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Forest structure and species diversity as predictors of aboveground biomass in a temperate forest of northern Mexico

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Abstract

Background: Understanding the biotic factors that drive aboveground biomass, including species and structural diversity, is essential for improving forest productivity and informing management under climate change.

Hypotheses: We evaluated whether species diversity and structural diversity positively influence aboveground biomass in a temperate forest of northwestern Mexico, hypothesizing that structural diversity would exert a stronger and more consistent effect.

Data description / Mathematical model: Aboveground biomass was estimated using species- and genus-specific allometric equations. Species diversity indices (richness, Shannon, and evenness) and structural metrics (tree density, number of diameter and height classes, and tree-size diversity indices) were calculated. Partial correlations guided variable selection, followed by linear regression relating diversity metrics to plot-level aboveground biomass.

Study site and dates: The study was conducted in the El Brillante ejido, Sierra Madre Occidental, Durango, Mexico (~2,500 m elevation), using data collected in 2023 from 40 randomly distributed plots.

Methods: Pearson and partial correlations evaluated bivariate and independent relationships between predictors and aboveground biomass. The final model included tree density, number of diameter classes, and the Shannon index of height classes; assumptions were verified using residual diagnostics and variance inflation factor.

Results: Mean aboveground biomass was 82 Mg ha^{-1}. Species richness showed weak and non-significant relationships, whereas structural variables explained 82 % of biomass variation.

Conclusions: Structural diversity is a strong predictor of aboveground biomass, while species richness plays a limited role.

Keywords: forest biomass, linear regression, climate change, niche complementarity.

Resumen

Antecedentes: Comprender los factores bióticos que determinan la biomasa aérea, incluida la diversidad de especies y la diversidad estructural, es fundamental para mejorar la productividad forestal.

Hipótesis: Evaluamos si la diversidad estructural y de especies influyen positivamente en la biomasa aérea en un bosque templado del noroeste de México, planteando que la diversidad estructural ejercería un efecto más fuerte y consistente.

Descripción de datos / Modelo matemático: La biomasa aérea se estimó mediante ecuaciones alométricas. Se calcularon índices de diversidad de especies (riqueza, Shannon y equidad) y métricas estructurales (densidad arbórea, número de clases diamétricas y de altura, e índices de diversidad de tamaños). La selección de variables se basó en correlaciones parciales y posteriormente se ajustó un modelo de regresión lineal.

Sitio y fechas de estudio: El estudio se realizó en el ejido El Brillante, Sierra Madre Occidental, Durango, México (~2,500 m de altitud), utilizando datos recolectados en 2023 en 40 parcelas distribuidas aleatoriamente.

Métodos: Se aplicaron correlaciones parciales, y el modelo final incluyó densidad arbórea, número de clases diamétricas e índice de Shannon de clases de altura; los supuestos se verificaron mediante diagnósticos de residuos y factor de inflación de la varianza.

Resultados: La biomasa aérea promedio fue de 82 Mg ha^{-1}. La riqueza de especies mostró relaciones débiles, mientras que las variables estructurales explicaron el 82 % de su variación.

Conclusiones: La diversidad estructural es un predictor sólido de la biomasa aérea, mientras que la riqueza de especies tiene una influencia limitada.

Palabras clave: biomasa forestal, regresión lineal, cambio climático, complementariedad de nichos.

Aboveground biomass (AGB) constitutes one of the largest and most dynamic carbon pools in forest ecosystems and is therefore widely used as a proxy for estimating forest carbon stocks (Ma *et al*. 2024). Because a relatively constant proportion of dry biomass is composed of carbon, variations in AGB directly reflect changes in forest carbon storage (Rodríguez-Veiga *et al*. 2017). Consequently, quantifying AGB is a fundamental step for assessing the role of forests as carbon sinks (Chave *et al*. 2014).

Given the importance of forests as carbon sinks, it is essential to identify the variables that drive biomass accumulation to develop strategies that contribute to climate change mitigation (Ondei *et al*. 2023). Both abiotic and biotic factors have direct and indirect effects on AGB (Ayushi *et al*. 2023). In particular, the role of species diversity in forest biomass has long been debated (Ondei *et al*. 2023). It is often assumed that higher species richness leads to greater biomass (Hordijk *et al*. 2023). However, species-specific contributions to stand-level AGB are rarely documented, which has limited the development of generalizable patterns and principles across forest types (Wang *et al*. 2016).

Empirical evidence linking species diversity to AGB varies across ecosystem types. Positive relationships have been reported in wetlands and subtropical broadleaf forests (Espinar 2006, Chen *et al*. 2022), where high species turnover and functional complementarity may enhance biomass accumulation, whereas weaker or context-dependent relationships have been observed in temperate and Mediterranean forests (Bravo *et al*. 2021). Global-scale analyses further suggest that species richness–biomass relationships are not universally transferable across biomes, highlighting limitations in generalization and the importance of ecosystem context (Gillman & Wright 2006).

In contrast, structural diversity reflecting variation in tree size, height, and canopy architecture (Gadow *et al*. 2012), has shown more consistent positive associations with AGB, particularly in temperate forests (Fischer *et al*. 2019, Hai *et al*. 2024). Structural heterogeneity can influence biomass through complementarity effects, allowing efficient resource capture among differently sized trees, while species richness can contribute via selection effects, where highly productive species dominate stand-level biomass (Zeller & Pretzsch 2019). As a result, structural attributes may represent a more direct and integrative predictor of AGB than taxonomic diversity alone, especially in managed or semi-managed forests (Dănescu *et al*. 2016).

This global variability is also evident at regional scales, including Mexico, where local-scale studies have revealed contrasting species diversity–biomass relationships. For example, in dry tropical forests, a log-linear positive relationship has been observed (Balvanera & Aguirre 2006). In Tamaulipan thornscrub forests of northeastern Mexico, negative linear relationship has been documented (Navar *et al*. 2014). In temperate forests, U-shaped (Návar-Cháidez & González-Elizondo 2009), positive linear, and hump-shaped relationships have been reported (Vargas-Larreta *et al*. 2021, Padilla-Martínez *et al*. 2024). Regarding structural diversity–biomass relationships, positive linear trends have been found in temperate forests of the Sierra Madre Occidental and Sierra Madre Oriental (northwestern and northeastern Mexico, respectively) (Návar-Cháidez & González-Elizondo 2009, Návar-Cháidez 2010, Padilla-Martínez *et al*. 2024). Together, these findings indicate that species diversity–biomass relationships are highly context-dependent across forest types in Mexico, whereas structural diversity appears to be a more consistent predictor of aboveground biomass in temperate forests.

Given these contrasting results, further efforts are needed to better understand how different dimensions of biodiversity relate to AGB, particularly in temperate forests of the Sierra Madre Occidental of Durango, where mixed conifer–broadleaf stands dominate and management practices create heterogeneous stand structures. The objective of this study was to analyze the relationships between species diversity, structural diversity, and aboveground biomass (AGB) in a temperate forest of the Sierra Madre Occidental (Durango, Mexico). We hypothesized that species and structural diversity would be positively associated with AGB, with structural diversity showing a more consistent relationship.

Materials and methods

Study area. The study was conducted in a forest within the El Brillante ejido, located in the Sierra Madre Occidental, Durango, Mexico (geographical extent: 23° 37’ 12.9”-23° 50’ 55.7” N and 105° 18’ 56.2”-105° 31’ 09.8” W; Figure 1).

The average elevation is 2,500 m, and the local climate types are semi-cold humid C(E)(m) and temperate sub-humid C(w) (García 2004). Mean annual temperature ranges from 10 °C to 18 °C, while mean annual precipitation is approximately 1,000 mm (INEGI 2017). The dominant soil types in the area are Luvisols and Regosols (INEGI 2017). The study area is covered by temperate forests, characterized by ecosystems dominated by mixed coniferous stands interspersed with broadleaf species typical of this region, primarily species of the genera *Pinus* and *Quercus* (González-Elizondo *et al*. 2007).

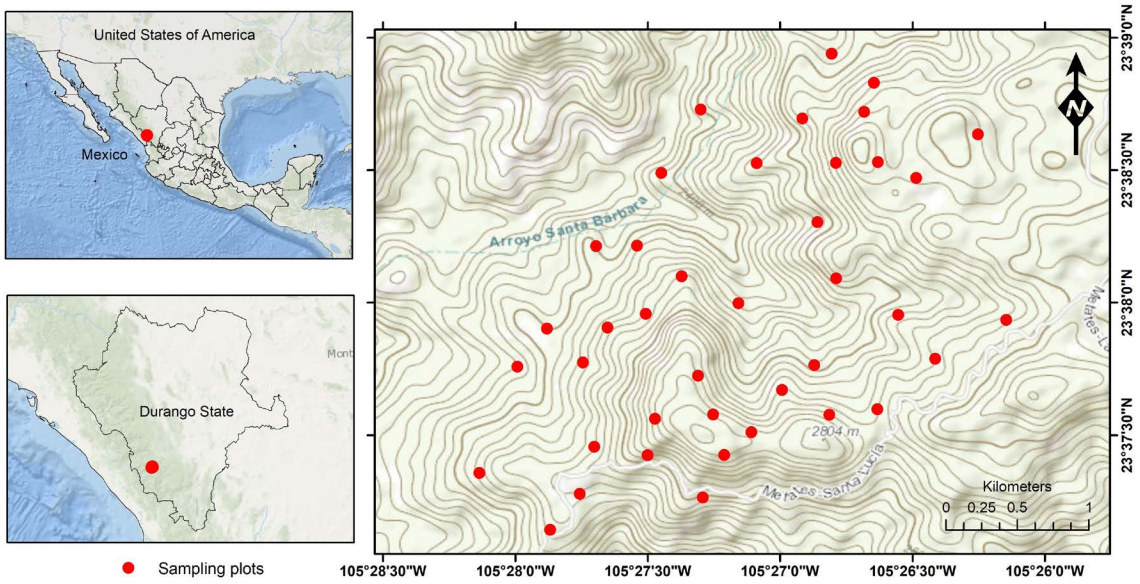

Figure 1. Location of the study area and distribution of sampling plots (red dots).

The El Brillante ejido has a legal area of 9,516 ha, of which approximately 9,100 ha are currently forested and managed. Forest management has been conducted for more than 60 years under an authorized management program based on a mixed silvicultural system, combining principles of the Mexican Method for the Management of Irregular Forests (MMOBI) and the Silvicultural Development Method (MDS). Timber extraction is regulated and primarily selective, resulting in a mosaic of stands with varying structural conditions. Although the forest is subject to episodic disturbances such as forest fires typically frequent but of low severity and occasional pest outbreaks, the study area maintains continuous forest cover and a heterogeneous stand structure. This management and disturbance context is representative of many temperate ejido forests in the Sierra Madre Occidental and provides an essential framework for interpreting patterns of diversity, structure, and aboveground biomass.

Data collection. Dendrometric data were collected from 40 randomly distributed circular plots, each with an area of 1,000 m², established across an approximate spatial extent of ~500 ha within the managed forest area. This study was framed as a pilot investigation aimed at exploring relationships between species diversity, structural diversity, and AGB.

Plots were located within a temperate forest representative of the dominant forest conditions of the study area, avoiding roads, forest edges, and areas affected by recent stand-replacing disturbances at the time of sampling. Within each plot, all trees with a diameter at breast height (DBH) ≥ 5 cm were measured. For each individual, species identity, DBH (cm), total height (TH; m), and crown diameter (CD; m) were recorded.

Aboveground biomass calculation. AGB was estimated using allometric equations developed by Vargas-Larreta *et al.* (2017), which are based on permanent silvicultural research plots established in temperate forests of the Sierra

Madre Occidental in Durango. These plots represent forest stands with similar floristic composition, structural characteristics, management history, and climatic conditions to those of the present study, and some are located in close proximity to the study area. The equations encompass a wide DBH range consistent with the diameter distribution of the measured trees, supporting their applicability for biomass estimation in this region.

For *Alnus* spp., an allometric equation developed in Oaxaca (Acosta-Mireles *et al*. 2002) was used due to the absence of regional models for northern Mexico. This choice represents the closest approximation available and its limitations are acknowledged. Individual tree biomass values (kg) were summed at the plot level and converted to megagrams per hectare ($Mg \cdot ha^{-1}$) considering the fixed plot area (1,000 m^2). These plot-level AGB values were used as the response variable in all subsequent analyses.

Species diversity and structural diversity calculation. At each sampling site, species richness (S; Equation 1) was calculated along with species diversity using the Shannon index (H; Equation 2) and Evenness index (E; Equation 3). Structural diversity was defined in terms of tree size heterogeneity and quantified using the number of diameter and height classes (NDC and NHC, respectively), along with Shannon diversity and evenness indices derived from diameter- and height-class distributions (Equations 5 and 6, respectively). Diameter classes were defined using 5-cm DBH intervals, and height classes were defined using 2-m height intervals. In addition, tree density (number of trees per plot) was included as a key structural variable given its direct influence on stand-level biomass. All indices were calculated in R version 4.4.1 using the *BiodiversityR* package (Kindt 2024).

Statistical analysis. Pairwise Pearson correlations were initially calculated to explore bivariate relationships between AGB and diversity and structural metrics. To disentangle direct relationships from spurious correlations driven by shared variance among predictors, partial correlation analyses were performed, controlling for the remaining variables. These analyses were used as an exploratory step to guide variable selection and to avoid redundancy among highly collinear metrics.

Based on partial correlation results and ecological interpretability, a single linear model was fitted to evaluate the relationship between AGB and forest structure and diversity. The model included tree density (number of trees per plot), NDC and HH as predictors, as these variables showed the strongest and most independent associations with AGB while minimizing redundancy among correlated metrics. Multicollinearity among predictors was evaluated using variance inflation factors (VIF), with all selected predictors showing VIF < 5. Model assumptions were evaluated through visual inspection of residuals and standard diagnostic plots. All analyses were conducted in R version 4.4.1 (R Core Team 2025).

Results

Aboveground biomass. Aboveground biomass (AGB) showed substantial variability among plots (Table 2). Plot-level AGB values ranged from 5.06 to 208.80 Mg ha^{-1}, with a mean of 82.18 Mg ha^{-1}.

Species contributions to total AGB were uneven, with *Pinus durangensis* Martínez accounting for 44.94 % of total biomass, followed by *Quercus rugosa* Née (12.61 %). Together, the dominant species represented more than 57.5 % of the total AGB, highlighting their structural importance at the study site. The lower contributions were observed for *Pinus herrerae* Martínez (0.44 %), *Arbutus madrensis* S. González (0.33 %), and *Juniperus deppeana* Steud. (0.31 %) (Table 3).

Species diversity and structural diversity. Out of a total of 1,965 trees analyzed, 17 species were identified, belonging to the families Pinaceae (8), Fagaceae (5), Cupressaceae (1), Ericaceae (2), and Betulaceae (1). On average, each plot contained six species, eight diameter classes, and four height classes. A statistical summary of species diversity and structural diversity indices is presented in Table 4.

Table 1. Equations for calculating species diversity and structural diversity indices.

	Index	Equation	
Species diversity	Species richness	$S = NS$	(1)
	Shannon index	$H = -\sum_{i=1}^{NS} n_i \times ln(n_i)$	(2)
	Eveness	$E = \frac{H}{ln(NS)}$	(3)
Structural diversity	Total number of diameter or height classes	NC	(4)
	Shannon index	$H = -\sum_{j=1}^{NC} n_j \times ln(n_j)$	(5)
	Eveness	$E = \frac{H}{ln(NC)}$	(6)

NS = total number of species at sampling plots i. ln = natural logarithm. n_i *= individual number of the i-th species.* n_j *= individual number of the j-th diameter or height class. NC = total number of diameter or height classes* (*class width* was 5.0 cm for diameters and 2.0 m for heights).

Table 2. Summary statistics of plot-level aboveground biomass (AGB, Mg·ha^{-1}).

n	Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
40	5.062	37.816	71.884	82.183	118.05	208.804

Table 3. Statistical summary of individual-tree aboveground biomass (Mg·ha^{-1}) by species.

Specie	Total AGB	Mean	Standard deviation	Minimum	Maximum	% of total AGB
Alnus acuminata Kunth	115.692	0.587	1.657	0.043	14.833	3.519
Arbutus madrensis S.González	11.148	0.485	0.849	0.058	3.668	0.339
Arbutus xalapensis Kunth	113.322	0.553	0.988	0.026	6.600	3.447
Juniperus deppeana Steud.	10.392	0.315	0.574	0.010	2.594	0.316
Pinus strobiformis Engelm.	78.638	1.123	1.720	0.036	8.651	2.392
Pinus cooperi C. E. Blanco	154.874	3.367	4.596	0.062	22.086	4.711
Pinus durangensis Martínez	1,477.401	2.442	3.857	0.047	47.453	44.942
Pinus engelmannii Carrière	78.098	2.231	2.436	0.145	8.372	2.376
Pinus herrerae Martínez	14.610	2.090	3.880	0.070	10.600	0.444
Pinus leiophylla Schiede *ex* Schltdl. & Cham.	72.989	2.212	2.776	0.017	8.730	2.220
Pinus lumholtzii B. L. Rob. & Fernald	72.017	1.263	1.381	0.100	6.550	2.191
Pinus teocote Schltdl. & Cham.	129.159	1.502	1.936	0.036	11.833	3.929
Quercus crassifolia Bonpl.	140.060	4.670	6.640	0.060	21.990	4.261

Specie	Total AGB	Mean	Standard deviation	Minimum	Maximum	% of total AGB
Quercus fulva Liebm.	24.800	2.760	3.660	0.110	10.800	0.754
Quercus rugosa Née	414.682	1.902	5.193	0.041	55.943	12.615
Quercus sideroxyla Bonpl.	334.795	1.200	3.587	0.022	48.085	10.184
Quercus urbanii Trel.	44.639	1.395	1.698	0.122	7.611	1.358

Table 4. Statistical summaries of species and structural diversity indices.

Variable	Mean	Standard error of the mean	Standard deviation	Minimum	Median	Maximum
Number of trees	49.15	4.62	29.22	13	38.5	128
S	6.025	0.241	1.527	3	6	9
Shannon (H)	1.3471	0.0441	0.2789	0.4709	1.4135	1.717
Evenness (E)	0.6723	0.0196	0.1241	0.3889	0.6852	0.9321
NDC	8.35	0.346	2.19	3	8	13
Shannon (HD)	1.6671	0.0559	0.3533	0.5924	1.731	2.113
Evenness (ED)	0.6774	0.0243	0.154	0.3617	0.6746	0.9806
NHC	3.85	0.132	0.834	2	4	6
Shannon (HH)	1.052	0.0434	0.2745	0.2988	1.1205	1.568
Evenness (EH)	0.7784	0.0245	0.1552	0.4494	0.8191	0.995

Correlation analysis. Values of the species diversity indices did not show a statistically significant relationship with AGB, except for species richness (S), which was positively correlated ($P = 0.018$). Among the structural diversity indices, NDC, HD, NHC, and HH exhibited statistically significant positive relationships with AGB ($P \leq 0.05$). The number of trees per plot also showed a positive and statistically significant association ($P = 0.001$). Figure 2 presents the correlation matrix of all variables used.

Partial correlation analyses revealed that AGB was significantly associated with tree density (Figure 3a), NDC (Figure 3b) and HH (Figure 3c) after controlling covariation among predictors.

Regression model. Based on partial correlation results, a linear model was fitted to quantify the joint effects of tree density, NDC and HH on AGB (Equation 7).

$$AGB = -111.8546 + 0.6991 \times Number\ of\ Trees + 10.3287 \times NDC + 69.78 \times HH \quad (7)$$

The model explained a substantial proportion of the variability in AGB across plots (adjusted $R^2 = 0.82$). Tree density emerged as the strongest predictor, with a significant positive effect on biomass, while NDC and HH also showed a significant independent contribution (Table 5).

Model diagnostics showed no evidence of influential observations or strong departures from linearity. Although residuals exhibited minor deviations from normality and a slight increase in variance at higher fitted values, these patterns were weak and did not compromise the overall interpretation of the results.

Discussion

This study provides one of the few empirical assessments of both species and structural diversity effects on aboveground biomass (AGB) in a temperate forest of northwestern Mexico, particularly under a long-term ejidal management context. Our results reinforce the role of structural heterogeneity as a consistent driver of AGB, highlighting the functional importance of stand structure for forest productivity and carbon storage.

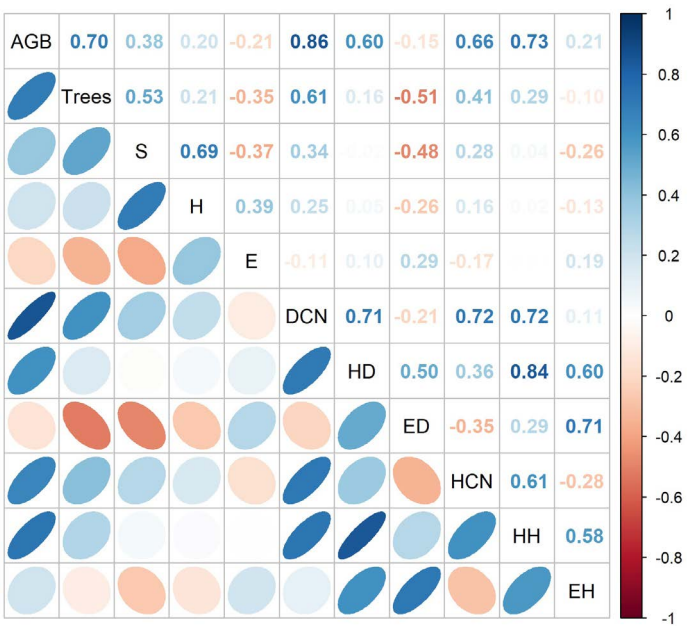

Figure 2. Correlation matrix between species diversity metrics, structural diversity metrics, and aboveground biomass (AGB). The lower-left panel shows Pearson correlation coefficients represented by ellipses, where ellipse orientation indicates the sign of the correlation (right-tilted = positive; left-tilted = negative) and ellipse shape and color intensity reflect correlation strength, with narrower and darker ellipses indicating stronger relationships. The upper-right panel displays the numerical values of the Pearson correlation coefficients.

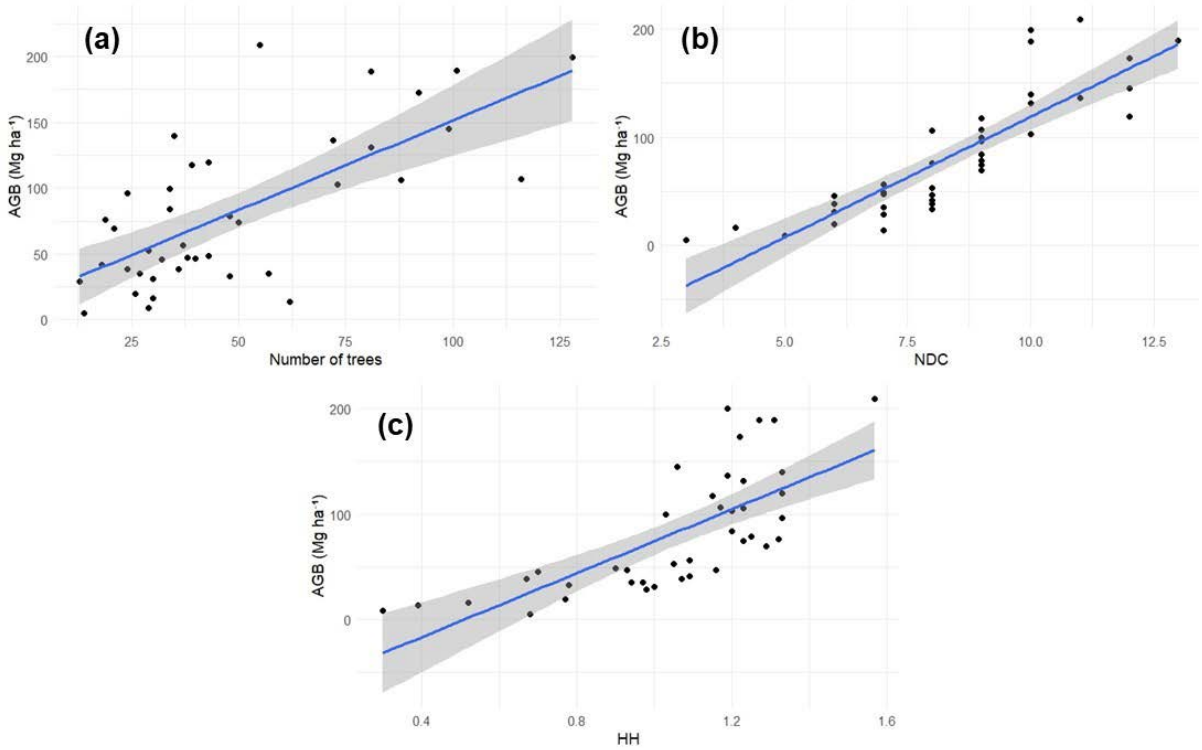

Figure 3. Relationships between AGB and (A) number of trees, (B) NDC, and (C) HH. The solid line represents the fitted linear regression, and the shaded area indicates the 95 % confidence interval.

Table 5. Summary of regression coefficient statistics.

Term	Coefficient	SE	*t*-value	*P*-value	VIF
Intercept	-111.8546	16.4323	-6.807	0.0000	
Number of trees	0.6991	0.1731	4.039	0.0002	1.71
NDC	10.3287	3.2001	3.228	0.0026	3.29
HH	69.78	21.1847	3.294	0.0022	2.27

SE= standard error of the coefficient; VIF= Variance inflation factor

The mean plot-level AGB in this study (~82 $Mg \cdot ha^{-1}$) falls within the range of values previously reported for temperate pine–oak forests in northern Mexico. For instance, field-based estimates of AGB in mixed conifer–broadleaf forests of Durango and adjacent regions have reported AGB values on the order of ~80-130 $Mg \cdot ha^{-1}$, reflecting similar structural conditions (Návar 2009, Graciano-Ávila *et al*. 2019). Results from remotely sensed AGB estimates in temperate forests of Durango also indicate substantial spatial variability in biomass stocks across the landscape (Rosas-Chavoya *et al*. 2023). Together, these findings indicate that the observed average AGB in our study is typical of temperate forests in the region and not unusually low or high. Importantly, the range of AGB values observed (from low to high) suggests a mosaic of stand conditions, consistent with long-term forest management, historical timber extraction, and naturally varying regeneration dynamics, rather than a uniformly old-growth or unmanaged stand (Soriano-Luna *et al*. 2018).

We acknowledge that applying equations outside their original geographic range may introduce some uncertainty (*i.e*., for *Alnus* spp., Acosta-Mireles *et al*. 2002); however, *Alnus acuminata* contributed a minor fraction of total plot-level biomass (< 2 %), and therefore any potential bias is unlikely to affect overall AGB estimates.

Among species diversity metrics, only species richness (S) showed a statistically significant correlation with AGB. However, when included in the regression model, S was not significant, likely because the richness–biomass relationship is mediated by environmental conditions, species interactions, and biogeographic factors (Jucker *et al*. 2016, Noreika *et al*. 2019, Ondei *et al*. 2023). In other words, abiotic factors can directly or indirectly influence AGB through their effects on biotic components (Alrutz *et al*. 2022, Xie *et al*. 2023, Simmavong *et al*. 2025).

Community uniformity may also mediate the biodiversity-biomass relationship. A negative correlation between species richness and uniformity in this study (Figure 2) suggests that sites with many individuals may still be dominated by a few species. This pattern implies that, at low richness, unequal communities can be more productive, whereas at high richness, more uniform communities perform better (Hordijk *et al*. 2023, Padilla-Martínez *et al*. 2024).

Structural diversity metrics, on the other hand, were positively and significantly related to AGB. Specifically, three simple metrics, the number of trees, NDC, and HH explained 82 % of the variance in AGB. Tree density influences diversity–biomass interactions: at low densities, interactions are weak, but they intensify as density increases (Forrester & Bauhus 2016). Additionally, forest biomass growth is affected by size inequality, quantified here using the Shannon index for tree sizes (Dănescu *et al*. 2016, Forrester 2019, Tan *et al*. 2021, Hai *et al*. 2024). High structural diversity likely enhances resource capture efficiency and biomass production via niche complementarity (Forrester 2019, Simmavong *et al*. 2025), suggesting that structural metrics better approximate actual niche occupation (LaRue *et al*. 2023).

These results are consistent with previous studies reporting positive relationships between forest structural diversity and aboveground biomass (Glatthorn *et al*. 2018, Fischer *et al*. 2019, Hai *et al*. 2024) and support the view that forest structure often exerts a stronger control on productivity than species diversity (Dănescu *et al*. 2016, Bohn & Huth 2017). In the temperate forests of northern Mexico, our findings indicate that variation in tree density and structural heterogeneity is directly linked to AGB, implying that forest management practices that alter stand structure such as thinning intensity or diameter distribution can have measurable consequences for biomass accumulation and long-term productivity (Padilla-Martínez *et al*. 2024).

On the other hand, considering climate change, managing structural and species diversity is crucial. Changing disturbance regimes, including increasing frequency and severity of droughts in Mexico, threaten forest stability (Seidl *et al*. 2017, Ehbrecht *et al*. 2021, Cabral-Alemán *et al*. 2022a). Managing tree density can mitigate competition stress and enhance drought tolerance, but must be balanced with maintaining species diversity (Ammer 2019, Cabral-Alemán *et al*. 2022b). Future studies could evaluate how density reduction affects AGB, structure, and species diversity under changing climatic conditions.

The high proportion of variance explained by our model is notable for ecological data, where unexplained variability is typically high. This is plausible in our study because the selected structural variables are strongly and independently associated with aboveground biomass in this temperate forest. These predictors were carefully selected using partial correlation analyses, minimizing redundancy and collinearity, which likely contributed to the high explanatory power. Model diagnostics, including residual inspection and variance inflation factor (VIF < 5), indicate that the model captures genuine ecological relationships rather than overfitting. Nonetheless, this study is pilot scale (40 plots), and caution is warranted when extrapolating results beyond the study area. Future research with larger and stratified sampling designs would help validate these findings and examine whether the high explanatory power holds across broader spatial and environmental gradients.

Although our linear model captured most of the variation in AGB, we acknowledge that potential non-linear relationships or interactions between tree density and species diversity may exist. For instance, biomass accumulation could saturate at high densities or exhibit threshold effects. Exploring these possibilities is an important avenue for future research, particularly under varying management regimes and disturbance histories.

Finally, we highlight that although species richness showed a positive relationship with AGB, forest structure emerged as a stronger predictor, with simple structural metrics explaining most of the variation. This pattern likely reflects niche complementarity, highlighting the functional importance of structural attributes in driving biomass accumulation. These results suggest that forest management strategies should focus on maintaining or enhancing structural diversity to support productivity.

Acknowledgements

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