwin 2009; Nogués-Bravo 2009; Nogués-Bravo et al. 2018; Alroy, Koch, and Zachos 2000). Thus far, we understand very little the role of these deep time climatic changes in shaping macroscale patterns in biodiversity (Myers, Stigall, and Lieberman 2015; Benson et al. 2021; Bartlein and Prentice 1989). This knowledge can be critical to make informed predictions about past, current, and future biodiversity distribution in light of ongoing climatic changes (Kiessling, Smith, and Raja 2023; Hagen 2023; Nogués-Bravo et al. 2018). Paleoclimate models—reconstructions of Earth’s climate over geological timescales—offer a promising avenue for integration with independent paleoecological data (Hargreaves and Annan 2009; Ludwig et al. 2019; Faith and Behrensmeyer 2013; Barr 2017). By combining paleoclimatic reconstructions, fossil data, and community assembly theory, we can model a relationship between historical climatic changes and the changes the compositional dissimilarity of fossil assemblages at macroecological scales across stratigraphic periods (**naglu2023across?**; Blanco et al. 2021; Mottl et al. 2021; Jabot et al. 2020). Here we aim to model the compositional dissimilarity of large-mammal fossil assemblages within North America and Europe and during the Neogene period. Specifically, we ask 1) Does the magnitude of climate change influence fossil assemblage dissimilarity? and 2) To what extent do temproal instability and spatial heterogeneity of climate contribute to fossil assemblage dissimilarity? While more extreme climatic shifts are expected to increase turnover through mechanisms such as origination, extirpation, and extinction, their impact on assemblage dissimilarity will be amplified if these shifts are also accompanied by significant climatic instability and fluctuations in spatial heterogeneity.

# Methods

## Data

### Study taxa

Fossils of large mammals are particularly useful to uncover macro-evolutionary trends as they are often preserved with higher spatial fidelity and therefore less prone to taphonomic biases compared to other fossil organisms. Moreover, the results of centuries of paleontological research are now digitally available in aggregated fossil databases with standardized taxonomic nomenclature and geotagged records. For this study, we gathered fossil data from the NOW database, excluding all records where the genus or species was classified as indeterminate (“indet.”).

### Temporal scope

The Neogene period (23-2.6 million years ago) provides an ideal case study to test these hypotheses, as this period was characterized by significant climatic changes. This period saw the emergence of many modern plant and animal families, as well as the extinction of many others that were widespread. During this time, the Earth’s climate transitioned from a greenhouse to an icehouse state, with the onset of the Northern Hemisphere glaciation around 3 million years ago. These led to the transformation of tropical areas in high latitudes into open landscapes such as savannas and prairies, and the expansion of temperate and boreal forests. These changes were driven by a combination of tectonic and oceanographic events, including the establishment of the modern-day Gulf Stream, the uplift of the Rocky Mountains and the Alps.

The Neogene is divided into several stratigraphic stages based on geologic time. We aggregated fossil observations into categorical stratigraphic ages based on their mid-point betwen the maximun and minumum radiocarbon based age estimates. The **Aquitanian** (23–21 Ma) marks the beginning of the Neogene and is characterized by early Miocene climate conditions. The **Burdigalian** (20–16 Ma) follows, marked by warmer climates, while the **Langhian** (15–14 Ma) and **Serravallian** (13–12 Ma) represent mid-Miocene periods of global cooling. The late Miocene stages, **Tortonian** (11–8 Ma) and **Messinian** (7–5 Ma), involve further cooling and tectonic shifts, culminating in the Mediterranean Salinity Crisis during the Messinian. The Pliocene stages, **Zanclean** (5–4 Ma) and **Piacenzian** (3–2 Ma), feature continued global cooling, setting the stage for the Pleistocene glaciations.

### Region of interest

The study area spans North-America and Europe. We divided continental masses into subregions: Eastern, Central, and Western USA, as well as Western Europe, Eastern Europe, and the Caucasus region. These geographic divisions capture key continental-scale gradients, allowing for analysis of species turnover and the regional variability in climatic effects. We aggregated present-day geographic coordinates of fossil observations using an equal-area hexagonal grid (100 Km spacing) rotated to Phanerozoic stratigraphic stages (Merdith et al. 2021), aggregating all coordinates within the same grid cell, implemented in the grid method of the paelorotate function of the paleoverse (Jones et al. 2023) package for R. Further, we aggregated fossil’ hexagonal binned records into square-gridded fossil paleocommunities, each of of 25 degree squared area. We computed sampling effort per grid as the count of all unique Locality Identification Numbers (LIDNUM), a unique identifier assigned to each fossil locality represented in the NOW database.

### Palaeoatmospheric data

We utilized paleo-atmospheric temperature reconstructions for the Northern Hemisphere (Hagen et al., 2019) as a proxy for macro-scale climatic variation across continental regions and Neogene time periods. The dataset from Hagen et al. (2019) spans the Cenozoic (60 Ma to the present), and we extracted a subset corresponding to the temporal range of our fossil data. To align the spatial resolution of the climate data with that of our fossil paleocommunities (5x5 degree grid cells), we aggregated the 1x1 degree grid cell temperature records by calculating simple means within each 5x5 degree grid cell.

To assess the distribution of temperature across regions within each stratigraphic stage, we aggregated 1 Ma temperature records by calculating simple means. To quantify the magnitude of climate change, we computed the temporal slope for each grid cell by fitting a linear regression model to the 1 Ma temperature records within each stratigraphic stage as a function of time. The slope of this model represents the rate of temperature change, while the standard deviation of the residuals from the regression captures temporal variability in climate for each region within a given stratigraphic stage.

## Statistical analyses

### Broad-scale fossil diversity patterns

#### Taxonomic richness

Our analysis began with quantifying the relative abundance of fossil genera across various grid cells and stratigraphic stages. For each grid cell, we normalized the genus counts by dividing the number of occurrences of each genus by the total species count at that site. This proportional representation enabled meaningful comparisons of genus composition across both spatial and temporal scales.

#### Paleocommunity composition

To evaluate the ecological dissimilarity between regions and time periods, we constructed genus-by-site matrices for each stratigraphic stage. We created these matrices by cross-tabulating the normalized genus abundances against the sites, with the exclusion of any sites lacking fossil records (i.e., those with zero total counts), ensuring our analysis was restricted to regions with available data (at least 3 unique genera recorded). We then calculated pairwise Bray-Curtis dissimilarities between grid cells within each stratigraphic stage. This approach provided an overview of taxonomic turnover of continental fossil communities across different stratigraphic stages.

### Paleoclimatic variables

From Hagen’s (2019) 1-million-year (1Ma) resolution paleoclimatic reconstructions, we derived a set of four paleoclimatic variables, each aggregated by stratigraphic period within the Neogene. Specifically, these variables include: 1) **Average atmospheric temperature (t\_var)**, calculated as the mean temperature across all 1Ma intervals within each stratigraphic stage; 2) **Magnitude of atmospheric temperature change (t\_slope)**, which represents the slope of a linear regression model fitted to the relationship between age and temperature for a given stratigraphic stage; 3) **Atmospheric temperature temporal instability (t\_inst)**, measured as the standard deviation of the residuals from the linear model used to estimate t\_slope; and 4) **Spatial heterogeneity of atmospheric temperature (t\_svar)**, computed as the mean difference between a focal temperature cell and its eight neighboring cells within a stratigraphic period, following the Horn algorithm.

#### Fluctuations in spatial heterogeneity of atmospheric temperature (t\_svar)

### General dissimilarity modelling

In this study, we applied General Dissimilarity Models (GDM) to explore spatial variation in fossil paleocommunity composition across environmental gradients and stratigraphic stages. GDMs offer a non-linear framework to quantify species turnover across environmental gradients while accounting for spatial effects on ecological dissimilarity. By focusing our analysis on fossil genera instead of species, we minimized biases associated with inconsistent taxonomic resolution across fossil sites. Separate GDMs were fitted to compositional dissimilarity matrices for each stratigraphic stage, modeling compositional turnover as a function of four paleoclimatic temperature variables: average atmospheric temperature (t\_mean), magnitude of temperature change (t\_slope), temporal temperature instability (t\_var), and spatial temperature heterogeneity (t\_svar). The geographic distance between fossil paleocommunities was included as a covariate, calculated as the Euclidean distance between site centroids within each paleocommunity grid. The relative contribution of each variable was determined through iterative adjustment of spline functions to maximize the fit between observed and predicted dissimilarity. We then examined how the explanatory power of each temperature variable shifted across stratigraphic stages. Lastly, by transforming and rescaling each environmental predictor to a common scale of biological relevance, we mapped geographic variation in community assembly processes over time, enabling a more meaningful comparison of climatic drivers of species turnover across regions and stages.

# Results

# Discussion

Ackerly, David D. 2003. “Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments.” *International Journal of Plant Sciences* 164 (S3): S165–84.

Alroy, John, Paul L Koch, and James C Zachos. 2000. “Global Climate Change and North American Mammalian Evolution.” *Paleobiology* 26 (S4): 259–88.

Barr, W Andrew. 2017. “Signal or Noise? A Null Model Method for Evaluating the Significance of Turnover Pulses.” *Paleobiology* 43 (4): 656–66.

Bartlein, PATRICK J, and IC Prentice. 1989. “Orbital Variations, Climate and Paleoecology.” *Trends in Ecology & Evolution* 4 (7): 195–99.

Benson, Roger BJ, Richard Butler, Roger A Close, Erin Saupe, and Daniel L Rabosky. 2021. “Biodiversity Across Space and Time in the Fossil Record.” *Current Biology* 31 (19): R1225–36.

Blanco, Fernando, Joaquı́n Calatayud, David M Martı́n-Perea, M Soledad Domingo, Iris Menéndez, Johannes Müller, Manuel Hernández Fernández, and Juan L Cantalapiedra. 2021. “Punctuated Ecological Equilibrium in Mammal Communities over Evolutionary Time Scales.” *Science* 372 (6539): 300–303.

Cavender-Bares, Jeannine, David D Ackerly, Sarah E Hobbie, and Philip A Townsend. 2016. “Evolutionary Legacy Effects on Ecosystems: Biogeographic Origins, Plant Traits, and Implications for Management in the Era of Global Change.” *Annual Review of Ecology, Evolution, and Systematics* 47: 433–62.

Chang, Cynthia, and Janneke HilleRisLambers. 2016. “Integrating Succession and Community Assembly Perspectives.” *F1000Research* 5.

Davis, Margaret B, and Ruth G Shaw. 2001. “Range Shifts and Adaptive Responses to Quaternary Climate Change.” *Science* 292 (5517): 673–79.

Davis, Margaret B, Ruth G Shaw, and Julie R Etterson. 2005. “Evolutionary Responses to Changing Climate.” *Ecology* 86 (7): 1704–14.

DiMichele, William A, Anna K Behrensmeyer, TD Olszewski, Conrad C Labandeira, John M Pandolfi, Scott L Wing, and Rene Bobe. 2004. “Long-Term Stasis in Ecological Assemblages: Evidence from the Fossil Record.” *Annu. Rev. Ecol. Evol. Syst.* 35 (1): 285–322.

Erwin, Douglas H. 2009. “Climate as a Driver of Evolutionary Change.” *Current Biology* 19 (14): R575–83.

Faith, J Tyler, and Anna K Behrensmeyer. 2013. “Climate Change and Faunal Turnover: Testing the Mechanics of the Turnover-Pulse Hypothesis with South African Fossil Data.” *Paleobiology* 39 (4): 609–27.

Fuente, Alejandro de la, Andrew Krockenberger, Ben Hirsch, Lucas Cernusak, and Stephen E Williams. 2022. “Predicted Alteration of Vertebrate Communities in Response to Climate-Induced Elevational Shifts.” *Diversity and Distributions* 28 (6): 1180–90.

Fukami, Tadashi. 2015. “Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects.” *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 1–23.

Gerhold, Pille, Marcos B Carlucci, Şerban Procheş, and Andreas Prinzing. 2018. “The Deep Past Controls the Phylogenetic Structure of Present, Local Communities.” *Annual Review of Ecology, Evolution, and Systematics* 49: 477–97.

Hagen, Oskar. 2023. “Coupling Eco-Evolutionary Mechanisms with Deep-Time Environmental Dynamics to Understand Biodiversity Patterns.” *Ecography* 2023 (4): e06132.

Hargreaves, JC, and JD Annan. 2009. “On the Importance of Paleoclimate Modelling for Improving Predictions of Future Climate Change.” *Climate of the Past* 5 (4): 803–14.

Harrison, Susan, Marko J Spasojevic, and Daijiang Li. 2020. “Climate and Plant Community Diversity in Space and Time.” *Proceedings of the National Academy of Sciences* 117 (9): 4464–70.

Jabot, Franck, Fabien Laroche, François Massol, Florent Arthaud, Julie Crabot, Maxime Dubart, Simon Blanchet, François Munoz, Patrice David, and Thibault Datry. 2020. “Assessing Metacommunity Processes Through Signatures in Spatiotemporal Turnover of Community Composition.” *Ecology Letters* 23 (9): 1330–39.

Jackson, Jeremy BC, and Douglas H Erwin. 2006. “What Can We Learn about Ecology and Evolution from the Fossil Record?” *Trends in Ecology & Evolution* 21 (6): 322–28.

Jackson, Stephen T, and Jessica L Blois. 2015. “Community Ecology in a Changing Environment: Perspectives from the Quaternary.” *Proceedings of the National Academy of Sciences* 112 (16): 4915–21.

Jones, Lewis A., William Gearty, Bethany J. Allen, Kilian Eichenseer, Christopher D. Dean, Sofía Galván, Miranta Kouvari, et al. 2023. “Palaeoverse: A Community-Driven r Package to Support Palaeobiological Analysis.” *Methods in Ecology and Evolution*, 1–11. <https://doi.org/10.1111/2041-210X.14099>.

Khattar, Gabriel, Margarete Macedo, Ricardo Monteiro, and Pedro Peres-Neto. 2021. “Determinism and Stochasticity in the Spatial–Temporal Continuum of Ecological Communities: The Case of Tropical Mountains.” *Ecography* 44 (9): 1391–1402.

Kiessling, Wolfgang, Jansen A Smith, and Nussaı̈bah B Raja. 2023. “Improving the Relevance of Paleontology to Climate Change Policy.” *Proceedings of the National Academy of Sciences* 120 (7): e2201926119.

Kraft, Nathan JB, Peter B Adler, Oscar Godoy, Emily C James, Steve Fuller, and Jonathan M Levine. 2015. “Community Assembly, Coexistence and the Environmental Filtering Metaphor.” *Functional Ecology* 29 (5): 592–99.

Ludwig, Patrick, Juan J Gómez-Navarro, Joaquim G Pinto, Christoph C Raible, Sebastian Wagner, and Eduardo Zorita. 2019. “Perspectives of Regional Paleoclimate Modeling.” *Annals of the New York Academy of Sciences* 1436 (1): 54–69.

Merdith, Andrew S, Simon E Williams, Alan S Collins, Michael G Tetley, Jacob A Mulder, Morgan L Blades, Alexander Young, et al. 2021. “Extending Full-Plate Tectonic Models into Deep Time: Linking the Neoproterozoic and the Phanerozoic.” *Earth-Science Reviews* 214: 103477.

Mottl, Ondřej, Suzette GA Flantua, Kuber P Bhatta, Vivian A Felde, Thomas Giesecke, Simon Goring, Eric C Grimm, et al. 2021. “Global Acceleration in Rates of Vegetation Change over the Past 18,000 Years.” *Science* 372 (6544): 860–64.

Myers, Corinne E, Alycia L Stigall, and Bruce S Lieberman. 2015. “PaleoENM: Applying Ecological Niche Modeling to the Fossil Record.” *Paleobiology* 41 (2): 226–44.

Nogués-Bravo, David. 2009. “Predicting the Past Distribution of Species Climatic Niches.” *Global Ecology and Biogeography* 18 (5): 521–31.

Nogués-Bravo, David, Francisco Rodrı́guez-Sánchez, Luisa Orsini, Erik de Boer, Roland Jansson, Helene Morlon, Damien A Fordham, and Stephen T Jackson. 2018. “Cracking the Code of Biodiversity Responses to Past Climate Change.” *Trends in Ecology & Evolution* 33 (10): 765–76.

Sonne, Jesper, Bo Dalsgaard, Michael K Borregaard, Jonathan Kennedy, Jon Fjeldså, and Carsten Rahbek. 2022. “Biodiversity Cradles and Museums Segregating Within Hotspots of Endemism.” *Proceedings of the Royal Society B* 289 (1981): 20221102.

Vasconcelos, Thais, Brian C O’Meara, and Jeremy M Beaulieu. 2022. “Retiring ‘Cradles’ and ‘Museums’ of Biodiversity.” *The American Naturalist* 199 (2): 194–205.

Weiher, Evan, Deborah Freund, Tyler Bunton, Artur Stefanski, Tali Lee, and Stephen Bentivenga. 2011. “Advances, Challenges and a Developing Synthesis of Ecological Community Assembly Theory.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1576): 2403–13.

Zachos, James, Mark Pagani, Lisa Sloan, Ellen Thomas, and Katharina Billups. 2001. “Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present.” *Science* 292 (5517): 686–93.