https://doi.org/10.46341/PI2026013
UDC [581.526.3 : 574.24] (234.421.1)

RESEARCH ARTICLE

Structural stability and compositional reorganization of high-mountain grasslands under anthropogenic load in the Ukrainian Carpathians

Andriy Novikov [1,*], **Viktor Nachychko** [2]

[1] State Museum of Natural History, National Academy of Sciences of Ukraine, Teatralna str. 18, 79008 Lviv, Ukraine; * novikoffav@gmail.com

[2] Ivan Franko National University of Lviv, Hrushevskoho str. 4, 79005 Lviv, Ukraine

Received: 07.10.2026 | **Accepted**: 23.10.2026 | **Published**: 27.10.2026

Abstract

Anthropogenic pressure can alter plant communities without immediately causing changes in total species richness or broad vegetation structure. We assessed the response of high-mountain grasslands to anthropogenic load across five mountain regions of the Ukrainian Carpathians using 30 vegetation relevés, including 15 pairs of control and anthropogenically loaded plots. Vegetation responses to anthropogenic load were examined comprehensively across different structural levels. Total species richness and broad vegetation structure remained highly similar between control and loaded plots. In contrast, reaction to the anthropogenic load was associated with changes in the distribution of species richness among dominant plant families and functional groups, particularly after accounting for regional heterogeneity. Loaded plots showed higher grass richness and lower forb richness, while their overall functional-group cover remained largely unchanged. Differences between paired control and loaded plots were predominantly attributable to species turnover rather than nested species loss, although turnover did not exceed the high background beta diversity of the studied grasslands. The community ecological specialization (cover-weighted) was significantly higher in loaded plots, mainly reflecting reduced dominance of species-generalists, whereas species evenness remained unchanged. Overall, the results indicate that anthropogenic load is associated with compositional reorganization of high-mountain grasslands within a broadly persistent vegetation structure, rather than with straightforward species- and biodiversity-level loss. Species functional identity, within-group species richness structure, and abundance-weighted community properties may therefore provide more sensitive indicators of anthropogenic change than evaluation of species richness or vegetation cover alone.

Keywords: high-mountain grasslands, Ukrainian Carpathians, anthropogenic load, compositional reorganization, species turnover, vegetation stability

Authors' contributions: Andriy Novikov – Conceptualization, Supervision, Funding acquisition, Project administration, Resources, Data curation, Methodology, Investigation, Visualization, Writing – original draft. Viktor Nachychko – Resources, Formal analysis, Investigation, Validation, Writing – review & editing.

Funding: The project 2025.07/0155 "Investigation of biodiversity, functional traits and phylogenetic structure of high-mountain meadows of the Ukrainian Carpathians in the context of habitat transformation" within the call 2025.07 "Excellent Science in Ukraine 2026-2028" is implemented with grant support from the National Research Foundation of Ukraine.

Competing Interests: The authors declare no conflict of interest.

Declaration of AI Use: The authors acknowledge the use of ChatGPT 5.6 Sol to assist with data analysis and statistical calculations, as well as for English language editing, proofreading, and stylistic corrections during the manuscript preparation. The generated statistical outputs were independently reviewed, cross-checked, and verified by the authors using conventional calculation methods to ensure full scientific accuracy. The core intellectual contributions, analytical interpretations, and conclusions remain entirely the work of the human authors.

© The Authors. This content is provided under CC BY 4.0 license.

Introduction

High-mountain grasslands are among the most species-rich semi-natural ecosystems in Europe and are strongly shaped by both natural environmental constraints and long-term human land use. Traditional mowing and grazing have helped maintain high plant diversity in many European grasslands, whereas changes in land use can alter vegetation composition, dominance structure, and species richness (Klimek et al., 2007; Schneider & Hering, 2024; Dayneko et al., 2027). Anthropogenic impacts on grasslands do not necessarily result in an immediate decline in total species richness. Land-use intensification can reduce plant species richness while increasing plant community overall production. Anthropogenic pressure may modify vegetation not only by altering the number of species present but also by changing species identity, dominance, and the relative representation of taxonomic or functional groups (Tanţău et al., 2014; Stanisci et al., 2020; Dainese et al., 2024). The magnitude and direction of these complex responses vary among ecosystems and management regimes (Beckmann et al., 2019). In mountainous ecosystems, it is often accompanied by shifts in the upper forest line and the intensified spread of woody species at higher elevations (Durak et al., 2015; Feurdean et al., 2016; Mitka et al., 2022).

Consequently, total species richness alone may provide an incomplete measure of community response to anthropogenic pressure. Communities with similar numbers of species may differ substantially in species identity and in the relative contribution of different ecological groups. Beta diversity provides a complementary framework for quantifying such compositional differences among communities. Importantly, beta diversity can be partitioned into turnover and nestedness components, thereby distinguishing species replacement from compositional differences resulting primarily from species loss or gain (Doležal & Šrůtek, 2002; Baselga, 2010, 2012; Hurdu et al., 2016; Zeidler et al., 2023). This distinction is particularly relevant when evaluating anthropogenic impacts because communities with similar total richness may nevertheless undergo substantial species replacement without a decline in overall alpha diversity (Ujházy et al., 2018; Sabatini et al., 2022; Coldea et al., 2026; Midolo et al., 2025). Hence, the analysis of the ecological characteristics of species that contribute most strongly to the community may provide an additional dimension for detecting vegetation responses. Zelený & Chytrý (2019) developed Ecological Specialization Indices (ESIs) for plant species based on their realized distributions along environmental gradients. Such indices can be used to examine whether changes in vegetation are associated with shifts in the ecological characteristics of species contributing to community composition and dominance. The ESIs were developed primarily for the Czech flora but, with certain limitations and caution, can also be extrapolated to other floristic regions.

The Ukrainian Carpathians are medium-high mountains, with the high-mountain zone (over 1500 m a.s.l.) covering about 1.7% of their territory (Kruhlov, 2008). At the same time, the mountains are one of the leading centers of biodiversity in Ukraine, with numerous endemic, rare, and relict plant species and corresponding plant communities, which makes this territory of high priority for nature conservation (Kricsfalusy, 2013; Novikov & Sup-Novikova, 2022). In particular, the strict high-mountain zone of the Ukrainian Carpathians is an environment for 104 vascular plant species listed in the Red Book of Ukraine (Didukh, 2009), most of which are associated with grassland communities (Kricsfalusy, 2013; Kobiv, 2017). Thus, given the intensifying land use and overall transformation of high-mountain plant communities, the Ukrainian Carpathians provide an important setting for examining the response of grasslands to anthropogenic loading (Kricsfalusy, 2013; Cherepanyn, 2018; Kobiv & Kobiv, 2020; Dmytrakh, 2021). Previous studies have demonstrated that vegetation responses to land-use changes in the Carpathians can involve shifts in species composition and dominance rather than a uniform response in total species richness (Csergő et al., 2013; Kyyak et al., 2015, 2019; Coldea et al., 2026). At the same time, strong spatial heterogeneity among mountain regions can obscure comparatively subtle anthropogenic effects if regional variation is not explicitly considered. Hence, this study aimed to assess whether

anthropogenic load is associated with changes in total species richness and broad vegetation structure, and to determine exactly how the effects of the anthropogenic load are expressed.

Material and methods

Study area and vegetation dataset

The study was conducted in high-mountain grasslands of the Ukrainian Carpathians during the 2026 vegetation season. To achieve comparable results, we focused on trivial plant communities representing the common grassland high-mountain vegetation of the Ukrainian Carpathians, most of which had signs of intermediate condition due to overgrowth by *Vaccinium* sp. (e.g., *Poo chaixii-Deschampsietum* / *Vaccinietum myrtilli*, *Vaccinietum myrtilli* / *Calluno-Nardetum*, *Soldanello-Nardetum* / *Antennario dioicae-Nardetum strictae*, *Caricetum sempervirentis* / *Nardetum strictae*). The vegetation dataset comprised 30 vegetation relevés distributed across the subalpine, (1250–)1500–1750 m a.s.l., vegetation belt in five mountain regions: the Beskyds, Chornohora, Polonynas, Svydovets, and Gorgany. The comprehensive initial dataset containing raw data is available from Zenodo (Novikov & Nachychko, 2026).

Within each mountain range, the plots were selected with the exposition as similar as possible. Between different mountain ranges, the exposition varied from E-SE to SW-W, but we tried to keep it as similar as possible too. Within each region, three control and three anthropogenically loaded plots were analyzed, yielding 15 pairs. As controls were selected the plots (10×10 m, i.e., 100 m^2), which were located at least 20 m from the roads, had the floristic composition typical of the general landscape, and showed no signs of intense anthropogenic disturbance. Some signs of pasture or trampling could still persist, as the Ukrainian Carpathians are generally exposed to various forms of irregular anthropogenic disturbance, even in restricted areas. The loaded plots were selected for having excessive evidence of anthropogenic pressure (primarily dumping and trampling). In a practical sense, all plots were evaluated for anthropogenic load by three 0–9 scales (i.e., recreation, pasture, and mowing). Plots that received at least 5–6 points were designated as loaded. It was not possible to precisely estimate the duration of the anthropogenic load, but we avoided the fresh trails and paths. So, all evaluated, loaded plots were located along roads/paths/trails that have existed for at least five years. As the anthropogenic load in the subalpine meadow communities of the Ukrainian Carpathians showed no signs of gradualism and disappeared already at distances of 1–2 m from the roads/paths/trails, the loaded plots were allocated along the roads/paths/trails as strips 0.5×100 m (50 m^2). The longer strips were not considered, as they showed significant changes in vegetation structure associated with micro-landscape peculiarities during the pilot (test) research and, hence, cannot be compared with the control ones due to heterogeneity. For each relevé, vascular plant and bryophyte taxa were recorded together with their projective cover within a single projection layer (i.e., bryophytes that were present in the community but covered by other plants were not considered to contribute to the common projection). Blank cover values were interpreted as an absence and assigned a value of zero. A taxon was considered present when its projective cover was greater than zero.

A species-by-relevé matrix was constructed from data on the projective cover of each registered species. Because the summed projective cover differed among relevés, cover values were normalized within each relevé so that the proportional contribution of all recorded taxa summed to 100 %. This procedure allowed comparisons of vegetation structure among plots while minimizing the influence of differences in total recorded cover. Species richness was calculated for each relevé as the number of taxa with projective cover greater than zero. All subsequent analyses were conducted at the individual-relevé level rather than on pooled species lists.

Species- and family-level vegetation composition

To assess the overall response of vegetation to anthropogenic load, the full species-by-relevé matrix of proportional projective cover was analyzed. Bray-Curtis (Bray & Curtis, 1957) dissimilarities were calculated among all relevés. Differences in species

composition between control and anthropogenically loaded plots were tested using permutational multivariate analysis of variance – PERMANOVA (Anderson, 2001). Two permutation schemes were used. First, unrestricted permutations were used to characterize the overall difference between control and loaded vegetation. Second, permutations were restricted within the five mountain regions. The latter analysis was used to account for strong spatial heterogeneity among the Carpathian regions while testing the overall association between plot status and vegetation composition. The proportion of multivariate variation associated with plot status was expressed as R^2. Statistical significance was assessed at $\alpha = 0.05$. Multivariate analyses were conducted using the R statistical environment and the vegan package for community ecology (Oksanen et al., 2026), emulated via ChatGPT 5.6 Sol. Where PERMANOVA indicated a treatment-associated difference of particular interest, homogeneity of multivariate dispersion was assessed using PERMDISP. This procedure tests whether groups differ in their multivariate dispersion around their centroids or spatial medians, thereby helping distinguish differences in group location from differences in within-group heterogeneity (Anderson, 2006). The graphs were visualized using the RAWGraphs 2.0 online environment.

To examine whether anthropogenic load affected vegetation at a broader taxonomic level, species were aggregated by family, following POWO (2026). For each relevé, family-level projective cover was calculated as the sum of the projective cover of all species belonging to a given family. Family-level species richness was calculated independently as the number of species belonging to each family recorded in the relevé. Two complementary analyses were conducted. First, all recorded families were included to evaluate general changes in family-level vegetation structure. Second, a targeted analysis was conducted for the ten families with the highest mean normalized projective cover across the complete dataset. These families were Poaceae, Ericaceae, Juncaceae, Asteraceae, Cyperaceae, Rosaceae, Onagraceae, Ranunculaceae, Amaryllidaceae, and Gentianaceae. Bray-Curtis dissimilarities and PERMANOVA were calculated separately for family-level projective cover and family-level species richness. Both unrestricted and region-restricted permutation procedures were applied.

Species evenness

Species evenness was quantified using Pielou's evenness index (J′), which expresses the distribution of relative abundance among species (Pielou, 1966). For each relevé, proportional projective-cover values were used as abundance measures. Shannon diversity was calculated as:

$$H' = -\Sigma p_i \ln(p_i),$$

where p_i is the proportional projective cover of species i.

Pielou's evenness was then calculated as:

$$J' = H'/\ln(S),$$

where S is the number of species recorded in the relevé.

The index ranges from 0 to 1, with higher values indicating a more even distribution of projective cover among species. Control and loaded plots were compared using a paired permutation test based on the 15 corresponding control/loaded relevé pairs.

Functional groups, life strategy, and life forms

Recorded taxa were assigned to seven broad functional groups: grasses, sedges, rushes, forbs, woody plants (including shrubs and young trees), mosses, and lycophytes. For each relevé, projective cover was summed within each functional group. Species richness was calculated as the number of species in each functional group present in the relevé. Separate Bray-Curtis dissimilarity matrices were generated for functional-group projective cover and functional-group species richness. Differences between control and loaded plots were tested using PERMANOVA with both unrestricted and region-restricted permutations.

Vascular plants were additionally classified according to their annual or perennial life-history strategy. For each relevé, both projective cover and species richness were calculated for annual and perennial taxa. Because annual species were extremely rare in the dataset, this classification was treated as a supplementary analysis rather than as a principal functional classification. Differences between control and loaded plots were

evaluated using Bray-Curtis dissimilarities and PERMANOVA.

Analyzed plant taxa were also classified according to the Raunkiaer (1934) life forms. The principal categories represented in the dataset were hemicryptophytes, chamaephytes, geophytes, phanerophytes, and therophytes. Life-form assignments followed the European trait sources used for the study. Bryophytes were retained as a separate descriptive category but were not assigned to Raunkiaer life forms in the formal analysis of vascular plants. For each relevé, projective cover and species richness were calculated for each life-form category. Bray-Curtis dissimilarities were then calculated separately for cover and richness profiles, and differences between control and loaded vegetation were evaluated using PERMANOVA with unrestricted and region-restricted permutations.

Beta-diversity partitioning

To determine whether compositional differences between control and loaded vegetation were primarily associated with species replacement or differences in species richness, beta diversity was partitioned into turnover and nestedness resultant components following Baselga (2010, 2012). Presence/absence data were used for this analysis. For each paired comparison, Sørensen dissimilarity (β_sor) was partitioned additively into the Simpson turnover component (β_sim) and the nestedness resultant component (β_sne):

$$\beta_sor = \beta_sim + \beta_sne.$$

The turnover component represents species replacement between assemblages, whereas the nestedness-resultant component represents dissimilarity associated with differences in species richness and nested composition (Baselga, 2010, 2012).

For the direct control–loaded comparison, relevés were paired within each mountain region according to replicate number, resulting in 15 corresponding control/loaded comparisons. For each pair, the number of shared species, the number of species occurring only in the control relevé, the number of species occurring only in the loaded relevé, total Sørensen dissimilarity, turnover, and nestedness were calculated. The relative contribution of turnover to total beta diversity was expressed as β_sim/β_sor.

To place treatment-associated dissimilarity against the background compositional heterogeneity of the dataset, pairwise Sørensen dissimilarity and turnover were also calculated among control/control, loaded/loaded, and control/loaded combinations within the dataset's regional structure. A permutation test restricted within mountain regions was then used to determine whether turnover between control and loaded plots exceeded background turnover within treatment categories.

Ecological specialization

A supplementary analysis was conducted to determine whether control and anthropogenically loaded vegetation differed in the ecological specialization of their constituent vascular plants.

Species-level Ecological Specialization Index (ESI) values were obtained from Zelený & Chytrý (2019). The ESI quantifies the degree of ecological specialization of a species relative to its realized niche, based on species co-occurrence across vegetation plots. Because specialization may differ between forest and non-forest vegetation, the non-forest ESI dataset (ESI_nf) was used in the present study.

Taxonomic names recorded in the Carpathian vegetation dataset were matched against the ESI database. Exact taxonomic matches were preferred; where nomenclature differed, established synonyms or taxonomically compatible aggregates were used. Taxa for which a defensible correspondence could not be established were excluded from the specialization analysis. Of the 94 vascular taxa recorded in the vegetation dataset, 54 could be matched to ESI_nf values. These matched taxa represented approximately 83 % of vascular-plant projective cover in both control and loaded plots. The completeness of ESI coverage was compared between plot categories to ensure that differences in specialization metrics were not attributable to unequal representation of taxa with available ESI values.

Two community-level specialization measures were calculated for each relevé. First, a presence-based Community Specialization Index (CSI) was calculated as the arithmetic mean of the ESI_nf values for

all matched species present in the relevé. Second, a cover-weighted CSI was calculated by weighting each species' ESI_nf value by its proportional projective cover. The latter metric, therefore, characterized the ecological specialization of species by their contribution to vegetation cover rather than by their mere presence. Differences in community specialization between control and loaded plots were evaluated using permutation tests, with permutations restricted within mountain regions.

For an additional descriptive comparison, species were classified as generalists, intermediate species, or specialists using thresholds derived from the external ESI_nf distribution. Species in the lowest quartile of the external ESI_nf distribution (ESI_nf ≤4.278) were classified as generalists, species in the highest quartile (ESI_nf ≥ 5.560) as specialists, and the remaining species as intermediate.

For each relevé, the proportional projective cover and proportional species richness of these three categories were calculated. Because the ESI values were derived from the Czech National Phytosociological Database, these categorical analyses were interpreted as exploratory comparisons rather than as absolute classifications of ecological specialization in the Ukrainian Carpathians. Zelený & Chytrý (2019) noted that the ESI values are geographically conditioned by the source vegetation-plot database and may be affected by sampling bias, particularly for less frequent species.

Results

Species-level composition

Species-level composition was highly heterogeneous among individual relevés. Bray-Curtis dissimilarity between the mean species-cover profiles of control and loaded plots was 0.222. In the unrestricted PERMANOVA, plot status accounted for 3.94% of total compositional variation (pseudo-F = 1.149, R^2 = 0.0394, p = 0.311), indicating no significant overall separation of control and loaded plots. Mean pairwise Bray-Curtis dissimilarity was approximately 0.578 among control plots, 0.553 among loaded plots, and 0.569 between control and loaded plots. Thus, variation among plots within the same treatment category was comparable to the average difference between treatments. Multivariate dispersion did not differ significantly between plot categories (PERMDISP F = 0.375, p = 0.609). Regional structure was a much stronger component of variation in floristic composition than plot status (control/loaded). When permutations were restricted to certain mountain regions, the treatment-associated signal became stronger but remained marginally insignificant (p = 0.0598).

Family-level composition

Aggregation to families revealed an even more stable vegetation structure. Only a slight shift among the top-ten families has been detected (Fig. 1). Across all families, the Bray-Curtis dissimilarity between the mean control and the loaded covers was 0.083. Plot status explained less than 1% of variation in family-level projective cover (pseudo-F = 0.212, R^2 = 0.0075, p = 0.969). The same pattern was observed for the ten dominant families (i.e., Poaceae, Ericaceae, Juncaceae, Asteraceae, Cyperaceae, Rosaceae, Onagraceae, Ranunculaceae, Amaryllidaceae, and Gentianaceae). Bray-Curtis dissimilarity between their mean cover profiles was approximately 0.065, and treatment accounted for only about 0.7% of variation (pseudo-F ≈ 0.195, R^2 ≈ 0.0069, unrestricted p ≈ 0.934). Restricting permutations within regions did not alter the conclusion (p ≈ 0.853). Several directional changes were nevertheless apparent. In particular, the average Poaceae projective cover increased from approximately 38.5% in control vegetation to 41.6% in loaded plots, while Ericaceae cover increased from 28.3% to 30.6%, respectively. In contrast, the Juncaceae projective cover declined from 9.1% to 7.1%, and that of Cyperaceae from 4.3% to 2.6% (Fig. 2). These changes therefore represented shifts in mean dominance within a broadly conserved family-level cover structure rather than a significant overall reorganization.

Total species richness per relevé was almost identical between control and anthropogenically loaded plots, averaging 18.67 species in control plots and 18.60 species in loaded plots (Fig. 3). When species richness was distributed among all recorded families, no significant overall treatment effect was detected (pseudo-F = 1.299,

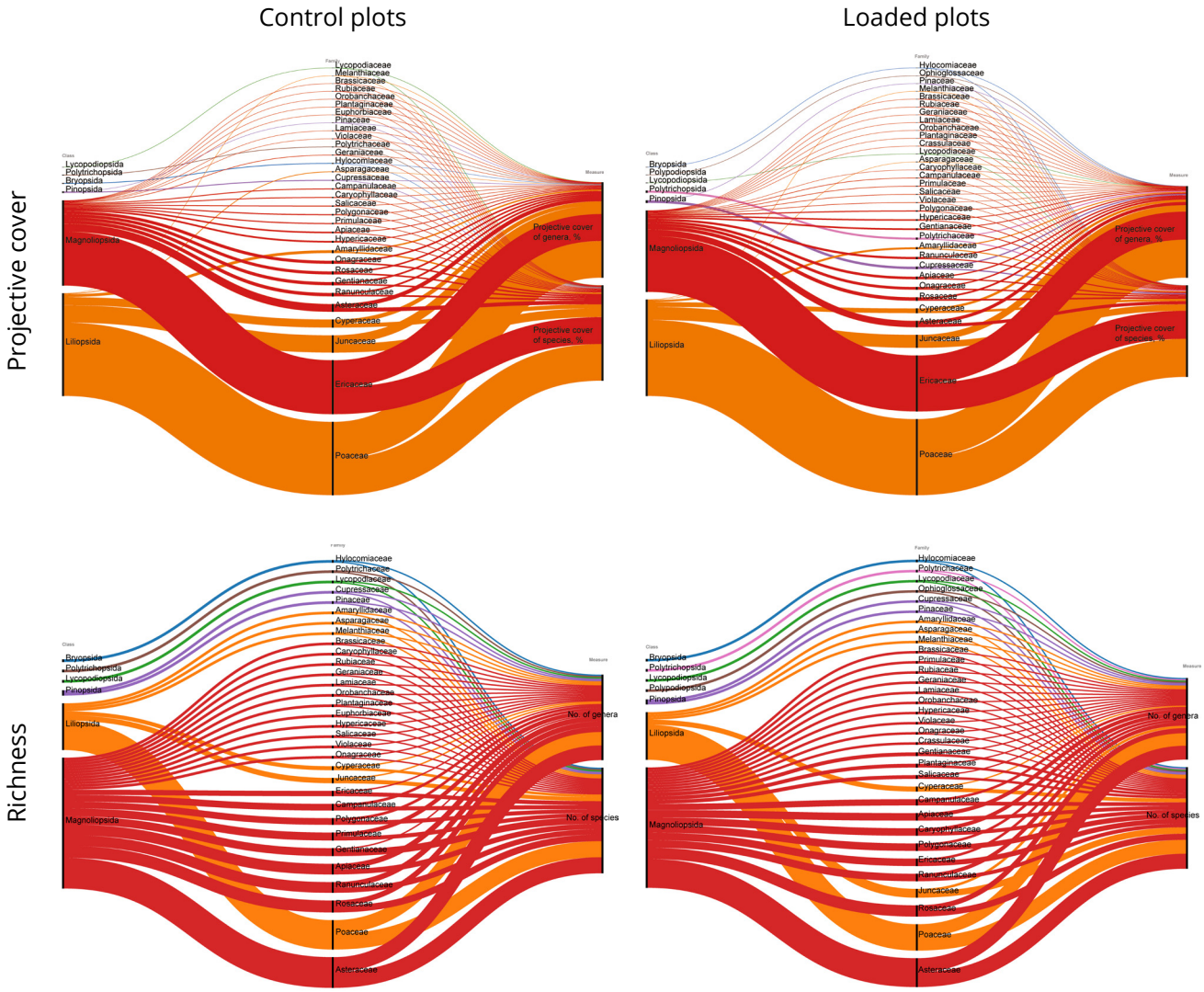


Figure 1. The family-level taxonomic circumscription of the high-mountain grasslands of the Ukrainian Carpathians.

R^2 = 0.0444, p = 0.250). A stronger pattern emerged in the targeted analysis of the ten dominant families. Bray-Curtis dissimilarity between the mean family-richness profiles was approximately 0.133. The unrestricted PERMANOVA detected a treatment-associated difference (pseudo-F = 2.386, R^2 = 0.0785, p = 0.0473). When permutations were restricted within certain mountain regions, the observed pseudo-F and R^2 remained unchanged, whereas the permutation probability decreased to approximately p = 0.012. Thus, plot status (i.e., control/loaded) accounted for approximately 7.9% of the multivariate variation in species richness distributed among the ten dominant families. This result was not attributable to unequal multivariate dispersion. Mean distance to the spatial median was 0.187 for control plots, and 0.183 for loaded plots, and PERMDISP showed no evidence of heterogeneity in dispersion (F = 0.042, p = 0.841; region-restricted p = 0.841). Consequently, the dominant-family analysis suggested a redistribution of species richness among the top-ten families despite the near absence of change in total plot-level richness and family-level projective-cover structure.

Functional-group composition

The general functional composition was relatively stable in both control and anthropogenically loaded plots. Grass cover increased from an average of 38.5% in control plots to 41.6% in loaded plots, and woody cover increased from 29.9% to 32.6% (Fig. 4). Conversely, forb cover declined from 17.3% to 14.7%, rush cover from 9.1% to 7.1%, and sedge cover from 4.3% to 2.6%. Mosses

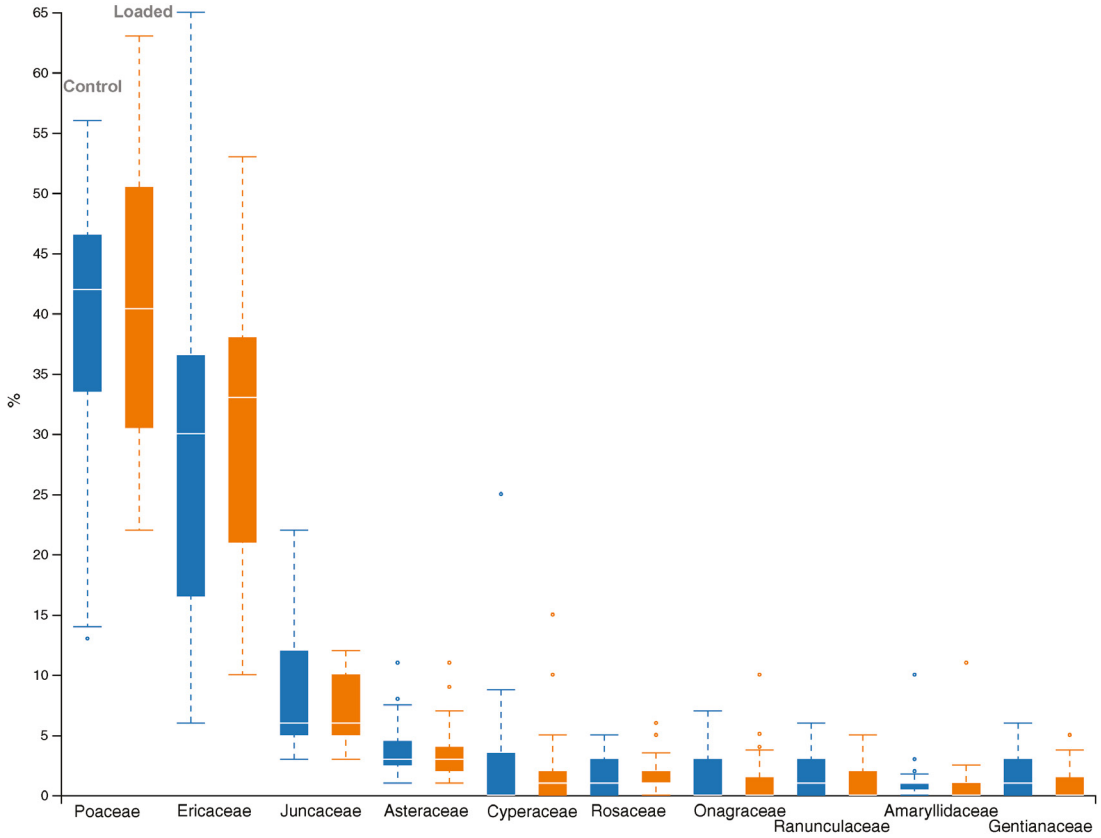


Figure 2. The projective cover of top-ten families in the high-mountain grasslands of the Ukrainian Carpathians.

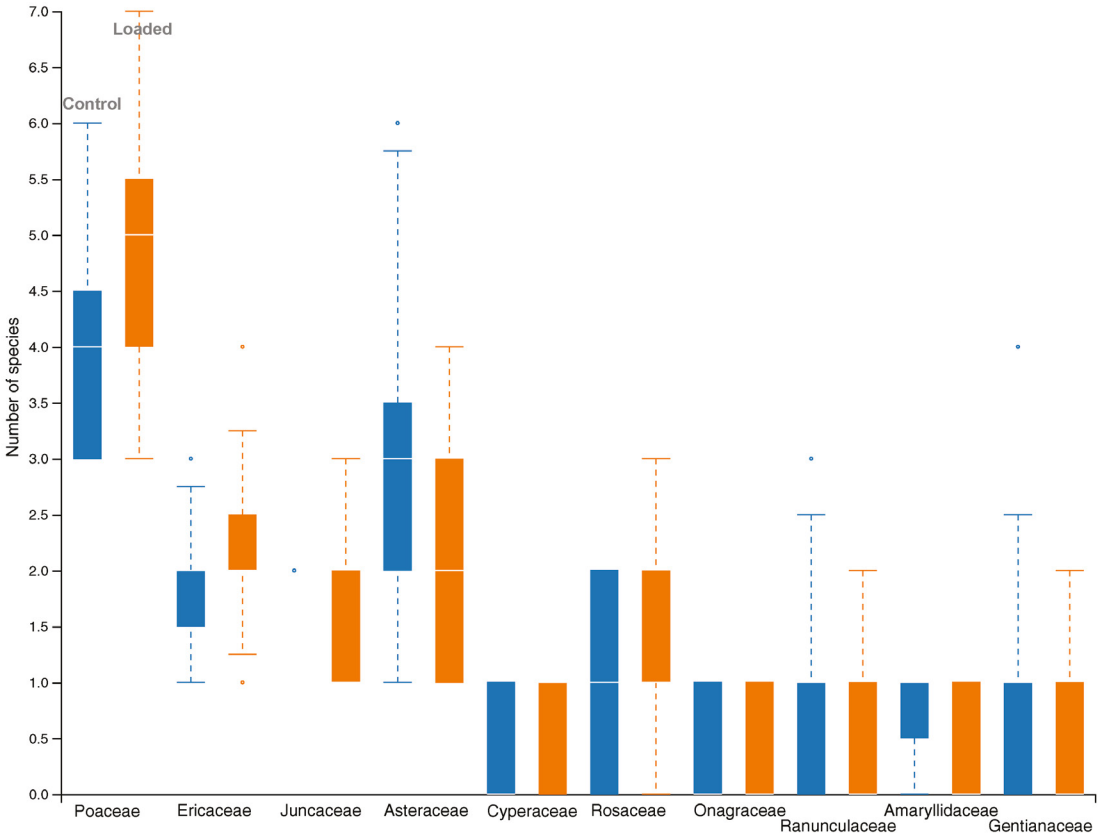


Figure 3. The species richness of the top-ten families in the high-mountain grasslands of the Ukrainian Carpathians.

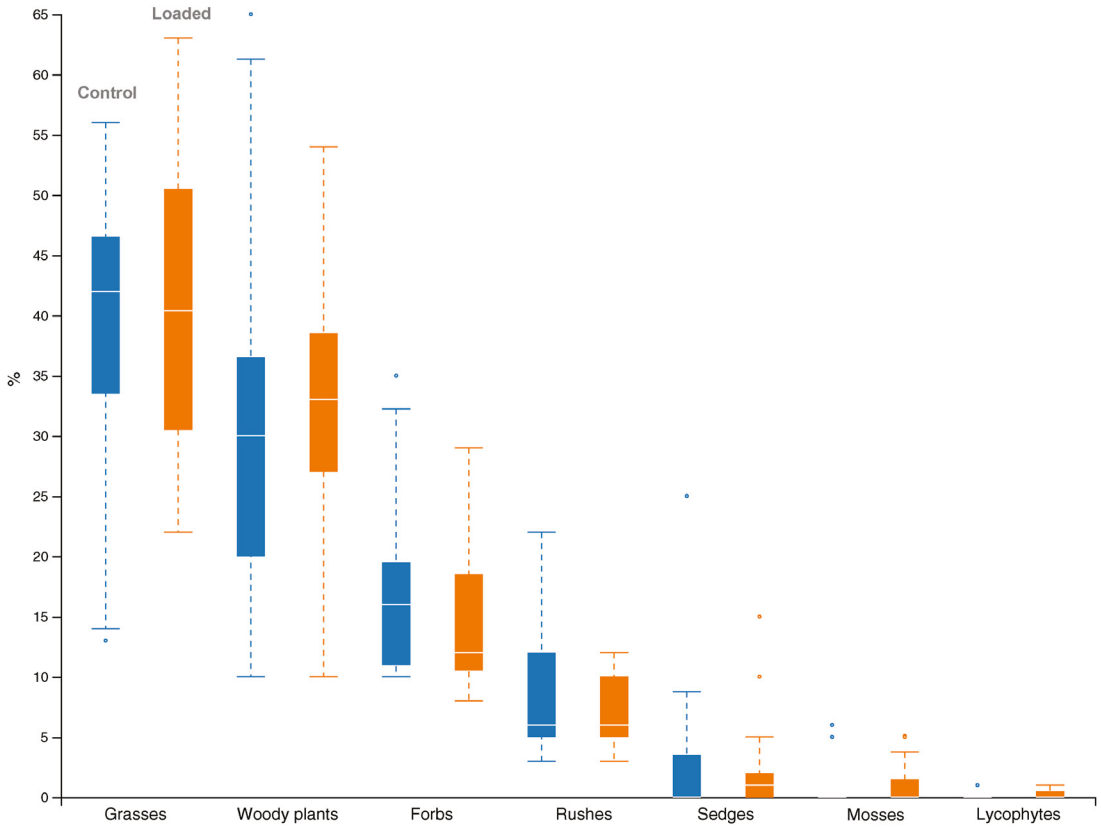


Figure 4. Projective cover of the principal functional groups in the high-mountain grasslands of the Ukrainian Carpathians.

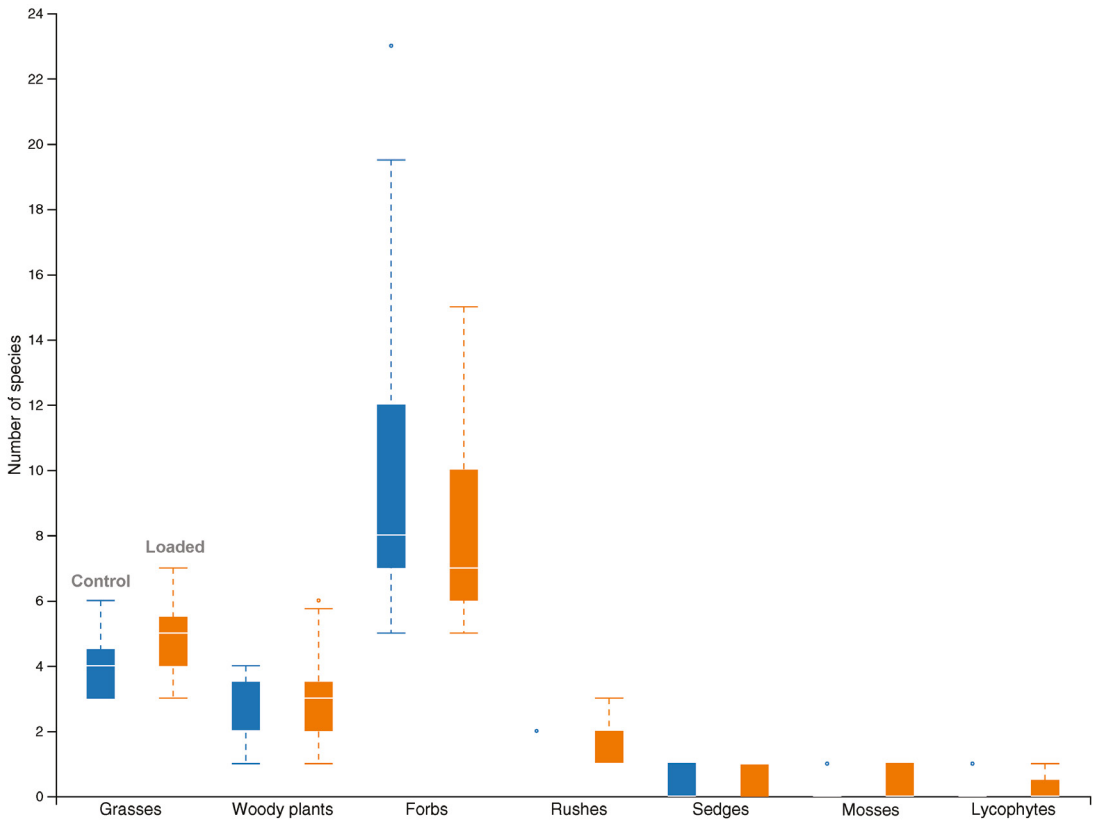


Figure 5. Species richness of the principal functional groups in the high-mountain grasslands of the Ukrainian Carpathians.

and lycophytes represented relatively small proportions of overall cover. Despite these directional shifts, Bray-Curtis dissimilarity between mean functional-cover profiles was only approximately 0.064. PERMANOVA detected no significant overall treatment effect (pseudo-F = 0.253, R^2 = 0.0090, p = 0.861). The conclusion was unchanged when permutations were restricted within certain mountain regions (p = 0.763). Thus, anthropogenic loading was not associated with the broad replacement of major plant functional groups.

Species richness showed a stronger functional response than projective cover (Fig. 5). Mean grass richness increased from 4.00 species per control relevé to 4.87 species per loaded relevé. The richness of woody plants increased from 2.53 to 2.87 species. In contrast, forb richness decreased from 10.27 to 8.20 species per relevé. Smaller increases occurred among rushes, sedges, mosses, and lycophytes. Bray-Curtis dissimilarity between the mean functional-group richness profiles was approximately 0.109. In the unrestricted PERMANOVA, plot status accounted for approximately 5.7% of multivariate variation but did not reach statistical significance (pseudo-F = 1.695, R^2 = 0.0571, p = 0.169). When permutations were restricted within certain mountain regions, the treatment-associated effect was significant (p = 0.035). The performed PERMDISP showed no evidence of unequal multivariate dispersion between control and loaded plots (p ≈ 0.782). Thus, although total species richness remained nearly unchanged, species were redistributed among functional groups, with the greater grass richness and lower forb richness in loaded plots.

Life strategy spectrum

The annual/perennial distinction was largely uninformative because almost all recorded taxa were perennial. Only one species, *Melampyrum pratense* L. (Orobanchaceae), was found to be clearly annual, while other species can perform both strategies depending on ecological preferences. At the same time, *M. pratense* was recorded only in one control and one loaded relevé with identical cover. Hence, it did not influence the overall results. Consequently, the average cover of annuals was approximately 0.07% in both plot categories, while perennials accounted for approximately 99.93% of the projective cover. Surely, PERMANOVA detected no difference in the annual/perennial cover spectrum (p = 1.000). Species-richness patterns were similarly invariant. Mean annual richness was 0.067 species per relevé in both categories, and no significant treatment effect was detected for the richness profile.

Hemicryptophytes dominated both in control and loaded vegetation plots, accounting for approximately 65.4% and 63.4% of projective cover, respectively (Fig. 6). Chamaephyte cover increased from approximately 28.5% in control plots to 31.1% in loaded plots. In contrast, geophyte cover declined from 3.7% to 2.3%, respectively. Phanerophytes and therophytes remained minor components. The overall Raunkiaer cover spectrum did not differ significantly between treatments (Bray-Curtis ≈ 0.032; pseudo-F = 0.306, R^2 = 0.0108, p = 0.695; region-restricted p = 0.490). The same was true considering the Raunkiaer's life forms accounted through the species richness (Fig. 7). Hemicryptophyte richness averaged 14.13 species in control and 13.93 species in loaded plots. Chamaephyte richness increased from 2.07 to 2.60 species, whereas geophyte richness declined from 1.60 to 1.00. Nevertheless, the overall life-form richness spectrum remained statistically similar (pseudo-F = 0.431, R^2 = 0.0152, p = 0.699; region-restricted p = 0.502).

Species turnover and nestedness

Despite the near-absence of differences in total species richness, paired control/loaded plots showed substantial compositional dissimilarity. Across the 15 corresponding plot pairs, an average of 12.47 species was shared between control and loaded relevés. In contrast, 6.20 species occurred only in the control member of the pair, and 6.13 occurred only in the loaded member (Fig. 8). Mean total Sørensen dissimilarity was β_sor = 0.325. Most of this dissimilarity was attributable to species replacement: mean turnover was β_sim = 0.270, whereas the nestedness-resultant component was only β_sne = 0.055. Turnover, therefore, represented approximately 82.6% of total pairwise beta diversity. This indicates that compositional differences between corresponding control and loaded plots

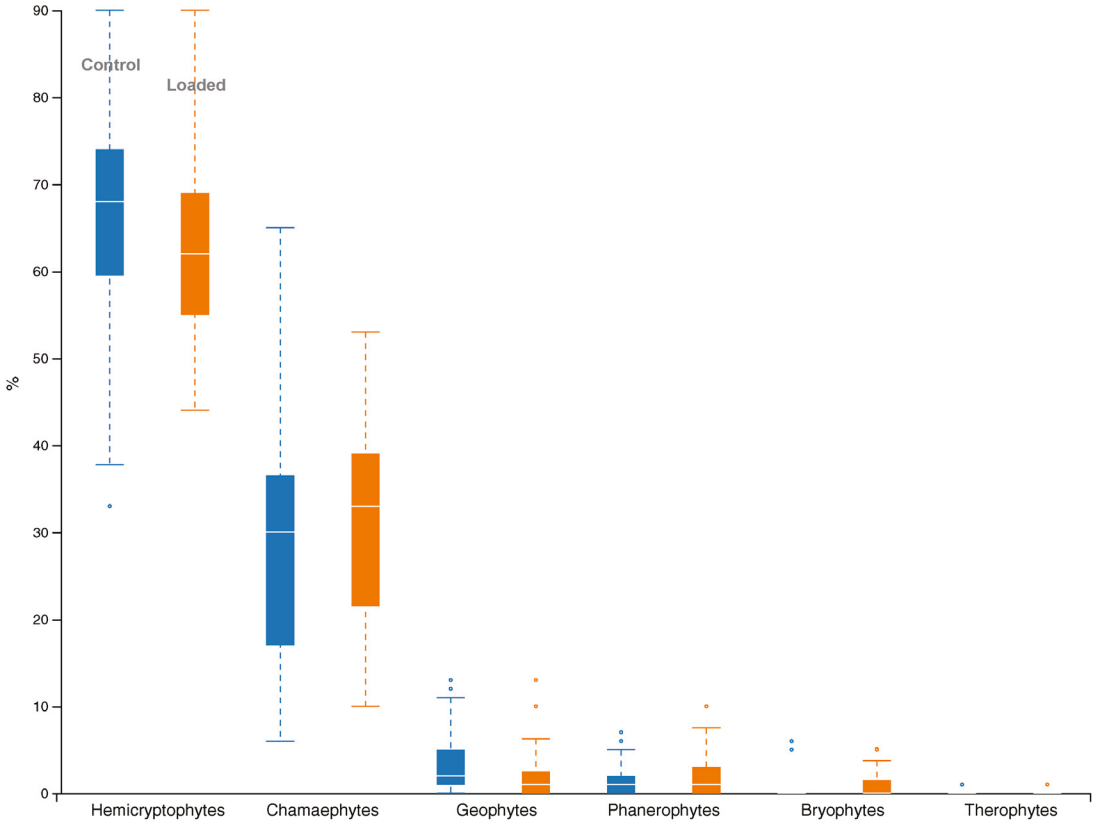


Figure 6. Projective cover of the Raunkiaer's life forms in the high-mountain grasslands of the Ukrainian Carpathians.

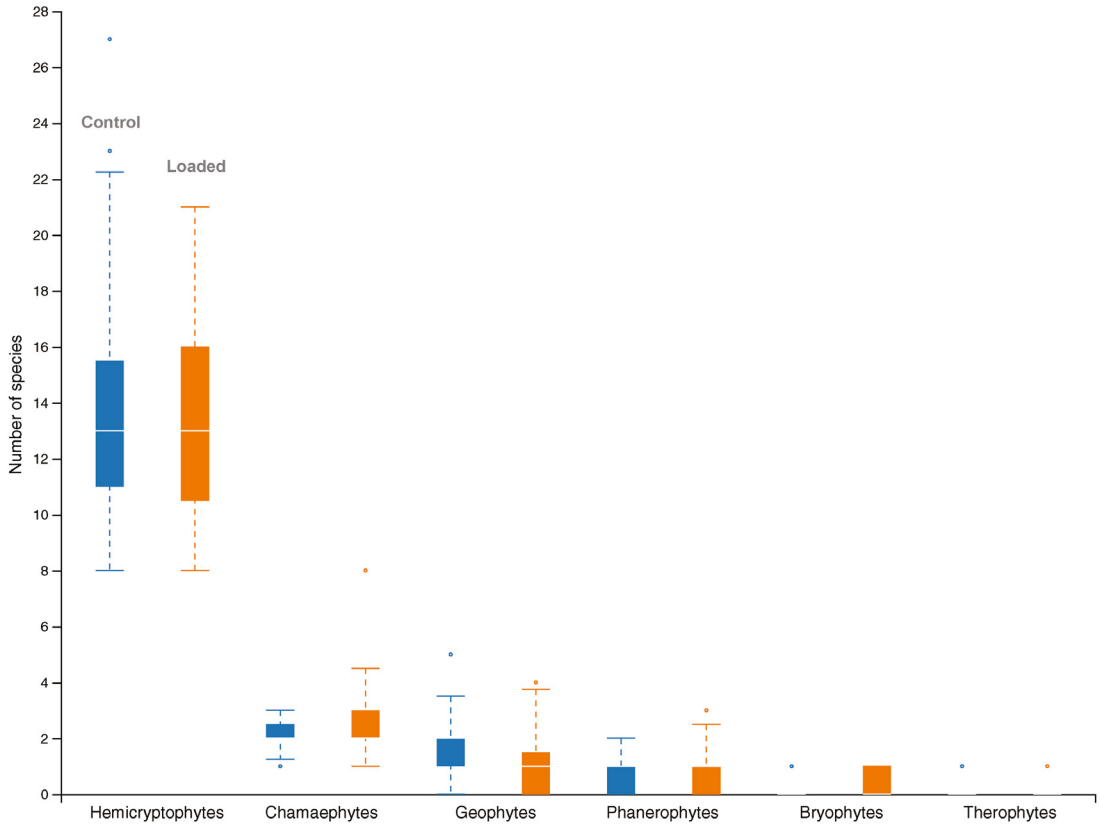


Figure 7. Species richness of the Raunkiaer's life forms in the high-mountain grasslands of the Ukrainian Carpathians.

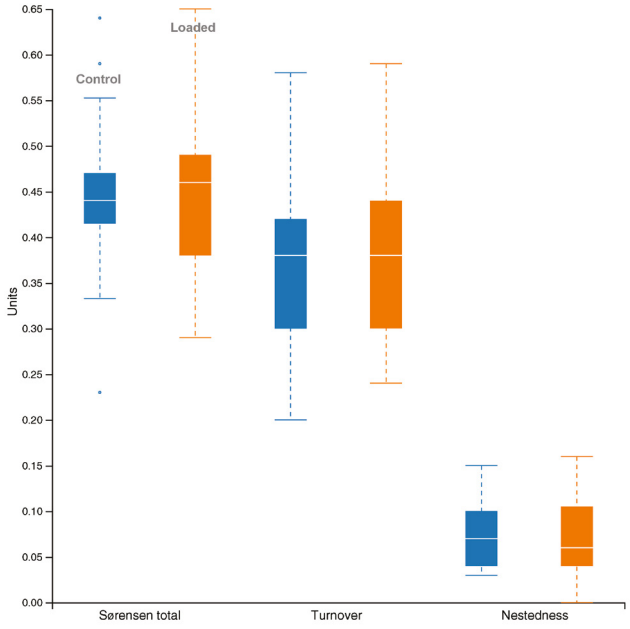


Figure 8. Species turnover and nestedness in the high-mountain grasslands of the Ukrainian Carpathians.

primarily reflected species replacement rather than a simple loss of species from the loaded plots. However, turnover between treatment categories did not exceed background plot-to-plot heterogeneity. Mean Sørensen dissimilarity was approximately 0.445 among control plots, 0.453 among loaded plots, and 0.418 between control and loaded plots. Corresponding mean turnover values were 0.371, 0.383, and 0.355, respectively. A region-restricted permutation test did not detect elevated turnover specifically associated with the control/loaded comparison ($p = 0.357$). Thus, replacement was the principal factor in the compositional differences between the tested plots.

Species evenness

Species evenness was highly similar between control and anthropogenically loaded vegetation. Mean Pielou's evenness was $J' = 0.776 \pm 0.067$ J'=0.776 \pm 0.067 in control plots and $J' = 0.781 \pm 0.074$ J'=0.781 \pm 0.074 in loaded plots. Median values were 0.794 and 0.787, respectively. The mean paired difference between loaded and control plots was only +0.004. A paired permutation test provided no evidence of a treatment-associated difference in evenness ($p = 0.883$). Thus, despite the compositional changes detected in species identity, functional-group richness, and ecological specialization, the overall distribution of projective cover among species remained essentially unchanged.

Ecological specialization

Fifty-four of 94 vascular taxa were matched to non-forest ESI values. Although this represented only part of the vascular flora, matched species accounted for 83.04% of vascular-plant projective cover in control plots and 82.88% in loaded plots. ESI coverage, therefore, did not differ between plot categories ($p = 0.973$), indicating that subsequent specialization comparisons were not driven by differential representation of taxa with available ESI values (Fig. 9). Presence-based community specialization showed only a weak difference. Mean CSI increased from 4.643 in control plots to 4.741 in loaded plots, but the region-restricted permutation test was non-significant ($p = 0.188$). A stronger pattern emerged when specialization was weighted by projective cover. Mean cover-weighted CSI increased from 4.362 in control vegetation to 4.559 in loaded vegetation, a difference of 0.197 ESI units. This difference was significant in the unrestricted permutation analysis ($p = 0.0165$) and became stronger when permutations were restricted within mountain regions ($p = 0.0023$). Thus, the species dominating in projective cover in loaded plots tended to have higher externally derived ESI scores, even though the mean specialization of species did not differ significantly.

The categorical analysis, which subdivided participating species into generalists and specialists, supported the CSI interpretation primarily through changes in generalist dominance. Species falling within the lowest quartile of the external ESI distribution accounted for approximately 48.16% of vascular-plant cover in control vegetation but only 36.69% in loaded vegetation, representing a decline of 11.47 percentage points (Fig. 10). This difference was significant under region-restricted permutation ($p = 0.0114$). Specialist cover increased from approximately 3.54% to 5.74%, but this individual change was not statistically significant ($p = 0.235$). Similarly, categorical species richness did not show significant differences. Generalists represented approximately 38.6% of matched species richness in control plots and 34.1% in loaded plots ($p = 0.156$), whereas specialists

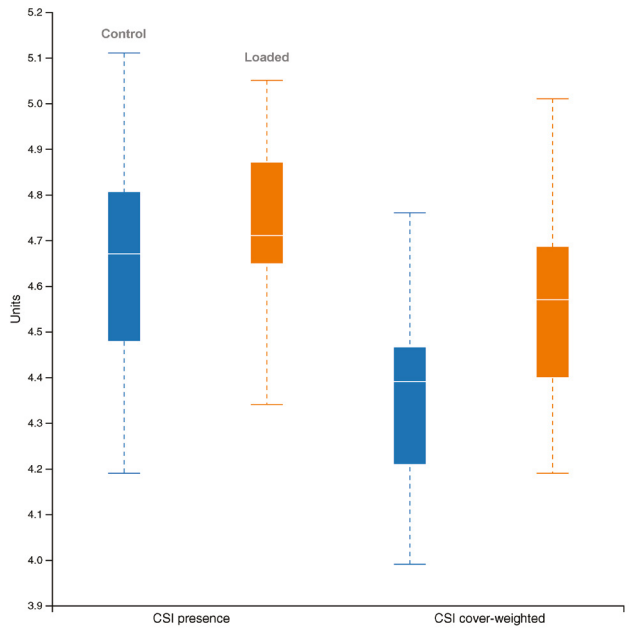


Figure 9. Community specialization index (CSI) calculations for the high-mountain grasslands of the Ukrainian Carpathians.

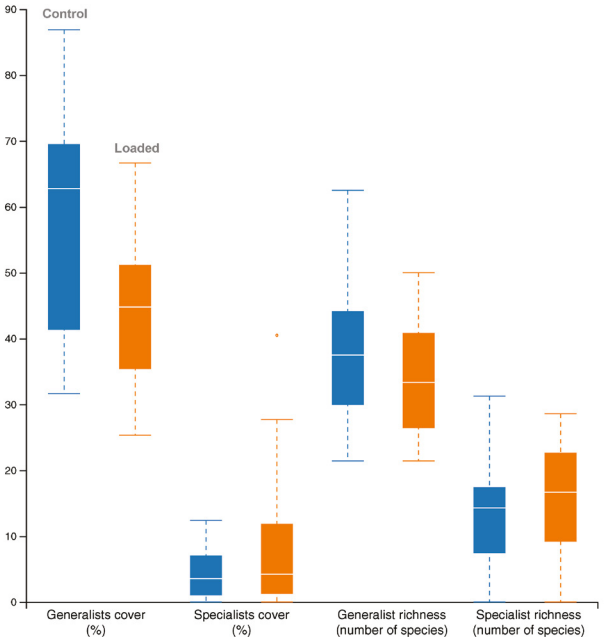


Figure 10. Ecological specialization within the high-mountain grasslands of the Ukrainian Carpathians.

increased from approximately 13.5% to 15.8% ($p = 0.527$). The specialization signal, therefore, reflected primarily a change in relative dominance rather than a clear gain or loss in the number of specialist or generalist species.

Integrated response

Across the different organizational levels, a consistent pattern emerged. Total species richness, broad family-level projective cover, functional-group cover, annual/perennial composition, Raunkiaer life-form spectra, and species evenness were comparatively stable between control and loaded vegetation. Mean Pielou's evenness was nearly identical in control and loaded plots ($J' = 0.776 \pm 0.067$ and 0.781 ± 0.074, respectively), and the paired permutation test provided no evidence of a treatment-associated difference ($p = 0.883$). Nevertheless, this overall structural stability concealed changes at finer levels of organization. Species richness was redistributed among dominant families and major functional groups, while differences in species composition between corresponding plots were predominantly generated by species replacement rather than nested species loss. In addition, the species contributing most strongly to projective cover in loaded vegetation showed higher community-weighted ecological specialization scores, accompanied principally by reduced cover of externally classified generalists.

Taken together, these results indicate that anthropogenic load was associated with complex compositional reorganization of the investigated plant communities rather than a simple alteration of their vegetation structure. Species identity and the distribution of richness among taxonomic and functional groups changed. In contrast, total species richness, broad structural attributes, and the overall evenness of species' projective cover remained essentially unchanged. Thus, the observed response was characterized less by general species loss, shifts in structural types, or dominance of certain plant ecological groups than by species replacement and changes in the ecological characteristics of the species that contribute to general community composition, and their projective cover.

Discussion

Structural stability and compositional reorganization

The combined analyses indicate that the response of high-mountain grasslands to anthropogenic load in the Ukrainian Carpathians was subtle and scale-dependent. Total species richness, broad family-level

cover, functional-group cover, annual/perennial composition, Raunkiaer (1934) life-form spectra, and species evenness remained stable between control and loaded plots, which can be explained by the general stability of such ecosystems and their ability for resistance (Cole & Monz, 2002; Berauer et al., 2021; Xiang et al., 2024). At the same time, finer-scale analyses revealed changes in species identity, the distribution of richness among dominant taxonomic and functional groups, beta-diversity structure, and abundance-weighted ecological specialization in the loaded communities. Thus, the absence of a strong response in conventional measures of alpha diversity or vegetation structure should not be interpreted as ecological invariance (Graham et al., 2019; Sabatini et al., 2022).

Similar decoupling between species richness and community composition has been reported in many disturbed grasslands. For example, a recent meta-analysis found higher plant diversity under extensive grazing or mowing than under abandonment, while emphasizing substantial heterogeneity among studies and strong effects of plot size (Schneider & Hering, 2024). Similarly, global analyses of land-use intensification generally report reductions in species richness, although the magnitude of these effects varies strongly among systems and intensity levels (Klimek et al., 2007; Beckmann et al., 2019). The relatively weak richness response observed here may therefore reflect the particular intensity and type of anthropogenic pressure represented in our study, as well as the environmental filtering already imposed by high-elevation conditions. Disturbance in grasslands often results in the recovery of species richness and evenness, while species composition and community functional characteristics remain different from those of undisturbed vegetation (Smith et al., 2022; Ulrich et al., 2025). Likewise, land-use effects on grassland vegetation may differ among regions and among diversity components, with species richness, evenness, and functional-group composition responding differently to management (Socher et al., 2013; Mauchamp et al., 2014; Berauer et al., 2021). These studies support the hypothesis that richness and evenness alone may not capture compositional responses to environmental change (Hillebrand et al., 2018; Avolio et al., 2021).

Species replacement rather than simple species loss

The partitioning of beta diversity provides a more informative interpretation of the observed differences. Approximately 83 % of the Sørensen dissimilarity between corresponding control and loaded plots was attributable to turnover, whereas nestedness contributed only a minor fraction. Thus, loaded plots were not simply species-poor subsets of control plots; differences were predominantly attributable to species replacement. This distinction is important because turnover and nestedness represent different mechanisms of compositional change. Turnover indicates replacement between species assemblages, whereas nestedness is more consistent with differences in species richness caused by ordered species loss or gain (Baselga, 2010). Studies of anthropogenically impacted grasslands have shown that similar turnover and nestedness may be driven by different ecological and historical factors, including environmental filtering, dispersal limitation, and land-use history (Ronikier, 2011; Conradi et al., 2017; Flantua et al., 2018). In our study, however, treatment-associated turnover did not exceed background turnover among plots within the same treatment. Therefore, the results should not be interpreted as strong evidence that anthropogenic load clearly increased overall beta diversity. Rather, anthropogenic load was associated with compositional replacement of certain plant species within a highly heterogeneous regional species pool. Such interpretation is also consistent with observations from Carpathian mountain meadows, where changes following abandonment can depend strongly on the identity and competitive characteristics of dominant species rather than on a uniform loss process (Korzeniak, 2005; Csergő et al., 2013; Collins et al., 2022). The present results extend this perspective by showing that substantial compositional differences can occur even when total species richness remains almost unchanged.

Changes in ecological specialization without increased dominance inequality

The ecological-specialization analysis revealed an additional dimension of community change. Presence-based

community specialization did not differ significantly between treatments, whereas cover-weighted specialization was higher in loaded plots. This indicates that the shift was related primarily to the relative contribution of species to vegetation cover rather than to a change in the specialization of the species pool itself. The categorical analysis further suggested that the increase in cover-weighted specialization was driven mainly by a reduction in the cover of externally classified generalists rather than by a significant increase in the cover or richness of specialists. This result should therefore not be interpreted as a simple transition toward specialist-rich vegetation. Instead, it suggests a change in which species contributed most strongly to community cover. Such abundance-weighted changes can remain undetected when species are treated only as present or absent. Ecological specialization indices are particularly useful in this context because they characterize species according to their realized niche breadth across environmental gradients (Zelený & Chytrý, 2019; Zinnen et al., 2021; Douda et al., 2026).

The result is also noteworthy because anthropogenic disturbance is frequently expected to favor broadly tolerant species. However, the relationship between disturbance and biodiversity is context dependent, and moderate disturbance can maintain or even increase diversity in some grassland systems (Hobbs et al., 1992; Yuan et al., 2016; Zarzycki et al., 2022). At the same time, high species diversity in native plant communities can serve as a strong barier for invasion of alien species and demonstrate the increased resistance to disturbance reaction (Buzhdygan et al., 2026). In our study, the observed increase in community-weighted specialization was not accompanied by a significant increase in specialist richness or cover. At the same time, no notable invasion of alien plants has been observed. Several mechanisms could therefore produce the pattern, including selective reduction of some widespread species or stronger environmental filtering under anthropogenic pressure. These mechanisms cannot be distinguished with the present observational design and should be considered hypotheses for future study.

Species evenness provides an important constraint on interpretation

The absence of a treatment effect on Pielou's evenness adds an important qualification to the specialization result. Mean evenness was almost identical in control and loaded plots ($J' = 0.776 \pm 0.067$ and 0.781 ± 0.074, respectively), with no evidence of a difference in the paired permutation test ($p = 0.883$). Thus, the increase in cover-weighted ecological specialization did not result from a general increase in dominance inequality. Such a distinction is important because richness, evenness, and taxonomic composition represent different dimensions of community structure and may respond independently or in contrasting ways to environmental change. In particular, investigations of semi-natural grasslands have shown that species richness and evenness can respond differently to landscape context (Krauss et al., 2004), while experimental studies have documented changes in species composition and functional characteristics despite the recovery or stability of richness and evenness (Smith et al., 2022). In the present study, the combination of stable evenness with altered species identity and specialization indicates that the relative distribution of projective cover among species remained broadly similar even though the identity and ecological characteristics of those species changed.

Regional heterogeneity and ecological interpretation

Our study revealed the strong contribution of the mountain region to the structure of plant communities. Regional differences explained substantially more variation in species composition than the simple control–loaded contrast did, and several treatment-associated patterns became clearer when permutations were restricted to regions. This demonstrates that the five investigated mountain regions responded differently to anthropogenic loading and cannot be treated as a single, integrated unit. Strong background floristic and environmental heterogeneity can obscure comparatively small anthropogenic effects when regional structure is ignored. This regional context is particularly important in mountain grasslands, where environmental gradients are sharp and can strongly structure

species composition over relatively short geographic distances. The observed treatment effects should therefore be understood as changes superimposed on a pronounced regional species turnover rather than as a uniform response of a single homogeneous vegetation type.

Implications for detecting anthropogenic change

Overall, the results indicate that anthropogenic load was associated with compositional reorganization within a structurally persistent vegetation framework. Total species richness and broad vegetation structure changed little, whereas species identity, the distribution of richness among functional and taxonomic groups, and abundance-weighted ecological specialization were more sensitive. At the same time, species evenness remained unchanged, indicating that the observed compositional reorganization was not accompanied by a general increase in dominance inequality. These findings suggest that studies based solely on total species richness or broad vegetation cover may underestimate subtle anthropogenic effects in high-mountain grasslands. Metrics incorporating species identity, turnover/nestedness partitioning, within-group richness, and abundance-weighted ecological characteristics can reveal changes that remain invisible at the level of total richness. Importantly, however, the high background beta diversity and relatively small number of sampled plots indicate that these patterns should be interpreted as evidence of compositional differentiation rather than a large-scale loss of biodiversity.

Conclusions

The studied high-mountain grasslands exhibited neither complete resistance nor straightforward biodiversity loss in response to anthropogenic loading. Instead, the response was expressed primarily through species replacement and changes in the ecological characteristics of species contributing to community cover. In particular, the anthropogenically loaded plots showed greater grass richness and lower forb richness, and species that dominated here in their projective cover tended to have higher available ESI scores. At the same time, total richness, broad vegetation structure, and species evenness remained comparatively stable in both loaded and control plots. Such a combination of changes in taxonomic structure and structural persistence in the studied plant communities suggests that species identity and abundance-weighted community properties may provide more sensitive indicators of subtle anthropogenic effects than measures of either characteristic alone.

Acknowledgements

We thank the National Research Foundation of Ukraine for the support of the project 2025.07/0155 "Investigation of biodiversity, functional traits and phylogenetic structure of high-mountain meadows of the Ukrainian Carpathians in the context of habitat transformation" implemented within the call 2025.07 "Excellent Science in Ukraine 2026-2028".

References

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology, 26,* 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anderson, M.J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics, 62*(1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Avolio, M.L., Komatsu, K.J., Collins, S.L., Grman, E., Koerner, S.E., Tredennick, A.T., Wilcox, K.R., Baer, S., Boughton, E.H., Britton, A.J., Foster, B., Gough, L., Hovenden, M., Isbell, F., Jentsch, A., Johnson, D.S., Knapp, A.K., Kreyling, J., Langley, J.A., … & Tognetti, P.M. (2021). Determinants of community compositional change are equally affected by global change. *Ecology Letters, 24*(9), 1892–1904. https://doi.org/10.1111/ele.13824

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography, 19,* 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography, 21,* 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceauşu, S., Kambach, S., Kinlock, N.L., Phillips, H.R.P., Verhagen, W., Gurevitch, J., Klotz, S., Newbold, T., Verburg, P.H., Winter, M., & Seppelt, R. (2019). Conventional land-use intensification reduces species richness and increases production: a global meta-analysis. *Global Change Biology, 25,* 1940–1951. https://doi.org/10.1111/gcb.14606

Berauer, B.J., Wilfahrt, P.A., Schuchardt, M.A., Schlingmann, M., Schucknecht, A., & Jentsch, A. (2021). High land-use intensity diminishes stability of forage provision of mountain pastures under future climate variability. *Agronomy, 11*(5), Article 910. https://doi.org/10.3390/agronomy11050910

Bray, J.R. & Curtis, J.T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs, 27*(4), 325–349. https://doi.org/10.2307/1942268

Buzhdygan, O., Baldauf, S., Tietjen, B., Iemelianova, S., Borovyk, D., Vynokurov, D., Chusova, O., Budzhak, V., Bergmann, J., Dengler, J., Dembicz, I., Janišová, M., Vasheniak, I., Chase, J., & Kuzemko, A. (2026). Drivers of plant invasions and their scale-dependency in grasslands. *Biological Conservation, 313,* Article 111584. https://doi.org/10.1016/j.biocon.2025.111584

Cherepanyn, R.M. (2018). Effect of climate changes on the habitat of rare arctic-alpine plant species in the high mountain part of the Ukrainian Carpathians. *Studia Biologica, 12*(1), 73–86. https://doi.org/10.30970/sbi.1201.544

Csergő, A.M., Demeter, L., & Turkington, R. (2013). Declining diversity in abandoned grasslands of the Carpathian Mountains: do dominant species matter? *PLoS ONE, 8*(8), Article e73533. https://doi.org/10.1371/journal.pone.0073533

Coldea, G., Gafta, D., Filipaş, L., & Stoica, A.I. (2026). No decline in plant species diversity despite noticeable land use changes over 58 years (Carpathian foothills, Romania). *Earth Systems and Environment, 10*, 4345–4361. https://doi.org/10.1007/s41748-025-00853-2

Cole, D.N., & Monz, C.A. (2002). Trampling disturbance of high-elevation vegetation, Wind River Mountains, Wyoming, USA. *Arctic, Antarctic, and Alpine Research, 34*(4), 365–376. https://doi.org/10.1080/15230430.2002.12003507

Collins, C.G., Elmendorf, S.C., Smith, J.G., Shoemaker, L., Szojka, M., Swift, M., & Suding, K.N. (2022). Global change re-structures alpine plant communities through interacting abiotic and biotic effects. *Ecology Letters, 25*(8), 1813–1826. https://doi.org/10.1111/ele.14060

Conradi, T., Temperton, V.M., & Kollmann, J. (2017). Beta diversity of plant species in human-transformed landscapes: control of community assembly by regional productivity and historical connectivity. *Perspectives in Plant Ecology, Evolution and Systematics, 24,* 1–10. https://doi.org/10.1016/j.ppees.2016.10.001

Dainese, M., Crepaz, H., Bottarin, R., Fontana, V., Guariento, E., Hilpold, A., Obojes, N., Paniccia, C., Scotti, A., Seeber, J., Steinwandter, M., Tappeiner, U., & Niedrist, G. (2024). Global change experiments in mountain ecosystems: a systematic review. *Ecological Monographs, 94*(4), Article e1632. https://doi.org/10.1002/ecm.1632

Dayneko, P., Borovyk, D., Borsukevych, L., Kuzemko, A., Magnes, M., Škodová, I., Vynokurov, D., Devánová, K., Iuga, A., Širka, P., Iosif, C., & Janišová, M. (2027). Fast post-ploughing recovery of traditionally managed semi-natural mountain grasslands in the Romanian Carpathians. *Agriculture, Ecosystems & Environment, 414,* Article 110754. https://doi.org/10.1016/j.agee.2026.110754

Didukh, Y.P. (Ed.). (2009). *Red book of Ukraine. The plant world.* Globalconsulting, Kyiv. (In Ukrainian)

Dmytrakh, R. (2021). Impact of natural factors on populations changes of herbaceous plants species and assessment of their state in present high-mountain conditions of the Ukrainian Carpathians. *Studia Biologica, 15*(1), 67–78. https://doi.org/10.30970/sbi.1501.646

Doležal, J., & Šrůtek, M. (2002). Altitudinal changes in composition and structure of mountain-temperate vegetation: a case study from the Western Carpathians. *Plant Ecology, 158,* 201–221. https://doi.org/10.1023/A:1015564303206

Douda, J., Doudová, J., Král, P., Häusler, J., Holeštová, A., Eusebio, L., Květoň, J., & Havrdová, A. (2026). A trait-based integration of competition and abiotic tolerance underlies plant success. *New Phytologist, 252*(1), 87–99. https://doi.org/10.1111/nph.71465

Durak, T., Żywiec, M., Kapusta, P., & Holeksa, J. (2015). Impact of land use and climate changes on expansion of woody species on subalpine meadows in the Eastern Carpathians. *Forest Ecology and Management, 339*, 127–135. https://doi.org/10.1016/j.foreco.2014.12.014

Feurdean, A., Gałka, M., Tanţău, I., Geantă, A., Hutchinson, S.M., & Hickler, T. (2016). Tree and timberline shifts in the northern Romanian Carpathians during the Holocene and the responses to environmental changes. *Quaternary Science Reviews, 134,* 100–113. https://doi.org/10.1016/j.quascirev.2015.12.020

Flantua, S.G., Hooghiemstra, H., & Hoorn, C. (2018). Historical connectivity and mountain biodiversity. In C. Hoorn, A. Perrigo & A. Antonelli (Eds.), *Mountains, climate and biodiversity* (pp. 171–185). Wiley-Blackwell.

Graham, S.I., Kinnaird, M.F., O'Brien, T.G., Vågen, T., Winowiecki, L.A., Young, T.P., & Young, H.S. (2019). Effects of land-use change on community diversity and composition are highly variable among functional groups. *Ecological Applications, 29*(7), Article e01973. https://doi.org/10.1002/eap.1973

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., ... & Ryabov, A.B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology, 55*(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hobbs, R.J., & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology, 6*(3), 324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Hurdu, B.I., Escalante, T., Puşcaş, M., Novikoff, A., Bartha, L., & Zimmermann, N.E. (2016). Exploring the different facets of plant endemism in the South-Eastern Carpathians: a manifold approach for the determination of biotic elements, centres and areas of endemism. *Biological Journal of the Linnean Society, 119*(3), 649–672. https://doi.org/10.1111/bij.12902

Klimek, S., Richter gen. Kemmermann, A., Hofmann, M., & Isselstein, J. (2007). Plant species richness and composition in managed grasslands: the relative importance of field management and environmental factors. *Biological Conservation, 134*(4), 559–570. https://doi.org/10.1016/j.biocon.2006.09.007

Kobiv, Y. (2017). Response of rare alpine plant species to climate change in the Ukrainian Carpathians. *Folia Geobotanica, 52,* 217–226. https://doi.org/10.1007/s12224-016-9270-z

Kobiv, Y., & Kobiv, V. (2020). Impact of environmental change on a rare high-mountain tall-herb species: a case study on *Achillea lingulata* in the Ukrainian Carpathians. *Botany Letters, 167*(2), 232–240. https://doi.org/10.1080/23818107.2019.1679249

Korzeniak, J. (2005). Species richness and diversity related to anthropogenic soil disturbance in abandoned meadows in the Bieszczady Mts. (Eastern Carpathians). *Acta Societatis Botanicorum Poloniae, 74*(1), 65–71. https://doi.org/10.5586/asbp.2005.010

Krauss, J., Klein, A.-M., Steffan-Dewenter, I., & Tscharntke, T. (2004). Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation, 13*, 1427–1439. https://doi.org/10.1023/B:BIOC.0000021323.18165.58

Kricsfalusy, V.V. (2013). Mountain grasslands of high conservation value in the Eastern Carpathians: syntaxonomy, biodiversity, protection and management. *Thaiszia, 23*(1), 67–112.

Kruhlov, I. (2008). Delimitation, metrisation and classification of morphogenic ecoregions of the Ukrainian Carpathians. *Ukrainian Geographical Journal, 3,* 59–68. (In Ukrainian)

Kyyak, V.H., Bilonoha, V.M., Dmytrakh, R.I., Gynda, L.V., Nesteruk, Y.Y., & Shtupun, V.P. (2015). Trends in plant population pattern changes under natural and man-induced ecosystem transformations of the high mountain zone in the Ukrainian Carpathians. *Studia Biologica, 9*(2), 169–180. https://doi.org/10.30970/sbi.0902.431

Kyyak, V., Kobiv, Y., Zhilyaev, G., Bilonoha, V., Dmytrakh, R., Mykitchak, T., Reshetylo, O., Kobiv, V., Nesteruk, Y., Shtupun, V., & Gynda, L. (2019). Changes in population structure of rare species in the high-mountain zone of the Ukrainian Carpathians and problems of their conservation. *Acta Biologica Universitatis Daugavpiliensis, 19*(1), 77–85.

Mauchamp, L., Mouly, A., Badot, P.M., & Gillet, F. (2014). Impact of management type and intensity on multiple facets of grassland biodiversity in the French Jura Mountains. *Applied Vegetation Science, 17*(4), 645–657. https://doi.org/10.1111/avsc.12116

Midolo, G., Clark, A.T., Chytrý, M., Essl, F., Dullinger, S., Jandt, U., Bruelheide, H., Argagnon, O., Biurrun, I., Chiarucci, A., Ćušterevska, R., De Frenne, P., De Sanctis, M., Dengler, J., Divíšek, J., Dziuba, T., Ejrnæs, R., Garbolino, E., Illa, E., ... & Keil, P. (2025). Six decades of losses and gains in alpha diversity of European plant communities. *Ecology Letters, 28*(11), Article e70248. https://doi.org/10.1111/ele.70248

Mitka, J., Kucharzyk, S., Capelo, J., & Stachurska-Swakoń, A. (2022). Subalpine woody vegetation in the Eastern Carpathians after release from agropastoral pressure. *Scientific Reports, 12*(1), Article 17897. https://doi.org/10.1038/s41598-022-22248-3

Novikov, A., & Nachychko, V. (2026). UCarpHT plant and soil dataset. Zenodo. https://doi.org/10.5281/zenodo.23499511

Novikov, A., & Sup-Novikova, M. (2022). Endemic vascular plants in the Ukrainian Carpathians. *Biodiversity Data Journal, 10,* Article e95910. https://doi.org/10.3897/BDJ.10.e95910

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., De Cáceres, M., Durand, S., Evangelista, H.B.A., Hannigan, G., ... & Weedon, J. (2026). *vegan: Community Ecology Package. R package version 2.8-0.* R-universe. https://cran.r-project.org/web/packages/vegan/index.html

Pielou, E.C. (1966). Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology, 10*(2), 370–383. https://doi.org/10.1016/0022-5193(66)90133-0

POWO. (2026). *Plants of the World Online.* Royal Botanic Gardens, Kew. https://powo.science.kew.org/

Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography.* Clarendon Press.

Ronikier, M. (2011). Biogeography of high-mountain plants in the Carpathians: an emerging phylogeographical perspective. *Taxon, 60*(2), 373–389. https://doi.org/10.1002/tax.602008

Sabatini, F.M., Jiménez-Alfaro, B., Jandt, U., Chytrý, M., Field, R., Kessler, M., Lenoir, J., Schrodt, F., Wiser, S.K., Arfin Khan, M.A.S., Attorre, F., Cayuela, L., De Sanctis, M., Dengler, J., Haider, S., Hatim, M.Z., Indreica, A., Jansen, F., Pauchard, A., ... & Bruelheide, H. (2022). Global patterns of vascular plant alpha diversity. *Nature Communications, 13*, Article 4683. https://doi.org/10.1038/s41467-022-32063-z

Schneider, A.R., & Hering, D. (2024). Effects of extensive grazing and mowing compared to abandonment on the biodiversity of European grasslands: a meta-analysis. *Applied Vegetation Science, 27*(4), Article e70003. https://doi.org/10.1111/avsc.70003

Smith, E.A., Holden, E.M., Brown, C., & Cahill Jr., J.F. (2022). Disturbance has lasting effects on functional traits and diversity of grassland plant communities. *PeerJ, 10,* Article e13179. https://doi.org/10.7717/peerj.13179

Socher, S.A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., Hemp, A., Schöning, I., Wells, K., Kalko, E.K.V., Weisser, W.W., & Fischer, M. (2013). Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic and Applied Ecology, 14*(2), 126–136. https://doi.org/10.1016/j.baae.2012.12.003

Stanisci, A., Bricca, A., Calabrese, V., Cutini, M., Pauli, H., Steinbauer, K., & Carranza, M.L. (2020). Functional composition and diversity of leaf traits in subalpine versus alpine vegetation in the Apennines. *AoB PLANTS, 12*(2), Article plaa004. https://doi.org/10.1093/aobpla/plaa004

Tanţău, I., Feurdean, A., De Beaulieu, J.-L., Reille, M., & Fărcaş, S. (2014). Vegetation sensitivity to climate changes and human impact in the Harghita Mountains (Eastern Romanian Carpathians) over the past 15 000 years. *Journal of Quaternary Science, 29*(2), 141–152. https://doi.org/10.1002/jqs.2688

Ujházy, K., Ujházyová, M., Bučinová, K., Čiliak, M., Glejdura, S., & Mihál, I. (2018). Response of fungal and plant communities to management-induced over storey changes in montane forests of the Western Carpathians. *European Journal of Forest Research, 137,* 169–183. https://doi.org/10.1007/s10342-017-1096-6

Ulrich, W., Borges, P.A.V., Fattorini, S., ter Steege, H., Gotelli, N.J., Magurran, A.E., Marguet, P.A., Schrader, J., & Matthews, T.J. (2025). Species and trait abundance distributions as tools for understanding disturbance effects and community assembly in applied ecology. *Journal of Applied Ecology, 62*(9), 2096–2110. https://doi.org/10.1111/1365-2664.70140

Xiang, Q., Yu, H., Huang, H., Yan, D., Yu, C., Wang, Y., & Xiong, Z. (2024). The impact of grazing activities and environmental conditions on the stability of alpine grassland ecosystems. *Journal of Environmental Management, 360,* Article 121176. https://doi.org/10.1016/j.jenvman.2024.121176

Yuan, Z.Y., Jiao, F., Li, Y.H., & Kallenbach, R.L. (2016). Anthropogenic disturbances are key to maintaining the biodiversity of grasslands. *Scientific Reports, 6,* Article 22132. https://doi.org/10.1038/srep22132

Zarzycki, J., Korzeniak, J., & Perzanowska, J. (2022). Impact of land use changes on the diversity and conservation status of the vegetation of mountain grasslands (Polish Carpathians). *Land, 11*(2), Article 252. https://doi.org/10.3390/land11020252

Zeidler, M., Husek, V., Banaš, M., & Krahulec, F. (2023). Homogenization and species compositional shifts in subalpine vegetation during the 60-year period. *Acta Societatis Botanicorum Poloniae, 92,* Article 171689. https://doi.org/10.5586/asbp/171689

Zelený, D. & Chytrý, M. (2019). Ecological Specialization Indices for species of the Czech flora. *Preslia, 91*(2), 93–116. https://doi.org/10.23855/preslia.2019.093

Zinnen, J., Spyreas, G., Zaya, D.N., & Matthews, J.W. (2021). Niche ecology in Floristic Quality Assessment: are species with higher conservatism more specialized? *Ecological Indicators, 121,* Article 107078. https://doi.org/10.1016/j.ecolind.2020.107078

Структурна стабільність та реорганізація складу високогірних лук під дією антропогенного навантаження в Українських Карпатах

Андрій Новіков [1,*], Віктор Начичко [2]

[1] Державний природознавчий музей НАН України, вул. Театральна, 18, Львів, 79008, Україна; * novikoffav@gmail.com

[2] Львівський національний університет імені Івана Франка, вул. Грушевського, 4, Львів, 79005, Україна

Антропогенний тиск може змінювати рослинні угруповання, не викликаючи негайних змін видового багатства чи загальної структури рослинності. Ми оцінили реакцію високогірних лук на антропогенне навантаження у п'яти гірських масивах Українських Карпат, використавши 30 геоботанічних описів, що представляють 15 пар контрольних та антропогенно навантажених ділянок. Реакція рослинності на антропогенне навантаження була всебічно досліджена на різних структурних рівнях. Загальні видове багатство та структура рослинності залишалися дуже схожими між контрольними та навантаженими ділянками. Натомість реакція на антропогенне навантаження була пов'язана зі змінами у розподілі видового багатства серед домінантних родин рослин та функціональних груп, зокрема після врахування регіональної гетерогенності. Навантажені ділянки загалом демонстрували вище видове багатство злаків і нижче багатство різнотрав'я, тоді як проективне покриття функціональних груп залишалося здебільшого незмінним. Відмінності між парними контрольними та навантаженими ділянками були переважно зумовлені заміщенням видів (turnover), а не їх поступовим вилученням (nestedness), хоча заміщення не перевищувало високого фонового бета-різноманіття досліджених лук. Екологічна спеціалізація угруповань (зважена за покриттям) була виразно вищою на навантажених ділянках, що головним чином відображало зниження домінування видів-генералістів, тоді як рівномірність розподілу (evenness) видів залишалася незмінною. Загалом, результати вказують на те, що антропогенне навантаження радше пов'язане з реорганізацією складу високогірних лук в межах загалом стійкої структури рослинності, а не з простим збідненням видового складу і біорізноманіття. Таким чином, видовий склад, структура видового багатства в межах окремих функціональних груп, а також характеристики угруповань, зважені за чисельністю, можуть слугувати чутливішими індикаторами антропогенних змін, ніж оцінка лише видового багатства чи характеру рослинного покриву.

Ключові слова: високогірні луки, Українські Карпати, антропогенне навантаження, реорганізація складу, заміщення видів, стабільність рослинності