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Integrating fine-scale topography and stand structure to explain herb-layer diversity in forest ecosystems

CARLA-MARIA APARASCHIVE

Department of Forestry, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania

PAUL SESTRAS

Department of Land Measurements and Exact Sciences University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania ; Academy of Romanian Scientists, Bucharest, Romania

ALINA M. TRUTA

Department of Forestry, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania

IRINA M. MORAR

Department of Forestry, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania 3Academy of Romanian Scientists, Bucharest, Romania

CATALINA DAN

*Department of Horticulture and Landscape, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania*Follow this and additional works at: <https://journals.tubitak.gov.tr/agriculture>

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Integrating fine-scale topography and stand structure to explain herb-layer diversity in forest ecosystems

Authors

CARLA-MARIA APARASCHIVE, PAUL SESTRAS, ALINA M. TRUTA, IRINA M. MORAR, CATALINA DAN, MONICA BOSCAIU, FLORIN IORAS, and ADRIANA F. SESTRAS

Integrating fine-scale topography and stand structure to explain herb-layer diversity in forest ecosystems

Carla-Maria APARASCHIVE¹ , Paul SESTRAS^{2,3,*} , Alina M. TRUTA¹ , Irina M. MORAR^{1,3} , Catalina DAN⁴ ,
Monica BOSCAIU⁵ , Florin IORAS⁶ , Adriana F. SESTRAS¹ 

¹Department of Forestry, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania

²Department of Land Measurements and Exact Sciences, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania

³Academy of Romanian Scientists, Bucharest, Romania

⁴Department of Horticulture and Landscape, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania

⁵Mediterranean Agroforestry Institute, Polytechnic University of Valencia, Valencia, Spain

⁶Department of Research and Enterprise, Buckinghamshire New University, High Wycombe, United Kingdom

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Abstract: Herb-layer diversity in temperate forests emerges from the interaction between stand structure and fine-scale environmental variation. We studied eight mixed beech–hornbeam and oak–hornbeam plots distributed along a short altitudinal gradient (170–310 m) and contrasting slope aspects in East Europe. For each plot, we measured tree diameter, height and crown-base height, and derived stand structural indices (tree density, basal area, Gini coefficients for DBH diameter at breast height and total height, and median crown-base height). Herb-layer communities were characterized using standard diversity indices and Ellenberg indicator values. We then used Jaccard similarity to explore tree–herb cooccurrence and Spearman correlations to relate stand structure to herb-layer diversity. Stands differed markedly in structure along the combined elevation–aspect gradient. Basal area peaked at middle elevation on the north-facing slope and at high elevation on the south-facing slope, whereas size inequality and crown-base height showed contrasting patterns among plots, reflecting a mosaic of dense, structurally heterogeneous stands and more open, even-sized canopies. Herb-layer richness and evenness increased with higher median crown-base height and lower size inequality, but declined with increasing basal area and stem density. Ellenberg values confirmed that open mixed stands supported more light-demanding herbs, while dense, beech-dominated stands were characterized by a few shade specialists. Tree–herb cooccurrence patterns were generally weak, indicating mostly generalist herbs with a few consistent associations. Overall, our results show that simple stand structural indices, combined with fine-scale topography, can effectively predict herb-layer diversity and provide useful indicators for biodiversity-oriented forest management.

Key words: Altitudinal gradient, slope aspect, ground vegetation, beech, microsite, indicator plant species

1. Introduction

Forests are among the most structurally complex and biodiverse terrestrial ecosystems on Earth, and they underpin a wide range of ecological processes and ecosystem services, including carbon sequestration, nutrient cycling, soil protection, and habitat provisioning for numerous taxa (Brockerhoff et al., 2017; Mori et al., 2017). In temperate Europe, mixed deciduous forests dominated by *Fagus sylvatica*, *Quercus* spp., and *Carpinus betulus* represent a major component of the natural vegetation matrix and play a central role in regional biodiversity conservation (Mucina et al., 2016). These forests are increasingly exposed to multiple interacting

pressures, including climate warming, altered natural disturbance regimes, long-lasting land-use legacies, and intensified forest management, all of which can profoundly affect stand structure, species composition, and functional diversity (Morris et al., 2014; Seidl et al., 2014; Thom et al., 2021). A distinguishing feature of temperate forests is that a large proportion of vascular plant diversity resides not in the tree canopy but in the herbaceous layer of the forest floor (Gilliam, 2007). Herb-layer plants contribute disproportionately to ecosystem functioning relative to their biomass, influencing nutrient cycling, decomposition, fine-scale microclimate, and forest regeneration dynamics. Because herb-layer species respond sensitively to variation

* Correspondence: paul.sestras@usamvcluj.ro

in light availability, soil moisture, nutrient status, and canopy structure, they are widely regarded as accurate bioindicators of forest condition and management history. Understanding how herb-layer communities respond to environmental gradients is therefore essential for assessing forest ecological integrity and for developing biodiversity-friendly silvicultural practices (Gilliam, 2007; Barbier et al., 2008; Helbach et al., 2022).

Fine-scale topography, reflecting variations in altitude, slope inclination, and slope aspect over distances of tens to hundreds of meters, is a major source of environmental heterogeneity in temperate landscapes. Such gradients shape microclimatic conditions by modifying solar radiation, temperature profiles, evaporative demand, and soil moisture regimes. In many temperate deciduous forests, north-facing slopes are cooler and moister, supporting more mesophilous species, whereas south-facing slopes experience higher radiation loads and seasonal water stress, often favoring more xerophilous assemblages. Altitudinal gradients further impose changes in temperature, growing-season length, and disturbance exposure, generating shifts in community structure and species turnover (Zhang et al., 2016; Sangry et al., 2024). However, despite substantial research on topographic gradients, interactions among topography, canopy structure, and forest-floor biodiversity remain underexplored, especially in colline mixed forests where environmental contrasts can be strong over short distances.

Stand structural attributes strongly influence understory vegetation through control over the quantity, spatial distribution, and temporal variability of light at the forest floor (McElhinny et al., 2005; Storch et al., 2018). Canopy architecture, including crown depth, crown-base height (CBH), canopy layering, and foliage density, modulates understory light heterogeneity, which is a key driver of ground-layer species richness in deciduous forests. In forest ecology, stand structural complexity is often approximated using simple metrics derived from standard tree inventories, such as stem density, basal area, and measures of size and height variability, because these attributes integrate key aspects of resource use, competition, and habitat heterogeneity (McElhinny et al., 2005; Staudhammer and LeMay, 2011). Among such inventory-based descriptors, Gini coefficients of diameter at breast height (DBH) and tree height provide concise measures of size inequality and structural heterogeneity, and they have been successfully used to distinguish between managed and unmanaged stands and to relate stand structure to biodiversity and functional responses (Pach and Podlaski, 2015; Reich et al., 2022). In addition, CBH and related crown metrics are increasingly recognized as important indicators of vertical stratification, light penetration, and tree vigor, with direct implications for

understory microclimate and ground vegetation (Matsuo et al., 2022). By combining tree density and basal area with Gini indices for DBH and height and median CBH, it is possible to capture major gradients in stand structural complexity using relatively simple field measurements.

These indices encapsulate variation in competition intensity, growth allocation, mechanical stability, and stand developmental stage and are therefore useful for predicting patterns of forest biodiversity and structural complexity. Furthermore, tree-species diversity itself can influence forest-floor vegetation by altering litter quality, nutrient availability, and root competition, as well as by generating variation in crown structure and phenology (Barbier et al., 2008; Storch et al., 2018; Helbach et al., 2022). Mixed-species stands often exhibit greater structural heterogeneity than monospecific stands, which may promote higher plant diversity at lower layers through niche diversification and increased spatiotemporal heterogeneity. However, the strength and direction of tree–herbaceous layer diversity relationships vary contextually, being strongly mediated by local environmental conditions and stand structure (Brockhoff et al., 2017).

Overall, these considerations indicate that overstory structure and tree-species diversity jointly shape herb-layer communities, but their effects are difficult to disentangle because they vary with forest type, management history, and local environmental conditions (Gilliam, 2007; Barbier et al., 2008; Evy et al., 2016). In particular, there is still a lack of plot-level studies that combine explicit inventory-based metrics of stand structural complexity (e.g., density, basal area, tree-size and height inequality, or CBH) with a detailed set of diversity and dominance indices for both tree and herb layers. This gap motivated the present study, in which we use a small set of intensively sampled mixed deciduous stands to explore how simple structural attributes and tree-species diversity relate to patterns of herb-layer richness, evenness, and dominance. In this study, we used mixed beech–hornbeam and oak–hornbeam stands in temperate broadleaf forests to investigate how tree diversity, stand structure, and fine-scale topography jointly shape forest-floor vegetation. Specifically, we quantified the α - and β -diversity of tree and herb layers across a short altitudinal gradient (170–310 m) and contrasting slope aspects, characterized stand structure using simple inventory-based indices (tree density, basal area, Gini coefficients of DBH and tree height, median CBH), and assessed how herb-layer species richness and composition respond to topographic variation and overstory structural and compositional attributes. We hypothesized that forest structural complexity and microtopographic gradients (elevation and aspect) significantly influence herb-layer diversity. By integrating data on tree structure, tree diversity, and ground-layer vegetation into a multiscale

framework, we aimed to provide new insights into the structural mechanisms shaping understory biodiversity in colline deciduous forests and to evaluate the usefulness of stand structural metrics as ecologically meaningful proxies for habitat conditions relevant to forest conservation and management.

2. Materials and methods

2.1. Plot selection and sampling design

To capture fine-scale topographic variation, we established eight sample plots distributed across four altitudinal levels (approximately 170, 230, 270, and 310 m a.s.l.), each level being represented by two plots on contrasting slope aspects (north vs. south or northeast vs. southwest). Although the number of plots was limited, their placement was designed to strategically encompass the main altitudinal and aspect-driven environmental contrasts within a compact, well-preserved forest matrix, allowing for a focused investigation of fine-scale topographic effects on forest structure and ground layer diversity (Clark and Clark, 2000; Cheng et al., 2023). Numerous studies highlight that field data availability is often limited, and national forest inventories typically provide small forest samples, with only a few measured trees per plot. As noted by Mey et al. (2021), national forest inventory plots generally contain only a few tree observations, which inherently restricts the number of usable sampling units in many forest studies. Moreover, Mey et al. (2021) further argued that reduced datasets are common in structural analyses and lead to the development of a statistical framework tailored to derive stand-level diameter distributions and structural descriptors from “small sample data,” although plots with as few as five measured trees can still provide useful structural information. In light of this, our use of eight intensively sampled plots should be understood as a compact design that is suitable for exploring stand structural patterns at the scale of the studied forest, while we acknowledge that larger plot networks would be needed for broader spatial generalization.

The study was conducted in a continuous forest block of approximately 20 km² (≈2000 ha) located in the low-elevation hilly (colline) sector of the Moldavian Plateau in northeastern Romania (Figure 1), an area characterized by mixed beech–hornbeam and oak–hornbeam stands and pronounced microsite variability. Plot selection followed a two-step procedure. First, we identified potential sampling locations that captured the main combinations of altitude and slope aspect present within the forest block, regardless of differences in forest type, stand age, or structural characteristics. These contrasts in stand structure and composition were preserved, as they represent the natural variability of beech–hornbeam and oak–hornbeam forests in the region. Second, all selected locations were visited

in the field, and one plot was established within each site using a systematic random approach to position the plot center, ensuring a representative coverage of the local topographic gradient.

Each plot was circular, with an area of 500 m² (radius: 12.62 m), centered on a point temporarily marked during the inventory process. After visually locating the approximate center, a forest compass was mounted on a pole at 1.3 m in height and fixed to magnetic north. This provided a stable reference for orienting measurements, delineating the circular plot boundary, and laying out transects for ground vegetation sampling, while also ensuring consistency among plots. The inclusion criterion for trees was that the horizontal distance from the plot center to the midpoint of the stem at breast height not exceed 12.62 m. Distances were checked with a Vertex IV hypsometer (Haglöf Sweden AB, Långsele, Sweden) for all trees with diameters of ≥5 cm to avoid edge effects and misclassification. For each plot, geographic coordinates, altitude, slope, and aspect were recorded in the field and soil type was assigned based on existing soil survey data, indicating the presence of one main soil type (Luvisol) and one plot with eroded soils (Figure 2).

Plots are referred to by their altitudinal levels and slope aspects (170N, 230N, 270N, 310N and 170S, 230S, 270S, 310S), with their corresponding site characteristics summarized in Table 1. For each plot, aspect was determined on site using a compass and recorded as northern (N), southern (S), northeastern (NE), or southwestern (SW) exposure. Elevation was obtained with the digital altimeter and mean stand age was taken from the corresponding forest management plans. Slope was measured at the plot center with the clinometer function of a handheld hypsometer, taking readings along the line of steepest descent, following standard forest inventory procedures (Avery and Burkhart, 2002).

2.2. Tree inventory and ground-layer vegetation survey

Within each 500-m² plot, all living trees with DBH (measured at 1.3 m above ground) of at least 5 cm were inventoried, following standard forest mensuration practice (Figure 3a). For each individual tree, we recorded species identity, DBH (an example of a beech stem is provided in Figure 3b), total height (H), and CBH (Husch et al., 2003). CBH was defined as the height from ground level to the lowest living branch (or whorl of branches), and it provides an estimate of the vertical position and length of the live crown, a key attribute in crown structure and growth analyses for representative canopy structures (Figures 3c and 3d) (Pretzsch, 2010). Tree diameters were measured with a forest caliper and expressed in centimeters, while total height and CBH were measured using the Vertex IV hypsometer and an electronic transponder and expressed in meters. Tree measurements

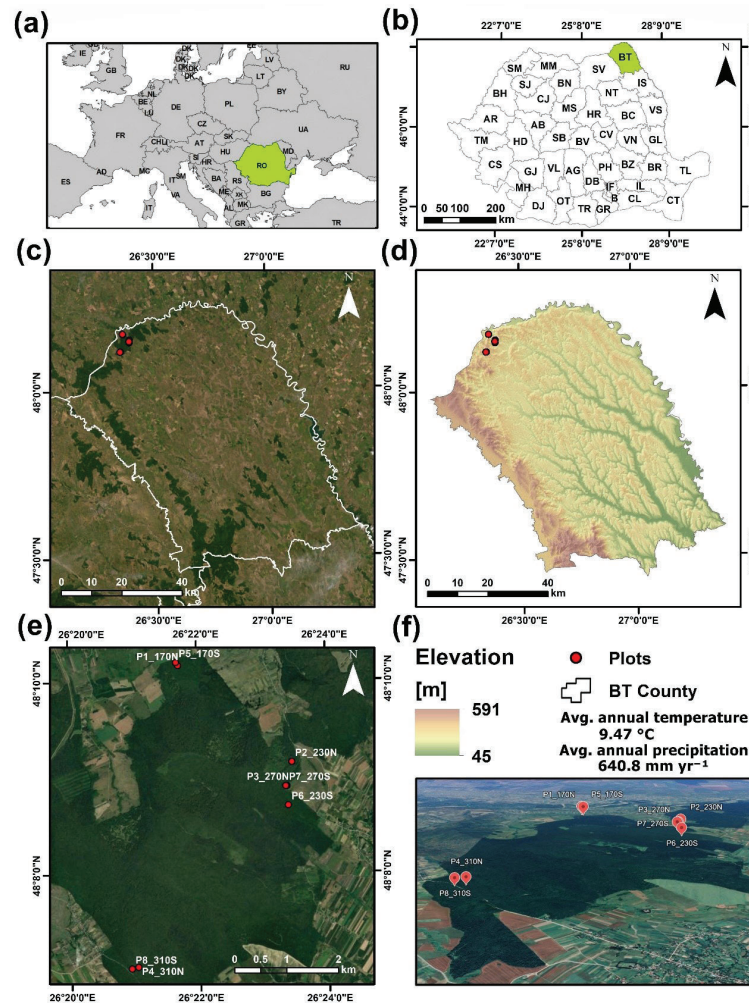


Figure 1. Location of the study area in Romania: (a) regional location of Romania within Europe; (b) national administrative context highlighting Botoșani County; (c) satellite view of Botoșani County with the study area marked; (d) elevation map of Botoșani County; (e) detailed satellite view showing the location of the sampling plots; (f) map of the study area with plot distribution and main topographic features.

were collected during several field studies in May under comparable phenological and visibility conditions.

Ground-layer vegetation (herb layer) was surveyed using a belt transect with fixed-area quadrats, following standard procedures for forest ground-layer sampling in temperate forests (Küchler et al., 1976; Kent, 2011). Within each 500-m² plot, a belt transect was laid out along the east–west axis passing through the plot center. Along this transect, four 1-m² quadrats (Q1–Q4) were positioned at fixed distances from the center, with two quadrats at 5 m and 10 m on the eastern side and two quadrats at 5 m and 10 m on the western side (Figure 4). In each quadrat, all vascular plant species occurring in the ground layer and reliably identifiable in the field were recorded, and the number of individual plants per species was counted.

Individuals were counted as distinct aboveground shoots or clumps (ramets) for each species, including species that often form distinct ramets through clonal propagation (e.g., *Carex*, *Galium*, *Vinca*), using the same counting rule across all plots so that the values represent species relative abundance rather than the number of genets. Quadrat-level data were then used directly to explore the within-plot heterogeneity of ground-layer vegetation and aggregated at plot level by summing the abundances of each species across the four quadrats, thereby producing a species-by-plot matrix for the calculation of diversity indices and for multivariate analyses.

To characterize the ecological preferences of each ground-layer species, we assigned Ellenberg indicator values for light (L), moisture (F), soil reaction (R), and nitrogen (N).

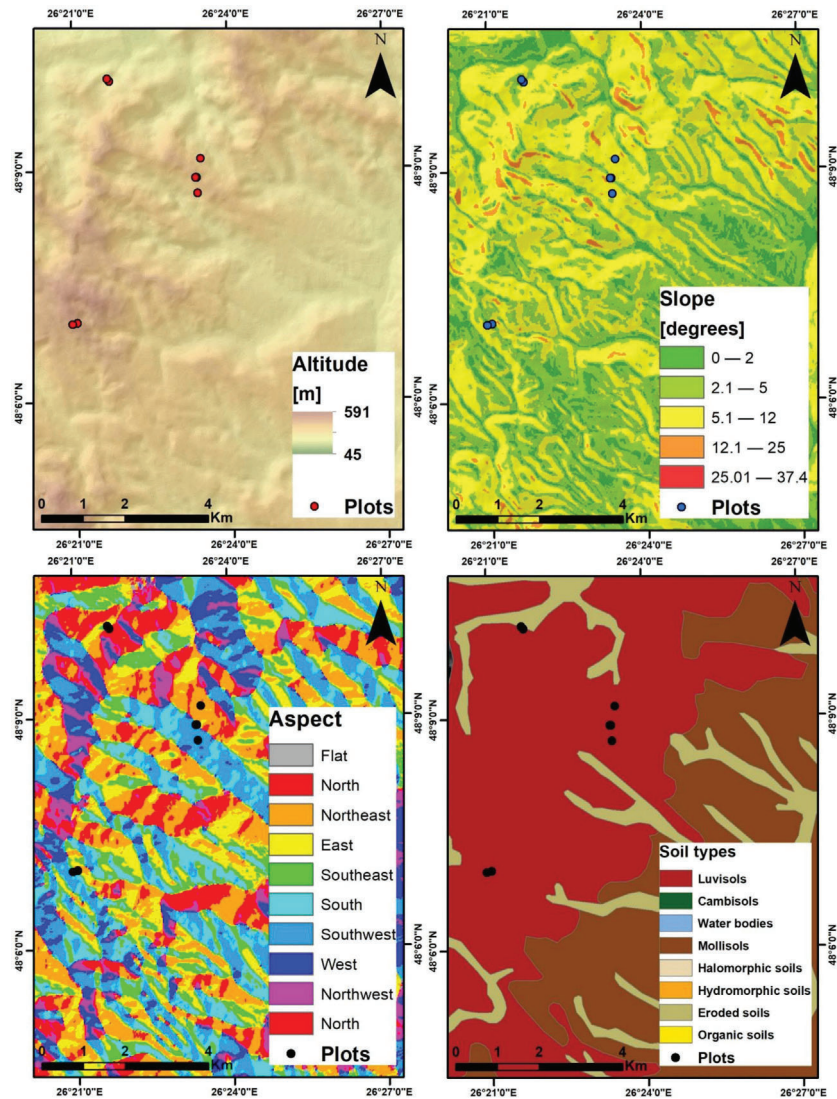


Figure 2. Topographic, aspect, and soil characteristics of the study area in Botoșani County, Romania.

Table 1. Environmental characteristics of the eight plots.

Plot name	Latitude (°N)	Longitude (°E)	Elevation (m)	Aspect	Slope (°)	Mean stand age	Dominant soil type
P1_170N	48.16917	26.36028	174	NNE	5	35	Luvisols
P2_230N	48.15222	26.38944	233	NE	7	125	Luvisols
P3_270N	48.14806	26.38806	271	NE	4	125	Luvisols
P4_310N	48.11694	26.34889	307	NE	5	85	Luvisols
P5_170S	48.16972	26.35972	173	SE	5	35	Eroded soils
P6_230S	48.14472	26.38833	234	SSW	10	60	Luvisols
P7_270S	48.14806	26.38778	271	S	5	50	Luvisols
P8_310S	48.11667	26.34722	306	SW	2	70	Luvisols

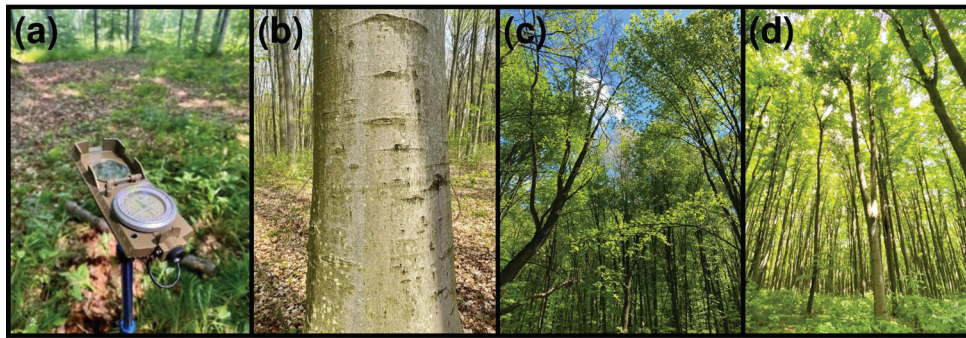


Figure 3. Field procedures and structural characteristics of the sampled stands: (a) marking the plot center with a forest compass to guide the identification of trees within the circular plot; (b) stem of European beech (*Fagus sylvatica*), one of the dominant canopy species; (c) mixed canopy showing variation in stem density and crown layering; (d) structurally uniform beech canopy dominated by tall and straight stems.

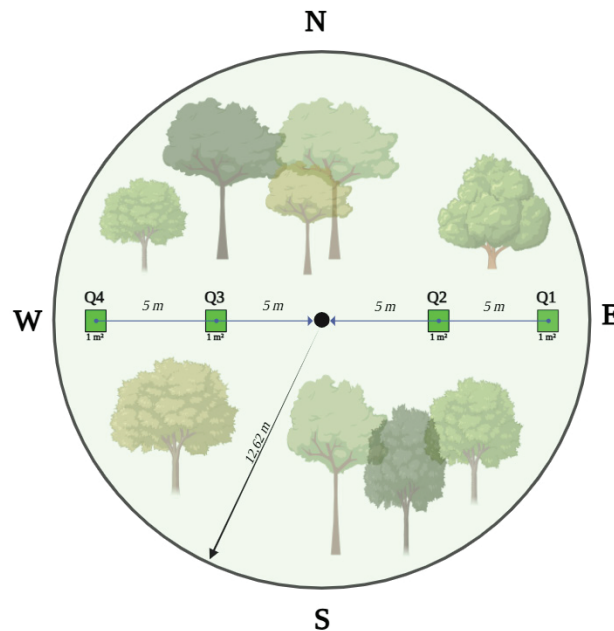


Figure 4. Schematic representation of the sampling design within each 500-m² plot, showing the east-west transect and the four 1-m² quadrats (Q1–Q4) positioned at fixed distances from the plot center.

These values are semiquantitative scores, typically ranging from 1 (very low) to 9 (very high), that describe the realized ecological niche of each species along major abiotic gradients and they are widely used to infer habitat conditions and environmental gradients in Central European forests (Ellenberg et al., 1991; West, 2015). In our case, indicator values were attributed to all herb-layer species and used to aid in the ecological interpretation of species composition and ordination patterns.

2.3. Stand structural indices

Stand structural indices were calculated for each plot. First, tree density (trees ha⁻¹) was obtained by counting

all live trees within the plot and scaling the counts to a per-hectare basis according to plot area. Basal area (BA; m² ha⁻¹) was then computed as the sum of the cross-sectional areas of all tree stems at breast height (1.3 m), using the formula $BA = \pi \times DBH^2/4$ for each tree and dividing by plot area (Avery and Burkhardt, 2002).

To quantify size inequality, we calculated Gini coefficients for the distributions of diameter at breast height (Gini_DBH) and tree height (Gini_H). The Gini coefficient is derived from the Lorenz curve and ranges from 0 (all individuals equal in size) to 1 (maximum inequality), providing a concise measure

of structural heterogeneity in tree size and height distributions (Staudhammer and LeMay, 2011; Pach and Podlaski, 2015). Finally, median CBH was defined as the median height from the ground to the lowest live branch among all measured trees in a plot, characterizing the typical height of the canopy base and contributing to the description of vertical stand structure. Together, these indices capture complementary aspects of stand density, size distribution, and vertical stratification that are widely used in forest structural analyses (Pretzsch, 2010).

2.4. Diversity metrics and statistical analyses

For each plot, and separately for the tree and herb layers, we calculated a suite of classical α -diversity indices commonly used in community ecology (Magurran, 2004). Besides species richness (Taxa_S) and number of individuals, we computed dominance and evenness metrics based on relative abundances, including Simpson's index expressed as its complement $1 - D$ (Simpson, 1949), Shannon entropy H (Shannon, 1948), Pielou-type evenness measures (Evenness_{ e^H/S } and Equitability_J) (Pielou, 1966, 1975), the Brillouin index, and the Berger-Parker dominance index (Berger and Parker, 1970). Additional richness-standardized measures included the Menhinick index (Menhinick, 1964), the Margalef richness index (Margalef et al., 1958), and Fisher's α derived from the log-series model (Aylmer Fisher et al., 1943). All indices were obtained from species-by-plot abundance matrices using PAST software (Hammer et al., 2001) and are summarized for trees in Table A1 and for herbaceous species in Table A2 in Appendix A. Redundancy analysis (RDA) was used to assess how environmental and stand structural variables were related to variation in species composition. Because these analyses were conducted at the plot level, two separate RDAs were performed: one for tree species and one for herb-layer species (Appendix B).

Tree-layer structure was assessed at plot level by recording all individual trees within each 500-m² plot and counting the number of tree species and total number of individuals per plot. Plot-level herb species richness (γ) was calculated as the total number of herb species recorded in the four 1-m² quadrats within each plot. Within-plot heterogeneity of the herb layer was quantified using Whittaker's multiplicative β -diversity, defined as $\beta_{(w)} = \gamma/\alpha$, where γ is the total herb species richness recorded across the four 1-m² quadrats within each 500-m² plot and α is the mean quadrat-level richness, following the original α - β - γ framework and its interpretation as proportional diversity (Whittaker, 1972; Tuomisto, 2010). All herb-layer richness and β -diversity metrics (γ , α , and Whittaker's β_w) pertain to this pooled 4-m² sampling area per plot.

Hierarchical cluster analyses were used to explore similarities in species composition among plots for both the tree and herb layers. Analyses were based on plot-level

species abundance matrices and computed using the Bray-Curtis similarity index. Dendrograms were produced by hierarchical agglomerative clustering with the unweighted pair-group average linkage method. All cluster analyses were also performed with PAST software (Hammer et al., 2001).

To explore plot-level associations between tree species and the herb layer, we quantified pairwise cooccurrence similarity using the Jaccard index based on presence-absence data. The Jaccard index was originally introduced for floristic similarity by Jaccard at the beginning of the 20th century and it remains a standard measure for presence-absence community data. For each tree-herbaceous species pair, the Jaccard similarity value J_{ij} was computed as $J_{ij} = a_{ij}/(a_{ij} + b_{ij} + c_{ij})$, where a_{ij} is the number of plots in which both species occur, and b_{ij} and c_{ij} are the numbers of plots in which only one of the two species occurs. The index ranges from 0 (no shared presence) to 1 (identical plot occupancy) and it is widely used to compare community composition based on binary (presence-absence) data (Hammer and Harper, 2006). Jaccard similarities were calculated in PAST from a species $\times$ plot presence-absence matrix separately for the tree and herbaceous layers, and the results were arranged into a rectangular matrix with tree species as rows and herbaceous species as columns. The resulting tree-herb cooccurrence matrix was visualized as a heatmap using the SRplot web platform.

To examine how overstory structure relates to herb-layer diversity, we quantified monotonic associations between the five stand structural indices (number of trees per hectare, basal area per plot, Gini coefficients of DBH and tree height, and median CBH) and the set of herb-layer diversity and dominance metrics described above using the Spearman rank correlation (ρ). The resulting 5×11 correlation matrix (structural indices $\times$ herb-layer indices) was visualized as a matrix heatmap using the SRplot web platform to emphasize the sign and relative strength of the relationships. The Spearman rank correlation coefficient (ρ) was used because it does not assume linear relationships or normality and is well suited for small sample sizes and variables with different scales, as in our case (eight plots and a mix of diversity and structural indices) (Spearman, 1904).

3. Results

3.1. Tree diversity and stand structural attributes

Tree density and species diversity differed both along the altitudinal gradient and between aspects within each level. Tree density ranged from low values in some higher-elevation plots to more than 30 trees per 500 m² in the low-elevation north-facing plot (Figure 5a). At 170 m, the north-facing plot supported the highest tree

density, whereas at intermediate and higher elevations (230–310 m) the south-facing plots tended to have equal or higher densities than their north-facing counterparts. Tree species richness per 500 m² showed a similar but less pronounced pattern: richness generally decreased with elevation on the north-facing slope, while south-facing plots maintained intermediate and relatively comparable richness values across the gradient (Figure 5b). Diversity indices calculated for each plot largely mirrored these patterns in richness (Appendix A, Table A1). The Shannon diversity index (H') and Simpson index ($1 - D$) indicated overall low-to-moderate tree diversity at stand level, with H' values close to zero in almost monospecific plots and approaching 2 in the most diverse plots. Plots with higher tree species richness, typically at lower elevations or where mixtures of several broadleaved species occurred, also showed higher Shannon and Simpson values. In contrast, plots dominated by a single species exhibited high dominance (Berger–Parker and dominance D close to 1) and very low Shannon and Simpson diversity, reflecting a strong contribution of the dominant species to total abundance. Evenness and equitability indices (e.g., Pielou's J , $e^{H'/S}$) were generally high in plots where several species cooccurred, suggesting a relatively balanced distribution of individuals among species despite the small plot size. In monospecific or nearly monospecific stands, evenness indices reached values close to 1 by definition, but in these cases they mainly reflected the absence of subordinate species rather than a truly even community structure. Fisher's α and the Margalef and Menhinick indices showed a similar differentiation between structurally simple stands and more mixed stands along the gradient.

The ordination biplot for the tree layer (Appendix A, Figure A1) provides a synthetic view of how

environmental and structural variables jointly structure canopy composition. Along the first canonical axis, plots dominated by beech at higher elevations on the north-facing slope (e.g., P3_270N, P4_310N) are clearly separated from sessile oak–hornbeam mixtures on the south-facing slope (P6_230S–P8_310S) and from the more species-rich low-elevation plots (P1_170N, P5_170S). This axis is aligned with increasing elevation and basal area and, in our dataset, captures a gradient from lower, more heterogeneous stands with mixed broadleaves to taller, denser stands dominated by a single canopy species. The second axis reflects residual variation related to slope and aspect, distinguishing, for example, the south-facing low-elevation stand (P5_170S), characterized by high diameter inequality, from north-facing plots with similar elevation.

Taken together, these results suggest that aspect and elevation, as components of the fine-scale topographic gradient, are associated with marked variation in local stand structure and tree diversity at the study site. North-facing low-elevation plots tended to have higher tree densities and richer assemblages, whereas some higher or more exposed plots showed simplified compositions dominated by one or a few species. Given the small number of intensively sampled plots and the observational design of this study, these patterns are best interpreted as a detailed description of stand-level variability along microtopographic gradients, providing initial evidence of potential topographic effects on tree communities in beech–hornbeam and oak–hornbeam stands of northeastern Romania.

Tree species composition differed visibly among plots and between aspects along the altitudinal gradient (Figure 6). The north-facing plots (P1–P4) were generally dominated by mixtures of *Carpinus betulus* and *Fagus*

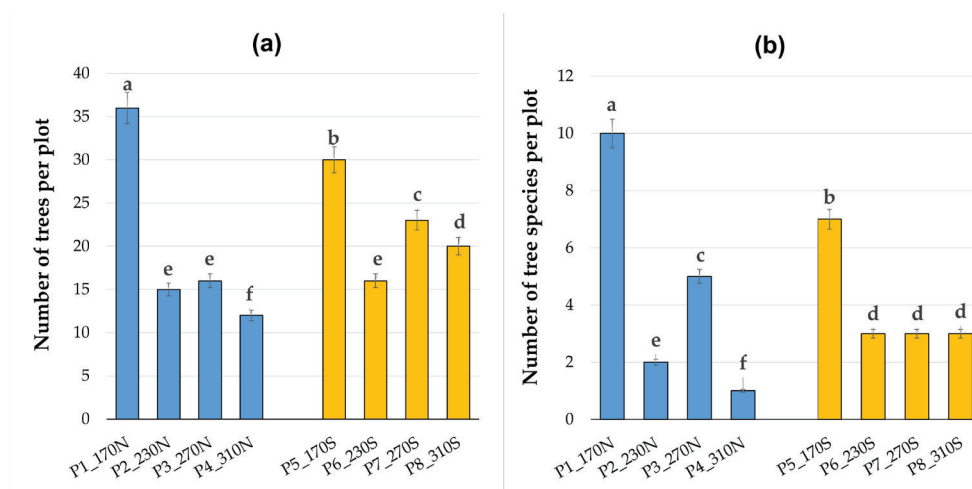


Figure 5. Tree density and species diversity in northern vs. southern plots: (a) number of trees per plot; (b) tree species richness (number of species per plot).

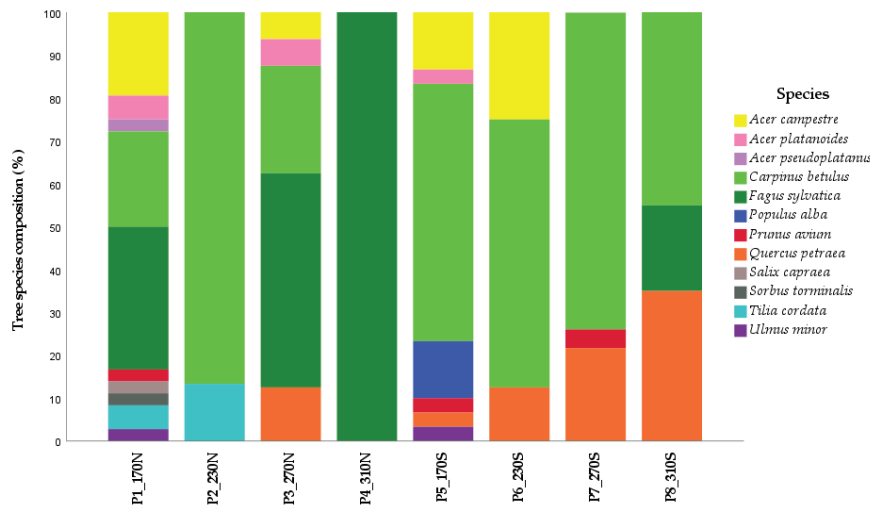


Figure 6. Tree species composition (% of individuals) in the eight plots.

sylvatica, together with several broadleaved associates such as *Acer campestre*, *A. platanoides*, and *Tilia cordata*. At 170 m (P1_170N), a relatively diverse mixture of hornbeam, beech, and several minor broadleaved species was observed. With increasing elevation, the contribution of *Fagus sylvatica* increased, culminating in the highest-elevation north-facing plot (P4_310N), which was almost monospecific and dominated by beech.

On the south-facing slope (P5–P8), *Carpinus betulus* remained an important component, but *Quercus petraea* played a much larger role than in the north-facing plots. At a low elevation (P5_170S), hornbeam cooccurred with *Populus alba* and several other broadleaved species, whereas at intermediate and higher elevations (P6_230S–P8_310S) the stands were dominated by mixtures of *Q. petraea* and *C. betulus*, with only small proportions of additional tree species. The highest south-facing plot (P8_310S) showed a particularly strong dominance of *Q. petraea*. Overall, these patterns indicate that, within the studied stands, north-facing plots tend to be characterized by beech–hornbeam mixtures and, at higher elevations, by nearly pure beech, whereas south-facing plots are dominated by sessile oak–hornbeam mixtures along the fine-scale topographic gradient. The observed differences in species composition are best regarded as a detailed, site-specific description of current stand structure along microtopographic gradients, providing hypotheses for potential topographic effects on tree communities rather than definitive evidence of causal relationships.

Two-way cluster analysis of standardized relative tree species abundances provided a synthetic view of compositional similarity among plots and species along the fine-scale topographic gradient (Figure 7). The north-facing plots at intermediate and high elevations (P2_230N,

P3_270N, P4_310N) formed a relatively tight cluster and were most similar to the mid- and high-elevation south-facing plots (P6_230S, P8_310S), all characterized by beech–hornbeam or oak–hornbeam mixtures with only a few subordinate species. In contrast, the two low-elevation plots (P1_170N and P5_170S) were more distinct, particularly P1_170N, which hosted a broader set of mesophytic broadleaves. At the species level, the clustering grouped several shade-tolerant broadleaved species (*A. campestre*, *A. platanoides*, *A. pseudoplatanus*, *T. cordata*, *U. minor*) that tended to cooccur mainly in the more species-rich plots, usually north-facing, whereas the main canopy dominants (*C. betulus*, *Q. petraea*) and locally restricted species such as *P. alba* formed separate branches. These multivariate patterns are consistent with the univariate results, highlighting a transition from more diverse mesophytic assemblages in lower and more shaded positions to simpler stands dominated by one or a few canopy species in higher or more exposed plots.

Table 2 summarizes the main stand structural attributes for the eight forest plots. Tree species richness ranges from only one species in plot P4_310N to 10 species in P1_170N, indicating a marked gradient from nearly monospecific to highly mixed stands. Basal area, the Gini indices for DBH and tree height, and the median CBH and corresponding coefficients of variation (CVs) all show wide ranges across the plots, pointing to pronounced differences in stand density, size differentiation, and vertical structure. Overall, the table indicates that the investigated stands encompass a continuum from relatively even, low-diversity structures to highly heterogeneous, species-rich mixtures. The between-plot variation in these structural indices and their CVs is examined in more detail in the following section using graphical representations. Height

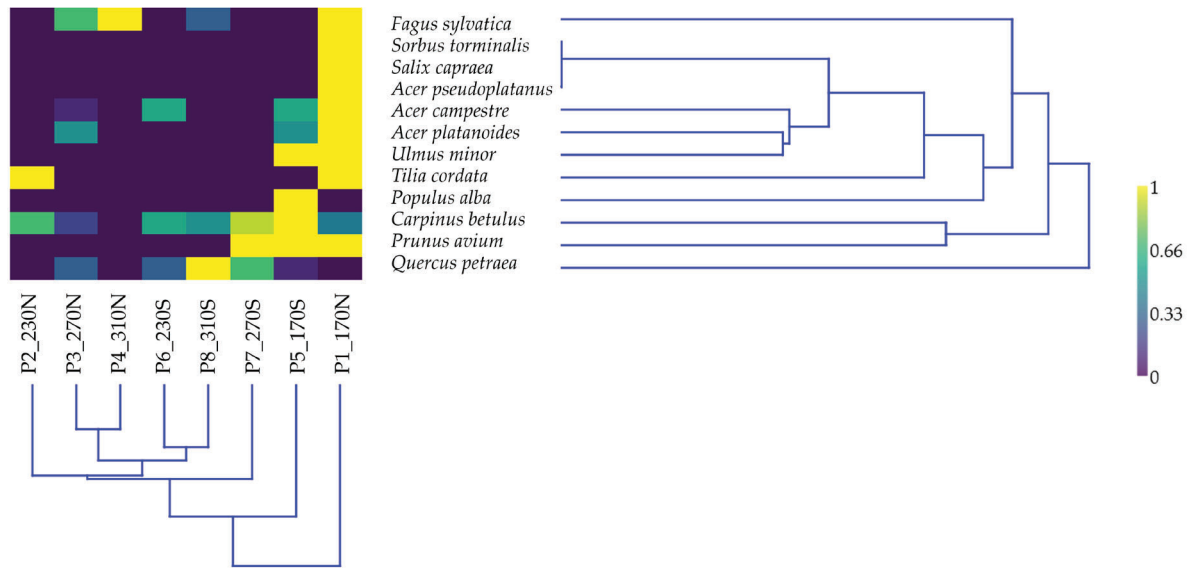


Figure 7. Heatmap and hierarchical clustering of relative tree species abundances in the plots along the fine-scale topographic gradient. Colors represent the normalized relative abundance of each tree species in each plot (0 = absence, 1 = maximum value in the dataset).

Table 2. Summary of stand structural attributes and variability measures for the eight forest plots.

Plot	Number of trees ha ⁻¹	Tree species richness	Basal area (m ² ha ⁻¹)	Gini (DBH)	Gini (H)	Median CBH	CV (Hcb) (%)
P1_170N	720	10	19.27	0.283	0.176	7.85	40.20
P2_230N	300	2	43.19	0.163	0.067	5.4	48.14
P3_270N	320	5	75.04	0.276	0.194	4.25	75.30
P4_310N	240	1	36.31	0.127	0.062	18.85	30.93
P5_170S	600	7	23.39	0.363	0.267	5.75	56.63
P6_230S	320	3	30.27	0.221	0.134	6.55	54.25
P7_270S	460	3	15.11	0.190	0.086	7.3	35.19
P8_310S	400	3	58.19	0.235	0.15	8.3	63.75

inequality, expressed as Gini (H), was generally low, ranging from about 0.06 to 0.27 among plots. The CVs of CBH differed markedly between plots, from about 31% in P4_310N to over 75% in P3_270N, indicating that some stands contain a much broader spread of CBH values than others and thus exhibit a more strongly differentiated vertical structure.

Figure 8 illustrates the variation in four key structural indices among the eight plots. Basal area differs strongly with both elevation and aspect. The highest values occur in P3_270N and P8_310S, where a large proportion of the growing space is occupied by relatively thick trees, whereas P7_270S shows the lowest basal area, indicating a stand dominated by small-diameter stems. Within elevation pairs, contrasts between north- and south-facing plots are evident, particularly at 270 m and 310 m, where the basal area is shifted toward the north-facing plot at 270 m and toward the south-facing plot at 310 m.

Median CBH also varies considerably among plots. P4_310N is characterized by very high crown bases, suggesting strong vertical stratification and intense competition for light, while the lowest median CBH is observed in P3_270N, where crowns start close to the ground and the vertical profile is more compressed. South-facing plots generally exhibit intermediate CBH values, reflecting more even vertical layering.

The Gini indices reveal substantial differences in size inequality. Diameter inequality (Gini (DBH)) is greatest in P5_170S, followed by P1_170N and P3_270N, indicating stands with a wide range of tree diameters and a pronounced mixture of size classes. In contrast, P4_310N shows the lowest Gini (DBH), consistent with a relatively even diameter structure. A similar pattern emerges for the Gini index for height, with the tallest inequality again in P5_170S and comparatively low values in P4_310N. Together, these indices reveal that the south-facing stands

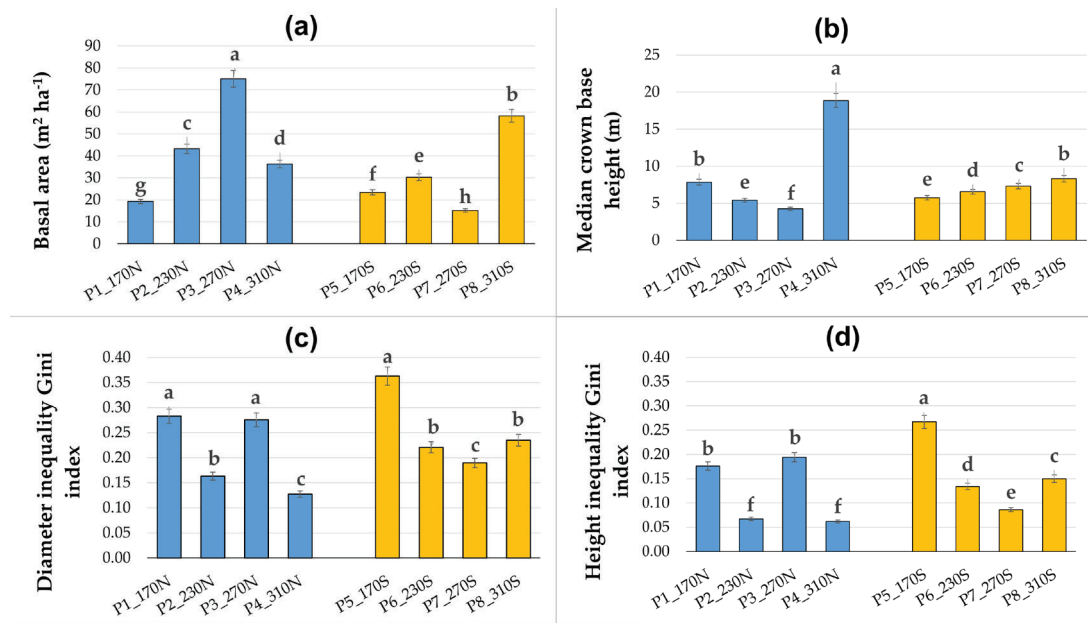


Figure 8. Variation in key stand structural indices among plots: (a) basal area (m² ha⁻¹); (b) median crown-base height (m); (c) Gini index for diameter inequality; (d) Gini index for height inequality.

at low elevation and the middle-elevation north-facing stand are structurally most heterogeneous, whereas the high-elevation north-facing stand is markedly more uniform.

3.2. Herb-layer diversity and composition

Across the sampled plots, the ground-layer vegetation comprised 15 vascular plant species belonging to 10 botanical families (Figure 9). The recorded flora was typical of mesophilous beech–hornbeam forests of the colline zone, including early-spring geophytes, shade-tolerant forest herbs, and clonal evergreen species. The species identified were as follows: *Anemone ranunculoides*, *Carex sylvatica*, *Corydalis solida*, *Ficaria verna*, *Galium aparine*, *Galium odoratum*, *Geranium robertianum*, *Lamium galeobdolon*, *Lathyrus vernus*, *Maianthemum bifolium*, *Pulmonaria officinalis*, *Salvia glutinosa*, *Urtica dioica*, *Viola reichenbachiana*, and *Vinca minor* (Figures 9a–9o).

To summarize the ecological characteristics of the ground-layer vegetation, we assembled species traits and Ellenberg indicator values for light, moisture, soil reaction, and nitrogen (Table 3). The resulting profile reveals a community dominated by sciaphilous forest herbs ($L = 3–5$) associated with mesic, moderately acidic-to-neutral soils ($F = 5–6$, $R = 5–7$), together with several early-spring geophytes typical of old-growth broadleaved forests (Ellenberg et al., 1991). These traits are consistent with the ecological conditions of beech–hornbeam and oak–hornbeam stands of the Moldavian Plateau.

Herb-layer diversity varied considerably among the plots (Figure 10). Plot-level richness (γ) ranged from 2 to 9 species per plot, with both north- and south-facing slopes including relatively species-poor and species-rich plots rather than following a simple altitudinal or aspect-related trend (Figure 10a).

The ecological indices calculated for individual herb-layer species summarized their patterns of dominance, frequency, and distribution along the microtopographic gradient (Appendix A, Table A2). Typical mesophytic forest herbs such as *C. sylvatica*, *G. odoratum*, *V. reichenbachiana*, and *M. bifolium* showed comparatively high values of Shannon diversity (H), Simpson index ($1 - D$) and Fisher's α , together with moderate Menhinick and Margalef richness values. This combination indicates that these species are not only frequent but are also relatively evenly represented across several plots, forming the core of the ground-layer flora in both beech–hornbeam and oak–hornbeam stands. In contrast, early-spring geophytes, such as *A. ranunculoides* and *C. solida*, and some nitrophilous or edge-associated taxa (e.g., *U. dioica*, *G. aparine*) were characterized by dominance and Berger–Parker values close to 1 and by very low or zero Shannon and Simpson indices. These patterns reflect their highly aggregated occurrence, with high local abundance in one or a few plots and virtual absence elsewhere. Several other species, including *F. verna*, *P. officinalis*, *S. glutinosa*, and *G. robertianum*, showed intermediate index values, suggesting a more restricted but still ecologically relevant contribution to understory diversity.

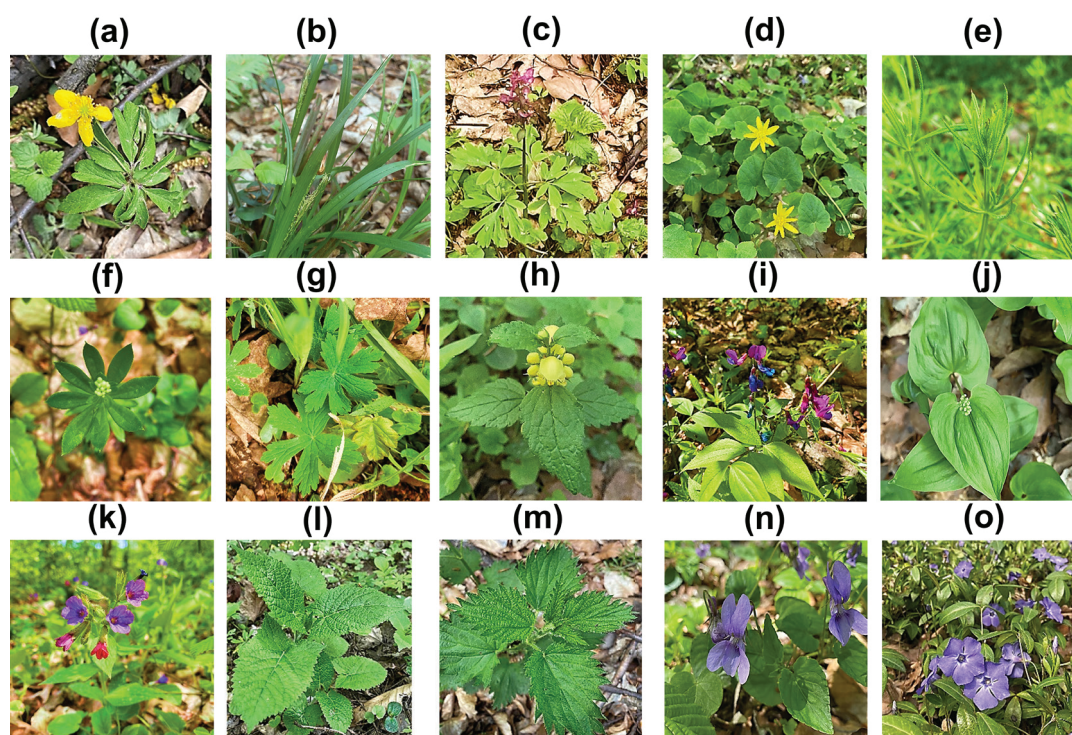


Figure 9. Representative ground-layer vascular plant species recorded across the studied plots: (a) *Anemone ranunculoides*; (b) *Carex sylvatica*; (c) *Corydalis solida*; (d) *Ficaria verna*; (e) *Galium aparine*; (f) *Galium odoratum*; (g) *Geranium robertianum*; (h) *Lamium galeobdolon*; (i) *Lathyrus vernus*; (j) *Maianthemum bifolium*; (k) *Pulmonaria officinalis*; (l) *Salvia glutinosa*; (m) *Urtica dioica*; (n) *Viola reichenbachiana*; (o) *Vinca minor*.

Table 3. Ecological traits and Ellenberg indicator values of the ground-layer vascular plant species recorded across the eight study plots.

Species	Strategy	L	F	R	N	Ecological meaning	Plot occurrence
<i>Anemone ranunculoides</i>	EG	3	5	6	4	Ancient forest geophyte	P6
<i>Carex sylvatica</i>	ST	4	6	5-6	4	Mesophilous forest indicator	P1, P2, P4, P6, P7, P8
<i>Corydalis solida</i>	EG	4	5-6	6	4	Spring ephemeral; old-growth indicator	P6
<i>Ficaria verna</i>	EG	5	5	6	7	Nitrogen-tolerant geophyte	P1, P2, P4, P5, P6, P7
<i>Galium aparine</i>	NF	6	6	6	7-8	Disturbance/nitrogen indicator	P4, P6
<i>Galium odoratum</i>	ST	3	6	6	4	Classic beech–hornbeam indicator	P1, P2, P3, P4, P7, P8
<i>Geranium robertianum</i>	NF	6	5	7	7	Nitrophilous forest-edge herb	P4, P6
<i>Lamium galeobdolon</i>	ST	5	6	6	6	Forest herb, semi-shade	P1, P5, P6
<i>Lathyrus vernus</i>	ST	4	5	6	4	Mature deciduous forest indicator	P7
<i>Maianthemum bifolium</i>	ST	3	5	4-5	3	Old humid mixed forests	P2, P4, P5,
<i>Pulmonaria officinalis</i>	ST	4	6	6-7	6	Mesic deciduous forest indicator	P2, P4, P5, P6
<i>Salvia glutinosa</i>	ST	5	6	6-7	5	Moist forest herb	P2, P4, P5
<i>Urtica dioica</i>	NF	7-8	7	7	9	Strong nitrogen indicator	P2
<i>Viola reichenbachiana</i>	ST	5	5	6	4	Shade-tolerant deciduous forest herb	P1 – P8
<i>Vinca minor</i>	CS	3-4	5	7	5	Clonal species, stable shade	P8

Strategy: Ecological/phenological strategy (EG: early-spring geophyte; ST: shade-tolerant herb; NF: nitrophilous species; CS: clonal spreader). L, F, R, N: Ellenberg indicator values for light, moisture, soil reaction (pH), and nitrogen. Ecological meaning: The species' indicative value for forest site conditions. Plot occurrence: Presence of each species across plots.

The RDA ordination of herb-layer communities (Appendix A, Figure A2) mirrors these patterns and links them explicitly to stand structure and topography. Along the first canonical axis, plots with high basal area and dense, shade-casting canopies (notably P3_270N and P4_310N) are separated from more open stands with lower basal area or higher CBH (e.g., P1_170N, P5_170S, P7_270S). Shade-tolerant forest specialists such as *Galium odoratum*, *Carex sylvatica*, *Maianthemum bifolium*, and *Viola reichenbachiana* are positioned toward the high-basal-area, north-facing stands, consistent with their low Ellenberg light values and preference for mesic, moderately acidic soils. In contrast, nitrophilous and more light-demanding species (e.g., *Urtica dioica*, *Galium aparine*, *Ficaria verna*) are associated with plots characterized by lower basal area, higher median CBH, or south-facing aspects, where understory light and nutrient availability are locally higher. The second canonical axis captures additional variation related to aspect and within-plot heterogeneity (β_W), separating the particularly species-rich south-facing plot at an intermediate elevation (P6_230S) from the remaining stands.

Taken together, the species-level ecological indices highlight a herb layer structured around a set of widespread mesic forest specialists, over which are superimposed more patchily distributed geophytes and nitrophilous species linked to particular microhabitats. This underlines the key role of the herb layer in capturing fine-scale environmental variation along the topographic gradient and complements the plot-level patterns described for ground-layer diversity and composition.

Within-plot β -diversity (β_W) also differed among plots, from ≈ 1.3 to >3.0 (Figure 10b), where $\beta_W \approx 1.3$

indicates almost no within-plot turnover and values of >3 indicate high small-scale heterogeneity layer across the four 1-m² quadrats. Overall, γ and β_W together show that both the amount of herb-layer diversity and its fine-scale spatial heterogeneity vary along the microtopographic gradient.

Cluster analysis of the herb layer provided an integrated view of how fine-scale topography structures understory communities across the eight plots (Figure 11). The heatmap shows that several characteristic mesophytic forest herbs, such as *G. odoratum*, *L. galeobdolon*, *C. solida*, *V. reichenbachiana*, *M. bifolium*, *V. minor*, and *L. vernus*, occur in most plots but with clearly differing relative abundances. The south-facing plot at 230 m (P6_230S) stands out by hosting high abundances of spring geophytes and shade-tolerant herbs (e.g., *F. verna*, *P. officinalis*, *A. ranunculoides*, *C. solida*, *V. reichenbachiana*), together with generalist species such as *V. minor* and *L. vernus*. The high-elevation north-facing plot (P4_310N) also supports a relatively rich assemblage of typical beech–hornbeam forest herbs, including *G. odoratum*, *C. sylvatica*, and *V. reichenbachiana*.

The dendrogram of plots indicates that the majority of north- and south-facing plots share a broadly similar herb-layer composition, forming a main cluster, whereas P6_230S appears more distinct due to its combination of numerous forest specialists and a few nitrophilous species. At the species level, nitrophilous and edge-associated taxa such as *U. dioica* and *G. aparine* are grouped separately from the core group of forest specialists, reflecting their more restricted occurrence in plots with locally higher resource availability. Overall, the herb-layer clustering emphasizes a gradient from plots dominated by typical

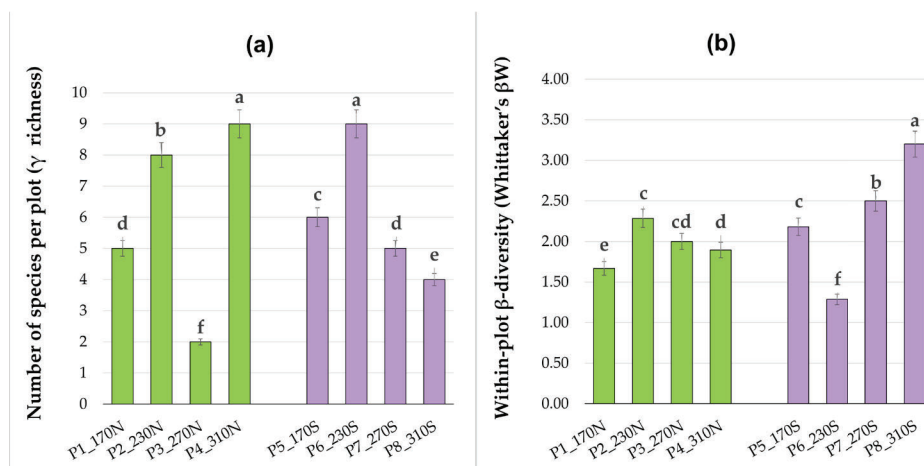


Figure 10. Herb-layer richness and within-plot β -diversity along the fine-scale topographic gradient: (a) plot-level herb species richness (γ); (b) within-plot β -diversity of the herb layer (i.e., Whittaker's β_W).

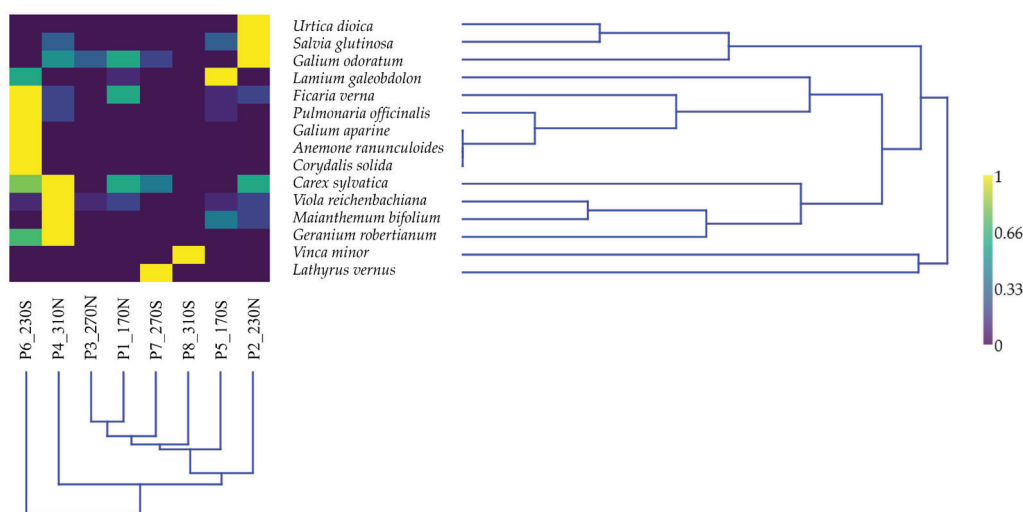


Figure 11. Heatmap of herb-layer species occurrence and hierarchical clustering of plots and species along the fine-scale topographic gradient. Colors represent the normalized relative abundance of each herbaceous species in each plot (0 = absence, 1 = maximum value in the dataset).

mesic deciduous-forest herbs in cooler or more shaded microtopographic positions to plots where these species are less abundant and the understory is characterized by a simpler set of widespread perennials or by locally abundant nitrophilous species.

3.3. Relationships between herbaceous species diversity and stand structural variables

The Jaccard heatmap (Figure 12) summarizes how consistently individual tree species cooccur with herbaceous species across the eight plots. Most tree-herb pairs show low to moderate similarity (Jaccard values of <0.5), indicating that many understory species cooccur with a given tree species in only a small subset of plots, or that they are more broadly distributed than any particular canopy species. Only a limited number of combinations reach higher Jaccard values (>0.6), highlighting a few relatively tight plot-level associations. For example, *A. campestre* and *L. galeobdolon*, *C. betulus* and *V. reichenbachiana*, *F. sylvatica* and *G. odoratum*, or *U. minor* and *L. galeobdolon* tend to cooccur in several plots while being absent together from others, which results in comparatively high similarity coefficients.

Because the Jaccard index is defined based on binary presence-absence data and is highly sensitive to how often species share plots, we use the heatmap as a qualitative summary of cooccurrence structure for the eight intensively sampled stands rather than as a basis for formal significance testing. In this representation, two main features emerge: most tree-herb pairs show weak or inconsistent cooccurrences at the plot scale, and a small group of shade-tolerant tree species is repeatedly associated with characteristic forest-understory herbs, suggesting a

gradient from more generalist to more specialist tree-herb assemblages that complements the stand-level diversity patterns described above.

The correlation heatmap (Figure 13) shows a clear and coherent pattern linking stand structure to herb-layer diversity. Basal area and tree-size inequality (Gini_DBH and Gini_H) are positively related to dominance-based indices (Dominance_D, Berger-Parker) and negatively related to Shannon and richness-type indices (Shannon_H, Brillouin, Margalef, Fisher_alpha), with Spearman ρ values reaching magnitudes of about 0.6–0.7. Taken together, these trends indicate that denser and more structurally unequal stands tend to support herb layers that are less diverse and more strongly dominated by a few species, whereas structurally simpler stands are associated with richer and more even herbaceous assemblages.

Median CBH shows the opposite tendency: plots with higher crown bases tend to have more even and species-rich herb layers, consistent with a more open vertical structure. The number of trees per hectare exhibits similar, but generally weaker, correlations than basal area and the Gini indices, suggesting that overall stem density contributes to these patterns but is less informative than metrics that explicitly describe size and height inequality.

4. Discussion

4.1. Structural complexity and herb-layer diversity along fine-scale topographic gradients

The results of this study reveal that even subtle topographic differences within these mixed deciduous stands correspond to marked variations in forest structure and herb-layer

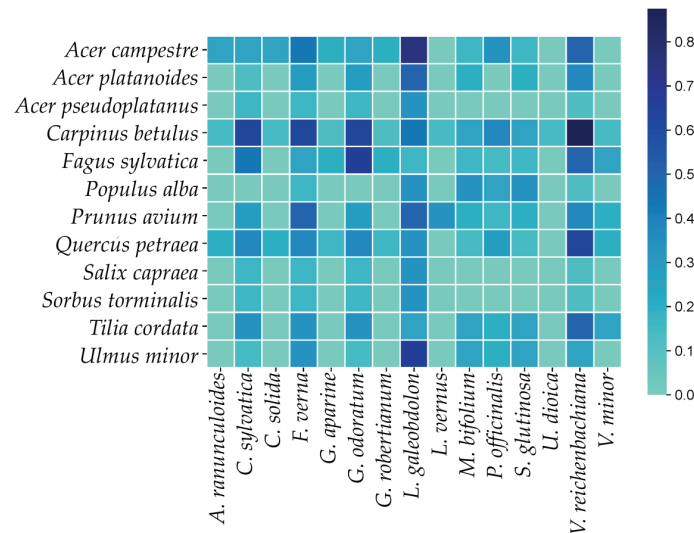


Figure 12. Heatmap of Jaccard similarity between tree species and herbaceous species.

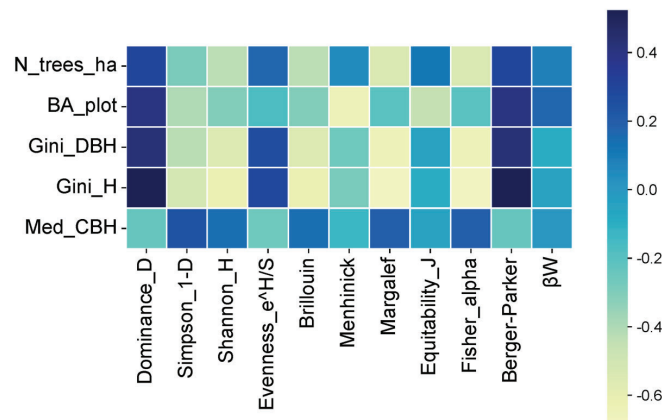


Figure 13. Heatmap of Spearman correlations between stand structural attributes and herb-layer diversity indices across eight forest plots.

diversity, consistent with previous work highlighting topography as a key driver of local plant diversity patterns in temperate forests (Moeslund et al., 2013; Chudomelová et al., 2017). Stands at different microtopographic positions exhibited distinct tree size distributions, as captured by the Gini coefficient, a measure of tree size inequality. Higher Gini values in certain microsites indicate more uneven diameter distributions, a signal of greater structural heterogeneity, whereas lower values reflect more uniform stand structures. Such structural complexity is not merely a statistical curiosity; it often reflects multiage cohorts or localized disturbance regimes creating varied tree sizes and canopy gaps (Reich et al., 2022). Differences in CBH further highlight structural adjustments along the gradient.

At more sheltered or resource-rich microsites, trees tended to self-prune the lower branches, raising the crown base, due to intense competition for light, whereas at harsher or drier microsites, trees retained lower limbs, resulting in a lower CBH. These contrasts in crown architecture imply differences in light penetration and vertical stratification among microhabitats. Notably, stands with higher average CBH likely allow more light to reach the understory, potentially facilitating a richer herb layer (Helbach et al., 2022). These structural contrasts are also consistent with the Ellenberg indicator values of the recorded herbs, which show that the ground-layer flora is dominated by shade-tolerant, mesophilous species and that structurally more open plots tend to host slightly more light-demanding

taxa. Overall, the use of the Gini index and CBH in tandem proved effective for quantifying this fine-scale structural complexity, underscoring how microtopography can shape the physical architecture of forests.

Our finding that simple stem density (trees ha⁻¹) was a weaker predictor than the composite indices implies that not just the quantity of stems but also their size distribution and vertical arrangement are critical in shaping the herb layer. In practice, this means that two stands with equal tree density can have very different understory outcomes if one consists of even-sized trees with high crowns (more light penetration) versus another with an uneven, many-layered canopy (deep shade in lower layers).

A central contribution of our study is the quantitative linking of stand structural metrics to understory diversity patterns. Using a Spearman rank correlation approach, we identified a coherent pattern of relationships: stands with greater basal area and higher size inequality (Gini coefficients for DBH and height) tended to support less diverse, more dominance-skewed herb layers, whereas stands with simpler, even-sized structures (lower Gini coefficients) and higher median CBH were associated with richer and more even herbaceous communities. In practical terms, this means that heavily stocked, uneven-aged stands, which in our case often coincided with monodominant canopies, created conditions where one or two shade-tolerant herb species (e.g., *Galium odoratum* or *Vinca minor*) dominated the ground layer. Conversely, stands with moderate stocking and a more uniform, open structure allowed a broader suite of herb species to coexist. This result resonates with findings from other European studies that have examined forest structure–biodiversity linkages. Kermavnar et al. (2021) showed that herb-layer species richness across 50 temperate forest plots was negatively impacted by strong canopy shading and positively influenced by features like lower tree-layer density and the presence of light-permitting canopy gaps. Similarly, Mestre et al. (2017) found that in southern temperate forests, purely deciduous stands, which generally have higher seasonal light transmittance and lower stem density, exhibited greater understory diversity than stands with evergreen or dense canopies. Our data add fine-scale support to these observations by demonstrating clear correlations ($|\rho| \sim 0.6\text{--}0.7$) between easily measurable inventory indices (basal area, Gini_H, Gini_DBH) and multiple herb-layer diversity metrics. This suggests that forest managers could use such structural indices as proxies or indicators for understory biodiversity in similar forest types. For example, a very high Gini coefficient for DBH in a stand may warn of a strongly stratified, perhaps overtopped canopy structure that is likely suppressing understory richness. On the other hand, a higher median CBH, indicative of a tall bole clearance and thus more light

near the forest floor, could be a positive sign for understory plant development.

4.2. Mechanisms linking overstory and ground-layer communities and implications for forest management and biodiversity conservation

In addition to these structural correlations, our analysis of tree–herb species cooccurrences via the Jaccard similarity heatmap provides insight into the specificity (or lack thereof) of overstory–understory associations. We found that most herbaceous species in our study are not tightly bound to a single tree species; rather, they appear opportunistic, colonizing any plot where suitable microhabitat exists, irrespective of which particular canopy species are present. This is evidenced by the generally low Jaccard similarity values (<0.5) for most tree–herb pairs. In other words, a given herb, such as *Carex sylvatica* or *Pulmonaria officinalis*, occurred with multiple different canopy compositions across the eight plots, indicating broad tolerance. Nevertheless, a few notable higher Jaccard values emerged, highlighting relatively consistent associations: for example, *Fagus sylvatica* and *Galium odoratum* frequently cooccurred (both were present together in several plots), as did *Carpinus betulus* with *Viola reichenbachiana*, and *Acer campestre* with *Lamium galeobdolon*. These pairings make ecological sense as *G. odoratum* and *V. reichenbachiana* thrive under the deep shade and moist litter often provided by beech or hornbeam, whereas *Lamium* (a semishade, nutrient-loving herb) benefits from the lighter conditions and richer soils often found in mixed maple stands.

While our dataset is too limited for rigorous tests of association, the cooccurrence analysis qualitatively supports the idea that certain understory plants are favored by the microenvironment created by specific canopy trees. This is in agreement with broader vegetation studies; for example, classical Central European phytosociology recognizes *Galium odoratum* as a characteristic herb of beech-dominated forests and *Lamium galeobdolon* as frequent in oak–hornbeam settings on fertile soils (Novák et al., 2020, 2023). However, our results also underscore that these relationships are not exclusive; the ground flora is largely composed of generalist forest herbs that can subsist under any canopy providing sufficient shade and moisture. Thus, maintaining the diversity of canopy species might not lead to one-to-one correspondence with unique herb species, but it ensures a range of microhabitats that collectively support a higher gamma-diversity of understory plants.

From an applied perspective, the above findings carry several important implications. First, they highlight that structural complexity is a double-edged sword: while a multilayered, high-biomass stand may be structurally “complex” in forestry terms, it can actually impoverish the

herb layer due to intense light competition. In our study, the most structurally heterogeneous plots (e.g., P3_270N with very high DBH Gini coefficient and dense basal area) had lower herb richness than more “simple” open stands (e.g., P7_270S). This suggests that forest managers aiming to enhance vascular plant diversity should avoid uniformly heavy canopy stocking. Thinning interventions or partial harvest that reduce basal area and create gaps can release the herb layer without necessarily sacrificing tree regeneration, a conclusion supported by numerous studies on beech and oak forests. For example, selective thinning in German beech forests has been shown to increase herb cover and species number by increasing light heterogeneity, with no loss of typical shade-tolerant species (von Oheimb and Härdtle, 2009). Similarly, a study in Romania found higher herb-layer Shannon diversity in coppiced beech forests compared with beech high forests, suggesting a positive effect of coppicing on understory plant diversity (Šebesta et al., 2017).

Our results provide mechanistic backing for these observations: greater light availability via higher CBH and lower stand density directly correlates with richer herb communities. This implies that mixed-species stands, especially those combining species with different crown architectures or phenologies (e.g., early leafing vs. late leafing), could foster a longer or more varied light period for the herb layer, thus accommodating more species. Indeed, a pan-European analysis by Evy et al. (2016) concluded that, when environmental context is accounted for, higher tree diversity can promote greater understory plant diversity, likely through increased resource heterogeneity. However, that study and others also caution that the relationship is context-dependent: in very fine-grained mixtures or in certain fertile sites, overstory diversity per se may have neutral or even negative effects if one species such as beech functionally dominates the light environment. In our case, the positive tree–herb diversity linkage likely reflects the complementary traits of *Quercus*, *Carpinus*, and minor broadleaves creating a mosaic of light conditions. The takeaway for management is that simply maximizing tree species count is not a silver bullet for herb diversity; one must also consider the identity and functional traits of the canopy species. Mixtures that include highly shade-casting species will need structural management, like thinning or group selection cuts, to ensure that understory light levels remain sufficient for diverse herbs.

5. Conclusion

In summary, our study demonstrates that even subtle fine-scale topographic differences (on the order of 100–150 m altitude and contrasting slope aspects) can drive significant variation in forest structure and understory plant diversity. Altitude and slope aspect jointly shaped

tree density, species composition, and vertical structure, which in turn governed the richness and composition of herb-layer communities. These findings highlight a clear mechanistic link between overstory architecture and understory biodiversity, underscoring the scientific value of integrating stand structural metrics with microtopographic gradients. The results are not only scientifically novel, filling an important knowledge gap for East European colline forests; they also carry practical implications. Forest managers and conservation planners can apply this knowledge to biodiversity-oriented management, for example by preserving a mosaic of microsites and structural conditions to maintain high understory diversity.

While the observed trends are compelling, the results should be interpreted with caution given the observational nature of the study and the sample size, and further research based on larger samples and extended timeframes will be needed to support broader generalizations. Overall, this study’s original approach and findings contribute to a more nuanced understanding of forest diversity patterns, emphasizing that fine-scale environmental heterogeneity is a key driver of biodiversity even in managed temperate forests.

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Appendix A

Appendix A.1

Table A1. Diversity indices of tree species in the studied plots.

Plot	P1_ 170N	P2_ 230N	P3_ 270N	P4_ 310N	P5_ 170S	P6_ 230S	P7_ 270S	P8_ 310S
Taxa_S	10	2	5	1	7	3	3	3
Individuals	36	15	16	12	30	16	23	20
Dominance_D	0.18	0.75	0.29	1	0.38	0.43	0.58	0.33
Simpson_1-D	0.81	0.25	0.70	0	0.62	0.57	0.42	0.67
Shannon_H	1.96	0.43	1.42	0	1.39	0.96	0.73	1.1
Evenness_e^H/S	0.71	0.76	0.83	1	0.58	0.87	0.69	1
Brillouin	1.53	0.31	1.01	0	1.06	0.73	0.58	0.89
Menhinick	1.67	0.52	1.25	0.29	1.28	0.75	0.62	0.67
Margalef	2.51	0.37	1.44	0	1.76	0.72	0.64	0.67
Equitability_J	0.85	0.61	0.88	NA	0.72	0.88	0.67	1
Fisher_alpha	4.59	0.62	2.5	0.26	2.87	1.09	0.92	0.98
Berger-Parker	0.33	0.87	0.5	1	0.6	0.62	0.74	0.45

Cells with "NA" indicate plots where Equitability_J is not defined ($S = 1$).

Appendix A.2

Table A2. Diversity indices of herbaceous species in the studied plots.

Plot	P1_ 170N	P2_ 230N	P3_ 270N	P4_ 310N	P5_ 170S	P6_ 230S	P7_ 270S	P8_ 310S
Taxa_S	5	8	2	9	6	9	5	4
Individuals	166	156	28	206	71	350	49	203
Dominance_D	0.27	0.29	0.65	0.24	0.43	0.17	0.36	0.91
Simpson_1-D	0.73	0.71	0.35	0.76	0.57	0.83	0.64	0.09
Shannon_H	1.39	1.47	0.54	1.66	1.20	1.96	1.25	0.24
Evenness_e^H/S	0.80	0.54	0.85	0.58	0.56	0.79	0.70	0.32
Brillouin	1.33	1.37	0.45	1.57	1.06	1.89	1.08	0.21
Menhinick	0.39	0.64	0.38	0.63	0.71	0.48	0.71	0.28
Margalef	0.78	1.39	0.30	1.50	1.17	1.37	1.03	0.56
Equitability_J	0.86	0.71	0.77	0.75	0.67	0.89	0.78	0.17
Fisher_alpha	0.97	1.78	0.49	1.92	1.56	1.68	1.39	0.71
Berger-Parker	0.38	0.43	0.79	0.34	0.63	0.30	0.55	0.95

Cells with "NA" indicate plots where Equitability_J is not defined ($S = 1$).

Appendix B
Appendix B.1

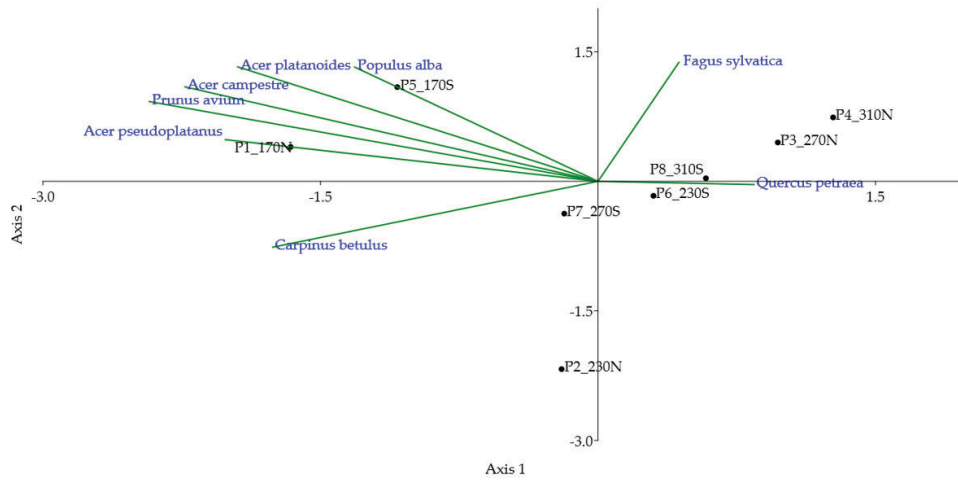


Figure A1. Ordination biplot of tree species and sample plots based on species composition

Appendix B.2

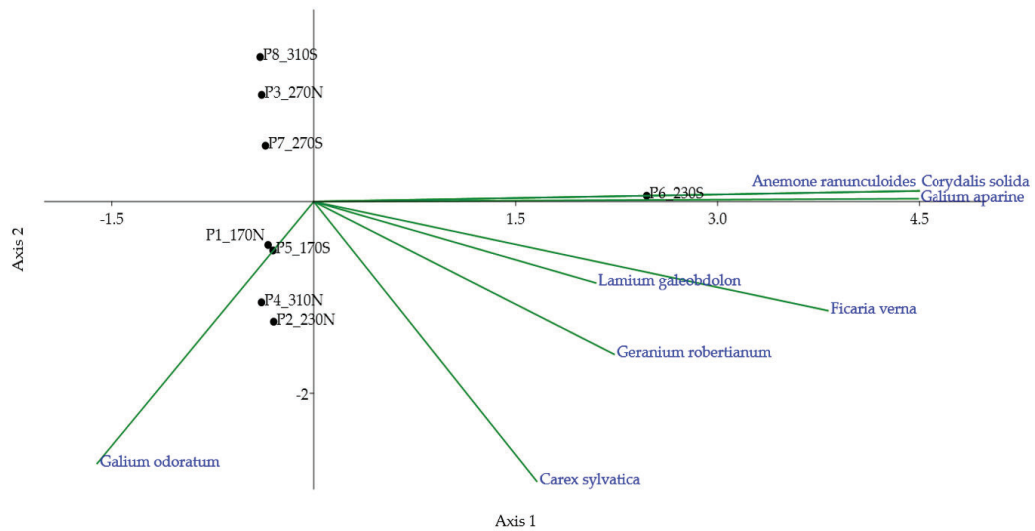


Figure A2. Ordination biplot of herbaceous species and sample plots based on species composition