The Relative Effects of Functional Diversity and Structural Complexity on Carbon Dynamics in Late-Successional, Northeastern Mixed Hardwood Forests

Samantha Myers

University of Massachusetts Amherst
THE RELATIVE EFFECTS OF FUNCTIONAL DIVERSITY AND STRUCTURAL COMPLEXITY ON CARBON DYNAMICS IN LATE-SUCCESSIONAL, NORTHEASTERN MIXED HARDWOOD FORESTS

A Thesis Presented

by

SAMANTHA R. MYERS

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SAMANTHA R. MYERS

Approved as to style and content by:

Malcolm Itter, Chair

Paul F. Catanzaro, Member

Miranda T. Curzon, Member

Paige Warren, Department Head
Department of Environmental Conservation
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ABSTRACT

THE RELATIVE EFFECTS OF FUNCTIONAL DIVERSITY AND STRUCTURAL COMPLEXITY ON CARBON DYNAMICS IN LATE-SUCCESSIONAL, NORTHEASTERN MIXED HARDWOOD FORESTS

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SAMANTHA R. MYERS, B.A., WASHINGTON UNIVERSITY IN ST. LOUIS

M.S., UNIVERSITY OF MASSACHUSETTS

Directed by: Professor Malcolm S. Itter

Late-successional forests provide a unique opportunity to explore adaptive management approaches that mitigate atmospheric carbon dioxide levels through carbon storage while also enhancing ecological resilience to novel climate and disturbances. Typical benchmarks for adaptive forest management include species diversity and structural complexity, which are widely considered to increase ecosystem stability and productivity. However, the role of functional trait diversity (e.g., variation in leaf and stem traits) in driving forest productivity and ecosystem resilience remains underexplored. We leveraged existing continuous forest inventory (CFI) data and collected local functional trait observations from CFI plots within late-successional forests in western Massachusetts to explore links between aboveground carbon storage and different types of forest diversity. We then fit a linear model within a Bayesian hierarchical framework applying functional diversity, species diversity, and structural complexity as predictors of live aboveground biomass (AGB) within CFI plots. Our framework integrates local functional trait information with database species mean trait values using a multivariate structure to account for inherent trait syndromes and estimate functional diversity in each plot. Across 626 plot-timepoints, we found that integrating...
individual functional trait information from co-located plots yielded the best predictions of live AGB. Contrary to expectations, functional diversity had a negative relationship with live AGB. Whereas plots with low functional diversity and higher AGB were dominated by mid-to-late successional hardwood species, plots with high functional diversity had more shade-intolerant species and lower AGB mediated by recent small-scale disturbances. Our results reveal an ontogenetic shift in the effects of functional diversity on AGB productivity over the course of succession in northeastern temperate forests. Corroborating with classical models of biomass development in late-successional northern hardwood forests, our findings support the need for adaptive forest carbon management to facilitate a mosaic of different forest successional stages across the landscape to maximize live aboveground carbon benefits in northeastern mixed hardwood forests.
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CHAPTER 1

INTRODUCTION

Global change, including extreme temperatures and novel disturbances (e.g., pest invasions, extreme droughts, and flooding), can shift ecosystem structure and result in the loss of critical ecosystem functions. Global change is already altering disturbance regimes and contributing to shifts in the composition and structure of eastern temperate forests, impacting their capacity to store and sequester carbon (Seidl et al. 2017, McDowell et al. 2020). These unprecedented impacts necessitate the development of adaptive management strategies to maintain ecosystem function in the face of changing conditions (Millar et al. 2007, Jandl et al. 2019). At the same time, there is increasing interest in forest carbon management as a climate mitigation tool, especially in the heavily forested northeastern U.S. (Birdsey et al. 2006, Nunery and Keeton 2010, Fahey et al. 2010, Gunn et al. 2014, Ford and Keeton 2017). Since the promotion of forest ecosystem resilience directly relates to the long-term sustainability of forest carbon stores, existing adaptive management strategies are often used as a starting point for forest carbon management (Ontl et al. 2020).

Ecologists and land managers often use diversity metrics including species diversity and structural complexity as adaptive management benchmarks since high species diversity and structural complexity are widely considered to increase ecosystem stability and productivity (Tilman 1999, Franklin et al. 2002, Reich et al. 2004, Gough et al. 2019). Whereas species diversity indicates the variation and relative abundance of species present in the forest, structural complexity is a measure of the variation in vertical and horizontal stand structure including variability of tree size, canopy strata, abundance
of standing deadwood and downed woody material, and frequency and size of forest gaps (Franklin et al. 2002, McElhinny et al. 2005). In general, greater ecological diversity (i.e., containing a variety of species or organisms from different functional groups) has been shown to contribute to higher productivity and ecosystem stability driven by niche complementarity in a variety of terrestrial ecosystems (Holling 1973, Lehman and Tilman 2000, Loreau and Hector 2001, Gonzalez and Loreau 2008, Tilman et al. 2014, Gross et al. 2014). In forests globally, studies have found positive effects of biodiversity on productivity, including strong effects in boreal forests and weaker positive effects in temperate hardwood forests (Paquette and Messier 2011, Liang et al. 2016). Other studies, however, have found differing effects of diversity on forest productivity, especially when looking across different carbon pools (Hooper et al. 2005, Adair et al. 2018). A range of studies over the past two decades have demonstrated a positive relationship between structural complexity and carbon storage across both natural and managed stands (Franklin et al. 2002, Nunery and Keeton 2010, D’Amato et al. 2011, Hardiman et al. 2011, Bradford and D’Amato 2012, Ruiz-Benito et al. 2014, Dănescu et al. 2016, Thom and Keeton 2019, 2020). However, the magnitude of the effects of structural complexity on aboveground biomass (AGB) production may depend on the structural metrics used (Forrester and Bauhus 2016).

Functional trait diversity (hereafter, “functional diversity”) is linked to species diversity and structural complexity (i.e., functional traits relate to a species’ life history strategy and growth form), yet its potential impact on forest carbon and resilience in the context of adaptive management is not well explored. Functional traits (e.g., specific leaf area, leaf nutrient content, and wood density) contribute to a species’ fundamental niche,
thereby impacting population fitness, community dynamics, and myriad ecosystem functions (Reich et al. 2003, Violle et al. 2007, Reich 2014, Kraft et al. 2015, Laughlin et al. 2020). Functional diversity has been found to lead to higher ecosystem stability and productivity in grassland ecosystems and may enhance AGB productivity in forests (Tilman et al. 1997, Reich et al. 2004). A number of studies have found that functional traits drive forest productivity in temperate and boreal forests (Paquette and Messier 2011, Ziter et al. 2013, Ruiz-Benito et al. 2014, Lin et al. 2016, Yuan et al. 2016, Espelta et al. 2020) and that functional diversity better explains variation in AGB than species diversity (Ziter et al. 2013, Ruiz-Benito et al. 2014, Yuan et al. 2018). Most of these studies have used species-level univariate trait analyses. However, accounting for intraspecific variability in functional traits is crucial to understanding different demographic responses to variable biotic and abiotic conditions leading to variation in stand-level AGB (Reich 2014, Laughlin and Messier 2015, Kunstler et al. 2016, Laughlin et al. 2020). Contemporary trait-based approaches suggest that we can better assess the role of functional diversity on long-term forest AGB dynamics by integrating intraspecific variability within local trait observations, moving beyond existing species-level mean trait values (e.g., Kattge et al. 2020) while also modeling covariation among traits related to inherent trait syndromes (Wright et al. 2004, Chave et al. 2009, Reich 2014, McGill et al. 2006, Laughlin et al. 2012, 2020, Reich 2014, Laughlin and Messier 2015, Clough et al. 2017, Cardou et al. 2022).

Diversity-productivity relationships in forests are further complicated by successional dynamics which cause broad shifts in species composition and functional groups (e.g., shade tolerance), forest structure, and other ecological processes over time.
Some studies have found that positive biodiversity-productivity relationships become stronger over time in forests, particularly early in stand development (Urgoiti Otazua et al. 2022), and weaken in later successional stages (Lasky et al. 2014). Stand complexity and functional diversity, in particular, may have a greater impact on productivity in early to mid-successional forests than in late-successional or old-growth forests (Hardiman et al. 2011, Fahey et al. 2015, Yuan et al. 2016).

Late-successional forests are important model systems in the context of carbon management since they have high carbon stores and high structural complexity. Given these forests are dominated by late-successional species with higher shade tolerance and slower growth rates, we expect them to have lower overstory tree species diversity and accordingly lower functional diversity than other forest successional stages (Spies and Franklin 1996, Scheller and Mladenoff 2002, Gravel et al. 2010). Though classical stand development models predict declining sequestration rates in late-successional forests (Odum 1969) others predict late-successional forests exist within a ‘dynamic steady-state’ in terms of biomass accumulation in which total biomass (carbon stores) fluctuates about a constant equilibrium (Bormann and Likens 1979). Further, late-successional forests in the Northeast may have a higher capacity to store and sequester carbon in AGB than previously considered (Keeton et al. 2011, Gunn et al. 2014, Pontius et al. 2016). Late-successional forest ecosystems provide key characteristics to disentangle the effects of diversity (species, functional, structural) on long-term forest carbon dynamics and reach a clearer consensus on the multifaceted biodiversity-productivity relationships in forests needed to inform adaptive management.
The goal of this study is to understand the relative contributions of forest structural complexity, functional diversity, and species diversity on long-term live AGB in late-successional mixed hardwood forests in the northeastern U.S. We focus on quantifying the effects on live AGB since it is one of the largest and most variable pools of carbon in forest ecosystems and therefore has a strong correlation with forest carbon storage. To do this, we combined long-term forest inventory data and local functional trait observations within a Bayesian hierarchical model to advance understanding of the relationships between live AGB dynamics and different types of diversity in late-successional, northeastern mixed hardwood forests. Our model synthesizes local, individual functional trait observations with existing species-level mean trait values applying a multivariate structure that accounts for inherent trait syndromes. We applied our model to quantify the relative effects of species diversity, functional diversity, and structural complexity as drivers of live AGB in order to inform forest carbon management practices in late-successional, northeastern mixed hardwood forests.
CHAPTER 2

METHODS

2.1 Site selection and continuous forest inventory

We conducted our study at 304 existing Massachusetts Department of Conservation and Recreation (DCR) continuous forest inventory (CFI) plots across 7 state forests in western Massachusetts. The CFI network consists of over 2,000 1/5-ac fixed-area plots established beginning in 1957 and located on half-mile grid on public land in the state across a variety of management designations. These plots are measured periodically (every 8–20 years), providing forest inventory measurements including tree species, status, crown class, and diameter at breast height (DBH) of all trees greater than 5-inches DBH. Recent inventories also included tree height measurements and coarse woody debris sampling along three transects (including all pieces ≥ 3 inches in diameter and ≥ 3 feet in length).

Using the most recent CFI data from 12 state forests known to contain late-successional or old-growth mixed hardwood stands, we classified the successional stage of each plot via a modified version of the classification method in Lorimer and Halpin (2014). This method is based on total basal area and relative proportions of basal area within four defined size classes (sapling, pole, mature, and large) in each plot. Plots that were identified as late-successional (including early-to-late transitional and steady state phases) were targeted for functional trait sampling. During functional trait sampling (described in greater detail below), we recorded observations of tree status, diameter at breast height, height, crown class, and coarse woody debris abundance within CFI plots.
which had not been measured in the last three years (2018-2021). We then expanded our analysis to include all plots within the 7 state forests in which the late-successional plots were located. Though many plots in our analysis fall within areas currently designated as forest ‘reserves’ (designated in 2010, after which no timber harvests may occur), each property has variable land-use history, including potential agricultural or timber harvesting activity (William VanDoren, PC).

2.2 Functional trait sampling

Functional traits were sampled from all live trees at least 5 inches in DBH located within three 15.2-ft fixed-radius subplots established 76 ft from CFI plot center along the three course woody debris transects (30°, 150°, 270°). We measured five functional traits related to plant productivity and photosynthetic capacity common in plant trait literature: leaf nitrogen content, leaf carbon to nitrogen ratio, leaf phosphorus content, specific leaf area (SLA; fresh leaf area over dry mass), and wood density (green volume over dry mass) (Reich et al. 2003, Wright et al. 2004, Chave et al. 2009, Reich 2014).

Traits were measured using methods modified from Pérez-Harguindeguy et al. (2013). From each tree, we collected two increment cores using a 5.15 mm increment borer and 3-4 g of sun-exposed leaves using an arborist throwline (200ft, 2mm width), 10-12 oz weighted throw bags, and Tru Shot™ Line Launcher (Jameson) (Youngentob et al. 2016). For broadleaf species, 3-7 disks were cut out of 4-7 leaves per tree using a 0.75-in diameter hollow steel hole punch (General Tools). To calculate SLA, leaf disks from broadleaf trees were dried at 60-70°C for 24 hours and weighed. The area of the hole punch device was calibrated according to Loustau et al. (2018) and used to calculate
fresh leaf area. Needle leaves were imaged and leaf area was calculated using ImageJ (Schneider et al. 2012). Needles were then dried at 60-70°C for 24 hours and total weight was recorded for each sample. For all leaf samples, weight was measured to the closest 0.001 g twice and averaged. For leaf nutrient content analysis (total C, N and P), leaves were dried at 60-70°C for 24 hours and petioles were removed from broadleaf samples. Leaves collected from each individual were pooled and grinded. Leaf total carbon and nitrogen content (percent of dry mass) was determined via combustion method using a Primacs SNC-100 TN/TC Analyzer (Skalar, Inc). For leaf phosphorous analysis, ground leaf material was asched at 550°C for 8 hours, then digested with reverse aqua regia at 90°C for 1 hour. Fresh green volume of increment cores was taken in the field by measuring water displacement before samples were dried at 103°C for 18-24 hours and weighed. Wood density was averaged across the two samples per tree.

2.3 Functional diversity

Functional diversity, species diversity, structural complexity indices, and total live AGB were calculated for CFI plots during all remeasurement years from 2000-2021 (hereafter, “plot-year”). Plots were dropped if they had no trees present in the inventory and/or were recently harvested (7 plots). Functional dispersion, a multivariate functional diversity index, was calculated with the FD package in R (Laliberte and Legendre 2010, Laliberté et al. 2014) using species mean trait values for 29 species within the CFI plots in the study region. Mean trait values for the five traits (wood density, specific leaf area, leaf percent nitrogen and phosphorus, and leaf carbon to nitrogen ratio) were derived from TRY plant trait database (see Appendix B for more details) and weighted by species’ relative basal area to calculate functional dispersion for each plot-year (Kattge et
al. 2020). Basal area calculations included only live species and species were dropped from the analysis if they did not meet the following criteria: a) species is present at a minimum of 5 plot-years and makes up at least 5 percent of the total live AGB in at least one site or b) species is present at less than 5 plot-years but makes up at least 10 percent of total live AGB at a minimum of one of those timepoints. Chestnut oak, which accounted for a small fraction of the basal area in a few plots, was the only species not represented in the TRY database, so white oak mean trait values were used instead. Hickory species were pooled and trait means for three common hickory species (pignut, bitternut, shagbark) were averaged for the functional dispersion calculation. Additionally, trees coded as unknown or other species were dropped. This resulted in 22 species included in the model analysis.

2.4 Structural complexity, species diversity, and live aboveground biomass

Stand density and structural complexity metrics were calculated for all CFI plot-years from 2000 to 2021 based on available data. For all plot-years, we calculated total live basal area, stems per acre, Reinke’s stand density index, quadratic mean diameter, percent softwood composition (by basal area), number of large trees per acre (DBH > 50 cm), Shannon’s effective diameter diversity index of live trees (bins of 5 inches), diameter variance, snags per acre, and large snags per acre (DBH > 50 cm). For recent inventory years (2010-2021), we also calculated Shannon’s effective height diversity (bins equally spaced from min to max), height variance, Shannon’s effective crown class diversity, foliage height diversity (Shannon’s effective diversity in upper and lower foliage extent weighted by basal area), number of foliage strata (bins of 3m), and coarse woody debris biomass (tons per acre) (McElhinny et al. 2005, Woodall and Monleon
2008, Thom and Keeton 2019) (see Appendix C). For all plot-years we also calculated Shannon’s effective species diversity index weighted by live relative basal area, excluding species designated as unknown or other.

Total live AGB was estimated by applying Jenkins AGB equations for each plot-year (Jenkins et al. 2003). In total, missing species which were excluded from functional dispersion, species diversity, and AGB calculations made up more than 5 percent of basal area in 22 out of 626 plot-years (3.5 percent) with a maximum percent of overall basal area of 16.2 percent.

2.5 Modeling approach

We fit a Bayesian hierarchical model estimating total live AGB in CFI plot-years from 2000 to 2021 as a function of varying combinations of forest density, relative abundance of softwoods, structural complexity, species diversity, and functional diversity. Plot-years without any species present for which functional traits were collected were dropped from the analysis (3 plot-years), resulting in 626 plot-years total across 304 plots. All study plots had 2-3 measurements that were 5-20 years apart (except for 5 plot-years which were measured less than 5 years apart). We tested three candidate models of live AGB following from our study objectives. The general model form was as follows: Live AGB ~ Forest density + Percent softwood composition + Structural complexity + Species/functional diversity + Error.

All three models included basal area per acre and percent softwood composition (by basal area) to control for the effects of forest density and softwood composition on total live AGB. Further, all models included Shannon’s diameter diversity, snags per acre, and large snags per acre as measures of structural complexity. The three structural
complexity variables were selected given high correlation with live AGB and low correlation among variables. The three models differed in their inclusion of species versus functional diversity as predictors of total live AGB. The first model included species diversity in addition to density and structure, while in the second and third models, species diversity was replaced with functional diversity.

The two functional diversity models were used to explore the effects of local functional trait values on live forest AGB. In the first of these two models, we used existing species-level mean trait values from the TRY database to calculate functional dispersion. In the second model, we applied a functional trait sub-model to update species-level mean trait values based on local trait observations at the individual scale. Specifically, we modeled individual trait observations as, $t_{ij} \sim \text{MVN}(\mu_j, \Omega)$, where $t_{ij}$ denotes a 5-dimensional vector of trait observations from the $i^{th}$ individual and the $j^{th}$ species, $\mu_j$ is the 5-dimensional species-level mean trait value, $\Omega$ is a 5-dimensional trait covariance matrix, and $\text{MVN}(\cdot)$ denotes a multivariate trait distribution. Individual trait observations are modeled jointly among traits as a function of species-level trait means and individual trait variability with inherent trait syndromes modeled explicitly through the trait covariance matrix. Existing species-level mean values and associated measures of uncertainty from the TRY database are integrated through the prior distribution on species-level trait means: $\mu_{jk} \sim N(\theta_{jk}, \nu_{jk})$. Here, $\mu_{jk}$ is the univariate species-level mean for the $j^{th}$ species and $k^{th}$ trait (i.e., an individual element of $\mu_j$), while $\theta_{jk}$ and $\nu_{jk}$ are species-level mean traits and species-specific standard deviation values for each trait mean compiled from the TRY database (when standard deviation was not available, $\nu_{jk}$ was set at 10 percent of $\theta_{jk}$, or in rare cases was set equal to the mean; n=7 species-trait
combinations; see Appendix B). Under this approach, species-level trait means are allowed to shift depending on individual trait observations and associated uncertainty (Fig. 1).

All models were fit using Markov chain Monte Carlo (MCMC) simulation to numerically estimate the joint posterior distribution using the RStan package in R (Stan Development Team 2022). Details on model implementation including prior specification are provided in Appendix D.

We used the Watanabe-Akaike information criterion (WAIC) to evaluate and compare the three candidate models in terms of their ability to predict live AGB. WAIC provides a fully-Bayesian measure of in-sample model prediction based on the posterior predictive distribution subject to a penalty term (Gelman et al. 2014, Hooten and Hobbs 2015). WAIC is well suited to the current analysis where interest is on in-sample inference rather than out-of-sample prediction. We further estimated Bayesian R-squared values for each of the three models to determine the proportion of variability of live AGB explained by each model (Gelman et al. 2019) as well as estimating the proportion of variability explained by forest density and softwood composition (combined), structural complexity, and species or functional diversity (Schulz et al. 2021). More details on the estimation of Bayesian R-squared values and variance partitioning are provided in Appendix D.
Figure 1: Schematic of model-updated species mean trait values. Given the database mean and standard deviation in database mean species-trait values (blue) and distribution of local species-trait observations (orange), the updated species mean trait value (asterisk) will shift according to one of four scenarios: If there is no difference between the mean values, there will be no change in the mean trait value. (Scenario 1). If the mean values are different between the two data sources, the trait may or may not shift depending on the relative amount of variation in the two data sources (Scenarios 2A-C). If the variability in the database means is small, the updated trait mean will stay at the database mean trait value (Scenario 2A). If the variation in the local trait observations is small, the updated trait mean will shift towards the local trait mean (Scenario 2B). If the variation in the database mean trait values is similar to the variation in local trait observations, the updated trait mean will fall between the two mean values (Scenario 2C).
CHAPTER 3
RESULTS

3.1 Forest aboveground biomass model results

After fitting three models that integrated functional diversity or species diversity and structural complexity to predict live AGB, we found that the models with functional diversity explained about the same amount of variation in AGB as the model with species diversity (Table 1). Though all three models were comparable in terms of predictive ability, the model with functional diversity that integrated local trait information (WAIC= -2111) performed slightly better than both the model with functional diversity using database species mean trait values (WAIC= -2118) and the model with species diversity (WAIC= -2120). We also compared these models to a null model without functional or species diversity to test the value of including these diversity metrics and found that it was comparable but performed slightly worse than the other three models (WAIC= -2129). In the top model, most of the variation in total live AGB was explained by basal area and softwood composition (proportion of variability= 0.73 [0.70, 0.75]), followed by structural complexity (proportion of variability= 0.07 [0.06, 0.08]), and functional trait diversity (proportion of variability= 0.004 [0.001, 0.008]) (Table 3). Further, though functional diversity and species diversity explained very small proportions of variability in live AGB, the model with local trait information increased the amount of variation explained by functional diversity compared with the model that used database species mean values (proportion of variability= 0.003 [0.0007, 0.006]) and explained more than species diversity (proportion of variability= 0.002 [0.0003, 0.005] (Table 3).
Functional diversity was predicted to have a negative relationship with AGB, whereas different structural covariates had varying effects on AGB that were generally consistent across all three models (Table 2). In the top model, diameter diversity was predicted to have a positive relationship with live AGB whereas snags per acre was predicted to have a negative relationship with live AGB. In the third model, species diversity was also estimated to have a negative association with live AGB with a similar magnitude to the functional diversity coefficient estimates (posterior coefficient estimate = -2.92 [-4.68, -1.11]).

Table 1: Comparison of three models using functional diversity or species diversity along with structural complexity metrics to predict live AGB. Model comparison using Watanabe-Akaike information criterion (WAIC) and overall R \(^2\) values with 95% credible intervals are displayed for each model.

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<tr>
<td>FDis (local trait update)</td>
<td>BA/ac, diameter diversity, snags/ac, large snags/ac (&gt;50cm), Proportion softwood</td>
<td>-2111.215</td>
<td>0.95 [0.94,0.96]</td>
</tr>
<tr>
<td>FDis (database species means)</td>
<td>BA/ac, diameter diversity, snags/ac, large snags/ac (&gt;50cm), Proportion softwood</td>
<td>-2117.788</td>
<td>0.95 [0.94,0.95]</td>
</tr>
<tr>
<td>Species diversity</td>
<td>BA/ac, diameter diversity, snags/ac, large snags/ac (&gt;50cm), Proportion softwood</td>
<td>-2119.852</td>
<td>0.95 [0.94,0.95]</td>
</tr>
</tbody>
</table>

Table 2: Posterior mean coefficient estimates with 95% credible intervals for parameters in the top model (includes functional diversity with local trait update).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient estimate (+/ - 95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-14.71 [-18.3, 11.27]</td>
</tr>
<tr>
<td>Density (BA/ac)</td>
<td>91.1 [88.8, 93.3]</td>
</tr>
<tr>
<td>Diameter diversity</td>
<td>31.5 [28.6, 34.32]</td>
</tr>
<tr>
<td>Snags/ac</td>
<td>-2.22 [-3.14, 1.28]</td>
</tr>
<tr>
<td>Large snags/ac</td>
<td>0.38 [-0.21, 0.96]</td>
</tr>
<tr>
<td>Proportion softwood</td>
<td>-10.24 [-11.13, 9.34]</td>
</tr>
<tr>
<td>Functional diversity</td>
<td>-4.2 [-5.88, 2.42]</td>
</tr>
</tbody>
</table>
Table 3: Proportion of variability in live AGB explained by the covariates of each model, partitioned between basal area per acre and proportion softwood (combined), diversity metric (functional or species diversity), and structural complexity metrics (diameter diversity, snags per acre, and large snags per acre combined). Overall R^2 values included with their 95% credible intervals.

<table>
<thead>
<tr>
<th>Model</th>
<th>Density/Prop. softwood</th>
<th>Diversity (functional or species)</th>
<th>Structural complexity</th>
<th>Overall R^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1: FDis with local trait update</td>
<td>0.726 [0.702,0.751]</td>
<td>0.004 [0.001,0.008]</td>
<td>0.072 [0.062,0.084]</td>
<td>0.95 [0.94,0.96]</td>
</tr>
<tr>
<td>Model 2: FDis</td>
<td>0.723 [0.697,0.749]</td>
<td>0.003 [0.001,0.006]</td>
<td>0.075 [0.064,0.087]</td>
<td>0.95 [0.94,0.95]</td>
</tr>
<tr>
<td>Model 3: Species diversity</td>
<td>0.721 [0.696,0.747]</td>
<td>0.002 [0.005]</td>
<td>0.075 [0.065,0.087]</td>
<td>0.95 [0.94,0.95]</td>
</tr>
</tbody>
</table>
Under the local functional trait model, estimates of species-level mean trait values had largest shifts from database mean values when the variation in the database values was high and differences between species mean trait values were high. On the other hand, moderate changes in the mean trait value reflected moderate differences between mean values and lower standard deviation in local observations than database values (Fig. 2). The variance between most observed traits values was lower than the variance between database mean trait values except for a few mean values for leaf P and a few species-trait values where the sample size of local observations was ≤ 5. Small to no changes in estimated mean trait value reflected small differences in mean trait value between observed traits and database values.

![Figure 2: Percent change between database mean value (theta) and the posterior mean estimate for each species mean trait value (mu_t): (posterior mean of mu_t - theta)/theta with sample sizes of local trait observations for each species in parentheses.](image-url)
3.2 Trends in species composition and structure across high and low functional diversity plot-years

Upon investigating the negative relationship between functional diversity and live AGB, we found that plot-years with high and low functional diversity differed in species composition and structure. For example, plot-years with low functional diversity were dominated by shade tolerant and mid-tolerant hardwood species (e.g., sugar maple, northern red oak, red maple, and beech) whereas plot-years with high functional diversity were more likely to have a mixture of species, including softwood species (e.g., white pine, red pine, red spruce, Norway spruce, hemlock, balsam fir) and shade-intolerant species (e.g., white birch, trembling aspen, black cherry, black birch, red pine) than plots with low functional diversity (Fig. 3). Accordingly, plot-years with high functional diversity also tended to have higher species diversity than plots with low functional diversity but species diversity was slightly more variable. Only 4 out of the 40 plot-years with the lowest functional diversity had more than 10 percent softwood species by relative basal area. These plot-years were dominated by Eastern hemlock, white pine, or Norway spruce.

Plot-years with high and low functional diversity also differed in stand structural attributes (Fig. S1-S2). Low functional diversity plot-years had on average higher quadratic mean diameter (QMD) and diameter diversity and fewer snags per acre on average than high functional diversity plot-years. They also had lower and less variable stand density and total basal area on average than high functional diversity plot-years. Changes in live AGB over the inventory time period (2000-2021) were slightly positive, on average, and increased with increasing functional diversity at the first timepoint,
suggesting slightly higher AGB accrual rates in plot-years with higher functional diversity (Fig. 4).

Figure 3: Proportion of species with low, medium, and high shade tolerance in the plot-years with the lowest and highest functional dispersion calculated using posterior model parameter estimates (n=40 in each group). Each vertical bar represents a plot-year, ordered by ascending functional dispersion values from left to right. Plot-years with low functional diversity are primarily dominated by Northern red oak, sugar maple, red maple, and beech, while plot-years with high functional diversity are dominated by a range of low to high shade-tolerant hardwood and softwood species.
Figure 4: Change in total live AGB between inventory timepoints (T1 and T2) at all CFI plot-years 2000-2021 as a function of total live AGB (A) and mean posterior functional diversity (B) at T1 (n= 322). Similar trends are found when the y-axis is normalized by time between inventory years (i.e., converted to biomass increment). Distribution of the change in live AGB (C) and change in live AGB increment (D) across all CFI plot-years 2000-2021 (n= 322).
CHAPTER 4
DISCUSSION

Elucidating the relationships between various measures of forest diversity and carbon storage is of critical importance to further adaptive forest carbon management in the Northeast. Within this context, the role of functional diversity in forest carbon dynamics remains underexplored. We found that incorporating local functional trait information to estimate plot-level functional diversity yielded the best predictions of live AGB (Table 1). Contrary to expectations, functional diversity had a negative relationship with live AGB across 626 plot-years (Table 2). Together, our results illuminate the critical role that successional dynamics play in mediating the diversity-productivity relationship in mixed hardwood forests, including shifting the direction and magnitude of the effects of functional diversity on live AGB.

4.1 Structural complexity, density, and softwood composition were stronger predictors of live AGB than functional and species diversity

As opposed to previous studies that found that functional traits explain variability in ecosystem provisioning better than species richness alone (Balvanera et al. 2005, Bunker et al. 2005, Paquette and Messier 2011, Ziter et al. 2013, Ruiz-Benito et al. 2014, Yuan et al. 2018), we found little difference in the variability of live AGB explained by functional diversity and species diversity. Instead, variability in live AGB was explained most strongly by forest density, softwood composition and structural complexity of the overstory. Rather than functional and species diversity, we find that overstory forest composition (i.e., proportion softwood) and structure are larger drivers of live AGB, reflecting both physiological differences in the carbon storage capacity of hardwood and
softwood species and the variation in structural complexity in late-successional forests (Franklin et al. 2002).

Though there was a slight preference towards the models with diversity metrics, there was no practically significant difference between the predictive ability of the models with functional diversity, species diversity, and the null model without either metric. Further, neither functional diversity nor species diversity were strong predictors of live AGB across the plots (Table 1, Table 3). These results reflect the low levels of and low variability in species and functional diversity of overstory trees typical in late-successional mixed hardwood forests dominated by shade-tolerant species (Oliver and Larson 1996, Spies and Franklin 1996, Franklin et al. 2002, Scheller and Mladenoff 2002, Gravel et al. 2010, D’Amato et al. 2011). This illuminates the ability of ontogenetic shifts across forest successional stages to shape diversity-productivity relationships, particularly in the context of functional trait diversity and its impact on community assembly and function (Lasky et al. 2015). For example, in early-successional forests, overstory species diversity has been found to have increasingly positive effects on forest productivity driven primarily by increasing complementarity effects (Urgoiti Otazua et al. 2022). This positive effect has been found to decline in mid-successional forests (Lasky et al. 2014) and disappear in some late-successional and old-growth forests (Hardiman et al. 2011, Fahey et al. 2015). Notably, diversity in trait strategies may only impact demographic rates (i.e., growth) and total AGB if environmental conditions are diverse enough within or across stands to facilitate dominance-tolerance trade-offs (Grossman et al. 2018, Zheng et al. 2021). In contrast to the strong positive diversity-productivity relationship found in early-to-mid-successional forests with higher variability in
functional and species diversity, in late-successional forests we see a small effect of functional and species diversity on live AGB stores. This highlights the need for more studies integrating functional diversity to investigate the multifaceted diversity-productivity relationships across forest successional stages.

4.2 Functional diversity has a negative effect on aboveground biomass in late-successional forests

The negative effect of functional diversity on live AGB suggests that productivity is driven by disturbance-mediated compositional shifts in late-successional mixed hardwood forests. Plot-years with low functional diversity were composed of mid-to-late-successional canopy-dominant hardwood species (e.g., Northern red oak and sugar maple), which have similar slow resource acquisition strategies, exemplified by mid-to-high shade tolerance (Fig. 3; Reich 2014). At the tree level, these dominant hardwood species store more biomass than other dominant species (e.g., eastern hemlock), which contributes to higher overall live AGB compared to late-successional stands that are less hardwood-dominated, barring tree mortality events (Jenkins et al. 2003). On the other hand, plot-years with high functional diversity were composed of a variety of hardwood and softwood species with a range of shade tolerances and trait strategies. Particularly, the higher proportion of shade intolerant hardwood species in these plots suggests that small-scale disturbances may be driving the negative functional diversity-biomass productivity relationship. Our results suggest that differences in species trait values play a minor role compared to the role of disturbance in driving the negative functional diversity-productivity relationship. The dominance of mid-to-high shade-tolerant hardwood species in low functional diversity plots compared to a mix of species
including shade-intolerant species in high functional diversity plots suggests that disturbance-mediated stand development/successional dynamics, rather than competitive dominance or complementarity effects, shape the negative diversity-productivity relationship we find in the current study. Our findings are similar to another study that found that managed sugar maple stands also had a negative functional diversity-productivity relationship due to the key driver of anthropogenic disturbance (Ziter et al. 2013).

4.3 The role of disturbance in shaping the structure, function, and carbon dynamics in late-successional forests

Inextricably linked to successional dynamics, disturbance plays a key role in shaping functional, species, and structural diversity and driving late-successional forest carbon dynamics. Disturbances affecting northeastern mixed hardwood forests are semi-frequent, non-stand replacing events such as wind and ice storms which cause variability in composition and structure of mid-to-late-successional forests that are in the late-transition or dynamic steady-state phase of stand development (Bormann and Likens 1979). In the dynamic steady-state that characterizes late-successional forests, total ecosystem biomass is predicted to stay relatively constant over the long-term but fluctuate in the short term due to non-stand replacing disturbances (as a “dynamic but relatively unchanging condition”) until a catastrophic stand-replacing disturbance occurs. We see similar patterns across our study plot-years which show slightly positive changes in live AGB on average, contrary to previous expectations that biomass accumulation rates will decline over time in late-successional northern mixed hardwood forests (Odum 1969) but in line with more recent studies (Fig. 4; (Keeton et al. 2011, Gough et al. 2013,
Pontius et al. 2016, Curtis and Gough 2018). In our plots, this likely relates to the lack of recent large-scale disturbance leading to equilibrium in biomass levels, with some variation around this equilibrium as a result of recent small-scale disturbances. In addition to causing a temporary decrease in live AGB, these small-scale disturbances have likely increased functional diversity and biomass accrual rates in recently-disturbed plot-years (Fig. 4). In this dynamic steady-state, the system is able to return to equilibrium shortly after small-scale disturbances, maintaining key ecosystem functions, unless disturbed past a tipping point (i.e., a large patch cut or stand-replacing disturbance). Adaptive forest management strategies can take advantage of the natural resilience within the dynamic steady-state which preserves long-term carbon stores by focusing active management on early-to-mid successional stands wherein facilitation of high functional diversity is expected to yield higher net productivity and aboveground carbon stores. In late-successional forests, such management serves to reduce live aboveground carbon stores with limited residual productivity benefit.

4.4 Integrating local trait information shifted mean species trait values and improved model prediction

Although we found that functional diversity explained only a small proportion of the variability in live AGB across plot-years, integrating local trait information improved model predictions and increased the proportion of variability explained by functional diversity (Table 1, 3). The traits we considered (wood density, leaf nutrient content, and specific leaf area) relate to life history strategies that impact plant growth mediated by environmental conditions. Further, the mean value and intraspecific variability within traits may shift across an individual tree’s lifetime (Spasojevic et al. 2014, Lasky et al.)
2015, Chun and Lee 2019) and across forest successional stages (Hulshof and Umaña 2022). Whereas most studies estimate functional diversity using species mean trait values derived from global trait databases, compiled across a variety of environmental conditions including successional stages, climate, and other stand-level variables, our estimate of functional diversity utilizes “updated” species mean values informed by local trait information (reflecting both local environmental conditions and successional stage) that accounts for intra-specific trait variability (Fig. 1).

Species mean trait value updates reflect the differences in both mean value and variation within the database and local trait information for each species-trait combination (Fig. 1, 2). Since variability within local trait observations was often smaller than variability between database mean trait values, when the database mean value differed from the local trait mean, the updated trait mean was either a compromise between the two mean values or strongly shifted towards the local trait mean when local variability was magnitudes smaller. Whereas contemporary trait-based approaches require large samples sizes to connect individual demographic processes (e.g., growth, mortality) to individual functional traits accounting for intraspecific variability and inherent trait syndromes (Laughlin and Messier 2015), our modeling approach enables the use of local trait information to improve mean species trait estimates and inform site-specific analyses, even when per-species sample sizes are small at local sites. As a result of updating database species mean trait values, our functional dispersion estimates captured more variability in AGB across the late-successional plots which had similar stand-level and climatic conditions to the subset of plots where traits were collected. Our findings highlight the need for the continued collection of local functional trait
information in forest functional diversity studies, as our approach enables ecologists to make use of limited trait information and trait datasets with low sample sizes, especially when making inferences about functional diversity driving forests processes across climatic gradients and stand development stages (Laughlin and Messier 2015, Urgoiti Otazua et al. 2022).
CHAPTER 5

MANAGEMENT IMPLICATIONS

This study illuminates the need to broadly integrate functional diversity along with species diversity and structural complexity in the context of adaptive forest carbon management. While enhancing functional and species diversity may be crucial in biodiversity conservation, forest resilience, and other ecosystem processes, managers may primarily consider stand structural complexity when managing for live aboveground carbon benefits within late-successional, northeastern mixed hardwood forests. Our results emphasize the trade-offs between creating small-scale gaps in late-successional forests stands to promote resilience by facilitating the regeneration of low-to-mid shade tolerant species, which may slightly increase functional diversity and lead to temporarily lower live aboveground carbon stores without an additional long-term growth benefit. Rather, management should consider broadening strategies across the landscape, where distinct stands can be managed differently to enable different successional stages, as laid out as the “shifting mosaic steady state” which mimics the natural disturbance regime in northeastern hardwood forests (Bormann and Likens 1979). For example, managers may enhance early-to-mid-successional forests to reap carbon sequestration benefits from cutting, while preserving late-successional and old-growth stands elsewhere with their high carbon stores in a “dynamic steady state equilibrium” barring a stand-replacing disturbance. Though these stand-replacing disturbances are unpredictable and temporarily reduce carbon stores, actively diversifying the representation of successional stages across the landscape enables a broader inventory of aboveground carbon stores that in itself can serve as a landscape-scale dynamic steady state. This can mirror the concept of
functional redundancy amongst species in eastern temperate forests and create landscape-level forest carbon resilience whereby after a stand-replacing disturbance, mid-successional stands elsewhere on the landscape can re-gain the carbon stores more quickly than the reset stand can recover on its own (similar to other modular landscape management approaches such as the functional complex network (Messier et al. 2019)). By enhancing structural complexity at the stand scale and supporting a mix of functional groups and successional stages in different stands across the landscape, northeastern forests can act as a mosaic at equilibrium to support high aboveground carbon stores over the long term.
Figure S1: Forest structure and composition in plot-years (2000-2021) with the lowest and highest functional dispersion calculated using posterior model parameter estimates (n=40 in each group). Quadratic mean diameter (QMD) and diameter diversity were slightly higher in low functional diversity plot-years whereas stand density (stems per acre and Reinke’s stand density index) were lower in these plots. Plots with high functional diversity are more likely to have greater density of standing snags than plots with low functional diversity. Plots with low functional diversity had a smaller proportion of softwood species by relative basal area, on average.
Figure S2: Mean posterior functional diversity as a function of forest structure and composition in plot-years from 2000-2021 with a 95% credible interval. Plot stand density (stems per acre and Reinke’s stand density index) and snags per acre tend to increase whereas diameter diversity and quadratic mean diameter (QMD) tend to decrease with increasing functional diversity. Functional diversity is low for plot-years with a very low proportion of softwood species and generally is maximized at 40-60 percent softwood composition by relative basal area.
Figure S3: Mean posterior estimates of functional diversity for plot-years (2000-2021) with relative softwood basal area ≤ 20 percent (A), >20 percent and < 60 percent (B), and ≥ 60 percent (C) plotted on a stand density curve with stems per acre as a function of quadratic mean diameter (QMD).
APPENDIX B

PRE-PROCESSING OF TRAIT DATA

TRY trait database cleaning
In all, we paired down dataset from 30917 to 16590 total trait values (16381 individual measurements and 209 means values). First, we took out duplicates based on origObsID according to the TRY protocol (n=14255 or 46 percent removed). Then, for observations missing standardized values, we converted the original units into the standardized values. There were still some observations missing values which we removed (n=37 removed). Finally, we removed value types (ValueKind) that were “best estimate”, “min” or “max” (n=2298 removed). We pooled all specific leaf area traits together (traitID= 3115, 3116, 3117; with or without petiole, or not specified) and pooled all hickory species together at this point (CFI data did not distinguish between hickory species).

Setting prior trait means and standard error from TRY trait database
We assembled independently derived trait means from each study that reported either a mean trait value or individual measurements for each species-trait combination from TRY. We then quantified the overall mean and standard deviation of the independently derived trait means for each species-trait combination (hereafter, ‘database mean’ and ‘database standard deviation’).

We set the prior values of theta and nu as the database mean and database standard deviation, respectively, of each species-trait combination when available. The only species without mean trait values was chestnut oak, for which we pooled with white oak and used white oak trait values. For species-trait combinations without a database standard deviation (i.e., there was only one independently derived trait mean from TRY), we used the standard error of the observations when the sample size was available (n= 2 species-trait combinations with 3 observations each from Reich et al. (2009)). For one species-trait combination where the database standard deviation was 0 likely due to two studies contributing the same value from the same original source, we set nu as 10% of the mean. Additionally, there were four species-trait combinations that had suspiciously equal values derived from one reference in the database for which we set the SD equal to the mean (value=65 for leaf C:N ratio from Liebegesell et al. (2016)).

Data cleaning of local trait observations
Individual trait data was examined for potential outliers and one true outlier for wood density was removed before two wood density measurements were averaged for each individual. Before fitting the model, individuals were dropped if they did not have all five traits measured, which resulted in dropping all white birch trait observations (for which one individual was sampled for an incomplete set of traits). Local trait observations for basswood individuals were also dropped since the species was dropped from the abundance matrix used to fit the model (species was in relatively low abundance across CFI plot-years).
APPENDIX C

STRUCTURAL COMPLEXITY METRICS

We selected structural complexity variables by examining correlation among variables and fitting multiple linear regression models in R. All exploratory models included one metric of stand density (e.g., basal area per acre), structural diversity metrics, and FDis. Many of the structural variables were correlated (Fig. S4) and ultimately diameter diversity, snags per acre, and large snags per acre were included in the model. Height diversity was included in initial models with smaller dataset but dropped later due to lack of data availability during the 2000-2010 inventories and low explanatory power (Table S1).

Table S1: Number of plot-years with data available for structural metrics.

<table>
<thead>
<tr>
<th>Structural metric</th>
<th>Number of plot-years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total live basal area per acre</td>
<td>629</td>
</tr>
<tr>
<td>Live stems per acre</td>
<td>629</td>
</tr>
<tr>
<td>Stand density index</td>
<td>629</td>
</tr>
<tr>
<td>Standard deviation DBH</td>
<td>629</td>
</tr>
<tr>
<td>Minimum DBH</td>
<td>629</td>
</tr>
<tr>
<td>Maximum DBH</td>
<td>629</td>
</tr>
<tr>
<td>Diameter diversity (exp)</td>
<td>629</td>
</tr>
<tr>
<td>Number of large trees per acre (DBH&gt;50cm)</td>
<td>629</td>
</tr>
<tr>
<td>Quadratic mean diameter</td>
<td>629</td>
</tr>
<tr>
<td>Height diversity (exp) of all standing trees</td>
<td>326</td>
</tr>
<tr>
<td>Height diversity (exp) of all live trees</td>
<td>326</td>
</tr>
<tr>
<td>Snags per acre</td>
<td>629</td>
</tr>
<tr>
<td>Large snags per acre (DBH&gt;50cm)</td>
<td>629</td>
</tr>
<tr>
<td>Coarse woody debris (tons/acre)</td>
<td>325</td>
</tr>
<tr>
<td>Crown class diversity (exp)</td>
<td>326</td>
</tr>
<tr>
<td>Proportion softwood by basal area</td>
<td>629</td>
</tr>
<tr>
<td>Strata diversity</td>
<td>26</td>
</tr>
<tr>
<td>Number of strata</td>
<td>26</td>
</tr>
<tr>
<td>Variance in crown ratio</td>
<td>26</td>
</tr>
<tr>
<td>Mean litter depth</td>
<td>26</td>
</tr>
<tr>
<td>Mean duff depth</td>
<td>26</td>
</tr>
<tr>
<td>Crown ratio diversity</td>
<td>26</td>
</tr>
</tbody>
</table>
Figure S4: Correlation between mean posterior functional diversity, species diversity, and structure metrics.
APPENDIX D

SUPPLEMENTAL MODEL DETAILS

Model specification
We applied a multiple linear regression model within a broader Bayesian hierarchical framework to estimate live AGB as a function of plot-level variables including forest density (basal area per acre), proportion of softwoods (calculated in terms of basal area per acre), structural complexity variables (diameter diversity, snags per acre, large snags per acre), and either species diversity or functional diversity under three alternative models. The model is expressed in general form as, $y_i = x_i^{T} \beta + \epsilon_i$, where $y_i$ is the live AGB in plot-year $i$ ($i = 1, 2, ..., n$), $x_i$ is a $p$-dimensional vector of observed plot-level variables, $\beta$ is a $p$-dimensional vector of regression coefficients, and $\epsilon_i$ is a residual error term ($\epsilon_i \overset{iid}{\sim} N(0, \sigma^2)$). The three alternative models applied either species diversity or functional diversity as part of the covariate set $x_i$ as defined in the main article.

As described in the main article, one of the two functional diversity models integrated local, individual functional trait information. Specifically, we modeled individual trait observations as, $t_{ij} \sim \text{MVN}(\mu_j, \Omega)$, where $t_{ij}$ denotes a 5-dimensional vector of trait observations from the $l^{th}$ individual and the $j^{th}$ species, $\mu_j$ is the 5-dimensional species-level mean trait value, $\Omega$ is a 5-dimensional trait covariance matrix, and $\text{MVN}(\cdot)$ denotes a multivariate trait distribution. Existing species-level mean values and associated measures of uncertainty from the TRY database are integrated through the prior distribution on species-level trait means: $\mu_{jk} \sim N(\theta_{jk}, \nu_{jk})$. Here, $\mu_{jk}$ is the univariate species-level mean for the $j^{th}$ species and $k^{th}$ trait (i.e., an individual element of $\mu_j$), while $\theta_{jk}$ and $\nu_{jk}$ are species-level mean traits and species-specific standard deviation values for each trait mean compiled from the TRY database. Modeled species-level trait means ($\theta_{jk}$) are used to generate plot-year estimates of functional dispersion (FDs) using the methodology of Laliberte and Legendre (2010). Local estimates of FDs are subsequently included as a model covariate within the general regression equation provided above.

Priors and model implementation
The model is completed by specifying prior distributions for remaining model parameters. We apply a multivariate normal shrinkage prior for the regression coefficients, $\beta \sim \text{MVN}(0, \Sigma)$, where $\Sigma$ is a $p$-dimensional covariance matrix. We decompose the covariance matrix as, $\Sigma = \text{diag}(\tau_\beta) L_\beta L'_\beta \text{diag}(\tau_\beta)$, where $\text{diag}(\tau_\beta)$ is a $p$-dimensional diagonal matrix with scale parameter $\tau_\beta$ along the diagonal and $L_\beta$ is the Cholesky decomposition of a $p$-dimensional correlation matrix for $\beta$ (Stan Development Team 2022). We apply a non-informative prior to the Cholesky decomposition of the correlation matrix, $L_\beta \sim \text{LJCorr}(1.0)$ and fix $\tau_\beta$ at 10.0 shrink unimportant regression coefficients to zero (Hooten and Hobbs 2015). We apply a similar decomposition for the trait covariance matrix: $\Omega = \text{diag}(\tau_t) L_t L'_t \text{diag}(\tau_t)$. Here, each trait is assigned its own unique scale parameter contained in the 5-dimensional vector $\tau_t$. We assign each element of $\tau_t$ a half-Cauchy prior, $\tau_{t\ell} \sim \text{Cauchy}(0, 2.5)$ for $\ell = 1, ..., 5$, and again apply a non-
informative $L|	ext{Corr}(1.0)$ prior on $L_t$. Finally, the residual standard deviation ($\sigma$) is assigned an improper uniform prior: $\sigma \propto 1$.

The joint posterior distribution of all model parameters was estimated using Markov chain Monte Carlo (MCMC) simulation using RStan (Stan Development Team 2022). Three independent MCMC chains were run for a total of 2,000 iterations with a burn-in period of 1,000 iterations. Convergence was assessed using Gelman-Rubin statistics and by visually inspecting traceplots of posterior samples. All model inference was based on a total of 1,500 posterior samples (500 samples per chain) collected following model convergence.

**Variance partitioning**

Variance partitioning was conducted following model convergence to estimate the overall proportion of variance explained by each model. We calculated Bayesian R-squared values for each model as follows (as defined in Gelman et al. 2019),

$$\frac{\sum_{i=1}^{n} \hat{y}_i^{(s)} \hat{y}_i^{(s)}}{\sum_{i=1}^{n} \hat{y}_i^{(s)} + \sigma^2(x)} \quad \text{where} \quad \hat{y}_i^{(s)} = x_i^{(s)'} \beta^{(s)}$$

where $V_i^{n} = \frac{1}{n-1} \sum_{i=1}^{n} (y_i - \bar{y})^2$, the variance among the $n$ observations and $s$ indexes the posterior sample (these exist for all regression coefficient and the residual variance under all models; we have posterior samples of plot-level covariates $x_i$ only under the model where functional diversity is estimated using local, individual trait observations). Note that by calculating R-squared values as above, we obtain posterior samples of these statistics and thus have an estimate of their posterior distribution.

Variance partitioning is carried out applying the approach defined in Schulz et al. 2021. Specifically, variance partitioning is carried out by defining calculating the variance of each model component, $V_i^{n} x_i^{(s)'} \beta^{(s)}$, where the ($\cdot$) indicates a subset of the covariates. Here, we break our covariates into four sets comprising different plot-level variables: (1) basal area per acre; (2) proportion softwoods; (3) structural complexity; (4) species/functional diversity (which one depends on the model). We then estimate the proportion of variability explained by each subset of covariates as:

$$\frac{\sum_{i=1}^{n} \hat{y}_i^{(s)} \hat{y}_i^{(s)}}{\sum_{i=1}^{n} x_i^{(s)'} \beta^{(s)}}$$
BIBLIOGRAPHY


