Article

Resistance of Lichens and Mosses of Regenerated Alpine Communities to Repeated Experimental Trampling in the Belianske Tatras, Northern Slovakia

Veronika Piscová [1],*, Michal Ševčík [2], Andrej Sedlák [2], Juraj Hreško [2], František Petrovič [2] and Terézia Slobodová [2]

[1] Institute of Landscape Ecology of Slovak Academy of Sciences, Akademická 2, 949 10 Nitra, Slovakia
[2] Department of Ecological and Environmental Sciences, Faculty of Natural Sciences and Informatics, Constantine the Philosopher University in Nitra, Trieda A. Hlinku 1, 949 01 Nitra, Slovakia
* Correspondence: veronika.piscova@savba.sk

Abstract: Due to the destruction of alpine ecosystems by extreme human trampling, some alpine areas are closed to tourists. After years of regeneration, a tendency toward reopening these areas for tourism is envisaged. Although numerous studies have documented vegetative responses to trampling disturbance, research that thoroughly examines the trampling impacts on the vegetation at different organizational levels is often limited. Most of the previous studies on the human disturbance of vegetation focused on the impacts on vascular plants, while the impacts on lichens or mosses are less well-documented. To understand how regenerated communities respond to further trampling disturbance, we repeated the experimental research on short-term trampling after 14 years in three high-altitude communities in the Tatras in northern Slovakia. According to Cole and Bayfield's protocol, we evaluated the resistance of communities trampled in 2008 and 2022, with a focus on groups of lichens and mosses and their individual species. This research brings new knowledge regarding the different behaviors of regenerated vegetation, especially lichens and mosses, to trampling disturbance. The results show that human trampling in alpine communities has a large negative impact and, therefore, management plans should discourage off-trail hiking and limit recreational activities in sensitive or reopened alpine areas.

1. Introduction

The intensity of recreation in protected areas has increased significantly, especially increasing the pressure on wildlife ecosystems [1,2]. Recreational and tourism activities are causing disturbances in natural ecosystems worldwide [3–6]. Particularly in high-mountain areas, these human-related activities are increasing the pressure on alpine ecosystems [7–9].

Alpine ecosystems respond very sensitively to disturbance, recovering slowly due to the short growing season and harsh climate combined with poor soil conditions [10–12]. Activities such as hiking or mountain biking affect alpine vegetation [6,8,13,14]. In addition, visitors often stray away from the designated trails and cause trampling damage to the vegetation [15–17]. More specifically, these activities can alter the cover and dominance hierarchies of bryophytes, lichens and vascular plants [18–20]. Human recreational activities cause direct mechanical disturbances in natural ecosystems, with undesirable effects on the vegetation, such as changes in the cover, species composition, diversity and plant height as well as an increased risk of invasive species [21–27]. The trampling process causes direct physical loss or damage to individual species, changing their morphological and physiological characteristics [28,29].

Disturbances caused by tourism have been shown to have stronger effects on plant communities than physiographical factors (i.e., elevation and slope) in vegetation, with disturbed areas having different species compositions distinguished by unique indicator species [30]. Its negative impacts might be propagated to higher levels, such as weakening the ecosystem stability and functioning due to the fact of species loss [19,31].

Trampling disturbance can also cause soil erosion, soil compaction, changes to the soil hydrology, trail widening and exposure of roots, rocks and bedrocks in existing trails [4,32]. Apart from human disturbances, alpine areas are also frequently affected by the grazing activities of the natural fauna [33,34].

Alpine plant communities may be able to tolerate a certain level of tourism, but extreme situations may lead to, for example, a substantial reduction in the plant cover [7]. Under harsh climate conditions with poor soil development, low productivity and a short growing season, the process of vegetation recovery due to the fact of trampling in sensitive regions may be slow [19]. This indicates that the plant communities in more sensitive areas, such as alpine grasslands, may have only a moderate tolerance to human disturbances [24]. Hence, site management can play an important role in counteracting the effects of tourism and human disturbance [35].

Although numerous studies have documented vegetation responses to trampling disturbance, research on trampling impacts at different organizational levels is often limited [36]. Most of the previous studies on vegetation disturbance by trampling have focused on the impacts on communities and vascular plants [14,21,24,37–40], but the impacts of trampling on lichens and bryophytes are less well documented [25,41,42].

In terms of species richness [43,44], biomass [45–47] and, especially, nutrient cycling [46,48–50], lichens and mosses play a role, especially, at higher latitudes and altitudes [43,44]. Lichens and bryophytes are significant parts of ecosystem functioning in areas that are considered to be particularly vulnerable to human disturbance [41]. Knowledge concerning the trampling of lichens and mosses in a recreational alpine area is important. In addition, the regeneration of severely degraded alpine grasslands after trampling will probably take more than a century [12].

In addition to their importance for ecosystem functioning, lichens and bryophytes also interact intensively with vascular plants in communities [51–54]. Vascular plants have a profound influence on cryptogam performance and abundance [55,56] and can affect natural vegetation succession [52,53,57]. Competition with bryophytes and vascular plants is not the only stressful factor for lichens in dry grasslands; however, there are only a few correlations between traits and disturbance factors. Trampling is regarded as the main threat to *Cladonia* lichens [58], but the positive correlation with richly branched podetia suggests that a moderate trampling could be a positive factor in open habitats, e.g., as a major driver of dispersal [47,59,60]. Trampling has the positive effect of producing and dispersing thallus fragments and, therefore, it could be particularly beneficial for lichens with large and fragile thalli [18].

Moreover, climate warming is expected to amplify the aboveground productivity of vascular plants, which could enable faster-growing plant species to outcompete lichens and bryophytes [55,61–65]. Although recent climate change may primarily cause the observed changes in vegetation, the combined effects with nonclimatic factors (e.g., grazing and trampling) are likely important as well [61]. According to [66], multiple aspects of climate change will affect biocrusts (communities of mosses, lichens, cyanobacteria and heterotrophs living at the soil surface) to the same degree as physical disturbance.

Lichens are the dominant life form in approximately 8% of terrestrial ecosystems [67]. They often inhabit niches with extreme environmental conditions. For successful growth in these habitats, they must be adapted to a wide range of temperatures, changing conditions of humidity and lighting [68]. Lichen growth is often expressed as a linear measurement (mm year^{-1}) (i.e., as an increase in the radius of foliose and crustose lichens) or as an increase in the apex length of fruticose species. Foliose species grow 0.5–4 mm year^{-1}, fruticose species grow 1.5–5 mm year^{-1} and crustose species grow 0.5–2 mm year^{-1} [69], but

many lichens do not fall within this range and show a lower insole growth rate [46]. It is convenient to express the growth of lichens as a relative increase in the area or weight compared to the initial area or weight [70]. Their growth rate slows down with an increasing cold intensity [71].

However, lichens also grow in other habitats together with mosses. In these ecosystems and habitats, for example, bogs, springs, rocky habitats and tundra, bryophytes can form a dominant part of the vegetation. Bryophytes play an important role in retaining water and strengthening the soil cover, and they represent important habitats for other organisms (invertebrates, cyanobacteria and algae). Despite their low nutritional value and high content of indigestible cellulose, under certain conditions, they can be a component of the food of herbivores, which consume them together with vascular plants or lichens [72].

The process of how higher plants, lichens and mosses respond to repeated trampling is not well known. The vulnerability of plant communities exposed to trampling is determined by their ability to resist trampling and their ability to regenerate after the impact of trampling ends [73,74]. However, trampling's effects on the species richness and diversity of lichens and bryophytes have seldom been examined [42,75,76], and the impacts on the abundance and cover vary. The abundance of both bryophytes and lichens may be reduced [7,41] or increased [20,42], or there may be a delayed reduction in the lichen and bryophyte abundance [20]. The importance of lichens and mosses in alpine ecosystems is understudied and, therefore, further studies on the effects of trampling are needed [74].

From a lichen regeneration perspective, it can also be problematic in areas damaged by enormous visitation and tourist activities in the past and that have been closed for regeneration but with a tendency to make these areas accessible to tourists again. Such a case occurred in Slovakia, in the Belianske Tatras, which closed to tourists in 1978 due to severe destruction. We therefore investigated the impact of trampling on the vegetation in the vicinity of the trail, which reopened in 1993, in the Belianske Tatras and on the border with the High Tatras, where tourists descend from the Belianske Tatras.

We tested the hypothesis of whether there was resistance of the vegetation, especially lichens and mosses, to trampling changes after 14 years of regeneration. In 2008 and 2022, we established short-term trampling experiments according to the standard procedure of Cole and Bayfield [77]. This method makes it possible to compare the damage to species and communities by a specific amount of trampling [78] as well as the relationship between the intensity of use, damage to the vegetation and the diversity of plant communities. This research brings new knowledge concerning the resistance of the studied communities, E1 and E0 layers (E1—herb layer; E0—layer of mosses and lichens), lichens and mosses and the individual species of the undergrowth to repeated trampling after several years of regeneration. Decreasing or increasing the coverage of the sensitive groups of lichens and bryophytes can be used to monitor the effects of trampling on the vegetation in protected areas.

2. Materials and Methods

2.1. Study Area

This study was conducted in high-altitude alpine communities located within the National Nature Reserve Belianske Tatry and outside on the border with the High Tatras (Figure 1). Due to the damage caused by the enormous number of tourists, the National Nature Reserve has been closed to visitors since 1978, with the exception of one hiking trail that has been opened to tourists since 1993. The High Tatras, as the highest part of the Carpathians, is the most visited part of the Tatras.
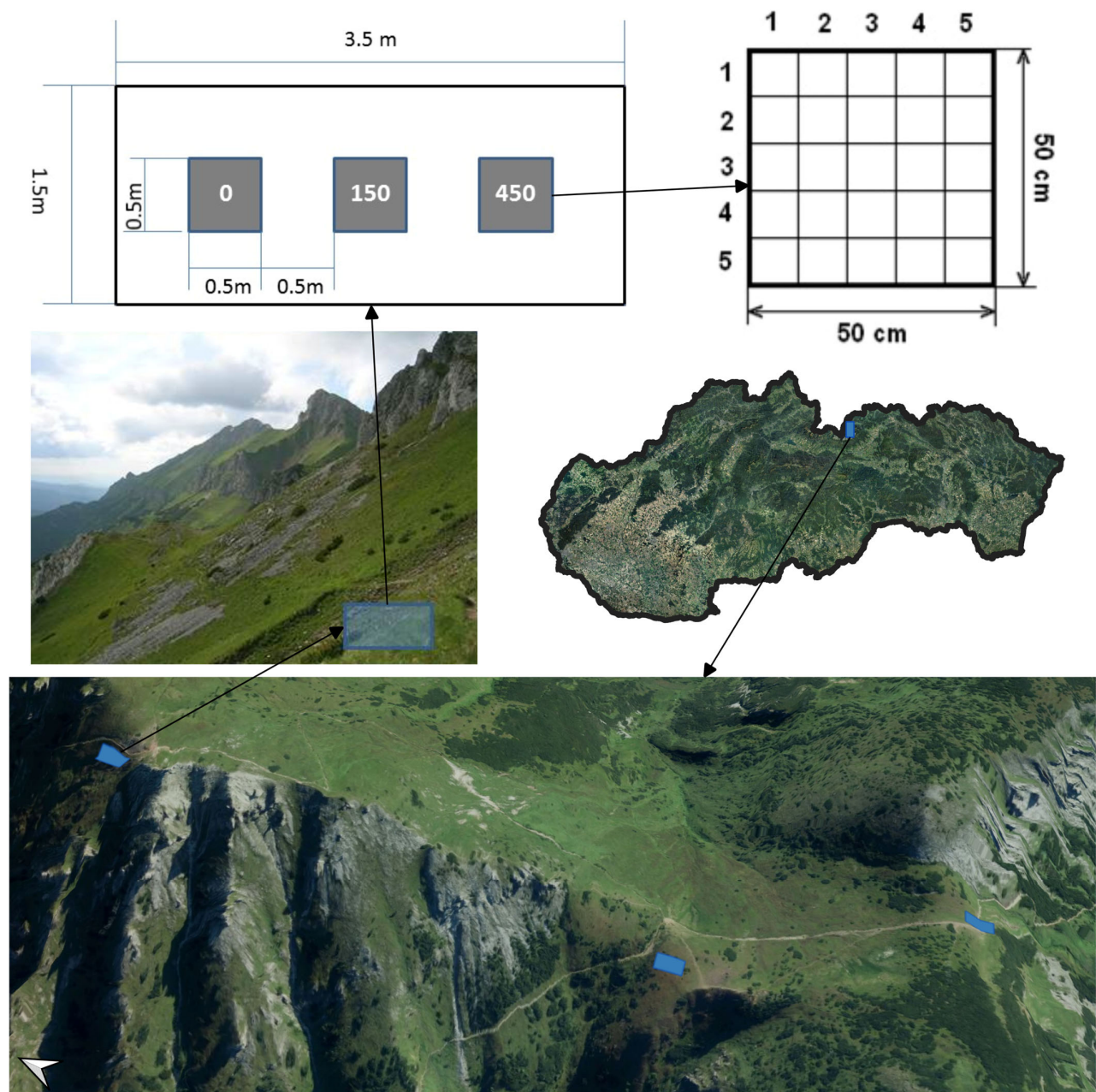
Figure 1. Study area and the experimental design (source: Mapy.cz: © GKU Bratislava, National Forestry Center of the Slovak Republic).

The Belianske Tatras belong to a climatically cold region, where the average annual air temperature is 2–4 °C, the temperature in July (the warmest month) is 10–12 °C and the average temperature in January (the coldest month) is −8–10 °C [79]. The average annual precipitation reaches 900–1200 mm. In summer, the amount of precipitation is variable, from 250 to over 700 mm; in spring, it is similar to summer; and in autumn, it is 125–450 mm [79]. At the alpine level of the Belianske Tatras, the average number of days with snow cover is 200–250 [80]. Trampling experiments were conducted in three alpine plant communities: *Juncetum trifidi* (49°13.751 N; 20°13.179 E), *Junco trifidi-Callunetum vulgaris* (49°13.591 N; 20°13.313 E) and *Seslerietum tatrae* (49°23.471 N; 20°21.829 E).

According to the SHMI data from the Skalnate pleso meteo-station (altitude: 1778 m), during the period under review, from 2008 to 2020, the annual average air temperature

was 3.25 °C and the average annual precipitation was 1547.77 mm (Figure 2). The duration of the compact snow cover in the area of the Kopske sedlo saddle was 174 days for the period 2015 to 2022. The duration of the snow cover was determined using images from the Sentinel satellite.
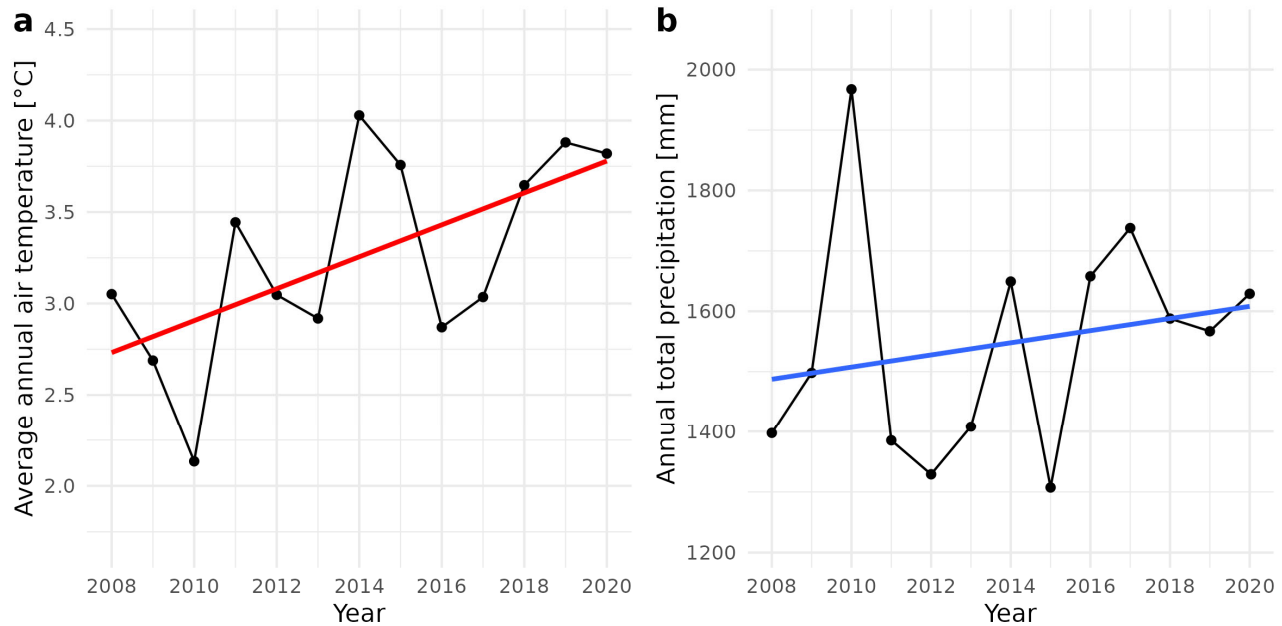
Figure 2. (**a**) Average annual air temperatures (°C); (**b**) annual rainfall totals (mm) of the Skalnate pleso meteo-station at an altitude of 1778 m (years: 2008–2020). The colored lines represent simple linear regression lines (source: SHMI).

The community Juncetum trifidi (Krajina 1933) is a pioneering community with an important soil protection function. It is not one of the endangered phytocenoses, although it contains endemic taxa (Campanula tatrae, Leucanthemopsis tatrae and Soldanella carpatica). The community is dominated by tufted hemicryptophytes (Juncus trifidus, Oreochloa disticha and Festuca supina) and rosette hemicryptophytes (Campanula alpine and Hieracium alpinum). Shrub chamaephytes (Vaccinium vitis-idaea and Vaccinium myrthillus) are nondominant but play an important role in trampling. The undergrowth consists of lichens (Alectoria ochroleuca, Cetraria islandica, Cladonia rangiferina, Cladonia squamosal and Thamnolia vermicularis) and mosses (Pleurozium schreberi, Polytrichastrum alpinum and Niphotrichum canescens). The bedrock consists of limestone, dolomites and shales. The community spreads over rankers on the border of the High and Belianske Tatras. An experimental block was established on the NW site with a slope of 22° at an altitude of 1754 m.

The Junco trifidi-Callunetum vulgaris community (Krajina 1933) Hadač ex Šibík et al. 2007 is rare and is not threatened yet. Its occurrence is at a small scale in the western Carpathians. The community is dominated by shrub chamaephytes (Calluna vulgaris, Vaccinium myrthillus and Vaccinium vitis-idaea) and hemicryptophytes (Avenella flexuosa, Campanula alpine, Hieracium alpinum and Juncus trifidus). The undergrowth consists of lichens (Alectoria ochroleuca, Cetraria islandica, Cladonia pyxidata, Cladonia rangiferina, Cladonia squamosa and Thamnolia vermicularis) and mosses (Pleurozium schreberi and Polytrichastrum alpinum). The bedrock consists of limestone, dolomites and shales. The community spreads over rankers on the border of the High and Belianske Tatras. An experimental block was established on the NE site with a slope of 4° at an altitude of 1778 m.

The community Seslerietum tatrae Domin 1929 corr. Climent et al. 2005 needs a long-lasting high snow cover. It occurs at the altitudinal range 1.900–2.000 m a.s.l. in the Tatras. The community is dominated by hemicryptophytes (Sesleria tatrae, Carex tatrorum, Anthoxanthum alpinum, Bastrsia alpina, Bistorta vivipara, Campanula tatrae, Helianthemum grandiflorum, Homogyne alpina, Pedicularis verticillata, Potentilla aura, Soldanella carpatica and Thymus pulcherrimus). Shrub chamaephytes (Salix silesiaca and Salix reticulata) are nondominant. The undergrowth consists of mosses (Pleurozium schreberi). The bedrock consists of limestone, dolomites and shales. The community spreads over lithosols in the National Nature Reserve Belianske Tatry. An experimental block was established on the SW site with a slope of 39° at an altitude of 1924 m.

2.2. Experimental Design

Following the standard procedure according to Cole and Bayfield [77], one experimental block was established in the uniform vegetation in each plant community. An experimental block consisted of three trampling plots (0.5 m wide and 0.5 m long) separated by 0.5 m wide buffer zones [81]. Each plot was divided into 25 subplots, and each subplot was 0.1 m wide and 0.1 m long. Subplots should be selected by a botanical grid.

One plot was a control plot and received no pedestrian pressure, while the other plots received successive trampling intensities of 150 and 450 passes, i.e., crossing the area with 75 visitors and 225 visitors on the same day. The direction of the trampling should simulate the path, so the trampling should be in two directions [81].

2.3. Trampling Treatment and Timing

The trampling treatment should depend on the average traffic of the trail in sunny and adverse weather. In high mountain landscapes, the size and configuration of the plots should be adapted to the rugged terrain and 2 passes per plot (one-person trampling) [70]. Each pass represents one footprint. Cole and Bayfield [40] recommend using walkers of moderate weight (75 ± 10 kg). One trampling procedure should occur on the same day for all treatments, 4 times during the vegetation season, in June, July, August and September [81].

In the study area, each experimental plot should be assigned one of the three trampling treatments: control (i.e., no trampling), 150 passes and 450 passes, i.e., crossing the area with 75 visitors and 225 visitors on the same day [81]. The trampling process was conducted in June, July, August and September in 2008 and 2022. We used a walker with a weight of 65 kg. The trampling was conducted in both directions.

The parameters measured in each subplot follow:

1. Coverage (%) of the vascular plant species (E1 layer), mosses and lichens (E0 layer; the lichens and mosses were determined by a specialist). Only green photosynthetic material should be included in the cover estimates. It is inappropriate to include the cover of the surviving stems that have been defoliated by the trampling. The cover values were round integral numbers, and if the cover was less than 1%, a value of 0.5% or 0% was used, indicating a complete lack of cover.

   (a) Visual estimates of the top coverage perpendicular to each subplot;
   (b) Visual estimates of the coverage of each vascular plant species, mosses and lichens per subplot.

2. Coverage (%) of the bare ground (i.e., ground not covered by live vegetation). Bare ground can be either mineral or soil.

   (c) Visual estimates of the top coverage of the bare ground perpendicular to each subplot;
   (d) Visual estimates of the coverage of the bare ground per subplot.

3. Coverage (%) of the litter (including the litter of the recently trampled plants).

   (e) Visual estimates of the top coverage of the litter perpendicular to each subplot;

(f)   Visual estimates of the coverage of the litter per subplot.

2.4. Data Analysis

2.4.1. Relative Cover

The relative cover (RC) can be used to characterize the vulnerability of the different vegetation types [67]. Vulnerability is the ability of a vegetation type to resist being altered by trampling; it is also referred to as resistance. RC is based on the sum of the coverage of all species rather than a single estimate of the total vegetation of the vascular plats, mosses and lichens, which allows for more accurate estimates of the trampling response. RC was calculated as follows:

$$RC = \frac{\text{surviving cover on trampled plots}}{\text{initial cover on trampled plots}} \times cf \times 100$$

where cf is the correction factor:

$$cf = \frac{\text{initial cover on control plots}}{\text{surviving cover on control plots}}$$

In the absence of any change in the cover caused by trampling, the RC will be 100%. Therefore, the extent to which the relative cover after the trampling deviates from 100% provides a measure of the damage response to the trampling. We evaluated the resistance in the range: 0–20%, very low; 20–40%, low; 40–60%, medium; 60–80%, high; and 80–100%, very high.

2.4.2. Statistical Processing

To better describe the changes in the relative cover over time, we used linear regression models. The time variable represents the number of days from the first day of the first month (June) of every sampling session. Due to the nonlinear nature of some of the relationships, second-order polynomial regression models were used. To determine which model described the collected data best and most simply (i.e., linear or polynomial), the adjusted coefficient of determination (R^2) was used. All analyses were performed in the R environment [82].

3. Results

The coverage resistance of the high mountain communities (*Juncetum trifidi, Junco trifidi-Callunetum vulgaris* and *Seslerietum tatrae* together) to the trampling changed from medium (RC 55.02%) in 2008 to high (RC 61.49%) in 2022. We can state that the average resistance of the studied regenerated high mountain communities was higher by 6.47%. However, we cannot generalize this statement for all species and life forms. In particular, some lichens and mosses reacted to the trampling with a delayed response. In 2022, the high mountain communities showed, on average, a high resistance to the trampling in July (RC 69.98%), a medium resistance in August (RC 47.57%) and a low resistance in September (RC 34.43%). Some species of lichens and mosses were missing in the regenerated communities in 2022; they became extinct a few years after the trampling in 2008. Some regenerated communities may appear to be more resistant to repeated trampling, but they may lack some species of lichens and mosses or vascular plants. The changed communities appeared to be more resistant to the trampling at the expense of species change.
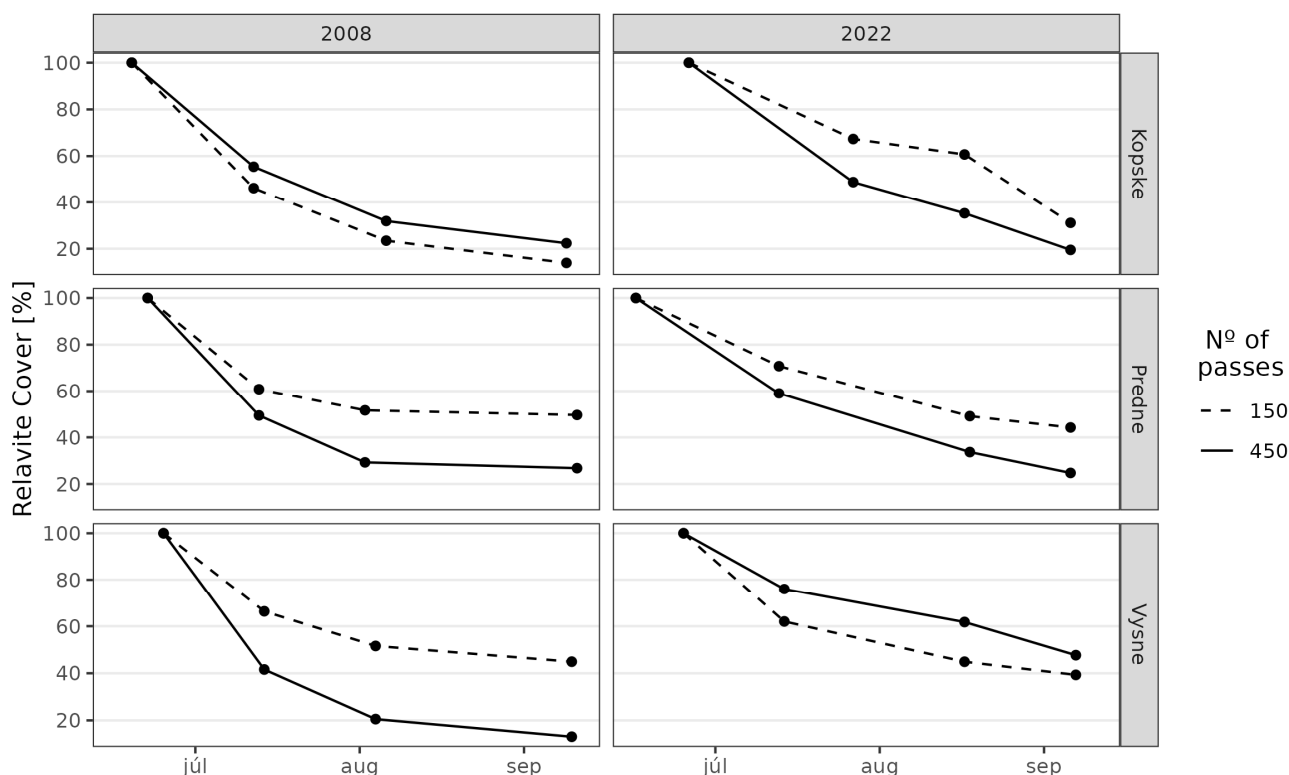
3.1. Juncetum trifidi Community

The *Juncetum trifidi* community is dominated by hemicryptophytes (88%) and woody chamaephytes (12%). The initial vegetation before the trampling in 2008 consisted of higher plants (42% cover), which was followed bryophytes (41% cover) and lichens

(39% cover). In 2008 and 2022, this community responded from a medium to a high resistance to the trampling.

In 2008, the RC values were as follows: 45.90% on the 150 passed plot and 52.42% on the 450 passed plot. In 2022, the situation was different, and the RC values were as follows: 64.79% on the 150 passed plot and 50.89% on the 450 passed plot.

On the 150 passed plot, the community resistance to the trampling was medium in July (RC 46.19%), low in August (RC 23.47%) and very low in September (RC 13.93%) in 2008 (Figure 3). In 2022, the community response to the trampling was different. While the community resistance was medium in July (RC 67.32%) and medium in August (RC 60.69%), it decreased to low in September (RC 31.14%) (Figure 3). On the 450 passed plot, the community resistance to the trampling was medium in July (RC 55.40%), low in August (RC 31.91%) and low in September (RC 22.38%) in 2008 (Figure 3). In 2022, the community response to the trampling was different. The community resistance was high in July (RC 48.78%) and high in August (RC 35.27%), and it decreased to low and very low in September (RC 19.51%) (Figure 3). The average difference in the RC of the communities per month in 2008 and 2022 reached the range of 22–29% (Supplementary Materials File S1).
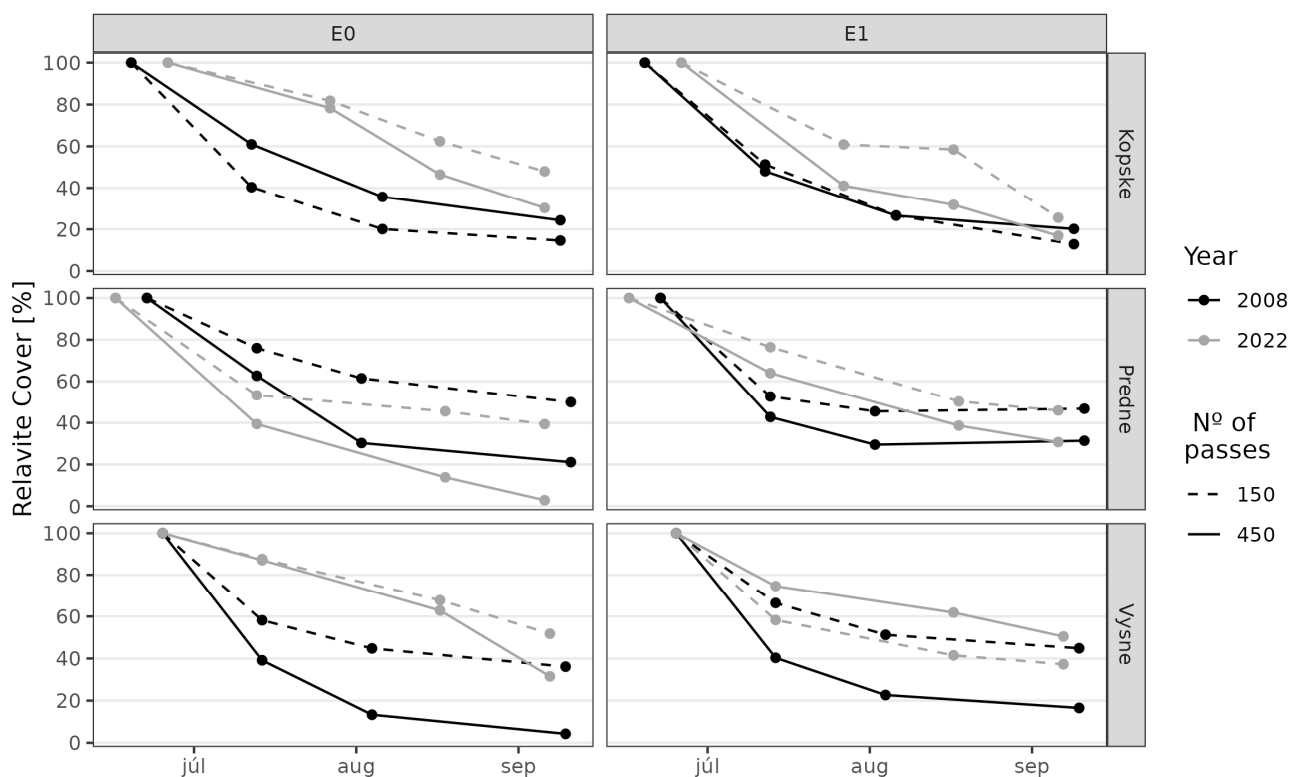

Figure 3. Relative cover of the communities *Juncetum trifidi* (Kopske sedlo), *Junco trifidi-Callunetum vulgaris* (Predne Kopske sedlo) and *Seslerietum tatrae* (Vysne Kopske sedlo) in 2008 and 2022.

During 2008–2022, the E0 layer of the *Juncetum trifidi* on the 150 passed plot community responded similarly to the E1 layer but differently on the 450 passed plot (Figure 4). While in 2008, the E1 layer of the 150 passed plot reached a medium resistance (RC 47.71%), it reached a high resistance (RC 61.23%) in 2022. In addition, while the E0 layer reached a medium resistance (RC 43.76%) in 2008, it reached a high resistance (RC 73.03%) in 2022 as well. In both years, the E1 layer on the 450 passed plot reached a medium resistance (RC 48.70% in 2008; RC 47.44% in 2022). While the E0 layer on the 450 passed plot reached a medium resistance (RC 55.23%) in 2008, it reached a high resistance (RC 63.75%)

in 2022. The average difference in the RC of the E1 and E0 layers per month in 2008 and 2022 reached the range of 17–30% (Supplementary Materials File S2).
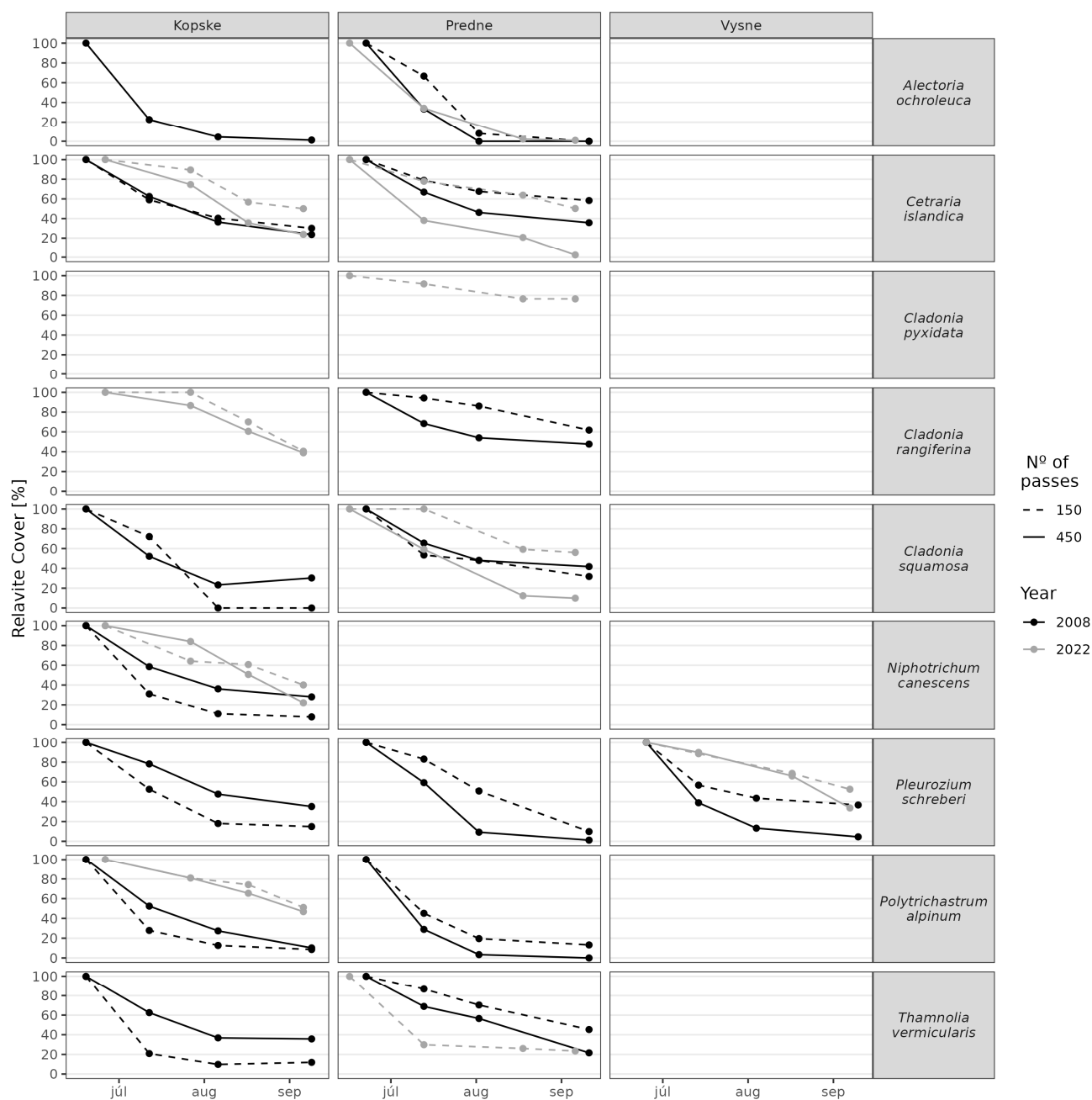

Figure 4. Relative cover of the E1 and E0 layers of the communities *Juncetum trifidi* (Kopske sedlo), *Junco trifidi-Callunetum vulgaris* (Predne Kopske sedlo) and *Seslerietum tatrae* (Vysne Kopske sedlo) in 2008 and 2022.

During 2008–2022, the lichens of the *Juncetum trifidi* community on the 150 passed plot responded similarly to the mosses on both plots (Figure 5). While in 2008, the lichens on the 150 passed plot reached a medium resistance (RC 52.89%), they reached a high resistance (RC 74.28%) in 2022. However, while the mosses of this community on the 150 passed plot reached a low resistance (RC 38.14%) in 2008, they reached a high resistance (RC 71.28%) in 2022. The lichens on the 450 passed plot reached a medium resistance (RC 53.97%) in 2008 and medium resistance, again, in 2022 but stronger (RC 59.48%). While the lichens on the 450 passed plot reached a medium resistance (RC 55.15%) in 2008, they reached a high resistance (RC 70.09%) in 2022. The average difference in the RC of the lichens and mosses per month in 2008 and 2022 reached the range of 16–31% (Supplementary Materials File S3).
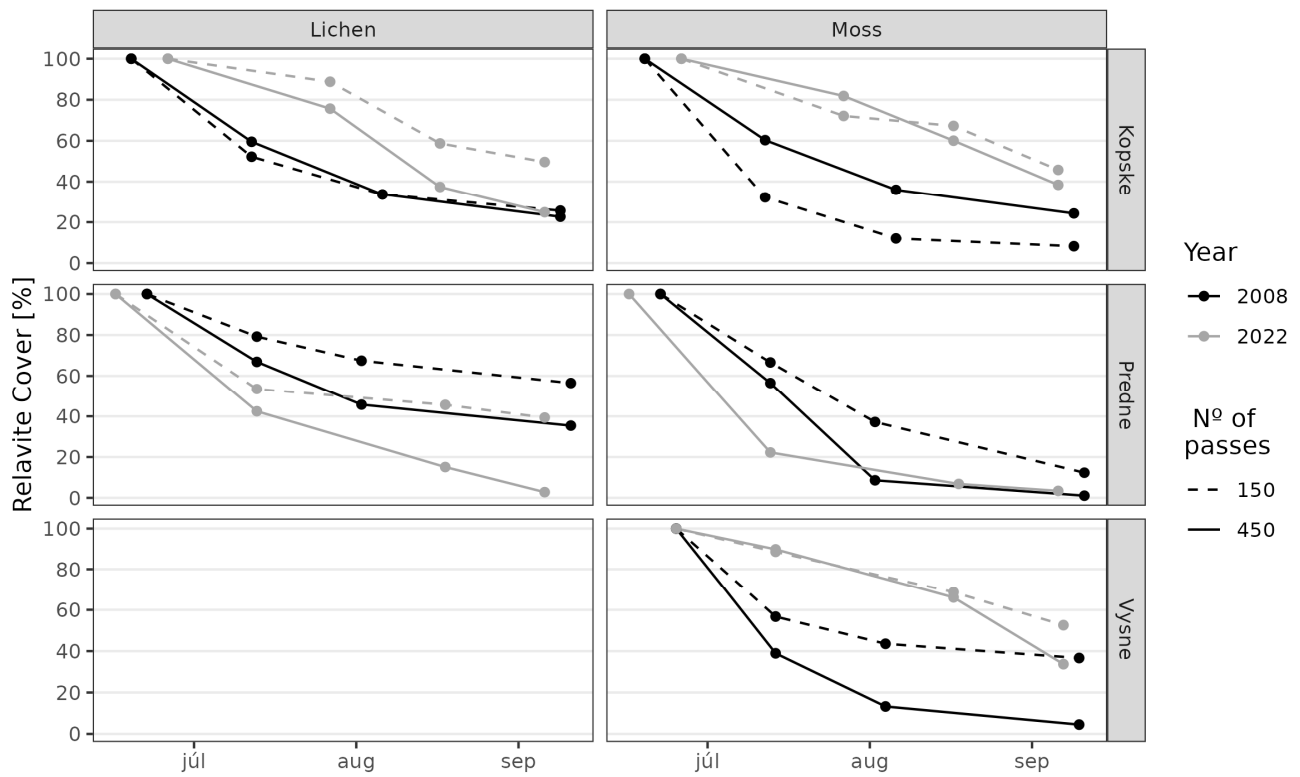
Figure 5. Relative cover of the lichens and mosses of the communities *Juncetum trifidi* (Kopske sedlo), *Junco trifidi-Callunetum vulgaris* (Predne Kopske sedlo) and *Seslerietum tatrae* (Vysne Kopske sedlo) in 2008 and 2022.

Alectoria ochroleuca (Hoffm.) Massal. (a fruticose lichen) was recorded only on the 450 passed plot in 2008 (Figure 6). In 2008, the lichen reached a low resistance (RC 32.07%), but in 2022, it became extinct.

Figure 6. Relative cover of the individual species of lichens and mosses of the communities *Juncetum trifidi* (Kopske sedlo), *Junco trifidi-Callunetum vulgaris* (Predne Kopske sedlo) and *Seslerietum tatrae* (Vysne Kopske sedlo) in 2008 and 2022.

Cetraria islandica (L.) Ach. (a fruticose lichen) was recorded on all of the plots (Figure 6). In 2008, the lichen reached a medium resistance (RC 57.37%), but in 2022, it reached a high resistance (RC 74.07%) on the 150 passed plot. In 2008, the lichen reached a medium resistance (RC 55.65%) and in 2022 a medium resistance, again, but a little stronger (RC 58.50%) on the 450 passed plot (Supplementary Materials File S5). The average difference in the RC of the species per month in 2008 and 2022 was in the range of 16–26% (Table 1).

Table 1. Mean difference (decrease) of the relative cover (RC) of individual species per month in 2008 and 2022.

Area	Trampling	Species	2008 Formula	R^2	Mean Change [1]	2022 Formula	R^2	Mean Change [1]
Kopske	450	*Alectoria ochroleuca*	$96.31 - 3.42x + 0.03x^2$	0.91	32.92			
Kopske	150	*Cetraria islandica*	$98.84 - 1.9x + 0.01x^2$	0.98	23.3	$103.4 - 0.76x$	0.87	16.64
Kopske	450	*Cetraria islandica*	$99.92 - 1.89x + 0.01x^2$	0.99	25.44	$101.99 - 1.12x$	0.95	25.39
Kopske	150	*Cladonia rangiferina*				$100.8 + 0.41x - 0.02x^2$	0.96	19.84
Kopske	450	*Cladonia rangiferina*				$104.94 - 0.86x$	0.92	20.37
Kopske	150	*Cladonia squamosa*	$93.87 - 1.33x$	0.76	33.33			
Kopske	450	*Cladonia squamosa*	$100.32 - 2.63x + 0.02x^2$	0.99	23.23			
Kopske	150	*Pleurozium schreberi*	$100.63 - 2.6x + 0.02x^2$	0.99	28.37			
Kopske	450	*Pleurozium schreberi*	$96.39 - 0.81x$	0.92	21.61			
Kopske	150	*Polytrichastrum alpinum*	$96.32 - 3.14x + 0.03x^2$	0.9	30.48	$101.35 - 0.64x$	0.93	16.3
Kopske	450	*Polytrichastrum alpinum*	$98.85 - 2.2x + 0.01x^2$	0.99	29.94	$101.6 - 0.73x$	0.99	17.73
Kopske	150	*Niphotrichum canescens*	$97.19 - 3.13x + 0.03x^2$	0.94	30.71	$96.7 - 0.79x$	0.92	19.98
Kopske	450	*Niphotrichum canescens*	$99.36 - 2.03x + 0.01x^2$	0.99	24	$106.72 - 1.1x$	0.92	25.98
Kopske	150	*Thamnolia vermicularis*	$95.53 - 3.41x + 0.03x^2$	0.86	29.37			
Kopske	450	*Thamnolia vermicularis*	$100.36 - 2.04x + 0.02x^2$	0.99	21.43			
Predne	150	*Alectoria ochroleuca*	$105.05 - 2.9x + 0.02x^2$	0.85	33.33			
Predne	450	*Alectoria ochroleuca*	$99.42 - 3.72x + 0.03x^2$	0.99	33.33	$99.18 - 2.9x + 0.02x^2$	0.99	33.01
Predne	150	*Cetraria islandica*	$99.66 - 1.1x + 0.01x^2$	0.99	13.88	$97.66 - 0.57x$	0.97	16.59
Predne	450	*Cetraria islandica*	$99.99 - 1.85x + 0.01x^2$	0.99	21.42	$87.32 - 1.09x$	0.84	32.57
Predne	150	*Cladonia pyxidata*				$99.55 - 0.31x$	0.93	7.83
Predne	150	*Cladonia rangiferina*	$102.74 - 0.48x$	0.96	12.75			
Predne	450	*Cladonia rangiferina*	$99.37 - 1.65x + 0.01x^2$	0.99	17.44			
Predne	150	*Cladonia squamosa*	$96.77 - 1.93x + 0.01x^2$	0.84	22.73	$105.83 - 0.63x$	0.82	14.64
Predne	450	*Cladonia squamosa*	$99.58 - 1.86x + 0.01x^2$	0.99	19.39	$94.67 - 1.15x$	0.94	30.04
Predne	150	*Pleurozium schreberi*	$101.88 - 1.15x$	0.98	30.06			
Predne	450	*Pleurozium schreberi*	$103.37 - 2.99x + 0.02x^2$	0.93	32.94			
Predne	150	*Polytrichastrum alpinum*	$99.11 - 2.94x + 0.02x^2$	0.99	28.94			
Predne	450	*Polytrichastrum alpinum*	$97.95 - 3.65x + 0.03x^2$	0.97	33.33			
Predne	150	*Thamnolia vermicularis*	$99.98 - 0.68x$	0.99	18.24	$96.74 - 2.82x + 0.02x^2$	0.84	25.52
Predne	450	*Thamnolia vermicularis*	$94.95 - 0.93x$	0.97	26.15			
Vyšne	150	*Pleurozium schreberi*	$97.69 - 2.2x + 0.02x^2$	0.93	21.11	$100.51 - 0.63x$	0.99	15.81
Vyšne	450	*Pleurozium schreberi*	$97.75 - 3.32x + 0.03x^2$	0.97	31.83	$103.94 - 0.86x$	0.93	22.1

[1] Mean difference (decrease) in the relative cover (RC) per month.

Cladonia rangiferina (L.) F. H. Wigg. (a fruticose, cup lichen lichen) was recorded on all of the plots only in 2022 (Figure 6). The lichen reached a high resistance (RC 77.65%) on the 150 passed plot. It reached a high resistance (RC 71.54%) on the 450 passed plot (Supplementary Materials File S6). In 2022, it became a new species on both the trampled plots in the *Juncetum tridifi* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 19–21% (Table 1).

Cladonia squamosa (Scop.) Hoffm. (a cup lichen) was recorded on all of the plots only in 2008 (Figure 6). The lichen reached a medium resistance (RC 43.03%) on the 150 passed plot. On the 450 passed plot, it reached a medium resistance again but a little stronger (RC 51.45%) (Supplementary Materials File S7). The average difference in the RC of the species per month in 2008 and 2022 reached the range of 23–24% (Table 1).

Thamnolia vermicularis (Swartz) Ach. Ex Schaerer (a fruticose lichen) was recorded on all of the plots only in 2008 (Figure 6). The lichen reached a low resistance (RC 35.63%)

on the 150 passed plot. On the 450 passed plot, it reached a medium resistance (RC 58.74%) (Supplementary Materials File S8). In 2022, it became extinct on both of the trampled plots in the *Juncetum tridifi* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 21–30% (Table 1).

Pleurozium schreberi (Brid.) Mitt. Was recorded only in 2008 (Figure 6). In 2008, the species reached a medium resistance (RC 46.37%) on the 150 passed plot. In 2008, the moss reached a high resistance (RC 65.26%) on the 450 trampled plot (Supplementary Materials File S9). In 2022, it became extinct on both of the trampled plots in the *Juncetum tridifi* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 21–29% (Table 1).

Polytrichastrum alpinum (Hedw.) G.L. Sm. Was recorded on all of the plots in 2008 and 2022 (Figure 6). In 2008, the moss reached a low resistance (RC 37.26%) on the 150 passed plot, but in 2022, it reached a high resistance (RC 76.53%). In 2008, the moss reached a medium resistance (RC 47.49%) on the 450 trampled plot, but in 2022, it reached a high resistance (RC 73.27%) (Supplementary Materials File S10). The average difference in the RC of the species per month in 2008 and 2022 reached the range of 16–31% (Table 1).

Niphotrichum canescens (Hedw.) Bednarek-Ochyra & Ochyra was recorded on all of the plots in 2008 and 2022 (Figure 6). In 2008, the moss reached a medium resistance (RC 37.47%) on the 150 passed plot, but in 2022, it reached a high resistance (RC 66.23%). In 2008, the moss reached a medium resistance (RC 55.66%) on the 450 trampled plot, but in 2022, it reached a high resistance (RC 64.18%) (Supplementary Materials File S11). The average difference in the RC of the species per month in 2008 and 2022 reached the range of 19–26% (Table 1).

3.2. Junco trifidi-Callunetum vulgaris Community

The *Junco trifidi-Callunetum vulgaris* community, which occurs at a small scale, in the Western Carpathians is rare but not yet endangered. This community is dominated by hemicryptophytes (86%) and woody chamaephytes (14%). The initial vegetation before the trampling in 2008 consisted of higher plants (66% cover) followed by lichens (31% cover) and bryophytes (13% cover).

In 2008 and 2022, the community responded from a medium to a high resistance to the trampling. In 2008, the RC values were as follows: 65.52% on the 150 passed plot and 51.37% on the 450 passed plot. In 2022, the situation was very similar, and the RC values were as follows: 66.03% on the 150 passed plot and 54.35% on the 450 passed plot.

In 2008, the resistance of this community decreased with the increase in the trampling intensity. In 2022, the community response to the trampling was different. On the 150 passed plot, the community resistance to the trampling was high in July (RC 60.82%), medium in August (RC 51.63%) and medium in September (RC 49.63%) in 2008 (Figure 3). In 2022, the community response to the trampling was different. The community resistance was high in July (RC 70.76%), medium in August (RC 49.11%), and medium in September (RC 44.23%) (Figure 3). In 2022, the community resistance was high in July (RC 70.76%), medium in August (RC 49.11%) and medium in September (RC 44.23%) (Figure 3). On the 450 passed plot, the community resistance to the trampling was medium in July (RC 49.43%), low in August (RC 29.27%) and low in September (RC 26.78%) in 2008 (Figure 3). In 2022, the community resistance was medium in July (RC 58.99%), low in August (RC 33.68%) and low in September (RC 24.73%) (Figure 3). The average difference in the RC of the communities per month in 2008 and 2022 reached the range of 18–26% (Supplementary Materials File S1).

During 2008–2022, the E0 layer of the *Junco trifidi-Callunetum vulgaris* community responded differently than the E1 layer on the 150 passed plot (Supplementary Materials File S4). While in 2008, the E1 layer of the *Junco trifidi-Callunetum vulgaris* community on the 150 passed plot reached a high resistance (RC 61.23%), it reached a high resistance again in 2022 but a little stronger (RC 68.16%). The E0 layer of the community reached a

high resistance (RC 71.85%) in 2008 but a medium resistance (RC 59.54%) in 2022. We recorded the same situation on the 450 passed plot. While the resistance of the E1 layer increased in July and August and decreased in September at both intensities, the resistance of the E0 layer decreased in all months (Figure 4). On the 450 passed plot, the E1 layer of the community reached a medium resistance (RC 50.91%) in 2008 and a medium resistance again in 2022 but a little stronger (RC 58.34%). The E0 layer of the community reached a medium resistance (RC 53.52%) in 2008 but a low resistance (RC 39.03%) in 2022. The average difference in the RC of the E1 and E0 layers per month in 2008 and 2022 reached the range of 17–33% (Supplementary Materials File S2).

During 2008–2022, the lichens of the *Junco trifidi-Callunetum vulgaris* community responded differently than mosses (Figure 5). On the 150 passed, the lichens of the *Junco trifidi-Callunetum vulgaris* community reached a high resistance (RC 75.79%) in 2008 but a medium resistance (RC 59.64%) in 2022. The mosses of the community reached a medium resistance (RC 54.02%) in 2008, but they were missing in 2022. On the 450 passed plot, the lichens of the community reached a high resistance (RC 62.01%) in 2008 but a medium resistance (RC 40.09%) in 2022. The mosses of the community reached a medium resistance (RC 41.53%) in 2008 and a low resistance (RC 33.11%) in 2022. The average difference in the RC of the lichens and mosses per month in 2008 and 2022 reached the range of 14–33% (Supplementary Materials File S3).

Alectoria ochroleuca (Hoffm.) Massal. (a fruticose lichen) was recorded on the 150 and 450 passed plots in 2008 and on the 450 passed plot in 2022 (Figure 6). On the 150 passed plot, the lichen reached a medium resistance (RC 43.71%) in 2008, but it was missing in 2022 (Supplementary Materials File S4). On the 450 passed plot, the lichen reached a low resistance (RC 33.33%) in 2008 and a low resistance again in 2022 but stronger (RC 34.11%). The average difference in the RC of the species per month in 2008 and 2022 was in the range of 33–34% (Table 1).

Cetraria islandica (L.) Ach. (a fruticose lichen) was recorded on all of the plots in this community (Figure 6). On the 150 passed plot, the lichen reached a high resistance (RC 76.22%) in 2008 and a high resistance again in 2022 but a little weaker (RC 72.99%). On the 450 passed plot, while the lichen reached a high resistance (RC 62.21%) in 2008, it reached a medium resistance (RC 40.27%) in 2022 (Supplementary Materials File S5). The average difference in the RC of the species per month in 2008 and 2022 was in the range of 13–33% (Table 1).

Cladonia pyxidata (L.) Hoffm. (a cup lichen) was recorded only on the 150 passed plot in 2022 (Figure 6). The lichen reached a very high resistance (RC 86.18%) in 2008. In 2022, it became a new species in the *Junco trifidi-Callunetum vulgaris* community. The average difference in the RC of the species per month in 2008 and 2022 reached 7.83% (Table 1).

Cladonia rangiferina (L.) F. H. Wigg. Was recorded on all of the plots only in 2008 (Figure 6). On the 150 passed plot, the lichen reached a very high resistance (RC 85.54%). It reached a high resistance (RC 67.54%) on the 450 passed plot (Supplementary Materials File S6). In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 12–18% (Table 1).

Cladonia squamosa (Scop.) Hoffm. was recorded on all of the plots (Figure 6). On the 150 passed plot, the lichen reached a medium resistance (RC 58.36%) in 2008 and a high resistance (RC 78.84%) in 2022. On the 450 passed plot, the lichen reached a high resistance (RC 63.85%) in 2008 and a medium resistance (RC 45.37%) in 2022 (Supplementary Materials File S7). The average difference in the RC of the species per month in 2008 and 2022 reached the range of 14–31% (Table 1).

Thamnolia vermicularis (Swartz) Ach. ex Schaerer was recorded on all of the plots except for the 450 passed plot in 2022 (Figure 6). On the 150 passed plot, the lichen reached a high resistance (RC 75.59%) in 2008 but a medium resistance (RC 44.81%) in 2022. On the 450 trampled plot, while the lichen reached a high resistance (RC 61.73%) in 2008, it

became extinct in 2022 (Supplementary Materials File S8). The average difference in the RC of the species per month in 2008 and 2022 reached the range of 18–27% (Table 1).

Pleurozium schreberi (Brid.) Mitt. was recorded in 2008 and 2022 (Figure 6). On the 150 passed plot, the species reached a high resistance (RC 60.94%) in 2008. On the 450 trampled plot, the moss reached a medium resistance (RC 42.41%) in 2008 (Supplementary Materials File S9). In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 30–33% (Table 1).

Polytrichastrum alpinum (Hedw.) G.L. Sm. was recorded only in 2008 (Figure 6). On the 150 passed plot, the species reached a medium resistance (RC 44.48%). On the 450 trampled plot, the moss reached a low resistance (RC 33.08%), but it was not recorded in September (Supplementary Materials File S10). In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 28–34% (Table 1).

3.3. Seslerietum tatrae Community

The community *Seslerietum tatrae* occurs in a narrow altitudinal range of 1900–2000 m a.s.l. with long-lasting high snow cover. This community is dominated by hemicryptophytes (67%), woody and herbaceous chamaephytes (26%), annual terophytes (4%) and geophytes (3%). The initial vegetation before the trampling in 2008 consisted of higher plants (86% cover) and bryophytes (23% cover); lichens were missing.

In 2008 and 2022, the *Seslerietum tatrae* community responded from a medium to a high resistance to the trampling. In 2008, the RC values were as follows: 65.72% on the 150 passed plot and 43.80% on the 450 passed plot. In 2022, the situation was different, and the RC values were as follows: 61.56% on the 150 passed plot and 71.36% on the 450 passed plot. On the 150 passed plot, the community resistance to trampling was medium in July (RC 66.36%), medium in August (RC 51.60%) and medium in September (RC 44.91%) in 2008 (Figure 3). In 2022, the community resistance was medium in July (RC 62.03%), medium in August (RC 44.89%) and low in September (RC 39.31%) (Figure 3). On the 450 passed plot, the community resistance to the trampling was medium in July (RC 41.60%), low in August (RC 20.53%) and very low in September (RC 13.05%) in 2022 (Figure 3). In 2022, the community resistance was high in July (RC 75.98%), high in August (RC 61.78%) and medium in September (RC 47.68%) (Figure 3). The average difference in the RC of the communities per month in 2008 and 2022 reached the range of 17–29% (Table 1).

During 2008–2022, the E0 layer of the *Seslerietum tatrae* community responded differently than the E1 layer on the 150 passed plot but similarly on the 450 passed plot (Figure 4). On the 150 passed plot, the E1 layer of the *Seslerietum tatrae* community reached a high resistance (RC 65.63%) in 2008 and a medium resistance (RC 59.27%) in 2022. The E0 layer reached a medium resistance (RC 59.77%) in 2008 but a high resistance (RC 76.78%) in 2022. On the plot trampled by 450 passes, the E1 layer of the community reached a medium resistance (RC 44.88%) in 2008 and a high resistance (RC 71.72%) in 2022. The E0 layer of the community reached a low resistance (RC 39.18%) in 2008 but a high resistance (RC 70.35%) in 2022. The average difference in the RC of the E1 and E0 layers per month in 2008 and 2022 reached the range of 16–32% (Supplementary Materials File S2).

We did not record the presence of lichens in the *Seslerietum tatrae* community. During 2008–2022, the mosses of the community responded to the trampling by increasing their resistance (Figure 5). On the 150 passed plot, the mosses of the community reached a medium resistance (RC 59.23%) in 2008 but a high resistance (RC 77.44%) in 2022. On the 450 passed plot, while the mosses of the community reached a low resistance (RC 39.18%) in 2008, they reached a high resistance (RC 72.39%) in 2022. The average difference in the RC of the lichens and mosses per month in 2008 and 2022 reached the range of 15–32% (Supplementary Materials File S3).

Pleurozium schreberi (Brid.) Mitt. was recorded on all of the plots in 2008 and 2022 (Figure 6). On the 150 passed plot, while the moss reached a medium resistance (RC 59.24%) in 2008, it reached a high resistance (RC 77.44%) in 2022. On the 450 trampled plot, the moss reached a low resistance (RC 39.18%) in 2008 but a high resistance (RC 72.39%) in 2022 (Supplementary Materials File S9). The species became a new species on both of the trampled plots in the *Seslerietum tatrae* community in 2022. The average difference in the RC of the species per month in 2008 and 2022 reached the range of 15–32% (Table 1).

3.4. Community Resistance Scheme

The resistance of both the mosses and lichens may decrease or increase. After a delayed reduction in their abundance, some species of lichens and mosses may become extinct during the regeneration of the destroyed vegetation (Figure 7).

	Juncetum trifidi				*Junco trifidi-Callunetum vulgaris*				*Sesleretum tatrae*			
	2008		2022		2008		2022		2008		2022	
	150	450	150	450	150	450	150	450	150	450	150	450
Community												
E1 layer												
E0 layer												
Mosses												
Lichens												
Alectoria ochroleuca												
Cetraria islandica												
Cladonia pyxidata												
Cladonia rangiferina												
Cladonia squamosa												
Thamnolia vermicularis												
Pleurozium schreberi												
Polytrichastrum alpinum												
Niphotrichum canescens												

Legend:

Color	Meaning	Color	Meaning
High resistance		Missing	
Medium resistance		Extinct	
Low resistance		Very high resistance	

Figure 7. Resistance of the communities and their parts to the trampling in 2008 and 2022.

4. Discussion

Many authors are concerned with the question of how to reconcile increasing tourism with a sustainable environment [83–91]. Therefore, many of them conducted trampling

experiments on different types of vegetation, and studies are being conducted all over the world.

Most of the previous studies on the human disturbance of vegetation, based on the methodology of Cole and Bayfield [77], focused on the impacts on vascular plants [14,21,24,38–40], while the impacts on plant community composition, bryophytes or lichens are less well documented [25,41,42]. The trampling effects on the species richness and diversity of lichens and bryophytes have seldom been examined [42,73,74], and the impacts on the abundance and cover vary. The abundance of both bryophytes and lichens may be reduced [7,41,75] or increased [20,42], or there may be a delayed reduction in the lichen and bryophyte abundance [20].

Studies on the effects of experimental short-term trampling are conducted on different types of vegetation and their regeneration. However, on the Earth, there are not only protected areas under the constant pressure of tourist trampling. Due to the enormous visitation, excessive tourist activities and destruction, some areas have been closed to tourists in the past. Depending on the intensity of the damage, the vegetation, in particular, takes different lengths of time to recover [12,81]. After the regeneration comes the tendency to reopen these closed areas. However, there are questions concerning the management of such protected areas: "when should such areas be reopened?" and "what visitation is allowed for this area?"

In an attempt to find out how the regenerated community of a closed high mountain area would respond to trampling again in the years after its reopening, we repeated the experimental trampling after 14 years in the alpine communities of *Juncetum trifidi*, *Junco trifidi-Callunetum vulgaris* and *Seslerietum tatrae*. The research was conducted in the National Nature Preserve (due to the destruction from the enormous amount of tourism, it has been closed since 1978), in the surroundings of the path that was reopened in 1993, and in its border with the High Tatras, the most visited part of the whole Tatras. The methodology was based on a previous study [62]. Due to the high fragmentation of the high mountain environment and due to the average distance of two steps while walking, the size of the trampled plots was adjusted to 0.5 m × 0.5 m. Therefore, we studied the impact of 150 and 450 passes, i.e., crossing the area with 75 visitors and 225 visitors on the same day.

The hypothesis that the regenerated community reacts differently to trampling was confirmed. The studied communities after regeneration behaved as more resistant to the trampling. In 2008 and 2022, the vegetation responded from a medium to a high resistance to the trampling. The coverage resistance of the studied high mountain communities to the trampling changed from medium (RC 55.02%) in 2008 to high (RC 61.49%) in 2022. We can state that the average resistance of the studied regenerated high mountain communities was higher by 6.47%. While the mean difference in the RC on the 150 passed plot per month was 18.36% in 2008, it reached 20.23% in 2022. The situation on the 450 passed plot was different. While the mean difference in the RC per month was 28.98% in 2008, it reached 17.43% in 2022.

The E1 and E0 layers of the studied communities responded to the trampling differently. In the *Juncetum trifidi* community, the resistance of both of the layers increased for the 150 passed plot. On the 450 passed plot, while the resistance of the E1 layer decreased, the resistance of the E0 layer increased in 2022. In the *Junco trifidi-Callunetum vulgaris* community, the resistance of the E1 layer increased in July and August, and it decreased in September for both of the plots in 2022. The resistance of the E0 layer decreased significantly for both of the plots in 2022. In the *Seslerietum tatrae* community, the resistance of the E1 layer decreased for the 150 passed plot and increased for the 450 passed plot in 2022. The resistance of the E0 layer increased significantly for the 150 passed plot and increased for the 450 passed plot in 2022.

In the *Juncetum trifidi* community, the resistance of the lichens increased for both plots in 2022. Very similarly, the resistance of the mosses also increased but more significantly. In the *Junco trifidi-Callunetum vulgaris* community, the resistance of the lichens decreased

for both of the plots in 2022. However, the resistance of the mosses decreased and then increased for the 450 passed plot in 2022. In the *Seslerietum tatrae* community, the resistance of the mosses increased for both of the plots and significantly for the 450 passed plot in 2022.

However, a community is a dynamic system, and its parts can behave differently. Especially, the individual species of the lichens and mosses responded to the trampling differently. Previous studies have argued that the abundance of both bryophytes and lichens may be reduced [7,41,75] or increased [20,42], or there may be a delayed reduction in the lichen and bryophyte abundance [20]. After a delayed reduction in abundance, the species may become extinct during the regeneration of the destroyed vegetation. The regenerated community appears to be more resistant to trampling at the expense of species change. We assume that the regenerated community will become more resistant again after the delayed response of some lichens and mosses at the expense of species change, mainly loss.

In the *Juncetum trifidi* community, three species of lichens became extinct on some of the trampled plots during the regeneration: *Alectoria ochroleuca*, *Cladonia squamosa* and *Thamnolia vermicularis*. In 2022, one species, *Cladonia rangiferina*, became a new species of this community. *Alectoria ochroleuca* reached a low and a very low resistance in 2008 after being trampled; in 2022, we did not record it. *Alectoria ochroleuca*, which was trampled by 225 visitors in 2008, became extinct during the regeneration. According to [81], species losses occurred after 2014. The statement in [20] was confirmed. *Cetraria islandica* reached a medium resistance in 2008 after being trampled, and it reached a high resistance to trampling by 75 visitors and a medium resistance to trampling by 225 visitors in 2022. The resistance of *Cetraria islandica* gradually decreased with repetitions of the trampling in 2008 and 2022. *Cladonia rangiferina* reached a high resistance in 2022, and it became a new species on both of the trampled plots in the *Juncetum tridifi* community. *Cladonia squamosa* reached a medium resistance to trampling by 75 and 225 visitors in 2008. In 2022, it became extinct on both of the trampled plots in the *Juncetum tridifi* community. *Cladonia squamosa* became extinct during the regeneration. According to [81], species losses occurred after 2014. The statement in [20] was confirmed. *Thamnolia vermicularis* reached a low resistance to trampling by 75 visitors and a medium resistance to trampling by 225 visitors in 2008. In 2022, it became extinct on both of the trampled plots during the regeneration. According to [81], species losses occurred after 2014. The statement in [20] was confirmed

Compared to the *Juncetum trifidi* community, the lichens in the *Junco trifidi-Callunetum vulgaris* community responded to the trampling differently. We expect that lichens are probably more protected by woody chamaephytes, mainly by the heather *Calluna vulgaris*. However, three species of lichens became extinct on some of the trampled plots during the regeneration as well; two of them are *Alectoria ochroleuca* and *Thamnolia vermicularis*. *Cladonia rangiferina* is the third species that became extinct in this community during the regeneration. In 2022, one species, *Cladonia pyxidate*, became a new species of this community. *Alectoria ochroleuca* reached a medium resistance to trampling by 75 visitors, but in 2022, it became extinct. According to [81], species losses occurred after 2014. The statement of [20] was confirmed. After being trampled by 225 visitors, the lichen reached a low resistance in 2008 and a higher resistance within the same level in 2022. *Cetraria islandica* reached a high resistance to trampling by 75 and 225 visitors in 2008. However, in 2022, the species reached a high resistance to trampling by 75 visitors and a medium resistance to trampling by 225 visitors. The resistance of *Cetraria islandica* gradually decreased with the repetitions of the trampling in 2008 and 2022. *Cladonia pyxidata* reached a very high resistance to trampling by 75 visitors in 2008. In 2022, it became a new species in the *Junco trifidi-Callunetum vulgaris* community. *Cladonia rangiferina* reached a very high resistance to trampling by 75 visitors and a high resistance to trampling by 225 visitors in 2008. In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. According to [81], species losses occurred after 2014; therefore, this species became extinct during the regeneration. The statement in [20] was confirmed. *Cladonia*

squamosa reached a medium resistance to trampling by 75 visitors in 2008 and a high resistance in 2022. Its resistance to trampling by 225 visitors was high in 2008 and medium in 2022. The resistance of this species gradually decreased with the repetitions of the trampling in 2008 and 2022. *Thamnolia vermicularis* reached a high resistance to trampling by 75 and 225 visitors in 2008. In 2022, the species reached a medium resistance to trampling by 75 visitors, but it became extinct on the plot trampled by 225 visitors. According to [81], species losses occurred after 2014. The statement in [20] was confirmed.

The mosses behaved differently from the lichens to trampling. Our research confirmed the statement in [20] that there may be a delayed reduction in the abundance of mosses. In the *Juncetum tridifi* community, the species *Pleurozium schreberi* reached a medium resistance to trampling by 75 visitors and a high resistance to trampling by 225 visitors. In 2022, it became extinct on both of the trampled plots. According to [81], species losses occurred after 2014. Therefore, *Pleurozium schreberi* became extinct during the regeneration. The statement in [20] was confirmed. *Polytrichastrum alpinum* reached a low resistance to trampling by 75 visitors in 2008 and a high resistance in 2022. The resistance to trampling by 225 visitors changed from medium in 2008 to high in 2022. The resistance of *Polytrichastrum alpinum* gradually decreased with the repetitions of the trampling in 2008 and 2022. *Niphotrichum canescens* reached a medium resistance to trampling by 75 visitors in 2008 and a high resistance in 2022. The resistance to trampling by 225 visitors changed from high in 2008 to medium in 2022. The resistance of *Niphotrichum canescens* gradually decreased with the repetitions of the trampling in 2008 and 2022.

In the *Junco trifidi-Callunetum vulgaris* community in 2008, the species *Pleurozium schreberi* responded to the trampling very similarly to the *Juncetum trifidi* community. However, the species *Polytrichastrum alpinum* responded differently. *Pleurozium schreberi* reached a high resistance to trampling by 75 visitors and a medium resistance to 225 visitors. In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. According to [81], species losses occurred after 2014. Trampled *Pleurozium schreberi* became extinct during the regeneration. The statement in [20] was confirmed again. *Polytrichastrum alpinum* reached a medium resistance to trampling by 75 visitors and a low resistance to trampling by 225 visitors in 2008. In 2022, it became extinct on both of the trampled plots in the *Junco trifidi-Callunetum vulgaris* community. According to [81], species losses occurred after 2014. *Polytrichastrum alpinum* became extinct during the regeneration. The statement in [20] was confirmed again. While the species *Pleurozium schreberi* became extinct in the *Juncetum trifidi* and *Junco trifidi-Callunetum vulgaris* communities during the regeneration between 2008 and 2022, it reached a high resistance in the *Seslerietum tatrae* community in 2022. However, this species reached a medium resistance to trampling by 75 visitors and a low resistance to trampling by 225 visitors in 2008.

The hypothesis that regenerated communities respond to the repeated trampling differently was confirmed. The statements that the abundance of both bryophytes and lichens may be reduced [7,41,76] or increased [20,42], or there may be a delayed reduction in the lichen and bryophyte abundance [20], was confirmed as well. However, after a delayed reduction in abundance, the species may become extinct during the regeneration of the destroyed vegetation. Delayed responses of lichens to trampling can also be caused by their slow growth [18,47,62,63] as well as the way they spread [46,68,69,71].

However, following this research, many questions regarding the response of lichens and mosses to trampling are offered for discussion. We expected that lichens in the *Junco trifidi-Callunetum vulgaris* community are probably more protected by woody chamaephytes, mainly by the heather *Calluna vulgaris*. While the resistance of *Cetraria islandica* increased in the *Juncetum trifidi* community, it decreased in the *Junco trifidi-Callunetum vulgaris* community. This response is the opposite of our expectation. The fruticose lichens responded to the trampling differently; thus, the biological form probably does not play a major role.

The response of the mosses to the trampling also offers many questions. The communities are certainly affected by climate change, and its influence was captured in the results thanks to a formula [78] and the repetitions of the trampling during the growing season. The species *Pleurozium schreberi* became extinct in both of the *Juncetum trifidi* and *Junco trifidi-Callunetum vulgaris* communities. Therefore, woody chamaephytes did not protect the undergrowth sufficiently. Compared to the *Juncetum trifidi* community, the species *Polytrichastrum alpinum* became extinct in the *Junco trifidi-Callunetum vulgaris* community. Probably, the pressure of the compressed woody chamaephytes on the lichens and mosses affected its resistance to the trampling more intensively. The species *Pleurozium schreberi* became extinct in both of these communities in 2022, but its resistance increased in the *Seslerietum tatrae* community. The experimental blocks were established on the site with a slope of 22° in the *Juncetum trifidi* community, 4° in the *Junco trifidi-Callunetum vulgaris* community and 39° in the *Seslerietum tatrae* community. The slope of the *Seslerietum tatrae* community was the steepest. Does the slope of a site play any role in trampling? Or is *Pleurozium schreberi* protected by the dominant hemicryptophytes (*Sesleria tatrae* and *Carex tatrorum*)? In addition, lichens are often presented as an association of two symbionts, but because they have evolved several times [92,93], few generalizations are applicable to all. Moreover, lichens are marked by slow growth rates and, thus, natural succession [55] and might show a delayed response to changing environmental conditions.

This research confirms the need to expand the study of lichens and mosses and to monitor trampled, attacked and destroyed high mountain communities over time. This study claims that some lichens and mosses respond to trampling with a delayed reduction in their abundance or a delayed species loss. Now, we understand that the appropriate time to reopen a closed high mountain area and the intensity of visitation are, for individual communities, different. Nature conservation managers should therefore pay particular attention to high-altitude communities with a rich diversity of lichens and mosses. Given the role of lichens and bryophytes in alpine ecosystems, further studies on the effects of trampling are needed.

5. Conclusions

Experimental trampling was conducted in three high mountain communities of *Juncetum trifidi*, *Junco trifidi-Callunetum vulgaris* and *Seslerietum tatrae* in 2008 and 2022. Trampling has a destructive effect on some lichen and moss species. The abundance of both lichens and mosses may be reduced [7,41] or increased [20,42], or there may be a delayed reduction in the lichen and bryophyte abundance [20]. The species of lichens and mosses in the regenerated high mountain communities responded differently to the trampling in 2022. After a delayed reduction in abundance, some species of lichens and mosses became extinct during the regeneration in 2008–2022.

In the *Juncetum trifidi* community, three lichen species became extinct, and one became a new species during the regeneration. The fruticose lichen *Alectoria ochroleuca* (Hoffm.) Massal. was already extinct in 2022. Another fruticose lichen, *Cetraria islandica* (L.) Ach. (a fruticose lichen), responded in the *Juncetum trifidi* community to both intensities of the trampling, with a stronger resistance in 2022. The species *Cladonia rangiferina* (L.) F. H. Wigg. (a fruticose, cup lichen) became a new species on both of the trampled plots in the *Juncetum tridifi* community in 2022. The cup lichen *Cladonia squamosa* (Scop.) Hoffm. and the fruticose lichen *Thamnolia vermicularis* (Swartz) Ach. ex Schaerer became extinct in 2022.

In the *Junco tridifi-Callunetum vulgaris* community, three lichen species became extinct and one became a new species during the regeneration. The fruticose lichen *Alectoria ochroleuca* (Hoffm.) Massal. survived being trampled in 2022, but only with a very low resistance (0.97%). The resistance of the fruticose lichen *Cetraria islandica* (L.) Ach. to the trampling decreased in 2022. The cup lichen *Cladonia pyxidata* (L.) Hoffm. became a new species on both of the trampled plots in 2022. *Cladonia rangiferina* (L.) F. H. Wigg., a fruticose cup lichen, became extinct in 2022. The resistance of the cup lichen *Cladonia squamosa*

(Scop.) Hoffm. increased on the 150 passed plot and decreased on the 450 passed plot in 2022. The fruticose lichen *Thamnolia vermicularis* (Swartz) Ach. ex Schaerer on the 450 passed plot was already extinct in 2022. On the 150 passed plot, its resistance decreased in 2022.

Lichens were missing in the *Seslerietum tatrae* community.

Mosses, similar to lichens, responded differently to the trampling in 2022. In the *Juncetum tridifi* community in 2022, the species *Pleurozium schreberi* (Brid.) Mitt. became extinct on both of the trampled plots. The resistance of the species *Polytrichastrum alpinum* (Hedw.) G.L. Sm. increased on the 150 and 450 passed plots in 2022. The species *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra behaved as tolerant of the trampling in the *Juncetum trifidi* community. The resistance of this species increased on both of the passed plots in 2022.

In the *Junco trifidi-Callunetum vulgaris* community, the resistance of *Pleurozium schreberi* (Brid.) Mitt. increased on the 150 passed plot and decreased on the 450 passed plot in 2022. The species *Polytrichastrum alpinum* (Hedw.) G.L. Sm. became extinct in 2022.

In the *Seslerietum tatrae* community, the resistance of *Pleurozium schreberi* (Brid.) Mitt. increased in 2022.

This study offers more questions for discussion. We expected that lichens and mosses would be protected by woody chamaephytes or by the dominant hemicryptophytes. However, the answer is not clear. Probably, trampled woody chamaephytes can disturb lichens and mosses and decrease their resistance. Moreover, hemicryptophytes such as *Sesleria tatrae* can probably protect mosses during the trampling process. We expected that the biological forms of lichens play an important role in the trampling process. The responses of the individual species of lichens did not confirm this idea. The research on lichens and mosses in relation to trampling is only in the beginning stage. Considering the importance of lichens and mosses in alpine ecosystems, more studies on the effects of trampling are very necessary.

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