

Ecological heterogeneity in global warming across terrestrial biomes

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Abstract

Global mean temperature is the dominant indicator of climate change, but it provides limited information about how warming is experienced across the Earth’s ecosystems. Because biodiversity, ecosystem functioning and climate adaptation are organized around ecological systems rather than global averages, understanding the ecological distribution of warming is essential for assessing climate risk. Here we examine global temperature change through the lens of terrestrial biomes and show that warming is structured in ways that are largely hidden by conventional climate metrics. Some biomes, particularly at high latitudes, exhibit strong and accelerating warming, whereas tropical and temperate systems experience more gradual but persistent increases. Other biomes are characterized by substantial variability that can amplify or obscure long-term trends. These contrasting trajectories reveal that ecosystems are exposed not only to different magnitudes of warming but also to different rates and patterns of change. We further find that climate dynamics are organized along ecological boundaries, indicating that biome structure helps shape how warming is expressed across the planet. By translating global temperature records into biome-specific measures of climate exposure, our framework connects large-scale climate change with ecosystem-level impacts and provides a scalable basis for improving biodiversity risk assessment, conservation planning and climate adaptation in a warming world. These findings provide a quantitative basis for prioritizing conservation efforts and informing regional adaptation strategies.

Analysis

Global mean temperature is an indispensable indicator of climate change, yet it is a poor proxy for how warming is organised across the terrestrial biosphere. Species distributions, ecosystem processes and conservation strategies are not defined by geopolitical boundaries or coarse spatial averages, but by ecological units with distinct vegetation, energy balance, hydrology and seasonal regimes. Climate exposure that is meaningful for biodiversity and adaptation must therefore be evaluated in ecologically coherent units rather than in global aggregates[1–3, 5].

This distinction is not merely conceptual. The same global forcing produces markedly different thermal trajectories across terrestrial systems. High latitudes experience amplified warming driven by surface–atmosphere feedbacks[8], while tropical and wetland systems respond through coupled hydrological and land–atmosphere processes[5]. As a result, climate-related risks to ecosystems and human systems are unevenly distributed in space[10]. Despite this, empirical analyses often represent temperature either as a global average or as a continuous spatial field defined independently of ecological structure. While appropriate for monitoring, these representations are less suited to understanding ecosystem-specific climate exposure. By aligning climate exposure with

biome structure, our framework provides a direct bridge to assessments of ecosystem service vulnerability, enabling more targeted evaluations of where climate change threatens water availability, agricultural productivity, and coastal protection—resources that underpin human welfare across the globe.

Here we recast global temperature change as an explicitly biome-structured problem. We combine the RESOLVE ecoregions framework, comprising 846 terrestrial ecoregions nested within 14 major biomes[1], with monthly near-surface air temperature from the NCEP/NCAR Reanalysis[11, 12] from 1948 to 2025. We discuss the choice of NCEP/NCAR Reanalysis data over other datasets in the Supplementary Material. On this basis, we estimate a hierarchical Bayesian spatio-temporal model in which each biome is characterised by its own long-run stochastic trend, seasonal cycle and medium-term dynamics, while sub-biomes evolve with flexible temporal deviations, and controlling spatial dependence across biomes and sub-biomes. Alternative spatial specifications allow us to test whether residual climate dependence follows ecological adjacency or continuous geographic distance.

This reframing yields two advances. First, it transforms a global temperature record into an exposure metric that is directly interpretable for ecological systems, bridging the gap between climate detection and ecosystem-level impact assessment. Second, it separates long-run warming from seasonal structure and medium-term variability, revealing biome-specific climate trajectories that are obscured in aggregate analyses. The result is a global, uncertainty-aware characterization of warming that is both statistically rigorous and ecologically meaningful.

Methods

Understanding how climate change manifests heterogeneously across biomes requires a framework capable of disentangling long-run forcing, short-run variability, and spatial dependence while respecting ecological boundaries. The proposed hierarchical spatio-temporal methodology directly addresses this challenge by integrating biome-level stochastic trends with sub-biome heterogeneity and alternative spatial structures, allowing the data to reveal whether temperature dynamics are better explained by continuous geophysical processes or by discrete ecological organization. This distinction is central for advancing climate change measurement, as biomes represent coherent land–atmosphere systems with shared vegetation, albedo, and feedback mechanisms, yet they also exhibit substantial internal variability driven by local conditions. By combining interpretable temporal components with flexible spatial representations, ranging from adjacency-based dependence to continuous fields on the sphere, the framework provides a unified and computationally scalable approach to quantify how climate signals propagate across ecological systems at the global scale.

We model monthly surface temperature observations as Gaussian responses conditional on a latent spatio-temporal linear predictor. The predictor decomposes temperature variability into sub-biome effects, biome-specific long-term trends, seasonal structure, short-run temporal dynamics, and spatial dependence.

Biome-level temporal dynamics are represented through three components. Long-term trends are modeled as first-order random walks, allowing permanent responses to cumulative climate forcing.

Seasonality is captured via stochastic monthly effects constrained to sum to zero within each year, isolating intra-annual variation. Short-run dynamics are modeled using stationary autoregressive processes of order two, allowing for persistent and potentially oscillatory behavior consistent with interannual variability.

Sub-biome effects account for baseline thermal differences across ecological units. Because no global intercept is included, these effects absorb mean temperature levels. We consider three alternative specifications for the spatial effects: (i) time-invariant exchangeable effects capturing persistent spatial heterogeneity; (ii) temporally evolving effects following autoregressive dynamics, allowing gradual shifts in local baselines; and (iii) fully exchangeable space–time effects representing unconstrained heterogeneity across both dimensions.

To characterize residual spatial dependence, we compare three alternative structures. First, a null specification assumes no additional spatial field beyond ecological grouping and temporal dynamics. Second, we adopt a discrete spatial model based on intrinsic conditional autoregression, which smooths temperature across adjacent ecological units and captures spatial coherence aligned with biome boundaries. Third, we model spatial dependence as a continuous Gaussian random field with Matérn covariance defined on the sphere. This field is implemented via a stochastic partial differential equation (SPDE) representation, enabling computationally efficient inference while preserving interpretable parameters for spatial range and smoothness.

All structured components are constrained for identifiability, and inference is conducted within a Bayesian hierarchical framework using integrated nested Laplace approximations (INLA). This setup enables scalable estimation while allowing direct comparison between discrete and continuous representations of spatial climate dependence. A detailed description of the methodology is provided in the Online Methods and Supplementary Material.

Results

Warming is widespread but not uniform across biomes

Simple contrasts between the first and last five years of the record already reveal strong ecological heterogeneity in warming magnitude (Table 1). The largest increase is observed in tundra (+1.62 °C), consistent with strong high-latitude amplification. Large positive changes also appear in tropical and wetland-associated systems, including tropical and subtropical grasslands, savannas and shrublands (+1.14 °C), mangroves (+0.95 °C), tropical and subtropical moist broadleaf forests (+0.94 °C), and flooded grasslands and savannas (+0.92 °C). Mediterranean forests, woodlands and scrub also show a relatively large end-of-period increase (+0.87 °C).

Several temperate biomes warm more modestly in this simple comparison. Temperate broadleaf and mixed forests rise by only +0.15 °C, boreal forests/taiga by +0.16 °C, and deserts and xeric shrublands by +0.50 °C. Two biomes—montane grasslands and shrublands, and temperate conifer forests—show negative first-versus-last five-year differences of −0.89 °C and −0.80 °C, respectively. These negative contrasts should not be read as evidence against warming in those systems. They are descriptive edge comparisons that remain sensitive to internal variability, biome composition,

and the timing of multi-year fluctuations at the endpoints of the sample. As we show below, a decomposition of long-run trend, seasonality, and cyclical variation is necessary to interpret these patterns correctly and to distinguish structural forcing from medium-frequency oscillations.

Dynamic sub-biome effects improve model fit

We compared five hierarchical model specifications that differ in their treatment of sub-biome heterogeneity and spatial dependence. All models include biome-specific stochastic trend, seasonal, and cyclical components, but differ in whether sub-biome effects are modeled as static or dynamic and in how spatial dependence is represented. Specifically, spatial dependence is either omitted (Model 1), represented by a discrete Besag (ICAR) model defined over the ecological adjacency graph (Models 2, 4, and 5), or modeled as a continuous Matérn spatial field using the SPDE approach on the sphere (Model 3) (see Online Methods and the Supplementary Material for complete model specifications).

Model 1 serves as the baseline specification, incorporating time-invariant exchangeable sub-biome random effects without an explicit spatial component. Model 2 extends this baseline by adding a Besag (ICAR) spatial effect to capture boundary-based dependence among neighboring sub-biomes. Model 3 instead replaces the discrete spatial effect with a continuous Matérn SPDE field defined on a spherical mesh, allowing spatial dependence to decay smoothly with geodesic distance. Model 4 further extends the baseline by introducing time-varying sub-biome random effects following an AR(1) process together with a Besag spatial component, thereby capturing persistent temporal evolution in local deviations. Finally, Model 5 replaces the AR(1) dynamics with independent Gaussian innovations over time, allowing sub-biome effects to vary freely across years without temporal persistence while retaining the Besag spatial structure.

Model comparison (Table 2) strongly favours the specification that combines dynamic sub-biome deviations with ecological adjacency-based spatial smoothing (Model 4). This model achieves the best log marginal likelihood ($-19,707,756$) and the lowest WAIC ($39,077,899$) and DIC ($39,246,324$), improving materially on both the baseline hierarchical model and the continuous-field alternative (Table 2). The result indicates that global temperature dependence is not captured fully by geographic distance alone once biome structure is introduced. Residual coherence also follows ecological neighbourhoods, and much of the medium-term variation that would otherwise be absorbed by the long-run trend is better interpreted as persistent but evolving sub-biome heterogeneity.

This finding is substantively important. In climate-exposure applications, overly rigid models can confound structural warming with shorter-horizon local deviations, while overly flexible models can obscure interpretable broad-scale signals. The preferred specification strikes a useful balance: it preserves biome-level trend trajectories while allowing local ecological units to depart from the group mean in persistent and temporally evolving ways. This separation is especially consequential for biomes with high internal heterogeneity, where dynamic sub-biome effects absorb local variability that would otherwise distort the estimated long-run signal.

Biome trajectories show distinct warming shapes

The estimated long-run trends from the preferred model reinforce pronounced ecological heterogeneity in warming dynamics (Fig. 2). Differences across biomes are not limited to magnitude but extend to the shape, curvature, and timing of warming.

Tundra exhibits the strongest and most clearly accelerated increase, particularly from the late twentieth century onward, consistent with Arctic amplification driven by snow–albedo feedbacks and atmospheric heat transport[7, 8]. The acceleration visible in this trajectory is captured endogenously by the first-order random walk specification for the long-run trend, which allows warming increments to vary over time rather than imposing a linear rate. This shape carries ecological implications beyond the cumulative thermal shift: systems adapted to slowly shifting baselines may face disruption from the pace of change itself, compounding exposure to the total magnitude of warming.

Tropical and subtropical moist broadleaf forests, as well as tropical and subtropical grasslands, savannas and shrublands, display sustained upward trajectories with smoother curvature and less abrupt acceleration, in line with evidence that tropical systems experience persistent but less amplified warming signals[4, 5]. The smoothness of these trajectories does not imply lesser ecological significance. Tropical species are often adapted to narrow thermal ranges, and a persistent upward trend without acceleration may translate into proportionally greater physiological stress than a numerically larger but more variable signal in higher-latitude zones.

Wetland-associated systems, including mangroves and flooded grasslands, also show positive trends but with wider posterior uncertainty bands. This pattern likely reflects the spatial fragmentation of these biomes, limited grid-cell coverage in some regions, and genuine hydrological and coastal variability that introduces additional noise in the temperature record. The wider credible intervals should be interpreted as appropriate uncertainty quantification rather than evidence of weak warming: in several cases, the lower bound of the posterior interval remains positive throughout the sample, providing probabilistic evidence of sustained warming even where the posterior mean is modest.

Temperate broadleaf and mixed forests, and Mediterranean forests, woodlands and scrub, display moderate but steady positive trajectories. Deserts and xeric shrublands present relatively small long-run shifts. These patterns are consistent with the more modest descriptive contrasts in table 1 and reflect the moderate thermal forcing experienced by mid-latitude systems relative to polar and tropical zones.

Negative and irregular trajectories reflect heterogeneity, not absence of warming

Figure 2 shows that montane grasslands and shrublands and temperate conifer forests exhibit flat, irregular, or weakly negative trajectories. These cases illustrate two mechanisms by which biome-level aggregates can obscure underlying warming signals in a globally warming world.

Montane grasslands and shrublands encompass steep altitudinal gradients across geographically and climatically distinct regions, including the high-altitude grasslands of the Andes, the Tibetan

Plateau, the East African highlands, the Drakensberg range, and the Australasian alpine zone. Within each of these regions, temperature dynamics are governed by elevation-dependent lapse rates, aspect and slope orientation, local orographic circulation, snow cover duration, and land-surface energy balance, all of which vary substantially over short spatial distances. The global aggregate of these sub-biomes therefore mixes warming signals of different magnitudes, rates, and directions, producing a composite trajectory that reflects partial cancellation rather than a coherent forced response.

Under the preferred model decomposition, the irregular behavior of montane grasslands is largely absorbed by the cyclical and dynamic sub-biome components (See Figures 2 and 3 in Supplementary Material), while the latent trend remains flat and uncertain, with wide posterior credible intervals. This outcome is itself informative: it indicates that the montane grassland biome cannot be meaningfully summarized by a single monotonic warming trajectory at the global aggregate scale. Local warming signals within individual mountain ranges and altitudinal zones are well documented in the literature[4], but they are not spatially coherent enough at the biome scale to produce an identifiable aggregate trend in the present analysis. The preferred specification handles this correctly by assigning the unresolvable heterogeneity to dynamic sub-biome effects rather than forcing it into the long-run trend component.

Temperate conifer forests present a qualitatively different case. Unlike montane grasslands, this biome is less globally fragmented and occupies more contiguous zones, primarily in western North America, parts of East Asia, and the Palearctic. The irregular long-run trajectory in Figure 2 reflects the dominance of medium-frequency variability over the long-run forced signal at biome-aggregate scales. Temperature dynamics in this biome are strongly influenced by the Pacific Decadal Oscillation and associated atmospheric circulation patterns, which can sustain multi-year cool anomalies that affect endpoint averages in the descriptive comparison. The spatial position of temperate conifer forests in a transitional latitudinal zone, subject to competing influences from Arctic amplification to the north, subtropical warming to the south, and strong oceanic modulation from the Pacific, further complicates the aggregate thermal signal. In the preferred model, the AR(2) cyclical component absorbs the dominant oscillatory behavior, preventing it from being misattributed to the stochastic trend. The resulting latent trend is weakly positive with wide credible intervals and a non-monotonic shape, consistent with a system where weak persistent warming coexists with strong interannual to decadal variability.

These results underscore the value of hierarchical decomposition. By separating long-run trends, cyclical variability, and sub-biome heterogeneity, the framework avoids conflating distinct processes and provides a more ecologically meaningful interpretation of climate exposure. The diversity of trajectory shapes, from accelerating tundra warming to persistent tropical trends, moderate Mediterranean increases, irregular temperate conifer dynamics, and uncertain montane signals, illustrates how a common global forcing is filtered through ecologically distinct systems with different feedbacks, variability structures, and spatial organization.

Seasonality and cyclical variability remain biome specific

Supplementary results (Supplementary Figure 2) show that heterogeneity extends beyond the long-run component. High-latitude biomes, particularly tundra and boreal forests, exhibit the largest seasonal amplitudes, reflecting strong intra-annual thermal contrasts[8]. Tropical forests and mangroves display narrower seasonal ranges but persistent upward shifts in mean temperature levels. The explicit cyclical component captures biome-specific multi-year variability, preventing medium-frequency fluctuations from being conflated with structural warming trends, an issue highlighted in studies of climate extremes and variability[9]. This role of the cyclical component is especially important for biomes such as temperate conifer forests and montane grasslands, where it absorbs the dominant oscillatory signal and thereby enables a cleaner identification of the long-run trend.

This decomposition reveals that temperature dynamics operate across multiple interacting layers: a biome-level long-run trajectory, a climatic-regime-dependent seasonal structure, and a persistent medium-term deviation component. Separating these elements improves interpretability and aligns with the view that climate variability and long-term change jointly shape ecological exposure[5].

Discussion

This study reframes global warming as an ecological exposure problem, emphasizing how temperature change is organized across biomes rather than summarized by global averages. While global mean temperature remains the standard indicator of climate change, it provides limited insight into how warming is experienced by ecological systems, where biodiversity risk, resilience, and adaptation are structured around ecological units rather than planetary aggregates [2, 3].

Our results show that global means and latitudinal averages systematically obscure the ecological structure of warming. Although global mean temperature captures planetary energy imbalance, it masks substantial spatial and temporal heterogeneity across biomes [4, 6]. Biome-specific warming trajectories differ not only in magnitude but also in shape, with distinct rates of acceleration and peak long-run increases. Strong warming in tundra, consistent with Arctic amplification [8], contrasts with smoother trends in tropical systems, moderate increases in temperate and Mediterranean forests, and flat or highly variable trajectories in montane and temperate conifer biomes.

Latitude captures broad climatic gradients but is insufficient to characterize ecological climate exposure. Biomes within the same latitudinal zone often exhibit markedly different warming trajectories due to vegetation, land-surface feedbacks, and hydrological processes [5].

Flat or irregular biome trajectories are particularly informative. For montane grasslands and shrublands, weak aggregate trends arise from spatial averaging across sub-biomes with contrasting local dynamics. In temperate conifer forests, modest warming is largely obscured by strong interannual and decadal variability linked to ocean-atmosphere oscillations.

These results have important implications for climate impact assessment. Because biological responses depend on local exposure and variability rather than global averages [2, 3], biome-specific warming trajectories provide a more meaningful basis for assessing ecological risk [10]. By separat-

ing persistent warming trends from oscillation-driven variability, the framework identifies systems experiencing the most rapid increases in climate exposure and those where variability may obscure long-term change, informing biodiversity monitoring, conservation, and adaptation planning.

More broadly, this work helps bridge the gap between global-scale climate detection and ecosystem-level impact assessment. Organizing temperature dynamics along ecological boundaries reveals patterns hidden by aggregate metrics while providing an interpretable, data-driven measure of climate exposure that complements physically based climate models and can be readily integrated into ecological and conservation analyses. This finding has direct implications for climate modeling and prediction: embedding temperature dynamics within an ecologically coherent hierarchy can reduce extrapolation errors in impact assessments and improve the representation of land–atmosphere feedbacks, because biomes integrate the vegetation structure, surface energy balance, and hydrological regimes that mediate regional climate responses—processes that physically based models must parameterize but often treat as independent of ecological organization.

The analysis has several limitations. It relies on a single long-term reanalysis dataset and considers only air temperature. However, this focus reflects the central objective of the study: to understand how the primary signal of global climate change is distributed across ecological systems. Temperature remains the most widely monitored and consistently measured dimension of climate change and provides a common basis for comparing exposure among biomes at the global scale. The patterns identified here should therefore be viewed as a first step toward an ecological characterization of climate change rather than a complete assessment of climate impacts.

Future work should test the robustness of these results using alternative datasets, including ERA5 and Berkeley Earth, and extend the framework to precipitation, aridity, and compound extremes, which are critical determinants of ecosystem vulnerability and adaptation [4, 9]. Greater spatial disaggregation of highly heterogeneous biomes, particularly montane systems, may also help reveal localized climate signals that remain masked by global biome-level aggregation.

Despite these limitations, the main conclusion is clear: the terrestrial biosphere is not warming in a uniform manner. Global warming decomposes into a set of biome-specific trajectories with distinct magnitudes, temporal structures, and variability patterns. Some biomes are warming strongly and with acceleration; others persistently but smoothly; others show weak forced trends dominated by internal variability; and others aggregate such diverse sub-regional dynamics that no single trajectory adequately represents the whole. Recognizing and quantifying this full spectrum of ecological heterogeneity, including its irregular and apparently anomalous cases, provides a more complete and informative basis for understanding climate impacts and for designing adaptation strategies in a rapidly changing world.

Online Methods

Ecological units and temperature data

We used the RESOLVE Ecoregions 2017 dataset to define the ecological hierarchy [1]. The database maps 846 terrestrial ecoregions nested within 14 major biomes and broader biogeographic realms

(Figure 1). These units are widely used in biodiversity and conservation research and provide a natural scaffold for analysing climate exposure in ecologically coherent regions.

Temperature data come from the NCEP/NCAR Reanalysis 1 project, using monthly mean near-surface air temperature at 2 m from 1948 to 2025 [11, 12]. The monthly fields were spatially overlaid with the RESOLVE polygons so that each grid-cell observation could be assigned to an ecoregion and biome. The resulting dataset preserves global coverage while enabling inference in ecological units rather than only in the native atmospheric grid.

Hierarchical decomposition

Let $y_{i,t}$ denote monthly temperature observed in location i at time t , where location i belongs to sub-biome $c(i)$ and biome $b(i)$. We modelled

$$y_{i,t} = \mu_{c(i),t} + T_{b(i),t} + S_{b(i),t} + C_{b(i),t} + \mathcal{S}_i + \varepsilon_{i,t},$$

where $\mu_{c(i),t}$ is a sub-biome effect, $T_{b(i),t}$ is a biome-specific long-run stochastic trend, $S_{b(i),t}$ is a biome-specific seasonal component, $C_{b(i),t}$ is a biome-specific cyclical component and $\mathcal{S}_i$ is an optional spatial effect. Observation errors were Gaussian.

The long-run trend was represented as a first-order random walk, allowing warming rates to evolve flexibly over time. Seasonality was modelled with monthly stochastic effects under a sum-to-zero constraint, and the medium-term cycle was represented through an AR(2) component. Competing specifications differed in whether $\mu_{c(i),t}$ was static, AR(1)-persistent or exchangeable through time, and in whether $\mathcal{S}_i$ followed no spatial structure, a Besag/ICAR ecological adjacency field [13], or an SPDE approximation to a Matérn field on the sphere [14]. See Supplementary Section: Methodology for a detailed presentation of the methodology.

Inference and model comparison

Inference was conducted in the latent Gaussian framework using integrated nested Laplace approximations (INLA) [15]. Weakly informative priors were used for precisions and penalised-complexity style shrinkage was applied to favour simpler components unless the data supported additional structure [16]. Structured spatial and temporal effects were centred where necessary to reduce confounding.

Models were compared using log marginal likelihood, WAIC and DIC (Table 2). The preferred model was the one with dynamic AR(1) sub-biome effects and Besag spatial dependence. We interpret this model as the best compromise between ecological interpretability, separation of long-run versus medium-term variability, and statistical fit.

Table 1: **Simple warming contrasts by biome.** Mean temperature in the first and last five years of the sample and the associated absolute change.

Biome	First 5 years (°C)	Last 5 years (°C)	Change (°C)
Boreal forests/taiga	-4.31	-4.15	0.16
Deserts & xeric shrublands	18.17	18.67	0.50
Flooded grasslands & savannas	18.09	19.01	0.92
Mangroves	24.67	25.62	0.95
Mediterranean forests, woodlands & scrub	15.82	16.69	0.87
Montane grasslands & shrublands	1.33	0.44	-0.89
Temperate broadleaf & mixed forests	8.43	8.58	0.15
Temperate conifer forests	3.70	2.91	-0.80
Temperate grasslands, savannas & shrublands	8.00	8.39	0.39
Tropical & subtropical coniferous forests	18.65	19.32	0.67
Tropical & subtropical dry broadleaf forests	23.77	24.58	0.81
Tropical & subtropical grasslands, savannas & shrublands	23.23	24.37	1.14
Tropical & subtropical moist broadleaf forests	22.23	23.17	0.94
Tundra	-12.15	-10.53	1.62

Scope of inference

The results describe how warming is organised across ecological units in one long global temperature record. They should not be interpreted as causal attribution of warming mechanisms, nor as a substitute for process-based climate modelling. Their contribution is to provide a statistically coherent, uncertainty-aware exposure layer aligned with biome structure.

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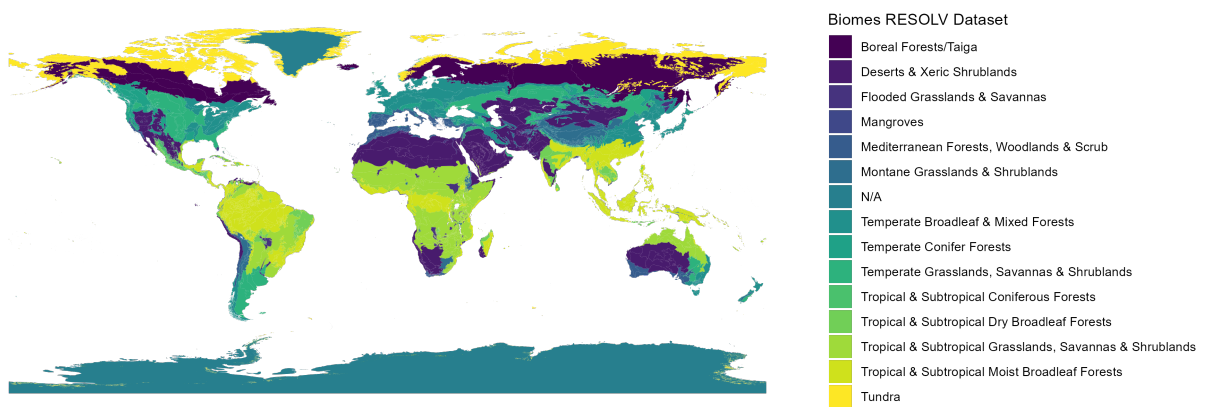


Figure 1: **Global ecological partitions used in the analysis.** The RESOLVE Ecoregions 2017 dataset provides the ecological hierarchy used to organise temperature observations into terrestrial biomes and ecoregions.

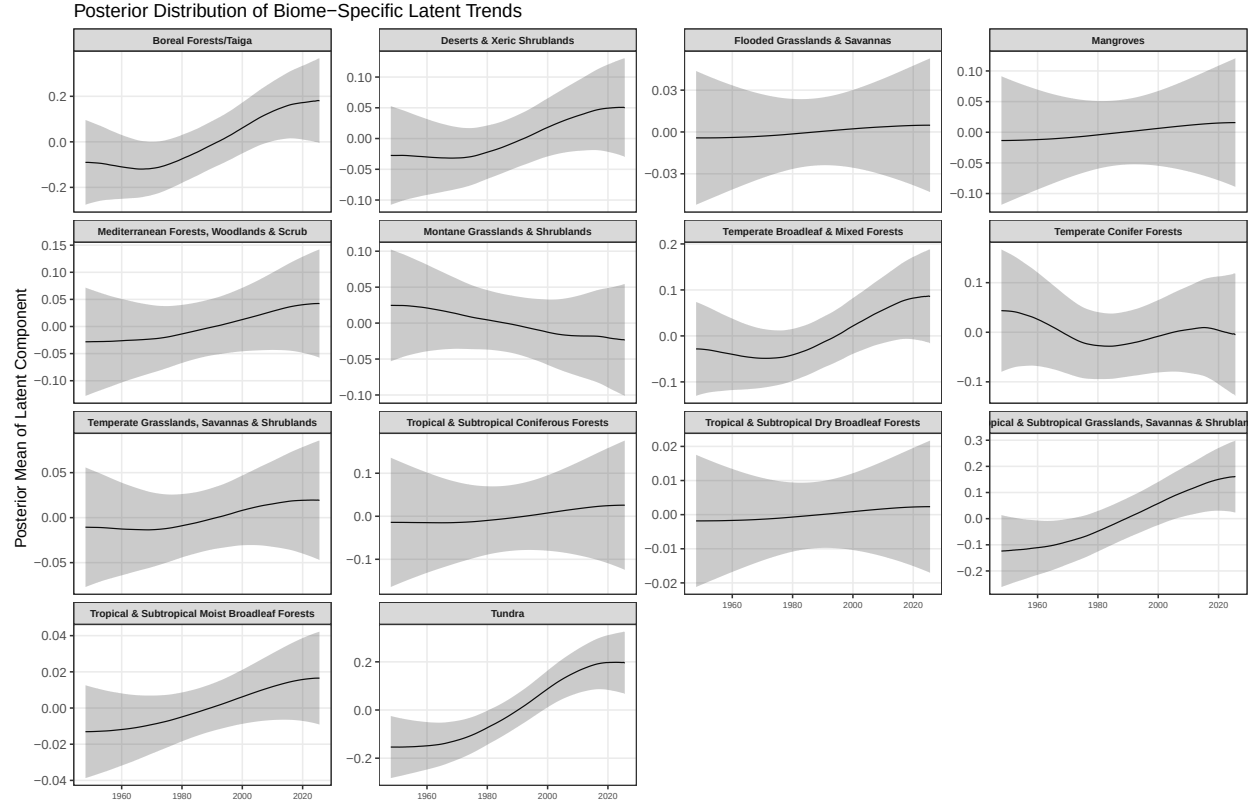


Figure 2: **Estimated biome-level long-run temperature trajectories in the preferred model.** Curves show posterior means and shaded bands indicate 95% credible intervals. The preferred specification includes dynamic sub-biome effects and ecological adjacency-based spatial dependence.

Table 2: **Model comparison.** Lower WAIC and DIC indicate better fit.

Model	Log marginal likelihood	WAIC	DIC
Model 1	-21,005,141	41,989,023	41,990,773
Model 2	-21,017,127	41,987,810	41,989,746
Model 3	-20,609,575	41,190,131	41,191,695
Model 4	-19,707,756	39,077,899	39,246,324
Model 5	-19,817,993	39,247,975	39,451,217

Notes. Model 1 is the baseline hierarchical specification including biome-specific stochastic trends, seasonal and cyclical components, and time-invariant (static) exchangeable sub-biome random effects, without an explicit spatial dependence structure. Model 2 extends Model 1 by incorporating a Besag (ICAR) spatial effect defined over the ecological adjacency graph, capturing boundary-based spatial dependence among neighboring sub-biomes. Model 3 extends Model 1 by replacing the discrete spatial effect with a continuous Matérn SPDE spatial field on the sphere, using a mesh with 1,618 triangles to capture geodesic-distance spatial dependence. Model 4 includes biome-specific stochastic trends, seasonal and cyclical components, time-varying sub-biome random effects following an AR(1) temporal structure, and a Besag spatial component, allowing persistent sub-biome deviations that evolve over time. Model 5 is similar to Model 4 but assumes time-varying exchangeable sub-biome effects as independent Gaussian innovations, allowing sub-biome heterogeneity to vary freely over time without temporal persistence.

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Supplementary Information

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Justification for the Use of NCEP/NCAR Reanalysis

The use of the NCEP/NCAR Reanalysis dataset is justified by the objectives and spatial scale of this study. Our goal is not to reconstruct local surface temperatures with maximum precision, but rather to characterize long-term warming trajectories across broad terrestrial biomes. Because the analysis is conducted at a highly aggregated ecological scale, the primary requirement is a temporally consistent global record capable of capturing large-scale climate variability and long-run trends.

NCEP/NCAR provides an appropriate foundation for this purpose. As one of the longest-running and most extensively used global reanalyses, it offers a physically consistent representation of the climate system by combining observations with atmospheric dynamics. This framework produces spatially complete temperature fields, which are particularly valuable when aggregating temperatures across biomes that span regions with highly uneven observational coverage. Moreover, the dataset has served as a benchmark in numerous studies of climate variability and long-term climate change, facilitating comparison with an extensive literature.

Although ERA5 provides substantially higher spatial resolution and a more sophisticated data assimilation system, these advantages are primarily relevant for regional climate analyses, local-scale applications, and the study of extreme events. Furthermore, the quality and density of assimilated observations vary substantially through time, particularly before the satellite era. As a result, part of the apparent improvement in climate reconstruction reflects changes in the observing system itself. For a study focused on multi-decadal biome-level warming patterns, the additional spatial detail offered by ERA5 is unlikely to materially alter the large-scale ecological signals of interest while introducing potential complications associated with temporal inhomogeneities in observational coverage.

Berkeley Earth presents a different set of limitations. Although it provides a longer temperature record and is specifically designed for surface temperature estimation, it remains an observational reconstruction whose historical coverage depends on the spatial and temporal distribution of weather stations. Coverage is particularly sparse in earlier decades across parts of the tropics, polar regions, and other remote areas that are ecologically important for global biome analyses. In addition, Berkeley Earth does not provide the dynamically consistent global climate fields available from a reanalysis product. For a study aimed at identifying broad ecological structures in global warming rather than estimating local temperature anomalies, the spatial completeness and physical consistency of a reanalysis framework constitute important advantages.

Because the present analysis emphasizes relative warming trajectories, long-run trends, and differences among biomes rather than local temperature estimates, NCEP/NCAR represents a suitable and well-established data source. Nevertheless, future research should evaluate the robustness of the identified biome-level patterns using alternative datasets such as ERA5 and Berkeley Earth. Agreement across independent climate products would strengthen confidence that the ecological organization of warming documented here is not an artifact of a particular dataset but a robust feature of the global climate record.

Supplementary Table 1: Biomes and associated realms

Biome	Realms
Tropical & subtropical moist broadleaf forests	Afrotropic, Australasia, Indomalayan, Neotropic, Oceania, Palearctic
Tropical & subtropical dry broadleaf forests	Afrotropic, Australasia, Indomalayan, Nearctic, Neotropic, Oceania
Tropical & subtropical coniferous forests	Indomalayan, Nearctic, Neotropic
Temperate broadleaf & mixed forests	Australasia, Indomalayan, Nearctic, Neotropic, Palearctic
Temperate conifer forests	Indomalayan, Nearctic, Palearctic
Boreal forests/taiga	Nearctic, Palearctic
Tropical & subtropical grasslands, savannas & shrublands	Afrotropic, Australasia, Indomalayan, Nearctic, Neotropic, Oceania
Temperate grasslands, savannas & shrublands	Afrotropic, Australasia, Nearctic, Neotropic, Palearctic
Flooded grasslands & savannas	Afrotropic, Indomalayan, Neotropic, Palearctic
Montane grasslands & shrublands	Afrotropic, Australasia, Indomalayan, Neotropic, Palearctic
Tundra	Antarctica, Australasia, Nearctic, Palearctic
Mediterranean forests, woodlands & scrub	Afrotropic, Australasia, Nearctic, Neotropic, Palearctic
Deserts & xeric shrublands	Afrotropic, Australasia, Indomalayan, Nearctic, Neotropic, Palearctic
Mangroves	Afrotropic, Australasia, Indomalayan, Neotropic

Supplementary Table 1 lists the terrestrial biomes considered in the analysis and their associated biogeographic realms based on the RESOLVE ecoregions framework. Each biome aggregates ecologically similar ecoregions characterized by shared vegetation structure, climatic conditions, and land-atmosphere interactions. The corresponding realms indicate the broad biogeographic regions in which each biome occurs, reflecting large-scale evolutionary and geographic patterns. This classification underpins the hierarchical structure of the empirical model by linking local temperature observations to ecologically meaningful units, allowing the analysis to capture both within-biome heterogeneity and cross-realm variation in climate dynamics.

Supplementary Table 2: Temperature change by biome, 1948–2025

Supplementary Table 2 compares the average temperatures of the first five and last five years of the sample, providing a robust measure of long-run climate change while smoothing short-term interannual variability. The results indicate widespread warming across most global biomes. Positive absolute changes dominate, with particularly pronounced increases in high-latitude and tropical systems.

The Tundra exhibits the largest absolute increase (1.62 °C), corresponding to a 13.3% rise relative to the early-sample mean. This result is consistent with Arctic amplification, whereby polar regions warm at rates exceeding the global average. Tropical & Subtropical Grasslands, Savannas & Shrublands also show substantial warming (1.14 °C), followed by Mangroves (0.95 °C), Tropical & Subtropical Moist Broadleaf Forests (0.94 °C), and Flooded Grasslands & Savannas (0.92 °C).

Table 2: Descriptive statistics of monthly surface temperature by biome (1948–2025).

BIOME_NAME	temp_first5	temp_last5	delta_abs	delta_pct
Boreal Forests/Taiga	-4.31	-4.15	0.16	3.78
Deserts & Xeric Shrublands	18.17	18.67	0.50	2.76
Flooded Grasslands & Savannas	18.09	19.01	0.92	5.11
Mangroves	24.67	25.62	0.95	3.84
Mediterranean Forests, Woodlands & Scrub	15.82	16.69	0.87	5.47
Montane Grasslands & Shrublands	1.33	0.44	-0.89	-66.68
Temperate Broadleaf & Mixed Forests	8.43	8.58	0.15	1.81
Temperate Conifer Forests	3.70	2.91	-0.80	-21.51
Temperate Grasslands, Savannas & Shrublands	8.00	8.39	0.39	4.83
Tropical & Subtropical Coniferous Forests	18.65	19.32	0.67	3.61
Tropical & Subtropical Dry Broadleaf Forests	23.77	24.58	0.81	3.41
Tropical & Subtropical Grasslands, Savannas & Shrublands	23.23	24.37	1.14	4.90
Tropical & Subtropical Moist Broadleaf Forests	22.23	23.17	0.94	4.21
Tundra	-12.15	-10.53	1.62	13.30

Mediterranean Forests, Woodlands & Scrub display an increase of 0.87 °C, reflecting the well-documented warming and drying trends in Mediterranean-type climates.

Deserts & Xeric Shrublands and most temperate biomes also show positive temperature changes, although of smaller magnitude (between 0.15°C and 0.50°C). These patterns suggest that warming is globally pervasive but spatially heterogeneous in intensity. The magnitude of warming appears particularly strong in high-latitude and certain tropical systems, consistent with theoretical and observational climate dynamics.

Two biomes—Montane Grasslands & Shrublands and Temperate Conifer Forests—exhibit negative differences between the first and last five-year averages. Given the high interannual variability and potential altitudinal heterogeneity within these biomes, these declines may reflect localized dynamics or compositional shifts rather than a reversal of global warming trends. The contrast with the widespread positive changes elsewhere underscores the importance of accounting for biome-specific heterogeneity in climate assessments.

Supplementary Figure 1: Annual biome-level boxplots

Supplementary Figure 1 summarizes the evolution of annual temperature distributions within each biome using cross-sectional boxplots over time. The dominant pattern is a systematic upward shift in the median and interquartile range across most biomes, indicating that warming is spatially pervasive rather than driven by isolated grid cells.

High-latitude biomes, particularly Tundra and Boreal Forests/Taiga, display the most pronounced upward displacement, consistent with Arctic amplification. Tropical biomes exhibit smaller dispersion but clear and steady increases in median temperatures, reflecting persistent warming even in climatically stable regions. Temperate systems show moderate upward shifts combined with substantial spatial heterogeneity, suggesting uneven regional responses within biomes.

Overall, the figure provides distributional evidence that global warming operates as a structural shift in temperature distributions across terrestrial ecosystems, with magnitude and variability

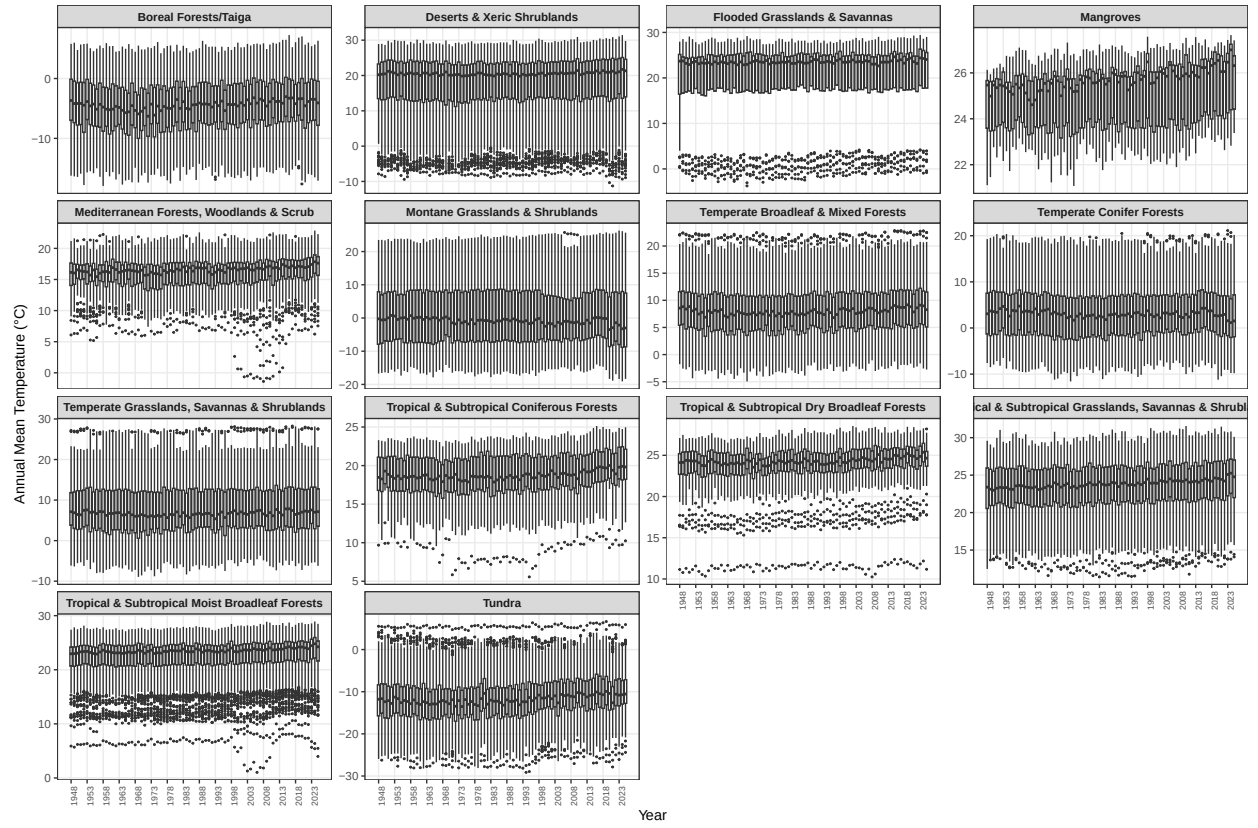


Figure 1: Biome-level annual temperature distributions using boxplots.

differing systematically by biome.

Supplementary Section: Methodology

Hierarchical spatio-temporal model and alternative spatial specifications

We model monthly surface temperature observations y_i observed at spatial location $s_i \in \mathbb{S}^2$, time t_i , sub-biome $c(i)$, and biome $b(i)$. Conditional on the latent linear predictor η_i , we assume

$$y_i \mid \eta_i \sim \mathcal{N}(\eta_i, \tau_\varepsilon^{-1}),$$

where τ_ε denotes the observation precision.

Linear predictor. The linear predictor common to all specifications is

$$\eta_i = \mu_{c(i),t_i} + T_{b(i)}(t_i) + S_{b(i)}(t_i) + C_{b(i)}(t_i) + \mathcal{S}_i,$$

where:

- $\mu_{c,t}$ denotes the sub-biome effect, - $T_b(t)$ is the long-run biome-specific trend, - $S_b(t)$ is the seasonal component, - $C_b(t)$ is a short-run AR(2) cycle, - $\mathcal{S}_i$ is the spatial component.

All structured temporal and spatial effects are constrained to sum to zero to ensure identifiability. No global intercept is included; baseline levels are absorbed by $\mu_{c,t}$.

Biome-specific temporal dynamics. Long-run trend (RW1). For each biome b , the trend follows a first-order random walk:

$$T_b(t) = T_b(t-1) + \epsilon_{b,t}, \quad \epsilon_{b,t} \sim \mathcal{N}(0, \tau_{T_b}^{-1}).$$

This specification implies that shocks have permanent effects, capturing the cumulative nature of anthropogenic climate forcing.

Seasonal component. Monthly stochastic seasonality is modeled, for each biome b , by a set of month-specific random effects,

$$S_{b,1}, \dots, S_{b,12},$$

The monthly effects are assumed Gaussian with precision τ_{S_b} and are subject to the sum-to-zero constraint in each year (12 periods):

$$\sum_{m=1}^{12} S_{b,m} = 0.$$

This restriction ensures identifiability in the absence of a global intercept and guarantees that the seasonal component captures only intra-annual deviations around the biome-specific annual mean level.

Short-run cycle (AR(2)). Higher-frequency persistence is modeled as

$$C_b(t) = \phi_{1,b}C_b(t-1) + \phi_{2,b}C_b(t-2) + \nu_{b,t}, \quad \nu_{b,t} \sim \mathcal{N}(0, \tau_{C_b}^{-1}),$$

allowing damped oscillatory behavior consistent with intra-annual and interannual variability. The stationary condition is imposed on the estimation of this component, using a partial autocorrelation representation. Detailed discussions and justifications for the use of these climate modeling specifications can be found in [1].

Sub-biome random effects. The sub-biome component $\mu_{c,t}$ captures structural temperature differences across ecological partitions. Because the global intercept is omitted from the model specification, these effects absorb the baseline mean level of each sub-biome. For this reason, we do not impose a sum-to-zero constraint on $\mu_{c,t}$; they are interpreted as sub-biome-specific intercepts.

We consider three alternative specifications.

(i) Time-invariant exchangeable effect.

$$\mu_c \sim \mathcal{N}(\bar{\mu}, \tau_\mu^{-1}),$$

where $\bar{\mu}$ is an unknown hyper-mean estimated from the data. This specification captures persistent thermal differences across sub-biomes arising from geography, elevation, vegetation structure, and surface energy balance, and assumes that these spatial effects remain constant over time.

(ii) Time-varying AR(1) group dependence.

$$\mu_{c,t} = \rho\mu_{c,t-1} + \xi_{c,t}, \quad \xi_{c,t} \sim \mathcal{N}(0, \tau_\mu^{-1}),$$

with $|\rho| < 1$. This formulation allows sub-biome-specific deviations to evolve dynamically over time, capturing gradual shifts in local baseline climate conditions while preserving temporal persistence within each ecological unit.

(iii) Fully exchangeable space–time variation.

$$\mu_{c,t} \sim \mathcal{N}(\bar{\mu}, \tau_\mu^{-1}),$$

independently across sub-biomes c and time periods t . Under this specification, sub-biome effects vary freely across both spatial units and time, representing idiosyncratic deviations that are not constrained by temporal dynamics or spatial smoothing. In all cases, the absence of a global intercept implies that $\mu_{c,t}$ captures the mean temperature level associated with each sub-biome (and, when applicable, each time period), ensuring that ecological baseline heterogeneity is explicitly modeled rather than absorbed into an overall constant term.

Alternative spatial specifications. We compare three competing representations for $\mathcal{S}(s)$. The first assumes no structured spatial field $\mathcal{S}(s) = 0$. This baseline assumes that ecological grouping and temporal dynamics fully explain spatial structure. The second specification adopts a discrete areal dependence structure based on the Besag/ICAR model introduced by [2]. Let $G = (V, E)$ denote the adjacency graph of ecological units. The spatial field is specified as an intrinsic conditional autoregressive (ICAR) model:

$$\mathcal{S}_i \mid \mathcal{S}_{-i} \sim \mathcal{N}\left(\frac{1}{n_i} \sum_{j \sim i} \mathcal{S}_j, \frac{1}{\tau_S n_i}\right),$$

where n_i is the number of neighbors of region i and $j \sim i$ denotes adjacency. In matrix form:

$$\mathcal{S} \sim \mathcal{N}\left(0, \tau_S^{-1} Q^{-}\right), \quad Q = D - W,$$

where W is the adjacency matrix and D the diagonal matrix of neighbor counts. This specification smooths across adjacent ecological units and captures discrete regional coherence. The Besag (ICAR) spatial structure is justified because climate similarity depends not only on geographic distance but also on shared ecological characteristics. Adjacent sub-biomes often exhibit gradual transitions in vegetation, soils, moisture regimes, and land-surface feedbacks, so the Besag model allows temperatures in one region to borrow strength from neighboring ecological units, capturing climate coherence aligned with ecological boundaries.

Unlike continuous spatial fields, which smooth across geographic space in all directions, the Besag formulation respects discrete ecological partitions and avoids oversmoothing across sharp biome or land-cover transitions. By conditioning only on adjacent regions, it captures localized spatial dependence without imposing global smoothness. The ICAR/BESAG model is a Gaussian Markov random field with a sparse precision matrix, which makes it computationally efficient and well suited for hierarchical models estimated with INLA, as discussed by [4]. The approach is also widely used in environmental and spatial epidemiology applications, as noted by [2] and [3]. In this context, the Besag component represents regional climate coherence driven by ecological adjacency, allowing us to evaluate whether temperature similarity follows biome boundaries rather than continuous geographic distance.

The third form assumes that $\mathcal{S}(s)$ is modeled as a spatially continuous Gaussian random field with Matérn covariance:

$$\text{Cov}(\mathcal{S}(s), \mathcal{S}(s')) = \sigma^2 \frac{2^{1-\nu}}{\Gamma(\nu)} (\kappa d)^\nu K_\nu(\kappa d),$$

where d is geodesic distance on the sphere, ν controls smoothness, κ the spatial scale, and K_ν is the modified Bessel function. Following [5], this field is represented as the weak solution of the Stochastic Partial Differential Equation (SPDE)

$$(\kappa^2 - \Delta)^{\alpha/2} \mathcal{S}(s) = \mathcal{W}(s),$$

with $\mathcal{W}(s)$ Gaussian white noise on $\mathbb{S}^2$.

The motivation for this specification is threefold. Global temperature fields reside on the sphere rather than on a Euclidean plane. Planar distance approximations distort separation distances, particularly at high latitudes, potentially biasing inference on spatial range and long-distance dependence. The SPDE approach allows the Matérn field to be defined directly on a spherical mesh using geodesic distance, ensuring projection-invariant interpretation of spatial correlation. This property is especially important in global climate applications where polar amplification and cross-hemispheric dependence are central features of the data.

Classical Gaussian random fields scale poorly for global datasets due to dense covariance matrices. The SPDE approach addresses this limitation by approximating the continuous Matérn field with a finite element representation that produces sparse precision matrices, enabling efficient large-scale Bayesian inference within INLA while retaining interpretable parameters for spatial smoothness and correlation range. Widely used in climate and environmental applications such as temperature

and precipitation modeling, climate downscaling, and extreme-event analysis, the SPDE–Matérn framework combines physical interpretability with computational efficiency. In this study, the SPDE spatial field captures continuous residual climate dependence after accounting for biome-level temporal dynamics and sub-biome heterogeneity, allowing comparison with the discrete Besag specification to assess whether global temperature dependence is better represented as continuous spatial processes or structured along ecological adjacency boundaries.

Prior Structure

The hierarchical model uses weakly informative but structured priors, with particular emphasis on penalized complexity (PC) priors that favor simpler base models unless the data support additional complexity. Precision parameters for the iid, Besag, and RW1 components follow a log-Gamma(1, 5e-05) prior, implying a heavy-tailed variance distribution that allows flexibility while maintaining computational stability. For the AR(2) temporal component, PC priors are applied to both the innovation precision—`pc.prec(3, 0.01)`—and the partial autocorrelations—`pc.cor0(0.5, 0.5)` and `pc.cor0(0.5, 0.4)`—which regularize persistence toward simpler temporal dependence structures. The spatial SPDE–Matérn field also uses PC priors on the range and marginal standard deviation, favoring shorter-range dependence and limiting excessive spatial variability in order to reduce potential confounding with biome-level effects. More generally, [6] define PC priors by penalizing departure from simpler base models using Kullback–Leibler divergence, yielding interpretable shrinkage and invariance to reparameterization.

Identification and Inference Methodology

The model assumes that long-run trends, seasonal patterns, and short-run cyclical dynamics are homogeneous within each biome, meaning that all locations in a biome share the same stochastic trend, seasonal structure, and persistence parameters. Spatial heterogeneity within biomes is instead captured through sub-biome random effects and spatial components (Besag or SPDE–Matérn), which absorb local deviations from the common temporal signal. This restriction is motivated both conceptually and statistically. From a climatological perspective, the ecological grouping of biomes and ecoregions described by [7], together with the broader climate synthesis provided by [8], suggests that areas within the same biome may share important surface and ecological characteristics relevant to climate dynamics. From an econometric perspective, imposing common dynamics within biome groups limits overparameterization and can improve identification of persistent components; this is broadly consistent with the panel-data perspective discussed by [9].

Biome-specific trends are identified by separating permanent temporal dynamics from spatial and cross-sectional heterogeneity. Sub-biome exchangeable effects capture persistent baseline temperature differences, while spatial fields model coherent cross-sectional deviations. With temporal components centered and structured spatial effects constrained, the stochastic trend is interpreted as the cumulative warming signal common to the biome rather than as a collection of local anomalies. This hierarchical separation uses partial pooling in the spirit of [10] and is compatible with latent Gaussian spatio-temporal modeling as discussed by [4]. It is also consistent with the distinction, common in climate analysis, between large-scale forced signals and regional variability, as discussed by [11] and [8]. Under this interpretation, the biome-specific trend represents the long-run warming trajectory of each ecological regime, while seasonal and cyclical components capture shared short-run dynamics and spatial or sub-biome effects represent localized departures.

The model combines exchangeable and Besag spatial effects, which raises identifiability issues because the intrinsic CAR (Besag) model is invariant to constant shifts within connected components of the spatial graph. Without additional constraints, baseline temperature levels could be attributed either to the exchangeable effect or to the structured spatial component. To address this issue, sum-to-zero constraints are imposed on the Besag effect within each connected component, ensuring that it captures spatial contrasts rather than baseline levels. Since the model excludes a global intercept, the exchangeable sub-biome effects absorb baseline mean temperatures, while the Besag component represents spatially structured deviations. When temporal components (trend, seasonal, and persistence terms) are included, centering constraints are applied only to structured spatial and temporal effects in order to reduce confounding with global levels while preserving meaningful ecological variation across sub-biomes.

Estimation of the hierarchical spatio-temporal models is performed using Integrated Nested Laplace Approximations (INLA), following [4]. INLA is a deterministic Bayesian inference approach for latent Gaussian models, a class that naturally accommodates spatial fields, stochastic trends, and mixed-effects structures. Because the proposed framework combines biome-level stochastic trends, temporal dynamics, sub-biome random effects, and alternative spatial structures (Besag and SPDE–Matérn), it fits naturally within this class. INLA replaces simulation-based MCMC with nested Laplace approximations and numerical integration to obtain posterior marginals while exploiting the sparse precision structure of Gaussian Markov random fields, which makes computation feasible even for large global spatio-temporal datasets. The method also facilitates uncertainty quantification and model comparison using criteria such as marginal likelihood, DIC, and WAIC. In the empirical analysis, differences in fit are attributed to the spatial specifications because the temporal and sub-biome components are held constant across competing models.

Supplementary Figures 2 and 3: Seasonal and cyclical components

Supplementary Figures 2 and 3 show the estimated posterior distribution of the Seasonal and Cycle components estimated by preferred model. The seasonal components exhibit pronounced biome dependence. High-latitude biomes, including Boreal Forests and Tundra, display the largest seasonal amplitudes, reflecting extreme annual cycles in temperature and radiation. This strong seasonal signal is consistent with well-documented phenological and energy-balance dynamics in polar and sub-polar ecosystems. Temperate forests and grasslands show intermediate seasonal amplitudes, corresponding to marked but less extreme annual climatic cycles. Tropical moist forests exhibit comparatively low seasonal amplitude, consistent with limited annual temperature variation, though hydrological seasonality may still play a role. The robustness and clarity of the seasonal components suggest a high signal-to-noise ratio in the annual cycle, and their structure remains stable across alternative spatial specifications, reinforcing confidence in their identification.

The latent cyclical components capture multi-year oscillations beyond the deterministic seasonal cycle. In tropical systems, the estimated cycles exhibit moderate amplitude and persistence, potentially reflecting sensitivity to large-scale modes of climate variability such as ENSO-scale oscillations. Temperate and Mediterranean biomes show weaker but discernible multi-year fluctuations, while boreal regions display somewhat clearer low-frequency oscillations consistent with documented decadal variability in northern climate systems. Importantly, the presence of a distinct cyclical component allows the stochastic trend to remain smoother and more interpretable. This decomposition is most coherent under Model 4, where the combination of AR(1) sub-biome effects and explicit

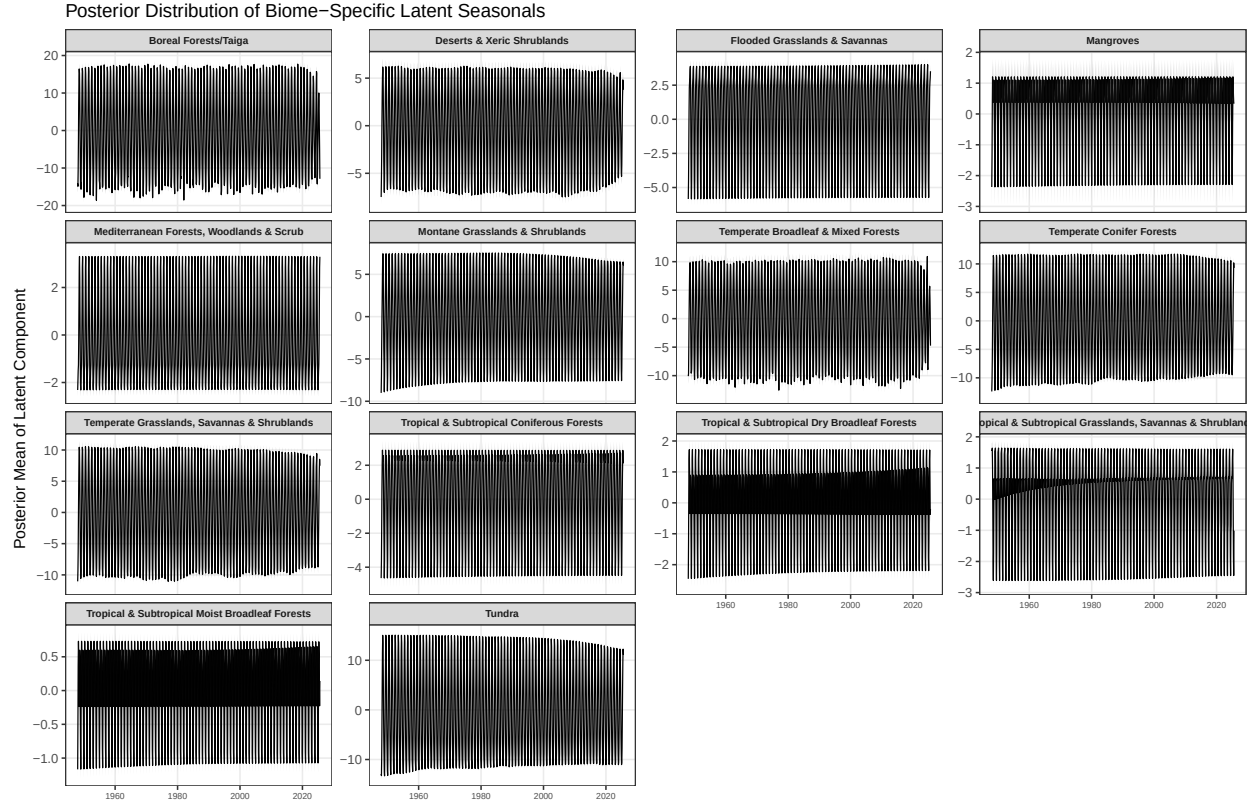


Figure 2: Posterior distribution of seasonal components by biome.

cyclical structure reduces the risk that medium-frequency variability is misattributed to long-run structural change.

The differences in credibility intervals for cycle components across biomes largely reflect the number of observations and the spatial extent of each biome. Biomes with dense sampling and broad coverage tend to have narrower intervals, as the model can more confidently estimate seasonal or interannual cycles. In contrast, sparsely sampled or spatially heterogeneous biomes show wider intervals, reflecting greater uncertainty due to limited data and variability across space. These patterns highlight that wider credibility intervals do not necessarily indicate weaker cycles, but rather the limits of data support in representing the biome's average behavior.

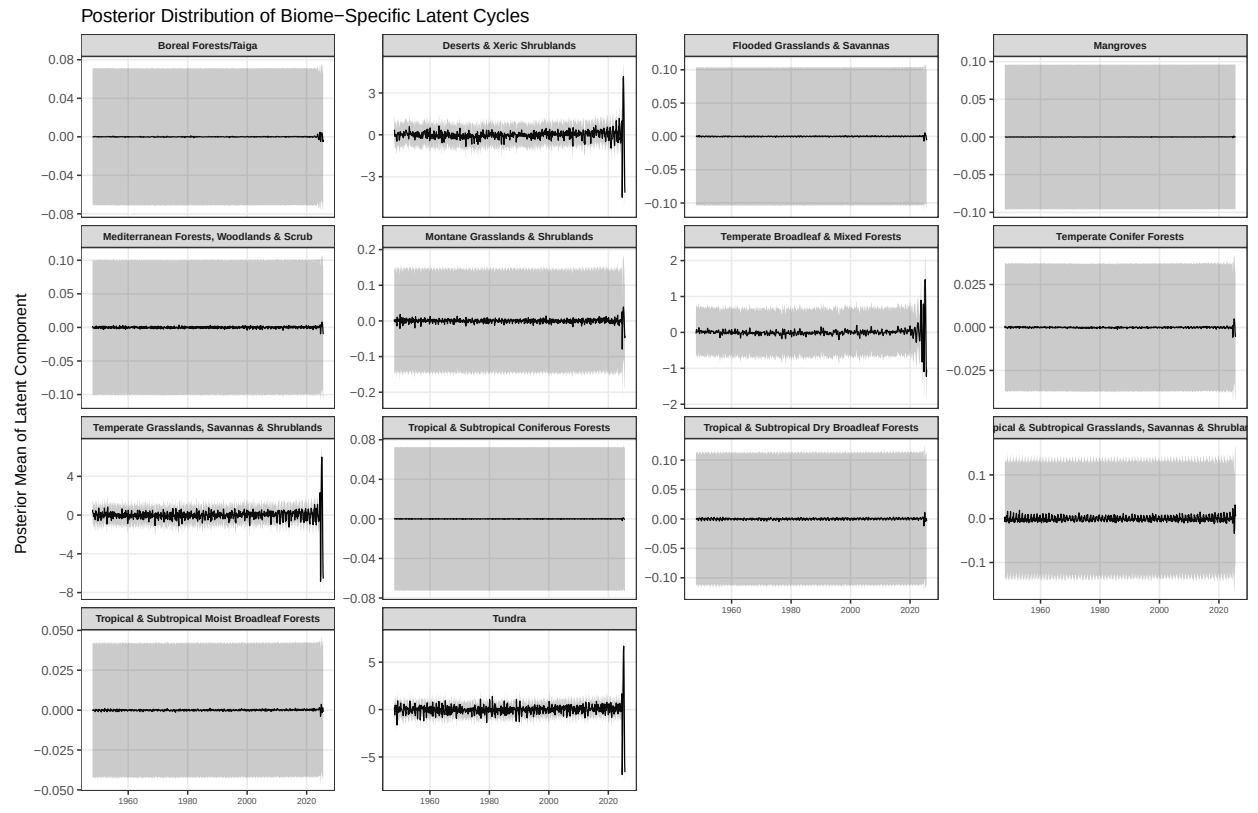


Figure 3: Posterior distribution of multi-year cycle components by biome.

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