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Biodiversity as a Driver of Ecosystem Stability under Multi-Year Droughts: Global Patterns of Resistance and Resilience

GEO 511 Master's Thesis

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18.12.2025

Abstract

Extreme multi-year droughts are becoming an increasing threat to how ecosystems function as climate change intensifies. Biodiversity is often seen as a stabilizing factor that reduces vegetation loss during droughts and promotes faster recovery afterwards. However, comprehensive global evidence supporting this notion remains limited. This thesis explores how biodiversity affects an ecosystem's ability to resist and recover from multi-year droughts, and how these effects differ among the world's major biomes. Using a global dataset with 10 km spatial resolution covering 1980–2018, vegetation responses were measured with the kernel NDVI (qkNDVI). Biodiversity was assessed through species richness and alpha diversity, while drought severity was described using the Standardised Precipitation–Evapotranspiration Index (SPEI). The analysis focused on the 100 most severe multi-year droughts worldwide. Spatially explicit Bayesian Additive Models (BAMs) were used to capture nonlinear relationships, biome-specific effects, and large-scale spatial patterns. Results show that biodiversity enhances ecosystem resistance to multi-year droughts, with species richness increasing resistance and alpha diversity buffering extreme drought impacts. Post-drought recovery shows weaker and more context-dependent biodiversity effects, dominated by alpha diversity rather than species richness. Strong differences appear between biomes. To resist droughts, biodiversity has the largest effect in boreal forests and temperate grasslands, moderate effects in tropical and subtropical forests, and the weakest effects in tundra and montane forests. For recovery, biodiversity shows the strongest influence in temperate grasslands, moderate in boreal forests, and limited effects elsewhere. Overall, the findings highlight that biodiversity helps maintain ecosystem stability under extreme droughts, but its role varies between resistance and recovery, drought intensity, and ecological context.

Acknowledgements

I would like to express my sincere gratitude to my supervisors, Dr. Dirk Karger (Swiss Federal Institute for Forest, Snow and Landscape Research, WSL) and Prof. Dr. Ross Purves (University of Zurich), for their continuous guidance, constructive feedback, and scientific support throughout this thesis. I am especially thankful for the opportunity to conduct this research in collaboration with the WSL, which provided an inspiring scientific environment and valuable institutional support. Their expertise and critical input greatly contributed to the development and refinement of this work. I am also deeply grateful to my friends and fellow students for their encouragement, helpful discussions, and moral support during the writing process. Their willingness to exchange ideas and provide perspective made this demanding period both more productive and enjoyable. Finally, I would like to thank everyone who supported me throughout my studies and contributed, directly or indirectly, to the completion of this thesis.

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1. Introduction

Climate change is leading to increasingly extreme weather, including more frequent and intense heatwaves, as well as severe drought events (IPCC 2021). Those intensified drought events endanger natural systems such as ecosystems and anthropogenic systems worldwide (Anderegg et al. 2015). The IPCC report of 2021 found with high confidence that under all future emissions scenarios (SSPs), droughts are projected to become more frequent as well as more intense with increasing global temperatures. Even if global warming stabilizes at 2°C, many regions are, with high confidence, projected to face more intense drought conditions (IPCC 2021). SPEI is a suitable indicator for evaluating drought severity because it provides a clearer representation of drought conditions and will therefore be used in this study. It is vital to distinguish between a single-year drought and multi-year droughts. Multi-year droughts are droughts which last for at least two years (Chen et al. 2025). The multi-year droughts are becoming drier, hotter, and expanding by about $49{,}279 \pm 14{,}771$ km^2 every year since 1980 (Chen et al. 2025).

In ecosystems, the variety of species is threatened due to climatic impacts, plant life is disrupted, and ecosystem productivity is decreasing due to more intense and frequent droughts (Bai and Tang 2024). However, the effects are not uniform across ecosystems. Certain regions are more resistant to extreme drought events, meaning they are less affected during the drought itself, while others exhibit exceptional resilience, recovering more quickly after the drought has ended. In an ecosytsem, biodiversity appears to be a major contributor to both resistance and resilience. Ecological research has long focused on the notion that species-rich ecosystems are more resilient to climate stress. This is due to the fact that species in diverse ecosystems tend to be more resilient than others. They work together in complementary ways and adapt to changing conditions (Isbell et al. 2015; Pardos et al. 2021). At the same time, biodiversity may also increase resistance by buffering ecosystems against immediate impacts and reducing the extent of vegetation loss during droughts (Isbell et al. 2015). Numerous research on ecosystems' resilience and resistance to drought are focused at the regional level instead of globally and are not focusing on multi-year droughts. Furthermore, the connection between biodiversity and improved tolerance to and resilience to droughts is frequently overlooked. Classifying various ecosystems by grouping them into biomes is a straightforward and widely used approach. In order to determine whether global spatial patterns in biodiversity

and ecosystem responses to multi-year droughts differ among biomes, this study uses a geospatial approach. It investigates whether biodiversity, assessed by species richness and alpha diversity, improves ecosystem stability during multi-year droughts by fusing data from remote sensing data as well as spatial statistics. Finding biomes that serve as hotspots for biodiversity and show a significant resistance and recovery against drought stress is a major goal of the study. By revealing when and where biodiversity supports resilience, this study offers valuable insights for identifying at-risk biomes and guiding conservation and climate adaptation efforts. The motivation for this work arises from the increasing need to connect biodiversity–stability theory with global evidence under intensifying multi-year droughts.

The central research questions are:

1. How does biodiversity influence the resistance of ecosystems to vegetation loss during multi-year droughts?

2. How does biodiversity influence ecosystem recovery after multi-year droughts?

3. How do the effects of biodiversity on multi-year drought resistance and recovery vary across major global biomes?

The overarching hypothesis is that biomes with high biodiversity, such as tropical forests, exhibit greater resistance and resilience to multi-year droughts, whereas biomes with lower baseline biodiversity, such as boreal forests or tundra, benefit more strongly from increases in species richness. Higher biodiversity tend to keep ecosystems stable even under extreme climate conditions. Understanding these links has become increasingly important as long-lasting droughts are expected to become more frequent worldwide, even as biodiversity continues to decline in many areas (IPCC 2021). However, it is still uncertain whether the stabilizing benefits of biodiversity seen in smaller-scale studies also apply globally or under extended drought conditions. By revealing when and where biodiversity supports resilience, this study offers valuable insights for identifying at-risk biomes and guiding conservation and climate adaptation efforts.

2. Literature Review

Climate change is causing more extreme weather conditions such as more frequent and more severe heat waves, as well as extreme drought events (IPCC 2021). Those intensified drought events endanger natural systems such as ecosystems and anthropogenic systems worldwide (Anderegg et al. 2015). With global warming, droughts are intensifying in terms of heat, dryness, and duration (Chen et al. 2025), with vegetation recovery often trailing structural regrowth, particularly when atmospheric dryness is elevated (Zhang et al. 2023).

A key question in global change ecology is whether biodiversity continues to buffer ecosystem functioning under these shifting conditions and whether species-rich systems recover more effectively from droughts. Chapin et al. (2013) emphasized that biodiversity is closely linked to climate, and as the climate changes, shifts in biodiversity and biodiversity loss are expected. However, they point out that while many correlations between biodiversity and climate have been identified, these cannot be generalized as easily as the well-established relationships between climate and the distribution of different plant functional types (Chapin et al. 2013). This indicates that investigating how biodiversity affects ecosystem resistance and resilience is essential for improving our understanding of how biodiversity can be beneficial.

In drought and vegetation studies, small-scale experiments often use linear mixed-effects models or ANOVA to pinpoint treatment effects. At broader, biome-scales, researchers usually turn to correlation-based methods to connect drought indices like the SPEI with vegetation responses. On a global level, studies tend to rely on multiple regression models and satellite-based indicators to measure drought severity and recovery. However, these large-scale analyses rarely consider biodiversity as a factor and often lack spatially detailed modelling. As a result, we still lack a clear, global understanding of how biodiversity influences ecosystems' resistance and resilience to droughts across different biomes.

2.1 Definitions of relevant terms

2.1.1 Drought definition

In the literature, there are different types of drought definitions, such as meteorological-, agricultural-, hydrological-, socioeconomic-, and ecological- droughts. However, meteorological, agricultural, and ecological droughts are used the most to investigate droughts and their intensity. Meteorological drought is typically defined as a drought with a deficit in precipitation over a certain period of time, relative to the long-term average for a specific region. It acts as a trigger for the formation of drought in the hydrological cycle. Meteorological drought is measured with the Standardized Precipitation Index (SPI) or the Standardized Precipitation Evapotranspiration Index (SPEI) (You et al. 2025). The difference between SPI and SPEI is that SPI measures the deviations of precipitation from the long-term mean, standardized by the variability of the record, so it only has precipitation as an input variable. SPEI on the other hand is a multi-scalar drought index which also takes into consideration both precipitation and temperature via potential evapotranspiration which provides a simple water balance. SPEI is more sensitive to temperature driven droughts which makes it the better choice for identifying more severe and prolonged droughts especially in regions where high temperatures increase evapotranspiration whereas SPI does not account for that. The standardization which both SPI and SPEI have, allows comparisons between regions as well as between different years (Tirivarombo et al. 2018). In this study, only SPEI was used, since it is more precise due to the consideration of both precipitation and temperature.

Agricultural and ecological droughts are typically detected through deviations in the Normalized Difference Vegetation Index (NDVI), a widely used remote sensing proxy for vegetation greenness and health based on the contrast between near-infrared (NIR, ∼0.7–1.1 µm) and red light (∼0.6 -0.7 µm). NDVI is calculated as

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{Red}}{\mathrm{NIR} + \mathrm{Red}} \tag{2.1}$$

It is valued for its ability to quickly delineate vegetation status and detect vegetative stress due to the strong absorption of red light by chlorophyll and the enhanced reflection of near-infrared light by healthy plant cell structures (Huang et al. 2021). Agricultural droughts focus only on crops or pasture and how they respond to droughts, ecological droughts on the other hand focus on how water shortages degrade the health, structure, and function of entire ecosystems, not just agricultural productivity.

It is vital to distinguish between a single-year drought and multi-year droughts. Multi-year droughts are droughts which last for at least two years. When compared to single-year droughts, they are a different statistical phenomenon. According to Power and Gillett

(2025), the probability and impact of multi-year droughts are not only an extension of the odds of a single-year drought but rather, they necessitate distinct study and comprehension. Chen et al. (2025) use the SPEI index mentioned earlier to classify drought years. A year is classified as a drought year if the annual SPEI ≤ -1.0. A multi-year droughts event is then defined as a period where at least two consecutive years are meeting the criteria SPEI ≤ -1.0. The paper looked at multi-year droughts between 1980 and 2018 and found that multi-year droughts have occurred on all continents excluding Antarctica and that the global occurrence of multi-year droughts have increased significantly over time. The multi-year droughts are becoming drier, hotter, and expanding by about $49{,}279 \pm 14{,}771$ km^2 every year since 1980 (Chen et al. 2025). Some high impact multi-year droughts hotspots were found by Chen et al. (2025) in Mongolia, Southeastern Australia, Western United States and parts of central and southern Africa, Argentina and central Asia. Mid-latitude regions were affected most severely from multi-year droughts where strong declines in vegetation greenness, measured with kNDVI, were measured. Multi-year droughts in tropical regions were less frequently classified as severe. Chen et al. (2025) attribute this pattern to high vegetation density and persistent cloud cover, which can mask or delay detectable vegetation stress when assessed via NDVI.

2.1.2 Ecosystem Resistance and Resilience

Given the rising frequency and severity of droughts, multi-year droughts as well as single-year droughts, it is crucial to explore how this has an effect on ecosystems and if and how biodiversity contributes to the stability of ecosystems. One key aspect of ecosystem stability in the face of climatic extremes is the ability to either withstand or recover from disturbance. These two capacities are commonly referred to as resistance, the ability of an ecosystem to remain largely unaffected during a drought, and resilience, its ability to recover after the drought has ended (Pimm, Stuart L. 1984). Therefore resistance captures the immediate impact of drought on ecosystem functioning, whereas resilience describes the speed and extent of post-drought recovery.

2.1.3 Definition of Biodiversity

In this study, biodiversity is represented by two complementary measures: species richness and alpha diversity. Species richness refers to the total number of species within an ecosystem and is one of the most widely used metrics of biodiversity. It provides an estimate of the potential diversity reservoir that may contribute to ecosystem functioning (Bai and Tang 2024; Ammer 2019).

Alpha diversity was originally introduced by Whittaker (1960), and describes the species diversity within a local habitat or community which is often referred to as “point diversity”. It reflects the number of species occurring within a defined area and, when

combined with evenness measures, captures how individuals are distributed among these species. Therefore alpha diversity, includes both the total number of species and how evenly their individuals are distributed. It characterizes the structure of the local community and the balance between dominant and subordinate species (Sabatini et al. 2022).

Although neither measure directly represents functional diversity, both can influence the range and effectiveness of functional traits present in an ecosystem. Functional diversity, such as the presence of deep-rooted species or species with contrasting phenologies, helps maintain biomass production when dominant species fail (Mariotte et al. 2013).

Therefore, both dimensions of biodiversity considered here are ecologically relevant for understanding ecosystem responses to drought. Higher species richness may buffer ecosystems through mechanisms like functional complementarity and redundancy, while higher alpha diversity indicates more even contributions of species to ecosystem functioning, which can enhance stability under stress.

2.1.4 Insurance Effect

The insurance effect, introduced by Yachi and Loreau (1999), explains how biodiversity helps ecosystems stay stable and perform well even as the environment changes. It works through two main mechanisms. The first is the buffering effect, which smooths out fluctuations in ecosystem processes. Since different species respond differently to changing conditions, a drop in one species can be balanced by a rise in another, keeping overall productivity steady. The second is the performance-enhancing effect, which boosts the average level of ecosystem functioning. In diverse communities, it's more likely that at least some species will thrive under any given set of conditions, lifting overall productivity over time. Together, these mechanisms show that biodiversity not only reduces environmental ups and downs but can also improve long-term ecosystem performance. How strong these effects are depends on how independently species respond to change and how their growth patterns vary with the environment.

2.1.5 Definition of Biomes

To study ecosystem functioning and resilience at a global scale, it is useful to group ecologically similar regions into broader ecological units known as *biomes*. Biomes are broad regions where similar types of vegetation and life-forms thrive. Traditionally, scientists have also defined biomes based on their geography and climate, connecting each type of biome to specific climate conditions which are often referred to as its climatic envelope (Woodward et al. 2004). There are several ways to classify biomes, but one of the most widely adopted frameworks is the Beck et al. (2023). This system divides global climates into five primary types and thirty subtypes based on long-term averages of temperature and precipitation and defines the biomes based on long-term climatic

trends and their associated vegetation structures. The five main climate groups include tropical (A), arid (B), temperate (C), cold or continental (D), and polar (E). Each group is further divided by seasonal precipitation and temperature regimes, producing familiar multiple-letter codes such as Af (tropical rainforest), Csa (Mediterranean, hot summer), Dfb (humid continental, warm summer), and ET (tundra). Because vegetation patterns are closely linked to climate, the Köppen–Geiger system serves as a valuable bioclimatic proxy for ecological zonation and is frequently applied in ecological, ecohydrological, and biodiversity studies assessing the impacts of climate change (Beck et al. 2023).

2.2 Ecosystem Stability

2.2.1 Biodiversity as a Driver of Ecosystem Stability

Numerous scientific studies have shown that ecosystems with greater species richness tend to be more stable over time. In this context, the stability of ecosystems refers to their ability to maintain their structure and function even when faced with disturbances such as extreme weather events. For example, a stable ecosystem can better withstand and recover from challenges such as droughts, floods, storms, or other natural influences that might disrupt its normal processes and is therefore more resilient (Oliver et al. 2015). Ecosystem stability is a broad concept that includes components such as resistance, resilience, and temporal stability, which describes how steadily an ecosystem functions over time. Ecosystems with high temporal stability show only small year-to-year fluctuations in their productivity, meaning their overall performance remains relatively constant despite changing environmental conditions. Increased biodiversity can result in ecosystems suffering fewer losses in their functionality, because a wider variety of species offers more reliable support than relying on only a small number of species. This implies that some species will continue to maintain the functioning of the ecosystem even if others do not succeed (Yachi and Loreau 1999), making that ecosystem more stable. Bai and Tang (2024) investigated how species richness influences forest resistance and resilience to drought by using global tree-ring data from over 4000 sites. In that study, there is some evidence that species richness improved resistance to droughts in about half of global forests, especially under high drought intensity and climatic water deficit, but its role in resilience (recovery after drought), particularly under prolonged drought, remains unclear. A substantial amount of research indicates that biodiversity enhances ecosystems' ability to withstand extreme climate conditions. For example, data from 46 grassland experiments show that higher plant species richness increases ecosystem stability across various intensities and durations of climatic stress (Isbell et al. 2015). Long-term studies further indicate that these biodiversity-stability connections intensify over time as interactions among species promote greater asynchrony and complementarity, thereby stabilizing productivity through

insurance effects (Wagg et al. 2022; Schnabel et al. 2021). Ecosystem stability rises with diversity when species react asynchronously, which means that their reactions to the environment are not perfectly correlated. The more varied and distinct these responses are, the stronger the insurance effects become, although this also means that at lower levels of diversity, some species may become redundant. Ecosystem redundancy occurs when a few species dominate productivity, so adding additional species no longer significantly improves stability or productivity. The point at which this happens depends on how variable and unique the species' responses are to environmental changes (Langenheder et al. 2012). Understanding how species respond at different times is key to determining whether ecosystems with higher biodiversity are more resistant and resilient to extreme droughts. Asynchronous species responses can buffer vegetation performance and enhance recovery following severe climatic events.

Concerning recovery, specifically resilience, the evidence is more inconsistent. Experiments and long-term studies suggest that diverse communities can recover faster after drought due to complementary traits and species responding at different times (Schnabel et al. 2021; Wagg et al. 2022). Previous exposure to drought can also strengthen these benefits, creating a kind of ecological memory that enhances recovery in diverse communities (Chen et al. 2022). In contrast, forest ecosystems show a more complex pattern. A global tree-ring analysis across 4,072 sites found that species richness, higher biodiversity, tends to boost resistance to drought but can actually reduce resilience afterward, which means that richer forests sometimes recover more slowly after prolonged dry periods (Bai and Tang 2024). These patterns point to a strong biome- and timescale-dependence. Bai and Tang (2024) found that species richness enhanced the resistance but weakened the resilience of trees to drought globally, with these effects being stronger during prolonged droughts. The researchers also noted that the beneficial effects of biodiversity were less pronounced or even reversed in boreal regions, indicating that there is biome-specific variability in ecosystem responses to drought. In contrast, in grassland ecosystems, biodiversity has been shown to increase both the resistance and the rate of recovery following short-term droughts (Isbell et al. 2015). This comparison highlights that while biodiversity can buffer ecosystem functioning under moderate stress, its benefits may diminish under prolonged or severe drought conditions, when facilitative interactions among species become tempered or even reverse toward competitive interactions, thereby weakening both resistance and recovery (Bai and Tang 2024). Functional redundancy can help maintain ecosystem function even when some species decline, though recovery often hinges on the traits and dominance of key species (Bazzichetto et al. 2024). The strength of biodiversity effects can shift depending on drought intensity, background aridity, nutrient enrichment, which can weaken diversity-stability relationships, and the maturity of the community (Hautier et al. 2014; Wagg et al. 2022; Bai and Tang 2024). The resilience of ecosystems is influenced by a mixture of two aspects that are both complementary and occasionally contradictory:

resistance and the ability to recover after a drought (resilience). High resistance can reduce the need for recovery by buffering impacts from the outset, whereas in systems with lower resistance, rapid recovery may compensate for initial vulnerability. This illustrates that resistance and recovery are not independent properties but dynamically interconnected aspects of ecosystem resilience (Oliver et al. 2015). Altogether, these mechanisms form the foundation for investigating whether ecosystems with higher biodiversity show greater resistance and resilience to multi-year droughts across biomes.

2.2.2 Stability Drivers Other Than Biodiversity

Other studies say that biodiversity does not have a strong effect on stability of an ecosystem. The study from Pennekamp et al. (2018) found that biodiversity does not necessarily stabilize ecosystems, it can both increase and decrease different components of ecosystem stability. They found that the temporal stability, so less variation in biomass over time, increased in ecosystems with higher biodiversity. In contrast, resistance to warming decreased as biodiversity increased. Across diversity gradients, temporal stability and resistance negatively covaried, meaning that higher biodiversity increased one aspect of stability while decreasing another. This supports the idea that biodiversity's role in an ecosystem or biome in terms of stability is multifaced and context dependent. A greater number of species can improve the average productivity of an ecosystem over time when mechanisms such as competitive dominance allow the most productive species to thrive under specific environmental conditions (Langenheder et al. 2012; Yachi and Loreau 1999). However, the stability benefits of biodiversity depend on how species respond to environmental fluctuations. Understanding this complex relationship between biodiversity and ecosystem stability is therefore essential for evaluating if ecosystems with higher biodiversity are better able to withstand and recover from prolonged droughts across different biomes.

It is emphasised that the composition of species before and after a disturbance does not necessarily have to be identical for the function of the ecosystem to be maintained. Conversely, by employing functional replacement, which involves substituting vanished species with others that fulfill similar ecological roles, the ecosystem's performance can be preserved even though the community's structure changes. Some studies increasingly emphasise that the positive effects of biodiversity on drought resilience often result from complementary functional characteristics of different species, such as varying root depths, strategies for regulating stomata, or differing phenological patterns. These differences enable more efficient water use and a temporal distribution of resource use (Pardos et al. 2021; Loreau and De Mazancourt 2013). Therefore, certain traits are functions of plants important for resistance and resilience of ecosystems. In mixed forests, such mechanisms can lead to greater resistance as well as faster recovery after drought events,

especially in drier and hotter regions (Pardos et al. 2021). However, these advantages are not universal and are strongly influenced by other factors such as species composition, population structure and local climatic conditions (Pennekamp et al. 2018). In this context, the resilience of ecosystems arises from the interaction of processes that take place at several ecological levels. At the species level, characteristics such as growth rate, drought tolerance, genetic diversity and phenotypic plasticity determine the ability of individual organisms to resist and adapt to environmental stresses (Oliver et al. 2015). At the community level, mechanisms such as functional redundancy, asynchrony in species responses and the complexity of ecological interaction networks help to mitigate the effects of disturbances (Yachi and Loreau 1999). At the landscape level, factors such as habitat heterogeneity, ecological connectivity, and the presence of intact natural vegetation play a crucial role in modulating disturbance effects and facilitating recovery. These processes enable ecosystems to thrive and regenerate under changing environmental conditions, and their complex, context-dependent interactions mean that the influence of biodiversity on resilience can vary across biomes and disturbance types and is not always uniform (Oliver et al. 2015; Yachi and Loreau 1999; Pennekamp et al. 2018).

2.3 Drought Impacts on Vegetation Across Biomes

More research is needed to understand which biomes are most affected by droughts, especially multi-year droughts, and to reveal clearer patterns of resilience across different biomes. multi-year droughts are becoming more severe and spreading over larger areas globally. Temperate grasslands are notably experiencing significant reductions in greenness, whereas boreal and tropical forests generally exhibit less pronounced short-term declines (Chen et al. 2025). Identifying which ecosystems can better withstand prolonged droughts is crucial, since recovery rates and vegetation dynamics differ widely among biomes. This study explores how biodiversity supports drought resistance and recovery both within and across biomes, highlighting the importance of vegetation diversity in maintaining ecosystem stability under climate stress.

This study focuses on the following biomes: tundra, temperate grasslands, boreal forest, montane forest, and tropical & subtropical forest (Figure 2.1), following the grouping used in Chen et al. (2025). Deserts and Xeric Shrublands which are in the Arid biome were excluded because persistent dryness makes them less meaningful for drought–response analyses such as this.

2.3.1 Tundra

Tundra ecosystems occur in high-latitude Arctic regions and north of the climatic treeline (Gabriel 1984). They are characterized by extremely cold climates, long and severe winters,

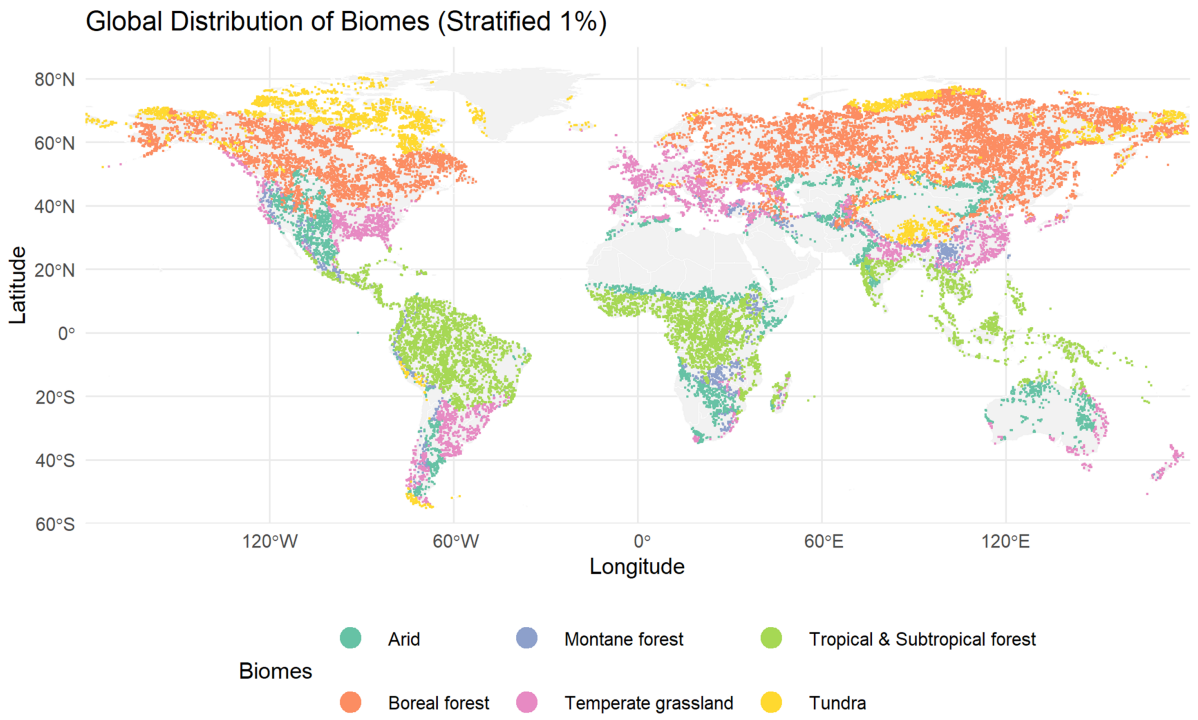

Figure 2.1: Global distribution of the biomes used in this study: Tundra, Temperate Grassland, Boreal Forest, Montane Forest, Arid, and Tropical & Subtropical Forest. The plot shows a 1% random sample of the full dataset (∼2.5 million data points), which is sufficient to represent the overall spatial patterns due to the regular and dense global coverage of the underlying raster data.

and short, cool summers, with mean annual air temperatures typically below 0 °C. Annual precipitation is low, generally under 1000 mm, most of which falls as snow (Woodward et al. 2004). The tundra biome is characterized by its low biodiversity (species richness) and its dependence on the seasons. The variety of species is linked to summer temperatures (Chapin et al. 2013). Chapin et al. (2013) also mentions that climate change is anticipated to significantly affect the Arctic, particularly in terms of the projected alterations in tundra biodiversity.

Geographically, tundra biomes are distributed across the circumpolar Arctic, which includes northern Alaska, Canada, Greenland, Scandinavia, and Siberia, as well as at high elevations in mountain systems such as the Rocky Mountains, the European Alps, and the Tibetan Plateau. These ecosystems store vast amounts of organic carbon in permafrost soils, estimated to exceed 1300 Gt, and are highly sensitive to warming and permafrost degradation, which may release greenhouse gases and amplify global climate feedbacks (Hugelius et al. 2014; Faber-Langendoen et al. 2016).

The tundra biome shows mixed responses to drought, with some studies highlighting its sensitivity and others suggesting comparatively high resistance due to temperature-limited vegetation growth. During the extreme 2020 drought in north-eastern Siberia, Rietze et al.

(2024) found that tundra vegetation lost much of its cooling effect through evapotranspiration, creating a positive feedback loop that intensified warming. Communities dominated by mosses and sedges maintained cooling longer, likely supported by permafrost meltwater, while drier or high-altitude sites such as tussock-sedge or lichen tundra showed reduced resistance. More diverse plant communities partly buffered neighbouring sites, indicating some biodiversity-driven resistance. At larger scales, Chen et al. (2025) observed only slight vegetation declines (kNDVI) during multi-year droughts in the Russian Arctic, suggesting persistence under prolonged drought. However, recovery is very slow: tundra belongs to the "barren" biomes, where low temperatures and biodiversity limit regrowth, leading to some of the longest recovery times globally (Schwalm et al. 2017). Thus, tundra ecosystems combine moderate resistance with poor resilience, highlighting the strong constraints of cold environments. Cold biomes such as tundra are mainly temperature-limited rather than water-limited. Water is primarily found in a solid, frozen state. Drought responses are therefore muted in the short term, but recovery from severe droughts can be slow due to short growing seasons and low productivity (Vicente-Serrano et al. 2013).

2.3.2 Temperate Grassland

Temperate Grassland ecosystems are located in mid-latitude regions (approximately 23°–55° N/S) across all continents, acting as a transition zone between temperate forests and deserts. They span across North and South America, Eurasia, and parts of Africa and Australia. These ecosystems are dominated by mesomorphic perennial grasses, forbs, and shrubs that have adapted to both moist and semi-arid conditions. The plant life extends from vast open grasslands to drier meadows found within wooded areas (Faber-Langendoen et al. 2016; Chapin et al. 2013). Grasslands are recognized as ecosystems that are limited by water availability, with droughts typically occurring at least once during a year. The annual precipitation in grasslands is ranging between 150 and 1200mm/year and temperatures are ranging between 0 and 25°C (Lieth and Whittaker 2012; Chapin et al. 2013). Chapin et al. (2013) argue that biodiversity in temperate grasslands shows significant variation throughout the biome. For instance, certain grasslands in southern South America represent a high-diversity system, while other regions such as some grasslands in Patagonia show much lover diversity. Overall, temperate grasslands possess high biodiversity, though they are quite uniform in plant species across broader areas.

Temperate grasslands are among the most drought-affected biomes. According to Chen et al. (2025), the most significant reductions in NDVI were observed during multi-year droughts, with productivity decreasing by up to three times compared to normal years, particularly in the Western USA, Mongolia, and Southeastern Australia. Repeated droughts caused cumulative degradation, where insufficient recovery left systems increasingly vulnerable. Biodiversity can enhance resistance by reducing productivity losses

(Hossain et al. 2022; Vogel et al. 2012). Functional diversity, such as deep-rooted or phenologically diverse species, sustains biomass when dominant species fail (Mariotte et al. 2013). Resilience, however, varies in temperate grasslands. Legume-rich communities recover faster (Mackie et al. 2019), whereas degraded or intensively managed grasslands often recover more slowly (Vogel et al. 2012). However, extended or repeated droughts can still overpower grassland ecosystems, demonstrating that biodiversity offers only limited defense against prolonged stress (Craine et al. 2013). Consequently, grasslands show low resistance and often only partial recovery when droughts are frequent or intense (Craine et al. 2013). Temperate grasslands demonstrate that biodiversity can strengthen resistance and promote recovery during moderate droughts. However, their limited resilience in prolonged or repeated droughts indicates that the stabilizing effect of biodiversity diminishes as drought severity increases. Temperate grasslands exhibit slower responses (8–10 months), tolerating moderate drought but becoming vulnerable under extended stress. Mixed species strategies provide some buffering but do not prevent declines during long droughts (Vicente-Serrano et al. 2013).

2.3.3 Boreal Forest

Boreal forests cover northern North America and Eurasia and are dominated by evergreen conifers with some deciduous trees. They experience long, cold winters and short summers, with soils generally poor in nutrients. Boreal forests store large amounts of carbon and are strongly shaped by disturbances such as fire and insect outbreaks (Martínez-García et al. 2024; Faber-Langendoen et al. 2016). The average yearly temperature in the biome fluctuates from -5 to 5°C, while the average annual precipitation varies from 400 to 2000mm (Woodward et al. 2004). In general, boral forest show a relatively low biodiversity comapred to other forests (Woodward et al. 2004).

Boreal forests exhibit low resistance and slow recovery after drought events. During the 2018 European drought for example, net ecosystem production (NEP), the balance between carbon uptake through photosynthesis and carbon release via respiration, dropped by 57% in Swedish boreal forests, revealing a strong reduction in drought resistance (Martínez-García et al. 2024). This decline shows that drought severely disrupts carbon assimilation, temporarily weakening the forest's capacity to function as a carbon sink. Although older stands can buffer short-term stress more effectively, both young and mature forests experience substantial productivity losses under prolonged droughts. On a global scale, NDVI declines in boreal forests during multi-year droughts are smaller than in grasslands (Chen et al. 2025), yet recovery is among the slowest of all biomes, often taking years to decades due to low growth rates and limited biodiversity (Schwalm et al. 2017). Structural and demographic factors influence recovery. It was found that younger forests tend to regenerate faster but are less resistant, whereas older trees maintain higher resistance

yet recover slowly. Regional conditions such as permafrost persistence in Siberia can further limit resilience (Berner et al. 2013). Even modest species diversity may enhance post-drought recovery (D'Orangeville et al. 2018), though repeated droughts can exceed adaptive limits and drive shifts toward more drought-tolerant species (Seidl et al. 2017). In summary, boreal forests exhibit both low resistance and limited resilience, making them particularly vulnerable to the exacerbating effects of repeated droughts. This highlights how boreal forests, with their low biodiversity and slow ecosystem dynamics, illustrate the constraints on both drought resistance and resilience. In cold, productivity-limited ecosystems, biodiversity provides only a modest buffering capacity against extended or recurrent droughts.

2.3.4 Montane Forest

Montane forests are found in the elevation zone between the lower submontane areas and the higher subalpine regions. Exactly where these changes happen depends on the location in the world, especially the latitude. The top of the montane forest zone, called the treeline, is where hardier, cold-tolerant trees start to appear but grow more thinly. On the lower end, montane forests blend into drier steppe or desert-like areas, creating a clear boundary known as the lower timberline (Price 1986). These forests usually grow in temperate climates, with average temperatures ranging from roughly 6 °C to 12 °C, and they get between 1,000 and 2,500 millimeters of precipitation yearly. As you go higher, precipitation tends to increase and can come as rain or snow depending on how high and where you are in the world (Lugo et al. 1999). Montane forests exist on many continents, including North and South America, Europe, Asia, Africa, and Australia. They typically form a middle zone between lowland forests below and alpine regions above, supporting a wide variety of plant life (Faber-Langendoen et al. 2016). The soil in these forests is usually thin and low in nutrients because of steep slopes and erosion (Faber-Langendoen et al. 2016). These forests play a key ecological role as transition zones in mountain ecosystems. Because they react sensitively to changes in climate and human activities, they are important indicators of environmental change (Faber-Langendoen et al. 2016).

Montane forests are adapted to seasonal droughts but remain vulnerable to prolonged multi-year events that test both resistance and resilience. High tree density, often resulting from fire suppression, reduces resistance by intensifying competition for water (North et al. 2016). Even large, old trees can die under severe stress (Allen et al. 2010). Droughts often act indirectly by weakening trees and increasing their susceptibility to insects or pathogens, which further limits both resistance and post-drought recovery (Stephens et al. 2012). Open, mixed-species stands tend to show more localized damage and faster regrowth, while dense, single-species plantations experience widespread mortality and slower recovery (Stephens et al. 2012). During the 2012–2016 California drought, 32.8% of basal area was

lost and NDVI remained low even after the event, with lower montane forests showing the weakest recovery (Hankin et al. 2024). Multi-year legacy effects on growth and carbon assimilation indicate that drought impacts can persist for several years, further constraining resilience (Szejner et al. 2019). Wildfire risk compounds these effects by adding additional disturbance before recovery is complete. Overall, montane forests show moderate resistance to short-term droughts but limited resilience to prolonged or repeated events. Structural and species diversity can enhance both properties, yet biodiversity alone cannot fully buffer these ecosystems against the cumulative effects of long-term water stress. Montane forests exhibit slower responses (8–10 months), tolerating moderate drought but becoming vulnerable under extended stress. Mixed species strategies provide some buffering but do not prevent declines during long droughts (Vicente-Serrano et al. 2013).

2.3.5 Tropical and Subtropical Forest

Tropical and subtropical forests are one of the most prominent biomes worldwide, with an estimated global coverage of 1.4 billion hectares (Reid 1992). The biome occurs near the equator and is characterized by warm, wet climates and extraordinary biodiversity (Malhi et al. 2014). Tropical forests are typically found in areas without frost and relatively high levels of precipitation. The area is characterised by a relatively stable temperature of about 20 to 30°C (Woodward et al. 2004) throughout the year, yet there is a notable variation in the total annual precipitation, ranging from roughly 1 to 8 meters. Additionally, the duration and intensity of the dry season vary significantly (Chapin et al. 2013). Even though tropical rainforests cover just a small fraction of Earth's land area, they are home to more than half of all known terrestrial species (Chapin et al. 2013).

Tropical and subtropical forests show both high resistance and variable resilience to drought. Global studies show only moderate reductions in vegetation during multi-year droughts (Chen et al. 2025). During the 2015–2016 El Niño event, intact forests were no more sensitive than in past droughts, overall indicating stable conditions (Bennett et al. 2023). Their high biodiversity and functional diversity contribute to this stability by allowing compensatory growth and asynchronous species responses that buffer short-term productivity losses (Xu et al. 2024). Diverse root depths, hydraulic traits, and phenological strategies allow these ecosystems to maintain carbon uptake even under temporary water stress (Xu et al. 2024). Humid biomes, including tropical, subtropical, also respond quickly to drought but for the opposite reason: plants are poorly adapted to water shortages. Droughts in these areas can rapidly reduce growth and greenness. While recovery is usually fast due to high growth rates, resilience declines sharply under prolonged or recurrent droughts (Vicente-Serrano et al. 2013).

However, resilience is increasingly constrained. In the Amazon, more than one-third of

the forest shows progressively slower post-drought recovery, signaling potential approach toward ecological tipping points (Van Passel et al. 2024). Extreme droughts have doubled the tree mortality, reducing resistance and altering species composition even where smaller, drought-tolerant taxa persist (Bonal et al. 2016). Recurrent droughts can cause cumulative canopy loss and alter recruitment, indicating that recovery mechanisms are weakening over time. Thus, while tropical and subtropical forests display strong short-term resistance supported by high biodiversity, their long-term resilience is diminishing under intensifying and repeated droughts, raising concern that biodiversity's stabilizing role may not prevent eventual functional decline in a warmer, drier future (Tao et al. 2022).

2.4 Research Gap

Numerous studies have been conducted examining the effects of droughts on vegetation at small spatial scales. Biodiversity–drought analyses are often limited to controlled conditions in specific regions such as Europe, North America, or Siberia, where biodiversity levels and drought intensity are experimentally manipulated in field setups rather than observed in natural large-scale ecosystems (Vogel et al. 2012; Mariotte et al. 2013; Berner et al. 2013). Larger studies have examined drought responses across biomes or within the Amazon basin (Vicente-Serrano et al. 2013; Van Passel et al. 2024), but their spatial focus remains regional or limited to one biome.

Nonetheless, global-scale assessments do exist. For example, the research by Schwalm et al. (2017) investigated drought recovery across various biomes, while Chen et al. (2025) examined the global occurrence and intensity of multi-year droughts using remote sensing and climate indices. The study from Vogel et al. (2012) found that grassland drought resistance is primarily driven by management intensity, while species richness consistently enhances biomass production regardless of management or climatic conditions and used linear mixed effects models (LME). Mariotte et al. (2013) show that subordinate species substantially increase community drought resistance, as their removal caused a ten-times stronger decline in resistance and prevented the compensatory biomass gains that normally buffer dominant species during drought. This insurance effect arises not from physiological advantages, but from reduced competition by drought-weakened dominants, enabling subordinates to increase biomass particularly in low-productivity plots and thereby stabilizing overall community functioning under drought. The used method was a combination of statistical tests such as ANOVA and lineare Regression. Vicente-Serrano et al. (2013) used SPEI, NDVI, tree-ring and aboveground net primary productivity data to identify the drought durations at which vegetation responds most strongly and found that vegetation across global biomes exhibits characteristic drought response time-scales. Arid and humid biomes were found to react to short-term droughts, whereas semiarid and subhumid biomes respond only to long drought durations, making drought sensitivity

strongly biome-dependent. The study was done by using pearson correlation analysis. Schwalm et al. (2017) used multiple linear regression models combined with an SPEI-based threshold analysis to identify the climatic and environmental drivers of global drought recovery times and finds that drought recovery times vary strongly across the globe and are longest in the tropics and high northern latitudes, driven mainly by post-drought temperature and precipitation conditions rather than by drought severity itself. However, these studies primarily emphasize vegetation responses without systematically comparing biome-specific patterns and the role of biodiversity in drought resistance and resilience on a global scale. A key limitation of prior work is that biodiversity has rarely been integrated as a predictor in large-scale analyses of global drought impacts. Many studies emphasize climatic drivers and vegetation greenness indices, but the potential buffering effect of species richness under prolonged multi-year droughts has been largely overlooked. Furthermore, existing global assessments tend to rely on aggregated statistics instead of spatially explicit methods that enable comparisons of biodiversity and vegetation dynamics across various biomes. This gap underscores the need for global high-resolution approaches that explicitly link biodiversity patterns with remote-sensing based measures of drought resistance and resilience over extended time periods.

In addition to these thematic gaps, most previous global studies have used linear or correlation-based statistical methods. While useful, these approaches struggle to capture the non-linear and spatially complex nature of drought–vegetation interactions. Research in ecology and remote sensing shows that vegetation responses to climate anomalies differ across regions, biomes, and environmental settings, highlighting the need for more flexible modelling techniques (Wood 2017; Bivand et al. 2013). Therefore, large-scale analyses of biodiversity and drought effects can benefit greatly from models that handle non-linear dynamics and account for broad spatial dependencies.

These gaps require a flexible modelling approach capable of representing nonlinear responses, absorbing broad-scale spatial structure, and integrating biodiversity and climate predictors across a global extent. By applying the Bayesian Additive Models (BAM) on a global 10 km raster grid, this study introduces a large-scale assessment of drought resistance and resilience. As a GIS-based geostatistical approach, it integrates ecological and climatic drivers using georeferenced biodiversity and climate datasets. It explicitly addresses spatial autocorrelation and coordinate-based trends. This raster-based modelling framework enables consistent biome-level comparisons across the globe and ensures that spatial structure is incorporated into the analysis. It thereby bridges the gap between local plot experiments and regional case studies on the one hand and broad-scale but aggregated global analyses on the other hand.

2.5 Synthesis and Open Questions

In conclusion, the reviewed literature offers a detailed depiction of how biodiversity acts as a buffer against droughts in both resistance to drought events and in the recovery after a drought. While many studies support the assumption that higher biodiversity can improve ecosystem stability through mechanisms such as functional redundancy, asynchronous responses and complementary resource use, these benefits are not universal. Positive effects depend heavily on the identity and characteristics of the species present, the nature of their interactions with each other, and the ecological context. In some cases, biodiversity increases certain aspects of stability, such as temporal stability or recovery rates, but may reduce other aspects, such as resilience to certain stressors such as severe or recurrent droughts, high vapor pressure deficit, or heat stress. Overall, biodiversity can act as a buffer against droughts, but its effectiveness is environmentally-dependent, and the ability to maintain important ecosystem functions under drought events depends more on the composition and functional diversity of the community than on biodiversity alone. It is quite a generalised statement to claim that biodiversity in general acts as a buffer against extreme drought events because in reality it is much more complex. It is therefore important to examine this more closely to see whether such a statement applies, at least in certain biomes and how much biodiversity contributes to resistance and resilience compared to other factors. Evidence suggests that greater biodiversity within specific ecosystems contributes to their stability and may enhance their resistance or resilience.

3. Methodology

3.1 Data

This study integrates multiple global datasets to assess multi-year drought impacts and the buffering role of biodiversity.

3.1.1 Sources of data used

Multi-year drought Data The multi-year drought dataset was derived from the CHELSA (Climatologies at High Resolution for Earth's Land Surface Areas) product, developed and maintained by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). CHELSA provides monthly time series of precipitation (*pr*) and potential evapotranspiration (*pet*) from 1980–2018 at a spatial resolution of approximately 1/24° (∼5 km), expressed in units of $\mathrm{kg\,m^{-2}\,month^{-1}}$ (equivalent to $\mathrm{mm\,month^{-1}}$). Potential evapotranspiration (PET) was estimated using the Penman–Monteith FAO-56 reference method, assuming a short reference crop of 12 cm height and using CHELSA-BIOCLIM+ meteorological inputs (air temperature, radiation, humidity, wind).

For each grid cell, the climatic water balance was computed as:

$$\mathrm{WB}_t = \mathrm{pr}_t - \mathrm{PET}_t, \tag{3.1}$$

and accumulated over a 12-month moving window to capture drought persistence:

$$S_t^{(12)} = \sum_{i=0}^{11} \mathrm{WB}_{t-i}. \tag{3.2}$$

To obtain a standardized drought index, the distribution of $S_t^{(12)}$ was fitted to a log–logistic probability distribution function:

$$F(x) = \left[1 + \left(\frac{\alpha}{x-\gamma}\right)^{\beta}\right]^{-1}, \tag{3.3}$$

where α, β, and γ are the scale, shape, and origin parameters estimated using the L-moment

method. The cumulative probability $F(x)$ was then transformed into a standardized normal variable using the approximation of Abramowitz and Stegun (1965):

$$\text{SPEI} = W - \frac{C_0 + C_1 W + C_2 W^2}{1 + d_1 W + d_2 W^2 + d_3 W^3}, \tag{3.4}$$

with

$$W = \begin{cases} \sqrt{-2\ln(P)}, & P \leq 0.5, \\ \sqrt{-2\ln(1-P)}, & P > 0.5, \end{cases} \tag{3.5}$$

and $P = 1 - F(x)$. The constants are $C_0 = 2.515517$, $C_1 = 0.802853$, $C_2 = 0.010328$, $d_1 = 1.432788$, $d_2 = 0.189269$, and $d_3 = 0.001308$. This transformation produces a dimensionless index with a mean of 0 and variance of 1, enabling spatial and temporal comparability across climate zones.

A 12-month integration period (*SPEI-12*) was chosen, and the December *SPEI-12* value was used to represent the annual drought condition per grid cell, aligning with the temporal scale of vegetation response.

Following the standard interpretation by Vicente-Serrano et al. (2010) and Chen et al. (2025), the standardized SPEI values indicate the relative wetness or dryness of a location compared to its long-term climatic mean. Negative values represent drier-than-normal conditions, while positive values indicate wetter-than-normal conditions. The classification is summarized in Table 3.1.

Table 3.1: Classification of drought and wetness conditions based on the Standardized Precipitation–Evapotranspiration Index (SPEI).

SPEI value range	**Interpretation**
> 0	Wetter than normal
$= 0$	Average condition
< 0	Drier than normal
< -1.0	Moderate drought
< -1.5	Severe drought
< -2.0	Extreme drought

In this study, a threshold of SPEI ≤ -1.1 was applied to delineate drought conditions, corresponding to moderate-to-severe droughts as used in Chen et al. (2025). This threshold ensures that only prolonged and ecologically relevant droughts are captured for subsequent analysis.

Vegetation Data Vegetation responses during and after drought events were quantified using the Kernel Normalized Difference Vegetation Index (*kNDVI*), which reduces the well-known saturation effects of NDVI in dense vegetation. The kNDVI is a nonlinear

transformation of NDVI that captures greenness anomalies more effectively in highly vegetated regions (Camps-Valls et al. 2021; Chen et al. 2025).

The kernel NDVI is calculated as:

$$kNDVI = \tanh\left(\frac{NIR - Red}{2\delta}\right)^2, \tag{3.6}$$

where NIR and Red are near-infrared and red reflectance, and δ is a length-scale parameter that controls sensitivity to vegetation density. Following Camps-Valls et al. (2021), δ is set to $0.5 \times (NIR + Red)$, which simplifies to:

$$kNDVI = \tanh\left(\mathrm{NDVI}^2\right). \tag{3.7}$$

Annual kNDVI layers were computed from the PKU GIMMS NDVI v1.2 product (Li et al. 2023), which provides globally consistent NDVI observations from 1982–2018 at 1/12° (∼10 km) resolution. The kernel NDVI anomaly (qkNDVI) represents deviations from the long-term mean (1982–2018) and is computed as:

$$\mathrm{qkNDVI}_t = \frac{kNDVI_t}{\overline{kNDVI}}. \tag{3.8}$$

Values $\mathrm{qkNDVI}_t < 1$ indicate reduced greenness (negative anomalies), whereas values $>$ 1 indicate enhanced vegetation conditions. To minimize confounding influences unrelated to droughts, pixels identified as croplands (MODIS MCD12Q1.061, class 12) and snow-affected regions (Köppen–Geiger classes 30 and 31) were excluded. This filtering ensures that the resulting qkNDVI dataset reflects genuine vegetation responses to drought conditions rather than anthropogenic or snow-related effects. The resulting dataset provides a robust measure of vegetation greenness anomalies globally, enabling the evaluation of ecosystem resistance and recovery in response to drought events.

Biodiversity Data Species richness was represented by rasterized species richness (SR), derived from the study by Cai et al. (2023), which is based on the GIFT database (Global Inventory of Floras and Traits). This dataset provides global models and predictions of plant diversity using advanced machine learning techniques.

Alpha diversity was represented by rasterized data of vascular plant alpha diversity derived from the global study by Sabatini et al. (2022). The dataset provides modelled estimates of local species richness based on more than 170,000 georeferenced vegetation plots from the *sPlot* database and additional regional datasets. By using boosted regression tree models, alpha diversity was predicted globally at a resolution of 2.5 arcminutes for both forest and non-forest ecosystems, and across multiple spatial grains (from 10 m^2 to 1 ha). The models incorporated climatic, edaphic, topographic, and biogeographical

predictors, allowing the relationships between environmental variables and local species richness to vary across spatial scales. For this study, the bias-corrected raster layers of vascular plant alpha diversity were used in their harmonized GeoTIFF format, and resampled to a 10 km grid to match the resolution of the other environmental predictors.

Topographic Data Elevation was incorporated as an additional explanatory variable to account for the influence of topography on drought exposure and ecosystem response. Topography can strongly affect local climatic and hydrological conditions by modulating temperature, precipitation patterns, runoff, and soil water availability, thus shaping the vulnerability and adaptive capacity of ecosystems. In particular, elevation gradients often create distinct vegetation zones and microclimates that mediate both the resistance of ecosystems during droughts and their recovery afterwards.

Elevation values were extracted from the global `DEM_latlong3` raster dataset, which provides consistent and spatially continuous elevation information on a global scale. The data were resampled to match the 10 km resolution of the climatic and vegetation layers, ensuring spatial comparability across all predictor variables. By integrating elevation into the modelling framework, the analysis accounts for orographic effects and improves the robustness of biome-level comparisons.

Biome Classification To capture biome-specific vegetation–climate interactions, each grid cell was assigned to a biome derived from the Köppen–Geiger climate classes. The Köppen–Geiger raster (ASCII with latitude, longitude, and class code) was imported and spatially matched to the response grid in `R` using `sf` via nearest-neighbor assignment (`st_join()` with `st_nearest_feature()`).

Following a study-specific crosswalk, original Köppen–Geiger codes were aggregated to six biome groups used in this work (see also Figure 2.1):

Table 3.2: Aggregation of Köppen–Geiger climate classes into study biomes.

Study biome	**Köppen–Geiger classes**
Tropical & Subtropical Forest	Af, Am, As, Aw
Temperate Grassland	BSh, BSk
Montane Forest	Cwb, Cwc, Cfb, Cfc, Csb, Csc
Boreal Forest	Dfa, Dfb, Dfc, Dfd, Dsa, Dsb, Dsc
Tundra	ET, Dwa, Dwb, Dwc, Dwd
Excluded classes	All remaining classes (e.g. BWh, BWk, EF)

This custom aggregation aligns the climate codes with the ecological focus of the analysis (e.g., separating Montane Forest from other temperate classes, assigning continental D subclasses to Boreal Forest, and mapping high-latitude/short-season climates including ET and Dw to Tundra).

3.1.2 Data Preparation

All datasets were harmonized to a common 10 km grid and joined to prepare the response–predictor table used in the BAM analyses: resistance and recovery. The workflow was implemented in `R` (R Core Team 2024) using spatial and data wrangling libraries (Pebesma 2018; Hijmans 2023; Wickham et al. 2023; Dowle and Srinivasan 2021).

Response and predictors. Table 3.3 summarises the response and predictor sets for resistance and recovery in plain terms.

Table 3.3: Response and predictors used in the resistance and recovery analyses.

Model	Response	Predictors
Resistance (during drought)	qkNDVI	Species richness, Alpha diversity, Drought severity, Elevation, Event length, Year, Biome, Spatial location, Drought event ID
Recovery (post-drought)	qkNDVI	Years since drought, Species richness, Alpha diversity, Drought severity, Elevation, Event length, Biome, Spatial location, Drought event ID

For the resistance analysis, drought severity was represented as the negative, standardised SPEI (larger values = stronger drought). For the recovery analysis, drought severity was instead mean-centred (SPEI_c), so that $\mathrm{SPEI}_c = 0$ corresponds to the average drought conditions in the modelling table. Rows with missing values (NA) in any required variable were removed before modelling.

To ensure comparability among predictors and to improve numerical stability, all continuous covariates were standardised using the base R function `scale()` (R Core Team 2024). For a variable x, `scale(x)` computes

$$x_{\text{scaled}} = \frac{x - \overline{x}}{s_x},$$

where $\overline{x}$ denotes the empirical mean and s_x the empirical standard deviation of x. This transformation centres predictors at zero and expresses their values in units of standard deviations. It prevents variables with large numeric ranges from dominating the estimation, stabilises interaction terms, and allows coefficient estimates to be interpreted as the expected change in qkNDVI per one–standard-deviation increase in the predictor.

For the resistance models, the following continuous variables were standardised to zero mean and unit variance: species richness, alpha diversity, drought severity (negative SPEI), elevation, and drought–event length. For the recovery models, species richness, alpha diversity, elevation, and event length were likewise standardised, whereas SPEI was

only mean-centred rather than fully standardised. This ensures that the model intercept represents average drought conditions while preserving the original variance structure relevant for temporal recovery.

Categorical predictors such as biome identity and drought-event ID (MYMD10) were not standardised, as scaling is not meaningful for nominal factors. The response variable qkNDVI was also not transformed, because it already represents a standardised greenness anomaly relative to local climatology and further scaling would reduce its ecological interpretability.

Spatial harmonization and keys. All CHELSA layers (SPEI and qkNDVI) were aggregated to ∼10 km and aligned on the same grid. Each grid cell received unique spatial identifiers and projected coordinates (`x_proj`, `y_proj`) in a metric CRS for spatial smoothing in BAM. Elevation values were extracted from the global DEM to the 10 km grid using raster sampling (`terra::extract`) and stored as a continuous covariate.

Biome assignment (Köppen–Geiger). The Köppen–Geiger ASCII raster (lat/lon/code) was read with `sf`/`terra` and joined to the response grid via nearest-neighbor matching (`sf::st_join` with `st_nearest_feature`) (Pebesma 2018). Original climate classes (e.g., Af, Am, Dfb) were mapped to the six study biomes (Tundra, Temperate Grassland, Boreal Forest, Montane Forest, Tropical & Subtropical Forest, Arid) using the study-specific crosswalk (vgl. Figure 2.1).

Drought events and severity. From the annual SPEI-12 series (CHELSA), the top-100 multi-year drought events in 1982–2018 were taken by global intensity ranking and constructed an event factor (`MYMD10`) that tags each observation to its multi-year drought. Drought severity at the cell level was used as

$$\texttt{drought\_sev} \;=\; -\,\mathrm{scale}(\texttt{SPEI}),$$

so that larger values indicate a stronger drought (more negative SPEI). This yields a consistent numeric gradient for interaction terms with biodiversity predictors. For the recovery analysis, drought severity was mean-centred as

$$\mathrm{SPEI}_c \;=\; \mathrm{SPEI} - \overline{\mathrm{SPEI}},$$

so that $\mathrm{SPEI}_c = 0$ denotes average drought conditions in the modelling table (no variance rescaling). Centering improves interpretability of main effects and of interactions with years since drought and biodiversity, and stabilises estimation when biome-specific random slopes are included.

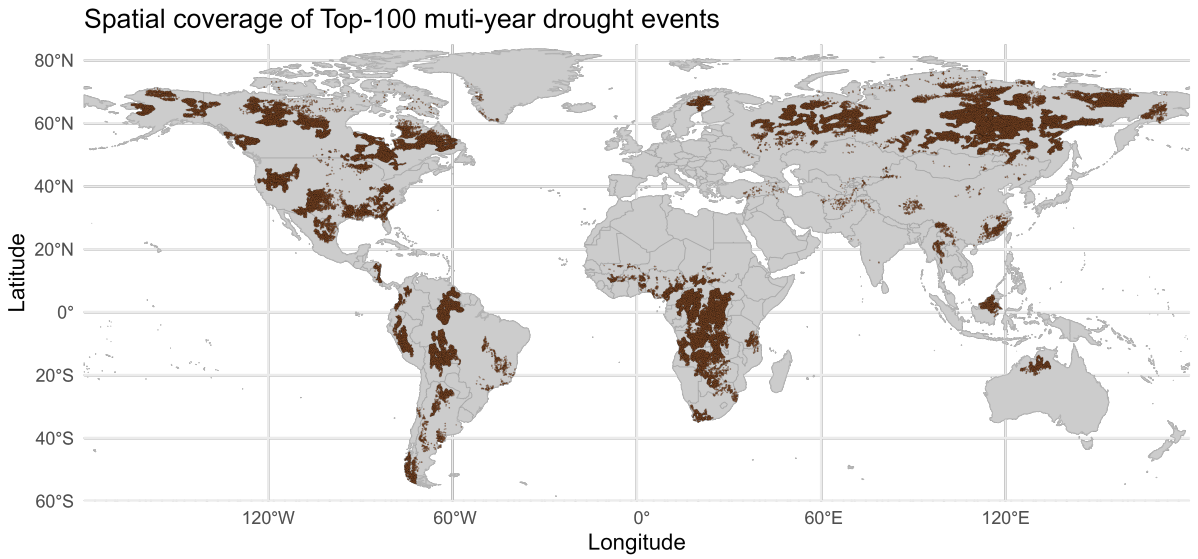

Figure 3.1: Global spatial coverage of the *Top-100* multi-year drought events (1982-2018). Each point marks a cell tagged by the event factor `MYMD10`.

3.1.3 Model-ready tables

After data preparation, all predictors and the response variable were managed as a raster stack on a common 10 km grid. All layers were reprojected to a metric coordinate reference system and co-registered to ensure consistent spatial alignment. Continuous rasters, such as SPEI (originally at approximately 1 km resolution), elevation, and biodiversity metrics, were aggregated to the 10 km grid using area-weighted cell means following reprojection. The qkNDVI layer, already available at roughly 10 km resolution, required only co-registration. The categorical biome layer was transferred to the 10 km grid using nearest-neighbour assignment. A unique cell ID was assigned to each grid cell. For each cell and year, two values were extracted on the common grid: the December SPEI-12 (a 12-month SPEI ending in December) and the annual qkNDVI. Finally, the multi-year drought catalogue was overlaid in space and time with the cell–year table, so that each record received an event ID and the corresponding drought-event duration (the number of years spanned by each defined event). No upscaling to finer resolutions was performed; any bilinear resampling occurred only during reprojection or co-registration and does not generate sub-grid information. From this master cell–year table, two model-ready tables were derived and stored in long format (one row per grid cell $\times$ drought event $\times$ time step):

(A) ***Resistance table*** *(during drought).* Contains one row per cell × event for the drought year only. Dynamic variables are taken for that specific drought year (qkNDVI, December SPEI-12). Drought severity was defined as the negative, scaled SPEI (larger values = stronger drought). Static covariates (species richness, alpha diversity, elevation, biome) are attached once per row.

(B) ***Recovery table (post-drought).*** For each cell–event, the drought year is defined as the year with the lowest December SPEI-12 within the multi-year event. The table then contains the drought year and the next four years (t_0–t_4), i.e., one row per cell–event–time step. Year-varying fields are qkNDVI and December SPEI-12 which shows the values for the next four years after the drought to analyse the vegetation recovery. For interpretability, SPEI is mean-centered for recovery ($\text{SPEI}_c = \text{SPEI} - \overline{\text{SPEI}}$). The same static covariates (species richness, alpha diversity, elevation, biome) are attached to every row.

Both tables retain projected coordinates (for spatial smoothing) and the event identifier (for event-level random effects).

3.2 Model definition

3.2.1 Generalized Additive Models (GAM)

Generalized Additive Models (GAMs) are an extension of classical regression approaches which allows predictor effects to vary smoothly rather than assuming strictly linear relationships (Hastie and Tibshirani 1990; Wood 2017). This flexibility is particularly useful for ecological and environmental data, where responses often change nonlinearly along climate, biodiversity, or spatial gradients. In GAMs, the expected response is modelled as an additive combination of linear terms and smooth functions of predictors. These smooth functions are estimated using penalised regression splines, where the degree of smoothness is selected automatically via restricted maximum likelihood (REML). This allows complex patterns to be captured while avoiding overfitting and retaining interpretability. In spatial analyses, GAMs commonly include smooth terms of geographic coordinates (e.g. $s(x, y)$) to account for broad-scale spatial structure and residual spatial dependence caused by unmeasured environmental drivers (Wood 2017).

3.2.2 Bayesian Additive Model (BAM)

The Bayesian Additive Model (BAM), implemented in `mgcv::bam`, expands upon the GAM framework and is tailored for extremely large datasets (Wood 2017). It introduces computational optimisations that enable global-scale and high-resolution spatial analyses while maintaining the flexibility of GAMs. In terms of mathematics, BAM and standard GAMs have the same additive predictor structure; the differences come from computational

optimisation rather than the underlying model formulation (Wood 2017).

Penalised likelihood with smoothness selection using fast restricted maximum likelihood (fREML) is the foundation for model estimation (Wood 2017). Quadratic penalties are used to regularise smooth terms. This stabilises estimation and provides approximate Bayesian uncertainty estimates for model parameters and predictions. BAM uses techniques like discretisation of covariates, block-wise data processing, sparse penalty structures, and parallel computation to effectively handle large sample sizes. These characteristics make it possible to fit complicated models with numerous smooth terms and random effects without incurring excessive computational costs (Wood 2017).

In this study, BAM is used to incorporate hierarchical structure for biomes and drought events using random-effect smooths and to model broad spatial patterns using Gaussian-process smooths. This allows for partial pooling across ecological contexts, enhancing biome-specific estimates' stability while preserving the possibility of biome-specific variations in biodiversity–drought relationships.

Overall, BAM offers a strong and adaptable framework for examining the connections between global biodiversity and droughts while specifically taking spatial structure, hierarchical variation, and model uncertainty into account.

3.3 Model Structure

3.3.1 Resistance

The core model is specified as

$$\begin{aligned} qkNDVI \sim\ & SR + \alpha\text{-diversity} + \textit{drought\_sev} + \textit{elevation} + \textit{event\_length} \\ & + s(x_{\text{proj}}, y_{\text{proj}}) + s(\text{Year}) \\ & + s(\text{MYMD10}) + s(\text{Biome}) \\ & + s(\text{Biome, by} = SR) + s(\text{Biome, by} = SR \times \textit{drought severity}) \,. \end{aligned} \tag{3.9}$$

The resistance question asks whether higher biodiversity is associated with smaller immediate losses during multi-year droughts and how this association differs among different biomes. The response is annual qkNDVI during the drought. Lower qkNDVI values indicate stronger loss of vegetation condition during drought. Larger drought intensity values represent harsher droughts. The inclusion of species richness and alpha diversity tests whether more diverse systems show smaller losses for a given drought intensity. In addition, biome-specific random slopes for the richness effect and for the richness$\times$*drought severity* term allow this buffering to differ among biomes, enabling explicit cross-biome comparison and evaluation of the expectation that tropical forests show the strongest resistance.

Elevation adjusts for topographic controls on water and energy that shape vegetation sensitivity. Event duration accounts for multi-year exposure so the estimated resistance reflects the acute loss in the focal drought year rather than accumulated pressure alone. A smooth function of calendar year absorbs broad secular trends (e.g., sensor changes, global greening/browning) to keep comparisons across events and regions on a common baseline.

The spatial Gaussian-process surface $s(x, y)$ captures broad geographic gradients and residual spatial dependence. Random-effect smooths (`bs="re"`) for drought events and for biomes absorb clustering by episode and baseline differences among ecological domains, while enabling partial pooling across groups. Taken together, the specification yields predictions of drought-year qkNDVI that are adjusted for space, time, and background environment, isolating the contribution of biodiversity and drought intensity to resistance and allowing those effects to vary across biomes in direct alignment with the research question.

The model is fitted globally using `mgcv::bam` with fast REML. In this structure, the spatial smoother $s(x_{\text{proj}}, y_{\text{proj}})$ models broad spatial trends, elevation accounts for topographic modulation of vegetation response, and biome-specific random slopes allow the effects of species richness (and its interaction with drought severity) to vary across biomes while sharing information via partial pooling. Model fitting follows standard `mgcv` practice: variables are centered/scaled for numerical stability, smoothness is selected by (f)REML, and inference relies on approximate Bayesian covariance for smooth terms. Remaining spatial dependence is assessed on Pearson residuals (e.g., Moran's I), and partial-effect plots are produced for interpretation (Wood 2017).

3.3.2 Recovery

The core model is specified as

$$
\begin{aligned}
qkNDVI \sim\ & \text{years since drought} + \big(\text{species richness} + \text{alpha diversity}\big) \times \text{SPEI}_c \\
& + \text{elevation} + \text{event duration} \\
& + \text{years since drought} : \text{species richness} + \text{years since drought} : \text{SPEI}_c \\
& + s(x, y) + s(\text{drought event}) + s(\text{biome}) \\
& + s(\text{biome, by} = \text{years since drought}) \\
& + s(\text{biome, by} = \text{species richness}) + s(\text{biome, by} = \text{SPEI}_c)\ .
\end{aligned}
$$

Here, $s(\cdot)$ denotes penalised smooths. This includes a Gaussian-process surface $s(x, y)$ for space, random-effect smooths for drought events and biome intercepts, and biome-specific random slopes (all implemented as penalised smooths) that allow the effects of time since drought, species richness and centred SPEI to vary among biomes via partial

pooling. One of the central questions asks whether higher biodiversity increases resilience to multi-year droughts and how these effects differ among biomes. The response is annual qkNDVI. The trajectory across years since the drought captures post-drought recovery and therefore resilience.

Years since drought define the recovery timeline and allow the model to estimate how quickly vegetation returns toward its baseline state after droughts. Annual drought conditions are represented by the centred December SPEI-12 ($SPEI_c$), which reflects relative moisture anomalies compared to average conditions and aligns with the annual qkNDVI observations. Centering SPEI-12 ensures that main effects are interpretable under average moisture conditions, while interaction terms describe how recovery trajectories change under relatively drier or wetter years.

Biodiversity is represented by species richness and alpha diversity. Their main effects and their interactions with $SPEI_c$ test the hypothesis that diverse systems recover faster after droughts. Interactions between years since drought and biodiversity quantify whether recovery accelerates with diversity, which operationalises resilience in this analysis.

Biome terms and biome-specific random slopes allow biodiversity–drought relationships to vary among biomes, enabling explicit cross-biome comparisons and evaluation of the expectation that tropical forests show the steepest recovery. The spatial surface and the drought-event effect reduce confounding by geography and episode-specific shocks, so predicted qkNDVI trajectories reflect the contribution of biodiversity and moisture to recovery within each biome, directly addressing the research question.

3.4 Stratified Subsampling & Spatial Autocorrelation

3.4.1 Definition of Moran's I and Spatial Dependence

According to Tobler's First Law of Geography, nearby locations tend to be more similar than distant ones (Tobler 1970). To quantify these patterns, spatial autocorrelation was evaluated using Moran's I (Anselin 1995), where positive values indicate clustering, values near zero indicate randomness, and negative values indicate spatial dispersion.

3.4.2 Stratified subsampling in SR–SPEI space

Both the resistance and recovery analyses use the full global 10 km dataset but apply stratified subsampling to achieve a balanced representation of biodiversity and drought conditions. Species richness (SR) and drought severity (SPEI or $SPEI_c$) are divided into bins, and an equal number of grid cells is randomly drawn from each combination. This avoids over-representation of drought-prone areas and ensures that the SR–SPEI relationship is estimated from a well-distributed sample.

3.4.3 Spatial autocorrelation: model-based treatment

Residual spatial autocorrelation was addressed through several spatial components within the GAM/BAM framework.

(1) Global spatial smooth. A two-dimensional Gaussian-process smooth

$$s(x_{\text{proj}}, y_{\text{proj}}, bs = \text{“gp”})$$

captures broad geographic gradients and removes large-scale spatial structure.

(2) Biome-level smooths. Random-effect smooths assign each biome its own baseline, and interaction smooths allow biodiversity and drought responses to differ among biomes. In recovery models, biome-specific timepoint smooths capture differences in multi-year recovery trajectories.

(3) Event-level effects (Recovery only). A random-effect smooth for drought events

$$s(\text{MYMD10}, bs = \text{“re”})$$

accounts for spatially contiguous drought episodes and reduces event-specific spatial clustering.

(4) Efficient estimation. Both models use `bam()` with `method = ''fREML''` and `discrete = TRUE` to reduce computational load and to stabilise smoothness estimation.

3.4.4 Resistance vs. Recovery: differences in spatial structure

Resistance. The resistance model includes the global spatial smooth and biome-level random effects, representing spatial structure at the drought peak.

Recovery. Recovery models also include event-level effects and timepoint-specific biome smooths, capturing multi-year spatial patterns during post-drought regrowth.

Residual spatial autocorrelation (Moran's I). Moran's I was computed on model residuals using a 10 km neighbourhood graph. Spatial autocorrelation was substantially reduced compared to non-spatial GAMs, indicating that most spatial structure was absorbed by the global spatial smooth and the hierarchical biome and event terms. Remaining autocorrelation is minor and expected in global kilometre-scale datasets.

4. Results

4.1 Drought Resistance

4.1.1 Smooth Terms and Model Performance of the BAM

The Bayesian Additive Model (BAM) includes smooth terms which represent spatial structure, temporal variation, biome-level heterogeneity, and drought-event identifiers. These smooth components allow the model to capture nonlinear patterns and group-level variation that cannot be represented by linear terms alone.

Table 4.1 lists the effective degrees of freedom (edf), the reference degrees of freedom (Ref.df), the F-statistics (F), and the associated significance levels. The edf quantify how flexible each smooth term is, where values close to 1 indicate near-linearity, while larger values indicate increasing complexity. The F-statistic tests whether each smooth explains substantial variation in the response. Larger F-values indicate a stronger contribution of the smooth term to explaining variation in the response relative to its complexity. The Ref.df specify the degrees of freedom used for the significance test and are typically larger than the edf because they account for uncertainty in smoothing parameter estimation. Small p-values (e.g. $p < 0.05$) indicate that the smooth term is statistically significant, whereas large p-values suggest that the effect is weak or indistinguishable from zero.

Table 4.1: Smooth terms in the BAM model (Gaussian, fREML).

Term	**edf**	**Ref.df**	**F**	**p-value**
Spatial effect (x,y)	94.539	2	5.923e+07	<0.001
Year	8.972	3	3.589	<0.001
Biome	4.972	3	1.989	<0.001
Biome × SR	4.926	3	1.970	<0.001
Biome × (SR × drought severity)	4.897	3	1.959	<0.001
Drought event ID (MYMD10)	91.314	3	3.653e+01	<0.001

The spatial effect shows very high edf (94.5), indicating complex spatial structure. The drought-event smooth (MYMD10) also has high edf (91.3), reflecting large differences between individual drought events. Smooths involving biome and biodiversity metrics

show moderate edf values around 5, consistent with flexible but comparatively less complex group-level variation. The model performance metrics are presented in Table 4.2. The adjusted $R^2 = 0.493$ indicates that the BAM model explains nearly half of the variance in qkNDVI during droughts. The deviance explained (49.3%) provides an analogous measure for GAMs. The scale estimate (0.00517) represents the residual variance after accounting for all smooth and parametric terms.

Table 4.2: Model performance diagnostics for the BAM model.

Metric	**Value**
Adjusted R^2	0.493
Deviance explained	49.3%
Scale estimate	0.00517
Sample size (n)	226,822
Moran's I (residuals)	0.163 ($p < 0.001$; MC $p = 0.001$)

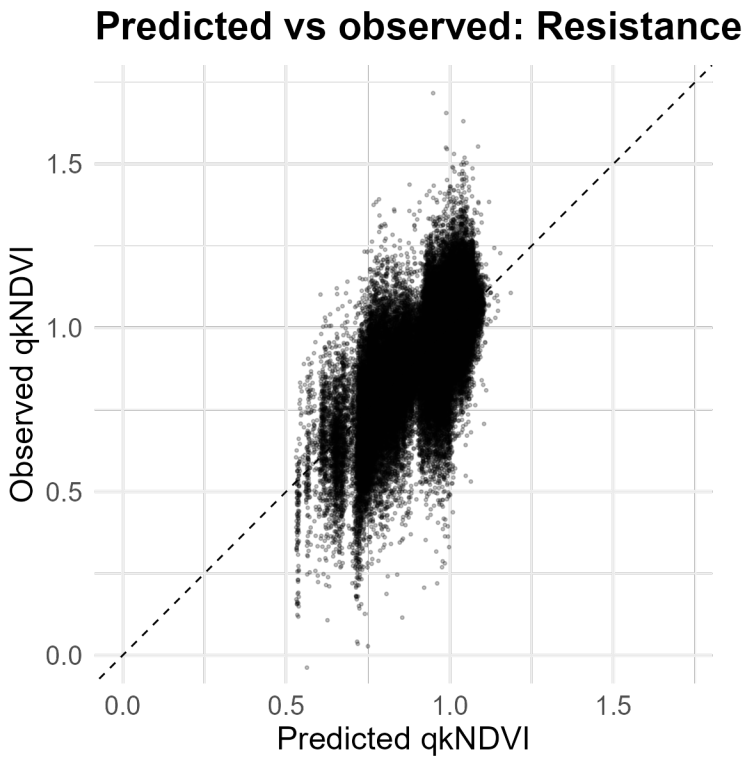

Figure 4.1: Predicted versus observed qkNDVI during drought. The dashed line indicates the 1:1 relationship.

4.1.2 Residual structure

Figure 4.1 compares predicted and observed qkNDVI values for all drought-year observations. Most points cluster tightly around the 1:1 line, indicating strong overall agreement between predictions and observations. The highest densities occur at intermediate qkNDVI

values, where the majority of data lie. Deviations from the 1:1 line are present at both low and high values, but they are approximately symmetric, suggesting no systematic bias across the response range.

Spatially mapped residuals (Figure 4.2) show both positive and negative deviations across regions, but no large-scale spatial bias. Moran's $I = 0.127$ indicates weak, though statistically significant, spatial autocorrelation, implying that most broad-scale spatial dependence was absorbed by the Gaussian-process smooth, while fine-scale spatial structure remains.

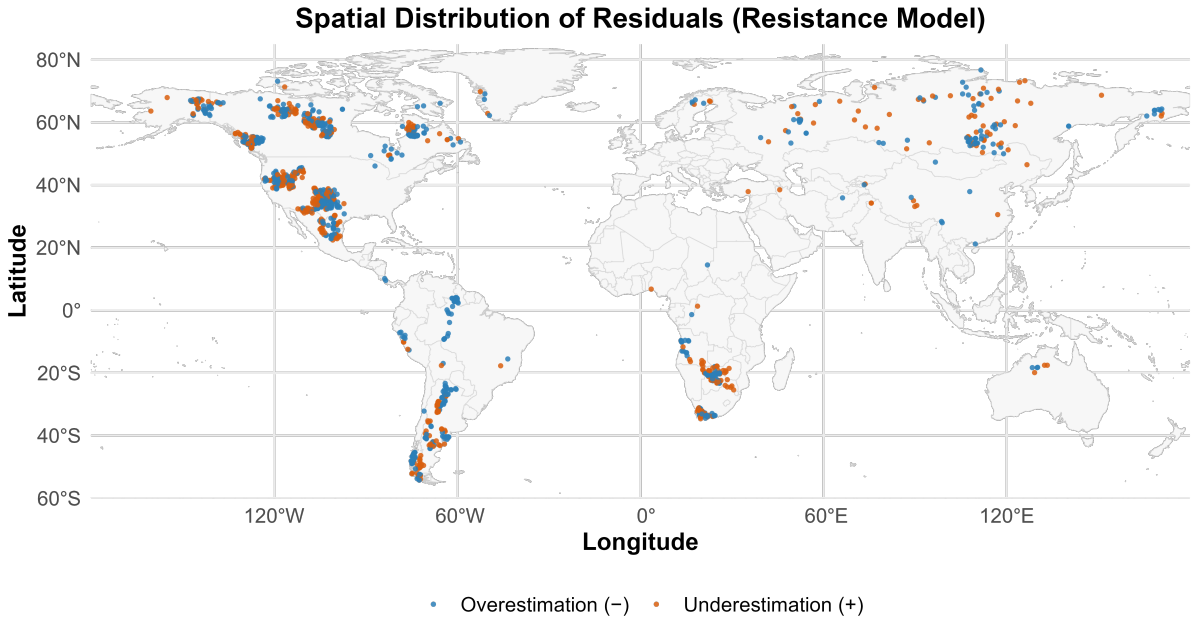

Figure 4.2: Spatial distribution of residuals in the Resistance Model. Blue points indicate *overestimation*, where predicted qkNDVI is at least 0.20 units higher than observed (residuals < -0.20). Orange points indicate *underestimation*, where predicted qkNDVI is at least 0.20 units lower than observed (residuals $> +0.20$). Only residuals with $|\text{residual}| \geq 0.20$ are displayed.

4.1.3 Parametric Effects

Table 4.3 summarises the parametric fixed effects of the BAM resistance model. All continuous predictors were centred and standardised before fitting, so that each coefficient represents the expected change in predicted qkNDVI associated with a one–standard deviation increase in the corresponding predictor, with all other variables held constant. Because all predictors were scaled, the effect sizes are directly comparable. The intercept reflects the expected qkNDVI at mean values of all predictors.

Species richness and alpha diversity both show significant positive effects, indicating that biodiversity is associated with higher vegetation greenness during droughts. Species richness exhibits a moderately strong positive effect, while alpha diversity shows a smaller but highly precise effect, reflected in its very small standard error. Drought severity has a strong and highly significant negative effect, confirming that more intense drought conditions reduce vegetation greenness. Elevation also shows a significant positive effect, whereas event length has a smaller but still significant positive influence. Predictors like elevation and event length had significant, though anticipated, effects, reinforcing their interpretation as environmental constraints rather than the main determinants of drought resistance in this study.

Interaction terms reveal how these effects vary with drought intensity. The interaction between species richness and drought severity is not statistically significant, suggesting that the positive biodiversity effect does not systematically strengthen or weaken under more severe droughts. In contrast, the alpha diversity–drought interaction is strongly positive and highly significant, indicating that ecosystems with higher local species diversity experience a reduced negative impact of droughts.

Table 4.3: Parametric coefficients of the BAM (Gaussian, fREML). Predictors were centred and scaled prior to fitting.

Term	**Estimate**	**Std. Error**	**t value**	**p-value**	**Sig.**
Intercept	0.9173	0.0297	30.93	< 0.001	***
Species richness	0.0201	0.00451	4.45	< 0.001	***
Alpha diversity	0.00281	0.00024	11.94	< 0.001	***
Drought severity	-0.00868	0.00025	-34.84	< 0.001	***
Elevation	0.00665	0.00043	15.45	< 0.001	***
Event length	0.01393	0.00549	2.54	0.011	*
Species richness × Drought	0.00125	0.00196	0.64	0.523	
Alpha diversity × Drought	0.00305	0.00017	17.85	< 0.001	***

4.1.4 Biome-specific patterns

Figure 4.3 displays marginal predictions of qkNDVI across biomes for varying species richness. Lines represent model predictions holding other covariates constant where the shaded ribbons show the central 80% prediction interval (corresponding to the 10th–90th percentiles of the predicted values). These intervals represent the spread of predicted greenness responses across the reference sets used for each biome.

The corresponding marginal slopes (Table 4.4) quantify the rate of change in predicted qkNDVI per one–standard deviation increase in species richness at drought severity = +1 SD. These slopes are presented with 95% confidence intervals, which describe the parameter uncertainty of the estimated biodiversity effect.

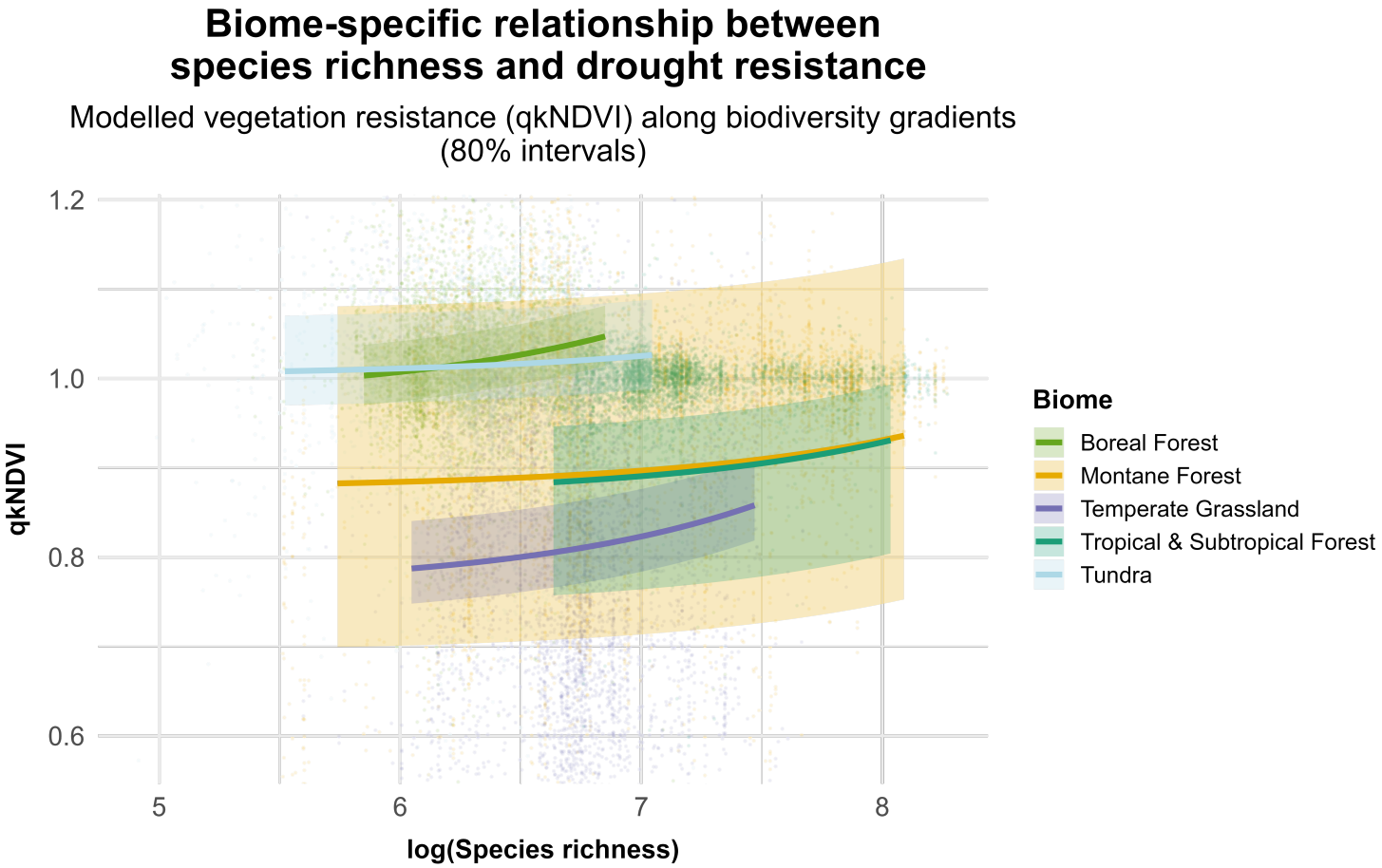

Figure 4.3: Relationship between predicted qkNDVI and species richness (biodiversity) across five biomes (boreal forest, montane forest, temperate grassland, tropical & subtropical forest, tundra). Coloured lines show biome-specific marginal predictions obtained by varying species richness while holding all other covariates (e.g. elevation, event length, year, drought severity, alpha diversity) at their biome-specific median values. Because species-richness values vary over several orders of magnitude, the x-axis uses log(Species Richness) to visualise the full gradient more clearly and to prevent high-richness values from dominating the scale. The shaded ribbons display the central 80% prediction interval (10–90 %), representing the spread of predicted qkNDVI across the richness gradient after accounting for model uncertainty (with event-level random effects excluded).

Table 4.4: Biome-specific biodiversity effects on drought resistance. Values represent how much predicted qkNDVI increases when species richness increases by one standard deviation, under drought severity = +1 SD. 95% confidence intervals quantify the uncertainty of these effects.

Biome	**Slope**	**Lower 95% CI**	**Upper 95% CI**	**Ranking**
Boreal Forest	0.0490	0.0453	0.0527	Strongest effect
Temperate Grassland	0.0248	0.0222	0.0274	Strong effect
Tropical & Subtropical Forest	0.0126	0.0113	0.0138	Moderate effect
Tundra	0.0088	0.0040	0.0137	Weak effect
Montane Forest	0.0069	0.0048	0.0090	Weakest effect

Across all biomes, species richness consistently increases with predicted vegetation greenness during droughts. Every slope is positive, and their 95% confidence intervals remain entirely above zero (see Table 4.4). Boreal forests show the steepest biodiversity effect, with a confidence interval that is different from all others. Temperate grasslands have the next strongest association, while tropical and subtropical forests show intermediate trends, overlapping somewhat with tundra and montane forests. These latter two biomes display the weakest positive effects, with confidence intervals that approach zero.

Figure 4.3 highlights biome-specific differences in uncertainty using 80% prediction ribbons. Boreal forests and tundra exhibit the widest 10–90% ranges, whereas montane and tropical forests show narrower ribbons. Absolute predicted qkNDVI values also vary across biomes, where tropical and temperate regions reach the highest greenness levels, while tundra and montane forests remain lower overall.

Overall, the biodiversity-greenness relationship appears roughly linear in all biomes, although the slope steepness differs. Boreal forests and temperate grasslands show the strongest increases across the observed richness range, while montane forests exhibit the flattest trends. The Bayesian additive model retained biome-specific random slopes for species richness and the richness-drought interaction, indicating clear, statistically supported differences among biomes in both biodiversity effect and drought response.

Figure 4.4 presents the global spatial distribution of predicted vegetation greenness (qkNDVI) during droughts. Teal colours indicate higher resistance (higher predicted greenness), while lighter shades indicate lower resistance. These spatial patterns complement the parametric effects by showing how the estimated relationships express geographically across biomes and climate regions.

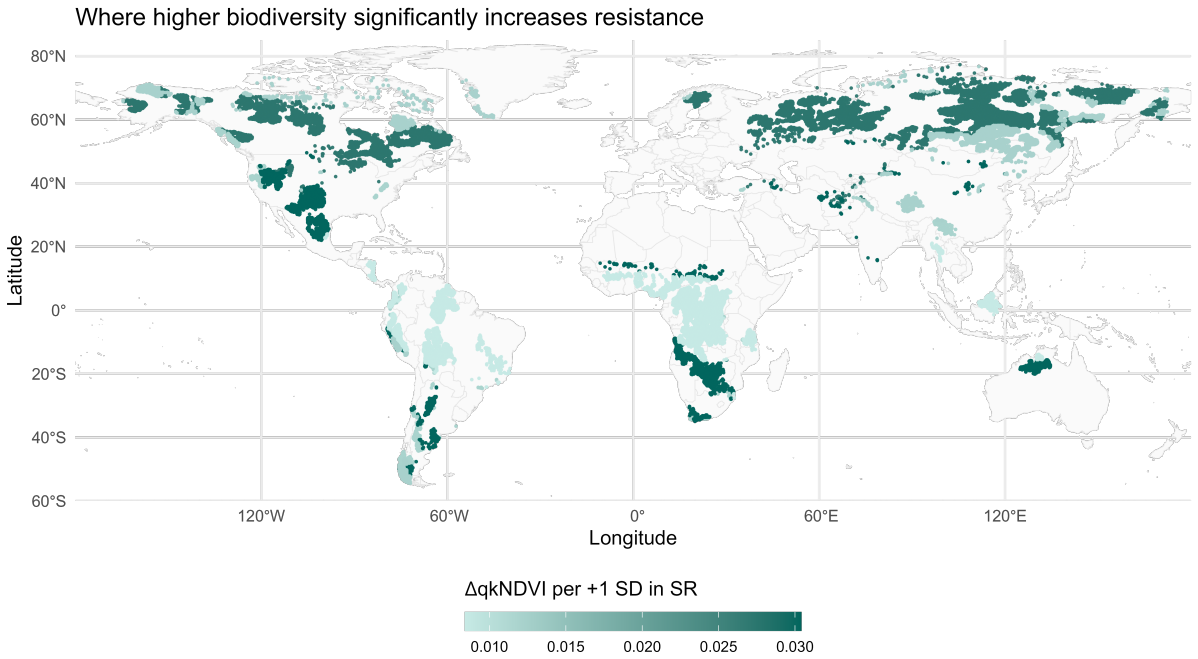

Figure 4.4: Global resistance map showing predicted vegetation greenness (qkNDVI) during droughts. Teal areas indicate higher predicted greenness (stronger resistance), while lighter shades represent lower resistance.

4.2 Vegetation Recovery after Droughts

4.2.1 Smooth terms and overall model performance

Table 4.5 and Table 4.6 summarise the smooth terms and performance metrics of the BAM fitted to vegetation recovery (qkNDVI). For each term, it reports the effective degrees of freedom (edf), the reference degrees of freedom (Ref.df), the F-statistic, and the p-value. All smooth terms show p-values below 0.001, which confirms that each smooth term contributes significantly to the model. The spatial effect displays the highest edf (98.18), reflecting a highly flexible and detailed spatial component. It also produces the largest F-statistic (7.37×10^8), indicating that spatial variation accounts for a large share of the model's explanatory power.

The smooth term for biome has an edf of 4.99 and a Ref.df of 5, with an F-statistic of 1.198. Comparable results are observed for the Biome × Timepoint (edf = 4.99, Ref.df = 5, $F = 1.199$), Biome × SR (edf = 4.96, Ref.df = 5, $F = 1.191$), and Biome × SPEI (edf = 5.00, Ref.df = 5, $F = 1.200$) terms. These four smooths show similar levels of complexity and statistical influence, suggesting that biome-level interactions contribute to the model in a consistent way. The Drought event ID (MYMD10) smooth has the second-highest edf (93.66), considerably higher than the biome-level terms. Although less

dominant than the spatial effect, it still captures meaningful variation, as reflected in its F-statistic of 22.48. Overall, the smooth terms vary strongly in complexity, with the spatial and event-level effects showing the highest flexibility, while biome-level smooths contribute more modest but consistent components to the model.

Table 4.5: Smooth terms in the Recovery BAM (Gaussian, fREML).

Term	**edf**	**Ref.df**	**F**	**p-value**
Spatial effect (x, y, GP)	98.179	2	7.368×10^8	< 0.001
Biome	4.990	5	1.198	< 0.001
Biome $\times$ timepoint	4.994	5	1.199	< 0.001
Biome $\times$ SR	4.963	5	1.191	< 0.001
Biome $\times$ SPEI	5.000	5	1.200	< 0.001
Drought event ID (MYMD10)	93.660	5	22.48	< 0.001

The model performance statistics for the recovery model are summarised in Table 4.6. The model achieves an adjusted $R^2 = 0.311$ and explains 31.1% of the deviance across more than 2.56 million observations, which is substantial given the global extent, the spatial heterogeneity of ecosystems, and the non-linear post-drought dynamics captured by the BAM. The estimated scale $\hat{\sigma}^2 = 0.005622$ suggests that there is relatively low residual variability after considering the spatial, biotic, and climatic predictors.

Table 4.6: Model performance diagnostics for the Recovery BAM.

Metric	**Value**
Adjusted R^2	0.311
Deviance explained	31.1%
Scale estimate	0.005622
fREML	-2.505×10^6
Sample size (n)	2,566,673
Moran's I (residuals)	0.075 ($p < 0.001$)

Figure 4.5 compares the predicted and observed qkNDVI values. The majority of points are clustered around the 1:1 line, suggesting that the model's predicted recovery strength corresponds closely with the observed values. The greatest point densities are found in the central region of the distribution, where the model's performance remains most consistent. Discrepancies from the 1:1 line are most noticeable at extreme points, where recovery values are either very low or very high, resulting in sparse data and more variable ecological responses. A slight tendency to underestimate high recovery and overestimate low recovery is expected in models that integrate highly diverse ecosystem types and matches the patterns seen in the partial dependence and biome-specific analyses discussed later.

Overall, these results show that the recovery BAM produces a reliable, well-calibrated global model with moderate explanatory strength and minimal remaining spatial bias, making it suitable for large-scale analyses of biodiversity–drought recovery dynamics.

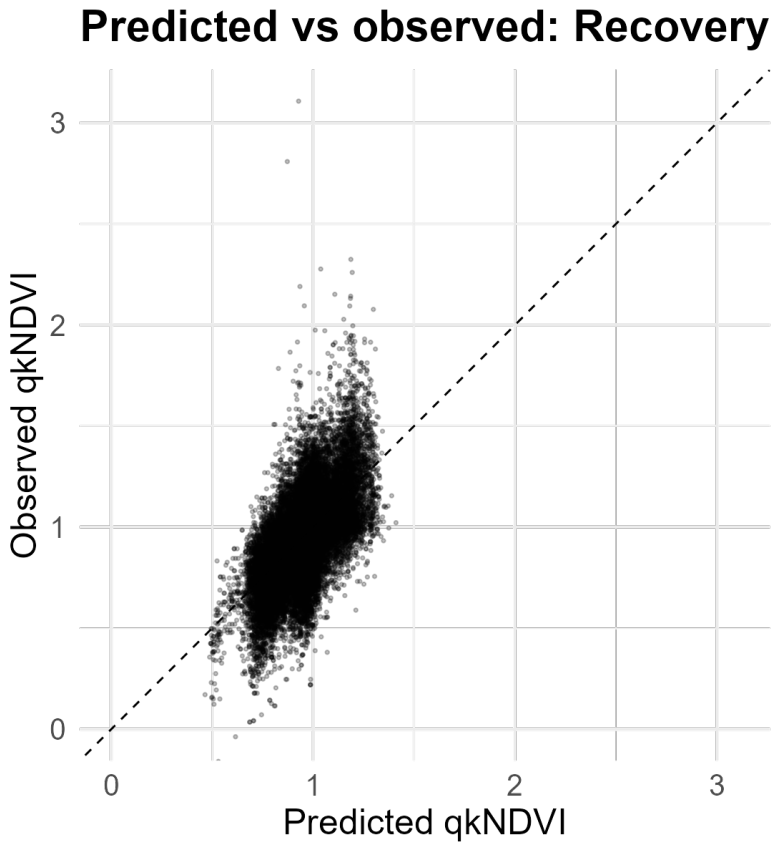

Figure 4.5: Predicted versus observed qkNDVI (vegetation recovery following drought). The dashed line marks the 1:1 relationship. Hexagon colour denotes count on a logarithmic scale.

4.2.2 Residual Structure

There is some residual spatial autocorrelation, but it is minimal (Moran's $I = 0.075$, permutation $p = 0.001$). This level of autocorrelation is expected in large global datasets with 10-km resolution, where regional clustering and biome boundaries naturally create some remaining spatial structure even after applying spatial smoothing. The relatively low value of Moran's I indicates that the Gaussian-process smoothing, along with the hierarchical random effects at biome and event levels, successfully captures the majority of large-scale spatial patterns.

Figure 4.6 maps the residuals from the Recovery Model. Only residuals with an absolute value of 0.20 or greater in qkNDVI ($|\text{residual}| \geq 0.20$) are shown, since smaller differences fall within normal model noise. Residuals represent the difference between observed and predicted qkNDVI values where the blue points mark areas where the model overestimates qkNDVI (predictions at least 0.20 higher than observed, residuals < -0.20),

while orange points mark areas where it underestimates (predictions at least 0.20 lower, residuals $> +0.20$).

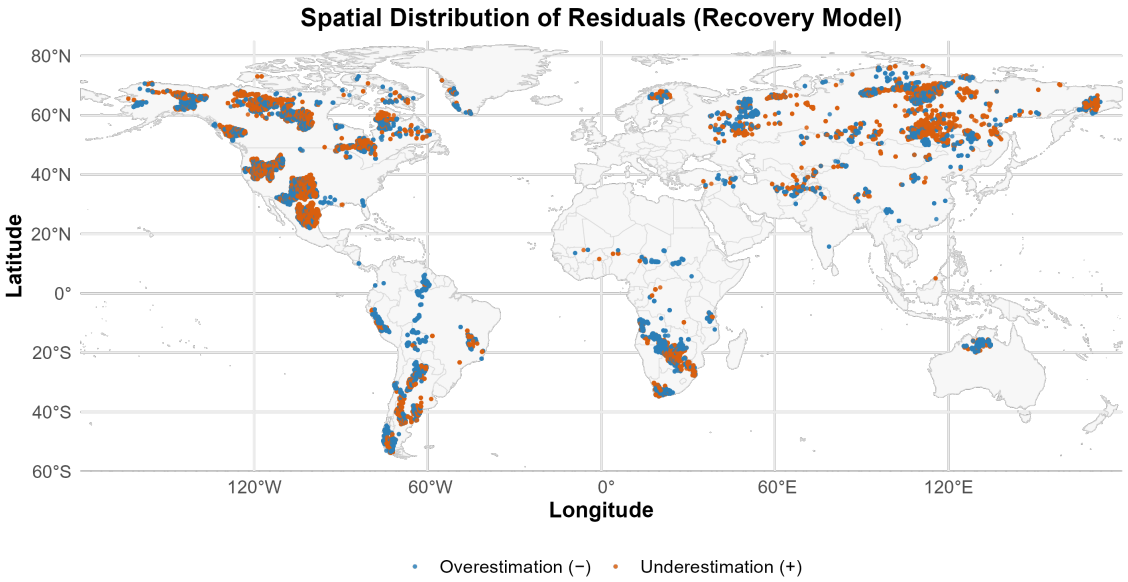

Figure 4.6: Spatial distribution of residuals in the Recovery Model. Blue points indicate *overestimation*, where predicted qkNDVI is at least 0.20 units higher than observed (residuals < -0.20). Orange points indicate *underestimation*, where predicted qkNDVI is at least 0.20 units lower than observed (residuals $> +0.20$). Only residuals with $|\text{residual}| \geq 0.20$ are shown.

Clear spatial patterns emerge. In North America, particularly across the southern Rocky Mountains and the Great Plains, both over- and underestimation frequently occur, which shows heterogeneous recovery dynamics in these regions. In Eurasia large contiguous areas exhibit positive residuals, indicating systematic underestimation of vegetation recovery. Additional clusters of positive and negative residuals appear in parts of southern Africa, Central Asia, and the Andes, though these are more spatially localized.

Overall, the spatial residual patterns highlight regions where the Recovery Model captures post-drought vegetation responses imperfectly, likely due to unmodelled processes such as soil characteristics, land-use history, or biome-specific vegetation strategies. This map complements the global model diagnostics by revealing geographically structured uncertainties in predicted recovery.

4.2.3 Parametric effects

Table 4.7 shows the estimated parametric coefficients of the recovery BAM model. For each term, the table provides the coefficient estimate, standard error, t-value, and p-value. All values are reported on the scale of the linear predictor. The Intercept has a positive and significant estimate (0.6753), with a t-value of 8.348 and a p-value below 0.001. The

coefficient for timepoint is also positive (0.00509) and statistically significant at the 5% level. The main effect of SR is small (0.00199) and not statistically significant (p = 0.4444).

The coefficient for alphadiv is positive (0.00105) and highly significant, with a t-value of 11.914. The effect of SPEI is positive (0.0275) but not statistically significant (p = 0.160). The coefficient for elevation is negative (−0.00113) and highly significant, with a t-value of −10.335. The coefficient for event length is positive (0.0408) and significant at the 1% level. The interaction SR × SPEI has a negative coefficient (−0.00180) and is highly significant (t = −16.014). The alphadiv × SPEI interaction is also negative (−0.00318) and highly significant, with the largest magnitude of any interaction term listed (t = −41.658). The timepoint × SR interaction is small (−0.00010) and not statistically significant (p = 0.0696). The timepoint × SPEI interaction is positive (0.00157) and highly significant, with a t-value of 31.964.

Overall, the parametric terms describe the linear components of the model and indicate which predictors and interactions show statistically detectable associations with the response, as expressed by their signs, magnitudes, and significance levels.

Table 4.7: Parametric fixed-effect coefficients of the Recovery BAM (Gaussian family, fREML estimation). Shown are linear effects and interaction terms included in the parametric component of the model; nonlinear smooth terms are not listed here. Estimates represent the direction and magnitude of each effect on predicted qkNDVI (vegetation recovery), with standard errors, t-values and significance levels indicating the strength of evidence for each effect.

Term	**Estimate**	**Std. Error**	**t value**	**p-value**	**Sig.**
Intercept	0.6753	0.0809	8.348	< 0.001	***
timepoint	0.00509	0.00210	2.430	0.0151	*
SR	0.00199	0.00261	0.765	0.4444	
alphadiv	0.00105	0.00009	11.914	< 0.001	***
SPEI	0.0275	0.0196	1.406	0.160	
elevation	-0.00113	0.00011	-10.335	< 0.001	***
event length	0.0408	0.0153	2.661	0.0078	**
SR × SPEI	-0.00180	0.00011	-16.014	< 0.001	***
alphadiv × SPEI	-0.00318	0.00008	-41.658	< 0.001	***
timepoint × SR	-0.00010	0.00006	-1.815	0.0696	.
timepoint × SPEI	0.00157	0.00005	31.964	< 0.001	***

Note. Significance codes: ******* $p < 0.001$, ****** $p < 0.01$, ***** $p < 0.05$, **.** $p < 0.1$.

4.2.4 Biome-specific patterns

The biome-specific patterns observed in Figure 4.7 complement the parametric effects reported in Table 4.7 and help to contextualise how biodiversity contributes to post-

drought recovery. The parametric effects show that alpha diversity has a strong and highly significant positive main effect on predicted recovery (estimate = 0.00105, $p < 0.001$), whereas species richness (SR) does not exhibit a significant global main effect (estimate = 0.00199, $p = 0.4444$). Instead, biodiversity influences recovery primarily through its interaction with drought severity. Both the SR×SPEI and alpha-diversity×SPEI interactions are negative and highly significant, indicating that higher biodiversity enhances recovery particularly under dry conditions. The interaction involving alpha diversity shows the strongest magnitude of all parametric terms.

These drought-modulated biodiversity effects are reflected in the biome-specific recovery trajectories shown in Figure 4.7. All biomes exhibit increasing predicted qkNDVI from the drought year (t_0) to the post-drought years (t_1–t_4), but the magnitude and temporal pattern of recovery differ substantially. Boreal Forest, Montane Forest, Temperate Grassland, and Tundra show clear separation between all timepoints, consistent with the significant main effect of timepoint (estimate = 0.00509, $p = 0.015$) and its strong interaction with drought severity. In contrast, Tropical and Subtropical Forests show smaller differences across years, which aligns with their comparatively muted recovery dynamics.

The letters above the boxplots indicate statistically distinct timepoint groups derived from Tukey post-hoc tests ($p < 0.05$), offering a within-biome view of how recovery progresses over time. In most biomes, t_0 consistently forms its own group with markedly lower predicted values, while the separation of later timepoints mirrors the modelled recovery gradients. These statistical groupings therefore confirm the parametric evidence that biodiversity modulates recovery strength across biomes.

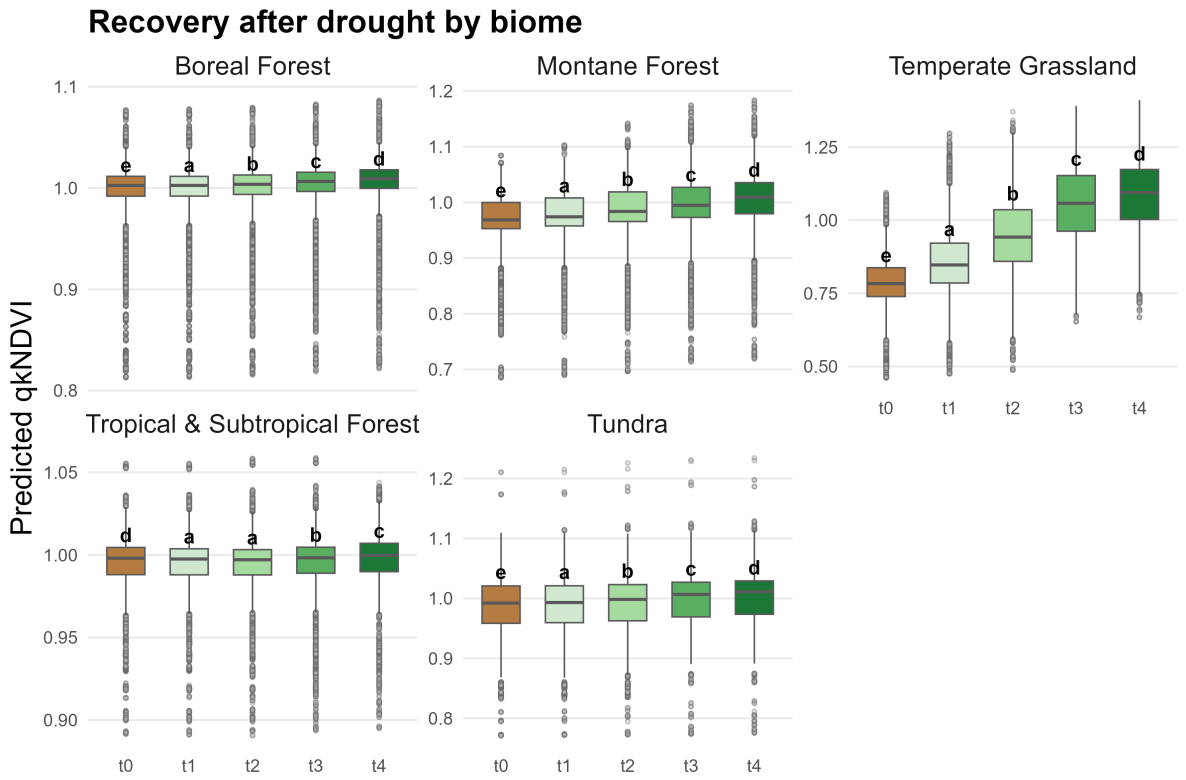

Figure 4.7: Predicted vegetation recovery (qkNDVI) after drought across biomes. Boxplots show modelled qkNDVI during the drought year (t_0) and in the four subsequent post-drought years (t_1–t_4). The brown boxplot represents the drought year (t_0), while the green boxplots represent recovery years (t_1–t_4). Letters above the boxplots indicate statistically distinct groups based on Tukey post-hoc tests ($p < 0.05$) applied within each biome; timepoints sharing a letter do not differ significantly, whereas timepoints with different letters show significant differences in predicted qkNDVI.

5. Discussion

5.1 Biodiversity and Drought Resistance

5.1.1 Interpretation of BAM resistance results

The results show that both species richness and alpha diversity have strong, statistically significant positive effects on the resistance of ecosystems during droughts. The interaction between alpha diversity and drought severity showed a strong positive effect, indicating that alpha diversity plays a stabilising role in an ecosystem when drought intensity increases. This was the strongest interaction effect in the entire BAM resistance model.

In contrast, the interaction between species richness and drought severity was not statistically significant, suggesting that species richness does not have an additional buffering effect as drought intensity increases. One possible explanation for this could be that species richness only captures the number of species present, but not the functional characteristics of the species. This shows that while higher species richness generally increases resistance, this relationship does not consistently change with drought intensity. Under severe droughts, alpha diversity provides a much stronger buffering effect than species richness. This suggests that insurance effects are driven more by the realised contributions of multiple species than by taxonomic richness alone.

Pennekamp et al. (2018) found that temporal stability and resistance can vary in opposite directions across biodiversity gradients. Meaning that higher biodiversity may strengthen one aspect of stability while weakening another. This highlights that biodiversity does not uniformly increase all aspects of stability, but rather influences different stability aspects in distinct and sometimes contrasting ways.

The results of the resistance analysis are also consistent with the insurance hypothesis described by Yachi and Loreau (1999). The positive effects of species richness and alpha diversity suggest that ecosystems with more species better maintain vegetation greenness (qkNDVI) during droughts. At the same time, the strong interaction between alpha diversity and drought severity demonstrates the buffering effect during increased environmental stress. Communities with a more uniform distribution of species experience smaller declines.

Together, these results provide empirical evidence for the insurance hypothesis and show how different aspects of biodiversity contribute to drought resistance in different ways (Wagg et al. 2022; Schnabel et al. 2021). Differences in how species respond to environmental stress prevent all species from declining at the same time, thereby strengthening the insurance effects during droughts. At lower levels of species richness, some species may become functionally redundant, limiting stability gains (Langenheder et al. 2012). Furthermore, biodiversity can stabilize ecosystem functioning even when species composition changes. Functional replacement and complementary traits, such as differences in root depth, stomatal control, or phenology, allow multiple species to maintain productivity under stress (Pardos et al. 2021; Loreau and De Mazancourt 2013). These mechanisms explain why diverse communities can maintain resistance even when species dominance shifts. They also show that biodiversity effects depend on species composition and local environmental context (Pennekamp et al. 2018).

Overall, these results provide a nuanced answer to the first research question: *How does biodiversity influence the resilience of ecosystems to vegetation loss during multi-year droughts?*. Species richness and alpha diversity capture the complementary aspects of biodiversity that are central to this study. Biodiversity influences drought resistance, but its components do so in different ways. Species richness increases the general resistance level of ecosystems, whereas alpha diversity enhances their ability to withstand increasingly severe droughts. This distinction reflects the way biodiversity was defined in this study. The pronounced interaction between alpha diversity and drought severity underscores that the structure of species contributions is particularly important when ecosystems face extreme climatic pressure. This shows that biodiversity does not uniformly strengthen ecosystem resistance to multi-year droughts, but enhances resistance through different and interacting dimensions of diversity.

5.2 Biodiversity and Post-Drought Recovery

5.2.1 Interpretation of BAM resilience results

As in the resistance analysis, several factors such as altitude and drought duration were considered. This allowed us to examine how and whether biodiversity affects vegetation recovery after multi-year droughts. Alpha diversity was strongly significant and had a strong positive main effect. Ecosystems with higher alpha diversity retain higher vegetation greenness at the start of post-drought recovery. Therefore, ecosystems with higher alpha diversity can maintain a stronger functional foundation even immediately after a drought, making them more resilient. The interaction between alpha diversity and SPEI was strongly negative, indicating that the positive effect of alpha diversity increases under more severe droughts.

Species richness on the other hand, showed a non significant main effect which means that species richness does not automatically enhance ecosystem recovery under average drought conditions. The increasing number of species alone does therefore not guarantee faster or stronger regrowth after a drought. The interaction between species richness and SPEI was also strongly negative, again because SPEI is negative during droughts. Similar to the interaction with alpha diversity, the negative interaction indicates that the effect of species richness becomes more positive under a severe drought.

In the recovery analysis, the interaction between timepoint and SPEI and timepoint and species richness was important. The results show a strongly positive interaction between timepoint and SPEI. This suggests that recovery strengthens over time, especially when drought conditions were less severe. This reflects the natural relaxation of stress and progression toward baseline functioning. The interaction between timepoint and species richness was slightly negative, which means that there is a weak trend suggesting that systems with higher species richness may recover slightly faster over time, although the effect is small and not robust. Across the full recovery trajectory (from t_0 to t_4), biodiversity effects remain present but are overall weaker than those observed for drought resistance. This reflects the growth-limited nature of post-drought recovery where ecosystems can only regain vegetation as fast as physiological, climatic, and resource constraints allow. While resistance captures the ability to maintain functioning during droughts, recovery depends on regrowth processes, which are inherently slower and more constrained. As a result, biodiversity mainly influences recovery by shaping community structure and functional balance. It does not equally accelerate biomass accumulation under all conditions.

The insurance effect presented by Yachi and Loreau (1999) shows that biodiversity enhances resilience through the buffering effect and through the performance-enhancing effect. The buffering effect is supported by the strong positive main effect of alpha diversity and the even stronger effect under severe drought conditions. According to Bai and Tang (2024) the evidence for whether biodiversity supports recovery after a drought is more inconsistent. Diverse communities may recover faster after a drought because complementary traits and different response timings among species strengthen resilience. This aligns with the BAM results, which show that alpha diversity strongly promotes post-drought recovery and becomes even more beneficial under severe conditions. Bai and Tang (2024) also found that species richness improves resistance, but not always resilience, and that this effect is highly biome-specific.

Since different species contribute to regrowth at different times, long-term experiments have demonstrated that complementary functional traits and asynchronous species responses can improve recovery (Schnabel et al. 2021; Wagg et al. 2022). Communities where species contribute more equally to ecosystem functioning are better able to sustain performance through compensatory dynamics. This matches the strong effect of alpha diversity observed in the BAM model. While species richness can speed recovery in some

ecosystems, like grasslands with strong functional complementarity (Isbell et al. 2015), its effects are weaker or nonexistent in others, especially in forests (Bai and Tang 2024). The mixed role of species richness found in the BAM results also reflects patterns reported in the literature. These findings highlight that biodiversity–recovery relationships are context dependent and can vary across biomes, a pattern that aligns with the broader ecological understanding of resilience.

To evaluate the second research question, *How does biodiversity influence ecosystem recovery after multi-year droughts?*, the recovery results demonstrate that biodiversity influences recovery, but that species richness and alpha diversity act through different mechanisms. Alpha diversity consistently supports ecosystem recovery, with particularly strong effects after severe drought events. This pattern is associated with balance, as more evenly represented communities allow species to compensate for each other and maintain essential ecosystem functions during recovery. Such balanced communities also promote functional complementarity, enabling species with different traits and recovery speeds to sustain vegetation regrowth over time.

Species richness, in contrast, does not always lead to stronger recovery and becomes more influential mainly under extreme drought conditions. In these cases, a higher number of species provides a broader range of traits that can contribute to recovery when dominant or drought-sensitive species decline. Overall, recovery is shaped by ecosystem structure and by how disturbances activate different species groups. Biodiversity therefore supports recovery by keeping species contributions balanced and by providing a reserve of traits that become particularly important under high environmental stress. Together with previous studies, the BAM results show that biodiversity enhances post-drought recovery through complementary diversity facets, whose importance depends on drought severity, ecosystem type, and climate.

5.3 Interpretation Biome Specific BAM Results

5.3.1 Tundra

The tundra biome shows a weak biodiversity effect. A reason for that could be the cold temperatures and short growing season. Due to the hard environmental conditions, species richness may matter less than other factors. The tundra biome is described to be temperature-limited but not water-limited (Vicente-Serrano et al. 2013) which is why a weak drought response, as shown in the results, was expected. But there is also mixed evidence for biodiversity buffering during multi-year droughts or droughts in general. Rietze et al. (2024) and Chen et al. (2025) showed that there is some local buffering due to higher biodiversity, but overall the evidence tends to low resistance.

The tundra biome has a very limited recovery capacity. Biodiversity has only a weak

effect on recovery, even under severe droughts. Recovery may be controlled by other factors, such as abiotic limits rather than species complementarity. Schwalm et al. (2017) found that recovery in tundra biomes is very slow due to short growing seasons and low productivity. Due to the fact that tundra is a temperature-limited area rather than water-limited, the responses to droughts are muted (Vicente-Serrano et al. 2013). Chen et al. (2025) found only slight vegetation declines during multi-year droughts but extremely long recovery times after multi-year droughts, which aligns with the trend seen in Figure 4.7.

Overall, tundra ecosystems show only weak biodiversity effects on both drought resistance and recovery. Vegetation responses are largely constrained by temperature, short growing seasons, and low productivity, which limits the role of species interactions. As a result, abiotic controls dominate tundra drought dynamics, and biodiversity contributes only marginally to ecosystem stability under multi-year droughts.

5.3.2 Temperate Grassland

Temperate grasslands show the second strongest biodiversity effect on drought resistance in the BAM results. These systems are often dominated by few species, so increases in species richness enhance functional complementarity and stabilise vegetation greenness during multi-year droughts. Despite experiencing some of the strongest global NDVI declines due to strong water limitation (Chapin et al. 2013; Chen et al. 2025), biodiversity effectively buffers productivity losses through functional diversity, such as deep-rooted and phenologically complementary species (Isbell et al. 2015; Mariotte et al. 2013). The resistance effect is substantial but weaker than in boreal forests, consistent with evidence that biodiversity buffering weakens under prolonged or repeated droughts (Craine et al. 2013). Regional variation in grassland biodiversity likely contributes to the moderate effect size observed at the global scale (Chapin et al. 2013).

Temperate grasslands also show the strongest biodiversity effect on post-drought recovery, with the fastest recovery among the studied biomes (Figure 4.7). Species richness and alpha diversity are particularly beneficial under severe drought conditions, supporting rapid regrowth through complementary rooting strategies, phenology, and the presence of legumes (Mariotte et al. 2013; Mackie et al. 2019). However, recovery remains constrained under repeated or prolonged droughts (Craine et al. 2013). Overall, biodiversity enhances recovery efficiency and timing in grasslands, but high drought sensitivity means that its stabilising role relies on rapid functional compensation rather than long-term resistance.

Taken together, temperate grasslands benefit strongly from biodiversity during both drought resistance and recovery, but through different mechanisms. While biodiversity buffers productivity losses during droughts by enhancing functional complementarity, its greatest contribution lies in enabling rapid post-drought recovery. This highlights

temperate grasslands as ecosystems where biodiversity is most effective by accelerating compensation processes rather than by preventing drought impacts altogether.

5.3.3 Boreal Forest

Biodiversity had the strongest effect on resistance in the biome boreal forest. Additional species provide disproportionately large gains in greenness under multi-year drought conditions and biodiversity acts as a strong buffer during this particular climatic stress. This pattern aligns well with ecological expectations. Boreal forests have relatively low baseline diversity (Woodward et al. 2004), which means that each additional species can introduce new functional traits that can substantially improve the stability of the ecosystem during droughts. Although boreal forests are known to be less drought resistance due to strong climatic limitations, as seen during events such as the 2018 European drought (Martínez-García et al. 2024), even modest increases in biodiversity can enhance short-term functional stability. This is supported by studies showing that small gains in tree species diversity improve drought responses and growth performance (D'Orangeville et al. 2018).

Boreal forests showed the slowest recovery after multi-year droughts. The influence of biodiversity on recovery was moderate, with species richness contributing most under severe drought conditions. Recovery may be limited by physiological constraints, so biodiversity plays a supporting but not dominant role. Schwalm et al. (2017) also states that boreal forests recover extremely slowly. It often takes them many years to decades to recover. Boreal forests have low biodiversity, which limits functional complementarity (Woodward et al. 2004). There is some evidence that more diversity can enhances recovery slightly (D'Orangeville et al. 2018). Multi-year droughts lead to moderate NDVI declines but long-lasting legacy effects (Chen et al. 2025; Martínez-García et al. 2024).

Overall, the results indicate that biodiversity provides the greatest marginal benefit in boreal forests, where low baseline diversity and slow ecosystem dynamics allow additional species to enhance functional complementarity and drought resistance. In contrast, recovery remains strongly constrained by physiological limits and slow growth rates, meaning that biodiversity supports regrowth only to a limited extent and resilience operates within tight environmental boundaries.

5.3.4 Montane Forest

Montane forests exhibit the weakest link between biodiversity and drought resistance in the BAM model. Although mixed-species stands can provide some local buffering, biodiversity cannot compensate for the dominant roles of climatic stress, structural rigidity, and disturbance legacies in determining drought outcomes (Szejner et al. 2019). A possible explanation could be the strong climatic and topographic constraints where biodiversity has limited influence on greenness during multi-year droughts. This finding aligns with

the ecology of montane ecosystems, where harsh environmental and structural conditions limit how much biodiversity can help. These forests often face intense competition for water because of dense stands which is a condition that is worsened by decades of fire suppression. As a result, drought stress is magnified, with trees becoming more vulnerable to insects and diseases (Stephens et al. 2012). On top of that, steep slopes and shallow, nutrient-poor soils place further strain on vegetation, leaving little room for additional species to meaningfully boost drought resilience.

Montane forests exhibit only a limited biodiversity response to recovery. The regrowth is rather slow and constrained. Therefore, biodiversity has only a limited effect on recovery in montane forests. The regeneration was overall slow and constrained. One possible explanation could be structural constrains such as steep slopes, shallow soils, competitions and water stress (Faber-Langendoen et al. 2016; North et al. 2016). Droughts are a stress factor in multivle ways, it can lead to vegetation sicknesses such as pests but also to fire supression (Stephens et al. 2012; North et al. 2016). After a drought NDVI remains low (Hankin et al. 2024), which indicates slow recovery. Szejner et al. (2019) states that biodiversity improves recovery only locally and not at biome scale, which is hard to argue with the BAM results, because the analyses was done at a biome scale.

Overall, montane forests show the weakest biodiversity effects on both drought resistance and recovery. Climatic and structural constraints dominate vegetation responses, leaving limited scope for biodiversity to enhance stability. While species diversity may provide local buffering, ecosystem-scale resistance and recovery are primarily governed by abiotic stress and slow regeneration dynamics, leaving little scope for biodiversity to substantially enhance resilience under multi-year droughts.

5.3.5 Tropical and Subtropical Forest

In tropical and subtropical forests biodiversity only showed a moderate resistance effect. Tropical and subtropical forests already have a very high baseline biodiversity and strong functional redundancy (Chapin et al. 2013), and adding more species may not provide additional protection against prolonged, multi-year droughts. However, biodiversity can still provide benefits, though its effects are less pronounced than in ecosystems with lower diversity. Although greater species richness does enhance resilience, the effect is smaller than in ecosystems with lower diversity. Studies show that tropical forests tend to experience only moderate NDVI declines during prolonged droughts (Chen et al. 2025), reflecting their strong inherent resistance. Mechanisms like compensatory growth and asynchronous species responses help stabilize productivity in the short term, but these benefits reach a saturation point as diversity increases (Xu et al. 2024).

Tropical and subtropical forests tend to recover strongly on their own, and greater biodiversity does not automatically lead to a better or faster recovery. Recovery in

this biome could be more dependent on other factors such as light availability and the dominance of certain species than on species richness alone. High functional diversity enables compensatory growth and rapid short-term recovery in tropical and subtropical forests (Xu et al. 2024). Multi-year droughts cause only moderate vegetation declines compared to other biomes (Chen et al. 2025). Recovery is usually rapid, but resilience declines under repeated droughts in parts of the Amazon.

Overall, tropical and subtropical forests exhibit high inherent resistance and recovery capacity, driven by high baseline biodiversity and functional redundancy. Biodiversity provides additional stabilisation, but its marginal benefits are limited, as many ecological functions are already filled. Consequently, ecosystem responses are increasingly constrained by repeated droughts and structural changes, particularly in parts of the Amazon, rather than by species richness alone.

5.3.6 Synthesis of biodiversity effects across biomes

Across biomes, biodiversity is associated with higher ecosystem resistance to multi-year droughts and contributes to post-drought recovery, but these effects are strongly biome dependent. This context dependence is consistent with the view that biodiversity–climate relationships are not easily generalised across systems (Chapin et al. 2013). In a climate where multi-year droughts are intensifying in heat, dryness, and duration (IPCC 2021; Chen et al. 2025), the BAM results indicate that biodiversity effects are shaped by baseline diversity and environmental constraints.

For resistance, biodiversity increases vegetation greenness across all biomes, with the strongest effects in boreal forests and temperate grasslands where baseline diversity is lower and additional species can increase functional complementarity. Effects are moderate in tropical and subtropical forests, where high baseline diversity already provides functional buffering, and weakest in tundra and montane forests, where climatic and topographic constraints dominate vegetation responses. Across biomes, species richness and alpha diversity contribute in distinct ways: species richness primarily elevates baseline resistance, whereas alpha diversity shows stronger drought-modulated effects, particularly under severe drought conditions (Table 4.3 and Table 4.7).

Recovery patterns also differ markedly among biomes. Tropical forests show high inherent recovery capacity, whereas tundra exhibits very limited regrowth potential, and biodiversity effects on recovery are generally weaker than for resistance. This aligns with evidence that recovery can lag behind regrowth, particularly under high atmospheric dryness (Zhang et al. 2023). Overall, the BAM results support the conclusion that biodiversity does not uniformly stabilise ecosystems under multi-year drought. Instead, resistance and recovery emerge from biome-specific mechanisms that interact with drought severity and time since disturbance.

Overall, these findings answer the third research question: *How do the effects of biodiversity on multi-year drought resistance and recovery vary across major global biomes?* Biodiversity effects differ strongly among biomes, with the greatest resistance benefits in boreal forests and temperate grasslands, moderate effects in tropical and subtropical forests, and weakest effects in tundra and montane forests, while recovery benefits are more limited and biome-dependent. Temperate grasslands exhibit the strongest and fastest recovery, with biodiversity playing a pronounced role under severe drought conditions. This confirms that biodiversity stabilises ecosystems under droughts through distinct, biome-specific mechanisms.

5.4 Methodological Considerations and Limitations

5.4.1 Resistance vs. Recovery: Conceptual and Analytical Differences

A comparison of the resistance and recovery models shows that ecosystem stability before and after droughts is shaped by different ecological processes. This directly reflects the core research question of how biodiversity influences resistance and recovery across biomes. The recovery model has a lower explanatory power, indicating that post-drought regrowth is influenced by additional factors. These include soil moisture recharge, physiological growth limitations, and species-specific regeneration traits. Such processes vary strongly among biomes and are difficult to capture statistically at a global scale. As a result, biodiversity effects appear more diffuse and context dependent during recovery than during resistance. Despite its lower R^2, the recovery model still reproduces large-scale patterns, showing that biodiversity and drought severity do influence recovery, though less deterministically than immediate drought responses. This separation between resistance and recovery underscores that ecosystem stability is multidimensional and the ability to withstand droughts does not necessarily predict the ability to recover afterward.

For this study, this means that biodiversity's role must be assessed separately for each stability component. While high biodiversity consistently buffers vegetation loss during droughts, its influence on post-drought recovery is less uniform and more strongly shaped by biome-specific ecological contexts. Analytically, this makes it explicit that resistance and recovery must be modelled with distinct predictors and interaction structures, as done in this study. More broadly, the results reinforce that relying solely on resistance metrics can provide an incomplete or misleading picture of resilience under climate extremes, highlighting the need for multi-dimensional stability frameworks that distinguish immediate drought impacts from longer-term recovery capacity.

5.4.2 Data Resolution and Global-Scale Limitations

Spatial Resolution

In global studies, the spatial resolution is often reduced to simplify the already very large datasets. The analysis uses a 10 km spatial resolution, at which individual grid cells often encompass multiple vegetation types, microclimates, and land-use histories. The upscaling of species richness and alphadiversity can lead to loss of fine-scale biodiversity patterns, especially in heterogeneous landscapes. The qkNDVI data was initially provided at a 10 km resolution, which reduces the resolution mismatch. However, fine-scale vegetation processes are still not captured and NDVI anomalies generally represent aggregated canopy responses rather than local dynamics. The 10-km harmonization inevitably smooths fine-scale ecological variation, which likely weakens biodiversity effects and results in conservative rather than exaggerated estimates. At this resolution, important local drivers cannot be captured. These include soil texture, microtopography, and disturbance legacies, even though they strongly influence drought impacts and post-drought recovery. As a result, the model reflects broad-scale biodiversity–drought relationships, while finer ecological mechanisms remain unresolved. This also means that some of the apparent differences between biomes may partly reflect unresolved internal heterogeneity rather than true ecological contrasts. Consequently, the estimated biodiversity effects should be interpreted with caution. They capture robust global tendencies but cannot represent the complexity of local processes or the full range of ecosystem responses.

Biome Aggregation

The aggregation of Köppen–Geiger climate classes into six broad biomes was necessary for a coherent global comparison, but it comes with important limitations. While this simplification improves interpretability, it masks substantial ecological variation within each biome. For example, tropical dry and evergreen forests, as well as different structural and functional subtypes within boreal forests, are grouped together. As a result, the biome effects in the model represent a combined signal of climate, vegetation structure, and functional traits rather than clean ecological categories. This means that some of the observed biome-level differences may partly reflect internal heterogeneity rather than true functional contrasts. Consequently, while the aggregation is appropriate for global-scale modelling, it limits the ability to draw fine-scale ecological conclusions and should be interpreted with caution.

Stratified Subsampling

The stratified subsampling in the SR–SPEI space was important to ensure that the analysis does not become dominated by drought-prone, low-diversity regions. This approach gives

a much fairer representation of biodiversity–drought combinations and helps the model focus on the actual shape of the SR–drought relationship. At the same time, it introduces some limitations. Rare combinations, such as very high species richness under severe droughts, remain underrepresented and therefore associated with higher uncertainty. This uncertainty is greatest in parts of the predictor space where ecological responses may be most informative. In addition, the global frequency of SR–SPEI combinations is not preserved, as the sampling strategy prioritised inference over reproducing global proportions. This means the models are well suited for understanding processes, but they cannot be used to quantify how common certain drought impacts are at the global scale.

Event Selection: Top 100 Multi-Year Droughts

The decision to focus only on the Top-100 multi-year drought events was mainly a practical one. Including every drought across the entire study period would have created a dataset far too large to handle, even for BAM, which makes the modelling much harder. This choice allows the analysis to capture the most severe and ecologically meaningful droughts, but it also means that the study is centred on rare, high-impact extremes. As a result, the patterns we observe reflect how ecosystems behave under exceptional stress, not under the far more common moderate droughts. This is a significant limitation, as moderate events shape long-term ecosystem dynamics and are underrepresented in the inferred biodiversity effects. By looking at Figure 3.1 it becomes evident that many regions of the globe were not taken into account. Large areas of Europe and Australia do not feature any of the top 100 drought events. Conversely, the figure also highlights where the majority of these severe events occur.

5.4.3 Strengths and Weaknesses of the BAM Framework

Strengths of the BAM Framework

The main strength of the BAM framework is its ability to efficiently handle very large datasets. This is achieved using discretization, chunking, and the fast REML (fREML) algorithm for smoothness selection. It also captures broad spatial structure via the Gaussian-process (GP) smooth. This helps reduce large-scale spatial autocorrelation. Another strength of the BAM is that it incorporates hierarchical variation through random-effect smooths for biomes and drought events. This allows the model to account for systematic differences among ecological contexts and event-specific dynamics that would otherwise bias global estimates. Partial pooling is an integral part of the BAM framework and helps stabilise estimates by shrinking extreme or noisy effects toward the group mean. This is particularly important in a global dataset where some biomes or rare SR–SPEI combinations are only sparsely represented. Without partial pooling, these

cases would easily lead to overfitting or ecologically unrealistic estimates. At the same time, the flexible nonlinear smooths in BAM allow biodiversity and drought effects to vary across biomes. This avoids enforcing a single global relationship. Together, these features ensure that the model captures meaningful ecological variation while keeping estimates robust in regions of low data density.

Weaknesses of the BAM Framework

The BAM framework does not only have strengths but also some limitations. One limitation is that BAM is fundamentally descriptive. This means that the smooth terms capture patterns in the data but cannot disentangle the underlying mechanisms. Therefore, the results should not be interpreted causally. Extrapolation is another challenge, particularly in parts of the species richness and SPEI space where data are sparse, such as very high biodiversity under extreme multi-year droughts. In these regions, smooth functions become less reliable and uncertainty increases.increasingly uncertain the further they move away from observed conditions. Although the spatial Gaussian-process smooth absorbs most broad-scale spatial structure, it cannot fully capture fine-scale ecological dependencies, which leaves some residual spatial autocorrelation in the model. Partial pooling, while stabilising estimates, can also shrink extreme responses toward biome-level means and may therefore obscure unique local or biome-specific dynamics. Additionally, the random-effect smooths assume that groups are exchangeable, which simplifies the modelling but may overlook meaningful ecological differences among biomes or drought events. Together, these limitations highlight that BAM provides a powerful but inherently constrained view of global biodiversity–drought relationships.

A related implication of this modelling choice becomes clear when comparing it with a simplified model specification. In that alternative setup, biodiversity effects are assumed to be globally homogeneous, and biomes are included only as random intercepts. In that alternative formulation, the interaction between species richness and drought severity was statistically significant at the global level (see Appendix Table A.4). However, once biome-specific random slopes were introduced in the final BAM, this global interaction was no longer significant. This indicates that the apparent buffering effect of species richness under increasing drought severity is not uniform across ecosystems, but instead reflects heterogeneous, biome-dependent responses. Allowing biodiversity–drought relationships to vary among biomes shifts explanatory power away from a single global interaction. Instead, it emphasises context-specific effects that are ecologically more plausible and better aligned with the study's research questions.

Conclusion of the BAM Framework

Overall, the BAM framework was a suitable and effective choice for this study. It enabled the analysis of a truly global dataset, captured key biodiversity–drought relationships, and handled spatial complexity in a way that would not have been feasible with more traditional modelling approaches. At the same time, remaining spatial dependence, the descriptive nature of the smooth terms, and uncertainty in data-sparse regions indicate scope for methodological improvement. Future work using additional spatial predictors, finer-resolution data, or more mechanistic models could help clarify biodiversity's role in drought resistance and recovery.

5.4.4 Residual Spatial Autocorrelation

Even after including a spatial Gaussian-process smooth, the residuals of both the resistance and recovery models show a positive Moran's I, indicating that some spatial dependence remains. The GP smooth removes broad spatial gradients but cannot represent finer ecological structure related to soils, land use, degradation history, or topography. This is also visible in the residual maps (Figure 4.2 and Figure 4.6), where clustered patterns remain in several regions. These patterns suggest that drought responses have a geographically structured component that extends beyond the predictors used in the models.

The differences between the resistance and recovery residuals also reveal important aspects of ecosystem behaviour. In the resistance model (Figure 4.2), residual clustering is comparatively weak, indicating that most spatial structure is well explained by drought intensity, biodiversity, biomes, and the spatial smooth. In contrast, the recovery residuals (Figure 4.6) show more pronounced clusters across regions such as southern Africa, Siberia, and parts of South America. This mirrors the lower R^2 of the recovery model and indicates that post-drought regrowth is driven by spatially structured processes not captured at 10 km resolution.

Some of the remaining spatial dependence is also inherent to the 10 km grid itself, which blends highly heterogeneous landscapes into single cells. This smoothing inevitably dampens fine-scale variation and makes it difficult for the model to fully represent local ecological dynamics. As a consequence, the effect estimates should be interpreted as broad global patterns rather than precise local predictions. Residual spatial autocorrelation highlights a key limitation of global-scale models, as some ecological processes remain beyond the reach of spatial smoothing.

5.5 Synthesis and Broader Implications

5.5.1 Contribution and synthesis of key findings

Before turning to the broader implications, it is important to clarify what this study contributes to the existing body of research. This study analyses biodiversity–drought relationships at a global 10 km scale and therefore provides a comparative perspective across biomes that is often missing from regional or experiment-based studies. At the same time, the BAM models used here describe correlations rather than processes, which means that the mechanisms behind the observed patterns cannot be directly determined. The strength of the study thus lies in identifying global-scale ecological tendencies and biome-specific contrasts, rather than explaining underlying physiological or community-level processes.

Taken together, the results show that biodiversity can act as an ecological buffer against multi-year droughts. However, this buffering is not uniform across stability dimensions or across biomes. Biodiversity contributes most strongly to drought resistance by reducing vegetation loss during extreme events, while its role in recovery mainly operates through balanced species contributions and functional complementarity.

In relation to the research gap identified in the literature review, this study provides a systematic global assessment of biodiversity–drought relationships that has so far been lacking. While earlier work has largely focused on regional case studies, single biomes, or experimental settings, the present analysis compares resistance and recovery processes consistently across multiple biomes using spatially explicit data. By explicitly integrating biodiversity metrics into a global drought framework and allowing their effects to vary across ecological contexts, this study moves beyond climate-only or vegetation-only perspectives that dominate existing global assessments. In doing so, it demonstrates that biodiversity effects on drought impacts are not universal but strongly biome dependent, thereby refining and qualifying the broadly stated assumption that biodiversity generally buffers ecosystems against drought.

5.5.2 Implications across biomes and for applied assessment

In terms of applied implications, the biome-specific patterns identified in this study are particularly relevant. Boreal forests and temperate grasslands emerge as biomes where additional biodiversity yields comparatively large gains in drought resistance and, in the case of grasslands, also in recovery. In these systems, conserving and restoring species-rich and functionally diverse communities can meaningfully strengthen ecosystem stability under increasing drought pressure.

In contrast, tundra and montane forests show much weaker biodiversity effects. Strong

abiotic and structural constraints limit how much additional species richness can improve resistance or recovery, indicating that biodiversity alone is unlikely to substantially enhance drought buffering in these ecosystems.

The results also suggest that biodiversity metrics should be more explicitly integrated into drought-risk assessments and climate adaptation planning. Species richness and alpha diversity capture different aspects of ecological stability, and their roles vary across biomes and along drought gradients. Incorporating these dimensions into risk models could help identify where biodiversity conservation is most effective and where other measures, such as soil protection or fire management, are more appropriate.

5.5.3 Geospatial Perspective and Spatial Integration

From a GIS perspective, this study uses geospatial methods primarily as an integrative framework rather than as a classical local-scale GIS analysis. GIS was essential to harmonize biodiversity, climate, and vegetation datasets from different sources and spatial resolutions into a consistent global grid. This spatial integration allowed a systematic comparison of biodiversity–drought relationships across biomes.

At the same time, the global 10 km scale, biome aggregation, and residual spatial autocorrelation underline that the findings should be used to guide broad priorities rather than to derive detailed local prescriptions. The coarse spatial resolution inevitably smooths the fine-scale ecological heterogeneity, which means that local processes related to soils, land use, or disturbance history cannot be resolved. As a result, the results should be interpreted as broad-scale patterns rather than site-specific insights.

5.5.4 Outlook

This study examines the relationship between biodiversity and drought on a global, cross-biome scale and demonstrates that the impact of biodiversity on ecosystem resistance and recovery is highly context-dependent. The patterns found here offer a solid basis for further research, despite the descriptive modelling approach and relatively coarse spatial scale limiting detailed, process-level insights.

Expanding on these findings might entail applying comparable frameworks at regional levels to gain a deeper understanding of local dynamics, or integrating biodiversity metrics with more detailed information on soil, land use, or functional characteristics. Assessing how biodiversity loss and biome shifts might impact ecosystem stability under increasingly frequent and severe droughts would also benefit from linking biodiversity–drought relationships to future climate projections.

In this sense, the present study should be understood as a stepping stone toward integrated, multi-scale assessments of ecosystem resilience in a changing climate.

6. Conclusion

This study investigated how biodiversity shapes ecosystem resistance and recovery during and after multi-year droughts, and how these relationships differ across the major global biomes: Tundra, montane forests, temperate grasslands, boreal forests and subtropical and tropical forests. The analysis addressed three questions concerning drought resistance, post-drought resilience, and biome-specific variation in biodiversity effects. The method used in this study was the BAM model, which extends the generalized additive model framework to efficiently handle very large spatial datasets while capturing nonlinear relationships, spatial structure, and hierarchical variation through penalised smooth terms and random-effect smooths.

The results show that biodiversity improves both drought resistance and recovery after dry periods, although the strength of these effects varies considerably depending on the biome. The greatest benefits are seen in boreal forests and temperate grasslands, where biodiversity leads to a significant increase in stability. Tropical and subtropical forests show only moderate biodiversity effects, likely due to high baseline diversity and functional redundancy. By contrast, tundra and montane forests exhibit very weak biodiversity buffering, as harsh abiotic constraints limit the extent to which additional species can support resistance or recovery.

These patterns represent broad-scale correlations rather than causal mechanisms, reflecting limitations of the global 10 km resolution and the descriptive nature of the BAM framework. Another key limitation is that only the 100 most severe multi-year droughts were included, resulting in a data gap because the events are not evenly distributed across the globe and across the biomes. Nevertheless, the study provides a global, cross-biome perspective on how different dimensions of biodiversity contribute to drought stability.

The findings highlight that biodiversity can strengthen ecosystem stability under increasing drought pressure, but that its benefits differ across stability dimensions and biomes. Conservation and management strategies should therefore be adapted to ecological context and incorporate biodiversity metrics into drought-risk and climate-adaptation planning. Future research should explore how climate-driven biodiversity loss and compositional change may alter these stability relationships, and how finer spatial scales, trait-based approaches, and mechanistic models can improve our understanding of biodiversity's role in drought resistance and recovery.

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A. Appendix

A.1 Exploratory Linear Mixed Model (LMM)

Linear Mixed Models (LMMs) extend classical linear regression by incorporating both fixed and random effects, allowing the analysis of hierarchical or grouped data (Gelman and Hill 2007; Pinheiro and Bates 2000). Random effects account for non-independence among observations arising from repeated measurements or shared group membership, thereby improving inference in ecological and spatial datasets (Bolker et al. 2009; Zuur et al. 2009).

In this study, an LMM was fitted as an initial exploratory model to quantify biodiversity–drought relationships while accounting for clustering by drought events. Vegetation greenness (qkNDVI) was modelled as a function of alpha diversity, species richness, drought severity (SPEI), elevation, year, and drought event length, including an interaction between alpha diversity and species richness:

$$qkNDVI \sim \text{alphadiv} \times SR + SPEI + elevation + Year + event\_length + (1 \mid MYMD10).$$

A random intercept for drought event ID (`MYMD10`) captured event-level heterogeneity and accounted for repeated observations within the same drought. The model was fitted using the `lme4` package with significance testing via `lmerTest`.

While LMMs are well suited for identifying hierarchical structure and broad ecological relationships, they do not explicitly model spatial autocorrelation and scale poorly for very large spatial datasets. These limitations motivated the use of spatially explicit GAM/BAM models as the primary analytical framework in this thesis.

A.1.1 Results Linear Mixed Model

The LMM revealed significant positive main effects of alpha diversity and species richness on vegetation greenness during droughts (Table A.1). Drought severity (SPEI) was positively associated with qkNDVI, indicating higher greenness under less severe drought conditions, while elevation and year showed small but significant negative effects. The interaction between alpha diversity and species richness was significantly negative,

suggesting diminishing marginal gains in greenness when both biodiversity components increase simultaneously.

Random-effects variance indicated substantial between-event variability (Table A.2), confirming that drought events differ markedly in their overall vegetation response. Overall, the LMM provided a useful baseline for understanding hierarchical drought effects but lacked the flexibility to capture nonlinear and spatially structured biodiversity–drought relationships, which were addressed using BAM in the main analysis.

Table A.1: Fixed effects of the exploratory Linear Mixed Model (LMM).

Predictor	Estimate	Std. Error	t value	p value
Intercept	0.986	0.0226	43.67	< 0.001
Alpha diversity	0.00596	0.00024	24.81	< 0.001
Species richness (scaled)	0.02252	0.00047	48.41	< 0.001
SPEI (scaled)	0.01022	0.00018	57.50	< 0.001
Elevation	−0.00948	0.00032	−29.38	< 0.001
Year (centred)	−0.00046	0.00014	−3.39	< 0.001
Event length	−0.00347	0.00430	−0.81	0.422
Alpha diversity × Species richness	−0.00302	0.00017	−17.68	< 0.001

Table A.2: Random effects variance components of the exploratory LMM.

Group	Effect	Variance	Std. Dev.
MYMD10	Intercept	0.00836	0.0914
Residual		0.00570	0.0755

Table A.3: Model diagnostics for the exploratory LMM.

Metric	Value
Number of observations	226,822
Number of drought events (MYMD10)	97
REML criterion	−527,658.4
Residual SD	0.0755

A.2 Alternative Model Specification

Table A.4 presents the summary of a simplified BAM without biome-specific biodiversity slopes. This model includes biome-level random intercepts only and assumes a global biodiversity–drought interaction.

Table A.4: Parametric coefficients of the alternative BAM for drought resistance (Gaussian, fREML). The model includes biome-level random intercepts only and does not allow biodiversity effects to vary across biomes. All predictors were centred and standardised prior to fitting.

Term	**Estimate**	**Std. Error**	**t value**	**p-value**	**Sig.**
Intercept	0.9156	0.0296	30.89	< 0.001	***
Species richness	0.0155	0.00049	31.60	< 0.001	***
Alpha diversity	0.00289	0.00024	12.28	< 0.001	***
Drought severity	-0.0107	0.00019	-56.89	< 0.001	***
Elevation	0.00636	0.00042	15.04	< 0.001	***
Event length	0.0131	0.00548	2.39	0.017	*
Species richness × Drought	0.00233	0.00020	11.82	< 0.001	***
Alpha diversity × Drought	0.00316	0.00017	19.06	< 0.001	***

Artificial Intelligence Statement

Artificial intelligence (AI) tools were used in the preparation of this thesis in a supportive and assistive capacity only. Their use was limited to technical assistance, language refinement, and clarification tasks. All scientific reasoning, methodological decisions, data interpretation, and conclusions are entirely my responsibility. AI tools were not used to replace independent analysis or scientific judgement.

Coding and data analysis

- **ChatGPT**: Assistance with coding-related questions in `R`, including troubleshooting, syntax clarification, and optimisation of analysis workflows.

All code was developed iteratively, critically reviewed, and validated. No code was implemented without full understanding. I take full responsibility for all analyses and their reproducibility.

Figures and workflow support

- **ChatGPT**: Support for the preparation of figures and schematic workflow overviews (e.g. conceptual models and visualisations).

AI assistance was limited to technical support. All analytical logic and design decisions originated from me.

Language and editorial support

- **ChatGPT**, **DeepL**, **QuillBot**, and AI-supported writing tools within **Overleaf**: Used for linguistic revision, paraphrasing of my own text, and stylistic refinement.

AI tools were not used to generate original scientific content or to paraphrase external sources. All revised text was reviewed and approved by me.

Literature and conceptual work AI tools were not used for literature search, literature selection, or conceptual development. All theoretical framing, hypothesis formulation, and interpretation of results were conducted independently. AI assistance was limited to clarification of general methodological concepts where needed.

Personal declaration

I hereby declare that the material contained in this thesis is my own original work. Any quotation or paraphrase from the published or unpublished work of another individual or institution has been duly acknowledged. This thesis has not been submitted, in whole or in part, to any other institution for assessment purposes.

Zurich, December 18, 2025

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