Received: 4 March 2019 | Revised: 15 December 2019 | Accepted: 19 December 2019

DOI: 10.1111/geb.13061

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology

WILEY

Beyond counts and averages: Relating geodiversity to dimensions of biodiversity

Quentin D. Read[1,2,15] | Phoebe L. Zarnetske[1,2] | Sydne Record[4] | Kyla M. Dahlin[2,5] | Jennifer K. Costanza[6] | Andrew O. Finley[3] | Keith D. Gaddis[7] | John M. Grady[1,8] | Martina L. Hobi[9] | Andrew M. Latimer[10] | Sparkle L. Malone[11] | Scott V. Ollinger[12] | Stephanie Pau[13] | Adam M. Wilson[14]

[1]Department of Integrative Biology, Michigan State University, East Lansing, Michigan

[2]Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, East Lansing, Michigan

[3]Department of Forestry, Michigan State University, East Lansing, Michigan

[4]Department of Biology, Bryn Mawr College, Bryn Mawr, Pennsylvania

[5]Department of Geography, Environment, and Spatial Sciences, Michigan State University, East Lansing, Michigan

[6]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina

[7]Earth Science Division, NASA, Washington, District of Columbia

[8]National Great Rivers Research and Education Center, East Alton, Illinois

[9]Swiss Federal Institute for Forest, Snow, and Landscape Research, Birmensdorf, Switzerland

[10]Department of Plant Sciences, University of California-Davis, Davis, California

[11]Department of Biological Sciences, Florida International University, Miami, Florida

[12]Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire

[13]Department of Geography, Florida State University, Tallahassee, Florida

[14]Department of Geography, University at Buffalo, Buffalo, New York

[15]National Socio-Environmental Synthesis Center, Annapolis, Maryland

Correspondence
Quentin D. Read, National Socio-Environmental Synthesis Center, 1 Park Place, Suite 300, Annapolis, MD 21401, USA.
Email: qread@sesync.org

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. Nonetheless, 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 USA.

Time period: 2007–2016.

Taxa studied: Birds and 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 fitted 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 fitted models including climate alone (temperature and precipitation), geodiversity alone (topography, soil and geology) and climate plus geodiversity.

Results: A combination of geodiversity and climate predictor variables fitted most forms of bird and tree biodiversity with < 10% relative error. Models using geodiversity and climate performed better for local (alpha) and regional (gamma) diversity than for turnover-based (beta) diversity. Among geodiversity predictors, variability of elevation fitted 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 with climate across ecoregions, but models tended to have a poor fit in ecoregions held out of the training dataset. Patterns of geodiversity could help to prioritize conservation

Funding information
National Aeronautics and Space Administration, Grant/Award Number: NNX14AP07G, NNX16AQ44G and NNX16AQ45G; National Science Foundation, Grant/Award Number: 1237491, 1637685, 1638688, DBI-1639145 and EF-1253225; National Institute of Food and Agriculture, Grant/Award Number: 1010055 and NH00634

Editor: Volker Bahn

efforts within ecoregions. However, we need to understand the underlying mechanisms more fully before we can build models transferable across ecoregions.

KEYWORDS
alpha diversity, beta diversity, biodiversity, breeding bird survey, conservation, forest inventory, gamma diversity, geodiversity

1 | INTRODUCTION

In the face of an ongoing sixth mass extinction, society is challenged to minimize biodiversity loss through conservation efforts (Ceballos et al., 2015). 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), but 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 the preservation of 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 geological, 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 (geological diversity, landscape complexity), soils (pH, organic matter and nutrient availability) or hydrology (variation of hydrological features, such as rivers, ponds and lakes; Hjort, Heikkinen, & Luoto, 2012; Kaskela et al., 2017; Wang et al., 2013). Some geodiversity definitions include climate, using variables such as temperature, precipitation, evapotranspiration, water balance and solar radiation, whereas others explicitly exclude climate from their definition (Gray, 2004; Parks & Mulligan, 2010; Tukiainen, Bailey, Field, Kangas, & Hjort, 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., 2015). However, little is known about how geodiversity of Earth's surface compares to climate in explaining the variation in biodiversity, whether relationships generalize across geographical 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, Boyd, & Field, 2018). Furthermore, conservation frameworks, including CNS, typically advance the idea that conservation of geodiversity will result in positive outcomes for biodiversity writ large (Beier & de Albuquerque, 2015). This assumption must be tested empirically, especially given the potential trade-offs among orthogonal dimensions of biodiversity within and among taxa; conservation of 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 USA to increase our understanding of biodiversity–geodiversity relationships. Geodiversity, in conjunction with climate, predicts patterns of species diversity of plants (Bailey et al., 2018; Tukiainen et al., 2017) and animals (Alahuhta et al., 2018; Parks & Mulligan, 2010) 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, Boyd, Hjort, Lavers, & Field, 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, Houtan, Pimm, & Sexton, 2015). Only a few have accounted for the three levels of biodiversity: alpha diversity, beta diversity (turnover among plots) and gamma diversity (Gossner et al., 2013; Meynard et al., 2011). 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 that of alpha diversity, because high geodiversity often reflects high diversity of habitats within regions and therefore more unique local species assemblages (Stein, Gerstner, & Kreft, 2014). This leads to prediction 2, which is that geodiversity will explain more variability in the beta and gamma levels of biodiversity than in 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, Faurby, & Svenning, 2018) in the face of the current biodiversity crisis. Given that phylogenetic (Winter, Devictor, & Schweiger, 2013) 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). Given that 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 geographical 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, topographical complexity generates a diversity of climatic conditions at small to intermediate spatial scales, ranging from metres (Bennie, Huntley, Wiltshire, Hill, & Baxter, 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, Keeler-Wolf, & Schoenherr, 2007). Inland, in contrast, the average climate of the Coast Range is more arid, and fog is absent (Ackerly et al., 2010), meaning that only the coolest facets of the landscape support any level of tree cover. In this context, topographical 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 topographical 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 USA 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 in 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.

2 | 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 USA. We used biodiversity and geodiversity data collected from 2007 to 2016.

2.1 | Breeding Bird Survey

The North American Breeding Bird Survey (BBS; https://www.pwrc.usgs.gov/bbs/) is an annual survey of breeding birds across the USA and Canada begun in 1966. Voluntary observers report species and counts of birds seen or heard during 3 min observations at 50 stops spaced every *c.* 800 m along routes *c.* 39.4 km in length (Sauer, Link, Fallon, Pardieck, & Ziolkowski, 2013). There are *c.* 3,480 active routes in the contiguous USA with continuous yearly stop-level data. We excluded any routes with an ambiguous midpoint coordinate (discontinuous transects), leaving 3,089 routes. We included only the surveys conducted under the standard protocol, discarding repeat surveys and any observations recorded by trainees.

2.2 | Forest Inventory and Analysis

The U.S. Department of Agriculture Forest Service's Forest Inventory and Analysis (FIA) program surveys the composition and status of forests throughout the USA, with data collected annually (Bechtold & Patterson, 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 & Patterson, 2005). Each tree is identified to species. We obtained the most recent survey from all forested, non-plantation FIA plots in the contiguous USA (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.

2.3 | 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 the Supporting Information (Appendix S1) for additional details.

2.4 | 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, because 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 on each route and pooled all surveys from 2007 to 2016. See the Supporting Information (Appendix S2) 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 Supporting Information Appendix S2). We took: (a) the median diversity of all sites in the radius, including the focal site (alpha); (b) the median pairwise diversity of all pairs of sites in the radius, including the focal sites (beta); and (c) the aggregated diversity of all sites in the radius (gamma). Each diversity level has three dimensions: taxonomic, phylogenetic and functional (Supporting Information Table S1). For taxonomic diversity, alpha diversity and gamma diversity were represented by species richness, and beta diversity was represented 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 the 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 the dependence on richness. Likewise, 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. Given that the BBS surveys provide poor estimates of the abundances of some species, we calculated incidence-based biodiversity metrics for both birds and trees in order that metrics are comparable between the two taxa.

2.5 | Geodiversity data sources and processing

We obtained and processed remotely sensed data for the contiguous USA 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; for example, WorldClim v.1 (Hijmans, Cameron, Parra, Jones, & Jarvis, 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 to weather stations, which measure air temperature several metres 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, Zhao, & Running, 2011). What is more, studies have shown that surface temperature might be more ecologically relevant than air temperature (Pau, Edwards, & Still, 2013; Still, Pau, & Edwards, 2014). The thermodynamic temperature of an organism, which drives its respiratory rate and vapour pressure deficit, is more closely related to the surface temperature than to 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, Hook, & Hulley, 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 geological 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 (Alahuhta et al., 2018; Austin & Smith, 1989). The 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 might capture additional spatial variation not accounted for by the other three geodiversity variables. See the Supporting Information (Appendix S3) 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 within the

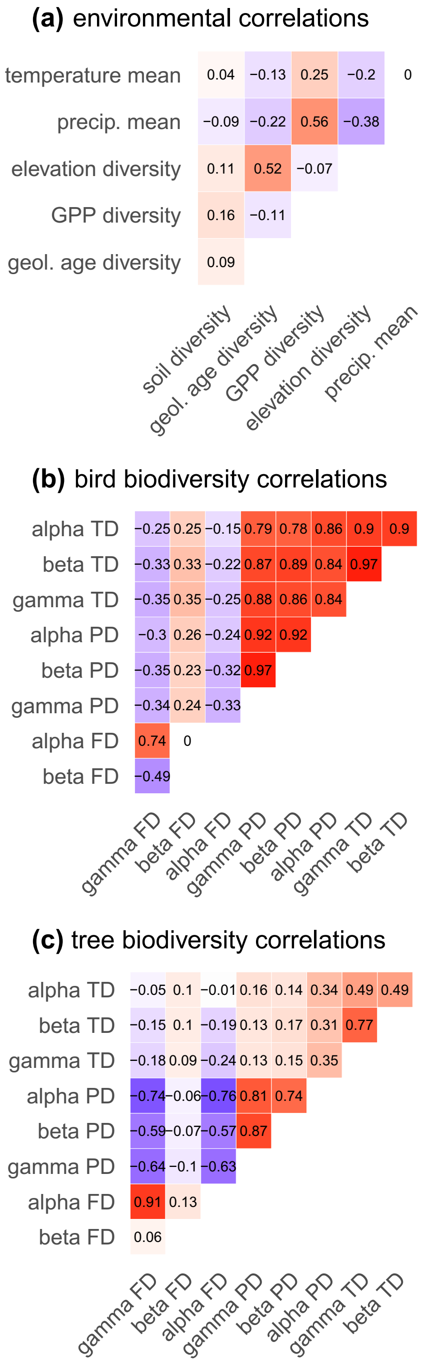

FIGURE 1 Heat maps showing correlations between pairs of environmental predictor variables, including: (a) geodiversity and climate; (b) bird biodiversity variables; and (c) tree biodiversity variables. Pearson correlation coefficients are shown, along with colours indicating the magnitude of the correlation coefficients. FD = functional diversity; GPP = gross primary productivity; PD = phylogenetic diversity; TD = taxonomic diversity

50 km radius, and we used the mean terrain ruggedness index (TRI; Wilson, O'Connell, Brown, Guinan, & Grehan, 2007) of the 3 × 3 pixel neighbourhood around all pixels to represent spatial variability. For discrete predictors, we used the Shannon entropy of all pixels in the radius to represent spatial variability. Shannon entropy has been shown to increase monotonically with an increasing number of landscape patch types, to behave consistently in both real and simulated landscapes and to be correlated positively with many other measures of landscape heterogeneity (Peng et al., 2010). Importantly, although many past studies have used variables extracted from spatially continuous layers at points to characterize environmental variation, we explicitly considered spatial variation in the regions around the points where biodiversity was measured. Defining geodiversity in terms of this variation is crucial for explaining biodiversity fully, because a single point value cannot capture the diversity of niche space that may determine biodiversity (Lawler et al., 2015).

Finally, we grouped geodiversity and biodiversity observations spatially using the terrestrial ecoregions of TNC (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 six border regions with insufficient data) is high enough to account adequately for spatial autocorrelation in biodiversity responses within the study area without overfitting.

2.6 | 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 USA 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).

2.7 | 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 zero and one in the model. No bird sites had a taxonomic beta diversity of exactly zero or one, but *c.* 16% of tree sites had taxonomic beta diversity of exactly zero or one, which is outside the domain of the logit function. Thus, we replaced zeroes with .001

and ones with .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 *c*. 3,000 sites, meaning that sample sizes were comparable between the datasets used to fit each model.

2.8 | Model fitting

We fitted spatial multivariate mixed models with the following fixed predictors: (a) all six predictor variables as fixed effects; (b) only the four geodiversity predictors as fixed effects; (c) only the two climate predictors as fixed effects; and (d) no fixed effects (null model with only spatial random effects). We fitted multivariate models for each diversity level (alpha, beta and gamma) and each taxon (birds and trees), totalling 24 models (four predictor sets × three diversity levels × two 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 fitted a random intercept and slope for each predictor in each TNC ecoregion. We excluded ecoregions with fewer than five sites, because random effects estimated with fewer than five data points are not robust. The excluded ecoregions were primarily in Canada or Mexico and have only a small area inside the contiguous USA that is ≥ 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, 2018).

We fitted the models in a hierarchical Bayesian framework using the R package *brms* (Bürkner, 2017). We modelled the error in response variables as normally distributed. Finally, we standardized both predictor and response variables before fitting the models in order 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.

2.9 | Model validation

To assess model predictive performance, we performed spatially blocked leave-one-location-out cross-validation (Roberts et al., 2017). We refitted 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 obtain a cross-validation RMSE for each model. We also calculated the RMSE of the models fitted to all the data. We divided all RMSE values by the range of the observed data to yield relative values that could 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 USA but does not correct fully for spatial autocorrelation.

We calculated the Bayesian R^2 (Gelman, Goodrich, Gabry, & Ali, 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.

3 | RESULTS

3.1 | Description of geodiversity and biodiversity variables

Correlations among geodiversity predictor variables were relatively low (Figure 1a). The pairwise correlation between elevation diversity and geological age diversity was relatively high (r = .52), indicating that geodiversity measured as topographical variability is correlated with geodiversity measured as the variety of geological substrate ages. Notably, the correlation between elevation diversity and mean annual temperature was low (r = −.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 be correlated 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, whereas geological and topographical variables varied at scales corresponding to major land features, such as mountain ranges (Figure 2). Biogeographical patterns were disparate across dimensions of biodiversity for birds (Figure 3) and trees (Figure 4). Bird diversity patterns were spatially idiosyncratic (Figure 3), whereas tree diversity showed a strong longitudinal pattern, with taxonomic diversity being highest in the east and functional and phylogenetic diversity highest in the west (Figure 4).

3.2 | 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

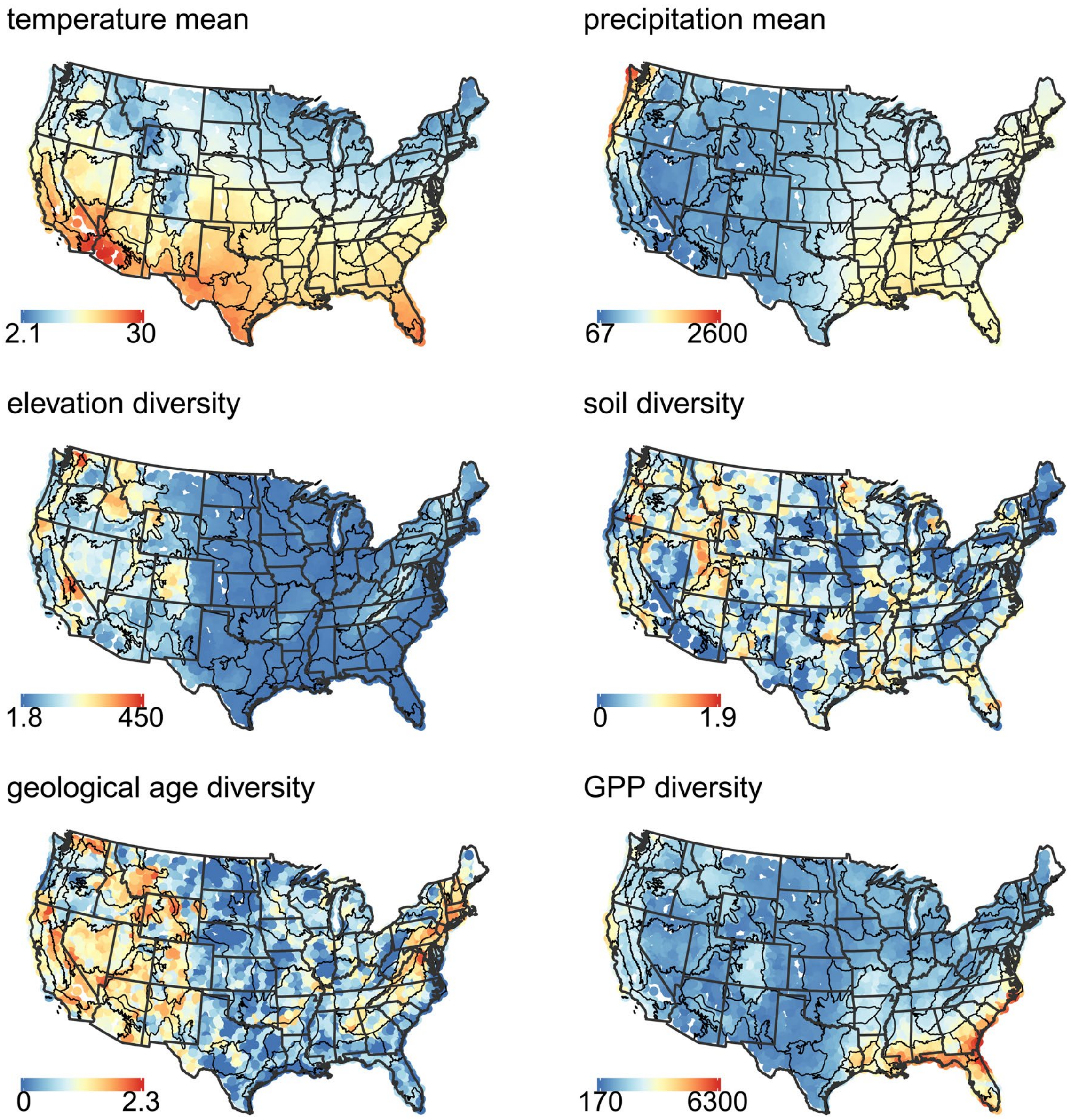

FIGURE 2 Maps of climate and geodiversity predictor variables across the contiguous USA, centred on Breeding Bird Survey (BBS) route midpoints and Forest Inventory and Analysis program (FIA) plots (fuzzed locations shown). GPP = gross primary productivity

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 geological age variability and soil type variability tended to be relatively weak, although for birds the soil type variability positively affected taxonomic diversity, and for trees the geological 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.

3.3 | 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

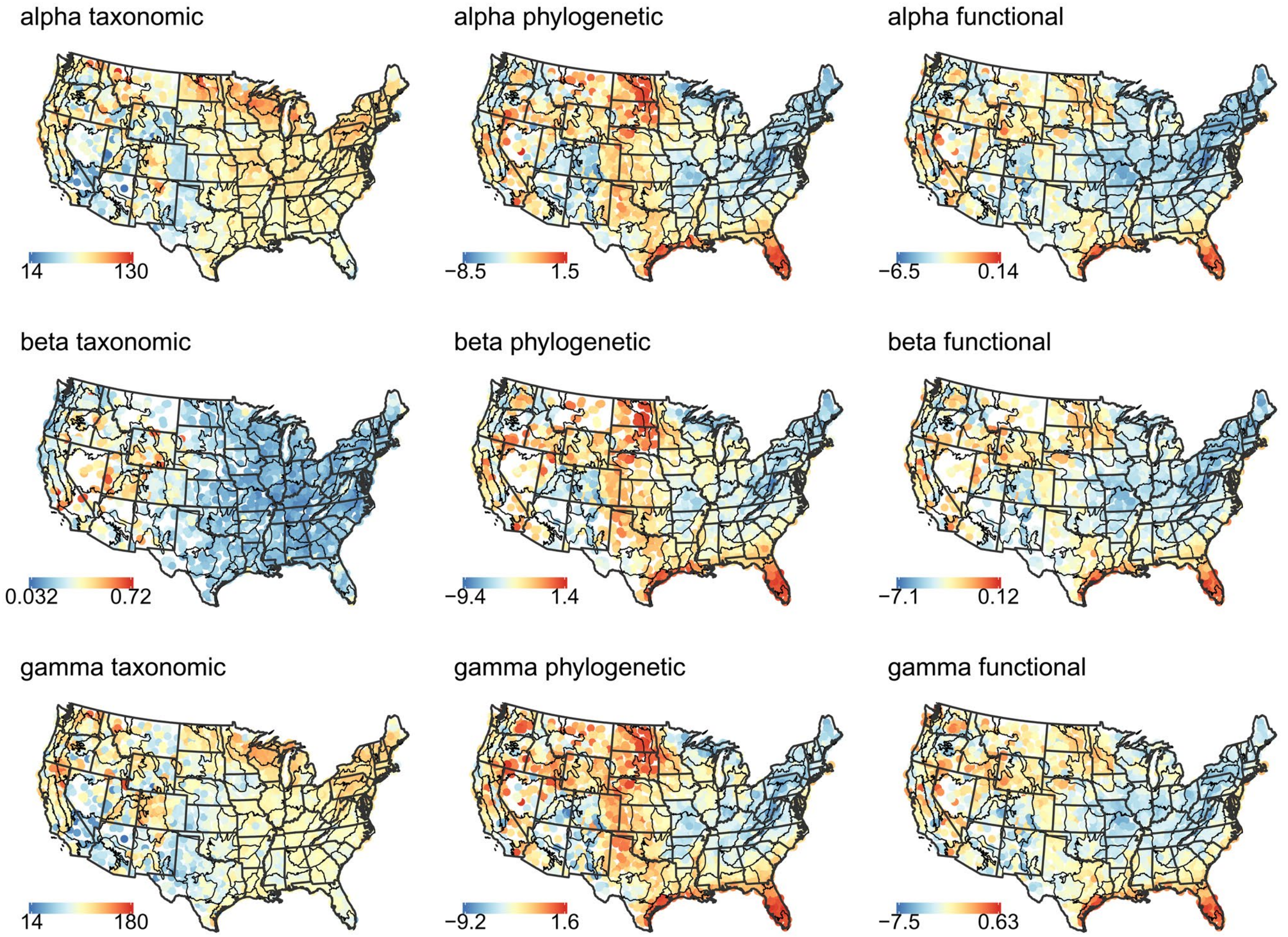

FIGURE 3 Maps of bird biodiversity at Breeding Bird Survey (BBS) routes, across three levels and three dimensions of biodiversity. For taxonomic diversity, richness is plotted for alpha and gamma diversity, and pairwise dissimilarity score is plotted for beta diversity. For phylogenetic and functional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

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^2 values (Supporting Information 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).

3.4 | Spatially varying biodiversity–geodiversity relationships

The strength of biodiversity–climate relationships varied more across ecoregions than the strength of biodiversity–geodiversity relationships (Supporting Information Figure S2). Individual geodiversity–biodiversity relationships varied idiosyncratically across space (Supporting Information Figures S3–S14). 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 (Supporting Information 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, might 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.

4 | DISCUSSION

The magnitude and direction of the relationships between environmental variability and biodiversity were intriguingly context dependent,

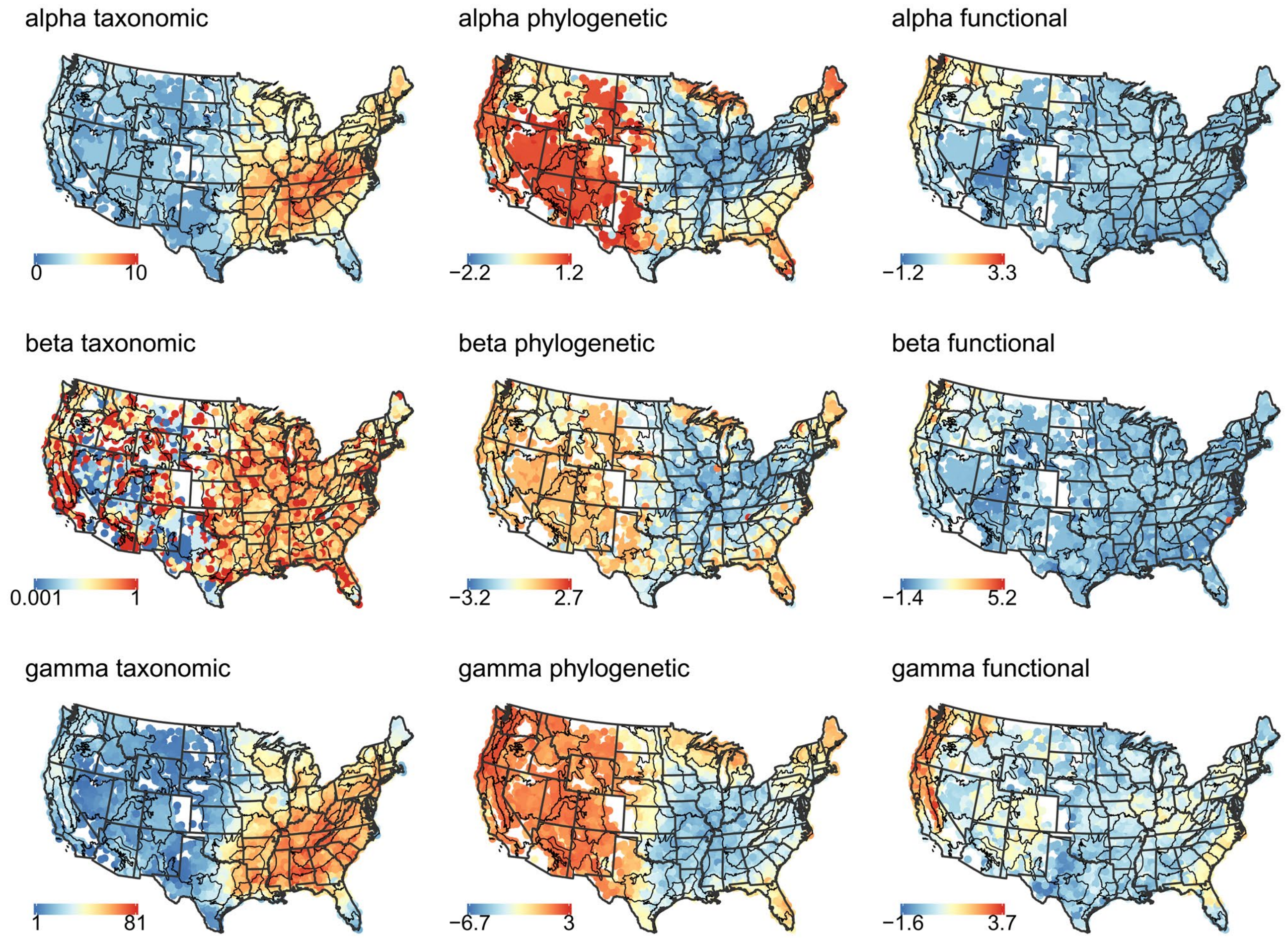

FIGURE 4 Maps of tree biodiversity at Forest Inventory and Analysis (FIA) program plots, across three levels and three dimensions of biodiversity. The same biodiversity metrics are shown as in Figure 3. Fuzzed locations of each FIA plot are shown on the map

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.

4.1 | 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 (Supporting Information 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 might 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 cautions against relying heavily on geodiversity or climate to predict biodiversity in regions far from where models are fitted.

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 (Supporting Information Figure S1), although neither climate nor geodiversity predictors increased prediction accuracy

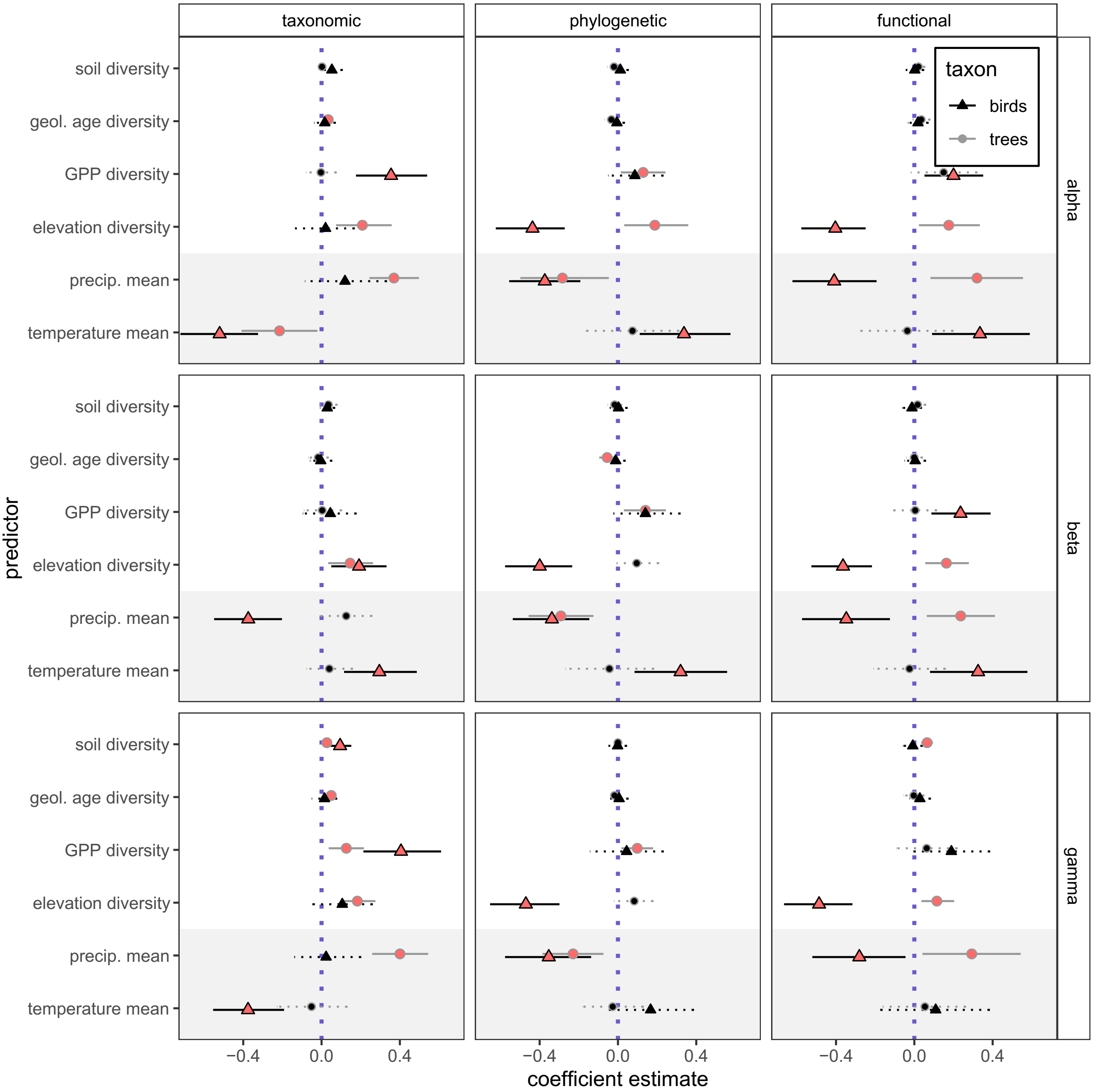

FIGURE 5 Scaled coefficients of fixed effects for birds and trees. Error bars show the 95% credible interval around the parameter estimate. Parameters with credible intervals that do not overlap zero are shown in red, and the credible intervals that do overlap zero are shown with dotted lines. Within 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. GPP = gross primary productivity

in spatially blocked cross-validation (Figure 6). Among geodiversity predictors, topographical variability had the largest effect on biodiversity. Interestingly, topographical variability had a positive relationship with tree diversity across levels but was associated with lower bird diversity. This might 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 might depend on the microhabitats created by topographical variation. Niche diversity for birds might be driven more by the diversity of food sources, which could be reduced in more topographically rugged regions. In contrast to topographical variability, geological 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 effect of geodiversity would be strongest on turnover (beta) and regional diversity (gamma). For trees, in particular, geodiversity combined with climate predicted beta

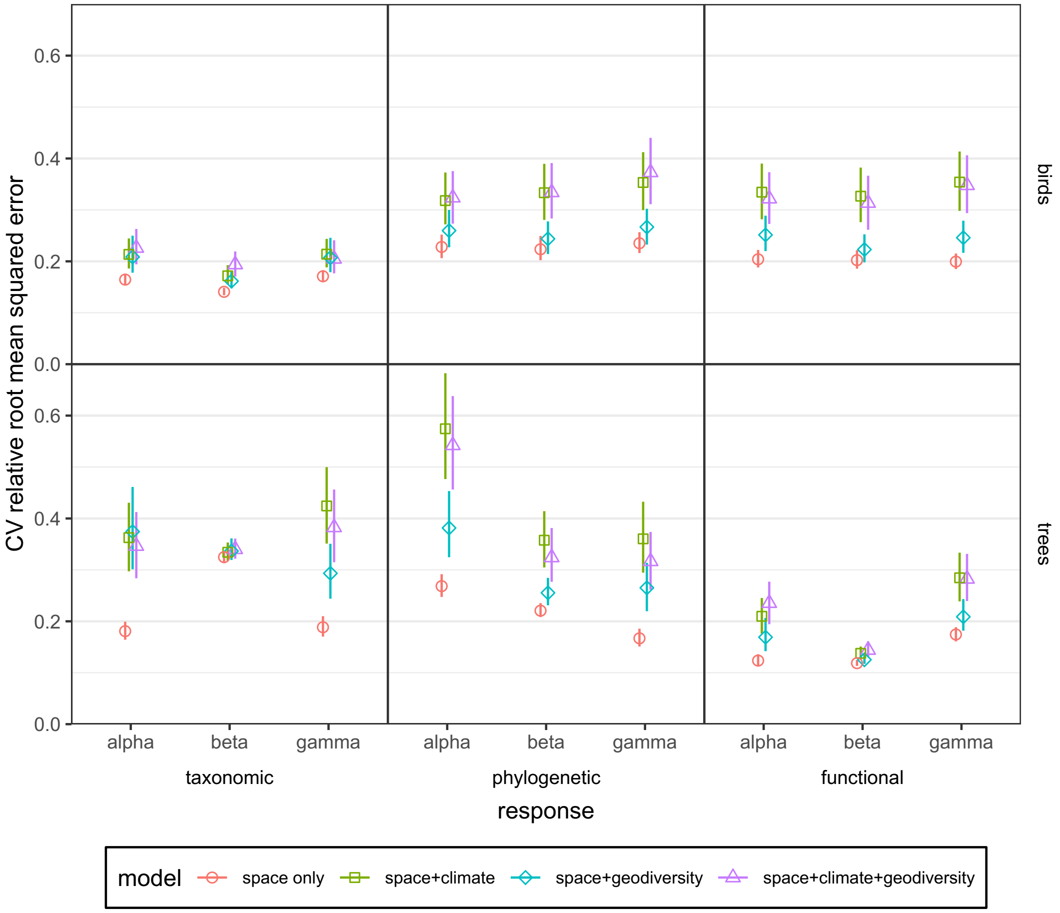

FIGURE 6 Model performance for bird biodiversity and tree biodiversity, assessed with spatially blocked leave-one-location-out cross-validation. This figure shows the root mean squared errors from the space-only or null models (red circles), models with climate predictors (green squares), models with geodiversity predictors (blue diamonds) and full models (purple triangles) for each taxon and each response variable. Individual models were fitted holding out all data points from one ecoregion, then the holdout data points were predicted, and the root mean squared error was 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. Given that each cross-validation (CV) fold excludes an entire region, the null model including only the spatial random effect tends to predict the held out values as well as or better than the models including climate and geodiversity predictors. However, models including geodiversity predictors tend to perform as well as or better than the models including climate predictors, especially for phylogenetic and functional diversity

diversity less well than alpha and gamma diversity. This result might be attributable to incomplete sampling of the local community by single FIA plots. If trees have patchy distributions at local scales, the small-sized FIA plots might 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 is integrated over many plots. We show that familiar maps of biodiversity, which are commonly created using species range maps (Brown & Lomolino, 1998; Currie & Paquin, 1987; 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 might indicate ecologically or evolutionarily meaningful relationships. In general, we found similar responses across biodiversity dimensions because they tend to be correlated positively with one another (Figure 1). This finding partly 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 topographical variability tended to have higher bird taxonomic diversity but lower phylogenetic and functional diversity. The taxonomic diversity of birds 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, Tilghman, & Anderson, 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 are likely to reflect increased taxonomic diversity within speciose guilds.

The discrepancy in relationships we observed among the dimensions of biodiversity we examined mirrors that of a previous study examining change in biodiversity over time. Increases in taxonomic diversity without corresponding changes in phylogenetic or functional diversity might indicate biotic homogenization of assemblages; 40 years of BBS surveys show a homogenizing trend over time (Jarzyna & Jetz, 2017). Although our study does not address change over time, the discrepancy between taxonomic and functional/phylogenetic diversity patterns with topographical variability and with temperature is notable. Jarzyna and Jetz (2017) 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 (2017), suggesting that bird communities at high elevations and in cold regions might be relatively homogeneous and thus relatively more vulnerable to changing climate. In the case of breeding birds in the USA, topographically diverse regions might, 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, although not all, traits are phylogenetically conserved (Devictor et al., 2010), such that phylogenetic diversity roughly approximates functional diversity (Winter et al., 2013). However, tree phylogenetic diversity increases with decreasing precipitation, whereas functional diversity and taxonomic diversity decrease. This suggests that the angiosperm and gymnosperm species that contribute to high phylogenetic diversity in low-precipitation regions might have convergently evolved suites of adaptations to dry environments (Méndez-Alonzo, Paz, Zuluaga, Rosell, & Olson, 2012), resulting in low functional diversity at those sites.

4.2 | Spatially varying biodiversity–geodiversity relationships

The relationship between geodiversity variables and biodiversity variables varied in direction and magnitude across the ecoregions of the USA. For example, elevational variability had a greater effect on tree biodiversity in the central and eastern USA, providing support for prediction 4. In the west, climatic factors and a smaller regional species pool set upper bounds on richness, meaning that the opportunity for increased richness with increased geodiversity is reduced relative to the east (Supporting Information Figure S11). In contrast, the effect of elevational variability on bird taxonomic diversity was more likely to be non-zero in regions of high topographical relief, such as the Appalachian ecoregion and the northern Rocky Mountains (Supporting Information Figure S5). For trees, the effect of precipitation on biodiversity was more likely to be significant in the drier central and western USA (Supporting Information 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 might depend on the spatial extent of the study region; a similar model fitted 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 might not be transferable across ecoregions. This might present a conundrum for organisms that are migrating to track climate conditions and might 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 USA (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.

4.3 | Conclusions and future directions

Our study found that topographical variability was related to biodiversity independently of climatic means and in different ways from climatic means. This result suggests that using remotely sensed temperature data, rather than values interpolated between weather stations using local elevation, might improve our ability to distinguish between the effects of climate and of topographical 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, Lobell, & Burke, 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. Past ecological research and the results of the present study show that climate explains much of the spatial variation in biodiversity of trees and birds, whereas geodiversity is related to biodiversity independently of climate. To disentangle the effects of climatic and topographical drivers, spatially continuous remotely sensed data are necessary. Biodiversity–geodiversity relationships depend on the taxonomic group, the 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 been characterized primarily in a few well-studied taxa (Hjort et al., 2012; Meynard et al., 2011; 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.

ACKNOWLEDGEMENTS

We would like to acknowledge Kevin Potter for providing tree phylogenies, Jens Stevens for providing tree trait data, Aaron Kamoske for compiling and manipulating raster datasets, Jay Jain for assisting with trait imputation and Kerri Brinegar for compiling precipitation data. We would also like to thank Volker Bahn and two anonymous reviewers for their helpful suggestions.

Funding for the bioXgeo working group was provided by the National Aeronautics and Space Administration (NASA) Ecological Forecasting Program, Earth Science Division, grant #NNX16AQ44G awarded to P.L.Z., K.M.D. and S.R. Q.D.R. was supported while writing this manuscript by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1639145. Additional support for P.L.Z., K.M.D., Q.D.R., J.M.G. and A.O.F. came from Michigan State University, and for P.L.Z.: USDA NIFA Hatch Project 1010055. Additional support for S.R. came from Bryn Mawr College. A.O.F. was also supportedby National Science Foundation (NSF) EF-1253225 and DMS-1916395, and National Aeronautics and Space Administration's Carbon Monitoring System project. Additional support for A.M.W. came from NASA grant #NNX16AQ45G. S.V.O. was also supported by NSF grants 1638688, 1237491 and 1637685 and USDA grant #NH00634. K.D.G. was supported by an AAAS Science & Technology Policy Fellowship served at NASA. M.L.H. was supported by NASA Biodiversity and MODIS Science Program #NNX14AP07G. We thank the National Center for Ecological Analysis and Synthesis (NCEAS) for hosting working group meetings. The views expressed in this paper do not necessarily reflect those of NASA, the United States Government or the American Association for the Advancement of Science. Forest Inventory and Analysis location data were provided through the Forest Service Agreement no. 17-MU-11261919-021. We provide no information that would enable the identification of individual Forest Inventory and Analysis plots based on tree inventory, and all plot locations displayed on maps are fuzzed for confidentiality.

DATA AVAILABILITY STATEMENT

Data and code for reviewers to reproduce all the model fitting and analysis presented in this manuscript are archived on FigShare at https://doi.org/10.6084/m9.figshare.7680083.v2. Code to replicate the data preparation and cleaning stages described in the Methods is also archived on the FigShare repository.

ORCID

Quentin D. Read https://orcid.org/0000-0003-4315-5582
Phoebe L. Zarnetske https://orcid.org/0000-0001-6257-6951
Sydne Record https://orcid.org/0000-0001-7293-2155
Kyla M. Dahlin https://orcid.org/0000-0002-6016-2605
Jennifer K. Costanza https://orcid.org/0000-0002-3747-538X
Andrew O. Finley https://orcid.org/0000-0002-2277-2912
Keith D. Gaddis https://orcid.org/0000-0002-5549-906X
John M. Grady https://orcid.org/0000-0001-6444-3300
Martina L. Hobi https://orcid.org/0000-0003-3537-9738
Andrew M. Latimer https://orcid.org/0000-0001-8098-0448
Sparkle L. Malone https://orcid.org/0000-0001-9034-1076
Scott V. Ollinger https://orcid.org/0000-0001-6226-1431
Adam M. Wilson https://orcid.org/0000-0003-3362-7806

REFERENCES

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: Implications for conservation biogeography. *Diversity and Distributions*, *16*, 476–487. https://doi.org/10.1111/j.1472-4642.2010.00654.x

Alahuhta, J., Ala-Hulkko, T., Tukiainen, H., Purola, L., Akujärvi, A., Lampinen, R., & Hjort, J. (2018). The role of geodiversity in providing ecosystem services at broad scales. *Ecological Indicators*, *91*, 47–56. https://doi.org/10.1016/j.ecolind.2018.03.068

Anderson, M. G., Barnett, A., Clark, M., Ferree, C. E., Olivero Sheldon, A., & Prince, J. (2014). *Resilient sites for terrestrial conservation in the Southeast Region*. The Nature Conservancy, Eastern Conservation Science. 127 pp.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., ... Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Anderson, M. G., & Ferree, C. E. (2010). Conserving the stage: Climate change and the geophysical underpinnings of species diversity. *PLoS ONE*, *5*, e11554. https://doi.org/10.1371/journal.pone.0011554

Anderson, S. H., & Shugart, H. H. (1974). Habitat selection of breeding birds in an East Tennessee deciduous forest. *Ecology*, *55*, 828–837. https://doi.org/10.2307/1934418

Austin, M. P., & Smith, T. M. (1989). A new model for the continuum concept. *Vegetatio*, *83*, 35–47. https://doi.org/10.1007/BF00031679

Badgley, C., Smiley, T. M., Terry, R., Davis, E. B., DeSantis, L. R. G., Fox, D. L., ... Yanites, B. J. (2017). Biodiversity and topographic complexity: Modern and geohistorical perspectives. *Trends in Ecology and Evolution*, *32*, 211–226. https://doi.org/10.1016/j.tree.2016.12.010

Bailey, J. J., Boyd, D. S., & Field, R. (2018). Models of upland species' distributions are improved by accounting for geodiversity. *Landscape Ecology*, *33*, 2071–2087. https://doi.org/10.1007/s10980-018-0723-z

Bailey, J. J., Boyd, D. S., Hjort, J., Lavers, C. P., & Field, R. (2017). Modelling native and alien vascular plant species richness: At which scales is geodiversity most relevant? *Global Ecology and Biogeography*, *26*, 763–776. https://doi.org/10.1111/geb.12574

Barbour, M., Keeler-Wolf, T., & Schoenherr, A. A. (2007). *Terrestrial vegetation of California* (3rd ed.). Oakland, CA: University of California Press.

Bechtel, B. (2015). A new global climatology of annual land surface temperature. *Remote Sensing*, *7*, 2850–2870. https://doi.org/10.3390/rs70302850

Bechtold, W. A., & Patterson, P. L. (Eds.). (2005). *The enhanced forest inventory and analysis program - National sampling design and estimation procedures* (General Technical Report SRS-80, p. 85, 080). Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

Beier, P., & de Albuquerque, F. S. (2015). Environmental diversity as a surrogate for species representation. *Conservation Biology*, *29*, 1401–1410. https://doi.org/10.1111/cobi.12495

Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., & Baxter, R. (2008). Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, *216*, 47–59.

Besag, J., & Kooperberg, C. (1995). On conditional and intrinsic autoregressions. *Biometrika*, *82*, 733–746.

Brown, J. H., & Lomolino, M. V. (1998). *Biogeography*. Sunderland, MA: Sinauer Associates Inc.

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*, e1400253. https://doi.org/10.1126/sciadv.1400253

Cody, M. L. (1981). Habitat selection in birds: The roles of vegetation structure, competitors, and productivity. *BioScience*, *31*, 107–113. https://doi.org/10.2307/1308252

Currie, D. J., & Paquin, V. (1987). Large-scale biogeographical patterns of species richness of trees. *Nature*, *329*, 326–327. https://doi.org/10.1038/329326a0

Davies, T. J., & Buckley, L. B. (2011). Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 2414–2425. https://doi.org/10.1098/rstb.2011.0058

Davis, M., Faurby, S., & Svenning, J.-C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences USA*, *115*, 11262–11267. https://doi.org/10.1073/pnas.1804906115

De Graaf, R. M., Tilghman, N. G., & Anderson, S. H. (1985). Foraging guilds of North American birds. *Environmental Management*, *9*, 493–536. https://doi.org/10.1007/BF01867324

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*, 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, *17*, 1022–1035.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., & Seal, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, *45*, 1–33.

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., … Michaelsen, J. (2015). The climate hazards infrared precipitation with stations—A new environmental record for monitoring extremes. *Scientific Data*, *2*, 150066. https://doi.org/10.1038/sdata.2015.66

Gelman, A., Goodrich, B., Gabry, J., & Ali, I. (2018). R-squared for Bayesian regression models. *The American Statistician*, *73*, 307–309. https://doi.org/10.1080/00031305.2018.1549100

Gossner, M. M., Getzin, S., Lange, M., Pašalić, E., Türke, M., Wiegand, K., & Weisser, W. W. (2013). The importance of heterogeneity revisited from a multiscale and multitaxa approach. *Biological Conservation*, *166*, 212–220. https://doi.org/10.1016/j.biocon.2013.06.033

Gray, M. (2004). *Geodiversity: Valuing and conserving abiotic nature*. Hoboken, NJ: John Wiley & Sons.

Gray, M. (2008). Geodiversity: Developing the paradigm. *Proceedings of the Geologists' Association*, *119*(3–4), 287–298.

Heft-Neal, S., Lobell, D. B., & Burke, M. (2017). Using remotely sensed temperature to estimate climate response functions. *Environmental Research Letters*, *12*, 014013. https://doi.org/10.1088/1748-9326/aa5463

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., … Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, *12*, e0169748. https://doi.org/10.1371/journal.pone.0169748

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hjort, J., Heikkinen, R. K., & Luoto, M. (2012). Inclusion of explicit measures of geodiversity improve biodiversity models in a boreal landscape. *Biodiversity Conservation*, *21*, 3487–3506. https://doi.org/10.1007/s10531-012-0376-1

Hobi, M. L., Dubinin, M., Graham, C. H., Coops, N. C., Clayton, M. K., Pidgeon, A. M., & Radeloff, V. C. (2017). A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. *Remote Sensing of Environment*, *195*, 142–152. https://doi.org/10.1016/j.rse.2017.04.018

Jarzyna, M. A., & Jetz, W. (2016). Detecting the multiple facets of biodiversity. *Trends in Ecology and Evolution*, *31*, 527–538. https://doi.org/10.1016/j.tree.2016.04.002

Jarzyna, M. A., & Jetz, W. (2017). A near half-century of temporal change in different facets of avian diversity. *Global Change Biology*, *23*, 2999–3011. https://doi.org/10.1111/gcb.13571

Jenkins, C. N., Houtan, K. S. V., Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences USA*, *112*, 5081–5086. https://doi.org/10.1073/pnas.1418034112

Kaskela, A. M., Rousi, H., Ronkainen, M., Orlova, M., Babin, A., Gogoberidze, G., … Zhamoida, V. (2017). Linkages between benthic assemblages and physical environmental factors: The role of geodiversity in Eastern Gulf of Finland ecosystems. *Continental Shelf Research*, *142*, 1–13. https://doi.org/10.1016/j.csr.2017.05.013

Kembel, S. W., Ackerly, D. D., Blomberg, S. P., Cornwell, W. K., Cowan, P. D., Helmus, M. R., … Webb, C. O. (2018). picante: Integrating phylogenies and ecology. Retrieved from https://CRAN.R-project.org/package=picante

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology and Evolution*, *22*, 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kress, M. C. (2018). *Hierarchical models for predicting vegetation characteristics* (Unpublished Master's thesis). Michigan State University, East Lansing, Michigan.

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Šímová, I., … Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA*, *111*, 13745–13750. https://doi.org/10.1073/pnas.1317722111

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., … Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology*, *29*, 618–629. https://doi.org/10.1111/cobi.12505

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., … Svenning, J.-C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*, 1470–1481. https://doi.org/10.1111/gcb.12129

Méndez-Alonzo, R., Paz, H., Zuluaga, R. C., Rosell, J. A., & Olson, M. E. (2012). Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology*, *93*, 2397–2406. https://doi.org/10.1890/11-1213.1

Meynard, C. N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., & Mouquet, N. (2011). Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography*, *20*, 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Mildrexler, D. J., Zhao, M., & Running, S. W. (2011). A global comparison between station air temperatures and MODIS land surface temperatures reveals the cooling role of forests. *Journal of Geophysical Research: Biogeosciences*, *116*, G03025.

Noss, R. F., Platt, W. J., Sorrie, B. A., Weakley, A. S., Means, D. B., Costanza, J., & Peet, R. K. (2015). How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Diversity and Distributions*, *21*, 236–244. https://doi.org/10.1111/ddi.12278

Olson, D. M., & Dinerstein, E. (2002). The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden*, *89*, 199–224. https://doi.org/10.2307/3298564

Parks, K. E., & Mulligan, M. (2010). On the relationship between a resource-based measure of geodiversity and broad scale biodiversity patterns. *Biodiversity Conservation*, *19*, 2751–2766. https://doi.org/10.1007/s10531-010-9876-z

Pau, S., Edwards, E. J., & Still, C. J. (2013). Improving our understanding of environmental controls on the distribution of C3 and C4 grasses. *Global Change Biology*, *19*, 184–196.

Peng, J., Wang, Y., Zhang, Y., Wu, J., Li, W., & Li, Y. (2010). Evaluating the effectiveness of landscape metrics in quantifying spatial patterns. *Ecological Indicators*, *10*, 217–223. https://doi.org/10.1016/j.ecolind.2009.04.017

Record, S., Dahlin, K. M., Zarnetske, P. L., Read, Q. D., Malone, S. L., Gaddis, K. D., … Ollinger, S. V. (in press). Remote sensing of geodiversity and biodiversity. In J. Cavender-Bares, J. A. Gamon, & P. Townsend (Eds.), *Remote sensing of biodiversity: Using spectral signals to understand the biology and biodiversity of plants, communities, ecosystems and the tree of life*. Springer Remote Sensing/Photogrammetry Series. Berlin: Springer.

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., … Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, *40*, 913–929. https://doi.org/10.1111/ecog.02881

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 2536–2544. https://doi.org/10.1098/rstb.2011.0024

Sauer, J. R., Link, W. A., Fallon, J. E., Pardieck, K. L., & Ziolkowski, D. J. (2013). The North American Breeding Bird Survey 1966–2011: Summary analysis and species accounts. *North American Fauna*, *79*, 1–32. https://doi.org/10.3996/nafa.79.0001

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*, 866–880. https://doi.org/10.1111/ele.12277

Steudel, B., Hallmann, C., Lorenz, M., Abrahamczyk, S., Prinz, K., Herrfurth, C., … Kessler, M. (2016). Contrasting biodiversity–ecosystem functioning relationships in phylogenetic and functional diversity. *New Phytologist*, *212*, 409–420. https://doi.org/10.1111/nph.14054

Stevens, R. D., & Gavilanez, M. M. (2015). Dimensionality of community structure: Phylogenetic, morphological and functional perspectives along biodiversity and environmental gradients. *Ecography*, *38*, 861–875. https://doi.org/10.1111/ecog.00847

Still, C. J., Pau, S., & Edwards, E. J. (2014). Land surface skin temperature captures thermal environments of C3 and C4 grasses. *Global Ecology and Biogeography*, *23*, 286–296.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tukiainen, H., Bailey, J. J., Field, R., Kangas, K., & Hjort, J. (2017). Combining geodiversity with climate and topography to account for threatened species richness. *Conservation Biology*, *31*, 364–375. https://doi.org/10.1111/cobi.12799

Wan, Z., Hook, S., & Hulley,G. (2015). MOD11A2 MODIS/Terra Land Surface Temperature/Emissivity 8-Day L3 Global 1km SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD11A2.006

Wang, X., Swenson, N. G., Wiegand, T., Wolf, A., Howe, R., Lin, F., … Hao, Z. (2013). Phylogenetic and functional diversity area relationships in two temperate forests. *Ecography*, *36*, 883–893. https://doi.org/10.1111/j.1600-0587.2012.00011.x

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, *11*, 3571–3594.

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, *30*, 3–35. https://doi.org/10.1080/01490410701295962

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology and Evolution*, *28*, 199–204. https://doi.org/10.1016/j.tree.2012.10.015

Zarnetske, P. L., Read, Q. D., Record, S., Gaddis, K. D., Pau, S., Hobi, M. L., … Wilson, A. M. (2019). Connecting biodiversity and geodiversity across scales with remote sensing. *Global Ecology and Biogeography*, *28*, 548–556. https://doi.org/10.1111/geb.12887

BIOSKETCH

The authors are members of a NASA Biodiversity working group, "bioXgeo". The goal of the working group is to connect biodiversity and geodiversity with remote sensing across scales in order to advance predictive models of biodiversity in an era of rapid global change. Collectively, they have expertise in global change ecology, biodiversity, community ecology, geodiversity, species distribution modelling, remote sensing and spatial statistics. The bioXgeo github site is available at: https://github.com/bioxgeo

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Read QD, Zarnetske PL, Record S, et al. Beyond counts and averages: Relating geodiversity to dimensions of biodiversity. *Global Ecol Biogeogr*. 2020;00:1–15. https://doi.org/10.1111/geb.13061