**Homogenization of vertical strategies under future climate scenarios**

Climate change is rapidly altering the taxonomic composition of species assemblages across the globe (Scheffers et al. 2016), as well as the composition of species traits (Feeley et al. 2020, Lajeunesse and Fourcade 2023, Chust et al. 2024, Borderieux et al. 2024). Changes in trait distributions over time can be predicted based upon predictable variation in traits across environmental gradients. For example, the thermal tolerance of species assemblages displays predictable variation across elevation gradients. As the climate warms and species shift toward higher elevations, the thermal tolerance of assemblages increases as cool-adapted species become locally extirpated and warm-adapted species immigrate into communities (a process known as thermophilization) (Feeley et al. 2020). The structure and function of future species assemblages may be predicted by forecasting changes in assemblage traits. However, examining changes in individual traits, such as thermal tolerance, may overlook how interacting traits can influence functional changes in species composition (Green et al. 2022).

Verticality is a trait syndrome that displays predictable variation across spatial and temporal environmental gradients (Scheffers et al. 2013, Oliveira and Scheffers 2019, Basham and Scheffers 2020, Basham et al. 2023) and represent several key ecological characteristics that influence geographic distributions and vulnerability to climate change, including fitness under different abiotic conditions and dispersal ability (Green et al. 2022). Here, we define verticality as the average height occupied by species in an assemblage across a gradient from fossorial (0) to terrestrial (0.5) to arboreal (1). Vertical use of habitat space influences exposure to abiotic conditions. Fossorial and terrestrial habitats experience greater climate stability, which limits species’ exposure to extreme hot, cold, and dry conditions relative to species living in the canopy where temporal climate fluctuations are more extreme. Some arboreal species exhibit physiological and/or morphological adaptations to extreme climate conditions, such as higher critical thermal maxima, larger size, or desiccation resistant skin (Tracy et al. 2010). These adaptations may reduce vulnerability to climate change relative to terrestrial species. In the absence of physiological adaptations arboreal species are faced with two options when exposed to more extreme climate conditions in the canopy: dispersal to more suitable habitat or local extirpation.

Arboreality is associated with improved dispersal capacity across horizontal and vertical dimensions relative to terrestrial species (Scheffers et al. 2017). Horizontal dispersal capacity may facilitate range shifts toward higher latitudes or elevations in response to climate change. Additionally, arboreal species can disperse across the vertical microhabitat gradient, which enables behavioral adaptation to extreme climate conditions. By moving toward the ground, arboreal species reduce their exposure to extreme hot and dry conditions that occur higher in the canopy (Basham and Scheffers 2020). If arboreal species exhibit range shifts at a greater rate than terrestrial species, vertical dispersal, or local extirpation in the absence of physiological adaptations or dispersal, verticality of assemblages may decline, a process we hereafter term ‘terrestrialization’. Despite associations between climate, verticality, and species’ geographic ranges, patterns of verticality across large spatiotemporal extents and changes in verticality in response to climate change are largely unknown. Here, we evaluate what environmental factors influence the verticality of vertebrate assemblages and predict how climate change may impact environmental conditions that have led to present day patterns of verticality globally.

We mapped species assemblages for birds, mammals, reptiles, and amphibians, which we defined as species that co-occur within 111 km grid cells based range maps from the IUCN, BirdLife International, and the Global Assessment of Reptile Distributions (Roll et al. 2017, BirdLife International and Handbook of the Birds of the World 2022, Caetano et al. 2022, IUCN 2023). For each species, we assigned a verticality score between zero (fully fossorial) and one (fully arboreal) based on vertical strategies described in TetrapodTraits and EltonTraits databases. We then calculated the mean verticality of each assemblage. To remove effects of the positive correlation between verticality and species richness, we calculated the standardized effect size (SES) of mean verticality, using biogeographic realms to define species pools (Oliveira and Scheffers 2019). We then used spatial autoregressive (SAR) models with a spatial error term to evaluate the impacts of climatic, topographic, and vegetative variables on assemblage verticality. Using models trained on historic climate data for the period 1981-2010, we predicted verticality for the time period 2071-2100 using future climate scenario SSP585, which represents the upper boundary of predicted warming under a scenario of fossil-fueled development. Though climate change will impact vegetation structure, we were unable to incorporate predictions of future vegetation into the models due to a lack of global future predictions of vegetation height and density.

# Global patterns of vertical stratification

Across vertebrate classes, there was a latitudinal gradient in assemblage verticality characterized by higher verticality than expected by chance in tropical regions (Figure 1). The latitudinal gradient in assemblage verticality remained apparent when only forested biomes were considered, indicating that lack of arboreality in temperate regions is not caused by lack of vegetation to support arboreal lifestyles (Fig. S 1).

Precipitation, climatic stability, temperature, and vegetative complexity impacted verticality, though the direction of impacts differed across vertebrate classes for some variables (Figure 2). Across all vertebrate classes, verticality was positively impacted by precipitation during the dry season and negatively impacted by precipitation seasonality. Water availability thus facilitates the occurrence of arboreal life strategies. In addition to reducing physiological stress, consistent moisture input from rain or cloud mist provides suitable conditions for high epiphyte abundance (cite), increasing niche diversity and resource availability in the canopy (cite). For example, cloud mist increases the consistency of water input to the canopy at high elevations (cite). High epiphyte abundance in these regions may increase resource availability in the canopy, thus favoring arboreality, as shown for birds. While positive impacts of elevation were not apparent for other taxa, increased density of understory vegetation at higher elevations may contribute to this result (Basham et al. 2023). In regions that receive less rain or longer dry seasons, the ephemeral availability of water in the canopy limits the viability of arboreal life strategies.

Impacts of temperature on verticality varied among vertebrate classes. Increasing minimum temperatures of the coldest quarter were associated with higher verticality for mammals and reptiles (Figure 2). Minimum cold temperatures could thus pose a poleward limit on geographic distributions of mammals and reptiles. Though the SES of amphibian verticality was not significantly associated with minimum temperature, mean verticality exhibited positive responses. Maximum temperatures in the warmest quarter had opposing effects on endotherms and ectotherms. High maximum temperatures positively impacted bird verticality and did not significantly impact mammal verticality. In contrast, maximum temperatures negatively impacted reptile and amphibian verticality. Though arboreal habitats can exhibit average temperatures over 2℃ higher than terrestrial habitats (Scheffers et al. 2013), critical thermal maxima of arboreal species may not substantially exceed that of terrestrial species (Carilo Filho et al. 2021). High temperatures simultaneously exacerbate negative impacts of low water availability in the canopy, possibly limiting arboreality.

Climate velocity represents climate instability across geographic timescales and negatively impacted verticality for all classes (Figure 2). Climate stability increases speciation rates and decreases extinction rates (Colville et al. 2020). In tropical forests where complex vegetation structure characterized by multilayered forests (Terborgh 1985) increases opportunities for diversification among arboreal niches, climate stability may therefore facilitate highly arboreal communities (see 11-13 Colville et al. 2020). These results are in contrast to positive associations between climate instability and arboreality at regional scales (Scheffers et al. 2017). Climate stability may therefore provide the conditions necessary for diversification in regions where climatic conditions are suitable for arboreal life strategies, while increased dispersal capacity of arboreal species throughout three-dimensional arboreal environments facilitates persistence in climatically unstable regions (Sandel et al. 2011, Scheffers et al. 2017).

# Terrestrialization and arborealization of assemblage verticality in response to climate change

Under future climate conditions, SAR models predict terrestrialization (i.e., a decline in the SES of verticality) in the tropics and a combination of terrestrialization and arborealization (i.e., an increase in the SES of verticality) in temperate regions (Figure 3). Behavioral thermoregulation (i.e., vertical dispersal) or range shifts (i.e., horizontal dispersal) may contribute to changes in assemblage verticality. Behavioral thermoregulation occurs when species avoid unfavorable climate conditions by sheltering in climatically buffered microhabitats. In the tropics, arboreal species have been observed to increase their use of terrestrial habitats in response to high temperatures and seasonal shifts in precipitation (Basham and Scheffers 2020) (cite). Just as low elevations are expected to experience biotic attrition as species’ ranges shift toward higher elevations (cite), terrestrialization may cause biotic attrition in the canopy. However, microclimatic diversity within the canopy may prevent widespread declines in verticality. For example, species may shelter in tree holes or large epiphytes (Scheffers et al. 2014b, 2014a, Seidl et al. 2020), cool off on tree trunks (cite), or climb higher in the canopy to reap the benefits of higher wind speeds on evaporative cooling (Zlotnick et al. 2024).

In temperate and arctic regions, future climate conditions are expected to favor a combination of terrestrialization and arborealization dependent on hemisphere and biome (Figure 3, Fig. S 2). Global SAR models predicated arborealization in the southern hemisphere as well as parts of the northern hemisphere. Increasing minimum winter temperatures and wet season precipitation without changes in dry season precipitation may favor increasing verticality in these regions (Fig. S 3 - Fig. S 7). Isolated case studies of range shifts across the tropical-temperate transition zone support these changes to the vertical composition of vertebrate assemblages. For example, poleward range edges of several semi-arboreal or arboreal tropical reptiles, including green iguanas, brown anoles, and the neotropical vine snake (*Oxybelis aeneus*), have occurred as increasing minimum winter temperatures release thermal barriers to colonization (Osland et al. 2021). Dispersal capacity of arboreal species (Scheffers et al. 2017) may facilitate latitudinal range shifts and colonization of temperate canopy habitats as the frequency of extreme minimum temperatures declines (Osland et al. 2021). Arborealization may therefore accompany patterns of tropicalization, which occur as the ranges of tropical species shift poleward (Osland et al. 2021).

While models predicted arborealization in the southern hemisphere would occur in forested habitats, SAR models trained on forested biomes indicated arborealization in the northern hemisphere predicted by the global models was restricted to largely non-forested biomes. These changes in verticality may be driven by increased use of terrestrial relative to fossorial habitats or colonization of habitats undergoing borealization (cite). In contrast, future climate conditions in temperate forest biomes in the northern hemisphere are largely predicted to favor terrestrialization. Though limits imposed on arboreal lifestyles by low winter temperatures may be removed under future climate conditions, increasing summer temperatures may exacerbate negative impacts of dry conditions on arboreal species in the northern hemisphere.

# Implications of climate-induced vertical niche shifts

Vertical niche shifts across the globe are predicted to cause global homogenization of vertical strategies as terrestrialization occurs in regions with high verticality and arborealization occurs in areas with low verticality (Figure 4). Vertical homogenization toward terrestrial habitats would impact ecosystem functioning, as arboreal species provide critical services including seed dispersal…. However, these predictions do not account for changes in forest structure or biotic interactions, which may mediate climate change impacts on assemblage verticality.

The presence and diversity of arboreal species is inextricably linked to the presence and complexity of vegetative structure (despite lack of significance of vegetative complexity in SAR models for some mammals and reptiles). Most studies on vertical stratification have suggested foliage density as a driving factor (Basham et al. 2023). Changes in precipitation regimes as the climate changes will impact forest structure, generally reducing height and structural complexity (McDowell and Allen 2015, Ehbrecht et al. 2021). Loss of taller trees favors the growth of understory vegetation, which could cause arboreal species to increasingly use lower positions in the forest (Basham et al. 2023). Climate change may also alter the spatial distribution of tree cover, and consequently the opportunity for arboreality, as borealization occurs at northern latitudes and desertification reduces tree cover in savannas (cite).

Changes in biotic interactions following vertical niche shifts may impede the vertical reorganization of assemblages. Stratification across vertical microhabitats reduces niche overlap between sympatric species, potentially facilitating high diversity in tropical ecosystems (Oliveira and Scheffers 2019). Homogenization of vertical habitat use may therefore increase competitive interactions, limiting the extent to which arboreal species can shift toward lower vertical positions (Scheffers et al. 2013, Oliveira and Scheffers 2019).

# Conclusions

We show that climate impacts the verticality of vertebrate assemblages and that future climate conditions will be suitable for global homogenization of vertical strategies toward terrestrial lifestyles. However, predictions should be cautiously interpreted because 1) models only consider changes in abiotic conditions and 2) spatial relationships between traits and environmental conditions do not always translate to temporal relationships between the same variables (Bjorkman et al. 2018). Vertical habitat use in temperate and tropical ecosystems should be monitored over time to improve our understanding of how climate change may impact the three-dimensional structure of species’ assemblages.

# Methods

## Assemblage verticality

We mapped the verticality of vertebrate assemblages in 111 km grid cells (~1° at the equator) using a cylindrical equal area projection. Range maps were obtained from the IUCN red list for mammals and amphibians (IUCN 2023), BirdLife Internation for birds (BirdLife International and Handbook of the Birds of the World 2022), and the Global Assessment of Reptile Distributions (GARD) (Roll et al. 2017, Caetano et al. 2022). To calculate the verticality of each assemblage (i.e., grid cell), we assigned each species a verticality score between zero and one and took the average verticality of all species whose ranges overlapped with the grid cell. For mammals, reptiles, and amphibians, verticality scores were based on their use of fossorial (0), terrestrial (0.5), and arboreal habitats (1) as defined in the TetrapodTraits database (Moura et al. 2024). This dataset uses phylogenetic imputation to identify traits if trait data is not available in the literature. For species where imputation was necessary, we considered them to use a given vertical niche if the imputation probability exceeded 0.7. For birds, we calculated verticality scores based on their occurrence in different foraging strata as identified in the EltonTraits database (Wilman et al. 2014). We classified foraging below the water surface, around the water surface, and on the ground as 0.5, in the understory as 0.667, mid-high canopy as 0.8337, and in or above the upper canopy as 1. If species used multiple vertical habitats, vertical scores were averaged. For example, if a species occurred in terrestrial (0.5) and arboreal (1) habitats, it would receive a verticality score of 0.75. Species that occupied only aerial vertical niches or that did not occur in terrestrial habitats were excluded from the analysis.

Verticality exhibited a strong positive correlation with species richness. To examine spatial patterns of verticality independently of species richness, we calculated the standard effect size (SES) of mean verticality. We defined species pools based on biogeographic realm (Dinerstein et al. 2017) and generated a null distribution of expected verticality given random chance for each grid cell using 100 simulations.

## Environmental data

We obtained present and future global climate data from CHELSA v2.1 (Karger et al. 2017, 2021). Present climate data represents the time period 1981-2010 and future climate data represents climate scenario SSP585 for the time period 2071-2100. Climate velocity represents the average rate of at which thermal isotherms have shifted between the last glacial maximum and present climate conditions (Sandel et al. 2011). Vegetative complexity was calculated as the product of vegetation density (Crowther et al. 2015) and canopy height (Lang et al. 2023). Elevation data was obtained from All environmental data was resampled to the resolution and projection of the assemblage data.

## Simultaneous autoregressive models

We used simultaneous autoregressive (SAR) models with a spatial error term to model the impact of environmental factors on the SES of mean verticality. Environmental variables included mean elevation, vegetative complexity, climate velocity, mean annual temperature, maximum temperature of the warmest quarter, minimum temperature of the coldest quarter, diurnal temperature range, temperature seasonality, annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation seasonality. We examined variable inflation factors (VIF) among variables and selected those which we thought would have the greatest ecological significance based on physiological and evolutionary constraints on verticality while retaining a VIF below five. Selected variables were mean elevation, vegetative complexity, climate velocity, maximum temperature of the warmest quarter, minimum temperature of the coldest quarter, precipitation of the wettest quarter, precipitation of the driest quarter, and precipitation seasonality.

Prior to modeling, independent variables were checked for linear relationships with the response variable and log10 transformed if the relationship was not linear. Independent variables were then scaled to a mean of zero and standard deviation of one. To determine the optimal neighborhood weights matrix, we visually examined the distance to which spatial autocorrelation occurred in the response based on correlograms. We then identified different neighborhood scenarios based on distance from the focal cell. The smallest distance included the eight neighbors immediately surrounding the focal cell and subsequently increased to include successive rings of cells up to the maximum distance at which spatial autocorrelation was present in the response variable. For each distance scenario, we produced three row-standardized neighborhood weights matrices based on distance, inverse distance, and inverse squared distance (Ver Hoef et al. 2018).

We produced SAR models using the additive effects of all scaled environmental variables for each neighborhood weight matrix and calculated Moran’s I for each model to determine if spatial autocorrelation remained in the residuals. Models in which spatial autocorrelation remained were discarded. Based on the remaining models, we selected the neighborhood weights matrix as the one used in the model with the lowest AICc. Initial model exploration indicated that spatial autocorrelation was present using larger spatial neighborhoods. To reduce computational demands, we therefore based subsequent model selection on spatial neighborhoods from a radius of one grid cell to seven grid cells. Using the optimal neighborhood weights matrix defined by the lowest AICc, we compared all possible combinations of independent variables using the ‘dredge’ function from the MuMIN R package. Models within two AICc of the best model were averaged to estimate coefficients. For each model within two AICc of the best model, we predicted the standard effect size of mean verticality to future environmental conditions and averaged predictions across these models. We repeated the modelling procedure with grid cells that occurred only in forested biomes.

# Figures

A map of the world

Description automatically generated

Figure 1. The standard effect size (SES) of mean verticality for bird, mammal, reptile, and amphibian assemblages. Red represents areas where verticality is higher than expected by random chance and blue represents areas where verticality is lower than expected by random chance. Species pools used to calculate SES were defined based on biogeographic realm.

A graph of a number of red dots

Description automatically generated with medium confidence

Figure 2. SAR model coefficients for impacts of environmental variables on the mean community verticality and the standardized effect size of community verticality for birds, mammals, reptiles, and amphibians.

A group of maps of different colors

Description automatically generated

Figure 3. Maps show change in the standard effect size of mean verticality based on model projections of SES mean verticality under future climate conditions. Histograms show the average difference between present and future SES of mean verticality for each latitudinal band. Positive numbers (blue) indicate increases in SES of verticality and negative numbers (red) indicate declines in SES of verticality.

A group of different types of verticality

Description automatically generated with medium confidence

Figure 4. Histograms of SES mean verticality across the globe under current and future climate conditions. Red dashed line indicates mean global verticality.

# Supplementary Figures

**A map of the world

Description automatically generated**

Fig. S 1. The standard effect size (SES) of mean verticality for bird, mammal, reptile, and amphibian assemblages in forested biomes. Red represents areas where verticality is higher than expected by random chance and blue represents areas where verticality is lower than expected by random chance. Species pools used to calculate SES were defined based on biogeographic realm.

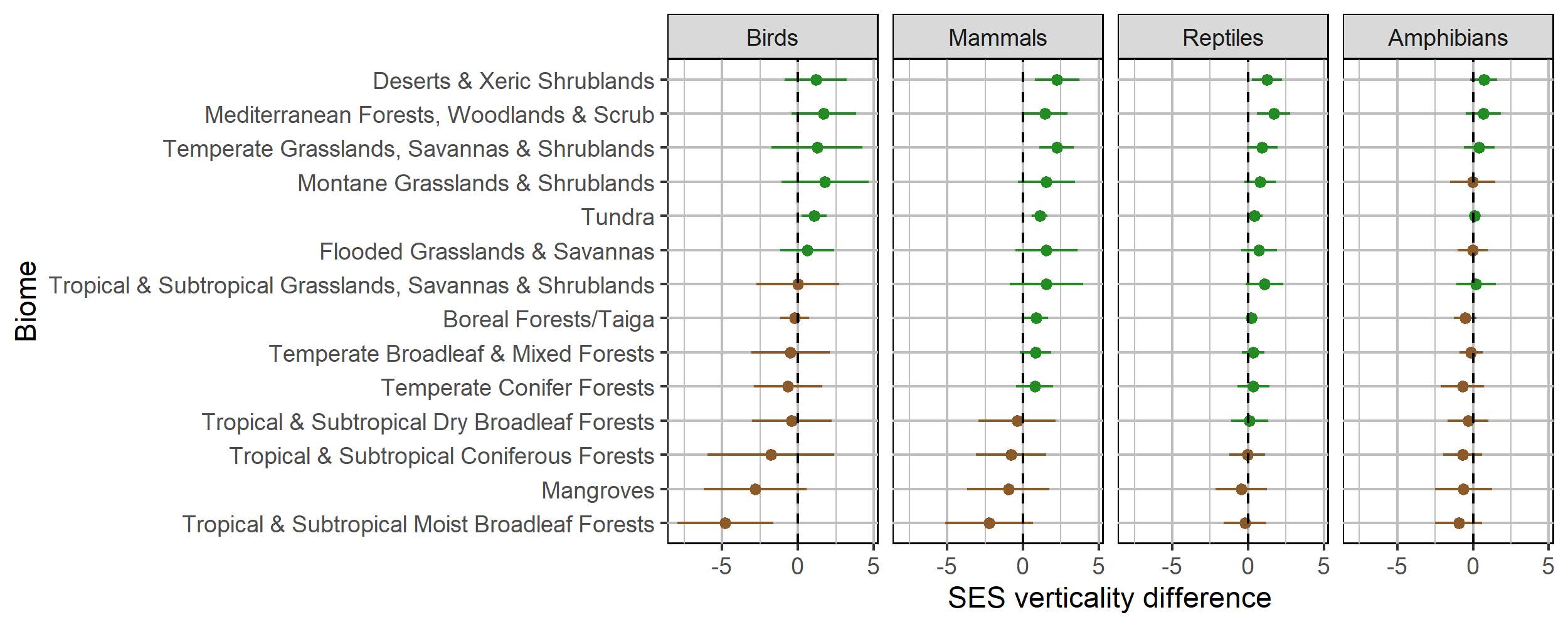


Fig. S 2. Mean assemblage verticality ± SD for each biome and class. Positive numbers (green) indicate increases in verticality and negative numbers (brown) indicate declines in verticality. From top to bottom, biomes are ordered by greatest increase to greatest decrease in verticality across all four taxonomic classes.

A map of the world

Description automatically generated

Fig. S 3 Difference between future and present maximum temperature of the warmest quarter. Positive numbers indicate increases in maximum temperatures.

A map of the world

Description automatically generated

Fig. S 4 Difference between future and present minimum temperature of the coldest quarter. Positive numbers indicate increases in minimum temperatures.

A map of the world

Description automatically generated

Fig. S 5 Difference between future and present precipitation seasonality. Positive numbers indicate increases in precipitation seasonality.

A map of the world

Description automatically generated

Fig. S 6 Difference between future and present wet season precipitation. Positive numbers indicate increases in precipitation.

A map of the world

Description automatically generated

Fig. S 7 Differences between future and present dry season precipitation. Positive numbers indicate increases in precipitation.

# TEXT GRAVEYARD

* + - Increase in community thermal index (CTI) for vertebrates and invertebrates in response to climate change = community restructuring (Lajeunesse and Fourcade 2023)
* Changes in trait distributions over time are influenced by immigration, localized extinction, phenotypic plasticity, and selection (Enquist et al. 2015)
  + - For example, range shifts toward higher elevations have caused average thermal tolerance within assemblages to increase over time as cool-adapted species become locally extirpated and warm-adapted species immigrate in (a process known as thermophilization) (Feeley et al. 2020)
* Understanding how the environment impacts community traits will improve our capacity to predict community responses to climate change
  + Understanding the relationship between the environment and community traits can improve our understanding of how climate change will impact functional diversity and ecosystem function in the future (Webb et al. 2010)
  + Predictable variation in assemblage traits across environmental gradients (see Cronwell and Ackerly 2009) enables traits to be predicted over space and time (see refs from Michel and Knouft 2014) and allows us to infer the structure of future species assemblages (see Merow et al. 2011; Shipley et al. 2011 from Michel and Knouft 2014)
* The reversal in effect direction for birds may be caused by birds in northern hemisphere boreal forests, which experience very cold minimum temperatures, occupying upper vertical strata in addition to terrestrial habitats while bird assemblages at higher latitudes in the southern hemisphere, which experience more mild temperatures, are primarily terrestrial.