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Effects of natural disturbances on environmental conditions, understory plant diversity, and functional strategies in montane forests

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Abstract: Natural disturbances are major drivers of forest ecosystem dynamics, yet their combined effects on soil properties, understory vegetation, and plant functional strategies remain insufficiently understood, particularly in mountain forests. We investigated the impacts of large-scale natural disturbances on understory plant communities in the Tatra Mountains (southern Poland). Using a paired twin-plot study design, we compared vegetation composition, species diversity, ecological CSR strategies, and selected soil physicochemical properties between sites of long-term forest continuity and disturbed ones.

A total of 86 vegetation plots representing 43 paired disturbed-undisturbed sites were surveyed in 2020 and 2021. Species composition differed significantly between disturbed and undisturbed forests, indicating reorganization of understory communities after disturbances. Disturbed plots were characterized by a higher abundance of ferns, grasses, and expansive species, whereas undisturbed forests supported species typical of mature beech and spruce stands. Contrary to expectations, disturbance did not significantly affect soil carbon, nitrogen, C/N ratio, pH, or sum of exchangeable base cations. In contrast, disturbed sites exhibited significantly higher soil moisture and capillary water capacity. Species richness was slightly higher in disturbed forests, while species evenness was significantly lower, particularly at higher elevations, suggesting increased dominance of a limited number of species. Analyses of plant life strategies based on functional traits revealed a significantly lower contribution of ruderals in disturbed plots, whereas species representing competitive and stress-tolerant strategies did not differ between disturbance categories.

Our results indicate that the ecological consequences of bark beetle outbreaks and wind disturbances in the Tatra Mountains are driven primarily by changes in microclimatic and hydrological conditions rather than by nutrient enrichment. The observed patterns suggest that understory vegetation responses reflect relatively advanced successional stages, where competitive species dominate while ruderal species remain of minor importance.

Keywords: plant diversity, natural disturbances, forest dynamics, herbaceous plants, forest ecology, plants life strategies

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Introduction

Natural ecosystems are increasingly affected by global environmental change, which alters the structure, functioning, and species composition of forest ecosystems worldwide (Franklin et al., 2016). One of the most visible drivers of these changes is the increasing frequency, extent, and severity of natural disturbances, including bark beetle outbreaks, windstorms, droughts, pathogens, and wildfires (Seidl et al., 2017; Turner, 2010). In temperate montane forests, such disturbances frequently result in extensive tree mortality, fundamentally transforming ecosystem structure and functioning (Kulakowski et al., 2017). Due to their longevity, large biomass, and dominant structural role, trees strongly regulate forest microclimate, nutrient cycling, hydrology, and biotic interactions (De Frenne et al., 2021; Ellison et al., 2005). Consequently, disturbance-driven canopy mortality affects not only tree populations but also the majority of organisms associated with forest ecosystems, particularly understory vegetation (De Frenne et al., 2021; Hart & Chen, 2008; von Oheimb et al., 2007; Roberts & Gilliam, 1995). Natural disturbances may alter forest environments through both physical and biogeochemical mechanisms. Canopy opening typically increases light availability and modifies temperature and moisture conditions (Sanczuk et al., 2023), while decomposition of dead organic matter may accelerate nutrient cycling and temporarily increase nutrient availability through resource release processes (Beudert et al., 2015; Bormann & Likens, 1979; Vitousek & Reiners, 1975).

Disturbance effects are highly heterogeneous and depend strongly on disturbance type, severity, spatial extent, and time elapsed since disturbance (Denslow, 1980). Different disturbance agents may generate contrasting ecological responses. For example, windthrow events are often associated with increased understory diversity due to creating higher habitat heterogeneity and light availability (von Oheimb et al., 2007; Ulanova, 2000), whereas the effects of high-severity fires on local species richness are context-dependent and may range from an initial decline caused by direct vegetation mortality to a temporary increase driven by species colonization and successional dynamics (Mahood & Balch, 2019; Schüle & Heinken, 2025). Similarly, the recovery dynamics after disturbance may vary considerably, with short-term declines in diversity followed by increases during subsequent successional stages. According to the intermediate disturbance hypothesis, disturbances of moderate severity may promote coexistence by increasing niche availability and reducing competitive exclusion (Connell, 1978; Wilkinson, 1999).

Forest understory vegetation is particularly sensitive to disturbances because its composition and diversity are strongly regulated by canopy structure and disturbance regimes. At the same time, the herb layer represents the most species-rich component of many temperate forest ecosystems and contributes substantially to total forest biodiversity (Gilliam, 2007). Despite the ecological importance of understory vegetation, responses of plant functional traits and functional strategies to natural disturbances remain considerably less studied than taxonomic responses (Cacciatori et al., 2022). Functional approaches may provide deeper insights into ecosystem processes by revealing changes in ecological strategies, stress tolerance, and regeneration potential, rather than focusing solely on species composition.

Natural disturbances affect not only aboveground vegetation structure but also belowground ecosystem processes associated with soil functioning and nutrient cycling (Błońska et al., 2018). Disturbance-driven changes in organic matter inputs, microclimatic conditions, and decomposition dynamics may substantially alter soil biological activity, carbon sequestration, and nutrient availability (Błońska et al., 2016). Because soil processes strongly regulate plant regeneration and resource acquisition, understanding the interactions between disturbance regimes, soil properties, and root functional traits is essential for predicting forest recovery trajectories. Soil-related responses to disturbance may therefore play a key role in shaping ecosystem resilience, regeneration dynamics, and long-term forest functioning (Lasota et al., 2020). Increased light availability and changes in soil temperature and moisture regimes may influence decomposition processes and nutrient turnover (Hou et al., 2025). Disturbance-related changes in microclimate may also alter patterns of organic matter accumulation and affect belowground ecosystem functioning (Tong et al., 2024). These processes may consequently influence forest regeneration following disturbance.

The aim of this study was to determine the effects of natural disturbances on forest vegetation and soil properties. Specifically, we addressed the following research questions:

1. How do natural disturbances modify environmental conditions, including soil physicochemical properties, and how are these changes reflected in plant species composition?

We expect that natural disturbances alter environmental conditions through changes in canopy cover, microclimate, and soil physicochemical properties. Disturbance-driven canopy reduction may increase light availability and soil moisture by reducing competition for water resources, while decomposition of dead biomass may enhance nutrient availability in the topsoil. These changes are expected to favor nitrophilous and moisture-demanding plant species, leading to shifts in species composition in disturbed

sites. However, increases in soil organic carbon and nutrient pools may become detectable only over longer time scales because of the slow decomposition rates and delayed nutrient cycling in mountain forest ecosystems.

2. How plant diversity and species composition respond to natural disturbances? We expect plant diversity to show varied responses, differing along environmental gradients?

Disturbances may promote the dominance of expansive species, potentially reducing species diversity at some sites. In other cases, disturbed areas may support higher plant diversity due to the emergence of numerous ecological niches associated with increased habitat heterogeneity. Under such conditions, both early- and late-successional species may coexist, resulting in relatively high species evenness. Regardless of disturbance occurrence, plant evenness is expected to decrease with increasing elevation, reflecting the general tendency of high-elevation communities to exhibit lower species richness and stronger dominance by a few species.

3. How natural disturbances influence plant species composition in terms of life-history strategies?

We expect that disturbances will alter the distribution of plant life-history strategies, although the direction and magnitude of these changes may vary among disturbed sites due to differences in post-disturbance environmental conditions. Disturbed sites may favor ruderal species (R), as canopy opening and increased resource availability can facilitate the colonization and dominance of pioneer species. In other cases, disturbed habitats may support a more balanced distribution of ecological strategies as a result of increased environmental heterogeneity. Under such conditions, species representing different life-history strategies, including ruderal (R), competitive (C), and stress-tolerant (S) species, may coexist within the same communities.

Methods

Study area

The study was conducted in the Tatra National Park, located in southern Poland. The park encompasses the Polish part of the Tatra Mountains (21 197 ha) and has been protected for more than 70 years since its establishment in 1955. The Tatra Mountains constitute the highest mountain range in the Carpathians and form the central-western part of the Carpathian Arc. Due to their alpine character, rapid transitions between climatic zones, and high habitat heterogeneity, the Tatra Mountains are considered a biodiversity hotspot within Central Europe. Approximately 1,300 species of vascular plants have been recorded within Tatra National Park (Piękoś-Mirkowa & Mirek, 2003; Szymura et al., 2023; Zięba et al., 2023). Currently, nearly 71% of the park area, including 56% of its forested area, is strictly protected (Parusel & Zwijacz-Kozica, 2018).

Prior to the establishment of the national park, Tatra Mountains forests were subjected to strong anthropogenic pressures, the effects of which are still reflected in contemporary vegetation (Foremnik et al., 2026). In particular, species-rich lower montane forests, originally dominated by European beech (*Fagus sylvatica*) and silver fir (*Abies alba*), were extensively transformed into Norway spruce (*Picea abies*) monocultures. These transformations resulted in reduced understory species diversity and decreased forest stand stability. Consequently, forests of the Tatra Mountains became highly susceptible to large-scale disturbances caused by the combined effects of windstorms and bark beetle outbreaks, which led to extensive tree mortality. As a result, the contemporary forest landscape of the Tatra Mountains represents a mosaic of different developmental stages, ranging from recently disturbed stands, through various phases of forest regeneration, to old-growth forests (Sproull et al., 2017; Szwagrzyk et al., 2021).

The Tatra Mountains exhibit pronounced altitudinal zonation typical of mountain ecosystems. Lower montane forests occur at elevations between 900 and 1,250 m a.s.l. and are characterized by a moderately cold climate, with a mean annual air temperature of approximately 5°C and annual precipitation around 1,100 mm. These forests are dominated by European beech, silver fir, and Norway spruce, often accompanied by rowan (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*). At higher elevations, up to 1,550 m a.s.l., upper montane forests are dominated primarily by Norway spruce. Climatic conditions in this zone are considerably harsher, corresponding to a cold mountain climate, with mean annual temperatures decreasing to approximately 3°C and annual precipitation increasing to around 1,400 mm (Bodziarczyk et al., 2019; Pielech et al., 2021). The highest forest stands in the Tatra Mountains are relict forests dominated by Swiss stone pine (*Pinus cembra*) (Zięba et al., 2018).

The geological substrates underlying the Tatra Mountains forests vary with elevation and across different parts of the mountain range. In general, the northern and central parts of Tatra National Park are composed primarily of sedimentary rocks (limestones and dolomites), whereas the southern part belongs to the Tatra Mountains crystalline massif formed by gneisses, granodiorites, and granites (Piotrowska et al., 2015).

Field sampling and laboratory works

Vegetation survey

This study is based on paired plots (also referred to as twin plots) located close to each other, where one of the plots was sampled in mature old-growth forest and the second one was sampled in an area affected by natural disturbances. During the 2021 and 2022 growing seasons, phytosociological studies were conducted in the forested part of the Tatra Mountains and focused on mature forest stands. As this data were collected not only for this study, but also for long-term analysis of vegetation change, their location followed approximate locations of research plots established in the 1920s (Pawłowski et al., 1928; Pawłowski & Stecki, 1927; Szafer, 1923; Szafer et al., 1927; Szafer & Sokołowski, 1927). For a detailed description of selecting plot localities, see Foremnik et al. (2026). Most of the research plots sampled in old-growth forests were located very close to areas that had been affected by disturbance events. In that case, the disturbed plot was paired with a nearby undisturbed plot, forming so-called "twin plots". Natural disturbance was defined as a reduction of the forest canopy across at least 80% of the plot area, i.e., the tree layer was absent from the majority of the plot. Disturbed areas were further characterized by the absence of a regenerated tree canopy exceeding 5 m in height. Based on these criteria, plot classification was determined by the current structural characteristics of the stands rather than by a predefined period elapsed since disturbance. The study area was primarily affected by large-scale bark beetle outbreaks during 2009–2013 and 2016–2017 (Bodziarczyk et al., 2019; Sproull et al., 2017), although disturbance history likely varied among individual plots.

Plot size was determined based on historical records whenever such information was available; otherwise, the median value of the documented range of historical plot sizes was applied. Most plots covered 400 m^2 (20 × 20 m), with the exception of two plots measuring 1500 m^2. The geographic coordinates of all plots were recorded using a high-precision GPS receiver (Ashtech MobileMapper 60) integrated with a mobile GIS database (Collector for ArcGIS, ESRI). Field topography and elevation were derived in a GIS environment (ArcGIS Pro 2.6.3, ESRI Inc.) using a high-resolution digital elevation model provided by the Tatra National Park and precise field-recorded GPS coordinates.

In total, 86 research plots were established, representing 43 paired twin plots. Phytosociological relevés were conducted following the Braun-Blanquet approach and using the Braun-Blanquet cover-abundance scale. Species cover was recorded separately for the tree, shrub, and herbaceous layers, while bryophytes were not surveyed. Taxonomic nomenclature was standardized according to the Euro+Med Plant Database (accessed 2 January 2024). Species data were collected in the field using the VegApp 2.0 application (developed by Sebastian Schmidtlein, Karlsruhe Institute of Technology) (Schmidtlein et al., 2026).

Soil samplings and lab analyses

Soil samples were collected from each plot and were taken from three locations arranged diagonally across the area to capture spatial variability (N = 258). After removing the surface litter layer consisting of fresh, undecomposed plant residues, soil samples were collected from the upper 0-10 cm, representing the first humus-accumulation horizon, where plant roots predominantly develop. Soil samples for chemical analyses were put into plastic bags to determine soil texture, pH, carbon (C) and nitrogen (N) content, and the sum of exchangeable base cations (cmol(+) kg^{-1}). Additionally, intact soil samples with undisturbed structure were collected using Kopecky cylinders for the determination of soil physical properties.

Soil samples collected for chemical analysis were oven-dried at 70 °C and sieved through a 2.0 mm mesh before analysis. Soil pH was determined potentiometrically in distilled water (H_2O). The carbon (C) and nitrogen (N) concentrations were measured using an elemental analyser (LECO CNS TruMac Analyser; LECO, St. Joseph, MI, USA), and the C/N ratio was subsequently calculated. Exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) were extracted using a 1 M ammonium acetate solution and analysed by inductively coupled plasma optical emission spectrometry (ICP-OES; iCAP 6500 DUO, Thermo Fisher Scientific, Cambridge, UK). Bulk density, dry bulk density, soil moisture, total porosity, capillary water capacity, and air capacity were determined using the Kopecký cylinder method (Šarapatka, 2015; Ostrowska et al., 1991) on undisturbed soil samples of known volume. The method allows the characterization of soil density, pore space, and water-air relationships based on the mass and water content of samples under different moisture conditions. Capillary water capacity represents the amount of water retained within the capillary pore space under standardized conditions and was therefore distinguished from soil moisture, which represents the actual water content of the soil at the time of sampling. The equations used to calculate the above-mentioned values are included in Supplementary Materials (S1).

Statistical analyzes

All analyzes were conducted and figures were drawn in R 4.4.3 (R Core Team, 2025). We used packages for data wrangling, statistical analyzes, and

graphical presentation, including 'tidyverse' (here 'tidyr', 'dplyr' and 'ggplot2'; Wickham et al., 2019), 'vegan' (Oksanen et al., 2022), 'MultiTraits' (He et al., 2026), 'ggpubr' (Kassambara, 2020), 'FD' (Laliberté et al.,2014), 'patchwork' (Pedersen, 2024) and 'egg' (Auguie, 2019).

Environmental variables and species diversity

Differences in species composition between paired twin plots representing areas with long-term forest continuity and forests affected by natural disturbances were tested using permutational multivariate analysis of variance (PERMANOVA). To assess the assumption of homogeneity of multivariate dispersion, a PERMDISP analysis was additionally performed. The non-significant PERMDISP result indicated similar within-group heterogeneity, suggesting that detected differences were attributable to shifts in community composition rather than differences in dispersion among groups (Anderson, 2006; Bakker, 2026). We additionally visualized the species composition of the studied plot types using Non-metric Multidimensional Scaling (NMDS) ordination. NMDS based on Bray–Curtis dissimilarities was selected because of its robustness in handling non-linear ecological relationships, high species turnover, and zero-inflated community datasets, making it particularly suitable for vegetation data (Borcard et al., 2018). The final two-dimensional solution achieved a goodness of stress value = 0.18, indicating an acceptable and ecologically interpretable ordination (Clarke, 1993). To improve interpretation of the ordination space, both study plots and the most informative species were visualized. Rare species occurring in fewer than five plots were excluded prior to plotting. From the remaining taxa, the 25 species with the greatest Euclidean distance from the ordination centroid were selected using the *slice_max()* function. Species located farther from the center of the ordination space were considered more strongly associated with major compositional gradients and therefore more informative for interpreting the NMDS structure.

To identify environmental variables distinguishing disturbed from undisturbed plots, environmental vectors were passively fitted onto the ordination space using the *envfit()* function. For each variable, the coefficient of determination (R^2) and statistical significance were calculated using permutation tests with 999 iterations. In addition to directly measured soil properties, we also included variables derived from species composition using Ecological Indicator Values for Europe (EIVE; Dengler et al., 2023). These indicator values describe species' ecological preferences along major environmental gradients, including light availability, soil moisture, temperature, soil reaction, and nitrogen availability. However, because several of these environmental characteristics were also quantified directly through soil measurements, only the indicator values for light and temperature were retained for further analyses in order to avoid redundancy between measured and inferred variables. Only variables significantly associated with the ordination structure ($p < 0.05$), together with elevation, species richness, and the Shannon Diversity Index (SDI), were fitted onto the ordination space. Correlations between selected environmental variables and NMDS axes were subsequently evaluated using Pearson correlation coefficients. The above-mentioned diversity metrics, namely species richness and SDI, were further compared between disturbed and undisturbed plots to assess the effects of natural disturbances on plant diversity. In addition, Pielou's evenness index was calculated, as it integrates both species richness and species diversity while reflecting the degree of dominance by particular species within a community.

Soil variables and diversity indices were compared between plot types using paired Wilcoxon signed-rank tests, reflecting the twin-plot study design. Relationships between soil properties, diversity indices, and elevation were additionally analyzed and significant or main results were presented in the main manuscript.

Plant life strategies

Plant ecological strategies were classified according to the CSR framework proposed by Grime (1977), which distinguishes three primary adaptive strategy types: competitors (C), stress-tolerators (S), and ruderals (R). To quantify these strategies, we applied the globally standardized CSR classification method developed by Pierce et al. (2017), which estimates plant ecological strategies based on functional trait relationships. This approach uses three key leaf functional traits: leaf dry matter content (LDMC; %), leaf area (LA; mm^2), and specific leaf area (SLA; $mm^2\ mg-1$), allowing consistent comparison of plant ecological strategies across different species and environmental conditions. Using the TRY Plant Trait Database (Kattge et al., 2020) and LEDA Traitbase databases (Kleyer et al., 2008), leaf functional trait data were assigned to approximately 90% of the species included in the study. Based on the CSR classification framework proposed by Pierce, the proportional representation of competitor (C), stress-tolerator (S), and ruderal (R) strategies was calculated for each species. Species were subsequently projected into CSR trait triangle space together with abundance-weighted community means visualized separately for disturbed and undisturbed plots. To facilitate comparison between plot types, centroids representing the average community-level CSR composition were also calculated and visualized

within the CSR triangle. The proportional contribution of each plant ecological strategy was compared between disturbed and undisturbed twin plots using paired Wilcoxon signed-rank tests, reflecting the twin plots structure of the study design.

The plant species recorded in the study plots and the corresponding values of their functional traits (Supplementary Materials S2 and S3).

Results

Changes in soil properties and species composition caused by disturbance

Species composition differed significantly between disturbed and undisturbed plots (PERMANOVA, $p < 0.001$), indicating clear differences in plant community structure between these two groups. PERMDISP analysis indicated no significant differences in multivariate dispersion between groups ($F = 0.172$, $p = 0.69$), suggesting that the significant PERMANOVA result reflected differences in community composition rather than differences in within-group heterogeneity.

Differences in species composition between the two plot types were also evident in the NMDS ordination space (Fig. 1). The separation between disturbed and undisturbed plots was driven primarily by the second ordination axis (NMDS2; Fig. 1, top panel). Species more strongly associated with disturbed plots included ferns such as *Athyrium distentifolium* and *Dryopteris dilatata*, grasses (e.g., *Hordelymus europaeus*, *Millium effusum*), and tall plant species that rapidly colonize disturbed areas and form dense patches (hereafter referred to as expansive species) such as *Rubus idaeus* and *Epilobium angustifolium*. In contrast, understory communities associated with long-term forest continuity were characterized by species typical of mature beech forests (e.g., *Actaea spicata*, *Dentaria bulbifera*, *Neottia nidus-avis*, and *Galium odoratum*) as well as subalpine spruce forests (e.g., *Vaccinium myrtillus* and *Lycopodium annotinum*). The gradient between fertile and nutrient-poor habitats was also strongly correlated with the NMDS1 ordination axis, as indicated by soil chemical properties such as soil pH, the sum of exchangeable base cations, and soil moisture (Fig. 1, bottom panel; Table 1). Elevation also followed this gradient, since soils are generally poorer at higher elevations, while they are richest at lower elevations. The NMDS analysis showed that vegetation composition was strongly related to soil properties. The most important factors differentiating the studied plots were soil pH and the sum of exchangeable base cations. An increase in soil pH and sum of exchangeable base cations was associated with a shift of plant communities toward those typical for more fertile habitats. Species richness and the Shannon Diversity Index (SDI) also increased with higher pH values and greater sum of exchangeable base cations, suggesting that more fertile soils supported higher floristic diversity. In contrast, the separation between disturbed and undisturbed plots was primarily associated with the NMDS2 axis (Fig. 1, bottom panel), which showed a positive correlation only with the light indicator value (Table 1). Elevation was primarily associated with temperature, but also exhibited a predictable positive relationship with moisture and light availability, while being negatively associated with diversity indices and soil pH.

Soil chemical properties did not change significantly following natural disturbance events (Fig. 2). This pattern was consistent both for key plant-related soil characteristics, such as carbon (C), nitrogen (N), and the C/N ratio, as well as for the sum of exchangeable base cations (including Na, Ca, K, and Mg). However, disturbed and undisturbed plots differed significantly in several moisture-related soil parameters. Disturbed plots exhibited significantly higher capillary water capacity and soil moisture compared to undisturbed plots.

Influence of natural disturbance on plant diversity

We found different effects of natural disturbances on forest vegetation across the analyzed diversity metrics, including species richness, the Shannon–Wiener diversity index (SDI), and species evenness (Fig. 3). Although the patterns of species richness varied considerably among study plots, disturbed sites showed, on average, slightly higher species richness compared to undisturbed forests (mean species richness: undisturbed = 39 ± 19; disturbed = 43 ± 19). However, a different pattern emerged when species abundances were taken into account. The Shannon–Wiener diversity index, which incorporates both species richness and the relative abundance of species, showed a slight decrease in disturbed

Table 1. Pearson correlation coefficients between environmental variables and sample scores of NMDS axes 1 and 2. Bold values indicate statistically significant correlations ($p < 0.05$)

Variable	Altitude [m a.s.l.]	Species richness	Species diversity	Indicator: light	Indicator: temperature	Soil pH	Gravimetric soil moisture	∑ Basic cations
NMDS1	**−0.582**	**0.768**	**0.784**	−0.196	**0.677**	**0.847**	**−0.368**	**0.627**
NMDS2	0.273	0.139	0.203	**0.430**	0.033	−0.13	0.017	−0.098

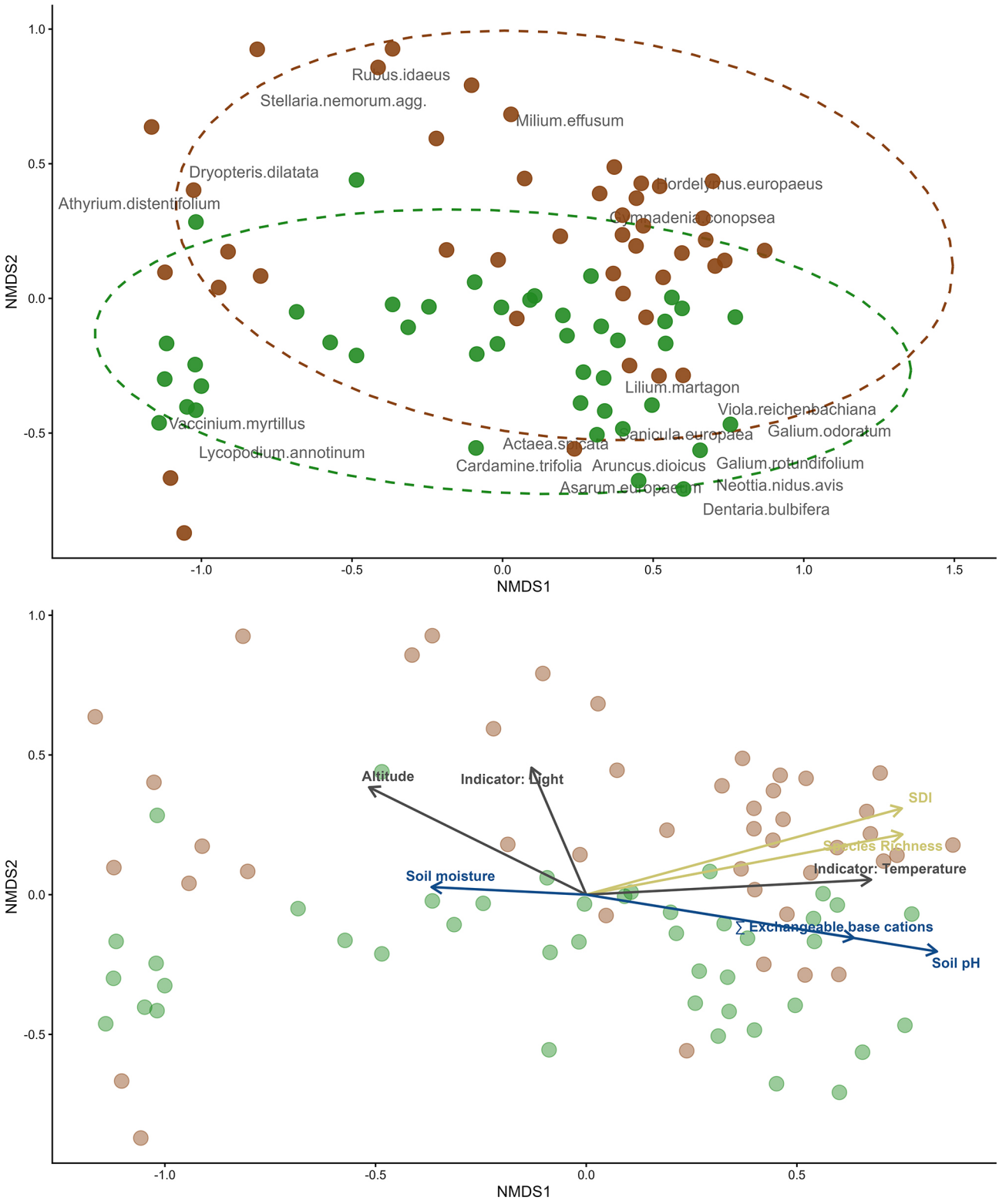


Fig. 1. Changes in plant community composition between undisturbed and disturbed forest sites visualized in multidimensional space using non-metric multidimensional scaling (NMDS). Colours of dots indicates studied plot type: green – forest continuity (Undisturbed), brown – affected by natural disturbance (Disturbed). Top panel: ordination of study plots (filled dots) showing differences in community similarity between undisturbed and disturbed sites; grey species labels indicate taxa associated with particular plot clusters. Bottom panel: ordination of the same study plots with passively fitted vectors representing selected significant soil properties, mean ecological indicator values and diversity indices. Arrow colors represent groups of variables: blue – soil properties, grey – mean indicator values and altitude, and gold – diversity indices

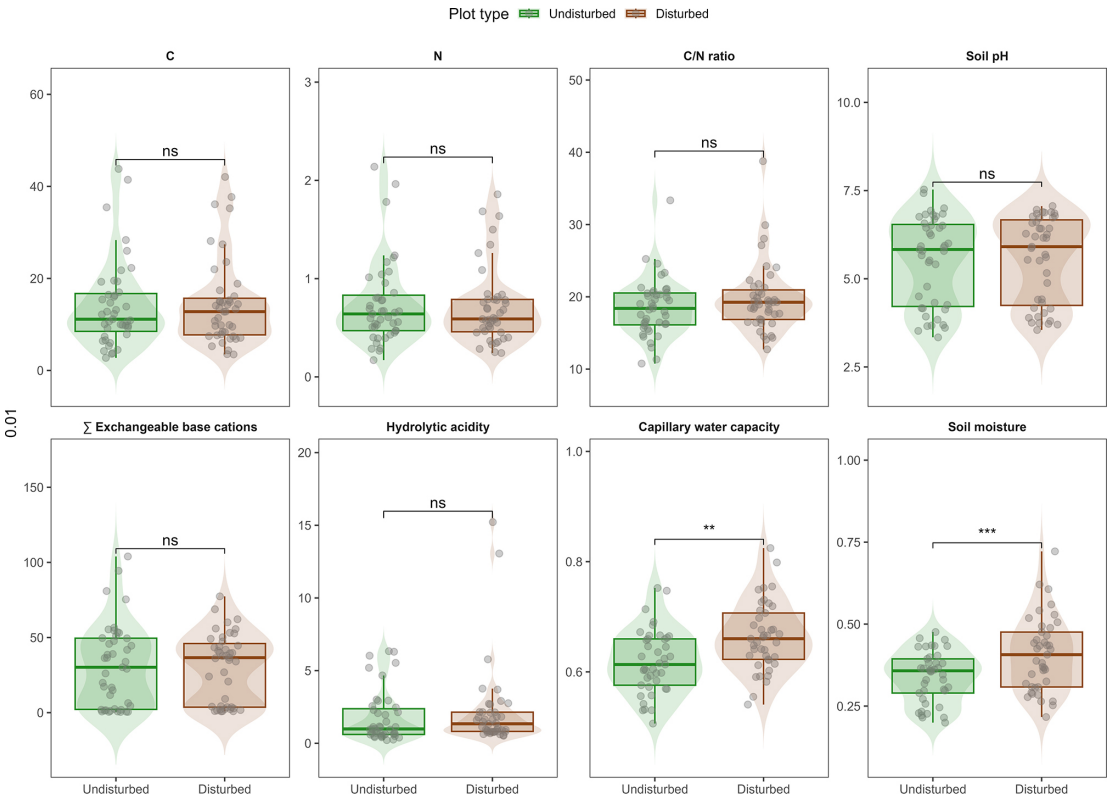


Fig. 2. Comparison of selected soil chemical and physical properties between disturbed and undisturbed plots. Differences between paired plots were tested using the Wilcoxon signed-rank test based on twin plots. Violin plots represent data distribution, boxplots indicate median and interquartile range, and points represent individual observations. Significance levels: ns – non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

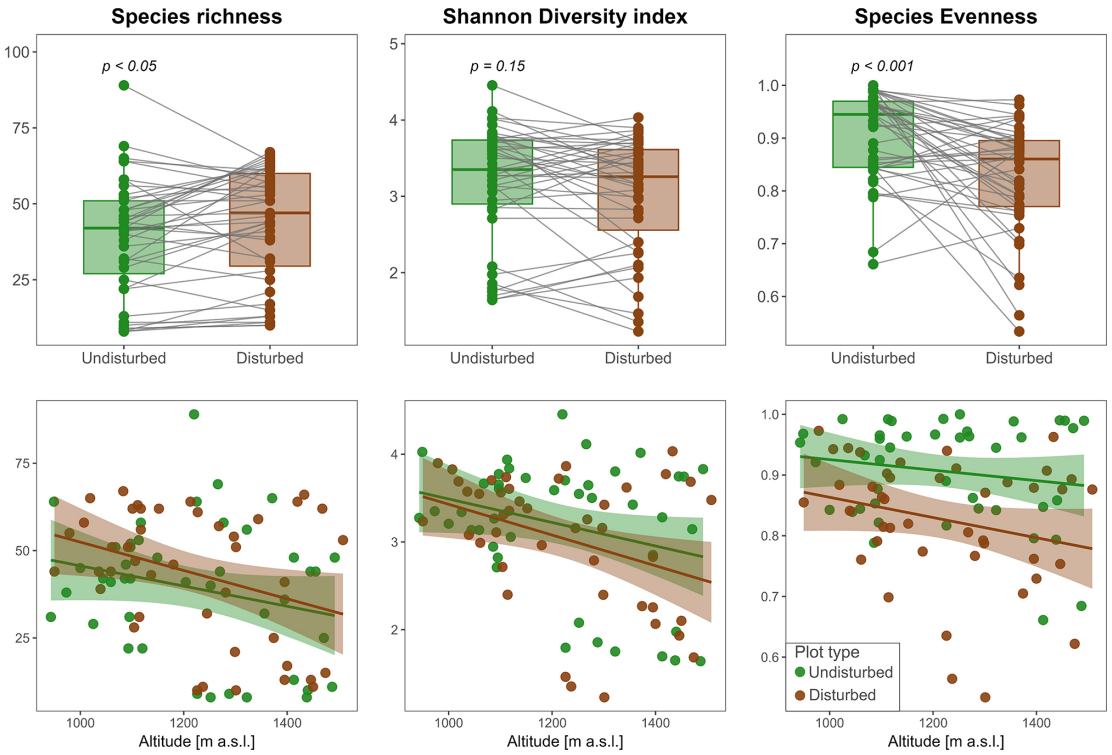


Fig. 3. Plant diversity metrics between plots with forest continuity (Undisturbed) and plots affected by natural disturbances (Disturbed) (top panel). Comparisons were performed for paired study plots connected by the same site identifier (linked by lines on the boxplots); significance was tested using the paired Wilcoxon signed-rank test. Relationships between diversity metrics and elevation gradient are shown in the bottom panel

sites (mean SDI: undisturbed = 3.19 ± 0.76; disturbed = 3.04 ± 0.75). A similar trend was found for species evenness, which showed a clear and significant decline in disturbed stands (mean evenness: undisturbed = 0.91 ± 0.08; disturbed = 0.83 ± 0.10). This pattern suggests a greater dominance of expansive species in disturbed forest communities. At the same time, no significant differences between the study areas were found in either species richness or the Shannon Diversity Index (SDI). As expected, both indices declined with increasing elevation. However, at higher elevations – particularly within subalpine forests (above approximately 1200 m a.s.l.) – their variability increased substantially, regardless of study area. In contrast, species evenness exhibited markedly different patterns between the two forest types. Although evenness decreased with elevation in both disturbed and undisturbed areas, this decline was not significant in forests with long-term continuity. Furthermore, species distribution in undisturbed forests remained relatively homogeneous, whereas disturbed areas showed a much broader range of evenness values, also between 0.6 and 0.7. This pattern suggests a pronounced post-disturbance dominance of only a few species.

Response of plant strategies to disturbances

Among all recorded plant species, the largest group consisted of taxa representing the CR strategy

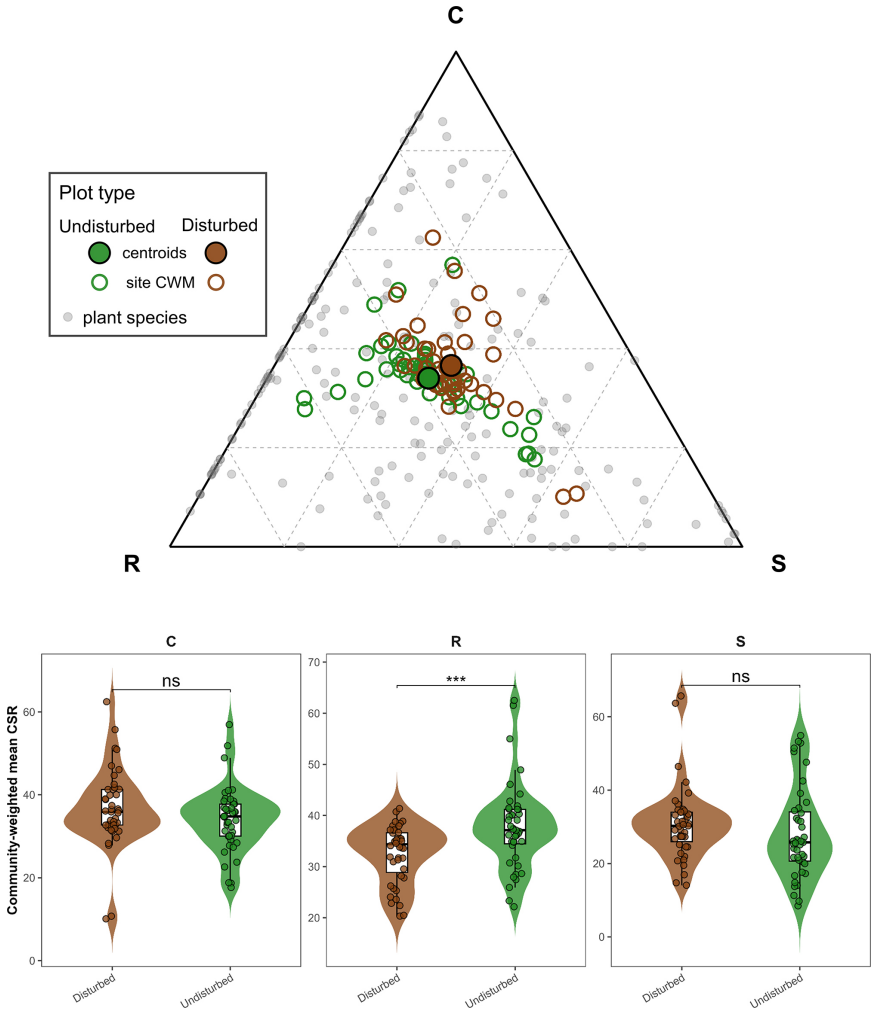


Fig. 4. Top panel: CSR triangle illustrating the distribution of plant ecological strategies and the community-weighted mean (CWM) CSR values for plots with forest continuity (Undisturbed) and plots affected by natural disturbance (Disturbed). Gray dots represent recorded species, open colored circles indicate CWM values for individual study plots, and filled colored circles represent centroids for disturbed and undisturbed plot types. Bottom panel: Boxplots comparing the community-weighted mean (CWM) proportions of CSR strategies between disturbed and undisturbed plots. Differences between paired plots were tested using the Wilcoxon signed-rank test based on the twin-plot design. Violin plots represent data distribution, boxplots indicate the median and interquartile range, and points correspond to individual plot. Significance levels are indicated as follows: ns – not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

type (including its variants C/CR, R/CR, and CR/CSR), which together accounted for approximately 35% of all species. The stress-tolerator (S) component had the lowest values, exhibiting, on average, 26% of the studied species. Community weighted means calculated for the study plots were generally clustered near the center of the CSR triangle, although they showed a clear tendency toward the CR strategy domain. The centroids representing disturbed and undisturbed plots were distinctly separated, primarily due to the influence of ruderal (R) species, which occurred significantly more frequently in undisturbed plots ($p < 0.001$). In contrast, the proportional contributions of competitor (C) and stress-tolerator (S) strategies did not differ significantly between plot types (Fig. 4).

Discussion

We found strong and significant differences between areas characterized by long-term forest continuity and those affected by natural disturbances in the Tatra Mountains. These differences were reflected not only in environmental conditions under which plant communities developed, but also in plant species composition, diversity, and ecological strategies.

Environmental changes following natural disturbances

The results of our research conducted in the Tatra Mountains are related to the nature of the disturbances that have occurred in this area, namely the European spruce bark beetle (*Ips typographus*) outbreaks, which often follow large-scale wind disturbances and lead to the replacement of the tree stand. These disturbance regimes create a characteristic structural mosaic in which some dead trees remain standing for decades, whereas others fall and contribute coarse woody debris to the forest floor (Edburg et al., 2012). Such conditions substantially alter understory microclimate and forest structure while maintaining partial continuity of the forest floor vegetation and belowground environment. Contrary to our expectations, we did not find significant differences in the concentrations of major soil nutrients, including carbon, nitrogen, or the sum of exchangeable base cations, between disturbed and undisturbed plots. This result contrasts with the classical concept of post-disturbance resource release, which predicts increased nutrient availability following canopy mortality and decomposition of dead biomass (Vitousek & Reiners, 1975). Resource release after natural disturbance is commonly associated with accelerated litter decomposition, increased mineralization, and reduced nutrient uptake by trees. However, bark beetle-induced mortality differs fundamentally from clear-cutting or severe soil-disturbing events because canopy mortality occurs without direct removal of biomass or major disruption of the soil surface (Huber, 2005). Although tree mortality may initially increase nitrogen availability through enhanced litterfall and decomposition processes, this effect can be temporary because nitrogen is simultaneously lost through nitrate leaching (Huber et al., 2004). Living trees normally act as major nitrogen sinks due to their large biomass and extensive root systems. Following stand dieback, nitrogen uptake by tree roots rapidly declines, whereas mineralization and nitrification continue, increasing concentrations of mobile nitrate ions in the soil.

At the same time, increases in understory biomass following disturbance are unlikely to fully compensate for the substantial reduction in nutrient uptake associated with the loss of mature trees, partly because understory vegetation typically has lower biomass and shallower rooting systems than mature trees (Deng et al., 2023; Gilliam, 2007). Consequently, the shallower rooting depth of understory species may reduce their capacity to intercept nitrate transported through deeper soil horizons (Pierret et al., 2016). Similar increases in nitrogen losses following bark beetle disturbance have been reported from montane spruce forests (Griffin et al., 2011; Huber et al., 2004). Despite the lack of significant differences in soil nutrient concentrations, disturbed plots exhibited significantly higher soil moisture and capillary water capacity. Increased soil moisture following bark beetle outbreaks and wind disturbances is a well-documented phenomenon and is primarily associated with reduced transpiration after canopy mortality (Bearup et al., 2014; Mikkelson et al., 2013). This process, often referred to as altered water partitioning, results from the sudden reduction in water uptake by trees, leading to greater water retention within the soil profile. In heavily disturbed stands, soil moisture may increase by more than 50% relative to intact forests (Norton et al., 2015; Brouillard et al., 2017). Elevated soil moisture may additionally enhance nitrate leaching, further limiting long-term nutrient accumulation in topsoil despite increased nutrient inputs from decomposing biomass (Krüger et al., 2021; Aber et al., 1989).

The lack of significant chemical changes following disturbance does not necessarily mean that soil-forming processes and nutrient cycling remained unaffected. In forest ecosystems, particularly in mountain forests, soil response may be strongly delayed due to the slow decomposition of organic matter and low temperatures limiting microbial activity (Błońska et al., 2023). Under such conditions, nutrients released from decomposing wood, litter,

and dead roots may accumulate gradually, and their influence on soil chemical properties may become visible only many years after the disturbance event (Schwarz et al., 2025). This may apply especially to mineral nitrogen and sum of exchangeable base cations, whose increased availability often appears only during later successional stages. At the same time, nutrients released shortly after disturbance may be rapidly immobilized by microorganisms or taken up by regenerating vegetation, which can limit the detection of short-term changes in soil chemical analyses (Gasch et al., 2014). The persistence of organic soil horizons may also play an important role. In forest ecosystems, a substantial proportion of nutrients is stored within the organic layer, which acts as a buffer stabilizing soil chemistry (Wilpert, 2022). Consequently, canopy disturbance may alter the rate of litter humification and soil organic matter accumulation, whereas changes in mineral-soil properties can occur gradually and depend on local environmental conditions (Ni et al., 2016). In this context, the obtained results may suggest that the studied disturbances initiated ecological processes that became visible earlier in vegetation structure and microclimatic conditions than in soil chemistry. Changes in species composition and increased soil moisture may therefore represent early stages of ecosystem transformation, whereas responses in soil chemical properties may only become apparent over a longer time scale (Canessa et al., 2021; Semeraro et al., 2025).

The lack of significant differences in soil chemical properties suggests that conventional physicochemical parameters may not be sufficiently sensitive to detect early ecosystem responses to disturbance. In this context, biological soil indicators could provide a more responsive measure of ongoing ecological changes (Błońska et al., 2024; Małek et al., 2021). Parameters such as enzymatic activity, microbial biomass, soil respiration, or the composition of microbial communities often respond more rapidly to alterations in moisture conditions, nutrient availability, and organic matter turnover than bulk chemical properties of soil (Aslam et al., 2026; Uzarowicz et al., 2020). Therefore, future studies could benefit from incorporating biological soil parameters to better understand the mechanisms and temporal dynamics of post-disturbance ecosystem transformation.

Our results therefore suggest that the dominant ecological consequences of bark beetle and wind disturbances in the studied forests were related primarily to shifts in hydrological conditions rather than to sustained nutrient enrichment. Disturbance significantly increased light availability and soil moisture, both of which are major drivers of understory community dynamics in temperate montane forests.

Vegetation alteration after disturbances

Species richness was significantly higher in disturbed plots than in undisturbed forests. Increased understory richness following natural disturbances has been widely reported in temperate forests and is commonly connected with environmental heterogeneity and increased resource availability, particularly light, following canopy opening (Seidl et al., 2017; Thom & Seidl, 2016; Roberts, 2004; Runkle, 1982). In forests affected by natural disturbances caused by bark beetle or strong winds, many forest species persist while additional light-demanding and early-successional species colonize newly available microsites, resulting in a temporary increase in local species richness (Connell, 1978). In contrast, species evenness differed significantly between disturbance categories, particularly at higher elevations, where disturbed plots exhibited lower evenness than undisturbed forests. This reduced evenness may reflect greater disturbance severity in subalpine spruce forests that occurred at higher elevations. Subalpine forests are often structurally simpler and dominated by Norway spruce, making them more prone to large-scale bark beetle outbreaks and windthrow events. Such disturbances may create conditions that favor rapid expansion of a limited set of competitive species, thereby reducing the relative abundance of other plant species and decreasing community evenness.

Additionally, most disturbed sites were affected several years or even decades before sampling. Consequently, the understory vegetation likely represents relatively advanced stages of succession after disturbances, dominated by highly competitive species such as *Rubus idaeus*, tall grasses (eg. *Calamagrostis* spp.), and ferns, rather than early-successional ruderal plants. This interpretation is consistent with the low representation of species assigned to the ruderal (R) strategy. Such species may establish shortly after severe disturbances that expose mineral soil, but are often rapidly replaced by competitively superior taxa as vegetation cover develops (Grime, 1977). Moreover, canopy mortality caused by bark beetle differs fundamentally from stand-replacing disturbances because the forest floor vegetation remains largely intact, limiting opportunities for ruderal species establishment (Jonášová & Prach, 2008). These findings also highlight the need for caution when applying Grime's CSR framework to forest ecosystems, as many species characteristic of disturbed forest habitats are classified as competitors rather than ruderals despite their association with post-disturbance environments.

Limitations of this study

In the present study, natural disturbances were analysed collectively, regardless of the time elapsed since their occurrence. The forests of Tatra Mountains constitute a highly heterogeneous landscape, characterized by a mosaic of habitats as well as different stages of post-disturbance regeneration and succession. Disturbances caused by bark beetle outbreaks are particularly complex because, although they may result in extensive tree mortality, they do not necessarily constitute stand-replacing disturbances. Tree mortality often develops gradually over several years, while standing dead trees may persist for decades, maintaining structural heterogeneity and driving progressive changes in local environmental conditions and ecosystem processes (Edburg et al., 2012; Kulakowski et al., 2017). Furthermore, the selection of study plots was constrained by the location of historical sampling sites (see *Methods* section), which limited the possibility of freely choosing research plots.

Consequently, the classification of disturbed stands in this study was based on structural criteria, namely canopy reduction, rather than on the time elapsed since disturbance. This approach reflects the current structural condition of the stands, but it should also be recognized as a limitation that may affect the interpretation of the results.

Conclusions

Natural disturbances significantly altered understory vegetation in the forests of the Tatra Mountains, leading to changes in environmental conditions, therefore, species composition, diversity patterns, and plant ecological strategies. The observed differences between disturbed and undisturbed stands were associated primarily with increased light availability and higher soil moisture following canopy mortality. Contrary to the expectations based on the resource-release hypothesis, we found no significant differences in soil nutrients, suggesting that bark beetle outbreaks and wind disturbances do not necessarily result in long-term nutrient enrichment of topsoil and that after disturbances, vegetation responses may be driven more strongly by microclimatic and hydrological changes than by alterations in soil chemistry.

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