

DRIVERS OF TREE COVER ACROSS HIMALAYAN FOREST HABITATS: INSIGHTS FROM STRUCTURAL EQUATION MODELING

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(Received 15th Oct 2025; accepted 22nd Jan 2026)

Abstract. Understanding the drivers of tree cover variation across different habitats is critical for ecosystem management and conservation. Although unified models often generalize ecological relationships, habitat-specific analyses may reveal divergent mechanisms that are otherwise overlooked. We used structural equation modeling (SEM) to assess the determinants of tree cover in dry temperate, moist temperate, and subtropical habitats, analyzing them both in a unified manner and in habitat-specific contexts. The unified model identified that elevation ($\beta = 0.81$, $p < 0.0001$) and moist habitats ($\beta = 0.40\text{--}0.47$, $p < 0.01$) promoted tree cover and biodiversity primarily through soil nitrogen pathways, while moderate degradation ($\beta = -0.20$ to -0.33 , $p < 0.05$) reduced both nitrogen and richness, lowering cover. Other habitat types and degradation levels showed no significant effects ($p > 0.05$). Habitat-specific models revealed deviations: in dry temperate systems, degradation reduced richness ($\beta = -0.318$, $p < 0.01$) and nitrogen ($\beta = -0.394$, $p < 0.001$); in moist temperate forests, elevation ($\beta = 0.340$, $p < 0.001$) and richness enhanced cover; and in subtropical forests, elevation ($\beta = 0.336$, $p < 0.001$) and richness ($\beta = 0.206$, $p < 0.01$) could increase cover, while nitrogen effects varied between habitats. These results show that unified models capture broad trends but risk obscuring biome-specific mechanisms where driver effects differ in magnitude or direction. Integrated conservation approaches that jointly address degradation, nutrient cycling, and biodiversity are therefore essential to maintain resilience in mountain ecosystems.

Keywords: *habitat specificity, structural equation modeling, elevation gradient, biodiversity-ecosystem functioning, forest structure, ecological drivers*

Introduction

As vital providers of ecosystem services, climate regulators, and repositories of biodiversity, forests are essential to the ecological integrity of the planet. More than 80% of terrestrial species live in forest ecosystems, which make up about 31% of the world's land area (Nesha et al., 2021). In addition to their importance for biodiversity, forests store approximately 662 gigatons of carbon in biomass and soil, making them significant carbon sinks that help mitigate climate change (Harris et al., 2021). Deforestation, land degradation, and climate-induced disturbances are among the anthropogenic pressures that pose an increasing threat to this ecological balance (Kumar et al., 2024). The Hindukush-Himalayan (HKH) mountain systems are unique among forested areas around the world due to their intricate topography, variable climate, and ecological diversity. The HKH region, which spans eight countries and contains a variety of forest types, is home to more than 10,000 plant species, many of which are endemic (Hyttén and Pearson, 2025; Nafees et al., 2024). More than 240 million people

in this region depend on forests for fuelwood, fodder, water regulation, and cultural values, making them the foundation of ecosystem services as well as being rich in biodiversity (Wester et al., 2019).

During the past few decades, the main focus of ecological research has been the connection between ecosystem functioning and biodiversity (BEF). Species richness improves several ecosystem functions, such as primary productivity, nutrient cycling, and resilience to environmental stressors, as numerous observational and experimental studies have shown (Huang et al., 2018; Schuldt et al., 2018). Due to processes such as resource partitioning, functional complementarity, and facilitative interactions among species, the richness of tree species is often linked to increased biomass accumulation and structural complexity in forest ecosystems (Jucker et al., 2016; Liang et al., 2022). Improved resource-use efficiency is one of the main ways species richness supports ecosystem function. Due to species-specific variations in rooting depth, nutrient uptake tactics, and canopy architecture, diverse plant communities typically use resources more thoroughly and reliably than monoculture (Jing et al., 2021). Over-production, in which mixed species forests generate more biomass than the most productive monoculture, is frequently caused by this complementarity effect (Feng et al., 2022). In addition, greater diversity can improve temporal stability by protecting ecosystems from shocks such as pests, diseases, and droughts (Hisano et al., 2024). Canopy cover is a structural characteristic of forest systems that is directly impacted by the diversity and composition of species. In order to improve canopy density and light interception, trees with different crown shapes, growth rates, and light requirements help to fill vertical and horizontal spaces more effectively (Williams et al., 2017). Furthermore, by promoting the growth of co-occurring species, some species can indirectly aid canopy development by increasing local soil fertility through nitrogen fixation or litter quality (Xu et al., 2022).

The significance of biodiversity for forest function is reaffirmed by recent studies conducted in temperate and tropical regions in China. In a large-scale biodiversity trial, they repeatedly shown that forest biomass and carbon storage increase greatly due to tree diversity (Liang et al., 2016; Dyola et al. (2022a)). Similar conclusions have been drawn from naturally occurring forests in the Americas and Europe, indicating that the relationship between biomass and biodiversity is stable across contexts and scales (Tuck et al., 2016). Plant growth and forest productivity are significantly influenced by soil fertility, especially nitrogen availability. Since it has a direct impact on photosynthesis, biomass accumulation, and canopy development, nitrogen is frequently the most limiting nutrient in terrestrial ecosystems (Zhu et al., 2015). Abiotic drivers such as elevation, climate and disturbance regimes, as well as biotic factors such as litter decomposition and microbial activity, influence soil nitrogen availability in forest systems (Hamid et al., 2021). Generally speaking, a higher nitrogen level encourages more plant growth and canopy closure, which can improve soil organic matter through litterfall and produce positive feedback loops (Elrys et al., 2023). A characteristic of the Himalayan landscape, elevation affects temperature, moisture availability and weathering rates, all of which have impacts on soil fertility and forest structure. Lower temperatures caused by elevation can slow the decomposition of organic matter and microbial activity, which can decrease nitrogen uptake and mineralization (McNichol et al., 2024). However, due to their higher moisture content, moderate temperatures, and fertile soils from organic accumulation, mid-elevation zones often have the best conditions for tree growth (Hamid et al., 2021). Due to these intricate relationships, elevation affects the types of vegetation and the availability of soil nutrients, which indirectly affects the structure of the canopy. These

elevation-induced effects are further mediated by habitat types, such as dry versus moist forests. Compared to dry forests on the ridges, moist forests, which are usually found in the valley bottoms or on windward slopes, tend to have richer soil and a greater variety of species (Rahman et al., 2022).

Given that moist conditions typically promote faster growth and higher accumulation of biomass, these variations in soil fertility and microclimate can have a substantial impact on the cover of the forest canopy (Requena Suarez et al., 2021). In this situation, soil nitrogen serves as a bridge connecting fine-scale vegetation structure and broad-scale abiotic elements such as elevation. The composition and function of forests are also influenced by disturbance regimes, which include both anthropogenic (such as logging and grazing) and natural (such as landslides and fire) forms of degradation. By eliminating biomass and changing the nutrient cycle, especially nitrogen retention and turnover, moderate degradation can reduce canopy cover and soil fertility (Araya et al., 2023). However, the effects of degradation vary depending on the situation; in certain situations, secondary succession can progressively restore biodiversity and nutrient levels, particularly in damp or low-elevation settings (Liu, 2025). Thus, one of the main factors that influence the recovery and structure of forests is the interplay between degradation and soil nitrogen. By combining biotic and abiotic perspectives, this study explores the factors that influence tree canopy cover in HKH forests, building on the theoretical and empirical foundations mentioned previously. This study investigates the following three hypotheses: (1) The richness of tree species directly enhances canopy cover and indirectly contributes through increased soil nitrogen availability, (2) Elevation and degradation effect tree cover indirectly through their effects on habitat type and soil fertility, and (3) The strength and direction of ecological drivers that regulate tree cover differ significantly between habitat types, indicating that habitat-specific models explain vegetation dynamics better than a unified model across all forest types. The purpose of this study is to test these hypotheses and better understand the relative and interdependent roles that biodiversity, soil fertility, and abiotic controls play in the structure of Himalayan forest ecosystems. This will help inform more effective conservation and reforestation strategies in this ecologically vulnerable area.

Materials and methods of the study

Study sites

The study was carried out in dry-temperate, moist-temperate and subtropical regions of the Malakand division (MKD), Khyber Pakhtunkhwa province, Pakistan. Malakand division consists of Swat, Chitral, Dir lower, and Dir upper. The study area lies between 36° 55' N latitude and 72° 10' E to 73° 55' E longitude (*Fig. 1*). The altitude of the mountains varies between 450 and 7782 m. The region experiences a climate ranging from subtropical to temperate, with mean annual temperatures varying between -6°C and 40°C. The level of annual precipitation varies from 500 to 1600 mm. The forests cover approximately 27% of the area, covering 0.8 million ha. The study area comprises diverse forest types, including subtropical broadleaved, semi-evergreen, subtropical chir, moist temperate, dry temperate, and alpine forests in certain locations. Common evergreen and broad-leafed forest species of the area are *Cedrus deodara*, *Pinus roxburghii*, *Pinus wallichiana*, *Pinus gerardiana*, *Picea smithiana*, *Abies pindrow*, *Taxus baccata*, *Quercus incana*, *Juglans regia*, *Olea ferruginea*, *Betula utilis*, *Morus alba*, *Acacia modesta* and *Populus ciliata* (Champion et al., 1965).

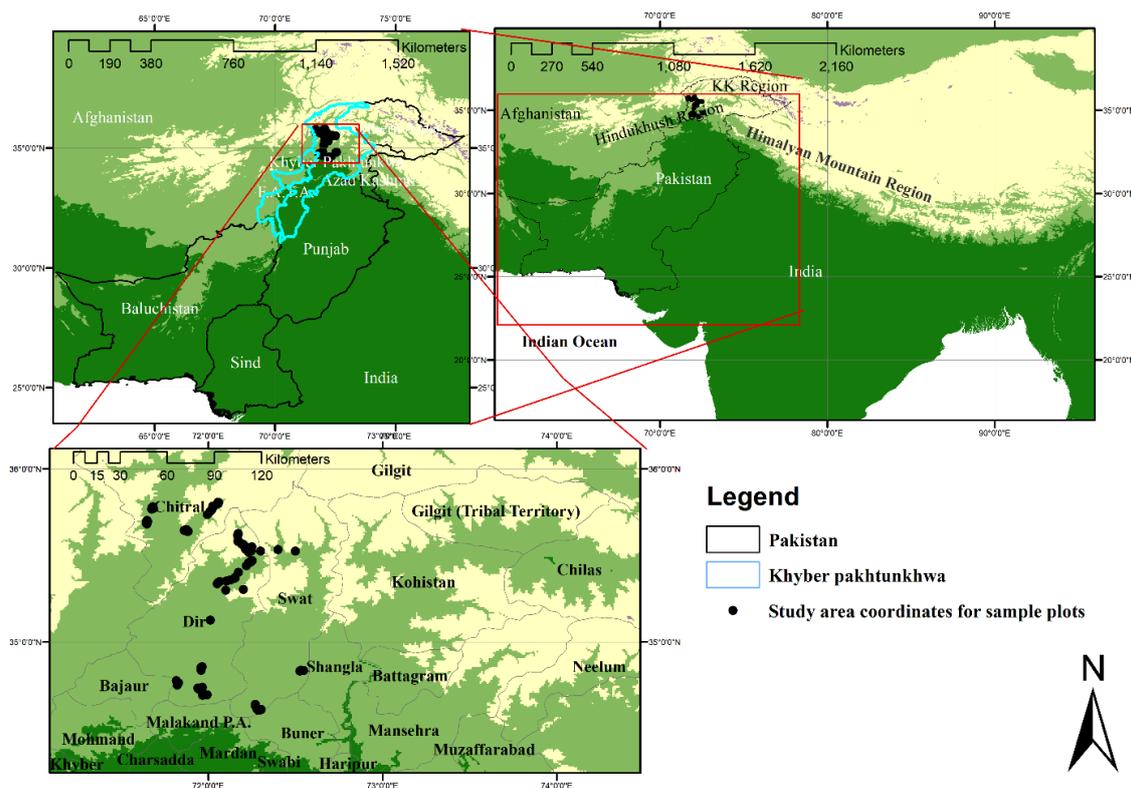


Figure 1. Study area map showing the various forest types selected for data collection in the eastern Hindukush region

Sampling design

This study used data from 225 randomly selected plots, with 75 plots per forest type (Table A1). Field sampling was carried out in 2023-24 during April to September. The sampling design used for this study was intended to capture spatial variability within each type of forest. The sampling plots were systematically distributed across each forest type, with a distance of 1 km between each plot and an elevation difference of 500 m, to cover various microhabitats and environmental gradients.

Forest habitat classification along the moisture gradient

The forests in the study area were categorized along a moisture gradient based on established habitat types that show distinct climatic and ecological conditions (Fig. 2). The classification combined elevation range, dominant vegetation composition, and long-term climatic attributes, mainly mean annual temperature and precipitation linked to each habitat type. Subtropical forests occur at lower elevations and are characterized by relatively higher temperatures and moderate precipitation, moist temperate forests occupy mid-elevations with cooler temperatures and higher precipitation, while dry temperate forests are found at higher elevations with lower precipitation and cooler climatic conditions. These habitat types were used as proxy variables for moisture availability, as each represents a distinct and ecologically significant temperature–precipitation regime. This classification approach is widely applied in mountain forest ecosystems and allows an effective representation of climatic influences on vegetation and soil processes without relying on plot-level climatic measurements.



Figure 2. Representative photographs illustrating the major forest habitats sampled in the study area

Measurement of canopy cover

To estimate canopy cover at the plot level, individual tree measurements were used to calculate the total crown area. This method provides a detailed, tree-specific approach based on the measured field dimensions of the tree crowns and their spatial extent. The diameter at breast height (DBH) was measured for all trees within the 20×20 m plots that had a stem diameter of at least 5 cm. For trees on slopes, measurements were taken 1.3 m above ground level on the uphill side, using a diameter tape. DBH values were primarily recorded for structural characterization and biomass estimation, and were not used directly in crown cover calculations. The spread of the crown of each tree was measured in two perpendicular directions: (1) North–South (NS) diameter and (2) East–West (EW) diameter (Wang et al., 2025). Measurements were taken using a measuring tape, and the values were recorded as the maximum horizontal extent of the live crown in each direction. These measurements were used to estimate the crown area, assuming an elliptical shape for the canopy projection of each tree. The location of each tree was mapped within the plot using a simple local coordinate system. The distances from the plot boundaries (usually measured from the southwest corner as the origin) were determined using a tape and a compass to locate each tree in two dimensions (X, Y). This step ensured that crown areas could be accurately accounted for within the fixed plot boundary.

$$A = \pi \times (D_{NS} / 2) \times (D_{EW} / 2) = (\pi \times D_{NS} \times D_{EW}) / 4 \quad (\text{Eq.1})$$

where:

D_{NS} = Crown diameter in North–South direction (m)

D_{EW} = Crown diameter in East–West direction (m)

To estimate total canopy cover for the plot, the summed crown area was divided by the total plot area (400 m^2) and expressed as a percentage:

$$\text{Canopy Cover (\%)} = (\Sigma A_i / 400 \text{ m}^2) \times 100 \quad (\text{Eq.2})$$

where:

ΣA_i = Total crown area of all trees in the plot (m^2)

400 m^2 = Area of plot ($20 \times 20 \text{ m}$)

A_i = Area of individual tree crowns

This method provides a reliable estimate of canopy cover that accounts for the size of the individual tree and the dimensions of the crown. However, it does not account for overlapping crowns, which may lead to a slight overestimation in denser plots.

Aboveground biomass estimation

Aboveground biomass (AGB, t ha^{-1}) was assessed using a two-step method. Stem volume ($\text{m}^3 \text{ ha}^{-1}$) was first calculated using species-specific or generalized allometric equations based on diameter at breast height (DBH) and tree height (H). For species lacking specific models, a generic volume equation was applied. Stem biomass was then derived by multiplying stem volume by species-specific basic wood density values. Total AGB was estimated by applying a biomass expansion factor (BEF) of 1.51, consistent with values reported for tropical and subtropical forests.

Soil analysis

A soil auger was used to randomly collect soil samples from three discrete points within each plot at a depth of 0-15 cm (*Fig. 3*). The subsamples were then thoroughly mixed to form a composite sample for each plot. The samples were air-dried, milled, and sieved through a 2 mm mesh before analysis. Standard analytical procedures were used to determine the total and available nutrient concentrations and organic matter contents in the soil. Soil organic matter content was measured using the Walkley–Black dichromate oxidation method (Walkley and Black, 1934). Total nitrogen was examined using the Kjeldahl digestion method (Bremner, 1960), while available nitrogen was determined by the alkaline hydrolysis method described by Subbiah and Asija (1956).



Figure 3. Field sampling activities carried out during the study period

Measurement of degradation levels

Forest degradation was evaluated by evaluating the reductions in forest cover and biomass and the richness of species compared to minimally disturbed reference plots. The plots were classified into three levels of degradation: low, moderate, and high based on the reduction of aboveground biomass and changes in vegetation cover. Reference conditions were established using plots located in minimally disturbed forest stands with negligible evidence of human activity, grazing, or logging. These reference plots were used to define the baseline for canopy density, species composition, and biomass levels within each forest type. Based on deviations from reference conditions, degradation levels were defined as follows: Low degradation: canopy cover > 70%, and total aboveground biomass reduction < 25% relative to reference levels. Moderate degradation: canopy cover between 40 and 70%, and biomass reduction between 25 and 50%. High degradation: cover < 40%, and biomass reduction > 50%. These thresholds were informed by field observations, forest structure benchmarks, and relevant literature on disturbance impacts in Himalayan temperate forests (Tewari, 2016). Assessments were performed during the peak growing season to minimize seasonal variability and ensure consistency between sampling units. Degradation categories were applied consistently on all plots to facilitate statistical analysis of vegetation structure, biomass distribution, and ecological function.

Measurement of diversity indices

For plant diversity estimation, we used the following three indices: Species Richness index, Shannon Weiner (H'), Pielou's evenness index, and Simpson's index (D). The equations used to calculate these indices are as follows.

$$H' = - \sum (i = 1 \text{ to } N) [P_i \times \ln(P_i)] \quad (\text{Eq.3})$$

where:

- H' = Shannon–Weiner diversity index
- P_i = Proportion of individuals belonging to the i th species
- N = Total number of species
- \ln = Natural logarithm

$$D = 1 - \sum (i = 1 \text{ to } S) [P_i^2] \quad (\text{Eq.4})$$

where:

- D = Simpson's diversity index
- S = Total number of species
- P_i = Proportion of individuals belonging to the i th species

Here, D is the Simpson diversity index and S represents the total number of species found. P_i represents the i th species in the community. $J = H'/\ln S$ Where, J represents the Pielou evenness index, H' represents the Shannon–Weiner index, and S is the number of species.

Statistical analysis

A combination of statistical techniques, including bivariate analysis, correlation matrices, and structural equation modeling (SEM), was used to explore the interdependencies between forest cover, soil nitrogen availability, elevation, species

diversity, habitat typology, and degradation gradients. Initial bivariate analyses facilitated the examination of individual associations between predictor and response variables. The correlation among explanatory variables was assessed through a correlation matrix, while multicollinearity diagnostics were performed using variance inflation factors (VIF). Subsequently, SEM was implemented via the Lavaan package in R to test the hypothesized direct and indirect causal relationships. SEM permitted concurrent estimation of multiple dependent relationships among observed variables. The prior ecological theory and empirical evidence guided the researchers in the specification of the model. Standard fit indices, including the chi-square test statistic (χ^2), root mean square error of the approximation (RMSEA), the comparative fit index (CFI), and the Tucker-Lewis index (TLI), were used to evaluate the performance of the model. Further refinement was guided by the examination of the modification indices and standardized.

Results

Bivariate analysis

To evaluate the relative importance of elevation, habitat type, and degradation intensity on tree vegetation cover, we first examined the bivariate relationship between the dependent and independent variables. The total plant cover was strongly influenced by ecological factors. The richness of the species was the strongest predictor ($R^2 = 0.41$, $p < 0.001$), followed by soil nitrogen ($R^2 = 0.33$, $p < 0.001$). Elevation had a weaker but significant effect ($R^2 = 0.07$, $p < 0.001$). Degradation significantly reduced plant cover significantly ($p < 0.001$), with least cover in severely degraded sites. The type of habitat was also significant ($p < 0.001$), with moist temperate forests showing the highest cover, followed by dry temperate and subtropical forests (*Fig. 4*).

The Heat map shows the relative contributions of independent variables to tree cover. Soil nitrogen as a key predictor of forest cover, strongly correlated with species richness ($r = 0.54$) and moist habitat ($r = 0.43$), suggesting moisture-driven nitrogen cycling and interdependence of nutrients and biodiversity. Elevation had weaker links with richness ($r = 0.22$) and nitrogen ($r = 0.35$), while degradation showed minimal correlations ($r < 0.04$), indicating hydrological decoupling and possible resilience of the ecosystem (*Fig. 5*).

Species richness exerts the strongest direct effect on forest cover (53.2%), followed by soil nitrogen (38.9%), with minimal degradation contribution (*Fig. 6*). The dominance of ecological factors (richness + nitrogen = 92.1%) over anthropogenic degradation highlights the importance of biodiversity and the conservation of nutrients to maintain forest cover.

Unified model

To evaluate the relative importance of elevation, habitat type, available nitrogen and degradation intensity on tree cover, we first examined direct and indirect relationships using structural equation modeling (SEM). The SEM showed good fit: $\chi^2(4) = 9.81$, $p = 0.044$; CFI = 0.980, RMSEA = 0.085, SRMR = 0.048 and identified the main pathways that influence forest cover in the Hindukush–Himalayan region (*Fig. 7*). Elevation strongly enhanced tree cover ($\beta = 0.81$, $p < 0.0001$) and soil nitrogen ($\beta = 0.32$, $p < 0.001$). The moist habitat improved soil nitrogen ($\beta = 0.47$, $p < 0.0001$) and species richness ($\beta = 0.40$, $p < 0.01$), while moderate degradation reduced both ($\beta = -0.20$ to -0.33 , $p < 0.05$). Soil

nitrogen strongly increased richness ($\beta = 0.99$) and tree cover ($\beta = 0.60$), with richness also promoting cover ($\beta = 0.55$). In general, elevation and moist habitats promoted biodiversity and tree cover mainly through soil nitrogen pathways, while degradation negatively affected nitrogen and richness, ultimately lowering cover. Other habitat types and degradation levels were not significant. These results confirm the hypothesis that tree species directly enhances canopy cover and indirectly contributes through increased soil nitrogen availability. Similarly, elevation and degradation had an indirect influences on tree cover primarily through changes in species richness and soil fertility.

Habitat specific models

Habitat-specific models revealed different drivers of tree cover (Fig. 8a–c). In dry temperate systems, elevation was insignificant, while degradation reduced richness ($\beta = -0.318$, $p < 0.01$) and nitrogen ($\beta = -0.394$, $p < 0.001$), suggesting niche partition in arid conditions. In moist temperate forests, elevation ($\beta = 0.340$, $p < 0.001$) and richness ($\beta = 0.973$, $p < 0.0001$) strongly promoted cover, probably due to reduced human pressure and microclimatic buffering. In subtropical zones, both elevation ($\beta = 0.336$, $p < 0.001$) and richness ($\beta = 0.206$, $p < 0.01$) increased cover, reflecting low disturbance at higher slopes. Soil nitrogen effects ranged from nonsignificant in subtropics to strongly negative in moist forests, underscoring habitat-specific nutrient constraints.

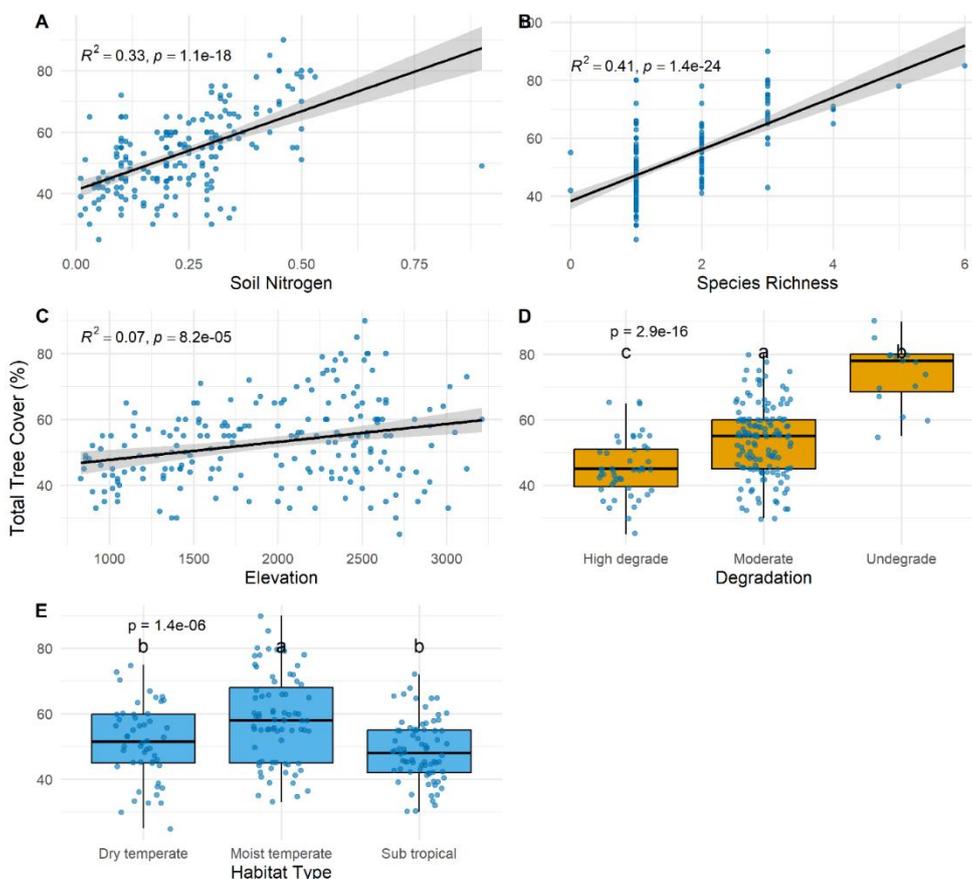


Figure 4. Relationships between total plant cover and key ecological drivers: (a) species richness, (b) soil nitrogen content, (c) elevation gradients, and (d) degradation levels across habitat types. Error bars represent 95% confidence intervals. Colors denote habitat categories (moist temperate, dry temperate, subtropical)

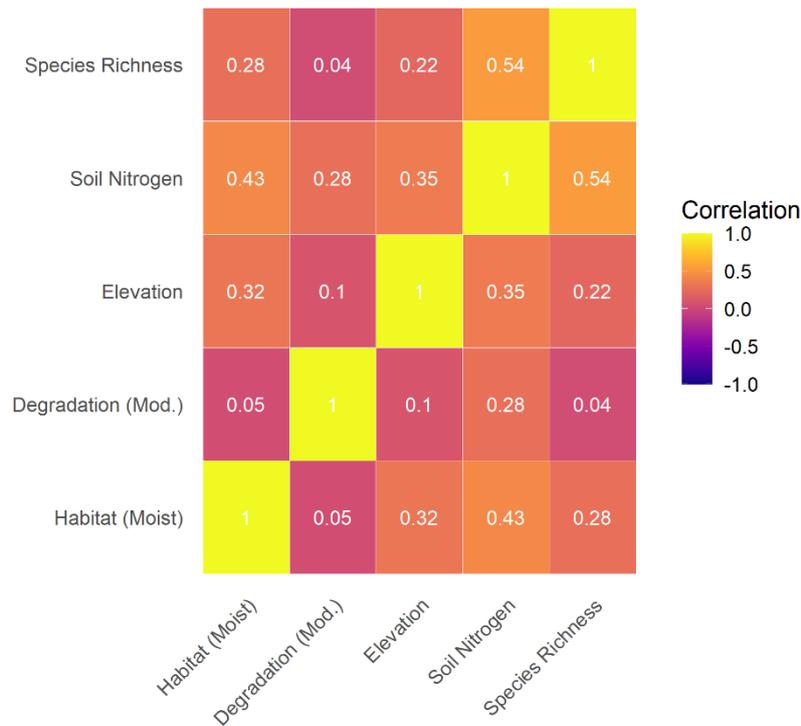


Figure 5. Correlation heatmap of key predictors of tree cover in the Hindukush-Himalayan region. Color intensity and direction (blue = positive; red = negative) reflect Pearson's correlation coefficients (r^*), with values labeled in each cell. Soil nitrogen emerged as a hub variable, strongly linked to species richness and habitat moisture. Weak elevation-degradation correlations suggest localized buffering of altitudinal gradients. All correlations are interpreted per Cohen's (1988) thresholds ($r^* > 0.3$ = moderate; $r^* < 0.2$ = negligible)

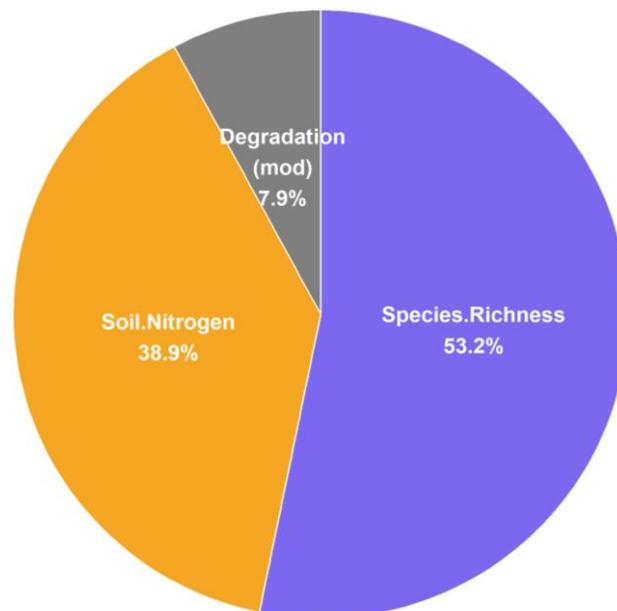


Figure 6. Relative direct effects of key predictors on tree cover in the Hindukush-Himalayan region. Species richness (53.2%, blue) emerged as the primary driver, followed by soil nitrogen (38.9%, green) and moderate degradation (7.9%, orange). Percentages reflect proportional contributions from partial regression analyses

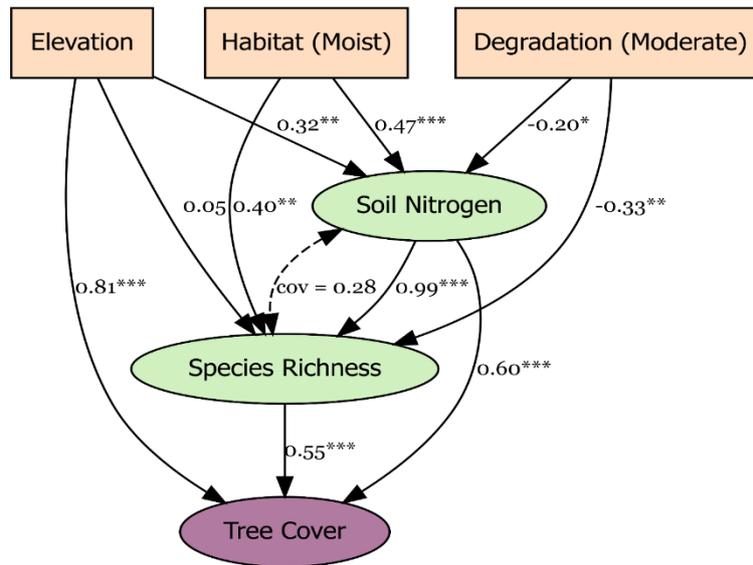


Figure 7. Structural equation model (SEM) of tree cover drivers in the Hindukush-Himalayan region. Standardized path coefficients (β) are shown for significant relationships $p < 0.05$, key pathways include: (1) strong direct effects of species richness and soil nitrogen on biomass, (2) indirect moisture effects mediated by nitrogen and richness, and (3) degradation's negative impact on nitrogen

Contrasts with the unified model

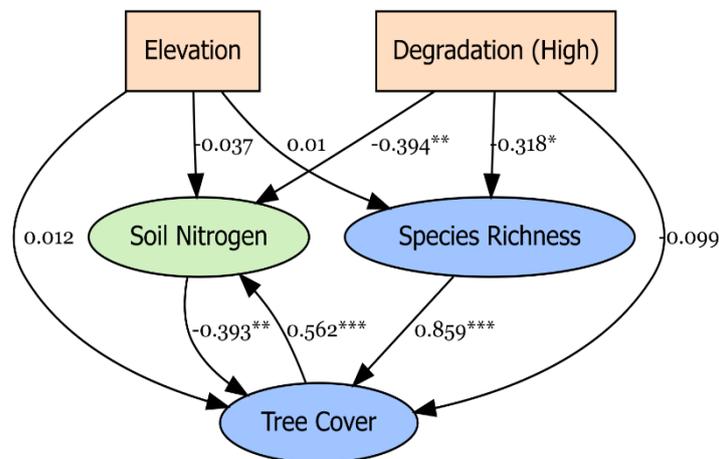
The unified model emphasized the type of habitat with elevation, nitrogen, and richness, but the habitat-specific models revealed key deviations. Dry temperate forests depended on segregation, moist temperate systems were constrained by cold-driven elevation, and subtropics showed nitrogen leaching. The unified model also overgeneralized species richness as universally positive, missing its weaker role in subtropics. Thus, while unified models capture broad trends, they risk obscuring biome-specific mechanisms where driver effects vary across habitats. These results confirm the hypothesis that the strength and direction of ecological drivers that regulate tree cover differ significantly between habitat types, indicating that habitat-specific models explain vegetation dynamics better than a unified model across all forest types.

Discussion

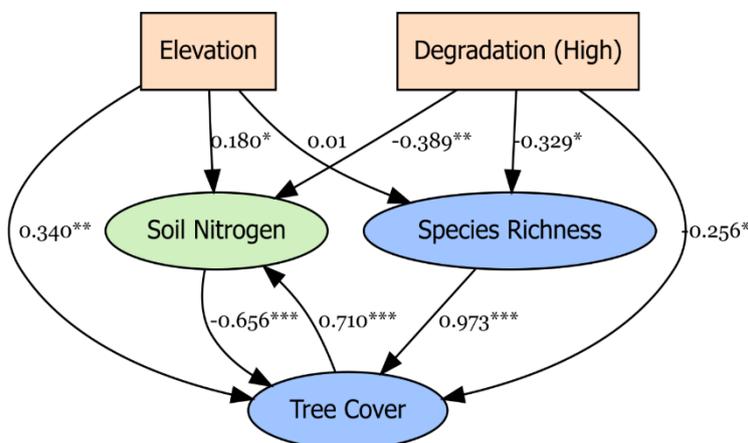
Species richness as the primary driver of forest cover

Our findings show that the species richness exerts the strongest direct effect on forest cover (53.2%), providing strong evidence for the role of biodiversity in maintaining ecosystem functioning within the HKH region. This result is consistent with recent global syntheses that demonstrate strong positive correlations between tree species richness and forest cover, with correlation coefficients that reach $r^2 = 0.96$ in protected forest areas (Yang et al., 2023). The dominance of species richness as a predictor reflects multiple underlying mechanisms, including complementary resource use, facilitation effects, and enhanced ecosystem stability through functional redundancy (Mayor et al., 2025; Hanson et al., 2020; Shennan-Farpón et al., 2021). The magnitude of the effect of the species richness observed in our study aligns with landscape-level analyzes carried out in the

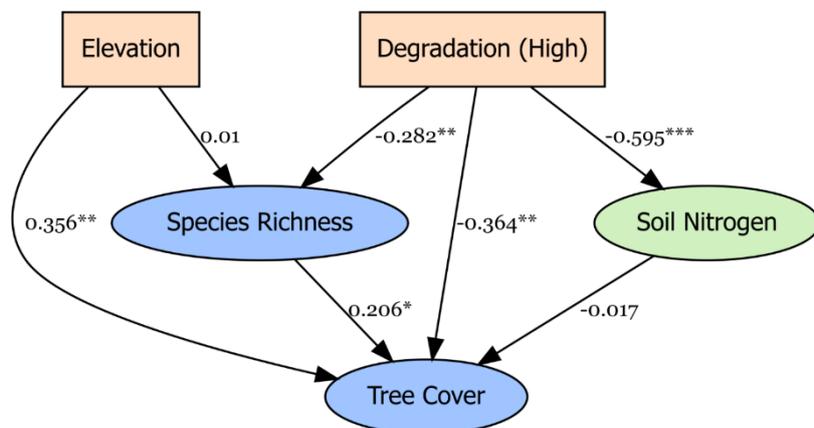
HKH and other regions (Mayor et al., 2025; Dyola et al., 2022b; Behera et al., 2017), where diversity was positively related to forest cover (Mayor et al., 2025). However, our findings extend beyond simple correlation analysis and highlight the causal pathways linking species richness with forest cover.



(a) Dry temperate forest



(b) Moist temperate forest



(c) Subtropical forest

Figure 8. (a–c) Structural equation models (SEMs) representing the relationships among elevation, degradation, soil nitrogen, species richness, and tree cover across three forest types in the study region. Arrows indicate the direction and standardized strength (β) of effects.

The SEMs show that the richness of species influences forest cover both directly and indirectly through its strong positive link with soil nitrogen ($\beta = 0.99$, $p < 0.001$), suggesting that diverse plant communities improve the nutrient cycling processes and thus promote forest productivity and cover. Biodiversity-rich ecosystems tend to be associated with greater temporal stability. Recent temporal studies showed that the positive effects of biodiversity can decrease with forest succession but remain significant across all stages of forest development (Zhang et al., 2025; Tian et al., 2023). This relationship represents a critical consideration for interpreting our results. This temporal variability suggests that the strong effects of species richness observed in our study may reflect the current stage of development of the forest stands examined, which has significant implications for long-term forest management and conservation planning. The persistence of biodiversity effects across forest succession stages supports the robustness of our findings and their relevance to understanding the dynamics of mature forest ecosystems. Mechanically, the dominance of species richness may reflect various synergistic processes that occur simultaneously within Himalayan forest communities. The functional diversity theory predicts that species with different resource acquisition strategies can use available environmental resources more efficiently, leading to enhanced productivity in diverse communities (Chen et al., 2025). In addition, ecologically diverse communities often show greater resilience to environmental stress and disturbances, which allows them to maintain a higher forest cover under the variable climatic conditions typical of mountain environments (Thompson et al., 2009). The consistent influence of species richness across various habitat types observed in this study supports this conclusion and emphasizes biodiversity conservation as a critical approach to preserving the functioning of the forest ecosystem in the region.

Soil nitrogen as a critical mediating factor

The high contribution of soil nitrogen to forest cover (38.9%) highlights the critical role of nutrient availability in restricting forest cover in the HKH region. This supports recent research that indicated that the impacts of tree functional diversity on carbon sequestration become more intense with greater availability of soil nutrients Chen et al. (2024). The good positive correlation between nitrogen in soil and species richness ($\beta = 0.99$, $p < 0.001$), as exposed by our structural equation model, indicates bidirectional feedback between plant diversity and nutrient cycling: rich plant communities fuel nitrogen availability, and nitrogen rich soils host richer plant assemblies, with both conducting to forest cover. The central position played by nitrogen in the habitat-inclusive scheme probably represents several interrelated processes that act on spatial and temporal scales. Plant communities with a variety of species can input soil nitrogen through differential litter quality, variations in root exudation, and symbiosis with nitrogen-fixing organisms (Liu et al., 2025). The functional microbial groups of the ectomycorrhizal fungi and oligotrophic bacteria decomposition genes further add to net ammonification processes, making nitrogen accessible to plants (Vitorisz et al., 2024). Collectively, these interactions suggest that the intense nitrogen impacts reported here are the result of intricate plant-soil-microbial feedbacks that maximize nutrient cycling in mountain forest ecosystems.

Forest management also influences nitrogen availability. The results of whole tree harvesting experiments indicate that management both directly, through regulation of litter biomass, and indirectly, through stimulation of plant productivity, can facilitate nitrogen cycling (Pang et al., 2024). Such processes suggest that historical land use and

management actions may have impacted the nitrogen–forest cover relationships identified here. The positive relationship of soil nitrogen with wet habitat conditions ($r = 0.43$) reinforces this interpretation, pointing to the role of moisture-controlled nitrogen cycling in maintaining forest productivity. Elevation gradients introduce additional complexity into nitrogen cycling. Forest growth along elevational gradients may improve nutrient mobilization through increased weathering and plant–soil feedback mechanisms (Fetzer et al., 2024). These phenomena can create feedback cycles in which nutrient-rich litter decomposes to release more nitrogen and phosphorus, helping to explain the positive elevation effects on soil nitrogen in the integrated model. But habitat-specific models break down considerably: nitrogen effects are not significant in subtropical forests, but strongly positive in moist and temperate forests. In particular, while in the unified model nitrogen is positively correlated with tree cover, it is negatively correlated in all three habitat-specific models.

This seeming paradox demonstrates a scale-dependent relationship in line with Simpson’s paradox, in which a trend that holds at the aggregate level reverses at the subgroup level, a phenomenon long familiar in ecological research on scale dependent processes and diversity productivity relationships (Blyth, 1972). In the integrated model, nitrogen rich environments will have more tree cover due to concomitant beneficial macro-environmental conditions such as moisture, organic resources, and lower temperatures. In other habitats, high nitrogen can correlate with those that inhibit tree cover, such as imbalances in nutrients, increased turnover or leaching under elevated rainfall, and competitive replacement in favor of noncontributing species that generate canopy instability in the long term. These results emphasize that nitrogen’s impact is context-specific and is influenced by interactions among climatic, edaphic, and historical conditions, and reinforce the need for habitat-specific management practices.

Elevation gradients and habitat heterogeneity

These nuanced elevation effects in our research mirror the complex mechanisms by which topographic gradients shape forest ecosystem processes in mountains. The robust positive effect of elevation on tree cover ($b = 0.81$, $p < 0.0001$) in our habitat-inclusive model contrasts with the more inconsistent elevation effects revealed in habitat-specific analyzes, indicating the importance of accounting for habitat context when interpreting elevation patterns. Recent research confirms this complexity, with evidence that upper altitudinal zones may have much higher tree biomass (568.8 Mg ha^{-1}) than lower zones (265.7 Mg ha^{-1}) in certain mountain systems (Sheikh et al., 2020), while other research indicates a decrease in productivity with elevation based on taxonomic groups and geographic regions. The processes behind elevation effects are likely to involve several interacting factors that act differently in different habitats. Temperature gradients, precipitation regimes, changes in atmospheric pressure, and soil development processes change systematically with elevation, producing contrasting environmental conditions that impact plant growth and community structure (Zhang et al., 2024).

Our result that elevation effects are quite different between habitat-specific models implies that these environmental gradients interact with the local habitat characteristics to produce context-dependent responses. For example, the non-significant elevation effects of dry temperate systems could be a sign of water limitations that take precedence over temperature advantages at higher elevations, whereas the positive elevation effects for moist temperate and subtropical systems could be a sign of less anthropogenic pressure or beneficial temperature-moisture combinations. The interaction of elevation

and anthropogenic disturbance is a key factor in the patterns in our study. Current studies show that the history of disturbance mediates the impacts of evolutionary diversity on the dynamics of forest biomass, with major negative correlations between diversity and productivity 5-8 years after disturbances (Borges et al., 2024). The positive elevation impacts reported in our subtropical model ($\beta = 0.336$, $p < 0.001$) could be partially due to decreasing human pressure at higher elevations, where accessibility restrictions limit anthropogenic use. These findings are validated by research that indicates that conversion from natural to modified habitat results in substantial loss of biodiversity, with consequences especially acute at certain elevations where biogeographic processes are most perturbed (Seastedt and Oldfather, 2021). The implications of climate change further complicate the impacts of elevation in our study. Mountain ecosystems are undergoing rapid environmental change that could change historical elevation-productivity relationships through changes in temperature and precipitation patterns, disturbance regimes, and species range shift (Altman et al., 2024). The prominent elevation effects found in our existing data will not hold under future climatic conditions, especially if rising temperatures remove the thermal benefits of high elevation or if altered precipitation patterns reroute moisture-elevation relationships. Appreciation of these temporal processes is essential to predict future forest reaction and create adaptive management plans for the preservation of mountain forests.

Forest degradation: context-dependent impacts

The comparatively low direct impact of degradation on forest cover patterns (7.9%) in our research contrasts with its stronger indirect impacts via soil nitrogen and species richness pathways, uncovering the intricate mechanisms through which anthropogenic disturbance affects forest ecosystem functioning. This result is supported by recent studies that demonstrate that disturbance effects on biodiversity ecosystem functioning relationships are strongly context dependent and mediated by multiple ecological factors Borges et al. (2024). The adverse impacts of moderate degradation on species richness ($b = -0.33$, $p < 0.01$) and soil nitrogen ($b = -0.20$, $p < 0.05$) in our combined model indicate that degradation affects forest cover mainly through cascade impacts on ecological processes and not direct structural effects. Habitat-specific models identified significant differences in the responses of forest types to degradation, and dry temperate systems exhibited especially strong negative responses to degradation for both species richness and nitrogen in the soil. This trend could be due to the increased susceptibility of arid ecosystems to disturbance, where reduced resource availability undermines the potential for recovery following degradation episodes. This interpretation is supported by recent work, showing that forest diversity experiment mortality is greater in monoculture plots with decreasing mortality as plot diversity increases (Cavender-Bares et al., 2024). This indicates that diversified communities are more resistant to degradation effects, and it is for this reason that the degradation effects reported here are mediated by diversity pathways.

The temporal dynamics of degradation effects is an important consideration when interpreting the present results. Evidence shows that the impacts of evolutionary diversity on forest dynamics change considerably with time since disturbance, with inverse relationships between diversity and productivity 5-8 years after disturbance events (Borges et al., 2024). This temporal variation indicates that the effects of degradation detected in our cross-sectional study may not represent the totality of the impacts of disturbance on the functioning of the forest ecosystem. Long-term monitoring would be

required to most clearly see how the effects of degradation change over time and interact with recovery processes operating in nature. The degradation effects vary with spatial scale, making our results more challenging to interpret. Habitat conversion research shows that biodiversity declines occur at multiple levels, with species richness reduced tenfold per plot and total abundance dropping 23 times when natural habitats are transformed into modified ones (Parra-Sanchez et al., 2024). The comparatively minor degradation effects in our landscape-scale analysis could be due to spatial averaging over more strongly affected local areas. This scale dependence also has significant conservation planning implications, indicating that preserving large blocks of forest could be more useful than targeting only localized restoration.

Habitat-specific mechanisms versus unified models

The significant differences among our combined and habitat-specific structural equation models uncover significant limitations of large-scale ecological generalizations and confirm the importance of taking into account ecosystem-specific processes in biodiversity-ecosystem functioning research. The combined model identified habitat type along with elevation, soil nitrogen, and species richness as the primary drivers; the site-specific models revealed important deviations that were concealed in the large-scale analysis. These findings mirror recent studies reporting a marked shift in diversity-productivity relationships in environmentally contrasting natural reserves, driven largely by site-specific factors shaped by local climate, elevation, rainfall and temperature seasonality (Zhu et al., 2024a). The site-specific models uncovered unique ecological mechanisms in diverse forest communities, with significant implications for determining biodiversity-ecosystem functioning relationships. In temperate dry systems, the fundamental reliance on species segregation and the high negative impact of degradation imply that niche partition mechanisms are especially significant in resource-poor environments. In contrast to dry temperate systems, elevation had a strong positive impacts on tree cover, perhaps through lowered anthropogenic pressure or microclimatic benefits. The subtropical model showed another pattern, where elevation and species richness favored tree cover but nitrogen effects were not significant, implying varying nutrient limitation patterns or leaching mechanisms. Recent research supports the importance of environmental heterogeneity in mediating the effects of diversity on ecosystem functioning.

Studies show that the effects of diversity on ecosystem functioning increase with environmental heterogeneity, with species richness being particularly important in mediating these effects (Wurz et al., 2024). Our habitat-specific findings illustrate this principle, demonstrating how the same ecological drivers can have intensely variable consequences as a function of local environmental conditions. The low correlation between degradation and habitat type ($r = 0.05$) for our correlation analysis implies that these habitat-specific processes are independent of anthropogenic disturbance patterns, suggesting that they represent true ecological differences rather than artifacts of management. The implications of these habitat-specific processes go beyond theoretical understanding to applied conservation and management. The variable importance of drivers by forest type indicates that conservation efforts must be optimized by individual habitat characteristics rather than taking a one-size-fits-all approach in the landscape. For example, the paramount importance of species segregation in dry temperate systems implies prioritizing the maintenance of habitat heterogeneity and avoiding homogenization in these systems. In contrast, the strong elevation effects in wet temperate

systems imply that the conservation of high-elevation habitats may be especially important to the preservation of forest cover in such systems. These habitat-specific patterns would be obscured in broader, aggregated analyses, underscoring the value of disaggregated approaches in ecological research.

Methodological insights and future directions

The application of structural equation modeling in our study demonstrates both the power and limitations of this analytical approach for understanding complex ecological relationships. Our models achieved adequate fit statistics, indicating that the hypothesized causal relationships reasonably represent the observed data structure. However, the substantial differences between unified and habitat-specific models highlight the importance of considering ecological context when applying SEM approaches to biodiversity-ecosystem functioning research. Recent methodological advances in structural equation modeling have emphasized the importance of incorporating temporal dynamics, spatial autocorrelation, and nonlinear relationships in ecological applications (Zhu et al., 2024b). Our study focused primarily on linear relationships and cross-sectional data, which may not capture the full complexity of biodiversity-ecosystem functioning relationships in mountain forest systems. Future research should consider incorporating temporal lags, threshold effects, and spatial dependence to better represent the dynamic nature of these ecological relationships.

The habitat-specific approach employed in our study provides a template for future research seeking to understand context-dependent ecological mechanisms. Rather than relying solely on broad-scale syntheses that may obscure important ecological details, our results demonstrate the value of disaggregated analyses that can reveal ecosystem-specific patterns. This approach is particularly important in mountain regions where environmental heterogeneity creates diverse ecological conditions within relatively small spatial extents. Future research directions should focus on several key areas identified by our study. First, long-term monitoring is needed to understand how the relationships observed in our cross-sectional analysis evolve over time, particularly under changing climate conditions. Second, experimental manipulations of species diversity and soil nutrients would help establish causal mechanisms underlying the correlative relationships revealed by our structural equation models. Third, expanded spatial sampling across broader elevation gradients and additional habitat types would help determine the generalizability of our findings to other mountain forest systems. Finally, integration of functional trait approaches with our taxonomic diversity measures could provide deeper insights into the mechanisms underlying biodiversity-ecosystem functioning relationships in these complex mountain ecosystems.

Conclusion

The Hindukush-Himalayan region's forest biomass and plant cover are primarily shaped by species richness and soil nitrogen, according to this study. The greatest predictor of vegetation structure turned out to be biodiversity, highlighting its fundamental significance in maintaining ecosystem productivity. The nutrient diversity synergy in these ecosystems was further strengthened by the role of soil nitrogen, which was a key mediating variable and was closely related to both species' richness and habitat moist. Despite having statistically significant effects, elevation and degradation primarily had an indirect impact through modifications to species composition and soil fertility.

Interestingly, degradation had little direct effect on biomass, indicating either the resilience of the ecosystem or the existence of degradation thresholds that linear models are unable to account for. Variations in plant cover by habitat, especially in moist temperate forests, highlight how important it is to preserve growth-promoting soil and microclimatic conditions. These hierarchical relationships were validated by the SEM, which showed that soil nitrogen and biodiversity together accounted for a sizable amount of biomass variation. All things considered, these results conservation tactics that give preservation of biodiversity and improvement of soil nutrients top priority. Such tactics are essential for maintaining forest carbon stocks and ecological stability in an area that is experiencing fast anthropogenic and climatic change. The dynamics of nutrient cycling across elevational gradients and non-linear degradation effects should be further investigated in future studies.

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APPENDIX

Table A1. Number of sample plots and their geographic coordinates (latitude and longitude) across different study regions

No of sample plots	Regions	Latitudes	Longitudes	No of sample plots	Regions	Latitudes	Longitudes
1	Lower Dir	34°41'58"	71°58'11"	23	Lower Dir	34° 51' 25"	71° 57' 42"
2	Lower Dir	34° 41' 53"	71° 58' 7"	24	Lower Dir	34° 51' 18"	71° 57' 35"
3	Lower Dir	34° 41' 49"	71° 58' 98"	25	Lower Dir	34° 50' 16"	71° 57' 33"
4	Lower Dir	34° 41' 46"	71° 58' 11"	26	Lower Dir	34° 50' 22"	71° 57' 17"
5	Lower Dir	34° 41' 44"	71° 58' 12"	27	Lower Dir	34° 50' 1"	71° 57' 20"
6	Lower Dir	34° 41' 41"	71° 58' 8"	28	Lower Dir	34° 49' 3"	71° 57' 24"
7	Lower Dir	34° 41' 38"	71° 58' 6"	29	Lower Dir	34° 48' 55"	71° 57' 12"
8	Lower Dir	34° 41' 48"	71° 58' 18"	30	Lower Dir	34° 48' 49"	71° 57' 19"
9	Lower Dir	34° 41' 58"	71° 58' 12"	31	Lower Dir	34° 48' 46"	71° 57' 15"
10	Lower Dir	34° 44' 24"	71° 57' 53"	32	Lower Dir	34° 49' 40"	71° 59' 24"
11	Lower Dir	34° 44' 23"	71° 58' 02"	33	Lower Dir	34° 49' 26"	71° 59' 37"
12	Lower Dir	34° 43' 49"	71° 56' 47"	34	Lower Dir	34° 94' 18"	71° 59' 44"
13	Lower Dir	34° 43' 46"	71° 56' 42"	35	Lower Dir	34° 49' 7"	72° 0' 2"
14	Lower Dir	34° 44' 08"	71° 56' 25"	36	Lower Dir	34° 49' 1"	72° 0' 2"
15	Lower Dir	34° 45' 54"	71° 49' 44"	37	Lower Dir	34° 51' 25"	71° 57' 0"
16	Lower Dir	34° 45' 60"	71° 49' 36"	38	Lower Dir	34° 51' 13"	71° 57' 3"
17	Lower Dir	34° 45' 57"	71° 49' 32"	39	Lower Dir	34° 51' 2"	71° 57' 2"
18	Lower Dir	34° 45' 7"	71° 49' 20"	40	Lower Dir	34° 50' 50"	51° 56' 53"
19	Lower Dir	34° 46' 12"	71° 49' 14"	41	Lower Dir	34° 50' 39"	71° 56' 52"
20	Lower Dir	34° 46' 41"	71° 48' 58"	42	Lower Dir	34° 50' 25"	71° 53' 54"
21	Lower Dir	34° 51' 26"	71° 57' 57"	43	Lower Dir	34° 50' 41"	71° 56' 37"
22	Lower Dir	34° 51' 26"	71° 57' 52"	44	Lower Dir	34° 50' 35"	71° 56' 27"
45	Swat	34° 36' 25"	72° 17' 26"	67	Swat	34° 50' 01"	72° 31' 34"
46	Swat	34° 36' 22"	72° 17' 29"	68	Swat	34° 50' 18"	72° 31' 57"
47	Swat	34° 36' 23"	72° 17' 15"	69	Swat	34° 50' 18"	72° 31' 60"
48	Swat	34° 36' 40"	72° 17' 14"	70	Swat	34° 50' 10"	72° 32' 50"
49	Swat	34° 36' 49"	72° 17' 6"	71	Swat	34° 50' 08"	72° 33' 08"
50	Swat	34° 36' 39"	72° 16' 59"	72	Swat	34° 50' 55"	72° 33' 30"
51	Swat	34° 36' 57"	72° 16' 46"	73	Swat	34° 49' 46"	72° 34' 19"
52	Swat	34° 37' 16"	72° 16' 43"	74	Swat	34° 49' 92"	72° 34' 22"
53	Swat	34° 37' 54"	72° 16' 19"	75	Swat	34° 48' 9"	72° 34' 22"
54	Swat	34° 38' 26"	72° 16' 12"	76	Swat	34° 48' 9"	72° 34' 22"
55	Swat	34° 36' 28"	72° 17' 30"	77	Swat	35° 29' 49"	72° 35' 31"
56	Swat	34° 36' 34"	72° 17' 33"	78	Swat	35° 29' 50"	72° 35' 31"
57	Swat	34° 36' 44"	72° 17' 50"	79	Swat	35° 23' 75"	72° 35' 71"
58	Swat	34° 36' 44"	72° 17' 55"	80	Swat	35° 28' 71"	72° 35' 98"
59	Swat	34° 36' 40"	72° 18' 5"	81	Swat	35° 23' 16"	72° 36' 07"
60	Swat	34° 36' 38"	72° 18' 12"	82	Swat	35° 27' 49"	72° 36' 36"
61	Swat	34° 36' 38"	72° 18' 13"	83	Swat	35° 27' 31"	72° 36' 42"
62	Swat	34° 36' 45"	71° 18' 14"	84	Swat	35° 37' 28"	72° 36' 47"
63	Swat	34° 36' 41"	72° 18' 13"	85	Swat	35° 28' 19"	72° 36' 44"
64	Swat	34° 36' 41"	72° 18' 13"	86	Swat	35° 27' 13"	72° 36' 49"
65	Swat	34° 50' 0"	72° 31' 33"	87	Swat	35° 27' 10"	72° 36' 50"
66	Swat	34° 50' 02"	72° 31' 35"	88	Swat	35° 27' 07"	72° 36' 54"
89	Swat	35° 27' 03"	72° 37' 16"	128	Chitral	35° 46' 38"	71° 40' 40"
90	Swat	35° 27' 12"	72° 36' 19"	129	Chitral	35° 46' 33"	71° 40' 37"
91	Swat	35° 82' 9"	72° 33' 23"	130	Chitral	35° 46' 29"	71° 40' 36"
92	Swat	35° 14' 02"	72° 55' 97"	131	Chitral	35° 46' 35"	71° 40' 54"

No of sample plots	Regions	Latitudes	Longitudes	No of sample plots	Regions	Latitudes	Longitudes
93	Swat	35° 82' 5"	72° 33' 37"	132	Chitral	35° 46' 7"	71° 40' 33"
94	Swat	35° 82' 3"	72° 33' 39"	133	Chitral	35° 46' 18"	71° 40' 40"
95	Swat	35° 83' 4"	72° 35' 65"	134	Chitral	35° 46' 18"	71° 40' 51"
96	Swat	35° 10' 35"	72° 34' 80"	135	Chitral	35° 46' 19"	71° 41' 1"
97	Swat	35° 14' 04"	72° 55' 98"	136	Chitral	35° 42' 37"	71° 40' 41"
98	Swat	35° 82' 6"	72° 33' 36"	137	Chitral	35° 43' 36"	71° 40' 35"
99	Swat	35° 82' 7"	72° 34' 39"	138	Chitral	35° 43' 24"	71° 40' 34"
100	Swat	35° 83' 9"	72° 35' 64"	139	Chitral	35° 44' 32"	71° 40' 53"
101	Swat	35° 10' 33"	72° 34' 81"	140	Chitral	35° 45' 7"	71° 40' 32"
102	Chitral	35° 48' 20"	72° 3' 33"	141	Chitral	35° 46' 23"	71° 40' 42"
103	Chitral	35° 48' 22"	72° 3' 31"	142	Chitral	35° 46' 22"	71° 40' 52"
104	Chitral	35° 48' 24"	72° 3' 29"	143	Chitral	35° 46' 21"	71° 41' 2"
105	Chitral	35° 48' 26"	72° 3' 26"	144	Chitral	35° 38' 38"	71° 52' 4"
106	Chitral	35° 48' 28"	72° 3' 23"	145	Chitral	35° 38' 41"	71° 51' 52"
107	Chitral	35° 48' 0"	72° 3' 30"	146	Chitral	35° 38' 42"	71° 51' 43"
108	Chitral	35° 46' 44"	72° 1' 45"	147	Chitral	35° 46' 51"	71° 40' 55"
109	Chitral	35° 46' 45"	72° 1' 43"	148	Chitral	35° 46' 48"	71° 40' 54"
110	Chitral	35° 46' 47"	72° 1' 43"	149	Chitral	35° 46' 47"	71° 40' 46"
111	Chitral	35° 46' 65"	72° 1' 37"	150	Chitral	35° 46' 20"	71° 41' 6"
112	Chitral	35° 45' 46"	72° 1' 11"	151	Chitral	35° 41' 9"	71° 38' 42"
113	Chitral	35° 45' 11"	72° 0' 35"	152	Chitral	35° 41' 32"	71° 38' 42"
114	Chitral	35° 44' 12"	71° 59' 41"	153	Chitral	35° 41' 31"	71° 38' 46"
115	Chitral	35° 38' 23"	71° 53' 8"	154	Chitral	35° 41' 33"	71° 38' 52"
116	Chitral	35° 38' 19"	71° 52' 58"	155	Chitral	35° 41' 34"	71° 38' 56"
117	Chitral	35° 38' 52"	71° 52' 43"	156	Chitral	35° 41' 36"	71° 39' 2"
118	Chitral	35° 38' 57"	71° 52' 20"	157	Chitral	35° 41' 46"	71° 39' 10"
119	Chitral	35° 38' 56"	71° 52' 11"	158	Chitral	35° 42' 7"	71° 38' 52"
120	Chitral	35° 38' 52"	71° 52' 7"	159	Chitral	35° 42' 5"	71° 38' 58"
121	Chitral	35° 38' 44"	71° 52' 9"	160	Chitral	35° 40' 58"	71° 38' 56"
122	Chitral	35° 38' 39"	71° 52' 4"	161	Chitral	35° 41' 51"	71° 38' 42"
123	Chitral	35° 38' 42"	71° 51' 52"	162	Chitral	35° 41' 40"	71° 38' 44"
124	Chitral	35° 38' 46"	71° 51' 43"	163	Chitral	35° 48' 21"	72° 3' 33"
125	Chitral	35° 46' 50"	71° 40' 55"	164	Chitral	35° 48' 23"	72° 3' 31"
126	Chitral	35° 46' 49"	71° 40' 54"	165	Chitral	35° 48' 25"	72° 3' 29"
127	Chitral	35° 46' 43"	71° 40' 46"	166	Chitral	35° 48' 27"	72° 3' 26"