Harmonizing spatial scales and ecological theories to predict avian richness and functional diversity within forest ecosystems

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Abstract

Classic ecological theory has proven that temperature, precipitation, and productivity organize ecosystems at broad scales and are generalized drivers of biodiversity within different biomes. At local scales, the strength of these predictors is not reliable across different biomes. To better translate these theories to localized scales, it is essential to determine the links between drivers of biodiversity. Here we harmonize existing ecological theories to increase the predictive power for species richness and functional diversity. We test the relative importance of three-dimensional habitat structure as a link between local and broad scale patterns of avian richness and functional diversity. Our results indicate that habitat structure is stronger than precipitation, temperature, and elevation gradients for predicting avian species richness and functional diversity across different forest ecosystems in North America. We conclude that forest structure, driven by climatic drivers, is essential for predicting the response of biodiversity with future shifts in climatic regimes.

Introduction

Whittaker's use of precipitation and temperature to predict the world's biomes (Whittaker, 1975) is fundamental to our understanding of how climate organizes ecosystems. Precipitation and temperature have also been used to predict habitat productivity, hypothesized to be a significant driver of terrestrial biotic diversity at large scales (Currie, 1991; Hawkins et al., 2003). These theories inform our understanding of global patterns in diversity and help define the fundamental niche of species based on abiotic factors but do not explain the processes at local scales where species interact, i.e. the biotic factors that define a species' realized niche and drive community assembly (Hutchinson, 1957; Griesemer, 1994).

At broad scales, climate, habitat productivity, and habitat heterogeneity are important predictors of spatial patterns in biodiversity (Currie, 1991; Hawkins et al., 2003; Stein et al., 2014). The habitat productivity and habitat heterogeneity hypotheses are potentially the best predictors of species diversity (Tews et al., 2004; Storch, Bohdalková, and Okie, 2018). Of these two, the habitat productivity hypothesis posits that energy in the form of resources such as vegetation productivity is known to limit the number of species able to co-occur in one space (Currie, 1991). The strength and importance of productivity-diversity relationships outperform other measures like habitat heterogeneity when investigating diversity trends at broad scales (Storch et al., 2006). However, when scaled down, the strength of productivity-diversity relationships is weaker and less consistent across different habitat types (Mittelbach et al., 2001), and the relative importance of factors explaining diversity is not well known (Field et al., 2009; Zellweger et al., 2016) nor consistent across biomes and ecoregions (He and Zhang, 2009). Thus, essential links between local and broad scale processes are needed for a better understanding of the associations between climate, habitat productivity, heterogeneity, and biodiversity.

Alternatively, at local scales the habitat heterogeneity hypothesis posits that habitat structure, the three-

dimensional arrangement of vegetation across the landscape, is elemental to the composition of species within a community; predicting that increased structural heterogeneity supports a greater number of species by providing a higher density of niches with unique microhabitats compared to more homogenous habitats (MacArthur and MacArthur, 1961; Vierling et al., 2008). Higher niche density in more structurally complex habitats, such as forests, is associated with greater partitioning of resources (Goetz et al., 2010; Carrasco et al., 2018), and accounting for differences in three-dimensional vegetation structure improves estimates of animal diversity (Huang et al., 2014; Zellweger et al., 2016). Three-dimensional structural vegetation heterogeneity also creates varied microclimates that allow species to persist in otherwise inhospitable environments (Huey et al., 2012), which will be increasingly important as climate continues to change. Habitat heterogeneity does predict avian richness at a local scale based on three-dimensional structure (Cooper et al., 2020a) and can scale up to a national level using satellite-based metrics (Huang et al., 2014; Farwell et al., 2020). However, little is known about the degree of similarity in habitat heterogeneity within or between biomes.

While species richness and species diversity are important indicators of the number of species and individuals in a community, functional diversity also informs us of the functional breadth, similarities, and distinctiveness of species in a community (Violle et al., 2012; Cadotte et al., 2011; Gagic et al., 2015). Thus, in addition to improving our knowledge of the relationships among habitat productivity, structure, and species richness, functional diversity can provide important linkages to the broader ecosystem. The decline and loss of species which are functionally connected to their ecosystems through seed dispersal, herbivory, predation, and pollination could lead to the decline of ecosystem resilience. Thus, understanding the functional diversity of species assemblages is important for understanding the stability and resilience of ecosystems.

Here we attempt to harmonize classic ecological theories over a broad range of ecosystems and scales to create a framework that can predict the extent to which climatic and vegetation structural characteristics drive variation in species and functional diversity. Our study focuses on forest ecosystems, the most biodiverse of terrestrial ecosystems, at National Ecological Observation Network (NEON) sites across North America. We use data from high resolution airborne sensors (light detection and ranging (lidar), and hyperspectral cameras), flux towers, and avian point count surveys to examine avian richness and functional diversity of North American forest ecosystems. The replicated nature of NEON samples and sites allows us to investigate ecological relationships within sites at local scales, between sites at regional scales, and between all sites at a national scale. We hypothesize that the combination of habitat heterogeneity and productivity within forests paired with precipitation and temperature (i.e. Whittaker's prediction of biomes) will more accurately predict avian richness and functional diversity across multiple spatial scales and forest ecosystems compared to temperature and precipitation alone, which will ultimately advance our understanding of links between broad and local scale drivers of species and functional diversity. We aim to answer the following questions:

Question 1: How are precipitation, temperature and three-dimensional forest structure related? Question 2: Does each forest ecosystem have a unique three-dimensional structural signature? Question 3: What is the relative strength of temperature, precipitation and forest structure in predicting differences in avian richness and functional diversity?

Methods

Study area

NEON operates at 47 terrestrial field sites located across 20 climatically and ecologically variable domains in the United States, and each domain has a core site and two satellite sites (Barnett et al., 2019). Forests occupy 24 terrestrial NEON sites across 12 domains and represent the major forest ecosystems throughout North America, north of Mexico (Figure 1; Table S1). NEON sites capture the wide variety of climatic conditions, disturbance regimes, habitat structures, and biodiversity of North America forests. These sites cover a large gradient of mean annual temperature (-7.8 – 27.0 °C) and precipitation (0 – 2,492 mm/yr) and cover a wide range of forest biomes, including boreal forests, temperate rainforests, temperate seasonal forests, and woodland/shrublands (Figure 2). We utilized data from NEON's bird and vegetation surveys, flux towers, and Airborne Observation Platform (AOP) (Table S2) to assess 12 variables of forest structure and productivity, 3 variables of topography, and 2 climate variables (Table S3). We use data from 2018 and 2019 as these data products were collected consistently across nearly all the selected sites at least once during this period. The area around each bird survey point within an 80m radius was used to average scale-dependent habitat heterogeneity and productivity measurements. This scale was selected based on the highest performing models, measured as the maximum mean Area Under the Receiver Operating Characteristic Curve (AUC), that predicted occupancy for a community of avian species within this study area (Cooper et al., 2020b).

Climate data

Climate data in the form of annual precipitation and mean annual temperature were derived from flux tower data for each site. However, some satellite sites did not have a flux tower to reference, and for these sites we calculated the distance to the nearest weather station collecting data for National Centers for Environmental Information (NCEI) using the 'GSOD' package in R version 4.1.0 (R Core Team, 2021). If there was a weather station closer than the core NEON site for that location we used the auxiliary weather station data, otherwise we used the core location's tower data for these nearby satellite sites without tower data from NEON. We derived temperature data for each site as the mean annual temperature ($^{\circ}C$) from the nearest weather station. Precipitation data for each site was compiled as annual precipitation totals (mm/year).

Structure data

Three-dimensional mapping sensors, such as lidar, measure habitat characteristics with high precision at fine scales (Davies and Asner, 2014). Productivity metrics derived from lidar data, such as Leaf Area Density (LAD, Bouvier et al., 2015) and heterogeneity metrics, such as LAD variability across a three-dimensional area, have more explanatory power for avian species richness than two-dimensional metrics such as canopy surface metrics (Carrasco et al., 2019). We standardized lidar height measures from NEON's classified discrete return point cloud before calculating standardized metrics for each sample location using the "lidR" package in R (Roussel et al., 2020; Roussel and Auty, 2021). Following the methods used by Carrasco et al. (2019), we selected habitat metrics that are representative and comprehensive in describing productivity and heterogeneity and are known to influence avian richness: Mean LAD in both horizontal and vertical planes; the Shannon index for LAD; the mean, maximum, and coefficient of variation of vegetation height; the vertical distribution ratio (VDR); the mean coefficient of variation (CV) of LAD in both horizontal and vertical dimensions; and the deep gap fraction across each area (see Table S3 for definitions). In addition to vertical habitat measurements, mean slope, aspect, and elevation metrics were calculated for each survey location from the lidar data using the same R package.

Raster products from NEON's hyperspectral imagery include enhanced vegetation index (EVI) which we used to determine the mean EVI for each location using the 'raster' package in R (Hijmans, 2021). The mean EVI represented a surrogate measure of vegetation productivity and health across a two-dimensional space, with high values indicating healthy vegetation (Huete et al., 2002).

$Bird\ data$

At each of the 24 preselected terrestrial forest NEON sites, we eliminated non-forest points and identified forest ecosystem type using the continental U.S. and Alaska Forest data (Ruefenacht et al., 2008). Based on these criteria, we compiled avian point count data for 253 survey points. The NEON point count method is adapted from Hanni et al. (2017). Depending on the size of the site, sampling occurs at randomly distributed individual points or 9-point grids. At larger sites, point count sampling occurs at five to fifteen 9-point grids. At smaller sites, point counts occur at the southwest corner of 5-25 distributed vegetation plots. Point counts are conducted once per breeding season at large sites and twice per breeding season at smaller sites. For larger sites, only the center points were used in our analyses to limit spatial autocorrelation and better match surveys from smaller sites. Prior to analysis we removed all non-forest/shrub bird species. Of the 343 species of birds detected across all sites, 231 species are dependent on forest habitats (IUCN, 2019).

Functional Diversity

To capture the functional diversity of the focus species at each point, site, and domain, we used the AVONET database (Tobias, 2021) which provides morphological, geographic, and ecological information about all bird species. Functional diversity measures from AVONET included bill length (cm), tail length (cm), wing length (cm), tarsus length (cm), mass (g), Hand Wing Index (HWI) (which is a measure of wing shape), diet percentage, range size, and foraging stratum. We identified two functional diversity metrics for this study: functional richness and redundancy. We also tabulated species' abundance and richness at each NEON survey point. Species richness and functional diversity metrics were calculated with the dbFD function in the R package 'FD' (Villeger et al., 2008; Laliberte and Legendre, 2010; Laliberte, Legendre, and Shipley, 2014). Functional richness represents the volume of trait space occupied by species. To estimate the amount of functional redundancy at each survey location, we calculated community-level functional redundancy using the 'adiv' package in R (Pavoine, 2020; Pavoine, 2021). Redundancy ranged between 0 and 1, with high values indicating high levels of overlap in species traits (Pavoine and Ricotta, 2019). Functional richness gives us the functional breadth of the avian community, while functional redundancy informs us about the overlap and similarity of species within a community at each point location.

Analysis

To assess the relationships between precipitation, temperature, and forest structure, we calculated Spearman rank correlation coefficients in R (R Core Team, 2021) for each pair of variables. We considered pairwise comparisons above a 0.6 to have a strong correlation. All pairwise comparisons with a p-value < 0.05 were considered significantly correlated.

To assess whether each forest ecosystem between the 12 forest domains has a distinct three-dimensional structure we tested the variations in structure, topography, and climate across forest ecosystems using a non-parametric Kruskal-Wallis one-way ANOVA test. We also used Kruskal-Wallis tests to assess whether the species richness and functional diversity in each forest ecosystem was distinct with a pairwise Dunn test to identify significant differences between forest ecosystems. Analyses were carried out using the function *ggbetweenstats* from the 'ggstatsplot' package in R, with violin plots to illustrate differences (Patil, 2021).

To assess the relative strength of temperature, precipitation, and forest structure in explaining the differences in species richness and functional diversity, we modeled the relationship of each functional diversity metric as a function of structure, climate, and topography. To model these relationships, we applied boosted generalized additive models (GAMs) to all data using the function *gamboost* in the package 'mboost' in R (Hothorn et al., 2021). These models are particularly suited for disentangling the effects of collinearity among variables and modelling non-linear relationships common to ecological systems (Hothorn et al., 2010), which is especially important for this study as structural metrics of forests can be highly correlated, in that structurally complex forests are also more productive (Fortis et al., 2018; Hardiman et al., 2011). Component-wise boosting optimized parameter estimates and prediction accuracy, including variable selection. Overfitting was mitigated with 25-fold bootstrap estimates of the empirical risk to determine the appropriate number of boosting iterations for each model using the function *cvrisk*. Finally, the selection frequencies of the 25 bootstraps were averaged to compare the effect size and importance of each structure, topographic, and climactic variable as a predictor for each functional diversity metric using NEON's domain classification as a random intercept.

Three-dimensional surfaces were generated to visualize how the relationships between temperature, precipitation, and structure predict species richness and functional diversity across North American forests. A smoothed surface was created with a GAM framework to model forest structure metrics across temperature and precipitation gradients. Both Shannon's Diversity of LAD and maximum canopy height resulted in two of the highest selection frequencies for our models of avian richness and functional diversity. However, maximum canopy height was selected in every model of avian richness and functional diversity. Thus, maximum canopy height was our third structural axis in the 3D modeled surface with precipitation and temperature. The predictive surface includes boreal and temperate forests, temperate rainforests, and woodlands. Using this modeled surface and fitted models, we predicted functional diversity and species richness across temperate forest biomes as defined by Whittaker (1975).

Results

Covariate correlations

Relationships between forest structure and climate variables were weakly correlated, with the absolute values of all Spearman rank correlation coefficients below 0.6 (Figure 3). Correlation coefficients revealed that the relationship between precipitation and temperature were weakly positive and significant ($R^2 = 0.25$, p-value = <0.001), but neither were strongly correlated with three-dimensional forest structure or productivity. For example, maximum canopy height was not correlated with precipitation ($R^2 = -0.01$, p-value = 0.88), but it was weakly correlated with temperature ($R^2 = 0.39$, p-value = <0.001). Most forest structure variables were weakly correlated with each other (Figure 3; Table S4). For example, maximum canopy height had positive correlations with the coefficient of variation in LAD vertically ($R^2 = 0.36$, p-value = <0.001) and horizontally ($R^2 = 0.17$, p-value = <0.001) and with Shannon's Diversity of LAD ($R^2 = 0.54$, p-value <0.001).

Forest Structure

There were strong differences in three-dimensional structure between many of the North American forest ecosystems (Also see Carrasco et al., 2019). Maximum canopy height was one of the strongest structural predictors of species richness and functional diversity in our models, and it was correlated with most other structure metrics; therefore, we generalize maximum canopy height to represent structural differences between forest ecosystems (see Table S4 for other comparisons). The maximum canopy height was significantly different across forest ecosystems ($X^2_{\text{Kruskal-Wallis}}(14) = 213.07$, p-value < 0.001) (Figure 4). The lowest canopy heights were recorded in spruce/fir forests with a mean height of 11.6m (SD = 5.8m), which was significantly shorter than 8 of the 14 forest ecosystems (p<0.05). The tallest canopy heights were recorded in the California mixed conifer forests with an average maximum height of 46.9m (SD = 8.8m), which was significantly taller than any other forest ecosystem (p<0.05) (Figure 4).

Bird and Forest Community Metrics

Across the 244 survey locations, 193 forest bird species were identified. Species richness ($X^{2}_{\text{Kruskal-Wallis}}(14) = 219.64$, p-value < 0.001) along with functional richness ($X^{2}_{\text{Kruskal-Wallis}}(14) = 206.39$, p-value < 0.001) varied significantly among forest ecosystems (Figure 3). The spruce/fir forests had the lowest mean number of species at a point, 4.4 (SD = 1.6), and average functional richness, 0.08 (SD = 0.08), while the California mixed conifer forests had the highest mean number of species observed, 16.1 (SD = 3.8), and average functional richness, 0.50 (SD = 0.09). Functional redundancy also varied significantly ($X^{2}_{\text{Kruskal-Wallis}}(14) = 123.87$, p-value < 0.001) across forest ecosystems. Spruce/fir forests had the lowest functional redundancy, 0.51 (SD = 0.20), while white/red/jack pine forests had the highest average functional redundancy, 0.83 (SD = 0.06).

Determinants of bird community structure

Structure, topography, and precipitation were consistently important covariates for species richness, functional richness, and redundancy models and outperformed climate only models (Table S5). The average selection frequencies were higher with structural variables for all three of our diversity measures (Figure 5). The strongest selection frequencies varied for each functional diversity and species richness model. However, the selection of maximum canopy height (9.1%, 8.1%, and 5.9% for species richness, functional richness, and functional redundancy respectively) and Shannon diversity of LAD (4.5%, 11.5%, and 12.7% for species richness, functional richness, and functional redundancy respectively) were consistently selected among the strongest structure metrics in these models. In the case of functional richness, the strongest single metric was elevation (18.2%) followed by the coefficient of variation in LAD (13.5%). The strongest metrics for species richness were elevation (14.8%) as well as precipitation (14.8%) followed by mean LAD (11.1%). The strongest metric for functional redundancy was mean LAD (18.1%) followed by precipitation (16.0%) and Shannon diversity of LAD (12.7%). On the other hand, the least selected metrics included mean aspect and slope. In the case of functional richness and species richness, temperature was much weaker (3.4% and 4.5% respectively).

Smoothed surface models of forest structure metrics across temperature and precipitation gradients revealed that maximum canopy height was projected to be the shortest in areas with relatively low precipitation and mean temperatures (Figure 6:A). The tallest canopies were projected across two major areas, one with a mean annual temperature of about 10° C and approximately 80 cm of precipitation per year and the other with mean temperature of roughly 0° C and annual precipitation amounts greater than 125cm per year. Using the surface models to predict species richness, functional richness, and redundancy across forest ecosystems resulted in different patterns for each diversity metric. Diversity metrics showed clear maxima and minima that were not constrained by biomes but instead were on a continuum or gradient across different forest biomes. Since each diversity metric responded differently to temperature, precipitation, and maximum canopy height, each resulting pattern was unique (Figure 6: B-D).

Discussion

Our results indicate that the three-dimensional structure of forests is an independent axis, along with precipitation and temperature, which help shape patterns of species richness and functional diversity for avian communities across spatial scales. In addition, forest structure varies significantly across forest ecosystems of North America, and this structural variation in forest structure is just as important, if not more important, in comparison to temperature and precipitation for organizing bird communities. The inclusion of habitat structure with temperature and precipitation also allows for the harmonization of leading ecological theories (habitat productivity, habitat heterogeneity) that aim to predict the species richness and functional diversity of communities of organisms.

Question 1: How are precipitation, temperature and three-dimensional forest structure related?

Neither precipitation nor temperature are correlated with forest structure as strongly as expected, and many structure metrics are largely independent of these variables. The correlation between lidar derived structure covariates and climate variables is consistent with other studies (Carrasco et al., 2019; LaRue at al., 2020); however, Ehbrecht et al. (2021) used different methods to measure structural complexity and found higher correlations between structure and mean annual precipitation but no significant correlation with mean annual temperature. For our study, precipitation and temperature were both weakly to moderately correlated with structure metrics. For example, precipitation had a larger influence on vegetation density, measured by mean LAD, than temperature in most forest ecosystems. In forests with more annual precipitation, forests tend to have denser canopies, while the forest canopy appears to be patchier in more arid regions. However, temperature is more correlated with metrics describing the spatial organization of LAD. The heterogeneity in LAD, measured as Shannon's Diversity of LAD, tends to increase with temperature. All of which suggests that warmer forests tend to be more heterogeneous and colder forests more homogeneous and denser. However, structural complexity and vegetation density were not always opposed to each other in extreme temperatures. For example, forest structure and density increase together at sites with lower mean temperatures and high precipitation, such as boreal forests, where our models predict taller, yet denser forests. Denser closed canopy forests can have a buffering effect in extreme cold, creating warmer microclimates underneath the canopy (Li et al., 2015; De Frenne et al., 2019), which can affect niche space by increasing the amount of suitable habitat in response to temperature regimes (Frey et al., 2016). This would help explain the increase in richness and functional diversity within boreal forests that our models predict, supporting the strength of forests serving as microrefugia for biodiversity under future climate change (De Lombaerde et al., 2022).

Question 2: Does each forest ecosystem have a unique three-dimensional structural signature?

Forest structure is influenced by many factors including the arrangement of individual trees, differences in species morphology, the availability of light, moisture, and soil nutrients, disturbance regimes, and forest management practices (Franklin et al., 2002; Onaindia et al., 2004; Vanwalleghem and Meentemeyer, 2009; Von Arx et al., 2013). These factors interact uniquely with climate variables at local scales to organize forests within different biomes and regions in North America (Hakkenberg and Goetz, 2021). We find that many of

the forest ecosystems across North America vary significantly in structure, but it is difficult to say that they are all unique based on any one metric. Based on canopy height, any given forest ecosystem was significantly different from 4 of the other 12 forest ecosystems on average, indicating a gradient of differences. Previous studies have shown similar structural differences in North American forests using different methods, such as grouping forests using the Environmental Protection Agency's level 1 and 3 ecoregion boundaries (Rishmawi et al., 2021). However, these ecoregions are delineated using geology, landforms, soils, vegetation, climate, land use, and many other factors known to influence natural vegetation. Thus, any differences in structure between ecoregions could be influenced by the abiotic factors that were used to delineate forest ecosystems, any significant differences in structure are more likely attributed to the forest arrangement itself, illustrating that many forest ecosystems are structurally different depending on how structure is measured.

Question 3: What is the relative strength of temperature, precipitation and forest structure in predicting differences in avian richness and functional diversity?

Harmonizing Whittaker's theory of ecosystem organization alongside the habitat productivity and heterogeneity hypotheses led to increased predictive power of species richness and functional diversity (comprised of functional richness and functional redundancy) both within and between forest biomes, thus connecting local and broad spatial scales. Temperature and precipitation are relatively robust predictors of average species richness and functional diversity gradients across all NEON sites but fail to describe the large variation of species richness and functional diversity within any given site or region. Forest structure metrics improved the ability for our models to predict variation in diversity, especially at local scales, which is consistent with studies that show vegetation structure to be secondary to vegetation productivity and climate variables when describing large scale diversity gradients (Roll et al., 2015). However, at extreme temperatures and amounts of precipitation, where energy becomes a limiting factor, the effect sizes of climatic variables were much larger than that of productivity and heterogeneity, which is consistent with patterns of species richness reported in other parts of the world (Coops et al., 2018).

The effect of climatic energy, in the form of temperature and precipitation, and habitat structure on bird diversity result in non-linear patterns (Carrasco et al., 2018; Bae et al., 2018). For example, increases in canopy heterogeneity, as indicated by coefficient of variation in LAD horizontally, increase both species and functional richness, and decrease functional redundancy, but only up to a point, before creating a bell-shaped curve (Figure S1). Beyond that point, canopy heterogeneity have a negative impact on species richness and functional richness but increase functional redundancy potentially in part to patchy habitats with elements such as edge effects or canopy gaps which create high structural heterogeneity that may not be conducive to many forest-dependent species. For example, increased edge density is known to decrease forest dependent avian richness and functional richness in Andean forests compared to larger continuous forests (Jones et al., 2021). Similarly, functional redundancy and species richness increase with increasing temperature up to roughly 3 °C and 12 °C respectively, after which they both decline with increasing temperature. On the other hand, species richness declines with increasing precipitation up to roughly 1200 mm/year. However, functional redundancy decreases with low levels of precipitation and increased with high amounts of precipitation. This is not the same as the biodiversity patterns of other organisms such as plants, where plant and tree diversity tend to be positive with increasing temperatures and precipitation totals (Chu et al., 2019). Thus, climate and structure simultaneously affect species richness and functional diversity relationships, independently driving broadscale patterns in the diversity of different taxonomic groups (Field et al., 2009) and forest structure conditions (Fahey et al., 2019), while interacting uniquely at local scales to form microclimates (Von Arx et al., 2013; Davis et al., 2019).

Studies of bird functional diversity provide a window into the causes and consequences of forest ecosystem resilience or degradation. While 85% of the current forests in the Americas are potentially threatened, with 40% of threatened forest ecosystems at risk of ecological collapse (Ferrer-Paris et al., 2019), understanding the drivers of functional diversity can provide insight into how we can maintain or potentially restore ecosystem integrity to these forests. Based on our models, avian functional diversity and species richness is highest

in forests with relatively warm temperatures with moderate amounts of rainfall as well as sites with high levels of habitat heterogeneity and structural complexity. Although we do not include tropical forests, we hypothesize that extreme temperatures would diminish species richness and functional diversity without a relatively large amount of heterogeneity in canopy structure or productivity. This would add support to the hypothesis that forest complexity is essential for stabilizing temperatures under the canopy (Davies-Colley et al., 2000; Vanwalleghem and Meentemeyer, 2009), which is an indicator of long-term temperature variability within a region and supports both avian richness and phylogenetic diversity (Voskamp et al., 2017). Therefore, a healthy and structurally complex forest is necessary to support avian species richness and functional diversity which in turn promote healthy forest ecosystems.

Here we present a new method for predicting species and functional diversity by harmonizing existing ecological theories to assess and predict diversity at local and macrosystem scales. We also conclude that climatic controls, such as a forest's ability to buffer and stabilize extreme temperatures (De Frenne et al., 2019), plays a substantial role in how forest structure relates to avian richness and functional diversity. A critical next step will be to expand the scope of these data to tropical forests and eventually to other types of ecosystems to assess the universality of this paradigm in driving and predicting species and functional diversity. The better we understand the foundation of these relationships and how they might vary across biomes, the clearer the picture will be for how local and regional factors combine to influence the biogeography of species diversity. We hope that this study will be a step towards building more accurate maps of biodiversity, microrefugia, and forest integrity across the continent, and eventually the globe, using remote sensing data. In addition, understanding how biodiversity is changing has urgent implications for conservation, land management decisions, and public policy at local, national, and international scales. The importance of forest structure, precipitation, and temperature in our models can be used to predict the response of species and functional diversity to shifting climatic regimes, which could be accounted for in future models of biodiversity responses to climate change.

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Figures:



Figure 1: Locations of the forested NEON sites. Colors indicate forested areas and specific forest ecosystems

as provided by the USDA Forest Service. Yellow points indicate core NEON terrestrial sites, and blue points indicate NEON's relocatable terrestrial sites.



Figure 2: Mean annual precipitation (mm) plotted against mean annual temperature (^oC) for each of the 24 forested NEON sites. These points were then overlaid on a Whittaker Diagram that highlights each biome (Whittaker, 1975).



Figure 3: Pairwise correlation coefficients for all climate, structure, productivity, and topography metrics. Pie areas are representative of \mathbb{R}^2 value as a percentage of the circle. Blue indicates positive correlation and red indicates negative correlations. Asterisks indicate significant correlations (p < 0.05). The absolute values of all Spearman rank correlation coefficients were below 0.6, suggesting that these metrics correspond to unique elements across different forest ecosystems.



Figure 4: To visualize and test for differences in species richness, functional diversity, and structure between North America's forest ecosystems, we generated violin plots of A) species richness, B) functional richness C) functional redundancy, and D) maximum canopy height. Each point represents one survey location at a NEON site. Horizontal lines between forest ecosystems indicate significant differences according to a pairwise Dunn's Test (p<0.05).



Figure 5: Average selection frequencies (%) of productivity, structure, precipitation, and temperature as fixed factors in boosted generalized additive models for species richness, functional richness, and functional redundancy. The selection frequencies were averaged from 25 bootstrap models.



Figure 6: To visualize a third axis on Whittaker's theory of ecosystem organization we generated a predictive three-dimensional surface model based on temperature, precipitation, and maximum canopy height using data from forested NEON sites across North America (A). The data from the three-dimensional surface was used to predict B) species richness, C) functional redundancy, and D) functional richness for each of Whittaker's overlapping forest biomes along precipitation and temperature gradients. For the model predictions we held all other covariates at their mean, allowing only temperature, precipitation, and maximum canopy height to vary.

Supporting Information

Additional supporting information may be found online in the Supporting Information Section at the end of the article.