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Beyond counts and averages: relating geodiversity to dimensions of biodiversity

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Running title: Geodiversity across dimensions of biodiversity

Abstract

Aim

We may be able to buffer biodiversity against the effects of ongoing climate change by prioritizing the protection of habitat with diverse physical features (high geodiversity) associated with ecological and evolutionary mechanisms that maintain high biodiversity. Yet, the relationships between biodiversity and habitat vary with spatial and biological context. In this study we compare how well habitat geodiversity — spatial variation in abiotic processes and features — and climate explain biodiversity patterns of birds and trees. We also evaluate the consistency of biodiversity-geodiversity relationships across ecoregions.

Location

Contiguous United States

Time period

2007-2016

Taxa studied

Birds, trees

Methods

We quantified geodiversity with remotely-sensed data and generated biodiversity maps from the Forest Inventory and Analysis and Breeding Bird Survey datasets. We fit multivariate regressions to alpha-, beta-, and gamma-diversity, accounting for spatial autocorrelation among

Nature Conservancy ecoregions and relationships among taxonomic, phylogenetic, and functional biodiversity. We fit models including climate alone (temperature, precipitation), geodiversity alone (topography, soil, geology), and climate + geodiversity.

Results

A combination of geodiversity and climate predictor variables fit most forms of bird and tree biodiversity with less than 10% relative error. Models using geodiversity and climate performed better for local (alpha) and regional (gamma) diversity than turnover-based (beta) diversity. Among geodiversity predictors, variability of elevation fit biodiversity best; interestingly, topographically diverse places tended to have higher tree diversity but lower bird diversity.

Main conclusions

Although climatic predictors tended to have larger individual effects than geodiversity, adding geodiversity improved climate-only models of biodiversity. Geodiversity was correlated with biodiversity more consistently than climate across ecoregions, but models tended to have poor fit in ecoregions held out of the training dataset. Patterns of geodiversity could help prioritize conservation efforts within ecoregions. However, we need to understand the underlying mechanisms more fully before we can build models transferable across ecoregions.

Keywords

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Introduction

In the face of an ongoing sixth mass extinction, society is challenged to minimize biodiversity loss through conservation efforts (Ceballos *et al.* 2015). While many conservation policies and strategies focus on conserving particular species (e.g., the United States Endangered Species Act, the International Union for Conservation of Nature Red List), there is growing interest in broadening conservation to include preserving parcels of Earth's surface that promote diversity even as species shift their ranges in response to climate change (Beier & de Albuquerque 2015). For example, The Nature Conservancy (TNC) prioritizes preserving areas with high geodiversity — variation in Earth's abiotic processes and features — through their 'Conserving Nature's Stage' (CNS) campaign (Beier & de Albuquerque 2015). Conserving nature's stage requires a firm understanding of biodiversity-geodiversity relationships, yet we know little about how these relationships vary across space, among taxa, and across different dimensions of biodiversity (Zarnetske *et al.* 2019). Addressing this knowledge gap is key to advancing conservation prioritization.

Geodiversity represents natural variation in geologic, geomorphic, and soil features (Gray 2004, 2008) and can be measured in a variety of ways. Most studies focus on elements of topography (roughness, elevation, slope and aspect), geology (geologic diversity, landscape complexity), soils (pH, organic matter, nutrient availability), or hydrology (variation of hydrological features such as rivers, ponds and lakes; Hjort *et al.* 2012; Wang *et al.* 2013; Kaskela *et al.* 2017). Some geodiversity definitions include climate, using variables such as temperature, precipitation, evapotranspiration, water balance, and solar radiation, while others explicitly exclude climate from their definition (Gray 2004; Parks & Mulligan 2010; Tukiainen *et al.* 2017). A comprehensive definition of geodiversity includes all abiotic features and processes found within Earth's atmosphere, lithosphere, hydrosphere, and cryosphere (Record *et al.* in press; Zarnetske *et al.* 2019).

Abiotic variation may promote increased variety of available niches for organisms (Tews *et al.* 2004), and high geodiversity is likely to indicate biodiversity hotspots (Lawler *et al.* 2015, but see Noss *et al.* 2014). However, little is known about how geodiversity of Earth's surface compares to climate in explaining variation in biodiversity, whether relationships generalize across geographic locations, and what types of biodiversity have the closest relationship with geodiversity. Despite the potential importance of geodiversity for explaining patterns of biodiversity, models explaining patterns of biodiversity rarely include geodiversity (Bailey *et al.* 2018). Furthermore, conservation frameworks, including CNS, typically advance the idea that conserving geodiversity will result in positive outcomes for biodiversity writ large (Beier & de Albuquerque 2015). This assumption must be tested empirically, especially given potential tradeoffs among orthogonal dimensions of biodiversity within and among taxa: conserving one aspect of biodiversity might have a neutral or even negative effect on other aspects. In this study, we use bird and tree occurrence data and remotely-sensed environmental data from across the United States to increase our understanding of biodiversity-geodiversity relationships. Geodiversity, in conjunction with climate, predicts patterns of species diversity of plants (Tukiainen *et al.* 2017; Bailey *et al.* 2018) and animals (Parks & Mulligan 2010; Alahuhta *et al.* 2018) across disparate biomes. Informed by these previously documented patterns, our **Prediction 1** is that combining geodiversity and climate predictors will significantly improve the goodness-of-fit of models explaining biodiversity of birds and trees.

Recent work shows that the biodiversity-geodiversity relationship depends on spatial grain and extent (Bailey *et al.* 2017; Zarnetske *et al.* 2019). Nevertheless, most studies have focused on alpha-diversity (local diversity) measured within a plot. In contrast, most large-scale mapping studies characterizing diversity have equated diversity with gamma-diversity, or the size of the regional species pool (Currie & Paquin 1987; Jenkins *et al.* 2015). Only a few have accounted for the three *levels* of biodiversity: alpha-diversity, beta-diversity (turnover among plots) and gamma-diversity (Meynard *et al.* 2011; Gossner *et al.* 2013). Beta-diversity represents compositional turnover among local communities, linking local diversity (alpha-diversity) to regional species pools (gamma-diversity). We expect that the relationship between geodiversity and beta- and gamma-diversity will be stronger than alpha-diversity, because high geodiversity often reflects high diversity of habitats within regions and therefore more unique local species assemblages (Stein *et al.* 2014). This leads to **Prediction 2:** Geodiversity will explain more variability in the beta and gamma levels of biodiversity than alpha-diversity.

The relationship between geodiversity and biodiversity may also vary with the *dimensions* of biodiversity (taxonomic, functional and phylogenetic diversity). Targeting functional and phylogenetic diversity is especially important for conserving unique ecological function (Steudel *et al.* 2016) and evolutionary history (Davis *et al.* 2018) in the face of the current biodiversity crisis. Because phylogenetic (Winter *et al.* 2012) and functional (Lamanna *et al.* 2014) biodiversity are explicitly linked to different ecological and evolutionary mechanisms, they may provide deeper insight into ecological and evolutionary processes that underlie regional variation in diversity. However, few studies of geodiversity have investigated these multiple dimensions of biodiversity (Meynard *et al.* 2011); most studies have considered only taxonomic diversity (e.g., Safi *et al.* 2011; Stevens & Gavilanez 2015). Because each dimension of biodiversity represents a unique mechanistic connection with the environment, we predict (**Prediction 3**) that the different dimensions of biodiversity will have different relationships with geodiversity.

Relationships between dimensions of biodiversity and geodiversity vary across geographic and environmental space. In some areas and environmental contexts, one form of geodiversity might be a more reliable predictor of biodiversity than elsewhere. For example, topographic complexity generates a diversity of climatic conditions at small to intermediate spatial scales ranging from meters (Bennie *et al.* 2008) to tens of kilometres (Badgley *et al.* 2017), which may buffer species against local extinctions as climate warms (Dobrowski 2011; Lenoir *et al.* 2013). Such buffering is, however, conditional on climatic context: if an entire landscape is far outside of the physiological range of tolerance for some taxonomic or functional groups, geodiversity is likely to be unimportant for maintaining local biodiversity. For example, along the central California coast, land and ocean surface temperatures contrast strongly and there is high heterogeneity in topography and associated cloud and fog patterns. Such conditions support relatively high local richness of tree species (Barbour *et al.* 2007). Inland, in contrast, the average climate of the Coast Range is more arid and fog is absent (Ackerly *et al.* 2010), so only the coolest facets of the landscape support any level of tree cover. In this context, topographic heterogeneity is still associated with higher tree diversity, but the relationship is likely to be weaker. For these reasons, we predict (**Prediction 4**) that the influence of different geodiversity predictors on biodiversity will vary across ecoregions. In particular, mountainous ecoregions with more mesic climates will have more positive relationships between topographic diversity and biodiversity than more arid mountain ranges.

In this study, we use bird and tree occurrence data and remotely-sensed environmental data from across the United States to increase our understanding of biodiversity-geodiversity relationships. We make the following predictions:

(1) Geodiversity will significantly increase the explanatory power of models explaining biodiversity of birds and trees.
(2) Geodiversity will explain more variability in beta- and gamma-diversity than alpha-diversity.
(3) The different dimensions of biodiversity will have different relationships with geodiversity.
(4) The influence of different geodiversity predictors on biodiversity will vary across ecoregions.

Methods

We used multivariate linear mixed models with spatial random effects to determine which geodiversity predictors explain the most variation across the levels and dimensions of bird and tree biodiversity in the contiguous U.S. We used biodiversity and geodiversity data collected from 2007-2016.

Breeding Bird Survey (BBS)

The North American Breeding Bird Survey (BBS, https://www.pwrc.usgs.gov/bbs/) is an annual survey of breeding birds across the U.S. and Canada begun in 1966. Volunteer observers report species and counts of birds seen or heard during 3-minute observations at 50 stops spaced every ~800 m along routes ~39.4 km in length (Sauer *et al.* 2013). There are ~3480 active routes in the contiguous U.S. with continuous yearly stop-level data. We excluded any routes with an ambiguous midpoint coordinate (discontinuous transects), leaving 3089 routes. We included only the surveys conducted under the standard protocol, discarding repeat surveys and any observations recorded by trainees.

Forest Inventory and Analysis (FIA)

The U.S. Department of Agriculture Forest Service's Forest Inventory and Analysis program (FIA) surveys the composition and status of forests throughout the United States, with data collected annually (Bechtold *et al.* 2005). Each FIA plot consists of four 7.2-m fixed radius subplots. Plots are spaced roughly on a 5-km grid across forested land. Each plot is surveyed approximately every 5 years (Bechtold *et al.* 2005). Each tree is identified to species. We obtained the most recent survey from all forested, non-plantation FIA plots in the contiguous United States (119,177 plots). Some plots in the Pacific Northwest Region included a larger "macroplot" around the central subplots; we excluded any trees outside the subplot boundary. The year of the most recent survey varied between 2012 and 2016.

Phylogenetic and Trait Data

We obtained phylogenetic trees and compiled trait information for all bird and tree species in the BBS and FIA databases, respectively, and used them to calculate the distance-based phylogenetic and functional diversity indices described below. See Appendix 1 for additional details.

Calculation of Biodiversity Metrics

For both tree and bird communities, we calculated biodiversity metrics based on species presence at the site level (here defined as a single FIA plot or BBS route). For trees in FIA, we used the most recent survey as a single time point for each site, as there is little turnover in species composition between surveys and the probability of imperfect detection is low. To minimize the effects of imperfect bird detection in the BBS survey, we pooled observations from all stops in each route and pooled all surveys from 2007-2016. See Appendix 2 for additional details.

We calculated alpha-, beta-, and gamma-diversity (referred to as *levels* of biodiversity) within a circle of 50 km radius around each site, originating at the centre of the FIA plot or midpoint of the BBS route. We defined any BBS route whose midpoint fell within the 50-km circle around the focal route midpoint to be a neighbour route (see Appendix 2). We took (1) the median diversity of all sites in the radius, including the focal site (alpha), (2) the median pairwise diversity of all pairs of sites in the radius, including the focal sites (beta), and (3) the aggregated diversity of all sites in the radius (gamma). Each diversity *level* has three *dimensions*: taxonomic, phylogenetic, and functional (Table S1). For taxonomic diversity, alpha-diversity and gamma-diversity were represented by species richness and beta-diversity by pairwise Sørensen dissimilarity. The Sørensen dissimilarity index represents the degree to which pairs of communities differ from one another in their species composition, independent of their species richness, and encompasses both species turnover and nestedness components of beta-diversity. This contrasts with beta-diversity indices based on multiplicative or additive partitions of alpha- and gamma-diversity (Anderson et al. 2011). To quantify phylogenetic diversity, we calculated mean pairwise phylogenetic distance (MPD) of each community with the R package *picante* (Kembel *et al.* 2018). We randomized the phylogenetic distance matrix 999 times and calculated the z-score of the observed phylogenetic distances relative to the distribution of phylogenetic distances of the randomized matrices to remove dependence on richness. Similarly, we calculated a distance-based metric of functional diversity by finding the Gower distance between the trait values for all possible species pairs, and then calculating the mean pairwise distance among all pairs of species in each community and its z-score. Because the BBS surveys poorly estimate abundances of some species, we calculated incidence-based biodiversity metrics for both birds and trees so that metrics are comparable between the two taxa.

Geodiversity Data Sources and Processing

We obtained and processed remotely-sensed data for the contiguous United States to generate geodiversity and climate data layers. Remotely-sensed geodiversity variables are particularly valuable in disentangling the independent effects of climate and geodiversity. Many biodiversity analyses use climatic data products that interpolate weather station data using elevation, e.g. Worldclim v.1 (Hijmans *et al.* 2005). Using elevation to derive temperature values makes it difficult to evaluate independent contributions from climate and topography (Körner 2007). Remotely-sensed temperature represents the temperature of the land surface, in contrast with weather stations that measure air temperature several meters above ground level (Bechtel

2015). In areas with very sparse coverage of meteorological stations and/or complex topography, the error introduced by interpolating between ground stations may be large. In many regions, especially grasslands, shrublands, and croplands, surface temperature shows large systematic deviations from air temperature (Mildrexler *et al.* 2011). What is more, studies have shown that surface temperature may be more ecologically relevant than air temperature (Pau *et al.* 2013; Still *et al.* 2014). The thermodynamic temperature of an organism, which drives its respiration rate and vapor pressure deficit, is more closely related to the surface temperature than the surrounding air temperature. Remotely-sensed data products provide spatially continuous, independent, and direct measures of climate and geodiversity for use in biodiversity models.

We generated predictors from the following remotely-sensed data products: elevation from SRTM (Farr *et al.* 2007), land surface temperature from MODIS MOD11A2 (Wan *et al.* 2015), precipitation from CHIRPS (Funk *et al.* 2015), and gross primary productivity (GPP) dynamic habitat index from MODIS (Hobi *et al.* 2017). We generated additional predictors from non-remotely-sensed products including soil type category from SoilGrids (Hengl *et al.* 2017), which uses remotely-sensed data to interpolate ground-based measurements, and geologic age category from USGS International Surface Geology. We included GPP because spatial variability in GPP integrates many geodiversity variables known to influence biodiversity via resource availability (Austin & Smith 1989; Alahuhta *et al.* 2018). GPP spatial variability is moderately correlated with mean annual precipitation but largely orthogonal to the other geodiversity variables we chose (Figure 1), indicating that it may capture additional spatial variation not accounted for by the other three geodiversity variables. See Appendix 3 for additional details.

We coarsened all environmental data layers by calculating the means within 25 km^2 pixels to equal the coarsest resolution of any layer, then we aggregated all geodiversity and biodiversity variables within a 50-km radius around the centre of each FIA plot and the midpoint of each BBS route. The 50-km scale of aggregation averages over a wide range of microhabitats and microclimates, capturing the geodiversity-biodiversity relationship at a coarse spatial grain; it is possible that a smaller grain of analysis would reveal different patterns (Zarnetske *et al.* 2019). For continuous predictors, we calculated the mean of all pixels partially or wholly in the 50-km radius, and we used the mean terrain ruggedness index (TRI; Wilson *et al.* 2007) of the 3×3 pixel neighbourhood around all pixels to represent spatial variability. For discrete predictors, we used Shannon entropy of all pixels in the radius to represent spatial variability. Shannon entropy has been shown to monotonically increase with increasing number of landscape patch types, to behave consistently in both real and simulated landscapes, and to correlate positively with many other measures of landscape heterogeneity (Peng *et al.* 2010). Importantly, while many past studies have used variables extracted from spatially continuous layers at points to characterize environmental variation, we explicitly consider spatial variation in the regions around the points where biodiversity was measured. Defining geodiversity in terms of this variation is critical for fully explaining biodiversity because a single point value cannot capture the diversity of niche space that may determine biodiversity (Lawler *et al.* 2015).

Finally, we spatially grouped geodiversity and biodiversity observations using TNC's terrestrial ecoregions (Olson & Dinerstein 2002) to account for spatial autocorrelation in response variables. We selected this classification scheme over alternatives because the regions are defined based on biodiversity analyses conducted across many taxa, and because the number of ecoregions in the contiguous USA (63 after excluding 6 border regions with insufficient data) is high enough to adequately account for spatial autocorrelation in biodiversity responses within the study area without overfitting.

Selection of Predictor Variables

We selected six predictor variables for our models: two climate variables to describe the climate norms inside the radius (mean annual temperature and mean annual precipitation), and four predictors to describe geodiversity or environmental heterogeneity (mean TRI of elevation and GPP, Shannon diversities of geological age category and soil type). Together, the six variables encompass most of the variation in geodiversity and climate among locations in the contiguous United States and are only modestly correlated with one another (Figure 1), meeting model assumptions. Based on our *a priori* hypothesis that geodiversity is related to biodiversity, we included one predictor to represent each of the unique geodiversity data sources available to us (elevation, soil type, and geological age category). In addition, we selected GPP diversity to represent other aspects of geodiversity not captured by the first three variables. Our choice of mean annual temperature and mean annual precipitation to represent long-run climate norms is reasonable because the two variables have no relationship to one another at our scale of observation (Figure 1).

Final Data Processing

First, we excluded any site within 50 km of the Canada or Mexico borders because the 50-km radius around those sites contained areas without biodiversity measurements. We logit-transformed the taxonomic beta-diversity variable, which is a raw dissimilarity metric varying between 0 and 1 in the model. No bird sites had a taxonomic beta-diversity of exactly 0 or 1, but ~16% of tree sites had taxonomic beta-diversity of exactly 0 or 1, which is outside the domain of the logit function. Thus, we replaced zeroes with 0.001 and ones with 0.999. We took a spatially stratified random sample of tree sites where each sampled site was a minimum of 20 km from any other site, to minimize spatial autocorrelation not captured by our model. This process left

~3000 sites, so that sample sizes were comparable between the datasets used to fit each model.

Model Fitting

We fit spatial multivariate mixed models with the following fixed predictors: (1) all six predictor variables as fixed effects, (2) only the four geodiversity predictors as fixed effects, (3) only the two climate predictors as fixed effects, and (4) no fixed effects (null model with only spatial random effects). We fit multivariate models for each diversity level (alpha, beta, and gamma) and each taxon (birds, trees), totalling 24 models (4 predictor sets × 3 diversity levels × 2 taxa = 24). Each model had three response variables corresponding to the three dimensions of biodiversity (taxonomic, phylogenetic, and functional). We used the null model z-scores to represent phylogenetic and functional biodiversity in all the models.

We fit a random intercept and slope for each predictor in each TNC ecoregion. We excluded ecoregions with <5 sites, because random effects estimated with <5 data points are not robust. The excluded ecoregions were primarily in Canada or Mexico and only have a small area inside the contiguous United States that is at least 50 km from a land border. After excluding these ecoregions, 63 ecoregions remained. We estimated random slopes and intercepts for each ecoregion with a multilevel conditional autoregressive (CAR) structure to model the spatial variability in the biodiversity-geodiversity relationship among ecoregions (Besag & Kooperberg 1995). We specified the neighbourhood structure with an adjacency matrix identifying all pairs of regions that share a border. The ecoregion random effects in the model were therefore spatially structured, accounting for spatial autocorrelation in the biodiversity values of neighbouring regions. We chose to model spatial dependence using discrete regions because of better out-of-sample prediction performance than simultaneous autoregressive models (Kress, unpublished).

We fit the models in a hierarchical Bayesian framework using the R package *brms* (Bürkner 2017). We modelled error in response variables as normally distributed. Finally, we standardized both predictor and response variables before fitting the models so that we could compare effect sizes across predictors and responses. The standard deviation of each coefficient represents the among-region variability of each predictor-response relationship.

Model Validation

To assess model predictive performance, we performed spatially blocked leave-one-location-out cross-validation (Roberts *et al.* 2017). We refit each of the models 63 times, each time holding out all data points from one of the 63 ecoregions. We found the root mean squared error (RMSE) of the predicted values of the withheld data from each fold to get a cross-validation RMSE for each model. We also calculated the RMSE of the models fit to all the data. We divided all RMSE values by the range of the observed data to yield relative values that can be compared among models. We also calculated RMSEs using resubstitution evaluation, in which no data points were held out in model fitting. This procedure assesses the goodness-of-fit of models across the entire contiguous U.S. but does not fully correct for spatial autocorrelation.

We calculated the Bayesian R-squared (Gelman *et al.* 2018) for each model to quantify the proportion of variation in the response explained by fixed and spatial random effects combined. Finally, we calculated the widely applicable information criterion (WAIC; Watanabe 2010) for each model.

Results

Description of geodiversity and biodiversity variables

Correlations among geodiversity predictor variables were relatively low (Figure 1a). The pairwise correlation between elevation diversity and geologic age diversity was relatively high (r = 0.52), indicating that geodiversity measured as topographic variability is correlated with geodiversity measured as the variety of geologic substrate ages. Notably, the correlation between elevation diversity and mean annual temperature was low (r = -0.20). In both birds (Figure 1b) and trees (Figure 1c), taxonomic and phylogenetic diversity were positively correlated with one another at all levels; this relationship was strongest for birds. However, local (alpha) and regional (gamma) functional diversity tended to correlate negatively with other forms of biodiversity in both birds and trees.

Geodiversity variables (Figure 2) had unique patterns and spatial grains of variability. Climate variables varied at broad scales, while geologic and topographic variables varied at scales corresponding to major land features such as mountain ranges (Figure 2). Biogeographic patterns were disparate across dimensions of biodiversity for birds (Figure 3) and trees (Figure 4). Bird diversity patterns were spatially idiosyncratic (Figure 3), while tree diversity showed a strong longitudinal pattern, with taxonomic diversity highest in the east and functional and phylogenetic diversity highest in the west (Figure 4).

Effects of climate and geodiversity across taxa and components of biodiversity

Among geodiversity variables, elevation variability tended to be the strongest predictor of biodiversity (Figure 5). Elevation variability was associated with increased bird taxonomic beta-diversity but with decreased bird phylogenetic and functional diversity at all levels. Interestingly, it had a positive effect across all levels and dimensions of tree biodiversity; it was the only predictor with such a consistently positive relationship. Higher mean annual temperature was associated with lower taxonomic diversity but higher phylogenetic and functional diversity in birds. In contrast, for trees, precipitation was a much more important climate driver than temperature (Figure 5). The effect size for temperature was not distinguishable from zero for most levels and dimensions of tree diversity. For birds, taxonomic alpha-diversity (local richness) was highest in colder and wetter areas, but most other levels and dimensions of biodiversity showed the opposite pattern. For trees, taxonomic and functional diversity were higher in wetter areas, but phylogenetic diversity was higher in drier areas.

The effects of geologic age variability and soil type variability tended to be relatively weak, although for birds, soil type variability positively affected taxonomic diversity, and for trees, geologic age variability positively affected taxonomic diversity. Spatial variability in GPP had a positive relationship with bird taxonomic and functional diversity and a positive relationship with tree turnover and regional diversity across the three dimensions of biodiversity.

Overall model performance

The spatially blocked cross-validation showed that the models with climate or geodiversity predictors performed no better than the null model when predicting all biodiversity values from an entire ecoregion held out during model fitting (Figure 6). However, cross-validation prediction error for models including climate tended to be higher than for models including geodiversity. Model evaluation using the full dataset without holding out any locations showed that models including the six fixed predictors were the best fit for biodiversity of trees and birds, as shown by the RMSEs, WAIC values, and Bayesian R-squared values (Figure S1; Table S2). Geodiversity explained a consistent proportion of variation in most forms of bird biodiversity. For trees, the explanatory power of geodiversity depended on the level of biodiversity considered: geodiversity explained local (alpha) and regional (gamma) biodiversity better than turnover (beta).

Spatially varying biodiversity-geodiversity relationships

The strength of biodiversity-climate relationships varied more across ecoregions than the strength of biodiversity-geodiversity relationships (Figure S2). Interestingly, the relationship between mean annual precipitation and tree taxonomic and functional biodiversity tended to be more strongly positive in drier western ecoregions where precipitation is limiting (Figure S10). Phylogenetic diversity showed an opposite spatial pattern: drier areas in the west had higher tree phylogenetic diversity. In those ecoregions, we observed high phylogenetic diversity at sites dominated by gymnosperms (*Pinus* and *Juniperus* spp.) with a few associated angiosperm species, notably *Cercocarpus ledifolius* and *Populus tremuloides*. These dry sites, which tended to have low to intermediate taxonomic and functional diversity, may be driving the negative relationship between precipitation and phylogenetic diversity in the western USA. Notably, the relationship between elevation variability and biodiversity was relatively consistent across ecoregions, being generally positive for trees, positive for bird taxonomic diversity, and negative for bird functional and phylogenetic diversity. Other geodiversity-biodiversity relationships varied idiosyncratically across space (Figures S2-S14).

Discussion

The magnitude and direction of the relationships between environmental variability and biodiversity were intriguingly context-dependent, varying between birds and trees, by diversity level (alpha, beta, and gamma), by diversity dimension (taxonomic, phylogenetic, and functional), and by ecoregion. Below we explore potential reasons for this context-dependence as they relate to the predictions we made initially.

Effects of climate and geodiversity across components of biodiversity

A combination of geodiversity and climate predictors predicted biodiversity within 10% relative error for most forms of biodiversity for both birds and trees (Figure S1). However, these more complex models performed worse than the null models in spatially blocked cross-validation, when predicting biodiversity values in ecoregions not used to fit the model (Figure 6). The poor performance of models outside the training dataset may indicate that similarity among neighboring communities of birds and trees explains the majority of variation in biodiversity, with deterministic effects of geodiversity and climate playing a smaller role. Alternatively this suggests that a large proportion of the relationship between geodiversity and bird and tree biodiversity is spatially context-dependent, providing only weak support for our prediction that geodiversity and climate together explain variation in biodiversity among ecoregions (Prediction 1). The high level of spatial autocorrelation and high variability in relationships among ecoregions prevented the statistical models from identifying spatially transferable relationships between geodiversity and biodiversity. Nevertheless, geodiversity variables performed relatively better than climate variables at out-of-sample prediction (Figure 6), suggesting a potential use of geodiversity to identify biodiversity hotspots at local to regional scales. The poor performance of the models relative to null models reveals the difficulty of disentangling environmental drivers of biodiversity from biogeographical and historical contingency and caution against relying heavily on geodiversity or climate to predict biodiversity in regions far from where models are fit.

Temperature and precipitation means had the strongest effects on diversity, across taxa and across the levels and dimensions of biodiversity. However, adding geodiversity predictors significantly increased explanatory power when evaluating models trained on the full dataset (Figure S1), although neither climate nor geodiversity predictors increased prediction accuracy in spatially blocked cross-validation (Figure 6). Among geodiversity predictors, topographic variability had the largest effect on biodiversity. Interestingly, topographic variability had a positive relationship with tree diversity across levels, but was associated with lower bird diversity. This may be because breeding bird diversity is driven by highly mobile migratory bird species seeking out high-productivity regions for breeding sites (Anderson & Shugart 1974; Cody 1981). The diversity of niche opportunities available to trees may depend on the microhabitats created by topographic variation. Niche diversity for birds may be driven more by the diversity of food sources, which could be reduced in more topographically rugged regions. In contrast with topographic variability, geologic age and soil type diversity tended to have little or no effect on biodiversity in the regions and taxa we studied.

We found that geodiversity has significant effects on all diversity levels. Gamma-diversity, which integrates the alpha and beta levels, is best predicted by a combination of geodiversity and climate. This finding contrasts with Prediction 2, that geodiversity's effect would be strongest on turnover (beta) and regional diversity (gamma). For trees in particular, geodiversity combined with climate predicted beta-diversity less well than alpha- and gamma-diversity. This result may be due to incomplete sampling of the local community by single FIA plots. If trees have patchy distributions at local scales, the small-sized FIA plots may overestimate beta-diversity because some species that are present throughout the region will be absent from a random subset of plots within the focal region (Figure 4). Therefore, local sampling might obscure the true pattern of turnover among plots, but not the regional diversity, which integrates over many plots. We show that familiar maps of biodiversity, which are commonly created using species range maps (Currie & Paquin 1987; Brown & Lomolino 1998; Jenkins *et al.* 2015), represent gamma-diversity patterns, but not necessarily other forms of biodiversity. Our results show that these different levels of biodiversity (Figures 3 and 4) exhibit different relationships with environmental gradients. Our maps promote a more nuanced view of biodiversity and emphasize that each level and dimension has a different relationship with spatial variability in the environment.

Although we found generally similar responses across biodiversity dimensions, differences may indicate ecologically or evolutionarily meaningful relationships. In general, we found similar responses across biodiversity dimensions because they tend to correlate positively with one another (Figure 1). This finding partially contradicts Prediction 3 that patterns would differ across dimensions. However, in support of Prediction 3, some environmental drivers had opposite effects on different dimensions of biodiversity (Jarzyna & Jetz 2016). This result parallels contrasting patterns across biodiversity dimensions previously documented in mammals (Davies & Buckley 2011). For example, areas with greater topographic variability tended to have higher bird taxonomic diversity but lower phylogenetic and functional diversity. Birds' taxonomic diversity might not have the same signal as phylogenetic or functional diversity because both the functional guilds and the phylogenetic lineages of birds differ greatly from one another in species richness (De Graaf *et al.* 1985). For example, there are many functionally similar and closely related species within the guild of small insectivorous songbirds. An increase of species richness in the insectivore guild would result in increased taxonomic diversity without influencing the other dimensions of diversity. The high numbers of bird species harboured by geodiverse regions likely reflects increased taxonomic diversity within speciose guilds.

The discrepancy in relationships we observed among the dimensions of biodiversity we examined mirror that of a previous study examining biodiversity change over time. Increases in taxonomic diversity without corresponding changes in phylogenetic or functional diversity may indicate biotic homogenization of assemblages; 40 years of BBS surveys show a homogenizing trend over time (Jarzyna & Jetz 2017). While our study does not address change over time, the discrepancy between taxonomic and functional/phylogenetic diversity patterns with topographic variability and with temperature is notable. Jarzyna and Jetz also observed that the greatest temporal changes in diversity occurred at higher elevations and latitudes, ascribing this pattern to climate change. We documented a positive association between temperature and beta-diversity for all dimensions, but we found lower phylogenetic and functional diversity in topographically diverse regions (Figure 5). This result echoes the temporal pattern documented by Jarzyna and Jetz, suggesting that bird communities at high elevations and in cold regions may be relatively homogeneous and thus relatively more vulnerable to changing climate. In the case of breeding birds in the United States, topographically diverse regions may in fact be the most sensitive to environmental change.

Phylogenetic and functional diversity have similar patterns with respect to most predictor variables. This finding makes sense given that many, though not all, traits are phylogenetically conserved (Devictor *et al.* 2010), such that phylogenetic diversity roughly approximates functional diversity (Winter *et al.* 2012). However, tree phylogenetic diversity increases with decreasing precipitation, while functional diversity and taxonomic diversity decrease. This suggests that the angiosperm and gymnosperm species that contribute to high phylogenetic diversity in low-precipitation regions may have convergently evolved suites of adaptations to dry environments (Méndez-Alonzo *et al.* 2012), resulting in low functional diversity at those sites.

Spatially varying biodiversity-geodiversity relationships

The relationship between geodiversity variables and biodiversity variables varied in direction and magnitude across the ecoregions of the United States. For example, elevational variability had a greater effect on tree biodiversity in the central and eastern United States, providing support for Prediction 4. In the west, climatic factors and a smaller regional species pool set upper bounds on richness, so the opportunity for increased richness with increased geodiversity is reduced relative to the east (Figure S11). In contrast, the effect of elevational variability on bird taxonomic diversity was more likely to be non-zero in regions of high topographic relief, such as the Appalachian ecoregion and the northern Rocky Mountains (Figure S5). For trees, the effect of precipitation on biodiversity was more likely to be significant in the drier central and western United States (Figure S10), where water tends to be limiting. This suggests that in regions where climatic factors strongly control species diversity, the influence of geodiversity on biodiversity is weaker. However, this result may depend on spatial extent of the study region; a similar model fit only for trees in the Pacific Northwest region shows a strong positive correlation between elevational variability and tree alpha- and gamma-diversity (Record *et al.* in press).

The form of the geodiversity-biodiversity relationship and the particular variables that are the best predictors of biodiversity may not be transferable across ecoregions. This may present a conundrum for organisms that are migrating to track climate conditions and may encounter novel geological features. The Nature Conservancy documented a similar pattern: when they initially developed the Conserving Nature's Stage framework, they identified geological variables as the best predictors of biodiversity in the Northeast U.S. (Anderson & Ferree 2010). Those variables did not predict biodiversity well when they extended the approach to the Southeast (Anderson *et al.* 2014), where geologically homogeneous regions of the Coastal Plain host high biodiversity.

Conclusions and future directions

Our study found that topographic variability was related to biodiversity independently from, and in different ways than, climatic means. This result suggests that using remotely-sensed temperature data, rather than values interpolated between weather stations using local elevation, may improve our ability to distinguish between the effects of climate and of topographic variability (Pau *et al.* 2013; Still *et al.* 2014). Remotely-sensed temperature has broader spatial coverage than interpolated temperature and is not inherently dependent on elevation. Therefore, it would be valuable to confirm whether remotely-sensed temperature is biologically relevant across a range of taxa (Heft-Neal *et al.* 2017).

With the increasing intensity of global change threatening biodiversity and ecological integrity, it is vital to conserve nature's stage and create refugia for organisms moving to track their optimal climatic conditions. While past ecological research and the results of this study show that climate explains much of the spatial variation in biodiversity of trees and birds, geodiversity is related to biodiversity independently of climate. To disentangle the effects of climatic and topographic drivers, spatially continuous remotely-sensed data are necessary. Biodiversity-geodiversity relationships depend on taxonomic group, spatial location, the level and dimension of biodiversity considered, and the grain of analysis (Zarnetske *et al.* 2019): there is no single relationship valid for all conditions. To date, biodiversity-geodiversity relationships have primarily been characterized in a few well-studied taxa (Meynard *et al.* 2011; Hjort *et al.* 2012; Wang *et al.* 2013; but see Kaskela *et al.* 2017; Tukiainen *et al.* 2017); our study of birds and trees only hints at potential mechanisms underlying differences in relationships among taxonomic groups. Future work across a wider range of taxa would allow us to identify the mechanisms behind the differences. Although we need to understand the underlying mechanisms more fully before we can build models that are transferable across ecoregions, globally available geodiversity predictors can inform conservation practitioners working at a local scale to conserve different dimensions of biodiversity in the face of climate change.

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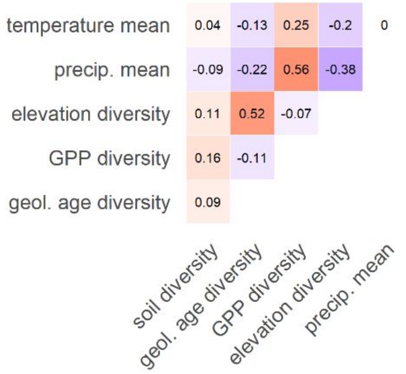
Data Accessibility Statement

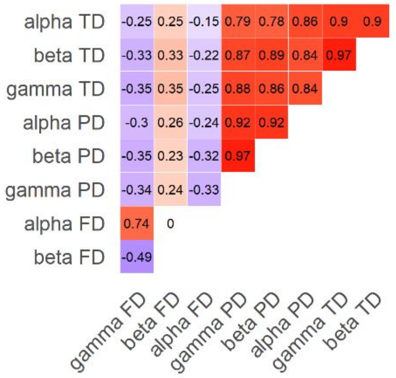
Data and code for reviewers to reproduce all the model fitting and analysis presented in this manuscript is archived on FigShare at doi.org/10.6084/m9.figshare.7680083.v1 (draft version). Code to replicate the data preparation and cleaning stages described in the methods is also archived on the FigShare repository.

Figures

(a) environmental correlations



(b) bird biodiversity correlations



(c) tree biodiversity correlations

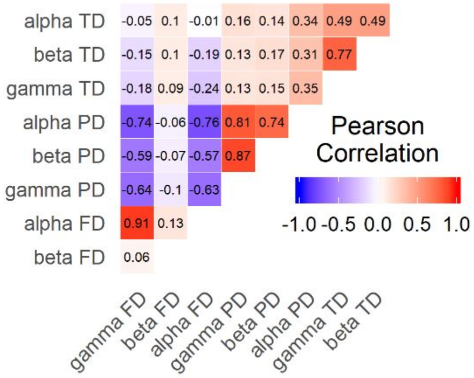


Figure 1. Heat maps showing correlations between pairs of environmental predictor variables including geodiversity and climate (a), bird biodiversity variables (b), and tree biodiversity variables (c). Pearson correlation coefficients are shown, along with colours showing the

magnitude of the correlation coefficients. TD = taxonomic diversity; PD = phylogenetic diversity; FD = functional diversity.

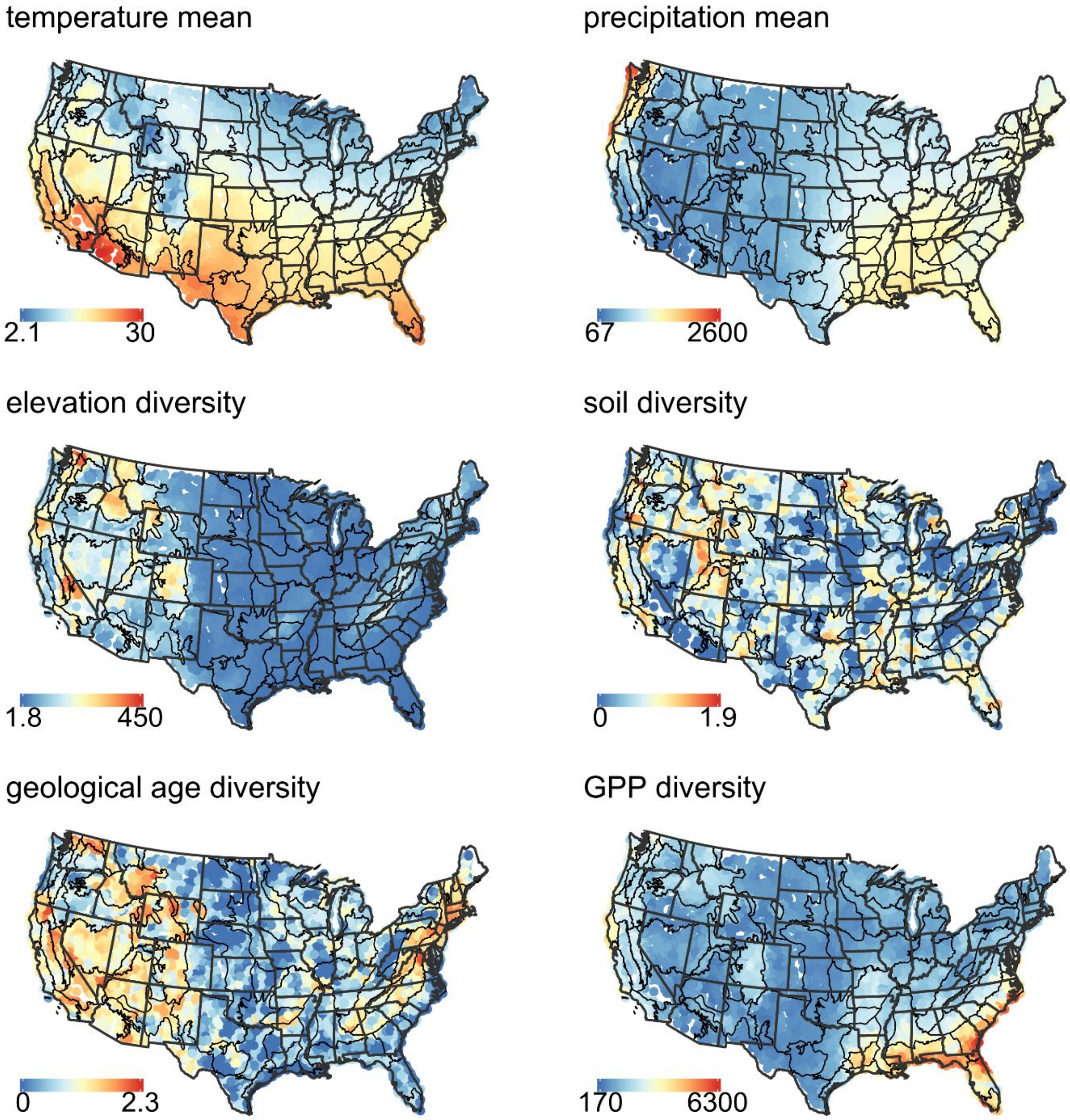


Figure 2: Maps of climate and geodiversity predictor variables across the contiguous United States, centred on BBS route midpoints and FIA plots (fuzzed locations shown).

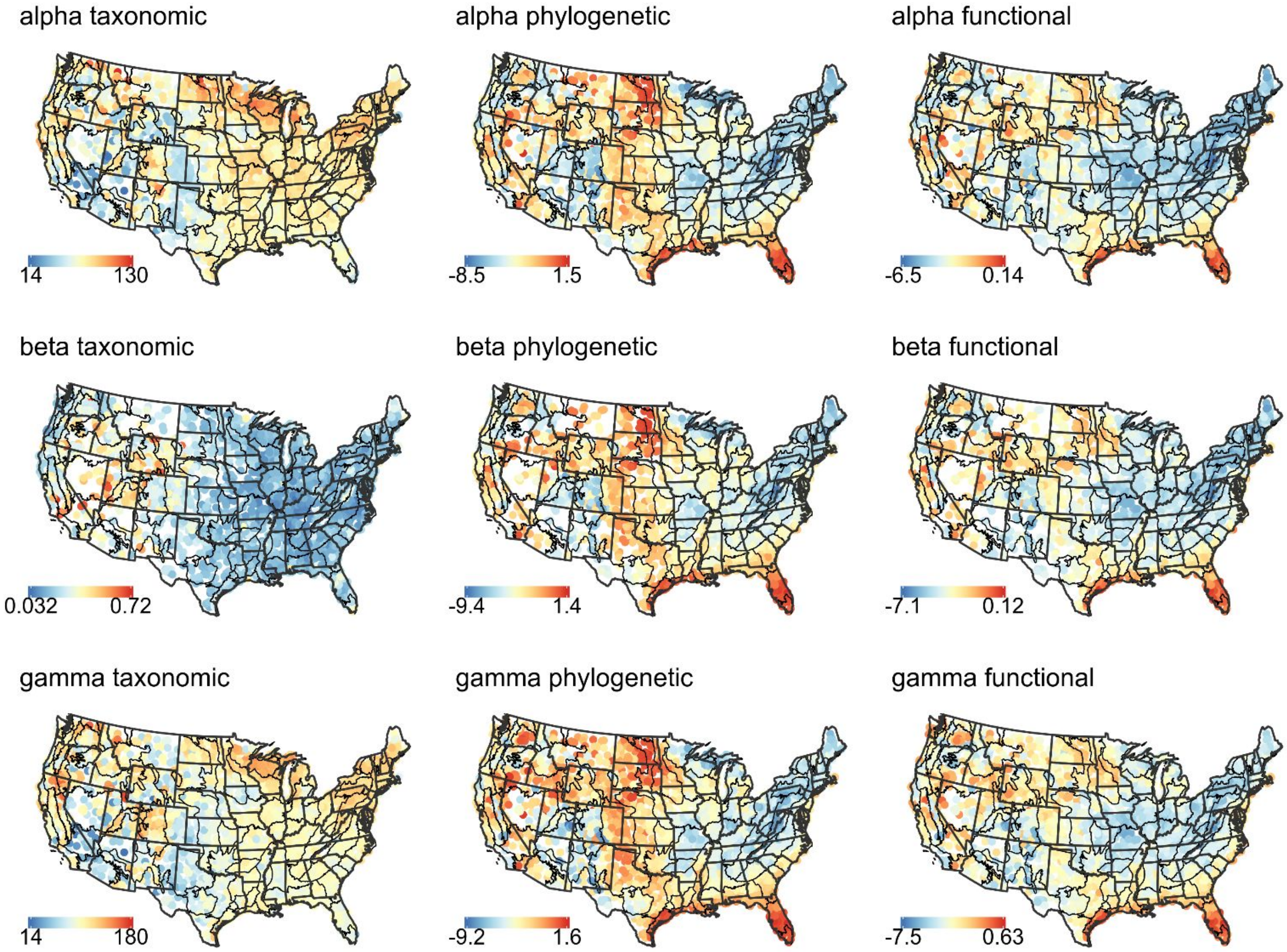


Figure 3: Maps of bird biodiversity at BBS routes, across 3 levels and 3 dimensions of biodiversity. For taxonomic diversity, richness is plotted for alpha- and gamma-diversity, and pairwise dissimilarity score is plotted for beta-diversity. For phylogenetic and functional diversity, z-scores are plotted for all levels. Midpoints of each route are shown on the map.

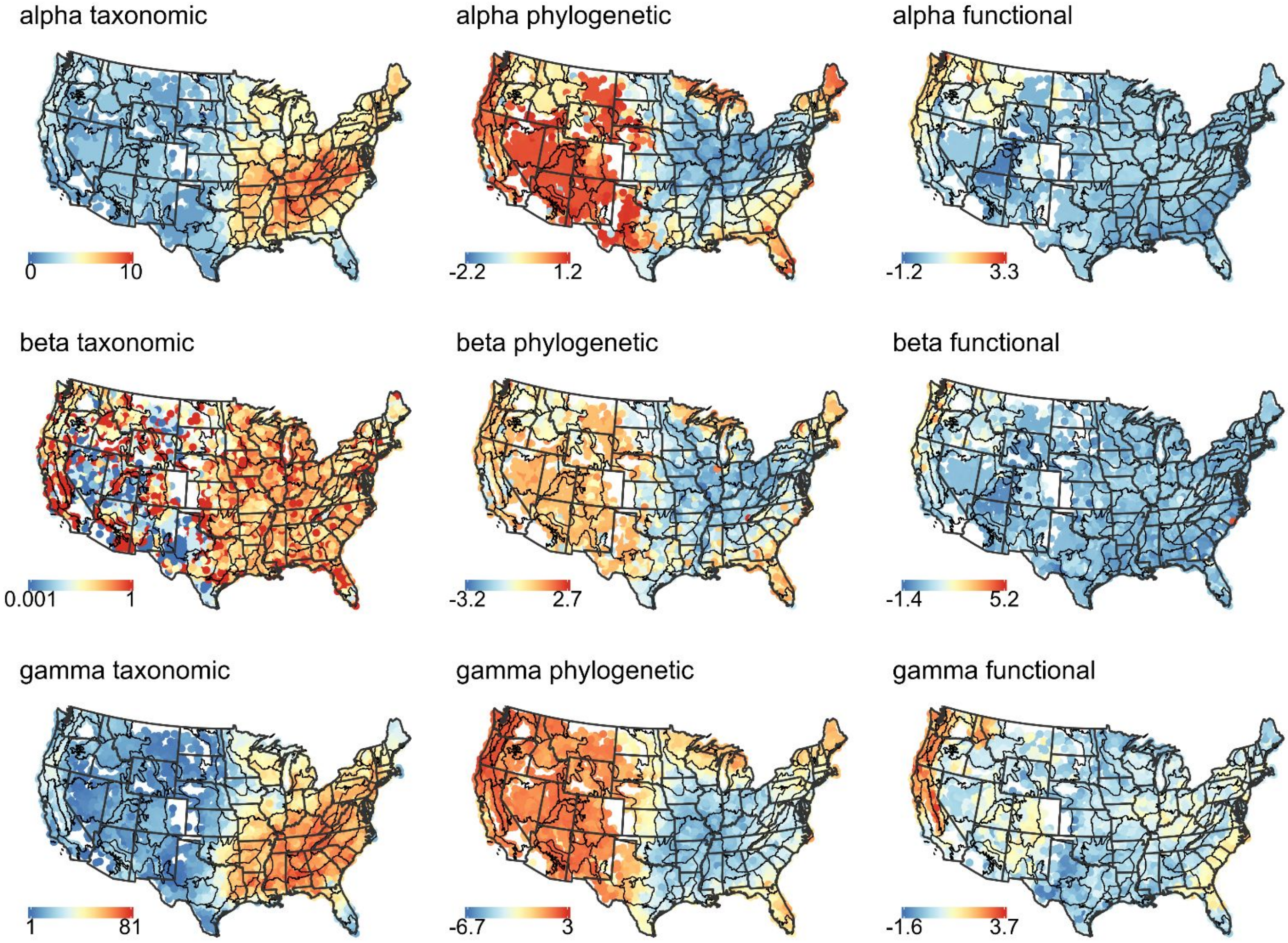


Figure 4: Maps of tree biodiversity at FIA plots, across 3 levels and 3 dimensions of biodiversity. The same biodiversity metrics are shown as in Figure 3. Fuzzed locations of each FIA plot are shown on the map.

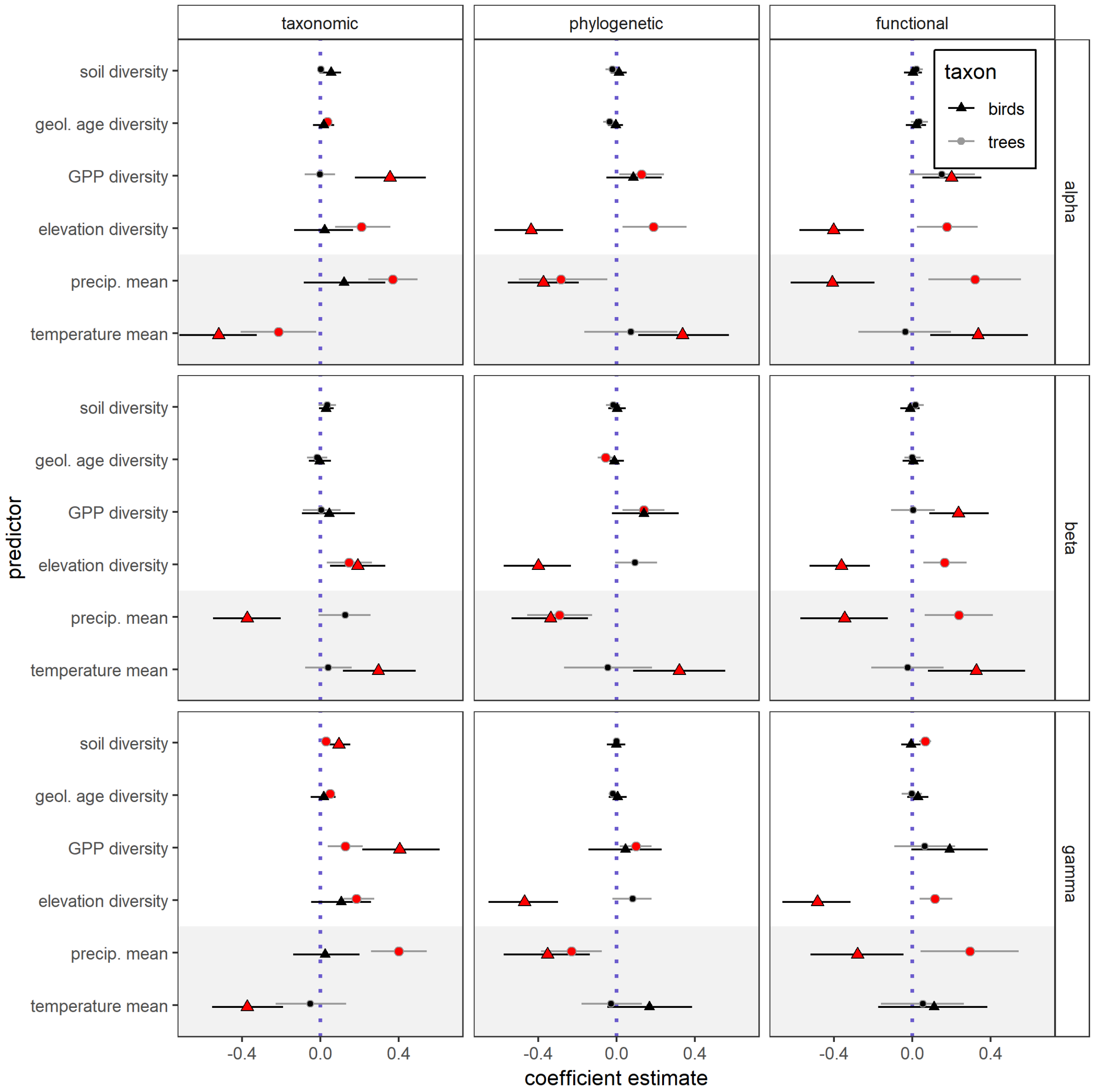


Figure 5: Scaled coefficients of fixed effects for birds and trees. Error bars show 95% credible interval around parameter estimate. Parameters with credible intervals that do not overlap zero are shown in red. Within each model, predictors are scaled so that coefficients can be compared across variables within the model. Predictors representing mean climate are shaded in grey; the other predictors represent geodiversity.

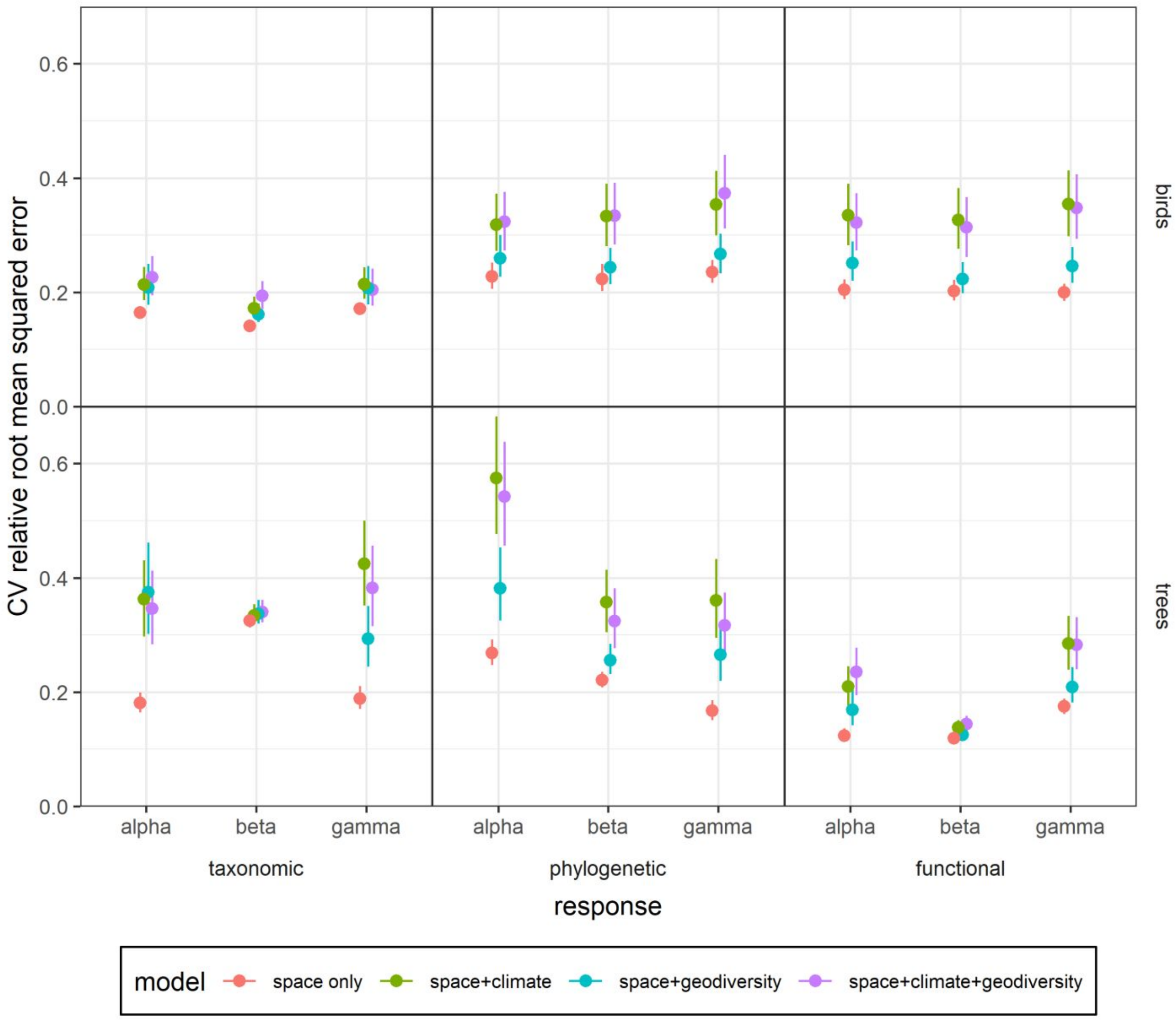


Figure 6: Model performance for bird biodiversity and tree biodiversity, assessed with spatially blocked leave-one-location-out cross-validation. This figure shows the root mean squared errors from the space-only or null models (red), models with climate predictors (green), models with geodiversity predictors (blue), and full models (purple) for each taxon and each response variable. Individual models were fit holding out all data points from one ecoregion, then the holdout data points were predicted and root mean squared error calculated across all ecoregions. The raw errors are divided by the range of the observed data to produce a relative value comparable among models. A lower value represents better performance of the model. Error bars are 95% credible intervals. Because each cross-validation fold excludes an entire

region, the null model including only the spatial random effect tends to predict the held out values as well or better than the models including climate and geodiversity predictors. However, models including geodiversity predictors tend to perform as well or better than the models including climate predictors, especially for phylogenetic and functional diversity.

Appendix 1: Assembly of functional traits and phylogenies for birds and trees

Birds: functional traits We obtained species mean trait values from the following two sources: the Amniote Life History Database (Myhrvold *et al.* 2016) and EltonTraits (Wilman *et al.* 2014). These databases provide measured or taxonomically imputed values for morphological and life-history traits, and foraging traits that define a species' resource niche, respectively. We used the following traits: proportion of the diet consisting of invertebrates, birds/mammals, reptiles/amphibians, fish, scavenged meat, fruit, nectar, and seeds; proportion of foraging time spent in the water below and above the surf line, on the ground, in the understory, at mid-height, in the canopy, and in the air; pelagic status; time to maturity of females and males; clutch size; number of clutches per year; average adult body mass; average and maximum longevity; mass at birth; egg mass; time of incubation; age at fledging. We also used the nocturnal status trait from EltonTraits to exclude nocturnal species, which are poorly detected by BBS protocol, from our analysis. Four traits (egg mass, mass at birth, male time to maturity, and average longevity) were correlated with other traits with Pearson's $r > 0.7$. Using a Mantel test implemented in the R package *vegan* (Oksanen *et al.* 2016), we compared the Gower pairwise distance matrix calculated from the full trait dataset with the matrix calculated from the reduced dataset without the four traits. The two matrices were highly correlated with one another (Mantel correlation statistic $r = 0.979$), indicating that the Gower distances among species are relatively insensitive to the inclusion of the correlated traits.

Birds: phylogeny We obtained a recent phylogeny of all bird species (Jetz *et al.* 2012). The phylogeny consists of a posterior distribution of 10000 trees. We randomly chose 1000 trees from this posterior distribution and generated a consensus tree with branch lengths using the R package *phytools* (Revell 2012). We used the branch lengths from this consensus tree to calculate the distance-based phylogenetic diversity indices described below.

We resolved any discrepancy in scientific names among BBS, the functional trait datasets, and the bird phylogeny by using the most recent taxonomy for each species found on Avibase (http://avibase.bsc-eoc.org/). We excluded all individuals not identifiable to the species level (excluding 0.17% of individuals) and all individuals listed as hybrids of two species (excluding 0.0003% of individuals). We assigned all taxa below the species level (subspecies or races) to the parent species (affecting 1.4% of individuals) and all species that were so recently split from another species in the dataset that they did not appear in the phylogeny or trait dataset (affecting 0.17% of individuals). After excluding the nocturnal species and unknown individuals and coarsening the subspecies to the species level, there were 605 unique species in the dataset.

Trees: functional traits We obtained all available trait data for all species in our survey dataset from the TRY database (http://try-db.org) (Kattge *et al.* 2011), and supplemented these traits with data compiled by Jens Stevens (unpublished). We restricted our analysis to continuous traits that have a documented link to species performance and niche and that have at least one available observation for the majority of species in our dataset. These criteria applied to the following traits: specific leaf area, leaf C content per area, leaf N content per area, leaf N content per dry mass, leaf P content per dry mass, leaf C:N ratio, leaf N:P ratio, leaf lifespan, photosynthetic rate per leaf area, photosynthetic rate per leaf dry mass, leaf thickness, litter decomposition rate, plant lifespan, plant shade tolerance category, rooting depth, seed dry mass, proportion vessel area per unit stem cross-sectional area, specific stem density, and stomatal conductance per leaf area. We used phylogenetic imputation implemented in the R package *Rphylopars* (Goolsby *et al.* 2017) to impute missing values. For the final analysis, we used the following six traits that had a value for almost all species to minimize the number of imputed traits: bark thickness, specific leaf area, specific stem density, seed dry mass, rooting depth, and plant lifespan.

Trees: phylogeny We obtained a phylogeny of all trees in the FIA survey area (Potter & Woodall 2012; Potter & Koch 2014). For this phylogeny, only a single tree was available rather than a distribution of trees, so all phylogenetic diversity metrics that we calculated for FIA trees are based on this single tree assuming that it represents a consensus tree. Any discrepancies in species names between the FIA, functional trait, and phylogenetic data sources were resolved using the most recent taxonomy listed by IUCN (iucnredlist.org).

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Appendix 2: Additional details on Breeding Bird Survey data processing

Dealing with imperfect detection in the Breeding Bird Survey

Imperfect bird detection is a known issue in estimating bird diversity from point count surveys (Link & Sauer 1998; Jarzyna & Jetz 2016). Because of this, when calculating biodiversity of Breeding Bird Survey (BBS) routes, we pooled observations from all stops in each route and pooled all surveys from 2007-2016. This yielded a single incidence value for each species at each route, with a species considered present if detected at any stop during the 10-year period. This method prioritizes minimizing false negatives due to imperfect detection, but may result in increased false positives because transient species are considered present. It is impossible to simultaneously minimize Type I and Type II errors when determining whether species are present or absent. An alternative approach would be to model detection probability for each species at each site explicitly (e.g. Dorazio & Royle 2005). Because our primary concern is relative differences in richness and diversity among sites rather than absolute diversity (Kéry & Royle 2008), generating species-specific estimates of occupancy and detection probability would be unlikely to qualitatively change our inference.

Determination of Breeding Bird Survey route neighbourhoods

Criterion used to determine neighbour status. Breeding Bird Survey routes are not points, but linear features. We obtained maps of the BBS routes and identified all routes for which we could unambiguously locate the midpoint of the route. This excludes any routes that are in multiple segments, routes that include loops, or routes that trace back on themselves, resulting in 3089 routes.

We identified all pairs of neighbouring routes as those whose midpoints were 50 km or less from one another. This method ensures that for almost all routes, at least 50% of the length of the neighbouring route was within the circle for which the environmental covariates were defined. If 50% of the neighbouring route is within the circle, the average environmental conditions of the circle should adequately represent the environmental conditions of the route. The following confusion matrix illustrates the point. 8520 of 8677 pairwise comparisons in our analysis both have midpoints that are within 50 km of one another and at least half of the neighbouring route within the 50-km circle around the focal route.

	Half of route not within 50 km	Half of route within 50 km	Total
Midpoint not within 50 km	—	**181**	**181**
Midpoint within 50 km	**157**	**8520**	**8677**
Total	**157**	**8701**	**8858**

As a result, the neighbourhood criterion is relatively insensitive to whether the midpoint or 50% criterion is chosen; 98.1% of pairwise comparisons are not affected by which criterion is chosen.

Number of neighbours for each route. Using the midpoint criterion to determine neighbourhoods, the number of neighbours for each BBS route varied between 0 and 15 (see table below). The 237 routes without neighbours did not have a beta-diversity value. These routes were not included in the beta-diversity regression models. The relatively low number of neighbours for some routes is a result of the relatively wide spacing of BBS routes, not the specific method we used to determine neighbour status.

Number of neighbours	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Number of routes	237	581	675	526	398	287	144	101	61	36	23	8	3	6	2	1

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Appendix 3: Compilation and processing of geodiversity data

All data were obtained for the contiguous U.S. or globally and processed using GDAL (GDAL/OGR Contributors 2018) and R (R Core Team, 2017) including the rgdal (Bivand *et al.* 2018), gdalutils (Mattiuzzi 2018), rts (Naimi 2018), RCurl (Lang & CRAN Team 2018), and raster (Hijmans *et al.* 2017) packages.

Elevation data were obtained from the NASA Shuttle Radar Topography Mission (SRTM; Farr *et al.* 2007) at 1 arcsecond (~30 m) resolution via USGS (https://e4ftl01.cr.usgs.gov/). From these data slope, aspect, and topographic position index (TPI) were calculated for a 3 × 3 pixel kernel around each central pixel. For each radius (see the section headed “Biodiversity Data Sources and Processing” in the main text), pixels were extracted and we calculated the mean, standard deviation, maximum, and minimum values.

Temperature variables were derived from land surface temperature (LST) data from the MODerate Imaging Spectrometer (MODIS; Wan *et al.* 2015) on board the Terra satellite (10:30 am descending node). We used the MOD11A2 product, which is LST averaged over an 8-day period at 1 km pixel resolution. These data were aggregated to monthly climatologies for 2001-2016.

Average monthly precipitation totals (mm) were calculated from the Climate Hazards group Infrared Precipitation with Stations (CHIRPS) monthly data from 2001-2015 (Funk *et al.* 2015). CHIRPS is a 0.05° resolution gridded rainfall product that combines satellite imagery and *in situ* station data, and has been shown to improve species distribution models in areas with sparse meteorological stations (Deblauwe *et al.* 2016). Monthly data were aggregated to monthly climatologies by averaging each month across the time period of 2001-2015.

The two main climate datasets - LST and precipitation - were aggregated into 19 bioclimatic variables (“bioclim variables”) as described in (Hijmans *et al.* 2005). Because LST and precipitation were available at different resolutions, and many of the bioclim variables require both, all 19 bioclim variables were calculated at both resolutions. LST was averaged to match the CHIRPS precipitation resolution and CHIRPS precipitation was simply re-gridded to the LST resolution. The bioclimatic variable calculation transformed the monthly climatologies into annual climatologies for each location. For each bioclimatic variable, we calculated the mean, standard deviation, minimum, and maximum values within each radius, as for the topographic indices.

Geologic and soil information included two polygon-based maps which we rasterized: geologic age (92 possible values) provided by USGS International Surface Geology (originally hosted by worldgrids.org; although the original page is no longer active, for an archived version of the page, see http://85.214.253.67/dkwk-stable/doku.php?id=wiki:geological_and_parent_materials_maps) and soil type (36 possible values) provided by the Harmonized World Soil Database (Fischer *et al.* 2008) and interpolated to a 250 m gridded product (Hengl *et al.* 2017). In contrast to the other geodiversity data layers, these products were not remotely sensed. We were concerned with the diversity of geological types within each radius, not the substrate and soil types themselves, so we calculated richness (number of types) and diversity (Shannon entropy) of substrate and soil types for each radius.

Gross primary productivity (GPP) was calculated as an indicator of cumulative vegetation productivity over the course of a year using the Moderate Resolution Imaging Spectroradiometer (MODIS) data (for details see Hobi *et al.* 2017). For this analysis the GPP MODIS Collection 5 product having a repeat period of 8 days and a spatial resolution of 1000 m was averaged for the time period of 2003-2014 (data freely available from the Dynamic Habitat Index project of the SILVIS lab: http://silvis.forest.wisc.edu/data/DHIs). Though GPP is not often considered a component of geodiversity, we chose to classify GPP as a geodiversity variable because it integrates across a number of biotic and abiotic variables.

Works cited (Appendix 3)

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Supplementary Information: Tables and Figures

Beyond counts and averages: relating geodiversity to dimensions of biodiversity. Quentin D. Read, Phoebe L. Zarnetske, Sydne Record, Kyla M. Dahlin, Andrew O. Finley, John M. Grady, Martina L. Hobi, Sparkle L. Malone, Jennifer K. Costanza, Adam M. Wilson, Andrew M. Latimer, Keith D. Gaddis, Stephanie Pau, Scott V. Ollinger

Supplementary Tables

Table S1: Overview of biodiversity metrics by level and by dimension.

		Diversity dimension		
		Taxonomic	**Phylogenetic**	**Functional**
Diversity level	**Alpha (local)**	Mean richness of local communities within a 50-km radius around the focal plot	Mean pairwise phylogenetic distance score of local communities in the radius, relative to null expectation	Mean pairwise functional distance score of local communities in the radius, relative to null expectation
	Beta (turnover)	Mean pairwise dissimilarity of local communities in the radius, logit-transformed	Mean pairwise phylogenetic distance among communities in the radius, relative to null expectation	Mean pairwise functional distance among communities in the radius, relative to null expectation
	Gamma (regional)	Richness of all communities in the radius, pooled to a single community	Mean pairwise phylogenetic distance of all communities in the radius, pooled to a single community, relative to null expectation	Mean pairwise functional distance of all communities in the radius, pooled to a single community, relative to null expectation

Table S2: This table shows model fit statistics for each response variable for each model. The RMSE is the root mean squared error of the model fit with all the data. The CV RMSE is the root mean squared error of the holdout data points in spatially blocked cross-validation. Both RMSEs are divided by the range of the data to produce a relative RMSE value that is comparable among models. Lower RMSE values indicate better model performance. The R^2 is calculated using the method of Gelman *et al.*. For all fit statistics, mean value as well as upper and lower bounds of 95% credible intervals are shown.

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## Warning: package 'knitr' was built under R version 3.6.1
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taxon	biodiversity level	biodiversity dimension	model	RMSE	CV RMSE	R^2
birds	alpha	taxonomic	space only	0.13 [0.13,0.14]	0.16 [0.15,0.18]	0.5 [0.48,0.52]
birds	alpha	taxonomic	space + climate	0.12 [0.11,0.12]	0.21 [0.19,0.24]	0.62 [0.6,0.63]
birds	alpha	taxonomic	space + geodiversity	0.11 [0.11,0.12]	0.21 [0.18,0.25]	0.63 [0.61,0.64]
birds	alpha	taxonomic	space + climate + geodiversity	0.11 [0.1,0.11]	0.23 [0.19,0.26]	0.68 [0.67,0.69]
birds	alpha	phylogenetic	space only	0.15 [0.15,0.16]	0.23 [0.21,0.25]	0.67 [0.66,0.68]
birds	alpha	phylogenetic	space + climate	0.13 [0.13,0.13]	0.32 [0.27,0.37]	0.76 [0.75,0.77]
birds	alpha	phylogenetic	space + geodiversity	0.13 [0.13,0.14]	0.26 [0.23,0.3]	0.75 [0.74,0.76]
birds	alpha	phylogenetic	space + climate + geodiversity	0.12 [0.12,0.12]	0.32 [0.27,0.38]	0.8 [0.79,0.81]
birds	alpha	functional	space only	0.15 [0.15,0.15]	0.2 [0.19,0.22]	0.62 [0.61,0.64]
birds	alpha	functional	space + climate	0.13 [0.12,0.13]	0.33 [0.28,0.39]	0.73 [0.72,0.74]
birds	alpha	functional	space + geodiversity	0.13 [0.12,0.13]	0.25 [0.22,0.29]	0.72 [0.71,0.73]
birds	alpha	functional	space + climate + geodiversity	0.11 [0.11,0.12]	0.32 [0.27,0.37]	0.78 [0.77,0.79]
birds	beta	taxonomic	space only	0.12 [0.12,0.13]	0.14 [0.13,0.15]	0.64 [0.62,0.65]
birds	beta	taxonomic	space + climate	0.12 [0.11,0.12]	0.17 [0.16,0.19]	0.67 [0.66,0.69]
birds	beta	taxonomic	space + geodiversity	0.11 [0.11,0.12]	0.16 [0.15,0.18]	0.68 [0.67,0.7]
birds	beta	taxonomic	space + climate + geodiversity	0.11 [0.11,0.11]	0.19 [0.17,0.22]	0.71 [0.7,0.73]
birds	beta	phylogenetic	space only	0.15 [0.14,0.15]	0.22 [0.2,0.25]	0.69 [0.68,0.7]
birds	beta	phylogenetic	space + climate	0.12 [0.12,0.13]	0.33 [0.28,0.39]	0.78 [0.77,0.79]
birds	beta	phylogenetic	space + geodiversity	0.13 [0.12,0.13]	0.24 [0.21,0.28]	0.77 [0.76,0.78]
birds	beta	phylogenetic	space + climate + geodiversity	0.11 [0.11,0.11]	0.33 [0.28,0.39]	0.83 [0.82,0.83]
birds	beta	functional	space only	0.14 [0.14,0.15]	0.2 [0.19,0.22]	0.64 [0.62,0.65]
birds	beta	functional	space + climate	0.12 [0.12,0.13]	0.33 [0.28,0.38]	0.74 [0.73,0.75]
birds	beta	functional	space + geodiversity	0.12 [0.12,0.13]	0.22 [0.2,0.25]	0.73 [0.72,0.74]
birds	beta	functional	space + climate + geodiversity	0.11 [0.11,0.11]	0.31 [0.26,0.37]	0.79 [0.78,0.8]
birds	gamma	taxonomic	space only	0.14 [0.13,0.14]	0.17 [0.16,0.18]	0.46 [0.43,0.48]
birds	gamma	taxonomic	space + climate	0.12 [0.12,0.13]	0.21 [0.19,0.24]	0.55 [0.53,0.57]
birds	gamma	taxonomic	space + geodiversity	0.12 [0.12,0.12]	0.21 [0.18,0.25]	0.58 [0.57,0.6]
birds	gamma	taxonomic	space + climate + geodiversity	0.12 [0.11,0.12]	0.2 [0.18,0.24]	0.62 [0.6,0.63]
birds	gamma	phylogenetic	space only	0.17 [0.16,0.17]	0.24 [0.22,0.26]	0.65 [0.64,0.66]
birds	gamma	phylogenetic	space + climate	0.15 [0.14,0.15]	0.35 [0.3,0.41]	0.73 [0.72,0.74]
birds	gamma	phylogenetic	space + geodiversity	0.14 [0.14,0.15]	0.27 [0.23,0.3]	0.74 [0.73,0.75]
birds	gamma	phylogenetic	space + climate + geodiversity	0.13 [0.13,0.13]	0.37 [0.31,0.44]	0.79 [0.78,0.8]

(continued)

taxon	biodiversity level	biodiversity dimension	model	RMSE	CV RMSE	R^2
birds	gamma	functional	space only	0.15 [0.15,0.16]	0.2 [0.18,0.22]	0.57 [0.55,0.59]
birds	gamma	functional	space + climate	0.13 [0.13,0.13]	0.35 [0.3,0.41]	0.68 [0.67,0.69]
birds	gamma	functional	space + geodiversity	0.13 [0.13,0.13]	0.25 [0.22,0.28]	0.69 [0.68,0.7]
birds	gamma	functional	space + climate + geodiversity	0.12 [0.11,0.12]	0.35 [0.29,0.41]	0.75 [0.74,0.76]
trees	alpha	taxonomic	space only	0.12 [0.12,0.13]	0.18 [0.16,0.2]	0.89 [0.88,0.89]
trees	alpha	taxonomic	space + climate	0.09 [0.09,0.1]	0.36 [0.3,0.43]	0.94 [0.93,0.94]
trees	alpha	taxonomic	space + geodiversity	0.1 [0.1,0.1]	0.37 [0.3,0.46]	0.93 [0.92,0.93]
trees	alpha	taxonomic	space + climate + geodiversity	0.09 [0.08,0.09]	0.35 [0.28,0.41]	0.95 [0.94,0.95]
trees	alpha	phylogenetic	space only	0.2 [0.2,0.21]	0.27 [0.25,0.29]	0.76 [0.75,0.77]
trees	alpha	phylogenetic	space + climate	0.15 [0.15,0.16]	0.57 [0.48,0.68]	0.86 [0.86,0.86]
trees	alpha	phylogenetic	space + geodiversity	0.17 [0.17,0.18]	0.38 [0.32,0.45]	0.82 [0.82,0.83]
trees	alpha	phylogenetic	space + climate + geodiversity	0.14 [0.14,0.14]	0.54 [0.46,0.64]	0.88 [0.88,0.89]
trees	alpha	functional	space only	0.09 [0.09,0.09]	0.12 [0.11,0.14]	0.73 [0.72,0.74]
trees	alpha	functional	space + climate	0.08 [0.08,0.08]	0.21 [0.18,0.25]	0.79 [0.79,0.8]
trees	alpha	functional	space + geodiversity	0.08 [0.07,0.08]	0.17 [0.14,0.21]	0.8 [0.8,0.81]
trees	alpha	functional	space + climate + geodiversity	0.07 [0.07,0.07]	0.24 [0.19,0.28]	0.84 [0.83,0.84]
trees	beta	taxonomic	space only	0.3 [0.29,0.3]	0.32 [0.31,0.34]	0.16 [0.14,0.19]
trees	beta	taxonomic	space + climate	0.29 [0.28,0.3]	0.33 [0.32,0.35]	0.2 [0.17,0.23]
trees	beta	taxonomic	space + geodiversity	0.29 [0.28,0.3]	0.34 [0.32,0.36]	0.2 [0.17,0.23]
trees	beta	taxonomic	space + climate + geodiversity	0.29 [0.28,0.29]	0.34 [0.32,0.36]	0.22 [0.2,0.25]
trees	beta	phylogenetic	space only	0.18 [0.18,0.19]	0.22 [0.21,0.24]	0.63 [0.62,0.64]
trees	beta	phylogenetic	space + climate	0.16 [0.16,0.17]	0.36 [0.3,0.41]	0.71 [0.7,0.72]
trees	beta	phylogenetic	space + geodiversity	0.17 [0.17,0.18]	0.26 [0.23,0.28]	0.68 [0.67,0.69]
trees	beta	phylogenetic	space + climate + geodiversity	0.16 [0.15,0.16]	0.32 [0.28,0.38]	0.73 [0.72,0.74]
trees	beta	functional	space only	0.1 [0.1,0.11]	0.12 [0.11,0.12]	0.51 [0.49,0.52]
trees	beta	functional	space + climate	0.1 [0.1,0.1]	0.14 [0.13,0.15]	0.54 [0.52,0.56]
trees	beta	functional	space + geodiversity	0.1 [0.1,0.1]	0.13 [0.12,0.14]	0.54 [0.52,0.55]
trees	beta	functional	space + climate + geodiversity	0.1 [0.09,0.1]	0.14 [0.13,0.16]	0.56 [0.54,0.58]
trees	gamma	taxonomic	space only	0.12 [0.12,0.13]	0.19 [0.17,0.21]	0.9 [0.9,0.91]
trees	gamma	taxonomic	space + climate	0.09 [0.09,0.09]	0.42 [0.35,0.5]	0.95 [0.95,0.95]
trees	gamma	taxonomic	space + geodiversity	0.09 [0.09,0.1]	0.29 [0.24,0.35]	0.94 [0.94,0.95]
trees	gamma	taxonomic	space + climate + geodiversity	0.08 [0.07,0.08]	0.38 [0.31,0.46]	0.96 [0.96,0.96]
trees	gamma	phylogenetic	space only	0.12 [0.11,0.12]	0.17 [0.15,0.19]	0.89 [0.89,0.9]
trees	gamma	phylogenetic	space + climate	0.08 [0.08,0.09]	0.36 [0.29,0.43]	0.94 [0.94,0.95]
trees	gamma	phylogenetic	space + geodiversity	0.1 [0.09,0.1]	0.27 [0.22,0.31]	0.93 [0.93,0.93]
trees	gamma	phylogenetic	space + climate + geodiversity	0.08 [0.07,0.08]	0.32 [0.26,0.37]	0.95 [0.95,0.96]

(continued)

taxon	**biodiversity level**	**biodiversity dimension**	**model**	**RMSE**	**CV RMSE**	R^2
trees	gamma	functional	space only	0.13 [0.13,0.13]	0.17 [0.16,0.19]	0.65 [0.64,0.67]
trees	gamma	functional	space + climate	0.11 [0.11,0.11]	0.28 [0.24,0.33]	0.75 [0.74,0.76]
trees	gamma	functional	space + geodiversity	0.12 [0.11,0.12]	0.21 [0.18,0.24]	0.73 [0.71,0.74]
trees	gamma	functional	space + climate + geodiversity	0.1 [0.1,0.11]	0.28 [0.24,0.33]	0.78 [0.77,0.79]

Table S3: This table shows the Widely Available Information Criterion (WAIC) for each model, along with the standard error of the WAIC. Lower WAIC values indicate a more parsimonious fit.

taxon	**biodiversity level**	**model**	**WAIC**	**standard error of WAIC**
birds	alpha	space only	15278.9	230.6
birds	alpha	space + climate	13189.6	259.3
birds	alpha	space + geodiversity	13307.8	246.9
birds	alpha	space + climate + geodiversity	11922.8	256.1
birds	beta	space only	13245.3	197.8
birds	beta	space + climate	11525.5	214.9
birds	beta	space + geodiversity	11698.0	203.9
birds	beta	space + climate + geodiversity	10407.8	213.2
birds	gamma	space only	16016.9	215.8
birds	gamma	space + climate	14375.7	243.3
birds	gamma	space + geodiversity	14053.7	231.8
birds	gamma	space + climate + geodiversity	12908.8	240.4
trees	alpha	space only	10308.1	205.6
trees	alpha	space + climate	6737.0	236.5
trees	alpha	space + geodiversity	7810.7	226.4
trees	alpha	space + climate + geodiversity	5412.5	248.2
trees	beta	space only	18052.9	257.3
trees	beta	space + climate	17223.2	276.8
trees	beta	space + geodiversity	17545.7	262.8
trees	beta	space + climate + geodiversity	16957.1	278.8
trees	gamma	space only	8349.6	205.3
trees	gamma	space + climate	4009.5	228.0
trees	gamma	space + geodiversity	5444.2	220.2
trees	gamma	space + climate + geodiversity	2541.7	245.6

Supplementary Figures

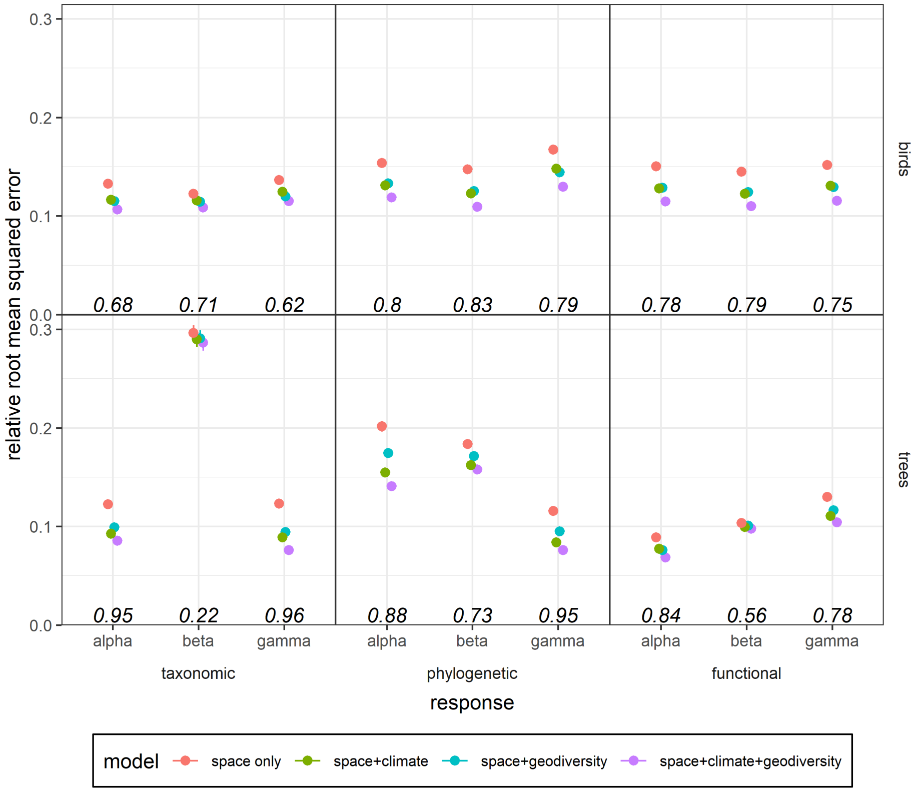

Figure S1: Model performance assessed with standard evaluation

Figure S1: This figure shows the relative root mean squared errors obtained from standard resubstitution evaluation, in which the models are fit using all data and the predicted and observed values compared. The raw errors are divided by the range of the observed data to produce a relative value comparable among models. A lower value represents better performance of the model predicting biodiversity. Error bars are 95% credible intervals. Here, we not only compare taxa but also the four types of model: space only (null), space + climate, space + geodiversity, and space + climate + geodiversity (full model). The Bayesian R-squared values for the full models are also shown. For most biodiversity variables, tree biodiversity is better predicted by a combination of space, climate, and geodiversity, compared to bird biodiversity. The exceptions are taxonomic and phylogenetic beta-diversity and phylogenetic alpha-diversity, which are predicted relatively poorly for trees.

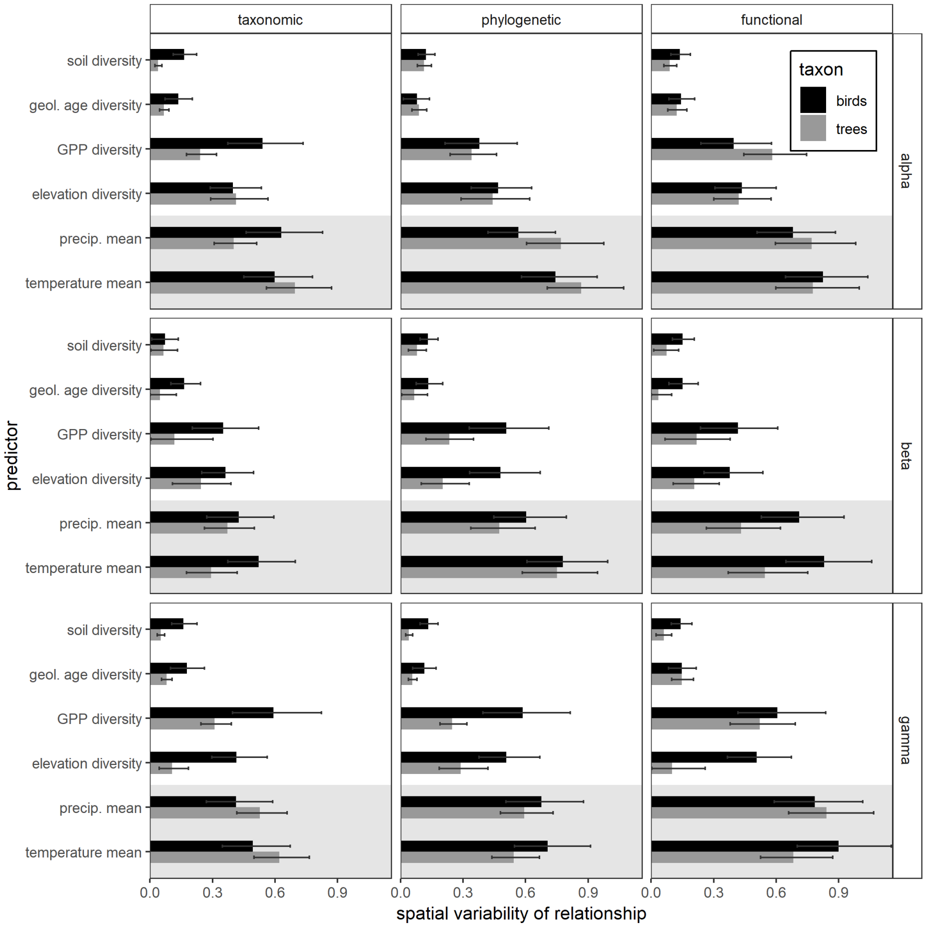

Figure S2: Spatial variation in geodiversity-biodiversity relationships

Figure S2: The spatial variability of the relationship between each predictor and each response, by taxon. The spatial variability is measured by the standard deviation of each coefficient value among ecoregions. Error bars represent the 95% credible interval of the standard deviation parameter. Higher values represent relationships that vary more spatially.

Supplementary Figures S3-S14

The following figures are maps of the coefficient on each climate or geodiversity predictor from the full multivariate models predicting alpha, beta, and gamma diversity for birds and for trees. Each figure shows the coefficients from the alpha, beta, and gamma models for each of the three biodiversity dimensions (taxonomic, phylogenetic, and functional) for one taxonomic group. Figures 3 through 8 show the coefficients for birds separately for each predictor, and figures 9 through 14 show the coefficients for trees.

In figures S3a, S4a, etc. below, the color of each TNC ecoregion is the region-level coefficient estimate from the model (USA-wide fixed-effect slope + random-effect slope from that region). The colors are scaled so that darker red ecoregions have more positive coefficients, and darker blue ecoregions have negative coefficients. White ecoregions have coefficients approximating zero, and dark gray ecoregions have coefficients that could not be estimated.

In figures S3b, S4b, etc., below, the ecoregions are shaded based on whether the 95% credible interval around the coefficient overlaps zero. Red shaded regions have entirely positive nonzero 95% credible intervals, while blue shaded regions have entirely negative nonzero 95% credible intervals. Dark gray shaded regions have 95% credible intervals that contain zero.

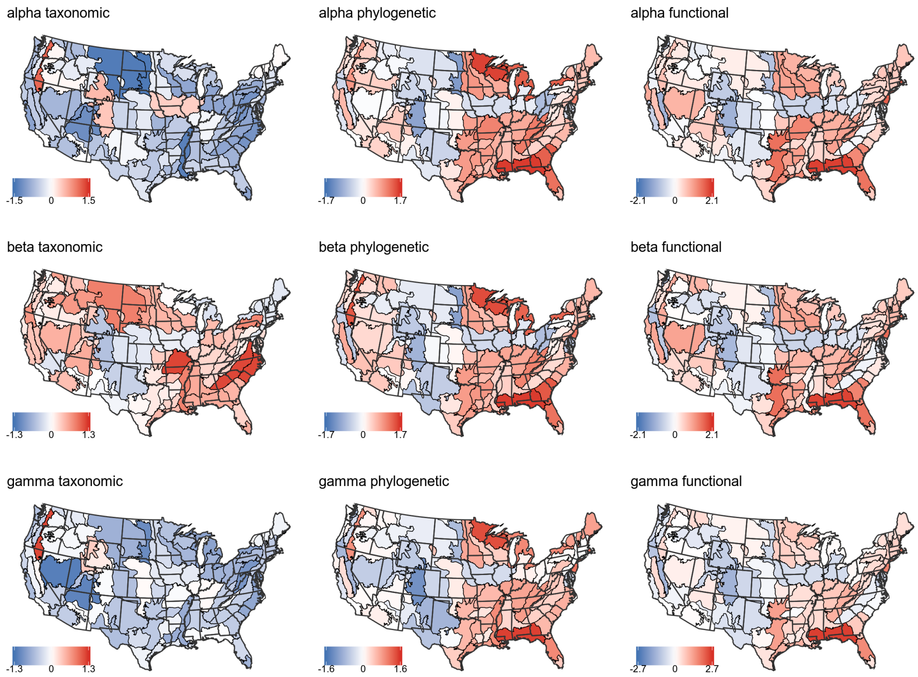

Figure S3a: Coefficients of mean annual temperature on bird diversity, values shown

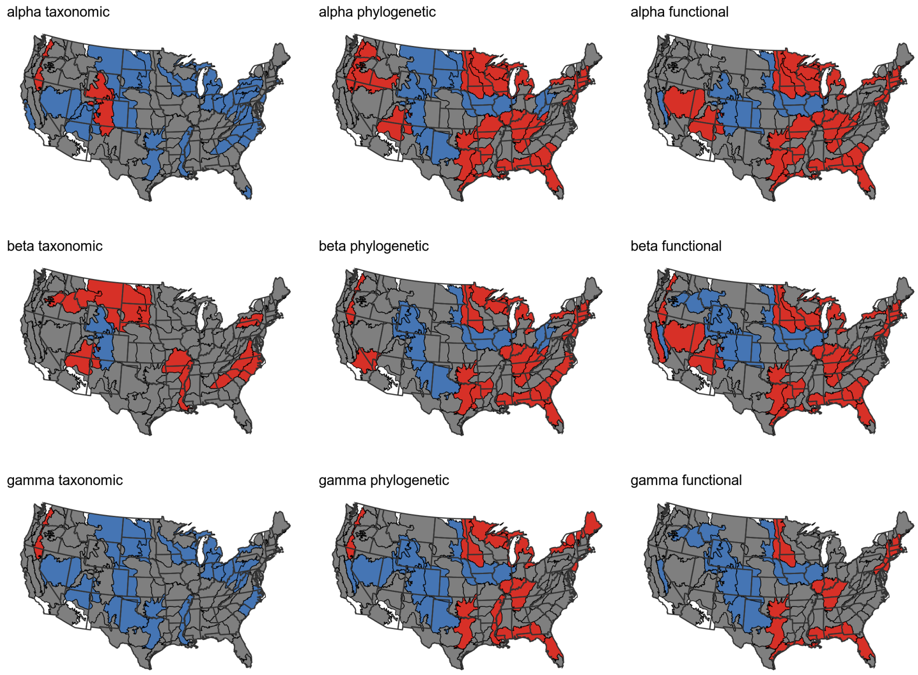

Figure S3b: Coefficients of mean annual temperature on bird diversity, nonzero regions shown

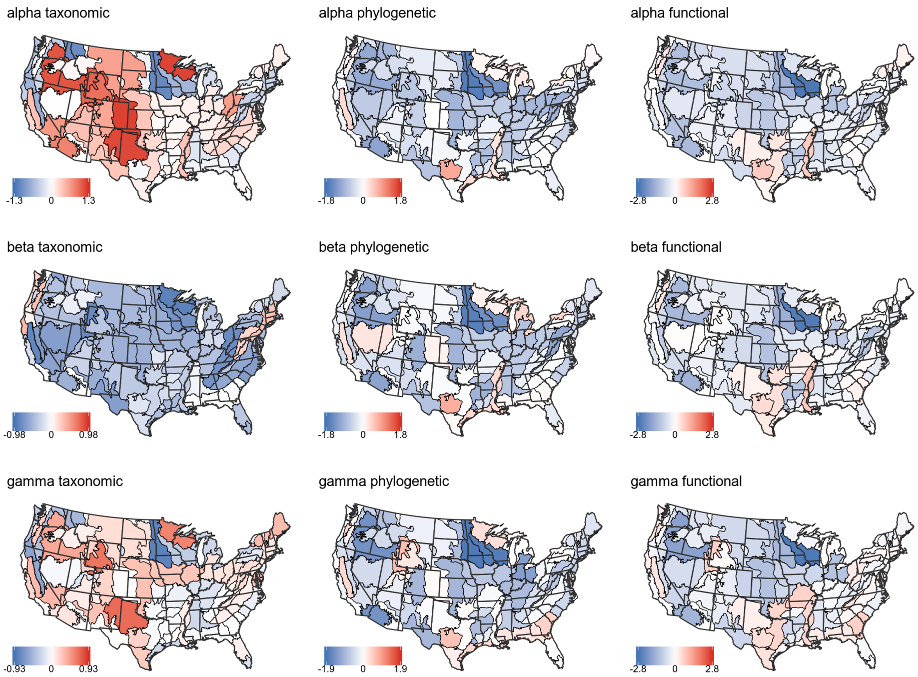

Figure S4a: Coefficients of mean annual precipitation on bird diversity, values shown

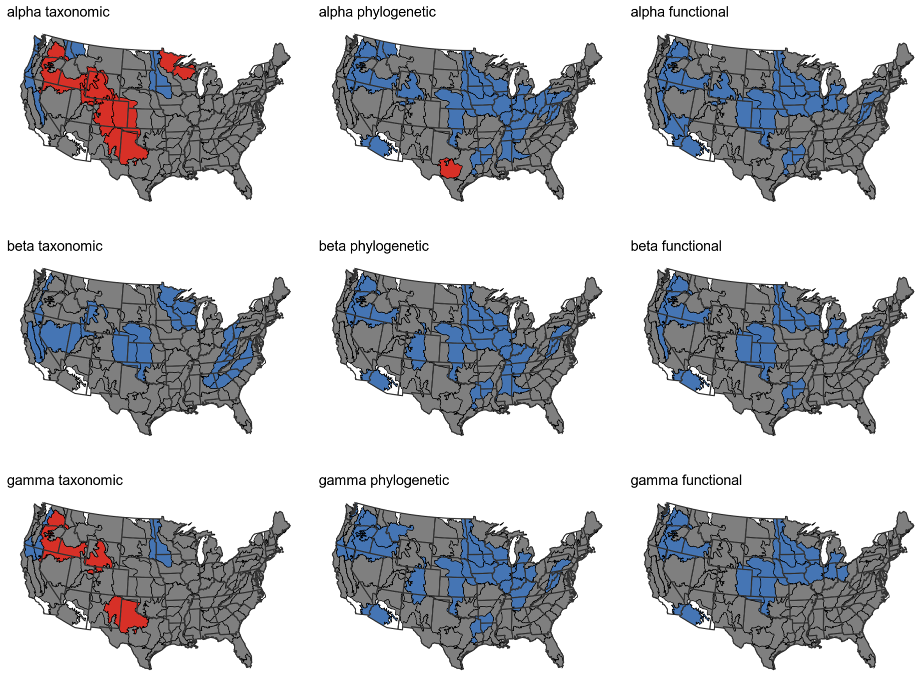

Figure S4b: Coefficients of mean annual precipitation on bird diversity, nonzero regions shown

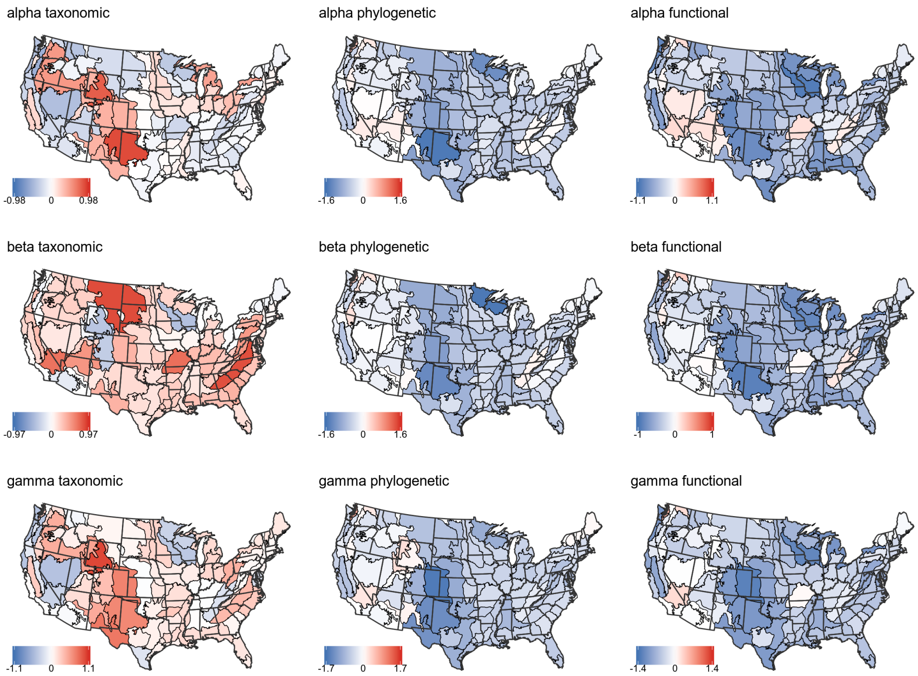

Figure S5a: Coefficients of elevation variability on bird diversity, values shown

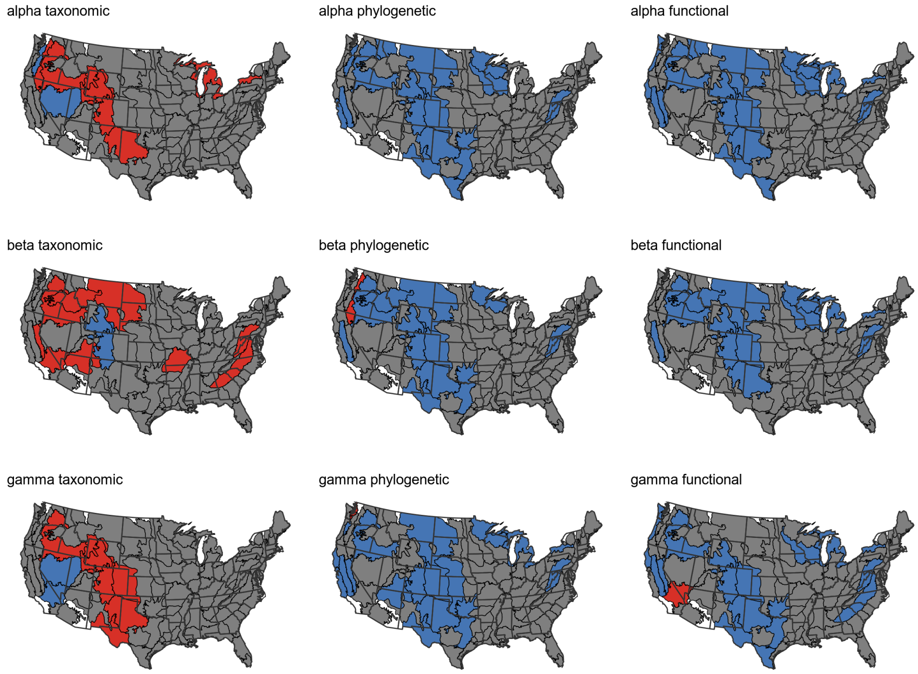

Figure S5b: Coefficients of elevation variability on bird diversity, nonzero regions shown

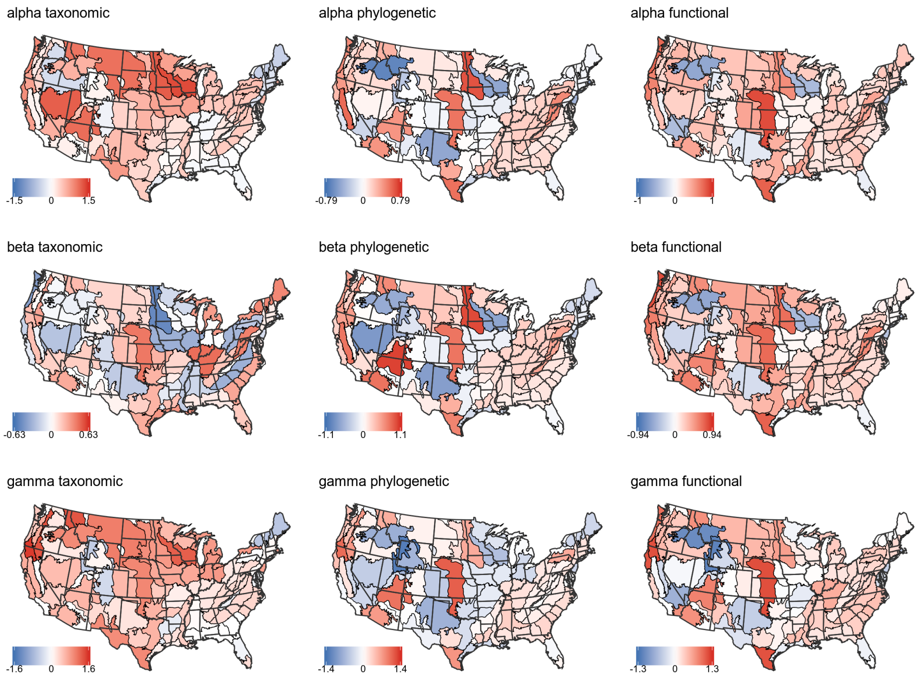

Figure S6a: Coefficients of GPP variability on bird diversity, values shown

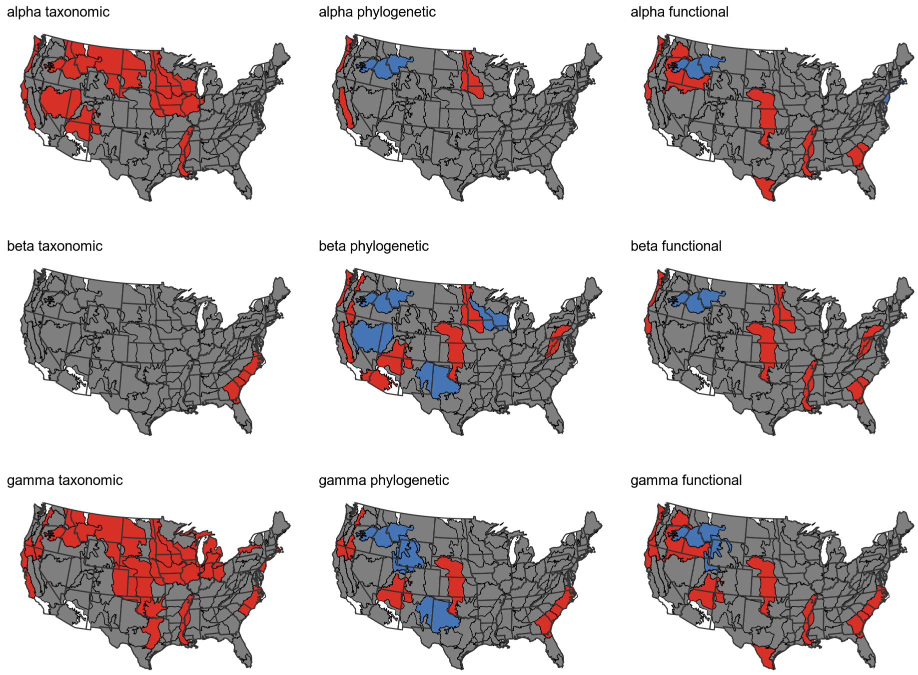

Figure S6b: Coefficients of GPP variability on bird diversity, nonzero regions shown

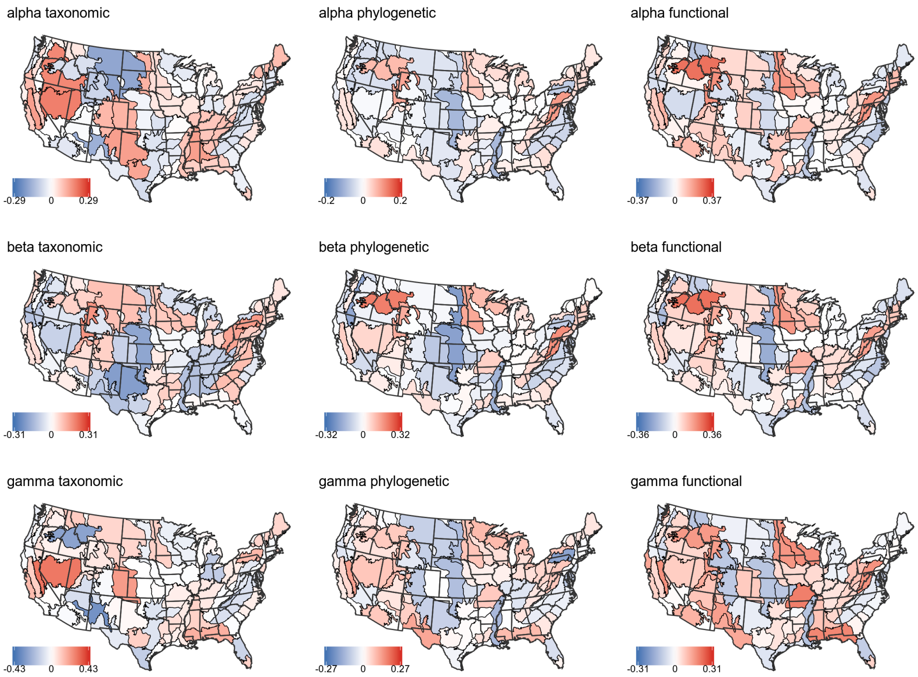

Figure S7a: Coefficients of geological age diversity on bird diversity, values shown

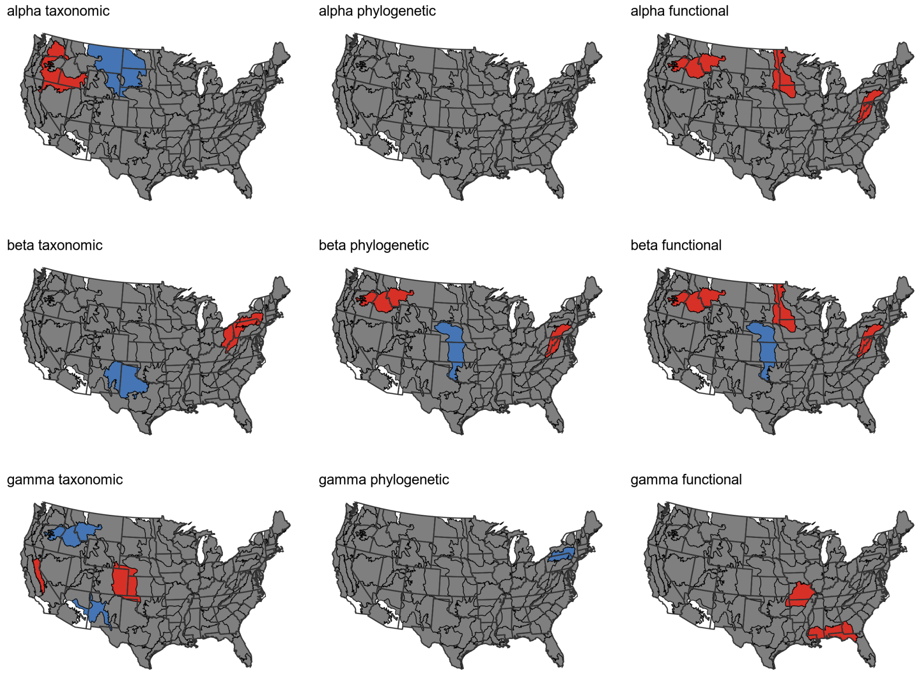

Figure S7b: Coefficients of geological age diversity on bird diversity, nonzero regions shown

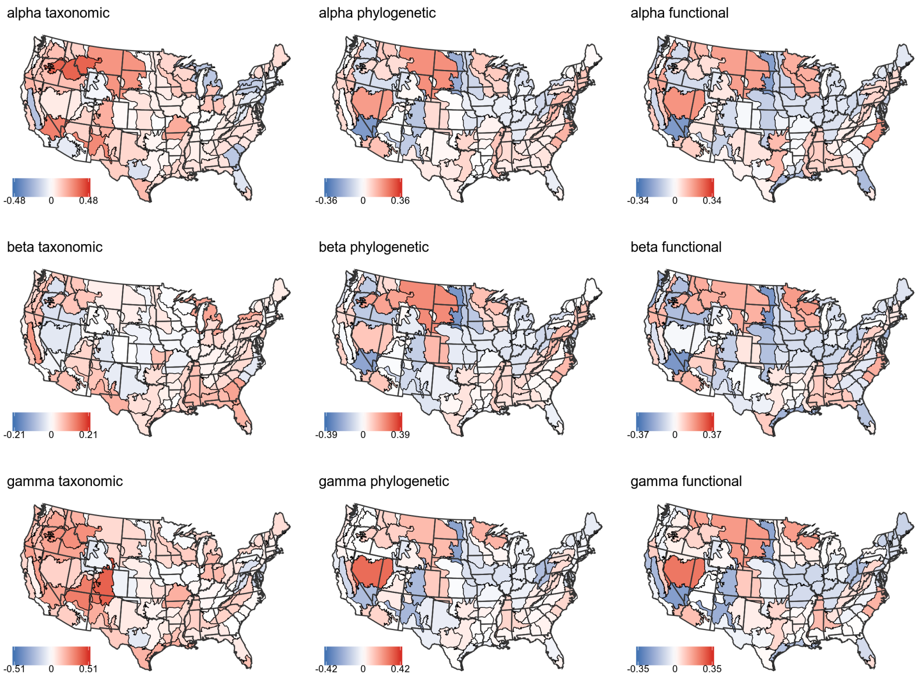

Figure S8a: Coefficients of soil type diversity on bird diversity, values shown

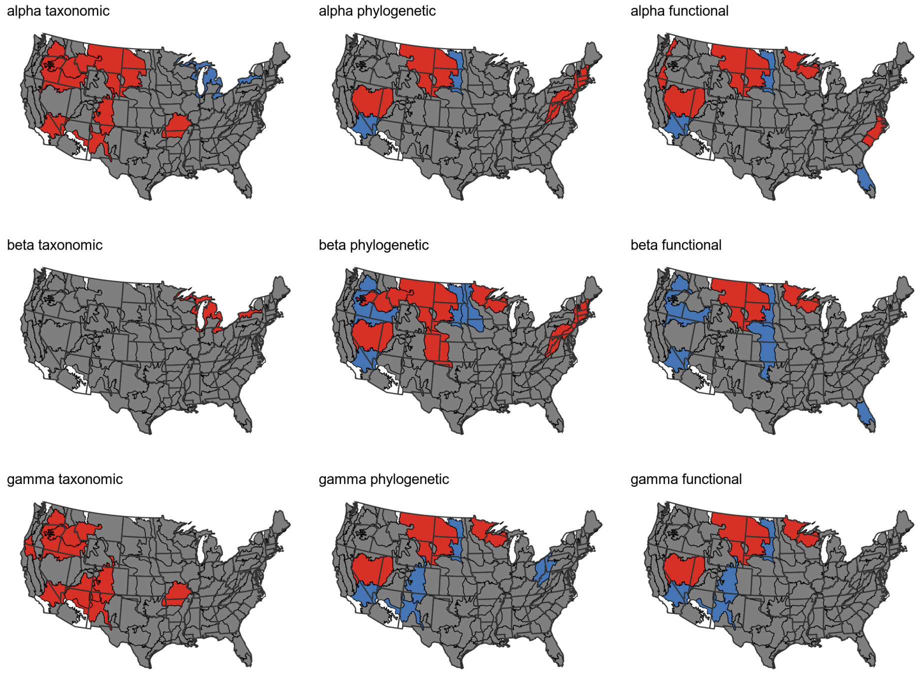

Figure S8b: Coefficients of soil type diversity on bird diversity, nonzero regions shown

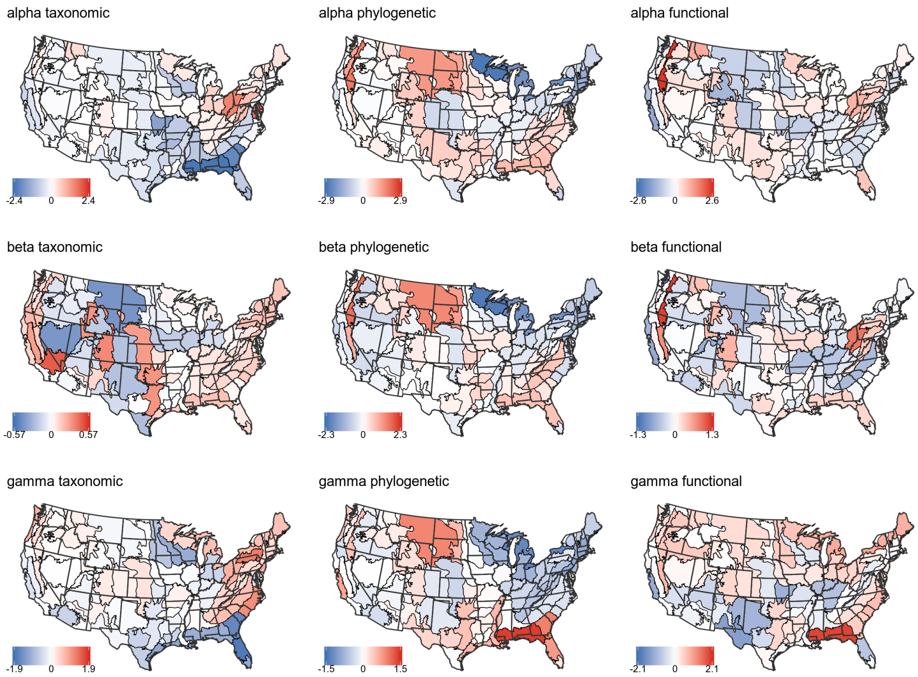

Figure S9a: Coefficients of mean annual temperature on tree diversity, values shown

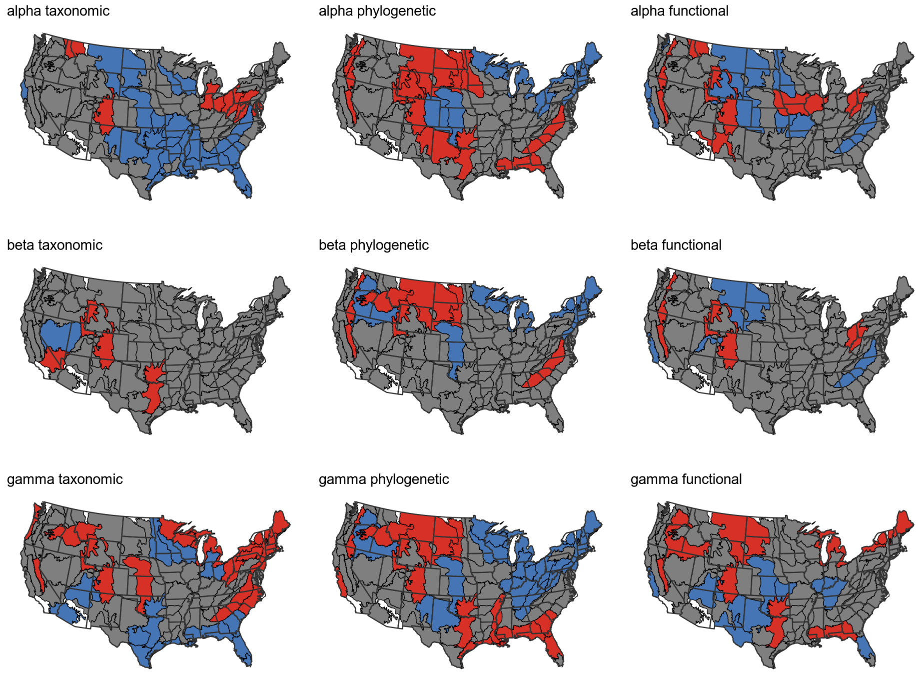

Figure S9b: Coefficients of mean annual temperature on tree diversity, nonzero regions shown

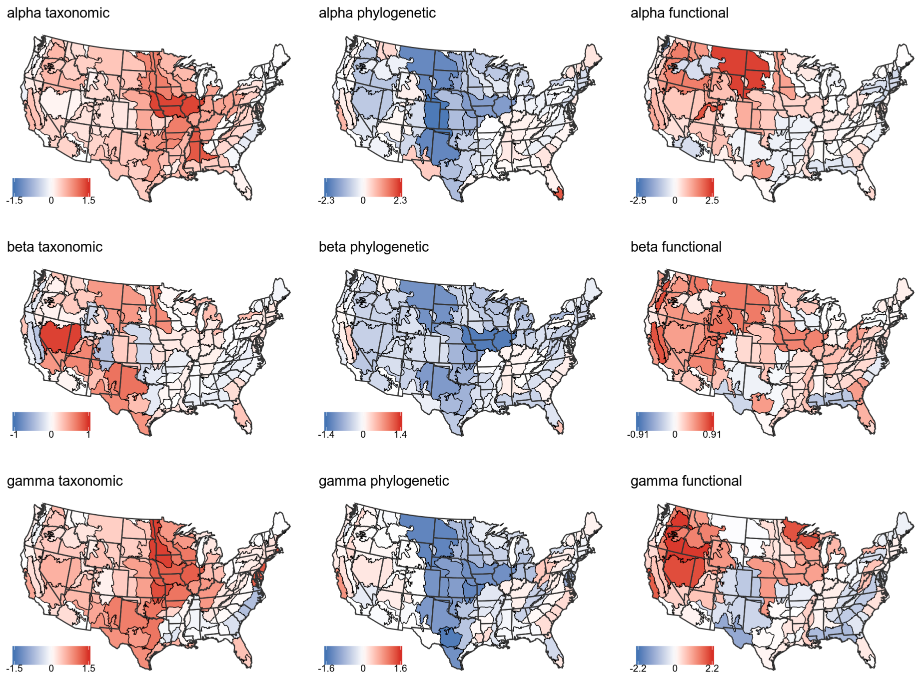

Figure S10a: Coefficients of mean annual precipitation on tree diversity, values shown

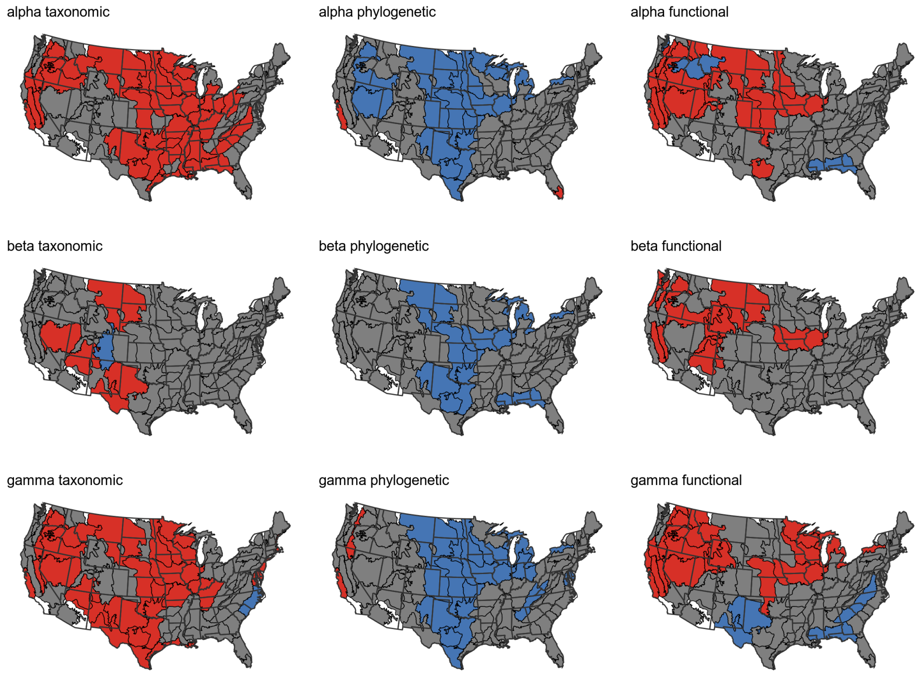

Figure S10b: Coefficients of mean annual precipitation on tree diversity, nonzero regions shown

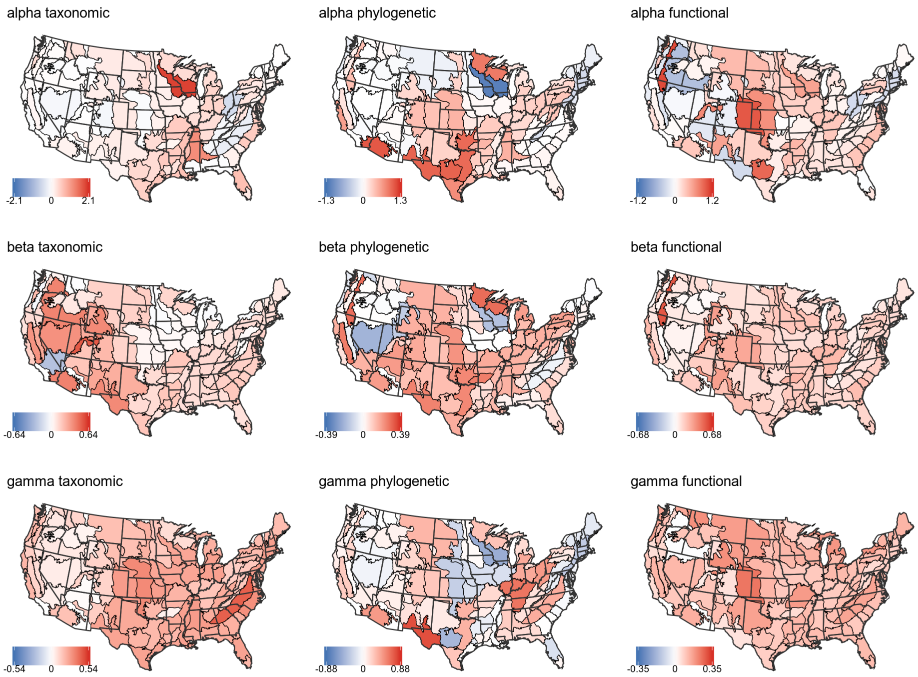

Figure S11a: Coefficients of elevation variability on tree diversity, values shown

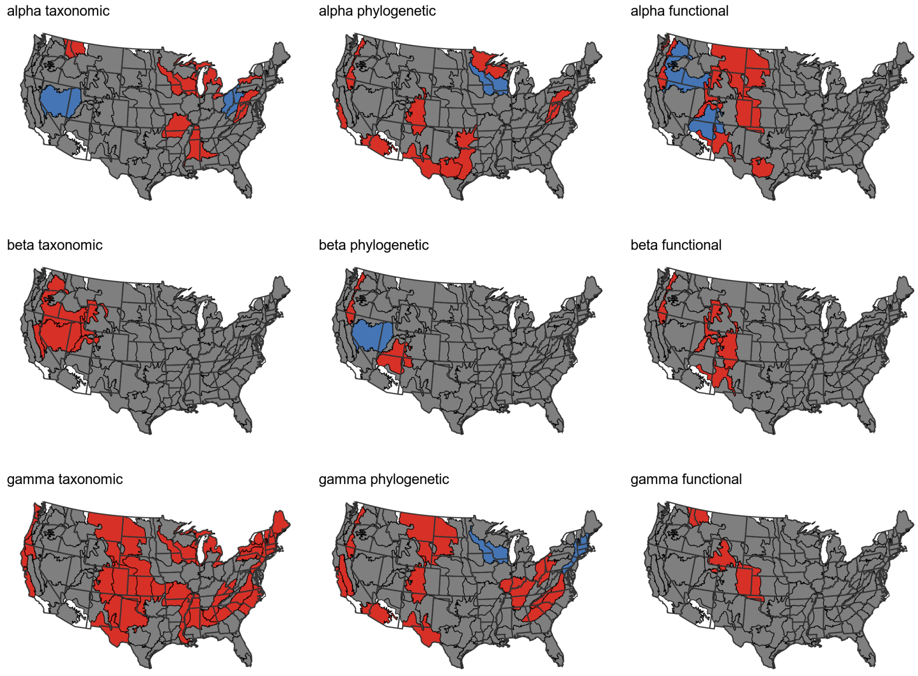

Figure S11b: Coefficients of elevation variability on tree diversity, nonzero regions shown

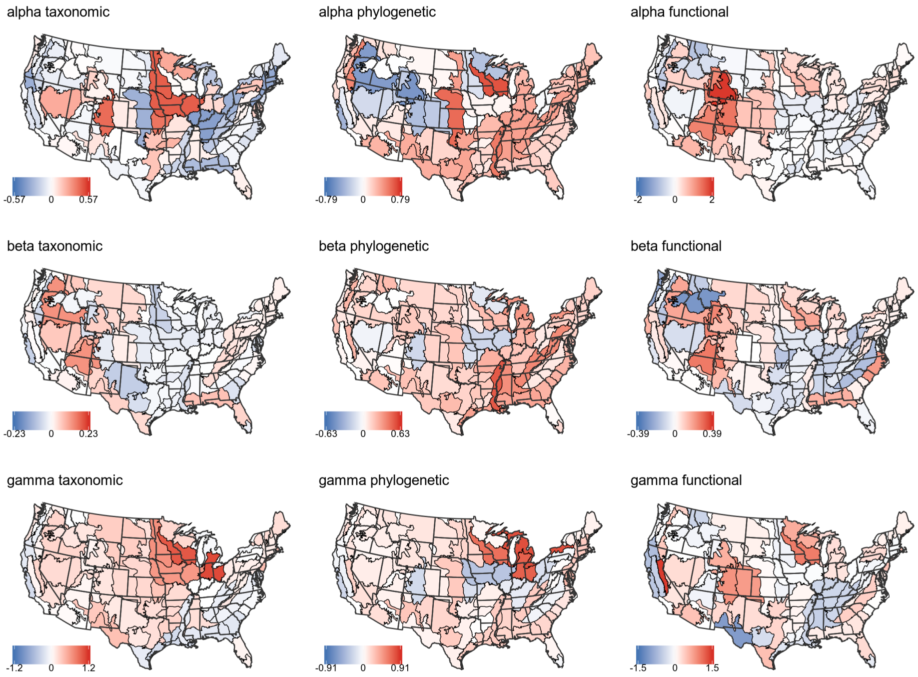

Figure S12a: Coefficients of GPP variability on tree diversity, values shown

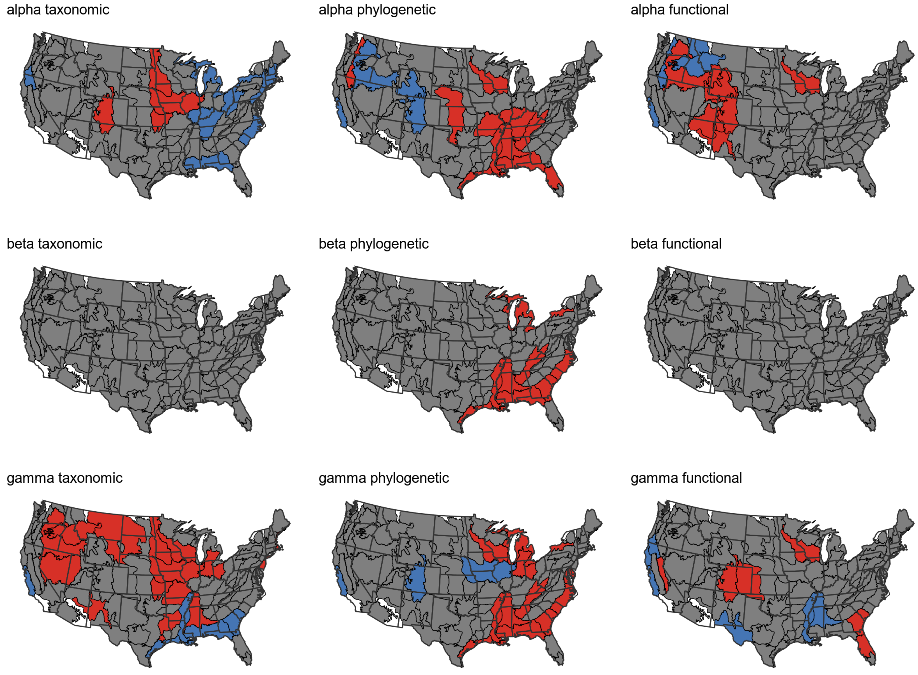

Figure S12b: Coefficients of GPP variability on tree diversity, nonzero regions shown

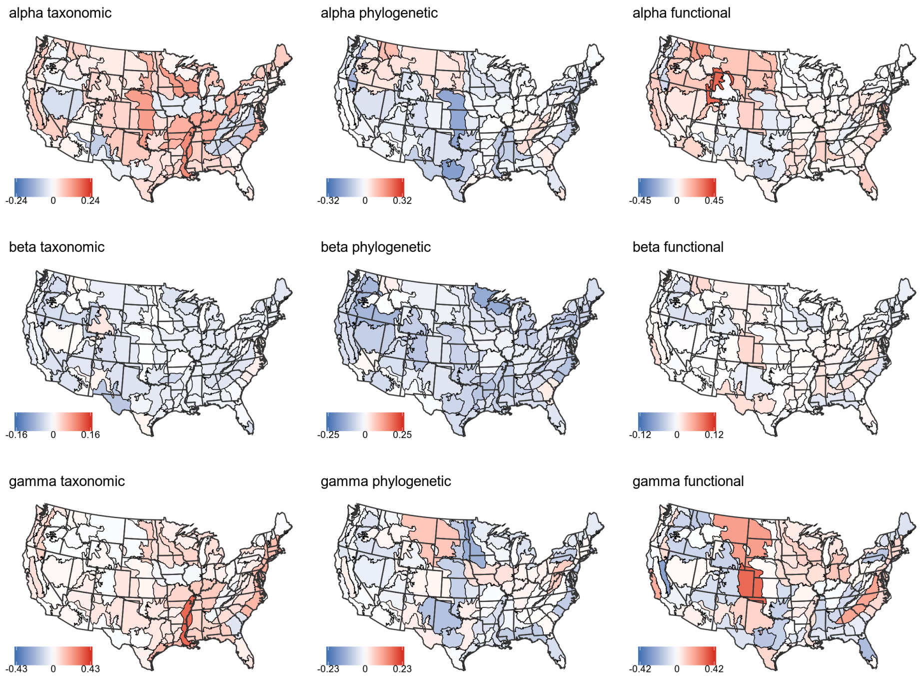

Figure S13a: Coefficients of geological age diversity on tree diversity, values shown

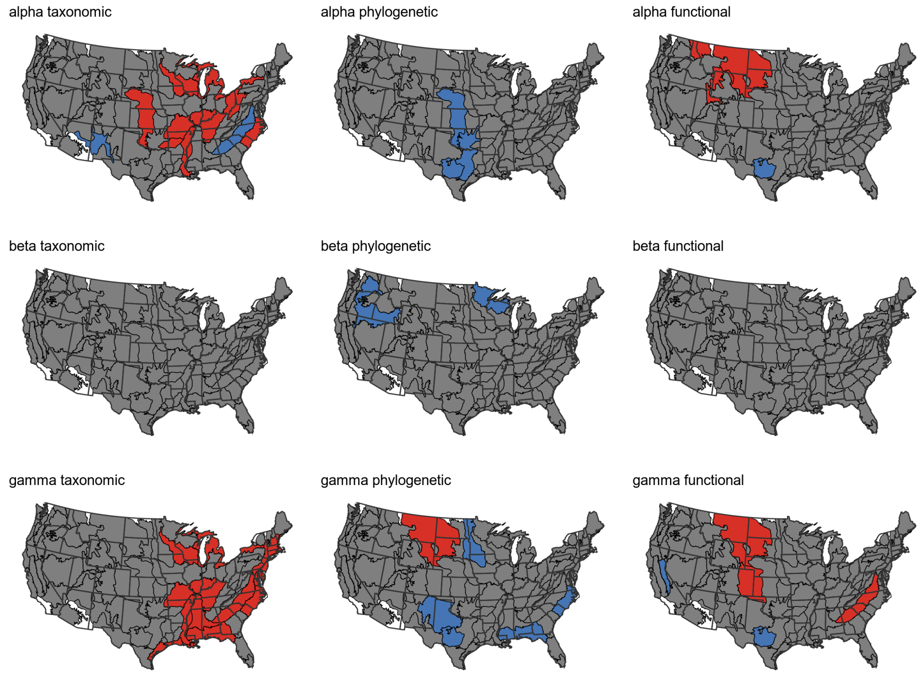

Figure S13b: Coefficients of geological age diversity on tree diversity, nonzero regions shown

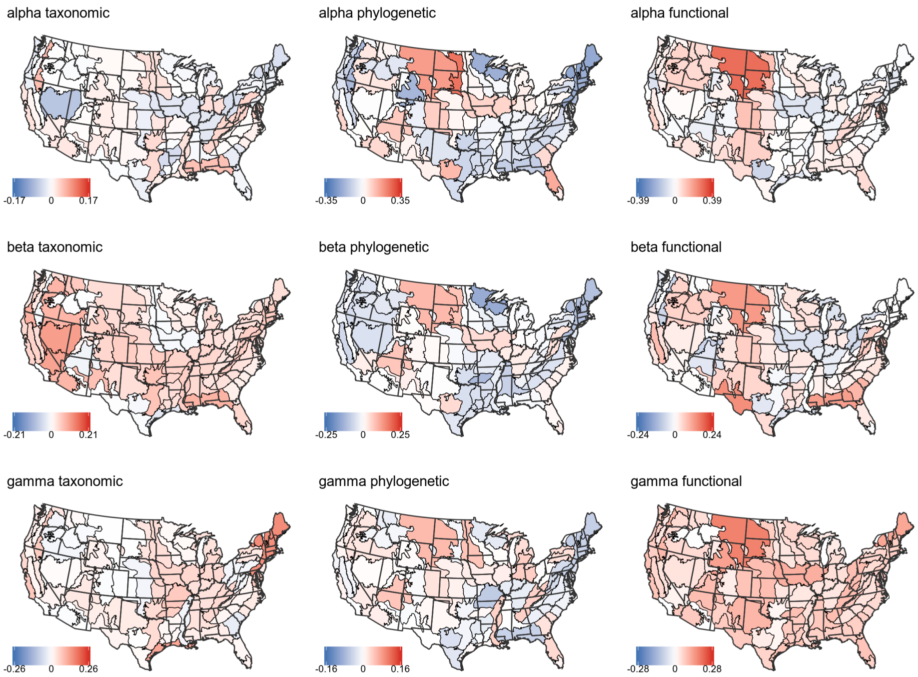

Figure S14a: Coefficients of soil type diversity on tree diversity, values shown

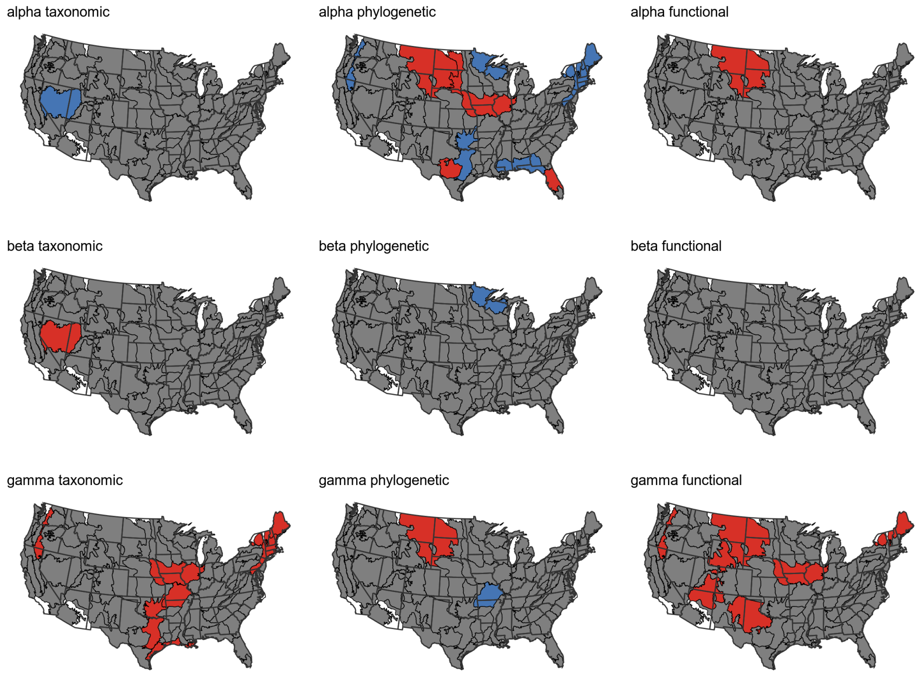

Figure S14b: Coefficients of soil type diversity on tree diversity, nonzero regions shown

Response to reviewers

***** Below we reproduce the reviewers' comments from the most recent round of peer review, with our responses to each individual comment printed in bold and preceded with ***.**

EDITOR'S COMMENTS TO AUTHORS
Editor: Bahn, Volker
Comments to the Author:

Thank you for your thorough revisions. You addressed most points well. Reviewer 1 only has some minor requests for changes in figures. Reviewer 2 and I are inclined to say that you did enough for a publishable manuscript but we both still have some reservations on the rigor and how you present your methodology and results. Please read over reviewer 2's comments carefully and see how far you can address them with reasonable effort.

To me one semantic issue remains (and I apologize if I didn't comment on that last iteration). You use the terms "predictive power" and "explanatory power" loosely, maybe even interchangeably, when really they are strong terms with important, somewhat distinct meanings. Predictive power means the ability of a model to predict onto independent, new data (here locations). In a spatial model, this can only be tested on locations that were held out and are outside the reach of spatial autocorrelation to training locations. The blocked CV achieves that partly (there can still be some autocorrelated test locations close to the borders). However, using that technique you actually find that you don't have any predictive power. Explanatory power implies a causal relationship. To prove such a relationship again requires that you apply the claimed relationships in a new context. Resubstitution (training data = test data) does not allow to evaluate explanatory power. What you find out with resubstitution is goodness of fit. Or in other words, correlation does not imply causation. I'm not dogmatic about this. I think that simple models with low risk of overfitting paired with much data make a correlation free of any causation pretty unlikely. Unfortunately, it has been shown repeatedly that in particular in spatial data correlation without causation is not only possible, but has an elevated probability to happen because of coincidence of spatial structure. Therefore, to me the much more parsimonious interpretation of your results (see your great summary at the beginning of the Discussion starting L 380) is that there is little functional relationship between environmental variables and the different measures of diversity. The goodness-of-fit achieved in resubstitution models would then be a reflection of coincidence in spatial structure in these variables. This interpretation much more parsimoniously explains your "intriguingly context-dependent" relationships that vary so much among regions and dependent variables and the lack of predictive power as evaluated on independent test data than that all functional relationships happen to be idiosyncratic to ecoregions and measures of diversity.

I personally think that we are about to see a paradigm shift toward finding very little functional relationship between coarse environmental variables and diversity, and that your study is a strong contribution toward that paradigm shift, but you are trying to interpret it according to the old paradigm, that is propped up by countless studies correlating diversity (and distributions) with environmental variables. I will not abuse my power as editor to enforce that view upon you, and you have already made some space in the discussion for that viewpoint. I will leave it up to you to think about this one more time and do as you see fit with this thought. The same goes for the comments of reviewer 2.

***** Thanks for your thoughts and interpretation. We agree that the body of work exploring the relationship between biodiversity and environmental variables is top-heavy with correlational studies and that there are few convincing demonstrations of mechanism. Our work is no exception. However we do not agree that the explanation that there is little or no functional relationship between coarse-scale environmental variables and biodiversity is most parsimonious. From what we know about biology, we can derive mechanistic hypotheses for large-scale environmentally-driven biodiversity trends from first principles, and the many correlational studies support those hypotheses. Furthermore, in noisy systems it is possible to mask true effects with conservative statistical tests designed primarily to minimize Type I error.**

L 81: here you use explanatory power. In the abstract it was predictive power. Most of your approaches don't evaluate either one. Explanatory power should be tested in a mechanistic sense, ie the predictors need to be shown to have a process-based relationship to the dependent variable. Predictive power needs to be evaluated by predicting onto independent data, ie locations outside of SAC distance of training locations. What you are looking at is goodness-of-fit.
L 303 That is actually assessing predictive performance and by implication explanatory power.
L 310 This only assesses goodness-of-fit, which need not be (but can be) related to explanatory power. It can be purely correlational.
L 358 Again, fit best rather than explained most

Dr. Volker Bahn, Editor

***** Thank you for your careful reading of the text. We have modified the text in the abstract and at the four places in the main text that you noted to more carefully distinguish between tests of predictive power and tests of goodness-of-fit.**

REVIEWER COMMENTS TO AUTHORS

Referee: 1

Comments to the Author
Thank you for addressing my comments. I have gone through the revisions that the authors have made and I am now satisfied with the manuscript. The only suggestion I would like to make is to make small changes to some figures. Specifically, please increase the font in figures 2-4 because the scales are not legible.

***** We increased the legend font size on Figures 2-4.**

Referee: 2

Comments to the Author
The authors made some efforts to respond to some of my concerns. Nevertheless, I am not really convinced to some of the responses.

First, obviously my suggestion to use an additive response was not as simple as it appeared to me. I understand that additive beta is correlated to gamma. But what happens if this beta is scaled by gamma? What is the difference compared to a simple Sorensen-Index? From a biological perspective, I want to know what is measured by the Sorensen-Index or any other index?

***** Thank you for your suggestion. We further tested our taxonomic beta-diversity model on the bird community data using the additive partition beta-diversity scaled by gamma-diversity (regional richness). The coefficients all had the same sign as the original Sorensen dissimilarity metric (see the figure below). The only difference in interpretation was that the credible intervals of the coefficients on elevation diversity and mean precipitation overlapped zero when the scaled additive beta-diversity was used for the response variable, though they did not for the dissimilarity beta-diversity. The broad overall similarity between the two sets of coefficients reassuringly indicates that the dissimilarity and additive partitioning metrics (when correctly scaled to remove dependence on gamma-diversity) are likely measuring the same latent variable -- the among-community variation. Therefore, we feel that we have thoroughly investigated the possibility of using additive partition beta-diversity and that it would not yield additional insight to include in the manuscript.**

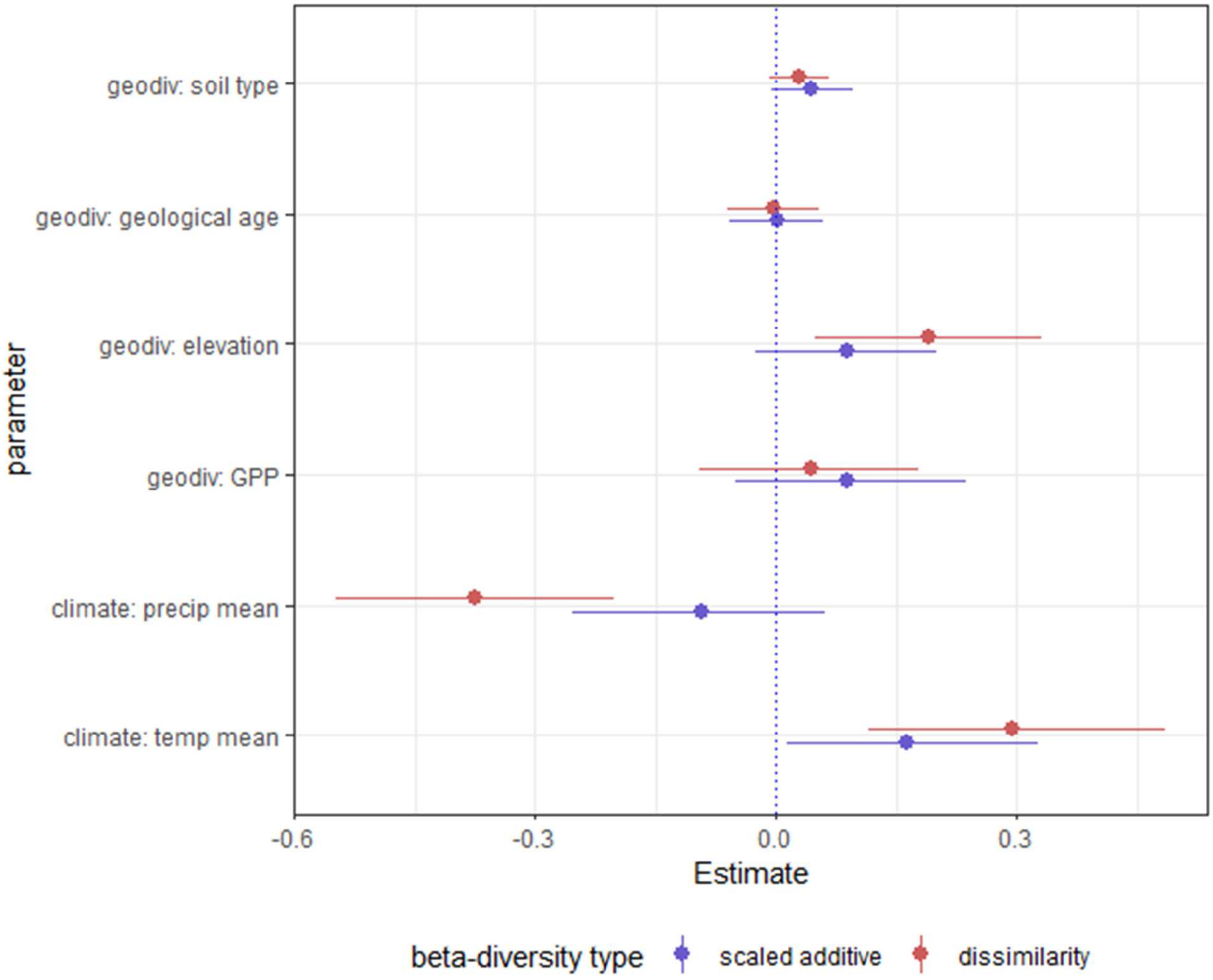

Figure: Comparison of standardized regression coefficients on predictors of taxonomic bird beta-diversity, using two different types of beta-diversity. The dissimilarity type is

the one used in the manuscript. Error bars represent 95% credible intervals around the parameter estimates.

To explain the biological meaning of our chosen beta-diversity index, we added text at line 193 as follows:

> **“The Sørensen dissimilarity index represents the degree to which pairs of communities differ from one another in their species composition, independent of their species richness, and encompasses both species turnover and nestedness components of beta-diversity. This contrasts with beta-diversity indices based on multiplicative or additive partitions of alpha- and gamma-diversity (Anderson et al. 2011).”**

Furthermore, I am still not happy of replacing zeros and ones of the beta-diversity in the tree data. It is very difficult to evaluate the effect of the arbitrary decision. 16 % of all tree sites have values of zero and 1. That´s a lot! What happens if we exclude such zeros and ones from the analysis? One might argue, if you have no beta-diversity at all (zeros) we have nothing to predict.

***** Thank you for your comment. As you suspect, since there are a large proportion of 0 and 1 values for tree beta-diversity, the model results are indeed sensitive to whether we exclude the values or adjust them. However, we disagree with the statement that no beta-diversity means that there is nothing to predict. A zero value of beta-diversity means that there is no species turnover among the focal plot and its neighbors, and a value of one indicates that no species are shared among the plots (complete turnover). It is important to note that 0 beta-diversity does not mean no species were present, it simply means the species are identical among the communities under consideration. FIA plots with no trees were not considered in our analysis. Because the 0 and 1 values represent true biological phenomena, extreme points on the continuum between no turnover and complete turnover, we were also interested in understanding which environmental factors are associated with locations where no turnover or complete turnover occurs. Therefore, we determined that adjusting the 0 and 1 values was the best of the imperfect options available to us.**

Second, I am still not happy about the procedures to estimate functional diversity. It was clear to me that morphological data of relevant traits are not available in books or data banks. But I am convinced that it would have been possible (of course with a little bit of effort) to measure the relevant traits of bill, legs, tail and wings at museum specimen. With such data at hand the authors would have the possibility to retrieve a rich picture of the functional diversity.

***** Thank you for your suggestion. Unfortunately collecting bird morphological trait data spanning the United States was outside the scope of our study, but we agree that this would be a fascinating avenue for future research that would yield a better understanding of patterns of variation in relevant bird functional traits.**

Furthermore, the author checked the impact of the correlation of several of their data used to estimate functional diversity with body size by correlating a distance matrix using a reduced set of variables to the original matrix. They found a high matrix correlation. To my opinion this is not the test needed; to my feeling this test shows only that these traits do not measure new aspects of the functional diversity. Why using them at all? An appropriate way of removing body size is to regress these variables on body size and to use the residuals for further calculations.

***** While we agree with the sentiment behind this comment, we feel that the test we ran in response to your comments on the previous revision adequately addresses this point. *(In that previous document, we compared the pairwise Gower functional distance matrices for all birds with and without the traits that were highly correlated with body size. A Mantel test shows that the two distance matrices were very highly correlated, with r = 0.979).* While we agree that this could be interpreted as justification for removing the traits, we intended our functional diversity metrics to include all traits for which we had adequate data for most of the bird species in our dataset. Our functional diversity metrics appear to be robust to the inclusion or exclusion of a small number of correlated traits among the set of possible traits, so we do not feel that any additional insight into important biological patterns can be gained by continuing to test out other possible trait combinations or scaling the morphological traits by body size.**

Nevertheless, after the revisions the paper has matured to an interesting contribution, although I am not always convinced by the theoretical predictions, data, procedures and results. Particularity some of the predictions in the introduction are not really informative. For example, that different measures of biodiversity have different relationships to geodiversity is to my opinion a bit empty. Different measures are different by definition and should have different relationships. But the finding that the relationships between biodiversity and climate as well as geodiversity is context dependent is an important message that might caution the increasing tendency to rely too much on remote sensing to predict biodiversity.

***** Thank you for your comment. We agree that the prediction that different dimensions of biodiversity should have different relationships with geodiversity may seem trivial. Our motivation for including this prediction was essentially rhetorical: we noticed that many conservation organizations are advancing the idea that "we must conserve geodiversity to conserve biodiversity." However, it is probable that focusing conservation efforts on geodiversity would only have a positive effect on conserving some aspects of biodiversity, and a neutral or even negative effect on other aspects. As you note, the various dimensions of biodiversity are inherently different by definition, and many of them are orthogonal to one another. In summary, we included this prediction primarily to underscore the context-dependence for readers and to make the point that this context-dependence has consequences for conservation such that the blanket statement that "geodiversity = biodiversity" is inadequate.**

We added text to the introduction section of the manuscript to emphasize this point (lines 79-83):

> **"Furthermore, conservation frameworks, including CNS, typically advance the idea that conserving geodiversity will result in positive outcomes for biodiversity writ large (Beier & de Albuquerque 2015). This assumption must be tested empirically, especially given potential tradeoffs among orthogonal dimensions of biodiversity within and among taxa: conserving one aspect of biodiversity might have a neutral or even negative effect on other aspects."**

Beyond counts and averages: relating geodiversity to dimensions of biodiversity

Running title: Geodiversity across dimensions of biodiversity

Abstract

Aim

We may be able to buffer biodiversity against the effects of ongoing climate change by prioritizing the protection of habitat with diverse physical features (high geodiversity) associated with ecological and evolutionary mechanisms that maintain high biodiversity. Yet, the relationships between biodiversity and habitat vary with spatial and biological context. In this study we compare how well habitat geodiversity — spatial variation in abiotic processes and features — and climate explain biodiversity patterns of birds and trees. We also evaluate the consistency of biodiversity-geodiversity relationships across ecoregions.

Location

Contiguous United States

Time period

2007-2016

~~Major t~~Taxa studied

Birds, trees

Methods

We quantified geodiversity with ~~spatially continuous~~ remotely-sensed data and generated biodiversity maps from the Forest Inventory and Analysis and Breeding Bird Survey datasets. We fit ~~separate~~ multivariate regressions to alpha-, beta-, and gamma-diversity, accounting for spatial autocorrelation among Nature Conservancy ecoregions and relationships among~~. The response variables for each model were~~ taxonomic, phylogenetic, and functional biodiversity. We fit models including climate alone (temperature, precipitation), geodiversity alone (topography, soil, geology), and climate + geodiversity.

Results

A combination of geodiversity and climate ~~predicted~~ predictor variables fit most forms of bird and tree biodiversity with less than 10% relative error. Models using geodiversity and climate performed better for local (alpha) and regional (gamma) diversity than turnover-based (beta) diversity. Among geodiversity predictors, variability of elevation ~~predicted~~ fit biodiversity best; interestingly, topographically diverse places tended to have higher tree diversity but lower bird diversity.

Main conclusions

Although climatic predictors tended to have larger individual effects than geodiversity, adding geodiversity improved climate-only models of biodiversity~~ for both taxa~~. Geodiversity ~~predicted~~ was correlated with biodiversity more consistently than climate across ecoregions, but models tended to have poor ~~predictive accuracy~~fit in ecoregions held out of the training dataset. ~~With ongoing climate change, ecoregion-scale geodiversity could help prioritize conservation regions for U.S. tree and bird biodiversity~~Patterns of geodiversity could help prioritize conservation efforts within ecoregions. However, we need to understand the underlying mechanisms more fully before we can build models transferable across ecoregions.

Keywords

biodiversity, geodiversity, Breeding Bird Survey (BBS), Forest Inventory and Analysis (FIA), alpha-diversity, beta-diversity, gamma-diversity, ~~phylogenetic diversity, functional diversity, richness~~conservation

Introduction

In the face of an ongoing sixth mass extinction, society is challenged to minimize biodiversity loss through conservation efforts (Ceballos *et al.* 2015). While many conservation policies and strategies focus on conserving particular species (e.g., the United States Endangered Species Act, the International Union for Conservation of Nature Red List), there is growing interest in broadening conservation to include preserving parcels of Earth's surface that promote diversity even as species shift their ranges in response to climate change (Beier & de Albuquerque 2015). For example, The Nature Conservancy (TNC) prioritizes preserving areas with high geodiversity — variation in Earth's abiotic processes and features — through their 'Conserving Nature's Stage' (CNS) campaign (Beier & de Albuquerque 2015). Conserving nature's stage requires a firm understanding of biodiversity-geodiversity relationships, yet we know little about how these relationships vary across space, among taxa, and across different dimensions of biodiversity (Zarnetske *et al.* 2019). Addressing this knowledge gap is key to advancing conservation prioritization.

Geodiversity represents natural variation in geologic, geomorphic, and soil features (Gray 2004, 2008) and can be measured in a variety of ways. Most studies focus on elements of topography (roughness, elevation, slope and aspect), geology (geologic diversity, landscape complexity), soils (pH, organic matter, nutrient availability), or hydrology (variation of hydrological features such as rivers, ponds and lakes; Hjort *et al.* 2012; Wang *et al.* 2013; Kaskela *et al.* 2017). Some geodiversity definitions include climate, using variables such as temperature, precipitation, evapotranspiration, water balance, and solar radiation, while others explicitly exclude climate from their definition (Gray 2004; Parks & Mulligan 2010; Tukiainen *et al.* 2017). A comprehensive definition of geodiversity includes all abiotic features and processes found within Earth's atmosphere, lithosphere, hydrosphere, and cryosphere (Record *et al.* in press; Zarnetske *et al.* 2019).

Abiotic variation may promote increased variety of available niches for organisms (Tews *et al.* 2004), and high geodiversity is likely to indicate biodiversity hotspots (Lawler *et al.* 2015, but see Noss *et al.* 2014). However, little is known about how geodiversity of Earth's surface compares to climate in explaining variation in biodiversity, whether relationships generalize across geographic locations, and what types of biodiversity have the closest relationship with geodiversity. Despite the potential importance of geodiversity for explaining patterns of biodiversity, models explaining patterns of biodiversity rarely include geodiversity (Bailey *et al.* 2018). Furthermore, conservation frameworks, including CNS, typically advance the idea that conserving geodiversity will result in positive outcomes for biodiversity writ large (Beier & de Albuquerque 2015). This assumption must be tested empirically, especially given potential tradeoffs among orthogonal dimensions of biodiversity within and among taxa: conserving one aspect of biodiversity might have a neutral or even negative effect on other aspects. In this study, we use bird and tree occurrence data and remotely-sensed environmental data from across the United States to increase our understanding of biodiversity-geodiversity relationships. Geodiversity, in conjunction with climate, predicts patterns of species diversity of plants (Tukiainen *et al.* 2017; Bailey *et al.* 2018) and animals (Parks & Mulligan 2010; Alahuhta *et al.* 2018) across disparate biomes. Informed by these previously documented patterns, our **Prediction 1** is that combining geodiversity and climate predictors will significantly ~~increase~~ improve the ~~explanatory power~~goodness-of-fit of models explaining biodiversity of birds and trees.

Recent work shows that the biodiversity-geodiversity relationship depends on spatial grain and extent (Bailey *et al.* 2017; Zarnetske *et al.* 2019). Nevertheless, most studies have focused on alpha-diversity (local diversity) measured within a plot. In contrast, most large-scale mapping studies characterizing diversity have equated diversity with gamma-diversity, or the size of the regional species pool (Currie & Paquin 1987; Jenkins *et al.* 2015). Only a few have accounted for the three *levels* of biodiversity: alpha-diversity, beta-diversity (turnover among plots) and gamma-diversity (Meynard *et al.* 2011; Gossner *et al.* 2013). Beta-diversity represents compositional turnover among local communities, linking local diversity (alpha-diversity) to regional species pools (gamma-diversity). We expect that the relationship between geodiversity and beta- and gamma-diversity will be stronger than alpha-diversity, because high geodiversity often reflects high diversity of habitats within regions and therefore more unique local species assemblages (Stein *et al.* 2014). This leads to **Prediction 2:** Geodiversity will explain more variability in the beta and gamma levels of biodiversity than alpha-diversity.

The relationship between geodiversity and biodiversity may also vary with the *dimensions* of biodiversity (taxonomic, functional and phylogenetic diversity). Targeting functional and phylogenetic diversity is especially important for conserving unique ecological function (Steudel *et al.* 2016) and evolutionary history (Davis *et al.* 2018) in the face of the current biodiversity crisis. Because phylogenetic (Winter *et al.* 2012) and functional (Lamanna *et al.* 2014) biodiversity are explicitly linked to different ecological and evolutionary mechanisms, they may provide deeper insight into ecological and evolutionary processes that underlie regional variation in diversity. However, few studies of geodiversity have investigated these multiple dimensions of biodiversity (Meynard *et al.* 2011); most studies have considered only taxonomic diversity (e.g., Safi *et al.* 2011; Stevens & Gavilanez 2015). Because each dimension of biodiversity represents a unique mechanistic connection with the environment, we predict (**Prediction 3**) that the different dimensions of biodiversity will have different relationships with geodiversity.

Relationships between dimensions of biodiversity and geodiversity vary across geographic and environmental space. In some areas and environmental contexts, one form of geodiversity might be a more reliable predictor of biodiversity than elsewhere. For example, topographic complexity generates a diversity of climatic conditions at small to intermediate spatial scales ranging from meters (Bennie *et al.* 2008) to tens of kilometres (Badgley *et al.* 2017), which may buffer species against local extinctions as climate warms (Dobrowski 2011; Lenoir *et al.* 2013). Such buffering is, however, conditional on climatic context: if an entire landscape is far outside of the physiological range of tolerance for some taxonomic or functional groups, geodiversity is likely to be unimportant for maintaining local biodiversity. For example, along the central California coast, land and ocean surface temperatures contrast strongly and there is high heterogeneity in topography and associated cloud and fog patterns. Such conditions support relatively high local richness of tree species (Barbour *et al.* 2007). Inland, in contrast, the average climate of the Coast Range is more arid and fog is absent (Ackerly *et al.* 2010), so only the coolest facets of the landscape support any level of tree cover. In this context, topographic heterogeneity is still associated with higher tree diversity, but the relationship is likely to be weaker. For these reasons, we predict (**Prediction 4**) that the influence of different geodiversity predictors on biodiversity will vary across ecoregions. In particular, mountainous ecoregions with more mesic climates will have more positive relationships between topographic diversity and biodiversity than more arid mountain ranges.

In this study, we use bird and tree occurrence data and remotely-sensed environmental data from across the United States to increase our understanding of biodiversity-geodiversity relationships. We make the following predictions:

(1) Geodiversity will significantly increase the explanatory power of models explaining biodiversity of birds and trees.
(2) Geodiversity will explain more variability in beta- and gamma-diversity than alpha-diversity.
(3) The different dimensions of biodiversity will have different relationships with geodiversity.
(4) The influence of different geodiversity predictors on biodiversity will vary across ecoregions.

Methods

We used multivariate linear mixed models with spatial random effects to determine which geodiversity predictors explain the most variation across the levels and dimensions of bird and tree biodiversity in the contiguous U.S. We used biodiversity and geodiversity data collected from 2007-2016.

Breeding Bird Survey (BBS)

The North American Breeding Bird Survey (BBS, https://www.pwrc.usgs.gov/bbs/) is an annual survey of breeding birds across the U.S. and Canada begun in 1966. Volunteer observers report species and counts of birds seen or heard during 3-minute observations at 50 stops spaced every ~800 m along routes ~39.4 km in length (Sauer *et al.* 2013). There are ~3480 active routes in the contiguous U.S. with continuous yearly stop-level data. We excluded any routes with an ambiguous midpoint coordinate (discontinuous transects), leaving 3089 routes. We included only the surveys conducted under the standard protocol, discarding repeat surveys and any observations recorded by trainees.

Forest Inventory and Analysis (FIA)

The U.S. Department of Agriculture Forest Service's Forest Inventory and Analysis program (FIA) surveys the composition and status of forests throughout the United States, with data collected annually (Bechtold *et al.* 2005). Each FIA plot consists of four 7.2-m fixed radius subplots. Plots are spaced roughly on a 5-km grid across forested land. Each plot is surveyed approximately every 5 years (Bechtold *et al.* 2005). Each tree is identified to species. We obtained the most recent survey from all forested, non-plantation FIA plots in the contiguous United States (119,177 plots). Some plots in the Pacific Northwest Region included a larger "macroplot" around the central subplots; we excluded any trees outside the subplot boundary. The year of the most recent survey varied between 2012 and 2016.

Phylogenetic and Trait Data

We obtained phylogenetic trees and compiled trait information for all bird and tree species in the BBS and FIA databases, respectively, and used them to calculate the distance-based phylogenetic and functional diversity indices described below. See Appendix 1 for additional details.

Calculation of Biodiversity Metrics

For both tree and bird communities, we calculated biodiversity metrics based on species presence at the site level (here defined as a single FIA plot or BBS route). For trees in FIA, we used the most recent survey as a single time point for each site, as there is little turnover in species composition between surveys and the probability of imperfect detection is low. To minimize the effects of imperfect bird detection in the BBS survey, we pooled observations from all stops in each route and pooled all surveys from 2007-2016. See Appendix 2 for additional details.

We calculated alpha-, beta-, and gamma-diversity (referred to as *levels* of biodiversity) within a circle of 50 km radius around each site, originating at the centre of the FIA plot or midpoint of the BBS route. We defined any BBS route whose midpoint fell within the 50-km circle around the focal route midpoint to be a neighbour route (see Appendix 2). We took (1) the median diversity of all sites in the radius, including the focal site (alpha), (2) the median pairwise diversity of all pairs of sites in the radius, including the focal sites (beta), and (3) the aggregated diversity of all sites in the radius (gamma). Each diversity *level* has three *dimensions*: taxonomic, phylogenetic, and functional (Table S1). For taxonomic diversity, alpha-diversity and gamma-diversity were represented by species richness and beta-diversity by pairwise Sørensen dissimilarity. The Sørensen dissimilarity index represents the degree to which pairs of communities differ from one another in their species composition, independent of their species richness, and encompasses both species turnover and nestedness components of beta-diversity. This contrasts with beta-diversity indices based on multiplicative or additive partitions of alpha- and gamma-diversity (Anderson et al. 2011). To quantify phylogenetic diversity, we calculated mean pairwise phylogenetic distance (MPD) of each community with the R package *picante* (Kembel *et al.* 2018). We randomized the phylogenetic distance matrix 999 times and calculated the z-score of the observed phylogenetic distances relative to the distribution of phylogenetic distances of the randomized matrices to remove dependence on richness. Similarly, we calculated a distance-based metric of functional diversity by finding the Gower distance between the trait values for all possible species pairs, and then calculating the mean pairwise distance among all pairs of species in each community and its z-score. Because the BBS surveys poorly estimate abundances of some species, we calculated incidence-based biodiversity metrics for both birds and trees so that metrics are comparable between the two taxa.

Geodiversity Data Sources and Processing

We obtained and processed remotely-sensed data for the contiguous United States to generate geodiversity and climate data layers. Remotely-sensed geodiversity variables are particularly valuable in disentangling the independent effects of climate and geodiversity. Many biodiversity analyses use climatic data products that interpolate weather station data using elevation, e.g. Worldclim v.1 (Hijmans *et al.* 2005). Using elevation to derive temperature values makes it difficult to evaluate independent contributions from climate and topography (Körner 2007). Remotely-sensed temperature represents the temperature of the land surface, in contrast with weather stations that measure air temperature several meters above ground level (Bechtel

2015). In areas with very sparse coverage of meteorological stations and/or complex topography, the error introduced by interpolating between ground stations may be large. In many regions, especially grasslands, shrublands, and croplands, surface temperature shows large systematic deviations from air temperature (Mildrexler *et al.* 2011). What is more, studies have shown that surface temperature may be more ecologically relevant than air temperature (Pau *et al.* 2013; Still *et al.* 2014). The thermodynamic temperature of an organism, which drives its respiration rate and vapor pressure deficit, is more closely related to the surface temperature than the surrounding air temperature. Remotely-sensed data products provide spatially continuous, independent, and direct measures of climate and geodiversity for use in biodiversity models.

We generated predictors from the following remotely-sensed data products: elevation from SRTM (Farr *et al.* 2007), land surface temperature from MODIS MOD11A2 (Wan *et al.* 2015), precipitation from CHIRPS (Funk *et al.* 2015), and gross primary productivity (GPP) dynamic habitat index from MODIS (Hobi *et al.* 2017). We generated additional predictors from non-remotely-sensed products including soil type category from SoilGrids (Hengl *et al.* 2017), which uses remotely-sensed data to interpolate ground-based measurements, and geologic age category from USGS International Surface Geology. We included GPP because spatial variability in GPP integrates many geodiversity variables known to influence biodiversity via resource availability (Austin & Smith 1989; Alahuhta *et al.* 2018). GPP spatial variability is moderately correlated with mean annual precipitation but largely orthogonal to the other geodiversity variables we chose (Figure 1), indicating that it may capture additional spatial variation not accounted for by the other three geodiversity variables. See Appendix 3 for additional details.

We coarsened all environmental data layers by calculating the means within 25 km^2 pixels to equal the coarsest resolution of any layer, then we aggregated all geodiversity and biodiversity variables within a 50-km radius around the centre of each FIA plot and the midpoint of each BBS route. The 50-km scale of aggregation averages over a wide range of microhabitats and microclimates, capturing the geodiversity-biodiversity relationship at a coarse spatial grain; it is possible that a smaller grain of analysis would reveal different patterns (Zarnetske *et al.* 2019). For continuous predictors, we calculated the mean of all pixels partially or wholly in the 50-km radius, and we used the mean terrain ruggedness index (TRI; Wilson *et al.* 2007) of the 3×3 pixel neighbourhood around all pixels to represent spatial variability. For discrete predictors, we used Shannon entropy of all pixels in the radius to represent spatial variability. Shannon entropy has been shown to monotonically increase with increasing number of landscape patch types, to behave consistently in both real and simulated landscapes, and to correlate positively with many other measures of landscape heterogeneity (Peng *et al.* 2010). Importantly, while many past studies have used variables extracted from spatially continuous layers at points to characterize environmental variation, we explicitly consider spatial variation in the regions around the points where biodiversity was measured. Defining geodiversity in terms of this variation is critical for fully explaining biodiversity because a single point value cannot capture the diversity of niche space that may determine biodiversity (Lawler *et al.* 2015).

Finally, we spatially grouped geodiversity and biodiversity observations using TNC's terrestrial ecoregions (Olson & Dinerstein 2002) to account for spatial autocorrelation in response variables. We selected this classification scheme over alternatives because the regions are defined based on biodiversity analyses conducted across many taxa, and because the number of ecoregions in the contiguous USA (63 after excluding 6 border regions with insufficient data) is high enough to adequately account for spatial autocorrelation in biodiversity responses within the study area without overfitting.

Selection of Predictor Variables

We selected six predictor variables for our models: two climate variables to describe the climate norms inside the radius (mean annual temperature and mean annual precipitation), and four predictors to describe geodiversity or environmental heterogeneity (mean TRI of elevation and GPP, Shannon diversities of geological age category and soil type). Together, the six variables encompass most of the variation in geodiversity and climate among locations in the contiguous United States and are only modestly correlated with one another (Figure 1), meeting model assumptions. Based on our *a priori* hypothesis that geodiversity is related to biodiversity, we included one predictor to represent each of the unique geodiversity data sources available to us (elevation, soil type, and geological age category). In addition, we selected GPP diversity to represent other aspects of geodiversity not captured by the first three variables. Our choice of mean annual temperature and mean annual precipitation to represent long-run climate norms is reasonable because the two variables have no relationship to one another at our scale of observation (Figure 1).

Final Data Processing

First, we excluded any site within 50 km of the Canada or Mexico borders because the 50-km radius around those sites contained areas without biodiversity measurements. We logit-transformed the taxonomic beta-diversity variable, which is a raw dissimilarity metric varying between 0 and 1 in the model. No bird sites had a taxonomic beta-diversity of exactly 0 or 1, but ~16% of tree sites had taxonomic beta-diversity of exactly 0 or 1, which is outside the domain of the logit function. Thus, we replaced zeroes with 0.001 and ones with 0.999. We took a spatially stratified random sample of tree sites where each sampled site was a minimum of 20 km from any other site, to minimize spatial autocorrelation not captured by our model. This process left

~3000 sites, so that sample sizes were comparable between the datasets used to fit each model.

Model Fitting

We fit spatial multivariate mixed models with the following fixed predictors: (1) all six predictor variables as fixed effects, (2) only the four geodiversity predictors as fixed effects, (3) only the two climate predictors as fixed effects, and (4) no fixed effects (null model with only spatial random effects). We fit multivariate models for each diversity level (alpha, beta, and gamma) and each taxon (birds, trees), totalling 24 models (4 predictor sets × 3 diversity levels × 2 taxa = 24). Each model had three response variables corresponding to the three dimensions of biodiversity (taxonomic, phylogenetic, and functional). We used the null model z-scores to represent phylogenetic and functional biodiversity in all the models.

We fit a random intercept and slope for each predictor in each TNC ecoregion. We excluded ecoregions with <5 sites, because random effects estimated with <5 data points are not robust. The excluded ecoregions were primarily in Canada or Mexico and only have a small area inside the contiguous United States that is at least 50 km from a land border. After excluding these ecoregions, 63 ecoregions remained. We estimated random slopes and intercepts for each ecoregion with a multilevel conditional autoregressive (CAR) structure to model the spatial variability in the biodiversity-geodiversity relationship among ecoregions (Besag & Kooperberg 1995). We specified the neighbourhood structure with an adjacency matrix identifying all pairs of regions that share a border. The ecoregion random effects in the model were therefore spatially structured, accounting for spatial autocorrelation in the biodiversity values of neighbouring regions. We chose to model spatial dependence using discrete regions because of better out-of-sample prediction performance than simultaneous autoregressive models (Kress, unpublished).

We fit the models in a hierarchical Bayesian framework using the R package *brms* (Bürkner 2017). We modelled error in response variables as normally distributed. Finally, we standardized both predictor and response variables before fitting the models so that we could compare effect sizes across predictors and responses. The standard deviation of each coefficient represents the among-region variability of each predictor-response relationship.

Model Validation

To assess model predictive performance~~fit~~, we performed spatially blocked leave-one-location-out cross-validation (Roberts *et al.* 2017). We refit each of the models 63 times, each time holding out all data points from one of the 63 ecoregions. We found the root mean squared error (RMSE) of the predicted values of the withheld data from each fold to get a cross-validation RMSE for each model. We also calculated the RMSE of the models fit to all the data. We divided all RMSE values by the range of the observed data to yield relative values that can be compared among models. We also calculated RMSEs using resubstitution evaluation, in which no data points were held out in model fitting. This procedure assesses the ~~explanatory power~~goodness-of-fit of models across the entire contiguous U.S. but does not fully correct for spatial autocorrelation.

We calculated the Bayesian R-squared (Gelman *et al.* 2018) for each model to quantify the proportion of variation in the response explained by fixed and spatial random effects combined. Finally, we calculated the widely applicable information criterion (WAIC; Watanabe 2010) for each model.

Results

Description of geodiversity and biodiversity variables

Correlations among geodiversity predictor variables were relatively low (Figure 1a). The pairwise correlation between elevation diversity and geologic age diversity was relatively high (r = 0.52), indicating that geodiversity measured as topographic variability is correlated with geodiversity measured as the variety of geologic substrate ages. Notably, the correlation between elevation diversity and mean annual temperature was low (r = -0.20). In both birds (Figure 1b) and trees (Figure 1c), taxonomic and phylogenetic diversity were positively correlated with one another at all levels; this relationship was strongest for birds. However, local (alpha) and regional (gamma) functional diversity tended to correlate negatively with other forms of biodiversity in both birds and trees.

Geodiversity variables (Figure 2) had unique patterns and spatial grains of variability. Climate variables varied at broad scales, while geologic and topographic variables varied at scales corresponding to major land features such as mountain ranges (Figure 2). Biogeographic patterns were disparate across dimensions of biodiversity for birds (Figure 3) and trees (Figure 4). Bird diversity patterns were spatially idiosyncratic (Figure 3), while tree diversity showed a strong longitudinal pattern, with taxonomic diversity highest in the east and functional and phylogenetic diversity highest in the west (Figure 4).

Effects of climate and geodiversity across taxa and components of biodiversity

Among geodiversity variables, elevation variability tended to be the strongest predictor of biodiversity (Figure 5). Elevation variability was associated with increased bird taxonomic beta-diversity but with decreased bird phylogenetic and functional diversity at all levels. Interestingly, it had a positive effect across all levels and dimensions of tree biodiversity; it was the only predictor with such a consistently positive relationship. Higher mean annual temperature was associated with lower taxonomic diversity but higher phylogenetic and functional diversity in birds. In contrast, for trees, precipitation was a much more important climate driver than temperature (Figure 5). The effect size for temperature was not distinguishable from zero for most levels and dimensions of tree diversity. For birds, taxonomic alpha-diversity (local richness) was highest in colder and wetter areas, but most other levels and dimensions of biodiversity showed the opposite pattern. For trees, taxonomic and functional diversity were higher in wetter areas, but phylogenetic diversity was higher in drier areas.

The effects of geologic age variability and soil type variability tended to be relatively weak, although for birds, soil type variability positively affected taxonomic diversity, and for trees, geologic age variability positively affected taxonomic diversity. Spatial variability in GPP had a positive relationship with bird taxonomic and functional diversity and a positive relationship with tree turnover and regional diversity across the three dimensions of biodiversity.

Overall model performance

The spatially blocked cross-validation showed that the models with climate or geodiversity predictors performed no better than the null model when predicting all biodiversity values from an entire ecoregion held out during model fitting (Figure 6). However, cross-validation prediction error for models including climate tended to be higher than for models including geodiversity. Model evaluation using the full dataset without holding out any locations showed that models including the six fixed predictors ~~and the random ecoregion spatial effect~~ were the best fit for biodiversity of trees and birds~~explained most of the spatial variation in biodiversity of trees and birds~~, as shown by the RMSEs, WAIC values, and Bayesian R-squared values (Figure S1; Table S2). Geodiversity explained a consistent proportion of variation in most forms of bird biodiversity. For trees, the explanatory power of geodiversity depended on the level of biodiversity considered: geodiversity explained local (alpha) and regional (gamma) biodiversity better than turnover (beta).

Spatially varying biodiversity-geodiversity relationships

The strength of biodiversity-climate relationships varied more across ecoregions than the strength of biodiversity-geodiversity relationships (Figure S2). Interestingly, the relationship between mean annual precipitation and tree taxonomic and functional biodiversity tended to be more strongly positive in drier western ecoregions where precipitation is limiting (Figure S10). Phylogenetic diversity showed an opposite spatial pattern: drier areas in the west had higher tree phylogenetic diversity. In those ecoregions, we observed high phylogenetic diversity at sites dominated by gymnosperms (*Pinus* and *Juniperus* spp.) with a few associated angiosperm species, notably *Cercocarpus ledifolius* and *Populus tremuloides*. These dry sites, which tended to have low to intermediate taxonomic and functional diversity, may be driving the negative relationship between precipitation and phylogenetic diversity in the western USA. Notably, the relationship between elevation variability and biodiversity was relatively consistent across ecoregions, being generally positive for trees, positive for bird taxonomic diversity, and negative for bird functional and phylogenetic diversity. Other geodiversity-biodiversity relationships varied idiosyncratically across space (Figures S2-S14).

Discussion

The magnitude and direction of the relationships between environmental variability and biodiversity were intriguingly context-dependent, varying between birds and trees, by diversity level (alpha, beta, and gamma), by diversity dimension (taxonomic, phylogenetic, and functional), and by ecoregion. Below we explore potential reasons for this context-dependence as they relate to the predictions we made initially.

Effects of climate and geodiversity across components of biodiversity

A combination of geodiversity and climate predictors predicted biodiversity within 10% relative error for most forms of biodiversity for both birds and trees (Figure S1). However, these more complex models performed worse than the null models in spatially blocked cross-validation, when predicting biodiversity values in ecoregions not used to fit the model (Figure 6). The poor performance of models outside the training dataset may indicate that similarity among neighboring communities of birds and trees explains the majority of variation in biodiversity, with deterministic effects of geodiversity and climate playing a smaller role. Alternatively this suggests that a large proportion of the relationship between geodiversity and bird and tree biodiversity is spatially context-dependent, providing only weak support for our prediction that geodiversity and climate together explain variation in biodiversity among ecoregions (Prediction 1). The high level of spatial autocorrelation and high variability in relationships among ecoregions prevented the statistical models from identifying spatially transferable relationships between geodiversity and biodiversity. Nevertheless, geodiversity variables performed relatively better than climate variables at out-of-sample prediction (Figure 6), suggesting a potential use of geodiversity to identify biodiversity hotspots at local to regional scales. The poor performance of the models relative to null models reveals the difficulty of disentangling environmental drivers of biodiversity from biogeographical and historical contingency and caution against relying heavily on geodiversity or climate to predict biodiversity in regions far from where models are fit.

Temperature and precipitation means had the strongest effects on diversity, across taxa and across the levels and dimensions of biodiversity. However, adding geodiversity predictors significantly increased explanatory power when evaluating models trained on the full dataset (Figure S1), although neither climate nor geodiversity predictors increased prediction accuracy in spatially blocked cross-validation (Figure 6). Among geodiversity predictors, topographic variability had the largest effect on biodiversity. Interestingly, topographic variability had a positive relationship with tree diversity across levels, but was associated with lower bird diversity. This may be because breeding bird diversity is driven by highly mobile migratory bird species seeking out high-productivity regions for breeding sites (Anderson & Shugart 1974; Cody 1981). ~~The tendency of topographic variability to promote microclimate variability may be less important for bird diversity relative to tree diversity.~~ The diversity of niche opportunities available to trees may depend on the microhabitats created by topographic variation. Niche diversity for birds may be driven more by the diversity of food sources, which could be reduced in more topographically rugged regions. In contrast with topographic variability, geologic age and soil type diversity tended to have little or no effect on biodiversity in the regions and taxa we studied.

We found that geodiversity has significant effects on all diversity levels. Gamma-diversity, which integrates the alpha and beta levels, is best predicted by a combination of geodiversity and climate. This finding contrasts with Prediction 2, that geodiversity's effect would be strongest on turnover (beta) and regional diversity (gamma). For trees in particular, geodiversity combined with climate predicted beta-diversity less well than alpha- and gamma-diversity. This result may be due to incomplete sampling of the local community by single FIA plots. If trees have patchy distributions at local scales, the small-sized FIA plots may overestimate beta-diversity because some species that are present throughout the region will be absent from a random subset of plots within the focal region (Figure 4). Therefore, local sampling might obscure the true pattern of turnover among plots, but not the regional diversity, which integrates over many plots. We show that familiar maps of biodiversity, which are commonly created using species range maps (Currie & Paquin 1987; Brown & Lomolino 1998; Jenkins *et al.* 2015), represent gamma-diversity patterns, but not necessarily other forms of biodiversity. Our results show that these different levels of biodiversity (Figures 3 and 4) exhibit different relationships with environmental gradients. Our maps promote a more nuanced view of biodiversity and emphasize that each level and dimension has a different relationship with spatial variability in the environment.

Although we found generally similar responses across biodiversity dimensions, differences may indicate ecologically or evolutionarily meaningful relationships. In general, we found similar responses across biodiversity dimensions because they tend to correlate positively with one another (Figure 1). This finding partially contradicts Prediction 3 that patterns would differ across dimensions. However, in support of Prediction 3, some environmental drivers had opposite effects on different dimensions of biodiversity (Jarzyna & Jetz 2016). This result parallels contrasting patterns across biodiversity dimensions previously documented in mammals (Davies & Buckley 2011). For example, areas with ~~increased~~ greater topographic variability tended to have higher bird taxonomic diversity but lower phylogenetic and functional diversity. Birds' taxonomic diversity might not have the same signal as phylogenetic or functional diversity because both the functional guilds and the phylogenetic lineages of birds differ greatly from one another in species richness (De Graaf *et al.* 1985). For example, there are many functionally similar and closely related species within the guild of small insectivorous songbirds. An increase of species richness in the insectivore guild would result in increased taxonomic diversity without influencing the other dimensions of diversity. The high numbers of bird species harboured by geodiverse regions likely reflects increased taxonomic diversity within speciose guilds.

The discrepancy in relationships we observed among the dimensions of biodiversity we examined mirror that of a previous study examining biodiversity change over time. Increases in taxonomic diversity without corresponding changes in phylogenetic or functional diversity may indicate biotic homogenization of assemblages; 40 years of BBS surveys show a homogenizing trend over time (Jarzyna & Jetz 2017). While our study does not address change over time, the discrepancy between taxonomic and functional/phylogenetic diversity patterns with topographic variability and with temperature is notable. Jarzyna and Jetz also observed that the greatest temporal changes in diversity occurred at higher elevations and latitudes, ascribing this pattern to climate change. We documented a positive association between temperature and beta-diversity for all dimensions, but we found lower phylogenetic and functional diversity in topographically diverse regions (Figure 5). This result echoes the temporal pattern documented by Jarzyna and Jetz, suggesting that bird communities at high elevations and in cold regions may be relatively homogeneous and thus relatively more vulnerable to changing climate. In the case of breeding birds in the United States, topographically diverse regions may in fact be the most sensitive to environmental change.

Phylogenetic and functional diversity have similar patterns with respect to most predictor variables. This finding makes sense given that many, though not all, traits are phylogenetically conserved (Devictor *et al.* 2010), such that phylogenetic diversity roughly approximates functional diversity (Winter *et al.* 2012). However, tree phylogenetic diversity increases with decreasing precipitation, while functional diversity and taxonomic diversity decrease. This suggests that the angiosperm and gymnosperm species that contribute to high phylogenetic diversity in low-precipitation regions may have convergently evolved suites of adaptations to dry environments (Méndez-Alonzo *et al.* 2012), resulting in low functional diversity at those sites.

Spatially varying biodiversity-geodiversity relationships

The relationship between geodiversity variables and biodiversity variables varied in direction and magnitude across the ecoregions of the United States. For example, elevational variability had a greater effect on tree biodiversity in the central and eastern United States, providing support for Prediction 4. In the west, climatic factors and a smaller regional species pool set upper bounds on richness, so the opportunity for increased richness with increased geodiversity is reduced relative to the east (Figure S11). In contrast, the effect of elevational variability on bird taxonomic diversity was more likely to be non-zero in regions of high topographic relief, such as the Appalachian ecoregion and the northern Rocky Mountains (Figure S5). For trees, the effect of precipitation on biodiversity was more likely to be significant in the drier central and western United States (Figure S10), where water tends to be limiting. This suggests that in regions where climatic factors strongly control species diversity, the influence of geodiversity on biodiversity is weaker. However, this result may depend on spatial extent of the study region; a similar model fit only for trees in the Pacific Northwest region shows a strong positive correlation between elevational variability and tree alpha- and gamma-diversity (Record *et al.* in press).

The form of the geodiversity-biodiversity relationship and the particular variables that are the best predictors of biodiversity may not be transferable across ecoregions. This may present a conundrum for organisms that are migrating to track climate conditions and may encounter novel geological features. The Nature Conservancy documented a similar pattern: when they initially developed the Conserving Nature's Stage framework, they identified geological variables as the best predictors of biodiversity in the Northeast U.S. (Anderson & Ferree 2010). Those variables did not predict biodiversity well when they extended the approach to the Southeast (Anderson *et al.* 2014), where geologically homogeneous regions of the Coastal Plain host high biodiversity.

Conclusions and future directions

Our study found that topographic variability was related to biodiversity independently from, and in different ways than, climatic means. This result suggests that using remotely-sensed temperature data, rather than values interpolated between weather stations using local elevation, may improve our ability to distinguish between the effects of climate and of topographic variability (Pau *et al.* 2013; Still *et al.* 2014). Remotely-sensed temperature has broader spatial coverage than interpolated temperature and is not inherently dependent on elevation. Therefore, it would be valuable to confirm whether remotely-sensed temperature is biologically relevant across a range of taxa (Heft-Neal *et al.* 2017).

With the increasing intensity of global change threatening biodiversity and ecological integrity, it is vital to conserve nature's stage and create refugia for organisms moving to track their optimal climatic conditions. While past ecological research and the results of this study show that climate explains much of the spatial variation in biodiversity of trees and birds, geodiversity is related to biodiversity independently of climate. To disentangle the effects of climatic and topographic drivers, spatially continuous remotely-sensed data are necessary. Biodiversity-geodiversity relationships depend on taxonomic group, spatial location, the level and dimension of biodiversity considered, and the grain of analysis (Zarnetske *et al.* 2019): there is no single relationship valid for all conditions. To date, biodiversity-geodiversity relationships have primarily been characterized in a few well-studied taxa (Meynard *et al.* 2011; Hjort *et al.* 2012; Wang *et al.* 2013; but see Kaskela *et al.* 2017; Tukiainen *et al.* 2017); our study of birds and trees only hints at potential mechanisms underlying differences in relationships among taxonomic groups. Future work across a wider range of taxa would allow us to identify the mechanisms behind the differences. Although we need to understand the underlying mechanisms more fully before we can build models that are transferable across ecoregions, globally available geodiversity predictors can inform conservation practitioners working at a local scale to conserve different dimensions of biodiversity in the face of climate change.

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Data Accessibility Statement

Data and code for reviewers to reproduce all the model fitting and analysis presented in this manuscript is archived on FigShare at doi.org/10.6084/m9.figshare.7680083.v1 (draft version). Code to replicate the data preparation and cleaning stages described in the methods is also archived on the FigShare repository.

Figures

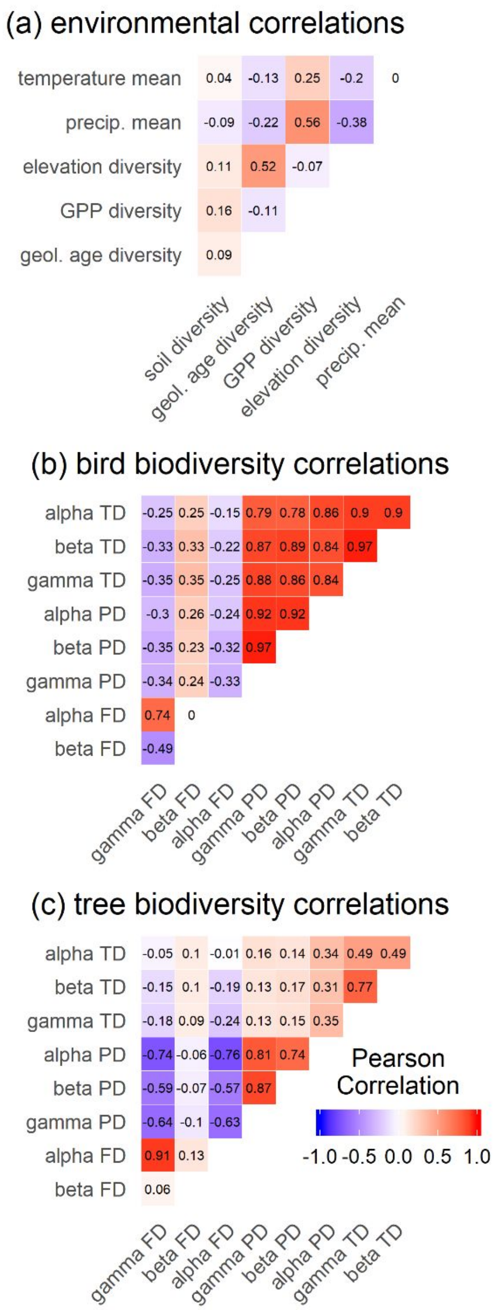

Figure 1. Heat maps showing correlations between pairs of environmental predictor variables including geodiversity and climate (a), bird biodiversity variables (b), and tree biodiversity variables (c). Pearson correlation coefficients are shown, along with colours showing the

magnitude of the correlation coefficients. TD = taxonomic diversity; PD = phylogenetic diversity; FD = functional diversity.

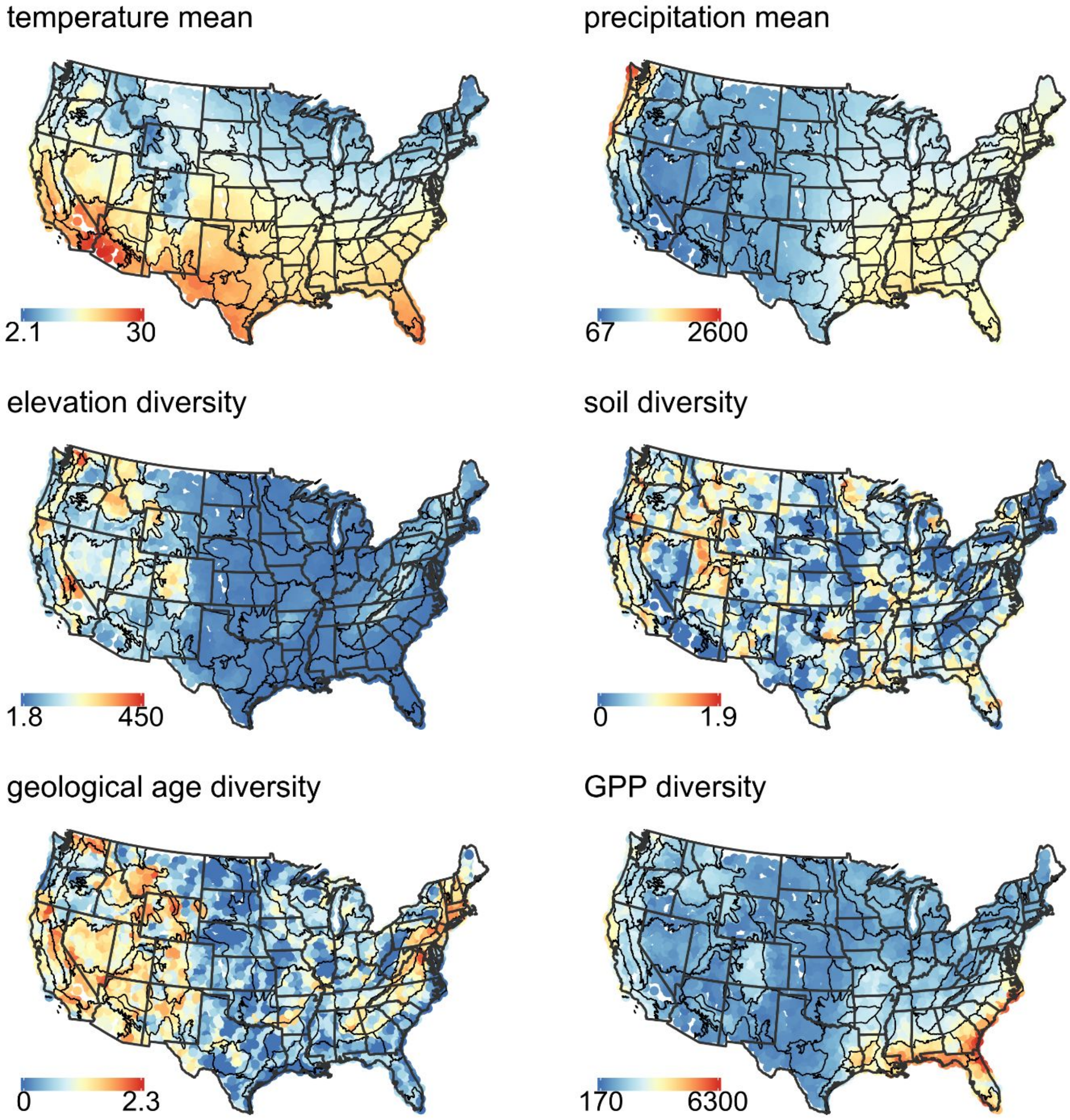

Figure 2: Maps of climate and geodiversity predictor variables across the contiguous United States, centred on BBS route midpoints and FIA plots (fuzzed locations shown).

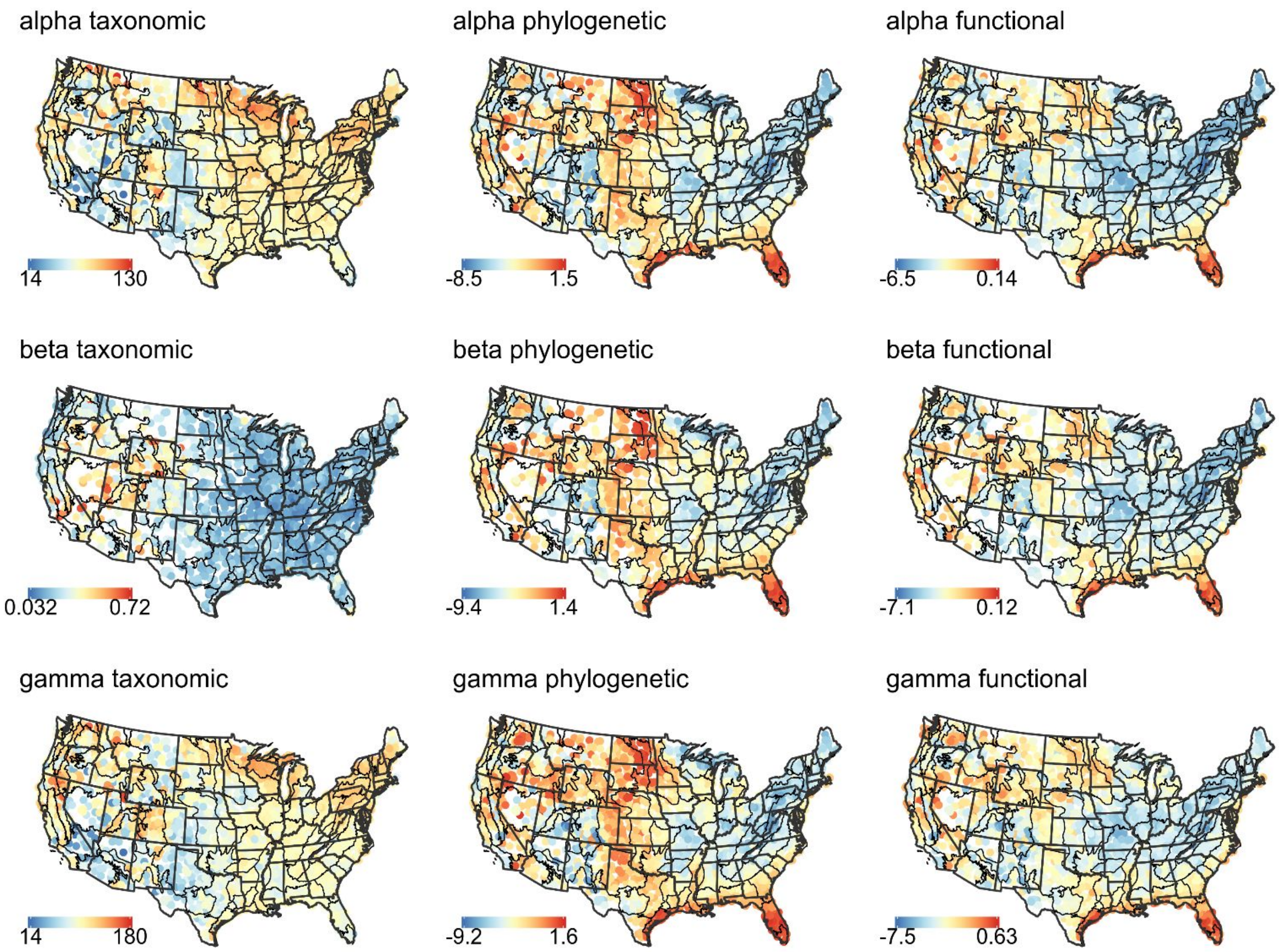

Figure 3: Maps of bird biodiversity at BBS routes, across 3 levels and 3 dimensions of biodiversity. For taxonomic diversity, richness is plotted for alpha- and gamma-diversity, and pairwise dissimilarity score is plotted for beta-diversity. For phylogenetic and functional diversity, z-scores are plotted for all levels. Midpoints of each route are shown on the map.

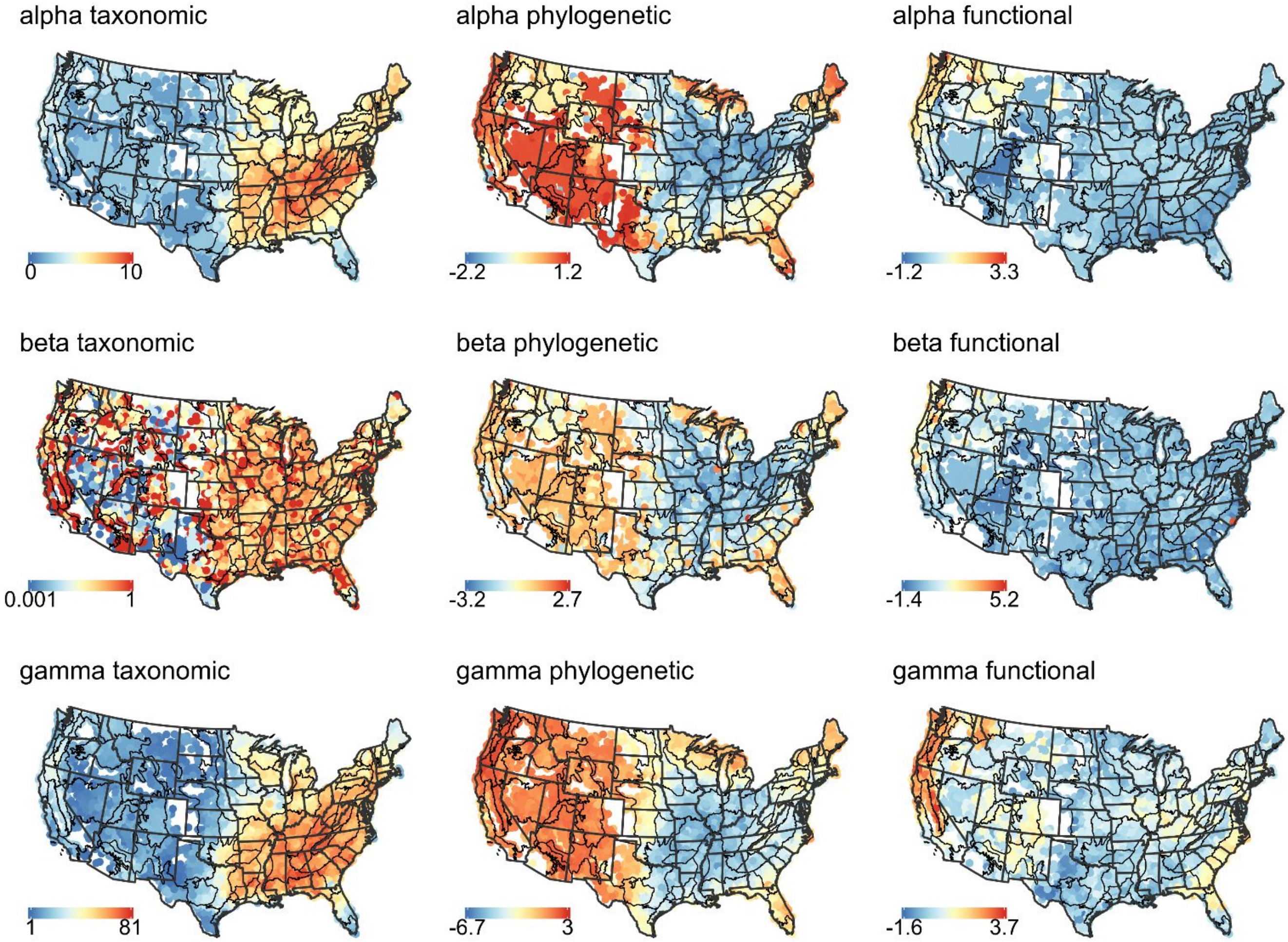

Figure 4: Maps of tree biodiversity at FIA plots, across 3 levels and 3 dimensions of biodiversity. The same biodiversity metrics are shown as in Figure 3. Fuzzed locations of each FIA plot are shown on the map.

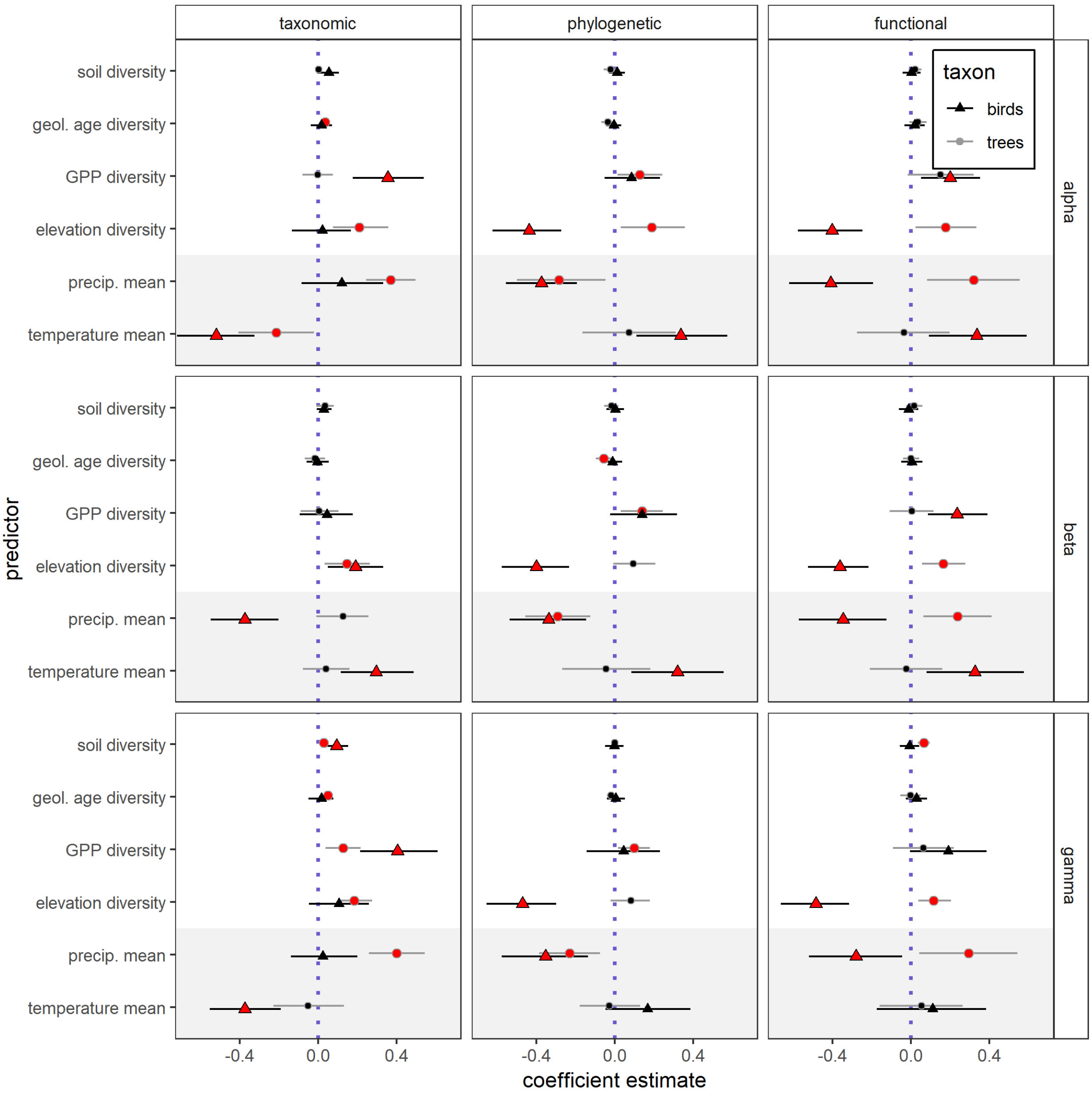

Figure 5: Scaled coefficients of fixed effects for birds and trees. Error bars show 95% credible interval around parameter estimate. Parameters with credible intervals that do not overlap zero are shown in red. Within each model, predictors are scaled so that coefficients can be compared across variables within the model. Predictors representing mean climate are shaded in grey; the other predictors represent geodiversity.

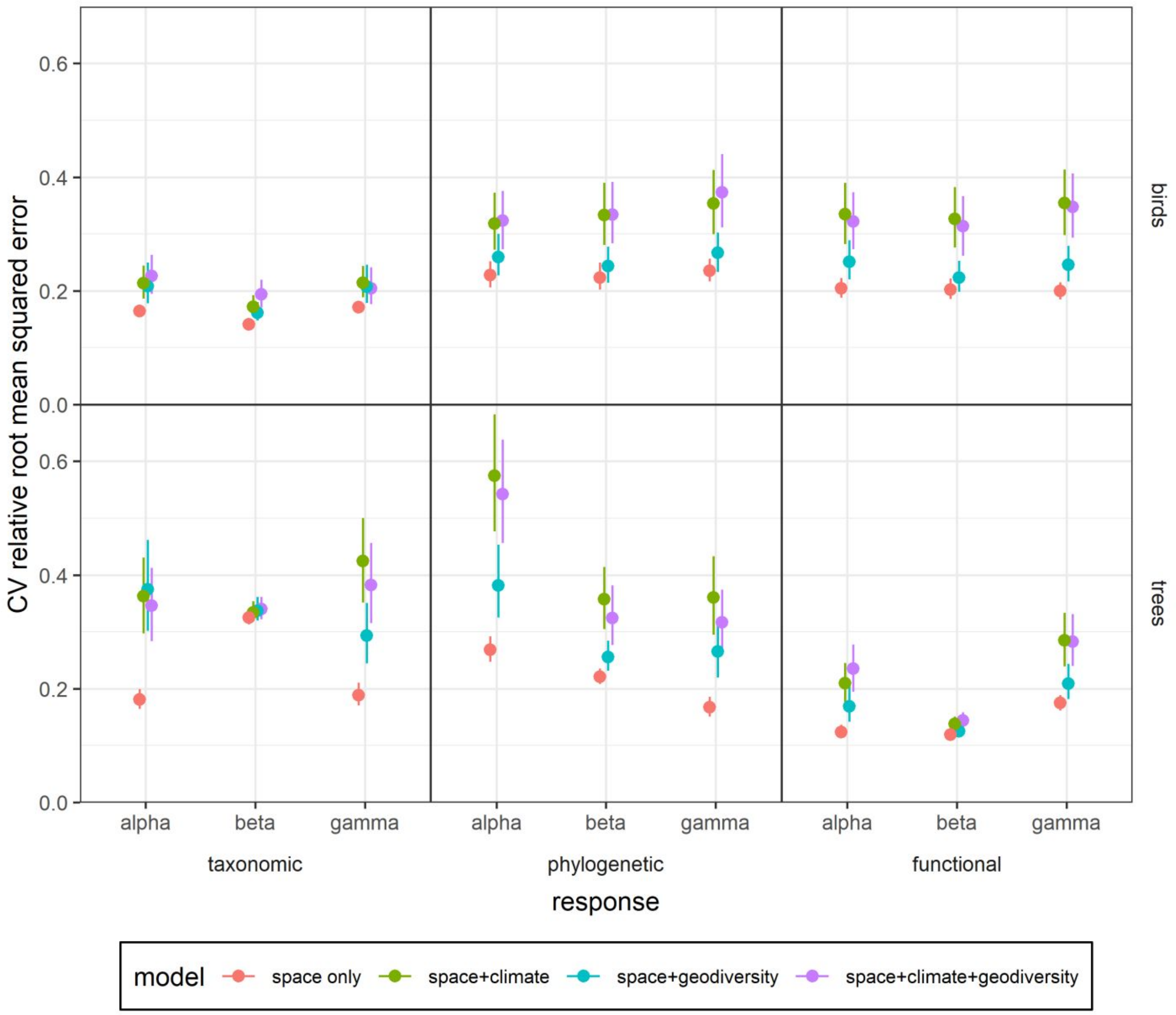

Figure 6: Model performance for bird biodiversity and tree biodiversity, assessed with spatially blocked leave-one-location-out cross-validation. This figure shows the root mean squared errors from the space-only or null models (red), models with climate predictors (green), models with geodiversity predictors (blue), and full models (purple) for each taxon and each response variable. Individual models were fit holding out all data points from one ecoregion, then the holdout data points were predicted and root mean squared error calculated across all ecoregions. The raw errors are divided by the range of the observed data to produce a relative value comparable among models. A lower value represents better performance of the model. Error bars are 95% credible intervals. Because each cross-validation fold excludes an entire

region, the null model including only the spatial random effect tends to predict the held out values as well or better than the models including climate and geodiversity predictors. However, models including geodiversity predictors tend to perform as well or better than the models including climate predictors, especially for phylogenetic and functional diversity.