Structural diversity as a reliable and novel predictor for ecosystem productivity

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The physical structure of vegetation is thought to be closely related to ecosystem function, but little is known of its pertinence across geographic regions. Here, we used data from over three million trees in continental North America to evaluate structural diversity – the volumetric capacity and physical arrangement of biotic components in ecosystems – as a predictor of productivity. We show that structural diversity is a robust predictor of forest productivity and consistently outperforms the traditional measure – species diversity – across climate conditions in North America. Moreover, structural diversity appears to be a better surrogate of niche occupancy because it captures variation in size that can be used to measure realized niche space. Structural diversity offers an easily measured metric to direct restoration and management decision making to maximize ecosystem productivity and carbon sequestration.

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Globally, ecosystems are increasingly threatened by ever-mounting pressure from environmental stressors. One major effort to mitigate these stressors is to understand how changes in the diversity of life forms impact ecosystem function (Loreau *et al*. 2001; Hooper 2002). The most common measure of diversity – species diversity – has been hypothesized to play an essential role in long-term sustainability, with a fundamental assumption that greater species diversity results in higher niche occupancy, resource use, and ecosystem function (Loreau *et al*. 2001; Hooper *et al*. 2005). Unfortunately, species diversity generally has limited usefulness for predictions of ecosystem productivity, with varying strength and directionality across environmental conditions (Winfree *et al*. 2015; Ratcliffe *et al*. 2017; Fei *et al*. 2018).

In a nutshell:

- The concept of structural diversity, a surrogate of niche occupancy, was developed from common forestry data
- Structural diversity varies across North America and serves as a better predictor of forest productivity than species diversity
- Along with the traditionally used species diversity, structural diversity can help practitioners to enhance ecosystem services, climate-change mitigation, and conservation across geographic regions
- Due to the consistent relationship between it and productivity, structural diversity has great potential to be applied in other ecosystems worldwide

Structural diversity – the volumetric capacity (total, occupied, and unoccupied) and physical arrangement of biotic components within ecosystems (LaRue *et al*. 2023) – has the potential to serve as an additional and possibly even superior predictor of productivity. Despite having roots in early ecology (MacArthur and MacArthur 1961), the idea that diverse vegetation structure plays a crucial role in ecosystem function has been given surprisingly little consideration since its origin (LaRue *et al*. 2023). In general, plants of varying sizes and structure are located across different horizontal and vertical spaces within an ecosystem, leading to the unique occupancy of niche axes such as light (Vieilledent *et al*. 2010; Forrester *et al*. 2017). The occupancy of more niche space, in turn, can be closely linked to essential ecosystem functions, such as an elevated capacity for ecosystem vegetation to convert more resources into growth (Tilman *et al*. 1997).

Unlike species diversity, which measures the potential niche space that organisms might occupy (Elton 1927), structural diversity offers a more direct measure of realized niche occupancy. Structural diversity captures variation in vegetation size and structure (Figure 1), and plants of different sizes – even those of the same species – can be functionally distinct in obtaining and utilizing resources. Therefore, structural diversity can provide estimations of not only the

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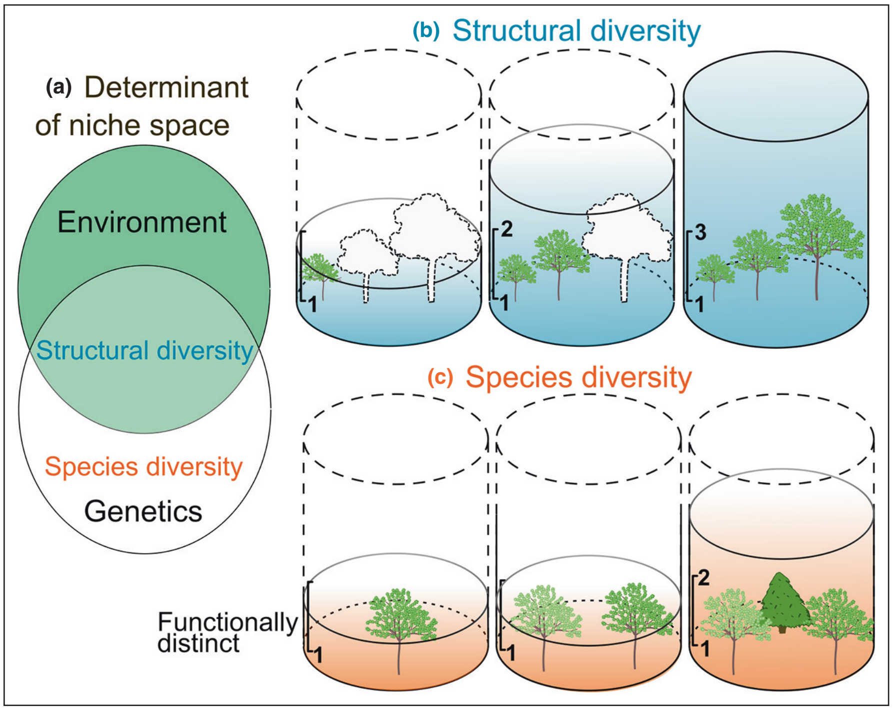

Figure 1. (a) Structural diversity captures variation in vegetation size that is representative of the genetic and the environmental determinants of realized niche space, whereas species diversity is genetically determined and representative of the theoretical niche. (b) Structural diversity considers which structural spaces are filled (solid icons) by trees of different sizes within ecosystem niche space (cylinder shading). The number of spaces filled by vegetation translates into canopy packing and higher resource use. (c) When the number of species increases (different colored tree icons), not all species are functionally distinct (unique shaped icons), and therefore niche occupancy does not always increase.

actual volumetric occupancy and arrangement of the niche space but also the total volumetric capacity of the niche space. Existing diversity measures, such as species diversity, cannot be used to directly measure niches filled by the presence of additional species or different-sized individuals of the same species. Furthermore, structural diversity is influenced by both genetics and environmental conditions, such that structural diversity can be high due to environmental conditions even when the genetic diversity of a community's component species is low.

For the above reasons, we hypothesized that structural diversity could serve as a more reliable predictor of ecosystem productivity than traditional diversity measures (Figure 1). To test this, we quantified structural diversity using metrics of forest stands that were measured from the most basic forest inventory data (eg national forest inventories [NFIs]) (MacArthur and MacArthur 1961; Tyrrell and Crow 1994; Sullivan *et al.* 2001). We first identified ecological factors associated with variability of structural diversity across North America, and then investigated structural diversity's relative ability versus species diversity to predict forest productivity across North America's climate gradients. Diversity–productivity relationships that are generalizable across biomes will provide practical management solutions to enhance forest productivity and carbon sequestration.

Methods

Forest inventory data

We obtained data for individual trees from NFI plots across North America, from the following sources: 102,072 plots from the most recent US Department of Agriculture Forest Service Forest Inventory Analysis (FIA) program sample (2004–2019, downloaded August 2021) (Smith 2002), 15,746 plots from Mexico's Comisión Nacional Forestal (CONAFOR) (2009–2014) (CONAFOR 2008), and 686 plots from the Natural Resources Canada (NRCAN) National Forest Inventory (1992–2007) (Gillis *et al.* 2005). FIA and CONAFOR plots are composed of four subplots, with FIA having a total area of 0.067 ha and CONAFOR of 0.16 ha; NRCAN has a single 0.04 ha plot design. Individual-level tree data of height, diameter, and species identity were obtained from trees with a diameter at breast height (DBH) greater than 12.7 cm, because this was the smallest DBH sampled across all NFIs. As NFI geographic coordinates are typically considered classified information, plot coordinates were assumed to be offset by up to several kilometers.

Structural diversity

We estimated the structural diversity of forest stands from metrics that measure horizontal, vertical, and three-dimensional (3D) structural richness using tree diameter and height size classes from forest inventory data. Structural richness provides a proxy of the number of structural niche spaces filled by trees of different sizes, because trees of different sizes will be able to capture resources at different horizontal and vertical locations within the canopy (that is, filling a unique niche space). Horizontal richness was measured as the number of different diameter size classes (Tyrrell and Crow 1994). We clarify that we refer to the number of diameter size classes as a measure of horizontal richness. We used 13 size intervals from DBH of each tree within plots, with a median DBH for each class of 15 cm, 20 cm, 25 cm, 30 cm, 35 cm, 40 cm, 45 cm, 50 cm, 60 cm, 70 cm, 80 cm, 90 cm, and 100 cm. Vertical richness was measured as the number of different tree height size classes (MacArthur and MacArthur 1961; Sullivan *et al.* 2001). We used 15 height classes to sort each tree into median height classes of 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 35 m, 40 m, 45 m, 50 m, 60 m, 70 m, 80 m, 90 m, and 100 m. We chose 10 cm and 10 m as intervals for classes greater than 50 cm DBH and 50 m height, respectively, because there would be fewer large trees than small trees and therefore doing so helped to even out the number of trees that fell into each size class. To provide a composite metric of 3D richness, we normalized the horizontal and vertical richness for each plot and then added them together.

The number of species and structural size classes is sensitive to the size of the area sampled (species–area relationship; MacArthur 1965). Therefore, given the unequal sampling areas of the three NFIs, we used Hill numbers (rarefaction and extrapolation; Hill 1973) to standardize sampling efforts via individual abundance (Chao and Jost 2012; Chao *et al*. 2014). Hill numbers provide a standardized estimate of the effective number of species or structural size classes from plots that do not have equal sampling areas. Hill numbers for structural size classes (q = 0) were estimated using the *estimateD* function in the R package *iNEXT* (Hsieh *et al*. 2016). Hill numbers for structural richness in our study can be interpreted as the number of structural size classes that would be expected from a sample of ten individuals. Extrapolations greater than twice the smallest sample can be biased (Hsieh *et al*. 2016), and therefore we used ten individuals as the reference sample size and discarded plots with fewer than five trees.

We initially measured six metrics of structural diversity, including three each of structural richness and structural evenness, but we discarded the evenness metrics from our analyses because their high correlations with richness meant that they did not add useful information (WebPanel 1; WebTable 1). The remaining structural diversity metrics revealed variations in their spatial patterns (Figure 2) and sometimes in the direction and strength of their correlation with ecological variables (WebTable 2). All analyses were conducted in R (v3.6.3; The R Group 2020).

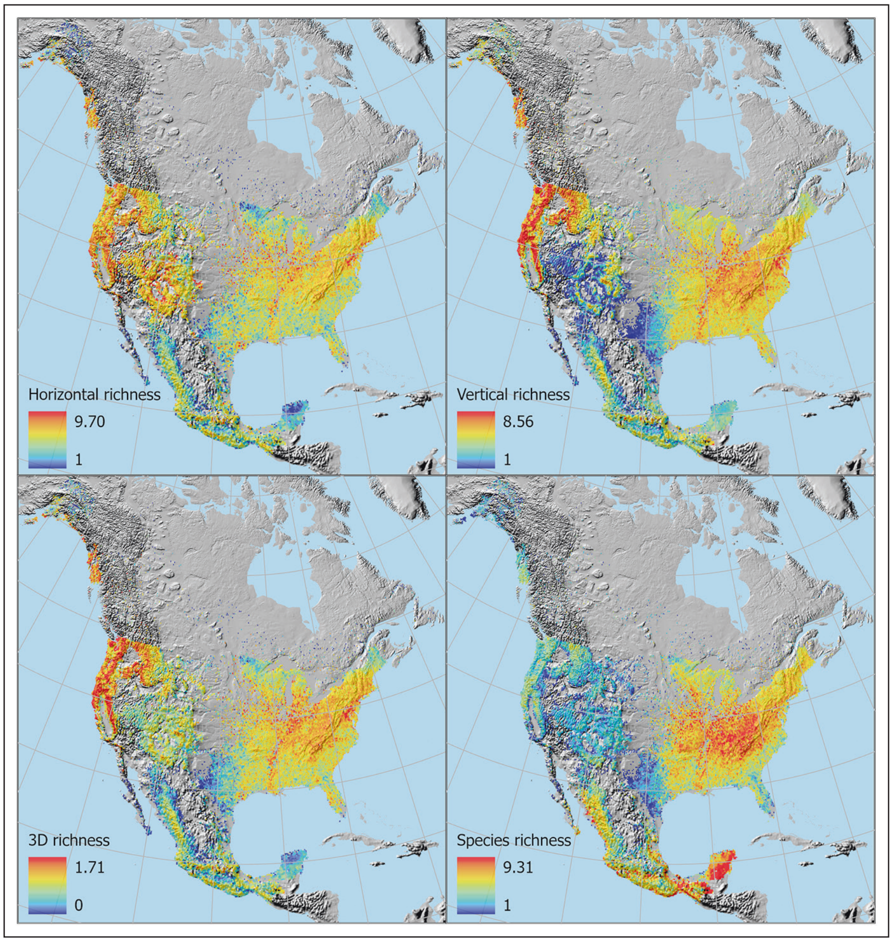

Figure 2. Spatial variation across North America for structural diversity as horizontal richness, vertical richness, and three-dimensional (3D) richness, and for species diversity as species richness. Plot values (N_{plots} = 118,504) were averaged within a 20-km × 20-km raster grid for visualization purposes. Horizontal, vertical, and species richness can be interpreted as the effective number of structural classes or species estimated from Hill numbers for a sample of ten individuals; 3D richness is a normalized richness value. The color scale indicates blue (low) to yellow (moderate) to red (high) values of richness.

Forest productivity

Given that forest productivity is directly related to aboveground biomass (Fei *et al*. 2018), we used mean annual increments (MAI) and periodic annual increments (PAI) of tree biomass and basal area increments (BAI) per plot to estimate forest productivity. MAI of biomass was calculated by dividing total aboveground biomass by stand age, whereas PAI of biomass was calculated by taking the difference between two time points (ranging from 3 to 15 years to maximize the number of sampling units included, N_{plots}) divided by the re-measurement period; both MAI and PAI were standardized to kilograms per hectare. These two variables were only available for plots in the US and do not include belowground biomass and trees <12.7 cm DBH. Plots used to measure PAI that did not have the same number of subplots sampled between the two time periods or that experienced high mortality or harvesting ($\text{PAI} < 0$) were excluded. FIA also did not contain re-measurements for plots in Wyoming and western Oklahoma. Our study accounts for the correlation between tree height and DBH variables used in the structural diversity metrics and the proxies of productivity by considering the variability in DBH and tree height instead of actual values. We also used BAI (basal area) as a proxy of productivity across North America, standardized as BAI expressed in square meters per hectare (m^2/ha). BAI from NRCAN and FIA data were calculated as the total basal area (m^2/ha) divided by stand age (standardized to hectare from subplot area). Because stand age was unavailable for plots in Mexico, we took the difference in the basal area between two time points divided by the re-measurement period (ranging from 2 to 10 years). Plots from Mexico with unequal sampling or a BAI < 0 were excluded. Finally, where age information was available, we removed plots <10 years old to filter out young forests that may not yet have reached the point of canopy closure.

Ecological correlates

We obtained variables that represent major ecological and compositional factors likely related to forest structural diversity: species diversity, stand density, stand age, elevation, and climate. For each forest inventory plot, we calculated species richness as the number of unique tree species that had a DBH > 12.7 cm and corrected for uneven sampling with Hill numbers as described for structural diversity. We measured stand density as the number of tree stems within the sampling area standardized to 1 ha. We obtained the stand age of forests and plot elevation from the NFI records, but stand age was only available for plots in Canada and the US. Climate variables were obtained by extracting mean annual temperature (MAT) and total annual precipitation (TAP) at 30-second resolution (1970–2000, WorldClim 1.4 [www.worldclim.org]) (Hijmans *et al.* 2005). Finally, we identified the North American ecoregions (level 1) within which each plot was located (CEC 1997).

Statistical analysis

To test for ecological correlates of structural diversity metrics, we relied on a mixed-effects modeling approach. We used the effect size of coefficients to assess the relative strength of the relationship between ecological correlates and structural diversity metrics, because statistical significance may not reflect ecological significance with the large sample sizes used here (Wasserstein *et al.* 2019). The predictor and response variables were *z*-score standardized to assess the effect size. The R package *lme4* was used to estimate the linear and quadratic coefficients between the three structural diversity metrics and each of the ecological variables (Bates *et al.* 2015). Ecological predictors were treated as fixed effects and level-1 ecoregion as a random intercept. The correlation of stand age with structural diversity metrics was assessed in a separate set of models because stand age was not available for Mexico. See WebPanel 1 for additional modeling details.

To assess the relationships between structural diversity and species diversity with productivity across climatic space, we defined ten quantile classes for MAT and TAP (together representing 100 units in climate space). Data for each climatic quantile unit were used to model productivity as a function of structural or species diversity metrics via a general linear model. We natural log $(1+x)$ transformed productivity variables to improve normality. Because previous research has shown that diversity can exhibit a linear or hump-shaped relationship with productivity (Fei *et al.* 2018), we ran a model with both linear and quadratic terms and a model with the linear term only; the best model was chosen using Akaike information criterion. For each of the 100 climate quantiles, we subtracted the adjusted R^2 (adj R^2) of the structural diversity metric from the species diversity adj R^2 to make a comparison of how much more of the variance in productivity was explained by structural diversity than species diversity in each climate quantile. We included one set of models for which stand age was a covariate predictor for one of the productivity variables, PAI (ie stand age was already incorporated into the other productivity variables). See WebPanel 1 for additional modeling details.

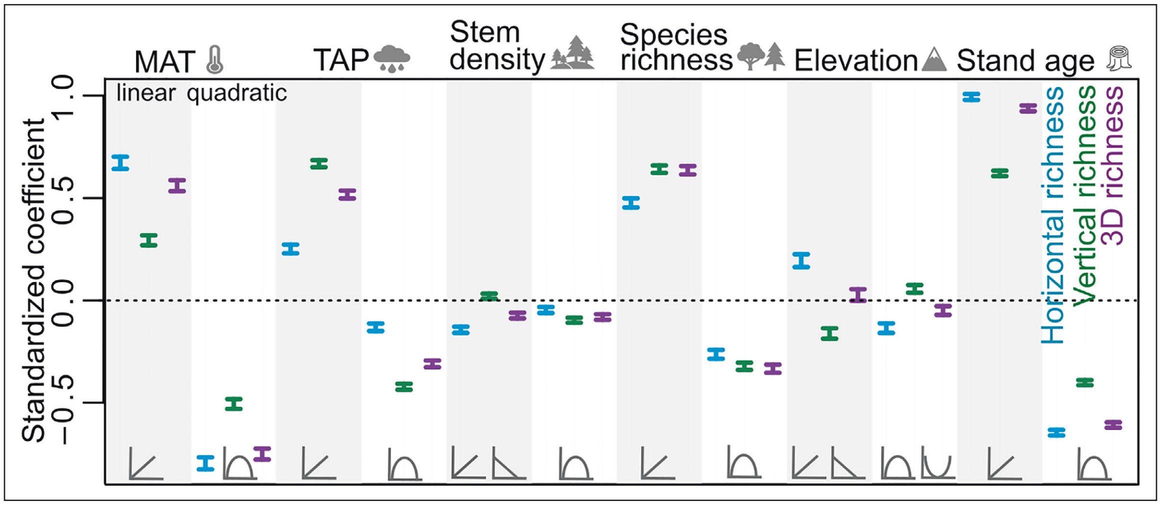

Figure 3. Ecological correlates of structural diversity at the continental scale (N_{plots} = 116,568). Stand age was run in separate models because stand age was only available for the US and Canada (N_{plots} = 99,982). A *z*-score standardization of the predictors and response variables was used to assess relative coefficient effect size. The error bars are a 95% profile-likelihood confidence interval (CI). MAT = mean annual temperature (°C); TAP = total annual precipitation (mm/year). Coefficients and CIs are shown in WebTable 2. For each ecological factor along the top, the simplified line graphs along the bottom depict linear (white shading) or quadratic (gray shading) relationships between that factor and structural diversity.

Results

Spatial variation in structural diversity and associated ecological factors

Several ecological factors were associated with variation in structural diversity (Figure 3; WebTable 2; see WebPanel 2 for bivariate scatterplots). All predictors except for elevation and stem density exhibited a strong and consistent direction in their correlation with structural diversity. Climate, tree species diversity, and stand age (though stand age was run in a separate, spatially restricted analysis) were among the strongest predictors (highest standardized coefficient values or effect size) of structural diversity; there was a positive hump-shaped relationship with species diversity, precipitation, temperature, and stand age. Stem density exhibited a negative hump-shaped relationship with structural diversity metrics, with the exception of a positive hump-shaped relationship with vertical richness. Elevation exhibited a positive hump-shaped relationship with horizontal and 3D richness, but a negative J-shaped relationship with vertical richness.

Structural diversity is a consistent and strong predictor of forest productivity

Our study shows that structural diversity is a more robust predictor of productivity than species diversity (Figure 4). We found that structural diversity was a stronger predictor of productivity when averaged across 100 climate quantile units (Figure 4; WebPanel 3). Horizontal, vertical, and 3D richness, on average, explained 11.4%, 18.4%, and 17.7% more variation in productivity from MAI, respectively, and explained 1.5%, 8.6%, and 6.7% more variation in productivity from PAI, respectively, than species diversity. With stand age added as a covariate predictor, horizontal, vertical, and 3D richness, on average, explained 1.7%, 8.3%, and 6.7% more variation in productivity in PAI, respectively, than species diversity. We also determined that the relationships between structural diversity and BAI confirmed that structural diversity had a stronger relationship with forest productivity than species diversity, with the exception of horizontal richness (Figure 4). Horizontal, vertical, and 3D richness, on average, explained 0.7%, 4.1%, and 3.0% more variation in productivity in BAI, respectively, than species diversity.

Discussion

Our study points toward the potential to use structural diversity as a management and conservation tool for predicting forest productivity, likely due to its capacity for quantifying the physically occupied niche spaces in ecosystems. Our results suggest that forests with high structural diversity, through the horizontal and vertical packing of individual trees (Hardiman *et al*. 2011), have high niche occupancy. As a result, structural diversity leads to efficient use of light, water, and other resources within the forest (Niinemets 2010). Structural diversity is an aspect of forests that could be manipulated and provide a supplemental approach to the management paradigms that utilize species diversity for enhancing overall productivity and carbon capture at a continental scale.

Structural diversity itself varied across North America in patterns that often followed climate variations, indicating potential physiological limitations to maximum structural diversity (Pan *et al*. 2013); for instance, structural diversity increased in regions with higher humidity and moderate temperatures. Regional climate conditions often influence different dimensions of diversity, including structural diversity (Franklin *et al*. 2002; Fotis *et al*. 2018; Fahey *et al*. 2019) and species diversity (MacArthur 1972; Ricklefs 1987). Climate was one of the strongest correlates of forest structural diversity in our analysis, and high temperature and precipitation are typically associated with highly productive ecosystems, which may have increased structural diversity and influenced its predictive strength of productivity within different areas of climate space. Despite some degree of spatial variation in the strength of structural diversity relationships with productivity (WebPanel 3), it was still a better predictor of productivity across North America. It is also notable that structural diversity does not continue to rise with the highest numbers of tree species (WebTable 2; WebPanel 2); this finding provides insight into why structural diversity relationships with productivity are stronger than species diversity as well as further support for our hypothesis. Structural diversity maintains that each unique structural size class should be functionally different (whether arising from inter- or intraspecific genetic variation or from environmental variation), which collectively is associated with an increase in niche space, whereas species diversity does not directly measure any functional differences between individuals (Figure 1). Conservation and climate-change mitigation initiatives that include structural diversity, in addition to traditional biodiversity measures, will increase ecosystem production and carbon capture (eg Dybala *et al*. 2019).

Stand age was a significant predictor of structural diversity, highlighting the important interconnections between age, tree size, and productivity, but it did not change the fact that structural diversity is a stronger predictor of productivity than species diversity when age was also included as a predictor of productivity. Tree size increases with age and larger trees can produce biomass faster than smaller trees (Lutz *et al*. 2018; Ouyang *et al*. 2019). Old growth forests can have high structural diversity (Franklin *et al*. 1981) and, as our results highlight, stand age is an important determinant of structural diversity. However, we detected a positive hump-shaped relationship between stand age and structural diversity, indicating that older stands are not always the most structurally diverse and that medium-age forests may have the highest structural diversity (ie Qiu *et al*. 2021). Furthermore, our results indicate that stand age does not substantially change the relative abilities of structural diversity versus species diversity to predict productivity when it was added as a covariate.

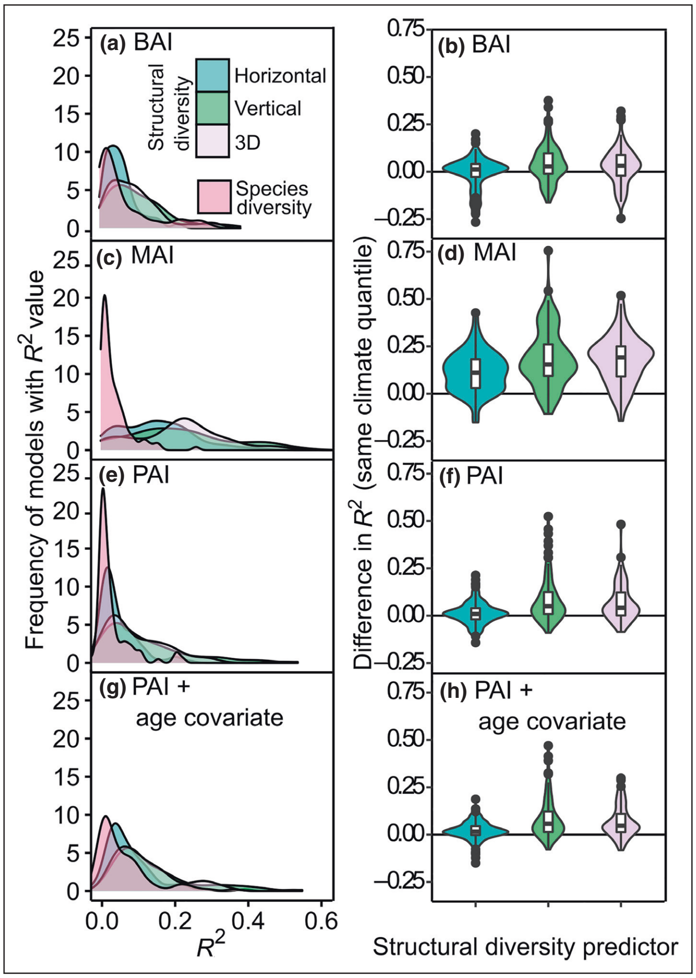

Figure 4. Structural diversity is a stronger predictor of productivity (response) than species diversity (richness) in climate space (100 climate quantiles) for (a, b) BAI (basal area) across North America (N_{plots} = 106,283), (c, d) MAI (biomass) across the US (N_{plots} = 99,343), and (e, f) PAI (biomass) as well as (g, h) PAI (biomass) with stand age as a covariate across the US (N_{plots} = 54,644). In (a), (c), (e), and (g), the distribution of adjusted R^2 (adj R^2) values across 100 climate quantile regressions is indicated on the *x* axis. In (b), (d), (f), and (h), differences in adj R^2 between the model within a climate quantile for a structural diversity metric and species diversity are shown. Equations used in the model are presented as Equation 4 in WebPanel 1. BAI = basal area increments, MAI = mean annual increments, PAI = periodic annual increments.

Conclusions

The results of our analyses demonstrate that forest structural diversity can consistently outperform species diversity in predicting forest productivity across a wide variety of climate conditions in North America, indicating that structural diversity is a superior predictor of ecosystem productivity. Structural diversity metrics may represent a closer approximation of the actual niche occupancy of an ecosystem and serve as a new approach to improve upon proxies for occupied niche space. Climate, species diversity, and stand age were among the strongest predictors of structural diversity across North America, indicating that, as with other dimensions of diversity (Paquette and Messier 2011; Grace *et al.* 2016), structural diversity is sensitive to ecological drivers at a continental scale; nonetheless, its relationship with productivity is consistently strong across different climate conditions. The fact that niche occupancy can be approximated with structural diversity based on only a few commonly measured variables in forest inventories is encouraging, as these structural metrics can be applied and manipulated in managed and natural forests to increase ecosystem production and carbon capture in an era of global change.

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Data Availability Statement

Code and aggregated data products from the US Forest Service will be deposited into Zenodo upon publication (doi.org/10.5281/zenodo.7242904). Data from CONAFOR and NRCAN forest inventories are protected under Material Transfer Agreements to SF.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2586/suppinfo