Disentangling Habitat-specific Pathways of Forest Biomass Loss: A Structural Equation Modeling Approach Across Temperate and Subtropical Forests

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This study examined how elevation, habitat diversity, and soil nitrogen interact to influence forest biomass across ecological zones. A field survey was conducted using 300 plots, systematically allocated across three habitat types with equal representation. The relationships were measured using bivariate analysis, correlation study, and structural equation modeling (SEM). The habitat-unified model revealed that elevation had a statistically significant direct effect on biomass ($\beta = 0.71$, $p < 0.001$), as well as indirect effects through species richness ($\beta = 0.37$, $p < 0.001$) and soil nitrogen ($\beta = 0.15$, $p < 0.05$). Moist forest habitats were shown to increase soil nitrogen content ($\beta = 0.37$, $p < 0.001$) and species richness ($\beta = 0.28$, $p < 0.001$) significantly. Habitat-specific models revealed that the strength and direction of these relationships varied between forest types. Degradation had a strong negative effect on biomass in subtropical ecosystems ($\beta = 0.34$, $p < 0.0001$) and in moist temperate forests ($\beta = 0.61$, $p < 0.0001$). Degradation reduced biomass in subtropical and moist temperate forests but had no significant effect in dry temperate forests. However, it strongly decreased soil nitrogen and, together with elevation, constrained biomass.

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INTRODUCTION

The Hindukush-Himalayan (HKH) forests are among the most ecologically important and carbon-rich ecosystems in the world and serve as primary biodiversity reservoirs, which have a decisive impact on local and planetary climate control (Bonan 2016; Sharma and Chettri 2021). However, the HKH area is now undergoing rapid environmental transformation due to deforestation, land-use change, and climate change, which, in turn, affect the structural integrity and functional activity of forest ecosystems (Hussain *et al*. 2021, 2024). The complexity of the topography, the diversity of climatic

conditions, and the wide range of ecosystems of the mountainous area create a heterogeneous mosaic of forest structures, each with unique structural and functional properties (Sundriyal and Sharma 2016; Manish and Pandit 2018). An array of biophysical variables modulates forest biomass, which is an important indicator of ecosystem productivity and carbon sequestration (He *et al*. 2020; Dyola *et al*. 2022). Among them, altitude, habitat type, and soil nitrogen levels are the main environmental gradients that determine vegetation patterns and biomass distributions (Singh 2018). Temperature, moisture, and solar radiation vary with elevation and, as a result, species composition and growth rates are affected (Shi *et al*. 2021; Lasway *et al*. 2023). Habitat variability promotes heterogeneity in forest structure, and soil nitrogen, a major macronutrient, directly affects plant growth and biomass gain (Gay *et al*. 2022; Wang *et al*. 2022). Although the two factors are recognized as playing key roles, the synergistic effects of these variables on forest biomass have not been extensively examined, particularly in the Himalayan-Karakoram (HKH) region. This study aims to bridge the existing knowledge gap by investigating the interactions among elevation, habitat diversity, and soil nitrogen levels to understand better their combined effects on forest biomass across different ecological zones in the study area. The research intends to make scientific contributions to inform sustainable forest management, biodiversity conservation, and climate change mitigation initiatives in mountainous ecosystems.

Elevation is a primary driver of microclimate, species, and ecosystem functioning, and mountain ecosystems in the HKH region have among the steepest environmental gradients worldwide (Johnstone 2021; Jia *et al*. 2024). The decrease in temperature with increasing altitude slows tree growth and reduces above-ground biomass in high-altitude forests (Zheng *et al*. 2021). Such a drop in temperature also reduces the levels of metabolism and extends the constraints of the growing season (Malhi *et al*. 2020; Testolin *et al*. 2020; Johnstone 2021). However, ideal moisture, temperature, and nutrient levels tend to support high biomass in middle-elevation regions (He *et al.* 2020). The effect of elevation on soil nutrient dynamics, in turn, has an indirect impact on forest biomass and a direct modulatory impact on climate. Nitrogen mineralization rates are usually slower at higher elevations due to decreased microbial activity and lower temperatures, resulting in reduced nutrient availability for plant uptake (Hobbie *et al*. 2005; Sundqvist *et al*. 2020). In forest ecosystems with high altitudes, the insufficiency of nitrogen may limit the photosynthetic rate and timber yield (Vitousek *et al*. 2002; He *et al*. 2020; Wang *et al*. 2022). In addition, alterations in species assemblages due to elevational gradients affect soil nitrogen cycling by changing litter quality and decomposition processes (Hewitt *et al*. 2022; Ostertag *et al*. 2022).

Habitat types play a critical role in tree biomass accrual by shaping environmental conditions, species composition, and ecological processes. Part of the forest habitats in the HKH area comprises temperate broadleaf and coniferous forests, as well as mixed forest types, each with distinct structural and functional characteristics (Ostertag *et al*. 2022; Hewitt *et al*. 2022). Each habitat type presents distinct microclimates, light availability, and soil characteristics, all of which directly influence tree growth, carbon sequestration potential, species composition, stand density, and resource use efficiency, ultimately making habitat a key determinant of biomass accumulation (He *et al*. 2020; Wang *et al*. 2022). Growing in colder and less-nutrient-rich areas, coniferous forests are often more likely to endure over longer periods due to the longevity and high density of the wood of conifer species (Hobbie *et al*. 2005; Johnstone 2021). Broadleaf forests, which are typically found in nutrient-rich, warmer regions, can sustain rapidly increasing species that accumulate AGB

rapidly but have shorter life spans (Hobbie *et al*. 2005; Johnstone 2021). Mixed forests are intermediate between broadleaf and coniferous forests and thus are more complex in structure and resource-use efficiency, potentially leading to higher biomass accumulation (Hobbie *et al*. 2005; Johnstone 2021). In addition, species diversity within specific habitats determines competition, complementarity, and resilience to environmental stressors, thereby mediating biomass dynamics; therefore, habitat type is an important factor in forest productivity, as it determines not only the rate but also the stability of biomass accumulation over time. Physicochemical properties of the soil are also indirectly influenced by habitat types through changes in organic matter inputs, vegetation composition, and microclimatic conditions (Singh *et al*. 2010; Chandra *et al*. 2016). Affected parameters of these changes include pH, nutrient availability, moisture content, and soil texture (Chadwick 1999; Rawat *et al*. 2021). Consequently, differences in soil fertility and ecosystem processes can be considerable due to changes in habitat structure and plant community dynamics (Perry *et al*. 2008; Lal 2015).

The nitrogen content of soil, an important determinant of plant productivity, mediates the effects of habitat on ecosystem productivity by influencing photosynthetic efficiency and lignocellulosic mass on biomass accrual (Vitousek 1997; LeBauer and Treseder 2008; Fay *et al*. 2015; Terrer *et al*. 2019). Nitrogen, a basic element of amino acids, nucleic acids, and chlorophyll, is essential for protein synthesis, enzyme catalysis, and photosynthetic performance; thus, it directly affects plant development and biomass accrual. Adequate nitrogen supply improves the leaf area index, promotes strong canopy growth, and increases net primary productivity (NPP) (Aber *et al*. 1998). Forest stands with suitable nitrogen inputs have been observed to accumulate greater amounts of above- and belowground biomass, which has been attributed to high levels of carbon assimilation and nutrient cycling. In contrast, nitrogen-limited soils hinder plant development, reduce biomass, and often produce a simplified species assemblage dominated by slow-growing, stress-tolerant taxa (Ritter *et al*. 2003). Moreover, nitrogen supply also controls the successional processes and structure of forests, especially in early successional or disturbed habitats with high nutrient demand. However, anthropogenic nitrogen inputs can lead to nutrient imbalances, soil acidification, and decreased biodiversity, which, in turn, can affect biomass accumulation trends and the overall activity of ecosystems (LeBauer and Treseder 2008; Fenn 2010). Thus, nitrogen input control is one of the central measures towards maintaining forest productivity and ensuring long-term carbon sequestration and ecological balance.

To accurately predict tree biomass under unstable environmental conditions, it is crucial to clarify how elevation, habitat typology, and nitrogen availability in forest ecosystems are affected. The nitrogen level in foliar tissues depends on nitrogen availability and is directly related to primary productivity and photosynthetic capacity (Bezerra *et al*. 2024). The most common adaptive strategies used by plants are slowed growth or increased root biomass to promote nutrient uptake in nitrogen-limited settings, shown by high-altitude coniferous forests (Camenzind *et al*. 2018; Zhao *et al*. 2024). In contrast, plants in low-altitude broadleaf forest ecosystems with high nitrogen levels invest a greater fraction of their resources in growth processes, thereby increasing biomass accumulation (Poorter *et al*. 2015). In addition, relationships with elevational gradients and habitat typology blur the connection between soil nitrogen levels and forest biomass. For example, coniferous forests are less associated with active nitrogen cycling due to acid soils and recalcitrant litter, which is explained by Ostertag *et al*. (2022); rather, the rate of nitrogen mineralization is higher in deciduous forests, which can be attributed to more

favorable litter chemistry and greater activity of microbes, as reported by Hewitt *et al*. (2022). These differences are also intensified by elevation, which changes moisture and temperature regimes, thereby affecting the release and decomposition of nutrients (Jiang *et al*. 2019). These relationships suggest that soil nitrogen is part of a complex system in which habitat traits and elevation collectively determine nutrient availability, which in turn determines forest biomass.

Although contemporary models have enhanced our understanding of ecosystem processes, they often overlook spatial heterogeneity. The processes of forming forest biomass are also controlled by a complex combination of abiotic and biotic factors, such as the availability of soil nutrients, topography, climatic environment, and human-made disturbances, but the mechanics of these interactions between these determinants in different habitats are not yet properly examined (Bayat *et al.,* 2021; Ullah *et al*. 2025; Yadav *et al*. 2024). The use of structural equation modeling (SEM) has become a highly useful tool for understanding these interrelations by quantifying both direct and indirect effects across environmental gradients (Fan *et al*. 2016; Zhu *et al*. 2024). Despite growing recognition of the role of environmental degradation in forest ecosystems, most existing studies remain focused on biomass estimation or remote sensing-based mapping, with limited efforts to quantitatively disentangle biome-specific responses and their interactions with soil nutrient dynamics and topographic stressors using integrated modeling approaches (Papucci *et al.* 2026; Latifah *et al*. 2025). Existing predictive models are more likely to generalize these complex relationships, thereby reducing interactions by applying the same assumptions to dissimilar habitats and obscuring crucial ecosystem-specific processes. To address this research gap, SEM was used in the present work to examine the direct and indirect relationships among forest degradation, soil nitrogen availability, and elevation in their effects on forest biomass across three forest biomes (moist temperate, subtropical, and dry temperate). This study aimed to evaluate how environmental degradation, soil nitrogen availability, and elevation interact to influence forest biomass across different habitat types, and to identify biome-specific ecological processes and key factors relevant to conservation planning using an SEM framework. Using a comparative analysis of a unified habitat model and habitat-specific frameworks, the study introduces a new multiscale approach to explaining forests' context-dependent responses to environmental stressors. The results have practical implications for focused conservation plans, particularly for identifying biome-specific weaknesses and prioritizing management actions to support forest resilience amid accelerating ecological change.

EXPERIMENTAL

Study Site

This study was conducted in subtropical, moist, and dry temperate forests of the Malakand Division (MKD) in Khyber Pakhtunkhwa Province, Pakistan. The Malakand division consists of Swat, Chitral, Dir lower, and Dir upper. The study area lies between 72° 00′ E and 35° 29′ 59.99" N with an altitudinal range of between 450 and 7,782 m (Fig 1). The Malakand division is known for its diverse and beautiful natural terrain. This region has diverse altitudinal, climatic, and geographical conditions responsible for the growth of different forests. The forest area is approximately 27% of the total land area, which is 0.8 million hectares (Ahmad *et al.* 2022). These forests hold significant ecological and economic importance and play a key role in mitigating climate change (Zeb *et al*. 2019).

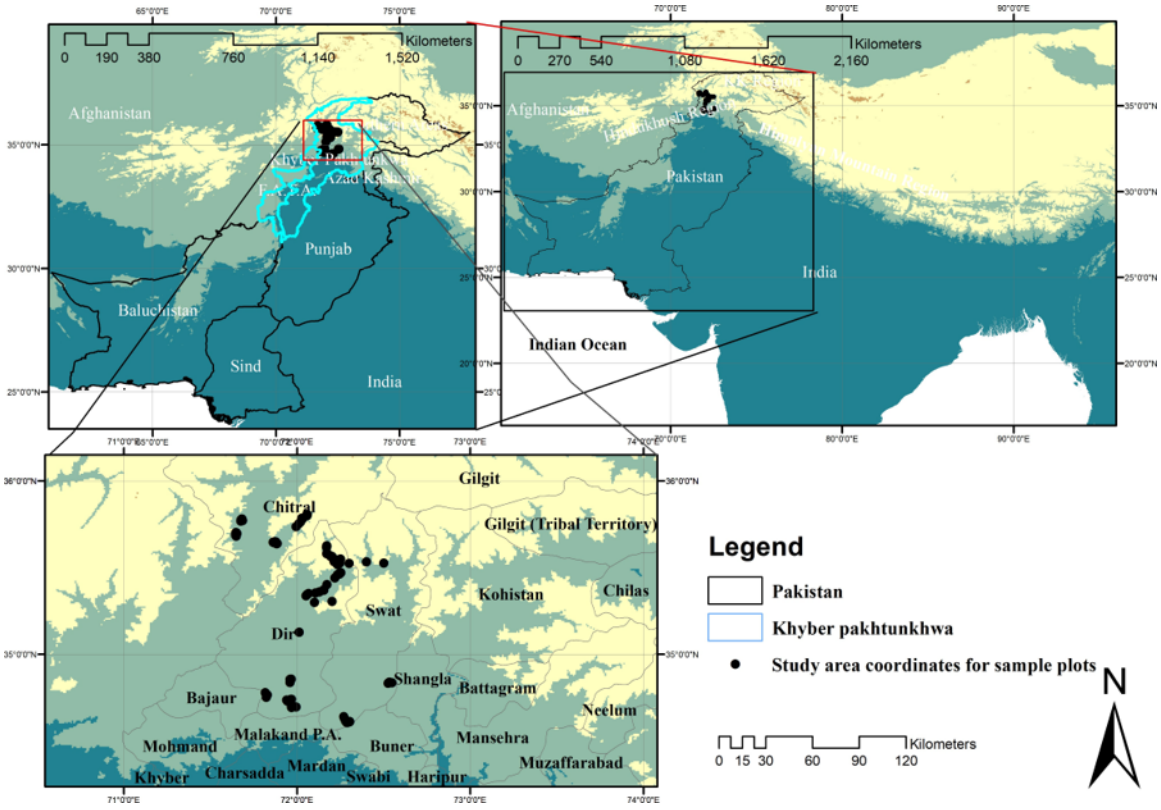

Fig. 1. Study area map

The Moist temperate forests are spread over the lower Swat and upper Dir regions at 1600 and 3100 m above sea level (asl). These are evergreen coniferous forests mixed with Oaks and other broadleaf vegetation. The mean annual temperature ranges from 13 to 18 °C, depending on altitude and location. The mean annual rainfall ranges from 700 to 1600 mm (Rahman *et al.* 2022). *Pinus wallichiana* (blue pine), *Cedrus deodara* (deodar cedar), *Abies pindrow* (Himalayan fir), *Quercus dilatata*, and *Quercus semicarpifolia* (brown oak) are common tree species found in these forests (Champion *et al*. 1965; Ullah *et al*. 2025).

Dry temperate forests occur in dry upper mountain regions at elevations of 1500 to 3350 m. The mean annual temperature ranges from 8 to 16 °C, and the mean annual precipitation is typically less than 500 mm (Rahman *et al.* 2022). However, these forests are under significant pressure from intense grazing and browsing by goats and sheep, which disrupts the natural balance of species composition. The key species include *Pinus gerardiana* (Chilgoza pine), *Pinus wallichiana*, *Picea smithiana* (West Himalayan spruce), *Juniperus macropoda* (juniper), *Juniperus excelsa*, *Taxus baccata* (yew), *Juglans regia* (walnut), and *Quercus ilex* (Champion *et al*. 1965; Ullah *et al*. 2025).

The subtropical chir pine forests are mainly composed of *Pinus roxburghii* (chir pine). They are found between elevations of 800 and 1600 m asl, particularly in the Lower Dir and Lower Swat regions. The area experiences mean annual temperatures ranging from 15 to 20° C, with precipitation between 700 and 1500 mm (Ahmad *et al.,* 2014; Rahman *et al.* 2022). The forests consist mainly of pure stands of chir pine, typically with almost even-aged trees. However, these forests are highly vulnerable to deforestation and degradation, particularly due to their proximity to human settlements. Grazing is

prevalent, often unmanaged, and intense. Common species are *Pinus roxburghii*, *Juglans regia*, and *Quercus incana* (Champion *et al.* 1965).

Tree and Soil Sampling

A stratified systematic sampling design was used in this work, with forest type as the primary stratification criterion. A total of 300 plots were established, with 100 plots assigned to each forest type. In each forest type, plots were established using a stratified design, ensuring at least 1 km of horizontal distance and approximately 500 m of elevation difference. This design was applied to minimize spatial autocorrelation and to fully capture environmental differences along the elevation gradient. This design has been extensively used in mountain forest landscapes to adequately capture environmental coverage while reducing spatial autocorrelation (Mueller-Dombois and Ellenberg 1974; Kent 2011; Thompson 2013). This sampling design was applied to balance logistical constraints with ecological representativeness in a large, topographically complex forest landscape. Each plot measured 20 × 20 m². Within each plot, a systematic tree-sampling approach was used to record all eligible stems, ensuring a complete inventory of tree structural attributes. Three representative points were randomly selected within each plot, and soil samples were collected from the upper 0 to 15 cm soil horizon. The soil sampling design ensured adequate representation of within-plot variability. The collected soil samples were transported to the laboratory, where concentrations of organic matter, total nitrogen, phosphorus, and potassium were analyzed following standard analytical protocols. Initially, all edaphic variables were included in the Structural Equation Modeling (SEM) analysis; however, only available soil nitrogen was significant and was therefore retained in the final model. The amount of available nitrogen was determined using the standard Kjeldahl digestion procedure, as described by Bremner (1960).

In this study, explicit climatic variables were not included because it was anticipated that classifying the study area into three distinct climatic zones would sufficiently capture the key climatic variation across the forest landscape. To address this further, both unified models and habitat-specific models were used, making it possible to examine patterns within and between these climatic zones. Likewise, climatic variables, such as temperature and precipitation, are often strongly correlated with elevation and with each other. Including these variables alongside elevation or climatic zones may introduce multicollinearity, thereby inflating standard errors and reducing the interpretability of SEM paths. Excluding redundant variables helps improve model stability. Climatic zones serve not only as proxies for climatic variables but also reflect ecological responses over time, including vegetation patterns, soil formation, and disturbance dynamics. Therefore, using climatic zones can sometimes be more ecologically reflective than raw climatic data (Kumar *et al.* 2024; Tercek *et al.* 2012).

In addition, altitude, aspect, slope, and geographic coordinates of each sampling plot were recorded. Topographic variables, slope, and aspect were initially considered and included in the preliminary SEM analysis. However, both variables were statistically insignificant and did not contribute meaningfully to the model. Therefore, only elevation was retained in the final analysis to maintain model parsimony.

Measuring Level of Degradation

Forest degradation was evaluated by quantifying reductions in forest cover, relative to the minimally disturbed reference plots. The plots were stratified into three levels of degradation, namely low, moderate, and high, based on changes in vegetation

cover. Reference conditions were defined for plots in forest stands with minimal anthropogenic disturbance and no evidence of human activity, grazing, or logging. The purpose of using these reference plots was to develop baseline measures of canopy density and species composition, as well as the proportion of biomass for each forest type. The degree of degradation was then classified based on the deviations of the reference conditions: low degradation was defined based on the canopy cover of above 70% relative to the reference baseline; medium degradation was determined based on the canopy cover of between 40 and 70%, and high degradation was based on the canopy cover of less than 40%. These limits were based on field observations, forest-structure standards, and the relevant literature on the effects of disturbances in Himalayan temperate forests (Food and Agriculture Organization of the United Nations 2011; Lal 2015). Measurements were taken during the most active period of the growing season to minimize seasonal variation and ensure some uniformity across sampling units. The categories of degradation were evenly distributed across all plots to enable statistical analysis of vegetation structure, biomass distribution, and ecological function. A statistical analysis was performed using R version 2.15.1 (R Core Team, Vienna, Austria). To estimate plant diversity, four indices were used: species richness, Shannon-Wiener index (H and H-), Pielou's evenness index, and Simpson's index (D). The equations used in the calculation of these indices are shown below,

$$H' = \sum_{i=1}^{s} P_i * \ln(P_i) \quad (1)$$

where H' is the Shannon-Weiner diversity index, P_i is the fractional contribution of the i^{th} species, and S is the total number of species enumerated. The $\ln(P_i)$ term is known as the natural logarithm of P_i. Equation 2 shows how the Simpson diversity index is calculated,

$$D = 1 - \sum_{i=1}^{s} (P_i)2 \quad (2)$$

where D is the Simpson diversity index, and S represents the total number of species observed. P_i represents the i^{th} species in the community. The Pielou evenness index equation is below,

$$J' = \frac{H\prime}{\ln(D)} \quad (3)$$

where J represents the Pielou evenness index, $\acute{H}$ represents the Shannon–Weiner index, and D is the number of species observed.

Aboveground Biomass Estimation

The biomass above ground (AGB) in $t\,ha^{-1}$ was estimated using a two-step procedure. First, stem biomass ($t\,ha^{-1}$) was calculated from stem volume and basic wood density. The total AGB was then obtained by applying a biomass expansion factor (BEF), as recommended in the literature (Adnan *et al*. 2014).

Stem volume estimation

Following the established literature on forest mensuration for the calculation of the stem volume ($m^3\,ha^{-1}$), species-specific or general allometric models that link the diameter of the tree at breast height (DBH) and the total height (H) to the volume were used (Guendehou *et al*. 2012; Hegde *et al*. 2025). However, for trees where no species-specific equation was available, the generic volume formula was used,

$$V = a + b \cdot (DBH)^2 \cdot H \quad (4)$$

where V is the volume of the stem (m^3), DBH is the diameter at breast height (cm), H is the height of the tree (m), and a and b are the model coefficients obtained from local area published allometric relationships. The volume per hectare was obtained by summing the volumes of individual trees and scaling to the hectare level.

Stem biomass and AGB calculation.

Stem biomass was calculated by multiplying the estimated stem volume by basic wood density (BWD), using values from the species-specific literature (Adnan *et al*. 2014):

$$\text{Stem biomass } (\text{tha}^{-1}) = V \quad (\text{m}^3\ \text{ha}^{-1}) \times \text{BWD } (\text{kgm}^{-3}) \tag{5}$$

The total aboveground biomass was then estimated as:

$$AGB\ (t\,\text{ha}^{-1}) = \text{Stem biomass}\ (t\,\text{ha}^{-1}) \times BEF \tag{6}$$

A BEF value of 1.51 was adopted, consistent with averages reported in the literature for tropical and subtropical forests (Intergovernmental Panel on Climate Change 2006; Adnan *et al*. 2014).

Statistical Analysis

A combination of statistical techniques, including bivariate analysis, correlation matrices, and SEM, was used to explore the interdependencies between forest AGB, soil nitrogen availability, elevation, species diversity, habitat typology, and degradation gradients. The exploratory analysis of the data included a preliminary bivariate analysis, which enabled the study of each association between the predictor and response variables separately. A correlation matrix was used to assess relationships among explanatory variables, and multicollinearity was diagnosed using variance inflation factors (VIFs). It was followed by SEM using the Lavaan package in R to test the hypothesized causal relationships (direct and indirect). The use of SEM enabled the concurrent estimation of several relationships among dependent observed variables. The researchers used the authors' previous ecological theory and empirical evidence to specify the model. The model's performance was assessed using standard fit indices, including the chi-square test statistic (χ^2), root mean square error of approximation (RMSEA), comparative fit index (CFI), and Tucker-Lewis index (TLI). Further improvement flowed from the examination of modification indices and standardized residuals.

RESULTS AND DISCUSSION

Bivariate Relations Between Driving Factors and Above-ground Biomass

The bivariate analysis revealed that the soil nitrogen was the strongest predictor, with the proportion of the variance in AGB explained ($R^2 = 0.54$, $p < 0.001$), and this implied that the nutrient content of the soil is a major determinant of the AGB accumulation (Fig. 2). Diversity of the species proved to be a very important predictor of AGB, with a variance of 45% ($R^2 = 0.45$, $p < 0.001$), and thus an important predictor of the forest biomass sustainability. Also, habitat type (moist) ($R^2 = 0.24$, $p = 0.000$) and elevation ($R^2 = 0.24$, $p = 0.000$) were statistically significant and were judged to play an important role in biomass accumulation (Fig 2).

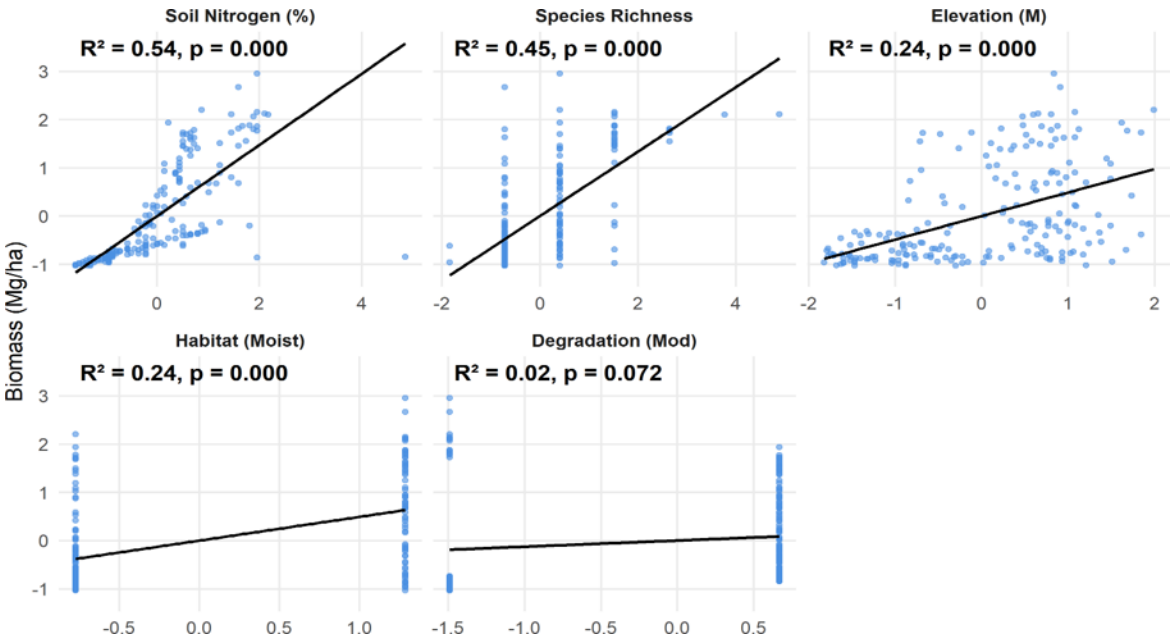

Fig. 2. The associations among tree biomass and the main biological and environmental factors. The positive effects of species diversity and soil nitrogen on tree biomass were highly significant, whereas the effects of elevation and habitat moisture were less important.

Fig. 3. A heat map of the Pearson coefficients of the biomass of trees based on their environmental and biotic predictors. The analysis shows moderate correlations between species richness and soil nitrogen, but none of the correlations approach the multicollinearity values.

To further support the above results, the correlation matrix provided in-depth information about the relationships of the predictor variables. The strongest positive correlation was between species richness and soil nitrogen (r = 0.54), which suggests a possible relationship between the higher nutrient content and the increase in tree diversity or that an increase in species richness can promote nitrogen deposition (Fig. 3). Moderate correlations between the soil nitrogen and the elevation (r = 0.35) and the moist habitat type (r = 0.43) were also observed (Fig. 3). Similarly, the moist habitat had a low correlation with elevation (r = 0.32) and species richness (r = 0.28) (Fig. 3). The other pairwise correlations were also weak to moderate. Importantly, all correlations were low relative to the generally accepted multicollinearity threshold (r < 0.7) and were therefore included in the subsequent multivariate methods (Fig. 3).

Relative Contribution of Driving Factors

As shown in Fig. 4, the predictor variable, habitat (moist), explained the highest percentage of AGB, with 33.6%, thus highlighting the important role played by water availability in determining forest productivity (Fig. 4). Elevation explained 29.8%, which is likely to be due to the effects of climatic and edaphic changes with the altitude gradients (Fig. 4). The percentage of variation attributed to soil nitrogen was 14.2%. It was clearly indicated that this is one of the main nutrients in the growth of trees. Species richness contributed 12.8%, indicating potential benefits associated with biodiversity. The moderate degradation was the least significant, and it explained only 9.6%, of the variations indicating that the disturbances have a moderate effect on biomass although relatively lower in comparison to the environmental and compositional variables (Fig. 4).

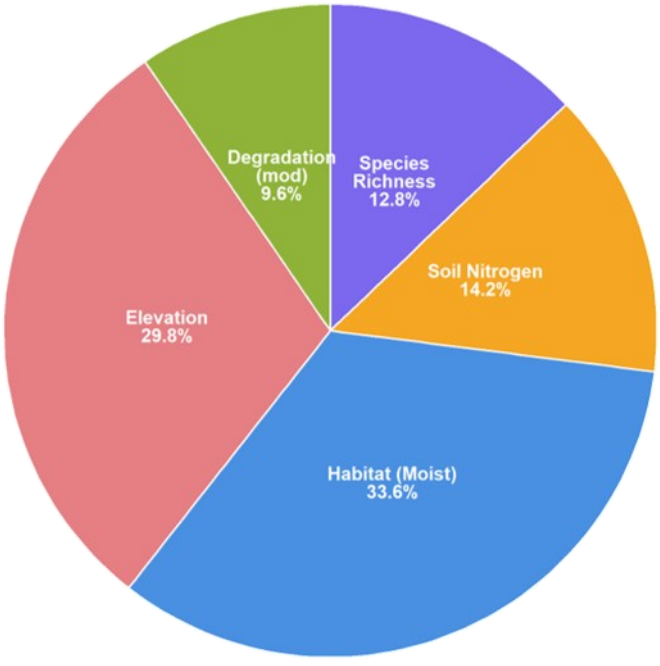

Fig. 4. The relative contribution of important predictors to tree biomass in the form of standardised path coefficients in the structural equation model. The pie chart illustrates the relative explained variance of the biomass of each predictor. The major factors are habitat moisture and elevation, with soil nitrogen and species richness coming next, with moderate degradation having the least impact.

Habitat-Unified Model

The final SEM that has been optimally fitted showed accepted model performance, where χ^2 (3) = 5.207, p = 0.157, RMSEA = 0.059(90% CI = 0.000 to 0.137), CFI = 0.99, TLI = 0.98, and SRMR = 0.040 (Fig. 6). The Unified SEM showed that the elevation and habitat degradation had a major impact on above-ground biomass indirectly and directly *via* species richness, biomass, and soil nitrogen (Fig. 5 & 6). Elevation had a strong direct positive impact on tree biomass (β= 0.54, p < 0.001) and an indirect impact through species richness (β = 0.36, p < 0.01) and soil nitrogen concentration (β = 0.51, p < 0.05). The moist habitat type had positive effects on soil nitrogen (β = 0.47, p < 0.001), elevation (β = 0.32, p < 0.001), and species richness (β = 0.28, p < 0.001), which consequently mediated vegetation responses (Figs. 5 and 6). Moderate degradation hurt the soil nitrogen (β = - 0.60, p < 0.001), and species richness (β = - 0.33, < 0.001) (Fig. 6). Altogether, SEM describes a sequence of elevation-mediated and degradation-mediated impacts on AGB pattern acts along the pathways involving species diversification and nutrient supply levels (Fig. 6), which shows the usefulness of habitat quality conservation in elevation gradients to sustain ecosystem functionality.

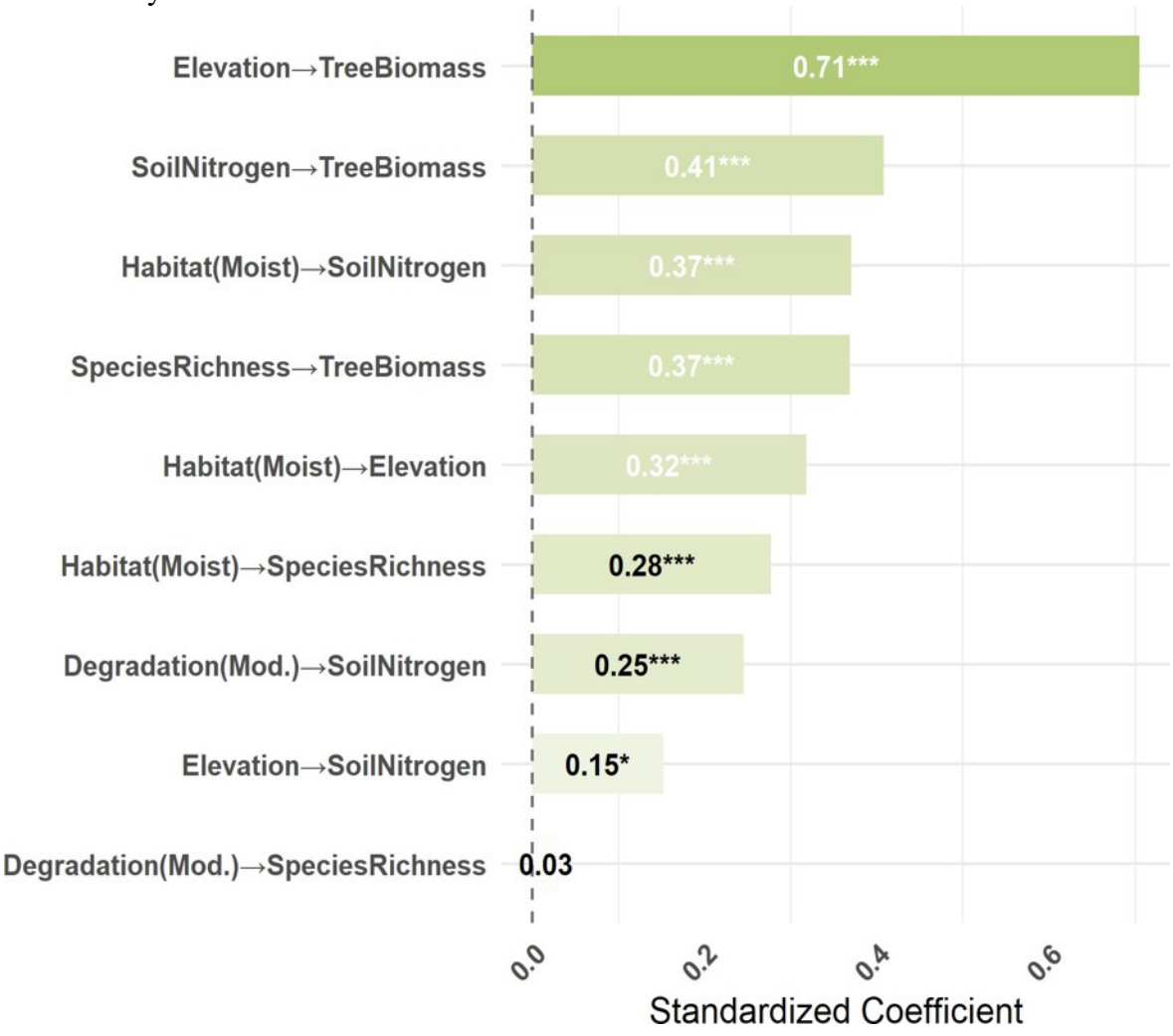

Fig. 5. Standardized path coefficients from the final structural equation model. All paths are significant at p < 0.05 unless otherwise indicated. Asterisks denote significance levels (*p < 0.05, **p < 0.01, and ***p < 0.001).

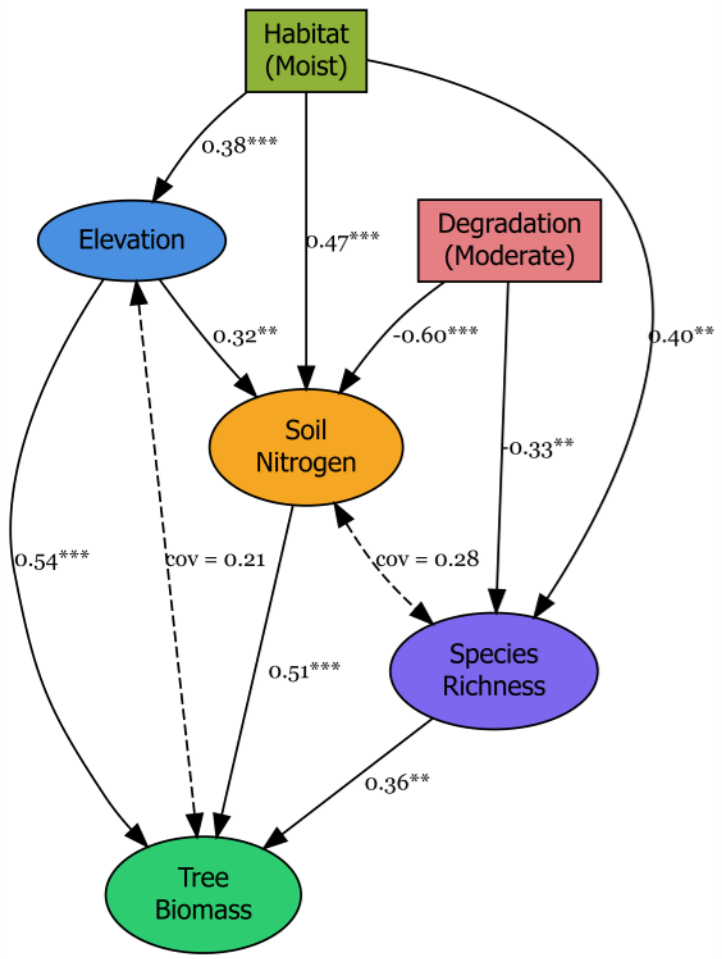

Fig. 6. Final SEM depicting direct and indirect pathways influencing tree biomass. The model demonstrates good fit, with elevation, habitat type, and soil nitrogen emerging as key drivers shaping biomass through their effects on species richness and nutrient availability. Model fit statistics CFI = 0.994, TLI = 0.981, RMSEA = 0.059, SRMR = 0.055.

Habitat-Specific Models

The division of SEMs by forest type, however, demonstrated that the magnitude and direction of relationships between environmental drivers and AGB varied widely across ecosystems, yielding important ecological information obscured in a coherent model. As an example, the direct effect of degradation on biomass in the case of subtropical ($\beta = 0.34$, $p < 0.0001$) and moist temperate forests ($\beta = 0.61$, $p < 0.0001$) was strong and statistically significant, indicating a high level of anthropogenic pressure in low-elevation stands located close to human settlements (Fig. 7a, b). Similarly, the moist temperate forest displayed the patterns that, to a large part, can be contrasted with those in the unified SEM, but emphasize that they had an increased value in the given forest type (Fig. 7 b). In contrast, in the dry temperate forest, degradation had a marginal impact on biomass but a strong impact on the soil nitrogen. Additionally, the effect of elevation on biomass was negative, unlike the unified model, which found a strong positive relationship (Fig. 7 c). These inconsistencies suggest that the overall models may conceal important ecosystem-specific processes. Even though the unified structural equation model captures general trends, the specific structural equation models capture the mechanisms and threshold values that determine each type of

forest. This type of comprehensive analytical method is essential for creating conservation plans that meet the specific needs of a particular ecosystem.

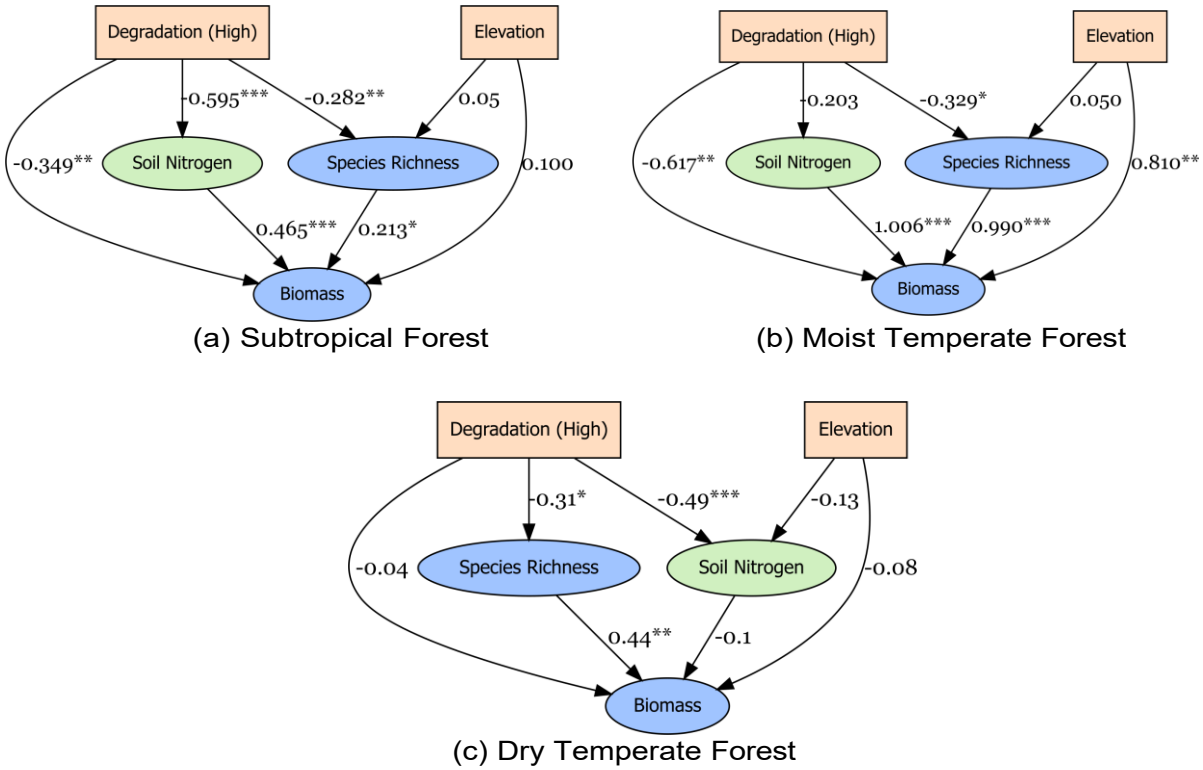

Fig. 7. Structural equation models illustrating standardised path coefficients for subtropical (a), moist temperate (b), and dry temperate (c) forests. Arrows indicate the direction and strength of relationships among degradation, elevation, soil nitrogen, species richness, and AGB. All paths shown are statistically significant. Positive effects are denoted by + values, and negative effects by − values.

The findings of this study demonstrated a complex system of interactions among abiotic and biotic drivers that determine tree biomass in forest ecosystems, and there were clear differences between the unified and habitat models. The comparison between the unified and habitat-specific SEM models was supported by differences in path coefficients, significance levels, and model fit indices, indicating that the strength and direction of associations among variables varied across forest habitats. The unified model provided the overall picture of ecosystem processes; the habitat-specific models then captured individual habitat-specific interactions, underscoring differences in the relative significance of habitat conditions, elevation, and soil nutrients in determining forest biomass. Soil nitrogen, elevation, and species richness had a direct effect on biomass in the unified model, and moist habitats increased the impact of elevation and soil nitrogen, thereby mediating the effect of environmental gradients on productivity. In particular, indirectly, degradation decreased biomass by depleting soil nitrogen, but it did not affect species richness significantly. In contrast, habitat-specific models revealed other direct impacts of degradation on biomass, particularly in sensitive dry temperate systems, in which its influence was strong and not mediated. Elevation had a continuous positive effect on biomass in a moist habitat and exclusive negative effects in a dry habitat, highlighting the context-dependent nature of elevation's effects. Together, these results suggest that, despite unified models' focus on indirect, nutrient-mediated interactions, stratified analyses reveal pronounced direct effects

of degradation that are obscured by generalised averaging. This emphasises the importance of scale and context in habitat for explaining ecosystem functionality, where soil nitrogen is a universal mediator and local degradation regimes predict immediate responses in biomass.

Soil Nitrogen as a Key Driver of Biomass

Soil nitrogen has both direct and indirect effects on ecosystem productivity, that is, by facilitating biomass accumulation and regulating species diversity (Fig. 6). The current discussion supports the existing theory that nutrient availability presents a leading limitation to plant productivity. This is reflected in the fact that soil nitrogen (N) had the greatest predictive relationship with biomass accretion. These findings correspond to the earlier studies that have suggested nitrogen limitation to be one of the key factors that govern the growth of forests, especially those established in tropical and temperate habitats where N is often the major limiting nutrient (Schulte-Uebbing and de Vries 2018; Du *et al*. 2020). The present study supports the resource ratio hypothesis, which argues that ecologies having a high level of nutrients support a larger biomass due to an increased rate of plant growth (Eskelinen and Harrison 2015). In addition, statistically significant correlations between soil nitrogen levels and species richness ($r = 0.54$) suggest that a reciprocal relationship may exist: more nutrient-rich soils support more biodiversity by maintaining higher species richness in the soil, and more heterogeneous assemblages of plant species increase nutrient trapping by using complementary resources (Bernhardt-Romermann *et al*. 2010). The current engagement highlights the importance of incorporating soil nutrient dynamics into research on biodiversity-ecosystem functioning, as these two aspects have the potential to complement each other to boost forest productivity. The results align with previous findings that the effect of biodiversity on ecosystem functioning is context-dependent and varies along environmental gradients. Biodiversity is typically higher in more favourable environments, such as lower elevations with warmer and more productive conditions, and tends to decline with increasing altitude. As a result, the contribution of biodiversity to forest biomass may differ across these gradients, with stronger effects observed in environments that support greater species richness (Ammer 2019).

Biodiversity's Role in Biomass Accumulation

Biodiversity is also important in biomass accumulation and is a critical determinant of ecosystem productivity and stability. The bivariate analysis and the SEM support the effect of species diversity on AGB. The result aligns with past empirical evidence that showed that the richer the ecosystem is in species, the higher primary productivity that is expected (Hossain and Li 2024). The positive connection is mainly viewed through the two main mechanisms: the niche complementarity and the selection effect (Furness *et al*. 2021; Tang *et al*. 2023). The niche complementarity hypothesis states that functionally different species can exploit the resources more effectively in combination, which increases biomass and the selection effect states that heterogeneous communities have a higher chance of including highly productive dominant species. The empirical covariance (0.28) that was found between soil nitrogen and species richness demonstrates that there was a small positive relationship, which means that the availability of nutrients can lead to the organization of plant diversity. The most relevant explanation is that an increase in soil nitrogen alleviates nutrient limitation, which promotes the growth of more species and their coexistence, which are also in line with the findings of previous studies (Bernhardt Römermann *et al*. 2010; Eskelinen and Harrison 2015; Ammer 2019).

Elevation as the Dominant Predictor

The relationship between biomass and elevation is normally non-linear, and in many cases it is affected by a range of interacting processes; higher temperatures result in shorter growing seasons, less available nutrients, and less biomass is expected to be grown at higher altitudes (Zhang *et al*. 2023; Hossain and Li 2024; Thakur *et al*. 2024). However, in the unified model, the direct correlation between elevation and biomass was the most significant ($\beta = 0.71$), compared with bio species and soil N. In individual models, the dry temperate forest showed a negative correlation between elevation and biomass, unlike the single SEM and the other forest types. This observation indicates that, in dry regions, elevation can cause the abiotic stressors of low temperatures, more wind, or less deep soils to inhibit arboreal growth despite any possible microclimatic advantages. Elevation does not consistently induce biomass growth; its effects depend on the ecosystem context and can be counterproductive in adverse environments, such as dry temperate forests. Therefore, the need for small-scale elevation modeling is reiterated by the need to measure productivity in water-limiting or even austere environments.

Results of this study support the crucial role of altitudinal gradients in the formation of forest structure, which is primarily determined by their effects on edaphic development, thermal conditions, and moisture flows (Su *et al*. 2023). Similarly, increased cooler temperatures and cloud cover associated with higher elevations dilute decomposition and metabolic activity, thus limiting vegetative growth and nutrient cycling (Fadrique and Feeley 2018). Elevation and biomass have a positive covariance in the residual values ($\beta = 0.21$), indicating that the relationship might be further mediated by additional unmeasured factors, including microclimatic stress or the species' adaptation to elevation (Salinas *et al*. 2021). These results underscore the need to have future research to include high-resolution climatic data in the analysis of elevation-biomass relationships.

Elevation had a stronger influence in the SEM results than in the bivariate analysis, due to its role as a significant environmental gradient that govern numerous ecological processes. Elevation simultaneously affects moisture regimes, temperature, and vegetation structure, which regulate forest biomass both directly and indirectly. It could be the reason that soil nitrogen was significant in the bivariate analysis, its effect may be mediated by elevation, as nutrient availability and cycling are often strongly controlled by altitudinal variation. It is because of these indirect pathways that SEM produced a more comprehensive understanding of how elevation shapes ecosystem functioning, thus clarifying its high relative importance in the model.

Indirect Effect of Habitat Type and Degradation

The assumption that the presence of moisture is one of the essential factors of the ecosystem processes (Gilliam 2016) is supported by the fact that the type of a moist habitat indirectly affects moister soils through their increase in nitrogen content and species richness. Moreover, the moderate correlation between moist habitat and elevation ($r = 0.32$) indicates that topographic position could bring some variation in water availability because higher elevations could receive more precipitation or maintain longer moisture because of reduced evapotranspiration. In the unified structure, degradation mainly affects the biomass indirectly *via* decreasing the amount of nitrogen in the soil, which in turn, undermines biomass due to the positive correlation existing between the level of soil nitrogen and biomass. This pathway is moderated by the moist habitat that buffers the loss of nitrogen. However, habitat-specific models indicate that there is also a direct negative impact of degradation on biomass, moderate in subtropical environments, and severe in moist temperate environments. The

perceived divergence implies that the unified model masks the details at the habitat level due to the aggregation that it includes. In turn, the effects of degradation are both direct and indirect, and the dominating one depends on the environment of a particular habitat. The effect of soil nitrogen in unstable arid ecosystems is insignificant, which means that the disturbed sites can experience nutrient loss through leaching or erosion, but not an immediate loss of biodiversity (Qu *et al*. 2024). Unified models are also likely to provide underestimates of the direct effects of degradation on biomass in susceptible habitats, *e.g.*, drylands, which justifies localized evaluations. It seems that the recovery of the soil fertility is more important than the actual reinstatement of the diverse range of species in the devastated landscapes, which is denoted by the latest empirical evidence and has serious implications to the forest restoration practice. The complexity of the relationship between biotic communities, habitat degradation, and abiotic constraints is supported by previous studies demonstrating that ecosystem productivity is jointly regulated by interacting biotic and abiotic drivers. Forest productivity is not controlled by a single factor, but rather emerges from the combined influence of species interactions, environmental conditions, and disturbance processes, which together shape ecosystem functioning and stability (Forrester *et al.* 2016; Ammer 2019).

The influence of habitat type differed between the bivariate analysis and the SEM results because SEM can account for both direct and indirect relationships among variables. While bivariate analysis captures only simple pairwise associations, it does not reflect the complex ecological interactions within forest systems. In the SEM framework, moist habitat emerged as a dominant factor, which was likely because it integrates multiple favourable conditions, including higher moisture availability, improved microclimate, and enhanced resource availability, that collectively support greater biomass accumulation. Furthermore, habitat type can indirectly influence biomass through its effects on soil properties and species composition, thereby increasing its overall importance in the SEM compared to bivariate analysis.

Ecosystem-specific Mechanisms Revealed by Integrated SEM Approaches

Although the unified structural equation model revealed strong correlations between elevation, degradation, biodiversity, and productivity in all forest habitats, the different models used in subtropical, moist, and dry temperate forest determined that there were strong ecosystem-specific differences in the magnitude and directionality of causal relationships. This two-level approach to methodology enabled macroscopic generalizations and fine-scale ecological explanations, which improved the understanding of the interactions in abiotic-biotic in a variety of forest systems. With the combination of both SEM methods, this research established ecological relations that have strength in all types of forests as well as those that are dependent on particular settings. The coherent framework found that general drivers, including elevation and soil nitrogen, occurred across the whole of all ecosystems, and the models that were particularly specific explained unique constraints and sensitivities within an individual ecosystem. Such results cannot be ignored in developing conservation plans that are specific to a specific type of forest; to mention but a few, this demonstrates the importance of soil rehabilitation initiatives in arid forested habitats and the need to protect biodiversity in mesic forests to maintain an ecologically productive system.

RECOMMENDATIONS

These results have strong implications in forest management as well as conservation practices. In humid forest systems, preservation should be focused on the maintenance of soil nutrient status, whereas in the dryland systems interventions should be focused on the minimization of degradation process as well as the preservation of biodiversity. The discussion between the unified and disaggregated modeling methods underscores the benefits of multiscale research: whereas unified models capture global processes, habitat-dependent research has its weaknesses and requires localized solutions to mitigate them. The complementary perspectives should be combined into future research to examine how ecosystems respond to drivers of global change, and the extensive applicability of principles and context-dependent dynamics will guide conservation planning. Such a twofold method will be particularly important for anticipating anthropogenic disturbances in a biome-specific warming climate.

CONCLUSIONS

1. This study has offered a multi-scale view of the forest biomass dynamics drivers and the underlying difference between unified and habitat-specific model approaches. Although the unified model emphasizes indirect, nutrient-mediated effects, especially the central role of soil nitrogen, the habitat-specific analyses indicate important direct effects of degradation that cannot be identified in broader-level assessments.
2. Findings suggest that the moist forests are resilient to factors due to nitrogen buffering in the soil. By contrast, dry regions biomass loss is instantaneous because of direct degradation stress.
3. Elevation acts as a context modulator, increasing productivity in moist environments and increasing stress in water-limited environments.
4. The application of separate spatial environmental models allows for ecologically sensitive and habitat-specific information to be obtained, which cannot be neglected in the development of specific management and restoration plans.
5. The conservation of dry temperate forests needs to be focused on minimizing degradation in the area, as it has very significant consequences on the biodiversity, and it is capable of breaking the vital nutrient-function interactions.
6. The maintenance of soil fertility and species abundance in the moist temperate forest ecosystems should take priority in conservation programs to ensure high productivity is maintained. In subtropical forest ecosystems, nutrient dynamics and resilience to disturbance exert a greater influence on ecosystem functioning than species diversity alone.

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Competing Interests

The authors declare no conflicts of interest.

Availability of Data and Material

All the data generated in this research work have been included in this manuscript.

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