



RESEARCH ARTICLE

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Linking hypothesized causal factors to aboveground biomass growth in forests of Alabama and the eastern United States

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Abstract

Aim of study: We analyzed the hypothesized causal effects of relative density, density, height, species richness, species diversity, temperature, precipitation, and slope on above ground biomass growth (AGBG).

Area of study: Eastern region of the USA.

Materials and methods: We used the USDA Forest Service's Forest Inventory and Analysis (FIA) database. A total of 2554 plots from all stand ages, regardless of disturbance history, were selected from the state of Alabama and 967 plots of stand age under 30 years and no prior disturbance were selected from the eastern US. We analyzed the data using descriptive statistics and structural equation modeling.

Main results: Relative stand density exhibited a strong positive direct effect on AGBG, especially in the young forests (path coefficient 0.79), but a weaker indirect effect through species richness/diversity. Tree height influenced positively AGBG directly and indirectly through relative density and species richness. The effect of temperature and slope was greater than the effect of species richness/diversity on AGBG in the young forests of the eastern US.

Research highlights: For the forests of the eastern US, greater tree species diversity did not appear to result in neither greater nor lower productivity. The diversity-productivity relationship was negative in forests of Alabama, however, where prior management likely resulted in removal of select dominant trees from valuable species (*i.e.*, high-grading).

Additional keywords: FIA; productivity; path analysis; relative stand density; species richness; Shannon's diversity index; temperature.

Abbreviations used: AGB (above ground biomass); AGBG (above ground biomass growth); CCR (compacted crown ratio); DBH (diameter at breast height); IVP (importance value percent); FIA (Forest Inventory and Analysis); SDI (stand density index); SEM (structural equation modeling).

Authors' contributions: LDD and SKO conceived and designed the research. Both authors read and approved the final manuscript. SKO acquired national forest inventory data from the USDA, Forest Service, Forest Inventory and Analysis (FIA), Knoxville Tennessee for the study. SKO extracted climatic variables from spatial data sources; he conducted statistical analysis and made figures and tables and prepared the first draft of the manuscript. LDD contributed to all parts and drafts of the manuscript.

Data acquisition and accuracy of analysis: The national forest inventory dataset was obtained with the help of the USDA Forest Service, Forest Inventory and Analysis (FIA) personnel. FIA data is publicly available at FIA DataMart (https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html). Climatic data was downloaded from the website of the PRISM Climatic Group, which is freely available for the public use (<http://www.prism.oregonstate.edu/normals/>). We assure that we had total access to the data and we are responsible for the integrity and accuracy of our analysis.

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Introduction

Forests play a critical role in reducing atmospheric carbon through sequestration (Woodall *et al.*, 2011). The

forests of the eastern United States (US) in particular are known for having high levels of carbon storage, species diversity, and structural diversity (Woodall *et al.*, 2011). There are uncertainties however, about how

changes in the drivers of forest growth will affect this carbon sequestration (Coulston *et al.*, 2015).

Forest structural diversity is one important factor among many that influence productivity (Zhang & Chen, 2015; Ali *et al.*, 2016). A stand with a combination of species differing in characteristics such as shade tolerance, height growth rate, crown structure, leaf phenology, and root depth, can be highly productive because of complementary resource use (Kelty, 1992).

Studies have shown that environmental and climatic factors are particularly important for productivity (Zuo *et al.*, 2012; Behera *et al.*, 2017). Quantitative analysis of the hypothesized causal relationships between various driving factors and productivity is useful to understand ecosystem functioning across various levels (Timilsina *et al.*, 2014; Grace *et al.*, 2016). Site variables influence individual tree growth rates for different species, which ultimately affects stand dynamics and structure (Fig. S1 [suppl.]). But stand structure and individual tree growth influence each other and both impact ecosystem services and productivity (Pretzsch, 2009). The competitive or facilitative interactions among trees are important structural mechanisms in forest dynamics, which may vary across environmental gradients and successional stages (Fichtner *et al.*, 2015).

Structural equation modeling (SEM) or path analysis (PA) is a method of analysis where covarying biotic and abiotic variables are connected in a network. It has been widely used for exploring complicated causal relationships among variables (Grace, 2008; Paquette & Messier, 2011; Lam & Maguire, 2012; Zuo *et al.*, 2012; Timilsina *et al.*, 2014; Zhang & Chen, 2015; Ali *et al.*, 2016; Dănescu *et al.*, 2016; Grace *et al.*, 2016). SEM models represent hypothesized cause-effect relationship between variables and describe complex interdependencies of the variables (Shipley, 2000). In SEM, the causal relationships are described by magnitude of effects, *i.e.*, direct, indirect, and total effects that independent variables have on dependent variables (Pugesek *et al.*, 2003). There is a need of observational studies to enhance our understanding of the multivariate relationships of the ecological and environmental drivers that affect aboveground biomass productivity or carbon storage in natural forests (Zhang & Chen, 2015).

We aimed to explore the relationships among above ground biomass growth (AGBG), stand structure, environmental, and climatic variables using structural equation models in forests of Alabama and the eastern United States. The objectives of the study were to examine if i) species diversity affects AGBG directly, ii) relative stand density affects AGBG directly or indirectly through its effect on species diversity, iii) height and tree density affect AGBG directly or

indirectly through their influence on relative density and species diversity, and iv) temperature, precipitation and slope affect AGBG indirectly through their influence on height, tree density, relative stand density and species diversity.

Material and methods

Study area

We conducted the study in two areas, the state of Alabama and the eastern region of the United States (Fig. 1) to examine if the models differ based on the type of dataset used. The Alabama data had fewer selection restrictions—no age limitations, regeneration mode, etc., while the regional data included only young naturally regenerated stands with no history of harvesting (more selection details in the next section). Alabama is in a humid subtropical climatic zone under the Köppen climate classification. Alabama is rich in floral diversity, contains about 200 tree species and 4000 species of vascular plants (Alabama Forestry Commission, 2010). Forests cover around 70% of the land area, comprising 46 forest types including loblolly pine (*Pinus taeda* L.) as the most common forest type covering a third of all forested area (Alabama Forestry Commission, 2010). About 57% of the state's forestland is covered by hardwood or mixed pine-hardwood forests. The hardwood species which are most common in the state are northern red oak (*Quercus rubra* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.), hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua* L.), and yellow poplar (*Liriodendron tulipifera* L.). Private landowners own about 94% of the total forest area, and plantations occupy about 30% of the forest area (Hartsell & Cooper, 2013). The major geographic ranges of Alabama are the Interior Plateau (Highland Rim), Southwestern Appalachians (or Cumberland Plateau), Piedmont, Ridge and Valley, and the East Gulf Coastal Plain (Alabama Dept. of Conserv. Nat. Resour., 2006). The average summer temperatures of the state range from 21 to 32°C, and average winter temperatures range from -1 to 10°C (Alabama Dept. of Conserv. Nat. Resour., 2006).

Our second study area, the eastern region of the US, consisted of the 31 conterminous eastern states, from North Dakota in the northwest to Texas in the southwest (Fig. 1). The area covers a large number of forest types and geographic variations. Under the Köppen climate classification, the climate of the eastern region is classified as temperate continental climate, humid subtropical climate, temperate oceanic climate, warm semi-arid climate, cold semi-arid climate, warm

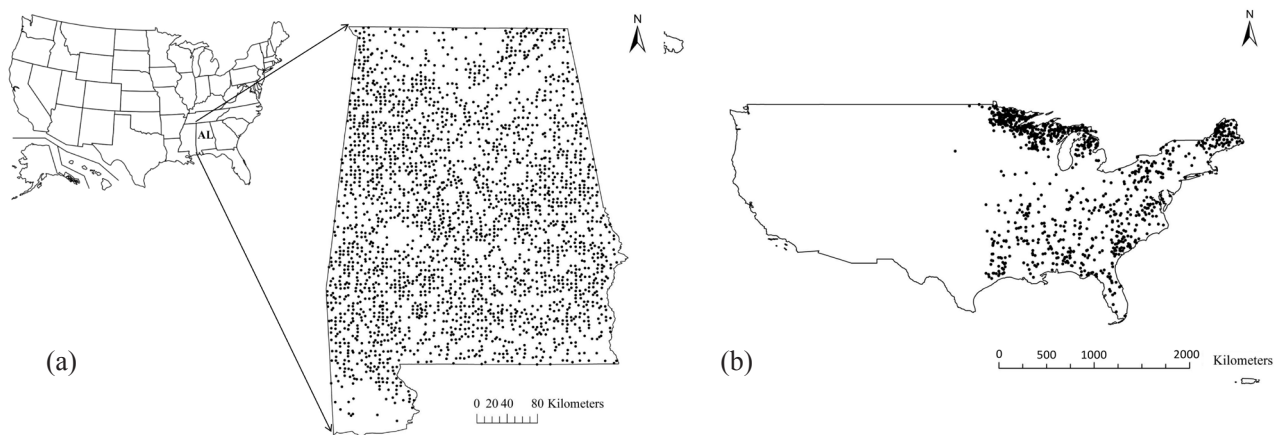


Figure 1. Approximate location of the plots in study area (a) Alabama and (b) eastern United States.

continental climate, temperate continental climate and cool continental climate (Zifan, 2016). The variability in climatic and geographical conditions is favorable for the high biodiversity in the region.

Data

We used publicly available forest inventory data from the USDA, Forest Service Forest Inventory and Analysis (FIA) database. The FIA applies a quasi-systematic sampling design that involves a nationally standardized sampling procedure with a sampling intensity of one plot for every 2428 hectares (Bechtold & Patterson, 2005). The area of the FIA standard plot size is 0.067 ha. The plot design consists of four 7.3 m radius subplots, each of approximately 0.0168 ha in size and set 36.6 m apart in a triangular form with three plots at the corners and one subplot at the center of the triangle.

For the Alabama study area, we used plots measured between 2005 and 2012. We selected plots that had at least 10% cover by trees and had no visible natural disturbance since the last measurement or within the last five years. Out of the 2554 selected plots, about two thirds were naturally regenerated and the rest were artificially regenerated. Almost 98% of the plots had two-storied stand structure, 1% had multistoried, and 1% had single-storied structure. The plots were under various ownership, including private, public (both federal and state government ownership), industrial, etc. Stand treatment and harvesting activities such as clearcut, various partial harvests, shelterwood harvest, commercial thinning, timber stand improvement, and salvage cutting had impact on about 20% of the plots since the last measurement.

For the second study area of the eastern US, we used plots measured between 1999 and 2009 across the eastern region. Our selection criteria for these plots were more restrictive. We selected all 967 plots

that had at least 10% forest cover, stand age of less than 30 years and established under the new FIA plot design implemented after 1999. The selected plots had no visible natural or anthropogenic disturbance since the last measurement or within the last five years. Our selection criteria for the eastern US was aimed at selecting only plots that did not have biomass loss due to harvesting activities. Harvesting is generally not carried out in such young stands, so a more accurate estimation of the biomass growth would be possible. The stand origin of the plots was from natural regeneration and had single-storied to multistoried stand structure. The plots were managed under various private, public (both federal and state government ownership) and industrial ownership.

The stand age of the Alabama plots ranged from 1 to 125 years, so we included all the trees from the subplots that had diameter at breast height (DBH, 1.37 cm above the ground) ≥ 12.7 cm. However, for the eastern region, the stand age of the selected plots was less than 30 years, so we also included all stems with DBH ≥ 2.54 cm.

Aboveground biomass growth (AGBG) and predictor variables

We used information from the FIA database on species, DBH, height, compacted crown ratio, stand age, slope, aspect, elevation, and site productivity class. We calculated the plot level variables species richness, Shannon's diversity index, trees per hectare, quadratic mean diameter (QMD), mean height, mean compacted crown ratio (CCR), dry above ground biomass of live-trees, and relative density.

Species richness and Shannon's diversity index were used to characterize species diversity. Species richness is simply a count of the number of species in the plot. Shannon's diversity index (H') was calculated with the formula:

$$H' = - \sum_{i=1}^s p_i \ln p_i \quad [1]$$

where S is the number of species and p_i is the proportion of species i relative to the total number of species (Magurran, 1988). We used basal area of the species for the calculation of Shannon's diversity index. Unlike most non-woody plants, trees can be highly divergent in size. Basal area accounts better than density for the space that each tree species occupies on a site (McMinn, 1992). Hereafter we refer to the term Shannon's diversity index as species diversity. We used each, species richness and species diversity, in the path models to test corresponding effect on AGBG.

CCR is the percent of the tree bole supporting live, healthy foliage that is measured at the individual tree level (Woudenberg *et al.*, 2010). Climatic data (temperature and precipitation) were extracted from spatial data of 800 m resolution (PRISM Climate Group, <http://www.prism.oregonstate.edu/normals>). The data values were the 30 year average for the period of 1981 to 2010.

We estimated aboveground biomass (dry) of each live tree as a total sum of the biomass of the tree components merchantable bole, top of the tree, and tree stump using the same method as the FIA, the Jenkins biomass equations (Jenkins *et al.*, 2003) and adjustment factors of the tree components. Plot level AGB was estimated by summing up the biomass of all individual live trees of the plot. AGBG is the mean annual increment of live AGB and we estimated AGBG of each plot by dividing the total live (AGB) of the plot by the stand age of the plot and expressed it in Mg/(ha·yr). We interchangeably referred to it as 'AGBG' or 'productivity'. Because of the nature of the dataset we could not account for the biomass that may have been removed in some of the Alabama plots, the estimate of AGBG in such plots was likely below its true value.

A square root transformation was applied to AGBG and tree density to make the data close to normal and meet the homogeneity assumptions (Legendre & Legendre, 2012). We refer to them as square root AGBG and square root tree density. A transformation was applied to modify aspect from 0-360° azimuth to values ranging from 0 to 2 (Beers *et al.*, 1966), where, 2 corresponds to northeast facing slopes (mesic) and 0 to southwest facing slopes (xeric). The arcsine transformation was applied to slope and CCR, which is generally used to transform percentages and fractions to make data close to normal (Legendre & Legendre, 2012).

Estimation of relative density

Relative density (RD) is the stand stocking, defined as the number of trees per unit area in a stand relative to

the potential maximum number of trees (Woodall *et al.*, 2011). The relative density of the plots was calculated by dividing the current stand density index (SDI) by the maximum SDI (Woodall *et al.*, 2005). SDI is based on tree density and size for fully stocked pure stands (Reineke, 1933). The formula was slightly modified for use in unevenaged stands using the additive or summation method. The SDI is determined on individual tree basis and then summed up for the stand (Long & Daniel, 1990), which is expressed as:

$$SDI = \sum tph_i \left(\frac{DBH_i}{25} \right)^{1.6} \quad [2]$$

where tph_i is number of trees/ha for the i th tree in the stand, and DBH_i is the diameter of the i th tree in the stand (cm).

To estimate stand specific maximum SDI of mixed species stands, we used a published regression equation (Woodall *et al.*, 2005) based on wood specific gravity (Miles & Smith, 2009) of each tree species in the stand. Relative density was used to characterize comparative stocking level of each plot and its values range from 0 to 1 representing understocked to overstocked plots.

Data analysis and construction of path analysis model

With the observational data, construction of the path model and interpretations about cause and effect of the model are done based on a priori conceptual knowledge of the complex system under observation (Grace, 2008). While constructing path analysis network, the knowledge about system functioning mechanisms, rather than mere associations are applied. The causal links were constructed based on empirical observations and theoretical explorations about how components of a forest system interrelate. The network of multiple causal links between the variables in the path model was constructed based on causal relationships found in the literature (Pretzsch, 2009; Paquette & Messier, 2011) as shown in Fig. 2. The causal links among the variables were slightly modified to retain significant paths and obtain best goodness of fit values.

A stepwise multiple linear regression procedure was used to select predictors of the response variable square root AGBG from among the stand variables (relative stand density, mean height, tree density, quadratic mean diameter, species diversity, species richness and compacted crown ratio) and from among the environmental variables (slope, aspect, mean precipitation, mean temperature, and elevation). Multicollinearity test was also applied to remove collinear predictor variables.

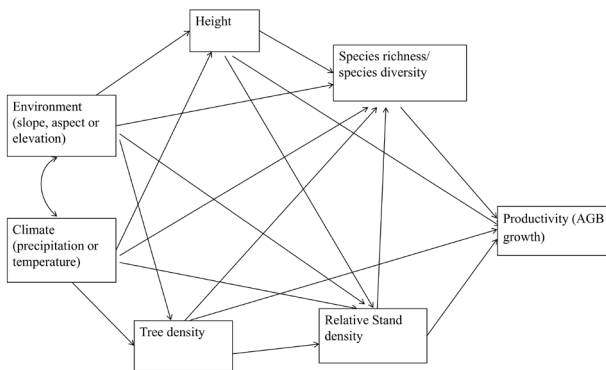


Figure 2. A conceptual path model depicting a complex causal links of stand-, climatic- and environmental- variables influencing aboveground biomass (AGB) growth in forest ecosystems (Pretzsch, 2009; Paquette & Messier, 2011).

We performed path analysis on the standardized data, displaying the simple correlations among independent variables, and the relationship of all independent variables with the dependent variable. Standardized path coefficient and t-value were used to compare the relative magnitude of the effects of different predictor variables in the model (Cramer *et al.*, 1999). The standardized path coefficients and the effects were produced through maximum likelihood estimation in covariance structure analysis. The direct effects, when one variable affects another directly, were estimated in the form of partial regression coefficients. The indirect effects, when one variable affects another indirectly through its effect on other variables, were estimated by multiplying the path coefficients by the simple correlation coefficients (Cramer *et al.*, 1999; Pugesek *et al.*, 2003). The total effect is estimated by adding the direct and indirect effects. In structural equation modeling the term exogenous variable refers to a variable that explains other variables in the model and whose variation is influenced by factors outside the model, while an endogenous variable refers to a variable whose variation is explained by using one or more of the other variables.

There are several indices available for describing the model fit and indicating how the model represents the data in structural equation modeling. We used the absolute fit indices root mean square of approximation (RMSEA), standardized root mean squared residual (SRMR), goodness of fit index (GFI), and adjusted goodness of fit index (AGFI) as well as the comparative fit indices Bentler's comparative fit index (Bentler's CFI), Bentler-Bonett normal fit index (Bentler-Bonett NFI), and Bentler-Bonett non-normal fit index (Bentler-Bonett NNFI) to determine the fit of the path models (Hooper *et al.*, 2008).

Good fit is indicated by RMSEA fit values from 0 to 0.08, or SRMR values between 0 and 0.05 (Hooper *et al.*, 2005). GFI and AGFI range between 0 and 1 and values of 0.9 or greater indicate well-fitting models (Pugesek *et al.*, 2003). The Bentler's CFI values range from 0 to 1 and values closer to 1 indicate good fit while more than 0.9 is considered adequate (Pugesek *et al.*, 2003; Hooper *et al.*, 2008). Values of Bentler's NFI and Bentler's NNFI also range between 0 and 1 and values greater than 0.9 indicates a good fit (Hooper *et al.*, 2008).

Chi-squared fit index has some limitations as it is sensitive to sample size and multivariate normality deviation, so it nearly always rejects the model when large sample size is used (Hooper *et al.*, 2008). Because of using large samples for each model construct, we did not report chi-squared fit index for our path models. The SAS PROC CALIS procedure with Levenberg-Marquardt optimization and McDonald method from the statistical package SAS[®] 9.3 was used for path analysis.

Results

A total of 113 tree and shrub species were found across the Alabama plots. Species richness ranged from 1 to 17. Out of the 2554 plots, the most common species richness was 1 (pure stands) on 12% of the plots, while the least common was species richness of 17, occurring on only one plot. About 50% of the plots had species richness of 5 or less. The range of current AGB was from 0.10 to 403.5 Mg/ha and of AGBG was from 0.01 to 15.7 Mg/(ha·yr). The top three dominant species on the basis of importance value percent (IVP) across Alabama were loblolly pine (31.58%), sweetgum (7.97%), and water oak (*Quercus nigra* L., 4.78%), all of which are shade intolerant species. The next three most dominant species were yellow-poplar, white oak, and red maple (*Acer rubrum* L.), with IVP values from 3.08% to 4.32%. The IVP of each species was the average of relative frequency percent, relative density percent, and relative dominance percent (Curtis & McIntosh, 1951). The stand age of about 45% of the plots was less than 25 years and over 95% of the plots were younger than 75 years. Descriptive statistics of the variables for the Alabama plots are shown in Table 1.

There were a total of 147 tree and shrub species in the data from across the eastern region (Table 1). Species richness ranged from 1 to 15, whereas current AGB and AGBG ranged from 0.06 to 246.84 Mg/ha and 0.01 to 15.04 Mg/(ha·yr), respectively (Table 1). The most common species richness (152 plots) was 3. The greatest observed species richness of 15 was found

Table 1. Mean, standard deviation, minimum and maximum values of the variables across 2554 FIA plots in Alabama and 967 plots in the eastern US.

Variables	Alabama plots				Eastern USA plots			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Quadratic mean diameter, QMD (cm)	23.1	5.73	12.7	94.1	7.5	4.11	2.5	43.5
Basal area (m ² /ha)	16.2	9.14	0.19	58.9	11.65	8.59	0.09	46.9
Height (m)	16.7	3.83	6.1	32.6	11.5	3.60	2.9	27.6
Tree density (trees/ha)	392	229	15	1324	3377	2705.28	15	16480
Relative stand density	0.4	0.15	0.00	0.83	0.23	0.16	0	0.92
Compacted crown ratio	0.39	0.10	0	0.99	0.44	0.17	0	0.99
Stand age (yr)	34	22	1	125	14.3	5.01	3	30
Total AGB (Mg/ha)	82.8	60.4	0.10	403.5	33.13	30.15	0.06	246.8
Mean annual AGBG (Mg/ha·yr)	2.7	1.8	0.01	15.7	2.3	1.94	0.01	15.04
Species richness (S)	5.8	3.36	1	17	4.6	2.98	1	15
Shannon's diversity index (species diversity)	1.11	0.69	0	2.54	0.86	0.56	0	2.29
Precipitation (cm)	142	8.4	121	172.7	102	25.7	51	166
Slope (%)	12	12	0	85	6.3	9.56	0	71
Elevation (m)	137.66	90.45	0	676.7	300.7	179.59	0	1109

on 4 plots. The IVP percent of the three top dominant species of the area in descending order were quaking aspen (*Populus tremuloides* Michx. 13.5%), loblolly pine (9.1%), and red maple (7.7%). The descriptive statistics of the variables for the eastern region plots are shown in Table 1.

The results for Alabama and eastern region are described separately below.

Alabama

The stepwise linear regression analysis showed that the best model for predicting square root AGBG included species richness/diversity, relative density, height, slope and precipitation. In the first path model,

the square root AGBG, species richness, height and relative density were treated as endogenous variables, while slope and precipitation were linked as exogenous variables (Fig. 3a).

All the predictors explained 31% of the variation in the dependent variable (square root AGBG). The effect of relative density on the response variable was the strongest among all variables and with the greatest path coefficient of 0.46 (Fig. 3a), followed by height, and species richness with path coefficients 0.32 and -0.24, respectively. Species richness had significant negative effect on square root AGBG. The effect of height, relative density, and slope on species richness was significant with path coefficients 0.31, 0.28, and 0.22, respectively ($R^2=0.29$; Fig. 3a), while

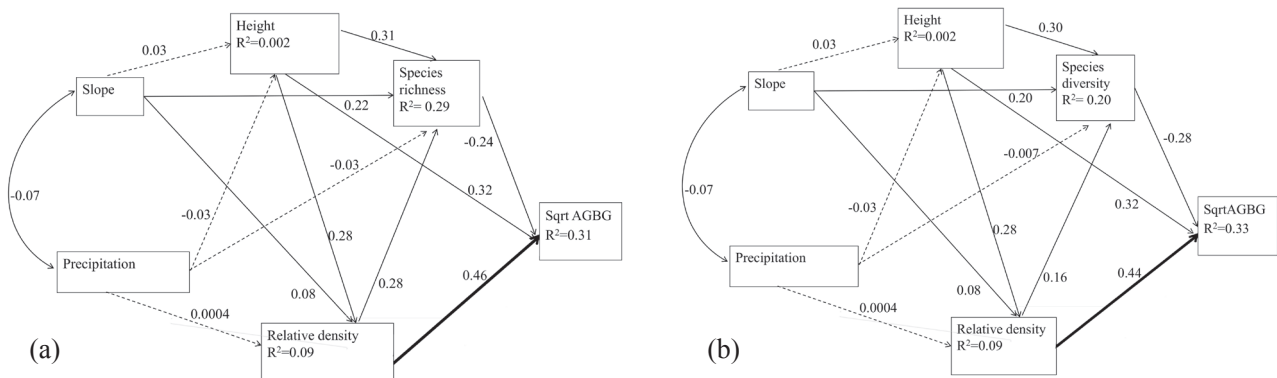


Figure 3. First path analysis model (a) showing the causal links between the square root aboveground biomass growth (AGBG) and predictor variables across the 2554 FIA plots in Alabama. The path coefficient signifies the effect of each respective predictor on the square root AGBG. The second path analyses model (b) uses species diversity instead of richness. The heavy black line indicates high and significant effect. The dotted line indicates no significant effect at $\alpha=0.05$.

Table 2. Goodness of fit and comparative fit indices of the path models.

Index	Alabama		Eastern region	
	Model I	Model II	Model I	Model II
Goodness of fit index (GFI)	0.99	0.99	0.99	0.99
Adjusted goodness of fit index (AGFI)	0.95	0.95	0.94	0.93
Bentler's comparative fit index (Bentler's CFI)	0.98	0.98	0.99	0.99
Bentler-Bonett normal fit index (Bentler-Bonett NFI)	0.98	0.98	0.99	0.99
Bentler-Bonett non-normal fit index (Bentler-Bonett NNFI)	0.88	0.87	0.95	0.94
Standardized root mean squared residual (SRMR)	0.02	0.02	0.01	0.01
Root mean square of approximation (RMSEA)	0.08	0.07	0.08	0.08

Table 3. Standardized effects of the predictor variables on the response variable square root aboveground biomass growth across the 2554 FIA plots in Alabama. The first path model uses species richness, the second uses species diversity. Values in parentheses are *p* values and effects are significant at $\alpha=0.05$.

Variable	Total	Direct	Indirect
1 st path model, using species richness			
Relative density	0.39 (<0.001)	0.46 (<0.001)	-0.07 (<0.001)
Height	0.36 (<0.001)	0.32 (<0.001)	0.03 (0.02)
Species richness	-0.24 (<0.001)	-0.24 (<0.001)	0
Precipitation	-0.005 (0.67)	0	-0.005 (0.67)
Slope	-0.009 (0.44)	0	-0.009 (0.44)
2 nd path model, using species diversity			
Relative density	0.39 (<0.001)	0.44 (<0.001)	-0.05 (<0.001)
Height	0.35 (<0.001)	0.33 (<0.001)	0.02 (0.03)
Species diversity	-0.28 (<0.001)	-0.28 (<0.001)	0
Precipitation	-0.009 (0.44)	0	-0.009 (0.44)
Slope	-0.01 (0.29)	0	-0.01 (0.29)

precipitation had a no effect on species richness (Fig. 3a). Height and slope had significant effect on relative density ($R^2=0.09$; Fig. 3a). Slope and precipitation had negligible influence on height and relative density. The model (Fig. 3a) was well-fitted, as indicated by the fit indices (model I for Alabama in Table 2).

Species richness had a significant negative direct effect on square root AGBG, and it had no indirect effect on it (Table 3). Relative density had a significant direct effect on square root AGBG but it had negligible indirect effect (-0.07) on it via species richness. The effect of height on square root AGBG was direct, while its effect through relative density and species richness was negligible (0.03). Slope and precipitation had no direct effect and also had insignificant indirect effect through height, species richness and relative density on square root AGBG (Table 3).

In the second path model we replaced only species richness with species diversity while keeping the other

variables the same as in the first path model (Fig. 3b, Table 3). The results were virtually the same. One exception was the relative density, which had lower effect (path coefficient 0.16) on species diversity than it had on species richness (0.28). The model fit indices of the path model (Fig. 3b) were adequate (model II for Alabama in Table 2).

Eastern region

For the eastern region, the variables relative density, height, square root tree density, species richness, slope, and temperature were significant predictors of square root AGBG. The square root AGBG, species richness, relative density, square root tree density, and height were linked as the endogenous variables, while temperature and slope were connected as the exogenous variables (Fig. 4a). As before, two path models were computed using species richness in one and species diversity in

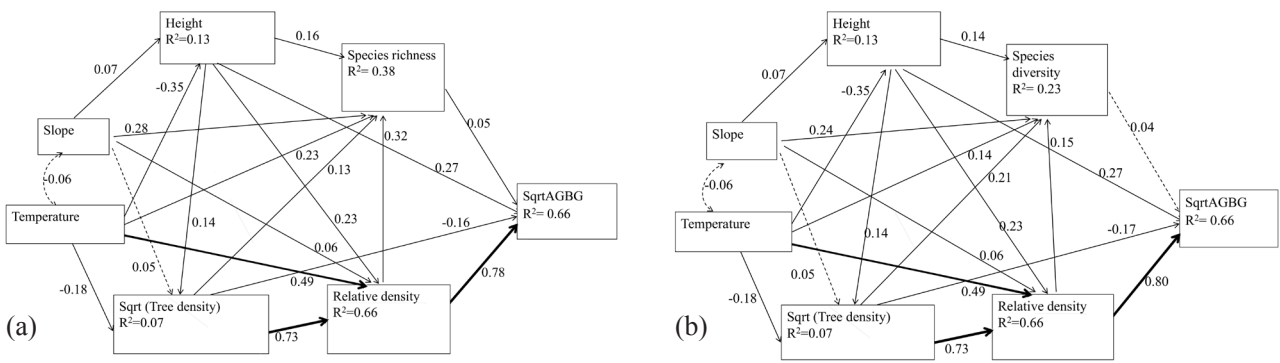


Figure 4. A first path analysis model (a) based on the 967 FIA plots in young forests of the eastern US, depicting the causal links between the square root aboveground biomass growth (AGBG) and predictor variables. The second path analyses model (b) uses species diversity instead of richness. The path coefficients signify the effect of each respective predictor on the square root AGBG. The heavy black lines indicate a strong significant effect. The dotted line indicates no significant relationship at $\alpha=0.05$.

the other, while keeping other variables the same in both models.

In the first path model for the data from the eastern US, the predictors explained 66% of the variation in square root AGBG (Fig. 4a). The predictors height, square root tree density, slope and temperature explained the same amount of variation (66%) in relative density. Relative density was the most influential factor for square root AGBG. Based on the path coefficients, the effect of relative density on square root AGBG was the strongest among the predictors with a path coefficient 0.78 (Fig. 4a). After relative density, height had the greatest effect on square root AGBG with a path coefficient of 0.27. The effect of square root tree density was negative and significant (-0.16). Species richness had a positive effect on square root AGBG, but it was weak compared to other stand variables (Fig. 4a). Relative density had stronger effect on species richness, with path coefficient 0.32, than the other variables. Similarly, slope, temperature, and height had positive effect on species richness with path coefficients 0.28, 0.23, and 0.16, respectively (Fig. 4a). The square root tree density also had a positive effect on species richness. Temperature had a greater effect on tree height and square root tree density than did slope. Slope had no effect on square root tree density. The effect of temperature and height on relative density was positive and significant, with path coefficients 0.49 and 0.23, respectively (Fig. 4a). The square root tree density had greatest effect (0.73) on relative density among the predictors. The values of the model (Fig.4a) fit indices were adequate (model I for the eastern region in Table 2).

Relative density had a very strong direct effect (0.78) on square root AGBG, while it had a very weak indirect effect (0.02) through species richness on square root AGBG. The direct and indirect effects of height on square root AGBG were almost equal (Table 4).

Height’s indirect effect through tree density, relative density and species richness on square root AGBG was substantial (0.25). The square root tree density showed a strong and positive indirect effect through relative density and species richness (0.59) on square root AGBG, while it had significant but comparatively low and negative direct effect (-0.16) on square root AGBG (Table 4). Species richness had significant but weak direct effect on square root AGBG (Table 4). Both temperature and slope showed significant and positive indirect effect on square root AGBG (Table 4).

In the second path model from the eastern US data, we replaced species richness with species diversity while keeping the other variables and causal paths the same. As with the Alabama data, there was no measurable improvement in the model (Fig. 4b, Table 4). In fact, the effects of the predictor variables on other predictors, particularly on diversity, were somewhat weaker. The path model (Fig. 4b) fit was adequate (model II for the eastern region in Table 2).

We found a non-significant indirect effect of relative stand density on square root AGB growth (Table 4), which was significant in the last model. Species diversity had no direct and indirect effect on square root AGBG (Table 4).

Discussion

The results from the Alabama data need to be evaluated with some important considerations: i) the stand age range of the plots was fairly large (1 to 125 years) and many plots were impacted by past forest management activities such as thinning, timber stand improvement, and harvestings, as well as by natural disturbances; ii) the common practice of selectively harvesting the largest trees of the most valuable species

Table 4. Standardized effects of the predictor variables on the response variable square root aboveground biomass growth across the 967 FIA plots in young forests in the eastern US. The first path model uses species richness, the second uses species diversity. Values in parentheses are *p* values and effects are significant at $\alpha=0.05$.

Variables	Total	Direct	Indirect
1 st path model, using species richness			
Relative density	0.80 (<0.001)	0.78 (<0.001)	0.02 (0.04)
Height	0.52 (<0.001)	0.27 (<0.001)	0.25 (<0.001)
Square root tree density	0.43 (<0.001)	-0.16 (<0.001)	0.59 (<0.001)
Species richness	0.05 (0.03)	0.05 (0.03)	0
Temperature	0.14 (<0.001)	0	0.14 (<0.001)
Slope	0.11 (<0.001)	0	0.11 (<0.001)
2 nd path model, using species diversity			
Relative density	0.80 (<0.001)	0.79 (<0.001)	0.01 (0.15)
Height	0.52 (<0.001)	0.27 (<0.001)	0.25 (<0.001)
Square root tree density	0.43 (<0.001)	-0.17 (<0.001)	0.60 (<0.001)
Species diversity	0.04 (0.10)	0.04 (0.10)	0
Temperature	0.14 (<0.001)	0	0.14 (<0.001)
Slope	0.11 (<0.001)	0	0.11 (<0.001)

(often referred to as highgrading) and not accounting for their volume (because it was not possible for us to do it with the available data), would have resulted in underestimation of the growth in the mixed stands; and iii) the pine stands are generally younger than the hardwood stands, as they are often harvested at a younger age than hardwood stands.

In all of our path models (Figs. 3 and 4), the effects on AGBG of the variables related to stand structure were stronger than the effects of the environmental variables. Relative density (stand stocking), tree density, and height were each found to influence AGBG directly and indirectly. However, the indirect effect of relative density through species richness/species diversity on AGBG was weak. The stand characteristics density and tree height were the main determinants, from the selected predictors, in the variation of AGBG in both datasets.

It is not surprising that dense stands accumulate more biomass than sparse stands where more growing space is unoccupied. Others have similarly found that among the processes and stand structural attributes that influence the diversity-productivity relationships in forests, density can be a stronger determinant of productivity than species richness (Forrester & Bauhus, 2016). Furthermore, the simultaneous interaction effects of stand density and other causal factors can influence the diversity-productivity relationship, and the complementarity effect in forests can increase or

decrease with increasing stand density depending on the limiting resources or climatic conditions (Forrester & Bauhus, 2016). In the temperate region, however, tree productivity and richness are primarily determined by the intensity of the competition, since competitive exclusion (low complementarity effect) and selection effects in this region are prominent due to a stable and productive environment (Paquette & Messier, 2011).

Relative density, age, and site productivity strongly affect forest growth (Innes *et al.*, 2005; Weiskittel, 2011) and we similarly found strong positive influence of relative density on AGBG. As stocking increases, the site occupancy grows, resulting in more complete use of the available site resources and an increase in growth.

The relationship between species diversity and AGBG in the forests of Alabama (significant and negative) was different from that for the eastern region (positive but very weak). As the selected plots from the forests in Alabama were older than those from the eastern US, they were much more likely to have experienced partial removal, whose volume is not accounted for in the data. In the rather common practice of removing the largest trees from commercially valuable species (high-grading), this would result in stands with somewhat lower diversity but greatly reduced biomass growth. Because the stands from the eastern US were young, such removals are less likely to have occurred or would have been uncommon. As a

result, the diversity-productivity relationship in the two datasets was different.

Based on the diversity-productivity relationship in the forests of the eastern US, it appears that while more diverse forests did not have a productivity advantage over less diverse forests, they were not less productive either. Species diversity has been reported in many studies as a significant factor for aboveground biomass productivity in naturally regenerated forests (Caspersen & Pacala, 2001; Liang *et al.*, 2007, 2016; Vilà *et al.*, 2007; Paquette & Messier, 2011), while others found stronger effects of species identity (referring to which species or set of species are in the community) than diversity (Nadrowski *et al.*, 2010). Forest ecosystem productivity and nutrient availability are not determined solely by the number of species, but are more likely to be determined by the characteristics of the species present (Firn *et al.*, 2007). Species identity or characteristics and spatial distribution are important factors that sometimes determine whether diverse stands are more productive than monospecific stands of similar age, tree stocking, soil characteristics, and management. Other studies (Vilà *et al.*, 2007) found that the dominant tree species is an important determinant for wood production in Spain. There are several factors that influence the relationships between species diversity and aboveground biomass productivity, such as environment (Hooper *et al.*, 2005; Vilà *et al.*, 2005; Ma *et al.*, 2010; Paquette & Messier, 2011), spatial scale (Chase & Leibold, 2002), plant density (He *et al.*, 2005; Potter & Woodall, 2014), successional status (Caspersen & Pacala, 2001; Vilà *et al.*, 2003), site productivity (Paquette & Messier, 2011; Potter & Woodall, 2014), soil fertility (Rodríguez-Loinaz *et al.*, 2008; Thoms *et al.*, 2010), evolutionary history and latitude (Pärtel *et al.*, 2007), and seed dispersal limitation (Pärtel & Zobel, 2007).

Precipitation and slope had no indirect effect on AGBG in the forests of Alabama, where the variation in these factors is not as great as that in the area covered by the other dataset. Precipitation was not in the models for the dataset from the eastern US, but of the examined climate variables that were in the model, temperature and slope had a significant indirect effect on AGBG. According to the Köppen climate classification (Zifan, 2016), the eastern region represents an area with substantial climate variability, whereas Alabama represents only humid subtropical climate. Temperature appeared to have a positive effect on species richness/diversity, which is not unusual as forests further from the poles tend to be more diverse (latitudinal diversity gradient (LDG)). Temperature also had a positive effect on relative stand density, as southerly forests of the US can grow at higher stocking levels in the more favorable temperature, precipitation and extended growing

season. Temperature generally increases tree and stand growth in temperate forests, where photosynthesis may exceed respiration in response to increased temperature (Ryan, 2010). However, temperature had a particularly strong and negative effect on tree height. Warmer climates do not necessarily mean greater tree height, as the determinants of tree height are complex. Previous work has shown that the tallest trees in the world are not necessarily in the equatorial regions where the growing season is the longest and there is plentiful precipitation. Instead, they are located in areas with thermally similar climates with average annual temperature around 10°C and seasonal temperature variation of approximately 10°C (Larjavaara, 2014).

Slope had a positive association with species richness/diversity. As slope becomes steeper, the conditions for plants become harder to a critical slope angle beyond which plants can no longer grow (Nadal-Romero *et al.*, 2014). It is harder for a species to become dominant in habitats with limited resources and harsher conditions (Tilman & Pacala, 1993). And as slopes become steeper and conditions less favorable, this likely contributes towards greater number of species occupying such sites, up to a point where the critical slope angle prevents vegetation from establishing and surviving.

We found that species richness had the lowest total effect (direct plus indirect), among the examined stand structure and environmental variables, on AGBG in the eastern forests. A similar result was found for the Mediterranean Aleppo pine forests in Spain, where Vilà *et al.* (2003, 2005) found that species richness is a less important factor than climate, successional stage, bedrock type, and solar radiation for wood production.

The predictors explained a relatively low (31% or 33%) amount of the variation in AGBG in the Alabama forests, which we contend could be due to factors such as disturbances, mortality, removals, and herbivory. In the path models of the eastern region, the predictors explained 66% of the variation in AGBG.

The study contributes to our understanding of the complex relationships between climatic, environmental and stand structure variables in forests of the eastern US.

Conclusion

We analyzed the hypothesized causal relationship between aboveground biomass productivity and stand structural (relative stand density, tree density, height), climatic (temperature, and precipitation), and environmental (slope) variables. The study used FIA data for path analysis and examined the direct and indirect effects of drivers of aboveground biomass

productivity in the forests of Alabama and the eastern US.

We found that the relative density, or stocking, was the most important variable among the selected predictors. Relative density showed a strong direct effect on AGBG, although it had a weak indirect effect through species richness/species diversity. Tree height and tree density were significant factor in influencing AGB productivity directly as well as indirectly through relative stand density and species richness. The environmental and climatic factors were more influential than species richness/species diversity for increasing AGB productivity in eastern forests. Species richness was negatively associated with AGB productivity in Alabama, where selective harvesting may have resulted in removal of the fastest growing trees. In the plots from the younger forests of the eastern US, the increase of species richness and diversity did not seem affect negatively, nor positively, productivity. Overall, increasing stocking appears to provide the greatest increase in productivity.

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References

- Alabama Dept. of Conserv. Nat. Resour., 2006. Alabama's comprehensive wildlife conservation strategy, Chapter 2. Wildlife Habitat—Alabama's Ecological Framework. <http://www.outdooralabama.com/sites/default/files/Chapter2.pdf>
- Alabama Forestry Commission, 2010. Forests at the Crossroads- Alabama Statewide Forest Assessment and Resource Strategy. http://www.forestry.alabama.gov/PDFs/Forests_at_the_Crossroads-AL-State_Assessment.pdf
- Ali A, Yan ER, Chen HYH, Chang SX, Zhao YT, Yang XD, Xu MS, 2016. Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. *Biogeosciences* 13: 4627-4635. <https://doi.org/10.5194/bg-13-4627-2016>
- Bechtold WA, Patterson PL (eds), 2005. The enhanced forest inventory and analysis program-national sampling design and estimation procedures. General Technical Report SRS-80. <http://www.treesearch.fs.fed.us/pubs/20371>. [2016, Nov 18].
- Beers TW, Dress PE, Wensel LC, 1966. Aspect transformation in site productivity research. *J For* 64: 691-692.
- Behera SK, Sahu N, Mishra AK, Bargali SS, Behera MD, Tuli R, 2017. Aboveground biomass and carbon stock assessment in Indian tropical deciduous forest and relationship with stand structural attributes. *Ecol Eng* 99: 513-524. <https://doi.org/10.1016/j.ecoleng.2016.11.046>
- Caspersen JP, Pacala SW, 2001. Successional diversity and forest ecosystem function. *Ecol Res* 16: 895-903. <https://doi.org/10.1046/j.1440-1703.2001.00455.x>
- Chase JM, Leibold MA, 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416: 427-430. <https://doi.org/10.1038/416427a>
- Coulston JW, Wear DN, Vose JM, 2015. Complex forest dynamics indicate potential for slowing carbon accumulation in the southeastern United States. *Sci Rep* 5: 8002. <https://doi.org/10.1038/srep08002>
- Cramer CS, Wehner TC, Donaghy SB, 1999. PATHSAS: A SAS Computer program for path coefficient analysis of quantitative data. *J Hered* 90: 260-262. <https://doi.org/10.1093/jhered/90.1.260>
- Curtis JT, McIntosh RP, 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32: 476. <https://doi.org/10.2307/1931725>
- Dănescu A, Albrecht AT, Bauhus J, 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 182: 319-333. <https://doi.org/10.1007/s00442-016-3623-4>
- Fichtner A, Forrester DI, Härdtle W, Sturm K, Oheimb G von, 2015. Facilitative-Competitive interactions in an old-growth forest: The importance of large-diameter trees as benefactors and stimulators for forest community assembly. *PLOS ONE* 10: e0120335. <https://doi.org/10.1371/journal.pone.0120335>
- Firn J, Erskine PD, Lamb D, 2007. Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia* 154: 521-533. <https://doi.org/10.1007/s00442-007-0850-8>
- Forrester DI, Bauhus J, 2016. A review of processes behind diversity-productivity relationships in forests. *Curr For Rep* 2: 45-61. <https://doi.org/10.1007/s40725-016-0031-2>
- Grace JB, 2008. Structural equation modeling for observational studies. *J Wildl Manag* 72: 14-22. <https://doi.org/10.2193/2007-307>
- Grace JB, Anderson TM, Seabloom EW, Borer ET, Adler PB, Harpole WS, Hautier Y, Hillebrand H, Lind EM, Pärtel M, *et al.*, 2016. Integrative modelling reveals mechanisms

- linking productivity and plant species richness. *Nature* 529: 390-393. <https://doi.org/10.1038/nature16524>
- Hartsell AJ, Cooper JA, 2013. Alabama's forests, 2010. *Resour Bull SRS-RB-193 Asheville NC USDA For Serv South Res Stn 87 P.* 193: 1-87.
- He JS, Wolfe-Bellin KS, Schmid B, Bazzaz FA, 2005. Density may alter diversity-productivity relationships in experimental plant communities. *Basic Appl Ecol* 6: 505-517. <https://doi.org/10.1016/j.baae.2005.04.002>
- Hooper D, Coughlan J, Mullen M, 2008. Structural equation modelling: Guidelines for determining model fit. *Electron J Bus Res Methods* 6: 53-60.
- Hooper DU, Chapin Iii FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, *et al.*, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75: 3-35. <https://doi.org/10.1890/04-0922>
- Innes JC, Ducey MJ, Gove JH, Leak WB, Barrett JP, 2005. Size density metrics, leaf area, and productivity in eastern white pine. *Can J For Res* 35: 2469-2478. <https://doi.org/10.1139/x05-174>
- Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA, 2003. National-scale biomass estimators for United States tree species. *For Sci* 49: 12-35.
- Kelty MJ, 1992. Comparative productivity of monocultures and mixed-species stands. In: *The ecology and silviculture of mixed-species forests*; Kelty MJ, Larson B & Oliver CD (Eds.). pp: 125-141. Kluwer Acad Publ, The Netherlands. https://doi.org/10.1007/978-94-015-8052-6_8
- Lam TY, Maguire DA, 2012. Structural Equation modeling: theory and applications in forest management. *Int J For Res* 2012: e263953. <https://doi.org/10.1155/2012/263953>
- Larjavaara M, 2014. The world's tallest trees grow in thermally similar climates. *New Phytol* 202: 344-349. <https://doi.org/10.1111/nph.12656>
- Legendre P, Legendre LFJ, 2012. *Numerical Ecology*, Vol 24. 3rd ed. Elsevier, Amsterdam.
- Liang J, Buongiorno J, Monsrud RA, Kruger EL, Zhou M, 2007. Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *For Ecol Manag* 243: 116-127.
- Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze ED, McGuire AD, Bozzato F, Pretzsch H, *et al.*, 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354 (6309): aaf8957. <https://doi.org/10.1126/science.aaf8957>
- Long JN, Daniel TW, 1990. Assessment of growing stock in uneven-aged stands. *West J Appl For* 5: 93-96.
- Ma W, He JS, Yang Y, Wang X, Liang C, Anwar M, Zeng H, Fang J, Schmid B, 2010. Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites: Diversity-productivity relationships in Chinese grassland. *Glob Ecol Biogeogr* 19: 233-243. <https://doi.org/10.1111/j.1466-8238.2009.00508.x>
- Magurran AE, 1988. *Ecological diversity and its measurement*. Princeton University Press; NJ, USA. https://books.google.es/books/about/Ecological_Diversity_and_Its_Measurement.html?hl=es&id=iHoOAAAAQAAJ. [2017, Feb 10]. <https://doi.org/10.1007/978-94-015-7358-0>
- McMinn JW, 1992. Diversity of woody species 10 years after four harvesting treatments in the oak-pine type. *Can J For Res* 22: 1179-1183. <https://doi.org/10.1139/x92-156>
- Miles PD, Smith BW, 2009. Specific gravity and other properties of wood and bark for 156 tree species found in North America. Newtown square PA 19073-3294: USDA For Serv North Res Stat. http://www.nrs.fs.fed.us/pubs/rn/rn_nrs38.pdf
- Nadal-Romero E, Petric K, Verachtert E, Bochet E, Poesen J, 2014. Effects of slope angle and aspect on plant cover and species richness in a humid Mediterranean badland. *Earth Surf Process Landf* 39: 1705-1716. <https://doi.org/10.1002/esp.3549>
- Nadrowski K, Wirth C, Scherer-Lorenzen M, 2010. Is forest diversity driving ecosystem function and service? *Curr Opin Environ Sustain* 2: 75-79. <https://doi.org/10.1016/j.cosust.2010.02.003>
- Paquette A, Messier C, 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests: The effect of biodiversity on the productivity. *Glob Ecol Biogeogr* 20: 170-180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>
- Pärtel M, Zobel M, 2007. Dispersal limitation may result in the unimodal productivity-diversity relationship: A new explanation for a general pattern. *J Ecol* 95: 90-94. <https://doi.org/10.1111/j.1365-2745.2006.01185.x>
- Pärtel M, Laanisto L, Zobel M, 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. *Ecology* 88: 1091-1097. <https://doi.org/10.1890/06-0997>
- Potter KM, Woodall CW, 2014. Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. *For Ecol Manag* 321: 117-129.
- Pretzsch H, 2009. *Forest dynamics, growth and yield*. Springer, Berlin, Heidelberg. <http://link.springer.com/10.1007/978-3-540-88307-4>. [2016, Aug 28]. https://doi.org/10.1007/978-3-540-88307-4_1
- Pugesek BH, Tomer A, Eye A von, 2003. *Structural equation modeling: Applications in ecological and evolutionary biology*. Cambridge University Press, UK. <https://doi.org/10.1017/CBO9780511542138>
- Reineke LH, 1933. Perfecting a stand-density index for even-aged forests. *J Agric Res* 46: 627-638.
- Rodríguez-Loinaz G, Onaindia M, Amezaga I, Mijangos I, Garbisu C, 2008. Relationship between vegetation

- diversity and soil functional diversity in native mixed-oak forests. *Soil Biol Biochem* 40: 49-60. <https://doi.org/10.1016/j.soilbio.2007.04.015>
- Ryan MG, 2010. Temperature and tree growth. *Tree Physiol* 30: 667-668. <https://doi.org/10.1093/treephys/tpq033>
- Shipley B, 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations, and causal inference. Cambridge University Press, UK. <https://doi.org/10.1017/CBO9780511605949>
- Thoms C, Gattinger A, Jacob M, Thomas FM, Gleixner G, 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in temperate deciduous forest. *Soil Biol Biochem* 42: 1558-1565. <https://doi.org/10.1016/j.soilbio.2010.05.030>
- Tilman D, Pacala S, 1993. The maintenance of species richness in plant communities. In: *Species Divers Ecol Communities*; Ricklefs RE, Schluter D (eds). University of Chicago Press; pp: 13-25. Available from: <http://www.cfbiodiv.org/userfiles/Tilman%201994%20species%20diversity.pdf>. [2017 Mar 3]
- Timilsina N, Escobedo FJ, Staudhammer CL, Brandeis T, 2014. Analyzing the causal factors of carbon stores in a subtropical urban forest. *Ecol Complex* 20: 23-32. <https://doi.org/10.1016/j.ecocom.2014.07.001>
- Vilà M, Vayreda J, Gracia C, Ibáñez JJ, 2003. Does tree diversity increase wood production in pine forests? *Oecologia* 135: 299-303. <https://doi.org/10.1007/s00442-003-1182-y>
- Vilà M, Inchausti P, Vayreda J, Barrantes O, Gracia C, Ibáñez JJ, Mata T, 2005. Confounding factors in the observational productivity-diversity relationship in forests. In: *For Divers Funct Temp Boreal Syst*; Scherer-Lorenzen M, Körner C, Schulze ED (eds). Vol 176, p. 65-86. [place unknown]: Springer. http://link.springer.com/chapter/10.1007/3-540-26599-6_4. [2016, Oct 22]. https://doi.org/10.1007/3-540-26599-6_4
- Vilà M, Vayreda J, Comas L, Ibáñez JJ, Mata T, Obón B, 2007. Species richness and wood production: A positive association in Mediterranean forests. *Ecol Lett* 10: 241-250. <https://doi.org/10.1111/j.1461-0248.2007.01016.x>
- Weiskittel AR (eds), 2011. *Forest growth and yield modeling*. Wiley, Hoboken, NJ, USA. <https://doi.org/10.1002/9781119998518>
- Woodall CW, Miles PD, Vissage JS, 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. *For Ecol Manag* 216: 367-377.
- Woodall CW, D'Amato AW, Bradford JB, Finley AO, 2011. Effects of stand and inter-specific stocking on maximizing standing tree carbon stocks in the eastern United States. *For Sci* 57: 365-378.
- Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL, 2010. The forest inventory and analysis database: Database description and users manual version 4.0 for Phase 2. <http://www.treesearch.fs.fed.us/pubs/37446>. [2016, May 20].
- Zhang Y, Chen HYH, 2015. Individual size inequality links forest diversity and above-ground biomass. *J Ecol* 103: 1245-1252. <https://doi.org/10.1111/1365-2745.12425>
- Zifan A. 2016, USA map of Köppen climate classification https://commons.wikimedia.org/wiki/File:USA_map_of_K%C3%B6ppen_climate_classification.svg. [2017, Feb 23].
- Zuo XA, Knops JMH, Zhao XY, Zhao HL, Zhang TH, Li YQ, Guo YR, 2012. Indirect drivers of plant diversity-productivity relationship in semiarid sandy grasslands. *Biogeosciences* 9: 1277-1289. <https://doi.org/10.5194/bg-9-1277-2012>