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Spatio-temporal distribution of European bison (*Bison bonasus* L.) in Poloniny National Park, East Carpathians, Slovakia

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Abstract. This study focused on analysis of spatio-temporal distribution of endangered European bison in Poloniny National Park (PNP). The main aim of the study was to analyse bison territory during both winter and the vegetation season for the whole period of reintroduction to show differences in occurrence at different altitudes, slopes and aspects as well as relationships between them during seasons and changes in territory utilization during 3-year periods. The animals change their habitat requirements according to actual season. Bison visit higher altitudes and steeper slopes mainly during the summer. During winter, bison remain in the valleys of displaced villages and feed on apple orchards and supplementary hay. The population is conservative in their territory and it still visits the same area.

Key words: altitudinal movements, habitat utilization, seasonal distribution, Poloniny National Park, East Carpathians

Introduction

The European bison (*Bison bonasus*) is Europe's largest terrestrial mammal. Pucek *et al.* (2004) state that in the past European bison were distributed all over the European continent, specifically in south-eastern, central and western Europe.

In Slovakia, the last bison was killed in the 16th-17th century (Pčola and Adamec 2007). Only two populations of European bison survived in the wild to the end of the 19th century; one in the Białowieża Forest at the borders between Poland and Belarus (*B. b. bonasus*) and the other in the West-Caucasus Mountains (*B. b. caucasicus*) (Pucek *et al.* 2004). History of the European bison extinction was summarised in studies by Pucek (1991, 1994). In many European countries the reintroduction of European bison is accomplished using animals previously kept in zoological enclosures (Pucek *et al.* 2004; Eliáš 2006, 2008). Release of captive animals into the wild to restore wild-living populations was at first attempted in the Polish part of Białowieża Forest in 1952 (Krasiński 1978, 1983) and then in forests in Belarus, Lithuania, Russia, Slovakia, Ukraine (Raczyński 2011, Pucek *et al.* 2004) and Kyrgyzstan (Pucek *et al.* 2004). However, all free-ranging as well as semi-free herds are isolated and these small populations quickly lose their genetic heterogeneity and are more vulnerable to extinction (Franklin 1980). High genetic similarity in all wild-living populations is indicative of inbreeding as the result of the bottleneck effect. Several studies reported the high (and still rising) inbreeding coefficient in European bison from Białowieża Forest (Matuszewska *et al.* 2004, Wołk and Krasińska 2004). Inbreeding has a detrimental effect on health, particularly on skeleton growth in females, and reduces disease and pathogen resistance of bison population (Kobryńczuk 1985, Olech 2008). Therefore, it is necessary to create conditions to facilitate migration of bison between herds. The first step should be to search for natural migratory routes and space use by individuals at sites of potential interconnections between neighbouring Slovak and Polish bison herds.

The State Nature Conservancy of the Slovak Republic developed and in 2004 implemented a project entitled "The Foundation of wild-living population of European bison in Slovak Carpathian Mountains, Poloniny National Park" (Adamec 2004, 2006; Eliáš 2008). This project aimed to create a stable population of European bison in Slovakia (Fig. 1). Five individuals from Italy, the Netherlands and Switzerland were imported in June 2004 and on December 10th, 2004 were released into the wild and monitored by telemetry (Adamec and Pčola 2004; Perzanowski *et al.* 2006; Pčola and Adamec 2007; Eliáš 2006, 2008). Shortly after their release, (December 25, 2004) one

Fig. 1. The European bison in the Poloniny National Park, Slovakia (Photo: M. Janiga, 2013).

wild-living bull called Pišta joined the group (Adamec 2006; Perzanowski *et al.* 2006; Pčola and Adamec 2007; Eliáš 2008). The chronology of reintroduction in Poloniny National Park was summarised in a study by Pčola and Gurecka (2008).

Different individuals often use the same area and their territories overlap considerably. Central parts of territories, including meadows and watering holes are the most intensively utilised (Krasiński *et al.* 1999). In Lithuania, animals frequented an area between 100 and 200 km^2 with large core areas measuring approximately 20 km^2 (Balčiauskas 1999; Pucek *et al.* 2004). A satisfactory area to sustain a population of 50-70 animals looks to be approximately 200 km^2 (Pucek *et al.* 2004).

The territories of European bison in Slovakia were analysed during the first four years following reintroduction (December 10th, 2004 to August 3rd, 2008) and mentioned in studies of Adamec (2006), Pčola and Adamec (2007) and Pčola and Gurečka (2008). At this time relationships were observed between distribution of European bison herds and individual animals and their occurrence at different altitudes, slopes and aspects during the year, but were never completely analysed. There are only a few free-ranging and semi-free herds of European bison in the world, and they occur in the wild only in a few places (Pucek *et al.* 2004). Therefore, the sustainable management of each population is key to survival of the species on a global scale.

Research on habitat utilization and patterns of herd movement during the whole period of population existence are essential to improving the reintroduction and the long-term management of European bison in European reserves.

We decided to compare winter and summer area of European bison and changes in their dimensions during years after reintroduction. The main objective of this paper is to analyse spatiotemporal distribution and identify potential connection of Slovak herd with Polish herd during the period of reintroduction of European bison populations in the Poloniny National Park, East Carpathians, Slovakia since 2004 to 2017.

Material and Methods

Poloniny National Park is located in north-eastern Slovakia, at the border with Poland and Ukraine, in the Bukovské vrchy mountain range. Areas of PNP (Poloniny National Park) are included in the East Carpathian Biosphere Reserve and several locations have been proclaimed by UNESCO as World Heritage Sites.

Data was collected between December 10th, 2004 and February 17th, 2017 (including 13 winter periods (December to March) and 12 vegetation periods (April to November)). It was collected by staff from The State Nature Conservancy of the Slovak Republic, the Administration of PNP, located in Stakčín and university students through telemetric monitoring. Monitoring was conducted once per week using the ICOM IC-R 10 receiver a Telonics RA 14 antenna (Pčola and Gurečka 2008, Eliáš 2008), and random observers. Between 2016 and 2017, data from authors' regular observations (several days each month) was added. Position data of herd and solitary individuals was collected, including date and coordinates as well as abundance and gender when possible (mainly since year 2010). Visual observations and field remnants (fresh droppings, footprints, lying areas, nibbled trees and shrubs) were recorded. Coordinates of hay feeders in the area, used as a source of food during winter were also recorded. Geographic information software (ArcGIS 10.0) was used for data analysis, specifically the ArcMap component. The data of basic matrix was analysed and standardized using the STATISTICA 12.1 program. Two-way analysis of variance (ANOVA) was used to determine significant differences between the means of two or more independent groups. The data is expressed as mean ± standard deviation (SD). Values of P less than 0.05 were admitted as statistically significant.

Results

540 out of a total of 560 position coordinates were used for analysis of area of territory. 20 coordinates (3.6%) were not used (11 of the Polish herd, one of migrating bull near Zboj village and 8 of migrating bull near Stakčín village). The Polish herd was observed in period between January 2016 and February 2017 and we found potential interconnection between Slovak and Polish bison herds near Hostovický creek. However, direct encounters of bison from two transboundary herds were not recorded (Fig. 2).

540 position coordinates were used for analysis during whole period. Total area included in analysis of the reintroduction period is 106.79 km^2 (Fig. 2). If we include the Polish herd and Slovak migrating bulls, the total area of European bison occurrence in the wild in Slovakia is 265.19 km^2. Maximal distance of occurrence data was 31.45 km (Svetlice – Zboj).

218 position coordinates were recorded during the period between October and March. The total area recorded in all winter periods was 81.33 km^2. Maximal distance of occurrence data in winter was 12.1 km (Fig. 3a).

322 position coordinates were recorded during the period between April and September. The total area recorded in all vegetation periods was 104.27 km^2. Maximal distance of occurrence data in vegetation period was 15.1 km (Fig. 3b).

In spring, eastern slopes were the most occupied by bison (39.3%), followed by western (23.6%), southern (20.2%) and northern slopes (16.9%) (Fig. 4). In summer, western slopes were the most occupied (28.0%), followed by southern (27.2%), eastern (26.4%) and northern slopes (18.4%). In autumn, western slopes were the most occupied (29.7%), followed by eastern (26.6%), southern (25.9%) and northern slopes (17.7%). In winter, eastern slopes were the most occupied (45.5%), followed by western (28.7%), southern (15.7%) and northern slopes (10.1%).

There were no seasonal differences observed between altitude of occurrence of herds and solitary animals. Herds inhabited lower altitudes in spring and then moved to higher altitudes. Conversely, individual animals inhabited higher altitudes in spring than herds and then moved to lower altitudes during summer. Nevertheless, interaction between these factors was deemed statistically insignificant.

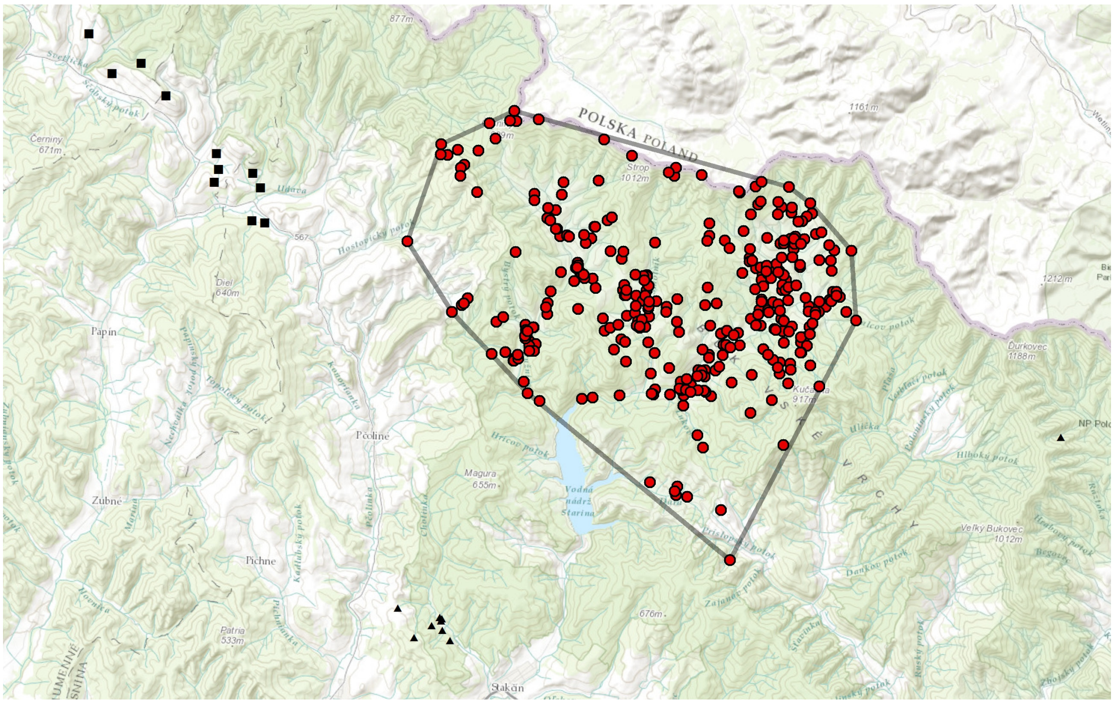

Fig. 2. Map of total area of the European bison occurrence in Poloniny National Park. Squares are data of Polish herd, which occurred on Slovak territory since January 2016 and triangles are data of Slovak migrating bulls. The data was not included to calculation of area of territory. Line encloses core area of bison occurrence in PNP.

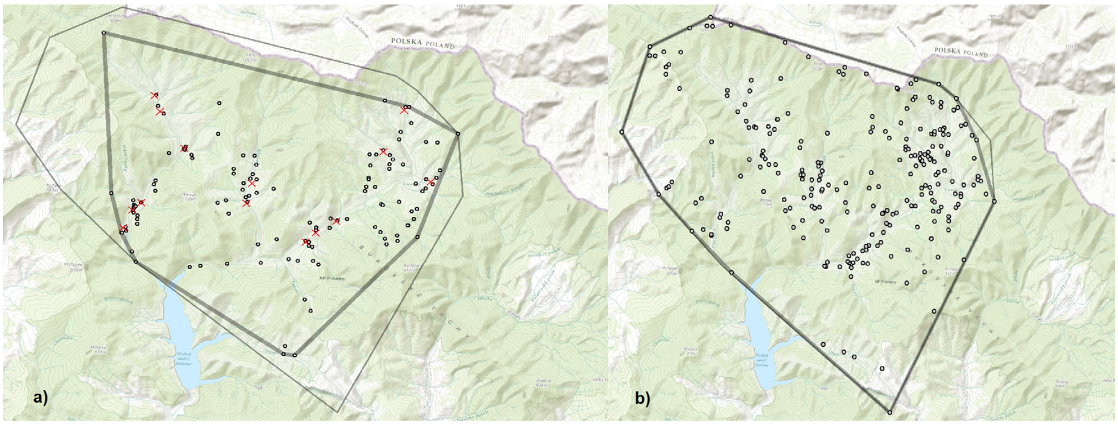

Fig. 3. Maps of territories of European bison in Poloniny National Park in **a)** winter season (October to March) and **b)** vegetation season (April to September). Thick lines show winter/summer area and thin lines total area of bison occurrence. Crosses show hay feeders. Data of Polish herd and Slovak migrating bulls are not included.

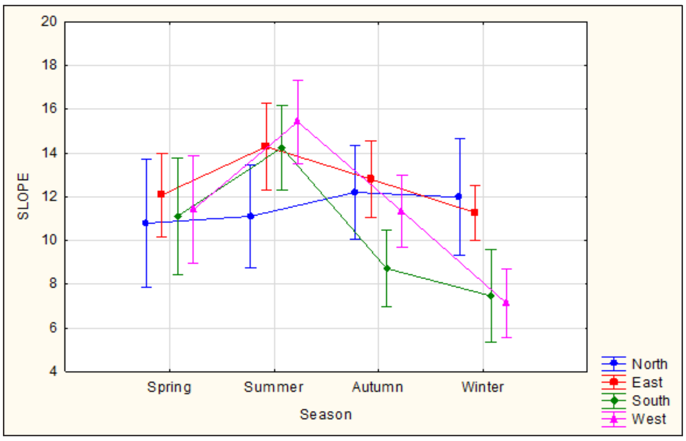

Fig. 4. Relationship between seasons, aspect and altitude. Southern and western slopes at higher altitudes from 620 to 650 m a.s.l. were commonly occupied by European bison in summer season (Two way ANOVA; effects: F(9. 534) = 3.0178; p = .00159; vertical bars denote 0.95 confidence limit). In spring, autumn and winter, bisons were at altitudes from 440 to 520 m a.s.l.

Period	Total area (km²)	Winter area (km²)	Vegetation period area (km²)
10 December 2004 to 2 February 2006	72.53	No data	No data
10 December 2004 to 3 August 2008	78.24	22.04	69.13
10 December 2004 to 17 February 2017	106.79	81.33	104.27

Table 1. Overview of territory expansion of European bison in Poloniny National Park. Processed according to Adamec (2006), Pčola and Adamec (2007), Pčola and Gurečka (2008).

Discussion

During the reintroduction period in Poloniny National Park between December 17th, 2004 and February 17th, 2017, the total area of territory was 106.79 km2. When compared to studies by Adamec (2006) and Pčola and Adamec (2007), this area grew from 72.53 km^2 to 106.79 km^2 (Table 1). Pucek *et al.* (2004) state that a satisfactory area for a population of 50-70 animals is approximately 200 km^2. According to observations, approximately 25 European bison live in PNP as part of the Slovak herd within a core area of 106.79 km^2 (not including the Polish herd and Slovak migrating bulls). Compared to Pčola and Gurečka (2008), the winter area (October to March) was larger, growing from 22.04 km^2 to 81.33 km^2 (59.29 km^2 growth) and the area inhabited during the vegetation period (April to September) grew from 69.13 km^2 to 104.27 km^2 (35.14 km^2 growth). Boundaries of total area were reached mostly in vegetation season, first in the period after reintroduction (December 10th, 2004 to December 31st, 2007). During other periods, bison inhabited the core area. This data confirms the conservation of European bison territory in PNP.

The individuals from Slovak herd were recorded several times at the border with Poland that runs along the ridge of the Poloniny Mountains. On the other side of the border are the Bieszczady Mountains, where the Polish population of European bison lives (Wołoszyn-Gałęza *et al.* 2016). Slovak individuals have repeatedly moved into the border area and might possibly get across the border into the Polish territory, but this behaviour was not recorded, because observers did not collected transboundary data. It can be assumed that potential interconnections with Polish herd could be near Hostovický creek and along the intersection of the boundary with the territory of the bison from Slovak area (Fig. 2).

Total average altitude for the year is 501 m a.s.l. Bison inhabit the lowest altitudes in winter, followed by spring. During autumn and summer animals inhabit the highest altitudes. Winter incidence at lower altitudes is influenced by the availability of supplementary food in hay feeders, long-lasting snow cover, low temperatures and decreased movements of visitors due to winter conditions. Occurrence at higher altitudes during vegetation period, specifically summer, may be due to a sufficient amount of food and higher movement of visitors in valleys of displaced villages, specifically owners of cottages and tourists. Seasonal migration could also be caused by bison preference for open habitats, which are more frequently used during winter period by both sexes. However, bison rarely move further than 5 km from the forest edge (Kowalczyk *et al.* 2013). The valleys with displaced villages in Poloniny achieve these conditions.

In general, eastern slopes were the most occupied (34.7%), followed by western (28.0%), southern (22.0%) and northern slopes (15.3%). Southern and western slopes at higher altitudes from 620 to 650 m a.s.l. were commonly occupied by bison during summer. Small incidence on northern slopes may be caused by the coldest climatic conditions and consecutive influence to composition of flora. On the other hand, incidence on slopes with eastern, southern and western exposures may be caused by long-lasting sunshine and stronger solar radiation. The quality of winter refuges depends on the amount of canopy cover and the dominant tree species (Wołoszyn-Gałęza *et al.* 2016). In winter, bison remained in displaced villages and fed mainly on apple orchards similarly to the reintroduced European bison in the Bieszczady Mountains (the Eastern Carpathians, Poland), which actively selected broken canopy forests with a high density of understory vegetation (Wołoszyn-Gałęza *et al.* 2016).

The European bison is a gregarious animal. The most observed units are small bull groups and groups composed of cows, calves and bulls. In this second type of group cows, calves aged 2-3 years and sometimes adult bulls were observed (Krasiński and Krasińska 1992, 1994; Krasiński *et al.* 1994b, 1999; Pucek *et al.* 2004). Groups of European bison are not family units and changes in structure and size of groups are influenced by other factors. Seasonal factors include bulls joining new groups in the rutting season and calves being introduced following calving. Others changes are a result of behavioural factors. Individuals move between groups at frequent group meets. Switching between groups is most common in young bulls (Krasińska *et al.* 1987). Environmental factors influence the average size of these groups. In different populations, groups are most often comprised of an average of 8-13 animals (Krasiński and Krasińska 1992, 1994; Krasiński *et al.* 1994b, 1999; Pucek *et al.* 2004) or 6-20 animals (Pčola and Adamec 2007). Occasionally, groups of 2-92 animals were observed in the Białowieża Forest, but more frequently groups of 20 animals (65-85%) were observed in this location (Krasińska *et al.* 1997, Pucek *et al.* 2004). Small bull groups occur in all populations and include two animals on average (1-11). A solitary life is led by more than 50% of the bulls (Krasiński and Krasińska 1994, Krasiński *et al.* 1994a, Pucek *et al.* 2004). Large mixed groups of cows, calves and bulls and groups comprised entirely of bulls are observed in winter around feeding sites. The number of groups of different sizes is affected by the size of population. Mean air temperature during the winter period and duration of permanent snow cover influence home ranges of bulls in winter. Mobility of individuals is limited by low temperatures and long-lasting snow cover (Krasińska *et al.* 2000, Pucek *et al.* 2004). Food supplementation can also be responsible for their low mobility and staying in valleys during winter (Krasińska *et al.* 2000). We found that during the winter period, bison remain close to the feeders when supplied with hay. However, supplementary feeding alone cannot represent a sustainable solution, because it causes bison aggregation and may lead to higher parasitic transmission (Ramos *et al.* 2016). Individuals wander the forest constantly due to its high claim to food. In the first year of life, calves eat 8.5 kg per day, while young animals (2-3 years) consume19.5-28.5 kg per day, and adults eat 23-32 kg of fresh food per day. 40% of this food is composed of leaves and sprouts (Gębczyńska and Krasińska 1972, Pucek *et al.* 2004). Feeding habits of European bison were researched mostly in Cejjskijj zakaznik in Russia, Białowieża Forest (Poland and Belarus) and Prioksko-Terrasnyjj reserve in Russia (Pucek *et al.* 2004). 131 plant species, with 27 species of trees and shrubs, 14 species of grasses and sedges and 96 species of dicotyledonous plants were described in the study of Borowski and Kossak (1972) as part of the bison diet in the Polish part of Białowieża Forest. Herbs, grasses and sedges represent 67% and trees and shrubs 33% of the whole diet. All wild-living groups formed in Białowieża Forest in winter are fed with supplementary food, specifically with hay (Krasiński 1978, 1983; Krasiński and Krasińska 1994; Pucek *et al.* 2004).

European bison went extinct in the wild until populations were restored during the 20th century. Today, the species is still listed by the International Union for Conservation of Nature (IUCN Red List of Threatened Species) as a species vulnerable to extinction. Despite of the increasing number of European bison, there are some specific problems regarding their sustainability in human inhabited areas (Hofman-Kamińska and Kowalczyk 2012), low genetic diversity (Oleński *et al.* 2018) and sufficient size of their territory with adequate habitat connectivity (Ziółkowska *et al.* 2016). Expansion of European bison populations is necessary, and analysing long-term data about bison space utilization, habits and movement patterns in existing populations may help to achieve this goal.

The European bison, as an extremely inbred extinct species requires effective management to sustain maximum genetic diversity (Oleński *et al.* 2018). Our results provide better understanding of bison space utilization and location of natural migratory routes during the period of their reintroduction to the Poloniny NP. The findings obtained in this study are beneficial for sustainable management of the European bison and for facilitate and subsequently maintenance migration of bison between neighbouring trans-border herds.

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Diversity of moths communities (Insecta, Lepidoptera) above tree line in Belianske Tatry Mts. (Hlúpy transect), the Western Carpathians

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Abstract. The research is focused on the evaluation of lepidopteran fauna investigated above the tree line in transect Hlúpy hill, which is situated in the central part of the Belianske Tatry Mountains. The investigation was carried out during 2016 and 2017. Light traps were used for trapping. Four to five traps were run simultaneously at different altitudinal gradients during four terms of night trapping. During the field investigation 203 species belonging to 30 families were identified. Many of the species were discovered over night using ultraviolet light. The most numerous test subjects came from the Noctuidae and Geometridae families. In total, 112 (55.72%) species and 2 127 (82.38%) individual moths were captured belonging to these families. A few eurytopic species, mainly *Noctua pronuba*, *Apamea monoglypha* and *Noctua fimbriata* (Noctuidae), were mos common, and significantly raised the proportion of all moth individuals. These three species comprised 46.65% of all individuals collected. The presence of these very abundant species may indicate disturbed habitats following the end of grazing in the 1950-60s.

Key words: Lepidoptera, mountains, alpine zone, subalpine zone, limestone, diversity partitioning

Introduction

The species composition, to a large extent, is due to the character of rock substratum. This can be best seen in the rock swards of the High Tatras, where there are definitely more Lepidoptera species on lime than crystalline substratum (Buszko and Nowacki 2010). In the High Tatras there are two lime areas with remarkable moth communities – the largely inaccessible Červené vrchy in the central Tatras, as well as Belianske Tatry, which is a more suitable area for investigations, due to a location on the edge of Tatras with quick access.

High Tatras National park is one of the best known parks in Slovakia with regard to recent knowledge about moths and butterflies. There is an abundance of research concerns butterflies (Rhopalocera), but few papers deal with each superfamiliy which consist of less known species. While we were focused on all moths except for the well known group, Rhopalocera, we have been trying to assemble scattered studies or only short reports about Belianske Tatry and moths.

In the past, Krampl and Marek (1988) summarized their sightings of the family Geometridae quite thoroughly. The authors mention exact characteristic of all species from this family, including a description of altitudes where specimens were collected. This is important for our assessment of changes which have been occuring over the last 30 years. Many locations that were selected by us, are same as those which have been visited by these authors, though nighttime trapping was not conducted in the same place. Krampl and Marek (1988) conducted their night investigations mostly in the vicinity of Plesnivec – Skalné vráta. This location is similar, but slightly warmer, and about 4 kilometres away from our study area, situated at a lower altitude (1 620 m) equal to that of the easernmost hill at Belianske Tatry.

New knowledge about moth communities in the zone above tree line of the Belianske Tatry range has been put together in our paper. Our results, gained from two years of fieldwork, were compared to those from older studies and unpublished manuscripts from the High Tatras. Our aim is to evaluate changes in species composition in accordance with Krampl and Marek's older study of Geometridae (Krampl and Marek 1988), detect new species in the High Tatras, and an evaluation of the 2016 and 2017 seasons. Comparing should lead to an assessment of how different conditions influence moth communities in alpine habitats.

Material and Methods

Description of the study area

Belianske Tatry constitutes it's own mountain range with a length of 14 km. The highest peaks are Havran (2 152 m), Ždiarska vidla (2 142 m) and Hlúpy (2 061 m). Široké sedlo (1 825 m), in the middle of the range is the lowest peak on this ridge. Nearby, Kopské sedlo (1 750 m) connects this geomorphologic part with the High Tatras. The Zadné Meďodoly valley borders the northeast side of the

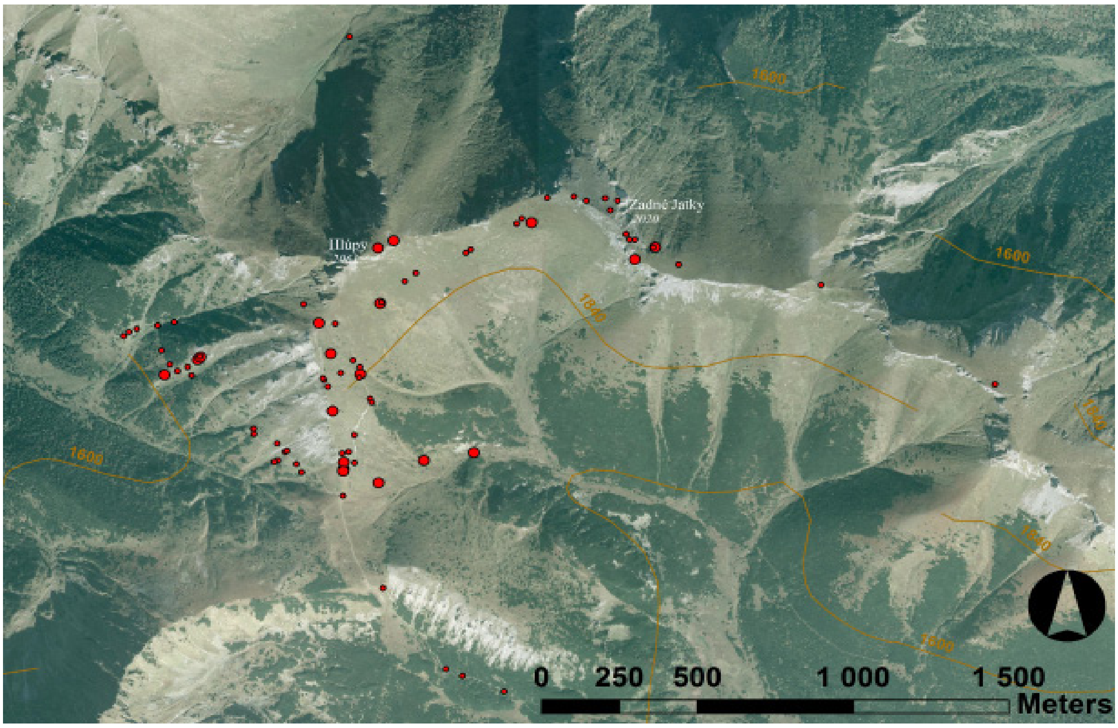


Fig. 1. Study area with 19 sites where the night investigation was realised (bigger dots) and findings of the moths found by netting on evenings, mornings (smaller dots).

mountains and splits Belianske Tatry and the High Tatras. The Predné Meďodoly borders the southwest side. While Belianske Tatry is composed of dolomites and limestone, the High Tatras are mostly formed of granodiorits (Kocian *et al.* 2010).

Predné Meďodoly valley and changes in the landscape structure are described in detail by Boltižiar (2006). A description of the secondary vegetation succession in the Belianske Tatry Mountains three decades after extensive grazing is provided by Hadač (1990).

Our selected study area includes various microhabitats and microclimates with significant altitudinal gradient. It is situated in the middle part of Belianske Tatry (Fig. 1, contain localities Predné Meďodoly, Zadné Meďodoly, Kopské sedlo, Hlúpy, Zadné Jatky, Monkova dolina) with an altitudinal range from 1 600 to 2 061 m. Each sampling site is distinguished by GPS coordinates measured by the Garmin Edge 510. The temperature was measured directly at the study site, (Zadné Jatky, Hlúpy) and other parameters like moisture and wind direction were taken from the Slovak Hydrometeorological Institute (station Tatranská Javorina).

Sampling and processing of moths

In this study, superfamilies were investigated as follows: Hepialoidea, Adeloidea, Gracillarioidea, Yponomeutoidea, Gelechioidea, Pterophoroidea, Choreutoidea, Tortricoidea, Pyraloidea, Lasiocampoidea, Bombycoidea, Geometroidea and Noctuoidea. To collect material in the field bucked light traps were used (UV lights 12V/8W BLB connected by lead-acid batteries 12V/4.5Ah). Chloroform was inserted into the buckets to immobilize the insects and they were transferred to egg cartons for preservation. This method provides almost uniform conditions and results in same time for each sampling site. We worked with 4-5 traps overnight. Because of insufficient time for fast processing material, it was necessary to freeze samples until processing. For exact determination of species, we macerated samples of abdomens in 10% potassium hydroxide and compare genital structures to the literature, using a stereomicroscope and a compound microscope. Afterwards, the preparates were preserved in glycerol filled tubes. The appendix lists which specimens were dissected. Part of the studied material is displayed in the author's private collection or at the Institute of High Mountain Biology Tatranská Javorina unless stated otherwise.

The following literature has been used for the determination of species: Nepticulidae (Laštůvka and Laštůvka 1997; only *Stigmella tatrica* – Tokár *et al.* 2017), Scythridae (Bengtsson 1997), Gelechiidae (Elsner *et al.* 1999; only *Sattleria dzieduszycki* – Povolný 2002), Tortricidae (Razowski 2008; Razowski 2009), Pterophoridae (Nel 2003), Pyralidae and Crambidae (Slamka 2008), Drepanidae, Geometridae (only *Entephria nobiliaria* – Hausmann and Viidalepp 2012), Sphingidae and Notodontidae (Fajčík and Slamka 1996), Noctuidae (Fajčík 1998), resting families with help of an internet source (www.mothdissection.co.uk 2018). With determination of species *Micropterix aureatella*, *Incurvaria vetulella*, *Psychoides verhuella*, *Bijugis bombycella*, *Argyresthia conjugella*, *Elachista argentella*, *E. irenae*, *Biselachista zonulae*, *Coleophora striatipennella*, *Prolita sexpunctella*, *Scrobipalpula diffluella*, lepidopterists Zdenko Tokár; *Phyllonorycter junoniella* Aleš Laštůvka; *Perizoma affinitata*, *Acronicta aceris*, *Noctua janthinana* Marek Dvořák and *Agonopterix astrantiae* Jan Šumpich helped.

Each species collected in the night traps was counted and listed in the matrix chart, and only species observed directly using the entomological net during the evenings or mornings were not included in this quantitative processing (Table 2, Fig. 2, Fig. 3). In Table 2 are included both cases.

Schedule of the field investigations

Altogether, 8 visits in the field were carried out. The samples were collected over a period of two years: July 11, August 20, and September 1 in 2016, and in June 9, July 5, July 19, August 9, and August 15 in 2017. Sampling was conducted twice with the assistance of Zdenko Tokár, and his findings fromJuly 5th 2017 and August 9th 2017 are included in this paper.

11. VII.16 – quite windy during the day, calm and mild, with no wind in the evening, but in the later part of the night, the winds began again.
20. VIII.16 – at noon, sunny. Shortly after noon windier and cloudy. Afternoon to evening, gradually cleared with no wind.
01. IX.16 – afternoon patchy clouds but calm, afternoon to evening calm westerly wind, that stopped after dark though cloud cover increased and it became foggy. The second half of the night, clear but windy.
09. VI.17 – all day patchy cloud - cloudy, silent wind, warm.
05. VII.17 – cooler, windy, patchy cloud – cloudy, but on the peak of the hill and by descending partially silence.
19. VII.17 – afternoon cloudy, in the evening completely clear almost calm, time to time windy over night.
09. VIII.17 – in the morning clear, by rising over the Vyšné Kopské sedlo saddle toward Zadné Jatky created local foggy cloud from the valley. At the peak firstly foggy, letter by descending the fog disintegrated. Warm.
15. VIII.17 – in the evening cloudy, calm, after dark, gradually brightening till completely clear and quite a strong wind and cold over night.

Statistical analysis

For each spot we counted the total number of species (S) and individuals (ni). From the relative abundance of each species, we calculated alfa diversity using Simpson's diversity index which measures the probability that two randomly selected individuals belong to the same species. Formula and ranges of the abundance categories are taken over Losos *et al.* (1984). For other analysis (ANOVA) was used program STATISTICA 8.0 (StatSoft Inc. 2008).

Results

In our field investigation 203 species belonging to 30 families were identified. The majority of species were discovered overnight, using ultraviolet light. Noctuidae and Geometridae, were the most numerous family, and 112 (55.72%) species and 2 127 (82.38%) of all collected moths belonged to these two families (Table 1). The mass occurrence of a few eurytopic species, mainly *Noctua pronuba*, *Apamea monoglypha* and *N. fimbriata* (Noctuidae), significantly raised the proportion of all moth individuals. These three species made up 46.65% of all collected individuals. The presence of these very abundant species may indicate disturbed habitats. All three species develop on different grasses, which are now expanding after the end of extensive grazing (about 1970) by mainly *Calamagrostis cf. varia*. It must be noted that abundance of *A. monoglypha* was approximately 2 times higher, *N. pronuba* 10 times higher, and *N. fimbriata*, 20 times higher on the north side of Zadné Jatky ridge than on the south side; although two comparable study plots were only a few metres apart.

The division of observed species to dominant classes shows an interesting detection. Over 2016, there was the distribution of species with different abundance quite equitable, while in 2017 few very abundant species from eudominant class prevailed. It could also be influenced by one sampling site situated on the north slope, close to ridge Zadné Jatky, with the most spacious radius of ultraviolet light. If we look at species division, there is clear decline in subrecedent class in 2017.

Dominance	species	ni	D
year 2016			
eudominant (> 10%)	*Apamea monoglypha*	260	17.87
	Noctua fimbriata	150	10.31
dominant (5-10%)	*Noctua pronuba*	122	8.39
	Entephria caesiata	118	8.11
	Mesapamea secalis	82	5.64
subdominant (2-5%)	*Dioryctria abietella*	68	4.67
	Eulithis populata	67	4.61
	Udea uliginosalis	48	3.30
	Xestia c-nigrum	35	2.41
	Dasypolia templi	35	2.41
recedent (1-2%)	*Platyptilia sp.*	25	1.72
	Amphipyra berbera	21	1.44
	Triphosa dubitata	19	1.31
	Anaplectoides prasina	17	1.17
	Perizoma minorata	17	1.17
	Xanthorhoe montanata	16	1.10
	Diarsia brunnea	15	1.03
subrecedent (< 1%)	124	290	23.37
year 2017			
eudominant (> 10%)	*Noctua pronuba*	471	41.76
	Udea uliginosalis	156	13.83
	Noctua fimbriata	137	12.15
dominant (5-10%)	*Apamea monoglypha*	65	5.76
subdominant (2-5%)	*Coenotephria salicata*	39	3.46
	Mesotype verberata	39	3.46
	Pharmacis sp.	31	2.75
	Entephria caesiata	25	2.22
recedent (1-2%)	*Mesapamea secalis*	14	1.24
	Triphosa dubitata	14	1.24
	Noctua interposita	12	1.06
subrecedent (< 1%)	53	134	11.08

Tab. 1 The survey of the species according to the scale of classes of dominance, with numbers of the caught individuals (ni) each year and value of dominance.

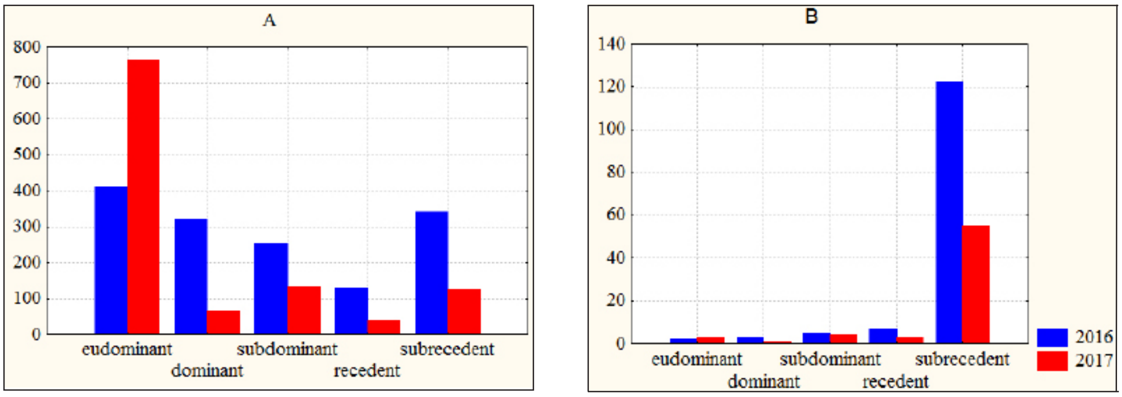


Fig. 2. Number of individuals (A) and species (B) belonging to dominant classes.

The division of observed species to dominant classes shows an interesting detection (Fig. 2). Over 2016, there was the distribution of species with different abundance quite equitable, while in 2017 few very abundant species from eudominant class prevailed. It could also be influenced by one sampling site situated on the north slope, close to ridge Zadné Jatky, with the most spacious radius of ultraviolet light. If we look at species division, there is clear decline in subrecedent class in 2017.

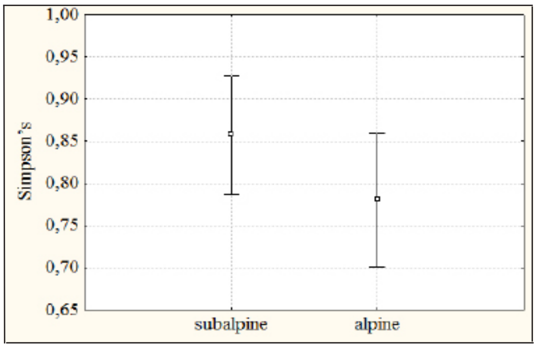


Fig. 3. Mean Simpson's diversity indices (with 95 percent confidence limits) in subalpine and alpine zone (9 and 7 study plots evaluated).

ANOVA analyse shows the differences in Simpson's diversity index (Fig. 3). The lower value of index in alpine zone could also be influenced by infiltration of a few very abundant species from lower altitudes (from the north part).

Description of selected findings

Rare species typical for high altitudes in Tatras

Stigmella tatrica (Tokár, Laštůvka and van Nieukerken, 2017) – Nepticulidae
Material: 1 ex. 9. VIII. 2017, Zadné Jatky

Lampronia splendidella (Heinemann, 1870) – Prodoxidae
Material: 7 ex. 5. VII. 2017, Zadné Jatky
Moths were observed on the ridge and south slope of Zadné Jatky peak and one under the Hlúpy near the saddle directed to Zadné Jatky at the altitude approximately 1 950 m.

Callisto coffeella (Zetterstedt, 1839) – Gracilariidae
Material: 2 ex. 5. VII. 2017, Belianska kopa
Moths netted on the south foot of Belianska kopa over daytime.

Kessleria zimmermanni (Nowicki, 1864) – Yponomeutidae
Material: 1 ex. 20. VII. 2017, Zadné Jatky
Only one moth was netted in the early morning hours on the ridge of Zadné Jatky close to the peak. Endemic species of Tatras.

Coleophora svenssoni Baldizzone, 1985 – Coleophoridae
Material: the caterpillars in cases feeding on *Astragalus frigidus*, 20. VIII. 2016, Zadné Jatky
Boreomontane species occurs, except for Belianske Tatry Mts., only in the Alps and Lapland. The population in Belianske Tatry is the biggest in the Carpathians. Other informations were evaluated by Marek and Krampl (1990).

Sattleria dzieduszyckii (Nowicki, 1864) – Gelechiidae
Material: 1 ex. 19. VII. 2017, Zadné Jatky, UV
Alpine species occuring mainly on granit basis of High and Low Tatras in range 1 700 – 1 900 m. (Tokár *et al.* 1996). Probably not native here, only infiltrated from the neighbouring granite zone.

Epinotia mercuriana (Frölich, 1830) – Tortricidae
Material: 2 ex. 20. VIII. 2016, Zadné Jatky; 19. VII. 2017, Kopské sedlo
On an altitude of around 1 750 metres was recorded already in 19. VII., while on the ridge of the Zadné Jatky was recorded one month later, 20. VIII. At the lower altitudes in subalpine zone, shows low abundance, at the ridges was one of the most abundant species.

Argyroploce noricana (Herrich-Schäffer, 1854) – Tortricidae
Material: 5 ex. 5. VII. 2017, Zadné Jatky
Arctoalpine species. Observed solely on the north slope of Zadné Jatky, with sparse vegetation. The most common moth in arctic tundra (Kullberg *et al.* 2013).

Eupithecia undata (Freyer, 1840) – Geometridae
Material: 1 ex. 11. VII. 2016, Kopské sedlo

One of the most remarkable species. We have discovered only a second individual in Tatras. Very similar to species *E. fennoscandica* occurring on cliffs in Lapland (Mironov 2003).

New species or unexpected species

The species have been compared to manuscripts of Slovak lepidopterists to reveal new species. The new species are signed by (*).

**Phylloporia bistrigella* (Haworth, 1828) – Incurvariidae
Material: 1 ex. 5. VII. 2017, Hlúpy, Tokár leg.
Moth has been found near the path leading under the peak Hlúpy, approximately at the altitude of 1 950 m. A very surprising finding in such high altitude, where the host plant absents. The species is feeding on birches. Third finding in Slovakia.

**Psychoides verhuella* Bruand, 1851 – Tineidae
Material: 1 ex. 19. VII. 2017, Zadné Meďodoly
Ocurring mainly in lower altitudes on limestones where *Asplenium* grows.

**Scrobipalpula diffluella* (Frey, 1870) – Gelechiidae
Material: 1 ex. 11. VII. 2016, Hlúpy, UV; 1 ex. 5. VII. 2017, Hlúpy
The first moth flew to the light trap under Hlúpy – in altitude 1 860 m., the second was found on a similar spot, but approximately 100 metres higher. Third place in Slovakia where the species occurs (Tokár *et al.* 2015).

**Pennithera firmata* (Hübner, 1822) – Geometridae
Material: 1 ex. 11. VII. 2016, Zadné Meďodoly, UV

**Venusia blomeri* (Curtis, 1832) – Geometridae
Material: 1 ex. 11. VII. 2016, Hlúpy, UV
One individual attracted to light. Quite rare species developing on *Ulmus*. The moth had to infiltrate from neighbouring area, where the host plant grows, probably Ždiar.

**Cucullia asteris* (Denis and Schiffermüller, 1775) – Noctuidae
Material: 1 ex. 11. VII. 2016, Predné Meďodoly, UV
Although the species ascends to the mountains, the genus *Cucullia* is more thermophilous.

**Lacanobia aliena* (Hübner, 1809) – Noctuidae
Material: 1 ex. 11. VII. 2016, Predné Meďodoly, UV; 1 ex. 19. VII. 2017, Zadné Meďodoly, UV
*Hadena compta (Denis and Schiffermüller, 1775) – Noctuidae
Material: 1 ex. 11. VII. 2016, Predné Meďodoly, UV

**Mythimna vitellina* (Hübner, 1808) – Noctuidae
Material: 3 ex. 1. IX. 2016, Kopské sedlo, Hlúpy, UV
Migrant from the Mediterranean, more common the last 20 years.

**Noctua interjecta* Hübner, 1803 – Noctuidae
Material: 4 ex. 19. VII. 2017, Zadné Jatky, UV
Moths attracted to light on the ridge of Zadné Jatky. The species is spreading eastwards. So far, the sixth locality of the species in Slovakia.

Catocala sponsa (Linnaeus, 1767) – Noctuidae
Material: 1 ex. 11. VII. 2016, Predné Meďodoly, UV
Very surprising finding in high mountains. The species occurs mainly in warm oak forests.

Amphipyra berbera Rungs, 1949 – Noctuidae
Material: 21 ex. 11. VII. 2016, more localities, UV; 2 ex. 19. VII. 2017, UV

**Chersotis rectangula* (Denis and Schiffermüller, 1775) – Noctuidae
Material: 1 ex. 19. VII. 2017, Zadné Meďodoly, UV
Local and rare species mainly in warm areas.

Expected, but not confirmed species

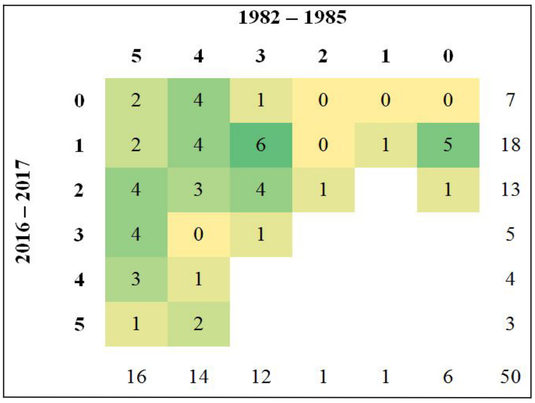
Scythris oelandicella Müller-Rutz, 1922 – Scythrididae – all our dissected *Scythrids* belonged to species *S. fallacella*

Colostygia austriacaria ssp. *distans* (Krampl and Marek 1991) – Geometridae

Discussion

In the study by Krampl and Marek (1988), species are divided into three categories according to the altitudinal level: A – montane (1 000 – 1 450 m), B – subalpine (1 450 – 1 800 m) and C – alpine (1 800 – 2 000 m). We focused specifically on the subalpine and alpine zone, but our range of altitudes was slightly different: subalpine (1 550 – 1 850 m) and alpine level (1 850 – 2 000 m). In addition, our data were transformed for the purpose of comparison. Also worth noting is that the most significant stenotopic species from the Geometridae family are often heliophilous at high altitudes and these species are not possible to find at night. This means that great portion of Geometridae stenotopic species in our study area might be compared.

Krampl and Marek (1988) collected 139 Geometrids from their entire study site in Belianske Tatry. At an altitude of above 1 450 m, 71 species were confirmed (69 from subalpine and 14 from alpine zone). Our investigation (Table 2) revealed 41 Geometrids



		1982 – 1985						
		5	**4**	**3**	**2**	**1**	**0**	
2016 – 2017	**0**	2	4	1	0	0	0	7
	1	2	4	6	0	1	5	18
	2	4	3	4	1		1	13
	3	4	0	1				5
	4	3	1					4
	5	1	2					3
		16	14	12	1	1	6	50

Table 2. Pivot table for the family Geometridae. Bold numbers represent abundance categories, where 0 = no individual; 1 = 1 ni; 2 = 2-5 ni; 3 = 6-20 ni; 4 = 20-50 ni; 5 = above 50 ni (Krampl and Marek 1988). Shaded numbers represent number of occasions. Total compared species – 50.

from altitudes of above 1 600 m (33 from subalpine and 23 from alpine zone). While we focused mainly on the zone above the tree line, few species from the altitude of 1 450 – 1 600 could be overlooked. For instance two – *Perizoma incultaria* (Herrich-Schäffer, 1848) and *Ematurga atomaria* (Linnaeus, 1758) were observed only in this zone. *Colostygia turbata* (Hübner, 1799) was found at this and only one other site, bringing the total species observed to 43.

We have not confirmed the presece of seven species found by Krampl and Marek (1988) within our study area: *Colostygia kollariaria* (Herrich-Schäffer, 1848), *Melanthia alaudaria* (Freyer, 1846), *Spargania luctuata* (Denis and Schiffermüller, 1775), *Eupithecia indigata* (Hübner, 1813), *E. tantillaria* Boisduval, 1840, *Odezia atrata* (Linnaeus, 1758) and *Odontopera bidentata* (Clerck, 1759). It should be mentioned that the rare species *M. alaudaria* have been observed by us at lower altitudes (up to 1 220 m). measured at Monková dolina. On June 9, 2017 it was the most abundant species observed in Javorová dolina, while one year ago only one individual was observed.

In contrast, according to our investigation, six new species were identified that were not collected by Krampl and Marek (1988) in Belianské Tatry: *Biston betularia* 1 (Linnaeus, 1758), *Campaea margaritaria* 2 (Linnaeus, 1761), *Chloroclysta miata* 3 (Linnaeus, 1758), *Pennithera firmata* 4 (Hübner, 1822), *Venusia blomeri* 5 (Curtis, 1832) and the higher stated *Ematurga atomaria* 6 (Linnaeus, 1758). These are species that develop on plants generally not native to the zone above the tree line, including: *Betula* 1; *Fagus* and other broadleaf trees and shrubs 2; *Vaccinium, Salicaceae, Betulaceae* 3; *Pinus* 4; *Ulmus* 5 and diverse plant food (polyphagous species) 6 (Patočka and Kulfan 2009). Therefore these species, except for *E. atomaria* are certainly not native to the study area and must have flown here from another location.

When our catalogue of species is compared to the from the paper by Turčáni *et al.* (1997) conducted in a neighbouring area in the Červené vrchy mountains, we found significant variation. A relative number of big species from Noctuidae are less abudant, while the authors also observe higher relative numbers of smaller species (for instance from the families Gelechiidae, Coleophoridae). This data could indicate changes in moth communities. The opposite situation seems to be occuring in the lowlands, where bigger species disappear more rapidly than small species (pers. comm. Buschmann, Liška or other lepidopterists).

Many species with high ecological value, that are, generally very common, have been confirmed. For instance *Plutella xylostella* (Linnaeus, 1758) and *Autographa gamma* (Linnaeus, 1758) are common and abundant almost everywhere in Slovakia, without any special habitat requirements. Sightings of some nocturnal moth species in our study area were remarkable and unexpected. Mainly finding of thermophilous Noctuid *Catocala sponsa* (Linnaeus, 1767), which is very rare in the mountains. It is spread mainly in oak forests of south Slovakia. Many of the observed species are typical for mountain spruce forests, which surround our study area. The largest category is represented by subalpine and alpine species.

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APPENDIX

Appendix 1. Checklist of observed species: direct observations are not highlighted (+), findings from the light traps are bolded (**+**), dissected species (D), leg. et coll. Zdenko Tokár (ZT).

	Supalpine zone					**Alpine zone**				**Date**		**Note**
Family Species	1600 – 1650	1650 – 1700	1700 – 1750	1750 – 1800	1800 – 1850	1850 – 1900	1900 – 1950	1950 – 2000	2000 – 2061	2016	2017	
Micropterigidae												
Micropterix aureatella (Scopoli, 1763)	+							+			5. VII	
Hepialidae												
Pharmacis fusconebulosa (de Geer, 1778)		**+**					+			11. VII		
Ph. carna (Denis & Schiffermüller, 1775)		**+**		**+**		**+**				11. VII		
Pharmacis sp.		**+**		**+**				**+**			19. VII	
Hepialus humuli (Linnaeus, 1758)				+							19. VII	
Nepticulidae												
Stigmella aeneofasciella (Herrich-Schäffer, 1855)									+		9. VIII	ZT
S. arbusculae (Klimesch, 1951)								+			5. VII	ZT
S. tatrica (Tokár, Laštůvka & van Nieukerken, 2017)								+			9. VIII	
Adelidae												
Cauchas rufimitrella (Scopoli, 1763)		+									5. VII	D
Nematopogon robertella (Clerck, 1759)		**+**								19. VII		
Prodoxidae												
Lampronia rupella (Denis & Schiffermüller, 1775)							+			12. VII		
L. splendidella (Heinemann, 1870)								+	+		5. VII	
Incurvariidae												
Incurvaria vetulella (Zetterstedt, 1839)						+	+				5. VII 20. VII	D
I. praelatella (Denis & Schiffermüller, 1775)			+							11. VII		D
Phylloporia bistrigella (Haworth, 1828)							+				5. VII	ZT
Psychidae												
Bijugis bombycella (Denis & Schiffermüller, 1775)								+			5. VII	
Epichnopterix sp.	+										9. VI	

Tineidae												
Psychoides verhuella (Bruand, 1851)		+									19. VII	
Gracillariidae												
Callisto coffeella (Zetterstedt, 1839)		+									5. VII	
Phyllonorycter hilarella (Zetterstedt, 1839)	+										9. VI	
Ph. junoniella (Zeller, 1846)									+	20. VIII		
Yponomeutidae												
Kessleria zimmermanni (Nowicki, 1864)								+			20. VII	
Swammerdamia compunctella Herrich-Schäffer, 1855							+				5. VII	D
Argyresthiidae												
Argyresthia glabratella (Zeller, 1847)							+				5. VII	ZT
A. conjugella Zeller, 1839		+		+				+		11. VII	19. VII	D
Plutellidae												
Plutella xylostella (Linnaeus, 1758)		+	+	+	+	+	+	+	+	11. VII 20. VIII	5. VII	
Rhigognostis marmorosella (Wocke, 1850)							+				9. VI	
Glyphipterigidae												
Glyphipterix bergstraesserella (Fabricius, 1781)			+				+			11. VII	5. VII	
Depressariidae												
Agonopterix astrantiae (Heinemann, 1870)		+								1. IX		
A. doronicella (Wocke, 1849)	+									1. IX		
Elachistidae												
Elachista exactella (Herrich-Schäffer, 1855)								+			5. VII	ZT
E. adscitella Stainton, 1851		+									19. VII	
E. albifrontella (Hübner, 1817)	+										19. VII	
E. argentella (Clerck, 1759)	+										9. VI	
E. dimicatella Rebel, 1903	+		+	+	+		+			11. VII	5. VII 19. VII	
E. irenae Buszko, 1989			+						+	11. VII	5. VII 9. VIII	
Biselachista zonulae Sruoga, 1992	+		+				+	+	+	20. VIII	5. VII 19. VII 9. VIII	
Ethmiidae												
Orophia ferrugella (Denis & Schiffermüller, 1775)				+						12. VII		
Scythrididae												
Scythris fallacella (Schläger, 1847)	+		+	+				+		11. VII 20. VIII	19. VII 9. VIII	D D
Coleophoridae												

Coleophora frischella (Linnaeus, 1758)						**+**				11. VII		D
C. svenssoni Baldizzone, 1985									+	20. VIII		
C. sylvaticella Wood, 1892					+					11. VII		D
C. virgaureae Stainton, 1857		**+**	**+**	+		**+**				11. VII		D
C. striatipennella Nylander, 1848								+			9. VIII	
C. nubivagella Zeller, 1849								+	+	12. VII	5. VII	
Gelechiidae												
Teleiopsis bagriotella (Duponchel, 1840)		**+**	**+**	+				+		11. VII 20. VIII		
Prolita sexpunctella (Fabricius, 1794)									+		5. VII	D
Scrobipalpula diffluella (Frey, 1870)						**+**	+			11. VII	5. VII	
Sattleria dzieduszyckii (Nowicki, 1864)								**+**			19. VII	D
Acompsia tripunctella (Denis & Schiffermüller, 1775)		**+**	+	**+**						11. VII 20. VIII	19. VII	D
Tortricidae												
Aethes smeathmanniana (Fabricius, 1781)				+			+			11. VII	5. VII	
Eana osseana (Scopoli, 1763)		+		**+**	**+**	**+**	+	**+**		11. VII 20. VIII 1. IX	19. VII 15. VIII	
E. argentana (Clerck, 1759)							**+**			1. IX		
E. penziana (Thunberg & Becklin, 1791)		**+**						**+**		1. IX	19. VII	D
Eulia ministrana (Linnaeus, 1758)									+		5. VII	
Clepsis rogana (Guenée, 1845)		+								20. VIII		
C. senecionana (Hübner, 1819)		+									9. VI	
Aterpia anderreggana Guenée, 1845				+			+	+		12. VII	5. VII	
A. corticana (Denis & Schiffermüller, 1775)			**+**							11. VII		
Apotomis sauciana (Frölich, 1828)								+			5. VII	ZT
Phiaris schulziana (Fabricius, 1776)								+			5. VII	
Ph. bipunctana (Fabricius, 1794)		**+**								11. VII		
Argyroploce noricana (Herrich-Schäffer, 1854)							+	+			5. VII	
Eriopsela quadrana (Hübner, 1813)	+					+					9. VI	
Epinotia mercuriana (Frölich, 1830)			+	+		+	+	+	+	20. VIII	19. VII 9. VIII	
E. tedella (Clerck, 1759)			+	**+**		+				11. VII	5. VII	
Zeiraphera griseana (Hübner, 1799)	**+**	**+**								1. IX		

Eucosma aspidiscana (Hübner, 1817)	+		+	+						11. VII	9. VI	
Epiblema turbidana (Treitschke, 1835)	+										19. VII	D
Pseudococcyx mughiana (Zeller, 1868)						+					5. VII	
Ancylis myrtillana (Treitschke, 1830)	+	+								11. VII	9. VI	
Lathronympha strigana (Fabricius, 1775)	+	+	+	+	+	+				11. VII	19. VII 15. VIII	
Dichrorampha montanana (Duponchel, 1843)				+			+			20. VIII	5. VII	D
Choreutidae												
Anthophila fabriciana (Linnaeus, 1767)			+							20. VIII		
Epermeniidae												
Phaulernis fulviguttella (Zeller, 1839)	+			+		+	+				5. VII	
Pterophoridae												
Platyptilia calodactyla (Denis & Schiffermüller, 1775)				+						11. VII		
Platyptilia sp.		+	+			+				11. VII		
Pyralidae												
Dioryctria abietella (Denis & Schiffermüller, 1775)	+	+	+	+		+				11. VII 1. IX		
Crambidae												
Gesneria centuriella (Denis & Schiffermüller, 1775)						+				11. VII		
Eudonia vallesialis (Duponchel, 1832)							+	+			5. VII 19. VII	
E. sudetica (Zeller, 1839)		+	+	+		+				11. VII 20. VIII		
Crambus lathoniellus (Zincken, 1817)						+				11. VII		
Catoptria permutatellus (Herrich-Schäffer, 1848)						+				11. VII		D
C. radiella (Hübner, 1813)		+	+	+		+		+	+	11. VII	9. VIII	
C. petrificella (Hübner, 1796)	+			+	+	+		+	+	11. VII	5. VII 19. VII	
Orenaia alpestralis (Fabricius, 1787)		+	+				+			11. VII	5. VII 19. VII	
Udea alpinalis (Denis & Schiffermüller, 1775)	+	+	+	+				+	+	11. VII	5. VII 19. VII	
U. uliginosalis (Stephens, 1834)		+	+	+		+	+	+	+	11. VII	5. VII 19. VII 15. VIII	
U. decrepitalis (Herrich-Schäffer, 1848)		+								11. VII		
Udea sp.						+				11. VII		
Lasiocampidae												
Trichiura crataegi (Linnaeus, 1758)							+			1. IX		
Cosmotriche lobulina (Denis & Schiffermüller, 1775)				+							19. VII	

Sphingidae												
Agrius convolvuli (Linnaeus, 1758)							+	+	+	1. IX	15. VIII	
Hyles gallii (Rottemburg, 1775)				+						11. VII		
Drepanidae												
Thyatira batis (Linnaeus, 1758)		+								11. VII		
Geometridae												
Biston betularia (Linnaeus, 1758)				+						11. VII		
Alcis repandata (Linnaeus, 1758)						+				11. VII		
Ematurga atomaria (Linnaeus, 1758)	+										9. VI	
Campaea margaritaria (Linnaeus, 1761)				+						11. VII		
Charissa glaucinaria (Hübner, 1799)			+							11. VII		
Elophos dilucidaria (Denis & Schiffermüller, 1775)		+									19. VII	D
E. vittaria (Thunberg & Sebaldt, 1792)				+						11. VII		D
E. operaria (Hübner, 1813)								+			19. VII	
Psodos quadrifaria (Sulzer, 1776)				+			+	+			5. VII	
Glacies canaliculata (Hochenwarth, 1785)									+		5. VII	
G. noricana (Wagner, 1898)						+				12. VII		
G. alpinata (Scopoli, 1763)									+		5. VII	
Xanthorhoe designata (Hufnagel, 1767)	+										9. VI	
X. spadicearia (Denis & Schiffermüller, 1775)	+	+								11. VII	9. VI	
X. montanata (Denis & Schiffermüller, 1775)		+	+	+		+		+		11. VII	19. VII	
X. fluctuata (Linnaeus, 1758)				+						11. VII		
Epirrhoe molluginata (Hübner, 1813)						+				11. VII		
Entephria nobiliaria Herrich-Schäffer, 1852								+			19. VII	D
E. flavicinctata (Hübner, 1813)								+			19. VII	D
E. caesiata (Denis & Schiffermüller, 1775)	+	+	+	+	+	+	+	+		11. VII 1. IX	19. VII 15. VIII	
Coenotephria salicata (Denis & Schiffermüller, 1775)		+	+	+				+		11. VII	19. VII	
Eulithis prunata (Linnaeus, 1758)	+	+		+						1. IX		
E. populata (Linnaeus, 1758)	+	+	+	+	+	+	+	+		20. VIII 1. IX	9. VIII 15. VIII	
Ecliptopera silaceata (Denis & Schiffermüller, 1775)								+			19. VII	
Chloroclysta miata (Linnaeus, 1758)	+							+		1. IX		

Dysstroma citrata (Linnaeus, 1761)	+	+								1. IX		
D. truncata (Hufnagel, 1767)	+	+	+	+				+		11. VII 1. IX	19. VII	
Pennithera firmata (Hübner, 1822)	+									1. IX		
Thera variata (Denis & Schiffermüller, 1775)	+		+							11. VII 1. IX		D
Colostygia turbata (Hübner, 1822)								+			19. VII	
Hydriomena furcata (Thunberg & Borgstroem, 1784)	+									1. IX		
Triphosa dubitata *(Linnaeus, 1758)*		+	+	+		+	+	+		11. VII 1. IX	19. VII 15. VIII	
Perizoma affinitata (Stephens, 1831)		+								11. VII		
P. alchemillata (Linnaeus, 1758)				+						11. VII		D
P. minorata (Treitschke, 1828)		+	+		+	+		+		11. VII	5. VII 19. VII	
P. albulata (Denis & Schiffermüller, 1775)				+		+				11. VII		
Mesotype verberata (Scopoli, 1763)		+	+	+	+	+	+	+	+	20. VIII 1. IX	9. VIII 15. VIII	
Eupithecia pyreneata Mabille, 1871				+						11. VII		D
E. undata (Freyer, 1840)				+						11. VII		D
E. veratraria Herrich-Schäffer, 1848		+		+						11. VII		D
E. absinthiata (Clerck, 1759)				+						11. VII		D
Eupithecia sp.				+						11. VII		
	+									1. IX		
Aplocera praeformata (Hübner, 1826)	+	+	+	+		+	+	+		11. VII 1. IX	19. VII 15. VIII	
Venusia blomeri (Curtis, 1832)						+				11. VII		
V. cambrica Curtis, 1839		+								11. VII		
Notodontidae												
Notodonta ziczac (Linnaeus, 1758)				+							19. VII	
Noctuidae												
Acronicta aceris (Linnaeus, 1758)				+						11. VII		
Catocala sponsa (Linnaeus, 1767)		+								11. VII		
Scoliopteryx libatrix (Linnaeus, 1758)	+				+					1. IX	15. VIII	
Polychrysia moneta (Fabricius, 1787)	+	+								1. IX		
Diachrysia chrysitis (Linnaeus, 1758)						+				11. VII		
Autographa gamma (Linnaeus, 1758)		+	+		+	+				11. VII	19. VII 15. VIII	
A. pulchrina (Haworth, 1809)			+							11. VII		

A. bractea *(Denis & Schiffermüller, 1775)*		+		+		+	+			11. VII 1. IX		
Cucullia umbratica (Linnaeus, 1758)			+	+						11. VII	19. VII	
C. asteris (Denis & Schiffermüller, 1775)			+							11. VII		
Amphipyra berbera Rungs, 1949		+	+	+		+		+		11. VII	19. VII	
A. tragopoginis (Clerck, 1759)	+		+	+		+		+		11. VII 1. IX	19. VII	
Charanyca ferruginea (Esper, 1785)			+							11. VII		
Euplexia lucipara (Linnaeus, 1758)		+								11. VII		
Hyppa rectilinea (Esper, 1788)		+	+	+		+				11. VII		
Cosmia trapezina (Linnaeus, 1758)				+						11. VII		
Sunira circellaris (Hufnagel, 1766)								+		1. IX		
Dasypolia templi (Thunberg & Sebaldt, 1792)	+	+		+	+		+	+		1. IX	15. VIII	
Lithophane socia (Hufnagel, 1766)				+			+			1. IX		
Mniotype adusta (Esper, 1790)			+	+		+				11. VII		
Apamea monoglypha (Hufnagel, 1766)	+	+	+	+		+		+		11. VII 1. IX	19. VII	
A. crenata (Hufnagel, 1766)		+	+	+		+				11. VII		
A. lateritia (Hufnagel, 1766)		+	+	+		+				11. VII		
A. rubrirena (Treitschke, 1825)		+	+	+						11. VII	19. VII	
Oligia strigilis (Linnaeus, 1758)				+						11. VII		D
Mesapamea secalis (Linnaeus, 1758)		+	+	+		+		+		11. VII	19. VII	D
Photedes captiuncula (Treitschke, 1825)	+	+									19. VII	
Lacanobia aliena (Hübner, 1809)		+		+						11. VII	19. VII	
L. oleracea (Linnaeus, 1758)	+									1. IX		
L. thalassina (Hufnagel, 1766)			+							11. VII		
Hada plebeja (Linnaeus, 1761)			+	+						11. VII		
Hadena compta (Denis & Schiffermüller, 1775)			+							11. VII		
H. confusa (Hufnagel, 1766)				+							19. VII	
Melanchra persicariae (Linnaeus, 1761)			+			+				11. VII		
Mamestra brassicae (Linnaeus, 1758)		+		+	+	+		+	+	11. VII	19. VII 15. VIII	
Polia hepatica (Clerck, 1759)			+							11. VII		
Mythimna conigera (Denis & Schiffermüller, 1775)				+						11. VII		

M. ferrago (Fabricius, 1787)				+					11. VII	
M. albipuncta (Denis & Schiffermüller, 1775)	+			+					1. IX	
M. vitellina (Hübner, 1808)				+				+	1. IX	
Cerapteryx graminis (Linnaeus, 1758)				+				+	11. VII 1. IX	
Eriopygodes imbecilla (Fabricius, 1794)		+		+					11. VII	19. VII
Diarsia mendica (Fabricius, 1775)		+	+	+		+		+	11. VII	19. VII
D. brunnea (Denis & Schiffermüller, 1775)		+	+	+		+			11. VII	
Noctua pronuba *(Linnaeus, 1758)*	+	+	+	+	+	+	+	+	11. VII 1. IX	19. VII 15. VIII
N. interposita (Hübner, 1790)	+	+		+		+	+	+	11. VII 1. IX	19. VII
N. fimbriata (Schreber, 1759)	+	+	+	+		+		+	11. VII 1. IX	19. VII
N. interjecta Hübner, 1803								+		19. VII
N. janthina (Denis & Schiffermüller, 1775)						+			11. VII	
Chersotis rectangula (Denis & Schiffermüller, 1775)				+						19. VII
Ch. cuprea (Denis & Schiffermüller, 1775)		+					+		1. IX	
Rhyacia simulans (Hufnagel, 1766)				+					11. VII	
Epipsilia grisescens (Fabricius, 1794)	+	+							1. IX	
Standfussiana lucernea (Linnaeus, 1758)			+			+		+	11. VII	19. VII
Eurois occulta (Linnaeus, 1758)			+						11. VII	
Opigena polygona (Denis & Schiffermüller, 1775)				+				+	1. IX	19. VII
Xestia speciosa (Hübner, 1813)		+	+						11. VII	
X. alpicola (Zetterstedt, 1839)				+						19. VII
X. c-nigrum (Linnaeus, 1758)	+	+		+	+		+	+	11. VII 1. IX	15. VIII
X. triangulum (Hufnagel, 1766)		+	+	+					11. VII	19. VII
X. baja (Denis & Schiffermüller, 1775)		+							11. VII	
Anaplectoides prasina (Denis & Schiffermüller, 1775)		+	+	+		+			11. VII	19. VII
Agrotis ipsilon (Hufnagel, 1766)	+	+		+			+	+	1. IX	19. VII
Panthea coenobita (Esper, 1785)		+							11. VII	
Calliteara pudibunda (Linnaeus, 1758)						+			11. VII	
Arctia caja (Linnaeus, 1758)	+			+					1. IX	
Callimorpha dominula (Linnaeus, 1758)			+						11. VII	

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Cottus poecilopus Heckel, 1836, in the river Javorinka, the Tatra mountains, Slovakia

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Abstract. This study focuses on the *Cottus poecilopus* from the river Javorinka in the north-east High Tatra mountains, Slovakia. The movement and residence of 75 Alpine bullhead in the river were monitored and carefully recorded using GPS coordinates. A map representing their location in the river was generated. This data was collected in the spring and summer of 2016 and in the autumn of 2017. Body length and body weight of 67 Alpine bullheads were measured. The largest bullheads were collected between 860-880 m a.s.l.. Bulheads found at the 1 000-1 100 m a.s.l. were significantly smaller. In favourable microhabitats of 850-900 m, mainly large light shade bullheads were collected. Fish monitoring in Javorinka was conducted aproximatelly 55 years following previous monitoring of this river performed by Václav and Sylvia Dyk.

Key words: Alpine bullhead, Javorinka river, Tatra Mountains, West Carpathians

Introduction

This work confims and monitors the presence of alpine bullhead (*Siberian sculpin*) in the Javorinka high-mountain stream in Belianske Tatras. The Javorinka stems from under the Javorový peak, 2 417.5 m a.s.l. and flows into the Biela voda (Bialka) river, which flows into the Baltic Sea north of Poland, east of Sweden and into the Atlantic Ocean. This work seeks to enhance current knowledge of bullheads, and the aim is to use this data to address ecological problems facing these fish today for the protection of their population and the preservation of the biodiversity of Europe and Slovakia.

Many authors have focused on the observation of fish in high altitude areas of the Tatra mountains. The German polyhistorian Johan Baptista Grossinger (1794) observed migrating salmon and eels in the influent streams of the river Dunajec in Slovakia. Reisinger (1830) and Kornhuber (1863) also noted fish populations in the Tatras. Fritsch (1859) and Mihályi (1954) summarized early information on fish from Bohemia and Hungary, respectively. In Tatranská Javorina under Muráň mountain, a small fish nursery was built by Christian Kraft von Hohenlohe around 1930. The most comprehensive studies on fish from the Tatra mountains were written by professor Václav Dyk (1957; 1961), Dyk and Dyková (1964a,b; 1965), who studied altitudinal distribution of fish, describing the highest points where fish were found. His studies on fish were likely the most complex studies of their kind during that period. Along with his wife Sylvia, who illustrated his studies, they published the first realistic studies on fish from the Tatra mountains including the river Javorinka (Dyk and Dyková 1964a). Ferianc (1948) published the first Slovakian nomenclature of fish in 1948. Eugen K. Balon (1964; 1966) was the next famous ichthyologist who became a recognised expert in the fish fauna of the streams of the Tatra mountains, the river Poprad, and various high mountain lakes. Data on fish species of the Dunajec and Poprad rivers was recorded by Kux and Weisz (1960). The next list of Tatra fish was published by Žitňan (1974), who found 26 species of fish and one species of lamprey in the Tatra mountains. The next studies of Tatra fish can be found in Holčík and Mihalík (1971) or Holčík and Nagy (1986). Salmon and bullhead are also mentioned in many general publications on fish from Slovakia – ex. Šimek (1954; 1959), Holčík *et al.* (1965), Oliva *et al.* (1968), and Sedlár *et al.* (1983).

Today, the ichthyofauna of alpine and mountain rivers and lakes is negatively influenced by fish farming at lower elevations, sport fishing and nonnative invasive species such as Brook trout. From year to year, climate change seems to be a very influential factor on fish dispersion. New species shift to higher elevations where they may act as concurrence or at least as a stress factor on the original species. For example, in the past, *Cottus gobio* were considered to be a more threatened species than *C. poecilopus*, but today the opposite is true.

This study is a step toward understanding the history of a group of Javorinka alpine bullhead over the last 50 – 100 years, as well as the history of these freshwater cottids and salmons; their ecological relatives in the river. The family Cottidae belongs to the suborder Cottoidei. In its entirety, Cottoidei is comprised of eleven families, and its distribution encompasses all the world's oceans. The diversity of the family Cottidae (sculpins) is the highest in the marine environments of the northern Pacific (Froese and Pauly 2003). Freshwater cottids outside Lake Baikal are confined to four genera: Mesocottus, Trachidermus, Myoxocephalus, and Cottus, which includes 40 species found within North America and Eurasia. Through these adaptive radiations, a tremendous diversity of morphological, ecological, physiological and life historical traits now exist in freshwater sculpins. A common anatomical feature for cottids, and also for Baikalian cottoids, is the lack of a swimming bladder, which determines their typically benthic life-style. Only three species of *Cottus* are widespread in Eurasia. The Alpine bullhead *C. poecilopus* is a cold-adapted fish, which inhabits rivers and lakes from the Russian Far East to restricted areas of Northern and Eastern Europe. The European common bullhead *C. gobio* is also a cold-adapted species, but in mountain areas it normally lives downstream of the *C. poecilopus* range (Witkowski 1979). Both *C. poecilopus* and *C. gobio* also thrive in the brackish coastal waters of the Baltic Sea (in salinities up to 6 and 7 p.p.t, Andreasson 1972). Alpine bullhead is a very polymorphic species, and alpine bullheads of Slovakian origin are members of the Sudeten - Carpathian group.

The majority of freshwater sculpins belong to the genus *Cottus*. This genus is suitable for studies of the evolutionary biology, fresh water and local habitual adaptations, as well as speciation in fishes derived from marine environments. Origins of the biodiversity in the *Cottus* species are very suitable for a general understanding of the phylogeny of coldwater adapted freshwater fishes in the Northern Hemisphere (Sideleva and Goto 2009). Like salmonids, bullheads are an important component of fish communities in rivers and lakes distributed in the middle to high latitudinal regions (Dyk 1961; Balon 1964; 1966). The species richness (64 species) of *Cottus* is similar to those of the salmonids, *Salvelinus* (56 species), and *Coregonus* (72 species) and exceeds those of *Phoxinus* (25 species) and *Thymallus* (13 species), all of which share Northern Hemisphere ranges similar to that of the *Cottus* species (Eschmeyer and Fricke 2010). Cottus species show regional specificity in their geographic distribution, with 16 species living in Europe, and they are generally sedentary (Oliva *et al.* 1968, Natsumeda 2007), tending to be isolated to specific areas within each habitat (Kozlowski *et al.* 2017). Because their local populations may adapt locally, a species may diverge both ecologically and morphologically. Such diverse features of individuals have contributed to the high species richness in this local region (Nolte *et al.* 2006). *Cottus* species inhabit a variety of freshwater environments that include lakes and the upper, middle and lower courses of rivers (Balon 1966; Holčík and Mihálik 1971). In addition, there are several species that inhabit marine coastal areas for a short period of their life, but are still categorized as freshwater amphidromous fishes. Amphidromous bullheads produce many small eggs in the lower reaches of streams and rivers. Hatched larvae rise to the surface of the river due to their phototactic response, and drift downstream. This strategy may contribute to the high survival of larvae (Goto 1993; McDowall 2007). The pelagic larvae spend some time in marine coastal areas before migrating to rivers. Such pelagic larvae occur in all lineages except the lineage of *Cottus poecilopus* from Eurasia. Fluvial species, which live in rivers for their entire lives, utilize the latter for both growth and reproduction, and usually produce a small number of large eggs (Dyk 1957). Larvae undergo direct development and are benthic after hatching (Jurajda 1992; Przybylski and Borowska 1998). Larval ecological characteristics of these species have not been reported on and pelagic larvae for this lineage are unknown (Pasko and Mašlak 2003). The lineage of the *Cottus poecilopus* group is distributed throughout northern Eurasia from Primorskii to the Siberian region of Russia, and in central Asia and Europe (Sideleva and Goto 2009). The aim of this study was to monitor the presence of mountain fish in the river Javorinka, to describe their local microhabitats and to understand the potential migration process. Another important goal of this study was to map favourable sites of high mountain Alpine bullheads and specimens of native wild brown trout.

Material and Methods

Study area

Sampling was carried out in the Javorinka river, which is part a of the Javorová mountain valley. Formation of the watershed of the Javorinka river in the Belianske Tatras in Slovakia and the assumed start of introduction of trout into mountain streams is assumed to be when the Poprad and Javorinka rivers began to form in the last interglacial period, 6 000-2 000 years ago. Many mountain albedoes exist as remnants of melted mountain glaciers, which were the last of the ice Wurme. The arrival of trout in mountain streams is anticipated to have occurred 3 000-300 years ago, when the Tatra forest stands developed into their current composition of fir beams, maples and others species. Relief of Javorinka is from the glacial valley to the north through Tatranská Javorina. Huge boulders in the channel are evidence of regular avalanches and rockfalls. The Belianske Tatry and the Javorinka river are situated on flysh subsoil (alternating layers of saplings and clay, slate). The best living conditions for fish fauna are in mountain stream stretches such as the Javorinka river where the shores are strengthened by old forest (Fig. 1) stands. Mature trees with deep roots are important as a support for the whole ecosystem.

Fig. 1. Profile photo of Javorinka river surrounded at many sites by 200 year old trees of *Abies alba*. At the left side, there is a deeper bank suitable for trouts, right sight may serve as microhabitat for alpine bullheads (Photo: Martin Janiga, 2017).

Field collections and laboratory measurements

The fish were observed or found in the river Javorinka in the spring and summer of 2016 and in the autumn of 2017. 75 Alpine bullheads in the river were monitored and carefully GPS coordinated. In the field, we recorded the elevation, relative slope and the geographic coordinates with GPS navigation, using Google Earth and Arcgis Arcmap 10.4 software for computer processing of samples. Photo documentation was performed at many of the sites. When deceased fish were found in the river, they were weighed with a spring balance and measured with callipers.

Statistical analysis

The allometric relationships between morphometric characters of fish were modelled by non – linear regression analysis. The body weights and body lengths among different groups of bullheads were compared by one-way analysis of variance (ANOVA) with significance level at P = 0.05. For all calculations, the STATISTICA 8. software was used. In the first analysis a simple exponential line and points graph was used to compare the relationship between body weight and length of fish. In the second analysis a polynomial points and line graph (regression) was used to show the relationship between elevation and body weight. A polynomial scatterplot graph was used to show the relationship between length, weight and elevation. The third analysis included a least square means ANOVA – one way analysis of variance, where I showed the relationship between two colours of bullheads and the elevation. In this last analyses the relationship between body characteristics was shown against the slope.

Results

The most important fish habitats are described in Fig. 2. The species utilizes a particular habitat, preferring a gravel substrate with many flat rocks on the riverbed, although some individuals were found on sandy substrate in areas of the river deeper than one meter. In general, brown trout were seen at higher elevations than alpine bullhead. Optimal habitats for bullhead are located in near Podspády, and stretch to approximately one hundred metres beyond the state border between the Slovak Republic and Poland.

An increase in body weight versus body length begins in sculpins approximately in the first third of their life cycle in the Javorinka (Fig.3). The largest bullhead were found between 860 – 880 m a.s.l. (Fig. 4), while bulhead found at 1 000 - 1 100 m a.s.l. were significantly smaller. In alpine bullheads, body length and body weight significantly decreased in habitats at a higher altitude.

The microhabitat between 870 and 900 metres was favourable for lighter coloured bullhead. In this altitudinal range, the heaviest (Fig. 5) and

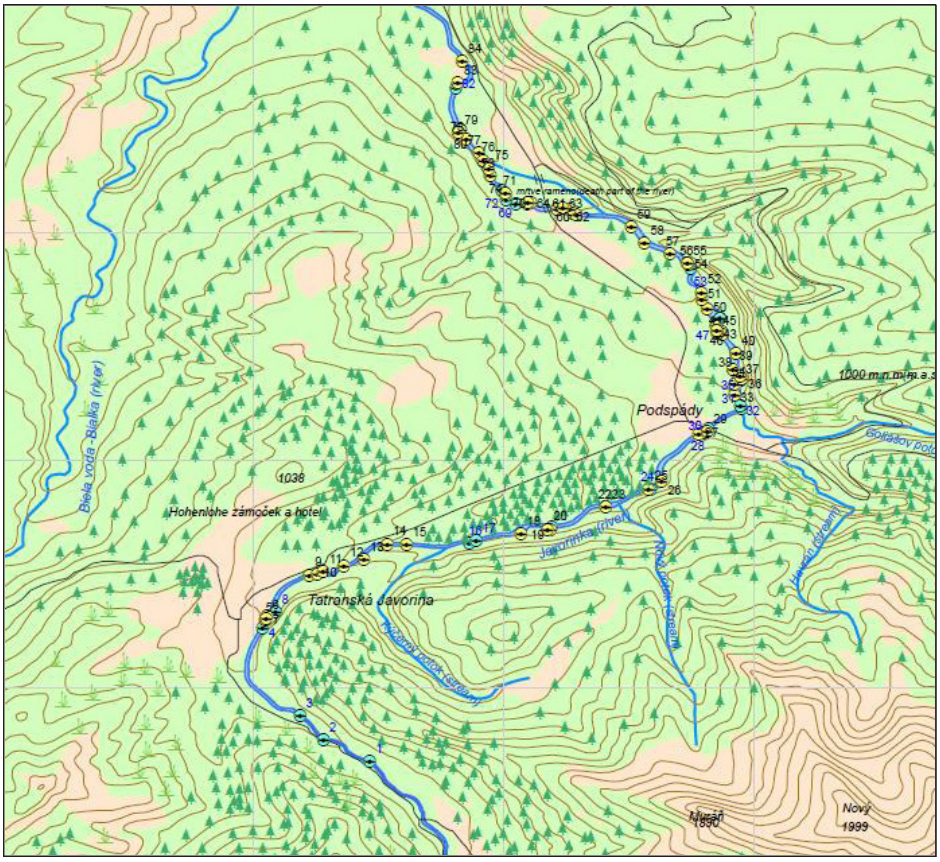

Fig. 2. The most important localities of fish occurence in the stream Javorinka – 2017 . Yellow – *Cottus poecilopus*, green *Salmo trutta* (Author: Martin Janiga).

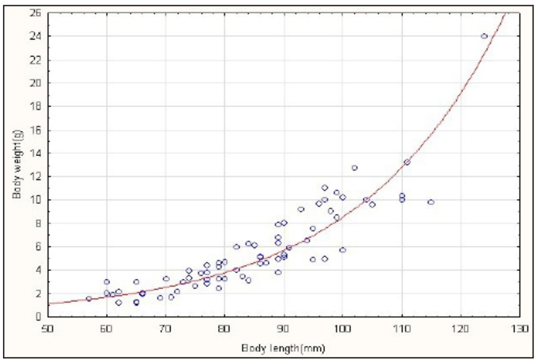

Fig. 3. Allometric (exponential) relationship between body length and body weight in Alpine bullheads in the river Javorinka. The body weight increases more rapidly when the animals reach the length of approximately 85 milimeters.

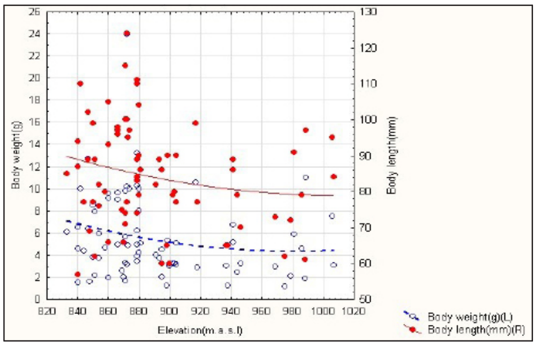

Fig. 4. Scatterplot of body weight and body length of *Cottus poecilopus* against the elevation The longest and biggest fish were found at the level from 860 to 880 m a.s.l. Both body characteristics decreased continually with increasing elevation.

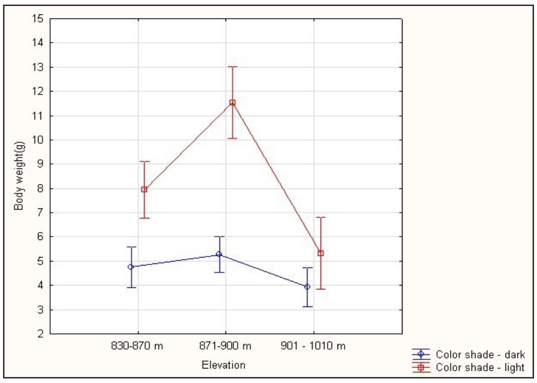

Fig. 5. Least square means with standard errors of body weight of *Cottus poecilopus*. Fish were the lightest in body weight at the higher elevations (F(2,65)=5.1, P=0.009) and the lighter bullheads (color shade) were significantly heavier than dark animals (F(1,65)=15.3, P=0.0002). At all elevations the light fish in color shade werer statistically significantly heavier than dark individuals. There was not interaction between the factor color shade and elevation (F(2,65)=2.1, P=0.12, NS).

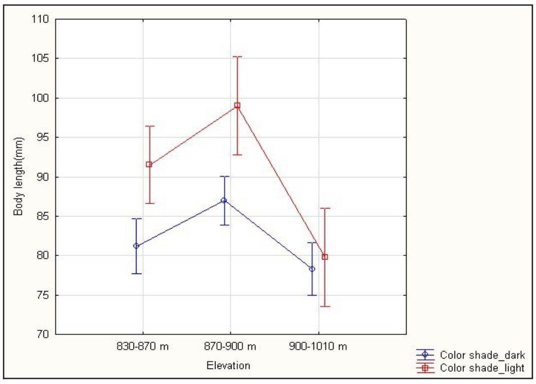

Fig. 6. Least square means with standard errors of body length of *Cottus poecilopus*. Fish were the shortest at higher elevations (F(2,65)=3.9, P=0.02) and the lighter bullheads were significantly longer than darker animals (F(1,65)=4.2, P=0.04). At lower elevations the light fish in color shade were statistically significantly longer than dark individuals. There was not interaction between the factor color shade and elevation (F(2,65)=0.7, P=0.52, NS).

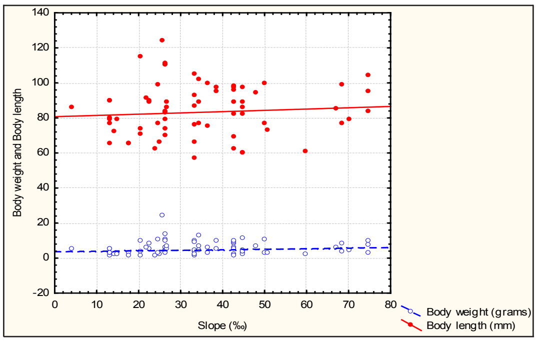

Fig. 7. Multiple exponential scatterplot graph showing relation between slope and both body weight and body length of Alpine bullheads *Cottus poecilopus*, bullheads were found mostly on 2,5 % steep site, the heaviest and the longest individuals were also found mostly in 2,5% steep slope.

the longest (Fig. 6) bullheads were found, and they were mainly fish of a lighter colour pattern (color shade).

Although there was a tendency for sculpins to increase in body length at steeper sites, the regressions were not statistically significant (Fig. 7).

Discussion

Elevation and morphomety of Cottus poecilopus

For *Cottus poecilopus,* the most suitable slope was 25% but bullhead were also found at a slope of 74% and an approximate elevation of 1 007 m a.s.l. Kozlowski *et al.* (2017) found bullhead at steeper slopes than reported by Balon (1966), such as in the Suchá voda stream at 101% slope. The highest point where the fish were present was Roztoka stream at 1 150 m a.s.l. Balon (1966) found the first Cottus poecilopus in the River Poprad close to the Štôla (elevation ca. 900 - 1 000 m a.s.l – ca. 26,7‰ relative slope). *Cottus poecilopus* usually prefer wider and lower channels of rivers with an average slope of 25%. Strong floods can really affect the lifecycle of this species, because they tent to remain in deeper waters without a sufficient amount of oxygen.

Allometry

Fish morphometrics have been a hot topic in ichthyological studies for many years, but the initial steps date back to the time of Galileo Galilei. The allometric model seems to be the most appropriate for describing morphometrics in fishe (Lleonart *et al.* 2002) and applies to the vast majority of relationships of morphological characteristics with body length. In the case of bulhead, growth is allometric. In the first third of their growth period, the species grows faster in length than in weight, but when the fish are older they gain weight faster than they increase in body length. The significance of allometry is related to the effect of the increasing body length to the relative efficiency of the intestine to absorb nutrients from digested food. Since growing organisms require more energy and nutrients, changes to the structural capacity, i.e. lengthier intestines, must occur in order for those needs to be met. Structural adaptation of the intestines will ensure that food can be retained longer in the tract, an thus, more nutrients will be absorbed, so additional receptors for the absorption of energy and nutrients will be available (Kramer and Bryant 1995). Typical allometric relationships between body weight and body length were noted in the bullhead found in Javorinka.

Species characteristics of the genus Cottus

Differences in characteristics between *Cottus poecilopus* and *Cottus gobio* are listed below. With regard to the European bullhead, abdomen fins are white, and they may have irregularly appearing grey spots, that do not join in contiguous strips as in the Alpine bullhead. European bullhead have two paired abdominal fins, which consist of four rays. Abdominal fins are short, do not reach the anal orifice and the inside fourth ray of abdominal fins is about half as long as the longest ray of the abdominal fin. The differences between European bullhead and Alpine bullhead are mainly in these abdominal fins. While both species have four rays of abdominal fins, there is a difference in their particular length. In case of European bullhead, the outside rays are about half as long as the two longest middle rays of abdominal fins and the aforementioned inner ray slightly exceeds half the length of the middle rays. The longest rays of *Cottus gobio* are the symmetrical middle rays.

Cottus poecilopus, the Alpine bullhead has abdominal fins that are proportionately longer than those of the European bullhead and they reach or exceed the anal orifice. The anal fin of the Alpine bullhead has 13 to 15 rays. In the front dorsal fin there are 9 rays, and in the back dorsal fin there are 17 rays. However, the most interesting-looking are the bizarre cheek spines above the branchiae, as well as the two outer perculae, which are better developed and larger than in the case of European bullhead. Comparatively, European bullhead have only one such spine or perculum placed above the branchiae, and it is more even. In males, the head is generally wider and larger, and the abdominal fins are longer compared to females.

Cottus poecilopus has four rays of abdominal fins that vary in length compared to the European bullhead, as each ray is of a different length. The longest ray is the middle outer ray. The middle inner is about 5/6 the length of the middle outer ray. The outer ray is about 2/5 the length of the inner rays. The internal ray is less than half as long as the middle rays, coming to a maximum of 1/6 to 2/5 of the longest middle ray when compared to the European bullhead.

Habitat of the Alpine bullhead

Alpine bullhead can be found from Scandinavia to the Kolymu River in Siberia, in the basin of the Amur, the Danube, and Dniester rivers as well as rivers flowing into the Sea of Japan. In Slovakia, its habitat includes the tributaries of the Danube, Visla, Poprad, Dunajec, and Javorinka rivers and the basins of the Black and Baltic Seas. In the Czech Republic, Alpine bullhead exist in the river basins of the Morava and Odra rivers. Alpine bullhead thrive at higher altitudes than European bullhead. According to Zelinka (1952), Alpine bullheads live only in water with an oxygen ratio of at least 8 mg of oxygen per 1 litre of water. They mainly live on *Hydropsyche* species. Bullheads hide under large flat stones that cannot be easily displaced by currents (Dyk 1957; Kozlowski *et al.* 2017).

The resting positions of bulheads and habitats are closely related to their reproduction sites, which runs from March to May. Balon (1966) described the entire ethological ritual of reproduction, sexual behaviour and methods of the solicitation of females by males before mating. Holčík *et al.* (1965), in the basin of the White Orava River, found where bullheads were abundant and where they were mating. They state, "... When a female stops in front of the hole with the waiting male, the male starts luring the female to get in by fluttering movements. The male comes out of the nest cavity several times and gets back... these preparatory ceremonies take sometimes more days until the female enters the hole and copulates with the male. After the copulation and laying eggs, the female remains lying for 20 minutes, then goes away and for the coming 15 days, the eggs are being taken care of by the male only. It fans them by the means of pectoral fins and cleans them from debris.'' It can be inferred from this, that in March, April, and May we can find mating bullheads in the stony side tributaries as well as in the main flow where males take care of the eggs in their resting positions. This is confirmed by an earlier claim of Dyk (1957) from research in the Bela River in 1937: "Alpine bullheads ... reproduce most abundantly in "teplice", i.e., powerful springs, which make up little creeks near the basin and after a few tens of meters flow into the main flow. Also in the side, mildly flowing basins, there are rich numbers of bullheads, but not in the bays and river arms with still water, and the bottom covered by detritus through which, under normal conditions, water does not flow." Male Alpine bullhead, however, is a territorial fish, and it defends its territory whether it protects eggs or not. European and Alpine bullheads lay around 100-1 400 eggs.

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Mercury concentration in feathers of *Prunella modularis* in spruce and dwarf pine forest

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Abstract. Levels of mercury contamination in bird feathers show some dependence of Hg contamination on habitat type or elevation. The aim of this study was to determine the level of Hg in the feathers of *Prunella modularis* from different habitats of the West Carpathians, Slovakia. No significant differences in the amount of mercury found in feathers was detected between spruce and dwarf pine habitats, and the level of Hg in the feathers also did not change with altitude.

Key words: mercury, feathers, *Prunella modularis*, spruce forest, dwarf pine forest

Introduction

Mercury (Hg), in contrast to other heavy metals, can be transported in the atmosphere around the world. European primary emission sources have a significant impact on mercury pollution, and due to the long residence time of gaseous mercury in the atmosphere, outside of Europe as well (Harmens *et al.* 2013). Hg is one of the most toxic environmental contaminants, and enters ecosystems through the air or water (Evers 2018). It is deposited in terrestrial and water surfaces, builds up in soils or sediments and may be persistent in the environment. In aquatic systems the metal is biologically converted into the toxic compound methylmecury (MeHg or CH_3Hg^+). Ingested methylmercury is often completely absorbed by the gastrointestinal tract because Hg is strongly bound with proteins and amino acids (methylmercury-cysteinyl complex) (Kerper *et al.* 1992). Chronic exposure causes a number of adverse effects, such as damage to the central nervous system, kidneys and stomach, and affects the immune system, blood pressure and heart activity (Kampa and Castanas 2008). Birds reduce the load of toxic Hg using several mechanisms, including feather growth. MeHg has a high affinity to the free thiol group (-SH) which is rich in keratin in the feathers (Crewther *et al.* 1965). During their growth, feathers are connected to the body by a blood vessel and circulating Hg can be transported to the feather and incorporated into the keratin structure. When rectrices growth is complete, after fledging in young birds or after each molt in adults, the feather is no longer supplied with blood and the Hg remains physically and chemically stable within the feather (Stettenheim 2000). Higher levels of Hg in circulating blood occurs during the growing period in adult feathers than young feathers (Westermark *et al.* 1975; Hughes *et al.* 1997). The levels of Hg in feathers can indicate the degree of environmental pollution by Hg (Berg *et al.* 1966).

Hg production has decreased in Central Europe over the last few decades (EEA 2016). The current Hg levels in mountainou areas of Slovakia are unknown and current studies are mostly focused on soils (Tóth *et al.* 2009), water environments (Kapustová 2009; Stobiński and Kubica 2016), and vascular plants (Ciriaková 2009).

Subalpine regions in the high mountains of Slovakia can be an indicator of the load of heavy metals for several trophic levels and habitats. To analyze levels of Hg in birds, dunnock (*Prunella modularis*, Linnaeus, 1758) was chosen as an indicator species. This species is particularly widespread in forested mountain areas where spruce predominates, but also in mountain ranges habitated by dwarf pine.

The aim of this study was to investigate the dependence of Hg contamination in feathers of dunnock on the type of forest habitat and altitude in mountain regions in Slovakia.

Material and Methods

Study area

Study areas included characteristic habitats of dunnock in the mountain and submountain zone of the Slovakian part of the Western Carpathians, including: The High Tatras (Veľká studená dolina), Belianske Tatras (Tatranská Javorina, Ždiar, Biele pleso, Kolové pleso), West Tatras (Červenec), Low Tatras and Hornádska kotlina (Chopok, Tri domky, Suchý vrch, Stredná hoľa), Oravské Beskydy (Babia hora, Oravská priehrada) and Chočské vrchy (Veľký Choč). Capture and sampling of birds were conducted between 1999-2017, mostly in the spring and summer periods.

Sampling analysis

Hg levels were analyzed in 39 dunnocks. They were frozen (at -20° C) and stored in the Institute of High Mountain Biology in Tatranská Javorina. From each individual two outer tail feathers (rectrices) were collected. All assembled samples wer dried, weighed and cut into small fragments. A direct

Hg Analyzer (DMA-80; Milestone, USA) was used to measure Hg levels in the feathers.

One way ANOVA and regression analysis was used to compare the levels of Hg at different altitudes and habitats (Statiscica 12 software).

Results

In total the feathers from 39 birds were investigated. Most individuals were collected from the area Belianske Tatry (Ždiar, Podspády, T. Javorina). Average levels of Hg in different months and localities are given in Table 1.

A statistically significant relationship between the amount of Hg in the dunnock feathers and the elevation at which they were collected was not found (Fig. 1). The dunnocks from lower elevation spruce habitats did not differ in the amount of Hg in their tail feathers from dunnocks living in the higher dwarf pine habitats (Fig. 2).

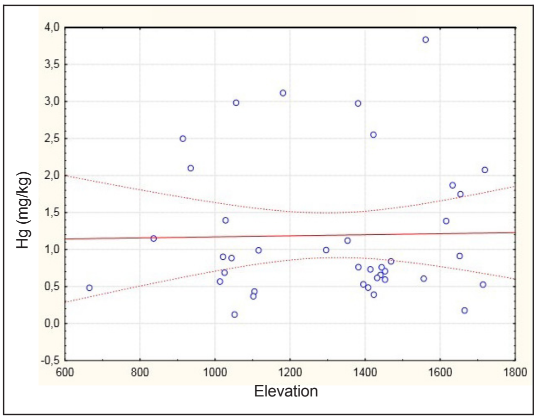

Fig. 1. Amount of mercury in the tail feathers of dunnocks in dependece on elevation in the West Carpathians. (Elevation: Hg (mg/kg): y=1.1004+7.0856 E-5*x; r=0.0209; p=0.8995).

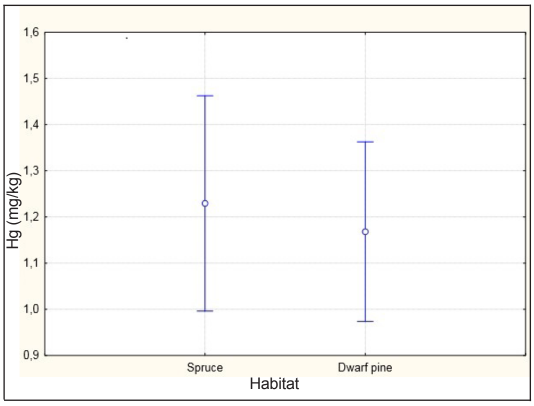

Fig. 2. Current effect levels of Hg between two vegetation lines. (LS Means + standard errors. Current effect: F(1, 37) = 0.04066, p = 0.84130)).

Discussion

Mercury levels are a major environmental burden for remote ecosystems that receive elevated deposition from long-range atmospheric transport (Blackwell and Driscoll 2015). The increased deposition of metals over large mountain areas of Europe is obvious (Janiga 2001). Examination of spatial deviations in Hg exposure of *P. modularis*, did not show any significant differences. Mountain ecosystems are exposed to higher levels of atmospheric Hg deposition as shown by accumulation patterns on the forest floor and associated high-elevation fauna (Townsend *et al.* 2014). Blackwell and Driscoll (2015) reported that total soil Hg concentrations increased with elevation from the deciduous to the alpine zone. Based upon soil characteristics, tree species, precipitation patterns, and expected Hg inputs, ecosystems at higher elevations are thought to receive higher Hg deposition and support greater methylation (Lawson *et al.* 2003; Yu *et al.* 2014). Findings of increased Hg concentrations in invertebrates, salamanders, and birds (Blais *et al.* 2006; Townsend *et al.* 2014), with increases in elevation support this hypothesis. Mercury enters ecosystems via wet or dry deposition, with inputs varying by forest cover type. Non significant differences among spruce and dwarf pine zones are attributed to the fact that both are within the coniferous tree line. Gerson *et al.* (2017) found that soil MeHg concentrations were highest in the mid-elevation coniferous zone (0.39 ± 0.07 ng/g) compared to the alpine tree zone (0.28 ± 0.04 ng/g) and deciduous tree (0.17 ± 0.02 ng/g), while the percent Hg as MeHg in soils decreased linearly with elevation. Higher concentration of Hg in

**Average levels of Hg (mg/kg) in different localities
(n – number of individuals)**

	Belianské Tatras	Central High Tatras	Low Tatras; Hornádska kotlina	West Tatras	Oravské Beskydy; Choč
April	1.43 (3)				
May	1.43 (2)	0.54 (2)	1.51 (2)	2.97 (1)	0.48 (1)
June	1.04 (2)		1.82 (2)		1.82 (1)
July	1.78 (3)		1.75 (1)	0.59 (8)	1.19 (5)
August	0.56 (2)				
September	1.35 (3)	2.08 (1)			

Table 1. Number of samples divided to the time in months.

soils in coniferous forests compared to deciduous forests have been reported by several studies (Fisher and Wolfe 2012; Graydon *et al.* 2008, Kolka *et al.* 1999).

Birds are often used as bioindicators of environmental contaminants, and their feathers are widely used for the indication of heavy metal contamination (Thompson and Furness 1989; Ahmadpour *et al.* 2016). It has been found that Hg binds with the growing feather, which gives a history of contamination at the time that the feather was grown (Thompson and Furness 1989). When molting is completed, the level of Hg in the feather remains stable, even if the bird feeds on contaminated food. The increase of Hg concentrations is then noted in internal organs (Dauwe *et al.* 2003). Results of this study show levels of Hg found in the *P. modularis* of the subalpine region from spring to late summer. Generally Hg levels in the feathers are low, but there are significant individual deviations from the average. This likely reflects the very 'eurytopic' way of life of the species.

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TECHNIQUES AND STRATEGIES

Alpine lichen-dominated heaths: ecology, effects of reindeer grazing, and climate change. A review

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Abstract. Lichens are important forage for reindeer during winter, making evaluation of lichen biomass important for reindeer population management. Lichen heaths have a scattered distribution at high latitudes and altitudes in Fennoscandia. During the last few decades, their decrease has been attributed to reindeer grazing and trampling as well as climate change. Some consider this decrease to be the result of competition from vascular plants. However, we believe that this is a far too simple an explanation. In many studies the most important factor - deep soils with long-lasting frost - has not been considered. As a result, anticipated long-term effects of climate change and grazing should be reconsidered. Lichens have no roots, and therefore, environmental and edaphic conditions have limited direct effects on lichen abundance. Vascular plants live in contact with two different environments; the atmosphere and the rhizosphere, and ecological factors within both affect them. It is imperative to know which environmental factors increase the possibility of maintenance and development of extensive lichen heaths. In this review, we use current ecological knowledge to discuss the ecology of alpine lichen heath distribution and possible reasons for their decline, both at present and in the future.

Key words: lichen, temperature, thaw, snow, competition, soil frost

Introduction

Macro-lichens (often called reindeer lichens or even reindeer mosses) can dominate the vegetation in alpine, boreal, and arctic ecosystems. In addition to being an important food resource for reindeer during winter, macro-lichens are also important for the functioning and biodiversity of cold ecosystems (Cornelissen *et al.* 2001; Asplund and Wardle 2017).

Lichen heaths in alpine ecosystems are dominated by lichen species with podetia that can reach heights of 12-14 cm, and the most important species belong to the *Cladonia* or *Flavocetraria* genera. They are frequently abundant at high elevations and latitudes in Fennoscandia (the alpine and northern boreal zone (Ahti *et al.* 1968; Moen 1999). Patches of lichen-dominated vegetation may also be found under highly variable environmental conditions. In lowland areas, lichen-dominated vegetation is often patchy and restricted to exposed naked rocks with very thin soils where the vegetation is frequently exposed to drought (Kleiven 1959). Lichens can also be common on sand dunes, on raised bogs and newly exposed substrates (Ahti and Oksanen 1990). The floristic composition and ecology of such communities is quite different from alpine lichen heaths. In continental parts of Fennoscandia, pine forests dominated by lichens have a wide distribution. In the present review, we will mainly discuss the ecology of alpine lichen heaths.

Lichen heaths often have scattered, patchy occurrences on exposed windblown sites in alpine areas. Their main distribution is confined to the continental parts of Scandinavia, indicating that they favor areas with low winter temperatures and low precipitation. The alpine zone in Scandinavia includes areas above the forest limit (Ahti *et al.* 1968; Moen 1999). The position of the forest limit is highly variable as shown by iso-line maps (Aas and Faarlund 2000; Moen 1999; Heikkinen 2005). The highest limits lie in the southern parts of Norway, mainly between 1 100 and 1 300 m, decreasing in all directions due to both climatic factors and mountain height (Odland 2015).

Ecologists have tried to explain the lichen heath distribution, and several possible factors have been suggested. It has frequently been emphasized that the distribution of lichens is primarily controlled by their inability to compete with faster-growing vascular plants. Apparently, lichen-dominated vegetation develops only in environments where competition from higher plants is excluded or reduced (Kershaw 1978; 1985). Consequently, a key to understanding lichen distribution can be to investigate ecological conditions where vascular plants are not growing. Crittenden (2000) reviewed knowledge on mat-forming lichen biology and their ecological relationships with reindeer. His conclusion was that factors controlling the development of lichen-dominated terrain remain incompletely understood.

Vascular plant and lichen abundance is significantly negatively correlated (Odland *et al.* 2015). Vascular plants easily outcompete lichens except under the most harsh ecological conditions, and

Corneliessen *et al.* (2001) found that the relationship between lichen biomass and vascular plants was consistently negative across alpine, subarctic and mid-arctic areas.

Lichens can survive extreme conditions, such as cold, heat, or drought. They grow in polar regions, high mountain areas, and arid deserts (Kappen *et al.* 1995; Körner 2003). Lichens can grow and metabolize at much wider ecological ranges than vascular plants, including at freezing or below-freezing temperatures, so long as the lichen thallus is sufficiently moist (Klein and Shulski 2011). In many ecosystems, such as on rocky coasts or otherwise bare mountaintops, lichens are often the most common and diverse organisms (Seaward 2008). This large lichen tolerance is an effect of being metabolically active only when wet; during dry periods, they can tolerate extreme temperature stress (Green *et al.* 2007).

Lichens are poikilohydric organisms, characterized by a high water absorption index, using atmospheric water as well as rain, dew and fog. Under the influence of evaporative forces, lichens lose water, becoming dry and largely metabolically inactive. After only 30 seconds of direct contact with water, the absorption exceeds the weight of the dry lichen biomass and maximum water absorption is reached during the first few minutes of exposure (Matwiejuk 2000).

Most lichen species require good light conditions. Light saturation for lichen photosynthesis is about 35 000 lux, which is higher than for vascular plants (20 000 – 30 000 lux) (Skre 1975). Lichens can begin photosynthesis early in spring, likely even before snowmelt. Lichens have a low optimum temperature for photosynthesis (between 7 and 10 ˚C), depending on temperature pretreatment. Apparent photosynthesis can continue down to -5 to -10˚C (Skre 1975). The growth rate of reindeer lichens is generally low (Kärenlampi 1971; Helle *et al.* 1983; den Herder *et al.* 2003).

Lichens produce a wide array of secondary compounds (Fahselt 1994; Molnár and Farkas 2010). Although the best studied lichen secondary compound is usnic acid (Cocchietto *et al.* 2002), there are countless other secondary compounds the functions of which are less well understood. Several laboratory studies have been executed to test allelopathic effects on plants and mosses (Huneck 1999; Sedia and Ehrenfeld 2003). Some studies indicate that substances inhibit growth of a variety of plants (Lawrey 1995), while other field studies have not shown any definitive effects (Kytöviita and Stark 2009).

Lichens are sensitive to different types of air pollution. Fertilization experiments show that the addition of approximately 150 kg N ha^{-1} produced a negative effect (23-73%) on a standing crop of *Cladina* spp. over a period of time exceeding eleven years compared to the control standing crop (Eriksson and Raunistola 1993).

Bryophytes and lichens are ubiquitous in cold ecosystems, and recently their roles in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). Studies show that moss-lichen layers function as important "thermal insulators," and strongly affect soil temperatures.

Development of mature lichen-dominated vegetation is a long-lasting process. It has been estimated that after a fire, it may take around 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In many cases, lichens fail to re-colonize sites after removal due to their inability to compete with faster-growing vascular species (Klein and Shulski 2011).

Lichen species are on the decline across the arctic, alpine and boreal (Joly *et al.* 2009; Fraser *et al.* 2014; Sandström *et al.* 2016), due to climate change and reindeer grazing (Joly *et al.* 2007). According to Bjerke (2011) and Bokhorst *et al.* (2012), lichen-dominated heaths appear to be one of the most vulnerable ecosystems in circumpolar regions. It is therefore important to have more information about which ecological factors are critical for lichen heath development, and which factors that threaten their future existence.

In this review, we will focus on the ecology of low alpine lichen heaths. Lichen-dominated heaths are characteristic for alpine landscapes, where they are considered to be a major winter food resource for wild and semi-domesticated reindeer. The following issues will be emphasized:

- Floristic variation of lichen-dominated heaths in Scandinavian alpine areas,
- Environmental factors associated with alpine lichen heath distribution and development,
- Effects of reindeer grazing, and
- Effects of ongoing climate change on the distribution of alpine lichen heaths

Alpine lichen heaths; distribution and flora

Distribution

Reindeer lichens have a wide circumpolar distribution and reach their maximum abundance in dry and oligotrophic sites around the coniferous timberline where competition with mosses, dwarf shrubs, and grass is low (Ahti and Oksanen 1990).

The distribution of lichen heaths is, however highly variable in the Scandinavian mountains. In general, lichen heaths are more common in the east than in the west, and they become more common toward the north (Du Rietz 1925; Ahti and Oksanen 1990). According to Moen (1999), alpine lichen heaths are mainly confined to the slightly continental and indifferent sections of Norway, characterized by an annual precipitation lower than 1 200 mm, and an air temperature frost-sum higher than 50 (Moen 1999; Odland *et al.* 2014; Falldorf *et al.* 2014; Sundstøl and Odland, 2017).

In oceanic areas, winter temperatures are generally warmer, and the winter conditions are often unstable. This gives important clues as to how environmental conditions are affecting the climatic tolerances of lichen-dominated heaths.

On the Hardangervidda mountain plateau (southern Norway), the chionophobous heaths where lichens are more or less dominant have been estimated to cover around 10% of the total area (Wielgolaski 1975; Hesjedal 1975; Rekdal *et al.* 2009). There are major geographic variations, with a strongly decreasing frequency toward the south and west (Moen 1999). According to Gaare and Skogland (1979), the cover of lichen heaths has been estimated to be 25% in the eastern region, and less than 1% in the snow-rich western region.

Studies of lichen heath elevation distribution in south central Norway (mostly on the Hardangervidda mountain plateau) show that they are mainly found at elevations between 1 150 and 1 400 m, in the low alpine zone (Fig. 1). A regression analysis of the data showed no significant trend within this elevational span.

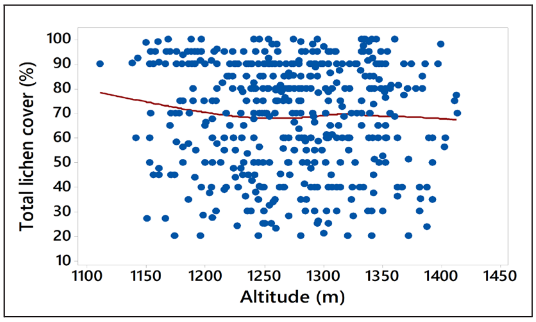

Fig. 1. Altitudinal distribution of lichen heath vegetation types around Hardangervidda. 437 plots where total lichen cover was higher than 20% have been plotted against altitude (data from Odland *et al.* 2014 and unpublished data). A Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Floristic variation

Lichens can be dominant in different types of vegetation. Alpine oligotrophic and chionophobous lichen-dominated vegetation types have been studied and described in Scandinavia for more than a century. The most ecologically successful terricolous lichens are mat-forming species within the genera *Cetraria*, *Cladonia*, *Flavocetraria*, *Stereocaulon*, and *Alectoria* (Ahti and Oksanen 1990). Lichens can also be dominant in alpine shrub vegetation dominated by *Salix glauca*, *Juniperus communis*, and *Betula nana* (DuRietz 1925; Nordhagen 1928; 1943; Jonasson 1981). Graminoids may also be abundant in lichen heaths, especially *Festuca ovina*, *Juncus trifidus*, and *Carex bigelowii* (Nordhagen 1943). Most commonly associated with lichen heaths are shrub species like *Loiseleuria procumbens*, *Arctous alpinus*, *Empetrum nigrum*, *Betula nana*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea*.

In the northernmost parts of Fennoscandia, Haapasaari (1988) described different heath types where macro-lichens were dominant, e.g. Arctic *Empetrum-Cetraria nivalis* type, Arctic-hemiarctic *Myrtillus-Lichenes* type, Hemiarctic *Empetrum-Lichenes* type, and *Betula nana-Lichenes* scrub type.

In coastal areas (oceanic sections sensu Moen 1999) exposed sites in alpine areas are mainly dominated by vascular plants and bryophytes, while lichens are less abundant (Reistad, 1997). Vegetation on exposed alpine sites in oceanic areas have been described by Odland (1981), Huseby and Odland (1981), Røsberg (1981), Löffler (2003), and Tveraabak (2004). *Cladonia arbuscula* and *C. rangiferina* may locally be abundant, but species like *Bryocaulon divergens*, *Alectoria nigricans*, *A. ochroleuca*, *Coleocaulon aculeatum*, *Flavocetraria cucullata*, *F. nivalis* and *Cladonia stellaris* are mostly rare or absent in oceanic alpine areas. The most abundant vascular plants at these sites are *Carex bigelowii*, *Scirpus cespitosus*, *Molinia caerulea*, and *Juncus trifidus*, in addition to several dwarf shrub species (*Empetrum nigrum*, *Vaccinium uliginosum*, *Betula nana*, and *Calluna vulgaris*). Mosses are also often highly abundant, especially *Racomitrium lanuginosum* and *Dicranum* spp.

Pine forest floors, often completely dominated by *Cladonia stellaris* are abundant in the continental parts of Fennoscandia (Kielland-Lund 1981; Ahti and Oksanen 1990; Haapasaari 1988). *Betula pubescens* forests at high elevations or latitudes can also be dominated by *C. stellaris* (Nordhagen 1943; Haapasaari 1988; Kumpula *et al.* 2011). These are not included in this review.

Importance of substrate and soil

Most alpine soils have developed since the last glaciations, during the last 9 000 years. The importance of lichens for soil development processes is not well known, but some information can be gleaned from recent succession studies in the front of retreating glaciers. Macro-lichens can be dominant in both boreal forests and in low alpine heaths, and one should therefore expect their soil conditions to be different. Lichens can have many direct and indirect effects on the substrate where they grow. Sedia and Ehrenfeld (2006) found that many biotic soil factors were significantly different under naturally occurring lichen and moss mats than under other ground covers.

Role of lichens in primary successions

Lichens and mosses are assumed to be pioneer species on recently exposed, dry minerogenic sediments, and in the early stages of primary successions (Cooper 1953; Ahti and Oksanen 1990). Studies on primary succession of exposed glacier moraines show, however, that species dominant in alpine lichen heaths arrive relatively late, long after bryophytes and many vascular plants. Studies from retreating glaciers indicate that reindeer lichens have minor ecological impacts during the early stages of primary successions (Stork 1963; Vetaas 1994; Rydgren *et al.* 2014). According to Ahti and Hepburn (1967), reindeer lichens require at least a thin soil layer for attachment because they cannot colonize bare rock. The role of reindeer lichens during primary succession in the front of retreating glaciers has been studied in different parts of the world (Matthews 1992). During the first stages (often 0-50 years), cryptogams (primarily mosses) are most abundant, followed by dwarf shrub heath and woodland, while macro-lichens are sparse (e.g. Fægri 1934; Cooper 1953; Ahti and Oksanen 1990; Coxson and Marsh 2001).

Vetaas (1994; 1997) studied vegetation on moraines of different ages in front of a retreating glacier in west central Norway. The youngest moraine ridges studied had been exposed for 54 years, and were primarily dominated by mosses, especially *Racomitrium* spp., *Dicranum* spp., *Polytrichum* spp., *Pohlia* spp., hepatics, and vascular plants. The most abundant lichen was *Stereocaulon* spp., while *Cladonia* spp. occurred only sporadically. *Alectoria* *ochroleuca, Flavocetraria nivalis*, and *F. cucullata* were abundant on moraines exposed for between 84 and 186 years. *Cladonia rangiferina*, *C. arbuscula*, and *C. uncialis* had a wider span, occurring on moraines between 54 and 226 years old. *C. stellaris* was most abundant on moraines around 200 years old. Moraines more than 200 years old were mainly dominated by birch, shrubs, herbs, graminoids, and bryophytes. Lichens were very rare in plots on moraines older than 200 years, likely outcompeted by trees and shrubs. In addition, lichens had different distribution on the moraine ridges, mainly confined to the ridge tops. Vascular plants (mainly shrubs) and mosses dominated both the distal and proximal slopes, probably a result of increased snow downward the slopes. Soil development on the moraines is a slow process, particularly at the highest altitudes. Mosses, especially *Racomitrium* spp. were the main source for the humus development (Vetaas 1986). Viereck (1966) also notes that mosses were most important for the development of humus on exposed moraine ridges.

Hestmark *et al.* (2005) studied the population biology of *Flavocetraria nivalis* on a glacier foreland. They found that the largest thallus was 96 mm in diameter, on moraines exposed for approximately 240 years. The fastest growth occurred during the first 60 years. The density of individual thalli (in m^{-2}) increased nearly linearly with time, and reached 10 after 240 years. The height of the thalli never exceeded 60 mm. Development of lichen-dominated vegetation appears to be a long-lasting process. It has been estimated that after a fire, it may take 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In general, during primary successions, soil organic matter and nitrogen content will increase with time. This can favor vascular plant dominance and in turn can decrease lichen abundance (Stork 1963; Tisdale *et al.* 1966; Vetaas 1994; Rydgren *et al.* 2014).

Lichens are slow-growing and produce a low volume of organic matter compared to most vascular plants and mosses. On Svalbard, Uchida *et al.* (2006) found that lichen primary production was 5.1 g dry weight m^{-2}, and represented 29% of moss and 5% of vascular plant primary production. Consequently, lichens have a limited effect on the development of organic humus layers, and during early stages of vegetation development vascular plants probably contributed most to soil development. Lichens could only become dominant when the soil layers were deep enough to remain frozen for long periods during the spring and early summer.

Lichen heath soil types and soil depth

Lichen-dominated forest communities have mostly been found on regosols or podsols (Nordhagen 1943; Löffler *et al.* 2008). Plant growth generally results in accumulation of organic residues, developing an organic layer (the O- and A-horizons). After sufficient time, a distinctive organic layer forms with humus (the A-horizon) which rest on mineral soils. Eluviation is driven by a downward movement of soil water. In time, this can develop an E-horizon. Beneath the E-horizon lies the B-horizon, a zone where the downward moving material is accumulated. The C-horizon is the relatively unaltered parent material, usually brightly colored directly from parent rock.

In alpine areas, conditions for soil development are unfavorable, and the humus layers are often less than 2 cm thick (Nordhagen 1943; Dahl 1956). During the warm Holocene period forest limits were up to 200 m higher than at present, and sites presently lichen-dominated were probably within the Boreal forest region. Alpine lichen heaths have been found on podsols, and an example is shown in Fig. 2.

Fig. 2. Soil profile from a lichen-dominated heath at Slondalen, central Norway (cf. Table 1).

Previous studies of alpine heath communities have shown they are mainly found on sites with variable soil thickness, but often the depth to the underlying bedrock can be more than 0.5 m. Lichen heaths have frequently been recorded at sites with a growth substrate of more than 30 cm, often with a humus-rich upper layer (Nordhagen 1943; Dahl 1956; Odland and Munkejord 2008a). The humus layer (O) is mostly between 1 and 10 cm thick, underlain by a bleached soil layer (E) often 5-12 cm thick.

Nordhagen (1943) described soil profiles from different types of lichen-dominated vegetation types from Sikilsdalen, southeast Norway. In all profiles, there was a humus-rich layer with a thickness between 1 and 8 cm. In some, there was a bleached soil layer 4-5 cm thick, followed by a B-layer 15-20 cm thick, underlain by moraine material. Dahl (1956) studied soil conditions in low alpine Alectorieto-Arctostaphyletum communities (extreme exposed sites), and found a thin humus layer and a 2-12 cm bleached soil layer below. On Hardangervidda, lichen-dominated plant communities presented with a 0-8 cm humus layer, and a 40 cm thick B layer (Hinneri *et al.* 1975). Lichen cover degree and lichen biomass have been studied in sites with different soil thickness (Myrvold 2013; Odland *et al.* 2014). These measurements include the thickness of the moraine material (the C-horizons), and indicate that high lichen abundance was mainly associated with a soil thickness between 10 and 40 cm (Fig. 3). Sundstøl (unpublished) found podsol profiles in most lichen dominated types (cf. Tab. 1).

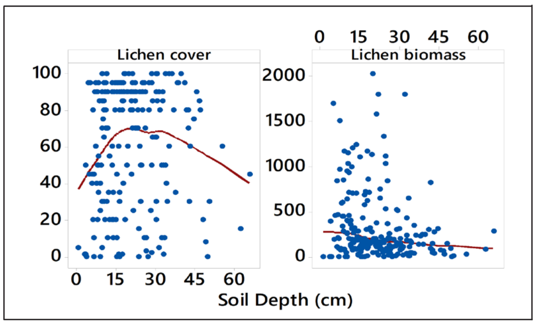

Fig. 3. Relationships between lichen cover (%), lichen biomass (g.m^{-2}) and soil depth (cm) (Based on data from Odland *et al.* 2014). Average lichen cover was 65±26%, average soil depth was 14.8±9.1 cm, and average lichen biomass was 533±405 g.m^{-2}. Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Soil richness

Previous studies have shown that alpine lichen-dominated heaths are mostly confined to oligotrophic soils with a pH mostly below 5.0 (Dahl 1956; Ahti and Oksanen 1990; Odland and Munkejord 2008; Sundstøl *et al.* unpublished).

Fig. 4 shows a plot of relationship between soil pH (upper 10 cm) and total lichen cover (data from Reinhardt *et al.* 2013; Odland *et al.* 2014). The data indicates that high lichen cover is mainly associated with pH values between 4.0 and 4.5.

The substrate has mostly low amounts of N and P, and is often subjected to frequent episodes of acute drought (Crittenden *et al.* 1994; Crittenden 2000). Lichens are adapted to growth in N-limited habitats, are quickly outcompeted in areas where N levels are higher (Hauck 2010), and are therefore sensitive to air pollution and nitrogen deposition. In an experimental study, Britton and Fisher (2010) found a critical N load for terricolous lichen communities (<7.5 kg N ha^{-1} yr^{-1}) and suggest that concentrations of N may have detrimental effects on the growth of sensitive species. Theodose and Bowman (1997) found that species diversity increased with nutrient additions to poor sites, while Natali *et al.* (2012) found that winter warming led to higher N availability. Higher soil temperatures in winter can also increase leaching of inorganic N compounds during snowmelt (Kaste *et al.* 2008). In a study by Klanderud (2008), which simulated environmental changes, the five most common lichen species decreased in abundance, and in some cases disappeared completely, likely due to a combination of increased temperatures and N inputs. Alpine lichen-dominated heaths are rarely found on calcareous sites. In these sites, the soils are generally less than 10 cm thick and the lichen cover is usually lower than 20% (Bringer 1961a, 1961b; Nordhagen 1955; Baadsvik 1974; Reinhardt *et al.* 2013). Table 2 shows data from soil chemical analyses from the upper 10 cm soil layer in 13 plots dominated by lichens.

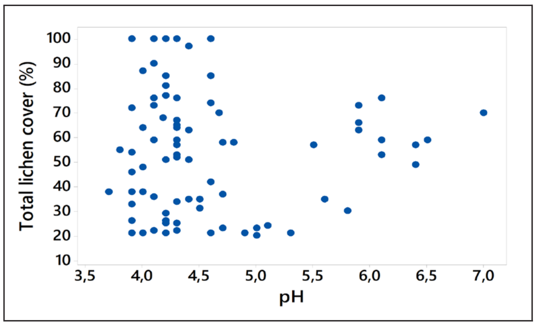

Fig. 4. Relationship between soil pH and total lichen cover (Based on data from Odland *et al.* 2014 and Reinhardt *et al.* 2013).

Soil horizon	**Depth**	**pH**	**% Organic matter (loss on ignition)**
Imingfjell, site 1 (ridgetop)			
OA	1-10	4.1	6.71
E	10-15	4.3	3.20
B1	15-26	4.9	1.00
B2	26-51	5.0	0.65
B3	51-68	5.2	0.34
BC	68+	5.1	0.33
Imingfjell, site 2 (midslope)			
O	0-8	3.7	56.40
E	8-14	4.0	1.92
Bs	14-29	4.7	5.48
Bh	29-40	4.7	9.69
BC	40+	5.2	0.88
Slondalen, site 1 (midslope)			
O	0-10	4.6	22.25
E	10-13	4.8	6.00
Bs	7-23	5.6	1.67
B2	23-43	5.8	1.62
C	43+	5.9	5.20
Slondalen, site 2 (snowbed)			
O	0-3	4.5	11.57
E	3-6	4.9	4.57
Bs	6-26	5.8	3.45
C	26+	6.1	2.60

Table 1. Data from four soil profile analyses in two alpine areas in S Norway (Data from Sundstøl *et al.* unpublished). Sites: I = Imingfjell (north-eastern part of Hardangervidda), L = Slondalen (Lesja mountain, Central Norway). Depth in cm, H = soil horizon. LOI = loss on ignition.

Lichen cover (%)	pH	Extracable P (mg/kg)	Extracable K (mg/kg)	Extractble Mg (mg/kg)	Extracable Ca (mg/kg)	Total C (%)	Total N (%)
95	4.4	0.6	2.5	3.8	18.4	4.4	0.2
100	4.1	1.4	3.1	3.2	20.0	3.7	0.2
75	4.2	0.6	0.9	2.4	19.8	4.3	0.2
78	3.8	2.0	16.9	10.8	48.0	8.9	0.3
60	3.9	0.9	2.8	2.4	22.6	4.8	0.2
73	4.3	0.6	3.0	3.2	17.9	5.0	0.3
83	4.2	1.0	2.5	2.9	20.1	3.3	0.2
95	4.3	0.6	3.3	5.2	24.2	3.3	0.2
90	5.2	0.9	3.1	15.0	129.0	4.8	0.3
95	4.4	0.7	2.2	6.5	28.8	3.1	0.2
85	4.4	0.9	6.6	10.5	35.8	8.3	0.4
80	4.4	1.9	8.6	12.0	51.3	9.6	0.6
73	4.7	0.7	6.8	18.3	55.0	5.2	0.3
AV	**4.3**	**1.0**	**4.8**	**7.4**	**37.8**	**5.3**	**0.3**
SD	**0.3**	**0.5**	**4.1**	**5.1**	**29.3**	**2.1**	**0.1**

Table 2. Results of soil chemical analyses from 13 lichen-dominated heaths (Data from Sundstøl *et al.* unpublished). LC = total lichen cover (%), P = phosphorous, K = Potassium, Mg = Magnesium, Ca = Calcium, C = Carbon, and N = nitrogen. AV = average values, SD = Standard deviation.

Mat-forming lichens are not dependent on soil conditions because they are able to sequester nutrients directly from atmospheric sources (Crittenden 1988; Ellis *et al.* 2004). They can efficiently recycle nutrients from senescent tissue to support growth, with high nutrient-use efficiency and residence times (Kytöviita and Crittenden 2007), and are physiologically able to survive long periods of desiccation (Kranner *et al.* 2008).

Importance of snow

Ecological gradients generated by spatial patterns of snow represent several correlated environmental factors influencing alpine plant life. Ecological effects of snow can be either direct or indirect, and these can have major impacts on both vegetation composition and grazing animals.

In Norway, snow can be quantified in different ways: maximum thickness, length of the snow cover period, timing of snow melt during spring, snow density, amount of water (snow water equivalent or SWE), and hardness. Snow has generally achieved maximum thickness and distribution during March/April, and by then most exposed sites are free from snow (Kohler *et al.* 2006: Odland and Munkejord 2008a; Löffler *et al.* 2008). Long periods with little snow resulted in extensive soil frost that can last until late June.

Estimation of the effect of snow is difficult because all variables change continuously during the snow season and from year to year. Long-term average values are the main factor defining vegetation distribution patterns that we can observe at present. According to Wahren *et al.* (2005) and Bidussi *et al.* (2016), direct effects of show depth, duration and quality on lichens in natural habitats are less recognized and only partly understood. Lack of snow cover reduces the degree of insulation and results in low soil temperatures, extensive soil freezing, and increases in freeze/thaw cycles (Edwards and Cresser 1992; Groffman *et al.* 1999; Freppaz *et al.* 2008). Schimel *et al.* (2004) focused on the importance of early snow accumulation during autumn. Previous studies have mostly concluded that the main factors associated with the occurrence of alpine lichen-dominated heaths are snow thickness and its effect on soil temperatures (Dahl 1956; Odland and Munkejord 2008a).

Snow thickness

Snow thickness is a very important factor associated with lichen heath occurrence. Dahl (1956) measured snow thickness (early spring) on the Cetrarietum nivalis association to between 0 and 0.4 m, and between 0.4 and 2.0 m on the *Cladonietum stellaris* association. He found that a snow layer less than 50 cm results in extensive soil frost during autumn/winter, which was associated with largest lichen communities dominated by *Flavocetraria nivalis*, while *Cladonia stellaris* was associated with a thicker snow layer.

According to Löffler (2007), there was an increased snow thickness where *Alectoria ochroleuca* was growing (mostly totally without snow cover) in comparison to the thinner snow cover (5-10 cm) present where *Flavocetraria nivalis* grew. And that of *Cladonia stellaris* (10-30 cm). This gradient was associated with late melting of frozen soil.

Sulkava and Helle (1975) and Kumpula *et al.* (1998) showed that *Alectoria* sp. and *Bryoria* sp. were accessible to reindeer during the winter, and these account for the main portion of the lichen biomass found where snow thickness was less than 2 m.

The relationship between maximum recorded snow thickness (early April) and total lichen species cover (Fig. 5) clearly indicate that lichen-dominated heath types were closely related to sites where the maximum snow cover was less than 1.0 m thick (Odland and Munkejord 2008a).

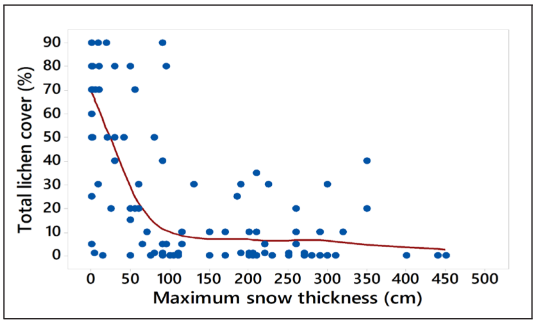

Fig. 5. Relationship between maximum recorded snow thickness (measured early April) and total lichen cover (Based on data from Odland and Munkejord 2008a). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Snow layer duration

In general, length of the snow cover duration is closely related to maximum snow thickness ($r = 0.86$, $p < 0.001$, Odland and Munkejord 2008a); however, air temperatures and their variations due to differences in altitude and aspect are also important. Date of snow-melt can be defined in the field or based on the date when soil temperature exceeds 1° C (Sundstøl and Odland 2017). Relationships between day of snow-melt and the total cover of lichens and vascular plants are shown in Fig. 6. The investigation indicates that lichens have their highest cover degree in sites where the snow had melted earlier than day 100 (April 10), while total vascular plant cover was highest in sites where the snow was melted around day 130 (end of May).

The rate of snowmelt is variable. It is mainly a function of air temperature, but can also be modified by factors such as rain, slope, aspect, and elevation. The melt rate has generally been measured to lie between 3 and 4 cm day^{-1} (Odland and Munkejord 2008a).

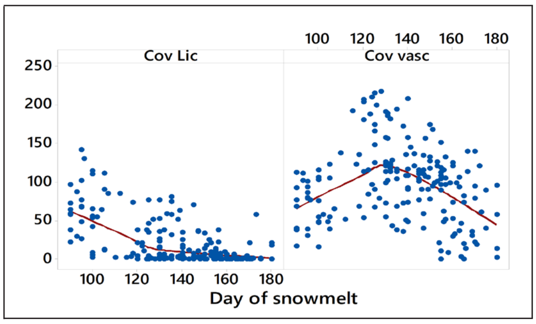

Fig. 6. Effects of snow layer duration (day of snowmelt) on the total cover of lichens (Cov Lic) and total vascular plant cover (Cov vasc) (Based on data from Odland and Munkejord 2008a). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Odland and Munkejord (2008b) have shown that some macrolichen species show statistically significant responses to snow layer duration (timing of snowmelt). Species with significant responses are listed in Table 3, where species with an indicator value of 1 are mainly found on sites with little or no snow cover (exposed early April). Species with an indicator value of 2 normally require a protective snow layer, and are mainly found on sites which are snow free 10 days later (before April 20). Species with higher indicator values are normally not abundant in lichen heaths.

Weighted average snow indicator values (WaSI) can be estimated for different alpine plant communities based on indicator values for both lichens, bryophytes and vascular plants (Odland and Munkejord 2008b; Odland *et al.* 2014). The WaSI-values can range from close to 1.0 (the most exposed lichen heaths) to below 6 (snow bed communities mostly without lichens). As shown in Fig. 7, lichen total cover and lichen volume (lichen height*lichen cover) decrease with increasing WaSI-value. The thickest lichen mats, with the highest volume are found in communities with a WaSI-value around 2, and in such communities (often dominated by *Cladonia stellaris*) there is normally a protective snow layer.

Effects of snow layer duration on the total abundances of lichens and vascular plants can be expressed in terms of WaSI-values (cf. Tab. 4 and Odland and Munkejord 2008b) as shown in Fig. 7. Figs. 6 and 7 indicate, however, that lichen abundance is highest where a thin snow cover is present.

Lichen biomass and lichen volume show major variation with estimated snow layer duration as

Species/Taxon	**Snow Index (SI)**
Alectoria nigricans	1
Alectoria ochroleuca	1
Bryocaulon divergens	1
Flavocetraria cucullata	1
Flavocetraria nivalis	1
Thamnolia vermicularis	1
Cladonia uncialis	2
Cladonia rangiferina	2
Cetraria ericetorum	2
Cladonia stellaris	2
Cladonia arbuscula	2
Cladonia gracilis	2
Cladonia macrophylla	2
Cladonia spp. (unidentified species)	4
Stereocaulon spp. (unidentified)	4
Cladonia ecmocyna	7

Table 3. Indicator values for lichen species (SI) and lichen taxa that show significant responses to snow layer duration (from Odland and Munkejord 2008b). Differences between the SI-values are explained in Table 4.

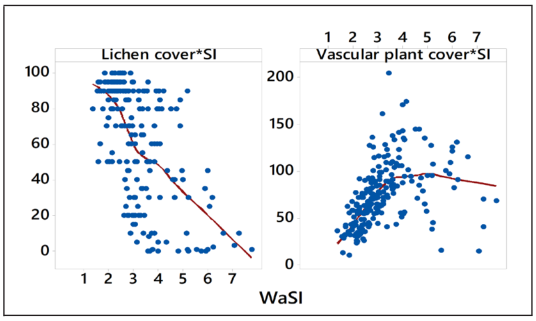

Fig. 7. Relationships between weighted average snow indicator values (WaSI), total lichen cover and vascular plant cover (Based on data from Odland *et al.* 2014) (cf. Table 4). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

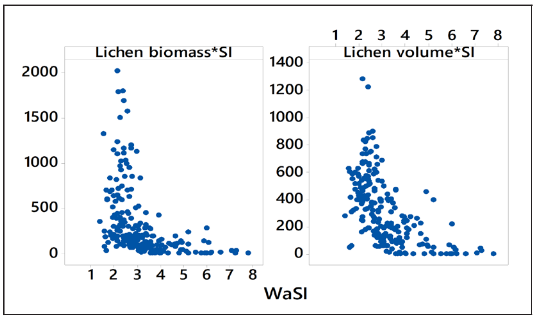

Fig. 8. Relationships between weighted average snow indicator values (WaSI), lichen biomass (g m^2) and lichen volume (lichen cover*lichen height) (cf. Table 4) (Based on data from Odland *et al.* 2014).

estimated by WaSI. As shown in Fig. 8, the highest biomass and volumes have been found in sites with a WaSI-value between 2 and 3. Sites with low WaSI-values are mainly dominated by *Alectoria nigricans, A. ochroleuca, Bryocaulon divergens, Flavocetraria cucullata, F. nivalis*, and *Thamnolia vermicularis*. Lichen heaths dominated by *Cladonia species* (especially *C. stellaris*) have higher biomass. The large differences in lichen biomass and volume as shown in Fig. 8 are mainly effects of reindeer grazing and trampling.

The gradient from the most exposed alpine sites mostly without a snow cover to sites with heavy snow loads are often separated into six zones (Odland 2012). Ecological characteristics between these zones have been quantified in Table 4. As shown in Figs. 7 and 8, lichens have their main abundances in zone 1 and 2, and these are mainly characterized by early snow-melt, WaSI-values lower than 3, a thin or missing snow cover and a long thaw period.

Bidussi *et al.* (2016) studied how increased snow accumulation affected lichen growth in dominant mat-forming arctic-alpine lichens. The species were transplanted for one year at different snow depths. Snow depth significantly affected lichen RGR (relative growth rate), but in species-specific ways. *A. ochroleuca* and F. nivalis, which are confined to sites with little or no snow, showed reduced RGR % when exposed to 120 cm of snow. *C. mitis* and *C. delicei* have a broader tolerance and showed relatively small reductions in RGR % when exposed to 200 cm snow. Their conclusion was that increased snow most likely reduces the abundance of dominant mat-forming lichens in alpine ecosystems of Scandinavia.

Lichen heath albedo and insulating effects

Albedo

Albedo is the proportion of incident solar radiation that is reflected by the land surface. The reflected solar radiation averages 80 – 90% on snow-covered surfaces, and there is a significant and rapid drop from about 80% to 10% when snowmelt begins and the vegetative surface emerges.

Vegetation zone	**SI**	**WaSI**	**Snow melt date**		**Thaw-period**	**SGS Day**	**Snow thickness**
			Day	**Date**			
1. Exposed ridge	1	<2	<99	Before April 9	>50	150	0–0.5 m
2. Snow protected heath	2	2-3	100–110	Before April 20	30-40	145	0.5–1 m
3. Lee-side	3	3-5	111–121	Before May 1	20	140-150	1.5–3 m
	4		122–127	Before May 7	15		
	5		128–135	Before May 15	10		
	6		136–146	Before May 26	6		
4. Early snow bed	7	5-6	147–153	Before June 2	5	155	3–4 m
5. Late snow bed	8	6-7	154–162	Before June 11	6	165	
6. Extreme snow bed	9	7-8	>162	Later than June 11	2	170	4–10 m

Table 4. Vegetation zonation along a snow gradient from an exposed lichen-dominated ridge, down to an extreme snow bed community. Six zones are separated (Odland 2012). SI = characteristic species indicator values (Odland and Munkejord 2008b). WaSI = Weighted average snow indicator values estimated from plant communities (Odland and Munkejord 2008b; Odland *et al.* 2014) (cf. Figs. 7 and 8). Snow-melt dates for different zones are given as day of the year (measured during 2004 which was a warm season when snow melt was approximately 2 weeks earlier than normal (Odland and Munkejord 2008b). The thaw period gives an average number of days between date of snow-melt and the start of the growing season determined by the day when soil temperature exceeded 6oC. Snow thickness gives values measured in early April. SGS = start of the growing season (day of the year).

Thus, albedo plays a critical role in the surface energy budget and is a direct feedback from vegetation to the climate system (Pitman 2003; Bala *et al.* 2007; Bonan 2008). Albedo varies substantially among different vegetation types, and changes with the development and senescence of the canopy. More specifically, the seasonal course of albedo is determined by the combined effect of seasonal changes in the reflectance of photosynthetically active (PAR, 400–700 nm wavelengths) and near-infrared (NIR) radiation. Lichen albedo has been measured at 0.31, mosses 0.24, and green vegetation 0.20 (Peltoniemi *et al.* 2010). This shows that lichens have high albedo compared to other vegetation surfaces. Where vegetation is sparse, the degree to which the soil warms up depends on its color, water and air content, and its structure (Larcher 1995).

The roles of bryophytes and lichens in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). With their high albedo and thermal conductivity, lichen mats also act as insulators that greatly impede the flux of heat into the underlying soil. A lichen mat 12 cm deep can reduce the soil heat flux by almost 50% and thereby significantly lower soil temperature (Bonan 1989). According to Kershaw (1985) and Gold *et al.* (2001), lichen mats will also reduce soil temperature during summer and dampen diurnal temperature fluctuations (cf. Figs 9 and 11). Reducing the lichen cover increases the heat flux between soil and the atmosphere, leading to higher soil temperatures in the summer and lower average soil temperatures in the winter (Olofsson *et al.* 2002). When the lichen canopy is disturbed, soils tend to warm up more quickly, especially at the beginning of the vegetation period, which could have positive feedback on plant growth since germination may begin earlier, thus lengthening the vegetation period.

Cohen *et al.* (2013) found that albedo was lower on the Norwegian side of a border fence than on the Finnish side during the snowmelt period, due to the presence of shrubs that stuck out from the snow surface. However, during the snow-free period, the Norwegian side had higher albedo which was attributed to the presence of lichens and lack of disturbance. Stoy *et al.* (2012), using satellite data, also found that the albedo in the snow-free season was higher on the less-intensively grazed Norwegian side of a border fence than on the overgrazed Finnish side.

Insulator effects

The effects of lichens and bryophytes as temperature insulators have been emphasized in several studies (Olofsson *et al.* 2002; Sofronov *et al.*, 2004; Peth and Horn, 2006; Fauria *et al.* 2008; Klein and Shulski 2011; Stoy *et al.* 2012). Consequently, changes in lichen cover that result from trampling during summer grazing alters the soil microclimate (Stark *et al.* 2000).

Well-developed lichen mats have been found to strongly affect the moisture and thermal regimes of forest soils, thereby reducing drought stress (Kershaw 1985; Bonan and Shugart 1989; Fauria *et al.* 2008). It is possible that the ecological effects are similar in alpine lichen heaths. Stoy *et al.* (2012) quantified the surface and subsurface temperatures and spectral reflectance of common moss and lichen species at field sites in Alaska and Sweden. Under alpine lichen heaths, temperatures were lowered by 10 to 11° C compared to bare soil. Similarly, cryptogams can also prevent warming of the soil. This is important for preventing permafrost from melting (van der Wal and Brooker 2004; Gornall *et al.* 2007). Field observations have revealed that at the beginning of June 2003, the soil underneath undisturbed lichen cover was still frozen at a depth of 30 cm, whereas no ice was encountered at that depth at the sites with moderately and heavily disturbed lichen cover. Similarly, Odland and Munkejord (2008a) found that in exposed lichen alpine heaths with a thick, moist humus layer in south Norway, soil temperatures needed more than two months to thaw on humus-rich soils. In exposed *Dryas octopetala* heaths without a thick humus layer, there was no delayed soil temperature increase during the spring (Reinhardt *et al.* 2013).

Effects of soil temperature and thaw period

Soil temperature

In Arctic tundra, lichens are commonly associated with permafrost and/or carbon-rich soils (Zimov *et al.* 2005; Schuur *et al.* 2008; Tarnocai *et al.* 2009). In Fennoscandia, previous lichen heath studies have reported that they are mainly found on sites with a seasonally frozen soil (Dahl 1956; Wielgolaski 1975). The amount and duration of soil frost has been associated with length of the thaw period, but this relationship has rarely been quantified. Soil temperature can be highly variable over very small distances, being dependent upon snow cover, type of vegetation cover and the heat capacity of the soil (Dahl 1956; Larcher 1995).

The presence or absence of snow determines the winter soil surface temperature (Dahl 1975; Löffler 2005), and snow acts as an insulator that influences both the temperature and the extent to which the soil is exposed to freeze-thaw events (Edwards *et al.* 2007). According to Kershaw (1985) and Rees (1993), studies of surface and subsurface temperatures and subsurface heat fluxes of bryophytes and lichens at the species level has rarely been undertaken. The relationship between air temperature and soil temperature is in itself fairly complex. Soil temperatures are dependent upon a number of factors such as moisture content, evaporation, albedo, and the thermal conductivity of the soil itself (Garcia-Suarez and Butler 2006) and is generally less variable than air temperatures (Gehrig-Fasel *et al.* 2008). Sundstøl and Odland (2017), investigated relationships between soil temperature and total lichen cover. Results (Fig. 9) show that a high lichen cover is associated with low soil temperatures, but also with relatively low summer soil temperatures. Total shrub cover correlated with differences in soil temperatures (Fig. 10), partly because some shrubs can be present in lichen heaths while other require a protective snow cover.

Different lichen and vascular plant species frequently found in alpine lichen heaths respond differently to the degree of frost sum (Sundstøl and

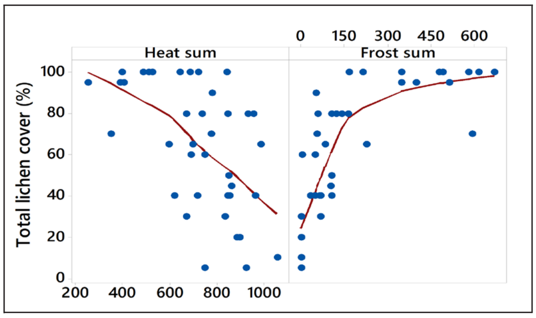

Fig. 9. Average lichen cover degree in relation to soil heat sum and soil frost sum measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

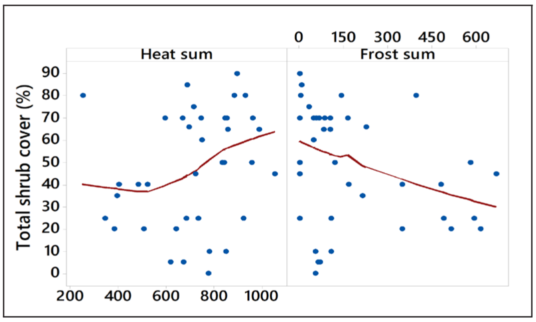

Fig. 10. Average shrub cover degree in relation to soil heat and frost sums measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Odland 2017). Lichen species characteristic of the most exposed heath types (cf. Table 2) such as *Alectoria ochroleuca, Bryocaulon divergens, Flavocetraria cucullata* and *F. nivalis* increase their abundance with increasing soil frost. *Cladonia arbuscula*, *C. rangiferina*, and *C. stellaris* however, decrease their abundance with increasing frost. *Betula nana* has a wide tolerance in relation to soil frost, while *Empetrum nigrum*, *Vaccinium myrtillus*, and *V. uliginosum* increase their abundance with decreasing frost sum. *Nardus stricta* was only found on sites with low or no frost while *Juncus trifidus* had a broad tolerance, but was most abundant where frost-sum was lower than 200. This indicates that many vascular plants do not tolerate high soil frost, and are therefore not competitors to lichen heaths so long as the soil frost remained unchanged.

Length of the growing season and the thaw period

The start and end of the vascular plant growing season are closely related to soil freezing and soil thawing (Ryden and Kostov 1980; Bonan and Shugart 1989). The start of the growing season during spring/summer has been defined in different ways (see review by Odland 2011). In general, biological activity is low when temperature is low, and, growing season start has frequently been defined by use of a soil temperature threshold of 5 - 6° C (Heikinheimo and Lappalainen 1997; Tuhkanen 1980; Karlsson and Weih 2001). This applies mainly for vascular plants with their roots in frozen soil where there is no available water. Low soil temperatures inhibit root elongation and increase water viscosity, inhibiting water uptake (Bonan and Shugart 1989). Lichens and bryophytes, however, have no roots, and they can grow when the substrate is frozen.

Thaw describes the change from a frozen solid to a liquid phase by gradual warming. The term "thaw period" has been defined in two ways: 1) On the most exposed sites without snow during most of the winter, the thaw period has been quantified as number of days from DOY 90 (day of the year) (April 1) which generally is the period when snow starts to melt (Odland and Munkejord 2008a). 2) In sites with a snow cover, start of the thaw period has been defined by timing of the event when soil temperatures reach + 1° C (Sundstøl and Odland, 2017). Odland and Munkejord (2008a) studied the distribution of oligotrophic alpine vegetation types in relation to length of the thaw period. Lichen-dominated types had thaw periods longer than 40 days, lee side vegetation less than ca. 20 days, and snow bed vegetation less than 8 days.

Thawing processes are highly influenced by the high heat capacity of water. Moist soil with a high heat capacity must be subjected to a long period of frost to freeze, but a long period with high temperatures is also needed to thaw the soil (Willis and Power 1975). Effects of air temperature on soil temperature are strongly influenced by the species composition of the surface and by soil (humus) water content. A relatively dry soil freezes more quickly and deeply than a wet soil, and thaws faster in the spring. Lichen cover reduces heat transfer to the soil below during warm periods because of its high albedo (Sofronov *et al.* 2004). Although summer temperatures often exceeded 40° C just above the surface of the moss-lichen layers, frozen soils remained under this coverage. The strong effect of lichen cover on soil temperatures is also evident from Fig 11. Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low.

Sofronov *et al.* (2004) showed that soil temperature increased from 0° C in an organic soil layer, to 8° C at the soil surface measured in August (in Larix forest in Siberia). Depth of the soil thawing was affected by surface vegetation dominated by mosses and lichens. There was a strong linear correlation between organic layer thickness and soil temperature.

Lichens and vascular plants have different responses in relation to the length of the thaw period (Fig. 12). Lichens have their highest cover degree where the thaw period is longer than 15 days, while vascular plant cover decreases when the thaw period is longer than 15 days. Betula nana, Arctous alpinus, and Empetrum nigrum can however, tolerate a long thaw period (Sundstøl and Odland 2017).

A relatively deep soil (cf. Fig. 3) has a decisive impact on the start of the growing season and length of the growing period. A moist, humus-rich soil is essential for development of a long soil frost period. Water has a high specific heat capacity, meaning that the soil needs to be exposed to extensive frost to freeze, and that the frozen soil needs to be exposed to high temperatures for a long period to thaw. Exposed sites with lichen heaths

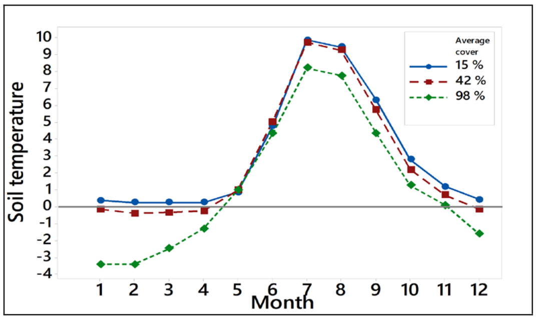

Fig. 11. Effects of variable average lichen cover in relation to average monthly soil temperatures. Sampled study sites were divided into three groups where lichen cover was >80% (average in 13 plots was 98%), cover 30 -50% (average in 7 plots was 42%), and cover <30% (average in 6 plots was 15%). Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low (Data from Sundstøl and Odland 2017).

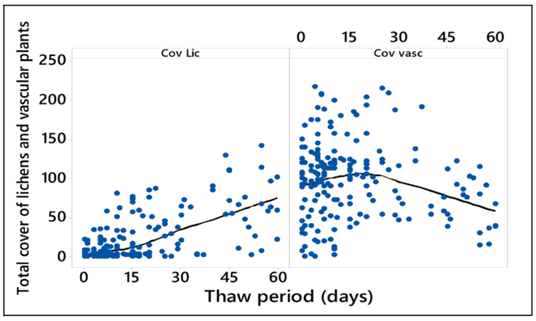

Fig. 12. Relationships between total lichen cover (Cov Lic) and total vascular plant cover (Cov vas) in relation to number of days needed to increase soil temperature from 1° C to 5° C. Start of the growing season is often defined as the day when soil temperature exceeds 5° C (Based on data from Odland and Munkejord 2008b and Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

may need more than 50 days to thaw (Odland and Munkejord 2008a). Exposed *Dryas octopetala* vegetation with a thin soil layer were, however, associated with less than 15-30 days to thaw (Reinhardt and Odland 2012; Reinhardt *et al.* 2013).

Even if the snow has melted on a site, vascular plants may not start to grow because the soil can be frozen. Lichens, however have no roots and can therefore initiate growth.

Lichen growth, biomass, and relationship to other plants

Lichen photobionts are concentrated in the apical part of the thalli (Nash *et al.* 1980). Experiments have shown that the relative growth rate of the apical parts is higher than that of the lower basal parts, which are constituted of fungal, sometimes senescent, tissues (Kärenlampi 1971; Kytöviita and Crittenden 2002; Gaio Oliveira *et al.* 2006).

The optimal growth temperature for lichens lie between 15-25° C, but in summer the temperature at the surface of lichen mats can reach 35-40° C without affecting their vitality (Tegler and Kershaw 1980; Coxson and Wilson 2004). Laboratory experiments show that lichens are extremely tolerant of freezing stress and of exposure to low temperatures. CO_2 exchange was already active at around -20° C, while the optimum temperature for net photosynthesis lies between 0 and 15° C.

Most vascular plants are not able to grow on sites with a long-lasting frozen soil. A precondition for lichen heaths is therefore a relatively thick and moist soil layer which will freeze solid. The great success of lichens in cold areas gives evidence of their physiological adaptation to areas with low temperatures. In general, lichens are able to persist through glacial periods, but extended snow cover and glaciation are limiting factors (Kappen *et al.* 1996).

Lichen growth and biomass

According to Ahti (1959), three growth stages exist throughout the reindeer lichen lifespan. The first stage, the growth-accumulation period, lasts an average of 10 years but can vary from 6 to 25 years. During this stage, size increases annually, and no part of the podetium dies. The internodes grow 10 to 15 times the height attained in the first year of life. During the second stage, podetium height still increases, but internode death occurs at the base. Despite some internode decay, height growth continues. This stage may continue for several decades and can exceed 100 years. During the third stage, the withering period, the podetium decays at the base faster than internodes lengthen. This stage of growth lasts some 10 to 20 years.

Maximum reindeer lichen height is around 12 cm, which is found when the top zone growth equals the rate of death and decomposition in the bottom zone (Morneau and Payette 1989). In old undisturbed lichen stands reaching heights of 12 cm, the lowermost 1-2 cm of the podetia are dead or decaying (Odland *et al.* 2014).

Lichen growth follows a logistic or sigmoidal curve with a maximum growth rate at an intermediate lichen height (Kumpula *et al.* 2000; Heggberget *et al.* 2002). Different methods have been used to determine the growth rate of reindeer lichens (see discussions in Kumpula *et al.* 2000), resulting in growth rates ranging from 2 to 6 mm year^{-1}. Kumpula *et al.* (2000) found that the maximum thickness increase in the living part of the whole lichen stand was only 1.5-1.6 mm year^{-1}, and the estimated biomass increase was 11% year^{-1}.

Standing biomasses in oligotrophic lichen heaths at Hardangervidda have been estimated to be 61, 7, and 380 g m^{-2} respectively for vascular plants, mosses and lichens (Wielgolaski 1975). Annual production in lichen heaths was 88 and 182 g m^{-2} year^{-1} respectively for lichens and vascular plants.
In Kevo, north Finland, the lichen biomass production was estimated to be 77 g m^{-2} year^{-1} and for vascular plants it was 375 g m^{-2} year^{-1} (Kallio 1975). The highest annual increase in lichen biomass has been estimated at approximately 120 kg ha^{-1} year^{-1} in a lichen mat with a biomass of ca. 800 kg ha^{-1} (Helle *et al.* 1990). According to Kumpula *et al.* (2000), the maximum lichen production has been estimated to be 170 kg dry matter ha^{-1} year^{-1} measured in a lichen stand that was around 40 year old, with a standing living biomass of nearly 3 000 kg dry matter ha^{-1}.

Estimations of lichen production in heath communities often include vascular plants growing in the heaths. In some cases, total production has been found to be as high as 250 – 300 g m^{-2} year^{-1} (Kjelvik and Kärenlampi 1975). When dominated totally by lichens, the total production was only around 100 g m^{-2} year^{-1} even in dense lichen heaths. The production to biomass ratio in lichen at Hardangervidda was estimated to be ca. 0.2 (Wielgolaski 1975). Lichen productivity was calculated from an estimated growth rate of 0.23 g g^{-1} year^{-1} (Kjelvik 1978).

Relationships to vascular plants

It is generally considered that lichens are very poor competitors (Grime 1977), growing in places where vascular plants and bryophytes are less successful. In areas where their competitors are suppressed by severe climate, lichens would expand to new habitats due to competitive release (Ahti and Oksanen 1990). It can therefore be assumed that lichens are in greatest abundance at sites where the establishment of vascular plants is difficult or unsuccessful. The main factor critical to most vascular plant growth is, as described, soil frost and a long period with frozen soil (Karlsson 1985; Sofronov *et al.* 2004). Several studies have emphasized the negative effects of low soil temperatures for the growth of vascular plants (Tranquilini 1979). There are, however, only a few vascular plant species which are able to grow on frozen soil together with lichens (Odland and Munkejord 2008b). Unfrozen soil is a prerequisite factor for the initiation of springtime root-zone processes and recovery of photosynthetic capacity (Karlsson and Nordell 1996; Sutinen *et al.* 2009).

Decrease of lichen poplations has frequently been described as an effect of strong competition from the expanding shrub cover due to increased leaf litter and subsequent shading which prevents the re-establishment of lichen cover (Gaare 1997; Heggberget *et al.* 2002; Fraser *et al.* 2014). These views are not in accordance with the conclusions above. Some alpine lichen heath communities can have a co-dominance of vascular plants, but the data shown in Fig. 13 indicates a negative correlation between total lichen cover and total vascular plant cover. Species with snow indicator values of 1 (cf. Table 3) rarely have a high cover of shrub species. *Cladonia* species with snow indicator values of 2 or higher, which have a relatively thin snow layer during the winter, can have a high cover of *Betula nana* which also has a snow indicator index of 2.

Effects of reindeer grazing

Reindeer grazing and trampling can locally be the most important factor affecting the state of lichen pastures. Reindeer prefer certain lichen species to others, and this selective grazing can change the species composition of lichen pastures. Lichen mats can be heavily affected by overgrazing and trampling which, in high-density populations, can cause substantial winter forage depletion and trigger large scale habitat shifts or population declines (Crittenden 2000; den Herder *et al.* 2003; Klein 1987; Manseau *et al.* 1996; Vistnes and Nelleman 2008; Falldorf *et al.* 2014, Heggenes *et al.* 2018).

Graminoids (grasses and sedges) have been found to increase under heavy grazing pressure from reindeer and caribou on lichen-dominated plant communities (Klein 1968; Thing 1984; Post and Klein 1999), and such species have also been predicted to increase under global warming scenarios (Chapin *et al.* 1995; Joly *et al.* 2009).

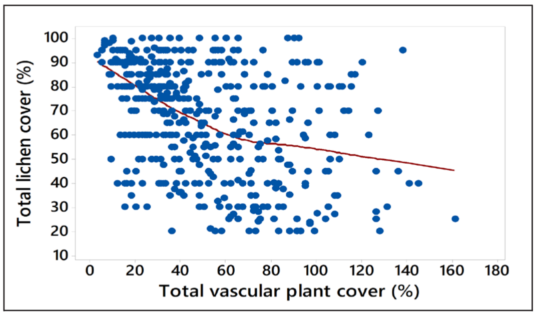

Fig. 13. The relationship between total vascular plant cover and total lichen cover from 471 study plots at the Hardangervidda mountain plateau, south Norway. Only plots where total lichen cover was higher than 20% were included (Based on data from Odland *et al.* 2014 and unpublished data). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) are drawn.

Intensive reindeer grazing reduces lichen biomass, being commonly 10% or even less of the biomass typical in un-grazed mature lichen associations (Mattila 1981; Tømmervik and Lauknes 1988; Kojola *et al.* 1995). On the Hardangervidda mountain plateau, lichen biomasses or volumes have been estimated to have decreased by more than 60% (Odland *et al.* 2014). Väre *et al.* (1996) found that grazing reduced lichen biomass from 790 to 86 g dw m^{-2}. Similarly, Akujärvi *et al.* (2014) found that the lichen cover was about five-fold greater and the biomass about fifteen-fold greater in the ungrazed (fenced) sites than in the grazed ones.

van der Wal (2006) reports that increased grazing pressure results in a transition to first a moss-dominated tundra and finally a graminoid-dominated vegetation. He suggested that lichens have to be protected by snow in winter to prevent overexploitation (cf. also Adamczewski *et al.* 1988; Ferguson *et al.* 2001). This may be valid for *Cladonia stellaris*-dominated forest vegetation but probably not for alpine lichen dominated vegetation. Increased snow would insulate the soil from extensive soil frost and thereby give vascular plants a chance to establish and outcompete lichens.

In the tundra, grazing by reindeer has been shown to reduce the cover of both lichens (Väre *et al.* 1995; den Herder *et al.* 2003; van der Wal *et al.* 2001) and dwarf shrubs (Olofsson *et al.* 2009; Dahlgren *et al.* 2009; den Herder *et al.* 2008). Stepwise transition from unproductive lichen-dominated vegetation to more productive moss and graminoid-dominated vegetation types have been hypothesized by Oksanen and Oksanen (2000), Zimov *et al.* 2005, and van der Wal (2006).

Destruction of cryptogamic vegetation by herbivore grazing and trampling can lead to extensive melting of permafrost, both directly and by accelerating the decomposition of organic matter, which in turn will increase soil temperatures (Woodin and Marquiss 1997; van der Wal and Brooker 2004). Sofronov *et al.* (2004) showed that the depth of soil thawing increased with a reduction in the moss-lichen layer thickness.

Effects of climate change

Reviews of effects of climate change on the winter food resources for reindeer (*Rangifer tarandus tarandus*), have been published by Suominen and Olofsson (2000), Heggberget *et al.* (2002), and Bernes *et al.* (2015). Most of these have, however, not included effects of soil frost and thaw period.

Ongoing climate change has had multiple effects on alpine lichen-dominated heaths. The main climate changes affecting lichen heaths can be assumed to be increased precipitation, both in the form of rain and snow, higher winter temperatures, and more unstable winter conditions. The general climate character will therefore be increasingly oceanic in most areas. Such changes have already resulted in both floristic and ecological changes, and those will probably be accelerated into the future.

Recent studies have found that the abundance of reindeer lichens have decreased in alpine heath communities. This has often been associated with increased dominance of shrub species (Cornelissen *et al.* 2001; Virtanen *et al.* 2003; van Wijk *et al.* 2003; Kullman 2005; Öberg 2002; Hudson and Henry 2009; Tømmervik *et al.* 2009; Pajunen *et al.* 2011; Danby *et al.* 2011; Fraser *et al.* 2014; Vuorinen *et al.* 2017). After resampling of *Loiseleuria procumbens* heaths, Virtanen *et al.* (2003) found that lichen abundance had decreased while *Empetrum nigrum* and mosses had increased. Other studies have also found that dense mats of lichens have been replaced by expanding *Empetrum nigrum* or other dwarf-shrubs (Kullman 2005; Öberg 2002).

Increased nutrient inputs combined with warming treatments have been found to decrease lichen abundance in northern Sweden (Jägerbrand *et al.* 2009), and a changing climate along with increased herbivory led to such losses of lichen cover in Arctic Canada that reintroduction was not viable (Klein and Shulski 2011).

Effects of changes in snow cover

So far, precipitation has increased in most parts of Fennoscandia. Increased rain, especially during the winter (rain on snow) has multiple effects on lichens, especially rate of snow-melt, soil temperatures, and soil thaw. Increased precipitation combined with low temperatures will increase snow depths. However, despite increased precipitation, the snow layer duration has decreased in most low-alpine areas. This is mainly an effect of faster snowmelt due to increased air temperature.

A reduction in snow depth could also lead to an increase in the depth and extent of frozen soil, which would have effects on biogeochemical and microbial processes and could result in direct injuries to roots (Hülber *et al.* 2011). However, in Norway, most models predict an increase in snow depths at higher elevations, coupled with a shorter snow season (Dyrrdal 2013; Klimaservicesenter 2015). Snow depth increases of about 2 cm per decade since the early 1900s have been recorded at Abisko in northern Sweden, despite there being no changes in snow season duration (Kohler *et al.* 2006). According to Bidussi *et al.* (2016), increasing snow depths will likely reduce the abundance and distribution of dominant mat-forming lichens in Scandinavian alpine ecosystems.

Autumn and winter climate change due to changes in snow regime and temperatures can have major impacts on northern plant communities. Vascular plants, particularly shrubs, appear to be most prone to damage while lichens appear tolerant (Bokhorst *et al.* 2012).

Turunen *et al.* (2009) suggested that increased winter precipitation, the occurrence of ice layers, deeper snow cover, and the appearance of molds beneath the snow cover may reduce the availability and/or quality of reindeer forage, but prolongation of snowless periods might have the opposite effect.

Effects of soil warming

Changes in the snow cover and higher air temperatures have been reported to increase soil temperatures and thereby the length of the growing season. This can change the competition between lichens and vascular plants. According to Sturm *et al.* (2001b, 2005), Bret-Harte *et al.* (2002), and Mack *et al.* (2004), the potential impacts of shrub expansion are warmer winter soils, enhanced nutrient cycling, and altered plant communities.

According to Lemke *et al.* (2007), the amount of seasonally frozen ground has decreased by about 7% during the last one hundred years. Henry (2006), reporting on data from weather stations across Canada, found that warmer winters resulted in fewer soil freezing days, associated with reductions in snow depth and number of days with snow on the ground.

Macias Fauria *et al.* (2008) found large differences in soil temperature values and dynamics between grazed and un-grazed heaths. Soils in the grazed part warmed up faster in spring, thawed 2–4 weeks earlier, and cooled down faster in autumn at all depths. Soil in the grazed parts reached lower winter temperatures, and higher summer temperatures at all depths. Indeed, significantly higher growing season degree-days were found in the grazed part of the stand at depths of –5 and –20 cm.

Porada *et al.* (2016) estimated average cooling effects of the bryophyte and lichen cover of 2.7° C on temperature in the topsoil for the region north of 50° N under the current climate. Locally, a cooling of up to 5.7° C was found. These results suggest that the reducing effect of the bryophyte and lichen ground cover on soil temperature should be accounted for in studies which aim at quantifying feedbacks between permafrost soil temperature and climate change.

Results from experimental warming suggest that lichens may become less competitive due to climate warming (Lang *et al.* 2012). According to Cornelissen *et al.* (2001), macrolichens in climatically milder Arctic ecosystems may decline if and where climate changes cause vascular plants to increase in abundance. They suggested that climate warming and/or increased nutrient availability leads to decline in macrolichen abundance as a function of increased abundance of vascular plants.

A decline in lichen biomass or abundance in artificially warmed fertilized ecosystems has been reported repeatedly in subarctic and mid-Arctic studies (Jonasson 1992; Chapin *et al.* 1995; Molau and

Alatalo 1998; Press *et al.* 1998; Graglia *et al.* 2001). This was suggested to be a response to increased shading by the taller vascular plants or the litter that they produce. Studies, both in situ and experimentally, have shown that warming increased height and cover of deciduous shrubs and graminoids, and decreased cover of mosses and lichens (Lang *et al.* 2012). Shrub abundance influences the summer albedo, and the effects of increasing shrub abundance on albedo will contribute to changes in the surface energy balance (te Beest *et al.* 2016).

General discussion and conclusions

It is of vital ecological importance to bear in mind that lichens are very poor competitors (Grime 1979), and that the distribution of alpine lichen heaths are primarily controlled by their inability to compete with fast-growing vascular plants (Kershaw 1985). Apparently, lichen heaths are mainly developed in environments where competition from vascular plants is excluded or reduced (Bonan 1989). As indicated in previous studies, the main factor associated with alpine lichen heath distribution is determined by the degree of soil frost and the length of the thaw period. It has been suggested that wind speed is the main factor for lichen heath distribution in alpine areas (Crabtree and Ellis 2010), but in our opinion, wind is an indirect factor which blows the snow cover away.

Lichen heath ecology

As shown above, alpine lichen heaths are developed on sites with a thick substrate and a humus layer on top, which is generally more than 5 cm thick. Based on results reviewed in the current paper, important factors influencing the distribution on an exposed low alpine ridge may be presented in a schematic way as shown in Fig. 14. The most exposed sites (zone 1) are dominated by species like *Bryocaulon divergens, Alectoria nigricans, A. ochroleuca, Coleocaulon aculeatum, Flavocetraria cucullata*, and *F. nivalis*. In zone 2 (snow protected heath), *Cladonia stellaris, C. arbuscula*, and *C. rangiferina* are more important. In zone 3 (lee sides), dwarf shrubs graminoids, and herbs dominate but *Cladonia* species can be important.

Any factor that changes the period with frozen soil will reduce the lichen abundance. Reindeer grazing and/or climate will change the surface albedo. The high albedo of a lichen mat decreases the heat influx to the soil, both during winter and summer. Consequently, a reduction of the lichen cover due to grazing and trampling will increase soil thawing during spring, and increase soil temperature during the summer and autumn. As a result, the growing season (defined as the period when soil temperature exceeds 5° C), will increase and this will again favor the growth of vascular plants.

Relationships to vascular plants

Numerous studies have recently reported decreasing lichen abundances in boreal, alpine and Arctic areas. This trend has often been explained by an increased dominance of vascular plants. In general, the total cover degree of vascular plants and lichens have opposite trends, and this can be explained by their different responses to snow and soil temperatures.

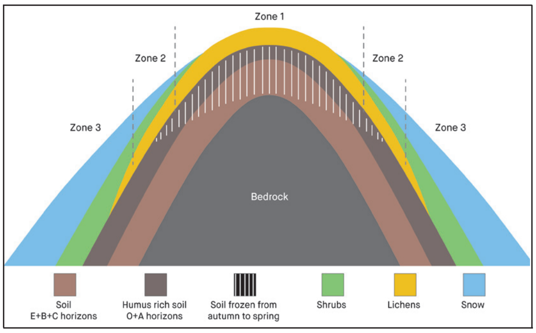

Fig. 14. Schematic drawing of an exposed low alpine ridge with important ecological factors influencing the distribution of lichens. The zones are described in Table 4.

Ongoing climate change involves changes in several environmental factors which can be critical to lichens. Numerous studies have concluded that vascular plants, especially shrubs, have increased as an effect of ongoing climate change. Few studies have linked this change to the underlying critical factor: soil temperatures have to be increased before vascular plants can outcompete lichens in the most exposed heaths. However, Brooker and van der Wal (2003) concluded that factors influencing soil temperature such as climate change or herbivory may also direct changes in vascular plant community composition. Fauria *et al.* (2008) and Porada *et al.* (2016) have also emphasized the negative effects of soil temperatures on lichens in a warmer climate.

Low temperatures and long-lasting soil frost may restrict vascular plant growth directly by limiting the rate of tissue respiration (Semikhatova *et al.* 1992) and thus nutrient uptake. Indirectly, soil frost slows the rate of soil decomposition and thus reduces the availability of essential nutrients (Jonasson 1983; Rustad *et al.* 2001). Frozen soils give vascular plants reduced soil water supply leading to tissue water deficits, especially if air temperatures increase before the soil is thawed (Gold and Bliss 1995). Winter desiccation happens when plants are rooted in frozen ground, but are trying to continue their metabolic processes anyway. Low soil temperature inhibits root growth as well as water uptake, and thus affects seedlings' water absorption and nutrient uptake rates (Mellander *et al.* 2004). This indicates that most vascular plants will probably not be able to invade lichen-dominated heaths, even if they have been well grazed before the frozen soil period has increased to a certain threshold.

Changed alpine lichen heath distribution

Climate change may modify the geographical distribution of lichen heaths in the future. Lichen heaths have their main distribution within the low-alpine zone in the continental parts of Fennoscandia where precipitation is relatively low, and winter temperatures and frost sum are low. An assumed general effect of climate change is that the climate character in Scandinavia will become increasingly oceanic, with more precipitation and less frost, even in continental regions. Consequently, the abundance of alpine lichen heaths in the future may become similar to the present situation in oceanic parts of Norway.

It has been suggested that lichen heaths may "move upward" as an effect of climate change (Heggberget *et al.* 2002). According to Moen *et al.* (2004), plant studies simulating climatic change indicate that a warmer and wetter climate may cause an altitudinal upward shift of macrolichens. This can result in an increased potential for lichen growth at high altitudes. At lower elevations, there may be increased competition from taller, faster-growing vascular plants, e.g. *Betula nana*. In our view, this is not a probable scenario, at least not in the near future. Lichen heaths are associated with a relatively thick soil layer, and in the mid-alpine zone (more than ca. 300 m above the forest limit), soils are shallow. Total thickness of organic and moraine substrate where the lichen cover was higher than 20% varied between 5 and 60 cm (average was 14.8±9.1 cm). Secondly, the snow amount may increase in high elevations due to increased precipitation and low temperatures.

Recent climate models indicate that the climate may become increasingly oceanic. Future climate in continental parts of Fennoscandia may then be similar to conditions in the western parts of Norway. In these areas, the distribution of alpine lichens heaths are generally small, and lichen abundance low.

Effects of grazing

Relationships between abundances of lichens and effects of reindeer grazing and climate have been discussed in several studies. It has frequently been reported that lichen abundances have decreased because of increased competition from expanding vascular plants, but this has rarely been verified by relevant studies. Certainly, lichen biomass will decrease with reindeer grazing and trampling, but the long-term effects remain unclear. Ecological effects of grazing have been discussed in several papers, however without reference to the importance of soil frost (e.g. Gaare 1997; Heggberget *et al.* 2002).

Cohen *et al.* (2013) suggested that effects of reindeer grazing with subsequent shrub expansion could cause climatic feedback through changed albedo. Similar feedback loops that couple vegetation changes, change in albedo and climatic feedback processes have been presented in other studies, particularly from Arctic areas (Hinzman *et al.* 2005; Sturm *et al.* 2005a; Chapin *et al.* 2005; Wookey *et al.* 2009; Myers-Smith and Hik 2013).

Sofronov *et al.* (2004) found that growth rates of young larch (*Larix* spp.) trees declined due to the reduction of the average soil thawing depth resulting from a recovery of the moss-lichen layer. This indicates that we cannot generally assume that vascular plants will outcompete and replace lichens. If vascular plants are to replace lichens, soil frost and thaw length must decrease first.

According to this, we suggest a possible explanation of lichen heath ecology, impacts of reindeer grazing, climate change, changed albedo, and soil temperature change (Fig. 15). Combined effects of extensive reindeer grazing and climate changes may result in feedback effects that in time may increase soil temperatures and thereby significantly decrease the distribution of the oligotrophic, chionophobous alpine lichen heaths.

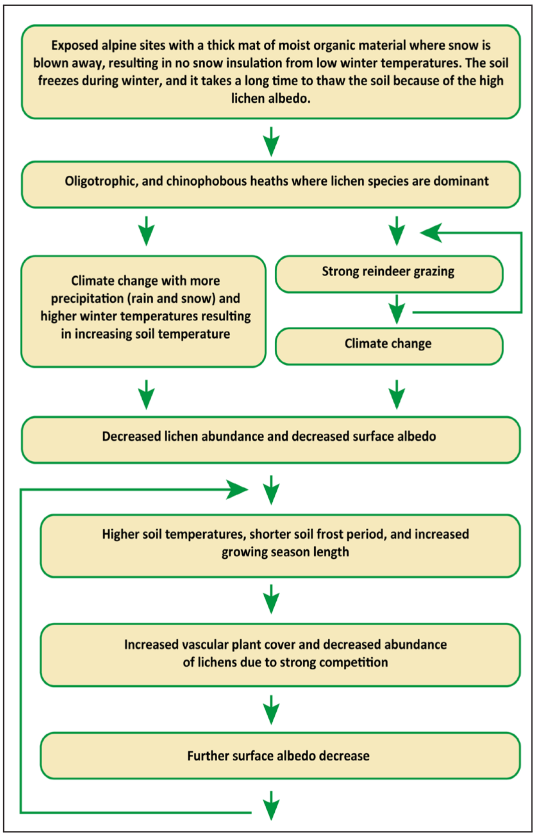

Fig. 15. Pathways for assumed relationships between lichen heath ecology, impacts of reindeer grazing, changes in climate, albedo, and soil temperatures. Feedback from reduced lichen cover result in reduced albedo and increasing soil temperatures. This may in turn give vascular plants favorable growth in the lichen heaths. Long-term impacts of lichen heaths without effects of climate changes are so far not known. As indicated, reindeer grazing may not necessary result in permanent loss of lichen heaths. A lichen-dominated heath can possibly be naturally reestablished if there are no effects of climate change.

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