

Cessation of livestock grazing and windthrow drive a shift in plant species composition in the Western Tatra Mts

Auflassung von Beweidung und Windwürfe führen zur Veränderung der Artenzusammensetzung der Vegetation in der westlichen Tatra

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Abstract

Mountain vegetation is considered highly sensitive to changes in land use, especially grazing regime and forest management. The aim of this study was to assess shifts in plant species composition in the Western Tatra Mts over the past 92 years and to determine environmental drivers that have caused changes in species composition. We resurveyed 47 vegetation plots assigned to three different types of vegetation, which were originally sampled in 1922. For each plot we recorded all vascular plant species, using the same methodology as in the original survey. For interpretation of the vegetation changes we used a set of ecological indicator values. The species composition of resampled grasslands was characterized by a higher proportion of nitrogen-demanding species on areas abandoned from livestock grazing. This reflects the higher susceptibility of grasslands located below natural treeline to changes in land use in comparison to those occurring on areas above the treeline, which may constitute a large threat to biological diversity of the Tatra Mts grasslands at the lower limit of their elevational range. Catastrophic windthrow constituted an important factor driving compositional dynamics in mountain spruce forests, creating a high diversity of microhabitats with suitable conditions for natural regeneration and development of the forest.

Keywords: alpine grassland, catastrophic wind events, ecological indicator values, grazing abandonment, natural treeline recovery, vegetation dynamics, vegetation resurvey

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Mountain areas have been exploited by humans for centuries, mainly for settlement, industry and shepherding (KOZAK 2003). As a result of human impacts, the elevational zonation of vegetation belts is often disturbed (e.g., AMEZTEGUI et al. 2016). For instance, most

mixed deciduous forests, typical of the lower forest belt in the Western Carpathians, were logged and replaced by planted spruce forests, or grazed by livestock (SOKOŁOWSKI 1936, MAYCOCK et al. 2000, BRUNET et al. 2010). Spruce forests of a higher forest belt were also transformed (e.g., SOKOŁOWSKI 1936, JONÁŠOVÁ et al. 2010), and disentangling natural forest stands from those with anthropogenic influences is often difficult or impossible (SVOBODA et al. 2010).

Both in managed and unmanaged forests, the main factor influencing vegetation dynamics is catastrophic windthrow, which is well documented on a wide geographical scale, in lowland temperate and boreal coniferous forest stands (e.g., ULANOVA 2000) as well as mountain forests (e.g., BUDZÁKOVÁ et al. 2013, WINTER et al. 2015). Catastrophic wind events may locally cause total damage of the tree canopy, leading to the colonization of forest by plants typical of non-forest vegetation (e.g., ULANOVA 2000, FISCHER et al. 2002).

Areas above treeline in the Tatra Mts are covered by dwarf pine communities and alpine grasslands (RADWAŃSKA-PARYSKA & PARYSKI 1995). As most of the more accessible areas were grazed for a long time, the upper treeline in mountain ranges of Central Europe has often been lowered by shepherding (PALOMBO et al. 2013). However, the economic importance of grasslands has decreased in most mountain regions, due to socio-economic changes following the Second World War (e.g., VEEN et al. 2009). The main reasons causing the abandonment of such areas were relatively low primary production and the short growing season in comparison to lower elevations (e.g., FISCHER & WIPF 2002).

The Chochołowska Valley in the Western Tatra Mts was used for shepherding, ore mining and metallurgy since the 15th century (FABIJANOWSKI 1962). The latter ceased in the 19th century and shepherding between the 1950s and 1970s, following establishment of the national park in 1955, which allowed the natural restoration of ecosystems. A few decades earlier, in 1922, the first historical vegetation survey of the Chochołowska Valley took place (SZAFER et al. 1923). It was one of the first phytosociological studies conducted in the Carpathians. This coincidence of the historical vegetation survey with the end of the period of intensive use of the area makes this valley an ideal place for exploring long-term shifts in plant species composition of ecosystems as a result of regeneration after release from long-term human impacts.

In this study we aimed to: (1) explore shifts in species composition of calcareous grasslands, granite grasslands and spruce forests over the past 92 years, and (2) identify environmental factors driving changes in the vegetation.

The cessation of sheep grazing resulted in colonization of the grasslands by tall herbs, shrubs and trees (e.g., AMEZAGA et al. 2004, BAUR et al. 2006, ONIPCHENKO et al. 2009). Therefore, we hypothesized that as a consequence of reforestation, the species composition of resampled non-forest plots would be characterized by higher proportions of more shade-tolerant species typical of the forest understory (EVJU et al. 2009, WESOŁOWSKA 2009, VASSILEV et al. 2011). Another effect of tree regeneration may be a higher proportion of warmth-demanding species, which may thrive under the canopy due to milder climate conditions in comparison to neighbouring open areas. Despite the relatively high insolation, open areas are strongly exposed to lower temperatures and stronger winds, which are the main factors determining the distribution of alpine plant species (HILLER et al. 2005, BATLLORI et al. 2010, AMEZTEGUI et al. 2016). Cessation of grazing also leads to a build-up of nutrient-rich soil humus, which in turn increases water storage capacity in the soil. In effect, more moisture- and nitrogen-demanding species may occur in grasslands where the grazing ceased (e.g., AUSTRHEIM & ERIKSSON 2001). Thus, we expected that on abandoned grasslands the

proportion of species tolerating more shade, preferring warmer climate, wetter soil conditions and higher nutrient contents in the soil, would be higher in comparison to their vegetation during the first sampling period (hypothesis 1).

Catastrophic windthrows can cause total damage of the tree canopy, leading to the colonization of disturbed forest stands by non-forest, open habitat species (e.g., ULANOVA 2000, FISCHER et al. 2002, ROBERTS 2004). Therefore we assumed that alongside successional processes in wind-disturbed forests, the cover of trees would increase (hypothesis 2). Windthrows also lead to increases in light availability, lower water and higher nutrient availability in the soil (e.g., ULANOVA 2000, ROBERTS 2004, BADE et al. 2015). Thus, we predict that in resampled forest plots the proportion of light-, nitrogen- and less water-demanding species (EIV-N) would be higher in comparison to the historical vegetation sites (hypothesis 3).

2. Material and methods

2.1 Study area

The Chochołowska Valley is the largest and longest valley in the Tatra Mts, covering an area of over 35 km² within a 10 km length and numerous side valleys. In comparison to other mountain valleys in the Tatra Mts (e.g., Mięguszowiecka Valley in the High Tatra Mts), the Chochołowska Valley is characterized by relatively few inaccessible steep slopes and rock walls. Since 1955 the whole valley has been in the zone of active conservation (except the strictly protected Kominiarski Wierch Massif) of Tatra National Park. The southern part of the Chochołowska Valley is composed of granitic and gneiss rocks and the northern part of sedimentary rocks - shale, limestone and dolomite, formed in the Triassic and Cretaceous periods (RADWAŃSKA-PARYSKA & PARYSKI 1995).

Shepherding and metallurgy started in the Tatra Mts in the 15th century, and in later centuries, covered all accessible areas and the whole elevational range. At the beginning of the 20th century, the intensity of grazing by sheep and cattle was relatively stable, and it peaked during the period between the First and Second World Wars, reaching approximately 30,000 animals (RADWAŃSKA-PARYSKA & PARYSKI 1995). Although grazing was most popular on open non-forest areas, it also affected forest and dwarf pine ecosystems (KOŁOWCA 1955). Between 1926 and 1953 the Chochołowska Valley was grazed by an average of 1200 sheep and 150 cattle in total (KOPCZYŃSKA-JAWORSKA 1985). After establishment of Tatra National Park (1955), the land ownership structure changed, and grazing by domestic animals progressively disappeared from the 1950s to the 1970s. Nowadays in this area, as well as in other parts of the National Park, only moderate grazing on some non-forest sites is still carried out (RADWAŃSKA-PARYSKA & PARYSKI 1995).

Forest ecosystems of the Chochołowska valley were exploited in the 18th century, mainly for the purposes of ore mining and metallurgy (FABIJANOWSKI 1962). European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) forests were logged, and replaced by spruce (*Picea abies*). Due to the establishment of Tatra National Park, the intensity of forest management decreased, and recently it has been restricted to designated low-elevation areas managed by the Community of Eight Villages in Witów (RADWAŃSKA-PARYSKA & PARYSKI 1995).

2.2 Study design

We carried out our resurvey in 2014, at elevations between 936 and 2170 m a.s.l. (Fig. 1), by resampling 47 historical vegetation plots. The plots were assigned to three types of vegetation, which are the most common in the Chochołowska Valley, and were characterized by a relatively high number of replications (Supplement E1): a) Norway spruce and silver fir forests (14 plots); b) granite grasslands with a dominance of *Agrostis rupestris*, *Calamagrostis villosa*, *Juncus trifidus* and *Oreochloa disticha* (19 plots) and c) species-rich calcareous grasslands, characterized by a high cover of *Festuca* spp., *Carex firma* and *Dryas octopetala* (14 plots; Fig. 2).

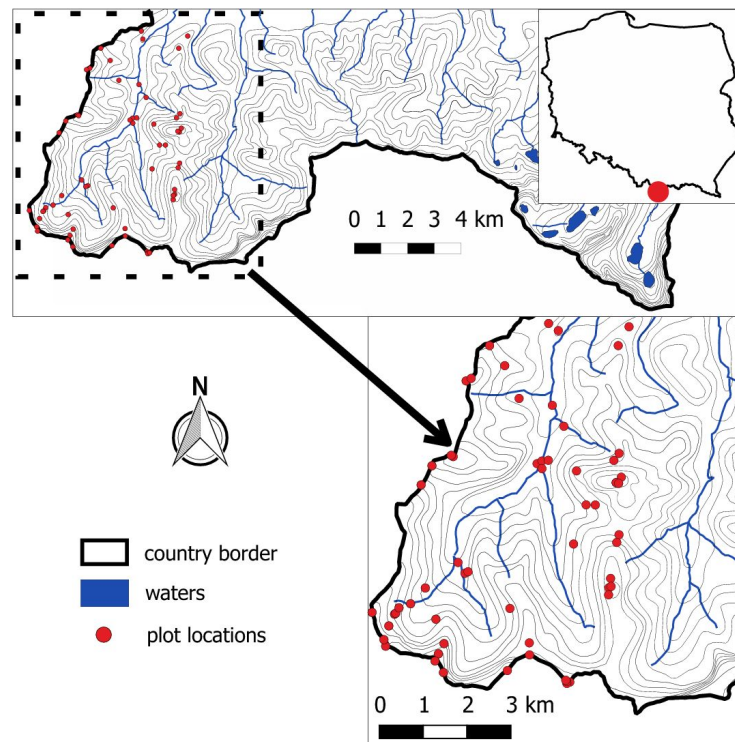


Fig. 1. Location of the study area. Elevation contour interval is 100 m.

Abb. 1. Lage des Untersuchungsgebietes. Die Intervalle der Höhenlinien betragen jeweils 100 m.

To relocate plots, we used map and plot descriptions (e.g., elevation above sea level, slope, and the presence of specific topographical features, such as rock shelves or steep faces) provided by SZAFER et al. (1923). This approach is commonly used in botanical resampling studies (e.g., VITTOZ et al. 2008, NAAF & WULF 2010, CZORTEK et al. 2018). To minimize the potential effects of plot relocation uncertainty in exploring vegetation shifts (STÖCKLI et al. 2011), we resurveyed only plots with the most precise descriptions.

At the time of initial sampling, an uniform and common phytosociological methodology did not exist in European botanical studies. SZAFER et al. (1923) did not provide any information about plot sizes used for the vegetation survey in the Chochołowska Valley. Therefore, to estimate the historical plot sizes (Supplement E1) we used the publication of PAWŁOWSKI et al. (1928), who carried out a vegetation survey of the nearby Morskie Oko Lake Region in 1927.

As B. Pawłowski is a co-author of both studies, we assumed that the methods used in the same period of time in the same geographical region and type of vegetation by researchers from the same scientific community were similar. The plot sizes used by PAWŁOWSKI et al. (1928) greatly varied between and within the described plant communities, e.g., from 30 m² to 3000 m² for granite grasslands and from 5 m² to 400 m² for snowbeds. Thus, they partly depended on the patch size of the plant community. In grasslands the plot sizes were probably equal to the whole area covered by the community that was studied, and limited by bedrock, soil moisture and the presence of specific topographical features, e.g., screens, rock shelves and steep rock faces. In order to minimize relocation bias, in the resurvey of forest plots we used all historical plot descriptions provided by SZAFER et al. (1923): name of specific valley, saddle and summit, elevation, aspect, slope, the presence of rock formations with characteristic shapes and specific landmarks, assuming that in the relocation of forest plots, detailed historical plot descriptions were more important than plot sizes. We further stated that due to homogeneous habitat



Fig. 2. Vegetation types resurveyed in the Chochołowska Valley: **a)** low-elevation calcareous grassland with spruce planted in the surrounding, **b)** high-elevation calcareous grassland above natural treeline, **c)** granite grassland in dwarf-pine vegetation belt, **d)** granite grassland above natural treeline, **e)** initial successional stage of spruce forest after catastrophic windthrow, **f)** more advanced successional stage of spruce forest (Photos: H. Ratyńska, July 2014).

Abb. 2. Wieder aufgenommene Vegetationstypen im Chochołowska-Tal: **a)** Kalkmagerrasen der niederen Lagen mit in der Umgebung gepflanzter Fichte, **b)** Kalkmagerrasen der Hochlagen über der natürlichen Waldgrenze, **c)** bodensaurer Magerrasen im Krummholzgürtel, **d)** Bodensaurer Magerrasen über der natürlichen Waldgrenze, **e)** Initiales Sukzessionsstadium eines Fichtenwaldes nach katastrophalem Windwurf, **f)** fortgeschrittenes Sukzessionsstadium eines Fichtenwaldes (Fotos: H. Ratyńska, Juli 2014).

conditions, the compositional heterogeneity of mountain spruce forests was relatively low in the same topographical feature (WOJTERSKA et al. 2004), characterized in details in historical plot descriptions. Moreover, catastrophic winds in the Tatra Mts cause drastic changes in the species composition of spruce forests at large spatial extents, i.e., covering the whole valleys, passes, slopes or summits (LIMANÓWKA et al. 2008). This allowed us to assume that relocation problems are a random factor, and therefore it should not undermine the results of our study, especially if focussed on changes in the proportion of species representing different ecological requirements, rather than shifts in species richness and Shannon's diversity, which are strongly dependent on plot size (DENGLER et al. 2009, CHYTRÝ et al. 2014, KOPECKÝ & MACEK 2015). For each vegetation plot, as was done by SZAFER et al. (1923), we recorded all vascular plants using the Braun-Blanquet seven-class abundance scale, and compared our lists with those recorded historically (Supplement E1). SZAFER et al. (1923) provided information about the abundance of trees in the tree layer only for forest plots dominated by spruce, whereas data about the cover of each tree species in the tree layer in sites with a prevalence of silver fir (*A. alba*) is missing. Therefore, in the resurvey of forest plots, we estimated a mean cover of trees, and also recorded the percentage cover of the tree layer. The same approach was used to estimate the historical mean percentage cover of trees in the spruce forest vegetation, according to the historical plot descriptions. Thus, as a proxy of succession in spruce forests, we adopted the mean percentage cover of trees. Following the definition of the forest (SZYMAŃSKI 2000), which assigns forest plant community status to vegetation patches with a tree canopy cover higher than 40%, we classified plots with a mean percentage cover of trees greater than 40% as representing advanced stages of succession. To avoid taxonomical differences between the historical and recent approaches to species identification, all species of *Alchemilla* spp. were excluded from the analyses. The nomenclature of species followed EURO+MED (2006-).

2.3 Vegetation characteristics and data analysis

We characterized the plant species' ecological requirements for light (EIV-L), temperature (EIV-T), moisture (EIV-F) and nitrogen (EIV-N) using ecological indicator values of ELLENBERG et al. (1991) as modified by ZARZYCKI et al. (2002), which includes Carpathian endemics and sub-endemics. As the indicator values for soil reaction (EIV-R) do not correspond in a clear manner with field pH measurements (e.g., SCHAFFERS & SÝKORA 2000, DZWONKO 2001) and, on the other hand, mean EIV-R are often positively correlated with EIV-N (e.g., DZWONKO 2001, CZORTEK et al. 2018), in our study we did not include EIV-R analyses.

In order to explore the shifts in species composition of the vegetation of the Chochołowska Valley, we focused our analyses on subsets of plots belonging to the three vegetation types (calcareous grasslands, granite grasslands and spruce forests), except for the analysis of biotic homogenization, which was done for the dataset with all types of vegetation combined. To explore changes in species composition of vegetation types resurveyed, for each historical and resampled plot we calculated mean values of ecological indicator values, weighted by cover of plant species.

To examine biotic homogenization of the vegetation types, understood as increasing compositional similarity between plots, for historical and resampled datasets compiling all plant communities studied, we calculated mean the Bray-Curtis compositional dissimilarity index. Statistical significance of the differences in Bray-Curtis index was evaluated by a t-test. The same Bray-Curtis index was also used to explore dissimilarities in plant species composition of the three types of vegetation with the highest plot number, and was calculated for each pair of plots (historical and resampled). To determine the effect of elevation above sea level on compositional dissimilarities of the resurveyed plant communities, we used linear regression. For inspection of outliers we checked Cook's distances and leverage values using *hat* statistics implemented in the *base::influence()* function in R (R CORE TEAM 2017). To identify outliers we used Bonferroni *p*-values for Studentized residuals t-tests using the *car::outlierTest()* function in R (R CORE TEAM 2017). After visual interpretation of diagnostic plots both for calcareous and granite grasslands we adopted 0.15 as threshold leverage values, as most of the observations had relatively low leverage values, ranging from 0.07 in calcareous and from 0.05 to 0.15 in granite grasslands. After that, we excluded two outliers: plot no. 71 (elevation 1039 m a.s.l.) from calcareous and plot no. 57 (elevation 1039 m a.s.l.) from granite grasslands.

tion 2123 m a.s.l.) from granite grasslands due to high leverage values (0.20 and 0.24, respectively) and due to the `car::outlierTest()` $p < 0.05$ in both cases.

To characterize the species composition of the three vegetation types, for each separate type of vegetation and for each sampling period, we performed six Detrended Correspondence Analyses (DCA) with passively fitted environmental vectors: ecological indicator values for light (EIV-L), temperature (EIV-T), moisture (EIV-F) and nitrogen (EIV-N).

To assess shifts in species composition between the two sampling periods, for each vegetation type we performed DCA using the `vegan::decorana()` function. To determine the relationships between the distribution of points representing plots in the DCA ordination space and EIV, we used the `vegan::envfit()` function, which fits the above-mentioned variables as passive vectors into an ordination space.

To check whether there were changes in the mean values of ecological indicators between the two periods studied we used a paired Wilcoxon test. To find whether there was a significant change in species frequencies (understood as the number of occurrences of each species in each sampling period) between the two sampling periods we used the χ^2 test (*Chi-squared* test) with a maximum level of significance set at $p = 0.05$. The distribution of alpine plant species is determined by high diversity microtopography and microclimates, contributing to the presence of a large number of specific microhabitats in a relatively small area (RADWAŃSKA-PARYSKA & PARYSKI 1995). Thus, alpine plants are often highly specialized, and due to high habitat heterogeneity, usually occur in low abundances (e.g., ERSCHBAMER et al. 2011). Therefore, in this procedure we analyzed species that appeared at least four times, either in historical or resampled datasets, reducing the tested number of species from 229 to 79 in calcareous grasslands, from 96 to 30 in granite grasslands, and from 175 to 62 in spruce forests. We did not adjust the p -values for multiple comparison corrections (e.g. Bonferroni), because according to MORAN (2003), in ecological studies of multiple species, these adjustments may lead to omitting possibly important results. We performed all analyses using R software (R CORE TEAM 2017).

3. Results

Mean Bray-Curtis compositional dissimilarity calculated for the three vegetation types together did not differ significantly between the two periods of sampling ($p > 0.05$). Both on calcareous and granite grasslands, the Bray-Curtis dissimilarity index on the plot level decreased significantly with increasing elevation above sea level ($R^2 = 0.49$, $p < 0.01$ and $R^2 = 0.25$, $p < 0.05$, respectively; Fig. 3a–b). No relationship between Bray-Curtis index and elevation was found in spruce forests (Fig. 3c).

We revealed that different factors characterized the species composition in different subsets (Supplement E2). In calcareous grasslands EIV-L had no significant correlation with the DCA axes in the dataset with the original plots, while the factor became important in the dataset with resampled plots. In granite grasslands EIV-F became non-significant in the new plots. In forest plots, EIV-L and EIV-T became non-significant in the resampled dataset in comparison with historical data.

The species composition of low-elevation (< 1300 m a.s.l.) resurveyed calcareous grasslands (Fig. 4a, Table 1, right side of the DCA plot) was characterized by relatively low values of EIV-L, and high values of EIV-N and EIV-T, whereas the most important factor associated with the historical plots were high values of EIV-L. EIV-N and EIV-T were positively correlated with each other, and negatively associated with EIV-L.

We observed that the species composition of the resurveyed granite grasslands at lower elevations was characterized by high values of EIV-F, EIV-T and EIV-N (Fig. 4b, Table 1, top-middle of the DCA plot). On the other hand, regardless of the time of sampling, the species composition of plots representing high-elevation granite grasslands (left side of the

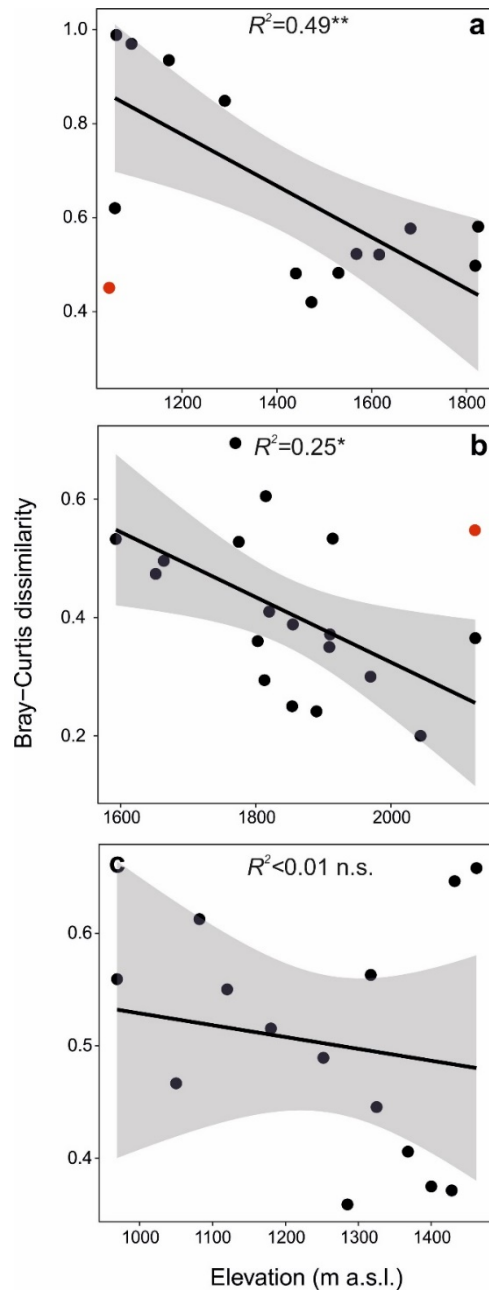


Fig. 3. Relationships between the Bray-Curtis index (compositional dissimilarity between historical and resampled plots) and elevation above sea level for: **a)** calcareous grasslands, **b)** granite grasslands and **c)** spruce forests. Red points represent two outliers (not included in regression analyses). Significance of results: $^{**}p < 0.01$, $^*p < 0.05$, n.s. – not significant.

Abb. 3. Beziehung zwischen dem Bray-Curtis-Index (der Unähnlichkeit der Vegetation zwischen alten und neuen Aufnahmen) und Höhe der Aufnahmeflächen in **a)** Kalkmagerrasen, **b)** bodensauren Magerasen, und **c)** Fichtenwäldern. Die roten Punkte bezeichnen zwei Ausreißer, die nicht in den Regressionsanalysen berücksichtigt wurden. $^{**}p < 0,01$; $^*p < 0,05$; n.s. – nicht signifikant.

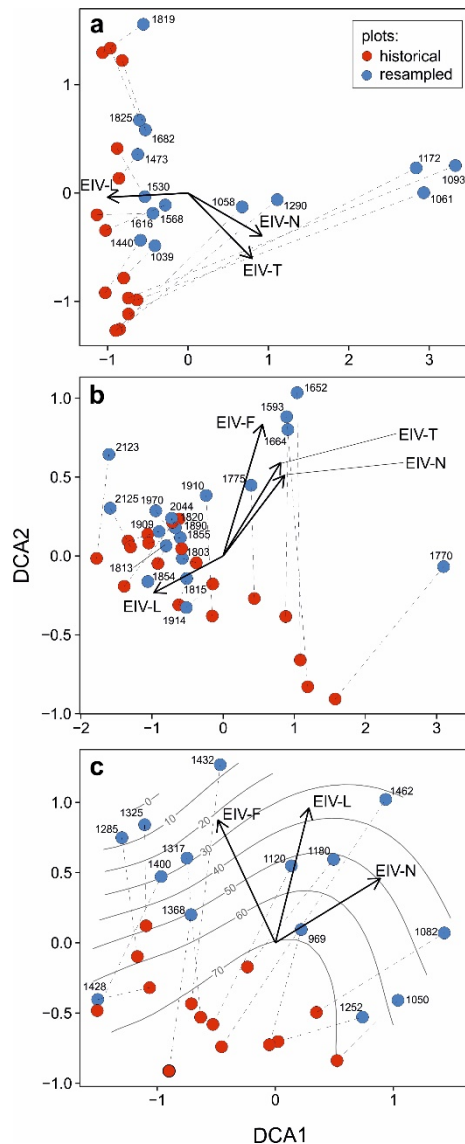


Fig. 4. DCA analyses for the three vegetation types: **a)** calcareous grasslands (axis 1 eigenvalue: 0.62, axis 2 eigenvalue: 0.37), **b)** granite grasslands (axis 1 eigenvalue: 0.63, axis 2 eigenvalue: 0.20) and **c)** spruce forests (axis 1 eigenvalue: 0.40, axis 2 eigenvalue: 0.28). Grey isolines in c) represent the percentage mean cover of trees in vegetation plots. Points represent plots, numbers – elevation above sea level, arrows – environmental variables significantly ($p < 0.05$) correlated with the ordination axes: EIV-L – light EIV, EIV-T – temperature EIV, EIV-F – soil moisture EIV, EIV-N – soil nitrogen EIV.

Abb. 4. DCA-Ordinationen für die drei Vegetationstypen: **a)** Kalkmagerrasen (Achse 1 - Eigenwert: 0,62; Achse 2 - Eigenwert: 0,37), **b)** bodensaure Magerrasen (Achse 1 - Eigenwert: 0,63; Achse 2 - Eigenwert: 0,20) und **c)** Fichtenwälder (Achse 1 - Eigenwert: 0,40; Achse 2 - Eigenwert: 0,28). Die grauen Isolinien in c) bezeichnen die mittleren Prozentwerte der Deckung der Baumschicht in den Aufnahme­flächen, die durch Punkte repräsentiert sind. Die Zahlen geben die Höhe über NN, die Pfeile die Stärke und Richtung des Einflusses signifikanter ($p < 0,05$) Umweltvariablen an: EIV-L (Licht), EIV-T (Temperatur), EIV-F (Bodenfeuchte), EIV-N (Bodenstickstoff).

Table 1. Parameters of variables fitted to the DCA analysis results focusing on particular vegetation types. R^2 and p values were calculated using a permutation test with 999 iterations. EIV – mean Ellenberg indicator value. Significance of results: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. – not significant.

Tabelle 1. Beziehung zwischen den DCA-Ordinationsachsen und Umweltvariablen, getrennt berechnet für die drei untersuchten Vegetationstypen. R^2 - und p -Werte beruhen jeweils auf einem Permutations-test mit 999 Iterationen. EIV – mittlere Ellenberg-Zeigerwerte. * $p < 0,05$; ** $p < 0,01$; *** $p < 0,001$; n.s. – nicht signifikant.

Parameter	Abbreviation	DCA1	DCA2	R^2
<i>Calcareous grasslands</i>				
Light EIV	EIV-L	-0.99926	-0.03855	0.8640***
Temperature EIV	EIV-T	0.79735	-0.60351	0.7408***
Moisture EIV	EIV-F	0.80565	0.59239	0.1327 n.s.
Nitrogen EIV	EIV-N	0.91905	-0.39414	0.9146***
<i>Granite grasslands</i>				
Light EIV	EIV-L	-0.97243	-0.23317	0.6873***
Temperature EIV	EIV-T	0.80662	0.59107	0.7576***
Moisture EIV	EIV-F	0.55163	0.83409	0.5641***
Nitrogen EIV	EIV-N	0.86008	0.51016	0.8690***
<i>Spruce forests</i>				
Light EIV	EIV-L	0.28419	0.95877	0.3533*
Temperature EIV	EIV-T	0.94672	0.32205	0.1349 n.s.
Moisture EIV	EIV-F	-0.48556	0.8742	0.3564**
Nitrogen EIV	EIV-N	0.88887	0.45817	0.5926**

DCA plot) was characterized by high values of EIV-L. In addition, EIV-T, EIV-F and EIV-N were associated negatively with EIV-L, and in parallel were positively correlated with each other.

The main shift in species composition of spruce forests was observed along DCA axis 2 (Fig. 4c, Table 1). The species composition of six resurveyed forest plots was characterized by a low mean percentage cover of trees (< 40%; upper-left side of the DCA plot). In contrast, eight plots showed a mean percentage cover of trees higher than 40%. The species composition of resurveyed plots was also characterized by high values of vectors describing plant ecological requirements: EIV-F, EIV-L and EIV-N, which were positively correlated with each other.

In recent calcareous grasslands, the share of more shade-tolerant (lower EIV-L), as well as more warmth-, moisture- and nitrogen-demanding species increased (higher EIV-T, EIV-F and EIV-N) significantly in comparison to the first sampling period. In resurveyed granite grasslands we observed significant increases in the proportions of more warmth- and nitrogen-demanding species in comparison to the historical plots. We found that recent forest plots were characterized by a significantly higher proportion of more light-, moisture- and nitrogen-demanding species in comparison to the initial sampling period (Fig. 5).

Of 79 plant species tested in calcareous grasslands, 16 had significantly increased in frequency in comparison to the first sampling period. Plant species that revealed the highest changes in frequency in calcareous grasslands were: *P. abies*, *Salix silesiaca* and *Pinus mugo*

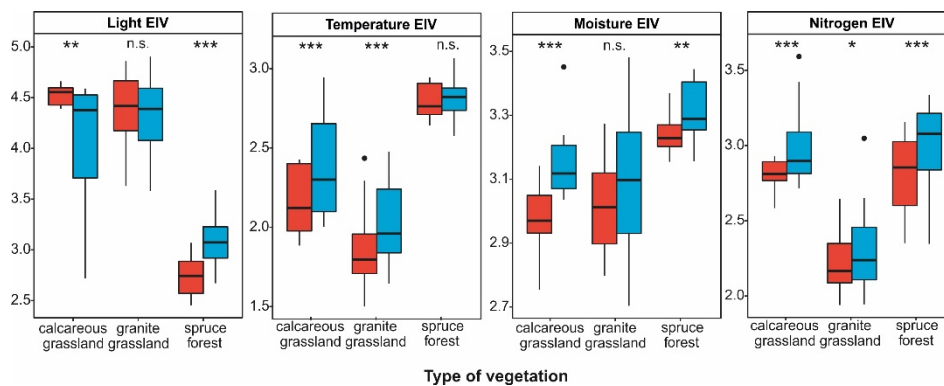


Fig. 5. Comparison of changes in mean values of ecological indicator values (EIV) between the two time periods of sampling for each vegetation type. Comparisons were based on paired Wilcoxon's test: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. – not significant. Box plots show range of observations: boundaries of box show interquartile range, line within a box – the median, black points – outliers (values below and over 1.5*interquartile range).

Abb. 5. Vergleich der mittleren Zeigerwerte (EIV) zwischen alten und neuen Aufnahme­flächen getrennt für die drei untersuchten Vegetationstypen (gepaarter Wilcoxon Text (*** $p < 0,001$; ** $p < 0,01$; * $p < 0,05$; n.s. – nicht signifikant)).

(Table 2). Of 30 plant species examined in granite grasslands, four had increased (*Calluna vulgaris*, *Huperzia selago*, *P. mugo* and *Veratrum lobelianum*) and two had decreased (*Festuca picturata* and *Luzula luzulina*) in frequency in comparison to the initial sampling (Table 2). We found that of 62 plant species analysed in spruce forests, 15 species had recently increased and four had significantly decreased in frequency. The highest increase in recent forest plots was shown by *Dryopteris carthusiana*, *Rubus idaeus*, *Calamagrostis villosa* and *S. silesiaca*, whereas significant decreases were found for *Moneses uniflora*, *Cardamine hirsuta*, *Goodyera repens* and *Neottia cordata* (Table 2).

4. Discussion

4.1 Plot relocation uncertainties

As information about the exact locations and sizes of plots is missing, the resurveyed vegetation represents the so-called semi-permanent plots with a relatively high risk of relocation error (e.g., DENGLER et al. 2009, CHYTRÝ et al. 2014, KOPECKÝ & MACEK 2015). This in particular could account for the high compositional dissimilarities observed in spruce forest vegetation, where the bias connected with plot relocation was the largest (see Materials and Methods). Therefore, the observed changes in species composition should be viewed with caution. Despite these limitations, resurvey studies are recently amongst the most popular in botanical investigations, constituting a proper method for studying plant species compositional change both over short (< 50 years; e.g., PAULI et al. 2012) and long time periods (> 50 years; e.g., MATTEODO et al. 2013).

Table 2. Changes in species frequency in the three vegetation types. χ^2 statistics calculated from the test are shown. Only species that showed significant differences in frequency are shown. Significance of results: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Tabelle 2. Signifikante Veränderungen der Arthäufigkeiten in den drei untersuchten Vegetationstypen. * $p < 0,05$; ** $p < 0,01$; *** $p < 0,001$.

Species	Calcareous grasslands		Granite grasslands		Spruce forests	
	χ^2	Change	χ^2	Change	χ^2	Change
<i>Rubus idaeus</i>	4.00*	4			8.33**	10
<i>Antennaria dioica</i>	4.00*	4				
<i>Cardaminopsis halleri</i>	4.00*	4				
<i>Clematis alpina</i>	4.00*	4				
<i>Epilobium montanum</i>	4.00*	4				
<i>Oxalis acetosella</i>	4.00*	4				
<i>Sorbus aucuparia</i> subsp. <i>glabrata</i>	4.00*	4				
<i>Viola biflora</i>	4.00*	4				
<i>Fragaria vesca</i>	5.00*	5				
<i>Hieracium murorum</i>	5.00*	5				
<i>Cardaminopsis arenosa</i> subsp. <i>borbasii</i>	6.00*	6				
<i>Juniperus communis</i> subsp. <i>alpina</i>	6.00*	6				
<i>Pinus mugo</i>	7.00**	7	5.00*	5		
<i>Salix silesiaca</i>	8.00**	8			8.00**	8
<i>Picea abies</i>	13.00***	13				
<i>Festuca picturata</i>			5.00*	-5		
<i>Luzula luzulina</i>			4.00*	-4		
<i>Calluna vulgaris</i>			4.00*	4		
<i>Veratrum lobelianum</i>			4.00*	4		
<i>Huperzia selago</i>			4.50*	6		
<i>Moneses uniflora</i>					5.33*	-8
<i>Cardamine hirsuta</i>					5.00*	-5
<i>Goodyera repens</i>					5.00*	-5
<i>Neottia cordata</i>					5.00*	-5
<i>Carex sylvatica</i>					4.00*	4
<i>Epilobium angustifolium</i>					4.00*	4
<i>Hypericum maculatum</i>					4.00*	4
<i>Listera ovata</i>					4.00*	4
<i>Taraxacum officinale</i>					4.00*	4
<i>Calamagrostis varia</i>					5.00*	5
<i>Petasites albus</i>					5.00*	5
<i>Senecio ovatus</i>					5.00*	5
<i>Senecio nemorensis</i>					5.00*	5
<i>Calamagrostis arundinacea</i>					6.00*	6
<i>Solidago virgaurea</i> subsp. <i>minuta</i>					6.00*	6
<i>Calamagrostis villosa</i>					7.00**	7
<i>Dryopteris carthusiana</i>					10.00***	10

4.2 General patterns of changes in species composition

Despite the fact that we did not find evidence that the species composition of resampled vegetation plots became more homogeneous, the vegetation of the Chochołowska Valley has changed significantly over the past 92 years. The magnitude of the compositional dissimilarities decreased with elevation above sea level, which is similar to results obtained by KUCHARZYK & AUGUSTYN (2010) and MAURSET (2015). This pattern was observed in calcareous and granite grassland communities, with bigger changes at lower elevations that are in the range of the spruce forest or dwarf pine vegetation belt. In contrast, at higher elevations such changes were less pronounced due to very slow recovery of the natural treeline, which in the period of intensive shepherding was lowered by more than 300 m and over the last 60 years shifted upward only about 20 m (KACZKA et al. 2015).

The rate of transformation in species composition depends on bedrock, indicating higher compositional dissimilarities on calcareous grasslands in comparison to granite ones (e.g., CASAS & NINOT 2003, BAŞNOU et al. 2009). Calcareous grasslands, which are hotspots of plant species diversity, are in general more sensitive to any change in environment due to high number of specialized species with relatively low tolerance to changes in soil humidity and nutrient contents (BAŞNOU et al. 2009). This is in line with our findings: the relationship between Bray-Curtis dissimilarity index and elevation above sea level was stronger on calcareous grasslands than those growing on granite. Therefore, the most specialized plant species may go extinct within large mountain ranges in Europe, which in historical times were grazed by livestock for a long time (DUPRÉ & DIEKMANN 2001, AMEZAGA et al. 2004, BAUR et al. 2006, SITZIA et al. 2010, HABEL et al. 2013, SHEIL 2016, CAMPAGNARO et al. 2017).

4.3 Impact of historical livestock grazing

In calcareous grasslands we found a higher number of species tolerating lower light conditions (lower EIV-L) in comparison to historical records, showing the highest decreases associated with the lowest elevation plots. Most of the shade-tolerant species were plants typical of forest understories (e.g., *Huperzia selago*, *Oxalis acetosella* and *Viola biflora*), which colonized calcareous grasslands excluded from grazing. In addition, calcareous and granite grasslands today are dominated by a higher number of species with high water (except granite grasslands), temperature and nitrogen demands (higher EIV-F, EIV-N and EIV-T), indicating the most dramatic shifts at the lowest elevations, and thus confirming hypothesis 1. These changes were probably caused by the colonization of such areas by more moisture-, warmth- and nitrogen-demanding tall herbs (e.g., *R. idaeus*, *Epilobium montanum* and *V. lobelianum*), shrubs (e.g., *Juniperus communis* subsp. *nana*, *P. mugo* and *S. silesiaca*) and trees (*P. abies* and *Sorbus aucuparia* subsp. *glabrata*), which showed significant increases in frequencies between the two sampling periods, and could have led to the establishment of a tall herb, shrub and tree canopy (KUCHARZYK & AUGUSTYN 2010, AMEZTEGUI et al. 2016). As an effect of land abandonment, specific microhabitat conditions were created under the canopy (BREUER et al. 2003). This could have led to the reduced exposure of species to low temperatures, strong winds, high evaporation and insolation, as well as a build-up of increased soil humus (HILLER et al. 2005, WESOŁOWSKA 2009, JIANG et al. 2015). The observed tendencies are evidence of natural treeline recovery, which historically had been lowered about 300 m on average in the Tatra Mts by livestock grazing, and has still not reached its potential limit set by climate (KACZKA et al. 2015).

4.4 Combined effect of cessation of grazing and afforestation

The largest changes in species composition between surveys were revealed for low-elevation calcareous grasslands. These plant communities historically were specific environmental islands in the belt of European beech and spruce forest, occupying steep limestone shelves and faces (BALCERKIEWICZ & BRZEG 1978). At the time of the first sampling, all such areas were covered by species-rich, non-forest plant communities. The possible spruce planting after cessation of grazing in the proximity of these species-rich vegetation patches could have promoted colonization by more shade-tolerant plants (low EIV-L) typical for the forest understory (i.e., *Clematis alpina*, *E. montanum*, *Hieracium murorum*, *O. acetosella* and *V. biflora*), thus compromising these local hotspots of biodiversity. This suggests that forest management may accelerate the treeline recovery.

4.5 Impact of wind disturbance in forest communities

There was a large compositional dissimilarity in the vegetation of spruce forests between the two sampling periods, which at the time of the historical survey represented mature forest stands. Currently, eight of the resampled forest plots are covered by more advanced stages of forest succession, which is expressed by mean cover of trees higher than 40% and relatively low compositional dissimilarities between the two sampling periods. The species composition of the remaining six plots was characterized by low mean cover of trees (below 40%), indicating more initial stages of succession. Observed tendencies confirm hypothesis 2 and are the consequences of catastrophic wind events, which are frequent phenomena in the Chochołowska Valley. Strong winds (> 36 km/h) occur in the Tatra Mts 196 times per year on average. The record wind speed of 270 km/h was recorded in 1968 on Kasprowy Wierch summit, and caused serious forest damage in the whole range of the Tatra Mts, resulting in 29,000 m³ of fallen trees, including the Chochołowska Valley (LIMANÓWKA et al. 2008). The latest catastrophic wind disturbance took place in this area in 2013, reaching a maximum speed of about 200 km/h, and caused damage to tree stands in the Chochołowska and Kościeliska Valleys, with approximately 153,000 m³ of spruce fallen (PAP 2014).

Windthrows often lead to total destruction of the tree canopy, which results in a drastic increase in light availability, soil temperature, and spatial heterogeneity of soil water content and nutrients (e.g., ROBERTS 2004). In effect, large disturbed areas became available for colonization by plants typical of open habitats (e.g., ULANOVA 2000, FISCHER et al. 2002). Due to higher insolation, most of the resurveyed forest plots were characterized by higher proportions of species with higher light demands, which may thrive due to the higher light availability in wind-disturbed forest sites (ROBERTS 2004). This tendency confirms hypothesis 3. Increased availability of nutrients from decaying coarse woody debris in the soil could drive the colonization of disturbed forest plots by nitrophilous tall herbs and shrubs, which corresponds with findings reported by FISCHER et al. (2002) and BUDZÁKOVÁ et al. (2013), and also confirms hypothesis 3. A supporting explanation of these patterns are significant increases in frequency of more light- and nitrogen-demanding tall herbs: *Calamagrostis arundinacea*, *Senecio ovatus*, *Petasites albus* and *Epilobium angustifolium*, as well as two shrubs: *R. idaeus* and *S. silesiaca*.

Along with tree canopy disappearance, more shade-tolerant plant species typical for the understory of low-productivity coniferous forest communities disappeared on wind-disturbed forest sites (e.g., *G. repens*, *L. cordata* and *M. uniflora*). A possible explanation

of this pattern may be the high insolation on plots without canopy, or that these specialized plant species could not successfully compete with generalists (i.e., nitrophilous tall herbs and shrubs).

We found that the share of species preferring wetter soil conditions increased in spruce forests in comparison to the first sampling period, which partially contradicts hypothesis 3. That inconsistency could be explained by the presence of pit and mound microtopography created by up-rooted trees - the specific wind-sheltered microsites with decreased soil evaporation (SWANSON et al. 2011), which could be suitable habitats for colonization by species with higher moisture requirements (e.g., *Petasites albus* and *Senecio nemorensis*), as well as by more shade-tolerant plants (e.g., *Dryopteris carthusiana*). In addition, pit and mound microsites with coarse woody debris may create suitable conditions for the survival of natural spruce regeneration (CHEČKO et al. 2015, WESOŁOWSKI et al. 2016). This pattern corresponds with our findings: the frequency of spruce was similar in both time periods, regardless of whether a given plot was at an advanced or initial successional stage of the forest.

5. Conclusions

Effects of the cessation of grazing and recent catastrophic wind disturbances are possibly the main factors driving transformations in plant species composition of the vegetation in mountain valleys of the temperate zone. The magnitude of compositional dissimilarities depended on elevation, as well as the type of bedrock: less pronounced shifts were found at higher elevations, and changes were more pronounced in calcareous grasslands. This reflects the high susceptibility of mountain plant communities at the lower limit of their elevational range to changes in land use in comparison to grasslands located above natural treeline. In our opinion, cessation of grazing may constitute a considerable threat to the biological diversity of Tatra Mts grasslands due to recovery of the natural treeline. Therefore, this factor should be taken into account during preparation and implementation of the national park's management plans, mainly by considering active protection of these areas by restoration of shepherding at a limited scale. In wind-disturbed forests compositional shifts are explained by catastrophic winds, which constitute a reasonably important factor that continually drives compositional dynamics in the mountain spruce forest vegetation belt. Strong winds favour the presence of pit and mound micro-topography created by uprooted trees and coarse woody debris, creating a high diversity of microhabitats and suitable conditions for natural regeneration, growth and survival of the forest.

Erweiterte deutsche Zusammenfassung

Einleitung – Bergregionen in Europa wurden über Jahrhunderte durch Besiedlung, Industrie und Weidewirtschaft beeinflusst (KOZAK 2003). Ziel dieser Untersuchung war es, Vegetationsveränderungen im "Chochołowska-Tal" in der westlichen Tatra (Polen) in den letzten 92 Jahren zu dokumentieren und die dafür verantwortlichen Umweltfaktoren zu beschreiben. Dafür wurden die Veränderungen der Anteile von Arten mit unterschiedlichen Umweltansprüchen analysiert.

Material und Methoden – Im Jahr 2014 wurden 47 alte Vegetationsaufnahmen von Gebirgsmagerasen auf Kalk (=Kalkmagerrasen) und Granit (=bodensaure Magerrasen) und Fichtenwäldern unter Verwendung der früher angewandten Methodik wiederaufgenommen. In jeder Fläche wurden die vorkommenden Gefäßpflanzenarten erfasst. Wir analysierten die Veränderungen in der Vegetation der

Magerrasen und Wälder über die Veränderungen der mittleren Ellenberg-Zeigerwerte (EIV) für Licht (EIV-L), Temperatur (EIV-T), Bodenfeuchte (EIV-F) und Bodenstickstoff (EIV-N). Die Ähnlichkeit zwischen alten und neuen Aufnahmen wurde über Bray-Curtis-Indizes erfasst.

Ergebnisse – Die Ähnlichkeit der Vegetation alter und neuer Aufnahmen von Magerrasen nahm signifikant mit steigender Meereshöhe zu (Abb. 3). Die neuen Aufnahmen von Kalkmagerrasen zeigten niedrigere EIV-L sowie höhere EIV-T und EIV-N im Vergleich zu den historischen Aufnahmen. In den bodensauren Magerrasen nahmen die mittleren Zeigerwerte für Temperatur, Bodenfeuchte und Stickstoff zu. Die neuen Vegetationsaufnahmen in Fichtenwäldern wiesen im Vergleich zu früher höhere Werte für EIV-L, EIV-F und EIV-N auf (Abb. 5).

Diskussion – Die Vegetation des Chochołowska-Tals in der westlichen Tatra hat sich über die vergangenen 92 Jahre stark verändert. Die Akkumulation einer stickstoffhaltigen Humusschicht ist vermutlich für die Zunahme nährstoffbedürftiger Arten in nicht mehr beweideten Magerrasen verantwortlich. Die milderen mikro-klimatischen Bedingungen in der dichteren Vegetation begünstigten auch die Besiedlung der Magerrasen durch wärmebedürftigere Bäume und Sträucher. Die Fichtenwälder der Region dagegen zeigten höhere Anteile an Licht- und Stickstoff-bedürftigen Arten, wahrscheinlich ausgelöst durch sturmbedingten starken Windwurf.

Schlussfolgerungen – Das Verschwinden der Bergweide im Untersuchungsgebiet ist hauptsächlich für die Veränderungen der Vegetation von Magerrasen und das Höherwandern der Baumgrenze verantwortlich. Die Grasländer niederer Lagen in der Tatra sind empfindlich gegenüber Veränderungen der Landnutzung, was eine Gefahr für den Erhalt der hohen Biodiversität der Region darstellt. Die Vegetationsdynamik in Berg-Fichtenwäldern ist stark durch den natürlichen Windwurf geprägt. Stürme schaffen durch umgeworfene Bäume eine starke Mikro-Topographie und damit eine hohe Diversität von Mikro-Habitaten, was die natürliche Regeneration fördert.

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Supplements

Supplement E1. Table of relevés recorded historically and recently with metadata of the plots.

Beilage E1. Vegetationstabelle der historisch und neu aufgenommenen Flächen mit ihren Metadaten.

Supplement E2. Results of DCA for each studied habitat and sampling date.

Beilage E2. Ergebnisse der DCA für jedes untersuchte Habitat und Aufnahmedatum.

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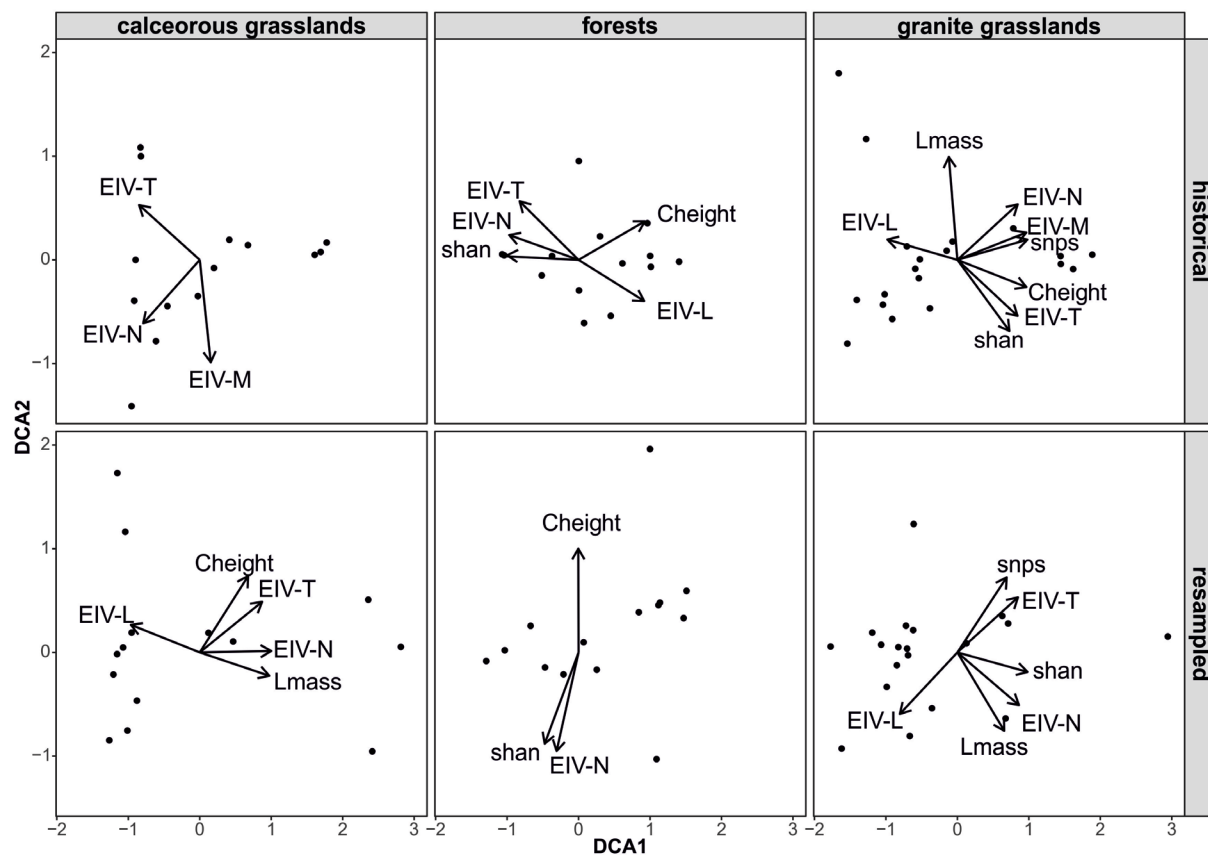
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Supplement E2. Results of DCA for each studied habitat and sampling date. For each analysis we passively fitted environmental vectors: ecological indicator values for light (EIV-L), moisture (EIV-M), soil fertility (EIV-N) and temperature (EIV-T), Shannon's diversity index (shan) and community weighted means of canopy height (Cheight), leaf mass (Lmass) and seed number per shoot (snps).

Anhang E2. Ergebnisse der DCA für jedes untersuchte Habitat und Aufnahmedatum. Für jede Analyse wurden Umweltvektoren passiv eingepasst: Zeigerwerte für Licht (EIV-L), Bodenfeuchte (EIV-M), Bodenstickstoff (EIV-N) und Temperatur (EIV-T), Shannon-Index der Diversität (shan) und gewichtete Mittelwerte der Bestandeshöhe (Cheight), Blattmasse (Lmass) und Samenzahl pro Spross (snps).



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