

Subalpine vegetation changes in the Eastern Sudetes (1973–2021): Effects of abandonment, conservation management and avalanches

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Abstract

Aims: The summit grasslands of many European mountain ranges were historically used for summer grazing, which ceased in the 20th century. These grasslands are changing, partly through succession after abandonment and partly owing to environmental changes. Subalpine vegetation is also affected by artificially reduced avalanche frequency. Recent conservation efforts have attempted to reverse the negative trends of change. We ask: (1) How has subalpine vegetation changed following the abandonment and avalanche control? (2) Was conservation management able to reverse the post-abandonment trend of vegetation change? (3) Did avalanche disturbance have a positive effect on plant species diversity?

Location: Summit area of the Hrubý Jeseník Mountains (1,491 m a.s.l.), Eastern Sudetes, Czech Republic.

Methods: Vegetation plots sampled in the 1970s were resurveyed in the 2000s and again in 2021. Subalpine vegetation was classified into six types, and transitions between these types over time were quantified. Vascular plant species richness and the proportion of threatened species were compared between periods, between areas with and without conservation management, and between areas affected vs unaffected by a large avalanche from 2019. Species composition was analysed using principal coordinate analysis and distance-based redundancy analysis.

Results: Vegetation types remained relatively stable except for species-rich grasslands, some of which changed to heathlands or tall-forb vegetation. Some competitive species have increased, and species specialized to threatened habitats declined. Conservation management systematically implemented after 2010 slowed the decline of habitat-specialized species but did not reverse it. Disturbance by an avalanche positively affected species richness but not the number of threatened species.

Conclusions: Subalpine vegetation is slowly losing its plant diversity owing to grazing cessation and possibly acidification from past atmospheric deposition. Recently

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implemented conservation management and restoration of avalanche activity are essential to stop this trend, but future monitoring is needed to evaluate the success of management actions.

KEYWORDS

alpine grassland, avalanche, conservation management, Hrubý Jeseník Mountains, subalpine scrub, succession, vegetation change, vegetation resurvey

1 | INTRODUCTION

Summer grazing by livestock was common in the past in the summit areas of many European mountains (Herzog et al., 2005). Treeless areas above the timberline were expanded, and summits of lower ranges that did not reach the climatic timberline were cleared to provide more pasture land (Pini et al., 2017). Extensive grazing contributed to the high species richness of mountain grasslands (Hoiss et al., 2013). However, mountain grazing became increasingly unprofitable during the 20th century, leading to the abandonment of many former pastures (MacDonald et al., 2000). The most obvious consequence of abandonment is the spread of forest and the upward shift in the previously artificially lowered alpine timberline (Didier, 2001; Gehrig-Fasel et al., 2007; Bracchetti et al., 2012; Treml et al., 2016; Mietkiewicz et al., 2017), and shrub encroachment above the timberline (Dullinger et al., 2003; Bühlmann et al., 2014; Palaj & Kollár, 2021; De Toma et al., 2022). In addition, there may be a significant loss of species diversity within grassland plant communities after management ceases (Dullinger et al., 2003; Schwaiger et al., 2022).

Abandonment of grazing and changes in land use are not the only causes of change in alpine and subalpine grasslands (Kulakowski et al., 2011). These grasslands are also affected by global warming (Klanderud & Birks, 2003; Walther et al., 2005; Pauli et al., 2007; Varricchio et al., 2022), increasing atmospheric nitrogen deposition (Britton et al., 2009) and acidification (McGovern et al., 2011; Ross et al., 2012). Because these processes are parallel, their effects are likely combined, and it is challenging to disentangle the main drivers of biodiversity change in mountain grasslands (Kaufmann et al., 2021).

Another factor affecting the diversity of alpine and subalpine grasslands is the alteration of the disturbance regime owing to anthropogenic suppression of avalanches. By disturbing subalpine forests and shrublands, avalanches maintain natural grasslands that can harbour high diversity, combining alpine belt species with forest belt species (Erschbamer, 1989; Rixen et al., 2007; Bebi et al., 2009). However, many artificial barriers have been created in mountain areas to protect against avalanches, resulting in lower avalanche frequency, which in turn triggers successional changes in vegetation (Kulakowski et al., 2006; Rixen et al., 2007).

In protected areas, conservation authorities are trying to halt the decline of mountain grasslands and their biodiversity by reintroducing extensive grazing or mowing (Krahulec et al., 2001; Lochon et al., 2018). In places without potential risk to humans, attempts are

also being made to restore the natural avalanche regime by removing protective barriers. However, in some areas, these measures were introduced several decades after avalanche regulation was abandoned. In the meantime, mountain grasslands have changed through succession, which may have led to biodiversity change that is difficult to reverse in the short term (Pecháčková et al., 2010). The question is how much of the former diversity has been lost and whether the mere reintroduction of historical or alternative management practices can restore it.

An example of a subalpine area that has gone through the journey from grazing through abandonment and avalanche control to conservation management is the summit of the Eastern Sudetes (Hrubý Jeseník) in the Czech Republic (Mackovčín et al., 2021). This area was used for livestock grazing from the 17th century but was abandoned in the 1940s. Beginning in the late 19th century, the non-native dwarf pine (*Pinus mugo*) was planted there to reduce avalanche activity. The lack of disturbance from grazing and avalanches led to successional changes in vegetation in the second half of the 20th century. Beginning in the late 1980s, conservationists have been gradually removing *Pinus mugo*, and in the 1990s, they also began mowing some areas of subalpine grasslands and heathlands. After several decades of no significant avalanche activity, a large avalanche was released in January 2019, destroying an extensive area of birch woodland.

Vegetation in this area has been surveyed repeatedly in the past, providing a unique opportunity to examine changes in subalpine plant communities following abandonment and avalanche regulation, and subsequent implementation of conservation management and restoration of natural avalanche dynamics. In 2021, we resurveyed vegetation plots from the 1970s and 2000s and asked the following questions: (1) How has subalpine vegetation changed following abandonment and avalanche control? (2) Was conservation management able to reverse the post-abandonment trend of vegetation change? (3) Did avalanche disturbance have a positive effect on plant species diversity?

2 | METHODS

2.1 | Study area

The study area is located in the Hrubý Jeseník Mountains (the highest mountain group of the Eastern Sudetes) in the northeastern Czech Republic. It includes the highest part of this mountain

range: Mount Praděd (1,491 m a.s.l.), the Vysokoholský hřbet range (Mount Vysoká hole, 1,464 m a.s.l.) and the Velká kotlina glacial cirque on the southeastern slope of the Vysokoholský hřbet (50°2'31"–50°5'6"N, 17°12'42"–17°14'46"E; Figures 1 and 2). Our sampling was conducted at elevations between 1,111 and 1,464 m a.s.l. The summit areas have flat topography with plateaus and rounded mountaintops, covered by monotonous vegetation of species-poor grasslands and heathlands. By contrast, the Velká kotlina cirque harbours a wide range of plant communities, many of which are species-rich (Jeník, 1961; Jeník et al., 1980; Hédli & Kočí, 2015; Bureš, 2022).

The bedrock consists mainly of Palaeozoic (Variscan) metamorphic rocks, mostly phyllite, but also gneiss, mica schist, schist with graphite, greenschist and metadolerite (<https://mapy.geology.cz/geocr50/>). The Velká kotlina cirque also contains patches of calcareous and alkaline igneous rocks (Novotný & Bureš, 2018). The most common soil type is acidic podzol, but there are also rankers on steep upper slopes and shallow peat accumulations on flat summit

areas (<https://mapy.geology.cz/pudy/>). The soil pH values we measured in the vegetation plots ranged from 2.9 to 6.0.

The mean annual temperature at the former climate station on Mount Praděd (1,490 m a.s.l.) in 1970–1997 was 1.2 °C (–6.5 °C in January, 9.7 °C in July), and the total annual precipitation was 1,094 mm (with a maximum in July) (Czech Hydrometeorological Institute, www.chmi.cz). There was no statistically significant change in mean annual temperature and total annual precipitation at Mount Praděd between 1970 and 1997. At Mount Šerák (1,328 m a.s.l.) station, located 17 km from the study area, there was also no change in these variables in the period 2004–2021 (Appendix S1). Continuous snow cover lasts on average until the second half of April, but small patches of snow often persist until June. Small avalanches fall in Velká kotlina at intervals of several years.

The timberline in the Hrubý Jeseník is, on average, at about 1,300 m a.s.l. (Tremil & Migoň, 2015) but is pushed down by avalanches in the Velká kotlina cirque (Figure 2c). The treeline ecotone is dominated by *Picea abies*, occasionally with an admixture of *Fagus*

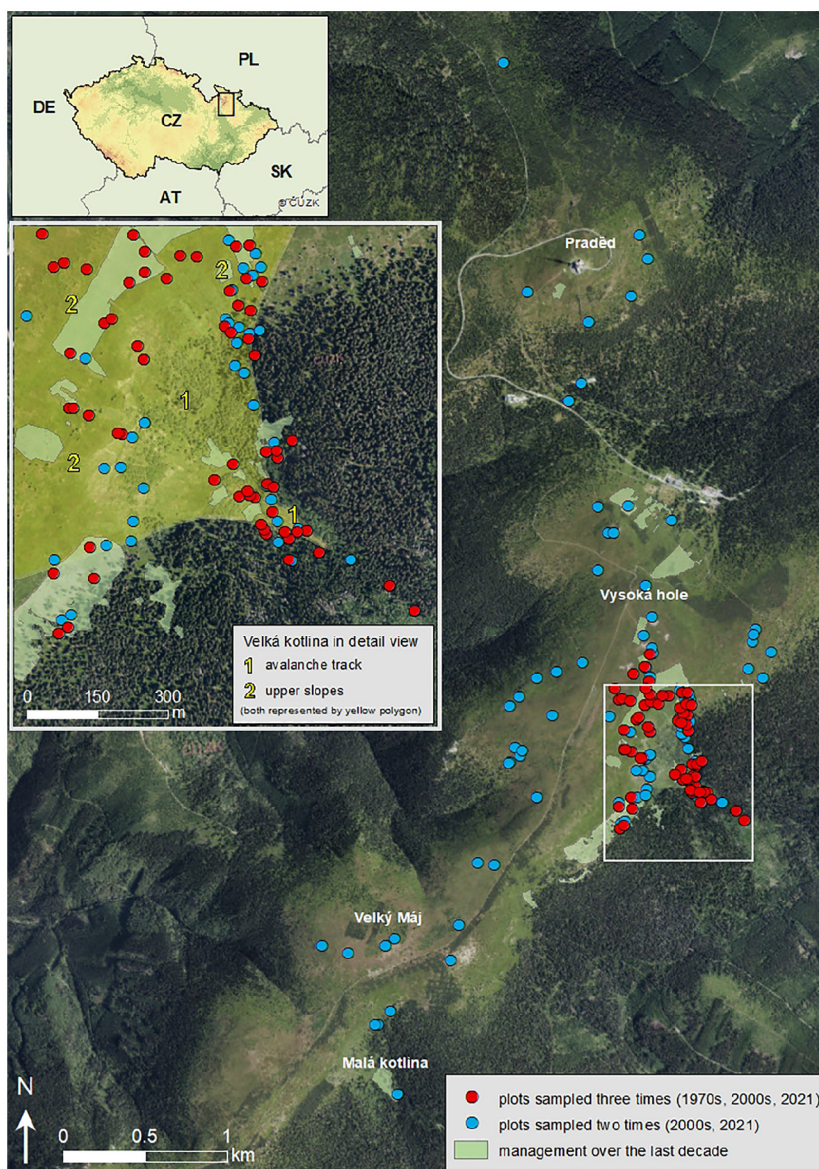


FIGURE 1 The treeless summit area of the Hrubý Jeseník Mountains with the locations of vegetation plots sampled three times (red, concentrated in the Velká kotlina cirque) and plots sampled twice (blue). Areas where conservation management (mainly mowing) was carried out after 2010 are shown in light green. An interactive map with a zoom option, showing the exact position of plots, small shifts between the 2000s and 2021 plot coordinates and photographs of plot sites in 2021, is available at <https://arcg.is/0uSrZ9>

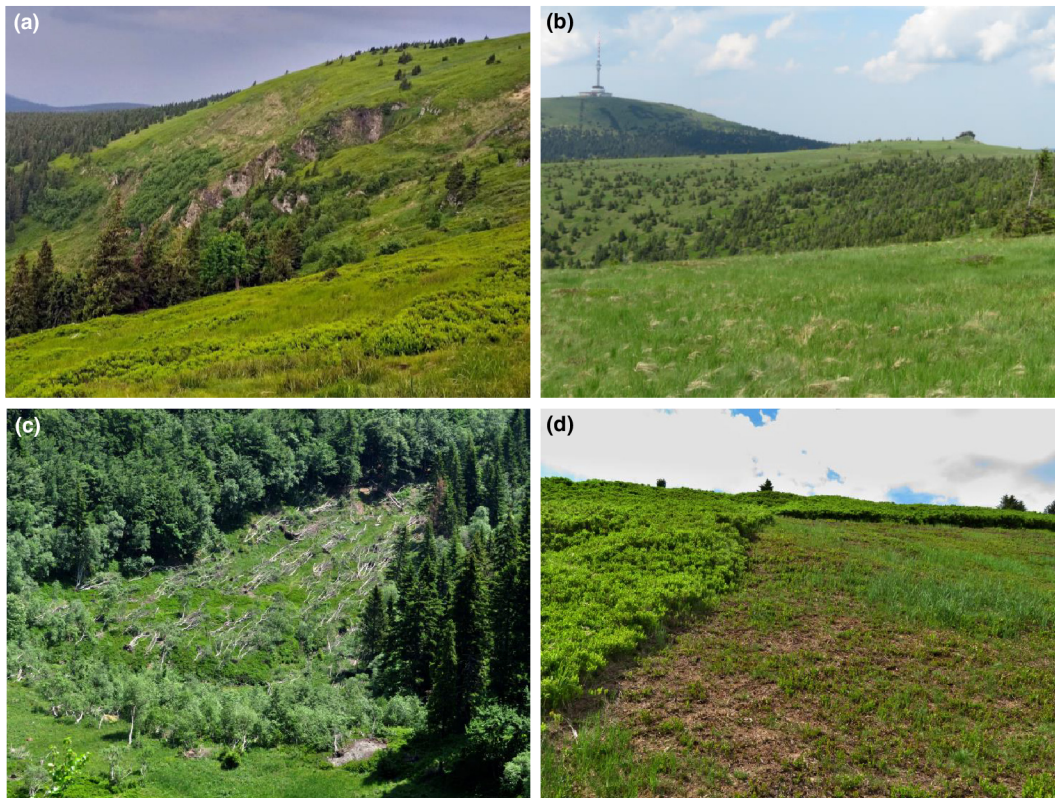


FIGURE 2 Study area and major disturbance regimes. The area includes (a) the Velká kotlina glacial cirque with steep slopes and rock outcrops and (b) treeless summit plateaus with gentle slopes. (c) Disturbed birch woodlands in a lower part of the 2019 avalanche track. (d) Formerly grazed but later abandoned grassland overgrown by extensive heathlands dominated by *Vaccinium myrtillus*. Some of these heathlands were recently mown as part of conservation management

sylvatica. The forest transitions directly into alpine grasslands, because there is no natural krummholz belt as in other Central European mountains. However, woodland or scrub of *Betula pubescens* subsp. *carpatica* and *Salix silesiaca* are present on avalanche tracks and sites with long-lasting, deep snow cover (Jeník et al., 1980).

It is likely that the summit areas were largely covered by forest in the mid-Holocene (Tremel et al., 2008; Novák et al., 2010), whereas open areas existed only on avalanche tracks and rocky slopes in the cirques. The continuous presence of natural grassland patches in this area is confirmed by the isolated occurrence of numerous subalpine grassland species, including some neo-endemics (Jeník, 1961; Jeník et al., 1983; Kaplan, 2017; Bureš, 2022). Large-scale deforestation by humans began in the 12th–13th centuries (Novák et al., 2010). The summit area was used for sheep and cattle grazing and hay-making from the 17th century (Hošek, 1972, 1973). As a result, the timberline dropped to its lowest level in the 18th and 19th centuries. In the late 19th and early 20th centuries, belts of non-native dwarf pine (*Pinus mugo*) were planted above the timberline to prevent avalanches (Hošek, 1972; Bureš et al., 2009). Livestock grazing began to decline already in the second half of the 19th century, and finally ended during World War II. Natural regeneration of spruce on abandoned grasslands and artificial afforestation led to a rise in the timberline and increasing forest density in the treeline ecotone (Tremel et al., 2016; Mackovčín et al., 2021). Birch woodland developed on the inactive lower part of the avalanche track in the Velká kotlina cirque.

Velká kotlina was designated a nature reserve in 1946, and protection was later extended to the entire study area and beyond. Nature conservation authorities have reintroduced mowing and locally (especially near the huts) also grazing. In small areas (ca. 0.1 ha), mowing was already being used experimentally in the 1990s. However, systematic mowing started only around 2010 and mowing of large areas in 2017. Areas managed after 2010, in most cases by mowing of expanding tall herbs and the dwarf shrub *Vaccinium myrtillus*, are shown in Figure 1. The frequency of mowing varied, and many places were mown only once in the past decade. In the late 1980s, nature conservation also began removing planted shrubs of *Pinus mugo* (Bureš et al., 2009). This likely contributed to the departure of an avalanche that fell in January 2019 and severely disturbed the birch woodland. This avalanche was the largest in at least 60 years and formed a 900-m track that ended at an elevation of 1,115 m a.s.l., whereas previous avalanches that fell during the past 50 years were shorter than 600 m.

2.2 | Vegetation sampling

In this study, vegetation change is analysed by comparing species composition in vegetation plots surveyed in three periods. The first survey (1970s) was conducted by Leo Bureš and Zuzana Burešová in the Velká kotlina cirque and the adjacent slopes of Mount Vysoká

hole in the summers of 1973–1978. This survey was conducted simultaneously with detailed vegetation mapping, and the location of each plot was assigned to a specific patch on the map, which contained 935 patches with 37 phytosociological associations and sub-associations.

The second survey (2000s) was conducted by Martin Kočí and Leo Bureš in the summers of 2004–2010 (Kočí, 2005; Bureš & Kočí, 2010). During this survey, plots in Velká kotlina were located in the same patch of the vegetation map as the corresponding plot in the 1970s, often with a spatial uncertainty of <10 m, based on the memory of Leo Bureš. In addition, several plots were sampled at new locations, particularly on summit plateaus. Plot coordinates were measured using GPS with an uncertainty of <10 m.

The third survey (2021) was conducted by the authors of this article, including Martin Kočí, in the second half of June 2021. Each plot position was determined based on the GPS coordinates from the 2000s. In a few cases, because of GPS measurement inaccuracies, the coordinates were found in a habitat different from the one sampled in the 2000s. In such cases, the location of the new plot was moved a few metres from the coordinates to sample the same habitat as sampled in the 2000s. If such a habitat was not nearby, the plot was rejected. In 2021, we measured the coordinates of most plots using a GPS with an accuracy of ca. 5 cm (Topcon HiPer SR with Getac PS336 Data Collector) in each corner of the plot. In such a way, we established a network of permanent vegetation monitoring plots. The size and shape of the plots varied by vegetation type. Repeated sampling always used the same plot size as the previous sampling. Most plots were squares of 100 m² in woodlands and 16 m² in grasslands or rectangles of 10 m² in springs. All species of vascular plants were recorded in each plot, and their cover was estimated using the nine-grade Braun-Blanquet scale (Westhoff & van der Maarel, 1978). Bryophytes and lichens were recorded in only some plots, focusing on the dominant species; they were not included in the analysis owing to inconsistent sampling. The final data set included data from 148 vegetation plots, of which 66 were sampled three times (1970s, 2000s, 2021) and 82 were sampled twice (2000s, 2021), i.e. 362 vegetation-plot records in total.

In 2021, soil samples were collected from the mineral soil horizon at a depth of 5–10 cm below the raw humus layer. Within each vegetation plot, soil samples were collected from four locations approximately in the middle of each plot quarter, mixed, dried at room temperature, sieved (mesh size 2 mm), and used to measure soil pH and electrical conductivity. A soil–water suspension (weight ratio 1:2.5) was shaken in the Biosan PSU-10i orbital shaker for 5 min at 280 rpm, and pH and conductivity were measured the next day using the HQ40D digital multimeter.

GIS layers indicating the areas managed (in most cases mown) for conservation purposes in the past 10 years were provided by the Administration of the Protected Landscape Area Jeseníky. Plot coordinates measured in the field were overlaid with these layers using ArcGIS 10.7 (ESRI). Based on this overlay (Figure 1), the plots were divided into managed and unmanaged. In addition, the plots were

divided into affected and unaffected by the 2019 avalanche based on the locations of damaged trees observed in the field.

2.3 | Data analysis

We entered vegetation-plot records from all three sampling periods into a database using the Turboveg 2 program (Hennekens & Schaminée, 2001). We then standardized the taxonomic concepts and nomenclature according to Kaplan et al. (2019) in the Juice 7.1 program (Tichý, 2002). We removed from the analyses the vernal species *Anemone nemorosa* and *Cardamine pratensis*, which were recorded frequently in 2021 but infrequently in the previous surveys because the 2021 sampling was conducted at a slightly earlier phenological stage.

To account for the different plot sizes in the comparisons of species numbers, we fitted the species-area curves in log–log space separately for birch woodlands and open habitats. Because the slopes of the curves were not significant, we compared species numbers without accounting for differences in plot sizes. We also analysed changes in the proportion of threatened species (IUCN categories critically endangered [CR], endangered [EN] and vulnerable [VU]) of all species between sampling periods. Species were classified according to the national Red List (Grulich, 2017); hybrids and species that could not be accurately identified were excluded from this analysis. Changes in species numbers and proportion of threatened species per plot over time were compared within groups of woodland plots and open-habitat plots and then separately for individual open-habitat types. Undisturbed and disturbed plots were also analysed separately to compare vegetation in the 2000s and 2021. For birch woodlands, disturbed plots were those affected by the 2019 avalanche, and for open habitats, disturbed plots were those cut as part of conservation management. The significance of changes in species numbers and proportions was tested using the Wilcoxon test for paired samples.

Because changes in alpine vegetation can differ among plant communities (Gritsch et al., 2016), we classified the entire data set of 362 vegetation-plot records from the three different periods into vegetation types. First, two types were distinguished based on the dominant species (birch woodlands and heathlands). All plot records with a total tree cover larger than 15% were assigned to birch woodland, and all non-woodland records with a total cover of heath species (*Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum hermaphroditum*) larger than 25% and a total cover of bog or spring species smaller than 10% were assigned to heathlands. We excluded two plots in beech forests and four plots on cliffs because these habitats were represented by only a few plots. For the remaining 267 plots, we used the modified TWINSPAN classification (Roleček et al., 2009) in the Juice 7.1 program (Tichý, 2002) with total inertia as a dissimilarity measure and three pseudospecies cut levels corresponding to 0%, 5%, and 25% species covers. The minimum group size for division was set at 2. We divided the data set into six clusters and then merged two

of them based on similar species composition, resulting in five vegetation types: bogs, species-poor grasslands, species-rich grasslands (created by merging two clusters), tall-forb vegetation and spring vegetation. The plot records of bogs ($n = 8$), beech forests and cliffs were included in the overall analyses, but were not analysed separately owing to the small number of plot records in these types. The types were interpreted as associations and alliances of the national vegetation classification (Chytrý, 2007).

Transitions between vegetation types on the same plots through time were visualized in alluvial plots created using the *ggalluvial* package in R (version 0.12.3; R Core Team, R Foundation for Statistical Computing, Vienna, AT). Data were visualized for three periods, using only plots surveyed three times (1970s, 2000s and 2021), and for two consecutive periods separately, including plots surveyed only in the 2000s and 2021. For the latter two periods, alluvial plots were also created separately for undisturbed and disturbed plots. The *gridExtra* package in R (version 2.3; R Core Team, R Foundation for Statistical Computing, Vienna, AT) was used to combine two alluvial plots into one display panel.

Because different numbers of plots were surveyed in the three periods (1970s, 2000s and 2021), we analysed changes in species richness and composition in two steps: between the 1970s and 2000s (66 plots) and then between the 2000s and 2021 (148 plots, including those first surveyed in the 2000s). We analysed overall changes across the data set and within each vegetation type (birch woodlands, heathlands, species-poor grasslands, species-rich grasslands, tall-forb and spring vegetation). Plots were assigned to these groups based on their vegetation classification at the time of initial sampling (either the 1970s or the 2000s). To allow comparison between the 2000s and 2021, we also conducted separate analyses of disturbed and undisturbed plots within each vegetation type.

To visualize changes in species composition, we calculated unconstrained ordination (principal coordinate analysis; PCoA) with square-root transformation of percentage species covers (derived from the Braun-Blanquet scale values) and Bray–Curtis dissimilarity. To analyse changes in species composition, we used a constrained ordination (distance-based redundancy analysis; db-RDA) with square-root transformation of species percentage covers and Bray–Curtis dissimilarity calculated using the *vegan* package in R (version 2.5-7; R Core Team, R Foundation for Statistical Computing, Vienna, AT). Time was used as a constraining variable. To test the significance of the change in species composition, we permuted observations from different periods within plots 999 times. We then determined which species significantly increased or decreased over time. To do this, we used the “*envfit*” function and tested the significance of the relationship between species and the constrained axis of db-RDA using a permutation test with 999 permutations within plots. Changes in species occurrence or abundance were considered significant if the p -value was <0.05 . For each comparison, unconstrained and constrained ordinations were plotted in R using the packages *ggplot2* version 3.3.5 (Wickham, 2016) and *gridExtra*

version 2.3 (R Core Team, R Foundation for Statistical Computing, Vienna, AT). When comparing overall changes in vegetation types over the entire period (1970s–2021), centroids were displayed for each vegetation type. The plots in this ordination were divided into vegetation types based on the 1970s classification.

Environmental changes in the resurveyed vegetation plots were assessed using Ellenberg-type indicator values for Czech flora (Chytrý et al., 2018). Differences in unweighted indicator values between pairs of observations from the same plots were tested using repeated measures ANOVA (“*aov*” function in the *stats* package in R). Row-based (randomization of sampling time) and column-based (randomization of indicator values for species before calculating plot means) tests were calculated with 999 permutations. The higher p -value of the two tests was considered (max test). The unweighted means of indicator values and permutations were calculated using the *weimea* package in R (Zelený, 2018).

3 | RESULTS

3.1 | Vegetation types

The following six vegetation types were distinguished and analysed (see the synoptic table of species composition in Appendix S2):

Birch woodlands (Figure 3a) are found mainly in the lower parts of the Velká kotlina cirque, especially near streams and at the edges of avalanche tracks. The dominant species in the tree layer is *Betula pubescens* subsp. *carpatica*, often accompanied by *Picea abies* and *Salix silesiaca*. In more disturbed areas, the dominant woody species grow as shrubs rather than trees. Typical herb-layer species include *Calamagrostis arundinacea*, *C. villosa*, *Chaerophyllum hirsutum*, *Cirsium oleraceum*, *Equisetum sylvaticum*, *Lunaria rediviva*, *Luzula sylvatica*, *Molinia caerulea*, *Rubus idaeus*, *Stellaria nemorum* and *Vaccinium myrtillus*. The average soil pH for this group is 4.4 (range 2.9–5.8). This vegetation belongs to the association *Salici silesiaca*–*Betuletum carpaticae* (alliance *Salicion silesiaca*).

Heathlands (Figure 3b) are dominated by ericoid plants, such as *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium myrtillus* and *V. vitis-idaea* accompanied by acidophilous graminoids, e.g. *Avenella flexuosa*, *Calamagrostis villosa*, *Festuca supina* and *Luzula sylvatica*. Heathlands are found mainly on the upper slopes and summit plateaus. They occur on acid soils with an average soil pH of 3.9 (3.1–5.3). They mostly belong to the association *Festuco supinae*–*Vaccinietum myrtilli* (alliance *Genisto pilosae*–*Vaccinion*), and some of them to *Avenello flexuosae*–*Callunetum vulgaris* (*Loiseleurio procumbentis*–*Vaccinion*).

Species-poor grasslands (Figure 3c, referred to as “Poor grasslands” in figures and tables) are found primarily on wind-affected summit plateaus on acidic soils. They are dominated by the grasses *Avenella flexuosa*, *Festuca supina* and *Nardus stricta*, which are accompanied by *Bistorta officinalis*, *Calamagrostis villosa* and *Carex bigelowii* subsp. *dacica*. The average soil pH is 3.8 (3.5–4.2). They belong to



FIGURE 3 The main vegetation types in the study area: (a) birch woodland, (b) heathland, (c) species-poor grassland, (d) species-rich grassland, (e) tall-forb vegetation and (f) spring vegetation

the associations *Carici bigelowii-Nardetum strictae* (alliance *Nardo strictae-Caricion bigelowii*), *Cetrario-Festucetum supinae* (*Juncion trifidi*), *Festuco supinae-Nardetum strictae* (*Nardion strictae*) and *Crepido conyzifoliae-Calamagrostietum villosae* (*Calamagrostion villosae*).

Species-rich grasslands (Figure 3d, “Rich grasslands” in figures and tables) occur on gentle slopes, especially in the Velká kotlina cirque. This vegetation is characterized by the presence of numerous forbs and graminoids that require deep and nutrient-rich soil.

The dominant species include *Anthoxanthum odoratum* agg., *Avenella flexuosa*, *Calamagrostis villosa*, *Carex montana*, *Deschampsia cespitosa*, *Geranium sylvaticum*, *Hypericum maculatum*, *Luzula sylvatica*, *Molinia caerulea*, *Nardus stricta*, *Poa chaixii*, *Potentilla aurea*, *Rumex arifolius* and *Trollius altissimus*. The average soil pH is 4.5 (3.7–5.8). These grasslands belong to the associations *Thesio alpini-Nardetum strictae* (alliance *Nardion strictae*), *Crepido conyzifoliae-Calamagrostietum villosae*, *Violo sudeticae-Deschampsietum cespitosae* (both *Calamagrostion villosae*) and *Bupleuro longifoliae-Calamagrostietum arundinaceae* (*Calamagrostion arundinaceae*).

Tall-forb vegetation (Figure 3e) is found on moist and nutrient-rich soils near springs and streams and in seepage areas. The vegetation is dominated by *Adenostyles alliariae*, *Alchemilla* spp., *Calamagrostis arundinacea*, *C. villosa*, *Carduus personata*, *Cirsium heterophyllum*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Filipendula ulmaria*, *Geranium sylvaticum*, *Hypericum maculatum*, *Laserpitium archangelica*, *Molinia caerulea*, *Poa chaixii*, *Rubus idaeus*, *Senecio nemorensis* agg. and *Trollius altissimus*. Shrubs of *Salix hastata* also dominate at some sites. The average soil pH is 5.3 (4.7–5.8). They belong to the associations *Ranunculo platanifolii-Adenostyletum alliariae*, *Trollio altissimi-Geraniatum sylvatici*, *Laserpitio archangelicae-Dactylidetum glomeratae* (all in the alliance *Adenostylin alliariae*) and *Violo sudeticae-Deschampsietum cespitosae* (*Calamagrostion villosae*).

Spring vegetation (Figure 3f) occurs on slopes where groundwater comes to the surface, especially in the Velká kotlina cirque. The dominant component of this vegetation is hygrophilous mosses and liverworts, e.g. *Bryum pseudotriquetrum*, *Hygrohypnum ochraceum*, *Palustriella decipiens*, *Philonotis caespitosa*, *Philonotis fontana*

and *Philonotis seriata*. Typical herbaceous plants include *Adenostyles alliariae*, *Allium schoenoprasum*, *Caltha palustris*, *Cardamine pratensis*, *Carex flava*, *Chaerophyllum hirsutum*, *Cirsium oleraceum*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Filipendula ulmaria*, *Molinia caerulea*, *Phalaris arundinacea*, *Phragmites australis* and *Senecio nemorensis* agg. The average soil pH is 5.4 (4.9–6.0). This vegetation belongs to the associations *Crepido paludosae-Philonotidetum seriatae*, *Swertietum perennis* and *Cardaminetum opicii* (alliance *Swertio perennis-Dichodontion palustris*).

3.2 | Transitions between vegetation types

Very few plots in birch woodlands and species-poor grasslands changed their vegetation type over time (Figure 4). Most of the changes occurred in the species-rich grasslands between the 1970s and 2000s, which often changed to heathlands and tall-forb vegetation. However, at some sites managed after 2010, the original vegetation type returned. In a few cases, primarily at disturbed sites, transitions occurred between spring and tall-forb vegetation.

3.3 | Changes in species richness and composition

In birch woodlands, there were no significant changes in the number of species or proportion of threatened species over time (Figure 5). However, in areas disturbed by the 2019 avalanche, species numbers increased between the 2000s and 2021 (Figure 6b). In open

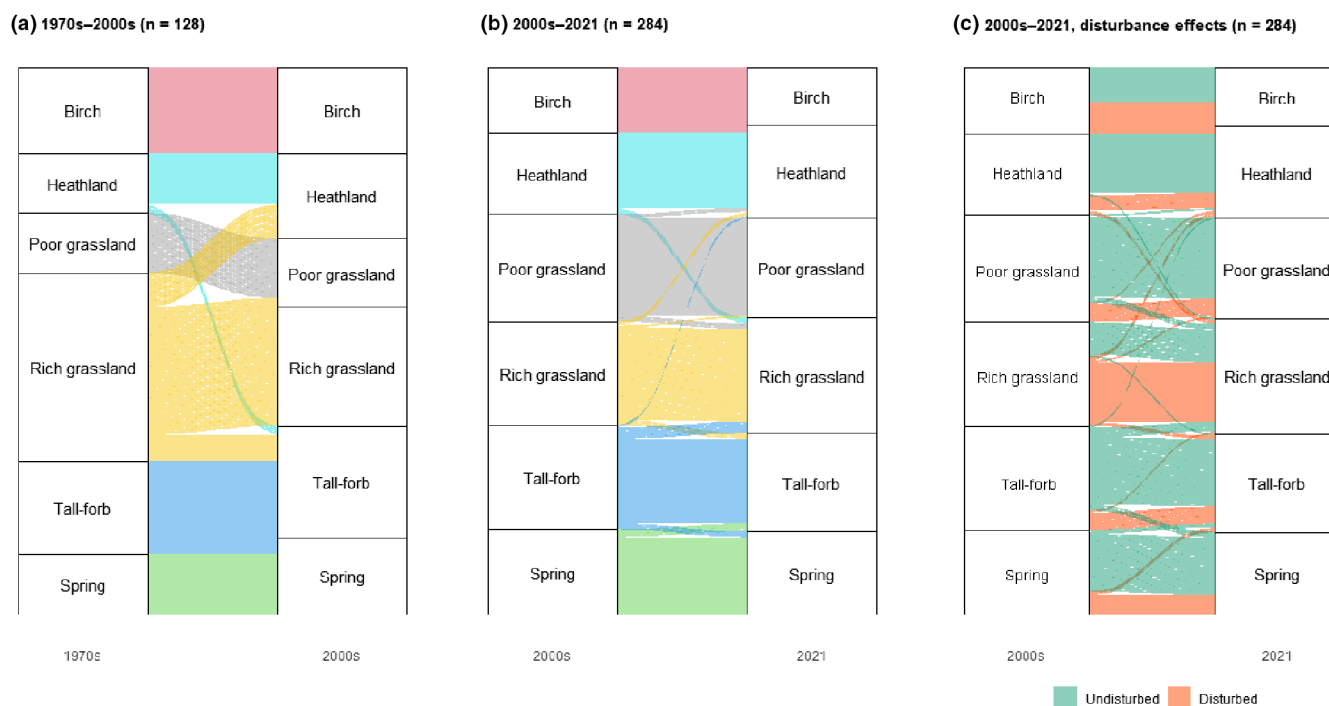


FIGURE 4 Alluvial diagrams showing transitions between vegetation types between two successive surveys (a, b) and the effects of disturbance regimes between the 2000s and 2021 (c)

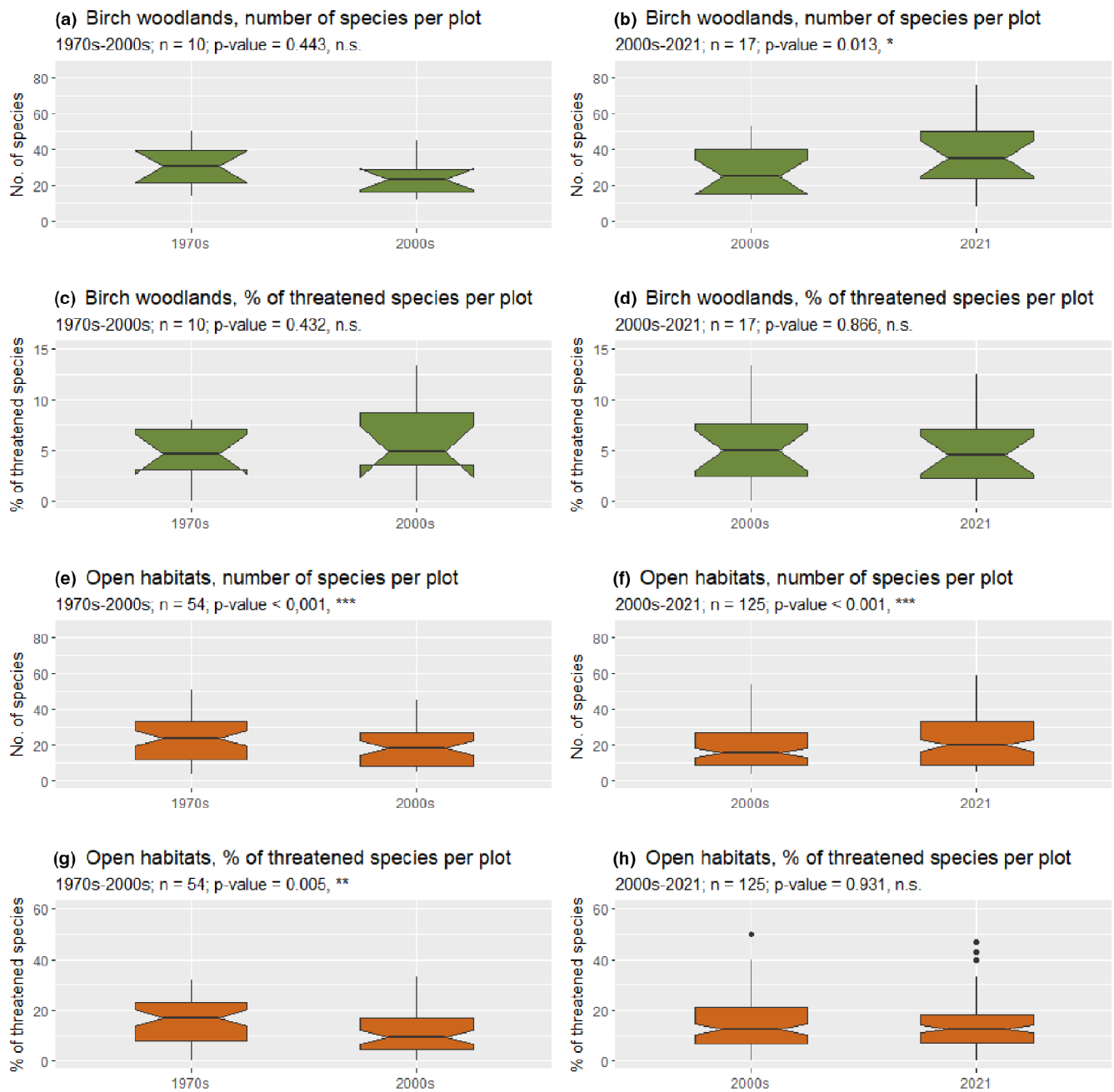


FIGURE 5 Comparison of the number of species per plot and the percentage of threatened species between the 1970s and 2000s and between the 2000s and 2021, separately for birch woodlands and open habitats. Values for the 2000s differ between the left and right graphs because a larger number of plots were used for the right graphs. Differences were tested using the Wilcoxon test for paired samples

habitats, the number of species decreased between the 1970 and 2000s and increased again between the 2000s and 2021. The proportion of threatened species decreased significantly between the 1970s and 2000s, but it did not change between the 2000s and 2021 (Figures 5 and 6). Trends in species richness and the proportion of threatened species for each open-habitat type are shown in Appendix S3.

The main trends of changes in species composition during the study period are shown in Figure 7. Separate analyses for the two periods and each vegetation type are shown in Appendix S4, and analyses for disturbed and undisturbed plots are presented

in Appendix S5. Species-level analysis (Table 1) shows declines in rare mountain species typical of species-rich grasslands and tall-forb vegetation (e.g. *Crepis conyzifolia*, *Dianthus superbus*, *Geranium sylvaticum*, *Gymnadenia conopsea*, *Hieracium prenanthoides*, *Hypochaeris uniflora*, *Rhinanthus riphaeus* and *Viola lutea* subsp. *sudetica*). By contrast, *Vaccinium myrtillus* and competitive herbs (*Hypericum maculatum*, *Luzula sylvatica*, *Poa chaixii* and *Veratrum album* subsp. *lobelianum*) spread and became dominant at many sites. The regionally invasive plant *Galium saxatile* and forest species (*Acer pseudoplatanus*, *Fagus sylvatica* and *Sorbus aucuparia*) also increased.

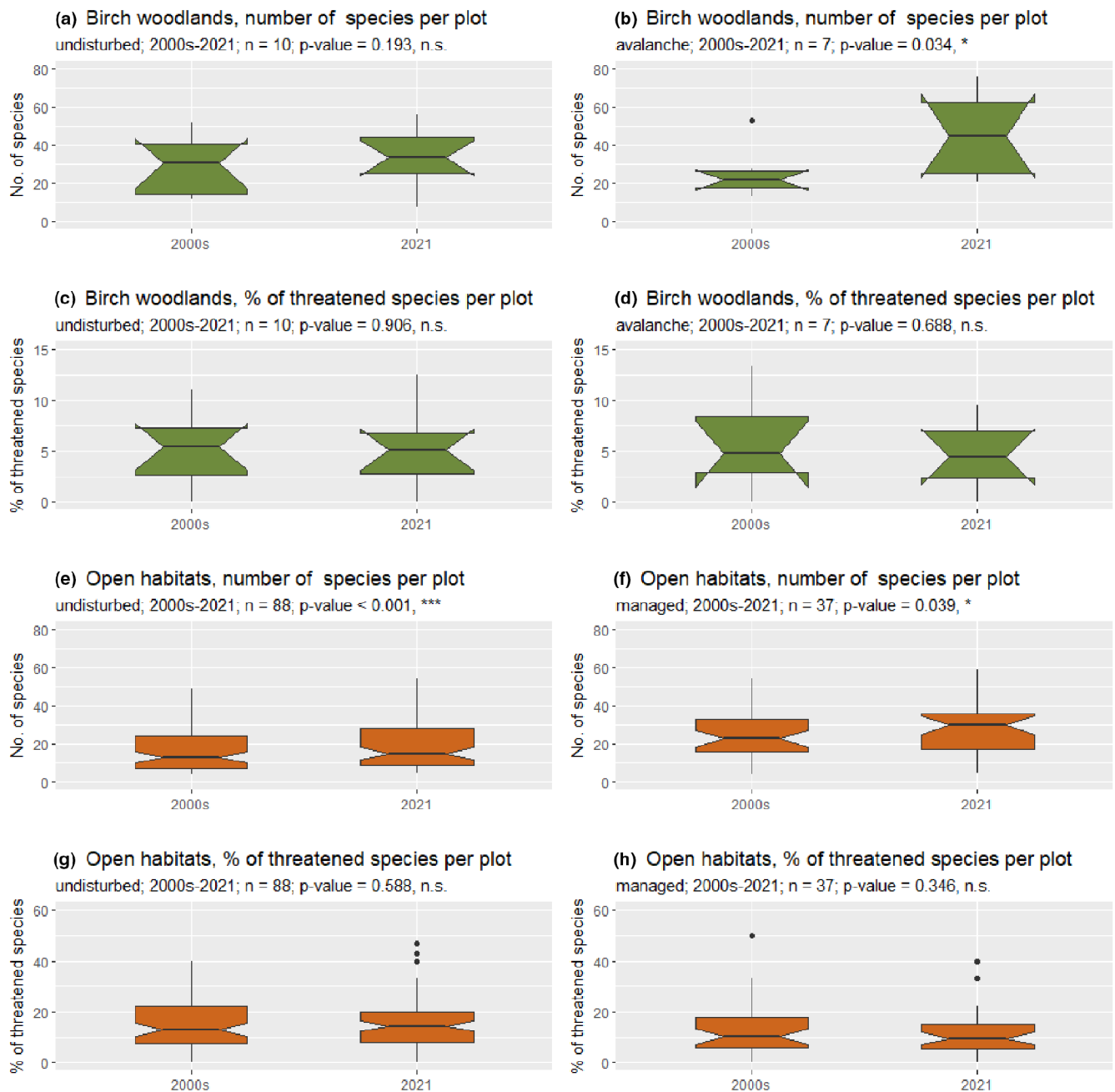


FIGURE 6 Comparison of the number of species per plot and the percentage of threatened species between the 2000s and 2021, separately for undisturbed and disturbed plots. Disturbances include the 2019 avalanche in birch woodlands and management in open habitats. Differences were tested using the Wilcoxon test for paired samples

In birch woodlands, spruce increased in the first period (1970s–2000s) when there were no severe avalanches (Table 2). In the second period (2000s–2021), *Acer pseudoplatanus* increased, and *Betula pubescens* subsp. *carpatica* decreased. In heathlands, *Vaccinium vitis-idaea* and *Trientalis europaea* increased in unmanaged areas. In species-poor grasslands, *Avenella flexuosa* increased in unmanaged areas during the first period, whereas *Festuca supina* increased between the 2000s and 2021. Species-rich grasslands lost several species in both periods, although more species disappeared in the first period. Tall-forb vegetation also lost some species, especially in undisturbed plots. Spring vegetation was relatively stable over the long term.

3.4 | Changes in indicator values

The unweighted mean Ellenberg-type indicator values for the plots showed very few significant changes over time. In the period from the 1970s to the 2000s, the only significant change was the increase in temperature indicator values in species-rich grasslands ($p = 0.012$, max test). In the period from the 2000s to 2021, light indicator values decreased in species-rich grasslands ($p = 0.038$) and in all managed open habitats taken together ($p = 0.026$), and temperature indicator values increased in heathlands ($p = 0.027$). In springs, indicator values in the latter period decreased for moisture ($p = 0.014$) and reaction ($p = 0.012$).

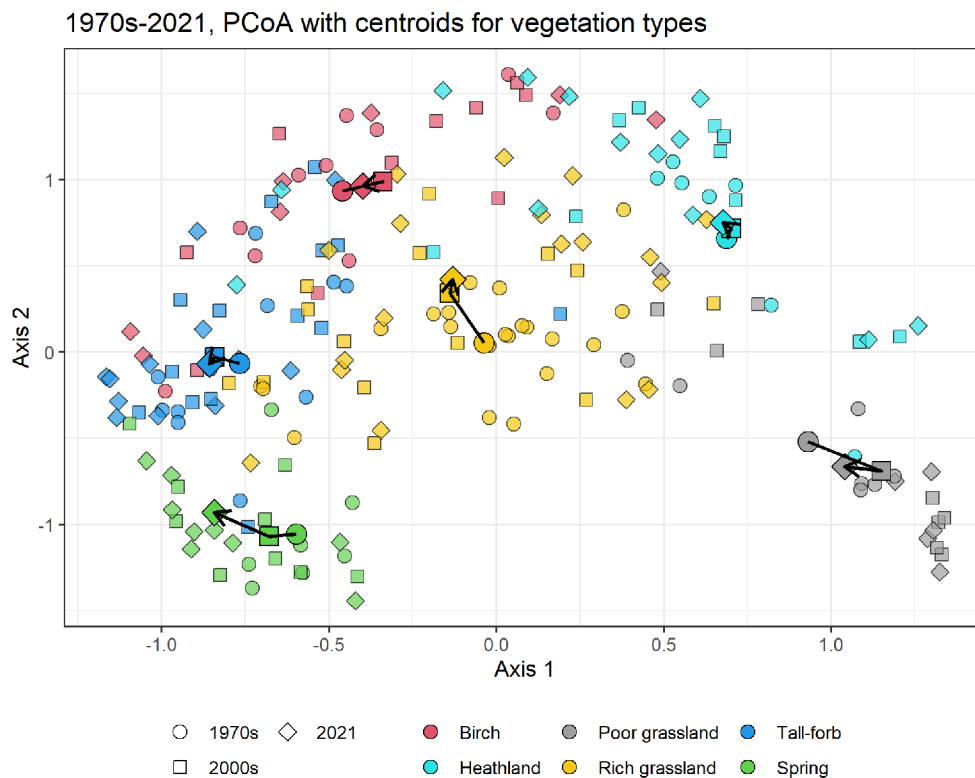


FIGURE 7 Changes in species composition of vegetation types throughout the whole study period (1970s–2021) analysed using unconstrained ordination (principal coordinate analysis; PCoA). Only the plots surveyed three times were used. Plots with different colours belong to different vegetation types according to the modified TWINSpan classification. Centroids for each vegetation type (larger symbols) were calculated based on the 1970s classification of plots. The arrows run from the centroid of plots in the 1970s to their centroids in the 2000s and 2021.

4 | DISCUSSION

Our comparison of vegetation-plot records from the 1970s, 2000s and 2021 shows that most types of subalpine vegetation in the Hrubý Jeseník Mountains have remained relatively stable over the past half-century. However, species-rich grasslands partially changed into tall-forb vegetation or species-poor heathlands. Vascular plant species richness in these grasslands declined, mainly due to the decline of habitat-specialist species, many of which are on the national Red List. Declines in habitat specialists continued over the past decade but have not been as severe as before. Conservation management and the 2019 avalanche have reduced some of the expanding dominant species, but so far, these factors have not restored the diversity of habitat-specialist and Red List species.

4.1 | Limited evidence of changes in the abiotic environment

Mean Ellenberg-type indicator values were relatively stable over time, suggesting a limited change in abiotic environmental factors. Although other studies of alpine grasslands (Evangelista et al., 2016; Gritsch et al., 2016) showed an increase in temperature indicator values, we found such an increase only for certain vegetation

types, namely species-rich grasslands between the 1970s and 2000s and heathlands between the 2000s and 2021. This weak response is consistent with the non-significant increase in temperature revealed by local climate station data (Appendix S1). The observed increase in temperature indicator values may be caused by the decline of specialized subalpine species, which have low temperature values, but their decline may also be caused by factors other than climate warming. At the same time, light indicator values decreased between the 2000s and 2021 in all managed open habitats combined, and specifically in species-rich grasslands. This suggests that light-demanding species are declining while grasslands are becoming denser. It is likely that the changes in grassland plant communities were not primarily caused by abiotic environmental changes such as temperature increase, eutrophication or acidification, although the area was subject to acidification from sulphur deposition in the 1970s–1980s (Rodhe et al., 1995; Hédli et al., 2011) and still receives high deposition of atmospheric nitrogen (Krupová et al., 2018). This is in contrast to some studies that have found impacts of temperature rise on alpine grasslands, especially on high mountain summits (Walther et al., 2005; Pauli et al., 2007; Steinbauer et al., 2018), or suggested impacts of atmospheric nitrogen deposition (Britton et al., 2009; McGovern et al., 2011; Ross et al., 2012). However, it is consistent with other studies that consider land abandonment in subalpine or alpine grasslands previously used for summer grazing as

TABLE 1 Increasing and decreasing species in the entire data set in the periods 1970s–2000s and 2000s–2021, determined by partial distance-based redundancy analysis (db-RDA) with time as the only constraining variable

| 1970s–2000s ($n = 132, p < 0.001$) | | 2000s–2021 ($n = 296, p < 0.001$) | |
|--|--|--|--|
| Increasing | Decreasing | Increasing | Decreasing |
| <i>Hypericum maculatum</i> *** | <i>Crepis mollis</i> (NT)*** | <i>Acer pseudoplatanus</i> *** | <i>Hypericum maculatum</i> *** |
| <i>Aconitum plicatum</i> ** | <i>Festuca supina</i> (VU)*** | <i>Anthoxanthum odoratum</i> agg.*** | <i>Geranium sylvaticum</i> ** |
| <i>Digitalis grandiflora</i> ** | <i>Potentilla erecta</i> *** | <i>Dactylorhiza fuchsii</i> ** | <i>Betula pubescens</i> subsp. <i>carpatica</i> ** |
| <i>Crepis paludosa</i> * | <i>Rhinanthus riphaeus</i> (EN)*** | <i>Festuca supina</i> (VU)*** | <i>Crepis conyzifolia</i> (VU)** |
| <i>Vaccinium myrtillus</i> * | <i>Dianthus superbis</i> (EN)** | <i>Luzula sylvatica</i> *** | <i>Delphinium elatum</i> (EN)** |
| <i>Trollius altissimus</i> (VU)* | <i>Festuca rubra</i> ** | <i>Poa chaixii</i> *** | <i>Calamagrostis arundinacea</i> ** |
| | <i>Crepis conyzifolia</i> (VU)** | <i>Trientalis europaea</i> *** | <i>Hypochaeris uniflora</i> (NT)** |
| | <i>Hieracium prenanthoides</i> (EN)** | <i>Veratrum album</i> subsp. <i>lobelianum</i> *** | <i>Senecio nemorensis</i> agg.** |
| | <i>Hypochaeris uniflora</i> (NT)** | <i>Taraxacum</i> sect. <i>Taraxacum</i> ** | <i>Crepis mollis</i> (NT)** |
| | <i>Polygonatum verticillatum</i> ** | <i>Galium saxatile</i> ** | <i>Digitalis grandiflora</i> ** |
| | <i>Viola lutea</i> subsp. <i>sudetica</i> (EN)** | <i>Paris quadrifolia</i> ** | <i>Juncus filiformis</i> ** |
| | <i>Ranunculus acris</i> ** | <i>Chrysosplenium alternifolium</i> ** | <i>Leontodon hispidus</i> * |
| | <i>Leontodon hispidus</i> ** | <i>Carex nigra</i> ** | <i>Phyteuma orbiculare</i> (EN)* |
| | <i>Ligusticum mutellina</i> (NT)** | <i>Ficaria verna</i> ** | <i>Parnassia palustris</i> (EN)* |
| | <i>Gymnadenia conopsea</i> (EN)** | <i>Lilium martagon</i> ** | <i>Carex echinata</i> * |
| | <i>Potentilla aurea</i> (NT)* | <i>Vaccinium myrtillus</i> * | <i>Ranunculus nemorosus</i> * |
| | <i>Angelica sylvestris</i> * | <i>Alchemilla</i> sp.* | |
| | <i>Ranunculus platanifolius</i> * | <i>Juncus effusus</i> * | |
| | <i>Silene vulgaris</i> * | <i>Primula elatior</i> * | |
| | <i>Primula elatior</i> * | <i>Luzula sudetica</i> * | |
| | <i>Paris quadrifolia</i> * | <i>Carex acuta</i> * | |
| | <i>Campanula barbata</i> (VU)* | <i>Poa trivialis</i> * | |
| | <i>Euphrasia officinalis</i> * | <i>Sorbus aucuparia</i> * | |
| | <i>Phyteuma spicatum</i> * | <i>Vaccinium vitis-idaea</i> * | |
| | <i>Geranium sylvaticum</i> * | <i>Carex vaginata</i> (EN)* | |
| | <i>Asarum europaeum</i> * | <i>Ranunculus acris</i> * | |
| | <i>Aconitum variegatum</i> * | <i>Ajuga reptans</i> * | |
| | <i>Hieracium lachenalii</i> * | <i>Helictochloa planiculmis</i> * | |
| | <i>Thalictrum aquilegifolium</i> * | <i>Fagus sylvatica</i> * | |
| | <i>Ranunculus nemorosus</i> * | <i>Veronica chamaedrys</i> * | |

Note: Numbers of plots (n) and p -values of partial db-RDA are indicated. Species with the same trends in both periods are shaded; species with opposite trends are bold. Red List categories critically endangered (CR), endangered (EN), vulnerable (VU) and near threatened (NT) are indicated in parentheses after species names. Species are listed in order of greatest increase or decrease.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

the main cause of vegetation change (Dullinger et al., 2003; Vittoz et al., 2009; Czortek et al., 2018). By contrast, the decline in moisture and reaction indicator values in springs may indicate the effects of the dry years 2015–2018 (Büntgen et al., 2021) and the spread of acidophilous species from grasslands to drying springs.

4.2 | Vegetation changes in abandoned subalpine grasslands

The main cause of changes in subalpine grasslands in the study area seems to be succession due to the abandonment of summer

grazing by sheep and cattle, accompanied by hay-making, which had already been declining since the second half of the 19th century and finally ceased during World War II (Klimeš & Klimešová, 1991). Zeidler et al. (2014) came to the same conclusion based on the assessment of vegetation changes between the 1950s and 2009 in a small part of our study area outside the glacial cirque. However, post-abandonment changes in vegetation must have occurred in the decades prior to our initial survey in the 1970s. Klimeš and Klimešová (1991) assessed changes in the dominant plant species on the summit plateaus in the study area based on botanical literature published between 1910 and 1987. Despite the inconsistent quality of the data, they observed a significant spread of *Avenella flexuosa*

TABLE 2 Increasing and decreasing species in individual vegetation types in the periods 1970–2000s and 2000s–2021, determined by partial distance-based redundancy analysis (db-RDA) with time as the only constraining variable

| | 1970s–2000s | 2000s–2021 disturbed | 2000s–2021 undisturbed |
|------------------------|--|---|--|
| Birch | n = 20, p = 0.014 | n = 14, p = 0.031 | n = 20, p = 0.067 |
| Increasing | <i>Picea abies</i> * | None | <i>Veratrum album</i> subsp. <i>lobelianum</i> * |
| Decreasing | <i>Solidago virgaurea</i> * | <i>Betula pubescens</i> subsp. <i>carpatica</i> * | <i>Acer pseudoplatanus</i> * |
| | None | | <i>Betula pubescens</i> subsp. <i>carpatica</i> * |
| | | | <i>Rumex arifolius</i> * |
| | | | <i>Calamagrostis arundinacea</i> * |
| | | | <i>Athyrium distentifolium</i> * |
| Heath | n = 14, p = 0.016 | n = 10, p = 0.563 | n = 32, p = 0.007 |
| Increasing | None | None | <i>Vaccinium vitis-idaea</i> * |
| Decreasing | None | None | <i>Trientalis europaea</i> * |
| Species-poor grassland | n = 14, p = 0.063 | n = 8, p = 0.250 | n = 48, p < 0.001 |
| Increasing | <i>Avenella flexuosa</i> * | None | <i>Festuca supina</i> (VU)*** |
| Decreasing | <i>Calamagrostis villosa</i> * | None | <i>Solidago virgaurea</i> * |
| | <i>Festuca supina</i> (VU)* | | |
| Species-rich grassland | n = 44, p < 0.001 | n = 36, p < 0.001 | n = 18, p < 0.398 |
| Increasing | <i>Hypericum maculatum</i> *** <i>Senecio nemorensis</i> agg.* <i>Aconitum plicatum</i> * | <i>Trientalis europaea</i> ** | None |
| Decreasing | <i>Crepis mollis</i> (NT)*** <i>Rhinanthus riphaeus</i> (EN)*** <i>Crepis conyzifolia</i> (VU)** <i>Dianthus superbus</i> (EN)** <i>Viola lutea</i> subsp. <i>sudetica</i> (EN)** <i>Hypochaeris uniflora</i> (NT)** <i>Ranunculus nemorosus</i> ** <i>Festuca rubra</i> ** <i>Gymnadenia conopsea</i> (EN)** <i>Ranunculus acris</i> ** <i>Hieracium prenanthoides</i> (EN)** <i>Potentilla aurea</i> (NT)** <i>Leontodon hispidus</i> * <i>Potentilla erecta</i> * <i>Campanula barbata</i> (VU)* <i>Euphrasia officinalis</i> * <i>Angelica sylvestris</i> * <i>Rumex arifolius</i> * <i>Festuca supina</i> (VU)* | <i>Geranium sylvaticum</i> *** <i>Hypericum maculatum</i> *** <i>Potentilla erecta</i> *** <i>Phleum alpinum</i> (NT)** <i>Trollius altissimus</i> (VU)** <i>Crepis mollis</i> (NT)* <i>Ligusticum mutellina</i> (NT)* <i>Potentilla aurea</i> (NT)* <i>Crepis conyzifolia</i> (VU)* <i>Ranunculus nemorosus</i> * <i>Deschampsia cespitosa</i> * | None |
| Tall-forb | n = 22, p = 0.002 | n = 10, p = 0.063 | n = 44, p < 0.001 |
| Increasing | <i>Hypericum maculatum</i> * <i>Aconitum plicatum</i> * | None | <i>Dactylorhiza fuchsii</i> * |
| Decreasing | <i>Geranium sylvaticum</i> * <i>Primula elatior</i> * | None | <i>Geranium sylvaticum</i> *** <i>Epilobium alpestre</i> (NT)** |

(Continues)

TABLE 2 (Continued)

| | 1970s–2000s | 2000s–2021 disturbed | 2000s–2021 undisturbed |
|--------------|---------------------------------------|----------------------|-------------------------------------|
| Birch | $n = 20, p = 0.014$ | $n = 14, p = 0.031$ | $n = 20, p = 0.067$ |
| | <i>Aconitum variegatum</i> * | | <i>Calamagrostis arundinacea</i> ** |
| | <i>Laserpitium archangelica</i> (EN)* | | <i>Senecio nemorensis</i> agg.* |
| | | | <i>Digitalis grandiflora</i> * |
| | | | <i>Hypericum maculatum</i> * |
| | | | <i>Delphinium elatum</i> (EN)* |
| Spring | $n = 14, p = 0.031$ | $n = 10, p = 0.063$ | $n = 34, p < 0.001$ |
| Increasing | None | None | <i>Dactylorhiza fuchsii</i> *** |
| | | | <i>Carex nigra</i> * |
| | | | <i>Rumex arifolius</i> * |
| Decreasing | None | None | None |

Note: The numbers of plots (n) and p -values of the partial db-RDA are indicated. Red List categories critically endangered (CR), endangered (EN), vulnerable (VU) and near threatened (NT) are indicated in parentheses after species names. Species are listed in order of greatest increase or decrease.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

in grasslands previously dominated mainly by *Nardus stricta*, which is considered an indicator of grazing (Klimešová, 1992; Hejman et al., 2006). In recent decades, *Avenella flexuosa* also increased in other mountain groups of the Sudetes, namely in the Krkonoše Mountains (1,602 m a.s.l.; M. Fabšičová, personal communication 2022) and on Mount Králický Sněžník (1,423 m a.s.l.; Husek, 2020). These authors suggested that the abandonment of grazing was the main cause of vegetation change in the summit grasslands. Consequently, the changes observed during our study period should be considered as a continuation of a long successional process that began much earlier. This succession may have also been influenced by grazing by red deer (*Cervus elaphus*), which are widespread in the study area, and introduced chamois (*Rupicapra rupicapra*), which find suitable habitat on the rocky slopes of the Velká kotlina cirque. However, both species differ from domestic livestock in their grazing preferences and impact on grassland vegetation.

As in some other studies of abandoned mountain pastures (Britton et al., 2009; Mayer et al., 2009; Schwaiger et al., 2022), we found no consistent trend of decline in species richness but noted changes in dominant species. The increase in *Avenella flexuosa* observed by Klimeš and Klimešová (1991) in species-poor grasslands on the summit plateaus continued into the 2000s. Interesting is the pattern of change in *Festuca supina*, another Red List species, a tussocky narrow-leaved grass that co-dominates species-poor grasslands on summit plateaus. It declined between the 1970s and 2000s and was gradually replaced by *Avenella flexuosa*, but it increased again in unmanaged areas between the 2000s and 2021. Its recent increase may be due to the summer droughts of 2015–2018, which resulted in the dieback of some patches of species-poor grasslands. In the subsequent wetter years of 2019–2021, *Festuca* may have regenerated more quickly than *Avenella* and increased its abundance. Similar effects of summer drought on narrow-leaved *Festuca* species have been observed in Central European lowlands (Kröel-Dulay & Garadnai, 2008; Fischer et al., 2020), and negative effects of

drought on the dominant species have also been found in experiments in Central European mountain grasslands (Stanik et al., 2021).

The most obvious vegetation change, however, was the transition from species-rich grasslands to heathlands dominated by *Vaccinium myrtillus* (on mesic, oligotrophic soils) or tall-forb vegetation (on moist, nutrient-rich soils). This change occurred mainly between the 1970s and 2000s, and was also observed in the other mountain groups with summit grasslands in the Sudetes (Krkonoše: M. Fabšičová, personal communication 2022; Králický Sněžník: Husek, 2020). It is interesting to note that Klimeš and Klimešová (1991), in their rough assessment of the change in dominant species on summit plateaus between the 1900s and 1980s, considered *Vaccinium myrtillus* to be a non-increasing, possibly even slightly decreasing species. This suggests that the expansion of *Vaccinium myrtillus* (and, to a lesser extent, an increase in *Vaccinium vitis-idaea*) found in our analysis across the study area may have occurred only since the 1980s. It is unclear whether this change was caused by a delayed response to grazing abandonment or by acid rains in the 1970s–1980s, which may have promoted these acidophilous dwarf shrubs in competition with herbaceous species. Another group of expanding species were some tall, nutrient-demanding plants, which spread mainly in the species-rich grasslands in the Velká kotlina cirque. Klimeš and Klimešová (1991) observed the spread of *Rubus idaeus*, which did not continue in our study period; however, we noticed the spread of *Senecio nemorensis* agg. (mainly *Senecio hercynicus*). Both of these species require nutrient-rich, ungrazed habitats. Their spread may be due in part to grazing abandonment and in part to enrichment by atmospheric nitrogen deposition.

Besides changes in dominant species, the most alarming trend in vegetation change since the 1970s has been the decline of several habitat-specialist species, including threatened species according to the national Red List (Grulich, 2017), such as *Campanula barbata*, *Crepis conyzifolia*, *Dianthus superbus*, *Gymnadenia conopsea*, *Hieracium prenanthoides*, *Rhinanthus rhiphaeus* and *Viola lutea* subsp. *sudetica*. At

the same time, total species richness per plot decreased between the 1970s and 2000s and increased again in the following period. The inconsistent pattern of total species richness could be due to methodological issues: most of the plots in the 2000s were sampled by a single researcher, whereas most of the 2021 plots were sampled by two to three researchers who had the 2000s plot record available. However, the trend of decline in habitat specialists occurred in both periods, although it was less severe between the 2000s and 2021. Declines in rare and habitat-specialist species have been observed in several plot-based studies of vegetation change in mountain and other grasslands (Britton et al., 2009; Prince et al., 2012; Ross et al., 2012; Husek, 2020). Currently, these threatened species are more frequently found at slightly disturbed sites along roads and trails, suggesting that their decline in the study area is primarily due to grassland abandonment and competition from species that have increased in cover. Nevertheless, other causes may also be involved. Acid rains in the 1970s–1980s (Klimeš & Klimešová, 1991) and current atmospheric nutrient deposition may have affected individual plant species, although indicator values for the whole community did not suggest any significant changes. Indeed, Hédli (2004) revealed a dramatic change in beech forest species diversity in a nearby mountain range as a result of acidification. Other possible causes could be pathogens or selective grazing of some rare species by introduced chamois (e.g. *Anemone narcissiflora*, *Campanula barbata*, *Crepis conyzifolia*, *Hypochaeris uniflora* and the endemic *Plantago atrata* subsp. *sudetica*; Klimeš & Klimešová, 1991). Monitoring and maintaining populations of rare plant species, possibly through the restoration of grazing in selected areas, should be among the priorities of nature conservation in the study area.

The area is not significantly affected by plant invasions, which is consistent with the generally low number of alien species in mountain areas of the Czech Republic (Chytrý et al., 2021). However, we have detected an increase in *Galium saxatile*, a species native to northwestern and western central Europe (including the Western Sudetes). It has been spreading in the mountains of the eastern part of the Czech Republic (including the Eastern Sudetes) since the first half of the 20th century, possibly supported by the transport of spruce seedlings for forestry plantations (Štěpánková & Kaplan, 2000).

4.3 | Effects of conservation management

Our results show contradictory effects of conservation management practised in some parts of the area during the past decade. Management reduced the cover of expanding *Vaccinium myrtillus*, which is cut in large areas. It also appears to have slowed or stopped the declines of some habitat-specialist and threatened species in tall-forb and spring vegetation. However, our data show that some habitat-specialist and Red List species of species-rich grasslands continue to decline in managed areas but not in unmanaged areas. This unexpected pattern can be caused by the fact that management was introduced primarily in areas with the greatest successional change

in vegetation, where these species had previously been largely lost. Large areas that have been managed since 2017 have actually become established primarily where *Vaccinium myrtillus* is spreading. Future monitoring is needed to show whether management is restoring species-rich grasslands and populations of their specialized species, as is the case of mountain grasslands in other protected areas (Schwaiger et al., 2022).

4.4 | Effects of avalanches on subalpine birch woodlands

In general, plant species diversity tends to be higher on avalanche tracks than in adjacent undisturbed mountain forests (Rixen et al., 2007). Our study took the unique opportunity to analyse vegetation change in a birch woodland on an avalanche track that had been inactive for several decades due to anthropogenic avalanche suppression and then disturbed by a large avalanche in January 2019. Successional changes were observed in the tree layer, namely an increase in spruce (*Picea abies*) between the 1970s and 2000s, followed by an increase in sycamore maple (*Acer pseudoplatanus*) associated with a decline in birch in undisturbed areas between the 2000s and 2021. These changes indicate that a late-successional forest community was replacing the pioneer birch woodland. However, the composition of the herb layer, species richness and the number of Red List species did not change significantly. After the tree canopy was disturbed by the avalanche, the total species richness increased considerably within two years. All new species that appeared were typical of natural subalpine grasslands, indicating that avalanches periodically increase species richness. This confirms the importance of the natural avalanche regime in maintaining high local plant species diversity, as shown in studies from the Alps (Rixen et al., 2007). The proportion of threatened species did not increase, nor did we observe a significant establishment of alpine plants from higher elevations on the avalanche track. Perhaps these species need more time to become established than just two years between the avalanche fall and our resurvey. However, if avalanches become more frequent in the future, aided by the removal of *Pinus mugo* planted as avalanche barriers, the transport of seeds and propagules of alpine and subalpine plants to lower elevations will likely increase (Erschbamer, 1989; Rixen et al., 2007). In such a case, threatened and alpine species could find suitable habitats for long-term occurrence on avalanche tracks.

5 | CONCLUSIONS

Over the past five decades, subalpine vegetation in the Eastern Sudetes has slowly changed, mainly due to the cessation of grazing, although other factors, such as acidification, may have played a role. The most notable change is the decline of species-rich subalpine grasslands and several threatened plant species typical of

these grasslands. Because palaeoecological and historical studies support the view that most grasslands in the study area are secondary, developed on formerly forested land due to long-term continuity of grazing, conservation plans should focus on management rather than a non-intervention approach. Conservation management applied over the past decade, replacing former grazing with mowing of stands with spreading competitive herbs and dwarf shrubs, is slowing negative trends in vegetation change. However, to date, there is limited evidence that these trends are reversing and that previous species diversity is being restored. It is likely that the time since 2010, when management became systematic, and especially from 2017, when it was introduced over large areas, has been too short for positive changes in biodiversity to appear. Therefore, we recommend continued mowing, possibly reintroducing extensive grazing in some areas and monitoring changes in plant species diversity. We also demonstrate that periodic avalanche releases have a positive effect on the maintenance of the subalpine birch woodland and its plant species richness, suggesting that the removal of avalanche barriers was a good decision for biodiversity in this mountain area. Plant community succession on the avalanche track also requires further monitoring. Our network of permanent vegetation plots provides a solid basis for such monitoring.

AUTHOR CONTRIBUTIONS

M.C. and M.K. conceived the idea. M.C. and J.D. supervised the project. M.K. conducted field sampling in the 2000s, and all authors conducted field sampling in 2021. All authors processed the collected materials and prepared the data sets. K.K., A.K., Š.P., V.S., D.S. and M.C. analysed the data. K.S. prepared the maps, including the online version. A.K., J.R. and K.S. conducted the literature review. M.C., K.K., A.K., Š.P. and V.S. wrote the text and all authors revised the text.

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DATA AVAILABILITY STATEMENT

The data used in this study are stored in the Zenodo repository (<https://doi.org/10.5281/zenodo.7338814>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Time series of climatic data for the study area.

Appendix S2. Synoptic table of species composition of the six vegetation types analysed in this study.

Appendix S3. Changes in species richness and the proportion of threatened species in individual types of open habitats (boxplots).

Appendix S4. PCoA ordination of observations from two periods (1970s–2000s, 2000s–2021) for all vegetation types combined and each vegetation type separately.

Appendix S5. PCoA ordination of observations from the 2000s and 2021 for each vegetation type, with separation of disturbed and undisturbed sites.

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