

Structural and species diversity explain aboveground carbon storage in forests across the United States: evidence from GEDI and forest inventory data

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Abstract

Since biodiversity often increases ecosystem functioning, changes in tree species diversity could substantially influence terrestrial carbon cycling. Yet much less is known about the relationships between forest structural diversity (i.e., the number and physical arrangement of vegetation elements in a forest) and carbon cycling, and the factors that mediate these relationships. We capitalize on spaceborne lidar data from NASA's Global Ecosystem Dynamics Investigation (GEDI) and on-the-ground forest inventory (FIA) data from 1796 plots across the contiguous United States to assess relationships among the structural and species diversity of live trees and aboveground carbon storage. We found that carbon storage was more strongly correlated with structural diversity than with species diversity, for both forest inventory-based metrics of structural diversity (e.g., height and DBH diversity) and GEDI-based canopy metrics (i.e., foliage height diversity (FHD)). However, the strength of diversity-carbon storage relationships was mediated by forest origin and forest composition. For both plot-based and GEDI-based metrics, the relationship between structural diversity (i.e., height diversity, DBH diversity, and FHD) and carbon storage was positive in natural forests for all forest types (broadleaf, mixed, conifer). For planted forests, structural diversity showed positive relationships in conifer planted forests, but not in mixed planted forests. Species diversity did not show strong associations with carbon storage in natural forests, but showed a positive relationship in mixed coniferous-broadleaf planted forests. Although plot-based structural diversity metrics refine our understanding of drivers of forest carbon balances at the plot scale, remotely sensed metrics such as those from GEDI can help extend that understanding to regional/national scales in a spatially continuous manner. Carbon storage showed stronger associations with plot-based structural diversity than with stand age, soil variables, or climate variables. Incorporating structural

diversity into management and restoration strategies could help guide efforts to increase carbon storage and mitigate climate change as nature-based solutions.

Keywords (6-10)

Biodiversity; biomass; carbon stocks; FIA; foliage height diversity; International Space Station; lidar; species diversity; structural diversity; temperate forests

1. Introduction

Increasing carbon storage in forests presents an opportunity for climate mitigation as a nature-based solution (Fargione et al., 2018; IPCC, 2021). Changes in forest carbon storage could influence the global climate, since forests cover approximately 30% of the world's lands and store 45% of the world's terrestrial carbon (Bonan, 2008). In addition to research on the general environmental conditions that influence forest carbon storage, considerable work has explored relationships between biodiversity and ecosystem functions and services (e.g., productivity, carbon storage, nutrient uptake, water quality, and pollination) (Grace et al., 2016; Liang et al., 2016; Naeem et al., 1994; Tilman and Downing, 1994), in part to assess when the twin goals of sustaining biodiversity and maintaining ecosystem services such as carbon storage may be aligned (Mori et al., 2021). Many experimental and observational studies have found positive associations between biodiversity and ecosystem functions (Cardinale et al., 2012; Hooper et al., 2005; Jochum et al., 2020), although the strength and significance of these relationships may vary among functions and ecosystems and across spatial scales (Gonzalez et al., 2020; Ricketts et al., 2016). However, fewer studies have examined relationships with *structural* diversity—which

in forests can refer to the variation in tree heights, stand density, clumping, canopy cover, and/or spatial heterogeneity in vertical arrangement (e.g., rugosity) (Atkins et al. 2018).

Theory underpinning biodiversity-ecosystem functioning research suggests that, on average, ecological communities with more species should be more productive than comparable communities with fewer species (Loreau et al. 2001; Hooper et al. 2005). Since individual species have different niches, communities with many species can use available resources more completely and efficiently than communities with few species, which in turn leads to higher productivity in species-diverse communities than in species-poor communities (Tilman et al., 2014). Although it may be true that more species can indeed use available niche space and resources more fully and complementarily, measuring all axes of the niche space and all resource use is intractable in real-world ecosystems. Biodiversity metrics such as species richness provide a proxy for the potential of species to occupy different niches in the community. Metrics of diversity that serve as better proxies for resource use and efficiency within communities should show stronger associations with ecosystem functioning. Structural diversity may be a better predictor of some ecosystem functions than biodiversity (Ali et al., 2019; Dănescu et al., 2016; Gough et al., 2019; Hardiman et al., 2011; Silva Pedro et al., 2017), as structural diversity may provide a more direct indicator of the niche space occupied within a community (LaRue et al., 2019; LaRue et al., 2023). For example, forest communities with differences in tree crown sizes and shapes have greater light absorption and stem biomass than forest communities where trees have similar crown architectures (Williams et al., 2017). More specifically, forest canopies with substantial vertical stratification, complementarity of crown shapes and heights, and

phenological differences among trees may lead to higher light use efficiency, resulting in higher biomass productivity (Forrester and Bauhus, 2016).

While scientists have developed numerous metrics of structural diversity (e.g., MacArthur and Horn, 1969; Staudhammer and LeMay, 2001), metrics are derived from two main sources of data: traditional plot-based measurements and lidar (light detection and ranging) remote sensing-based measurements. Traditional forest inventory data collected by field crews (e.g., manual height and diameter measurements) often provide information on the species' identities, stem diameters, and heights of trees in each forest plot (Burrill et al., 2021). Indices of structural diversity can be created from the heterogeneity (e.g. standard deviation) in tree stem diameters and heights, number of size and height classes, or with composite metrics combining different characteristics (Bohn and Huth, 2017; Storch et al., 2018; LaRue et al., 2022). Inventory and monitoring programs provide critical data but can be time consuming and costly to collect and curate, resulting in limited sampling in both space and time. Remotely sensed data, however, can bridge these gaps by offering substantial spatial coverage at landscape (e.g., air- and uncrewed aerial vehicles or UAVs) to global (e.g., satellite and other spaceborne platforms) extents. The combination of traditional stand structural data from inventory programs with remotely sensed data may help provide additional, important information about forest health, productivity, and carbon storage (Beland et al., 2019; Wehr and Lohr, 1999), while extending the utility of each across space and time.

Here, we use spaceborne lidar from NASA's Global Ecosystem Dynamics Instrument (GEDI), which provides near-global (between 51.6°S and 51.6°N latitude; Figure 1) estimates of forest

structure (see Dubayah et al. 2020 for GEDI details). Although GEDI has been used for applications such as estimating forest canopy heights (Liu et al., 2021; Potapov et al., 2021), estimating biomass and fuel loads across large areas (Dubayah et al., 2022; Duncanson et al., 2022; Leite et al., 2022), and coupling the structural information provided by GEDI with additional datasets to predict the biodiversity of trees and birds (Burns et al., 2020; Marselis et al., 2022), in this paper we examine the relative roles of structural and species diversity in explaining aboveground carbon storage. Building on previous work that found positive associations between structural diversity and net primary production using either lidar (Gough et al., 2019; Hardiman et al., 2011) or forest inventory data (Danescu et al., 2016; LaRue et al., 2023), our study integrates GEDI and forest inventory data to examine diversity-carbon storage relationships across the entire USA. Understanding how well GEDI-based metrics of structural diversity align with and/or complement plot-based metrics of structural diversity—and assessing relationships between metrics of structural diversity and carbon storage—could provide key insights when scaling up from individual forests plots to provide estimates of diversity and carbon storage across large spatial scales.

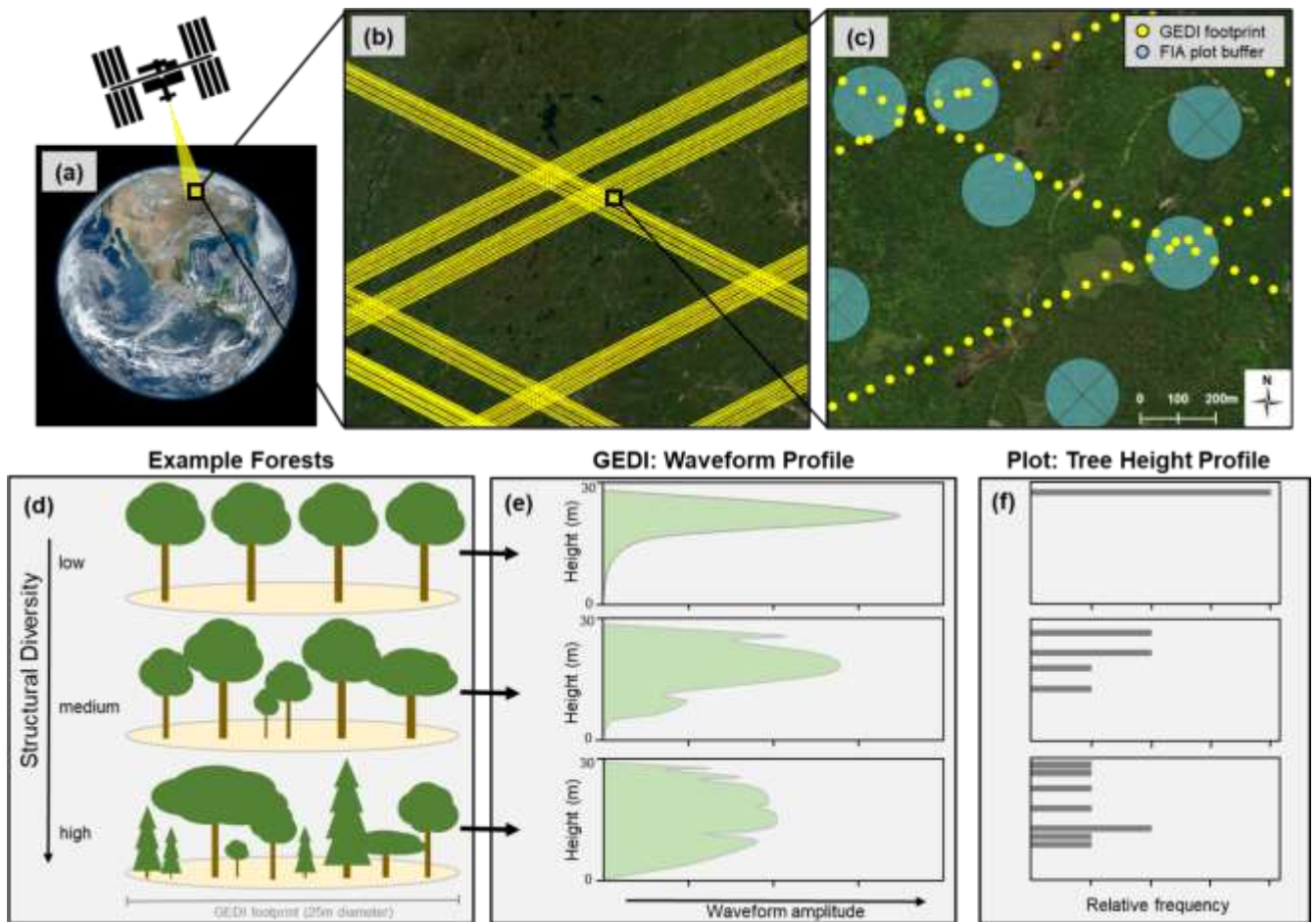


Figure 1. The GEDI sensor provides estimates of structural diversity. (a) The GEDI sensor has coverage tracks over the contiguous United States (and other regions between 51.6°S and 51.6°N latitude). (b) For each GEDI track there are eight beams spaced 600 m apart. (c) Within each beam there are footprints with a 25 m diameter spaced 60 m apart. We extracted GEDI footprints that were within a 100 m buffer zone of the FIA forest plots (hypothetical forest plots that were not included marked with an X). (d) Examples of different forests with low to high structural diversity. Indices of structural diversity can be generated from (e) the GEDI data and the lidar waveform, which is based on the return energy from all aspects of vegetation within the footprint (e.g., leaves, branches, tree trunks), or from (f) forest inventory plot data using metrics based on the relative frequency of individual tree heights (or DBHs).

Relationships between diversity and ecosystem functioning (e.g., carbon storage) may vary across different types of forests and between natural and planted forests. Scientists have proposed that the importance of plant species diversity for ecosystem functioning may be greater in more stressful environments than in more benign environments (Warren et al. 2009). In

support of this hypothesis, some studies found that biodiversity-productivity relationships vary among tropical, temperate, and boreal forests and among different regions (e.g., Paquette and Messier 2011; Liang et al. 2016), but it remains unclear how much these relationships vary across the broadleaf, coniferous, and mixed forests of the USA (Atkins et al., 2022). Since broadleaf and coniferous trees have very different shapes, we anticipate that the ways that individual trees interact and compete for resources may differ across broadleaf and coniferous forests, promoting different 2D and 3D arrangements of the vegetation, thus leading to different relationships between structural diversity and carbon storage. In addition, historical conditions may affect ecosystem functioning and could lead to differences in the relationships between diversity and carbon storage between natural and planted forests or between newly established and mature/old growth forests. Although evidence in grassland communities suggests that experimental and observational studies may show similar magnitudes of effects (Jochum et al., 2020), differences between natural and planted forests remain uncertain, but could be important due to the legacies of human actions. The majority of research on biodiversity-ecosystem functioning in forest communities has largely been conducted through observational studies in forests with little active management. Yet understanding differences between natural and planted forests is critical, as restoration projects present key opportunities to apply knowledge of relationships between biodiversity and ecosystem functioning (Srivastava and Vellend, 2005).

While we expect structural and species diversity to influence carbon storage at the site level (LaRue et al., 2023), other factors such as climate and soil conditions may influence forest biomass and carbon storage at the country-wide level (Pan et al., 2013). Temperatures vary greatly across latitudes and elevations in the USA, and warmer temperatures area often

associated with greater forest biomass in temperate forests (Keith et al., 2009). As temperate forests are mainly limited by water availability, increased precipitation leads to greater forest biomass (Stegen et al., 2011). Although in some forests, climate variables matter more than soil characteristics (Bennett et al., 2020), soil fertility is often associated with increased forest biomass (Paoli et al., 2008; Yuan et al., 2019). Nutrients such as nitrogen and phosphorus provide key elements for growth, while soil texture can influence the water availability for root uptake (Hofhansl et al., 2020; Laurance et al., 1999). Accounting for these types of additional factors that affect forest biomass can help show the relationships between structural diversity, species diversity, and carbon storage—the focus of this study.

In this paper, we explore the relationships of structural and species diversity with aboveground live tree carbon storage, an ecosystem service of critical importance for global climate change policy. First, we capitalize on detailed forest inventory program data and the newly available satellite-based GEDI data to assess the relative importance of structural and species diversity for aboveground carbon storage across the contiguous USA. Second, we investigate whether there are substantial differences in relationships between structural diversity and carbon storage when using plot-based versus GEDI-based structural diversity metrics. Third, we then explore whether relationships between diversity and aboveground carbon storage vary across different forest stand origins (natural or planted) and forest compositions (broadleaf, mixed, or conifer trees). Using observational rather than experimental data in this study, we do not directly evaluate directions of causality; we report the statistical relationships between diversity and carbon storage from spatial data across the USA.

2. Methods

Our study included data from the forested regions of the contiguous USA, with forest plots spanning 13 different EPA level II ecoregions (US EPA 2018; Figure 2). Based on the Daymet climate data (Thornton et al., 2020), the mean minimum annual temperature varied from -5.4°C to 15.8°C, the mean maximum temperature from 6.1°C to 29.1°C, and annual precipitation from 218 mm to 3742 mm over the past ten years at our forest plots. Individual forest plots contained 1 to 15 species, and all plots in the study region that were included in our analyses collectively contained 188 species. The analyses proceeded in three main steps: we selected suitable forest plots (section 2.1); extracted GEDI satellite data (2.2); and conducted statistical analyses to evaluate the effects of biological and structural diversity (2.3) (Figure 3). We conducted the analyses described below using R version 4.1.2 (R Core Team, 2021).

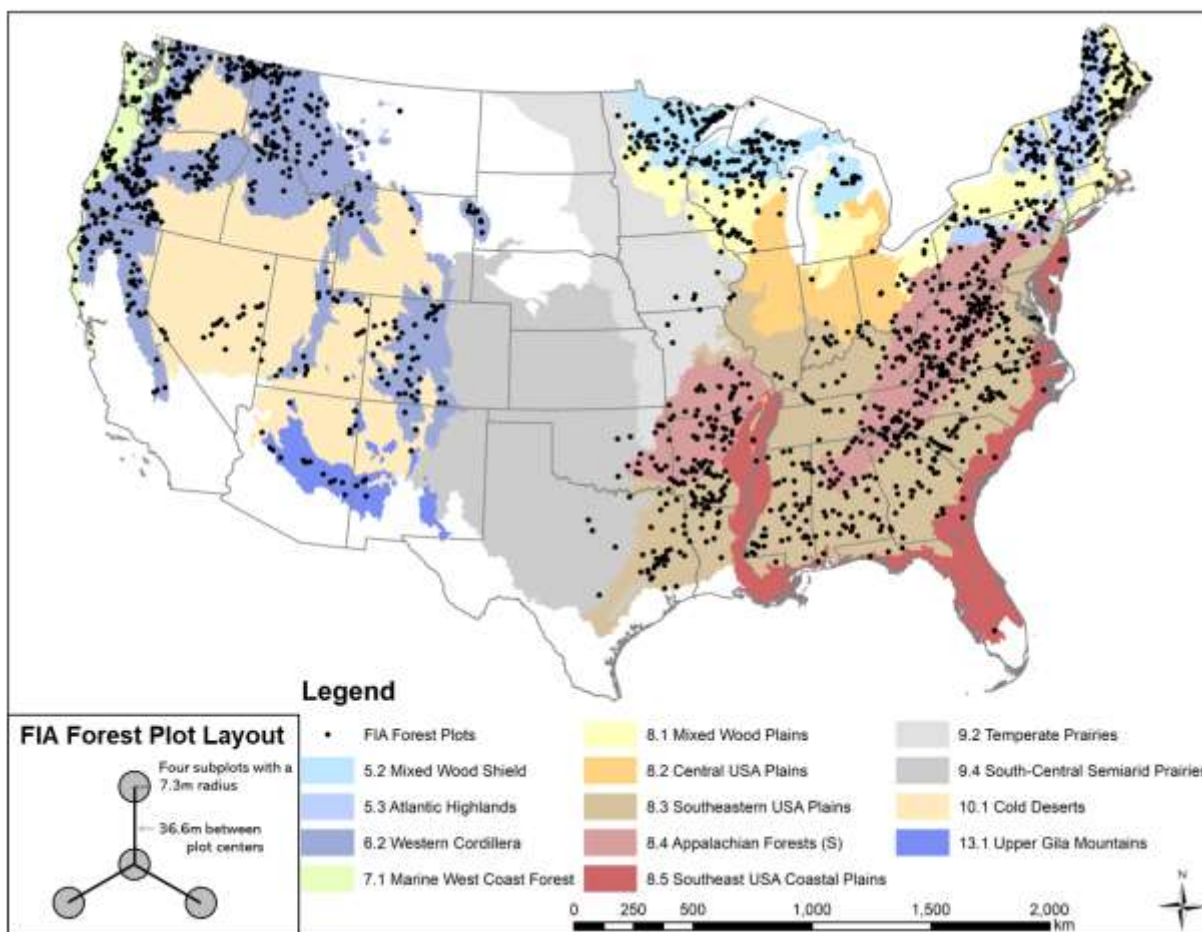


Figure 2. Our analysis includes 1796 Forest Inventory and Analysis (FIA) plots across the western and northeastern forests of the USA in 13 different EPA Level II Ecoregions. FIA plots are displayed using the publicly available perturbed coordinates.

2.1 Plot-Based Variables from Forest Inventory Data

We relied on Forest Inventory and Analysis (FIA) data to calculate estimates of aboveground carbon storage, metrics of species diversity, and other explanatory variables (Burrill et al., 2021).

FIA data were also used to calculate plot-based structural diversity metrics. Administered by the United States Department of Agriculture Forest Service, the FIA program provides the most comprehensive forest database currently available in the United States (Tinkham et al., 2018).

The FIA program divides each state into different strata (forested land and non-forested land)

using remotely sensed imagery, and conducts on-the-ground forest land sampling to match the relative area of forested strata, which results in a national sample intensity of approximately one plot per 2,428 ha (sampling ratio to total land of roughly 0.0028%; Bechtold and Patterson 2005). Forest land is defined as having >10% tree or woody canopy cover (or formerly having such cover that will be naturally or artificially regenerated) and being >0.4 ha in size and 37 m wide (Burrill et al., 2021). This incorporates both timberland and non-timberland, which includes woodland vegetation and reserved forest land (Oswalt et al., 2019).

We selected forest plots that were surveyed in 2017-2020, as these years corresponded most closely with the GEDI data (2019-2021) and provide a sample size of 1796 corresponding plots. The sampling protocols for these plots encompassed four subplots of 7.3 m in diameter for a total of 0.0672 ha per FIA forest plot (FIA plot design codes: 1, 501, 502). We selected FIA plots in which all four subplots contained trees and where at least 90% of the plot was specified as covered by forest. Our selection of FIA plots for the main analyses was further refined by the availability of GEDI data, as described in Section 2.2, but we also evaluated the representativeness of the sample of plots that spatially matched with GEDI footprints by using the most recent inventory measurement from all FIA plots that satisfied the above criteria (see Supplemental Information Section B for further details). Data for each subplot includes living trees that had a diameter at breast height (DBH) of at least 12.7 cm (5 inches). We excluded any trees in the FIA ‘macroplots’ (for plot design codes where macroplots existed)—regions surrounding the area of the ‘subplots’. The FIA database uses allometric equations from Jenkins et al. (2003) to provide estimates of biomass for different components of the tree—the stem, tops and limbs, and stump of each tree (see Woodall et al. 2011 for details). A conversion factor of

0.5 was used to estimate carbon storage from biomass, since carbon is roughly 50% of the tree biomass (but can vary between 46%-55%; Lamblom et al., 2003). We aggregated the carbon storage estimates for each living tree with a DBH greater than 12.7 cm to obtain aboveground carbon storage for each forest plot.

We calculated species diversity for each forest plot using metrics of species richness (simply a count of the number of species) and Shannon diversity, which weights species by the relative abundances according to Eqn (1):

$$Diversity = - \sum_{i=1} P_i * \log(P_i) \quad (1)$$

where P_i is the proportion of species (i.e., relative abundance) of species i within each forest plot. We report results from Shannon diversity in the main text, since it facilitates direct comparison with the plot-based and GEDI-based metrics of structural diversity described in the next paragraph and next section, but we include results from species richness in the supplemental information (Figures S5, S6).

Using the FIA plot-based data, we calculated structural diversity metrics for height and DBH diversity. For each forest plot, first we allocated trees into height classes with increments of 3.048 m (10 feet), and into DBH size classes with increments of 12.7 cm (5 inches). We used these bin widths to provide a range of size class values across the forest plots (1 to 14 and 1 to 10 size classes for height and DBH, respectively) comparable to the range of values species diversity (1-15 species). Then we calculated height and DBH diversity for each forest plot based

on the Shannon diversity formula used for species diversity (Eqn 1), but in this case P_i now represents the proportion of trees within size class i .

For calculations of other explanatory variables, the FIA dataset provides information on different forested conditions (i.e., subsections within subplots of the overall forest plot characterized by different stand ages, soil types, and/or levels of human influence). We calculated stand age for each forest plot using a weighted average, where age was weighted based on the area covered by each forested condition. We classified each forest plot into different forest compositions, where a forest plot was deemed ‘broadleaf’ if at least 70% of the total number of stems were broadleaf trees, ‘conifer’ if at least 70% of the stems were coniferous trees, and ‘mixed’ if conifer and broadleaf composition were between these two percentages (sensu Bonan et al., 2002). We categorized forests as ‘natural’ if the FIA data did not indicate any planted areas (0%) within the forest plot, and as ‘planted’ if more than 98% of the area was planted. Since there were few plots between these percentages, we excluded those plots from analyses and treated forest origin (natural/planted) as a categorical variable. Here, ‘planted’ forests are not necessarily ‘plantations’ and may contain multiple different species, including trees from natural regeneration. For disturbances, we include all plots in the results presented in the main text. In the supplemental information we provide results where we excluded any forest plot where the database indicated more than 5% disturbance (e.g., ice storm, fire, insect damage) (Figure S10 a,b). We used the USA EPA Ecoregions of North America dataset to identify the ecoregion associated with each forest plot (US EPA 2018). We report results from level II ecoregions since initial analysis showed that using level II (with 13 ecoregions in our study region) data explained

more of the variation in carbon storage than the broader level I ecoregion categories or an east/west division.

2.2 GEDI-derived Structural Diversity Metrics

With each overpass, GEDI collects data along 8 ground transects spaced approximately 600m apart, with footprints of 25 m in diameter spaced every 60 m along each transect (Figure 1). GEDI provides full waveform lidar returns from which metrics of forest structure are calculated. We used data from the GEDI Level 2B version 2 products (Dubayah et al. 2021), using the LPDAAC data prep scripts to find suitable GEDI tracks (Krehbiel, 2019) and the ‘rGEDI’ package in R to extract and process the data (Silva, 2021). We downloaded data for our study region during the years 2019, 2020, and 2021 for the months of July and August, peak summer months with leaf-on conditions in broadleaf forests. We then followed the latest GEDI user guide (Beck et al., 2021), selecting GEDI footprints where the algorithm and quality flags indicated that the measurements were suitable (values of 1), and where the footprints had at least a 95% beam sensitivity rating (i.e., the canopy cover percentage through which the beam would be able to detect the ground 90% of the time; Hancock et al. 2019). At lower beam sensitivities where the beam does not reach the forest floor, the relative height values provided in the GEDI data may not match on-the-ground conditions, and estimates of forest height and structural diversity may not be accurate representations. Because GEDI data cover all areas of the world (forests, cropland, urban areas, etc.), we extracted GEDI footprints that lined up with pixels that were classified as ‘forests’ on the ‘LCMAP’ national land cover map from 2019 (30 m resolution; USGS 2021).

The GEDI 2B provides metrics of forest structure and diversity, such as canopy gap fraction, plant area index (PAI), and foliage height diversity (FHD). The PAI is similar to the traditional concept of leaf area index (i.e., leaf area per unit ground area), but PAI incorporates all vegetation components (leaves, branches, and stems) as these components cannot be distinguished with GEDI (Tang and Armston, 2019). FHD measures the vertical heterogeneity of vegetation within the GEDI footprint by applying the Shannon diversity formula (Eqn 1); using bin widths of 1 m (Tang and Armston, 2019), P_i indicates the proportion of the PAI profile within the i^{th} vertical height band.

We extracted GEDI footprints that aligned with the FIA plots, where the footprint center was within a 100 m buffer zone around the center of the FIA plot (Figure 1). If there were multiple, suitable GEDI footprints within a given FIA buffer zone, we averaged these metrics of structural diversity across the footprints. By assessing the correlations between GEDI-derived height measurements (i.e., RH98 from the GEDI 2A version 2 product; Figure S2) and the maximum tree height in the FIA data, we found that choosing a reasonable buffer size involved a balance between the accuracy of GEDI measurements (i.e., better with a small buffer and with multiple GEDI footprints within the buffer region) and the sample size available for analyses (i.e., better with a larger buffer and a minimum of one GEDI footprint; Figure S3). Sensitivity analyses with different buffer sizes—using a 50 m buffer and a minimum of one GEDI footprint, a 100 m buffer and at least three GEDI footprints, and a 200 m buffer with at least three footprints—showed similar associations between metrics of diversity and carbon storage (Figures S7-S9); we report results in the main text using a buffer of 100 m and a minimum of three GEDI footprints

within each FIA buffer zone, which provided a total of 1796 plots suitable for our subsequent analyses.

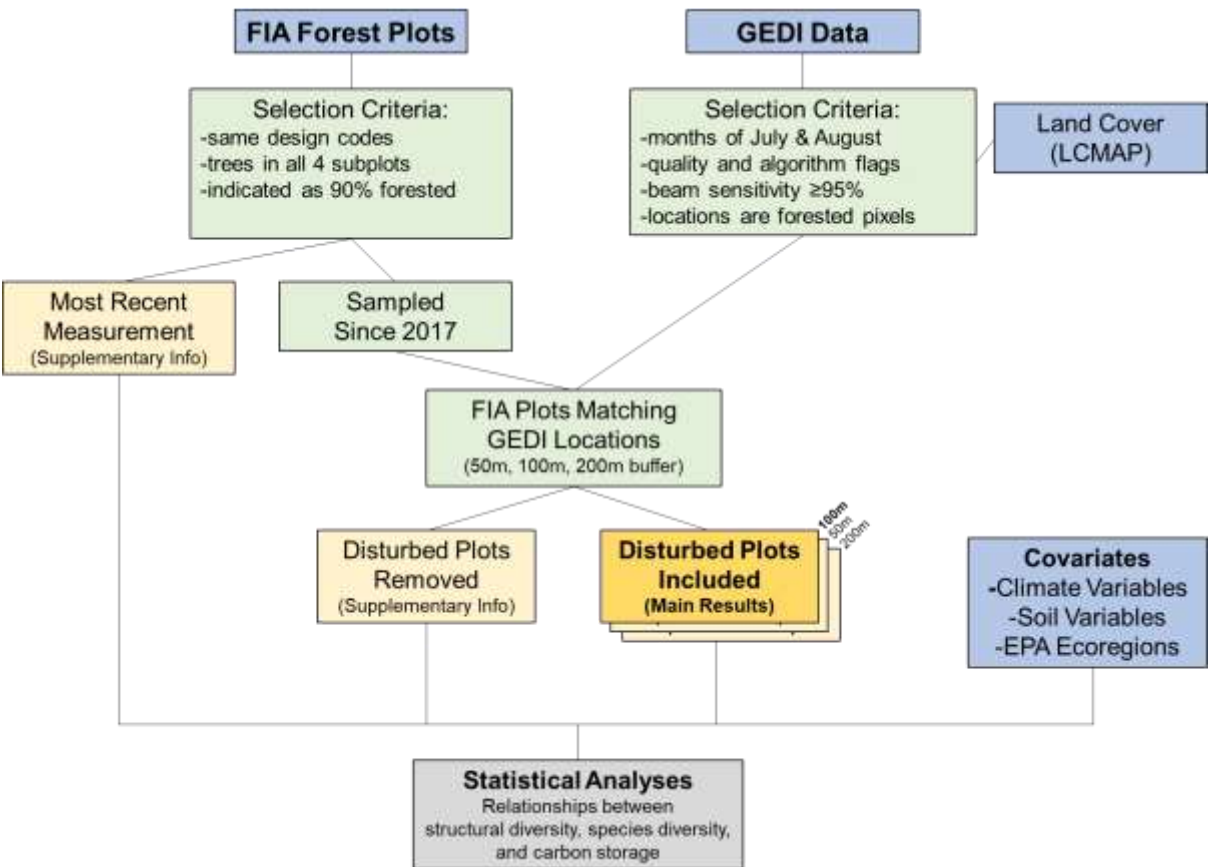


Figure 3. Schematic showing input data and how we selected appropriate plots for our main analyses and supplementary analyses. “Covariates” indicate datasets used to generate additional explanatory variables for the statistical modelling. Blue boxes indicate input datasets. Green boxes indicate selection criteria. Yellow boxes indicate results that are reported, with the results reported in the main text indicated in darker yellow and bold text. This figure is illustrative, not exhaustive, of all sensitivity analyses (see supplemental figures).

2.3 Statistical Analyses

We applied a generalized additive model (GAM) to model the relationships between carbon storage, species diversity, structural diversity, and other covariates. Using climate data from the Daymet dataset at a 1 km² pixel resolution (Thornton et al., 2020), we extracted the average annual temperature and precipitation at each forest plot over the past 10 years (2011-2020). We extracted soil data from the SoilGrids 2.0 database at a 1 km² resolution for pH, bulk density, clay and sand percentages, coarse fragments, and cation exchange capacity (ISRIC, 2022; Poggio et al., 2021). To approximate normal distributions for subsequent analyses, we log transformed carbon storage, mean annual maximum temperature, and precipitation, and square root transformed elevation. We scaled all variables to a mean of zero with unit variance, so that relationships of all variables with carbon storage could be compared on a common scale.

We built statistical models of increasing complexity to examine associations between diversity metrics and carbon storage and the amount of variation (i.e., R² value) explained by each variable or combination of variables. First, we modelled each of the metrics of structural diversity, species diversity, mean tree height, top canopy return (RH98), and several covariates individually with carbon storage, as well as models using the mean tree height, top canopy return (RH98), and several covariates individually to predict carbon storage. We then ran models that included both a height metric and a structural diversity metric as explanatory variables; this included mean tree height and height diversity or DBH diversity for the plot-based models, and RH98 and FHD for the GEDI-based model. We then ran models with several explanatory variables, with multiple metrics of diversity alone and with covariates; we conducted two full GAMs, where all variables remained the same except for the data source for structural diversity

and for height; one model used plot-based structural diversity (i.e., height and DBH diversity) and mean tree height and a second model used GEDI-based structural diversity (i.e., FHD) and canopy height (RH98). These full GAMs included carbon storage as the dependent variable and several explanatory variables and their interactions, including: smooth terms for species diversity and for structural diversity that simultaneously varied by forest origin (natural/planted) and forest composition (broadleaf, mixed, conifer); a smooth term for stand age; smooth terms for the pairwise interactions between stand age, structural diversity, and species diversity; and the factor variables forest origin, forest composition and EPA Ecoregion level II. We ran the GAM models with the ‘mgcv’ package v1.8.38 (Wood, 2011) using restricted maximum likelihood (REML) to estimate the model parameters. To compute these models within a reasonable time, we initially specified the number of basis dimensions at $k=4$ for each parameter, checked whether the basis dimensions of the resulting model were adequate, and increased k as necessary for each parameter. No evidence of spatial correlation was found via testing the residuals of the models with a Moran’s I index (Moran, 1950). To examine whether relationships between diversity and carbon storage varied by geography or by climate, we re-ran the models with an interaction term between each of the three diversity variables (i.e., DBH, height, and species diversity) and ecoregion, and also between the three diversity variables and climate categories; see supplemental information section C for further details. We visualized the GAM results with assistance from the ‘gratia’ package (Simpson, 2022). We tested for differences among the groups for the factor variables (forest origin, forest composition, and ecoregion) using a Kruskal-Wallis test with pairwise testing adjusted for multiple tests with Holm’s procedure (Holm 1979). In the following sections the results were ‘significant’ if $P < 0.05$, but we recognize that P -values are only one part of the overall relationships that we examined in this study.

3. Results

3.1 Associations Between Diversity and Carbon Storage

We found that structural diversity (both GEDI-based and plot-based metrics) explained more of the variation in carbon storage than did species diversity (Figure 4). When modelling each of the variables individually with carbon storage, FIA plot-based structural diversity metrics of height diversity and DBH diversity both explained 49.4% of the variation in carbon storage. A model that only included the mean tree height explained 61.2% of the variation in carbon storage, but adding height diversity or DBH diversity to this model increased the explanatory ability of model to 68.2% and 72.0%, respectively. GEDI-based metrics of FHD, PAI, and canopy gap fraction individually explained 37.9%, 21.2%, and 22.1% of the variation in carbon storage, respectively. A model with the canopy height (RH98) explained 44.9% of the variation in carbon storage, and adding FHD as well only increased the explanatory ability to 45.8%, while adding the gap fraction increased the explanatory ability to 46.5%. Species diversity (Shannon index) and species richness showed weaker associations with carbon storage than did any metric of structural diversity; species diversity and richness explained 4.8% and 6.1% of the variation in carbon storage, respectively. Similar to these results with each of the variables individually, the GAM using FIA plot-based metrics of structural diversity (height and DBH diversity) plus additional covariates (i.e., stand age, forest composition, forest origin, ecoregion, soil, climate variables) explained a higher proportion of the variation in carbon storage than the GAM using GEDI-based metric of structural diversity (i.e., FHD) with the same covariates (71.6% vs. 61.2% respectively).

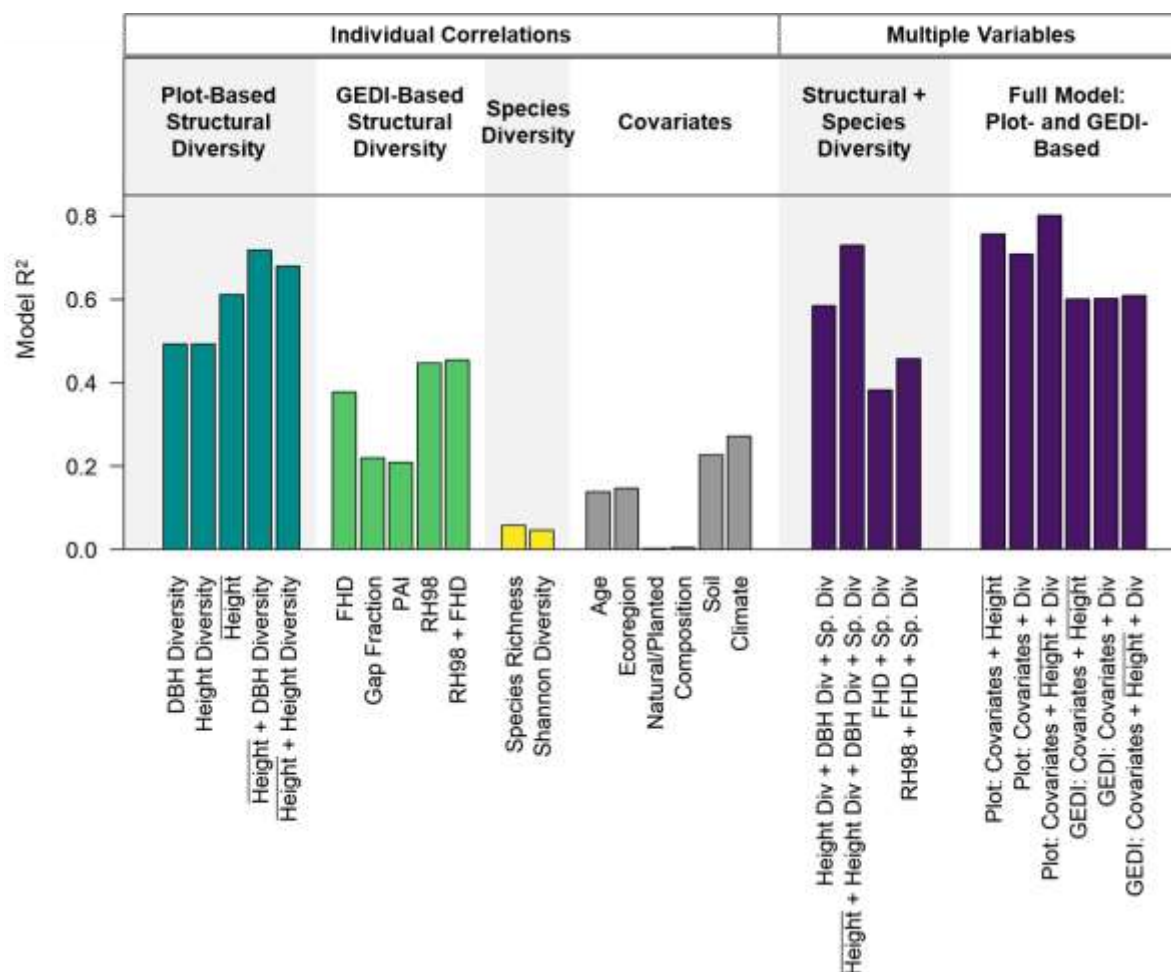


Figure 4. The amount of variation in carbon storage (adjusted R^2) explained by each variable individually or with one variable plus a height measurement (left-hand bars: “individual correlations”) and by models that included two or more diversity variables (right-hand bars: “multiple variables”). The “Full Model” included all variables (i.e., stand age, ecoregion, forest origin, forest composition, soil, and climate variables) and the interactions examined in this study when using the plot-based metrics of structural diversity and when using GEDI-based metrics. The axis label “composition” means forest composition (broadleaf, mixed, or conifer). Height indicates the mean tree height.

3.2 Relationships Among Metrics of Structural Diversity

The data show reasonable correlations between plot-based and GEDI-based metrics of structural diversity (Figure 5; see also Figure S1). In general, FHD saturates and levels off at higher levels of height diversity and DBH diversity, but we note that there are also fewer GEDI footprints which have the highest levels of FHD. Despite positive correlations, there remains considerable

scatter in the pairwise relationships between the three metrics (FHD, height diversity, and DBH diversity), indicating that they capture different aspects of structural diversity.

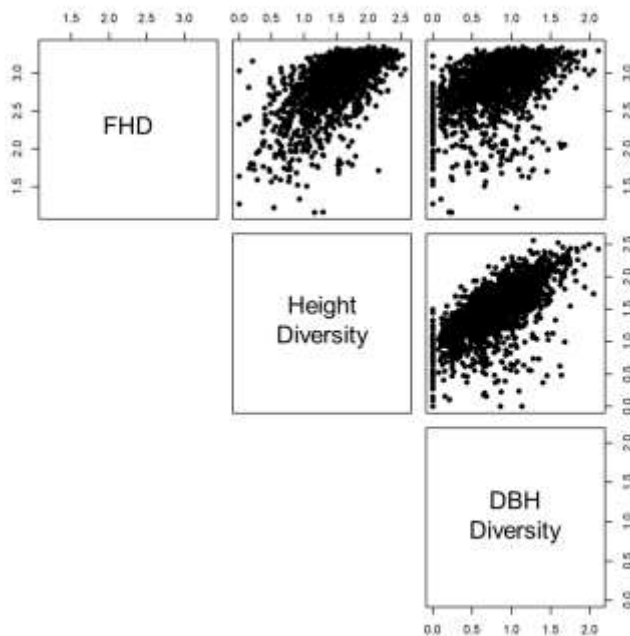


Figure 5. The main metrics of structural diversity used in this paper (FHD, height diversity, and DBH diversity) show positive correlations, although scatter in the relationships indicates that the metrics capture different aspects of structural diversity.

3.3 Plot-Based Models of Structural Diversity

Partial effects plots from the GAMs illustrate that the magnitude and significance of relationships between diversity and carbon storage varied between metrics of diversity and between natural and planted forests (Figure 6). With the FIA plot-based models, structural diversity metrics of both height diversity and DBH diversity showed positive associations with carbon storage across all forest types (broadleaf, mixed, and conifer) in natural and planted forests (GAM; $P < 0.001$ for all, except for height diversity in mixed planted forests where $P =$

0.10). We could not estimate diversity-carbon storage relationships in broadleaf planted forests since there was only one such plot in our dataset. Species richness did not show significant relationships with carbon storage in natural forests. Species richness showed a non-significant relationship in mixed planted forests, and a significant negative relationship in conifer planted forests ($P < 0.001$). In addition to these relationships between diversity and carbon storage, the mean values of height diversity, species diversity, and carbon storage were all slightly higher in natural forests than in planted forests (Figure 6; Kruskal-Wallis; $P = 0.049$ for carbon storage, and $P < 0.001$ for all others).

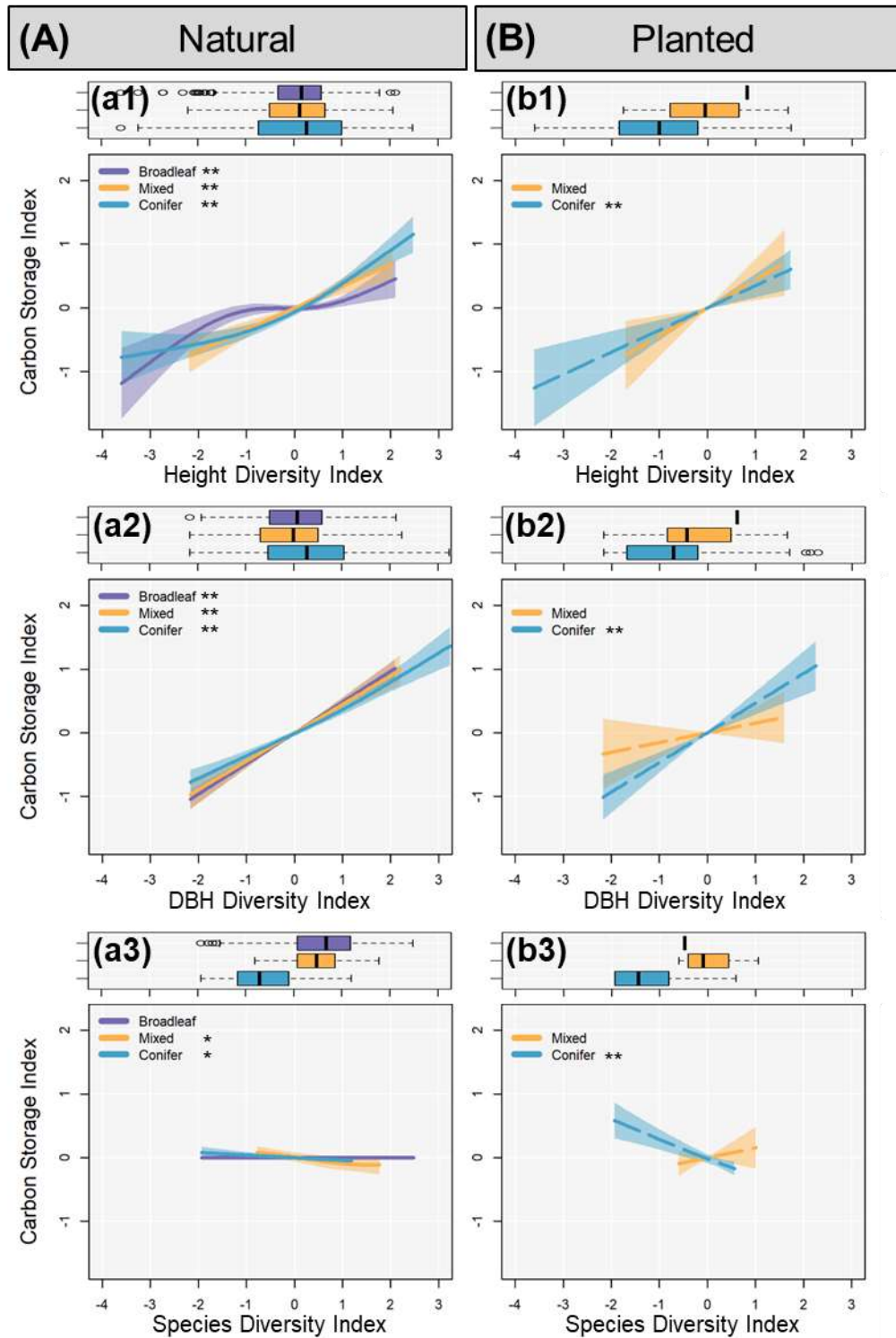


Figure 6. Partial effects plots from a GAM model using plot-based metrics of structural diversity show the relationship between diversity and carbon storage across forest types in (A) natural versus (B) planted forests. Boxplots (A and B subpanels) show the distributions of diversity metrics. Relationships different than 0 at the $P < 0.10$ level are shown with a *, and at the $P < 0.05$ level with a **.

430

431 **3.4 GEDI-Based Models of Structural Diversity**

432 Metrics of GEDI-based structural diversity showed contrasting results across broadleaf, mixed,
433 and conifer forests (Figure 7). In natural forests, the partial effects of structural diversity (i.e.,
434 FHD) showed a positive significant relationship with carbon storage in all forest types (GAM; P
435 < 0.001). In planted forests, FHD showed a significant positive relationship with carbon storage
436 in conifer forests ($P < 0.001$), but no significant relationship in mixed forests. As above, we
437 could not estimate relationships in broadleaf planted forests as there was only one forest plot. In
438 natural forests, species diversity showed positive associations with carbon storage in broadleaf
439 forests ($P = 0.019$), and no association in mixed forests or conifer forests. In planted forests,
440 species diversity showed no association with carbon storage in conifer forests and a positive
441 association in mixed forests ($P = 0.027$).

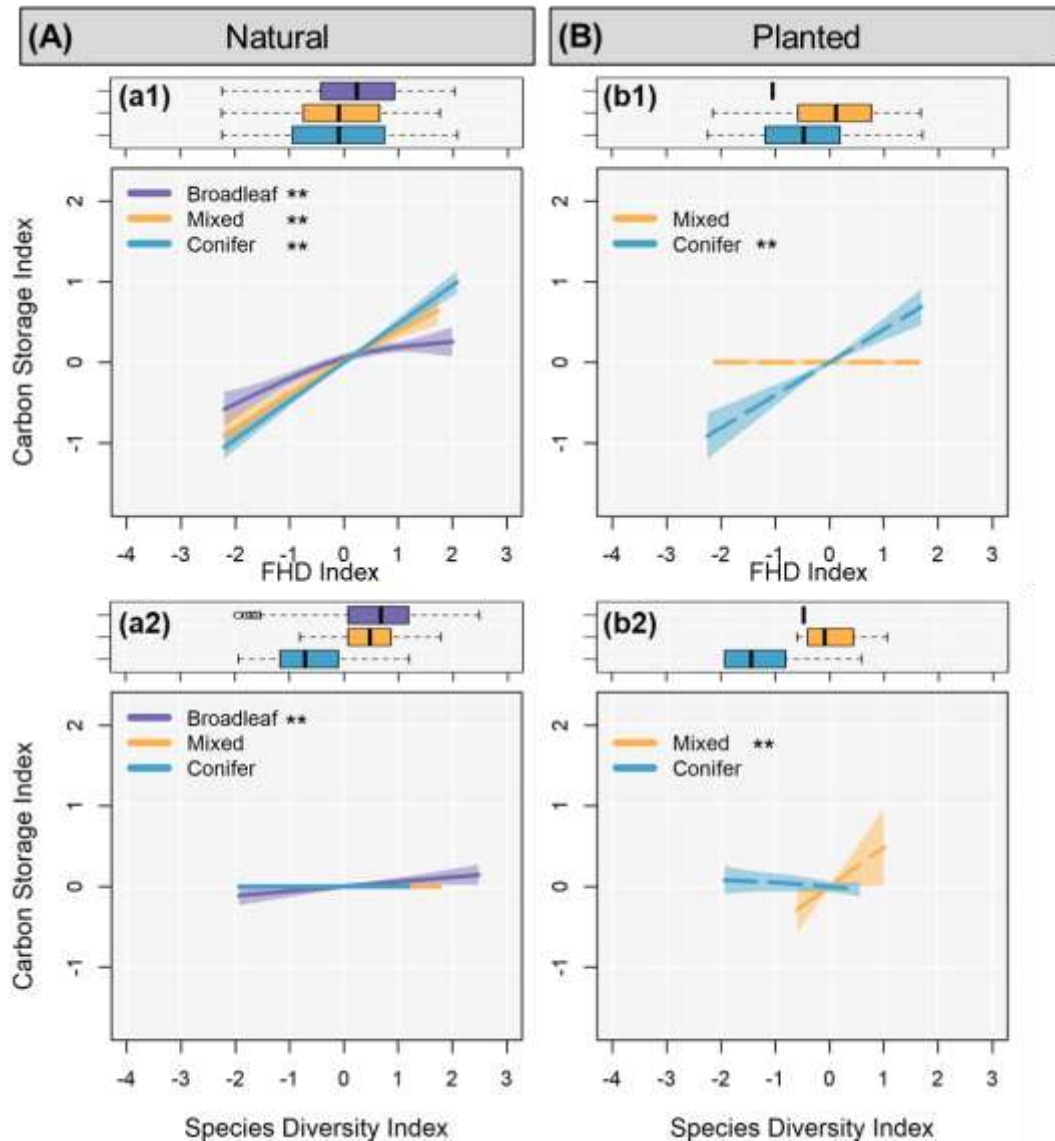


Figure 7. Partial effects plots from a GAM model with GEDI-based measurements of structural diversity and with plot-based measurements (B) show the relationship between diversity and carbon storage across forest types in (A) natural and (B) planted forests. Boxplots (A, B subpanels) show the distributions of carbon storage and diversity. Relationships significantly different than 0 at the $P < 0.05$ level are shown with a **).

3.5 Ecoregions

The mean values and degree of variation in carbon storage, structural diversity, and species diversity varied among some of the 13 EPA level II ecoregions (Figure 8). For example, the Marine West Coast Forests (region 7.1) had higher carbon storage and height diversity than the

Atlantic highlands (region 5.3). The Upper Gila Mountains (region 13.1) had lower species diversity than regions such as the Atlantic highlands (region 5.3) and the Appalachian forests (region 8.4). Although forests of the Temperate Prairies (region 9.2) showed relatively high variation in species diversity and DBH diversity between forest plots in this region, the temperate prairies had low variation in height diversity.

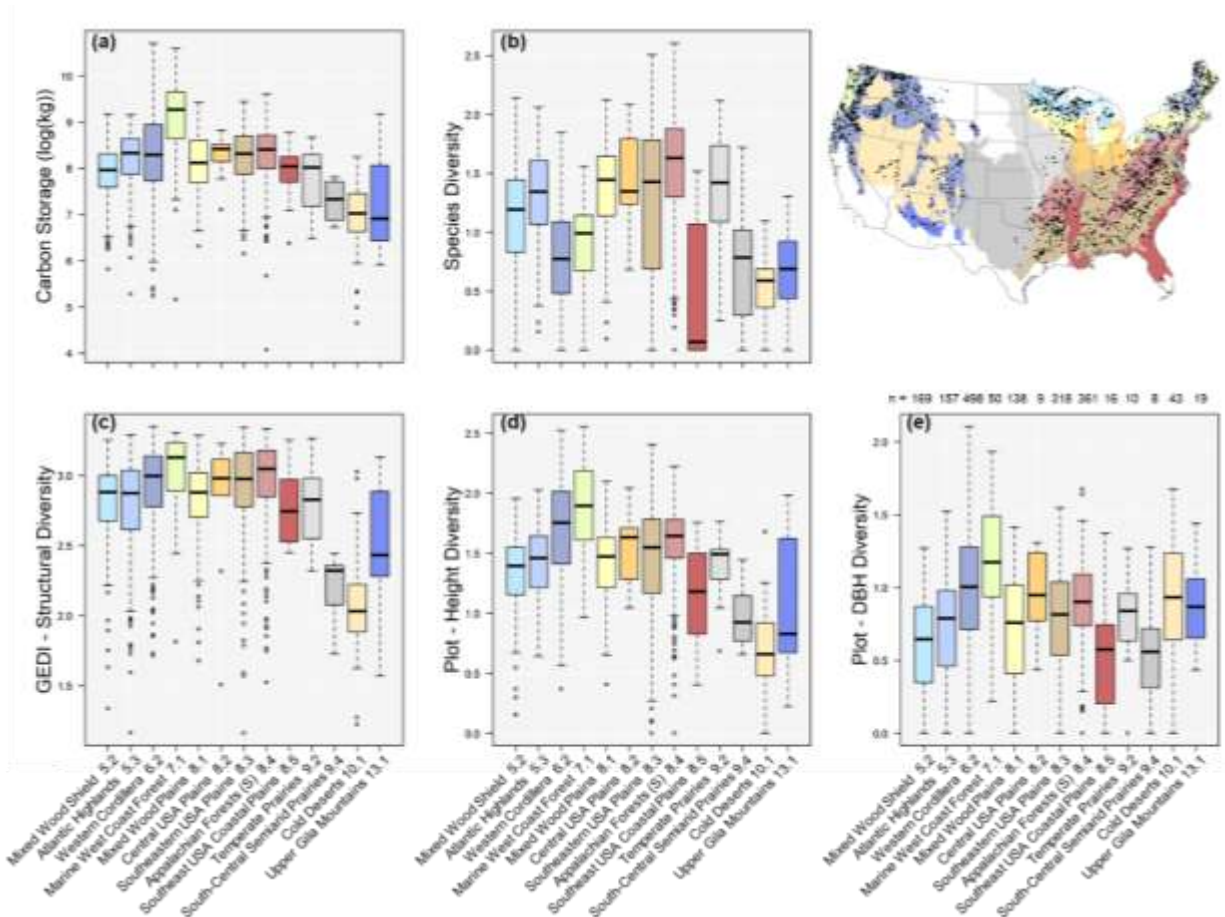


Figure 8. The distributions of (a) carbon storage, (b) GEDI-based structural diversity (FHD), (c) FIA plot-based structural diversity index, (d) and species diversity across the 13 EPA Level II Ecoregions. The number of forest plots in each ecoregion is shown above panel (d).

3.6 Stand Age

Stand age was a strong driver of carbon storage, as we found that, individually, stand age explained 14.1% of the variation in carbon storage. The amount of variation in carbon storage explained by the plot-based metrics of structural diversity, height diversity (49.4%) and DBH diversity (49.4%), was greater than the variation in carbon explained individually by stand age (14.1%), soil variables (23.3%), or climate variables (27.8%) (Figure 4).

For some metrics of diversity, the relationships between diversity and carbon storage varied modestly with forest stand age (Figures 9, S6). There were positive interaction effects on carbon storage (i.e., a more positive effect than expected based on the values of either variable on their own) for young stands with either very high or very low height diversity and for both very young and very old stands with low FHD. There were negative interaction effects for old stands with high height diversity and with high FHD. That said, the interaction effects of diversity and stand age on carbon storage were subtle compared to the main effects of these variables individually and incorporating interactions into the model added a minimal increase in the overall explanatory ability of the model.

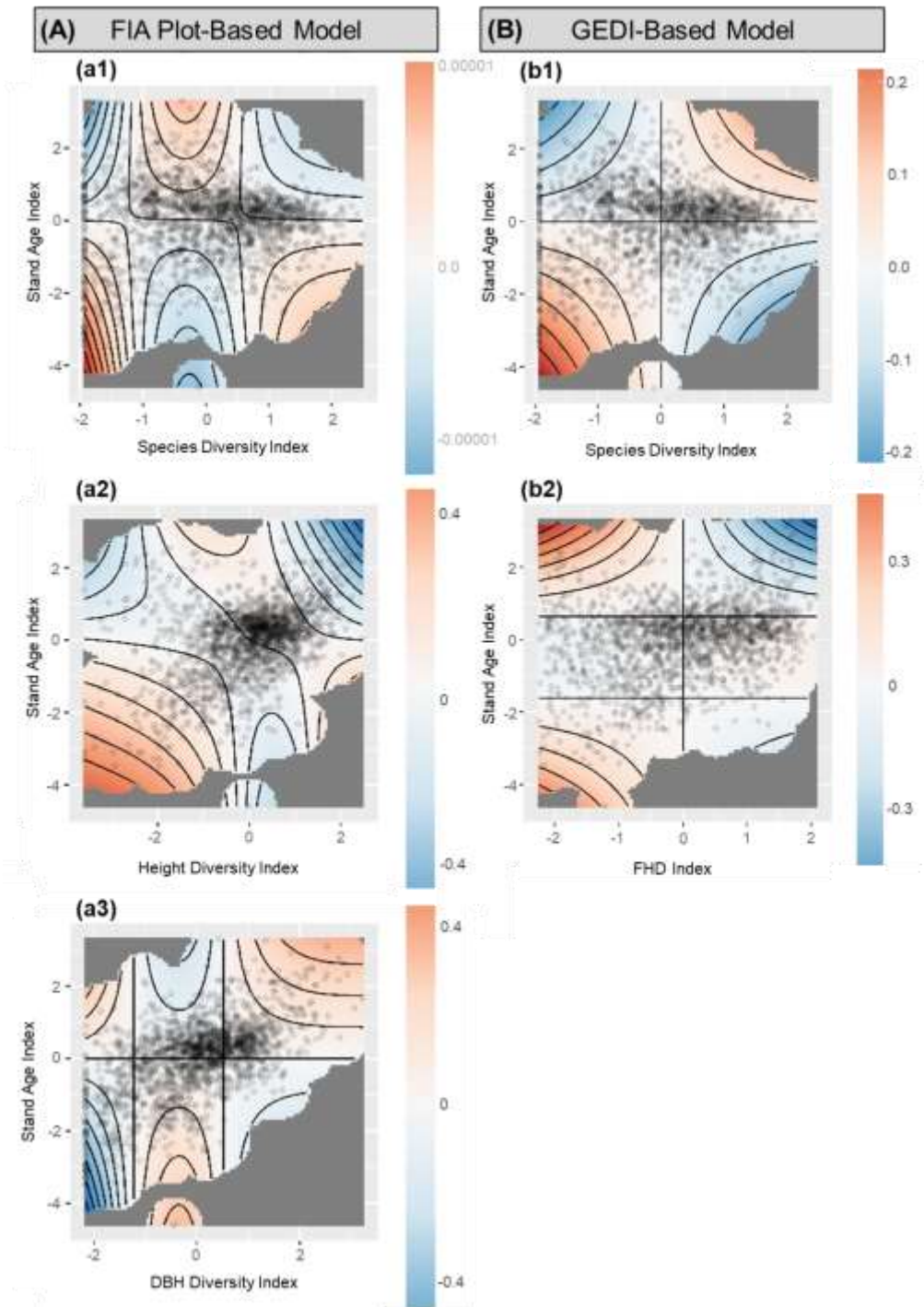


Figure 9. Partial effects plots showing interaction effects between stand age and diversity on carbon storage when using models with (A) plot-based metrics of structural diversity and (B) GEDI-based metrics of structural diversity. Warm (red) colors indicate positive interaction effects, while cold (blue) colors indicate negative interaction effects. Numbers next to the colour bar indicate the combined effect of stand age and diversity metrics on carbon storage. Areas in dark grey indicate too few data points to make reasonable estimates in those regions. Interactions that were not significant are indicated by light grey numbers beside the scale bar.

4. Discussion

4.1 Structural vs. Species Diversity

Our results based on FIA and GEDI data show that structural diversity explained more of the variation in carbon storage (i.e., higher R^2 values) than did species diversity, suggesting important considerations for management. Although we cannot measure species' niches directly in this observational study, our results are consistent with the idea that structural diversity may provide better estimates than species diversity of the niche space occupied by the community (LaRue et al., 2023). Previous work has demonstrated that structural diversity enhances light and resource use efficiencies, potentially explaining relationships with higher productivity and carbon storage (Atkins et al., 2018; Hardiman et al., 2013). One challenge of species diversity is that it remains difficult to partition the effects of composition versus the effects of diversity (Isbell et al., 2018; Loreau and Hector, 2001); differences in composition between sites could confound relationships between diversity and functioning. However, structural diversity approximates how the physical volume of a forest is utilized more directly, potentially reducing this challenge. From a management perspective, incorporating estimates of structural diversity into management considerations could help enhance carbon storage and mitigate climate change.

4.2 FIA Plot-Based vs. GEDI-Based Structural Diversity

FIA plot-based and GEDI-based metrics of structural diversity explained substantially different amounts of the variation in carbon storage, potentially because of uncertainty in the GEDI data, spatial and temporal differences in data collection, and distinctions between what aspects of the vegetation plot-based and GEDI-based metrics capture. Similar to previous studies (Fayad et al., 2021; Wang et al., 2022), we found that GEDI height measurements (RH98) did not match

perfectly with the maximum tree heights in the FIA plots (Fig S2, S3). Accurately estimating the canopy heights from GEDI requires accurate elevations of both the ground returns and top returns. The number of peaks in the lidar waveform, slope and elevation at the site, and forest canopy cover can all introduce error into the GEDI canopy height estimates (Adam et al., 2020; Wang et al., 2022). In addition, plot-based metrics of structural diversity measure diversity at the same location as the carbon storage estimates. On the other hand, some of our GEDI-based measurements come from adjacent locations (i.e., within the 100 m buffer region), and may or may not overlap directly with the trees used to calculate carbon storage. Geolocation uncertainty of up to 10 m in the GEDI footprints further complicates comparing FIA and GEDI data directly and may contribute to these differences between the relationships in plot-based and GEDI-based estimates of structural diversity on carbon storage (Dubayah et al., 2020; Roy et al., 2021); however, similar associations between diversity and carbon storage with the 50 m, 100 m, and 200 m buffer regions (Figures S7-S9), suggest that geolocation uncertainty likely had only minor effects on the core results. Similarly, plot-based measurements of structural diversity and carbon storage estimates are based on data collected at the same time. However, when relating GEDI-based structural diversity to carbon storage, there may be up to a four-year time difference between when data used to calculate structural diversity were collected by GEDI versus when field data used to estimate carbon storage were collected at the FIA plot. In addition to ongoing growth during this period, any disturbances during the intervening years could affect the strength of the structural diversity-carbon storage relationships. Since aggregating data from multiple GEDI footprints reduced the noise associated with individual data points (Figure S2), uncertainty in the GEDI height measurements due to site characteristics and spatial and temporal mismatches

between plot and GEDI data collection—which in turn influence FHD values—could have led to the stronger associations observed in plot-based diversity than GEDI-based structural diversity.

Notwithstanding uncertainty in the contributions of different vegetation elements to carbon storage (Radtke et al., 2017), the plot-based measurements of structural diversity are based on components of forests—the diversity of tree heights and DBHs—which one would expect to be closely related to carbon storage. However, all the vegetation elements in the plot, collectively influence the vertical distribution of lidar return energy, and thus determine the GEDI-based FHD metric. While the leaves, small twigs, and shrubs greatly affect the lidar waveform, these vegetation elements do not contribute nearly as much to carbon storage as the large branches and tree stems. As metrics of structural diversity from plot and remote sensing data are correlated but not identical (Figure S1; Fischer et al., 2019; Knapp et al., 2020), these differences in what components of the vegetation most influenced the FIA plot-based and GEDI-based metrics of structural diversity could explain why plot-based metrics explained much more of the variation in carbon storage.

Although the FIA plot-based metrics explained a greater fraction of the variation in carbon storage, the GEDI-based metrics showed qualitatively similar relationships to those from plot-based metrics (Figures 6, 7). GEDI data could be coupled with other satellite data (e.g., Landsat, Sentinel, NISAR, Tandem-X; Choi et al., 2021; Duncanson et al., 2020) and other data products to interpolate between GEDI footprints and provide spatially continuous estimates of forest structure and diversity in areas without forest inventory plots. While airborne lidar provide more detailed forest information than data from the GEDI satellite, data from satellite sensors such as

GEDI, and ICESat provide 3D structural information across large areas of the world that is freely and openly accessible—information that is highly useful for estimating carbon storage across entire countries and continents.

4.3 Planted vs. Natural Forests

Natural forests may have shown stronger associations with carbon storage than did planted forests for plot-based structural diversity (i.e., DBH diversity) due to management activities or systematic differences in species composition. If human influence on carbon storage through management activities substantially outweighed the influences of structural and species diversity, diversity-carbon storage relationships may appear weak (Guo and Ren, 2014). These ‘planted’ forests are not necessarily ‘plantations’, and the degree of human influence in each forest plot remains difficult to ascertain; some planted forests have experienced no management since planting, while others have been actively managed (Burrill et al., 2021). Thinning or harvesting in planted forests transfer carbon out of the forest plot and also affect structural diversity, thus confounding the relationship between the two. In addition, forest managers often select and plant species and within-species provenances that are particularly suited to the local environmental conditions and/or plant species with fast growth rates and high commercial value (e.g., for the purposes of timber harvesting). We found higher relative proportions of species such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), loblolly pine (*Pinus taeda* L.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), bigleaf maple (*Acer macrophyllum* Pursh), and red alder (*Alnus rubra* Bong.) in planted forests than in natural forests (Figure S12). These (non-random) systematic differences in species composition between planted and natural forests can confound diversity-carbon storage relationships (Sonkoly et al., 2019). This combination of management

actions and species composition differences could explain the one negative relationship observed in this study—between species diversity and carbon storage in conifer-dominated planted forests (Figure 6b3). Future research could explore the role of disturbances and management legacies, and should aim to understand relationships in planted forests since restoration work provides an important application of biodiversity-ecosystem functioning research (Srivastava and Vellend, 2005).

4.4 Future Research Directions and Implications for Restoration & Management

Although theory suggests explanations for why higher diversity may increase carbon storage (i.e., more efficient and complete resource use) (Hooper et al., 2005; Tilman et al., 2014), in this observational study we cannot determine the directions of causality in relationships between diversity and carbon storage, only the strength of their associations across space. Future experimental studies that intentionally create communities with different levels of structural diversity could help elucidate whether there is a causative effect. In addition, just as research has sought to disentangle the effects of species diversity versus species composition (Grime, 1998), future work could examine trade-offs and synergies between promoting structural diversity versus particular structural attributes (e.g., maximum height) for increasing forest productivity and maximizing resilience in the face of changing global conditions.

While forest management plans often include provisions for biological diversity and climate change, our results indicate that incorporating structural diversity into management decisions could help bolster carbon stocks and help meet climate change mitigation targets. For example, in forest restoration projects where planting many tree species may not be feasible (i.e., specific

species are desired, leading to low species diversity), planting seedlings of different sizes and ages, or continuing to plant in subsequent years to create uneven aged stands, could increase forest structural diversity (Laiho et al., 2011). In addition, management actions geared at fostering resilience in highly stocked and/or fire-prone stands might consider increasing the structural complexity of residual trees to encourage higher rates of carbon accrual. Management actions that consider how forest canopies will develop in decades to come (i.e., planning how tree heights, crown shapes and sizes will develop and occupy space) could promote greater light-use efficiency and in turn prompt greater productivity and carbon storage (Atkins et al., 2022, 2018).

5. Conclusions

The combination of spaceborne lidar data from GEDI and ground-based data from FIA enabled us to assess relationships of structural and species diversity with aboveground carbon storage for forests across the contiguous United States. Our results showed strong relationships between plot-based metrics of structural diversity and carbon storage. We found that the amount of variation in carbon storage explained by structural diversity was greater than the variation explained individually by stand age, soil conditions, and climate variables—variables all known to substantially influence carbon storage. Plot-based metrics of structural diversity showed positive relationships with carbon storage in both natural and planted forests, while GEDI based metrics of structural diversity showed positive associations in natural forests, but non-significant relationships in planted forests of mixed broadleaf and conifer trees. Plot-based metrics of structural diversity provided stronger associations with carbon storage than did species diversity or GEDI-based metrics of structural diversity, but using satellite-based lidar measurements of

forest structure and diversity in concert with field-based measurements may be useful for large-scale monitoring programs that strive to estimate carbon storage across the world's forests. Incorporating structural diversity alongside species diversity and climate considerations into management and restoration strategies could help guide efforts to increase carbon storage and mitigate climate change through nature-based solutions.

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Data Availability Statement

We used publicly available data (i) from NASA's GEDI spaceborne lidar (<https://lpdaac.usgs.gov/data/>), (ii) from the Daymet database for climate variables (<https://doi.org/10.3334/ORNLDAAAC/1852>), (iii) from the SoilGrids database 1000m² product

(https://files.isric.org/soilgrids/latest/data_aggregated/), (iv) from the LCMAP land cover map (<https://eros.usgs.gov/lcmap/apps/data-downloads>), and (v) for EPA Ecoregions (<https://www.epa.gov/eco-research/ecoregions-north-america>). Although much data about each FIA plot is publicly available, the locations of plots listed in public datasets are perturbed to protect plot integrity and landowner confidentiality. We acquired actual plot coordinates for this project from the US Forest Service after requesting special permissions and executing a material transfer agreement. For privacy reasons, maps shown in the paper use the perturbed publicly available coordinates.

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