

CHANGES IN ALPINE VEGETATION OVER 50 YEARS IN THE WESTERN TATRAS (SLOVAKIA)

ANDREJ PALAJ, JOZEF KOLLÁR

Department of Ecology and Environmental Sciences, Faculty of Natural Sciences CPU in Nitra, Trieda A. Hlinku 1, 949 74 Nitra, Slovak Republic; e-mail: andrej.palaj@savba.sk

Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, P.O.Box 254, 814 99 Bratislava, Slovak Republic; e-mail: j.kollar@savba.sk

Abstract

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This paper examines changes in alpine vegetation over 50 years in the Western Tatras part of the Western Carpathians Mountains in Slovakia. We focus on the following most widespread vegetation types: subalpine to subnival grasslands (alliance *Juncion trifidi* Krajina 1933), snow-bed vegetation (alliance *Festucion picturatae* Krajina 1933) and dwarf-shrub vegetation (alliances *Loiseleurio-Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926 and *Vaccinion myrtilli* Krajina 1933). The historical 1971–1977 sampling dataset was re-sampled in 2016–2017 and our research is based on a comparison of 40 pairs of these relevés. Herein, we studied (i) changes in species frequencies; (ii) changes in phytodiversity and site conditions using estimates of Ellenberg's eco-indices and (iii) comparison of historical and current relevés over time using the nonmetric multidimensional scaling gradient analysis (NMDS) ordination method. The frequency curves reveal differences; especially in the most frequent species at 37.5–80%, which reach higher values in the current data. The higher 7.5–25% value of medium-frequent species in the historical relevés indicates progressive homogenisation of the examined vegetation. In addition, the Shannon-Wiener index of individual vegetation types revealed no significant differences in diversity or average number of species. The historical relevés included 75 species while 74 were confirmed in the current data. Statistically significant differences were determined in light factor for all three vegetation groups. This was due to the retreat of some light-demanding species. While NMDS indicated changes in *Festucion* and *Vaccinion* relevés over time, the *Juncion* group relevés did not follow this trend, thus confirming their high stability. The observed changes between current and historical data are attributed to changes in climate and altered land use with the cessation of grazing.

Key words: alpine grasslands, snow-bed, dwarf-shrub, changes, environmental factors.

Introduction

Alpine vegetation is typical by its mosaic-like occurrence, the high presence of endemic and relic species and its dynamics (Kliment, Valachovič, 2007). The dynamics are linked to the alpine environment (Lukniš, 1973; Midriak, 1983) and climate changes (Grabherr et al., 1995; Bahn, Körner, 2003; Pauli et al., 2012). The commonly assumed high sensitivity of alpine vegetation to climate change is largely due to invasion processes, and these are most obvious

in azonal vegetation types such as snowbeds and at the uppermost limits of plant life (Grabherr, 2003). This paper focuses on alpine vegetation changes in the Western Tatras Mountains influenced also by land use changes that especially include the cessation of cattle and sheep grazing in the mid-1980s when this area was declared a national park (Bohuš, 1994). This is crucial for alpine vegetation changes, since the absence of grazing leads to significant accumulation of plant litter (Virtanen, 2000) and some species are vulnerable to decline or disappearance, especially those with annual life cycles and species that require canopy gaps for recruitment (Erschbamer et al., 2003).

Historical vegetation of the study area was sampled in the 1970s (Horák, 1970, 1971; Turečková, 1974; Dúbravcová, 1976; Dúbravcová et al., 1976; Pietorová, 1977). This inspired our analysis of alpine vegetation changes over the last decades. Herein, we focus on the most widespread vegetation types. These are the subalpine-to-subnival grasslands (alliance *Juncion trifidi* Krajina 1933), snow-bed vegetation (alliance *Festucion picturatae* Krajina 1933) and dwarf-shrub vegetation dominated by *Vaccinium* genus species.

Methods

Study area

The study area covers the 34 km² in the Jamnicka and Račkova valley parts of the Western Tatras Mountains. This area is formed from granite, migmatite and various metamorphic rocks (Nemček, 1994) and has Podzols soils that follow Cambisols spread at lower altitudes (Šály, 1964). The area also lies in the cold climate region (Plesník, 1974). The 1966–2016 temperature data were recorded at Kasper Peak meteorological station and were supplied by the Polish Institute of Meteorology and Water Management. Situated at 1,959 m a.s.l., this station is close to our study area and it established a mean annual temperature of 0.35 °C, with an average maximum of 7.81 °C in the warmest month and an average minimum of -7.95 °C in the coldest month. The 1966–2016 average monthly temperatures show a fluctuating course (Fig. 1). Long-term measurements from the Skalnaté pleso meteorological station at 1,786 m a.s.l. in the neighbouring High Tatras Mountains revealed a shift from a relatively warmer period in 1941–1960, through mild cooling in 1961–1990 to a warm period after 1990. The registered increase in average annual temperatures was 0.8–1.7 °C in 1991–2012 and 1.2 °C between 2005 and 2012 (Hlavatá, 2013). The highest point in the study area is the Bystrá peak at 2,248 m a.s.l., and this is also the highest peak in the Western Tatras. The timber line at 1,400–1,500 m a.s.l. is affected by historical land use.

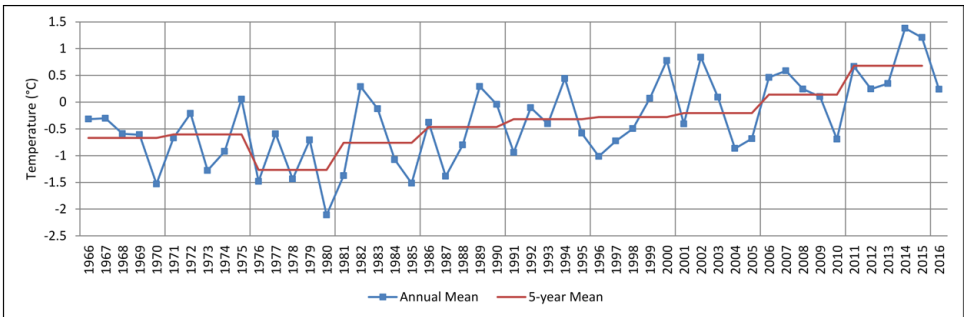


Fig. 1. Temperature change over the last 51 years (Kasper peak meteorological station).

Data sampling and analysis

Relevés were sampled in 2016–2017. The method of generalization of long-term monitoring sites and pair comparison is used to estimate changes in plant communities (Hédl, 2005). We resampled historical relevés of 1971–1977 stored in the Central database of phytocoenological relevés (CDF) (Hegedúšová, 2007; Šibík, 2012). The methods of Zürich-Montpellier School of Phytosociology (Braun-Blanquet 1964) were used to research plant communities. The 7-figure Braun-Blanquet scale was used to estimate species coverage, and while vascular plant nomenclature was modified according to Marhold, Hindák (1998), cryptograms are not included. A major part of the phytocoenological relevés, encompassing alliances *Festucion picturatae* and *Juncion trifidi*, was published in our previous study (Palaj, Kollár, 2017). Our syntaxonomical classification of the studied vegetation agrees with Jarolímek et al. (2008). The only exception here is the dwarf shrub vegetation, which we treated as a single vegetation type under the *Vaccinion* group because this includes communities similar in floristic composition, physiognomy and ecology. Statistical analysis of the phytocoenological relevés is based on comparison of 40 pairs of relevés; *Festucion* has 14 pairs, *Juncion* 17 and *Vaccinion* 9. The analysis included the following: (i) changes in species frequencies; (ii) changes in phytodiversity and site conditions estimated by Ellenberg's eco-indices and (iii) comparison of historical and current relevés over time, using the nonmetric multidimensional scaling ordination method (NMDS). Species frequency is expressed in percentages for all three vegetation groups in both historical and current relevés. The resultant values are depicted in frequency curves for all relevés and the relative frequency change for each group is shown separately (Magurran, 2004). Shannon–Wiener (SW) and evenness indices are calculated for all historical and current relevés and the values compared in box plots. Historical and current site conditions are estimated by bioindication using Ellenberg's eco-indices (Ellenberg et al., 1992) by employing Juice software (Tichý, 2002). The box plots provide results and the paired *t*-test was performed using RStudio software (RStudio Team, 2015). Relevé (di)similarity is estimated by NMDS indirect ordination methods with the RStudio Vegan package (Oksanen et al., 2017). Finally, NMDS is performed on log-transformed data using Bray–Curtis dissimilarity matrix, and species abundances are included in all analysis.

Results

Species frequency changes

Frequency curves (Fig. 2) reveal the differences, especially in species 1–15 where the most frequent species (37.5–80%) occur more frequently in current data and therefore have higher

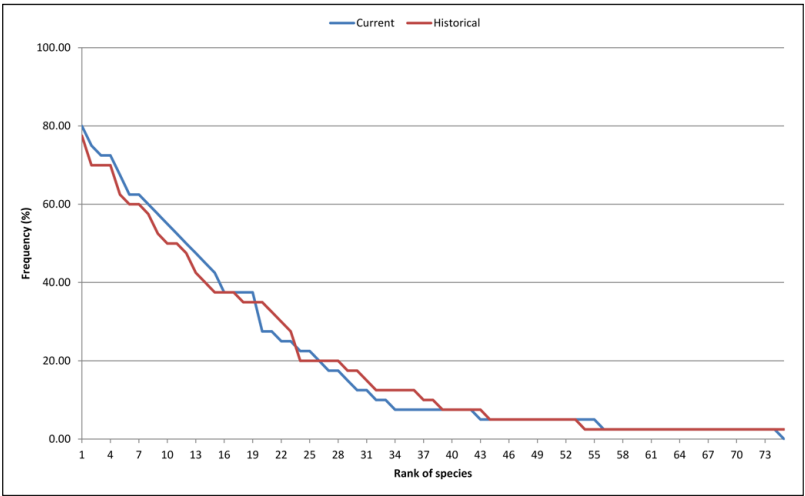


Fig. 2. Frequency curves of all species in the historical and current relevés groups. Species are ranked in descending order of frequency.

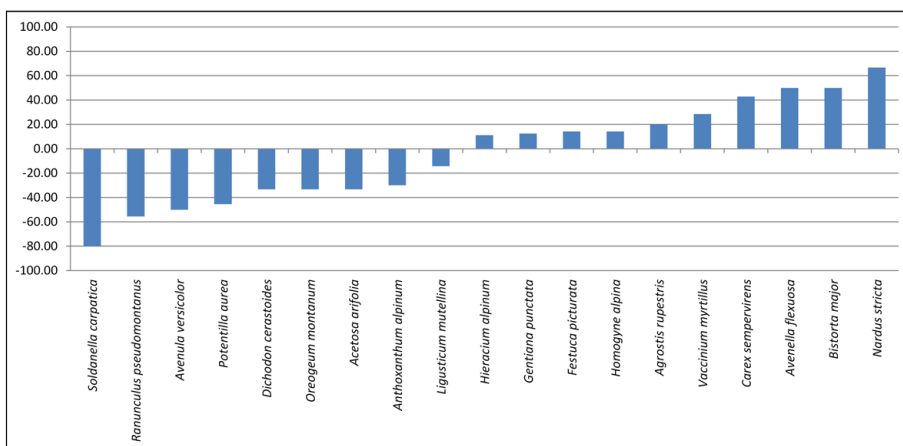


Fig. 3. Relative change in species frequency in the *Festucion* group.

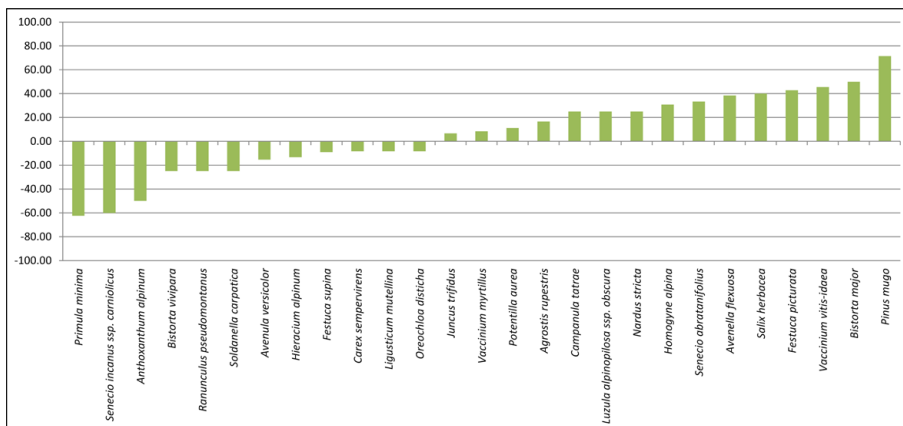


Fig. 4. Relative change of species frequencies in the *Juncion* group.

values. In contrast, species 19–39 has a frequency of 7.5–25% and higher values in the historical relevés. The historical data also included 75 species compared to 74 in our re-sampled relevés.

Relative frequency changes are shown for species with frequency exceeding 10% in the historical and current relevés. There is an obvious decrease in the frequency of current relevés in the *Festucion* group (Fig. 3). This is especially noted in alliance *Festucion picturatae* diagnostic species, including *Doronicum stiriacum* (-80%), *Soldanella carpatica* (-80%), *Ranunculus pseudomontanus* (-55.6%) and *Potentilla aurea* (-45.5%). These species are replaced by contact vegetation diagnostic species (classes *Caricetea curvulae*, *Loiseleurio-Vaccinieta* and *Nardetea strictae*). Important examples here are *Nardus stricta* +66.7%, *Vaccinium myr-*

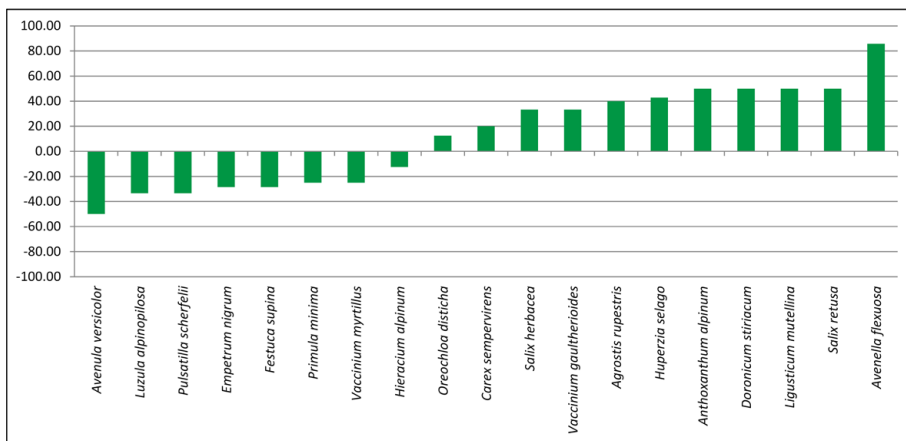


Fig. 5. Relative change in species frequency in the *Vaccinion* group.

tillus +28.6%, *Agrostis rupestris* +20% and *Hieracium alpinum* +11.1%. Additional species noted in current data include *Campanula serrata*, *Cardaminopsis neglecta*, *Primula minima*, *Juncus filiformis*, *Silene acaulis*, *Viola lutea* subsp. *sudetica*, *Achillea millefolium* subsp. *alpes-tris*, *Bartsia alpina*, *Carex nigra*, *Poa alpina*, *Pulsatilla scherfelii* and *Vaccinium gautherioides*. In contrast, the following species recorded in historical relevés are absent in current re-sampling: *Leucanthemopsis alpina*, *Rhodiola rosea*, *Poa granitica*, *Campanula tatrae*, *Adenostyles alliariae*, *Cerastium fontanum*, *Omalotheca supina* and *Sedum alpestre*.

Juncion vegetation group (Fig. 4) has an obvious increase in tree species, including *Pinus mugo* (+71.4%) and *Juniperus communis* (+66.7%). *Sorbus aucuparia* (+100%) was also sampled in one relevé. From neighbouring vegetation, especially from tall herb communities, *Gentiana punctata* (+100%), *Bistorta major* (+50%), *Festuca picturata* (+42.9%), *Avenella flexuosa* (+38.5%) and *Luzula alpinopilosa* subsp. *obscura* (+25%) have also penetrated. Current data also established an obvious decrease in the frequencies of *Primula minima* (-62.5%), *Senecio incanus* subsp. *carniolicus* (-60%) and *Anthoxanthum alpinum* (-50%). Additional species were recorded only in current relevés. These included typical alpine species, such as *Carex bigelowii*, *Gentiana punctata*, *Carex atrata* and *Ligusticum mutellinoides* as well as species inhabiting lower altitudes, including *Calluna vulgaris*, *Luzula sylvatica*, *Sorbus aucuparia*, *Dryopteris filix-mas*, *Hieracium murorum*, *Luzula luzuloides* and *Acetosa arifolia*. In contrast, the following species were recorded only in historical relevés: *Euphrasia tatrae*, *Pseudorchis albida*, *Diphasiastrum alpinum*, *Antennaria dioica*, *Carex flava*, *C. nigra*, *Phleum rhaeticum*, *Poa alpina*, *Pyrola minor*, *Selaginella selaginoides* and *Tofieldia calyculata*.

The *Vaccinion* vegetation group revealed changes in frequencies for *Avenella flexuosa* (+85.7%) and *Avenula versicolor* (-50%) (Fig. 5). The character and physiognomy of this vegetation is determined mainly by small shrubs, such as *Empetrum nigrum*, *Vaccinium myrtillus* and *V. vitis-idea*. Their current frequency, however, matches historical values. *Vaccinion* species recorded only in current data include *Nardus stricta*, *Pinus mugo* and *Veratrum*

album subsp. *lobelianum* and those sampled historically account for *Calamagrostis villosa*, *Potentilla aurea*, *Senecio incanus* subsp. *carniolicus* and *Soldanella carpatica*.

Changes in diversity and site conditions

Differences in diversity and site conditions were analysed by paired *t*-test. The null hypothesis contended that historical and current data are not significantly different ($\alpha=0.05$) (Table 1), and significant results are presented by box plot (Fig. 6). The *t*-test results revealed no obvious differences in diversity or in the average number of species over the last 50 years. In *Festucion* group the average number of species decreased from 14.8 to 12.9 and the SW index decreased from 1.77 to 1.57, but these changes were not statistically significant. In *Juncion* group, the SW index increased marginally from 1.96 to 2.05 and average species number from 17.02 to 17.51. In *Vaccinion* group, similarly, the SW increased from 1.78 to 1.84 and the average number of species increased by 0.45. In contrast, statistically significant differences were established in light factor

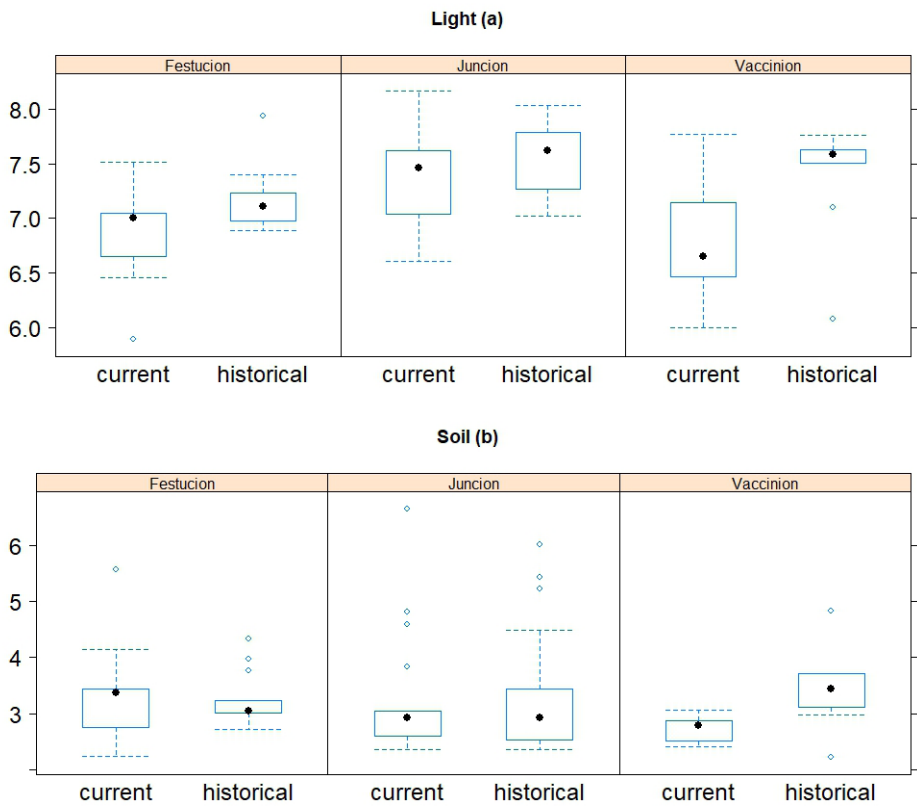


Fig. 6. Comparison of historical and contemporary site conditions estimated by Ellenberg's eco-indices (a, b).

T a b l e 1. Comparison of average values for historical and contemporary site conditions estimated by Ellenberg's eco-indices and results of the Paired t-test. Abbreviations: SW – Shannon-Wiener index, E – evenness index, NOS – number of species, temp – temperature, cont – continentality, mois – moisture, soil – soil reaction, nut – nutrients.

		SW	E	NOS	light	temp	cont	mois	soil	nut
<i>Festucion</i>	Historical	1.768	0.657	14.804	7.194	2.282	2.900	5.617	3.097	2.784
	Current	1.568	0.620	12.899	6.911	2.511	3.063	5.595	3.086	2.838
	t	1.238	0.465	1.738	2.189*	-1.861	-0.912	0.702	-0.482	-0.117
	p-value	0.238	0.650	0.106	0.047	0.085	0.379	0.495	0.638	0.909
<i>Juncion</i>	Historical	1.963	0.713	17.015	7.547	2.146	2.894	4.666	3.485	2.102
	Current	2.050	0.719	17.515	7.371	2.237	2.941	4.671	3.356	2.196
	t	-1.048	-0.656	-0.550	2.515*	-0.989	-0.929	-0.038	0.954	-0.865
	p-value	0.310	0.521	0.590	0.023	0.338	0.366	0.970	0.354	0.400
<i>Vaccinion</i>	Historical	1.781	0.694	13.222	7.388	2.461	3.820	5.129	3.407	2.119
	Current	1.837	0.711	13.667	6.821	2.453	3.768	4.908	2.733	2.272
	t	-0.330	-0.397	-0.222	3.234*	0.081	0.407	2.276	3.094*	-1.311
	p-value	0.750	0.701	0.830	0.012	0.937	0.694	0.052	0.015	0.226

Significance level: 0.05*

for all three groups. Light-demanding species not found in re-sampled sites included *Antennaria dioica*, *Diphasiastrum alpinum*, *Pseudorchis albida*, *Selaginella selaginoides* and *Tofieldia calyculata*. A significant decrease in soil reaction in the *Vaccinion* group is also observed.

NMDS ordination diagram of historical and current relevés

Figs 7 and 9 illustrate that NMDS ordination distinctly separated the historical and current relevés of *Festucion* and *Vaccinion*. This indicates that these vegetation types experienced a change in the studied period. However, the distribution of *Juncion* group relevés does not follow this pattern, and Fig. 8 highlights its stability in species composition and abundance.

Discussion

Our results on changes in the species *Festucion*, *Juncion* and *Vaccinion* mostly correspond with other authors' findings. With regard to climate change influences, Schei et al. (2015) report a similar pattern in species frequency changes in central Norway. This is explained by climate change, because some species' adaptation to gradual climate change is limited by competition with relatively thermophilous species migrating from lower altitudes (Abeli et al., 2012). Here, the *Festucion* group follows snowbed vegetation, which is the most sensitive to climate change, and similar species penetration from adjacent communities has also been observed in the Italian Rhaetian Alps (Carbognani et al., 2014). This phenomenon, and especially the increase in *Vaccinion* dwarf shrub abundance, is attributed to reduced snow cover duration and prolongation of the growth period (Klanderud, Birks, 2003; Cannone et al., 2007; Elmendorf et al., 2012; Grytnes et al., 2014; Vanneste et al., 2017). This increased dwarf shrub frequencies is also reported in other alpine habitats (Körner, 2003; Walker et al., 2006; De Witte, Stöcklin, 2010; Gottfried et al., 2012; Hedenäs

et al., 2016; Vanneste et al., 2017). Animal grazing is also implicated in frequency changes of species, with recognised trends due to reduction or cessation of grazing (Olofsson et al., 2001). However, the distinct increase in *Nardus stricta*'s frequency in the *Festucion* group is surprising because it does not agree with other authors' findings, which have reported the retreat of this species after a reduction in grazing (Austrheim et al., 2007; Speed et al., 2014; Korzeniak, 2016).

The relatively high stability of *Juncion* communities over time, especially the unchanged frequency of dominant graminoids, is supported by the findings of Grabherr (2003) and Dúbravcová and Jarolímek (2007). Here, the increased frequency of reptile chamaephytes (*Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*) appears linked to land use and climate changes. The most significant changes were found in dwarf pine stands (*Pinus mugo*) at lower al-

titudes. These are considered less typical in species composition (Zeidler et al., 2010). Neighbouring dwarf pines also affect both spatiotemporal snow distribution and airflow (Liston et al., 2002) and these altered site conditions gradually change the structure of communities that require strong, permanent winds because of their intolerance to deep snow. Expansion of dwarf pines and other tree species (*Juniperus communis*, *Sorbus aucuparia*) causes retreat of light-demanding species such as *Primula minima*, *Senecio incanus* subsp. *carniolicus* and *Avenula versicolor*. Similar trends have been reported in the Hrubý Jeseník Mts. alpine zone (Zeidler et al., 2010). The edge-

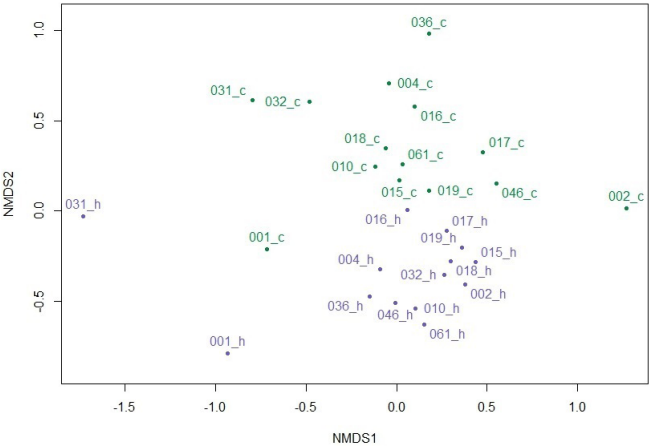


Fig. 7. NMDS ordination diagram (k=3) showing the distribution of current and historical relevés of *Festucion* vegetation group. Suffix _h indicates historical relevés.

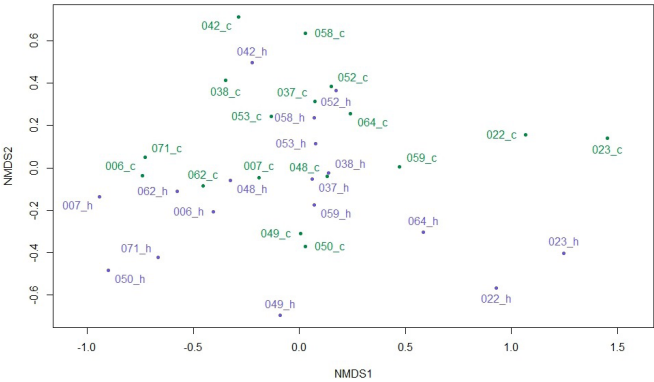


Fig. 8. NMDS ordination diagram (k=3) showing the distribution of current and historical relevés of *Juncion* vegetation group. Suffix _h indicates historical relevés.

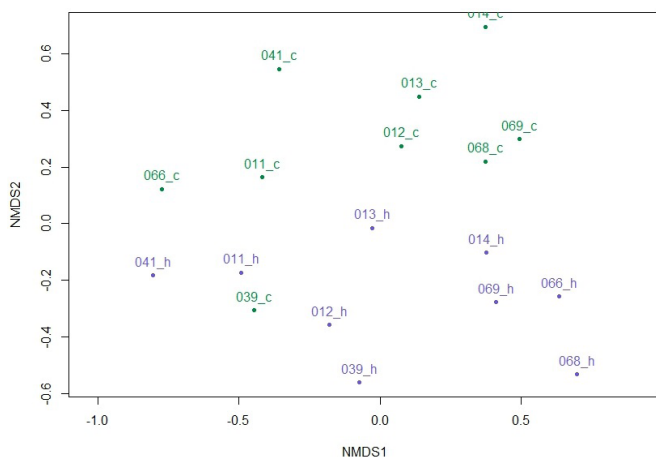


Fig. 9. NMDS ordination diagram (k=3) showing the distribution of current and historical relevés of *Vaccinium* vegetation group. Suffix _h indicates historical relevés.

effect of dwarf pine stands also establishes conditions for nutrient-demanding species from lower altitudes including *Dryopteris filix-mas*, *Hieracium muro-rum* and *Luzula luzuloides* (Soukopová et al., 2001).

While there was no change in *Vaccinium* group frequencies of small shrubs that determine stand physiognomy, the results indicate competition with increased *V. gaultherioides* and decreased *V. myrtillus*. Although similar results were reported by Gerdol et al. (2000) these were not con-

firmed in later research (Brancaloni, Gerdol, 2006). *Vaccinium vitis-idea* is the most sensitive reptile chamaephyte noted in climate change studies. While Kudo and Suzuki (2003) reported that it is suppressed by other small shrubs, especially *V. myrtillus*, we did not confirm this suppression. Acidophilous small shrub communities are considered very stable at high altitudes, but their succession can lead to dwarf pine stands (Šibík et al., 2007). This trend is indicated in our results by increased *Pinus mugo* frequency recorded in three relevés at lower altitudes, and together with strongly competitive species such as *Avenella flexuosa* and *Veratrum album* subsp. *lobelianum*, it has led to significant changes in Ellenberg indicator value for light. Increased soil reaction is caused by increased frequency of *Agrostis rupestris*, *Avenella flexuosa* and *Huperzia selago* and abundance at lower altitudes. Šmarda (1963) adds that soil reaction can also be changed by increased frequency of *Nardus stricta*, which strongly acidifies soils.

Although our studied vegetation groups include communities with different ecological demands, all three show significant changes in light conditions. The noted decrease in light-demanding species and those preferring nutrient-poor soils is related to grazing cessation (Witkowska-Żuk, Ciurzycki, 2000; Johansson et al., 2011; Korzeniak, 2016).

While our results show that changes in community structures are not generally reflected in diversity loss, exceptions here are a decrease in the light-demanding species such as *Antennaria dioica*, *Diphasiastrum alpinum*, *Pseudorchis albida*, *Selaginella selaginoides* and *Tofieldia calyculata*. Species competition is also evident in this study. Decrease in small species population density is often caused by competitive increase in taller neighbouring species (Tilman, 1988). Grazing cessation is also accompanied by promotion of expansion of phanerophytes, reptile chamaephytes and tall grasses. Our example of such a good competitor is *Avenella flexuosa* with its distinct 53.1% increase in frequency, and this is supported by similar trend in alpine pastures in the Polish part of the Tatras Mountains (Korzeniak, 2016) and in former alpine pastures in southern Norway

(Austrheim et al., 2007; Speed et al., 2014). The recovery and competitive ability of this species is largely due to cessation of previous vast cattle grazing. Further consequence of grazing cessation is seen in the accumulation of biomass, which has no consumers (Šmarda, 1963), and subsequent decomposition is limited by the harsh alpine climate (Gavazov, 2010). This also suppresses the terophyte and geophyte reproduction confirmed in this research by the decreases in the following species: *Euphrasia tatrae* (-100%), *Veronica alpina* (-100%), *Carex nigra* (-50%) and *Doronicum stiriaticum* (-37.5%).

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