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RESEARCH

Stand structural differences along a degradation gradient in the National forest inventory of Georgia

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Abstract
Forest degradation assessments grounded in measurable structural indicators provide a more reproducible basis for management decisions than qualitative field classifications alone, particularly in ecologically diverse forest systems. Based on data from the first National Forest Inventory of Georgia (2019–2021), we clustered samples into eight forest formations using a phylogenetically informed approach and compared stand structural indicators across field-assigned degradation severity classes within each formation. Indicators quantifying stand stocking, structure, and productivity were compared across severity classes using non-parametric tests with post-hoc pairwise comparisons. Across formations, significant structural differences relative to undisturbed conditions were detected in 52%, 69%, and 83% of tested indicator-formation combinations at low, moderate, and high severity, respectively. Field-assigned severity classes were associated with consistent structural differences, but the direction and magnitude of those differences varied substantially among formations and were often non-monotonic across severity levels. Stocking indicators showed the most consistent and significant differences across formations and severity classes. Productivity indicators were more formation-specific, with volume increment declining across most formations while diameter increment increased, particularly at lower severity levels, reflecting reduced competition following partial canopy opening. Regeneration indicators showed the highest formation-dependence, with significant differences confined to two formations, reflecting the high within-formation variability of regeneration density. These findings support formation-specific interpretation of degradation severity classes and demonstrate that quantitative inventory analysis captures structural dynamics beyond the resolution of field-based severity assessment. Grounding severity assessment in ecologically coherent forest units provides a consistent basis for condition monitoring and ecologically informed management decisions.

Keywords Forest degradation · Forest community classification · Stand structure · National forest inventory · Georgian forests

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Introduction

Situated between the Greater and Lesser Caucasus, with the Black Sea to the west and the semi-arid Transcaucasian steppes to the east, the forests of Georgia (Sakartvelo in Georgian) span a wide range of climatic zones despite the nation's relatively small size (60,700 km^2). The predominantly mountainous country is recognized for its ecological diversity and forms part of the globally significant Caucasus Biodiversity Hotspot (Myers et al. 2000; Mittermeier et al. 2011). According to the most recent assessments, forests cover approximately 2.3 Mio. ha or around 43% of the country's land area (Griesbach 2018; MEPA 2023). The combination of topographic and climatic complexity in Georgia has shaped diverse forest ecosystems, characterized by distinct ecological conditions and high shares of regional endemism (Akhalkatsi et al. 2014; Mumladze et al. 2019; Nakhutsrishvili et al., 2023). Georgia's forests are distinguished by the presence of unique and uncommon woody species admixtures (Nakhutsrishvili et al., 2023) and were long protected for their ecological functions, e.g. slope protection, with timber imports meeting the country's demand for wood during the Soviet era (UNECE, 2019). Since Georgia's independence in 1991, forest exploitation has remained small-scale, driven by subsistence needs and continued reliance on forests for grazing and firewood (Patarkalashvili 2016; Buchner et al. 2020; Chalatashvili et al. 2024; Stritih et al. 2024). Until the early 1990s, forest science in the country was dominated by botanical and biogeographical perspectives, e.g. the forest vegetation classification by Dolukhanov (2010). This foundational classification has been supplemented by more recent regional studies (Bohn et al. 2007; Nakhutsrishvili 2013) and is progressively being aligned with European vegetation classification standards (Barbati et al. 2014; Mucina et al. 2016; Chytrý et al. 2020; Knollová et al. 2024; Preislerová et al. 2024).

While recent advances in forest research, management reforms, and international support have strengthened the implementation of sustainable forestry in Georgia, substantial pressures on forest ecosystems continue (Lomsadze et al. 2019; Chalatashvili et al. 2024). Accordingly, forest degradation was assessed based on observable structural alterations and classified into hierarchical categories with three severity levels during the first National Forest Inventory of Georgia (GNFI, 2019–2021). National Forest Inventories provide systematic, large-scale forest data at national and regional scales, based on regular sampling grids (Tomppo et al. 2010; Vidal et al. 2016). Reported results indicate that 35.4% of forests in Georgia show signs of various forms of degradations (MEPA 2023). These impacts are associated with forest use, logging, and livestock grazing, as well as high fuelwood demand and weakened forest management bodies (Machavariani 2010; Gutman & Radeloff, 2017; Patarkalashvili 2017; Beridze and Dering 2021). Although remote-sensing based approaches have revealed relatively low rates of forest cover loss and large scale canopy disturbance in Georgia (Buchner et al. 2020; Chen et al. 2021), these estimates reflect canopy cover changes rather than necessarily deforestation in the FAO sense, defined as permanent conversion of forest to other land uses, and may therefore underestimate structurally degraded but still forested stands. Field based studies indicate more localized anthropogenic impacts, especially near settlements, which affect forest structure and composition without necessarily causing detectable forest cover loss (Cortner et al. 2024; Stritih et al. 2024). As systematic forest inventory data has only recently become available, quantitative analyses of stand structural properties have, to our knowledge, not yet been carried out in the country (Machavariani 2010). Hence, quantitative assessments of stand structure are especially valuable in countries such as Georgia, where degradation severity and structural impacts are typically small-scale and spatially heterogeneous, making them difficult to detect using remote sensing alone (Olofsson et al. 2010; Mikeladze et al. 2020; Stritih et al. 2024). The availability of such data creates an opportunity to develop ecologically grounded, quantitative frameworks for assessing the structural impacts of degradation and disturbance and for informing management decisions.

Forest disturbance and degradation are closely related yet conceptually distinct processes in forest ecology and management (Thompson et al. 2013; Vásquez-Grandón et al. 2018). Disturbance is broadly defined as a discrete, often stochastic event that alters structure, composition, or function, but may be followed by recovery through natural succession or management intervention (Pickett and White 1985; Mori 2011; Turner 2010; Seidl et al. 2017). In contrast, degradation represents a more persistent state of ecological decline in forest condition (Thompson et al. 2009; Ghazoul et al. 2015). Numerous definitions exist, reflecting different disciplinary or policy perspectives (Lund 2009). For example, the IPCC (2003) defines degradation primarily as a long-term human-induced reduction in forest carbon stocks that does not qualify as deforestation, reflecting a carbon-centered perspective. However, broader frameworks such as that adopted by Forest Europe define degradation as a reduction in biological or economic productivity, ecological complexity, or capacity to provide ecosystem services (Forest Europe, 2020). These broader definitions emphasize structural, functional, and compositional changes, including reductions in biomass productivity, biodiversity support, and protective functions (Sasaki and Putz 2009; Simula 2009; Ghazoul et al. 2015; Gunn et al. 2019). Distinguishing disturbance from degradation remains challenging due

to variability in severity, frequency, and spatial scale, and locally adapted quantitative thresholds remain scarce, especially in complex, species-rich systems (Senf et al. 2017; Vásquez-Grandón et al. 2018; Sturtevant and Fortin 2021). While the GNFI provides sample-based, country-wide data about diverse forest types and distinguishes between different causes of degradation, it does not explicitly differentiate between disturbance-related alterations and long-term functional degradation. Field assessments classify observable stand-level alterations into descriptive degradation categories based on inferred cause (e.g., pest outbreaks, stand damage) and severity.

In this study, we use a quantitative approach to assess whether field-assigned GNFI degradation severity classes are reflected in systematic differences in stand structural indicators, providing the first sample-based structural characterization of forest condition along a degradation gradient in Georgia. To account for the compositional heterogeneity of Georgian forests, samples were clustered into compositionally distinct forest groups, hereafter referred to as forest formations, which serve as the primary unit for all subsequent structural comparisons. We analyze differences in indicators related to stocking (basal area, canopy cover, stem number), structural heterogeneity (vertical distribution, quadratic mean diameter, stump basal area proportions), and growth (diameter and stand volume increment, regeneration density) across severity classes and forest formations. The following research questions guide the analysis: (i) Do field-assigned degradation severity classes correspond to quantitative differences in stand structural properties? (ii) Are structural differences among severity classes consistent across forest formations? (iii) Do structural indicators derived from NFI data provide a reproducible and interpretable basis for characterizing forest condition across severity classes?

Materials and methods

Study area

Georgia is located between 41°07′–43°35′N and 40°04′–46°44′E, bordered by the Russian Federation to the north, Türkiye and Armenia to the south, and Azerbaijan to the southeast. Approximately 55% of the country lies above 1000 m a.s.l., and 40% of its territory is characterized by slopes steeper than 20° (Mikeladze et al. 2020). The Greater and Lesser Caucasus mountain ranges shape Georgia's climate, with mean annual temperatures in mountainous areas ranging from −5 °C to 10 °C and precipitation levels from 800 to 1400 mm (Keggenhoff et al. 2014). The Likhi Range (ca. 1000 m a.s.l.) divides the humid, high-rainfall western regions (13–15 °C, 400–4000 mm) from the drier, more continental (10–13 °C, 500–600 mm) east (Denk et al. 2001; Elizbarashvili et al. 2006). This climatic and topographic variation supports diverse forest types, ranging from alpine coniferous forests dominated by *Abies nordmanniana* (Steven) Spach. and *Picea orientalis* (L.) Peterm. at higher elevations to open juniper woodland (*Juniperus foetidissima* Willd. and *J. polycarpos excelsa* subsp. *polycarpos* (K. Koch) Takht.) in the arid areas of the southeast (Dolukhanov, 2010; Lachashvili et al. 2020). The western lowlands feature humid Colchic forests, a Tertiary relict flora of high regional endemism characterized by stands of *Alnus glutinosa* subsp. *barbata* (C. A. Mey.) Yalt and *Castanea sativa* Mill., with a rich evergreen understory (Novák et al. 2021). Central Georgia hosts thermophilic to xerophytic oak forests dominated by *Quercus petraea* subsp. *iberica* (Steven ex M. Bieb.) Krassiln. and hornbeam species such as *Carpinus betulus* L., and *Carpinus orientalis* Mill. (Lachashvili et al. 2020; Novák et al. 2020, 2023b). These transition into mesophytic beech forests (*Fagus orientalis* Lipsky.) and hornbeam–beech associations in more humid regions, which represent the most widespread forest in Georgia (Dolukhanov, 2010; Patarkalashvili 2017; Nakhutsrishvili et al. 2021; Novák et al. 2023a) (Fig. 1, 2).

Data preparation

Sampling and plot design

Forests in Georgia are defined as *land area with a width of not less than 10 m and an area of not less than 0.5 ha covered with trees higher than 3 m and a canopy cover of more than 10%, or with trees able to reach these thresholds in situ* (Government of Georgia, 2020). The GNFI is based on a systematic sampling grid of 3.6 km × 3.6 km with a randomly selected origin. Field observations are recorded as cluster samples comprising three concentric sample plots, arranged in an L-shaped configuration with a distance of 100 m along both axes (Fig. 1). The GNFI has a ten-year repetition mandate under current legislation and field work of the first GNFI was carried out between 2019 and 2021 (MEPA 2023). As 18% of the country's territory is currently not accessible for government officials due to an ongoing political conflict, only approximately 74% of the national forest area of Georgia was sampled (Fig. 3).

Stems with DBH≥8 cm are tallied on the inner nested subplot with a radius of 5 m (0.008 ha), whereas stems with DBH≥15 cm and DBH≥30 cm are assessed on subplots with $r = 10$ m (0.0314 ha), and $r = 15$ m (0.071 ha), respectively. Stems equal to or exceeding the respective DBH-thresholds are recorded with polar coordinates (azimuth and distance from the plot center). Crown cover percentage

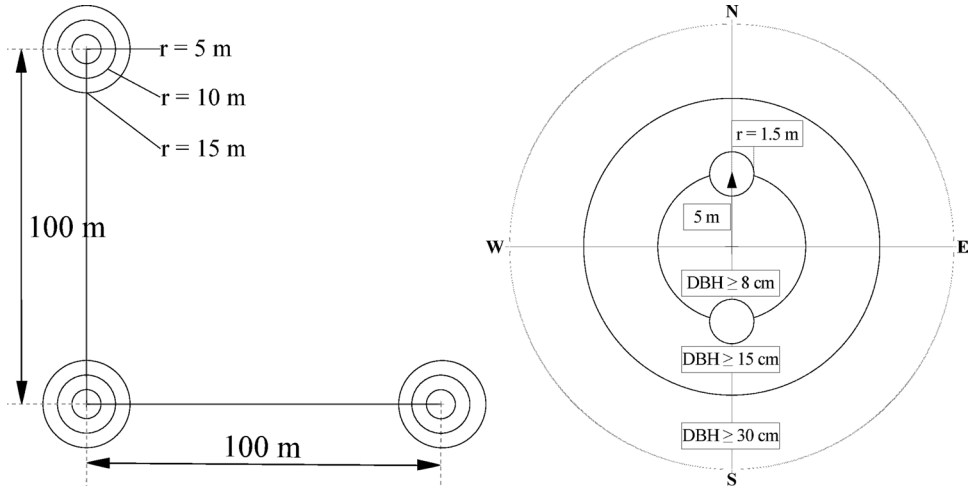

Fig. 1 Configuration of cluster plots (left) comprising three sample plots of the National Forest Inventory of Georgia. Sample trees are assessed within three nested subplots according to the diameter at breast height (DBH, at 1.3 m, right). For each stem, the tree and stem number, species and DBH measurement are recorded along with the polar coordinates of the stem axis. Regeneration is assessed on two subplots located 5 m from the sample plot center in a North-South direction (r = 1.5 m, MEPA, 2018)

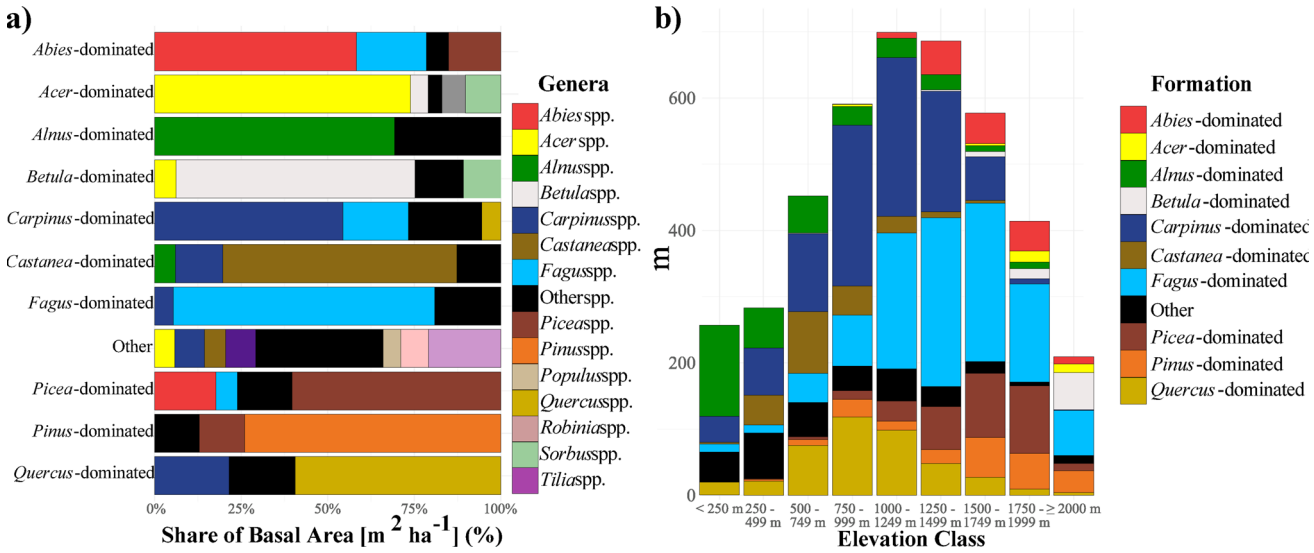

Fig. 2 Basal area proportions per genus and forest formation (**a**). Genera with total shares ≤ 10% of basal area are grouped as "Other spp." Distributions of samples (m) across elevation classes [m a.s.l] for all forest formation are shown in (**b**)

(CC%) is recorded as visual estimate of the area covered by crowns projected to the forest floor with the largest subplot (r = 15 m). As regeneration, all stems with DBH < 8 cm are assessed by stem counts in two smaller satellite subplots (r = 1.5 m) located at 5 m from the plot center (Fig. 1). In the first GNFI, increment sampling was stratified by canopy layer and species dominance. Species dominance is defined as the maximum relative basal area among all measured trees. In each layer, three stems per dominant and co-dominant species were selected for increment sampling to represent the lower, mean, and upper DBH classes. For subordinate species, one stem per species representing the mean DBH class of that species was sampled. Trees with stem deformities or crown damage were excluded (MEPA, 2018). On average, increment cores were extracted from 2.8 ± 0.9 stems per sample plot. In total, 13,356 cores were collected for subsequent laboratory analyses (MEPA 2023).

Stumps, defined as *remaining root collars of trees* ≤ 1.3 m in height, are recorded with a minimum diameter threshold of 10 cm and classified according to decay. Stump diameter and height are measured at the midpoint and the highest point of the remaining bole, respectively (MEPA, 2018).

Forest degradation

Within a 15 m radius around the sample plot center, the GNFI assesses forest degradation status as observable alterations that have negatively affected forest structure and function (MEPA, 2018). Field teams record specific degradation types, such as *stands of low density*, *quality reduction due to non-systematic cuts*, *damage caused by phyto- and entomological pests*, *fire impacts*, and other structural alterations observed within 15 m of the plot center. *Damage of regeneration and ground vegetation caused by browsing*

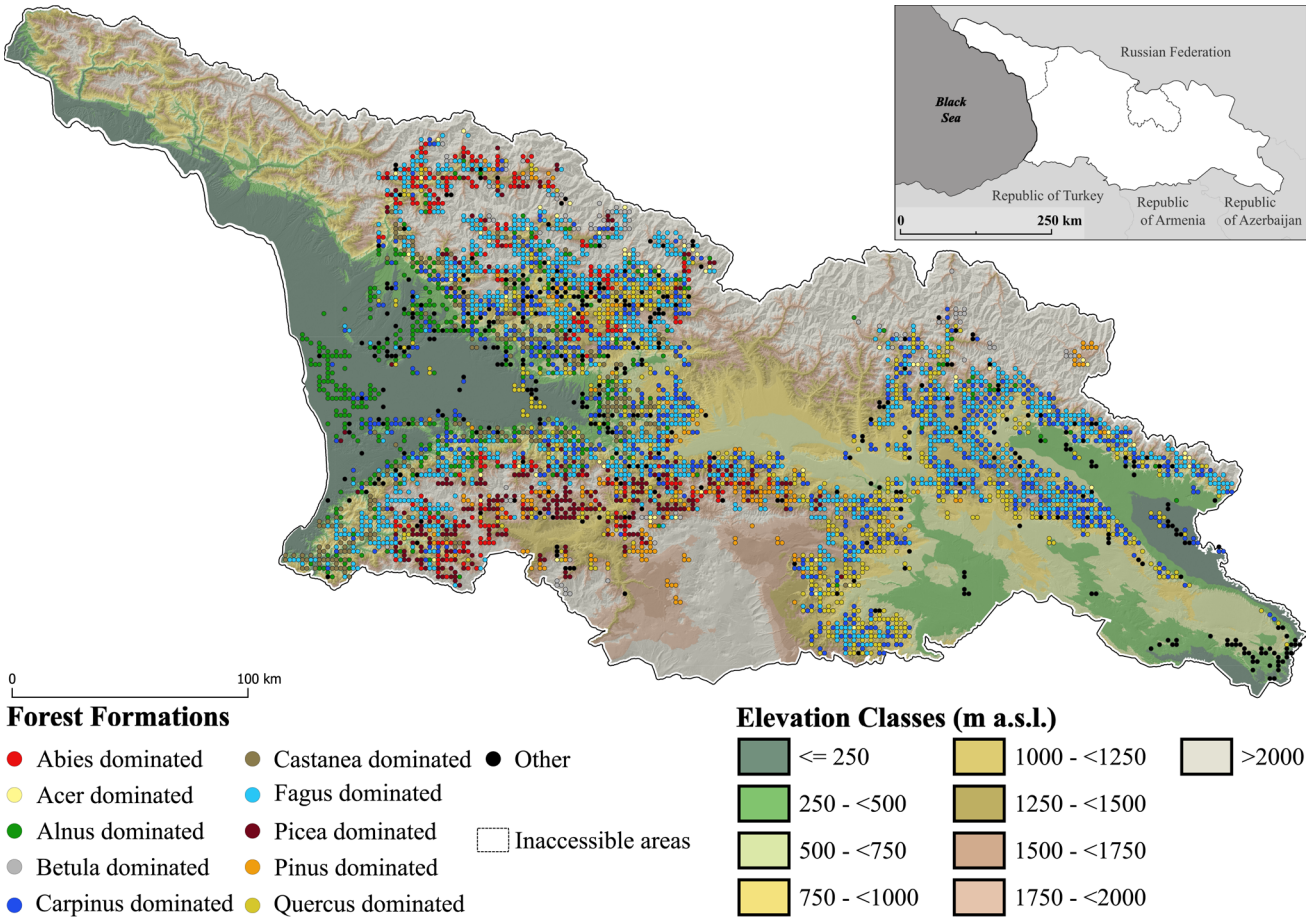

Fig. 3 Spatial distribution of GNFI samples (m = 4168), colored by assigned forest formation. Each point represents one individual sample location on the systematic 3.6 km × 3.6 km sampling grid. To reduce overplotting, locations are displayed with a 1.8 km offset along both axes

(grazing) is assessed within 25 m around the sample plot center. Multiple degradation types may be recorded for a given sample plot. Each degradation type is assigned a severity level according to standardized ordinal classes: *slightly degraded*, *average degraded*, or *strongly degraded* (MEPA, 2018). In this study, we used the GNFI degradation classifications as provided in the original dataset and retained the term *degradation* in accordance with the given nomenclature. We recoded severity classes into categories representing a gradient of structural alteration: undisturbed, low severity, moderate severity, and high severity. Where multiple degradation types co-occur at a single sample plot, the highest recorded severity level was used.

Data evaluation

We queried the GNFI dataset (m = 5970) to remove all sample plots that were inaccessible (m = 671) and not classified as "tree covered area" or "forest" (m = 1012) according to the local land cover categorization (MEPA 2023). Non-forest land cover categories excluded from analysis include *agricultural fields*, *meadows*, *shrubs*, and *other non-vegetated areas* (MEPA, 2018). To reduce the influence of edge effects on stand structure and species composition, we removed 342 sample plots that overlapped with the forest boundary (Ries et al. 2004; Willmer et al. 2022). The remaining dataset contained m = 4168 sample plot observations (n = 1717 clusters), henceforward referred to as "samples", of which m_{deg} = 2539 were degraded and m_{undeg} = 1629 were undisturbed according to GNFI records. Samples account for a total sampled area of approximately 294.6 ha, equal to 0.01% of the national forest area (MEPA 2023).

Classification of forest formations

To classify samples into broader forest formations, we applied cluster analysis using the *Isometric Partitioning around Medoids* algorithm (isopam, Schmidtlein et al. 2024). isopam performs iterative top-down partitioning, based on a given dissimilarity metric, ordination, and medoid-based clustering. The result is a hierarchical clustering of compositionally homogeneous groups (Schmidtlein

et al. 2010). We used the *Discriminating Avalanche* index as phylogenetically informed dissimilarity metric (Hao et al. 2019; Wellenbeck et al. 2024). Samples with species S < 2 (m = 660) and sample records that contained taxa identifications on genus level (m = 41) were excluded from the analysis. Consequently, a total of m = 3466 samples (83%) were clustered based on a species composition matrix in which abundance is expressed as basal area per hectare (BA [m^2 ha^{-1}]) per species, weighted by normalized interspecies phylogenetic distances. The resulting clusters were named after the genus contributing the largest share of total BA, provided this exceeded 10% of total BA within the cluster (Wellenbeck et al. 2024). Where no single genus met this threshold, the cluster was assigned to the group "Other". We allocated all monospecific samples and samples with incomplete species-level identification (m = 702) manually according to dominant species to the respective formation. To evaluate whether the resulting clusters reflect ecologically meaningful spatial patterns, their elevational distribution and spatial configuration across the country were inspected visually.

Stand structure

As structural indicators per sample we considered BA and CC% and calculated stem (N ha^{-1}) and regeneration (N_{reg} ha^{-1}) densities. CC% plays a key role in regulating light availability throughout the vertical stand profile and influences numerous ecological processes (McElhinny et al. 2005; Modica et al. 2015). Further, we calculated proportions of BA within 5 m height classes (H_p) as measure to quantify vertical structure, the quadratic mean diameter (D_q, Curtis and Marshall 2000) and the share of total stump BA in relation to the total BA of growing trees (%BA_{stp}). The vertical distribution index H_p is based on BA distributions across vertical strata derived from imputed tree heights using DBH–height regression analysis (Dees et al. 2020). With $p_{i,s} = BA_{H_i,s} / \sum_{j=1}^{k_s} BA_{H_j,s}$, where $BA_{H_i,s}$ is the basal area in height class i, $\sum_{j=1}^{k_s} BA_{H_j,s}$ is total basal area within sample s and k_s is the number of height classes present in that sample. H_p [0, 1] is expressed as the mean of these proportions across the k_s height classes present in each sample. Higher H_p values indicate that BA is concentrated in fewer height strata, reflecting a vertically simplified structure, whereas lower H_p values indicate that BA is distributed across more height strata, reflecting greater vertical stratification. Mean annual diameter increment (i_d [mm ha^{-1}]) and stand volume increment (iv [m^3 ha^{-1} a^{-1}]) were derived per sample. Tree ring analysis from extracted increment cores provided i_d as ten year average (n = 12,503). Estimates of iv were calculated from measured diameter increment (i_d) and heights derived from a DBH–height regression at current and projected DBH values (Dees et al. 2020). Tree heights not measured in the field were imputed using DBH–height regression models fitted for tree species groups and stratified by stand layer, age class, site index, and geobotanical district to account for variation in growth conditions (Dees et al. 2020). Stem volume was estimated using a three-parameter function based on DBH and tree height, with coefficients derived from national volume tables or statistical fitting (Gigauri and Dzebisashvili 1990). Forest productivity, measured as mean annual increment can signal degradation when it consistently falls below expected levels for a given forest type and site (Bahamondez and Thompson 2016).

Analysis

We applied a space-for-time substitution approach, in which plots representing different degradation severity levels were interpreted as positions along a structural degradation gradient. This approach is widely used in forest ecology and succession research to infer structural differences from independent observations (Walker et al. 2010; Wardle et al. 2004). In each forest formation, differences in indicator means were compared across four degradation severity classes. Per forest formation and structural indicator, we first applied the Kruskal–Wallis rank-sum test as a non-parametric test for differences among all severity classes simultaneously, which does not assume normality and is appropriate for the unbalanced group sizes present here (Kruskal and Wallis 1952). Subsequently, pairwise post-hoc comparisons were conducted using Dunn's test, restricted to indicators where the Kruskal–Wallis test was significant at $\alpha \leq 0.05$ (Dunn 1964). P-values from pairwise tests were adjusted using the Holm procedure to control the family-wise error rate within each forest formation and indicator (Holm 1979). Where no regeneration or stumps were recorded at a sample plot, N_{reg} and BA_{stp} were set to zero, treating absence of recorded values as observed zeros rather than missing data. We compared indicator means and Δ values across degradation severity levels per forest formation. Δ values represent absolute differences in indicator means between each severity class and the undisturbed class and are not subject to statistical testing. Extreme outlier values were retained in statistical tests but not plotted to maintain consistent Y-axis scales across formations. Only pairwise contrasts with Holm-adjusted $p \leq 0.05$ were labeled in the figures.

The analysis was carried out using R version 4.4.0 (R Core Team, 2024) in the RStudio environment (RStudio Team 2024). Phylogenetic distances were derived from a time-calibrated supertree based on the GBOTB extended phylogeny using the package V.PHYLOMAKER2 (Jin and Qian

2019, 2022). Cluster analysis was conducted using ISOPAM version 2.0 (Schmidtlein et al. 2024). Statistical tests were implemented using functions from the base R package RSTATIX (Kassambara 2019), graphs were created using GGPLOT2 (Wickham 2016). Spatial data was processed with QGIS version 3.34.8 (QGIS Development Team, 2024).

Results

We classified GNFI samples into forest formations via unsupervised hierarchical clustering of species BA distributions weighted by normalized interspecies phylogenetic distances (Supplement 1), with unclassified samples assigned manually. Cluster membership was evaluated against elevational distribution and mapped spatially to assess ecological plausibility. Structural indicators were compared across degradation severity classes within each formation, with descriptive statistics and pairwise test results provided in Supplements 3 and 5, respectively.

Forest formations

The hierarchical cluster analysis partitioned 3466 samples into 76 groups at the finest level (level VI), which were grouped into eleven forest formations by cutting the hierarchy at level III and characterizing each cluster by dominant genera with BA proportions ≥ 10% (Supplement 2). The resulting forest formations are "*Abies*-dominated" (m = 245), "*Picea*-dominated" (m = 241), "*Pinus*-dominated" (m = 221), "*Fagus*-dominated" (m = 1208), "*Carpinus*-dominated" (m = 768), "*Quercus*-dominated" (m = 419), "*Alnus*-dominated" (m = 354), "*Castanea*-dominated" (m = 223), "*Betula*-dominated" (m = 82), "*Acer*-dominated" (m = 61) and "Other" (m = 346). Species variability in clusters summarized in "Other" is high as this group encompasses diverse species assemblages. These include, e.g. *Juniperus* spp. and *Pistacia atlantica*-dominated (m = 31), but also *Tilia rubra* subsp. *caucasica* (Rupr.) V.Engl. dominated (m = 69) and *Robinia pseudoacacia* L.-dominated samples (m = 45), and samples dominated by fast-growing pioneer species e.g. *Salix caprea* L. and *Populus tremula* L. (m = 46). In total, 75% of all samples are distributed in formations dominated by broadleaves, whereas 17% are dominated by coniferous genera and 8% comprise mixed assemblages ("Other").

Spatially, formations largely align with elevational and regional gradients: coniferous formations dominate above 1,250 m a.s.l., *Fagus*- and *Carpinus*-dominated formations occupy mid-elevations, and *Alnus*- and *Castanea*-dominated formations are concentrated in the western lowlands below 1000 m a.s.l. (Fig. 2).

Abies-dominated forest formations occur predominantly (> 95%) above 1250 m a.s.l. in the western Greater and Lesser Caucasus, typically co-occurring with *P. orientalis*, *F. orientalis* and a minor share of other species, most importantly *Pinus sylvestris subsp. hamata* Steven, *Acer heldreichii* subsp. *trautvetteri* (Medvedev) A.E. Murray, and *C. betulus* (Dolukhanov, 2010; Nakhutsrishvili 2013). *Acer*-dominated formations overlap at these elevations but extend higher (76% above 1500 m a.s.l.) and further east (Fig. 3). *A. heldreichii subsp. trautvetteri*, *Acer platanoides* L., *Acer cappadocicum* Gled., *Acer campestre* L. and *Acer pseudoplatanus* L. comprise the dominant species of this forest formation with *Sorbus aucuparia* L. as notable associate (9.5% of total BA).

The highly diverse *Alnus*-dominated forest formations are primarily concentrated in the western part of the country, particularly within the Colchic lowlands, with 80% of all samples located below 1000 m a.s.l. These formations account for 34% of all samples below 500 m a.s.l. (Fig. 2) and are dominated by *A. glutinosa* subsp. *barbata* with *Alnus incana* (L.) Moench occurring at higher elevations in the eastern Greater Caucasus, where they form part of riparian forest systems (Dolukhanov, 2010; Nakhutsrishvili 2013; Novák et al. 2023b). In contrast, *Betula*-dominated formations are relatively species poor and are concentrated above 1750 m a.s.l. (89%), accounting for 30% of all samples above 2000 m a.s.l., along with formations dominated by *Fagus* (28%) and *Picea* (15%). Dominated by *Betula* spp. (*Betula pendula* Roth, *Betula medwediewii* Regel, and *Betula pubescens* var. *litwinowii (Doluch.) Ashburner & McAll.*), this formation occurs in association with *S. aucuparia* (Akobia et al. 2022). *Carpinus*-dominated formations are primarily located between 250 and 1500 m a.s.l. (89%) and account for 27% of all forest formations between 500 and 1000 m a.s.l. (Fig. 2). They are associated with *F. orientalis* and *Q. petraea* subsp. *iberica* and many understory and other woody species (S = 64), occupying a broad ecological range (Dolukhanov, 2010; Nakhutsrishvili 2013). *Castanea*-dominated formations are predominantly located between 250 and 1250 m a.s.l. (94%) in the western part of the country. *Fagus*-dominated formations are the most common formation between 1000 and 2000 m a.s.l. (41% of all samples in this range), while *Picea*-dominated formations are largely confined to the same elevational belt (89% between 1000 and 2000 m a.s.l.). *Pinus*-dominated formations occur mainly above 1500 m a.s.l. (63%) but extend into lower elevations (18% between 500 and 1000 m a.s.l.), and *Quercus*-dominated formations span the widest elevational range, with 66% of samples between 500 and 1500 m a.s.l. Formations grouped as "Other" are mostly distributed below 1000 m a.s.l. (71%). Because of limited sample sizes in formations dominated by *Betula* (m = 82), *Acer* (m = 61),

and high internal variability in "Other" (m = 346), these formations were excluded from further analyses (Fig. 4, 5, 6).

Differences in stand structure

Forest formations differed substantially in mean BA and N ha^{-1}, while mean CC% was similar (range: 54–62%) across all formations (Supplement 3). Among structural indicators, formation-specific variability was high for D_q (range: 20.8–43.3 cm), whereas H_p and $\%BA_{stp}$ were similar across all formations. Productivity indicators showed the largest spread in iv (range: 2.4–10.5 m^3 ha^{-1} a^{-1}), while i_d was similar across formations and N_{reg} exhibited high within-formation variability.

Differences among degradation severity classes varied in magnitude, pattern, and statistical significance across formations (Supplement 5). Differences were most consistent across formations for BA, CC%, and $\%BA_{stp}$, which showed directionally uniform deviations from the undisturbed class across all severity levels. D_q and iv showed moderately consistent negative differences across most formations, whereas differences in H_p, i_d, N ha^{-1}, and N_{reg} were largely formation-specific. Among all indicators, CC% showed the highest count of significant pairwise contrasts across formations ($n = 27$), followed by $\%BA_{stp}$ ($n = 25$) and BA ($n = 22$), with N_{reg}, N ha^{-1}, and D_q displaying markedly lower counts ($n = 6$, 6, and 9, respectively). In the following, we focus on the indicator in each variable group with the highest number of significant pairwise differences compared to the undisturbed class, namely CC% (stocking, Fig. 4), structure ($\%BA_{stp}$, Fig. 5), and productivity (iv, Fig. 7). In addition, we added N_{reg} (Fig. 6). All remaining indicators are provided in Supplement 4a–e.

BA and CC% were consistently lower at higher degradation severity, with significant differences most frequently observed between undisturbed and high severity classes across formations (Fig. 4, Supplement 4a). In *Abies*- and *Picea*-dominated formations, reductions in CC% and BA are non-significant at low degradation severity, but significant from moderate severity onward ($p \leq 0.01$ to $p \leq 0.001$). In *Pinus*-dominated formations, differences in BA reach significance only at high severity ($p \leq 0.001$), while CC% shows significant reductions across all severity classes at $p \leq 0.05$ (Fig. 4). Among broadleaves, *Fagus*-, *Carpinus*- and *Quercus*-dominated formations show significant reductions in both BA and CC% already at low severity ($p \leq 0.05$ to $p \leq 0.001$).

In *Alnus*-dominated formations, mean BA and CC% show significant differences at moderate and high degradation severity ($p \leq 0.01$ to $p \leq 0.001$). In *Castanea*-dominated

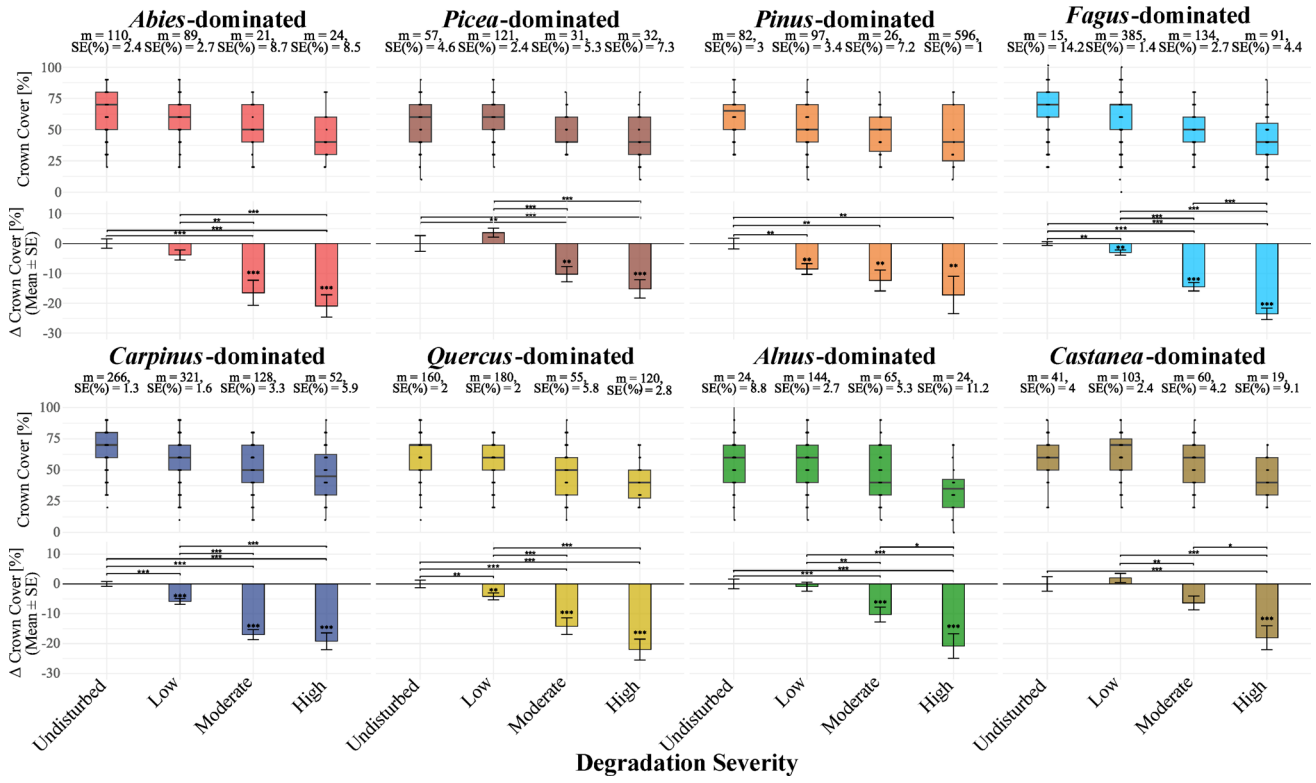

Fig. 4 Mean crown cover (CC%) and absolute differences (Δ) in mean CC% relative to the undisturbed class (severity 0) per forest formation. Significance of pairwise differences among severity classes based on Dunn's post hoc test with Holm adjustment (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Error bars represent ± SE

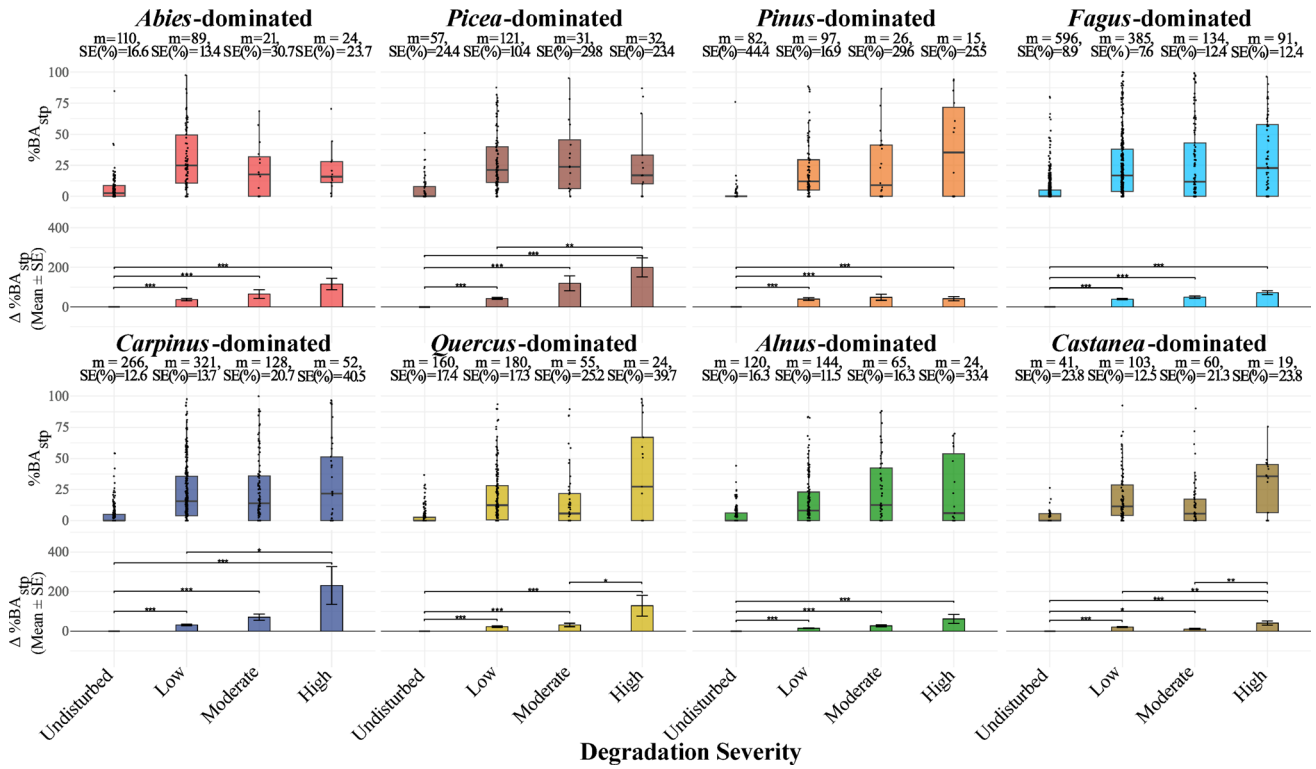

Fig. 5 Mean stump basal area as proportion of total basal area ($\%BA_{stp}$) and absolute differences (Δ) in mean $\%BA_{stp}$ relative to the undisturbed class (severity 0) per forest formation. Significance of pairwise differences among severity classes based on Dunn's post hoc test with Holm adjustment (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Error bars represent ± SE

formations, mean BA differs significantly only at high degradation severity ($p \leq 0.05$), while CC% shows significant differences from moderate severity onward ($p \leq 0.05$ to $p \leq 0.001$). *Abies*-, *Picea*-, *Fagus*-, *Alnus*-, and *Castanea*-dominated formations show a non-significant increase in mean N ha^{-1} from undisturbed to low degradation severity, whereas formations dominated by *Pinus*, *Carpinus*, and *Quercus* exhibit reduced mean N ha^{-1} already at low degradation severity (Supplement 4b).

Significantly lower mean D_q relative to undisturbed conditions was detected across all severity classes in *Fagus*- and *Carpinus*-dominated formations, at low and moderate severity in *Alnus*-dominated formations, at high severity in *Quercus*-dominated formations, and at low and high severity in *Castanea*-dominated formations ($p \leq 0.05$ to $p \leq 0.001$). Mean H_p was significantly higher across all severity classes in *Fagus*-, *Carpinus*-, and *Alnus*-dominated formations ($p \leq 0.001$ in *Fagus* and *Carpinus*), with significant differences at moderate and high severity in *Quercus*- and at high severity in *Pinus*-dominated formations (Supplement 4c and d). Differences in $\%BA_{stp}$ compared to undisturbed samples were significant across all severity classes in all formations ($p \leq 0.001$), except at moderate severity in *Castanea*-dominated formations ($p \leq 0.05$, Fig. 5). However, across severity classes the relative differences in mean $\%BA_{stp}$ do not uniformly increase across formations. In *Abies*- and *Picea*-dominated formations, increases of mean $\%BA_{stp}$ are marked, whereas in *Pinus*-dominated formations, differences in mean $\%BA_{stp}$ are relatively small. Among broadleaves, *Carpinus*-dominated formations show the highest increase, followed by *Quercus*-dominated formations. Mean $\%BA_{stp}$ increases in *Alnus*- and *Castanea*-dominated formations between undisturbed and high severity are relatively low.

Mean N_{reg} shows high overall variability across formations ranging from 2771 N_{reg} ha^{-1} in undisturbed *Alnus*-dominated formations to 19,201 N_{reg} ha^{-1} in *Quercus*-dominated formations at low severity (Supplement 5). Differences in mean N_{reg} varied strongly among formations, with increases at low or moderate severity observed in most formations (Fig. 6). Differences in mean N_{reg} ha^{-1} compared to undisturbed samples were significant across all severity classes in *Fagus*- and *Carpinus*-dominated formations ($p \leq 0.01$ to $p \leq 0.001$), whereas no significant differences were detected in any other formation.

Mean diameter increment (i_d) was significantly higher than in undisturbed samples across all severity classes in both *Fagus*- and *Carpinus*-dominated formations ($p \leq 0.01$ to $p \leq 0.001$), with the largest difference observed at moderate severity (Supplement 4e). In *Picea*-dominated

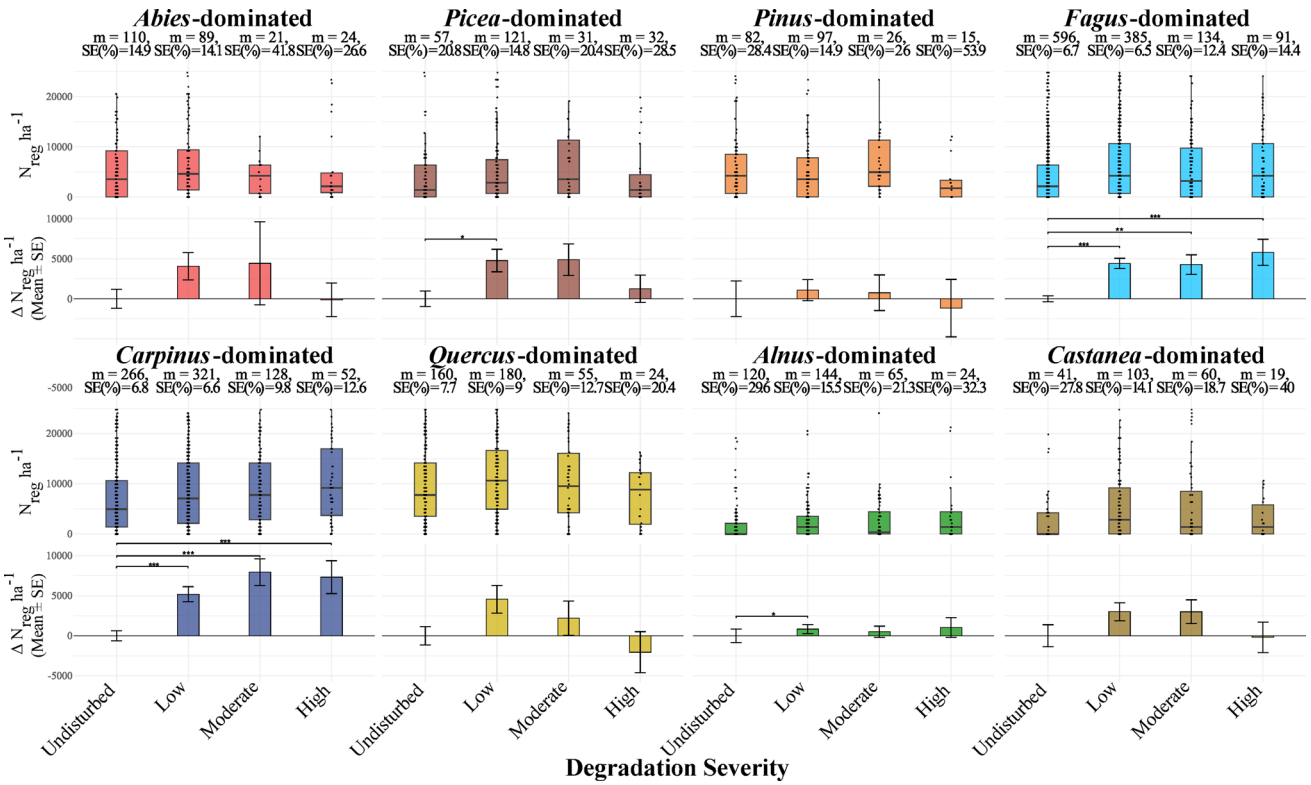

Fig. 6 Mean stem density per hectare for stems with DBH < 8 cm (N_{reg} ha^{-1}) and absolute differences (Δ) of N_{reg} ha^{-1} relative to the undisturbed class (severity 0) per forest formation. Significance of pairwise differences among severity classes based on Dunn's post hoc test with Holm adjustment (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Error bars represent ± SE

formations, differences in mean i_d were significant between undisturbed and high severity at $p \leq 0.01$. In *Abies*-, *Pinus*-, *Quercus*-, *Alnus*-, and *Castanea*-dominated formations, differences were not statistically significant. Unlike other productivity indicators, mean i_V was characterized by significant differences not only relative to undisturbed samples but also between low and moderate or high severity classes in *Picea*-, *Fagus*-, *Carpinus*-, and *Quercus*-dominated formations ($p \leq 0.05$ to $p \leq 0.001$, Fig. 7). In *Abies*- and *Picea*-dominated formations, mean i_V showed a non-significant increase at low severity, followed by a decline at moderate and high severity.

Significant reductions in mean i_V were observed at low severity in *Carpinus*-dominated formations ($p \leq 0.05$), and were limited to high severity in *Pinus*- and *Alnus*-dominated formations ($p \leq 0.05$ and $p \leq 0.01$, respectively). In *Castanea*-dominated formations, differences in mean i_V were not statistically significant.

Discussion

Forest formations derived from phylogenetically informed clustering of GNFI species composition data showed spatial patterns aligned with climatic and elevational gradients, reflecting known forest type zonation across Georgia (Bohn et al. 2007; Dolukhanov, 2010; Nakhutsrishvili 2013; Wellenbeck et al. 2024). This ecological coherence, reflecting environmental filtering along climatic and elevational gradients, provides the basis for a formation-specific interpretation of indicator responses to degradation severity (Wellenbeck et al. 2025). Mean BA, D_q, and i_V differed across formations, reflecting the ecological distinctiveness of the derived formations. Across degradation severity classes, indicator means differed in direction and magnitude among formations and were often non-monotonic, reflecting the context-dependence of disturbance responses across forest types (Seidl et al. 2017).

Stocking indicators showed the most consistent reductions across formations and severity classes, whereas differences in size differentiation, vertical structure, and productivity indicators were more formation-specific, underscoring the need for forest-type-specific indicator frameworks in degradation assessment (Thompson et al. 2013; Bahamondez and Thompson 2016). The absence of significant BA and CC% reductions at low and moderate severity in *Abies*- and *Picea*-dominated formations, in contrast to *Fagus*- and *Carpinus*-dominated formations, is consistent with their comparatively high baseline stocking (Supplement 3), which may reduce sensitivity to indicator

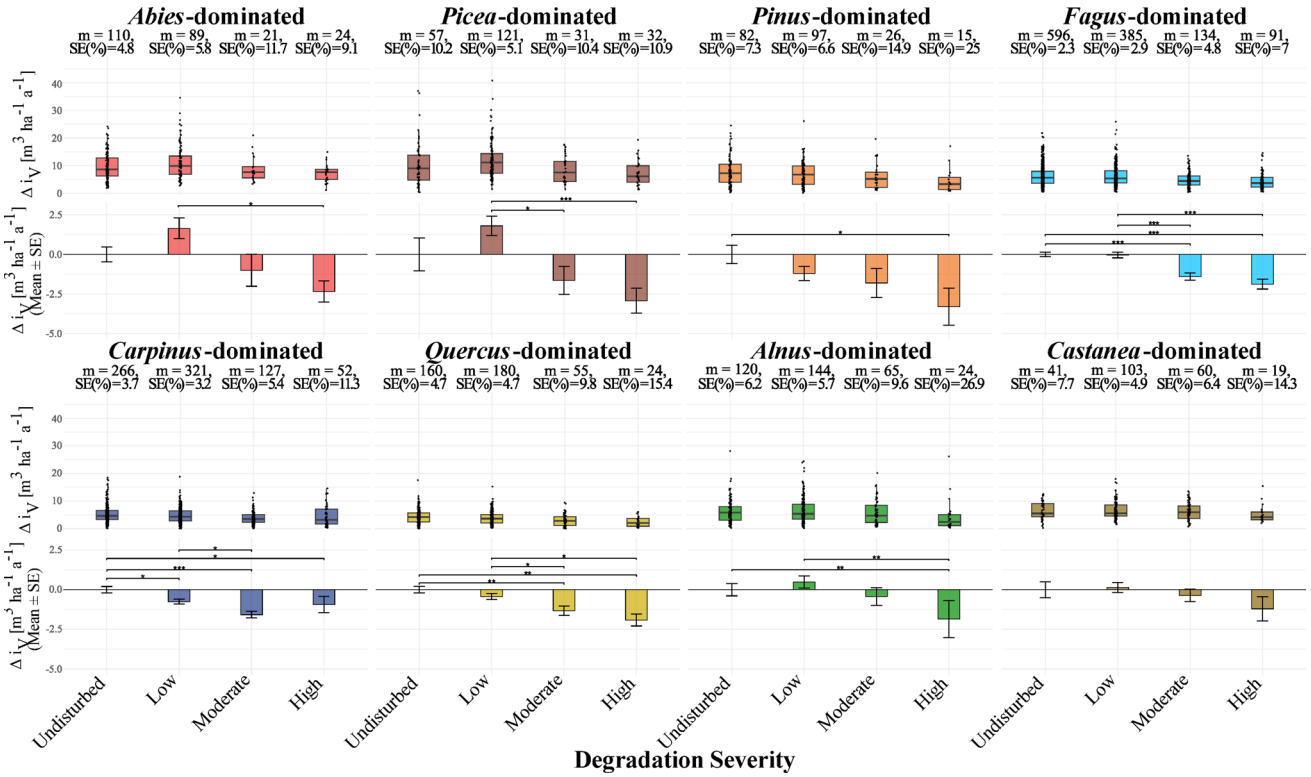

Fig. 7 Mean stand volume increment (i_V [m^3 ha^{-1} a^{-1}]) and absolute differences (Δ) in mean i_V relative to the undisturbed class (severity 0) per forest formation. Significance of pairwise differences among severity classes based on Dunn's post hoc test with Holm adjustment (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Error bars represent ± SE

change at lower degradation severity. Reduced mean D_q and H_p in several broadleaved formations point to decreased size differentiation and increased vertical homogenization at higher severity classes, consistent with selective removal of larger stems (Goode et al. 2020). $\%BA_{stp}$ showed the most consistent pattern across formations, with significant elevations at $p \leq 0.001$, except at moderate severity in *Castanea*-dominated formations ($p \leq 0.05$). However, mean values at high degradation severity should be interpreted carefully, as within-group variability was particularly high in several formations (with SE% > 23 at high severity except *Fagus*), driven by few plots with very high stump proportions (Fig. 5). Smaller sample sizes at high severity in several formations may further increase sensitivity of mean estimates to extreme values.

The higher mean i_d at low and moderate severity, significant in *Fagus*- and *Carpinus*-dominated formations, is consistent with reduced competition and increased growing space associated with partial canopy opening (Čada et al. 2020). The general decline in stand-level i_V is primarily attributable to reduced stand density and basal area, and reflects structural differences among severity classes rather than site productivity potential. Where reductions in both stocking and i_V were significant, concurrent structural and productivity losses may limit the capacity of affected stands to maintain pre-disturbance productivity levels (Knapp et al. 2021; Foster et al. 2022).

Regeneration density (N_{reg}) showed the most formation-dependent responses, with significant increases relative to undisturbed conditions detected only in *Fagus*- and *Carpinus*-dominated formations. Reduced canopy cover at higher severity levels may facilitate regeneration through increased light availability, particularly in *Fagus*-dominated formations where dense canopies typically suppress regeneration (Tinya et al. 2019). Gap dynamics play a key role in seedling establishment in these formations (Feldmann et al. 2018; Zenner et al. 2019; Martin-Benito et al. 2020; Droessler and Wolff 2023). Where regeneration increases were observed, even if not significant, they were generally stronger at low severity and weaker or inconsistent at higher severity classes (Fig. 6), suggesting dependence on formation context, including understory competition and soil disturbance (Puettmann and Ammer 2006; Kern et al. 2013; Pröll et al. 2015; Feldmann et al. 2020). The high variability of N_{reg} across formations and severity classes may reflect the small size of the regeneration subplots and limits the reliability of N_{reg} as an indicator of degradation severity.

Taken together, indicator-specific patterns suggest that GNFI severity classes correspond to quantifiable structural differences across forest formations, with stocking

indicators providing the most consistent signal across formations and severity levels. Productivity and regeneration indicators exhibit more formation-specific and non-monotonic responses, reflecting ecologically meaningful dynamics beyond the scope of the severity classification itself. The proportion of significant pairwise contrasts relative to the undisturbed class among indicators for which post-hoc testing was conducted increases from 52% at low severity to 69% at moderate and 83% at high severity, indicating that structural differences are more consistently detectable at higher severity classes. The relatively low proportion of significant contrasts at low severity suggests that detection of structural degradation may benefit from formation-specific thresholds, particularly at lower severity levels.

Different degradation types and stand contexts contribute to the formation-specific patterns observed across severity classes. In *Castanea*-dominated formations, the high prevalence of pest and pathogen-related disturbances (30% of all samples) may contribute to the observed irregularity in structural differences (Metreveli et al. 2023). Similarly, *Alnus*-dominated formations exhibit inconsistent regeneration and structural patterns, which may reflect their inherent variability and the relatively high grazing pressure (36% of *Alnus*-dominated samples) limiting regeneration success despite initial canopy opening (Novák et al. 2023b). These formations encompass both lowland swamp forests and alluvial forests at higher elevation (Novák et al. 2023b). *Abies*- and *Picea*-dominated formations, both with above-average shares of erosion-related degradation (~22%), showed steep reductions in stocking and stand increment under high severity, consistent with expected effects of soil destabilization (Worrell and Hampson 1997; Selkimäki et al. 2012; Rodrigues et al. 2020). *Pinus*-dominated formations, characterized by mixed samples of naturally regenerated and planted stands (Lachashvili et al. 2017; Akhalkatsi et al. 2019), display more gradual and heterogeneous responses. The high incidence of the degradation type *stands of low density* in *Fagus*-, *Carpinus*-, *Pinus*-, and *Quercus*-dominated formations (≥30%) is consistent with stronger stocking declines with increasing degradation severity. Where multiple degradation types co-occur, aggregation to the highest severity level may mask combined disturbance effects that could modify structural differences in ways not fully captured by the ordinal classification applied.

Observed structural differences among severity classes reflect associations with field-assigned degradation severity rather than directly observed temporal changes within individual stands, as samples represent independent observations from a single inventory cycle. Structural indicators are influenced not only by degradation severity but also by site conditions, stand development stage, and stand density, and although grouping samples by forest formation reduces ecological heterogeneity, residual variability from these factors may influence observed differences. CC% was visually estimated in the field and may not be independent of the assessor-assigned degradation severity class, which should be considered when interpreting its high frequency of significant contrasts across formations. Stump basal area may partly reflect legacy harvesting events and should therefore be interpreted as an indicator of cumulative disturbance rather than exclusively recent impacts, as decay rates vary with environmental conditions and wood properties. Although fixed-area sample plots may not fully capture fine-scale heterogeneity within stands (Portier et al. 2022; Moreno-Fernández et al. 2024), the systematic sampling design of the GNFI provides a consistent and spatially explicit basis for quantifying formation-specific structural differences across degradation severity classes at national scale.

The formation-specific structural patterns identified here demonstrate that quantitative analysis of systematic inventory data can complement field-assigned severity classifications, revealing indicator patterns that vary across forest formation and severity level. While single indicators are unlikely to provide reliable discrimination between severity classes given the within-class variability reported above, formation-specific multivariate combinations of stocking, productivity, and size differentiation indicators could form the basis for more robust, data-driven severity assessment, including the derivation of formation-specific structural thresholds. Incorporating degradation type as an explicit covariate alongside formation context would additionally allow type-specific structural signatures to be estimated separately from severity level, improving the interpretability of inventory-based assessments in terms of underlying disturbance processes. Long-term studies and comparison with near-natural reference conditions would further support the quantification of degradation and the development of formation-specific stocking guidelines (Schall and Ammer 2013; Bahamondez and Thompson 2016; Seidl and Rammer 2017; Nakhutsrishvili et al., 2023). Repeated inventory cycles in Georgia would allow structural change to be tracked directly over time, and the recently established marteloscope network offers valuable plot-level observations that could support and validate formation-specific severity assessments (Kruse 2022; Kruse et al. 2023). The ecologically coherent forest formations identified here show distinct structural characteristics that make them meaningful units for translating quantitative inventory analysis into management decisions and offer an ecologically grounded basis for forest classification that captures the diversity of Georgian forests.

Conclusions

Our findings show that field-assigned GNFI degradation severity classes are associated with quantifiable differences in stand structural properties, which vary among forest formations in an often non-monotonic manner across severity levels. Stocking indicators differed most consistently across formations and severity classes, while productivity and regeneration indicators varied in direction and magnitude depending on forest formation, with significant differences confined largely to moderate and high severity levels. The contrasting trends in stem diameter and stand volume increment at low severity illustrate the added value of a quantitative sample-based analysis compared to observational classification in the field. These findings support formation-specific interpretation of GNFI degradation severity classes and indicate that the approach is scalable, with reduced within-formation variability at higher sampling densities expected to sharpen structural differentiation among severity classes. Quantitative, formation-specific frameworks of this kind offer an ecologically grounded basis for translating inventory data into management decisions and forest classification, with potential for broader application where ecologically coherent forest classifications are lacking.

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Data availability The datasets generated and applied code are available from the author upon reasonable request. All required data and code are submitted.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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