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MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Impact of Selected Ecological Factors on Cryptogam Distribution in the Austrian Alps

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2020 / Vienna, 2020

Studienkennzahl lt. Studienblatt / UA 066 833
degree programme code as it appears on
the student record sheet:

Studienrichtung lt. Studienblatt / Masterstudium Ecology and Ecosystems
degree programme as it appears on
the student record sheet:

Betreut von / Supervisor:

Dipl.-Biol. Dr.rer.nat.habil. Christian Berg

Danksagung

Hiermit möchte ich mich bei all jenen bedanken, die mich bei der Verfassung dieser Masterarbeit begleitet und unterstützt haben.

An erster Stelle möchte ich mich bei Dr. Christian Berg bedanken, der meine Masterarbeit wissenschaftlich betreut und unterstützt hat. Seine Geduld und konstruktiven Beiträge haben diese Arbeit erst möglich gemacht. Weiters danke ich Prof. Helmut Mayrhofer und Peter Kosnik für die aufwendige Analyse und Identifizierung der Flechtenproben. Besonderer Dank gilt auch Patrick Schwager, MSc für die große Hilfe bei der statistischen Analyse und Martina Pörtl, MSc, die immer ein offenes Ohr für meine Fragen zu der Bestimmung von Bryophyten hatte.

Abschließend danke ich meinen Eltern, meinem Bruder und auch meinen FreundInnen, die mich immer unterstützt haben und jederzeit für mich da waren, um mich zu bestärken.

UNIVERSITÄT GRAZ
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Abstract

Cryptogams are closely related to their immediate environment. Hence, alpine bryophytes and lichens can be analysed with regard to environmental parameters for a better understanding of cryptogam distribution. The development of cryptogams in reaction to progressively changing environmental factors can help understand climate change implications for vegetation. The study is hence aimed at answering the following research questions: (1) How do cryptogams contribute to the species diversity of alpine grassland vegetation? (2) Which role play bioclimatic factors for the distribution of bryophytes and lichens? (3) Can inferences be made regarding bryophyte distribution in correlation with vascular plants? (4) How are bryophytes and lichens different regarding these questions? (5) Which conclusions can be drawn from the development of alpine cryptogams under global warming? Vegetation relevés were sampled throughout the Austrian Alps. Special focus was put on the Styrian North-Eastern Alps. Altogether, 694 species from 572 relevés were classified into vegetation communities of the Austrian Alps. Seven Classes of Alpine grassland vegetation could be characterized: *Molinio-Arrhenatheretea*, *Asplenieta trichomanis*, *Thlaspietea rotundifolii*, *Seslerietea albicantis*, *Thlaspietea rotundifolii*, *Caricetea curvulae*, *Salicetea herbaceae* and *Loiseleurio-Vaccinietea*. Within Classes, nine Orders with thirteen Alliances and eighteen Associations were identified. Relationships between alpine cryptogam distribution and selected environmental and bioclimatic variables, were inspected via Canonical Correspondence Analysis (CCA). Thirty bryophytes and eighteen lichens from 216 relevés were analysed in this regard. It can be inferred from CCA biplots cryptogam distribution in the Austrian Alps is predominately driven by EIV (continentality, moisture, nutrients, soil reaction and temperature) as well as by altitude, winter precipitation, precipitation seasonality, mean diurnal temperature range and vascular plant cover. Bryophytes and lichens show strong differences regarding these relationships. Under ongoing climate change, cryptogam distribution will likely change significantly in montane regions. Results of this study emphasize the importance of further research on current and future species distribution of bryophytes and lichens in alpine regions for a better understanding of the effects of climate change on cold-adapted vegetation. Consequently, conservation measures can be implemented accordingly.

Zusammenfassung

Kryptogamen sind eng mit ihrer unmittelbaren Umgebung vernetzt. Aus diesem Grund eignen sich alpine Bryophyten und Flechten gut, um verschiedene Umwelt- und Klimafaktoren zu analysieren und so die Verbreitung von Kryptogamen in Abhängigkeit von Umweltparametern besser zu verstehen. Die Entwicklung alpiner Kryptogamen in Reaktion auf sich fortschreitend ändernde bioklimatische Faktoren kann Information über den Einfluss des Klimawandels auf die Vegetation liefern. Die folgenden Fragen sollen in dieser Studie beantwortet werden: (1) Wie tragen Kryptogamen zur Artendiversität alpiner Graslandgesellschaften bei? (2) Welche Rolle spielen bioklimatische Faktoren für die Verbreitung von Bryophyten und Flechten? (3) Können Rückschlüsse aus der Beziehung von Kryptogamen und Gefäßpflanzen gezogen werden? (4) Wie unterscheiden sich Bryophyten und Flechten in Bezug auf diese Fragen? (5) Welche Schlüsse können aus der Entwicklung von Kryptogamen unter fortschreitendem Klimawandel gezogen werden? Vegetationsproben wurden im gesamten österreichischen Alpenraum gesammelt. Spezieller Fokus lag dabei auf den Steirischen Ostalpen. 572 Vegetationsaufnahmen mit insgesamt 694 Arten wurden klassifiziert und Pflanzengesellschaften der alpinen Felsrasenlandschaften zugeordnet. Sieben Vegetationsklassen wurden identifiziert: *Molinio-Arrhenatheretea Asplenetia trichomanis*, *Thlaspietea rotundifolii*, *Seslerietea albicantis*, *Thlaspietea rotundifolii*, *Caricetea curvulae*, *Salicetea herbaceae* und *Loiseleurio-Vaccinietea*. Innerhalb der Klassen wurden neun Ordnungen mit dreizehn Verbänden und achtzehn Assoziationen identifiziert. Beziehungen zwischen Kryptogamen und ausgewählten Umweltfaktoren wurden mittels Kanonischer Korrespondenzanalyse (CCA) untersucht. Dreißig Bryophyten und achtzehn Flechten aus 216 Vegetationsaufnahmen wurden diesbezüglich analysiert. Die Biplots der CCA zeigen, dass die Artenverbreitung von Kryptogamen in den österreichischen Alpen vorherrschend von Ellenberg-Indikatorwerten (Kontinentalität, Feuchtigkeit, Nährstoffe, Bodenreaktion und Temperatur), sowie Höhe, Winterniederschlag, Niederschlagssaisonalität, durchschnittlicher tageszeitlicher Temperaturspanne und der Vegetationsbedeckung von Gefäßpflanzen abhängt. Bryophyten und Flechten unterscheiden sich deutlich in Bezug auf diese Beziehungen. Die Kryptogamenverbreitung in alpinen Regionen wird sich unter Einfluss des aktuellen Klimawandels voraussichtlich stark verändern. Die Ergebnisse dieser Arbeit unterstreichen die Notwendigkeit weiterer Forschung an aktueller und zukünftiger Artenverbreitung von Kryptogamen im alpinen Raum, um die Auswirkungen des Klimawandels auf kalt-adaptierte Vegetation besser zu verstehen. Infolge können adäquate Schutzmaßnahmen umgesetzt werden.

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1. Introduction

Alpine biodiversity is driven by biogeographic, historical and evolutionary environmental factors as well as the physical environment more than by the influence of local species interactions. One of the main abiotic ecological parameters governing mountain ranges is known to be climate and related water availability (Kazakis et al. 2007; Cavieres et al. 2014) as the extensive land masses and specific topographic and orographic features of mountain ecosystems lead to specific local climate regimes (Keller, Goyette, and Beniston 2005). However, alpine plant diversity is not simply affected by the magnitude of these ecological factors but by their steep gradients which are typical for mountain ranges (Kazakis et al. 2007; Pickering, Hill, and Green 2008). These ecological gradients are mainly caused by complex mountain topography and related steep orographic gradients. High climatic and topographic variability generates high habitat diversity in Alpine mountains, thus further promoting alpine species diversity (Tribsch and Schönswetter 2003). The strong correlation between mountain biodiversity and climatic parameters renders mountain systems to be especially sensitive to climate change (Lamprecht et al. 2018). Rapid declines are expected in species richness and vegetation cover of vascular plants (Pauli et al. 2012) and cryptogams (Lang et al. 2012). Species adapted to high elevations (Berg and Schwager 2019) and latitudes (Lang et al. 2009) are especially at risk due to limited possibilities of migration (Pauli et al. 2012). Alpine mountain regions contribute substantially to global plant species diversity, containing approximately 4% of all known vascular plant species (Pickering, Hill, and Green 2008). This high species diversity together with high levels of endemism mark the European Alps as particularly important for research on climate change implications on vegetation (Tribsch 2004; Essl et al. 2009). High mountain ranges are particularly affected by increasing temperatures (Steinbauer et al. 2018) and winter precipitation as rain instead of snowfall results in distribution and diversity changes of alpine plant species (Niittynen, Heikkinen, and Luoto 2018; Pauli et al. 2007). Among alpine plant species, cryptogams are one of the most indicative species with respect to climate change (Spitale 2017) due to their strong dependency on topographic factors (Song et al. 2015) and climate-related parameters such as water availability (Zechmeister et al. 2003) which they require for growth and species distribution. Most research on vegetation responses to global warming has been carried out on vascular plants until now (Beringer et al. 2001), despite the fact that cryptogams are often accountable for the bigger part of biodiversity (Lang et al. 2012) and coverage (Nele Ingerpuu et al. 2001) than vascular plant in northern and high-altitude regions. They play significant roles in ecosystem functioning of these regions by strongly contributing to biomass production (Cornelissen et al. 2007), influencing carbon and nitrogen cycling (Turetsky 2003) as well as hydrology (Beringer et al. 2001). Thus, further knowledge on current and future species diversity and distribution of cryptogams in cold regions such as the Austrian high Alpine mountains plays an important role in understanding the effects of global warming on vegetation in these regions.

Results of this study are therefore aimed at contributing to fill the knowledge gap on ecological factors driving bryophyte and lichen distribution and their correlations with vascular plants.

1.1 Cryptogams in the Alps

While bryophytes and lichens are found in similar habitats, they are substantially different types of organisms. While lichens consist of a fungus, mycobiont and algae or cyanoobacterium (the photobiont) in symbiotic association (Lutzoni and Miadlikowska 2009) rather than being a plant, bryophytes are simply built, green land plants (Bell and Treshow 2002). Thus, both groups express diverging ecological habitat requirements (Vellak, Paal, and Liira 2003; Goffinet 2008; Flock 1978). Cryptogam distribution is mainly governed by topographic (e.g. aspect, slope, altitude) and soil factors such as pH and moisture as well as by vegetation cover (Song et al. 2015; Ellis et al. 2007). Bryophyte growth (Spitale 2017) and sexual reproductivity are subject to external water availability as they are poikilohydrous organisms (Zechmeister et al. 2003). Thus, most moss species are found in cool, moisture-rich and rather remote regions such as high mountain ranges. Despite the extreme habitat conditions in high alpine regions, which pose a severe challenge for most vascular plants (Grabherr and Mucina 1993), most mosses and lichens can handle these extreme climatic situations as they are, like many cryptogam species, desiccation tolerant, i.e. bryophytes and lichens endure the complete loss of water from their cells from several days to even years and can recover by rehydration. Length and success of the recovery process however, depend on individual species traits (Shaw and Goffinet 2000; Smirnov 1993). Due to their strong dependency on environmental and climate-related factors, mosses (Zechmeister et al. 2008) and lichens (Evju and Bruteig 2013) are particularly sensitive to ecological changes regarding their physiological and morphological properties as well as reproduction strategies. Thus, bryophytes (Lloret and González-Mancebo 2011) and lichens (Sancho, Allan Green, and Pintado 2007) are particularly important climate change indicators among plant species. Their close relationship with the environment also makes them important bioindicators for air pollution (Zechmeister 1999; Reckel, Aöschner, and Stock 1999). To fill the knowledge gap on species diversity and distribution in montane regions, Nimis et al. (2018) compiled an extensive checklist of lichens in the Alps, containing 3,163 species. Such analyses are essential for better understanding the role of cryptogam distribution in Alpine mountain regions and the effects of climate change in this regard. Extensive vegetation surveys are called for in order to cover the large diversity of meso- and microclimatic gradients and related habitat variability in the European Alps (Beniston, Diaz, and Bradley 1997). Only then, according conservation measures can be established to ensure alpine cryptogam diversity and distribution ranges in the face of climate change.

1.2 Alpine Climate

Due to the extensive land masses of mountain ranges combined with high altitude, latitude and continentality factors, mountain systems have distinct local climate regimes with rapidly changing temperature and precipitation (Keller, Goyette, and Beniston 2005). Climatic continentality refers to the relationship between the daily or seasonal oscillations of temperature and aridity/humidity. In the context of environmental variables, temperature becomes more influential with increasing elevation and latitude. Accordingly, continentality is higher in polar and montane regions. The term “thermic continentality” can hence also be applied. Low continentality can be referred to as “oceanity” as it coincides with higher humidity and less pronounced climatic seasonality (Berg, Welk, and Jäger 2017). The European Alps are located between three climate zones which further promotes local climate variability. In the West they boarder on the Atlantic climate zone, in the East the continental climate zone is dominant and the Mediterranean climate zone in the South (Wastl et al. 2013). Despite decreased precipitation and large temperature ranges with lower annual mean temperatures, mountain ecosystems ruled by continental climate may balance out low temperatures by increased sunshine availability (Beniston 2006). In Austria, where elevation ranges from 115 m a.s.l. in the lowermost eastern parts of the country to 3797 m a.s.l. at Großglockner, the highest Alpine mountain summit in Austria, variations in annual precipitation are documented between 500 and 2500 mm. Temperature varies between the warmest areas of Austria with an annual mean of 10°C to the highest peaks with below -5°C (Essl et al. 2009). Variation in mountain summit heights of the Austrian Alps and correlated difference in the altitudinal distribution of vegetation belts results in pronounced habitat variability in Alpine mountain ranges. Thus, rapidly changing climate factors such as temperature and precipitation in alpine mountains strongly affect plant species diversity and richness (Theurillat and Guisan 2001).

1.3 Climate Change in the Alps

With climate acting as the strongest influence on alpine mountain ecosystems, mountains react especially sensitive to climatic and related ecological changes. Current climate warming therefore already affects mountain ranges more strongly than other ecosystems. With increasing temperatures, substantial changes in alpine species distribution and richness as well as vegetation cover have already been documented (Lamprecht et al. 2018; Dullinger et al. 2012) demonstrating that mountain ecosystems are strongly susceptible to climate warming. Species are already trying to shift their distribution to higher altitudes and latitudes in order to escape increasing temperatures in their previous habitats (Pauli et al. 2007). While wind-dispersed species in high mountain ranges may have a chance of colonizing new higher situated sites, distribution of the remaining species is constrained by natural abiotic barriers (Theurillat and Guisan 2001). Mountain biodiversity changes can hence serve as important indicators of climate change impacts. Particularly interesting study sites can be

found within the European Eastern Alps (Dullinger et al. 2012) as they are home to a high percentage of endemic plant species and their comparably narrow summits provide almost no glaciers or other areas free of vegetation where species could colonize when re-distributing to higher elevations (Schwager and Berg 2019). Additionally, the upwards-shifting timberline will further decline distribution areas of alpine plants as studies have shown that most alpine species occurring above the timberline cannot persist in forests (Wessely et al. 2017).

1.4 Geology of the Austrian Alps

Two thirds of the 83,858 km² large area of Austria are dominated by Alpine mountain regions (Essl et al. 2009), thus enclosing 28.7% of the entire Alpine range (Nimis et al. 2018). The Austrian Alpine system belongs to the European Eastern Alps and comprises segments of the Northern Calcareous Alps (highest summit: 3031 m a.s.l.), the Central Eastern Alps (summits up to 3797 m) and the Southern Alps (up to 2780 m) (Andmann 2017). The Northern Calcareous Alps reach from Austria's easternmost part Vorarlberg to the southwestern regions of Vienna. Northern Calcareous Alpine mountains are composed of hard calcareous and dolomite bedrock as well as soft limestone and marl mountain ranges. South of the Northern Calcareous Alps adjoin the Central Eastern Alps which are dominated by siliceous bedrock such as amphibolite, slate and gneissic rock forming softer and rounder mountain ridges than those found in the Northern Calcareous Alps. Local limestone and dolomite mountain ranges within the Central Eastern Alps, like the Lienzer Dolomiten and Semmering region, resemble mountains of the Northern Calcareous Alps. At the southernmost end of Austria, the Southern Alps form the boarder to Italy and Slovenia with high mountain ranges mainly consisting of calcareous limestone and dolomite bedrock but slate and conglomerates are found as well (Geologische Bundesanstalt 2012). Generally, it can be observed that limestone and dolomite bedrocks dominate the narrower northern and southern parts of the Austrian Alps, whereas the higher central ranges are build up by siliceous bedrocks (Essl et al. 2009).

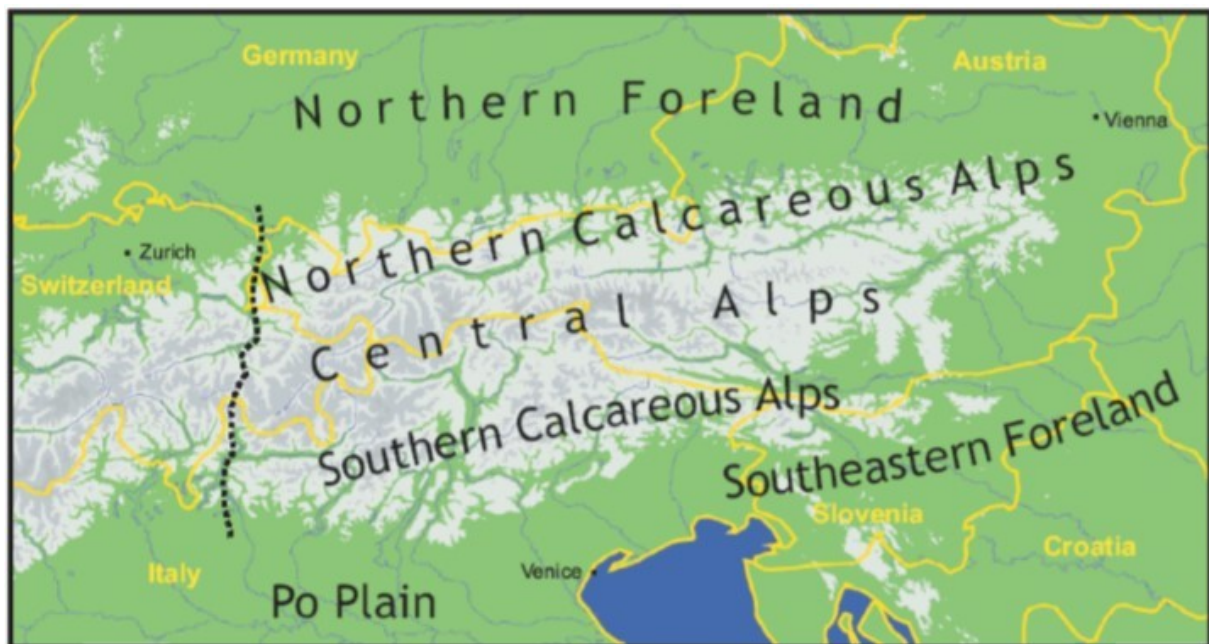


Figure 1: Map of the European Eastern Alps with focus on Austria (from Tribsch and Schönschwetter, 2003); colors: light grey indicates altitudes above 900 m; dark grey indicates altitudes above 2100 m; black dotted line separates Western and Eastern Alps; yellow line marks country borders

1.5 Vegetation Classification

Every phytocenosis (all living plants within a certain space-time-unit) can be assigned one specific vegetational community of a certain hierarchical level. In vegetation four main levels of communities can be distinguished: the highest hierarchical level is the vegetational Class which is subdivided in Orders. Orders comprise Alliances which are again subdivided into vegetation Associations (Dengler and Berg 2004). Vegetation communities are defined by so-called diagnostic species, often divided into “character species” which are indicative for one specific community and “differential species” which are present in several vegetation communities (Chytrý et al. 2002, Faber-Langendoen et al. 2020). The concept of defining vegetation communities via diagnostic species has been first introduced by Braun-Blanquet (1921, 1925). In the following decades Braun-Blanquet’s basic principle was revised and expanded by numerous authors. For the process of this study the vegetation classification concept described by Dengler and Berg (2004) was applied. In a specific plant community, a species must exhibit twice the occurrence frequency compared to any other community of the same hierarchical level to be considered a diagnostic species. Dengler and Berg (2004) then distinguish between differential species and character species. Differential species have twice the occurrence frequency in one or more community of the same hierarchical level compared to all communities of the next-higher level. Character species exhibit twice the occurrence frequency compared to all other plant communities of the same hierarchical level.

1.6 Research Questions

Cryptogams are closely related to their immediate environment. Hence, alpine bryophytes and lichens can be analysed with regard to environmental parameters for a better understanding of cryptogam distribution. The development of cryptogams in reaction to progressively changing environmental factors can help understand climate change implications for vegetation. The following hypotheses arise from this information: (a) Cryptogams are a prominent or even the dominant plant group in alpine grassland vegetation. (b) Cryptogam distribution in Alpine mountains is predominantly driven by environmental parameters. (c) Vascular plant cover plays a role in species distribution of cryptogams. (d) Bryophytes and lichens are different regarding these topics. (e) Cryptogams are well suited to analyse climate change implications on alpine vegetation. The study is hence aimed at answering the following research questions to test the hypotheses: (1) How do cryptogams contribute to the species diversity of alpine grassland vegetation? (2) Which role play bioclimatic factors for the distribution of bryophytes and lichens? (3) Can inferences be made regarding bryophyte distribution in correlation with vascular plants? (4) How are bryophytes and lichens different regarding these questions? (5) Which conclusions can be drawn from the development of alpine cryptogams under global warming?

2. Study Area

Vegetation sampling was carried out throughout the Austrian Alps (highest summit: 3797 m a.s.l.; Großglockner (Andmann 2017)). Selected sample sites from Carinthia, Salzburg, Styria and Tyrol were included. Special focus was put on the Styrian Alps which form the largely glacier-free (except for Dachstein) eastern margins of the European Alps and comprise a considerable part of the Northern Calcareous Alps (Figure 1). Mountain ranges in Styria extend over altitudes from 200 m to 2995 m a.s.l. According to Pilger, Podesser and Prettenhaler (2010) precipitation ranges around an annual mean of 700 to 2400 mm and temperature ranges around annual means of -5 to 10 °C. Particular attention in sampling was given to Angerkogel (2114m) within the Hochangern alpenstock north the city of Liezen and south of the Warscheneck plateau. The region is part of the karstic mountain range Totes Gebirge which belongs to the Northern Limestone Alps (Plan et al. 2009). The strong diversity in geology and climate between the Northern Calcareous Alps, the Central Alps and the Southern Alps leads to distinct contrasts in habitat conditions which are mainly accountable for species distribution in the Alpine mountains (Berg and Schwager 2019; Tribsch and Schönswetter 2003).

Main mountain ranges and regions of the Austrian Alps sampled for phytosociological relevés are marked in Figure 2.

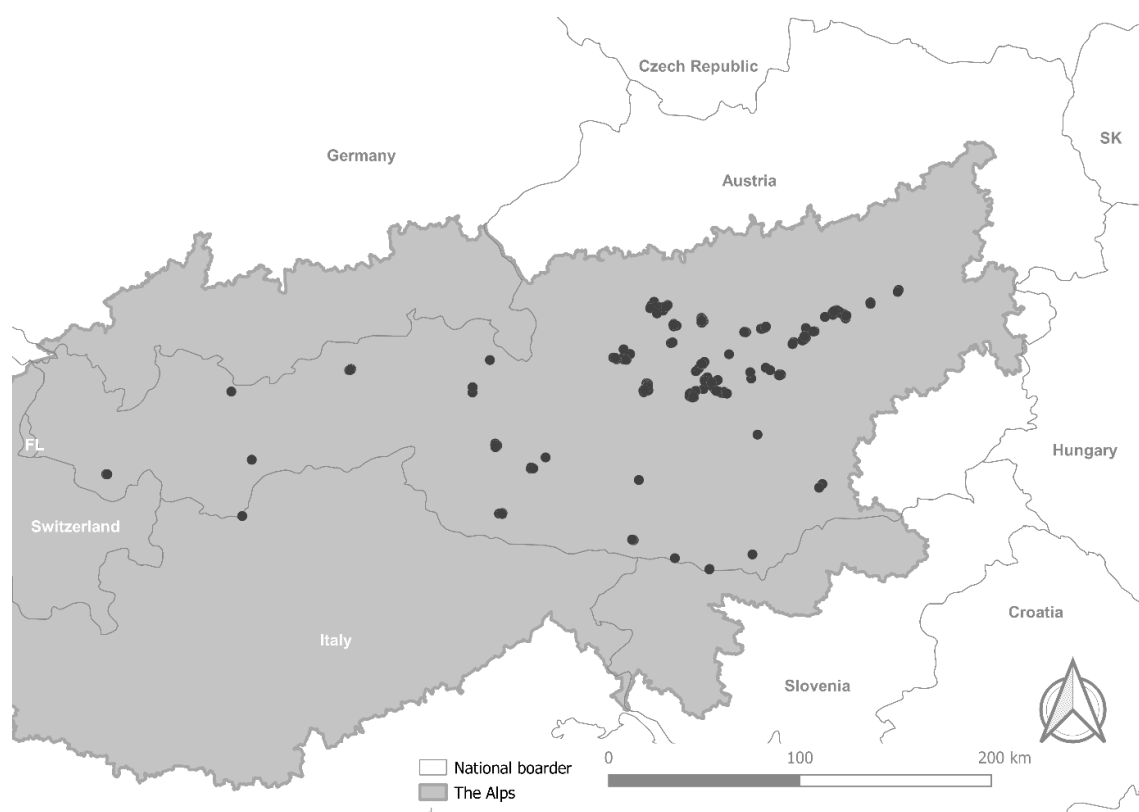


Figure 2: Map of main sampling areas in the Austrian Alps indicated by black dots; displayed across the Alpine Arc (grey coloured area); black lines indicate national borders; map was created via QGIS (Open Source Geospatial Foundation Project) using longitude and latitude data from phytosociological relevés.

3. Methods

3.1 Field Work and Prior Data Collection

The botanical institute of Karl-Franzens University of Graz has been committed to compile and expand the Austrian Vegetation Database (Willner, Berg, and Heiselmayer 2012), an extensive phytosociological data base containing information on the vegetation of the Austrian Alpine region. The data base was constructed using the computer software package TURBOVEG (chapter 3.2.1.3). In the years of 2015 to 2017 Patrick Schwager, MSc and Dietmar Cseh, MSc (Karl-Franzens University of Graz, Institute of Botany) collected vegetation samples during extensive field work in the alpine mountain ranges of the Austrian Alps (Table 1) to be added to the Database. Cseh focussed on samples sites on Angerkogel in the Styrian North-Eastern Alps as part of his master's thesis on Alpine Plant Species on Angerkogel for which he collected a considerable number of vegetation samples. For reproducibility of scientific analyses only relevés of 1 m² size were chosen to be included in the Austrian Vegetation Database. The highest sample site was located on Annakogel (Ötztal, Tyrol) with 3300 m a.s.l. while the lowest sample (1465 m) site was located on Tauplitz Alm (Totes Gebirge).

Table 1: Mountain ranges selected for relevé sampling, with number of relevés per area

State	Mountain range	No. of relevés	Sample area (with no. of relevés)
Styria	Totes Gebirge	276	• Angerkogel (171) • Hochangern-Plateau (29) • Schwarzkoppen (16) • Angeralm (10) • Nazogl (8) • Sattel Angeralm/Schwarzkoppen (7) • Luckerhütte (7) • Großer Woising (6) • Rotgschirr (5) • Elm (4) • Tauplitz Alm (4) • Wildgössl (4) • Redender Stein (2) • Hochkogel (1) • Lahngangsee (1) • Widderkogel (1)
	Wölzer Tauern	61	• Schoberspitz (9) • Rettlichkirchspitze (8) • Großer Zinken (5) • Haseneckscharte (5) • Funkelböden (3) • Gipfel (3) • Planneralm (3) • Plannerknot (3) • Eiskarspitze (2) • Kleiner Zinken (2) • Kleinhansl (2) • Krautwasch (2) • Plannerseekarspitze (2) • Rocklscharte (2) • Schießeck (2) • Großhansl (1) • Gstoder (1) • Hirnkogel (1) • Hochrettelstein (1) • Hohenwart (1) • Lachtal Bergstation Schönberg (1) • Stallertoerl (1)
	Grimming	1	• Martiner Scharte (1)
	Seetaler Alps	1	• Zirbitzkogel (1)
	Schladminger Tauern	19	• Hochwildstelle (8) • Sonntagskar See (3) • Äußeres Lämmerkar (2) • Äußeres Lamertal (2) • Klafferscharte (2) • Klafferessel (1) • Kleine Wildscharte (1)
	Dachstein	41	• Landfriedtal (23) • Dachstein mountain (6) • Landfriedstein (4) • Unterer Rumplersee (4) • Lausboden (2) • Feisterscharte (1) • Sinabell (1)
	Hochschwab	28	• Aflenzer Bürgeralm (5) • Mitteralm (5) • Hochturm (4) • Ochsenreichkar (3) • Voistalerhütte (3) • Hochschwab summit (2) • Ghacktes (2) • Schiestlhaus (2) • Häuselalm (1) • Trawiestal (1)

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Carinthia	Eisenerzer Alps	33	• Eisenerzer Reichenstein (16) • Wildfeld (6) • Rössl (4) • Große Scharke (3) • Reichenhals (2) • Speikkogel (1) • Stadlstein (1)
	Admont	5	• Riffel (1) • Sparafeld (4)
	Seckauer Tauern	4	• Hämmerkogel (2) • Seckauer Zinken (2)
	Johnsbach	6	• Rosskuppe (2) • Zinoedl (2) • Hochtör (1)
	Mürzsteger Alps	9	• Hohe Veitsch (7) • Schneealpe (2)
	Triebener Tauern	4	• Gaaler Törl (3) • Glaneck (1)
	Koralpe	12	• Großes Kar (11) • Bärentalalm (1)
	Melitzen	1	• Erlacheralm ob Radenthein (1)
	Hohe Tauern	7	
	Mallnitzer Tauern	1	• Jamingalm (1)
	Großglockner	9	• Glocknerhaus (5) • Leiter and Möll rivers (2) • Freiwanddeck (1) • Freiwandleiten (1)
	Finkenstein	2	• Mittagskogel (2)
	Hochstuhl	3	• Hochkar (3)
	Hochobir	1	
Tyrol	Dobratsch	10	
	Stubai glacier	1	• Schrankogel (1)
	Lienzer Dolomiten	6	
	Ötztal	1	• Annakogel (1)
	Rofan	18	• Gruberhochtal (5) • Dalfazer Joch (3) • Gruberplateau (2) • Riedl (2) • Dalfazer Kar (1) • Gamshals (1) • Haiderjochplateau (1) • Hoerndlschneid (1) • Rofankessel (1) • Törlfuß (1)
	Thajätörl	1	
Salzburg	Verwall	4	• Near Wiegensee (4)
	Kufstein	1	• Hochgrubkar (1)
	Saalach-Hinterglemm	3	

Thus, a notable amount of phytosociological data has already been compiled in the mentioned Austrian Vegetation Database prior to the process of this master's thesis. Regarding Schwager and Cseh's relevé samples, collected phytosociological information on the tree, shrub and herb layer have already been added to the Database. However, samples collected from the moss layer had not as yet been included. Cryptogam samples were stored in small paper bags and labelled with corresponding relevé numbers for later determination. These bryophyte and lichen samples are being identified and analysed in the course of this thesis as well as added to the Database. This extensive collection of vegetation data is aimed at facilitating further scientific research to reduce the existing knowledge gap

(Schröck et al. 2015; Zechmeister et al. 2003; Hernler-Steig 2002) on the phytosociology of cryptogams especially in the alpine region but also worldwide.

3.2 Cryptogam Distribution in Alpine Grassland Vegetation

3.2.1 Identification and Digitalization of Cryptogam Data

The collected moss and lichen samples from the years 2015 to 2017 could be analysed and identified for this thesis in 2019/2020s due to the mentioned desiccation tolerance of most cryptogam species (Shaw and Goffinet 2000; Smirnov 1993).

3.2.1.1 Identification of Bryophyte Species

From September 2019 to February 2020 bryophyte samples were identified. Species identification was carried out by means of stereo microscope and optical microscope. In the first step all mosses were analysed under the stereo microscope in their dry state as well as after rehydration in common tap water. Cross sections of leaves and stems were checked under the optical microscope. Many bryophyte species, especially such from the same family or even order, are not easily distinguished from each other. Individual species traits like the shapes, sizes, margins and tips of leaves and cells as well as leaf arrangement on the stems must be looked at collectively and be compared with other samples to be able to draw conclusions regarding species identification. Species identification keys are indispensable in order to arrive at reliable results. Volumes 1 to 3 of *Die Moose Baden-Württembergs* (Nebel and Philippi 2000, 2001, 2005) were utilized for this purpose. With Baden-Württemberg being one of the southernmost federal states of Germany, moss species of this region largely overlap with species occurrences and distributions in Austria. Additionally, *Moosflora* by Frahm and Frey (2004), *Moose einfach und sicher bestimmen* (Düll and Düll-Wunder 2012) and *Die Moose des Dachsteingebiets* (Schlüsslmayr 2019), were consulted for species identification. For visual comparison *Bildatlas der Moose Deutschlands* (Lüth 2011) and the web page *swiss bryophytes* (<https://swissbryophytes.ch/>) was utilized.

3.2.1.2 Identification of Lichen Species

During February and March 2020 lichen species were identified by Prof. Helmut Mayrhofer (Karl-Franzens University of Graz, Institute for Botany), an experienced lichenologist. Identification was achieved by means of stereo microscopy and thin-layer chromatography in a time- and material-consuming process as most lichen samples were rather small and of mediocre quality with regard to identification.

3.2.1.3 Qualifying of Alpine Vegetation Data in TURBOVEG

Identified species were digitalized via TURBOVEG. TURBOVEG is a data base management system for vegetational data which provides tools for creating phytosociological tables and record distinguishable plant Association types. The software has been developed for documenting vegetational relevés (Hennekens and Schaminée 2001). The TURBOVEG interface consists of the header data table

featuring recorded information on ecological parameters and location for each relevé, the species data table with cover and layer information and a third table displaying the numbers of most recently selected relevés (Berg and Magnes 2015).

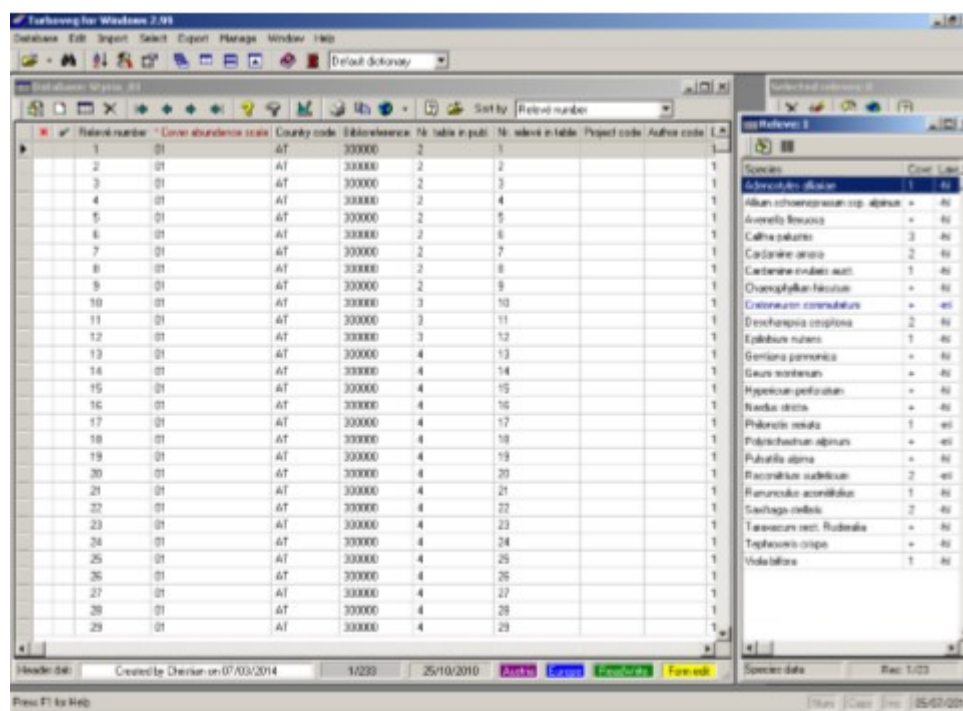


Figure 3: Structure of TURBOVEG user interface (Berg and Magnes 2015)

3.2.1.4 Data Input via TURBOVEG

Newly identified moss and lichen species were added to the species lists of their already digitalized corresponding relevés (by Schwager and Cseh) in TURBOVEG. The instruction paper for the software versions TURBOVEG 2.0 and JUICE 7.0 by Berg et al. (2015) and the user-friendly TURBOVEG interface facilitated a fast and efficient workflow for this phase of the study. Subsequently, the completed relevé data set consisting of species data and ecological data (header data) was exported from TURBOVEG as a standard XML file, for data exchange between the TURBOVEG and JUICE software.

3.2.2 Phytosociological Classification of Alpine Vegetation

Vegetation classification was carried out via JUICE. The software, initiated by Lubomír Tichý, was developed for phytosociological data analysis. As TURBOVEG is currently the most widely utilized software for digitalizing vegetation survey data (Tichý 2002) JUICE is targeted to work interconnected with TURBOVEG for uncomplicated data exchange between the two programs. The JUICE interface (Figure 4) provides the user with a vegetation table containing the species list with species data (e.g. number codes for vegetation layers, same as used in TURBOVEG), a species-abundance table and short headers to be filled with needed phytosociological information (Berg and Magnes 2015).

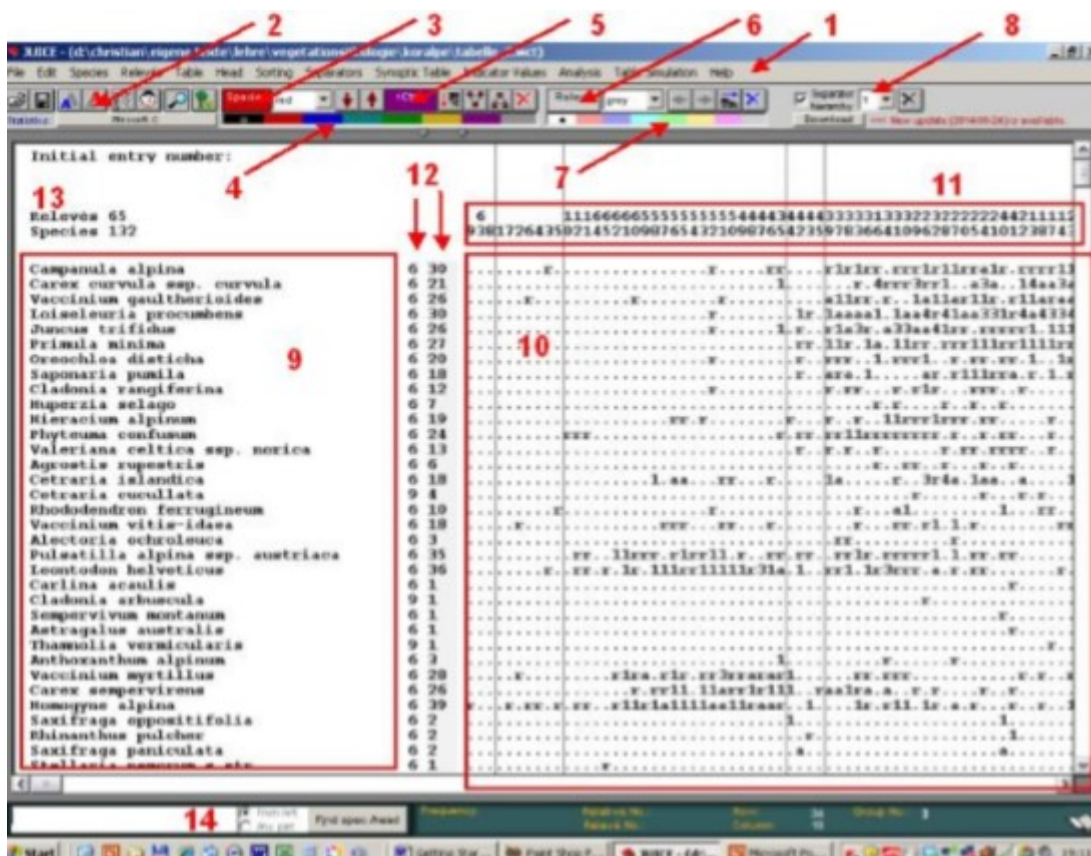


Figure 4: Structure of JUICE interface: task bar with pull-down and button menu (1-8), color menu for selecting species and relevés (3-7), species list (9), species-abundance table (10), short header data (11), species data field (12), number of species and relevés (13) and status row (14)

3.2.2.1 Organizing of Phytosociological Data

After uploading the vegetational data set from TURBOVEG into JUICE, phytosociological information stored in the header data table was checked and edited if needed to ensure correct denomination and numeration of ecological parameters. Manipulation of header data was carried out via EXCEL as this process can be quite intricate in JUICE (Berg and Mages 2015). Afterwards, the adjusted header data table was imported back into JUICE. Before starting phytosociological analyses, the vegetational raw data needs to be organized rid of any data inconsistencies. Following instructions of Berg et al. (2015) the species list was hence sorted alphabetically and vegetation layers were marked by colours. Next, relevés not featuring moss species were eliminated as they are not utilizable for analysis of the established research questions. Now, vegetation layer assignment and species nomenclature were investigated and adjusted if needed. Species occurring in more than one layer were merged and assigned the layer of highest species frequency to increase sample size per layer and account for significant analysis results. Thus, shrub layer species were merged into the herb layer. Relevés within the data set now consist of an herb and a moss layer. As relevés stem from alpine locations above the timberline, no tree layer exists in the data set. For subsequent phytosociological analysis, bioclimatic and environmental information about relevés and species needed to be included into the data set.

3.2.2.2 Ellenberg Indicator Values and Slope Exposition

Ellenberg indicator values (EIV) (Ellenberg et al. 1992) regarding species' ecological behavior in response to various environmental factors (Schaffers and Sýkora 2000) were appended to the JUICE data set. Therefore, an existing indicator value list (Berg, Welk, and Jäger 2017) following Ellenberg's nine-point scale (Ellenberg et al. 1992) was imported into the JUICE program. The following ecological indicators have been included: continentality (C), light (L), moisture (M), nutrients (N), soil reaction (R) and temperature (T). Indicator values were appended as individual columns to the header table. Indicator values were assigned to vascular plants only, thus, bryophyte and lichen data remained independent from environmental parameters. During field work, geographical exposition of mountain slopes have been assessed as values of aspect (degrees). As this variable is circular (0° to 360°) and hence not suitable for further analysis, it was converted into the linear variable of northing ($\cos(\text{Ex} \cdot 3.14159/180)$) with 1 (360°) representing northern-facing slopes and -1 (180°) representing southern-facing slopes.

3.2.2.3 Bioclimatic Data

Bioclimatic data for all relevé habitat locations were extracted from the CHELSA webpage (Climatologies at high resolution for the earth's land surface areas, (Karger et al. 2017)). They were added to the environmental header data table in JUICE as well. CHELSA provides climate data regarding temperature and precipitation from earth land surfaces as bioclimatic variables generated from thirty years of climatic data records for use in ecological analyses. Variable codes are derived from WORLDCLIM (<https://worldclim.org/data/bioclim.html>):

Table 2: Bioclimatic variables with abbreviation codes provided by CHELSA

Code	Bioclimatic variable	Code	Bioclimatic variable
Bio.1	Annual Mean Temperature	Bio.11	Mean Temperature of Coldest Quarter
Bio.2	Mean Diurnal Temperature Range	Bio.12	Annual Precipitation
Bio.3	Isothermality	Bio.13	Precipitation of Wettest Month
Bio.4	Temperature Seasonality	Bio.14	Precipitation of Driest Month
Bio.5	Max Temperature of Warmest Month	Bio.15	Precipitation Seasonality
Bio.6	Min Temperature of Coldest Month	Bio.16	Precipitation of Wettest Quarter
Bio.7	Temperature Annual Range	Bio.17	Precipitation of Driest Quarter
Bio.8	Mean Temperature of Wettest Quarter	Bio.18	Precipitation of Warmest Quarter
Bio.9	Mean Temperature of Driest Quarter	Bio.19	Precipitation of Coldest Quarter
Bio.10	Mean Temperature of Warmest Quarter		

The organized data set, supplemented with all important additional information, was now prepared for phytosociological calculations. Via JUICE, relative vegetation cover, relative and total species number for each vegetation layer and relevé were calculated and added to the header data.

Additionally, average indicator values weighted by species number were calculated for all relevés. The vegetational dataset is now prepared for classification of vegetation Associations.

3.2.2.4 Classification of Alpine Vegetation Communities

For analysis of plant communities JUICE is interconnected with several programs that are embedded in its software. The most widespread software for vegetation classification is the TWINSpan (“two way indicator species analysis”) software introduced by Hill (1979). TWINSpan offers six hierarchy levels into which a vegetation dataset can be partitioned (Hill 1979). Maximal variance in between and minimal variance within each section is expressed. TWINSpan hierarchical levels represent the hierarchy within species community relationships in nature (Berg and Magnés 2015; Hill 1979). The first division of the data set (hierarchy level 1) yields 2 columns of relevés partitioned by so-called Separators. Examination of these columns yielded two distinguishable main vegetation types: moor vegetation and grassland (forest-free) vegetation. Relevés belonging to moor vegetation consist almost exclusively of moss species which are not assigned any indicator values (see above). Thus, they were deleted from the JUICE data set as they cannot be utilized in further analyses. Now, the dataset comprised 572 grassland relevés. These were divided into sixteen columns (hierarchical level 4) which were used as baseline for classification phytosociological communities. Vegetation classification follows Berg and Dengler's concept (2004) on identifying diagnostic species for phytosociological communities. Thresholds for species fidelity and frequency were set to 20%, cover threshold to 50%. Measures above the thresholds were considered significant. To be considered diagnostic, species require occurrence frequencies of at least 20% in a column and additionally need to exhibit twice the frequency compared to all other columns in consideration. Species frequencies among relevés for each column are displayed in the JUICE Synoptic Table. TWINSpan cannot identify if high frequencies in a certain column are attributed to chance. However, JUICE provides analysis of interspecific associations between species and relevés which were compared with literature sources. Volume 1 and 2 of “*Die Pflanzengesellschaften Österreichs*” (Grabherr and Mucina 1993) were taken as reference for classifying diagnostic species into vegetation Associations based on the sixteen preselected columns. After determining vegetation Associations, superordinate phytosociological communities were delineated more sharply. TWINSpan hierarchical level 3 was utilized to represent the next higher-ranked phytosociological communities: Alliances. After diagnostic species for Alliances were selected, vegetation Orders (TWINSpan level 2) and Classes (level 1) were classified.

3.3 Relationships between Vegetation and Ecological Parameters

Strength and direction of relationships between plant species data and the following ecological parameters were calculated with Excel:

Table 3: Ecological parameters analysed with regard to species data, for full names of bioclimatic variables see Table 2

Ecological parameter	Abbreviations
Continentality EIV	C
Light EIV	L
Moisture EIV	M
Nutrients EIV	N
Soil Reaction EIV	R
Temperature EIV	T
Bioclimatic variables	bio.1 to bio.19
Altitude (m)	
Northing (1 for 360°, -1 for 180°)	

Relationships between these parameters and total and relative species numbers as well as vegetation cover of herb and moss layer were primarily calculate via Spearman correlation coefficients (Spearman 1904) to check for strong correlations.

3.3.1 Brief Insight into Multivariate Statistical Analysis in Ecology

In most instances, correlations of several corresponding biotic and abiotic ecological parameters of the habitat locations are responsible for species community patterns in vegetation. Correlation of vegetation data and ecological variables is generally unimodal with species expressing an optimum for various abiotic variables along ecological gradients (Legendre and Legendre 2012; Dormann and Kühn 2012). Vegetational data is therefore multivariate. When it comes to methods of data ordination in multivariate statistics, two main approaches need to be distinguished: unconstrained and constrained ordination methods (Leyer and Wesche 2007). In unconstrained ordination species-sample data is utilized to analyse gradients of species composition. Constrained ordination combines already fitted explanatory ecological variables to species data along linear axes, i.e. two matrices instead of one are being analysed in relation to each other (Økland 1999; Dormann and Kühn 2012). In this study, a constrained ordination method, (Canonical) Correspondence Analysis (CA or CCA) (Oksanen 2008), needs to be applied to the vegetation data as the cryptogam vegetation data is analysed with regard to gradients of separately measured ecological parameters (EIV of vascular plants). CCA has been introduced by Hill (1974) as effectual ordination method to reduce complex ecological datasets with numerous explanatory ecological variables from many dimensions to a few to facilitate maximization of accountable variability (Legendre and Legendre 2012). Variables are displayed as linear combinations on the axes of an ordination diagram (ter Braak 1988).

3.3.2 Cryptogam Distribution in Alpine Mountain Ecosystems

Correspondence analysis of vegetation data was conducted via open-source software R version 3.6.3. (R Core Team, 2020) embedded in RStudio (R Studio Team, 2019). The phytosociological dataset was

transferred from JUICE to the R program as CSV file. For computation of ordination methods, the R package “vegan” (Oksanen 2008) was installed into R. Species data was analysed with regard to ecological variables listed in Table 3.

CCA ordinations were separately conducted once with regard to Ellenberg indicator values and once to bioclimatic and environmental variables. Preliminary ordination plots yielded strongly skewed gradients of explanatory ecological variables that were not significantly interpretable. Reinspection of the vegetation dataset in JUICE confirmed a skewed ratio of relevés from siliceous to calcareous bedrock that distorted ordination plots and thereby comparability of species data. Consequently, relevés and corresponding environmental data were subdivided by bedrock type. Inspection of the separated data sets showed that the calcareous set contained disproportionately more relevés, namely 452, than the silicate set with 96 relevés. Hence, the calcareous dataset needed to be condensed in number of relevés. As the main focus of this study lays on inspecting cryptogam species distribution in the Austrian Alps, relevés containing considerable quantities of moss or lichen species are most relevant for statistical analysis. Therefore, calcareous relevés were checked for number of cryptogams. Relevés with less than two cryptogam species and most relevés containing only two cryptogam species were deleted from the JUICE dataset. The calcareous dataset was thus condensed to 96 relevés, which yielded a dataset of evenly distributed calcareous and silicate relevés. Furthermore, relevés with species of less than five occurrences in the dataset were excluded via EXCEL to downweigh the effect of rare species. Adjustment of the dataset yielded 30 bryophytes and 18 lichen species occurring at least five times in the data set; resulting in a total of 417 species (including 369 herb species) in 216 relevés. Now, correspondence analyses on EIV, and on climatic and environmental variables were computed on the new dataset. To emphasise predominant ecological variables affecting species distribution patterns, CCAs were computed again, containing those variables expressing the strongest correlations with species data.

3.3.3 Cryptogam Distribution in Relation to Vascular Plants and Ecological Factors

Relationships of species numbers, and relative cover of cryptogams with vegetation cover of vascular plants as well as selected ecological variables were analyzed via GLM (Generalized Linear Model) in R. Linear Models display dependencies of a certain variable from another (or several others) variable (Leyer and Wesche 2007), while Generalized Linear Models also explain how exactly the dependent variable is correlated with the explanatory variable (Dormann and Kühn 2012) by an assumed relationship between the response variable value and a linear predictor (from combined predictor variables) by a link function. (Guisan, Edwards, Jr., and Hastie 2002). For this analysis a Gaussian function was chosen, which is the default function provided by R as it is the most frequent form of distribution (Dormann and Kühn 2012) despite the fact that ecological data rarely follow a precise Gaussian distribution (Leyer and Wesche 2007).

Impact of Selected Ecological Factors on Cryptogam Distribution in the Austrian Alps

Table 4: Relationships analysed via GLM, Abbreviations: ml_%cov (cover of moss layer (%)), br_%cov (cover of moss species (%)), li_%cov (cover of lichen species (%)), br_SpN (total no. of moss species), li_SpN (total no. of lichen species), hl_%cov (cover of herb layer (%)).

Variable 1	Variable 2	Variable 1	Variable 2
ml_%cov	hl_%cov	Moisture (EIV)	Northing
br_%cov	hl_%cov	br_%cov	Continentality (EIV)
li_%cov	hl_%cov	li_%cov	Continentality (EIV)
br_%cov	li_%cov	br_SpN	Continentality (EIV)
br_SpN	li_SpN	li_SpN	Continentality (EIV)
ml_%cov	Mean Diurnal Temperature Range (bio.2)	ml_%cov	Continentality (EIV)
br_%cov	Mean Diurnal Temperature Range (bio.2)	ml_%cov	Winter Precipitation (bio.19)
li_%cov	Mean Diurnal Temperature Range (bio.2)	br_%cov	Winter Precipitation (bio.19)
br_SpN	Mean Diurnal Temperature Range (bio.2)	li_%cov	Winter Precipitation (bio.19)
li_SpN	Mean Diurnal Temperature Range (bio.2)	br_SpN	Winter Precipitation (bio.19)
Temperature (EIV)	Northing	li_SpN	Winter Precipitation (bio.19)

4. Results

4.1 Alpine Grassland Vegetation and the Role of Cryptogams

In this study 572 relevés comprising 694 species were classified regarding vegetation communities. They show distinct ecological variance as they were sampled throughout the wide-spread area of the Austrian Alps. Altogether, seven Classes of Alpine vegetation above the timberline could be characterized. Communities consist of phanerogams and cryptogams. Among limestone and dolomite Classes, Molinio-Arrhenatheretea with 4.6 % bryophyte cover and 2.8 % lichen cover on average, Asplenieta trichomanis (6.3 % bryophyte and 3.6 % lichen cover), Thlaspietea rotundifolii (8.9 % bryophyte and 2.6 % lichen cover) and Seslerietea albicantis (8.1 % bryophyte cover and 5.5% lichen cover) are found. Thlaspietea rotundifolii holds one exception: The Association Androsacetum alpinae is found on calcareous and siliceous bedrock. Caricetea curvulae with 19.7 % bryophyte cover and 0.4 % lichen cover, Salicetea herbaceae (3.0 % bryophyte cover and 4.8 % lichen cover) and Loiseleurio-Vaccinieta (2.9 % bryophyte and 18.5 % lichen cover) can be found on silicate, slate and amphibolite bedrock. Altogether, nine Orders with thirteen Alliances and eighteen Associations were classified. Grabherr and Mucina (1993) are taken as reference for denomination and general description of vegetation communities (4.1.1 to 4.1.7).

Table 5: Classification of alpine grassland vegetation, numeration of Association refers to subsequent results

Class Molinio-Arrhenatheretea R. Tx. 1937 em. R. Tx. 1970
Order Poo alpinae-Trisetetalia Ellmauer et Mucina ordo nov. hoc loco Alliance Poion alpinae Oberd. 1950 1) Association Crepido-Festucetum commutatae Lüdl 1948
Class Asplenieta trichomanis (Br.-Bl. in Meier et Br.-Bl. 1934) Oberd. 1977
Order Potentilletalia caulescentis Br.-Bl. in Br.-Bl. et Jenny 1926 Alliance Potentillion caulescentis Br.-Bl. in Br.-Bl. et Jenny 1926 2) Association Drabo stellatae-Potentilletum clusianae Hörandl et Greimler in Mucina ass. nova hoc loco Alliance Androsaco-Drabion tomentosae T. Wraber 1970 3) Association Potentilletum nitidae Wikus 1959
Class Thlaspietea rotundifolii Br.-Bl. 1948
Order Arabidetalia caeruleae Rübel ex. Br.-Bl. 1948 Alliance Arabidion caeruleae Br.-Bl. in Br.-Bl. et Jenny 1926 4) Association Arabidetum caeruleae Br.-Bl. 1918 5) Association Campanulo pullae-Achilleetum clusianae Wendelberger 1971 ad interim (Art. 2b) 6) Association Salicetum retuso-reticulatae Br.-Bl. in Br.-Bl. et Jenny 1926 Order Androsacetalia alpinae Br.-Bl. in Br.-Bl. et Jenny 1926 Alliance Androsacion alpinae Br.-Bl. in Br.-Bl. et Jenny 1926

7) Association Androsacetum alpinae Br.-Bl. 1918
Class Caricetea curvulae Br.-Bl. 1948 <i>Order Caricetalia curvulae Br.-Bl. in Br.-Bl. et Jenny 1926</i> Alliance Caricion curvulae Br.-Bl. in Br.-Bl. et Jenny 1926 8) Association Caricetum curvulae Rübel 1911 <i>Order Festucetalia spadiceae Barbero 1970 em. Grabherr</i> Alliance Festucion variaie Guinochet 1938 9) Association Pulsatillo albae-Festucetum variaie Theurillat 1989 Alliance Nardion strictae Br.-Bl. 1926 10) Association Sieversio-Nardetum strictae Lüdi 1948
Class Salicetea herbaceae Br.-Bl. 1948 <i>Order Salicetalia herbaceae Br.-Bl. in Br.-Bl. et Jenny 1926</i> Alliance Salicion herbaceae Br.-Bl. in Br.-Bl. et Jenny 1926 11) Association Polytrichetum sexangularis Frey 1922
Class Seslerietea albicantis Br.-Bl. in Br.-Bl. et Jenny 1926 <i>Order Seslerietalia coerulaea Br.-Bl. in Br.-Bl. et Jenny 1926</i> Alliance Caricion firmae Gams 1936 Association Caricetum firmae Rübel 1911 12) Variation with <i>Primula clusiana</i> 13) Variation with <i>Festuca pumilae</i> 14) Association Dryadetum octopetalae Rübel 1911 Alliance Seslerion coeruleae Br.-Bl. in Br.-Bl. et Jenny 1926 15) Association Seslerio-Caricetum sempervirentis Br.-Bl. in Br.-Bl. et Jenny 1926 Alliance Caricion ferruginae G. Br.-Bl. et J. Br.-Bl. 1931 16) Association Campanulo scheuchzeri-Festucum noricae Isda 1986
Class Loiseleurio-Vaccinietea Eggler 1952 <i>Order Rhododendro-Vaccinietalia Br.-Bl. in Br.-Bl. et Jenny 1926</i> Alliance Loiseleurio-Vaccinion Br.-Bl. in Br.-Bl. et Jenny 1926 17) Association Loiseleurio-Cetrarietum Br.-Bl. et al. 1939 18) Association Empetro-Vaccinetum gaultherioidis Br.-Bl. in Br.-Bl. et Jenny 1926 corr. Grabherr hoc loco

Species composition and number of relevés of the eighteen Associations can be seen in Table 6.

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Table 6: Percentage synoptic table of diagnostic vascular plant species and cryptogams (extract) with relative cover (ml_%cov) and species number (ml_%SpN) of the moss layer; for numeration of Associations see Table 5.

Percentage synoptic table

		Ass.																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No. of Relevés		36	22	6	16	68	14	24	8	14	22	12	87	107	20	61	15	26	14
ml_%cov		7.3	10.6	4.4	19.6	5.9	15.0	18.2	12.0	12.9	13.1	20.0	10.3	7.7	9.9	4.6	1.8	16.6	28.8
ml_%SpN		10.3	17.1	15.1	19.7	8.6	17.5	26.1	16.9	18.1	18.9	18.4	16.9	18.3	17.0	6.9	3.5	21.1	28.4
Abbr.																			
		Total Frequency																	
		Layer																	
Crepis alpestris	Cre.alp	6	84	81	.	.	.	29	.	.	.	.	.	2	.	.	54	.	.
Potentilla crantz Pot.cra		6	46	61	.	.	.	4	.	.	.	.	.	7	.	.	23	7	.
Luzula sudetica	Luz.sud	6	30	47	.	.	.	.	.	.	.	9	.	.	.	.	11	.	8
Crepis aurea	Cre.aur	6	30	39	.	.	19	4	.	.	.	5	17	1	.	5	5	7	4
Alchemilla glabr Alc.gla		6	18	28	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.
Potentilla clusiar Pot.clu		6	61	3	77	.	.	.	.	.	.	.	.	3	37	.	.	.	.
Draba stellata	Dra.ste	6	12	.	50	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Campanula coch Cam.coc		6	12	.	27	.	.	1	.	.	.	5	.	.	3	.	.	7	.
Saxifraga opposi Sax.opp		6	14	6	23	.	.	.	.	.	.	.	.	1	4	.	.	.	.
Potentilla nitida	Pot.nit	6	5	.	.	83	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula auricula	Pri.aur	6	28	.	23	83	.	.	.	.	.	.	.	2	14	5	.	.	.
Carex mucronat Car.muc		6	8	.	.	83	.	.	.	.	.	.	.	.	2	.	.	7	.
Saxifraga caesia	Sax.cae	6	22	.	14	33	.	.	.	.	.	.	.	1	14	5	.	.	.
Achillea atrata a Ach.atr.agg		6	34	3	.	.	56	25	7	.	.	.	8	.	2	.	5	.	.
Pritzelago alpina	Pri.alp	6	29	.	5	.	69	24	.	.	.	.	.	1	.	.	.	.	.
Saxifraga andros	Sax.and	6	24	.	.	.	63	6	36	8	.	.	8	.	1	5	.	.	.
Soldanella austri	Sol.aus	6	15	.	5	.	38	7	.	.	.	.	2	1	.	.	.	.	.
Arabis alpina	Ara.alp	6	10	.	.	.	31	7	.	.	.	.	.	.	.	.	.	.	.
Potentilla braun	Pot.bra	6	11	.	.	.	31	3	7	.	.	.	8	.	.	2	7	.	.
Arabis bellidifoli	Ara.bel	6	10	.	.	.	31	6	7	.	.	.	.	.	.	.	.	.	.
Moehringia cilia	Moe.cil	6	20	3	.	.	31	18	7	.	.	.	.	.	.	.	.	7	.
Campanula pullz	Cam.pul	6	60	.	.	.	25	74	.	.	.	.	.	2	1	.	5	.	.
Achillea clusiana	Ach.clu	6	54	6	.	.	13	65	.	.	.	.	.	2	.	.	7	.	.
Doronicum glaci	Dor.gla	6	13	3	.	.	.	1	36	13	.	.	.	.	2	5	.	.	.
Saxifraga bryoid	Sax.bry	6	16	.	.	.	.	.	63	13	.	.	.	.	.	.	.	.	.
Phyteuma globu	Phy.glo	6	19	.	.	.	.	7	63	38	.	.	.	.	.	.	.	.	.
Minuartia sedoi	Min.sed	6	80	6	14	.	19	10	14	50	.	.	.	22	22	5	11	.	.
Poa laxa	Poa.lax	6	5	.	.	.	.	.	.	21	.	.	.	.	.	.	.	.	.
Cerastium uniflo	Cer.uni	6	7	.	.	.	13	.	.	21	.	.	.	.	.	.	.	.	.
Carex curvula	Car.cur	6	24	3	.	.	.	7	4	63	7	9	17	.	.	.	.	38	7
Festuca varia	Fes.var	6	21	.	.	.	.	.	13	.	100	5	.	.	.	.	.	8	7
Pulsatilla alpina	Pul.alp	6	25	.	.	.	.	.	.	13	79	23	.	.	.	.	3	.	19
Anthoxanthum z	Ant.alp	6	52	42	.	.	.	3	7	4	13	21	68	.	3	.	13	7	4
Potentilla aurea	Pot.aur	6	38	19	.	.	.	4	.	.	.	7	64	25	1	.	15	3	13
Nardus stricta	Nar.str	6	40	42	.	.	.	.	7	.	.	.	59	25	.	.	5	3	8
Geum montanur	Geu.mon	6	19	.	.	.	.	.	.	.	14	55	25	.	.	.	2	.	4
Deschampsia ce	Des.ces	6	23	.	5	.	6	3	7	.	.	14	45	.	1	.	3	7	4
Campanula barb	Cam.bar	6	12	.	.	.	.	.	.	4	25	7	36	.	.	.	.	.	.
Gnaphalium sup	Gna.sup	6	24	.	5	.	.	1	.	8	13	.	27	100	.	.	.	7	.
Arenaria biflora	Are.bif	6	13	.	5	.	.	.	.	.	13	.	.	92	.	.	.	.	.
Polytrichastrum	Pol.sex	9	11	.	5	.	.	.	.	.	.	5	75	.	.	.	.	.	.
Sibbaldia procur	Sib.pro	6	14	.	.	.	.	1	7	.	13	.	5	75	.	.	.	7	.
Veronica alpina	Ver.alp	6	21	.	.	.	19	9	.	.	13	.	14	67	.	.	.	.	.
Pohlia drummor	Poh.dru	9	8	.	.	.	.	.	.	.	.	.	.	67	.	.	.	.	.
Salix herbacea	Sal.her	6	18	.	.	.	.	1	.	21	38	.	5	58	.	.	.	.	4
Taraxacum sect.	Tar.sec.Alp	6	10	.	.	.	19	1	.	.	.	.	.	50	.	.	.	.	.
Polytrichum juni	Pol.jun	9	27	6	.	.	.	1	7	4	13	.	23	50	.	10	2	7	8
Cerastium cerasi	Cer.cer	6	8	.	.	.	.	3	.	.	13	.	.	42	.	.	.	.	14
Primula clusiana	Pri.clu	6	116	3	.	.	6	4	.	.	.	.	.	70	33	5	23	.	.
Carex firma	Car.fir	6	240	3	50	.	25	28	7	.	.	.	.	94	85	40	38	.	.
Festuca pumila	Fes.pum	6	157	22	27	.	.	32	50	4	.	.	.	47	44	40	25	.	8
Dryas octopetal	Dry.oct	6	244	36	9	.	.	7	36	8	50	.	.	93	72	100	56	.	4
Sesleria varia ag	Ses.var	6	43	6	.	.	6	3	36	.	.	.	.	10	7	80	2	.	.
Carex sempervir	Car.sem	6	160	25	9	.	6	46	29	.	25	43	14	.	29	10	25	80	27
Sesleria albicans	Ses.alb	6	152	22	9	.	6	28	7	.	.	.	.	43	24	.	89	27	.
Festuca norica	Fes.nor	6	9	.	.	.	.	1	7	.	.	.	.	.	.	.	.	47	.
Carlina acaulis	Car.aca	6	9	3	.	.	.	.	.	.	.	.	.	1	.	.	3	33	.
Trifolium prat	Tri.pra	6	18	19	5	.	.	1	.	.	.	.	.	.	2	.	5	27	.
Helictotrichon p	Hel.par	6	8	.	.	.	.	.	.	.	.	.	.	.	.	.	7	27	.
Loiseleuria proc	Loi.pro	6	75	.	.	.	.	.	.	.	38	14	9	.	20	3	30	10	100
Cladonia arbusci	Cla.arb	9	28	.	5	.	.	14	21	.	7	14	.	.	.	5	2	12	79
Vaccinium myrti	Vac.myr	6	38	11	5	.	.	.	.	.	13	29	36	.	1	.	7	19	71
Cladonia gracilis	Cla.gra	9	9	.	.	.	.	.	8	.	.	.	.	.	.	.	2	8	29
Paraleucobryum	Par.ene	9	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
Cladonia mitis	Cla.mit	9	35	22	5	.	.	.	.	.	13	7	.	.	17	2	5	5	4

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Cladonia boreali Cla.bor	9	8	8	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.
Dichodontium p Dic.pel	9	6	.	.	.	13	4	.	.	.	.	.	.	1	.	.	.	.	.
Bryum pseudotr Bry.pse	9	19	.	.	.	38	9	.	.	.	.	.	.	5	1	.	3	.	.
Cratoneuron cor Cra.com	9	5	.	.	.	25	1	.	.	.	.	.	.	.	.	.	.	.	.
Lescurea incur Les.inc	9	19	.	5	.	25	13	.	.	.	.	14	.	1	.	.	2	.	.
Cratoneuron filic Cra.fil	9	24	.	5	.	25	22	.	.	.	.	5	.	.	2	.	2	.	.
Cladonia symph Cla.sym	9	29	.	.	.	.	13	.	.	.	.	.	.	7	9	.	7	.	.
Ptychodium plic Pty.pli	9	19	6	.	.	.	10	14	.	.	.	.	.	1	2	.	8	.	.
Sanionia uncinat San.unc	9	24	6	.	.	6	6	43	17	.	.	14	.	1	1	.	2	.	4
Campyllum stell Cam.ste	9	25	.	.	.	6	13	14	8	.	.	.	.	2	3	10	5	7	.
Cetraria nivalis Cet.niv	9	43	3	.	.	.	.	14	25	.	.	.	.	7	14	15	5	.	19 14
Polytrichastrum Pol.alp2	9	20	.	.	.	.	.	.	42	25	7	14	8	.	.	.	.	8	7
Thamnomia verm Tha.ver	9	112	6	9	.	.	.	29	58	38	21	.	.	36	30	35	8	.	35
Cladonia sp. Cla.sp.	9	18	.	.	.	.	.	.	13	.	7	9	.	2	6	5	3	.	4
Racomitrium lan Rac.lan	9	6	.	5	.	.	.	.	13	.	7	.	.	.	.	.	.	.	4
Polytrichum pilif Pol.pil	9	9	.	.	.	.	.	.	13	13	7	.	.	.	1	.	.	.	4 14
Cladonia unciali Cla.unc	9	8	.	.	.	.	.	.	.	.	14	.	.	3	.	5	.	.	8
Polytrichum con Pol.com	9	2	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.
Hylocomium spl Hyl.spl	9	29	8	.	.	.	1	29	17	.	21	.	.	6	2	20	2	.	4 7
Cladonia furcata Cla.fur	9	8	6	.	.	.	.	7	.	.	7	5	.	1	.	.	.	.	4 7
Dicranum brevif Dic.bre	9	6	.	.	.	.	1	.	.	.	7	9	.	1	.	.	2	.	.
Racomitrium sur Rac.sud	9	5	.	.	.	.	.	.	8	.	9	.	.	.	.	.	.	.	4
Dicranum scopi Dic.sco	9	23	8	.	.	.	1	14	8	.	7	23	.	2	1	.	5	.	8 7
Pohlia wahlenbe Poh.wah	9	10	3	.	.	6	6	.	.	.	.	18	.	.	.	.	.	.	.
Diplophyllum ta Dip.tax	9	3	.	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.
Racomitrium elo Rac.elo	9	7	6	.	.	.	1	.	.	13	.	14	.	.	.	.	.	.	.
Anthelia juratzk Ant.jur	9	6	3	.	.	.	.	.	4	.	.	5	25	.	.	.	.	.	.
Brachythecium f Bra.gla	9	2	.	.	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.
Pogonatum urni Pog.urn	9	9	.	.	.	.	1	.	8	.	.	5	17	1	1	.	2	.	.
Kiaeria sp. Kia.sp.	9	2	.	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.	.
Cetraria ericetor Cet.eri	9	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	12	7
Ptilidium ciliare Pti.cil	9	9	.	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.
Cladonia macro Cla.mac	9	27	11	.	.	.	.	.	4	.	7	.	.	17	2	5	3	.	4
Rhytidium rugos Rhy.rug	9	33	.	.	.	.	.	14	4	.	14	.	.	17	5	15	5	.	4 7
Cetraria tilesii Cet.til	9	39	3	9	.	.	1	.	.	.	.	.	.	6	27	.	2	.	.
Ditrichum flexic Dit.fle	9	99	6	32	.	31	9	14	.	.	7	.	.	21	37	5	26	7	.
Thamnomia subul Tha.sub	9	53	3	.	.	.	1	.	8	.	14	.	.	26	21	.	2	.	7
Hypnum cupres Hyp.cup	9	18	3	9	.	.	7	.	.	.	7	9	.	1	9	.	.	.	.
Barbilophozia ly Bar.lyc	9	9	6	.	.	.	1	.	4	.	.	9	.	.	1	.	2	.	7
Bryum elegans Bry.ele	9	7	.	.	.	.	3	.	4	.	.	.	.	.	3	.	2	.	.
Campyllum chry Cam.chr	9	9	.	.	.	.	4	.	.	.	.	.	.	1	4	.	.	7	.
Ctenidium mollu Cte.mol	9	19	6	5	.	6	9	.	.	.	.	.	.	2	6	.	2	.	.
Ctenidium proce Cte.pro	9	8	.	5	.	.	.	.	4	.	.	.	.	.	5	.	2	.	.
Dicranum spadic Dic.spa	9	16	6	.	.	.	.	7	4	.	7	5	.	6	1	5	5	.	.
Cladonia stellari Cla.ste	9	6	.	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	7
Rhytidiadelphus Rhy.tri	9	20	3	.	.	.	1	14	4	.	.	.	.	5	.	35	3	.	14
Pleurozium schr Ple.sch	9	9	.	.	.	.	.	7	4	.	7	5	.	.	.	15	2	.	7
Tortella tortuos Tor.tor	9	191	11	50	33	38	51	21	8	.	7	9	.	52	46	5	39	40	.
Cladonia pyxidat Cla.pyx	9	40	3	9	.	.	6	7	.	13	.	.	.	8	10	8	5	10	7 4 21
Alectoria ochrol Ale.och	9	18	.	.	.	.	7	17	25	7	.	.	.	1	1	10	.	.	19 7
Cetraria islandic Cet.isl	9	198	25	.	.	.	3	43	50	50	50	32	.	72	24	85	20	.	85 79
Cladonia rangife Cla.ran	9	40	.	.	.	.	.	.	4	38	29	9	8	1	5	30	.	.	46 36
Cetraria cucullat Cet.cuc	9	39	3	.	17	.	.	29	17	25	.	.	.	10	7	5	2	.	23 14

The contribution of alpine cryptogams to the eighteen vegetation Associations are displayed in Figure 5 and Table 7, along with selected ecological parameters assessed for each Association.

Impact of Selected Ecological Factors on Cryptogam Distribution in the Austrian Alps

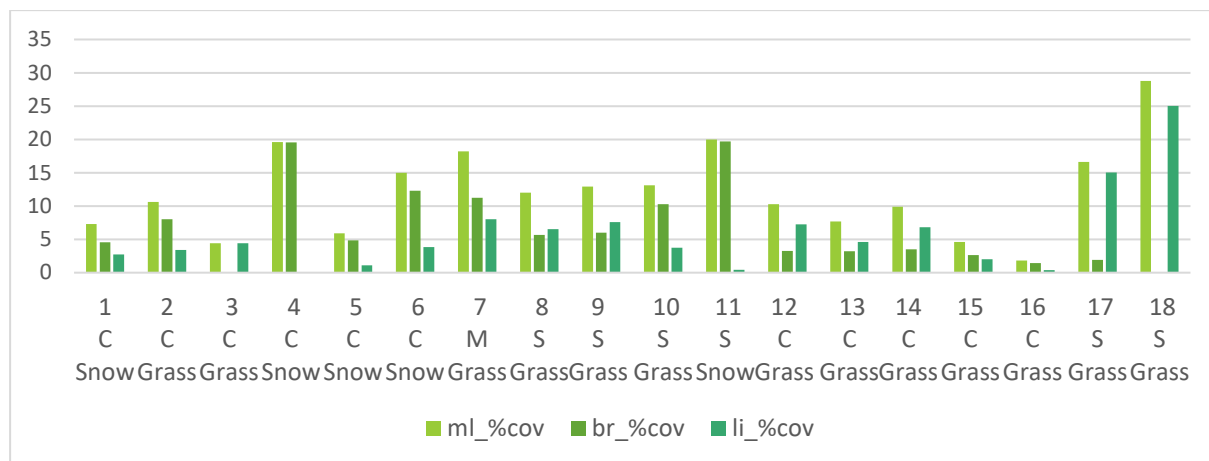


Figure 5: Relative cover of cryptogams (ml_%cov), with bryophytes (br_%cov) and lichens (li_%cov) separately, in alpine grassland Associations; cover percentages are displayed in Table 7, for numeration of Associations see Table 5.

Table 7: Ecological Parameters governing Associations; bedrock abbr.: calcareous (c), siliceous (s), mixed (m); for numeration of Associations see Table 5, for abbreviations of variables see Table 3 and Table 4.

Association	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No. of Relevés	36	22	6	16	68	14	24	8	14	22	12	87	107	20	61	15	26	14
bedrock	c	c	c	c	c	c	m	s	s	s	s	c	c	c	c	c	s	s
herbs hl_%cov	90.2	22.2	30.6	52.7	77.3	67.9	51.4	58.6	60.5	61.6	69.9	70.9	54.4	68.8	90.1	65.0	70.5	74.5
cryptogams	ml_%SpN	10.3	17.1	15.1	19.7	8.6	17.5	26.1	16.9	18.1	18.9	18.4	16.9	18.3	17.0	6.9	3.5	21.1
	ml_%cov	7.3	10.6	4.4	19.6	5.9	15.0	18.2	12.0	12.9	13.1	20.0	10.3	7.7	9.9	4.6	1.8	16.6
bryophytes	br_%SpN	1.1	1.4	0.0	3.3	1.6	2.6	2.3	0.6	1.7	2.8	2.8	1.0	1.2	1.4	1.0	0.5	0.7
	br_%cov	4.6	8.0	0.0	19.6	4.9	12.3	11.2	5.7	6.0	10.3	19.7	3.3	3.2	3.5	2.6	1.5	1.9
lichens	li_%SpN	1.1	0.6	1.5	0.0	0.4	1.9	2.4	2.1	1.9	0.8	0.3	2.4	2.0	2.5	0.7	0.1	3.0
	li_%cov	2.8	3.4	4.4	0.0	1.1	3.9	8.0	6.6	7.6	3.7	0.4	7.3	4.6	6.8	2.0	0.4	15.0
northing	average	0.0	-0.1	-0.5	0.3	-0.2	0.5	0.4	0.3	-0.3	0.3	0.1	0.2	0.0	0.5	-0.2	-0.6	0.7
altitude (m)	max	2535	2240	2320	2350	2450	2407	3300	2411	2385	2264	2560	2515	2570	2280	2306	2040	2258
	min	1828	1479	1990	1910	1711	1850	2170	1990	1686	1741	2050	1556	1465	1820	1625	1515	1851
	max	3.8	8.0	4.9	3.0	3.8	3.2	2.2	2.3	2.9	3.4	2.0	2.9	8.7	2.3	3.8	3.8	2.4
T (EIV)	min	1.3	1.3	2.9	1.4	1.5	1.6	1.0	1.1	2.0	1.9	1.5	1.2	1.2	1.8	1.6	1.8	0.0
	average	2.5	2.3	3.9	2.2	2.3	2.1	1.5	1.8	2.5	2.5	1.9	2.1	2.1	2.1	2.5	2.4	2.1
	max	5.9	5.4	6.0	5.0	6.0	5.9	5.7	5.9	5.9	5.8	6.6	6.8	6.6	5.7	5.7	6.0	6.0
C (EIV)	min	4.5	2.0	5.2	4.1	4.0	4.3	4.9	5.2	4.8	4.6	4.9	3.7	1.9	5.2	3.9	3.9	4.5
	average	5.3	4.8	5.6	4.7	4.9	5.4	5.4	5.6	5.6	5.0	5.4	5.2	5.2	5.7	5.0	4.7	5.6
	max	8.6	9.0	8.6	8.5	8.9	8.8	8.9	9.0	9.0	8.5	7.5	9.0	11.5	8.8	8.6	8.7	8.8
L (EIV)	min	6.3	0.0	6.9	6.0	4.5	7.0	7.6	7.2	6.4	5.8	7.0	5.4	7.2	7.3	6.0	7.3	5.5
	average	7.5	7.7	7.7	7.6	7.6	7.9	8.3	8.2	8.2	7.3	7.2	8.1	8.5	8.3	7.6	8.0	7.4
	max	6.5	7.0	4.0	4.6	5.9	4.2	3.1	3.7	2.6	3.1	4.8	4.7	8.5	3.6	5.3	4.3	3.0
N (EIV)	min	2.2	1.3	1.7	2.2	1.9	2.3	1.0	1.2	1.5	1.4	2.6	1.4	1.5	1.9	2.0	2.1	1.1
	average	3.7	2.5	2.8	3.5	3.6	3.2	1.9	2.2	2.1	2.5	3.7	2.8	2.8	3.0	3.2	3.1	2.0
	max	7.7	8.8	8.8	8.1	8.9	8.6	6.8	6.6	7.0	4.6	4.0	9.0	9.0	8.3	8.8	8.9	4.1
R (EIV)	min	36.0	22.0	6.0	16.0	68.0	14.0	24.0	8.0	14.0	22.0	12.0	87.0	####	20.0	61.0	15.0	14.0
	average	6.1	7.4	7.3	7.4	7.6	7.1	3.5	3.7	3.6	3.1	3.3	7.2	7.8	6.8	7.3	7.7	2.6
	max	6.7	7.0	4.1	7.2	8.0	7.6	5.8	6.0	5.2	6.6	7.0	6.8	7.7	5.0	5.9	6.2	5.8
M (EIV)	min	4.0	3.2	3.3	4.4	3.9	4.5	4.2	4.3	3.2	4.0	6.6	4.0	3.2	4.2	3.2	4.0	0.0
	average	5.0	4.5	3.7	6.1	5.3	5.7	4.9	4.9	4.1	5.5	6.9	4.8	4.4	4.4	4.9	4.8	4.8

4.1.1 Class Molinio-Arrhenatheretea

1) **Crepido-Festucetum commutatae: Association of sub-alpine milkwort pastures**

Milkwort pastures are found in high alpine ranges where snowbeds prevail the better part of the year. They develop successively on former spruce and knee timber forests after management and clearing of the forest as well as near mountain pastures on slopes and planes. Milkwort species (e.g. *Crepis aurea*) and grasses like *Luzula sudetica* are progressively accompanied by herbs (*Potentilla crantzii*). The Association prefers neutral to moderately acidic soils. As soils in alpine regions often acidify, *Crepido-Festucetum commutatae* is also found in mostly alkaline limestone regions. The moss layer consists of twenty-six bryophytes such as *Ctenidium molluscum*, *Ditrichum flexicaule* or *Sanionia uncinata* although none are expressing notable occurrence frequencies (see Table 7). Of the seventeen lichen species, *Cetraria islandica* and *Cladonia mitis* occur with mentionable frequencies.

4.1.2 Class Asplenieta trichomanis

2) **Drabo stellatae-Potentilletum clusianae: Association of *Potentilla clusiana* plots of the Eastern Alps**

As typical Association of Limestone crevices plots are mainly distributed in the highest alpine ranks of Northern Limestone Alps on sun-exposed mountain ridges and slopes in alpine summit regions (1647-2240 m.). Drought resistant and light-demanding herbs such as *Achillea clavennae*, *Potentilla clusiana*, *Draba stellata*, *Campanula cochleariifolia*, *Saxifraga oppositifolia* dominate the Association. With eighteen species, the moss layer consists mainly of bryophytes (see Figure 5 and Table 7), dominated by *Ditrichum flexicaule*. Ten Lichens, like *Peltigera rufescens* or *Thamnolia vermicularis*, occur scarcely throughout the community.

3) **Potentilletum nitidae: Association of *Potentilla nitida* plots**

The Association is endemic to South European dolomite and limestone cornices and thus features species endemic to the South-eastern Limestone Alps like *Paederota bonarota* and *Saxifraga squarrosa*. Low moisture and nutrient availability facilitate harsh local habitat conditions (see Table 7). Species such as *Potentilla nitida*, *Primula auricula*, *Carex mucronata* and *Saxifraga caesia* are well adapted to these conditions. The moss layer consists of four lichen species of which *Psora decipiens*, *Solorina saccata* and *Toninia candida* express high frequencies exclusively in this Association (Figure 5 and Table 7).

4.1.3 Class Thlaspietea rotundifolii

4) **Arabidetum caeruleae: Association of *Arabis caerulea* spots**

Habitats of this pioneer Association of calcareous, static boulder scree troughs are often permanently snow-covered. Most characteristic species, such as *Arabis caerulea*, *Pritzelago alpina*, *Saxifraga androsacea* or *Gnaphalium hoppeanum* are exclusively found in *Arabidetalia caeruleae* due to their

adaptations to these specific habitat conditions. These are accompanied by numerous hygrophilous species like *Achillea atrata*, *Veronia alpina* ssp. *pumila* and *Saxifraga stellaris* ssp. *robusta*. Regarding cryptogams, no lichen species are found throughout the Association. Twenty-nine bryophytes with frequent occurrences of *Bryum pseudotriquetrum*, *Cratoneuron commutatum*, *C. filicinum*, *Ditrichum flexicaule* and *Lescuraea incurvata* form the moss layer.

5) Campanulo pullae-Achilleetum clusianae: Association of calcareous scree grounds with persistent snow cover

Being endemic in a rather small areal within the Austrian north-eastern Limestone Alps, the eponymous *Achillea clusiana* has a well-defined distribution area. *Campanula pulla*, *Veronica aphylla* are characteristic as well. Although forty-four bryophytes and eleven lichens are reported, they are very scarce in number (see Table 7). *Cratoneuron filicinum* is the only cryptogam occurring frequently.

6) Salicetum retuso-reticulatae: Association of snow willow lines

Habitats on hill slopes and calcareous rocky ridges also feature persistent snow covers. Characteristic species *Salix retusa* and *Salix reticula* and accompanied by species with an affinity for high water availability such as *Doronicum glaciale*, *Pedicularis oederi*, *Carex fuliginosa*. The moss layer mainly comprises calciphile lichen and moss species. Of the twenty-three bryophytes and thirteen lichens, *Hylocomium splendens* and *Sanionia uncinata* are prevailing with *S. uncinata* being exclusively dominant in this Association. *Cetraria islandica*, *C. cucullata* and *Thamnolia vermicularis* are frequent companions.

7) Androsacetum alpinae: Association of Alpine rock-jasmine (*Androsace alpina*) plots

These pioneer communities are found on boulder screes of mountain summits, ridges and slopes. Habitats are notably more exposed to wind than those of Assoc. 6. Bedrock consisting of mica slate, slate and gneissic rock suggests acidic soils, but small incorporations of amphibolite scree are enough to result in a rather basophilic species composition dominated by *Saxifraga bryoides*, *Minuartia sedoides*, *Poa laxa* and *Cerastium uniflorum*. The acidophilic key species of *Androsace alpina*, is thus scarcely found in this Alliance. The moss layer is well pronounced in number of species and individuals. It comprises fifteen lichen species, dominated by *Cladonia arbuscular*, *Cetraria islandica*, *Cetraria nivalis* and *Thamnolia vermicularis*, as well as thirty-one bryophyte species, dominated by the alpine species *Polytrichastrum alpinum*.

4.1.4 Class Caricetea curvulae

8) Caricetum curvulae: Association of typical curved sage grasslands

Grassland plots are dominated by *Carex curvula* which is accompanied by persistent species such as *Campanula alpina*, *Pedicularis verticillata* and *Salix serpyllifolia*. The Association is found on calcareous mountain summits, ridges and slopes as well as rocky plateaus. With only 4 bryophytes and 9 lichens,

the moss layer is very species-poor (see Table 7). *Alectoria ochroleuca* is exclusively characteristic of this Association and is accompanied by frequent occurrences of *Cetraria cucullata* *C. islandica*, *Cladonia rangiferina*, and *Thamnolia vermicularis* and *Polytrichastrum alpinum* among the moss species.

9) Pulsatillo albae-Festucetum variae: Association of Eastern Alpine meadows of *Festuca varia*

Dense grasslands dominated by *Festuca varia* and *Pulsatilla alpina* are found on sun-exposed mountain summits, ridges and steep slopes. Featuring 20 bryophytes and thirteen lichens, the moss layer is rather species-poor but rich in individuals (Table 7). *Hylocomium splendens*, *Cetraria islandica*, *Cladonia rangiferina* are dominant here.

10) Sieversio-Nardetum strictae: Association of subalpine and alpine *Nardus stricta* pastures

The extensive community dominates alpine mountain pastures. *Nardus stricta* is accompanied by characteristic persistent shrub and herb species such as *Leontodon helveticus*, *Anthoxanthum alpinum*, *Potentilla aurea*, *Geum montanum* and *Deschampsia caespitosa*. The consistent moss layer (Figure 5 and Table 7) comprises thirty-four mosses, but only eight lichens. *Dicranum scoparium* exclusively characterizes this Association and is frequently accompanied by *Polytrichum juniperinum*, *Cetraria islandica* and *Cladonia rangiferina*.

4.1.5 Class Salicetea herbaceae

11) Polytrichetum sexangularis: Association of silicate snow grounds of alpine mountains

The acidophilic communities are adapted to cool, humid habitats with long-lasting or perennial snow cover. Hence, they are found in snowbeds on water saturated slate bedrock. Species composition is exclusively characterized by mosses (*Anthelia juratzkana*, *Polytrichastrum sexangulare*, *Pohlia drummondii*, *Polytrichum juniperinum*). Altogether, the moss layer consists of three lichen and nine moss species and is accompanied by small and persistent shrubs and herbs like *Arenaria biflora*, *Sibbaldia procumbens*, *Taraxacum alpinum* and *Veronica alpina*. Appearances of *Gnaphalium supinum* and *Salix herbacea* indicate a floristic transition to Salicetum herbaceae. Succession from Polytrichetum sexangularis into Salicetum herbaceae is however prevented by extreme snow conditions.

4.1.6 Class Seslerietea albicantis

Caricetum firmae: Association of *Carex firma* meadows

High habitat variability can be observed in these short sage grasslands which results in a classification into two Variations of Caricetum firmae in this study. *Carex firma*, *Saussurea pygmaea* and *Gentiana clusii* are persistent characteristic species of these Associations. The first Variation is dominated by *Primula clusiana* while the second Variation is dominated by *Festuca pumila*.

12) Caricetum firmae Variation with *Primula clusiana*

This Variation occurs in habitats slightly less exposed than the *Festuca pumila* Variation. Habitats include dolinas, snowbeds, hill slopes and rock terraces. *Carex firma* and *Primula clusiana* are accompanied by *Chamorchis alpina*. The well pronounced moss layer (Figure 5 and Table 7) features thirty bryophytes and twenty-nine lichens with *Cetraria islandica*, *Thamnolia subuliformis*, *Thamnolia vermicularis* and *Ditrichum flexicaule* occurring predominantly.

13) Caricetum firmae Variation with *Festuca pumila*

The Variation with *Festuca pumila* is found on exposed hill slopes (particularly their upper sections), mountain ridges, anticlinal folds, plateaus and terraces. *Carex firma* and *Festuca pumila* are predominantly accompanied by *Crepis terglouensis*. With forty-seven mosses and thirty-three lichens, the moss layer of this Variation is richer in species. However, it is dominated by the same species as the *Primula clusiana* Variation, with additional high occurrence frequencies of *Cetraria tilesi*.

14) Dryadetum octopetalae: Association of white dryas swards

Besides *Dryas octopetala*, Dryadetum octopetalae is dominated by calciphile scree vegetation such as *Sesleria varia* agg., *Vaccinium uliginosum*, *Bartsia alpina*, *Rhododendron hirsutum* and *Anthoxanthum odoratum*. Thirteen mosses and fourteen lichen species form a rather fragmentary moss layer (Table 7), dominated by *Hylocomium splendens* and *Rhytidiadelphus triquetrus* as well as *Cetraria islandica*, *Cladonia rangiferina*, *C. stellaris* and *Thamnolia vermicularis*.

15) Seslerio-Caricetum sempervirentis: Association of *Sesleria albicans* and *Carex sempervirens* sage heathlands

Habitats of sage grasslands dominated by *Sesleria albicans* and *Carex sempervirens* comprise calcareous rubble scree covered hillslopes, moraines, and rocky troughs. With twenty-eight bryophytes and fifteen lichens the moss layer is fragmentary and not well pronounced (Figure 5 and Table 7). *Ditrichum flexicaule* is the only species with notable occurrence frequencies.

16) Campanulo scheuchzeri-Festucum noricae: Association of *Festuca norica* meadows

The Association is dominated by *Festuca norica*, *Carex ferruginea*, *Carduus defloratus*, *Carlina acaulis*, *Trifolium pretense*, *Helictotrichon parlatorei*, *Silene vulgaris* and *Senecio abrotanifolius*. Meadows are distributed on calcareous hillside slopes, dolinas and troughs. The weakly pronounced moss layer (Figure 5 and Table 7) is species-poor with only eight bryophytes and two lichen species, none of which express characteristic occurrence frequencies.

4.1.7 Class Loiseleurio-Vaccinietea

17) Loiseleurio-Cetrarietum: Association of alpine azalea heathlands

Alpine azalea heathlands are adapted to extreme habitat conditions on wind-exposed hillside slopes, mountain ridges and plateaus. The densely growing dwarf shrub *Loiseleuria procumbens* (alpine azalea) is characteristically intertwined with dominant lichen species such as *Cetraria cucullata* and *C. islandica*. *Cladonia rangiferina* and *Thamnolia vermicularis* are found as well, resulting in one of the most extensive and well pronounced moss layers (dominated by lichens) of all Associations recorded in the course of study (Figure 5 and Table 7). Altogether, sixteen mosses and nineteen lichen species are recorded.

18) Empetro-Vaccinetum gaultherioidis: Association of *Empetrum* heathlands

The acidophile Association is found on moderately exposed hillside slopes and mountain ridges. As opposed to Loiseleurio-Cetrarietum, Vegetation of Empetro-Vaccinetum gaultherioidis is observably two-layered. The upper layer consists of dense scrubs of *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Vaccinium gaultheroides* and *Vaccinium vitis-idaea*. Lichens and mosses form the lower layer. The moss layer is well pronounced but dominated by lichen species. Of the seventeen bryophytes and fifteen lichens, *Cladonia gracilis*, *C. pyxidata* and *Paraleucobryum enerve* are exclusively characteristic of this Association. They are accompanied by frequently occurring *Cetraria islandica*, *Cladonia arbuscula* and *C. rangiferina*.

4.2 The role of Ecological Factors for Alpine Cryptogam Distribution

Vegetation classification of species and relevés demonstrates the high number of different recorded plant communities across the Austrian Alpine mountain ranges. However, vegetation classification alone yields no information on the ecological factors causing these vegetation patterns. Thus, I was interested in the fundamental ecological parameters responsible for species distribution patterns in alpine vegetation with special focus on cryptogam distribution.

4.2.1 Relationships between Vegetation and Ecological Factors

Analysis of herb and moss layer and environmental variables via Spearman correlations (Spearman 1904) yields an overview over the direction and strength of the relationships between vegetation and environment in the Alps.

Impact of Selected Ecological Factors on Cryptogam Distribution in the Austrian Alps

Table 8: Spearman Correlation Table showing relationships between vegetation and selected ecological variables; Abbreviations: for EIV see Table 3, for bioclimatic variables bio1 to bio19 see Table 2; herb layer: total species no. (hl_SpN), relative species no. (hl_%SpN), relative cover (hl_cov); moss layer: total species no. (ml_SpN), relative species no. (ml_%SpN), relative cover (ml_cov), colours: black framed fields indicate significant correlations referred to in this study, grey fields indicate min. and max. values, orange fields indicate separation between correlation coefficients (left) and p-values (right)

	Altitude (m)	Northing	hl_SpN	hl_%SpN	hl_cov	ml_SpN	ml_%SpN	ml_cov	L	T	C	M	R	N	bio_1	bio_2	bio_3	bio_5	bio_6	bio_10	bio_11	bio_12	bio_14	bio_15	bio_16	bio_17	bio_19
Altitude (m)	0.00	0.73	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.04	0.00	0.92	0.06	0.01	
Northing	-0.01	0.00	0.11	0.00	0.23	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.34	0.00	0.02	0.27	0.00	0.00	0.00	0.35	0.58	0.00	0.03	0.27	0.95	
hl_SpN	-0.13	-0.07	0.00	0.00	0.00	0.60	0.00	0.35	0.00	0.00	0.00	0.00	0.52	0.00	0.01	0.00	0.02	0.01	0.00	0.01	0.33	0.06	0.36	0.06	0.05	0.14	
hl_%SpN	-0.19	-0.23	0.34	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.00	0.00	
hl_cov	-0.07	-0.05	0.43	0.23	0.00	0.03	0.00	0.01	0.00	0.00	0.55	0.00	0.15	0.00	0.89	0.11	0.63	0.89	0.48	0.98	0.81	0.51	0.53	0.00	0.16	0.00	
ml_SpN	0.17	0.22	-0.02	-0.92	-0.09	0.00	0.00	0.25	0.00	0.00	0.02	0.00	0.02	0.01	0.02	0.01	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.09	0.00	0.00	
ml_%SpN	0.20	0.23	-0.34	-1.00	-0.23	0.92	0.00	0.00	0.01	0.00	0.00	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.00	0.00	
ml_cov	0.12	0.26	-0.04	-0.82	-0.11	0.87	0.82	0.00	0.92	0.00	0.00	0.00	0.00	0.03	0.05	0.14	0.07	0.10	0.01	0.07	0.03	0.00	0.00	0.00	0.20	0.00	
L	0.13	0.05	-0.24	-0.10	-0.24	0.05	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.69	0.60	0.17	0.22	0.15	0.27	0.01	0.00	0.00	0.06	1.00	
T	-0.33	-0.12	0.21	0.22	0.22	-0.17	-0.23	-0.14	-0.51	0.00	0.00	0.26	0.29	0.00	0.00	0.09	0.03	0.00	0.00	0.00	0.95	0.78	0.00	0.05	0.46	0.09	
C	0.22	0.26	-0.12	-0.20	-0.02	0.19	0.20	0.15	0.30	-0.20	0.00	0.03	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.02	0.04	0.07	0.00	0.00	0.55	0.00	
M	0.07	0.20	0.20	-0.02	0.15	0.10	0.02	0.15	-0.46	0.05	-0.09	0.00	0.00	0.00	0.18	0.02	0.03	0.24	0.09	0.23	0.13	0.36	0.75	0.32	0.06	0.27	
R	-0.22	-0.22	-0.03	0.12	-0.06	-0.14	-0.12	-0.18	0.32	-0.04	-0.33	-0.32	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00	
N	-0.06	-0.04	0.28	0.16	0.27	-0.10	-0.16	-0.09	-0.45	0.26	-0.19	0.41	0.10	0.00	0.83	0.00	0.86	0.84	0.14	0.96	0.47	0.00	0.00	0.00	0.76	0.00	
bio_1	-0.76	0.13	0.11	0.13	0.01	-0.11	-0.14	-0.08	-0.05	0.19	-0.09	-0.06	0.18	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.02	0.11	0.01	0.17	
bio_2	0.36	0.10	-0.13	-0.13	-0.07	0.10	0.12	0.06	-0.02	-0.07	0.25	0.09	-0.47	-0.17	-0.34	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.56	0.35	0.00	0.00	
bio_3	0.51	0.05	-0.10	-0.14	0.02	0.11	0.14	0.08	-0.02	-0.09	0.18	0.09	-0.34	0.01	-0.59	0.72	0.00	0.00	0.00	0.00	0.91	0.13	0.34	0.21	0.32	0.33	
bio_5	-0.76	0.14	0.11	0.12	-0.01	-0.10	-0.13	-0.07	-0.06	0.19	-0.09	-0.05	0.17	-0.01	1.00	-0.33	-0.61	0.00	0.00	0.00	0.81	0.03	0.09	0.14	0.05	0.71	
bio_6	-0.78	0.12	0.14	0.15	0.03	-0.13	-0.15	-0.10	-0.05	0.19	-0.13	-0.07	0.24	0.06	0.97	-0.39	-0.55	0.95	0.00	0.00	0.05	0.00	0.00	0.06	0.00	0.00	
bio_10	-0.76	0.12	0.12	0.13	0.00	-0.11	-0.13	-0.07	-0.06	0.19	-0.10	-0.05	0.18	0.00	1.00	-0.35	-0.62	1.00	0.96	0.00	0.00	0.92	0.04	0.04	0.25	0.06	
bio_11	-0.76	0.16	0.11	0.13	0.01	-0.12	-0.14	-0.09	-0.05	0.20	-0.09	-0.06	0.18	0.03	0.98	-0.30	-0.50	0.96	0.98	0.96	0.00	0.06	0.00	0.04	0.00	0.00	
bio_12	0.00	0.04	0.04	0.13	0.03	-0.13	-0.12	-0.13	0.11	0.00	-0.08	0.04	0.19	0.14	0.03	-0.08	0.00	0.01	0.08	0.00	0.08	0.00	0.00	0.00	0.00	0.00	
bio_14	-0.08	0.02	0.08	0.16	0.03	-0.14	-0.15	-0.14	0.12	0.01	-0.13	0.01	0.30	0.16	0.12	-0.18	-0.06	0.09	0.19	0.09	0.18	0.94	0.00	0.00	0.00	0.00	
bio_15	0.17	0.13	0.04	-0.12	-0.26	0.13	0.11	0.18	0.14	-0.15	0.19	0.04	-0.28	-0.22	-0.10	0.02	-0.04	-0.07	-0.16	-0.09	-0.14	-0.16	-0.23	0.00	0.00	0.00	
bio_16	0.00	0.09	0.08	0.09	-0.06	-0.07	-0.09	-0.05	0.14	-0.08	-0.02	0.08	0.01	0.01	0.07	-0.04	-0.05	0.06	0.08	0.05	0.08	0.84	0.74	0.28	0.00	0.00	
bio_17	-0.08	0.05	0.08	0.15	0.12	-0.13	-0.14	-0.12	0.08	0.03	-0.15	0.05	0.31	0.22	0.11	-0.18	-0.04	0.08	0.19	0.08	0.17	0.91	0.95	-0.33	0.68	0.00	
bio_19	-0.10	0.00	0.06	0.16	0.24	-0.14	-0.15	-0.16	0.00	0.07	-0.21	0.03	0.32	0.28	0.06	-0.17	0.04	0.02	0.16	0.02	0.13	0.72	0.74	-0.49	0.45	0.88	
Max	0.51	0.73	0.43	0.23	0.27	0.92	0.82	0.35	0.92	0.26	0.55	0.69	0.52	0.34	1.00	0.72	0.86	1.00	0.98	0.98	0.81	0.95	0.95	0.56	0.92	0.88	
Min	-0.78	-0.23	-0.34	-1.00	-0.26	-0.17	-0.23	-0.18	-0.51	-0.20	-0.33	-0.32	-0.47	-0.22	-0.59	-0.39	-0.62	-0.07	-0.16	-0.09	-0.14	-0.16	-0.23	-0.49	0.00	0.00	

Strong correlations can be observed between altitude and bioclimatic variables, relationships that are well documented in literature (Kazakis et al. 2007; Cavieres et al. 2014; Schwager and Berg 2019, Keller, Goyette, and Beniston 2005). Comparison of herb and moss layer, especially of relative species numbers, show strongly contrasting relationships with the various environmental and bioclimatic factors predominant in alpine ecosystems.

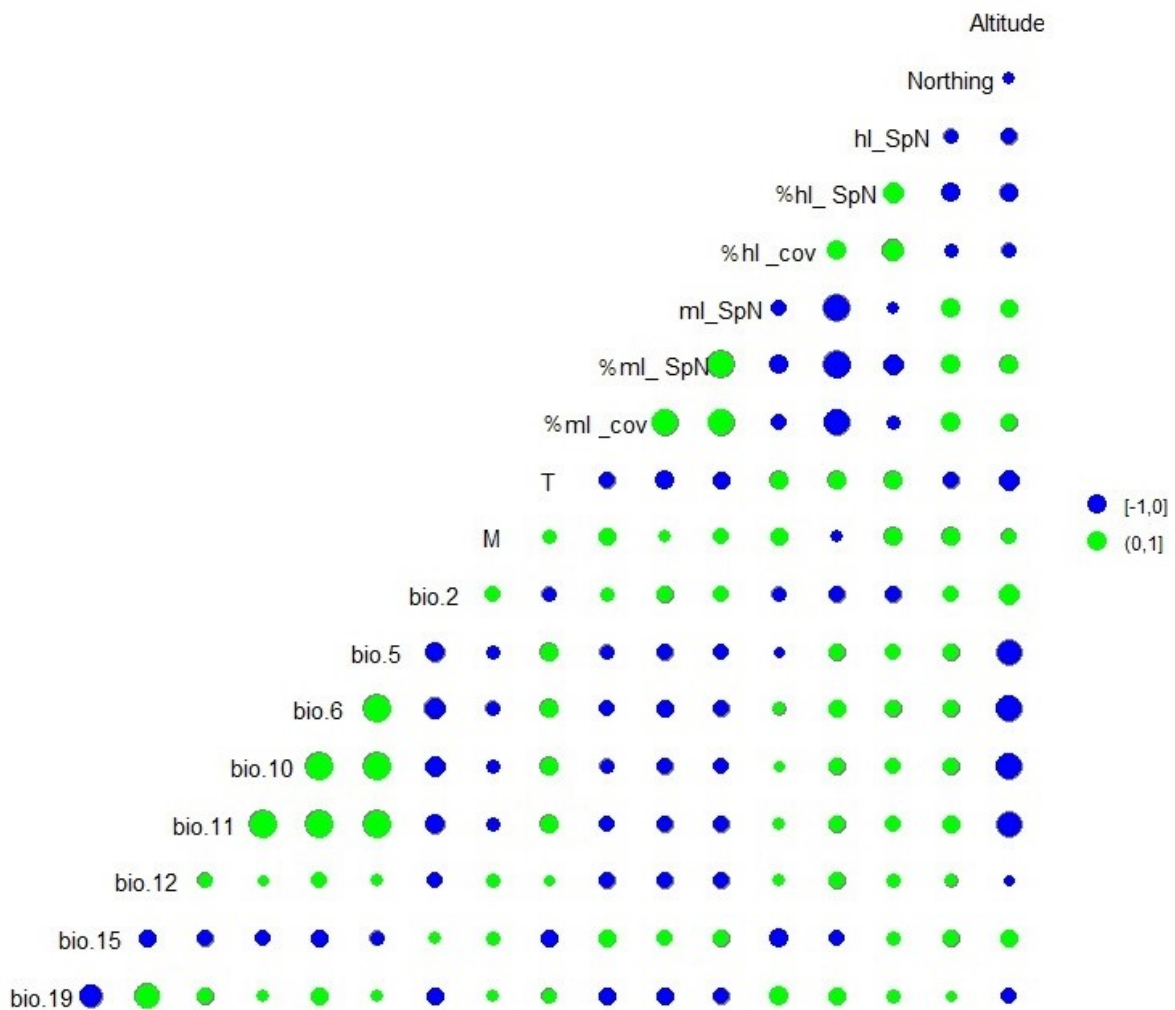


Figure 6: Graphical display of selected Spearman correlations; green dots indicate positive correlations, blue dots indicate negative correlation, size of dots indicates strength of relationships, for abbreviations see Table 8.

4.2.2 Cryptogam Distribution in Relation to Ecological Parameters in the Alps

Initial CCA featuring all environmental and bioclimatic variables as well as Ellenberg indicator values (EIV) yields distinct patterns concerning the magnitude of environmental influence on cryptogam species distribution. Regarding bioclimatic parameters, effects on moss layer and herb layer are strongly divergent.

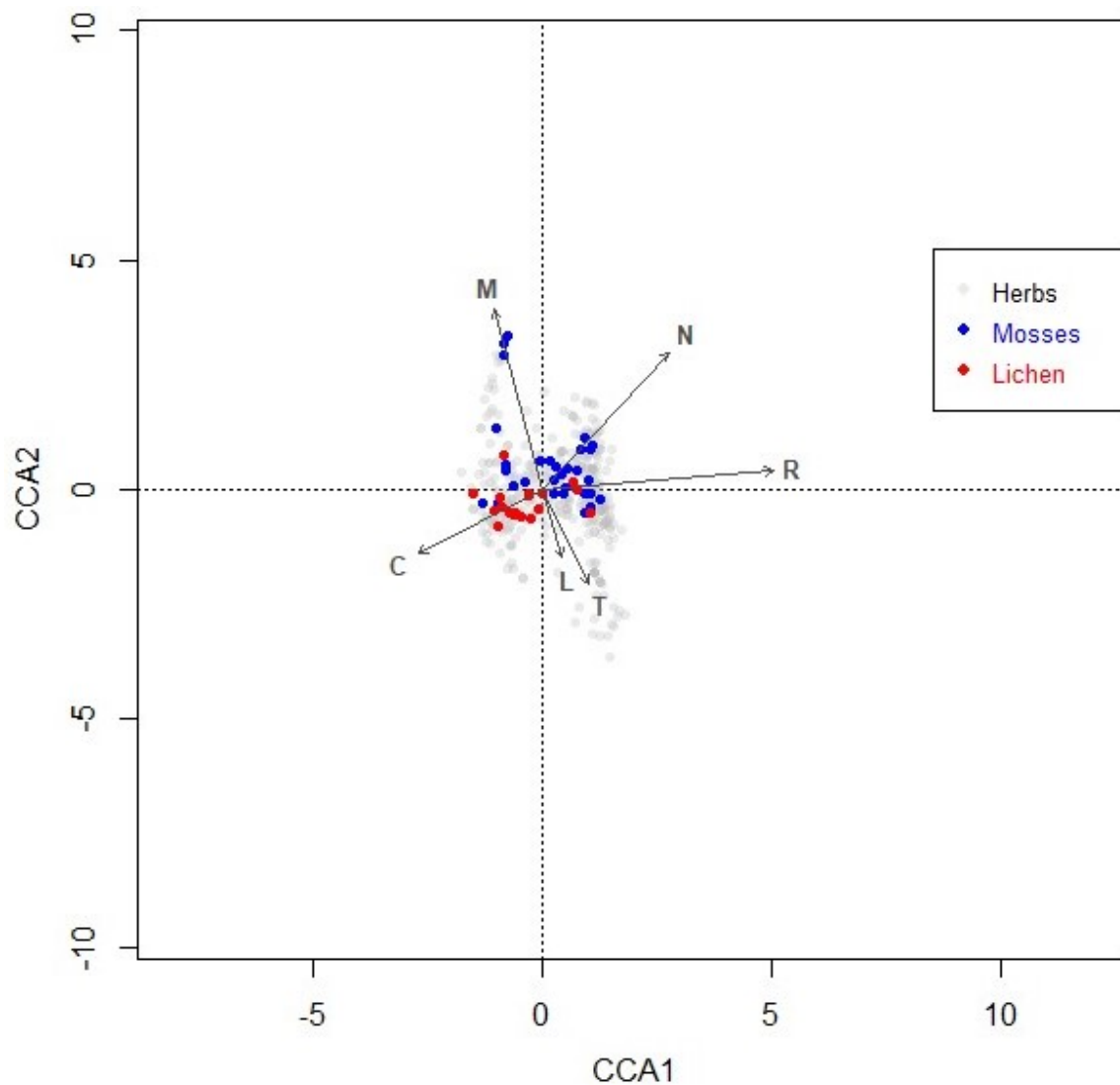


Figure 8: CCA of cryptogams and EIV, for abbreviations see Table 3

In Figure 7, altitude, relative cover of herb layer, bio.2, bio.15 and bio.19 express the longest arrows and thus the strongest relation with cryptogam distribution. Figure 8 shows that, except for Light (L) which expresses the same correlation with the data as Temperature (T) all CCA arrows are equally long. To emphasise the noted predominant explanatory variables affecting species data and inspect their effects on species distribution, the following CCA biplots display these variables only.

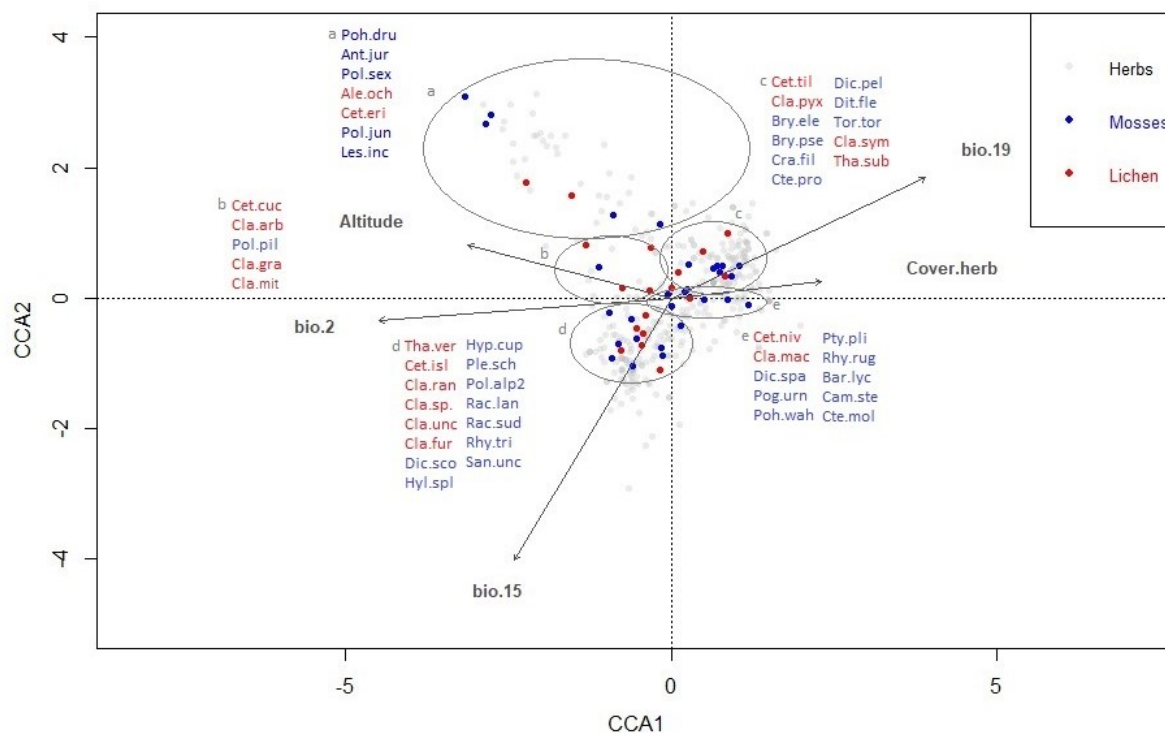


Figure 9: CCA ordination biplot constrained by five selected variables: altitude (m), relative cover of herb layer (Cover.herb), bio.2 (mean diurnal temperature range), bio.15 (precipitation seasonality) and bio.19 (winter precipitation). Circles indicate species groups a to e with corresponding species labels. Colours: grey points indicate herbs, red points and labels indicate lichens, blue points and labels indicate moss, black arrows and labels indicate explanatory variables.

Cryptogam species names in plots are abbreviated, for corresponding full species names see Table 6. Regarding ecological parameters, the CCA biplot diagram in Figure 9 shows positive correlations of winter precipitation (bio.19) and relative cover of herb layer with the first correlation axis while altitude, mean diurnal temperature range (bio.2) and precipitation seasonality (bio.15.) are negatively correlated with the first axis. Regarding cryptogam species, distinct species clusters can be identified in relation to the explanatory variables. Group a is located at the outer ranges of the species pool, these species show the strongest relationship with the altitudinal gradient. Group b is strongly related with altitude as well, however these species are not as distinct from rest of the cluster as Group a. Group c is predominantly affected by bio.19 while Group d is more strongly related with bio.15. Group e is predominantly related with relative herb cover.

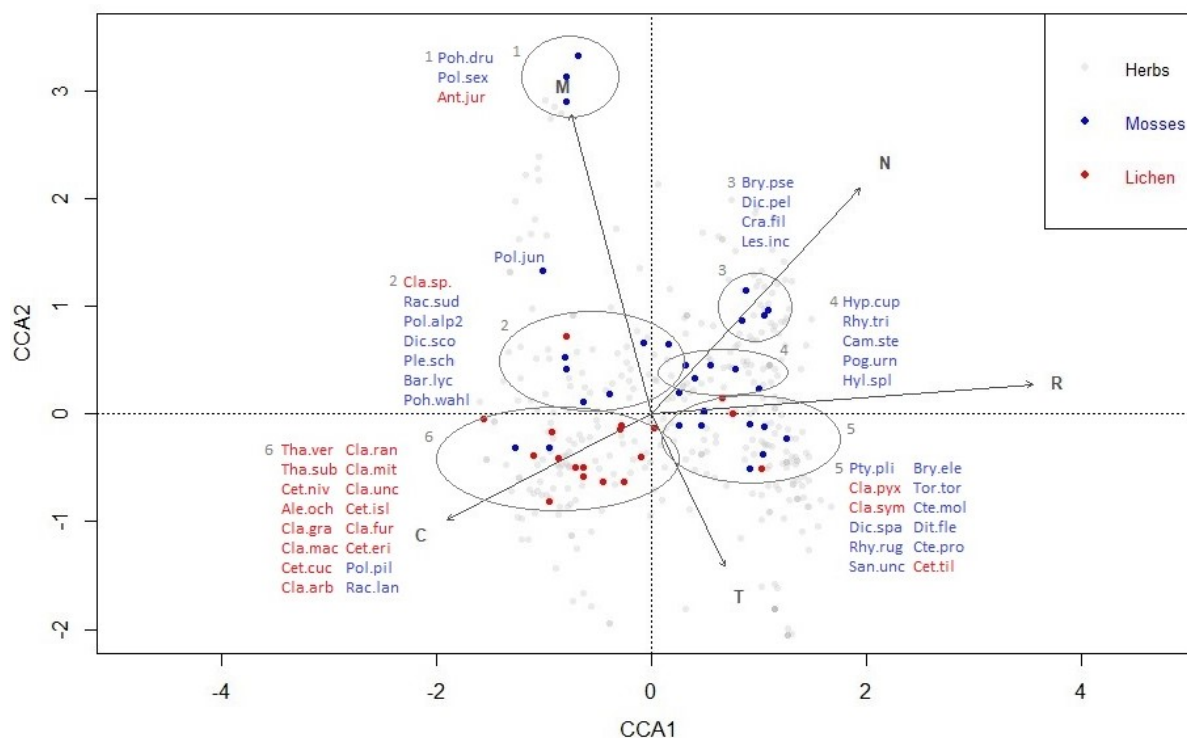


Figure 10: CCA ordination biplot constrained by five selected EIV: Continuity (C), Moisture (M), Nutrients (N), Soil reaction (R), Temperature (T). Circles indicate species groups 1 to 7 with corresponding species labels. Colours: grey points indicate herbs, red points and labels indicate lichens, blue points and labels indicate moss, black arrows and labels indicate explanatory variables

Regarding EIV, the CCA biplot in Figure 10 displays a positive correlation of the first ordination axis with R while it is negatively correlated with C. M and N are correlated with the second axis. Regarding relationships of the individual cryptogam species with EIV, species clusters can be identified in here as well. Group 1 is located at the outer range of the species cluster and shows the strongest relation with M. Cryptogams of Group 2 are located closely to coordinate system's origin but are also predominantly related to M. Group 3 shows a strong relationship with N while Group 4 is located close to the origin and also displays relations with R. Group 5 is most strongly correlated with the first axis and thus with R. Species of Group 7 are more loosely grouped but visibly related to the C variable.

CCA ordination biplots displaying relationships between cryptogams and environmental variables as well as EIV show that certain combinations of ecological parameters can be identified as responsible for cryptogam distribution patterns in the alpine mountain ranges.

4.3 Differences between Bryophytes and Lichens regarding Ecological Influences

Relationships between alpine vegetation and bio.2 (Mean Diurnal Temperature Range), bio.19 (Winter Precipitation) and continentality are displayed in the GLM diagrams below. Additionally, relations between northing and moisture as well as temperature are being inspected.

4.3.1 Influence of Mean Diurnal Temperature Range (bio.2) on Cryptogams

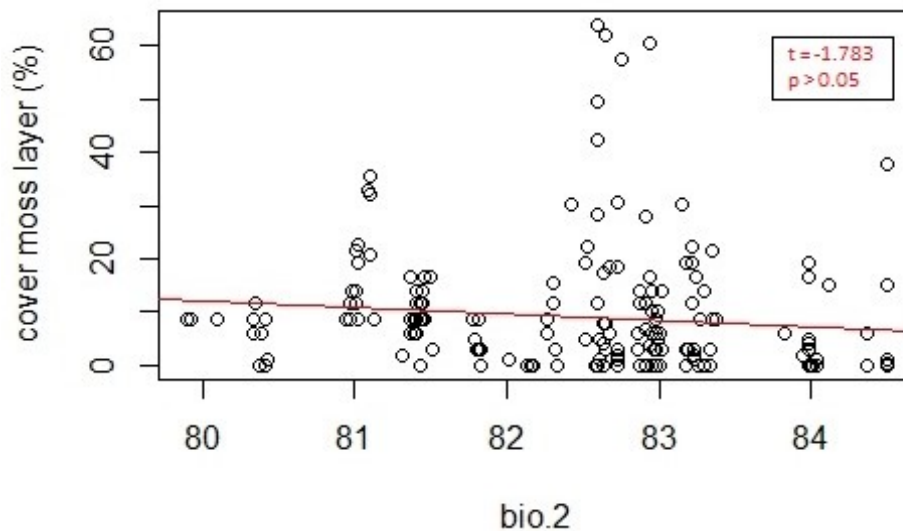


Figure 11: GLM analysis of relationships between bio.2 and relative moss layer cover, red line indicates direction of relationship, red t- and p-values indicate significance of results.

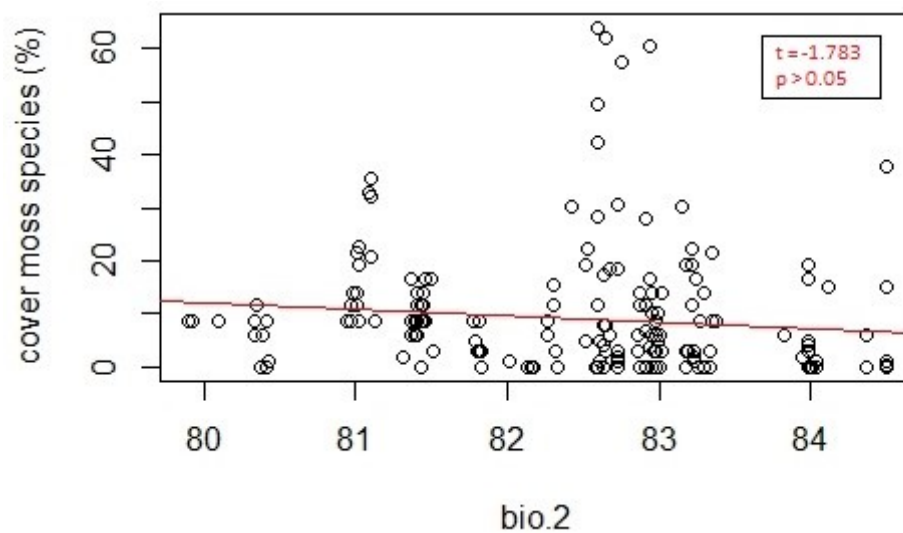


Figure 12: GLM analysis of relationships between bio.2 and relative cover of bryophytes, red line indicates direction of relationship, red t- and p-values indicate significance of results.

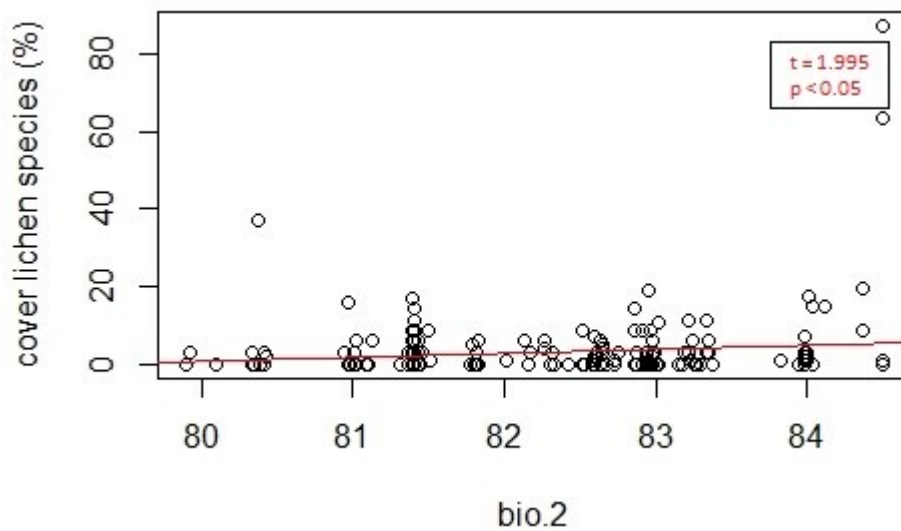


Figure 13: GLM analysis of relationships between *bio.2* and relative cover of lichens, red line indicates direction of relationship, red *t*- and *p*-values indicate significance of results.

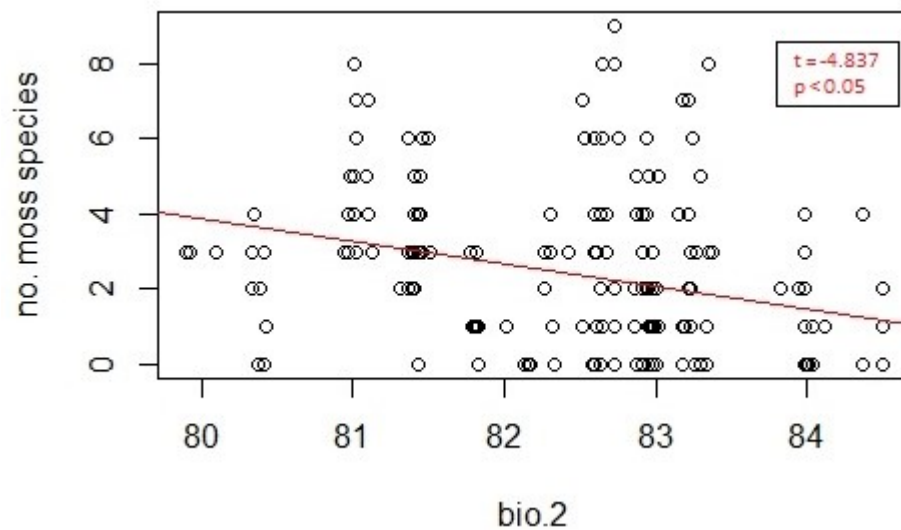


Figure 14: GLM analysis of relationships between *bio.2* and total number of bryophyte species, red line indicates direction of relationship, red *t*- and *p*-values indicate significance of results.

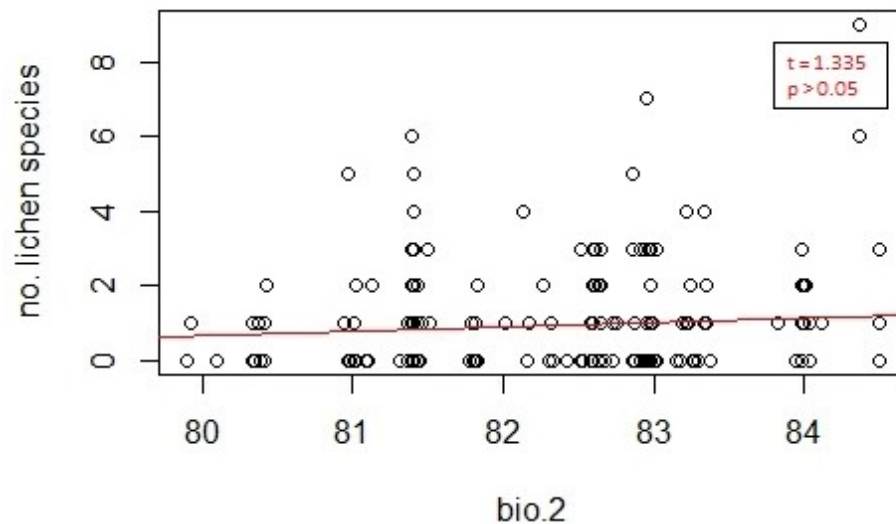


Figure 15: GLM analysis of relationships between bio.2 and total number of lichen species, red line indicates direction of relationship, red t- and p-values indicate significance of results.

There is no relationship between the mean diurnal temperature range (bio.2) and the relative moss layer cover (Figure 11). Separate analysis of bryophytes and lichens show contrary results: While bio.2 is not related with the relative bryophyte cover (Figure 12), lichen cover (Figure 13) shows a positive relationship. Regarding total species numbers, bryophytes show a negative relationship with bio.2 (Figure 14) while no relationships can be observed for lichens (Figure 15).

4.3.2 Influence of Winter Precipitation (bio.19) on Cryptogams

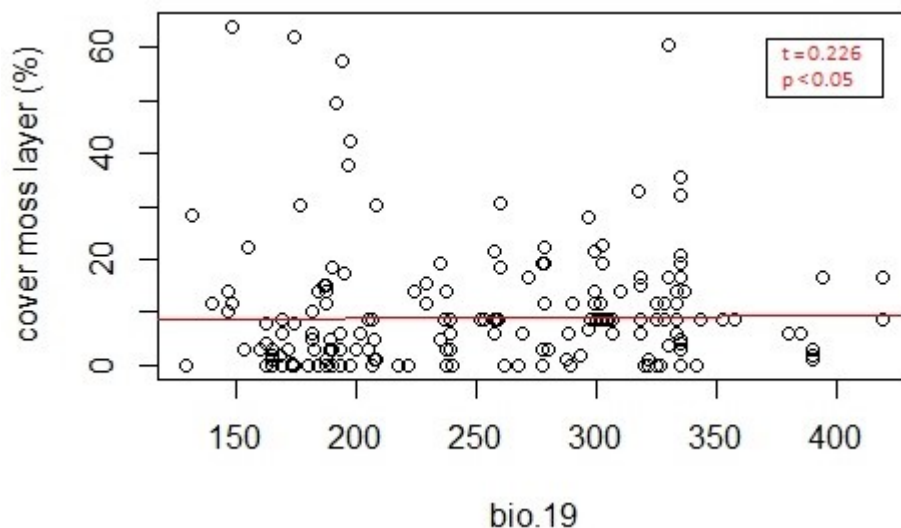


Figure 16: GLM analysis of relationships between bio.19 and relative moss layer cover, red line indicates direction of relationship, red t- and p-values indicate significance of results.

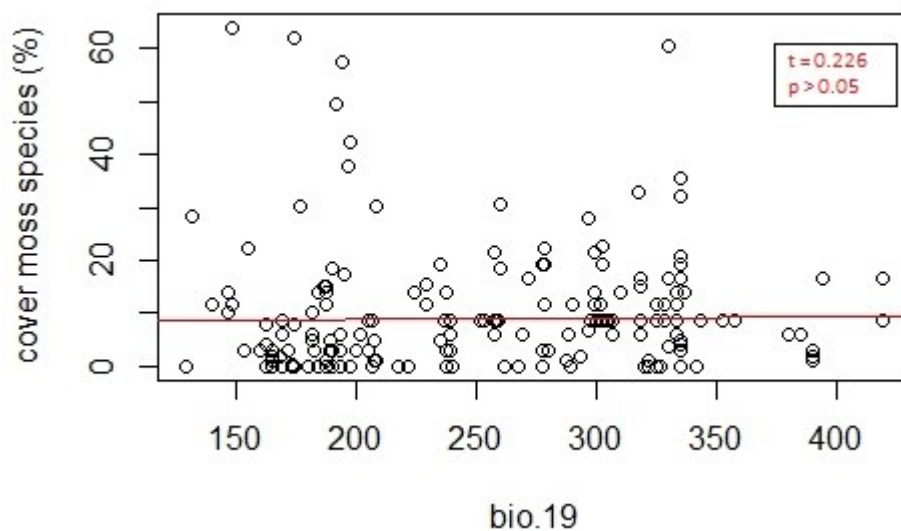


Figure 17: GLM analysis of relationships between bio.19 and relative cover of bryophytes, red line indicates direction of relationship, red t- and p-values indicate significance of results.

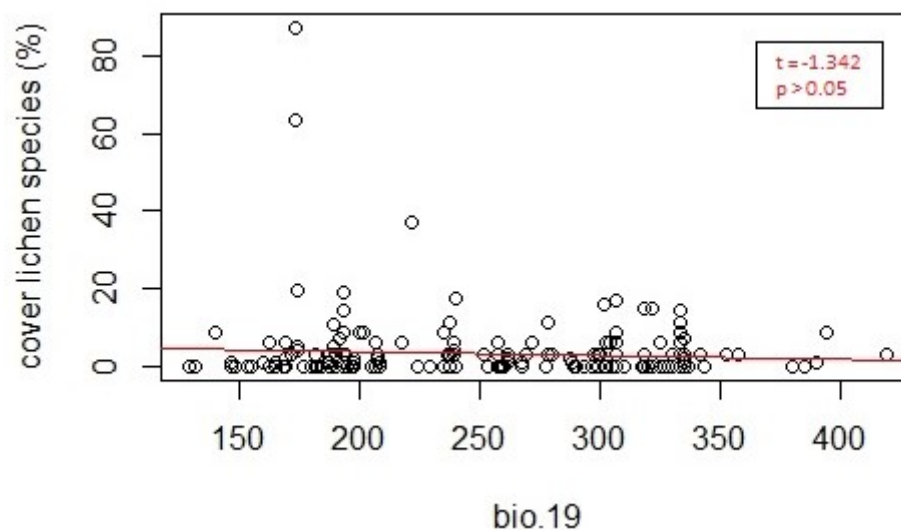


Figure 18: GLM analysis of relationships between bio.19 and relative cover of lichens, red line indicates direction of relationship, red t- and p-values indicate significance of results.

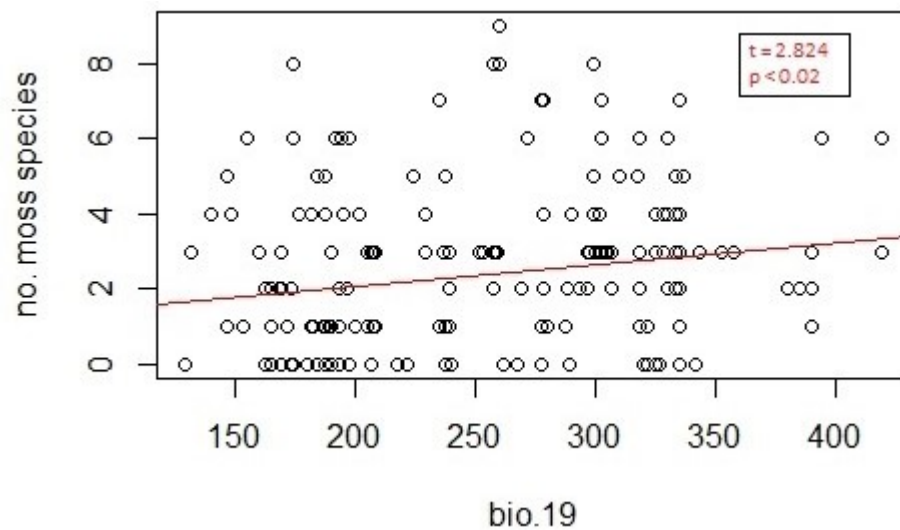


Figure 19: GLM analysis of relationships between bio.19 and total number of bryophyte species, red line indicates direction of relationship, red t- and p-values indicate significance of results.

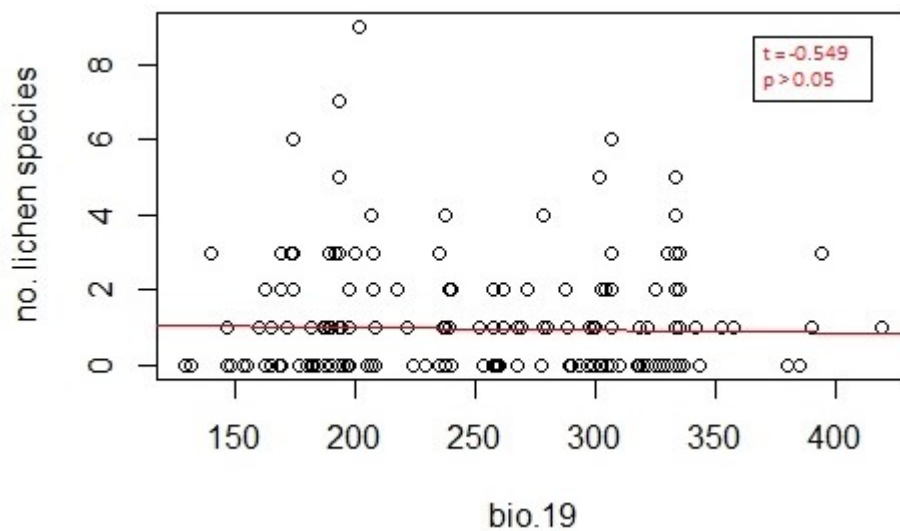


Figure 20: GLM analysis of relationships between bio.19 and total number of lichen species, red line indicates direction of relationship, red t- and p-values indicate significance of results.

There is no relationship between winter precipitation (bio.19) and the relative moss layer cover (Figure 16). Separate analysis of bryophytes (Figure 17) and lichens (Figure 18) yields the same result. Regarding total species numbers, a positive relationship with bio.19 can be observed for mosses (Figure 19).

4.3.3 Influence of Continentality (C) on Cryptogams

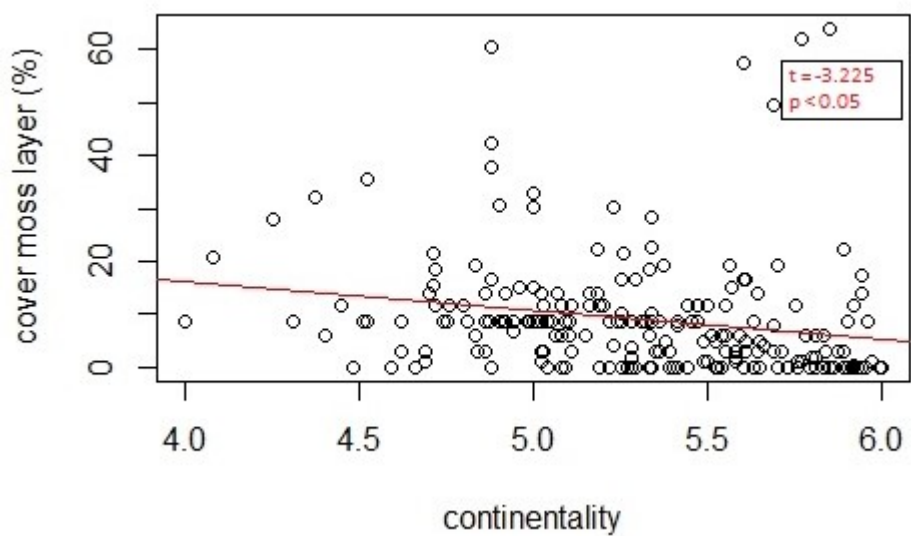


Figure 21: GLM analysis of relationships between EIV C (continentality) and relative moss layer cover, red line indicates direction of relationship, red t- and p-values indicate significance of results.

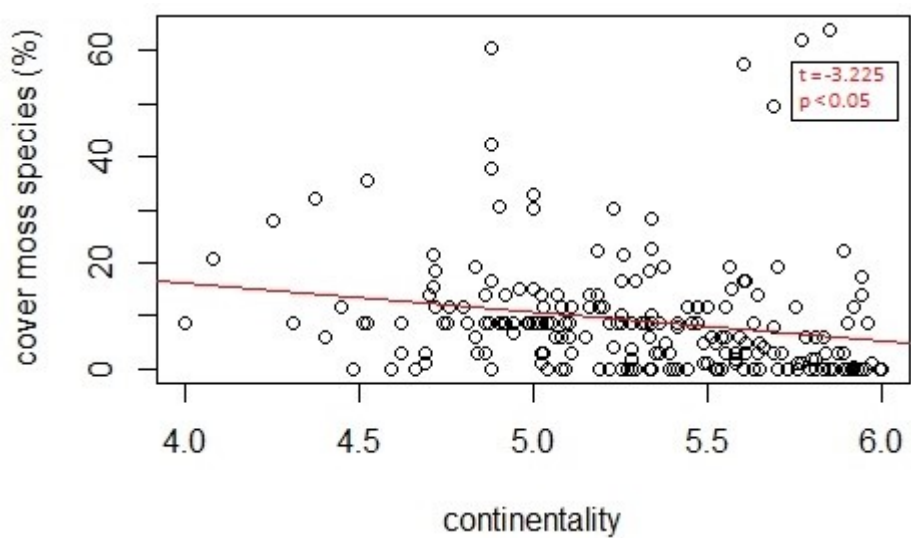


Figure 22: GLM analysis of relationships between EIV C (continentality) and relative cover of bryophytes, red line indicates direction of relationship, red t- and p-values indicate significance of results.

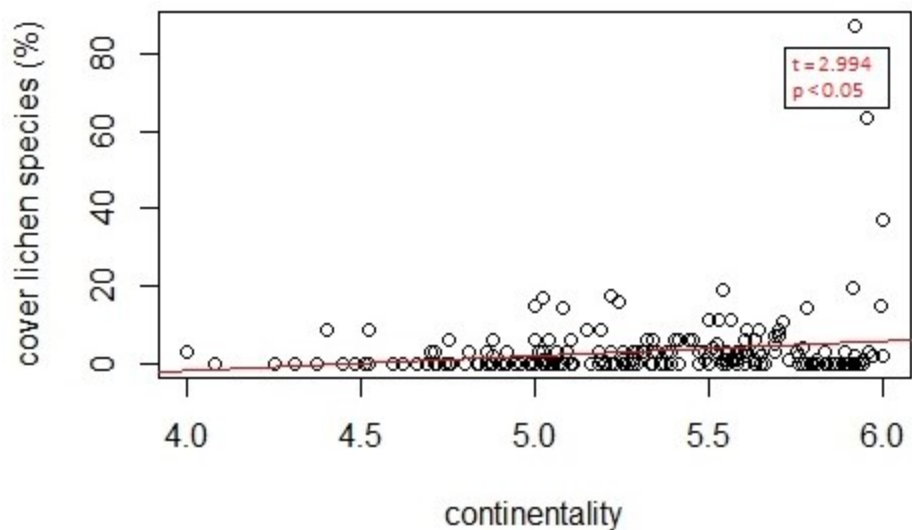


Figure 23: GLM analysis of relationships between EIV C (continentality) and relative cover of lichens, red line indicates direction of relationship, red t- and p-values indicate significance of results.

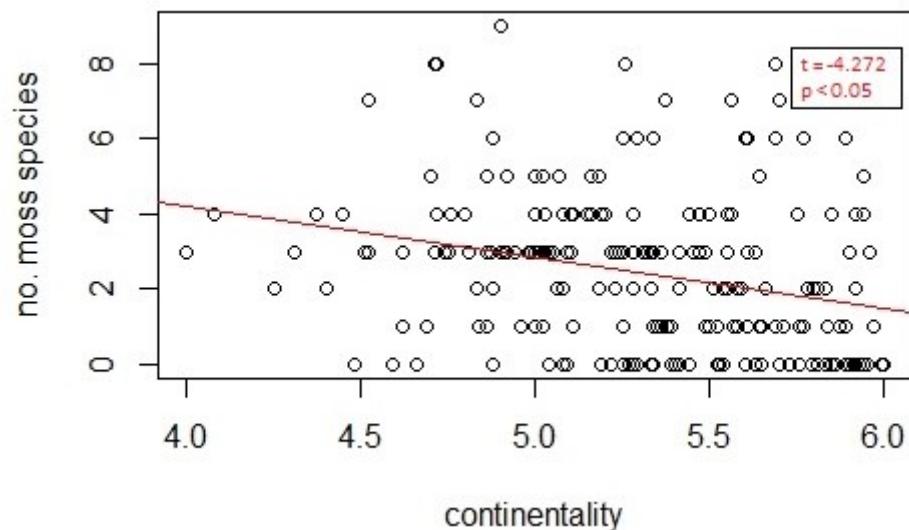


Figure 24: GLM analysis of relationships between EIV C (continentality) and total number of lichen species, red line indicates direction of relationship, red t- and p-values indicate significance of results.

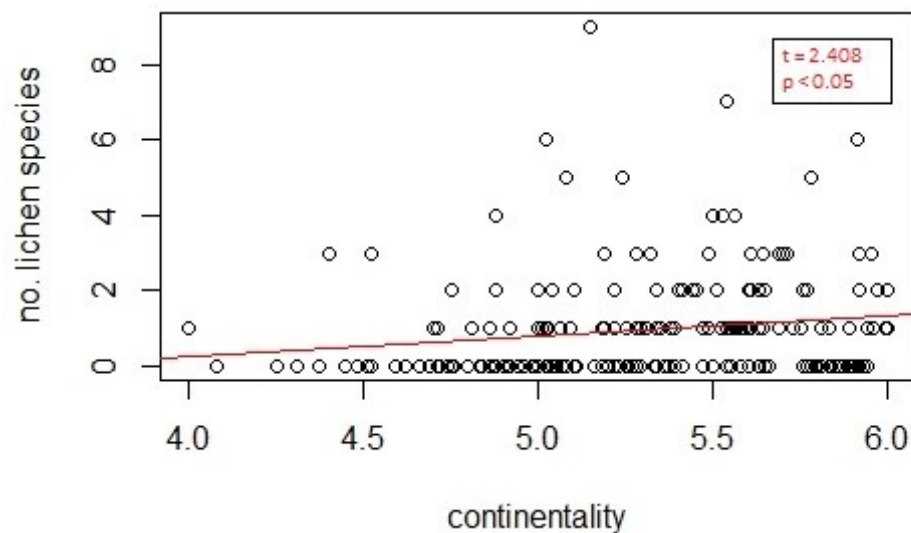


Figure 25: GLM analysis of relationships between EIV C (continentality) and total number of lichen species, red line indicates direction of relationship, red t- and p-values indicate significance of results.

The relative moss layer cover is negatively related with continentality (Figure 21). The pattern is reflected in cover (Figure 22) and species number (Figure 24) of bryophytes. Lichens on the other hand show positive relationships with continentality (Figure 23, Figure 25).

4.4 Influence of Relief on Climatic Factors

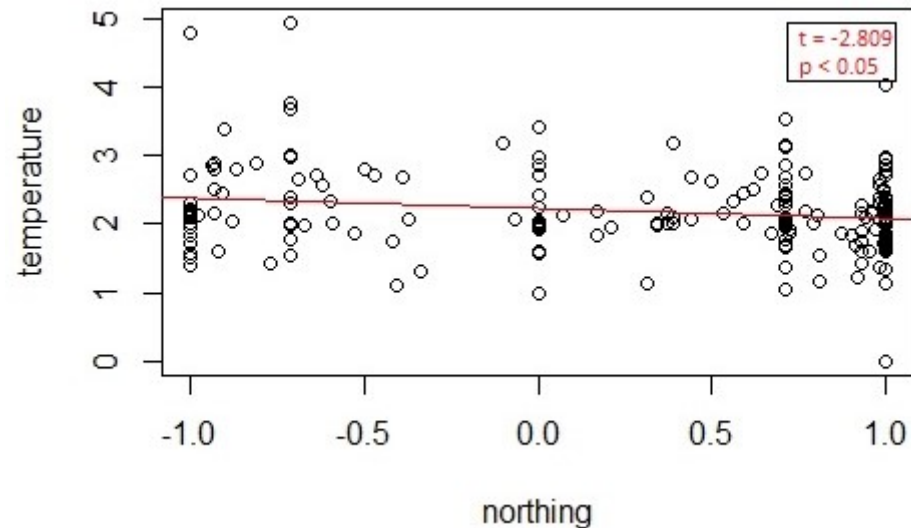


Figure 26: GLM analysis of relationships between northing and EIV T (temperature), red line indicates direction of relationship, red t- and p-values indicate significance of results.

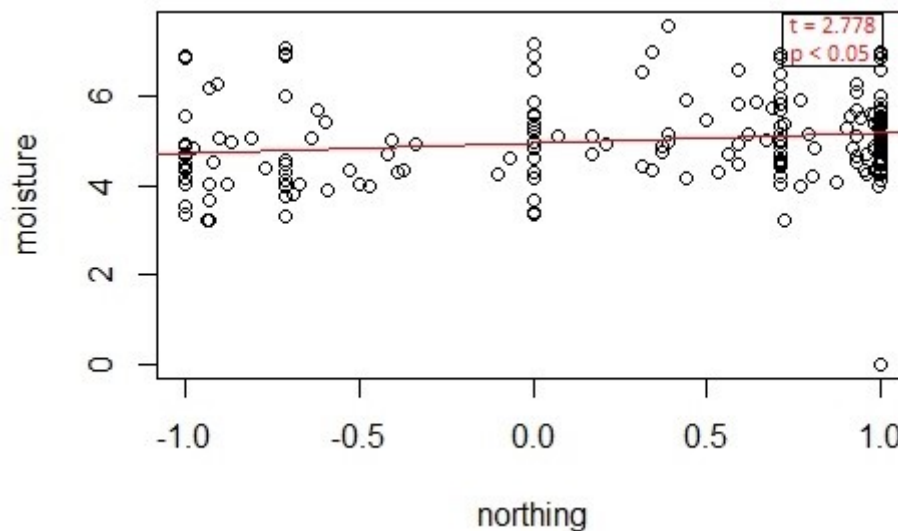


Figure 27: GLM analysis of relationships between northing and EIV M (moisture), red line indicates direction of relationship, red t- and p-values indicate significance of results.

Northing is negatively related to temperature (Figure 26) while a positive relationship with moisture (Figure 27) can be observed.

4.5 Cryptogam Distribution in Relationship to Vascular Plants

Relationships between cryptogam distribution and herb layer are displayed in the following GLM diagrams. Differences between bryophytes and lichens are being inspected.

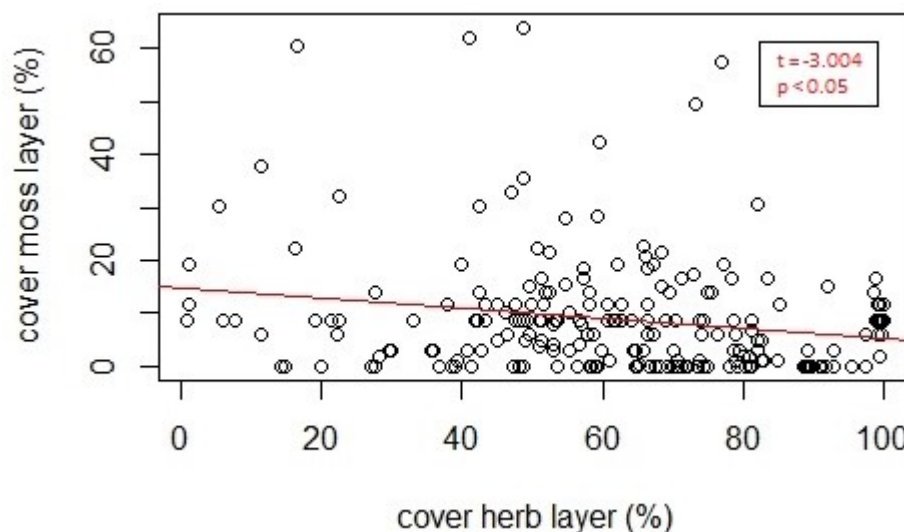


Figure 28: GLM analysis of relationships between relative covers of moss and herb layer, red line indicates direction of relationship, red t- and p-values indicate significance of results.

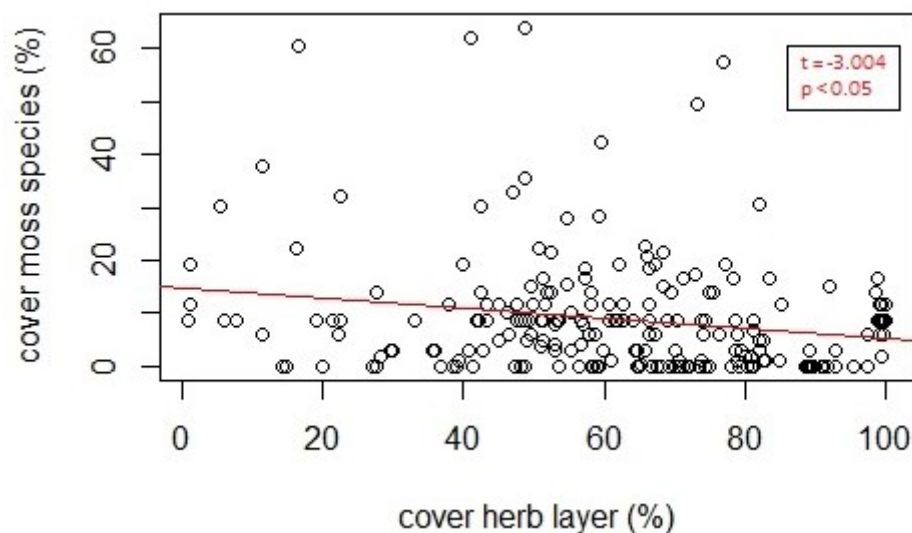


Figure 29: GLM analysis of relationships between) relative covers of bryophyte and herb layer, red line indicates direction of relationship, red t- and p-values indicate significance of results.

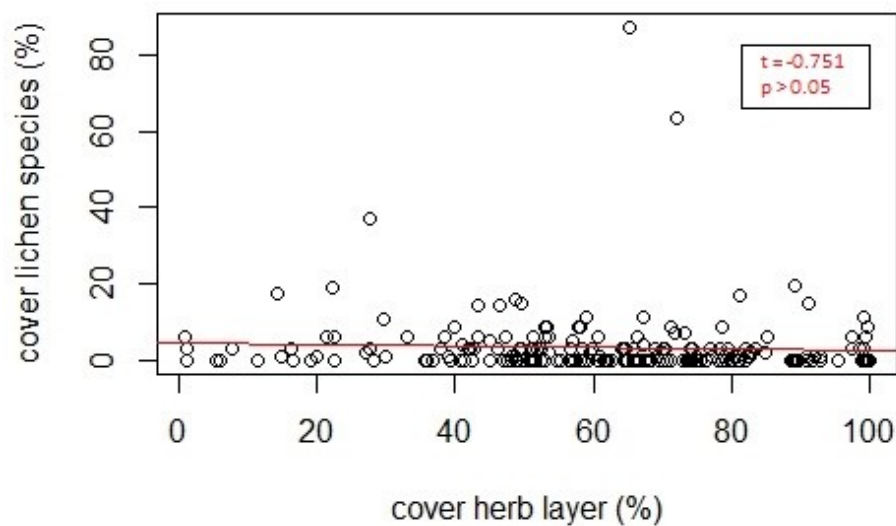


Figure 30: GLM analysis of relationships between relative covers of lichen and herb layer, red line indicates direction of relationship, red t- and p-values indicate significance of results.

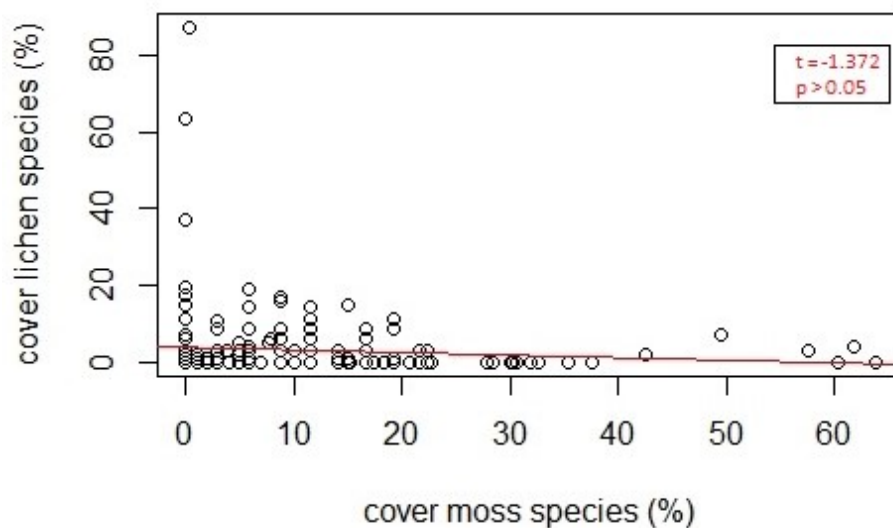


Figure 31: GLM analysis of relationships between relative covers of lichen and bryophytes, red line indicates direction of relationship, red t- and p-values indicate significance of results.

A negative relationship between covers of moss and herb layer can be observed (Figure 28). Separate inspection of mosses and lichens shows the relationship only refers to bryophytes (Figure 29). No relationship can be seen between herbs and lichens (Figure 30). Between bryophyte and lichen covers there is also no relationship (Figure 31).

5. Discussion

5.1 Alpine Grassland Vegetation and the Role of Cryptogams

The seven vegetation Classes were found throughout the Austrian Alps in grasslands above the timberline. Their ecological variability is reflected in the high number of identified Orders (nine), Alliances (thirteen) and Associations (eighteen). Species distribution is strongly affected by differences in altitude and bedrock which is reflected by three identified Classes predominantly occurring on siliceous bedrock (*Caricetea curvulae*, *Salicetea herbaceae*, *Loiseleurio-Vaccinietea*), three on calcareous bedrock (*Asplenietea trichomanis*, *Thlaspietea rotundifolii* and *Seslerietea albicantis*) and one indifferent Class (*Molinio-Arrhenatheretea*). Within the eighteen Associations clear patterns can be identified with regard to cryptogam species distribution. *Campanulo scheuchzeri-Festucum noricae* features the weakest cryptogam layer, surpassed only slightly by *Crepido-Festucetum commutatae*, *Seslerio-Caricetum sempervirentis*, and *Pulsatillo albae-Festucetum variaae*, which include moss as well as lichen species but only in scarce numbers and cover. The fragmentary occurrence of mosses and lichens in these Associations which primarily represent alpine meadows and heathlands rich in grass species suggests a negative relationship of vascular plants and cryptogams. Correlations have been inspected by numerous studies (Löbel et al. 2006; N. Ingerpuu 2002; Zamfir 2000), however, with divergent results. Alpine pastures of *Sieversio-Nardetum strictae* comprise weak cryptogam layers as well, with notably less lichens than bryophytes indicating different ecological preferences and species interactions with vascular plants among the two groups of cryptogams. Interactions between cryptogams and vascular plants are discussed more closely below (5.5). Inspection of *Drabo stellatae-Potentilletum clusianae* too indicates a weakly pronounced moss layer, which is partly attributed to the varying cryptogam occurrences throughout its relevés. As habitats of the typical vegetation of calcareous rock crevices are strongly sun-exposed on summits and sides of mountain ridges in the highest regions of the alpine belt (Grabherr and Mucina 1993), and is predominated by cushion plants, these habitats may not be attracting many bryophytes due to their preference of shade and moisture rich habitats (Berg and Martin 2008). High Alpine snowbed communities of *Arabidetum caeruleae*, *Campanulo pullae-Achilleetum clusianae*, *Polytrichetum sexangularis* and *Salicetum retuso-reticulatae* in contrast feature moss dominated cryptogam layers. Bryophytes benefit from extensive and long-lasting snow covers in these habitats which they utilize as water source for growth and sexual reproductivity (Spitale 2017; Zechmeister et al. 2003). Moss layers of *Potentilletum nitidae*, *Caricetum curvulae* and *Dryadetum octopetalae* on the other hand are dominated by lichen species which is accredited to very limited water and nutrient availability in these habitats. Lichen growth is not well supported by water-logged habitats and short vegetation periods in snowbeds (Fryday 2001). While many lichen species have developed adaptations to extreme sun-exposure and low temperatures at high elevations, these are not effective below a sun-isolating snow cover. By increasing parts of their

thallus to attain darker colouring lichens can warm up faster. Additionally, increased storing of usnic acid and sometimes a crystalline layer serves as protection from strong insolation (Obermayer 1997). Thus, higher lichen diversity can be found in dry and extremely exposed habitats of alpine grasslands. Although water availability is comparatively high within habitats of *Caricetum firmae* Variation with *Primula clusiana*, *Loiseleurio-Cetrarietum* and *Empetro-Vaccinetum gaultherioidis*, their cryptogam layers are lichen dominated too. Due to strong wind and sun exposure, these habitats are depleted of nutrients and hence not suitable for bryophytes. Evidently, bryophyte and lichen distribution is disparately influenced by nutrient and moisture availability, directed by wind and sun exposure. CCAs discussed below emphasize this inference. *Androsacetum alpinae* and *Caricetum firmae* Variation with *Festuca pumila* feature strongly pronounced cryptogam layers, regarding relative cover as well as species numbers. Vegetation communities of these Associations predominantly consist of cryptogam species as their habitats are found up to the highest alpine regions where climatic conditions are too extreme for many vascular plant species. Regarding anthropogenic impact, only one of the documented Classes in this study, *Molinio-Arrhenatheretea*, is defined as anthropogenic vegetation (Mucina, Grabherr, and Ellmauer 1993). However, human pressure (e.g. alpine livestock farming, fertilization) has shaped even the most remote areas of Alpine mountain ranges for millennia which continuously modified species distribution. It is hence uncertain whether the current vegetation is in a natural equilibrium with the Alpine ecosystem (Theurillat and Guisan 2001).

5.2 The role of Environmental Factors in Alpine Cryptogam Distribution

Correspondence Analyses of ecological impacts on cryptogam species indicate that distribution of numerous high alpine cryptogam species occurring in high mountain ranges (Group a) is predominately governed by elevation. The additional relation of *Anthelia juratzkana*, *Pohlia drummondii* and *Polytrichastrum sexangulare* and *Polytrichum juniperinum* with high availability of moisture and low temperatures (Group 1) emphasizes the well documented fact that elevation is essentially equivalent to increasing precipitation and decreasing temperature (Keller, Goyette, and Beniston 2005; Theurillat and Guisan 2001). Accordingly, species of these Groups are most frequently found in high Alpine snowbed communities of *Polytrichetum sexangularis*, while *Lescurea incurvata* is predominantly found in the snowbeds of *Arabidetum caeruleae*. This pattern is also reflected by Group b, where several species are strongly related with altitude and bio.2. Many species, such as *Anthelia juratzkana* are specifically adapted to these extreme habitat conditions. *Ant.jur* developed a wax coating that protects its growth structures from strong light exposure and minimize dehydration (Düll and Düll-Wunder 2012). Such adapted species express optimal photosynthesis rates under the cold and wet conditions in snowbeds (Lösch, Kappen, and Wolf 1983). As opposed to the moisture-requiring bryophytes, lichen distribution of Group a and b is dominated by continentality (Group 6) and low nutrient availability. Concurrently, these species are found in dry, wind- and sun-exposed,

nutrient-depleted habitats with high continentality, such as *Caricetum curvulae*, *Pulsatillo albae*-*Festucetum varia*e and *Loiseleurio-Cetrarietum*. The CCA with EIV shows that alpine lichen distribution is almost exclusively governed by pronounced continentality and lower nutrient levels. Considerable species overlap of Group 6 and d emphasizes the preference of lichens for a rather continental climate, as bio.2 is a marker of thermic continentality, and continental climate is characterized by low precipitation seasonality. On the contrary, most bryophytes prefer low continental influence, meaning an oceanic climate which is correlated with higher moisture availability, mediated by winter precipitation (bio.19). Moreover, their distribution is dominated by higher nutrient availability and soil reaction. This pattern is visible in the overlap of species from Group c with Groups 3, 4 and 5. These cryptogams occur in calciphile Associations such as *Drabo stellatae*-*Potentilletum clusianae* and both *Caricetum firmae* Variations. High moisture availability, low continentality and alkaline bedrock are habitat requirements primarily met in the mountain ranges of the Calcareous and Southern Alps. They are governed by a more oceanic climate than the Central Alps, due to their location at the outer ranges of the Austrian Alps. Correspondence analyses visualize significant differences regarding cryptogam species distribution patterns in alpine mountains. While lichens predominate nutrient-poor, siliceous habitats in highly continental climates, bryophytes are found in habitats with higher nutrient and moisture availability located in climate regions of high oceanity. The opposing relationships of lichens and mosses with regard to various environmental factors shall be inspected more closely in the following chapters.

5.3 Differences in Bryophytes and Lichens in Relation to Environmental Factors

Cryptogams are affected in the same way by bio.2 and continentality as these two factors are correlated, with bio.2 serving as marker for thermic continentality (Berg, Welk, and Jäger 2017). The already inferred opposing effect of continentality on bryophytes and lichens (5.2) can be attributed to their contrasting requirements for physiological and reproductive traits. Available free water in alpine regions, which is in large part correlated with the amount of winter precipitation (bio.19) falling as snow, the extent of snowpack and correlated runoff of melt-water (Beniston 2006) is paramount for sexual reproduction, fully functioning photosynthesis (Lange 2012) and maintaining cell turgor (Goffinet 2008) in bryophytes. Accordingly, bryophytes have a higher capacity for water accumulation than lichens. Hence, water-saturated snowbeds might be among the most important habitats for bryophytes as they provide suitable conditions for alpine mosses over extended periods of time. The rapid water absorbance and loss in lichen physiology on the other hand directly mirrors the moisture conditions of their immediate environment. Thus, a negative correlation between bio.19 and lichens (see 4.3.2) was expected. The lack thereof might be owed to an insufficient sample size. Under air dry conditions lichens arrest their metabolism and low levels of thallus water content are sufficient for them to start respiring. With increasing thallus moisture photosynthesis rates increase slowly until a

certain threshold. Thallus water contents beyond the threshold cause photosynthesis rates to reduce again (Flock 1978). Lichen species therefore avoid habitats with high moisture availability where their physiological properties would be impaired. Ecologists and conservationists widely consider lichens to be of essential importance for montane plant diversity in continental regions and bryophytes in oceanic regions (Fryday 2001). In conclusion, bryophytes are more abundant and diverse in habitats with oceanic climate which can be found in the Calcareous and Southern Alps and lichens are predominant in these with continental climate (Central Alps).

5.4 Influence of Relief on Climate and Species Distribution

It has already been assessed that alpine bryophytes are indicators for cold and moist climatic conditions in montane habitats. These conditions are most strongly pronounced on northern-facing mountain slopes due to low sun exposure. Due to their contrasting habitat preferences of mosses and lichens, the latter group was expected to prefer sun-exposed slopes. However, this preference cannot be confirmed by correlation analysis (Table 8). The smaller sample size of lichens as opposed to bryophytes might be the reason for this result. Regarding vascular plants, a clear preference for warmer temperate mountain slopes and corresponding overall milder climatic conditions as can be seen in Table 8. GLM diagrams in chapter 4.4 display the relationship between relief and climate. Consequently, the significance of montane relief regarding adaptations of alpine plants to climate can be confirmed.

5.5 The Relationship of Alpine Cryptogams and Vascular Plants

Opposing distribution patterns of vascular plants and cryptogam species are not owed to mountain relief alone. The negative relationship between the two plant groups has already been discussed with regard to decreased bryophyte diversity in alpine meadow and heathland communities, which are dominated by herbs and grasses (5.1). In the highest alpine ranges, sun exposure and low temperatures make habitat conditions too extreme for herbs, whereas cryptogams are well adapted to the harsh climatic conditions. As they do not have to fight for resources in these habitats, cryptogams are less competitive than vascular plants. Hence, they are easily replaced by strongly pronounced vascular plant cover (Pauli et al. 2007). The absence of measurable relationships between lichen cover and herbs or bryophytes might be attributed to the comparably low ratio of assessed lichens to bryophytes in most relevés. Pronounced soil depths typical of grasslands may negatively affect cryptogam species richness (Löbel et al. 2006) as cryptogams are known to be pioneer species on inorganic surfaces where they can promote formation of soil. Other authors found (species-specific) positive relationships between cryptogams and vascular plant cover owing to improved microclimate facilitated by vascular plants (Nele Ingerpuu, Liira, and Pärtel 2005). This hypothesis is not supported by results of this study. With ongoing climate change, competitive relations between

vascular plants and cryptogams will play an increasingly important role in governing species distribution patterns.

5.6 Development of Alpine Cryptogam Distribution under Global Warming

Due to global warming, changes in climate from continentality to more oceanic conditions have already been documented over the last decades (Boychenko et al. 2018; Stonevicius, Stankunavicius, and Rimkus 2018). With progressive global warming this trend will likely become stronger. Without regarding competitive influences of vascular plants, bryophyte distribution might be promoted by this development while lichens might suffer under increasing moisture availability in their habitats. However, under continuing global warming, winter precipitation will increasingly fall as rain instead of snow. Decreasing snow cover extent and duration (Rogora et al. 2018; Lamprecht et al. 2018) will likely decrease bryophyte distribution ranges and diversity and promote lichens in the highest alpine mountain systems. Cryptogams (especially bryophytes) living in alpine snowbed habitats might be affected most strongly by decreased precipitation as snow as these species are adapted to or even depend on persistent snow covers. Moreover, increased temperatures and less extensive snowpack in winter negatively affects water availability in the warmer months due to earlier snow-melt and a decrease in runoff of melt-water (Beniston 2012). Thus, cryptogams who are adapted to extreme alpine habitat conditions may rather be negatively affected by an increasingly mild climate while herbs possibly benefit from these changes (see 5.5). Due to their poikilohydric nature, cryptogams might be even more endangered by growing water deficits on mountains due to climate warming (Lloret and González-Mancebo 2011). Bryophytes may have an advantage over lichens in this regard as they are not dependent on light and might hence longer find suitable habitats on north-exposed mountain slopes. Pronounced habitat diversity in alpine ranges can thus help certain montane plants evade the effects of climate change a little longer. However, when temperatures rise to a point where northern-facing mountain slopes become warmer as well, in the long term, bryophytes might be more endangered than lichens due to their adaptation to cold climatic conditions. With increasing temperatures and precipitation as rain instead of snow, Evju and Bruteig (2013) hypothesize that lichen growth might even be promoted. Changes in snow cover can additionally have significant effects on winter and annual nutrient dynamics (Farrer et al. 2015) further changing current habitat conditions and inter-specific relationships (Evju and Bruteig 2013). Decreasing snow covers and overall milder climatic conditions in alpine regions would extend growing seasons which also promotes plants from lower elevations to shift upwards to now suitable habitats (Pauli et al. 2007; Lamprecht et al. 2018). Thus, high alpine species which typically do not need to compete for resources due to their adaptations to extreme montane habitat conditions, are progressively being replaced by low-land species (Rumpf et al. 2018; Pauli et al. 2007). As vascular plants predominate sun-exposed mountain slopes, lichens might be affected first by these changes. With time, the increasing vegetation cover of

vascular plants in high montane ranges will inevitably lead to a decline or even disappearance of the less competitive alpine cryptogams (Gottfried et al. 2012).

6. Summary and Conclusions

6.1 Cryptogam Distribution in Alpine Grassland Vegetation

Cryptogams strongly contribute to the species diversity and vegetation cover in Alpine vegetation. They are found throughout all grassland communities recognized in high mountain ranges. Divergent habitat preferences of bryophytes who predominate moisture saturated snowbeds and lichens who predominate dry rocky grasslands lead to the conclusion that moist and dry Alpine habitats are essential for alpine cryptogam diversity and distribution. Statistical analyses demonstrate the divergent climatic and habitat requirements of bryophytes and lichens. It has been confirmed that bryophyte distribution in alpine grasslands is driven by higher moisture and nutrient availability correlated with oceanic climate, conditions predominant in the Calcareous and Southern Alps, and especially on northern-facing slopes. Lichens are governed by dry, sun- and wind-exposed habitat conditions in more continental climates which can be found in the Central Alps and on sun-exposed mountain slopes. Hence, pronounced habitat diversity of high mountain systems is essential. Furthermore, the extent of cryptogam distribution ranges in alpine grasslands is endangered by an increasing vascular plant cover as alpine phanerogams are competitively stronger than bryophytes and lichens. In the light of current climate change these findings stress the importance of understanding ecological implications for alpine cryptogam distribution.

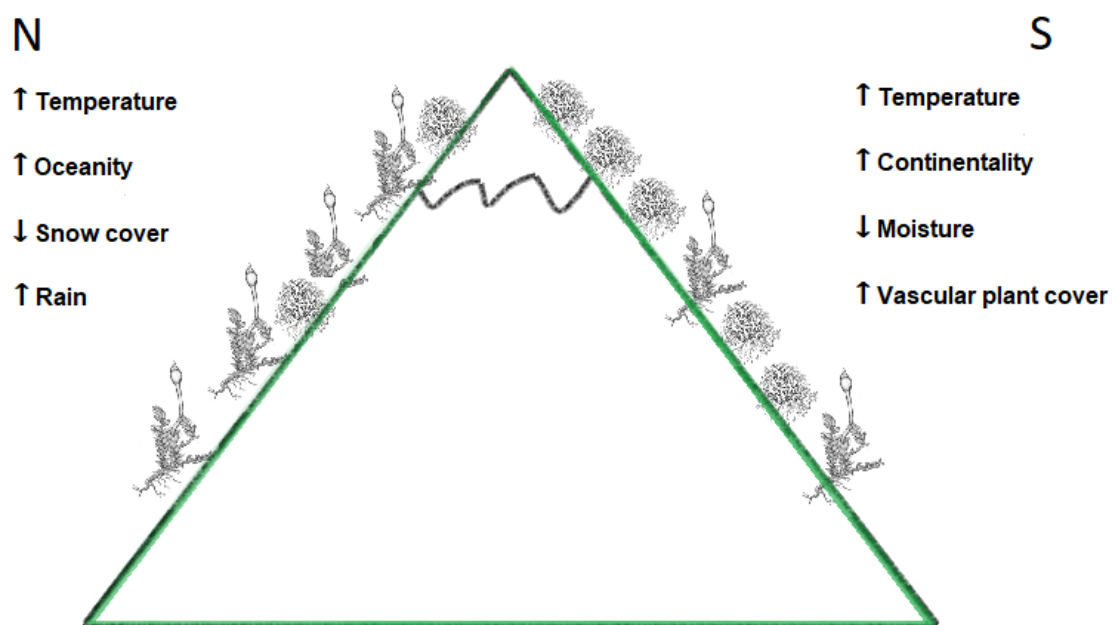


Figure 32: Graphical representation of ecological changes on northern (N) and southern (S) mountain slopes; bryophyte design from Seppelt and Stone 2016, lichen design from Harrison 2015

6.2 Climate Change Impact on Alpine Bryophyte and Lichen Distribution

Progressive increase of temperature as well as precipitation falling as rain instead of snow, decreasing snow cover duration (Niittynen, Heikkinen, and Luoto 2018) and earlier snowmelt time (Carbognani, Tomaselli, and Petraglia 2014) in alpine habitats will alter habitat conditions not only for cryptogams but also for vascular plants and will thus lead to changes in community composition and inter-specific relationships. Consequent upward-shifts of phanerogams endanger already limited cryptogam distribution ranges in the highest mountain ranges and, with time, might replace bryophytes and lichens in large part. Understanding the general and species-specific implications of these changes on bryophytes and lichens is of fundamental importance in alpine mountain systems in order to implement conservation measurements accordingly to the changing climate.

6.3 Future Outlook

The results of this study provide an analysis of the current state of alpine cryptogam distribution and may henceforth be used to construct predictive models on future developments of bryophyte and lichen distribution in response to changing climate and habitat conditions in the Austrian Alps. Computation of SDMs (species distribution models) can help predict potential responses of cryptogam distribution to global warming. Presence/absence data of selected species can thus be modelled in relation to ecological parameters to project distributions under future climatic scenarios (Engler et al. 2011). With this information, cryptogams which might be especially indicative or endangered regarding climate changes can be used to monitor future developments of bryophytes and lichens in the Austrian Alps.

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10. Appendix

Table 9: Percentage synoptic table of vascular plants and cryptogams, full version

Percentage synoptic table			Total frequency	Ass.																	
No. of Relevés	Abbr.	Herb layer		Ass. 1	Ass. 2	Ass. 3	Ass. 4	Ass. 5	Ass. 6	Ass. 7	Ass. 8	Ass. 9	Ass. 10	Ass. 11	Ass. 12	Ass. 13	Ass. 14	Ass. 15	Ass. 16	Ass. 17	Ass. 18
				36	22	6	16	68	14	24	8	14	22	12	87	107	20	61	15	26	14
Crepis alpestris	Cre.alp	84	81	0	0	0	29	0	0	0	0	0	0	2	0	0	54	0	0	0	
Potentilla crantzii	Pot.cra	46	61	0	0	0	4	0	0	0	0	0	0	7	0	0	23	7	0	0	
Luzula sudetica	Luz.sud	30	47	0	0	0	0	0	0	0	0	9	0	0	0	11	0	8	14		
Crepis aurea	Cre.aur	30	39	0	0	19	4	0	0	0	0	5	17	1	0	5	5	7	4	0	
Alchemilla glabra	Alc.gla	18	28	0	0	0	0	0	0	0	0	0	8	0	0	11	0	0	0		
Potentilla clusiana	Pot.clu	61	3	77	0	0	0	0	0	0	0	0	0	3	37	0	0	0	0		
Draba stellata	Dra.ste	12	0	50	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
Campanula cochleariifolia	Cam.coc	12	0	27	0	0	1	0	0	0	0	5	0	0	3	0	0	7	0		
Saxifraga oppositifolia	Sax.opp	14	6	23	0	0	0	14	0	0	0	0	0	1	4	0	0	0	0		
Potentilla nitida	Pot.nit	5	0	0	83	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Primula auricula	Pri.aur	28	0	23	83	0	0	0	0	0	0	0	0	2	14	5	0	0	0		
Carex mucronata	Car.muc	8	0	0	83	0	0	0	0	0	0	0	0	0	2	0	0	7	0		
Saxifraga caesia	Sax.cae	22	0	14	33	0	0	0	0	0	0	0	0	1	14	5	0	0	0		
Achillea atrata agg.	Ach.atr.agg	34	3	0	0	56	25	7	0	0	0	0	8	0	2	0	5	0	0		
Pritzelago alpina	Pri.alp	29	0	5	0	69	24	0	0	0	0	0	0	1	0	0	0	0	0		
Saxifraga androsacea	Sax.and	24	0	0	0	63	6	36	8	0	0	0	8	0	1	5	0	0	0		
Soldanella austriaca	Sol.aus	15	0	5	0	38	7	0	0	0	0	0	0	2	1	0	0	0	0		
Veronica alpina ssp. pumila	Ver.alp	5	0	0	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0		
Arabis alpina	Ara.alp	10	0	0	0	31	7	0	0	0	0	0	0	0	0	0	0	0	0		
Potentilla brauneana	Pot.bra	11	0	0	0	31	3	7	0	0	0	0	8	0	0	2	7	0	0		
Arabis bellidifolia s.str.	Ara.bel	10	0	0	0	31	6	7	0	0	0	0	0	0	0	0	0	0	0		
Moehringia ciliata	Moe.cil	20	3	0	0	31	18	7	0	0	0	0	0	0	0	0	7	0	0		
Arabis caerulea	Ara.cae	4	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0		
Saxifraga stellaris ssp. robusta	Sax.ste.rob	5	0	5	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0		
Carex ornithopodoides	Car.orn	8	3	0	0	13	0	0	0	0	0	0	0	2	2	0	2	0	0		
Alchemilla anisiaca	Alc.ani	3	0	0	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0		
Campanula pulla	Cam.pul	60	0	0	0	25	74	0	0	0	0	0	0	2	1	0	5	0	0		
Achillea clusiana	Ach.clu	54	6	0	0	13	65	0	0	0	0	0	0	2	0	0	7	0	0		
Salix retusa	Sal.ret	104	28	5	0	25	28	64	25	13	14	0	0	14	9	40	21	7	23		
Salix reticulata	Sal.ret2	24	0	0	0	0	1	57	0	13	7	0	0	6	4	10	2	0	4		
Doronicum glaciale	Dor.gla	13	3	0	0	0	1	36	13	0	0	0	0	0	2	5	0	0	0		
Pedicularis oederi	Ped.oed	13	0	0	0	0	0	36	8	13	0	0	0	0	0	10	2	0	8		
Carex fuliginosa	Car.ful	7	0	0	0	0	0	29	4	0	0	0	0	0	0	5	0	0	4		
Saxifraga bryoides	Sax.bry	16	0	0	0	0	0	63	13	0	0	0	0	0	0	0	0	0	0		
Phyteuma globulariifolium	Phy.glo	19	0	0	0	0	0	7	63	38	0	0	0	0	0	0	0	0	0		
Minuartia sedoides	Min.sed	80	6	14	0	19	10	14	50	0	0	0	0	22	22	5	11	0	0		
Poa laxa	Poa.lax	5	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0		
Cerastium uniflorum	Cer.uni	7	0	0	0	13	0	0	21	0	0	0	0	0	0	0	0	0	0		
Carex curvula	Car.cur	24	3	0	0	0	0	7	4	63	7	9	17	0	0	0	0	0	38		
Festuca varia	Fes.var	21	0	0	0	0	0	0	13	0	100	5	0	0	0	0	0	0	8		
Pulsatilla alpina s.lat.	Pul.alp	25	0	0	0	0	0	0	0	13	79	23	0	0	0	0	3	0	19		
Leontodon helveticus	Leo.hel	60	0	5	0	0	3	0	4	38	64	100	17	0	0	20	2	0	42		
Anthoxanthum alpinum	Ant.alp	52	42	0	0	0	3	7	4	13	21	68	0	3	0	0	13	7	4		
Potentilla aurea	Pot.aur	38	19	0	0	0	4	0	0	0	7	64	25	1	0	15	3	13	4		
Nardus stricta	Nar.str	40	42	0	0	0	0	7	0	0	0	59	25	0	0	5	3	0	8		
Geum montanum	Geu.mon	19	0	0	0	0	0	0	0	0	14	55	25	0	0	2	0	4	0		
Deschampsia cespitosa	Des.ces	23	0	5	0	6	3	7	0	0	14	45	0	1	0	0	3	7	4		
Campanula barbata	Cam.bar	12	0	0	0	0	0	0	4	25	7	36	0	0	0	0	0	0	0		
Gnaphalium supinum	Gna.sup	24	0	5	0	0	1	0	8	13	0	27	100	0	0	0	0	7	0		
Arenaria biflora	Are.bif	13	0	5	0	0	0	0	0	13	0	0	92	0	0	0	0	0	0		
Polytrichastrum sexangulare	Pol.sex	11	0	5	0	0	0	0	0	0	0	5	75	0	0	0	0	0	0		
Sibbaldia procumbens	Sib.pro	14	0	0	0	1	7	0	13	0	5	75	0	0	0	0	7	0	0		
Veronica alpina	Ver.alp	21	0	0	0	19	9	0	0	13	0	14	67	0	0	0	0	0	0		
Pohlia drummondii	Poh.dru	8	0	0	0	0	0	0	0	0	0	0	67	0	0	0	0	0	0		
Salix herbacea	Sal.her	18	0	0	0	0	1	0	21	38	0	5	58	0	0	0	0	0	4		
Taraxacum sect. Alpina	Tar.sec.Alp	10	0	0	0	19	1	0	0	0	0	0	50	0	0	0	0	0	0		
Polytrichum juniperinum	Pol.jun	27	6	0	0	0	1	7	4	13	0	23	50	2	0	10	2	7	8		
Cerastium cerastoides	Cer.cer	8	0	0	0	0	3	0	0	13	0	0	42	0	0	0	0	0	0		
Primula clusiana	Pri.clu	116	3	0	0	6	4	0	0	0	0	0	0	70	33	5	23	0	0		
Chamorchis alpina	Cha.alp	30	6	0	0	0	0	7	0	0	0	0	0	22	2	5	8	0	0		
Carex firma	Car.fir	240	3	50	0	25	28	7	0	0	0	0	0	94	85	40	38	0	0		
Festuca pumila	Fes.pum	157	22	27	0	0	32	50	4	0	0	0	0	47	44	40	25	0	8		
Dryas octopetala	Dry.oct	244	36	9	0	0	7	36	8	50	0	0	0	93	72	100	56	0	4		
Sesleria varia agg.	Ses.var.agg	43	6	0	0	6	3	36	0	0	0	0	0	10	7	80	2	0	0		
Vaccinium uliginosum	Vac.uli	20	0	5	0	0	0	0	0	0	7	5	0	2	0	55	0	0	12		
Bartsia alpina	Bar.alp	74	6	0	0	6	1	21	0	25	7	5	0	39	5	50	20	0	4		
Rhododendron hirsutum	Rho.hir	38	3	0	0	0	1	7	0	0	0	0	0	13	3	40	15	13	4		
Anthoxanthum odoratum agg.	Ant.odo.agg	15	0	0	0	0	0	0	0	0	14	17	0	0	30	0	0	12	7		
Carex sempervirens	Car.sem	160	25	9	0	6	46	29	0	25	43	14	0	29	10	25	80	27	12		
Sesleria albicans	Ses.alb	152	22	9	0	6	28	7	0	0	0	0	0	43	24	0	89	27	0		
Festuca norica	Fes.nor	9	0	0	0	0	1	7	0	0	0	0	0	0	0	0	0	47	0		
Carduus defloratus s.lat.	Car.def	29	3	0	0	0	10	0	0	0	0	0	0	2	1	0	20	40	0		
Carlina acaulis	Car.aca	9	3	0	0	0	0	0	0	0	0	0	0	1	0	0	3	33	0		
Trifolium pratense	Tri.pra	18	19	5	0	0	1	0	0	0	0	0	0	0	2	0	5	27	0		
Helictotrichon parlatorei	Hel.par	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	27	0		
Silene vulgaris	Sil.vul	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0		
Senecio abrotanifolius	Sen.abr	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	20	0		
Loiseleuria procumbens	Loi.pro	75	0	0	0	0	0	0	0	38	14	9	0	20	3	30	10	0	100		

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Cladonia arbuscula	Cla.arb	28	0	5	0	0	0	14	21	0	7	14	0	0	0	5	2	0	12	79
Vaccinium myrtillus	Vac.myr	38	11	5	0	0	0	0	0	13	29	36	0	1	0	0	7	0	19	71
Empetrum hermaphroditum	Emp.her	10	0	0	0	0	0	0	0	7	0	0	3	2	0	0	0	0	29	0
Cladonia gracilis	Cla.gra	9	0	0	0	0	0	8	0	0	0	0	0	0	0	2	0	8	29	0
Paraleucobryum nerve	Par.ene	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0
Betonica alopecuroides	Bet.alo	7	0	0	0	0	0	0	0	0	0	0	1	0	0	7	13	0	0	0
Agrostis schradleriana	Agr.sch	20	36	0	0	0	1	0	0	0	0	0	0	0	0	10	0	0	0	0
Thymus praecox agg.	Thy.pra.agg	13	22	0	0	0	1	7	0	0	0	0	0	0	0	5	0	0	0	0
Galium anisophyllum	Gal.ani	83	42	5	0	0	24	21	0	0	14	5	0	8	7	5	38	33	8	0
Ranunculus montanus agg.	Ran.mon.agg	40	25	5	0	19	9	0	0	13	14	9	0	2	2	5	11	27	0	0
Campanula scheuchzeri	Cam.sch	177	81	5	0	38	38	14	17	25	36	36	0	38	8	15	59	47	12	21
Gentianella germanica agg.	Gen.ger.agg	74	22	5	0	6	19	14	0	0	0	0	0	16	8	0	43	0	0	0
Homogyne discolor	Hom.dis	130	58	0	0	6	28	29	0	0	7	9	8	34	0	10	67	13	19	7
Saxifraga paniculata	Sax.pan	27	3	27	0	6	0	14	13	0	0	0	3	8	5	2	0	0	0	0
Trisetum alpestre	Tri.alp	9	0	23	17	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Festuca alpina	Fes.alp	12	0	23	17	0	6	0	0	0	0	0	0	2	0	0	0	0	0	0
Paederota bonarota	Pae.bon	4	0	0	67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Achillea clavennae	Ach.cla	20	0	18	50	0	0	0	0	0	0	0	0	10	0	2	7	0	0	0
Sesleria sphaerocephala	Ses.sph	4	0	0	50	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Saxifraga squarrosa	Sax.squ	2	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Valeriana saxatilis	Val.sax	12	0	0	33	0	1	0	0	0	0	0	1	7	0	0	0	0	0	0
Kernera saxatilis	Ker.sax	3	0	0	33	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gnaphalium hoppeanum	Gna.hop	50	3	5	0	31	53	7	0	0	0	0	3	0	0	3	7	0	0	0
Saxifraga aizoides	Sax.aiz	58	0	14	0	25	38	29	0	0	0	0	7	10	0	7	0	0	0	0
Poa minor	Poa.min	23	0	5	0	0	29	0	0	0	0	0	0	0	0	2	7	0	0	0
Veronica aphylla	Ver.aph	24	0	0	0	0	24	29	0	0	0	0	1	5	0	7	0	0	0	0
Carex parviflora	Car.par	34	3	0	0	31	22	0	0	0	0	0	9	0	0	8	0	0	0	0
Silene pusilla ssp. pusilla	Sil.pus.pus	24	0	5	0	25	21	14	0	0	0	0	1	0	0	3	0	0	0	0
Sedum atratum	Sed.atr	24	3	0	0	13	26	0	0	0	0	0	1	1	0	0	7	0	0	0
Viola biflora	Vio.bif	43	3	0	0	19	37	7	0	0	0	5	0	1	0	35	2	20	0	0
Senecio carniolicus	Sen.car	20	0	0	0	0	0	63	25	0	0	0	0	0	0	0	0	8	7	0
Ranunculus alpestris agg.	Ran.alp.agg	155	8	23	0	94	54	43	25	0	0	8	30	31	65	16	0	0	0	0
Campanula alpina	Cam.alp	42	3	0	0	0	7	17	75	7	0	10	5	0	2	0	46	14	0	0
Pedicularis verticillata	Ped.ver	26	0	0	0	10	7	17	25	0	0	7	3	5	2	0	4	0	0	0
Salix serpyllifolia	Sal.ser	25	6	0	0	0	0	13	25	0	0	2	8	30	2	0	0	0	0	0
Phyteuma hemisphaericum	Phy.hem	12	0	0	0	0	0	0	25	21	0	0	2	0	0	0	12	14	0	0
Valeriana celtica ssp. norica	Val.cel.nor	45	6	0	0	0	7	33	75	5	0	3	0	5	2	7	42	14	0	0
Avenella flexuosa	Ave.fle	16	0	0	0	0	0	0	0	14	36	17	0	0	0	0	15	0	0	0
Festuca picturata	Fes.pic	25	3	5	0	0	0	4	0	43	68	0	0	0	0	7	0	0	0	0
Leucanthemopsis alpina	Leu.alp	22	0	5	0	0	0	33	0	21	27	8	0	0	0	0	12	0	0	0
Sagina saginoides	Sag.sag	16	3	0	0	25	3	0	0	13	0	67	0	0	0	0	0	0	0	0
Phleum rhaeticum	Phl.rha	18	17	0	0	0	1	0	0	0	9	50	0	0	3	7	0	0	0	0
Cardamine alpina	Car.alp	5	0	0	0	0	0	0	0	0	0	42	0	0	0	0	0	0	0	0
Poa annua	Poa.ann	6	0	0	0	0	0	4	13	0	0	33	0	0	0	0	0	0	0	0
Soldanella pusilla	Sol.pus	26	0	5	0	13	0	4	13	7	45	75	0	0	0	0	0	0	7	0
Saussurea pygmaea	Sau.pyg	53	0	0	0	0	0	0	0	0	0	29	26	0	0	0	0	0	0	0
Gentiana clusii	Gen.clu	52	0	0	17	0	0	0	0	0	0	24	17	40	7	0	0	0	0	0
Crepis terglouensis	Cre.ter	64	0	0	0	6	0	0	0	0	0	18	40	0	2	0	0	0	0	0
Nocca crantzi	Noc.cra	45	6	0	0	26	0	0	0	0	0	10	0	0	26	0	0	0	0	0
Anthyllis vulneraria ssp. alpicola	Ant.vul.alp	32	0	0	0	6	6	0	0	0	0	7	2	25	21	0	4	0	0	0
Lotus corniculatus agg.	Lot.cor.agg	38	19	0	0	4	0	0	0	0	0	2	2	0	25	60	0	0	0	0
Heracleum austriacum	Her.aus	14	6	0	0	0	1	0	0	0	0	1	0	0	7	40	0	0	0	0
Helianthemum glabrum	Hel.gla	22	3	9	0	0	1	0	0	0	0	2	6	0	7	40	0	0	0	0
Knutia maxima	Kna.max	17	0	0	0	0	1	0	0	0	0	1	0	0	15	40	0	0	0	0
Carex ferruginea	Car.fer	24	8	0	0	0	12	0	0	0	0	0	2	4	0	3	33	0	0	0
Rumex scutatus	Rum.scu	3	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0
Meum athamanticum	Meu.ath	13	3	0	0	6	0	0	0	0	0	1	2	0	8	20	0	0	0	0
Hieracium sp.	Hie.sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0
Thymus pulegioides	Thy.pul	17	6	14	0	0	0	0	0	7	5	0	1	5	0	2	20	0	0	0
Leontodon hispidus	Leo.his	27	3	0	0	6	0	4	0	21	0	5	0	5	8	53	0	0	0	0
Huperzia selago	Hup.sel	23	0	0	0	0	0	29	13	0	7	5	0	5	0	2	0	23	14	0
Cetraria islandica	Cet.isl	198	25	0	0	3	43	50	50	32	0	72	24	85	20	0	85	79	0	0
Vaccinium gaultherioides	Vac.gau	54	0	0	0	1	0	38	7	9	0	14	2	0	10	0	54	93	0	0
Vaccinium vitis-idaea	Vac.vit	141	31	0	0	0	1	14	13	38	50	9	0	55	9	65	26	0	62	64
Hieracium alpinum	Hie.alp	29	0	0	0	0	0	8	25	7	23	0	1	0	0	0	50	36	0	0
Cladonia rangiferina	Cla.ran	40	0	0	0	0	0	4	38	29	9	8	1	5	30	0	46	36	0	0
Saponaria pumila	Sap.pum	23	0	0	0	0	0	38	38	14	0	0	0	0	0	0	31	7	0	0
Pulsatilla alpina ssp. alba	Pul.alp.alb	15	0	0	0	0	0	4	25	0	0	17	0	0	2	0	23	21	0	0
Cetraria cucullata	Cet.cuc	39	3	0	17	0	0	29	17	25	0	0	10	7	5	2	0	23	14	0
Achillea millefolium	Ach.mil	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0
Achillea moschata	Ach.mos	2	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0
Acinos alpinus	Aci.alp	4	0	0	0	0	0	0	0	0	0	0	0	2	0	0	13	0	0	0
Aconitum napellus agg.	Aco.nap.agg	2	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Aconitum sp.	Aco.sp.	1	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0
Aconitum tauricum	Aco.tau	2	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Adenostyles alliariae	Ade.all	3	0	0	0	3	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Adenostyles glabra	Ade.gla	3	0	0	0	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis agrostiflora	Agr.agr	5	3	0	0	0	0	0	0	14	9	0	0	0	0	0	0	0	0	0
Agrostis alpina agg.	Agr.alp.agg	155	42	0	0	6	29	0	4	0	5	0	60	22	35	52	0	4	7	0
Agrostis capillaris	Agr.cap	3	0	0	0	0	0	0	0	9	0	0	0	0	2	0	0	0	0	0
Agrostis rupestris	Agr.rup	47	3	0	0	6	4	7	17	25	14	36	42	0	10	0	46	43	0	0
Agrostis stolonifera	Agr.sto	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Ajuga pyramidalis	Aju.pyr	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Alcea sp.	Alc.sp.	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alchemilla alpigena	Alc.alp	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Alchemilla conjuncta agg.	Alc.con.agg	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alchemilla hoppeana	Alc.hop	6	0	0	0	4	0	0	0	0	0	0	0	0	2	13	0	0	0	0
Alchemilla sp.	Alc.sp.	6	0	0	0	3	0	0	0	0	0	0	0	0	3	13	0	0	0	0

Impact of Selected Ecological Factors on Cryptogam Distribution in the Austrian Alps

[illegible]

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Euphrasia minima agg.	Eup.min.agg	61	19	0	0	0	4	29	17	38	21	41	42	0	10	5	2	0	23	29
Euphrasia officinalis agg.	Eup.off.agg	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrasia officinalis ssp. picta	Eup.off.pic	5	3	0	0	0	1	0	4	0	0	0	0	0	0	0	2	7	0	0
Euphrasia officinalis ssp. rostkoviana	Eup.off.ros	2	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0
Euphrasia rostkoviana	Eup.ros	5	8	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Euphrasia salisburgensis	Eup.sal	186	28	5	0	25	44	29	0	0	0	0	0	54	48	20	52	20	0	0
Euphrasia sp.	Eup.sp.	6	0	0	0	0	0	0	0	0	9	0	1	3	0	0	0	0	0	0
Festuca nigrescens	Fes.nig	10	0	0	0	0	0	7	0	0	14	9	0	1	0	20	0	0	0	0
Festuca pseudodura	Fes.pse	24	8	0	0	0	0	14	29	38	7	0	0	0	3	0	2	0	8	14
Festuca pulchella	Fes.pul	6	0	0	0	0	1	0	0	0	0	0	2	2	0	0	0	7	0	0
Festuca rubra agg.	Fes.rub.agg	2	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	4	0
Festuca rupicaprina	Fes.rup	81	36	5	0	6	53	14	0	0	0	0	0	13	4	0	21	0	0	0
Festuca sp.	Fes.sp.	9	0	0	0	0	1	0	0	13	7	0	0	0	5	0	2	0	0	0
Festuca supina	Fes.sup	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Festuca versicolor	Fes.ver	10	0	18	0	0	1	0	0	0	0	0	0	5	0	0	0	0	0	0
Festuca versicolor ssp. brachystachys	Fes.ver.bra	2	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Festuca violacea agg.	Fes.vio.agg	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
Galeobdolon flavidum	Gal.fla	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0
Galium noricum	Gal.nor	128	6	0	0	31	46	14	0	0	0	0	0	53	21	5	28	7	0	0
Galium sp.	Gal.sp.	2	0	0	0	0	0	0	0	0	7	0	0	0	0	0	2	0	0	0
Genista germanica	Gen.ger	4	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Gentiana acaulis	Gen.aca	8	0	0	0	0	0	0	0	0	14	0	0	0	10	0	0	8	7	0
Gentiana bavarica	Gen.bav	23	0	0	0	19	15	0	0	0	0	0	2	4	10	3	0	0	0	0
Gentiana brachyphylla	Gen.bra	3	0	0	0	0	0	7	0	0	0	0	0	1	0	2	0	0	0	0
Gentiana frigida	Gen.fri	4	0	0	0	0	0	7	8	0	0	0	0	0	5	0	0	0	0	0
Gentiana nivalis	Gen.niv	11	3	0	0	0	1	14	0	13	0	0	3	1	0	2	7	0	0	0
Gentiana orbicularis	Gen.orb	6	0	0	0	13	3	0	0	0	0	0	0	0	2	0	0	0	0	0
Gentiana pannonica	Gen.pan	5	3	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	14
Gentiana pumila	Gen.pum	21	6	0	0	0	9	14	0	0	0	0	7	2	0	5	0	0	0	0
Gentiana punctata	Gen.pun	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
Gentiana sp.	Gen.sp.	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Gentiana verna	Gen.ver	18	0	0	0	0	3	0	0	0	0	0	1	9	25	0	0	0	0	0
Gentianella anisodonta	Gen.ani	3	0	0	0	0	0	7	0	0	0	0	0	0	0	0	7	4	0	0
Gentianella aspera	Gen.asp	8	3	0	0	6	0	0	0	0	0	0	1	4	0	2	0	0	0	0
Gentianella austriaca	Gen.aus	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Gentianella campestris	Gen.cam	3	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0
Geranium sylvaticum	Ger.syl	4	3	0	0	0	0	0	0	0	0	0	0	0	0	2	13	0	0	0
Globularia nudicaulis	Glo.nud	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	13	0	0
Gymnadenia conopsea	Gym.con	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	13	0	0	0
Gypsophila repens	Gyp.rep	7	0	9	17	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Hedysarum hedysaroides ssp. hedysaroides	Hed.hed.hed	36	0	9	0	0	0	21	4	13	14	0	0	5	13	20	7	0	4	0
Helianthemum alpestre agg.	Hel.alp.agg	185	19	23	50	6	24	36	0	0	0	0	0	56	61	30	46	0	0	0
Helianthemum nummularium agg.	Hel.num.agg	6	11	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Helianthemum ovatum	Hel.ova	2	0	0	17	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Helleborus niger	Hel.nig	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Hieracium bifidum	Hie.bif	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Hieracium glaciale	Hie.gla	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	7	0
Hieracium humile	Hie.hum	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hieracium intybaceum	Hie.int	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Hieracium lactucella	Hie.lac	2	0	0	0	0	0	0	0	7	5	0	0	0	0	0	0	0	0	0
Hieracium pilosella	Hie.pil	2	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0
Hieracium valdepiilosum	Hie.val	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium villosum	Hie.vil	7	0	0	0	0	1	0	0	0	0	0	0	2	0	7	0	0	0	0
Hippocrepis comosa	Hip.com	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Homogyne alpina	Hom.alp	72	28	0	0	0	1	0	0	13	29	77	17	3	0	45	10	0	46	50
Hypericum maculatum s.str.	Hyp.mac	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Hypericum perforatum	Hyp.per	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus jacquinii	Jun.jac	3	0	0	0	0	0	7	0	13	0	0	0	1	0	0	0	0	0	0
Juncus monanthos	Jun.mon	24	6	0	0	6	7	7	0	13	0	0	0	1	0	20	7	0	0	0
Juncus trifidus	Jun.tri	38	0	0	0	0	0	8	25	29	32	0	0	2	0	2	0	58	36	0
Juncus triglumis	Jun.tri2	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
Juniperus communis ssp. alpina	Jun.com.alp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Juniperus communis ssp. nana	Jun.com.nan	2	0	0	0	0	0	0	0	7	0	0	0	0	0	0	7	0	0	0
Kobresia myosuroides	Kob.myo	8	3	0	0	0	0	7	0	0	0	0	0	2	2	10	0	0	0	0
Kobresia simpliciuscula	Kob.sim	4	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0
Larix decidua	Lar.dec	10	6	0	0	0	0	0	0	0	0	0	3	1	0	5	7	0	0	0
Leontodon autumnalis	Leo.aut	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Leontodon montanus	Leo.mon	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Leontopodium alpinum	Leo.alp	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Leucanthemum atratum agg.	Leu.atr.agg	33	8	0	0	0	15	0	0	0	0	0	1	2	0	21	27	0	0	0
Ligusticum mutellina	Lig.mut	104	61	0	0	19	32	0	0	0	14	36	50	5	1	5	52	7	4	7
Ligusticum mutellinoides	Lig.mut2	14	6	0	0	0	3	7	4	13	0	5	0	1	2	0	2	13	0	0
Lilium martagon	Lil.mar	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Linaria alpina	Lin.alp	4	0	0	0	0	1	7	0	0	0	0	0	2	0	0	0	0	0	0
Linum alpinum	Lin.alp	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	7	0	0	0
Linum catharticum	Lin.cat	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Lloydia serotina	Llo.ser	9	0	0	0	0	0	21	13	13	0	0	0	0	5	0	0	0	0	7
Luzula alpina	Luz.alp	10	0	0	0	0	0	4	0	14	9	0	1	1	0	2	0	4	7	0
Luzula alpinopilosa	Luz.alp2	35	0	5	0	0	0	14	25	0	29	59	33	0	0	5	0	0	8	14
Luzula campestris	Luz.cam	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Luzula glabrata	Luz.gla	33	11	0	0	6	12	0	0	0	0	0	9	2	0	15	7	0	0	0
Luzula luzuloides	Luz.luz	1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Luzula multiflora s.lat.	Luz.mul	6	0	0	0	0	0	7	0	0	7	5	0	0	0	0	0	4	14	0
Luzula spicata	Luz.spi	7	0	0	0	0	0	13	0	0	9	8	0	0	0	0	0	4	0	0
Luzula sylvatica	Luz.syl	1	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0
Mercurialis perennis	Mer.per	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Minuartia austriaca	Min.aus	5	0	5	0	0	3	0	0	0	0	0	0	1	0	0	7	0	0	0
Minuartia cherlerioides	Min.che	10	0	14	0	0	4	0	0	0	0	0	3	0	0	2	0	0	0	0
Minuartia gerardii	Min.ger	19																		

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Solidago virgaurea	Sol.vir	6	0	0	0	0	0	0	0	0	14	9	0	0	0	0	2	0	0	7
Suaeda prostrata	Sua.pro	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Swertia perennis	Swe.per	2	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	4	
Taraxacum alpestre s.str.	Tar.alp	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Taraxacum alpinum agg.	Tar.alp.agg	10	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	
Taraxacum sect. Ruderalia	Tar.sec.Rud	3	0	0	0	0	3	0	0	0	7	0	0	0	0	0	0	0	0	
Taraxacum sp.	Tar.sp.	3	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	
Tephrosieris integrifolia ssp. capitata	Tep.int.cap	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Thalictrum alpinum	Tha.alp	7	3	0	0	0	0	21	8	13	0	0	0	0	0	0	0	0	0	
Thesium alpinum	The.alp	4	0	0	0	0	0	0	0	0	0	0	0	1	5	2	7	0	0	
Thlaspi alpestre	Thl.alp	7	0	0	0	6	4	0	0	0	0	0	3	0	0	0	0	0	0	
Thlaspi rotundifolium	Thl.rot	2	0	0	17	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Thymus praecox ssp. polytrichus	Thy.pra.pol	3	0	0	0	0	0	7	0	0	0	0	0	0	0	2	7	0	0	
Thymus sp.	Thy.sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	
Tofieldia calyculata	Tof.cal	52	8	0	0	0	0	0	0	0	0	0	0	32	7	25	13	0	0	
Tofieldia pusilla	Tof.pus	3	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	
Tortella tortuosa	Tor.tor	191	11	50	33	38	51	21	8	0	7	9	0	52	46	5	39	40	0	
Traunsteinera globosa	Tra.glo	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	
Trifolium alpestre	Tri.alp2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Trifolium badium	Tri.bad	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	
Trifolium repens	Tri.rep	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Trisetum distichophyllum	Tri.dis	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	
Trisetum spicatum ssp. ovatipanic	Tri.spi.ova	4	0	0	0	0	0	7	13	0	0	0	0	0	0	0	0	0	0	
Trollius europaeus	Tro.eur	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	7	0	0	
Tussilago farfara	Tus.far	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
Valeriana celtica	Val.cel	3	0	0	0	0	0	0	4	0	0	0	0	1	1	0	0	0	0	
Valeriana elongata	Val.elo	4	0	0	0	13	1	7	0	0	0	0	0	0	0	0	0	0	0	
Valeriana montana	Val.mon	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	
Valeriana supina	Val.sup	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Valeriana tripteris	Val.tri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	
Veratrum album	Ver.alb	10	0	0	0	0	4	0	0	0	0	9	8	0	0	0	3	13	0	
Veronica bellidioides	Ver.bel	5	0	0	0	0	0	0	0	0	5	17	0	1	0	0	0	4	0	
Veronica fruticans	Ver.fru	12	0	0	0	0	15	0	0	0	0	0	0	0	0	0	13	0	0	
Vincetoxicum hirundinaria	Vin.hir	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	
Viola alpina	Vio.alp	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Viola sp.	Vio.sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	
Moss layer																				
Abietinella abietina	Abi.abi	6	6	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	
Aulacomnium palustre	Aul.pal	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Heterocladium dimorphum	Het.dim	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Jungermannia gracillima	Jun.gra	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Tortula ruralis	Tor.rur	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cladonia deformis	Cla.def	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cladonia mitis	Cla.mit	35	22	5	0	0	0	0	0	13	7	0	0	17	2	5	5	0	4	
Cladonia borealis	Cla.bor	8	8	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	
Dibaeis baeomyces	Dib.bae	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Lecanora sp.	Lec.sp.	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Amblystegium serpens	Amb.ser	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Barbula crocea	Bar.cro	2	0	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Campylium calcareum	Cam.cal	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Campylium halleri	Cam.hal	2	0	5	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
Dicranum bergeri	Dic.ber	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Homalothecium lutescens	Hom.lut	2	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pseudoleskea catenulata	Pse.cat	4	3	9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Schistidium sp.	Sch.sp.	5	0	18	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Squamaria gypsacea	Squ.gyp	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Megaspora verrucosa	Meg.ver	5	0	5	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	
Peltigera rufescens	Pel.ruf	6	0	5	0	0	3	0	0	0	0	0	1	2	0	0	0	0	0	
Toninia sedifolia	Ton.sed	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Toninia sp.	Ton.sp.	2	0	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Psora decipiens	Pso.dec	6	0	0	50	0	4	0	0	0	0	0	0	0	0	0	0	0	0	
Solorina saccata	Sol.sac	2	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Toninia candida	Ton.can	3	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Asterella lindenbergiana	Ast.lin	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Barbula sp.	Bar.sp.	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Bryum pseudotriquetrum	Bry.pse	19	0	0	0	38	9	0	0	0	0	0	5	1	0	3	0	0	0	
Bryum sp.	Bry.sp.	6	0	0	0	19	0	0	0	0	0	0	8	0	1	0	0	7	0	
Cratoneuron commutatum	Cra.com	5	0	0	0	25	1	0	0	0	0	0	0	0	0	0	0	0	0	
Cratoneuron filicinum	Cra.fil	24	0	5	0	25	22	0	0	0	5	0	0	2	0	2	0	0	0	
Campylopus schimperi	Cam.sch2	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cephalozia ambigua	Cep.amb	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dichodontium pellucidum	Dic.pel	6	0	0	0	13	4	0	0	0	0	0	1	0	0	0	0	0	0	
Dicranella subulata	Dic.sub	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Distichium capillaceum	Dis.cap	5	0	0	0	6	3	0	0	0	0	0	0	2	0	0	0	0	0	
Ditrichum sp.	Dit.sp.	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Encalypta vulgaris	Enc.vul	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Lescurea incurvata	Les.inc	19	0	5	0	25	13	0	0	0	0	14	0	1	0	0	2	0	0	
Mnium sp.	Mni.sp.	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Orthothecium rufescens	Ort.ruf	2	0	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0	
Philonotis tomentella	Phi.tom	3	0	0	0	6	0	0	0</											

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Pogonatum urnigerum	Pog.urn	9	0	0	0	0	1	0	8	0	0	5	17	1	1	0	2	0	0	0
Dermatocarpon sp.	Der.sp.	1	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0
Anthelia juratzkana	Ant.jur	6	3	0	0	0	0	0	4	0	0	5	25	0	0	0	0	0	0	0
Barbula convoluta	Bar.con	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Fissidens osmundoides	Fis.osm	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Leiocolea alpestris	Lei.alp	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Ptilidium ciliare	Pti.cil	9	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0
Rhytidiadelphus loreus	Rhy.lor	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Rhytidium rugosum	Rhy.rug	33	0	0	0	0	0	14	4	0	14	0	0	17	5	15	5	0	4	7
Caloplaca sinapisperma	Cal.sin	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0
Cladonia ecmocyna	Cla.ecm	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cladonia macroceras	Cla.mac	27	11	0	0	0	0	0	4	0	7	0	0	17	2	5	3	0	4	0
Lecidella elaeochroma	Lec.ela	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lecidella wulfenii	Lec.wul	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rinodina conradii	Rin.con	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Solorina bispora	Sol.bis	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Thamnolia subuliformis	Tha.sub	53	3	0	0	0	1	0	8	0	14	0	0	26	21	0	2	0	0	7
Bryum algovicum	Bry.alg	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Campanula sp.	Cam.sp.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ceratodon purpureus	Cer.pur	5	3	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Ctenidium procerrimum	Cte.pro	8	0	5	0	0	0	0	4	0	0	0	0	0	5	0	2	0	0	0
Desmatodon latifolius	Des.lat	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Didymodon rigidulus	Did.rig	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ditrichum flexicaule	Dit.fle	99	6	32	0	31	9	14	0	0	7	0	0	21	37	5	26	7	0	0
Hypnum hamulosum	Hyp.ham	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hypnum sauteri	Hyp.sau	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Jungermannia atrovirens	Jun.atr	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Myurella julacea	Myu.jul	3	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0
Orthotrichum acuminatum	Ort.acu	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Buellia punctata	Bue.pun	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Caloplaca stillicidiorum	Cal.sti	4	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Caloplaca tirolensis	Cal.tir	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Cetraria tilesii	Cet.til	39	3	9	0	0	1	0	0	0	0	0	0	6	27	0	2	0	0	0
Cladonia pleurota	Cla.ple	4	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Cladonia pocillum	Cla.poc	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Dactylina madrepuriformis	Dac.mad	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lecanora epibryon	Lec.epi	10	3	0	0	0	1	0	0	0	0	0	0	7	0	2	0	0	0	0
Ochrolechia sp.	Och.sp.	5	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0
Ochrolechia upsaliensis	Och.ups	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Parmelia saxatilis	Par.sax	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Peltigera sp.	Pel.sp.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Physcia dubia	Phy.dub	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Physconia muscigena	Phy.mus	3	3	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Rinodina roscida	Rin.ros	3	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
Solorina octospora	Sol.oct	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Blepharostoma trichophyllum	Ble.tri	2	0	0	0	0	0	0	0	0	0	0	0	1	5	0	0	0	0	0
Homalothecium sp.	Hom.sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
Hypnum vaucheri	Hyp.vau	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
Pleurozium schreberi	Ple.sch	9	0	0	0	0	0	7	4	0	7	5	0	0	15	2	0	0	7	7
Rhytidiadelphus triquetrus	Rhy.tri	20	3	0	0	0	1	14	4	0	0	0	0	5	0	35	3	0	0	14
Cladonia stellaris	Cla.ste	6	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	7	7
Peltigera aphthosa	Pel.aph	2	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
Fissidens adianthoides	Fis.adi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Leskea polycarpa	Les.pol	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Tritomaria quinqueidentata	Tri.qui	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
Campyllum chrysophyllum	Cam.chr	9	0	0	0	0	4	0	0	0	0	0	0	1	4	0	0	7	0	0
Campyllum stellatum var. protensum	Cam.ste.pro	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0
Encalypta streptocarpa	Enc.str	4	0	5	0	6	0	0	0	0	0	0	0	1	0	0	0	7	0	0
Fissidens dubius	Fis.dub	4	0	5	0	0	0	0	0	0	0	0	0	0	0	3	7	0	0	0
Barbilophozia barbata	Bar.bar	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Entodon concinnus	Ent.con	3	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	0	0
Polytrichum pallidisetum	Pol.pal	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Cetraria ericetorum	Cet.eri	5	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	12	7	0
Stereocaulon sp.	Ste.sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Dicranum fuscescens	Dic.fus	4	0	0	0	0	0	0	4	0	0	0	0	2	0	0	0	0	7	7
Nardia scalaris	Nar.sca	4	0	0	0	0	0	0	4	0	0	5	0	0	0	0	0	4	7	7
Polytrichum piliferum	Pol.pil	9	0	0	0	0	0	13	13	7	0	0	0	1	0	0	0	4	14	14
Cladonia macrophylla	Cla.mac	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	7
Cladonia pyxidata	Cla.pyx	40	3	9	0	0	6	7	0	13	0	8	10	8	5	10	7	4	21	21
Lepraria neglecta	Lep.neg	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	7