

Resistance of plant life forms of native and regenerated alpine plant communities to experimental trampling

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Trampling of vegetation as a result of recreation can adversely affect natural habitats, leading to loss of vegetation and degradation of plant communities. Many studies indicated that intrinsic properties of plant communities appear to be the most important factors determining the response of vegetation to trampling disturbance. Specifically, the dominant life-form of a plant community accounts for more variation in the resistance of communities to trampling than the intensity of the trampling experienced, suggesting that simple assessments based on this trait could guide decisions on access to natural sites. We verify these claims in the Belianske Tatry National Nature Reserve in Slovakia, which has been closed since 1978 due to destruction by mass tourism, with the exception of one trail made accessible since 1993. In researching the resistance of communities according to dominant life forms we adjusted the number of passes according to the minimum (75 tourists) and maximum (225 tourists) daily visitation during the tourist season. The studied communities occur in close proximity to the trails on the saddles through which the open trail passes. Available evidence from our studies suggests that vegetation dominated by hemicryptophytes is more resistant to trampling and recovers from trampling to a greater extent than vegetation dominated by other life forms. Therefore, we selected three alpine communities dominated by hemicryptophytes. In the *Juncetum trifidi* community, they almost completely dominate, they are mainly composed of grasses. Although they dominate the *Juncetum trifidi-Callunetum vulgaris* community, the species, *Calluna vulgaris* has been added to the woody chamaephytes, and thus the woody *Chamaephytes* achieve a higher cover than in the *Juncetum trifidi* community. Although in the community *Seslerietum tatrae biscutelletosum laevigatae* hemicryptophytes dominate, it consists of several plant life forms and its grasses reach greater heights than in previous communities. We found that it is not possible to estimate the resilience of communities to trampling by dominant life forms. Life forms within one community react very similarly, but this statement cannot be generalized globally for all communities. At the same time, we found that if we damaged the native community, which subsequently regenerates, the life forms of the community behave differently when damaged repeatedly. More detailed research is needed worldwide, which would point out patterns of behaviour of alpine plant vegetation to trampling.

Keywords: experimental trampling; plant life form; alpine vegetation; Belianske Tatras Mts.; Tatra National Park; Tatra Biosphere Reserve.

Introduction

In last decades, recreational intensity in protected areas has increased considerably (Buckley, 2000). Especially, increased use of alpine natural and wilderness mountains for nature, eco- and adventure tourism and recreation has been identified as a worldwide trend (Pickering & Hill, 2007; Memoli et al., 2019). However, alpine ecosystems are generally considered to be sensitive and fragile to disturbance such as trampling and slow to recover, due to short growing seasons and the harsh climate, in combination with poor soil conditions (Körner, 2003).

The alpine landscape represents a unique biogeographical unit of the Earth. It occupies 4 million km², which represents almost 3% of the Earth's land surface (Körner, 2003). Alpine ecosystems support high diversity of terrestrial flora and fauna species. These communities provide essential ecosystem functions and services (Wang et al., 2015). They are home to highly diverse and endemic flora and fauna that play essential roles in sequestering atmospheric carbon dioxide, facilitating water storage and purification, and provide irreplaceable ecosystem services that sustain human society (Ram et al., 1989; Dhar, 2002; Price, 2004).

The ecological importance and economic potential of this unique type of ecosystem (Li et al., 2023) is being disrupted by recreational activities. Human recreational activities such as walking, hiking, and jogging cause direct mechanical disturbances in natural ecosystems with undesirable effects on vegetation, such as changes in cover, species composition, diversity, plant height and increased risk of invasive species (Pickering & Growcock, 2009; Crisfield et al., 2012; Barros et al., 2013). Trampling distur-

bance affects the morphological and physiological features of individual species by causing direct physical loss or damage to them (Cole, 1995a). It often leads to non-renewable changes in vegetation cover and species richness (Xu et al., 2013), they might be propagated to higher levels, such as weakening ecosystem stability and functioning due to species loss (Hill & Pickering, 2006; Jägerbrand & Alatalo, 2015).

Because of the uniqueness of alpine ecosystems, many scientists have sought a way to determine the resistance of alpine landscapes to trampling. Earlier short-term studies have focused on the effects of walkers on vegetation and soils (Cole, 2004; Roovers et al., 2004). These studies have found that plant morphology, particularly lifeform and height, explains much of the variation in resistance and resilience of plant communities to trampling (Pickering & Growcock, 2009; Crisfield et al., 2012). Trampling reduces the cover, height, and species density of ground vegetation (Liddle, 1975a; Jägerbrand & Alatalo, 2015). Several studies have shown that there is a delay between trampling impact and vegetation decline (Forbes et al., 2004; Pertierra et al., 2013).

The relevance of trampling studies for conservation managers and practitioners depends on the nature of the managed site, the plant communities contained within, and the type of access in use or being considered (Burden & Randerson, 1972; Cole, 1987). Authors studying trampling, in an effort to ascertain the information needed by conservation managers, have divided community responses to trampling into various categories and series with the intention of producing indicators or indices representing the responses of plant communities (Leung & Marion, 2000). The responses of vegetation to trampling have been reported to be affected by

trampling intensity (Cole, 1987; Cole, 1995a), frequency (Cole & Monz, 2002), distribution (Gallet et al., 2004), season (Gallet & Rozé, 2002), weather (Gallet & Roze, 2001), habitat (Liddle, 1975b), species (Gallet et al., 2004), Raunkiaer life-form (perennating bud position) and growth-form (Cole, 1995b), and soil type (Talbot et al., 2003). Most previous studies of human disturbance of vegetation have focused on the impacts on vascular plants (Bernhardt-Römermann et al., 2011; Pescott & Stewart, 2014), while the impacts on plant community composition, bryophytes or lichens are less well documented (Crisfield et al., 2012; Pertierra et al., 2013).

More studies indicated a significant heterogeneity in the impact of trampling on vegetation recovery. This was related to resistance and recovery time, and the interactions of these variables with Raunkiaer life-form, but was not strongly dependent on the intensity of the trampling experienced (Pescott & Stewart, 2014). The available evidence suggests that vegetation dominated by hemicryptophytes and geophytes recovers from trampling to a greater extent than vegetation dominated by other life-forms. Variation in effect within the chamaephyte, hemicryptophyte and geophyte life-form sub-groups was also explained by the initial resistance of vegetation to trampling, but not by trampling intensity (Pescott & Stewart, 2014). Intrinsic properties of plant communities appear to be the most important factors determining the response of vegetation to trampling disturbance. Specifically, the dominant Raunkiaer life-form of a plant community accounts for more variation in the resilience of communities to trampling than the intensity of the trampling experienced, suggesting that simple assessments based on this trait could guide decisions concerning sustainable access to natural areas.

Resistance, the intrinsic capacity of vegetation to withstand the direct effect of trampling (Liddle, 1975b), and resilience, the intrinsic capacity of vegetation to recover from trampling (Kuss & Hall, 1991), are most often used as indicators of impact. The response reported most frequently is vegetation cover, which can be used to quantify the vulnerability of vegetation on types using measures of resistance and resilience (Cole & Bayfield, 1993). Primary studies often present data on vegetation cover as 'Relative Vegetation Cover'; this is the cover on a trampled plot relative to its initial cover, adjusted for changes in cover on control plots during an experiment (Cole & Bayfield, 1993).

In Slovakia, the alpine landscape occupies 320 km², which represents 0.7% of the country's territory (National Biodiversity Strategy of Slovakia, 1997). The island character of the high mountains, their height and substratum ruggedness created suitable conditions for the creation of a varied mosaic of vegetation types with a number of naturally rare, relict and endemic plants. Especially the limestone mountains, Belianske Tatras Mts. and Červené vrchy Mts., the highest limestone mountains in Slovakia, are characterized by sensitive ecosystems with rare flora and fauna of endemic species and glacial relicts, with a diverse mosaic of unique forms of relief, soil cover and alpine karst.

As a part of the Tatra Mts., Belianske Tatras belongs to the Tatra National Park, which was established in 1949 and the Tatra Biosphere Reserve, established in 1993. Since 1991, the Belianske Tatras has been the under strict protection of the National Nature Reserve Belianske Tatry with the highest degree of protection. These mountains have been closed since 1978 to public access due to excessive visitors and the devastation of the rare natural ecosystems. The mountain massif of the Belianske Tatras is composed of limestones, dolomites, and shales with a clear karst topography, which is fundamentally different from the mostly granite hills of the High Tatras (the neighbouring part of the Tatras). Due to the fact that the high-altitude relief of the high mountains in the Belianske Tatras is fragmented and communities often cover small areas, they become even more threatened by excessive trampling.

Many studies indicated that intrinsic properties of plant communities appear to be the most important factors determining the response of vegetation to trampling disturbance (Pescott & Stewart, 2014). Specifically, the dominant life-form of a plant community accounts for more variation in the resistance of communities to trampling than the intensity of the trampling experienced, suggesting that simple assessments based on this trait should be used in decisions about public access. In this study, we verify these claims in the Belianske Tatry National Nature Reserve in Slovakia. We selected three alpine communities dominated by hemicryptophytes:

(1) the *Juncetum trifidi* community in the Kopské sedlo saddleback, (2) the *Junco trifidi-Callunetum vulgaris* community in the Predné Kopské sedlo saddleback, and (3) the *Seslerietum tatrae biscutellotosum laevigatae* community in the Vyšné Kopské sedlo. For evaluation of the resistance of these communities, we based our work on the standard protocol of Cole & Bayfield (1993). Due to the fragmentation of the territory, we modify the design of the areas for fragmented high mountain environments and small-area communities. Since the trail is accessible to tourists from 15th June to 1st November, we prefer repeated trampling during the growing season over design replications and one-time trampling as per the protocol. The communities were trampled in June, July, August and September, in 2008 as native and in 2022 as regenerated communities. Life forms were determined according to the study of Jurko (1990), who assigned life forms to specific alpine species of Slovakia. These life forms correlate with Raunkiaer life forms (Raunkiaer, 1934).

We found that although the species of one life form in one plant community react to trampling in a similar way, their reaction to different intensities of trampling cannot be generalized for all communities. At the same time, life forms react to trampling differently in the same native, later regenerated community. The resistance of life forms to smaller or larger intensities of trampling cannot be generalized. At the same time, reactions to the trampling of dominant life forms in the community also differ.

Recreational pressure can cause many problems for managers of nature reserves, countryside and wilderness (Leung & Marion, 2000). If the recreational use of natural habitats is to be in balance with the preservation of the natural value of the site, effective management is essential (Pescott & Stewart, 2014). In this context, managers of protected areas and researchers in Slovakia should identify the need for increased knowledge of the impact of recreational activities on biodiversity as one of the environmental issues of most importance to policy. Especially when considering the reopening of areas that have been severely damaged by mass tourism, such as the Belianske Tatry National Nature Reserve, it is necessary to know other possible consequences of recreational tourism in the country and to set limits for this activity.

Materials and methods

Study area. This study was conducted in alpine plant communities in the Tatras, in the northern part of Slovakia. The Tatras, as the highest part of the Carpathians, are the most visited mountains in Slovakia. The Tatra Mts. fall under the territorial protection of the Tatra National Park (established in 1949) and the Tatra Biosphere Reserve (established in 1993). The main objective of the national park/biosphere reserve is to protect the alpine character of the highest range in the Carpathian Mountain chain.

The study area (Fig. 1) is located within the National Nature Reserve Belianske Tatry. The National Nature Reserve (Fig. 2) has been closed to visitors since 1978, with the exception of one hiking trail that has been opened to tourists since 1993. The experimental research took place in the vicinity of the saddles trail reopened in 1993 (Fig. 3), which connects the Belianske Tatras with the High Tatras:

(1) The Kopské sedlo saddleback with the *Juncetum trifidi* (Krajina, 1933) community – the bedrock consists of limestone, dolomites and shales. An experimental block was established on the NW site with a slope of 22° at an altitude of 1,754 m ASL,

(2) The Predné Kopské sedlo saddleback with the *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al. 2007 community – the bedrock consists of limestone, dolomites and shales. An experimental block was established on the NE site with a slope of 4° at an altitude of 1,778 m ASL,

(3) The vyšné Kopské sedlo saddleback with the *Seslerietum tatrae biscutellotosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community – the community is spread 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 1,924 m ASL.

The northeastern part of the Tatras, including the Belianske Tatras, is included in a cold climate region with three subregions – moderately cool subregion, where the average temperature in July is from 12–16 °C, cool mountainous subregion with an average July temperature from 10 to 12 °C and a cold mountainous subregion with an average temperature in

July of less than 10 °C. The highest areas have an average temperature in January of –8 to 0 °C (Štátný et al., 2002). The average annual precipitation totals are in the range of 900–1200 mm, and the individual subregions

have a very humid climate. Especially in the summer season, we confirmed significantly uneven rainfall, when more than 40 mm/hour fell during the supercell storm in June 2016.

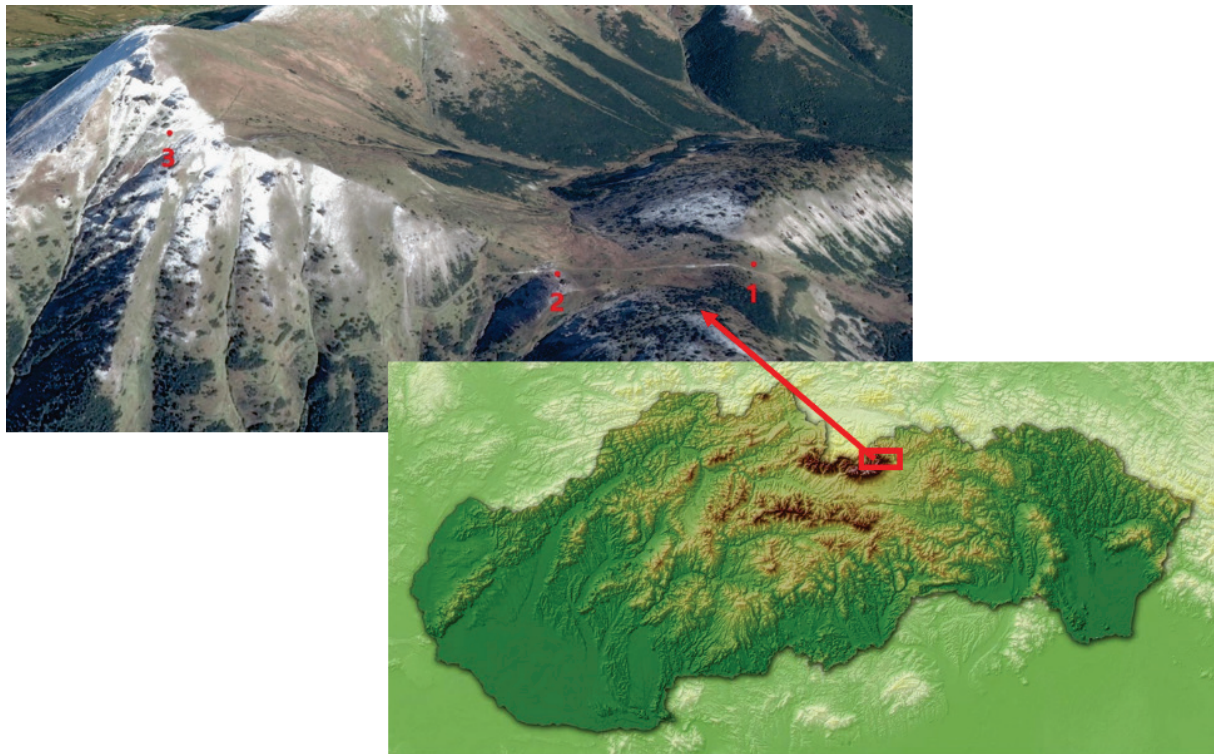


Fig. 1. Study area in the National Nature Reserve Belianske Tatry (www.mapy.cz): 1 – saddleback Kopské sedlo (1,750 m ASL), study block at 1,752 m ASL, *Juncetum trifidi* Krajina 1933 community; 2 – saddleback Predné Kopské sedlo (1,778 m ASL), study block at 1,778 m ASL, *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community; 3 – saddleback Vyšné Kopské sedlo (1,933 m ASL), study block at 1,924 m ASL, *Seslerietum tatrae biscutellatosum laevigatae* Kliment et al., 2005 community



Fig. 2. The National Nature Reserve has been the under strict protection of the National Nature Reserve Belianske Tatry with the highest degree of protection since 1991: it has been closed to visitors since 1978, with the exception of one hiking trail that has been opened to tourists since 1993; these mountains have been closed due to excessive visitor pressure and the devastation of the rare natural ecosystems since 1978; the mountain massif of the Belianske Tatras is composed of limestones, dolomites, and shales with a clear karst topography, which is fundamentally different from the mostly granite hills of the High Tatras (the neighbouring part of the Tatras)



Fig. 3. Part of the reopened trail between the Kopské sedlo saddleback (1,750 m ASL) and the Vyšné Kopské sedlo saddleback (date: 23.6.2010); the territory of the Belianske Tatras National Nature Reserve has been closed to tourists since 1978 due to destruction by mass tourism

During the growing season, the amount of precipitation is variable, from 250 to more than 700 mm per month; in spring it is similar to summer; and in autumn it is 125–450 mm (SHMI, 2015). According to (SHMI, 2015), there are 80 to 100 days with snowfall in the studied area. In the area of the alpine belt of the Belianske Tatras, the average number of days with snow cover is 200–250 (Šťastný et al., 2002). According to the Sentinel II satellite images, the duration of the compact snow cover in the area of Kopské sedlo saddle was 174 days for the period from 2015 to 2022, which is below the average compared to the reference period until 1990.

Life forms accordings to Jurko (Jurko, 1990). In the Slovak study of Jurko (1990), life forms are assigned to individual species from the Slovak territory, which, however, correspond to the life forms of Raunkier (1934). According to Jurko (1990), the life forms are described as follows:

- herbaceous chamaephytes – perennial herbs with renewal buds on above-ground stems, not higher than 25 cm;
- woody chamaephytes – low shrubs, semi-shrubs with renewal buds on above-ground stems, not higher than 25 cm;
- geophytes – renewal buds on permanent underground organs (tubers, bulbs, rhizomes, etc.);
- hemicryptophytes – perennial herbs and grasses with overwintering buds near the surface of the earth;
- annual therophytes – plants without renewal buds (overwinter only in seeds).

The studied alpine communities contain the following species and their life forms:

(1) The *Juncetum trifidi* (Krajina, 1933) community is a pioneering community with an important soil protection function. It is dominated by tufted hemicryptophytes and rosette hemicryptophytes (Table 1). Woody chamaephytes are nondominant but play an important role in trampling. It is not one of the endangered phytocenoses, although it contains endemic

taxa (*Campanula tatrae*, *Leucanthemopsis tatrae* and *Soldanella carpatica*).

Experimental design. In each plant community (native and regenerated), one experimental block was established in the uniform vegetation (Piscová et al., 2021). This experimental block consists of one control and two trampled plots. Due to the varied and complex division of the mountain range, and the occurrence of small-scale alpine communities, plots were not fixed, they can be arranged in a line (where slopes occurred, plots were oriented parallel to contours) or placed irregularly if this suited the site. Each plot is 0.5 m wide and 0.5 m long, separated by 0.5 m wide buffer zone (Fig. 4). Each plot was divided into 25 subplots, and each subplot was 0.1 m wide and 0.1 m long. Subplots were selected by a botanical grid (Fig. 5). The direction of the trampling simulated the path, so the trampling leads in two directions.

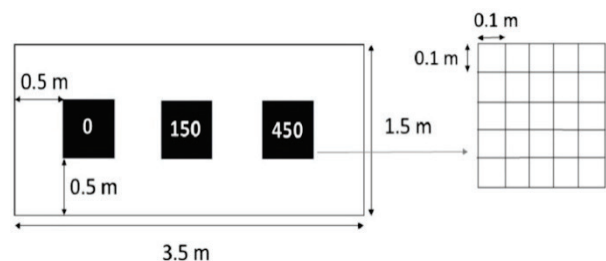


Fig. 4. Experimental block design: on the left side of the figure, the layout of the experimental plots is shown, with 0 passes – the control plot and plots trampled by 150 and 450 passes (75 tourists, lowest daily trail visitation in 2008, and 225 tourists, highest daily trail visitation in 2008); on the right side, a botanical grid is shown, its size corresponds to the size of one plot

Table 1

List of species and their life forms at the studied sites (Kopské sedlo saddleback, Predné Kopské sedlo saddleback and Vyšné Kopské sedlo saddleback) during 2008–2022

Site	Life form	Species
Kopské sedlo saddleback	Woody chamaephytes	<i>Vaccinium vitis-idaea</i>
Kopské sedlo saddleback	Hemicryptophytes	<i>Campanula alpina</i> , <i>Campanula tatrae</i> , <i>Festuca supina</i> , <i>Hieracium alpinum</i> , <i>Juncus trifidus</i> , <i>Oreochloa disticha</i>
Kopské sedlo saddleback	Hemicryptophytes or Geophytes	<i>Bistorta major</i>
Kopské sedlo saddleback	Lichens	<i>Alectoria ochroleuca</i> , <i>Cetraria islandica</i> , <i>Cladonia rangiferina</i> , <i>Cladonia squamosa</i> , <i>Thamnolia vermicularis</i>
Kopské sedlo saddleback	Mosses	<i>Niphotrichum canescens</i> , <i>Pleurozium schreberi</i> , <i>Polytrichastrum alpinum</i>
Predné Kopské sedlo saddleback	Woody chamaephytes	<i>Calluna vulgaris</i> , <i>Vaccinium vitis-idaea</i>
Predné Kopské sedlo saddleback	Hemicryptophytes	<i>Agrostis pyrenaica</i> , <i>Campanula alpina</i> , <i>Carex sempervirens</i> , <i>Festuca supina</i> , <i>Hieracium alpinum</i> , <i>Juncus trifidus</i> , <i>Luzula alpino-pilosa</i> subsp. <i>obscura</i> , <i>Potentilla aurea</i> , <i>Primula minima</i> , <i>Pulsatilla scherfelii</i>
Predné Kopské sedlo saddleback	Hemicryptophytes or Geophytes	<i>Bistorta major</i>
Predné Kopské sedlo saddleback	Lichens	<i>Alectoria ochroleuca</i> , <i>Cetraria islandica</i> , <i>Cladonia pyxidata</i> , <i>Cladonia rangiferina</i> , <i>Cladonia squamosa</i> , <i>Thamnolia vermicularis</i>
Predné Kopské sedlo saddleback	Mosses	<i>Niphotrichum canescens</i> , <i>Pleurozium schreberi</i> , <i>Polytrichastrum alpinum</i>
Vyšné Kopské sedlo saddleback	Herbaceous chamaephytes	<i>Selaginella selaginoides</i> , <i>Thymus pulcherrimus</i>
Vyšné Kopské sedlo saddleback	Woody chamaephytes	<i>Salix silesiaca</i> , <i>Salix reticulata</i> , <i>Vaccinium vitis-idaea</i>
Vyšné Kopské sedlo saddleback	Geophytes	<i>Bartsia alpina</i> , <i>Lloydia serrpotina</i>
Vyšné Kopské sedlo saddleback	Hemicryptophytes	<i>Agrostis pyrenaica</i> , <i>Alchemilla</i> sp., <i>Avenula versicolor</i> , <i>Carex atrata</i> , <i>Carex sempervirens</i> , <i>Festuca versicolor</i> , <i>Leontodon pseudotaraxaci</i> , <i>Ligusticum mutellina</i> , <i>Luzula alpino-pilosa</i> subsp. <i>obscura</i> , <i>Oreochloa disticha</i> , <i>Parnassia palustris</i> , <i>Pedicularis oederi</i> , <i>Phyteuma orbiculare</i> , <i>Poa alpina</i> , <i>Potentilla aura</i> , <i>Ranunculus alpestris</i> , <i>Rhodiola rosea</i> , <i>Sesleria tatrae</i> , <i>Soldanella carpatica</i> , <i>Thymus pulcherrimus</i>
Vyšné Kopské sedlo saddleback	Annual Therophytes	<i>Euphrasia tatrae</i>
Vyšné Kopské sedlo saddleback	Lichens	Missing
Vyšné Kopské sedlo saddleback	Mosses	<i>Pleurozium schreberi</i> , <i>Rhytidiadelphus triquetrus</i>

Note: some species form a life form of hemicryptophyte or geophyte, depending on environmental conditions; (2) the *Juncus trifidi*-*Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community is dominated by woody chamaephytes and hemicryptophytes (Table 1); this plant community is rare, but not threatened yet; its occurrence is at small scale in the Western Carpathians; (3) the *Seslerietum tatrae biscuetteletosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community needs a long-lasting high snow cover at the altitudinal range 1,900–2,000 m ASL; this plant community is dominated by hemicryptophytes (Table 1); woody chamaephytes are nondominant.

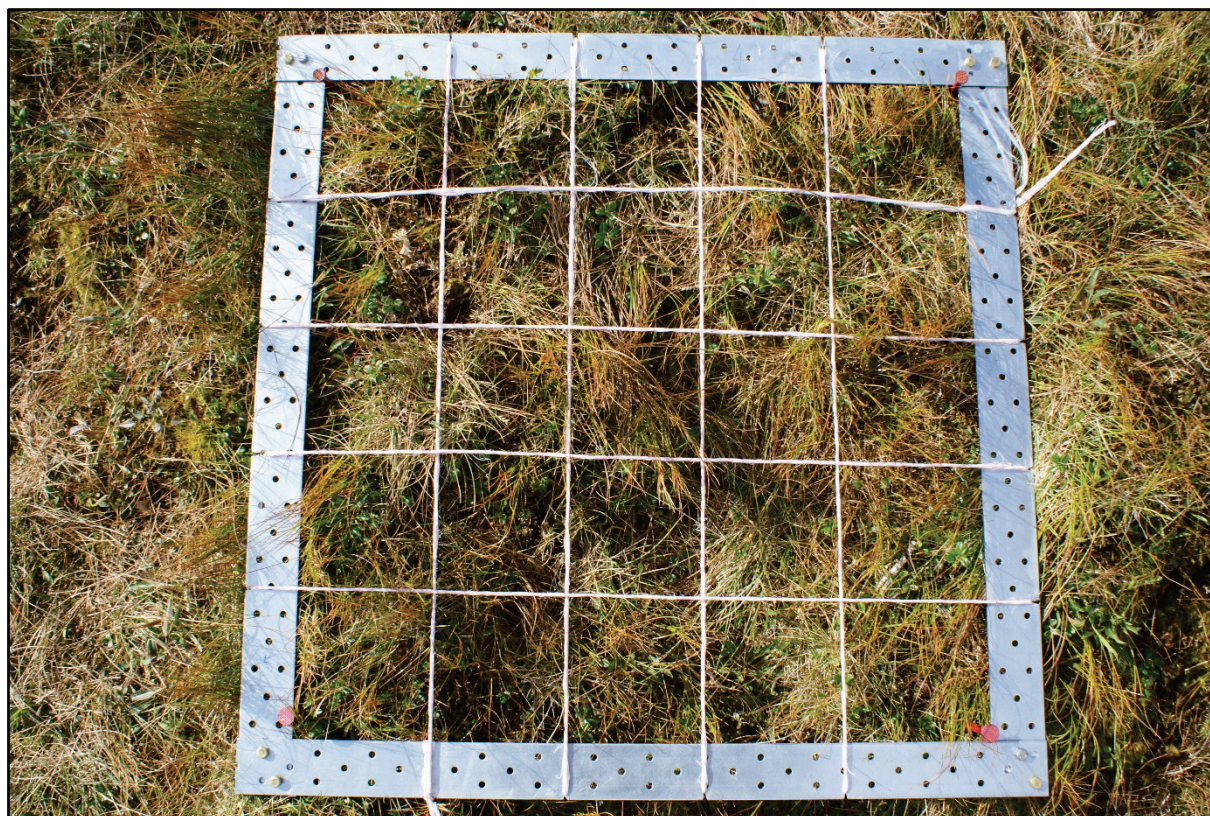


Fig. 5. Botanical grid, used in experimental trampling: its size is 0.5 x 0.5 m, in individual subplots with a size of 0.1 x 0.1 m we recorded the coverage of individual species in percentages; the photo shows the community of *Juncetum trifidi* in Kopské sedlo, a control area (17.08.2022)

The experimental plots are marked using metal nails treated with anticorrosion paint, their position is recorded by GPS coordinates. Nails are inspected annually with a metal detector unless they are visible to the naked eye. In case of loss, the nail is always replaced with a new nail. Be-

fore each step, the position of the nails is also verified by measuring their distance from permanently selected points in the area.

Trampling treatment and timing. We have trampled the same communities, in 2008 as native communities and in 2022 as regenerated

communities. The native communities were not trampled by humans before the experiment. In 2022, the Relative Vegetation Cover of communities trampled in 2008 reached almost 100%, therefore we consider the communities as regenerated.

The experimental block consists of one control plot without trampling and two trampling plots trampled by intensities of 150 passes (75 tourists) and 450 passes (225 tourists). These trampling intensities were determined according to the average lowest and highest daily visit rate between the studied saddles. Each pass represents one footprint. The weight of a walker is 70 kg. One trampling procedure occurred on the same day for all treatments, 4 times during the vegetation season, in June, July, August and September (Piscová et al., 2021). Each experimental plot is assigned one of the three trampling treatments: control (no trampling), 150 passes and 450 passes on the same day (Piscová et al., 2021). Following the Cole & Bayfield (1993) study, measured parameters were:

1) Cover (%) of the vascular plant species (E₁ layer – a herbal layer), mosses and lichens (E₀ layer – a layer of mosses and lichens; 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:

- (a) Visual estimates of the top cover perpendicular to each subplot;
- (b) Visual estimates of the cover of each vascular plant species, mosses and lichens per subplot.
- (2) Cover (%) 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 cover of the bare ground perpendicular to each subplot;
- (d) Visual estimates of the cover of the bare ground per subplot.
- (3) Cover (%) of the litter (including the litter of the recently trampled plants):
- (e) Visual estimates of the top cover of the litter perpendicular to each subplot;
- (f) Visual estimates of the cover of the litter per subplot.

Data analysis/relative vegetation cover: Resistance is the ability of a vegetation type to resist being altered by trampling. Relative vegetation cover can be used to characterize the resistance of different vegetation types (Cole & Bayfield, 1993). Relative Vegetation Cover is based on the sum of the cover of all species, rather than a single estimate of the total vegetation of vascular plants, mosses, and lichens. Cover of individual species changed during short-term trampling under the influence of trampling and seasonality.

Relative vegetation cover was calculated as follows:

$$\text{Relative Vegetation Cover} = \frac{\text{surviving cover on trampled plots}}{\text{initial cover on trampled plots}} \times \text{Correction Factor} \times 100\%$$

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

Relative Vegetation Cover will be 100% in the absence of any change in cover caused by trampling. Therefore, the extent to which relative cover after trampling deviates from 100% provides a measure of the damage response to trampling. The resistance is evaluated in the range: 0–20%

Table 2

Resistance of individual life forms to trampling by 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites in native and regenerated communities (each community was trampled as native in 2008, in 2022 as regenerated): the *Juncetum trifidi* (Krajina, 1933) community occurs in the Kopské sedlo saddleback, the *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community in the Vyšné Kopské sedlo saddleback

Life form	Site	Year of trampling	Trampling intensity	Resistance
Woody chamaephytes	Kopské sedlo saddleback	2008	150 passes/75 tourists	3
Woody chamaephytes	Kopské sedlo saddleback	2008	450 passes/225 tourists	3
Woody chamaephytes	Kopské sedlo saddleback	2022	150 passes/75 tourists	3
Woody chamaephytes	Kopské sedlo saddleback	2022	450 passes/225 tourists	2
Hemicryptophytes	Kopské sedlo saddleback	2008	150 passes/75 tourists	3
Hemicryptophytes	Kopské sedlo saddleback	2008	450 passes/225 tourists	2
Hemicryptophytes	Kopské sedlo saddleback	2022	150 passes/75 tourists	4
Hemicryptophytes	Kopské sedlo saddleback	2022	450 passes/225 tourists	2
Hemicryptophytes/Geophytes	Kopské sedlo saddleback	2008	150 passes/75 tourists	3
Hemicryptophytes/Geophytes	Kopské sedlo saddleback	2008	450 passes/225 tourists	0
Woody chamaephytes	Predné Kopské sedlo saddleback	2008	150 passes/75 tourists	3
Woody chamaephytes	Predné Kopské sedlo saddleback	2008	450 passes/225 tourists	3

very low; 20–40% low; 40–60% medium, 60–80% high and 80–100% very high.

For the individual native and regenerated communities, we selected the results of relative cover according to individual life forms.

Data analysis: To describe the changes in the relative cover over time, linear regression models were used. 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 (R²) was used. All analyses were performed in the R environment (R Core Team, 2022).

Results

Life forms of plants in the native community trampled in 2008 and in the regenerated community trampled in 2022 reached different resistances to the intensity of trampling (Table 2). Especially, the hemicryptophyte/geophyte life form, represented by one species (under certain conditions the species forms a hemicryptophyte, under others a geophyte), died during the regeneration during the years 2008–2022 in both the *Juncetum trifidi* and *Junco trifidi-Callunetum vulgaris* communities.

The *Juncetum trifidi* community. The community consists of woody chamaephytes, hemicryptophytes a geophytes/hemicryptophytes. Woody chamaephytes are formed by 1 species, hemicryptophytes by 6 species and 1 species can form a geophyte or a hemicryptophyte (Table 1). The native community, as well as individual life forms, reacted to 150 passes with medium resistance (Table 2). After community regeneration, woody chamaephytes responded with the same intermediate resistance, but resistance of chamaephytes increased (Table 3). Unfortunately, the hemicryptophyte/geophyte life form did not survive. After 450 passes, woody chamaephytes in the native community responded with intermediate resistance, as after 150 passes, but hemicryptophytes were less resistant. In the regenerated community, after 450 passes, the resistance of living forms decreased. For the evaluation of resistance of plant life forms, we needed to evaluate the resulting regression equations with the coefficient of determination and the size of the average change (Table 4).

Woody chamaephytes on the 150 passed plot. In July in both years 2008 and 2022, woody chamaephytes responded to trampling with medium resistance (Table 2, Fig. 6). Woody chamaephytes responded slightly more intensively in 2008 than in 2022. However, a different situation occurred in August. While the resistance of woody chamaephytes of the regenerated community was medium (2022), the species of this life form of the native community reacted with low resistance (2008). Woody chamaephytes of regenerated association reacted better in September 2022 too. While their resistance to trampling in the native community was very low (2008), in the regenerated community, these species were more resistant to trampling, their resistance was low (2022) (Table 3). This states that woody chamaephytes responded with a higher resistance in the regenerated community than in the native one.

Life form	Site	Year of trampling	Trampling intensity	Resistance
Woody chamaephytes	Predné Kopské sedlo saddleback	2022	150 passes/75 tourists	4
Woody chamaephytes	Predné Kopské sedlo saddleback	2022	450 passes/225 tourists	4
Hemicryptophytes	Predné Kopské sedlo saddleback	2008	150 passes/75 tourists	4
Hemicryptophytes	Predné Kopské sedlo saddleback	2008	450 passes/225 tourists	3
Hemicryptophytes	Predné Kopské sedlo saddleback	2022	150 passes/75 tourists	4
Hemicryptophytes	Predné Kopské sedlo saddleback	2022	450 passes/225 tourists	2
Hemicryptophytes/Geophytes	Predné Kopské sedlo saddleback	2008	150 passes/75 tourists	4
Hemicryptophytes/Geophytes	Predné Kopské sedlo saddleback	2008	450 passes/225 tourists	3
Herbaceous chamaephytes	Vyšné Kopské sedlo saddleback	2008	150 passes/75 tourists	2
Herbaceous chamaephytes	Vyšné Kopské sedlo saddleback	2008	450 passes/225 tourists	2
Herbaceous chamaephytes	Vyšné Kopské sedlo saddleback	2022	150 passes/75 tourists	4
Herbaceous chamaephytes	Vyšné Kopské sedlo saddleback	2022	450 passes/225 tourists	4
Woody chamaephytes	Vyšné Kopské sedlo saddleback	2008	150 passes/75 tourists	4
Woody chamaephytes	Vyšné Kopské sedlo saddleback	2008	450 passes/225 tourists	3
Woody chamaephytes	Vyšné Kopské sedlo saddleback	2022	150 passes/75 tourists	4
Woody chamaephytes	Vyšné Kopské sedlo saddleback	2022	450 passes/225 tourists	4
Geophytes	Vyšné Kopské sedlo saddleback	2008	150 passes/75 tourists	4
Geophytes	Vyšné Kopské sedlo saddleback	2008	450 passes/225 tourists	2
Geophytes	Vyšné Kopské sedlo saddleback	2022	150 passes/75 tourists	3
Geophytes	Vyšné Kopské sedlo saddleback	2022	450 passes/225 tourists	4
Hemicryptophytes	Vyšné Kopské sedlo saddleback	2008	150 passes/75 tourists	3
Hemicryptophytes	Vyšné Kopské sedlo saddleback	2008	450 passes/225 tourists	3
Hemicryptophytes	Vyšné Kopské sedlo saddleback	2022	150 passes/75 tourists	3
Hemicryptophytes	Vyšné Kopské sedlo saddleback	2022	450 passes/225 tourists	4
Annual Therophytes	Vyšné Kopské sedlo saddleback	2008	150 passes/75 tourists	2
Annual Therophytes	Vyšné Kopské sedlo saddleback	2008	450 passes/225 tourists	2
Annual Therophytes	Vyšné Kopské sedlo saddleback	2022	150 passes/75 tourists	3
Annual Therophytes	Vyšné Kopské sedlo saddleback	2022	450 passes/225 tourists	4

Note: resistance values: 1 – zero resistance (the life form did not survive trampling), 2 – low resistance (the life form reaches Relative Vegetation Cover values in the range of 20.1–40.0%, 3 – medium resistance (the life form reaches Relative Vegetation Cover values in the range of 40.1–60.0%, and 4 – high resistance (the life form reaches Relative Vegetation Cover values in the range of 60.1–80.0%); Relative vegetation cover will be 100% in the absence of any change in cover caused by trampling, which represents its highest degree.

Table 3

Values of relative vegetation cover of individual plant life forms in the Kopské sedlo saddleback in the native (2008) and regenerated (2022) *Juncetum trifidi* community; intensities of trampling are 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites; the *Juncetum trifidi* (Krajina, 1933) community occurs in the Kopské sedlo saddleback, the *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community in the Vyšné Kopské sedlo saddleback; Relative vegetation cover will be 100% in the absence of any change in cover caused by trampling, which represents its highest degree

Passes	Life form	June 2008	July 2008	August 2008	September 2008	June 2022	July 2022	August 2022	September 2022
150	Woody chamaephytes	100.00	45.87	19.08	12.89	100.00	48.51	46.78	21.72
450	Woody chamaephytes	100.00	42.73	24.34	22.36	100.00	10.74	6.00	5.45
150	Hemicryptophytes	100.00	50.85	26.68	13.02	100.00	68.01	66.29	29.42
450	Hemicryptophytes	100.00	48.60	25.06	21.00	100.00	43.30	33.51	17.10
150	Hemicryptophytes or Geophytes	100.00	27.86	17.82	16.25	0.00	0.00	0.00	0.00

Table 4

The resulting regression equations with the coefficient of determination and the size of the average change in percentage. Intensities of trampling are 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites in native and regenerated communities (each community was trampled as native in 2008, in 2022 as regenerated). The *Juncetum trifidi* (Krajina 1933) community occurs in the Kopské sedlo saddleback, the *Junco trifidi-Callunetum vulgaris* (Krajina 1933) Hadač ex Šibík et al. 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin 1929 corr. Climent et al. 2005 community in the Vyšné Kopské sedlo saddleback

Site	Passes	Life form	Formula	Coefficient of determination in percentage	Mean difference (decrease) of Relative Vegetation Cover (RC) per month in percentage	Formula	Coefficient of determination in percentage	Mean difference (decrease) of Relative Vegetation Cover (RC) per month in percentage
Kopské sedlo saddleback	150	Woody chamaephytes	$99.04 - 2.65x + 0.02x^2$	0.99	29.04	$93.9 - 1.02x$	0.88	26.09
Kopské sedlo saddleback	450	Woody chamaephytes	$97.93 - 2.65x + 0.02x^2$	0.96	25.88	$98.57 - 3.67x + 0.03x^2$	0.95	31.52
Kopské sedlo saddleback	150	Hemicryptophytes	$98.77 - 2.29x + 0.02x^2$	0.99	28.99	$100.63 - 0.90x$	0.87	23.53
Kopské sedlo saddleback	450	Hemicryptophytes	$98.92 - 2.50x + 0.02x^2$	0.99	26.33	$92.07 - 1.12x$	0.89	27.63
Kopské sedlo saddleback	150	Hemicryptophytes or geophytes	$95.78 - 3.06x + 0.03x^2$	0.85	27.92	–	–	–
Predné Kopské sedlo saddleback	150	Woody chamaephytes	$94.73 - 3.23x + 0.03x^2$	0.75	26.42	$97.25 - 0.51x$	0.96	14.48
Predné Kopské sedlo saddleback	450	Woody chamaephytes	$94.91 - 3.34x + 0.03x^2$	0.79	28.01	$95.27 - 0.65x$	0.93	18.97

Site	Passes	Life form	Formula	Coefficient of determination in percentage	Mean difference (decrease) of Relative Vegetation Cover (RC) per month in percentage	Formula	Coefficient of determination in percentage	Mean difference (decrease) of Relative Vegetation Cover (RC) per month in percentage
Predné Kopské sedlo saddleback	150	Hemicryptophytes	$98.98 - 2.08x + 0.02x^2$	0.98	16.71	$96.37 - 0.76x$	0.92	19.58
Predné Kopské sedlo saddleback	450	Hemicryptophytes	$98.71 - 2.76x + 0.02x^2$	0.98	21.28	$92.48 - 1.21x$	0.92	32.22
Predné Kopské sedlo saddleback	150	Hemicryptophytes or geophytes	$98.24 - 2.58x + 0.02x^2$	0.95	16.67	–	–	–
Predné Kopské sedlo saddleback	450	Hemicryptophytes or geophytes	$95.71 - 3.42x + 0.03x^2$	0.86	30.00	–	–	–
Vyšné Kopské sedlo saddleback	150	Herbaceous chamaephytes	$96.45 - 3.63x + 0.03x^2$	0.93	32.41	$98.28 - 1.62x + 0.01x^2$	0.93	14.36
Vyšné Kopské sedlo saddleback	450	Herbaceous chamaephytes	$94.79 - 4.14x + 0.04x^2$	0.87	33.33	$96.20 - 0.71x$	0.93	19.35
Vyšné Kopské sedlo saddleback	150	Woody chamaephytes	$99.01 - 1.36x + 0.01x^2$	0.97	14.26	$94.13 - 0.53x$	0.85	14.37
Vyšné Kopské sedlo saddleback	450	Woody chamaephytes	$96.00 - 3.07x + 0.03x^2$	0.87	27.27	$93.55 - 0.58x$	0.85	15.75
Vyšné Kopské sedlo saddleback	150	Geophytes	$97.83 - 1.73x + 0.02x^2$	0.81	7.46	$94.49 - 2.75x + 0.02x^2$	0.78	27.86
Vyšné Kopské sedlo saddleback	450	Geophytes	$94.76 - 3.87x + 0.03x^2$	0.86	33.33	$99.53 - 0.88x$	0.99	21.16
Vyšné Kopské sedlo saddleback	150	Hemicryptophytes	$98.33 - 2.42x + 0.02x^2$	0.97	23.33	$97.36 - 2.06x + 0.02x^2$	0.92	21.57
Vyšné Kopské sedlo saddleback	450	Hemicryptophytes	$97.26 - 3.00x + 0.03x^2$	0.94	27.53	$94.01 - 0.62x$	0.88	16.56
Vyšné Kopské sedlo saddleback	150	Annual Therophytes	$100.93 - 3.74x + 0.03x^2$	1.00	33.33	$97.46 - 2.49x + 0.02x^2$	0.93	22.22
Vyšné	450	Annual Therophytes	$90.96 - 4.39x + 0.04x^2$	0.64	33.33	$97.08 - 0.80x$	0.49	14.81

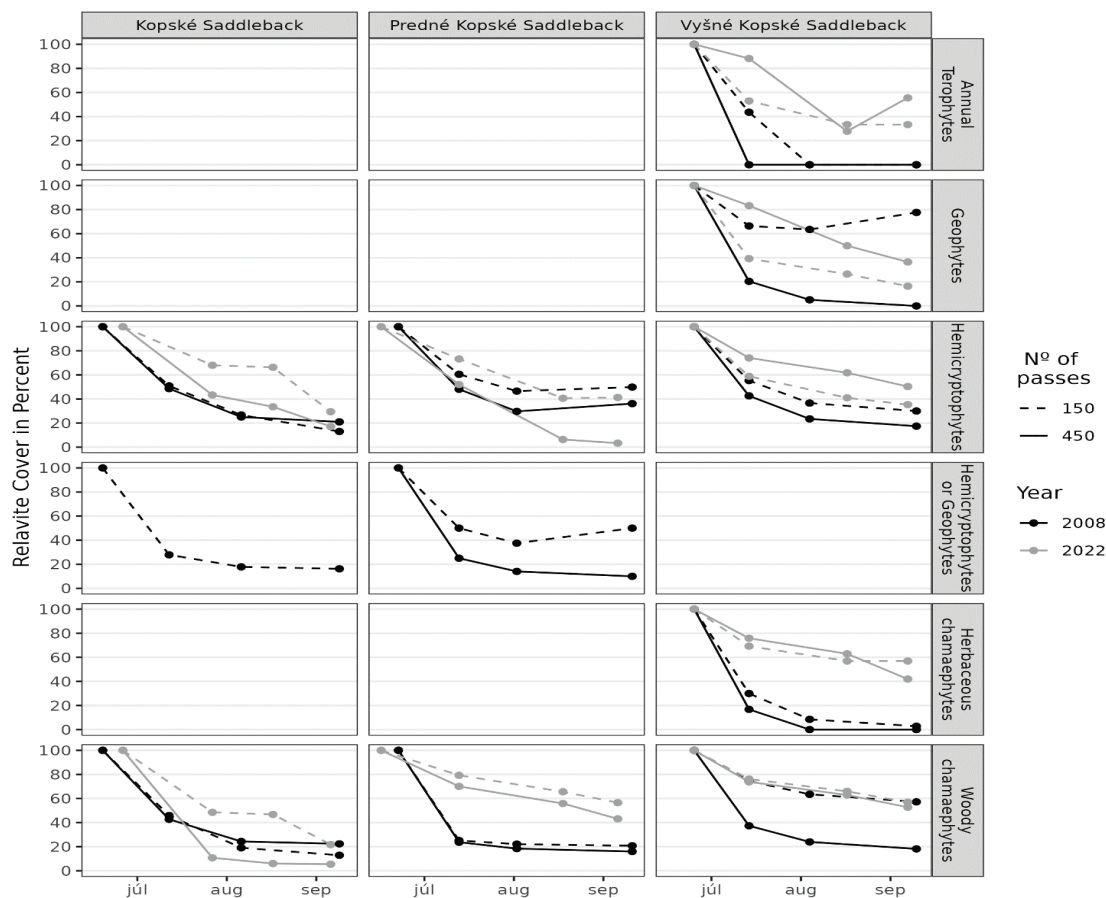


Fig. 6. Relative vegetation cover in percentage of individual life forms trampled in 2008 such as a native community and in 2022 such as a regenerated community: intensities of trampling are 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites; the *Juncetum trifidi* (Krajina, 1933) community occurs in the Kopské sedlo saddleback, the *Juncetum trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community in the Vyšné Kopské sedlo saddleback; Relative vegetation cover will be 100% in the absence of any change in cover caused by trampling, which represents its highest degree

Woody chamaephytes on the 450 passed plot. A completely different situation occurred in the regenerated community on the 450 passed plot. In July, while the woody chamaephytes of the native community responded to trampling with medium resistance, they showed very low resistance in the regenerated community (Table 3, Fig. 6). A similar situation occurred in August and September, when woody chamaephytes achieved low resistance in the native community, but only very low resistance in the regenerated community.

Hemicryptophytes on the 150 passed plot. Hemicryptophytes also reacted more resistantly to the 150 passed plot in July in the regenerated community (Table 3, Fig. 6). While they achieved medium resistance in the native community, they reacted with high resistance in the regenerated community. Even in August, while in the native community they reacted with only low resistance, in the regenerated community their resistance to trampling was high. In September, they reacted more resistantly in the regenerated community than in the native one.

Hemicryptophytes on the 450 passed plot. In July, contrary to the 150 passed plot, the hemicryptophytes reacted somewhat more resistantly to the 450 passed plot in the native community than in the regenerated. In August, the situation was different, hemicryptophytes reacted with higher resistance in the regenerated community (Table 3, Fig. 6). In September, hemicryptophytes of the native community were more resistant to trampling.

Hemicryptophytes/geophytes on the 150 passed plot. We only noticed this life form in the native community in 2008, when its resistance decreased due to repeated trampling (Table 3, Fig. 6). This species *Bistorta major* apparently died out during the late regeneration of the community, as a delayed response to trampling.

Table 5

Values of relative vegetation cover of individual plant life forms in the Predné Kopské sedlo saddleback in native (2008) and regenerated (2022) *Juncetum trifidi* community. Intensities of trampling are 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites; the *Juncetum trifidi* (Krajina, 1933) community occurs in the Kopské sedlo saddleback, the *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community in the Vyšné Kopské sedlo saddleback; Relative vegetation cover will be 100% in the absence of any change in cover caused by trampling, which represents its highest degree

Passes	Life form	June 2008	July 2008	August 2008	September 2008	June 2022	July 2022	August 2022	September 2022
150	Woody chamaephytes	100.00	25.11	22.12	20.75	100.00	79.26	65.60	56.55
450	Woody chamaephytes	100.00	23.70	18.39	15.98	100.00	70.06	55.86	43.08
150	Hemicryptophytes	100.00	60.50	46.54	49.87	100.00	73.26	40.63	41.26
450	Hemicryptophytes	100.00	48.07	29.71	36.15	100.00	51.98	6.35	3.35
150	Hemicryptophytes or geophytes	100.00	50.00	37.50	50.00	0.00	0.00	0.00	0.00

Hemicryptophytes on the 150 passed plot. Hemicryptophytes also reacted more resistantly to the 150 passed plot in July in the regenerated community (Table 5, Fig. 6). They achieved a high resistance in both the native and regenerated community. Even in August, they reacted with medium resistance in both the native and regenerated community. In September, they reacted more resistantly in the native community than in the regenerated one.

Hemicryptophytes on the 450 passed plot. In July, the hemicryptophytes reacted more resistantly in the regenerated community than in the native one. In August and September, the situation was different, hemicryptophytes reacted with higher resistance in the native community (Table 5, Fig. 6). While the resistance of hemicryptophytes in native vegetation was medium, their resistance in regenerated association was very low.

Hemicryptophytes/geophytes on the 150 passed plot. We only noticed this life form in the native community in 2008, when its resistance decreased in July, increased in August and increased again in September, due to repeated trampling (Table 5, Fig. 6). This species *Bistorta major* apparently died out during the late regeneration of the community, as a delayed response to trampling.

Hemicryptophytes/geophytes on the 450 passed plot. We only noticed this life form in the native community in 2008, when its resistance decreased to a very low level due to repeated trampling (Table 5, Fig. 6). This species *Bistorta major* apparently died out during the late regeneration of the community, as a delayed response to trampling.

The *Junco trifidi-Callunetum vulgaris* community. The community consists of woody chamaephytes, hemicryptophytes a geophytes. Woody chamaephytes are formed by 2 species, hemicryptophytes by 10 species and 1 species can form a geophyte or a hemicryptophyte (Table 1). In the native community, except for wood chamaephytes with medium resistance, life forms reacted with high resistance to 150 passes. In the regenerated community, the resistance of woody chamaephytes increased to a high level, but we did not observe the hemicryptophyte/geophyte life form. At 150 passes, life forms in the native community responded with medium resistance. After 450 passes, resistance of woody chamaephytes rose to high, but decreased to low in hemicryptophytes (Table 2). For the evaluation of resistance of plant life forms, we needed to evaluate the resulting regression equations with the coefficient of determination and the size of the average change (Table 4).

Woody chamaephytes on the 150 passed plot. In July, August and September on the 150 passed plot, woody chamaephytes responded to trampling as more resistant in the regenerated vegetation (Table 5, Fig. 6). With repeated trampling, their resistance decreased from low to very low in the native community. But in the regenerated community, their resistance changed from high to medium level.

Woody chamaephytes on the 450 passed plot. We recorded a similar situation on the 450 passed plot. In July, August and September on the 150 passed plot, woody chamaephytes responded to trampling as more resistant in the regenerated vegetation (Table 5, Fig. 6). With repeated trampling, their resistance decreased from low to very low in the native community. But in the regenerated community, their resistance changed from high to medium level.

The Seslerietum tatrae biscutellatosum laevigatae community. This community consists of herbaceous and woody chamaephytes, hemicryptophytes, geophytes and therophytes. Herbaceous chamaephytes are formed by 2 species, woody chamaephytes are formed by 3 species, geophytes by 2 species, hemicryptophytes by 20 species and annual therophytes by 1 species (Table 1). The life forms in the native community were restored for 150 transits with different resistance (Table 2), high resistance was achieved by woody chamaephytes and geophytes. While annual geophytes and herbaceous chamaephytes achieved low resistance in the native community, their resistance was high in the regenerated one. After 450 passes, the resistance of life forms was again different in the native community, lower for woody chamaephytes and geophytes than at 150 passes. However, the resistance of all life forms in the regenerated community increased to a high level (Table 2). For the evaluation of resistance of plant life forms, we needed to evaluate the resulting regression equations with the coefficient of determination and the size of the average change (Table 4).

Herbaceous chamaephytes on the 150 passed plot. This life form reacted better in the regenerated vegetation (Table 6, Fig. 6). While its resistance changed with gradual trampling in the native community from low to very low, in the regenerated community it was from high to medium.

Herbaceous chamaephytes on the 450 passed plot. Similarly, these herbaceous chamaephytes reacted to being trampled even on the 450 passed plot (Table 6, Fig. 6). While in the native community they achieved very low resistance in July and died out in August, they gradually reacted

through high and medium resistance in the regenerated area. Woody chamaephytes on the 150 passed plot. Woody chamaephytes reacted in

the native and regenerated vegetation very similar (Table 6, Fig. 6). Their resistance remained at a high level.

Table 6

Values of relative vegetation cover of individual plant life forms in the Vyšné Kopské sedlo saddleback in the native (2008) and regenerated (2022) *Juncetum trifidi* communities: intensities of trampling are 150 passes (75 tourists, lowest daily trail visitation in 2008) and 450 passes (225 tourists, highest daily trail visitation in 2008) at individual sites; the *Juncetum trifidi* (Krajina, 1933) community occurs in the Kopské sedlo saddleback, the *Junco trifidi-Callunetum vulgaris* (Krajina, 1933) Hadač ex Šibík et al., 2007 community in the Predné Kopské sedlo saddleback, and the *Seslerietum tatrae biscutellatosum laevigatae* Domin, 1929 corr. Climent et al., 2005 community in the Vyšné Kopské sedlo saddleback; Relative vegetation cover will be 100% in the absence of any change in cover caused by trampling, which represents its highest degree

Passes	Life form	June 2008	July 2008	August 2008	September 2008	June 2022	July 2022	August 2022	September 2022
150	Herbaceous chamaephytes	100.00	29.94	8.49	2.77	100.00	69.23	56.92	56.92
450	Herbaceous chamaephytes	100.00	16.75	0.00	0.00	100.00	75.81	62.90	41.94
150	Woody chamaephytes	100.00	74.48	63.48	57.22	100.00	76.16	65.93	56.89
450	Woody chamaephytes	100.00	37.33	23.95	18.18	100.00	73.81	62.90	52.76
150	Geophytes	100.00	66.42	63.47	77.63	100.00	39.29	26.43	16.43
450	Geophytes	100.00	20.41	5.10	0.00	100.00	83.33	50.00	36.51
150	Hemicryptophytes	100.00	55.27	36.60	30.00	100.00	58.82	40.97	35.30
450	Hemicryptophytes	100.00	42.58	23.46	17.42	100.00	74.11	61.76	50.33
150	Annual Therophytes	100.00	43.64	0.00	0.00	100.00	52.94	33.33	33.33
450	Annual Therophytes	100.00	0.00	0.00	0.00	100.00	88.24	27.78	55.56

Woody chamaephytes on the 450 passed plot. A different situation occurred on the 450 passed plot where woody chamaephytes reacted more resistantly in the regenerated community (Tables 6, Fig. 6). During gradual trampling their resistance changed from a low to very low level in the native community, in the regenerated community, their resistance changed from high to medium.

Geophytes on the 150 passed plot. Compared to the year 2022, geophytes reacted in the native community as more resistant in 2008 (Table 6, Fig. 6). In the native community, their resistance was high, it even increased in September. In the regenerated community, their resistance changed from low to very low with repeated trampling.

Geophytes on the 450 passed plot. Contrary to the 150 passed plot, geophytes reacted more resistantly in the regenerated community (Table 6, Fig. 6). In the native community, their resistance changed from low, very low to extinction in September. In the regenerated community, the resistance of this species varied from high to medium to low.

Hemicryptophytes on the 150 passed plot. Hemicryptophytes also reacted more resistantly to the 150 passed plot in July in the regenerated community (Table 6, Fig. 6). They achieved a medium resistance in both the native and regenerated communities. Even in August, they reacted with lower resistance in both the native and regenerated communities. In September, they reacted in the native and regenerated community very similarly, with a low resistance.

Hemicryptophytes on the 450 passed plot. Hemicryptophytes also reacted more resistantly to the 450 passed plot in July in the regenerated community (Table 6, Fig. 6). The resistance of hemicryptophytes to the 450 passed plot was weaker in the native community than in the regenerated. While their resistance varied from medium to very low in the native community, it reached high to medium values in the regenerated community.

Annual therophytes on the 150 passed plot. Therophytes also reacted more resistantly in the regenerated community (Tables 6, Fig. 6). They died out in the native community in August, their resistance in the regenerated community was moderate in August and September.

Annual therophytes on the 450 passed plot. Therophytes did not survive trampling 450 passes in the native community already in July (Table 6, Fig. 6). However, their resistance changed significantly in the regenerated community, namely high in July, low in August and medium in September.

The dominant form of hemicryptophyte. Although it is the dominant life form of all studied communities, the resistance of hemicryptophytes to the same intensities of trampling is different in different communities. While in native communities with greater cover woody chamaephytes (heather in the *Junco trifidi-Callunetum vulgaris* community and willows in the *Seslerietum tatrae biscutellatosum laevigatae* community) better resisted a lower intensity of trampling, in the native *Juncetum trifidi* community, with limited *Vaccinium* cover, they were more resistant to stronger trampling. On the plot trampled with higher intensity (450 passes/225

tourists), the species *Campanula alpina* and *Juncus trifidus* started to regenerate already in the time between trampling in July and August 2008 (Fig. 7 and 8). However, we did not observe this rapid regeneration of these two species in the regenerated community. At the same time, the hemicryptophytes of the regenerated *Juncetum trifidi* community in Kopské sedlo reacted as more resistant to the fence trampled with less intensity (150 passes/75 tourists, Fig. 6).

In native and regenerated *Junco trifidi-Callunetum vulgaris* community with heather, life forms reacted to the lower intensity of trampling (150 passes/75 tourists) very similarly. However, their resistance decreased rapidly in the regenerated community (Fig. 6).

Similar to the native *Junco trifidi-Callunetum vulgaris* community as well as the native *Seslerietum tatrae biscutellatosum laevigatae* community, hemicryptophytes responded with higher resistance to a lower intensity of trampling (150 passes/75 tourists). Hemicryptophytes reacted with greater resistance to both intensities of trampling in the regenerated *Seslerietum tatrae biscutellatosum laevigatae* community.

Discussion

Vegetation trampling resulting from recreation impacts natural habitats, leads to the loss of vegetation and the degradation of plant communities (Gomez-Limon & De Lucio, 1995; Forsberg, 2010; Pescott & Gavin, 2014). A considerable primary literature exists on this topic, therefore it is important to assess whether this accumulated evidence can be used to reach general conclusions concerning vegetation vulnerability to inform conservation management decisions. Therefore, in the presented study, we compare our results with other studies in an attempt to find agreement with other research and we are trying to make recommendations for the Administration of the Tatra National Park.

The resistance of plant species to disturbances, such as trampling, is strongly associated with the morphological characteristics of those species (Del Moral, 1979; Bratton, 1985; Roovers et al., 2004). Life-form and plant height are often good predictors of plant community responses to trampling (Sun & Liddle, 1993; Yorks et al., 1997; Amesen, 1999). In our experimental research, we found that higher hemicryptophytes in the *Seslerietum tatrae biscutellatosum laevigatae* community responded with greater resistance than lower hemicryptophytes in the *Juncetum trifidi* community. Bernhardt-Römermann et al. (2011) claims, that vegetation resistance is predicted by two plant functional traits: leaf size and leaf distribution. Resistance is negatively related with leaf size, meaning that plants with higher resistance tended to have smaller leaves. Yorks et al. (1997) and Bernhardt-Römermann et al. (2011) found that plants with smaller leaves were resistant to disturbance. According to Yorks et al. (1997), the herbaceous, typically broader-leaved (forb) life-form appeared most likely to suffer immediate losses. Shrubs have the longest-lasting decreases in diversity following trampling impact. Also according to

Bernhardt-Römermann et al. (2011), resistance of a trampled plant community is negatively related with leaf size, meaning that plants with higher resistance tended to have smaller leaves. Typically, resistant plant species had a rosette life-form: species forming rosettes were more resistant than semi-rosette plants, which were, in turn, more resistant than species with a regular stem leaf distribution. However, all life-forms had sensitive species. We agree with this statement only in the case of different species, such as *Hieracium alpinum* versus *Juncus trifidus*. In general, herbs are less resistant to trampling than grasses. However, in the comparison of grass species as hemicryptophytes among themselves, *Juncus trifidus* in the *Juncetum trifidi* community in Kopské sedlo suffered more damage than, for example, *Sesleria tatrae* in the *Seslerietum tatrae biscutellatosum laevigatae* community in Vyšné Kopské sedlo saddleback.

Studies of Cole (1995a, 1995b) and Cole & Monz (2002) suggested that hemicryptophytes and geophytes will be more resistant to trampling impacts relative to other life-forms. In contrast, chamaephyte-dominated vegetation did not show a main effect of recovery; indeed, chamaephyte-dominated communities have been shown to die-back after trampling

disturbance, despite initially high resistance. Hemicryptophytes have a greater ability to recover than chamaephytes (Yorks et al., 1997; Amesen, 1999). We agree with this statement, but only in native communities. Woody chamaephytes (mainly heather) in the *Juncus trifidi-Callunetum vulgaris* community, as well as woody chamaephytes (mainly creeping willows) and herbaceous chamaephytes (for example *Thymus*) in the *Seslerietum tatrae biscutellatosum laevigatae* community, were severely destroyed after trampling and their resistance was low (Fig. 6). But in 2022, they were already regenerated and reacted to trampling with higher resistance than in the native community.

Juvenile chamaephytes, with their buds at a distance from the ground, are more sensitive to trampling than hemicryptophytes or geophytes that have their buds at or below-ground level (Liddle, 1975a, 1975b; Roovers et al., 2004). During our experimental research, we did not trample juvenile chamaephytes. However, we found that regenerated individuals respond to high resistance in regenerated communities of *Juncus trifidi-Callunetum vulgaris* and *Seslerietum tatrae biscutellatosum laevigatae*.



Fig. 7. The recovering species *Campanula alpina* at the Kopské sedlo site in the native *Juncetum trifidi* community, between the 2nd (July) and the 3rd (August) by experimental trampling in 2008 (3.8.2008)



Fig. 8. The recovering species *Juncus trifidus* at the Kopské sedlo site in the native *Juncetum trifidi* community, between the 2nd (July) and the 3rd (August) by experimental trampling in 2008 (3.8.2008)

According to Roovers et al. (2004), perennial species with the ability to resprout are probably more resistant than annuals. In the studied area, we can evaluate annual therophytes to other life forms. One-year-old therophytes in the native *Seslerietum tatrae biscutellatosum laevigatae* community did not survive the first trampling in June (they were extinct in July) on the area trampled with a higher intensity (450 passes/225 tourists). They also died out on the fence trampled with a lower intensity (150

passes/75 tourists), one month later (after being trampled in July, they became extinct in August). However, we recorded them in the regenerated community of *Seslerietum tatrae biscutellatosum laevigatae* in Vyšné Kopské sedlo, where they survived the experimental trampling and thus reacted with higher intensity. Since there are several identical individuals, it is questionable why they reacted. Pescott & Gavin (2014) state that the intrinsic properties of plant communities appear to be the most important

factors determining the response of vegetation to trampling disturbance. Specifically, the dominant life form of a plant community accounts for more variability in community resilience to trampling than trampling intensity, suggesting that simple assessments based on this trait could guide decisions regarding sustainable access to natural areas (Liddle, 1975b; Roovers et al., 2004). This claim is questionable. In regenerated communities, individual life forms, even individual species, achieved almost identical relative vegetation cover before trampling in both native and regenerated communities. Not only did the dominant life form determine the resistance or resilience of the community, but there is a need for the interplay of life forms. For example, in the *Junco trifidi-Callunetum vulgaris* community, *Juncus trifidus* responded to trampling differently than in the *Juncetum trifidi* community because it was partially protected by heather. In the *Seslerietum tatrae biscutellatosum laevigatae* community, grasses grow over the creeping willows, which, however, protect their buds when trampled.

The study of Bernhardt-Römermann et al. (2011) claims that slow-growing plants with below-ground buds have a high resistance. In general, this statement was not confirmed by us (Fig. 6). Other studies (Grime & Campbell, 1991; MacGillivray et al., 1995; Fortunel et al., 2009) claim, in general, that plants with higher growth rates are predicted to have greater resilience. We can confirm this statement by the reaction of *Sesleria tatrae* in the *Seslerietum tatrae biscutellatosum laevigatae* community.

According to the study (Pescott & Gavin, 2014), the greatest general species and individual plant losses take place in the first few passes by feet. We agree with this statement both after the passage of 75 tourists (150 passes) and 225 tourists (450 passes), because there was a difference between the 1st and 2nd experimental trampling (1st trampling in June, 2nd trampling in July). Pescott & Gavin (2014) also claims, that limited recovery of chamaephytes may occur after dieback, given a period free from further disturbance. This statement was confirmed mainly by willows in the *Seslerietum tatrae biscutellatosum laevigatae* community, but also by *Calluna vulgaris* in the *Junco trifidi-Callunetum vulgaris* community. *Vaccinium vitis-idaea* recovered faster in *Juncetum trifidi* and *Junco trifidi-Callunetum vulgaris* communities. However, we claim that this restoration may not be limited, as the Relative vegetation cover of these species was almost identical in native and regenerated communities.

Several authors, for example (Yorks et al., 1997; Cole & Monz, 2002) do not recommend combining results of short-term and long-term experimental research. Yuejin et al. (2022) claims that the impacts of short-term trampling are both similar and different from those of long-term trampling, so it may be problematic to speculate on the impacts and trends of long-term trampling only from the results of short-term experimental trampling. However, we would like to draw attention to the fact that regenerated communities react to trampling differently than native communities, so even experimental short-term trampling, although repeated 4 times, will be reflected in the regenerated community. This fact is inevitable. Based on vegetation responses to human trampling, the study of MacGillivray et al. (1995) clearly revealed that resistance and resilience, the two components of ecosystem stability, are strongly affected by environmental factors. For resistance, their results highlight background anthropogenic disturbance leading to species adaptations that potentially increase the ability to withstand disturbances. This statement was confirmed by some life forms in the regenerated *Junco trifidi-Callunetum vulgaris* (for example woody chamaephytes) and *Seslerietum tatrae biscutellatosum laevigatae* communities (for example herbaceous chamaephytes) (Fig. 6).

Despite the results of many studies, such as that trampling leads to changes in the composition and structure of plant communities (Cole & Bayfield, 1993; Roovers et al., 2004; Pescott & Gavin, 2014), disturbance by trampling affects vegetation mainly directly by damaging plant tissues and indirectly by modifying soil structure and water regime (Kozłowski, 1999; Roovers et al., 2005), and nitrogen mineralization (Breland & Hansen, 1996) or, that the effects of trampling on soil compaction remain unclear (Lei, 2004) or are at least important only in areas with chronic disturbance, these results are not sufficient to establish general models of vegetation behaviour for trampling. Roovers et al. (2004) claims that to predict plant species responses following disturbance it is necessary to consider species relationships to the current abiotic (e.g. soil, climate) and

biotic (e.g. competitors) environment. The assembly of the vegetation in disturbed habitats will be determined by the adaptive strategies in the local species pool. We assume that this statement is correct. Apparently, all these factors also affect life forms within one community, and therefore the reactions of life forms in different communities is different.

Other authors claim, that within the same ecosystem type, the ability to withstand disturbance events is likely to be depend on nutrient (MacGillivray et al., 1995; Breland & Hansen, 1996) and water availability (Gallet & Roze, 2001). Some ecosystems adapted to drought are known to be very resistant to trampling (Andrés-Abellán et al., 2006), while in general wet habitats seem to be most sensitive (Chapin & Chapin, 1980; Grime & Campbell, 1991; Francis et al., 2005). Thus, resistance and resilience both show differences across climatic (Liddle, 1975) and elevation gradients (Kissling et al., 2009). Thanks to the resistance of individual life forms in the communities of *Juncetum trifidi* and *Seslerietum tatrae*, we assume the correctness of this statement.

Although we found agreement with some of the claims in the work, it is probably not possible to generalize all these claims. Therefore, it is necessary to systematically investigate the high mountain areas most attacked by trampling. The impact of trampling on vegetation has been reviewed on several occasions (Liddle, 1975b; Yorks et al., 1997; Bernhardt-Römermann et al., 2011); however, we agree, that for a transparent and comprehensive synthesis of the available evidence, a systematic methodology should be employed for the retrieval, critical appraisal and pooling of results (Pullin & Night, 2003; Sutherland et al., 2004; Pullin & Stewart, 2006; Stewart, 2010).

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