Herbaceous Biomass Dynamics and the Interacting Roles of Nitrogen and Plant Diversity across Elevational and Habitat Degradation Gradients

Rashid Ahmed,[a] Abd Ullah,[a] Alam Zeb,[a,b,]* Khalid Khan,[a] Muhammad Nawaz Rajpar,[a] Ghulam Nabi,[c,]* Muhammad Nauman Ahmad,[d] Maha Abdullah Alwaili,[e] Nawal Al-Hoshani [e] and Rewaa S. Jalal [f]

Mountain ecosystems are under increasing pressure from forest degradation, which can alter key ecological indicators, including herbaceous biomass production. This study considered how herbaceous above-ground biomass (AGB) is influenced by degradation intensity, nitrogen availability, elevation, and species richness in temperate and subtropical forests of the Hindu Kush Himalayas. Data from 200 systematically placed plots were analyzed using bivariate and correlation methods, followed by structural equation modeling (SEM) to assess both direct and indirect pathways affecting herbaceous biomass. The results showed that available nitrogen was the strongest predictor of biomass ($\beta = 0.77$, $p < 0.001$), followed by species richness ($\beta = 0.18$, $p < 0.05$). Degradation reduced biomass indirectly by decreasing nitrogen ($\beta = -0.72$, $p < 0.001$) and species richness ($\beta = -0.59$, $p < 0.001$). Moderate degradation also negatively influenced subtropical habitat ($\beta = -0.82$, $p < 0.001$) and nitrogen ($\beta = -0.43$, $p < 0.01$). Higher nitrogen levels were significantly associated with less degradation ($\beta = -0.47$, $p < 0.001$), suggesting a protective effect of nitrogen-rich soils. Elevation had no direct effect on biomass but reduced subtropical forests ($\beta = -0.82$, $p < 0.001$) and increased moist temperate forests ($\beta = 0.35$, $p < 0.01$). The model identified nitrogen as the main driver of productivity, while degradation disrupted soil fertility and biodiversity, especially in vulnerable low-elevation forests.

DOI: 10.15376/biores.21.2.4899-4918

Keywords: Forest degradation; Herbaceous biomass; Available nitrogen; Species richness; Elevation gradient; Himalayan forests

Contact information: a: Department of Forestry, Shaheed BB University, Sheringal Dir (Upper), P. O. Box 18050, Khyber Pakhtunkhwa, Pakistan; b: Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB, T6G 2H1, Canada; c: Center for Animal Sciences and Fisheries, the University of Swat, Swat, 19200, Pakistan; d: Department of Agricultural Chemistry and Biochemistry, University of Agriculture, Peshawar, Khyber Pakhtunkhwa Pakistan; e: Department of Biology, College of Science, Princess Nourah bint Abdulrahman University, P.O. Box 84428, Riyadh 11671, Saudi Arabia; f: Department of Biological Sciences, College of Science, University of Jeddah, 21493, Jeddah, Saudi Arabia;
**Corresponding authors: zeb@ualberta.ca and ghulamnabiqau@gmail.com*

INTRODUCTION

The mountain ecosystems of the Hindukush and Himalayan (HKH) regions are widely accepted for their ecological complexity and rich biodiversity. These landscapes are home to a wide range of endemic plant species that provide important environmental services such as carbon sequestration, water regulation, and biomass production (Xu *et al.* 2019). However, increasing human pressures, such as changes in land use, habitat fragmentation, and climate changes, are increasing the fragility of these habitats and threatening their ecological coherence and function (Wester *et al.* 2019; Pei *et al.* 2024).

Herbaceous biomass is a key component of these ecosystems, which serves not only as an essential energy source in food webs but also as an indicator of overall ecosystem productivity (Masese *et al.* 2022). The herbaceous layer also plays an important role in the nutrient cycle and biodiversity (Geng *et al.* 2024). The production of herbaceous biomass is a sign of ecosystem health because it is very sensitive to changes in biotic and abiotic conditions and their interactions (Ryś *et al.* 2024). Herbaceous biomass is governed by both abiotic and biotic factors, with elevation, soil fertility, nitrogen availability, and species richness playing an influential role (Qian *et al.* 2024). Among these, elevation gradients exert a strong influence on climate conditions, soil properties, and species distributions (Han *et al.* 2022; Ni and Vellend 2024). Although there is some insight, the interaction between elevation, habitat degradation, and mediating factors such as available nitrogen and species richness remains relatively understudied, particularly in high-altitude regions such as the eastern Himalayas.

The relationship between habitat modification, elevation gradients, and ecosystem productivity has become central, especially in light of how these elements work together to affect the dynamics of herbaceous layers (Seastedt and Oldfather 2021). In mountain ecosystems, elevation acts as a master environmental filter, generating comparatively different microclimates and habitat types at short distances (Fatunsin *et al.* 2024). HKH regions show distinct vertical forest stratification driven by elevational changes (Rawat and Negi 2021), in lower elevations, tropical broadleaf forests dominate, while mid-elevation is occupied by mixed temperate forests and high-elevation is dominated by alpine scrublands. Fundamental modifications in abiotic conditions cause these habitat transitions: precipitation patterns show complex orographic effects, and the temperature drops by about 0.6 °C for every increase in elevation of 100 m (Seastedt and Oldfather 2021).

More importantly, environmental gradients not only affect human disturbances on ecosystem function but also have a direct impact on vegetation structure and composition (Sundqvist *et al.* 2013). Recent studies have shown that about 25% of the forests in the HKH region have suffered significant degradation since 2000 mainly due to grazing pressure, agricultural development, and timber extraction. Several ecological characteristics, such as canopy structure, microclimate, and soil characteristics, are altered by this degradation, triggering a cascading effect in the communities of understory plants (Wang *et al.* 2023; Singh *et al.* 2025). Degradation, influenced by elevation-driven variations in forest habitat types, changes species richness and available nitrogen, thus indirectly affecting biomass productivity. Recent studies supported this theory by demonstrating that the impacts of degradation on soil properties vary significantly between elevation zones (McNichol *et al.* 2024). Degradation also indirectly affects elevation-based changes in temperature and moisture, which play a vital role in the regulation of nitrogen mineralization rates (Wang *et al.* 2023). For example, in low-altitude tropical forests, degradation increases soil temperature and accelerates organic matter decomposition, while in higher-altitude temperate forests it frequently causes soil compaction and decreased microbial activity (Sharma *et al.* 2022).

The availability of nitrogen becomes a central mediator, particularly in nitrogen-constrained forest landscapes. According to recent studies, 68% of the forests studied show considerable growth responses to nitrogen addition, showing that the HKH region has particularly severe nitrogen limitations (Elrys *et al.* 2023). Nitrogen cycling affects degradation through the decrease in nitrogen input through the reduction of litter production and nitrogen fixation, the increase in nitrogen losses through erosion and leaching, and the alteration of microbial populations are responsible for nitrogen conversions (Li *et al.* 2024). A meta-analysis found that the plant-available nitrogen in degraded HKH forests is 30% to 45% less than that in intact forests, with the most pronounced differences observed in mid-elevation zones (1,500 to 2,500 m) where the anthropogenic pressure is high (Malik and Ford 2025). These nitrogen reductions can significantly limit herbaceous productivity, specifically for species that require nitrogen (She *et al.* 2021).

Species richness is another significant mediator in the relation between the degradation of biomass productions. Diverse plant populations typically have higher productivity efficiency, mainly due to their supportive interactions and the utilization of complementary resources (Li *et al.* 2021). Forest degradation leads to decline in the richness of understory species by breaking the complexity of habitats, reducing the heterogeneity of the microsites and competition between species (Deng *et al.* 2023). Research studies in the HKH region have shown that the species richness in degraded forests is 20% to 35% lower than in non-degraded forests, which has a more severe effect on endemic and habitat-specific species (Shaheen *et al.* 2024). Importantly, the relationship between biomass productivity and species richness differs along elevations, with strong positive relations found at lower altitudes due to favorable growth conditions (Dani *et al.* 2023). This suggests that species richness may have an elevation-dependent mediation effect on the relationship between biomass and degradation. In ecology, structural equation modeling (SEM) has emerged as a powerful tool for disentangling the direct and indirect effects among variables. It enables researchers to measure the effects of mediation while accounting for the covariance between predictors (Zhu *et al.* 2024).

Current uses of these integrated analytical approaches have revealed critical information on elevation specific climate responses and the nonlinear effects of forest degradation (Sundqvist *et al.* 2013; Pu *et al.* 2025). Even with these advances, there are many questions regarding how elevation, degradation, and mediating factors combine to affect the dynamics of herbaceous biomass production (Lu 2024). Herbivore pressure and plant-soil feedback are biotic interactions that can modify vegetation dynamics to environmental change in ways that traditional models overlook (He *et al.* 2025). Few studies have explored the interactions between elevation and degradation, as most research has concentrated on these impacts in isolation, especially in the eastern HKH region (Hamid *et al.* 2021; Munkhzul *et al.* 2021; Han *et al.* 2022; Ni and Vellend 2024).

To fill this gap, this study focused on how elevation, habitat degradation, species diversity, and soil nitrogen directly and their interaction affect herbaceous biomass using the SEM approach. Specifically, this study has focused on the following two hypotheses: (1) available nitrogen and species richness mediate the negative impact of forest degradation on herbaceous biomass in mountain ecosystems; and (2) elevation indirectly influences herbaceous biomass by altering the type of forest habitat and levels of degradation, which subsequently affect nitrogen availability and species richness. The results of this study will have significant implications for the protection and sustainable management of HKH ecosystems. The findings will guide restoration efforts that identify the most vulnerable elevation zones and habitat types. In addition, the evaluation of the impacts of species richness will highlight the connections between biodiversity and ecosystem function in these systems, while the quantification of nitrogen mediation effects will aid in prioritizing locations for nutrient management interventions.

EXPERIMENTAL

Sampling Design

Data were collected from 200 sample plots spread over three habitat types: moist temperate, dry temperate, and subtropical. Each plot measured 20 × 20 m. Field sampling was carried out in 2023-24, from April to September, which represents the peak of vegetation development in the study area. However, seasonal differences were not considered due to logistical limitations, and the findings mainly reflect conditions during the sampling period. The sampling plots were systematically distributed across each forest type, with a distance of 1 km between each sampled plot and an elevation difference of 500 m. This design was used to capture spatial variability within each habitat of the forest and cover different microhabitats and ecological gradients.

Study Sites

The Malakand division lies in the northwestern part of Khyber Pakhtunkhwa (KP), Pakistan, and is among its largest divisions, occupying approximately 32,007 km^2, which is equivalent to 40% of the province. It is located approximately 72°00′E and 35°29′59.99″N (Fig. 1). The division is bordered by Gilgit Baltistan, Kohistan, and Battagram to the East, Afghanistan and the Bajaur Agency to the West, Nooristan province to the North, and Mardan and Charsadda to the South. Characterized by diverse terrain and climatic zones, the area supports a wide variety of forest ecosystems. These forests are not only ecologically and economically significant, but they also contribute to efforts to combat climate change (Zeb *et al.* 2019). The moist temperate regions in the study area spread over the lower Swat and upper Dir regions at 1600 m and 3100 m above sea level (asl). The mean annual temperature of the region varies between 13 and 18 °C, depending on altitude and location. The mean annual rainfall is between 700 mm and 1600 mm. The common herb species found in these forests are *Carex hirta*, *Cannabis sativa*, *Viola riviniana*, *Stipa capillata*, *Fragaria vesca*, and *Artemisia pontica* (Champion *et al.* 1965).

The dry temperate regions occupy the dry regions of the high mountain zones at elevations of 1500 m to 3350 m (asl). This region experience mean annual temperature between 8 °C to 16 °C, with annual precipitation generally remains below 500 mm. However, these regions are under considerable pressure from intensive grazing and browsing by goats and sheep, leading to alteration in species composition. The key herb species are *Artemisia pontica, Origanum majorana*, *Panicum miliaceum*, *and Elymus glaucus* (Champion *et al.* 1965; Khan *et al.* 2014).

The subtropical regions in the study area are found mainly 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. The forests of the region are highly susceptible to deforestation and degradation, mainly due to their closeness to human habitations. Grazing is widespread, often mismanaged, and intense. Common herb species in this area are

Origanum majorana, *Elymus glaucus, Panicum miliaceum, and Artemisia pontica* (Champion *et al.* 1965).

These habitat types were used as proxy variables for moisture availability, as each implies a different and ecologically significant temperature–precipitation regime. This categorization method is commonly used in mountain forest ecosystems and allows an effective representation of climatic impacts on vegetation growth and soil processes without using plot-level climatic measurements.

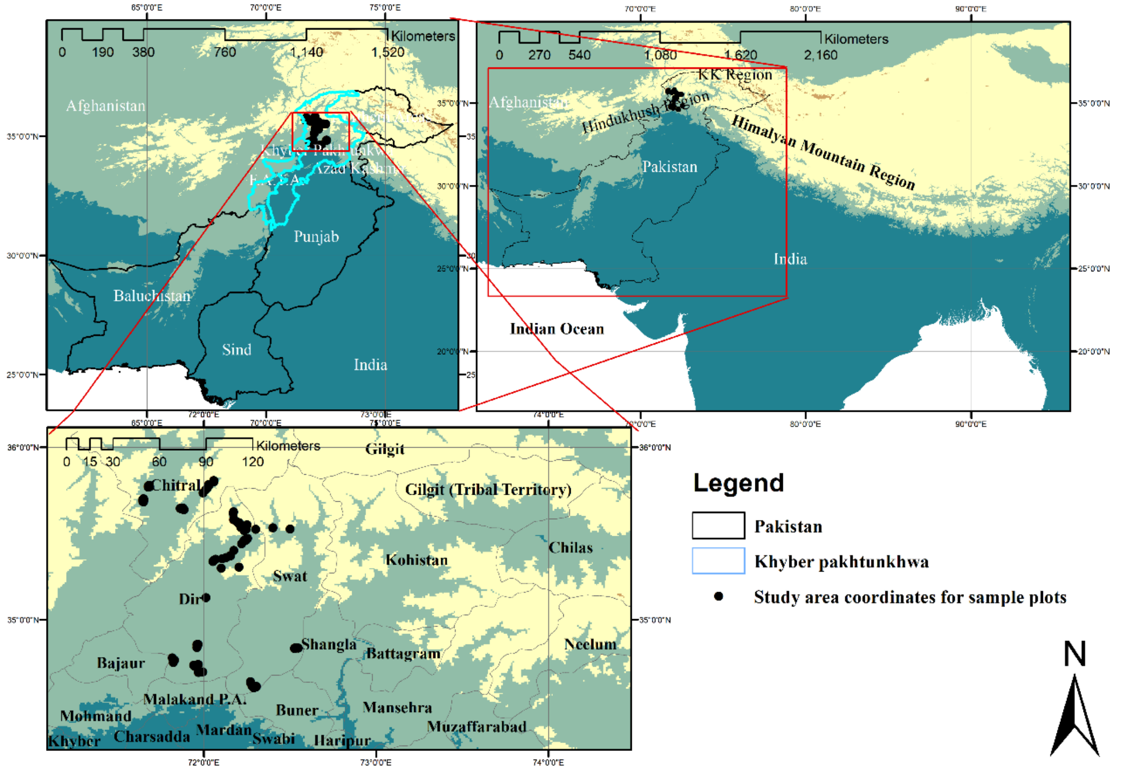

Fig. 1. Study area map showing the distribution of sample plots in various forest types in the Eastern Hindukush region

Soil Analysis

Soil sample was acquired within each plot at three different locations, with 1 × 1 m subplots from a depth of 0 to 15 cm using a stainless-steal soil auger. The samples collected at three different locations were then thoroughly mixed to form a composite sample for each plot. In rocky areas, when a designated sampling point concurred with a rock, the sampling site was adjusted within a short radius (*e.g.*, 0.5 to 1 m) to obtain representative soil sample. This method is consistent with typical ecological field techniques. Prior to analysis, the samples were air dried, mechanically crushed, and passed through a 2 mm sieve. Standard analytical procedures were used to determine the total and available forms of vital soil nutrients, as well as the content of organic matter. The organic matter of the soil was quantified using the Walkley-Black dichromate oxidation method Walkley and Black (1934). This procedure includes the oxidation of organic carbon by potassium dichromate in an acidic medium. Soil available nitrogen was measured following the alkaline potassium permanganate method (Subbiah and Asija 1956), which measures mineralizable nitrogen, mainly as ammonium (NH_4^+). It is significant to note that plant-available nitrogen in soils largely consist of both ammonium (NH_4^+) and nitrate (NO_3^-), which represent the core inorganic forms used by plants. Total potassium and phosphorus were calculated after wet acid digestion, then by measurement using flame photometry and spectrophotometry respectively. The soil available nitrogen was calculated through alkaline hydrolysis method with diffusion (Subbiah and Asija 1956), which captures hydrolyzed organic matter released ammonia. The soil available phosphorus was found using the method by Olsen *et al*. (1954). This procedure comprises of the extraction of sodium bicarbonate appropriate for neutral to alkaline soils. The available potassium was obtained with 1 M neutral ammonium acetate and measured by flame photometry. These analyzes give a thorough examination of the soil fertility status relative to vegetation growth and degradation gradients.

Herb Biomass Estimation

Herb biomass was measured using a destructive direct sampling method. The sample was collected from a uniform-sized quadrats (1 m^2), placed randomly throughout the sampling area to reflect spatial variations in vegetation cover. All above-ground herbaceous material within each quadrant was cut to the soil surface using scissors. To confirm consistency, only non-woody flora was harvested; woody stems and shrub were not included. The herb biomass collected was then kept in paper bags and were taken in time to the laboratory for onward procedure. The collected herb samples were dried in oven at 65 °C for at least 48 h, or until a uniform weight was obtained, and then weighed to the nearest 0.01 g using an analytical balance. The final values were standardized to grams per square meter (g/m^2) based on the area of the quadrant. In addition, we also recorded the altitude, aspect, slope, and geographic coordinates of the sample plots.

Classification of Degradation Intensity

A multifactor valuation was used to find the degradation status of each plot, comprising (i) the percentage of bare ground, (ii) the grazing pressure, and (iii) indicators of human disturbance such as the number of cut stumps per plot. The barren ground, measured as the area of soil without vegetation or litter, was taken as the main indicator of environmental degradation, a generally used indicator of vegetation loss and the risk of erosion (Teague *et al*. 2004). The percentage of bare ground in each plot was measured using the point intercept technique along systematically placed transects. The data were recorded at fixed intervals. The percentage of bare soil was calculated by dividing the number of bare points by the total number of intercept points within the plot. The intensity of grazing was visually assessed through field observation, based on signs of livestock activity such as trampled vegetation, presence of dungs, and visible grazing or browsing of herbaceous and woody plant materials. Human disturbance was assessed by documenting the presence of cut stumps, felled trees, bark removal, branch removal, and informal pathways. Based on the observations of these indicators, each graph was categorized into one of three degradation levels. Low degradation was assigned to mean less than 20% of bare ground, minimal or no grazing signs, and no visible human disturbance. The term moderate degradation was used for 20% to 50% bare ground, moderate grazing signs, occasional cutting or lopping. High degradation meant more than 50% of bare ground, heavy grazing and trampling, and frequent or severe evidence of tree cutting and bark removal. Established ecological thresholds served as the basis for this classification, where increased bare ground and human disturbance are strongly linked with decreased ecosystem outcomes, poor soil stability, and reduced ecosystem function. The grazing pressure was assessed using a semi-quantitative scale based on field observations (*e.g.*, low, moderate, high), which was subsequently converted into ordinal numerical values for statistical analysis. Table 1 summarizes the criteria used for classifying the intensity of degradation is provided.

Table 1. Degradation Levels Based on Vegetation, Grazing, and Human Impact

Degradation	Bare Ground	Grazing Status	Human Impact	Description
Low	< 20%	None or very light	Absent or rare	Closed canopy, negligible soil exposure, and low disturbance. Intact vegetation mostly intact
Moderate	20% – 50%	Moderate (trampling, dung, some browsing)	Occasional stumps or lopping	Partial canopy opening, sporadic understory, regular signs of disturbance.
High	> 50%	Intense (browsed saplings, heavy trampling)	Frequent cutting, bark stripping, trails	Open canopy, sparse vegetation, exposed soil, and severely impacted microhabitats

Statistical Analysis

To investigate the relationships between herbaceous biomass, soil nitrogen, altitude, species richness, habitat type, and levels of degradation, a combination of bivariate analyses, correlation analysis, and structural equation modeling (SEM) was used. These variables were selected based on their well-established ecological significance and their known influence on forest productivity, structure, and ecosystem services. These variables represent significant climatic, edaphic, biotic, and abiotic drivers that are widely recognized in the literature. Climatic variables (*e.g.*, temperature and precipitation) were not explicitly included, as habitat types served as proxy variables; each habitat type represents a distinct temperature and precipitation regime. However, these variables were not included as independent factors in the analysis, which may represent a limitation of the study. Bivariate analyzes were performed to explore individual pairwise associations between the response and predictor variables. The correlation between the independent variables was determined using the correlation matrix. The variance inflation factor (VIF) was used to check for multicollinearity in fitted models. To test direct and indirect hypothesized relationships between biomass and soil nitrogen, altitude, species richness, habitat type, and degradation levels, structural equation modeling (SEM) using the [lavaan package in R] was performed. Through SEM, multiple direct and indirect effects were estimated simultaneously among observed variables. The prior ecological theory and empirical evidence guided the researchers in the specification of the model. The fit of the model was evaluated using standard fit indices, including the chi-square test statistic (χ^2), the mean square error of the root approximation of the root (RMSEA), the comparative fit index (CFI) and the Tucker-Lewis index (TLI). Modified indices and standardized residuals were assessed to examine possible enhancements in model fit.

RESULTS

Bivariate Analysis

Bivariate analysis revealed that areas with higher available nitrogen levels exhibited significantly higher herbaceous biomass, with nitrogen availability accounting for a substantial portion of the variation ($R^2 = 0.68$, $p < 0.001$) (Fig. 2). The level of forest degradation demonstrated a negative and statistically significant relationship with herbaceous biomass ($R^2 = 0.18$, $p < 0.001$), indicating that severely degraded sites supported considerably less biomass than those with minimal disturbance. Although the effect was more modest, the species richness also showed a significant positive association with herbaceous biomass ($R^2 = 0.17$, $p < 0.001$) (Fig. 2).

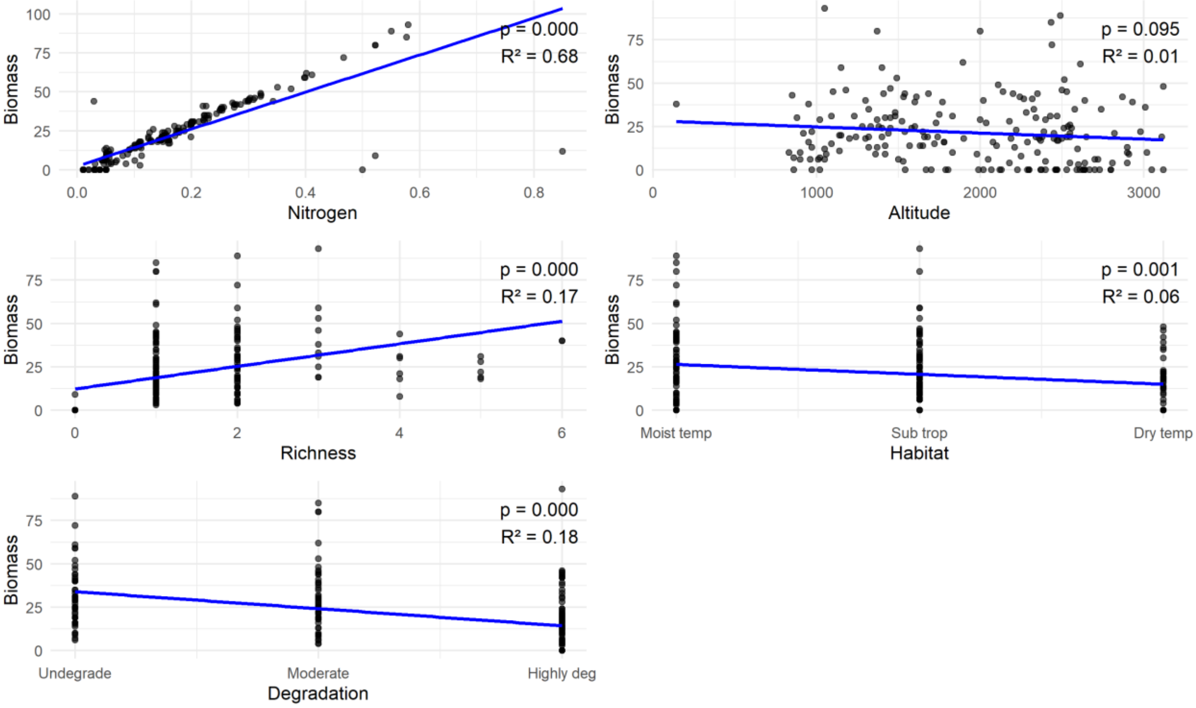

Fig. 2. Bivariate relationships between herbaceous above-ground biomass (AGB) and environmental variables, including available nitrogen, altitude, species richness, and forest degradation levels. Fitted regression lines are shown for statistically significant ($p < 0.05$) and marginally significant relationships ($p < 0.10$).

Elevation did not exhibit a statistically significant relationship with herbaceous biomass ($R^2 = 0.01$, $p < 0.05$), indicating a minimal direct effect of altitude on productivity. In contrast, habitat type significantly influenced biomass ($R^2 = 0.06$, $p < 0.001$), with lower values observed in dry temperate forests compared to moist temperate habitats. Taken together, these findings suggest that nitrogen availability and degradation are the primary determinants of herbaceous biomass, while habitat type and species richness contribute secondary but meaningful effects.

Figure 3 illustrates the relative contributions of different factors to biomass variation, revealing that highly degraded forest areas made the largest negative contribution (28.5%). This dominant share highlights forest degradation as the main constraint on the accumulation of herbaceous biomass in the studied ecosystem. Elevation (19.6%) and nitrogen availability (18. 4%) also played a significant role, likely due to their effects on plant growth conditions and soil fertility. Subtropical climatic conditions contributed moderately (14.8%). In general, the findings highlight the dominant role of forest degradation and abiotic factors in shaping biomass patterns, with climatic conditions and biodiversity playing relatively less important roles.

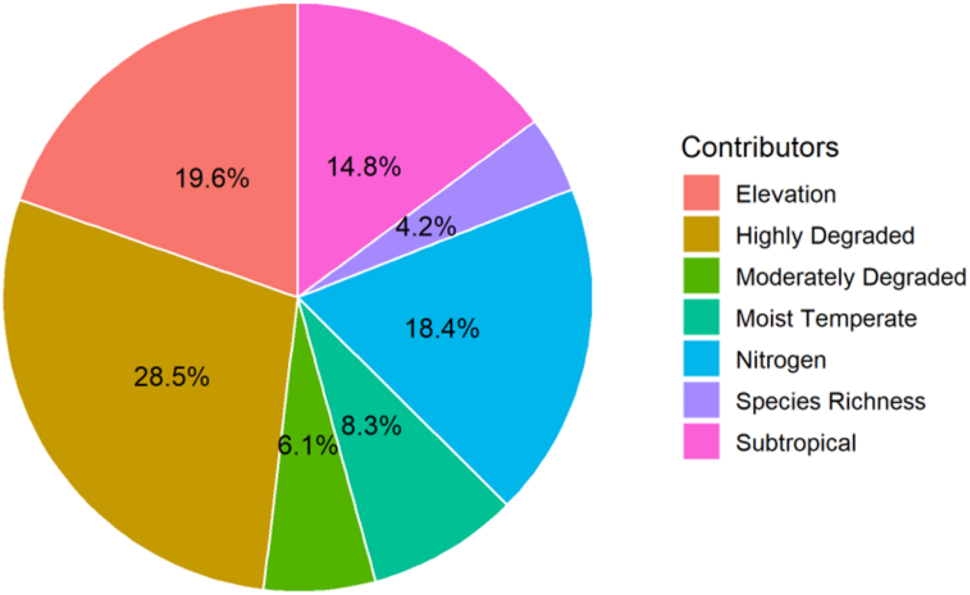

Fig. 3. Relative contribution of environmental and ecological factors to biomass variation. Highly degraded areas exhibited the greatest influence, followed by elevation and nitrogen availability.

Structural Equation Model (SEM)

The final structural equation model fitted the data well ($\chi2(11) = 11.86$, $p = 0.002$; CFI = 0.977; TLI = 0.942; RMSEA = 0.09; SRMR = 0.042). The analysis showed that nitrogen availability was the most significant predictor of biomass accumulation ($\beta = 0.77$, $p < 0.001$), indicating soil fertility's crucial role in productivity. Species richness showed a smaller but still statistically significant positive effect ($\beta = 0.18$, $p < 0.05$) (Figs. 4 and 5). Degradation showed strong negative-mediated effects on biomass through two key pathways: first by significantly decreasing available nitrogen ($\beta = -0.72$, $p < 0.001$), and second by reducing species richness ($\beta = -0.59$, $p < 0.001$). Additional significant pathways showed that moderate degradation negatively affected subtropical habitat ($\beta = -0.82$, $p < 0.001$) and available nitrogen ($\beta = -0.43$, $p < 0.01$). In particular, higher available nitrogen levels were significantly associated with significantly less high degradation ($\beta = -0.47$, $p < 0.001$), suggesting a potential protective effect of nitrogen-rich soils against degradation.

Elevation showed a significant but indirect effect on biomass. Although it had no direct effect, elevation strongly and negatively impacted subtropical habitats ($\beta = -0.82$, $p < 0.001$) while positively influencing moist temperate forests ($\beta = 0.35$, $p < 0.01$). Subsequently, these significant altitudinal patterns in habitat distribution affected degradation levels and available nitrogen availability, creating elevation-dependent productivity gradients.

Several paths showed non-significant relationships ($p > 0.05$), including some connections between elevation and degradation levels (Figs. 4 and 5). The model highlights nitrogen availability as the main driver of productivity, and degradation acts as a major stressor that disrupts both soil fertility and biodiversity. These statistically significant findings emphasize the importance of soil conservation and degradation control, particularly in sensitive subtropical systems, for maintaining ecosystem productivity across elevational gradients.

The model supports the hypotheses of the study: degradation reduces herbaceous biomass indirectly by diminishing soil available nitrogen and richness of species, whereas the effects of elevation on herb biomass is indirect through its influence on habitat structure and degradation intensity. These results underscore the importance of soil fertility and biodiversity in alleviating the adverse effects of forest degradation.

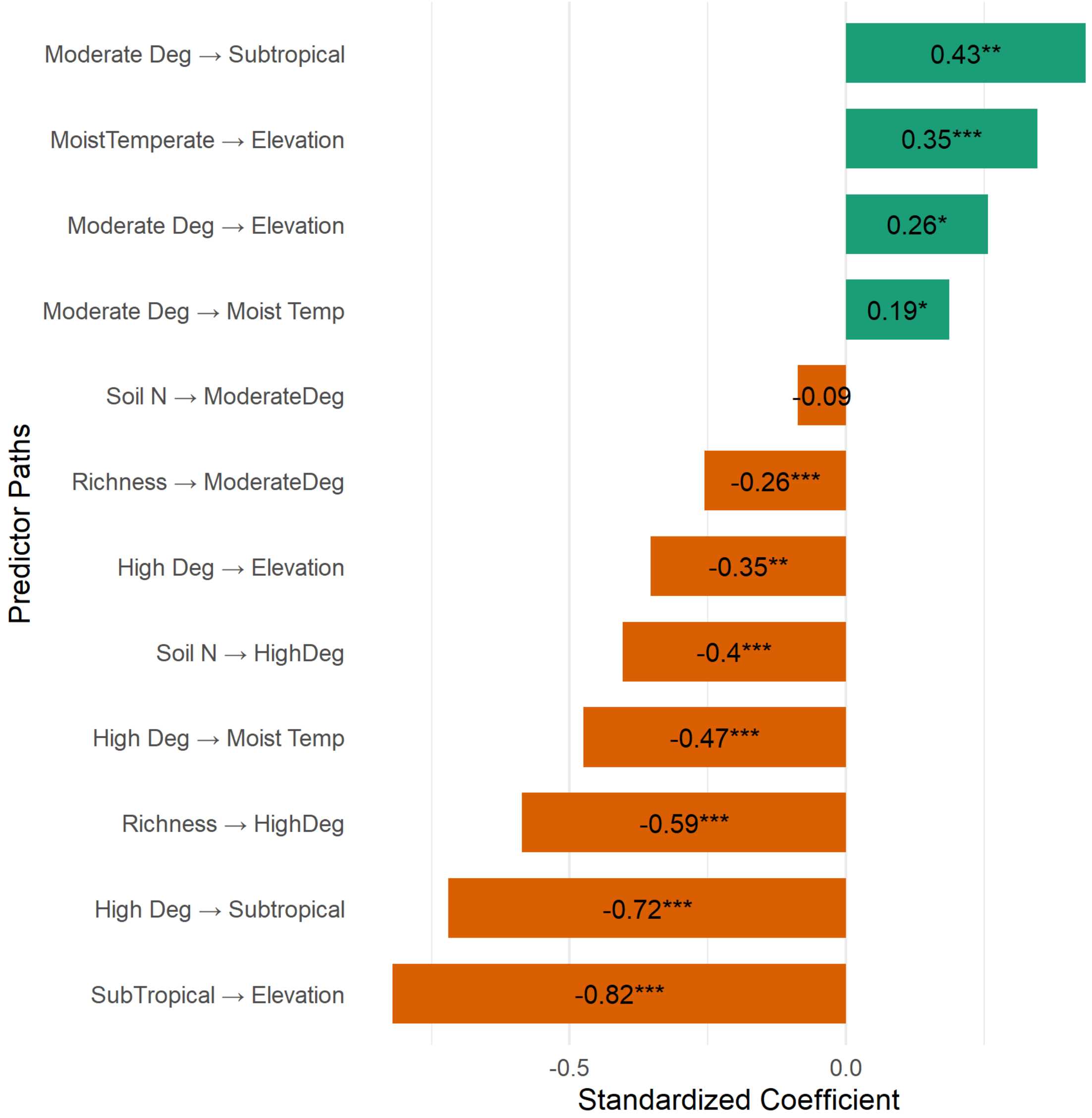

Fig. 4. Standardized effects of variables in the SEM. Green shows positive effects, and orange shows negative effects. The values of the standardized coefficients are represented by the bar length, showing the strength and direction of effect between variables. Strong negative relationship was observed between degradation levels and both nitrogen availability and habitat types and elevation and subtropical habitats.

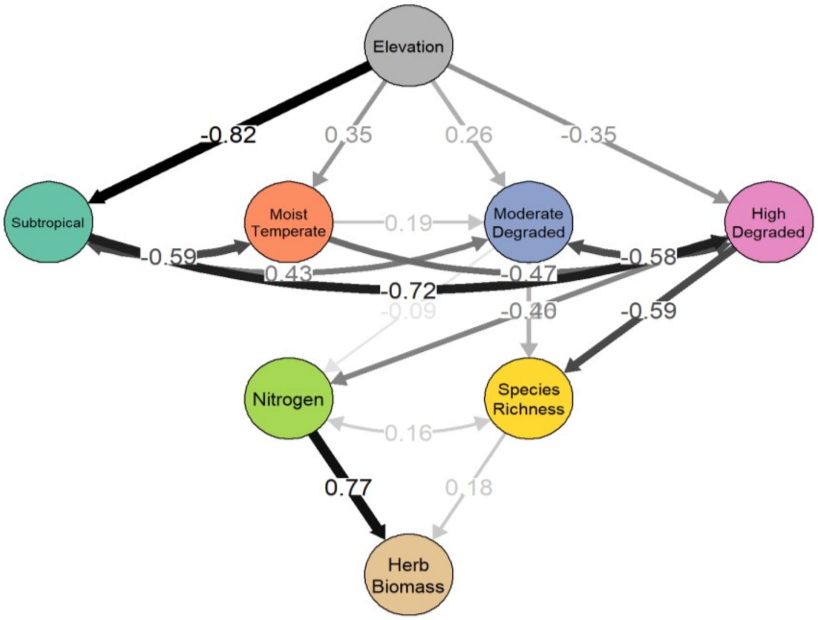

Fig. 5. Structure equation modeling (SEM) showing the direct and indirect effects of soil available nitrogen, species richness, elevation, degradation levels, and habitat type on above-ground biomass (AGB). Significant relationships are indicated through bold lines and lighter lines showed non-significant relation.

DISCUSSION

This study found degradation to be an important variable that indirectly suppressed herb biomass through two statistically significant pathways: first, by reducing soil available nitrogen, and second by decreasing biodiversity. Elevation showed no direct effect on herb biomass. However, elevation had significant influence on ecosystem properties through its robust effects on habitat distribution. Soil available nitrogen and species richness were the direct causes of herb biomass accumulation, which highlights its essential role in supporting herb productivity. These results collectively demonstrate how abiotic factors and anthropogenic disturbance interact through direct and mediated pathways to regulate primary productivity in these ecosystems.

Degradation by Losing Species Richness and Available Nitrogen

This study identified that the intensity of degradation and the availability of nitrogen in the soil had a critical non-linear relationship (Fig. 4). High intensity degradation resulted in a significant decrease (40.4%) in available nitrogen, but moderate degrees of degradation did not have a statistically significant effect on nitrogen levels. According to this threshold effect, ecosystems may initially be able to withstand some amount of nitrogen loss, but crucial nutrient cycling mechanisms are disrupted at a certain point of disturbance. For example, the three main mechanisms that fail simultaneously when degradation reaches a threshold. These are: loss of nitrogen-fixing plant species and their associated microbial communities, physical disruption of the soil structure that increases leaching of soluble nitrogen compounds and decoupling of plant microbe interactions that typically maintain mineralization levels (Schiere and Gregorini 2023). The model identified nitrogen availability as a major determinant of biomass, highlighting it as both a crucial driver of ecosystem productivity and a potential tipping point under degradation stress. The analysis identified a dangerous feedback loop where extreme degradation triggers sudden nitrogen depletion, which could cascade through the system *via*: (1) direct productivity declines, and (2) secondary biodiversity loss. This nonlinear relationship suggests that ecosystems can withstand moderate degradation before reaching a critical threshold where nitrogen cycling collapses dramatically.

Biodiversity responds in a graded manner to the increase in the intensity of degradation. High intensity degradation more than doubles the impact of moderate degradation, reducing species richness by 59% and 26%, respectively (Fig. 4). High intensity degradation reduces biodiversity by destroying microhabitats, disrupting ecological interactions, causing local extinctions, promoting community homogenization, and breaking down reproductive mutualisms (Bascompte and Scheffer 2023). Many species may endure modest disturbance but approach survival thresholds when degradation increases, as seen by the disproportionate loss of biodiversity under high degradation. The management and maintenance of ecosystems are significantly impacted by these non-linear interactions.

According to the nitrogen availability threshold, ecosystems can be spared from reaching crucial junctures where the cycle of nutrients is severely disrupted if degradation processes are addressed early (Sasaki *et al.* 2015). The nitrogen cycle includes a series of biogeochemical processes, starting with biological nitrogen fixation, through which atmospheric nitrogen (N_2) is transformed into plant-available forms such as ammonium (NH_4^+) (Stein and Klotz 2016; Aphirta *et al.* 2026). The next is mineralization and nitrification procedures, which further convert ammonium into nitrate (NO_3^-), a highly movable form quickly observed by plants. However, major nitrogen losses can occur through paths such as denitrification, where nitrate is converted back to gaseous forms (N_2 and N_2O) and released into the atmosphere, as well as through volatilization and leaching. These loss paths are specifically significant in hilly and degraded environments, where soil disruption, decreased vegetation cover, and change microclimatic conditions can increase nitrogen losses (Aphirta *et al.* 2026). In the context of this study, the perceived relationship between available nitrogen and vegetation traits underscore the significance of sustaining nitrogen balance for maintaining ecosystem productivity. Decreased nitrogen availability due to improved losses may limit plant growth and slow ecosystem recovery in degraded habitats. Consequently, understanding both the inputs and losses of nitrogen is crucial for effective forest management and restoration strategies aimed at improving soil fertility and ecosystem resilience.

Biodiversity loss due to high degradation prompts a recommendation that conservation strategies need to emphasis more on controlling the further deterioration of moderate degradation sites because ecological costs increase disproportionately. To overcome these thresholds, conservation efforts in rigorously degraded areas must address both biological components (microbial communities and plant and) and the physical environment (microclimate, soil structure) (Singh Rawat *et al.* 2023). This is because biological responses become significantly harsher after certain disturbance thresholds, the results underscore the significance of closely monitoring degradation levels rather than just its presence. According to Battisti *et al.* (2016), this requires the creation of sensitive indicators that can alert managers when ecosystems are about to reach these crucial transition points. According to the analysis, the most significant and direct predictor of plant biomass is nitrogen availability. These findings are in line with recent global syntheses that demonstrate that nitrogen availability mediates up to 70% of variation in primary productivity across terrestrial ecosystems (Mason *et al.* 2022).

The strength of this relationship suggests that these systems are severely nutrient-limited and that even modest increases in nitrogen availability can have a major impact on biomass output. The strength of this relationship between nitrogen and biomass has significant management implications for ecosystems, suggesting that some nitrogen conservation strategies could be able to maintain or even boost production. Although nitrogen has a greater impact, species richness still has a beneficial biological impact on plant biomass ($\beta = 0.187$). This moderate but significant effect aligns with the theory of ecosystem functioning of biodiversity, which suggests that diverse communities are more productive due to improved resource partitioning (Wang *et al.* 2012), a higher likelihood of including highly productive species (selection effect) (Feng*et al.* 2023), and facilitation among species (Bulleri *et al.* 2016). The results also showed a synergistic effect between nitrogen and species richness. This reciprocal enhancement creates a positive feedback loop in which nitrogen availability and biodiversity mutually reinforce ecosystem productivity. The ecological effects across the spectrum of disturbances are fundamentally different, as seen by the substantial negative correlation ($\beta = 0.586$) between moderate and high deterioration. Although moderate degradation may stimulate compensatory growth in the surviving vegetation, according to the intermediate disturbance hypothesis (Guo *et al.* 2024) high levels of degradation exceed the resilience of the ecosystem, leading to non-linear declines in function (Forzieri *et al.* 2022). These results have significant management implications, suggesting that controlling degradation outside critical thresholds is more effective than trying to restore highly degraded systems. However, forest degradation is fundamentally a multifactorial process. In addition to climate change and anthropogenic pressures, other factors such as biotic disturbances (*e.g.*, pest outbreaks), natural successional dynamics, and disturbance regimes (*e.g.*, fire) may also play significant roles.

Elevation Mediate Degradation and Habitat, Indirectly Affecting Herbaceous Biomass

The model demonstrates the dual role of elevation as a landscape filter, indirectly regulating herbaceous biomass through two interdependent pathways: (1) by changing habitat suitability and (2) by mediating degradation impacts. The results support the environmental filtering theory (Kraft *et al.* 2015; Deng *et al.* 2023; Fatunsin *et al.* 2024), in which elevation-mediated abiotic conditions limit the resilience of the ecosystem to anthropogenic stressors. The results revealed a distinct vegetation transition with opposite effects on the two forest types throughout the elevational gradient. Elevation reflects basic changes in environmental conditions with increasing altitude, having a considerable negative effect on subtropical forests and a moderately beneficial effect on moist temperate habitats. The spread of subtropical species is restricted by thermal thresholds, which are created by temperature drops of about 0.6 °C for every 100 m elevation increase (Körner and Hiltbrunner 2023). Given that even slight elevational changes have disproportionate effects on ecosystem composition, the greater detrimental effect on subtropical forests implies that these species function closer to their physiological limitations (Swenson and Rubio 2025). As temperatures rise, elevation-driven vegetation zones are likely to shift upward, potentially subjecting subtropical forests to increased degradation in their current ranges and exposing expanding temperate forests to new vulnerabilities (Kidane 2022). Therefore, conservation strategies must take into account both the dynamic nature of these vegetation transitions under global change and the current elevation-dependent degradation threats. Both types of forest are adversely affected by substantial degradation; however, according to the data, the effects are noticeably different.

Unlike moist temperate habitats, subtropical ecosystems have a stronger negative correlation, which shows that the resilience of the ecosystem is fundamentally different. Several biome-specific vulnerabilities in subtropical forests, such as their generally shallower root systems (Valverde-Barrantes *et al.* 2021), faster nutrient cycling rates (Yao *et al.* 2023), and increased reliance on delicate mutualistic relationships (Ellers *et al.* 2012), are probably the cause of this discrepancy. It is interesting to note that different types of forest exhibit different degradation patterns. Subtropical ecosystems have a stronger positive connection with degradation than moist temperate habitats. This probably reflects a number of unique vulnerabilities in each biome: subtropical forests tend to have thinner organic soil layers that are more vulnerable to erosion (Elrys *et al.* 2024), contain species that are less capable of coping with stress from compound disturbances (Philippot *et al.* 2021), and generally experience higher anthropogenic pressure at lower elevations (Elsen *et al.* 2020). The natural higher resistance to disturbance in temperate settings, such as more resistant litter that prevents nutrient loss and higher root biomass for soil stabilization (Bardgett *et al.* 2014), may be the cause of the correlation of softer degradation. Temperate forests may be more resistant to degradation pressures due to their evolutionary adaptation to disturbance, as evidenced by characteristics such as thicker bark (Schebeck *et al.* 2024), cold hardy tissues, and more extensive mycorrhizal networks (Allsup *et al.* 2023). Research studies also indicated that, compared to temperate systems, tropical and subtropical forests often suffer a 30% to 50% increase in biodiversity loss due to comparable disturbance intensities (Newbold *et al.* 2015). With significant consequences for focused conservation efforts along elevation gradients, the findings highlight how the natural biological distinctions among forest types regulate their reactions to human impacts.

A limitation of this study is the absence of direct measures of key climate drivers such as temperature and precipitation, which are well known to influence the structure of the grassland community and herbaceous biomass. However, the three eco-regions examined (dry, moist, and subtropical forests) inherently represent distinct climatic regimes, particularly with respect to rainfall and temperature, and thus provide an indirect gradient of these variables. As a result, while the observed differences in herbaceous biomass across ecoregions likely reflect both soil properties and broader climatic factors, future studies incorporating direct climatic measurements would strengthen the ability to disentangle their relative contributions.

RECOMMENDATIONS

This study has shown how the intensity of degradation, soil nitrogen, altitude, and species richness interact intricately to shape the structure and function of the ecosystem. The interrelations among these variables exhibit how biotic communities, disturbance regimes, and abiotic restrictions work together to shape ecosystem productivity. These results highlight the need for cohesive conservation approaches that concurrently address biodiversity protection, controlling degradation, and nutrient retention in soil. Maintaining ecosystem integrity below thresholds that trigger irretrievable state shifts is critical. This research offers a framework for predicting vegetation responses to environmental change and for designing targeted management approaches across elevational gradients. Future research should prioritize the identification of early warning indicators of ecological tipping points and the development of interventions that improve the resilience of the ecosystem under global change.

IMPLICATIONS AND FUTURE RESEARCH

The outcomes of this study provide key implications for the sustainable provision of biodiversity and ecosystem services in the face of climate change in mountain ecosystems. The observed associations between soil nitrogen availability and degradation levels underscore the need to prioritize forest landscape preservation by controlling degradation and restoring forest areas that have already degraded. This will increase the overall production of the forest ecosystem. Similarly, the conservation of soil fertility and biodiversity is important for mitigating environmental changes and strengthening ecological resilience under a changing climate. Furthermore, the findings also highlight the implication of using cohesive management strategies to capture the combined effects of climatic, edaphic, topographic, and human factors.

Future research should focus on combining high-resolution climatic data and exploring the relations between vegetative characteristics (tree and herbaceous strata), edaphic factors and microclimatic conditions to better understand the dynamics of forest biomass. Similarly, future research should consider quantifying nitrogen stored within plant biomass in addition to available soil nitrogen to provide a more complete understanding of the nitrogen dynamics of ecosystems. Furthermore, long-term monitoring and inclusion of factors such as pest outbreaks, fire regimes and grazing pressure would provide a more complete Knowledge of forest ecosystem responses to climate change.

CONCLUSIONS

1. As compared to temperate forests, subtropical forests are more sensitive to elevational changes and degradation impacts.
2. Nutrient cycling and species richness respond non-linearly to habitat degradation, with threshold effects that cause herb biomass to radically decline.
3. Nitrogen availability in soil emerges as the principal determinant of herb biomass productivity, while species richness maintains ancillary but ecologically significant enhancement effects.

ACKNOWLEDGMENTS

The authors are thankful to Princess Nourah bint Abdulrahman University Researchers Supporting Project number (PNURSP2026R227), Princess Nourah bint Abdulrahman University, Riyadh, Saudi Arabia.

Competing Interests

The authors declare that there are no conflicts of interest.

Availability of Data and Material

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

REFERENCES CITED

Allsup, C., Marquardt, S., and Lankau, R. (2023). "Mycorrhizal driven positive feedbacks and forest resilience to reduced rainfall," *Fungal Ecology* 65, article 101280. https://doi.org/10.1016/j.funeco.2023.101280

Aphirta, S., Rinanti, A., Muslih, E., Fachrul, M. F., Hendrawan, D. I., Marendra, S. M. P., Minarti, A., Sunaryo, T., and Pratiwi, R. (2026). "Nitrogen cycling in the ecosystem and its role in air, water, and soil pollution," in: *Nonpoint Source Nitrogen Pollution*, Elsevier, pp. 177-209.

Bardgett, R. D., Mommer, L., and De Vries, F. T. (2014). "Going underground: Root traits as drivers of ecosystem processes," *Trends in Ecology and Evolution* 29, 692-699. https://doi.org/10.1016/j.tree.2014.10.006

Bascompte, J., and Scheffer, M. (2023). "The resilience of plant–pollinator networks," *Annual Review of Entomology* 68, 363-380. https://doi.org/10.1146/annurev-ento-120120-091608

Battisti, C., Poeta, G., and Fanelli, G. (2016). *An Introduction to Disturbance Ecology*, Springer, Cham, pp. 13-29. https://doi.org/10.1007/978-3-319-32483-0_2

Bulleri, F., Bruno, J. F., Silliman, B. R., and Stachowicz, J. J. (2016). "Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning," *Functional Ecology* 30, 70-78. https://doi.org/10.1111/1365-2435.12496

Champion, S. H., Seth, S. K., and Khattak, G. M. (1965). *Forest Types of Pakistan*, Pakistan Forest Institute, Peshawar.

Dani, R. S., Divakar, P. K., and Baniya, C. B. (2023). "Diversity and composition of plants species along elevational gradient: Research trends," *Biodiversity and Conservation* 32, 2961-2980. https://doi.org/10.1007/s10531-023-02643-y

Deng, J., Fang, S., Fang, X., Jin, Y., Kuang, Y., Lin, F., Liu, J., Ma, J., Nie, Y., Ouyang, S., *et al*. (2023). "Forest understory vegetation study: Current status and future trends," *Forestry Research* 3, 6. https://doi.org/10.48130/forres-2023-0006

Ellers, J., Toby Kiers, E., Currie, C. R., McDonald, B. R., and Visser, B. (2012). "Ecological interactions drive evolutionary loss of traits," *Ecology Letters* 15, 1071-1082. https://doi.org/10.1111/j.1461-0248.2012.01830.x

Elrys, A. S., Desoky, E. S. M., Zhu, Q., Liu, L., Wang, Y. X., Wang, C., Tang, S., Wang, Y., Meng, L., Zhang, J., *et al*. (2024). "Climate controls on nitrate dynamics and gross nitrogen cycling response to nitrogen deposition in global forest soils," *Science of The Total Environment* 920, article 171006. https://doi.org/10.1016/j.scitotenv.2024.171006

Elrys, A. S., Zhu, Q., Jiang, C., Liu, J., Sobhy, H. H., Shen, Q., Uwiragiye, Y., Wu, Y., El-Tarabily, K. A., Meng, L., *et al*. (2023). "Global soil nitrogen cycle pattern and nitrogen enrichment effects: Tropical versus subtropical forests," *Global Change Biology* 29, 1905-1921. https://doi.org/10.1111/gcb.16548

Elsen, P. R., Monahan, W. B., and Merenlender, A. M. (2020). "Topography and human pressure in mountain ranges alter expected species responses to climate change," *Nature Communications* 11, article 1974.https://doi.org/10.1038/s41467-020-15732-9

Fatunsin, O. E., Staudhammer, C., Hart, J., and Ferguson, P. (2024). "Disentangling the contributions of ecological conditions to biomass in longleaf pine forests," *Forest Ecology and Management* 572, article 122297. https://doi.org/10.1016/j.foreco.2024.122297

Feng, H., Guo, J., Peng, C., Kneeshaw, D., Roberge, G., Pan, C., Ma, X., Zhou, D., and Wang, W. (2023). "Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: A global meta-analysis," *Global Change Biology* 29, 3970-3989. https://doi.org/10.1111/gcb.16711

Forzieri, G., Dakos, V., McDowell, N. G., Ramdane, A., and Cescatti, A. (2022). "Emerging signals of declining forest resilience under climate change," *Nature* 608, 534-539. https://doi.org/10.1038/s41586-022-05027-0

Geng, Q., Arif, M., Yin, F., Chen, Y., Gao, J., Liu, J., Liu, X., He, X., Wu, Y., Zheng, J., *et al*. (2024). "Characteristics of forest understory herbaceous vegetation and its influencing factors in biodiversity hotspots in China," *Ecological Indicators* 167, article 112634. https://doi.org/10.1016/j.ecolind.2024.112634

Guo, M., Guo, T., Zhou, J., Liang, J., Yang, G., and Zhang, Y. (2024). "Restored legume acts as a 'nurse' to facilitate plant compensatory growth and biomass production in mown grasslands," *Agronomy for Sustainable Development* 44, 1-13. https://doi.org/10.1007/s13593-024-00981-9

Hamid, M., Khuroo, A. A., Malik, A. H., Ahmad, R., and Singh, C. P. (2021). "Elevation and aspect determine the differences in soil properties and plant species diversity on Himalayan mountain summits," *Ecological Research* 36, 340-352. https://doi.org/10.1111/1440-1703.12217

Han, W., Chen, L., Su, X., Liu, D., Jin, T., Shi, S., Li, T., and Liu, G. (2022). "Effects of soil physicochemical properties on plant species diversity along an elevation gradient over alpine grassland on the Qinghai-Tibetan Plateau, China," *Frontiers in Plant Science* 13, article 822268. https://doi.org/10.3389/fpls.2022.822268

He, Y., Junker, R. R., Xiao, J., Lasky, J. R., Cao, M., Asefa, M., Swenson, N. G., Xu, G., Yang, J., and Sedio, B. E. (2025). "Genetic and environmental drivers of intraspecific variation in foliar metabolites in a tropical tree community," *New Phytologist* 246, 2551-2564. https://doi.org/10.1111/nph.20049

Khan, S., ul Hassan, M., Khan, A., and Qasim, S. (2014). "Climate change impacts and adaptation to flow of Swat River, glaciers and permafrost in Hindukush ranges, Swat district, Pakistan (2004-2013)," *Journal of Science and Technology* 38, 19-36.

Kidane, Y. (2022). *Vegetation Diversity and Distribution along the Bale Mountains Afroalpine Hotspot of Biodiversity in the Face of a Fast-Changing World*, Ph.D. thesis, Addis Ababa University, Ethiopia.

Körner, C., and Hiltbrunner, E. (2023). "The 0.6°C rule in mountain biogeography: Thermal constraints on subtropical species uplift," *Frontiers in Ecology and Evolution* 11, article 1125632. https://doi.org/10.3389/fevo.2023.1125632

Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., and Levine, J. M. (2015). "Community assembly, coexistence and the environmental filtering metaphor," *Functional Ecology* 29, 592-599. https://doi.org/10.1111/1365-2435.12345

Li, D., Wu, C., and Wu, J. (2024). "Soil fungal community has higher network stability than bacterial community in response to warming and nitrogen addition in a subtropical primary forest," *Applied and Environmental Microbiology* 90, article e00001-24. https://doi.org/10.1128/aem.00001-24

Li, Z., Liang, M., Li, Z., Mariotte, P., Tong, X., Zhang, J., Dong, L., Zheng, Y., Ma, W., Zhao, L., *et al*. (2021). "Plant functional groups mediate effects of climate and soil factors on species richness and community biomass in grasslands of Mongolian Plateau," *Journal of Plant Ecology* 14, 679-691. https://doi.org/10.1093/jpe/rtab021

Lu, X. (2024). "Degraded grassland vegetation and soil characteristics: Challenges, opportunities, and sustainable development," *Advances in Resources Research* 4, 205-220. https://doi.org/10.50908/arr.4.2_205

Malik, I. H., and Ford, J. D. (2025). "Monitoring climate change vulnerability in the Himalayas," *Ambio* 54, 1-19. https://doi.org/10.1007/s13280-024-02066-9

Masese, F. O., Fuss, T., Bistarelli, L. T., Buchen-Tschiskale, C., and Singer, G. (2022). "Large herbivorous wildlife and livestock differentially influence the relative importance of different sources of energy for riverine food webs," *Science of the Total Environment* 828, article 154452. https://doi.org/10.1016/j.scitotenv.2022.154452

Mason, R. E., Craine, J. M., Lany, N. K., Jonard, M., Ollinger, S. V., Groffman, P. M., Fulweiler, R. W., Angerer, J., Read, Q. D., Reich, P. B., *et al*. (2022). "Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems," *Science* 376, article eabh3767. https://doi.org/10.1126/science.abh3767

McNichol, B. H., Wang, R., Hefner, A., Helzer, C., McMahon, S. M., and Russo, S. E. (2024). "Topography-driven microclimate gradients shape forest structure, diversity, and composition in a temperate refugial forest. Plant-Environment Interactions," 5(3), article e10153. https://doi.org/10.1002/pei3.10153.

Munkhzul, O., Oyundelger, K., Narantuya, N., Tuvshintogtokh, I., Oyuntsetseg, B., Wesche, K., and Jäschke, Y. (2021). "Grazing effects on Mongolian steppe vegetation—A systematic review of local literature," *Frontiers in Ecology and Evolution* 9, article 703220. https://doi.org/10.3389/fevo.2021.703220

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., and Purvis, A. (2015). "Global effects of land use on local terrestrial biodiversity," *Nature* 520, 45-50. https://doi.org/10.1038/nature14324

Ni, M., and Vellend, M. (2024). "Soil properties constrain forest understory plant distributions along an elevation gradient," *Philosophical Transactions of the Royal Society B* 379, article 20230373. https://doi.org/10.1098/rstb.2023.0373

Olsen, S. R., Cole, C. V., Watanabe, F. S., and Dean, L. A. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*, Circular 939, USDA, Washington, D.C.

Pei, X., Zhao, X., Liu, J., Liu, W., Zhang, H., and Jiao, J. (2024). "Habitat degradation changes and disturbance factors in the Tibetan Plateau in the 21st century," *Environmental Research* 260, article 119616. DOI: 10.1016/j.envres.2024.119616

Philippot, L., Griffiths, B. S., and Langenheder, S. (2021). "Microbial community resilience across ecosystems and multiple disturbances," *Microbiology and Molecular Biology Reviews* 85, 10-1128. https://doi.org/10.1128/mmbr.00026-20

Pu, G., Han, L., Chen, L., Wan, D., and Teng, H. (2025). "Elevational dynamics of vegetation changes in response to climate change on the Tibetan Plateau," *Scientific Reports* 15, article 9813. https://doi.org/10.1038/s41598-025-94896-0

Qian, J., Ye, M., Zhang, X., Li, M., Chen, W., Zeng, G., and Che, J., Lv, Y. (2024). "Characteristics of grassland species diversity and soil physicochemical properties with elevation gradient in Burzin forest area," *Agriculture* 14, article 1176. https://doi.org/10.3390/agriculture14071176

Rawat, G., and Negi, H. (2021). "Altitudinal gradient and Himalayan vegetation in changing climate: A short overview," in: *Climate Change and Himalayan*

Ecosystems, E. Sharma and N. Chettri (eds.), Elsevier, Amsterdam, pp. 345-360. https://doi.org/10.1016/B978-0-443-23665-5.00023-5

Ryś, K., Chmura, D., Dyczko, A., and Woźniak, G. (2024). "The biomass amount of spontaneous vegetation concerning the abiotic habitat conditions in coal mine heaps as novel ecosystems," *Journal of Ecological Engineering* 25, 79-100. https://doi.org/10.12911/22998993/185586

Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M., and Mori, A. S. (2015). "Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances," *Ecological Indicators* 57, 395-408. https://doi.org/10.1016/j.ecolind.2015.05.019

Schebeck, M., Lehmann, P., Laparie, M., Bentz, B. J., Ragland, G. J., Battisti, A., and Hahn, D. A. (2024). "Seasonality of forest insects: Why diapause matters," *Trends in Ecology & Evolution* 39, 757-770. https://doi.org/10.1016/j.tree.2024.04.010

Schiere, J. B., and Gregorini, P. (2023). "Complexity, crash and collapse of chaos: Clues for designing sustainable systems, with focus on grassland-based systems," *Sustainability* 15, article 4356. https://doi.org/10.3390/su15054356

Seastedt, T. R., and Oldfather, M. F. (2021). "Climate change, ecosystem processes and biological diversity responses in high elevation communities," *Climate* 9, article 87. https://doi.org/10.3390/cli9050087

Shaheen, H., Attique, A., Riaz, M. T., Manzoor, M., Khan, R. W. A., and Riaz, M. T. (2024). "From biodiversity hotspot to conservation hotspot: Assessing distribution, population structure, associated flora and habitat geography of threatened Himalayan yew in temperate forest ecosystems of Kashmir," *Biodiversity and Conservation* 33, 553-577. https://doi.org/10.1007/s10531-023-02758-w

Sharma, S., Singh, P., Chauhan, S., and Choudhary, O. (2022). "Landscape position and slope aspects impacts on soil organic carbon pool and biological indicators of a fragile ecosystem in high-altitude cold arid region," *Journal of Soil Science and Plant Nutrition* 22, 2612-2632. https://doi.org/10.1007/s42729-022-00831-x

She, W., Bai, Y., Zhang, Y., Qin, S., Feng, W., Lai, Z., Qiao, Y., Liu, L., Zhang, W., and Miao, C. (2021). "Nitrogen-enhanced herbaceous competition threatens woody species persistence in a desert ecosystem," *Plant and Soil* 460, 333-345. https://doi.org/10.1007/s11104-020-04810-y

Singh, M., Bijlwan, A., Shukla, G., and Chakravarty, S. (2025). "Forest degradation and ecosystem functioning," in: *Forest Degradation and Management: An Indian Perspective*, S. Chakravarty (ed.), Springer, pp. 109-124.

Singh Rawat, V., Kaur, J., Bhagwat, S., Arora Pandit, M., and Dogra Rawat, C. (2023). "Deploying microbes as drivers and indicators in ecological restoration," *Restoration Ecology* 31, article e13688. https://doi.org/10.1111/rec.13688

Stein, L. Y., and Klotz, M. G. (2016). "The nitrogen cycle," *Current Biology* 26(3), R94-R98. https://doi.org/10.1016/j.cub.2015.12.021

Subbiah, B. V., and Asija, G. L. (1956). "A rapid procedure for the estimation of available nitrogen in soils," *Current Science* 25, 259-260.

Sundqvist, M. K., Sanders, N. J., and Wardle, D. A. (2013). "Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change," *Annual Review of Ecology, Evolution, and Systematics* 44, 261-280. https://doi.org/10.1146/annurev-ecolsys-110512-135750

Swenson, N. G., and Rubio, V. E. (2025). "The functional underpinnings of tropical forest dynamics—functional traits, groups, and unmeasured diversity," *Biotropica* 57, article e13360. https://doi.org/10.1111/btp.13360

Teague, W., Dowhower, S., and Waggoner, J. (2004). “Land degradation and variation in vegetation cover and bare ground across rangeland ecosystems,” *Journal of Arid Environments* 58, 477-486. https://doi.org/10.1016/S0140-1963(03)00122-8

Valverde-Barrantes, O. J., Authier, L., Schimann, H., and Baraloto, C. (2021). “Root anatomy helps to reconcile observed root trait syndromes in tropical tree species,” *American Journal of Botany* 108, 744-755. https://doi.org/10.1002/ajb2.1659

Walkley, A., and Black, I. A. (1934). “An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method,” *Soil Science* 37, 29-38.

Wang, C., Hou, Y., Hu, Y., Zheng, R., and Li, X. (2023). “Plant diversity increases above- and below-ground biomass by regulating multidimensional functional trait characteristics,” *Annals of Botany* 131, 1001-1010. https://doi.org/10.1093/aob/mcad058

Wang, M., Shi, S., Lin, F., Hao, Z., Jiang, P., and Dai, G. (2012). “Effects of soil water and nitrogen on growth and photosynthetic response of Manchurian ash (*Fraxinus mandshurica*) seedlings in northeastern China,” *PLoS ONE* 7, article e30754. https://doi.org/10.1371/journal.pone.0030754

Wester, P., Mishra, A., Mukherji, A., and Shrestha, A. B. (2019). *The Hindu Kush Himalaya Assessment: Mountains, Climate Change, Sustainability and People*, Springer Nature, Cham, Switzerland. https://doi.org/10.1007/978-3-319-92288-1

Xu, J., Badola, R., Chettri, N., Chaudhary, R. P., Zomer, R., Pokhrel, B., Hussain, S. A., Pradhan, S., and Pradhan, R. (2019). “Sustaining biodiversity and ecosystem services in the Hindu Kush Himalaya,” in: *The Hindu Kush Himalaya Assessment: Mountains, Climate Change, Sustainability and People*, P. Wester, A. Mishra, A. Mukherji, and A. B. Shrestha (eds.), Springer Nature, Cham, pp. 127-165. https://doi.org/10.1007/978-3-319-92288-1_5

Yao, T., Bolch, T., Chen, D., Gao, J., Immerzeel, W., Piao, S., Su, F., Thompson, L., Wada, Y., Wang, L., *et al.* (2022). “The Imbalance of Asian water tower,” *Nature Reviews Earth and Environment* 3, 618-632.

Zeb, A., Hamann, A., Armstrong, G. W., and Acuna-Castellanos, D. (2019). “Identifying local actors of deforestation and forest degradation in the Kalasha valleys of Pakistan,” *Forest Policy and Economics* 104, 56-64. https://doi.org/10.1016/j.forpol.2019.04.005

Zhu, Y., Liu, C., Peng, C., Zhou, X., Xie, B., Li, T., Li, P., Zou, Z., Tang, J., and Liu, Z. (2024). “Applications of structural equation modeling in plant functional trait research,” *Environmental Reviews* 32, 525-538. https://doi.org/10.1139/er-2023-0128

Article submitted: October 22, 2025; Peer review completed: March 21, 2026; Revised version received: April 7, 2026; Accepted: April 8, 2026; Published: April 20, 2026.
DOI: 10.15376/biores.21.2.4899-4918