Local and regional responses of alpine flora to climate change induced warming

Scientific thesis for the degree Master of Science (M.Sc.) at the School of Life Sciences at the Technical University of Munich

Supervisors	Prof. Dr. Anja Rammig (TUM School of Life Sciences) Dr. Sonja Wipf (Swiss National Park)
Submitter	Corinna Altmiks
Study programme	Conservation and Landscape Planning
Date	November 22, 2023

Abstract

Due to rising temperatures, the high alpine environment is currently exposed to climate change. Heightened vegetation productivity indicates ecotone shifts, which involve changes in species abundance and occurrence. In 2022, as part of the GLORIA network, permanent quadrats within and around the Swiss National Park in Grisons, Switzerland, were revisited to assess the impact of climate change on 51 alpine plant species. The findings were compared with data collected over two previous decades. These changes were labelled as local-scale and compared to regional-scale range edge shifts across Grisons, Switzerland, using data spanning a century. Findings reveal species responding differently, as twelve species benefited (winners), including dwarf shrubs and annuals, eight suffered (losers), and 31 showed no significant or clear directional change on local-scaled Gloria sites. In addition, winners on a regional scale have moved their leading edge significantly upwards, while losers have moved downwards. *Luzula spicata*, *Erigeron uniflorus*, *Poa alpina* and *Gentiana bavarica* exhibited not only local abundance declines but also reduced regional range areas, revealing their vulnerability. The study highlights the predictive capability of local-scale permanent quadrats for regional range area shifts. These findings suggest that dwarf shrubs and annuals, with diverse life cycle strategies (long vs. short cycles), hold an advantage in adapting to climate change. Winners, with the ability to colonize new habitats at their leading edge, are following their temperature niche, while losers face local extinction due to changing environmental conditions. Preserving vulnerable loser species is crucial for maintaining ecological balance in alpine environments responding to ongoing climate change effects.

Zusammenfassung

Aufgrund steigender Temperaturen ist das hochalpine Ökosystem gegenwärtig dem Klimawandel ausgesetzt. Dabei führt die gesteigerte Produktivität der Vegetation zu Ökotonverschiebungen, die Veränderungen in der Artenhäufigkeit und -verbreitung mit sich bringen. Im Jahr 2022 wurden im Rahmen des GLORIA-Netzwerks permanente Plots innerhalb und um den Schweizerischen Nationalpark in Graubünden, Schweiz, erneut untersucht, um die Auswirkungen des Klimawandels auf 51 alpine Pflanzenarten zu analysieren. Anschließend wurden die gewonnen Daten, mit denen der zwei vorangegangenen Jahrzehnte verglichen. Die daraus festgestellten lokalen Veränderungen wurden danach mit regionalen Verschiebungen der vertikalen Verbreitungsgrenzen in ganz Graubünden, Schweiz, verglichen, wobei Daten über einen Zeitraum von einem Jahrhundert verwendet wurden. Die Ergebnisse zeigen, dass verschiedene Arten unterschiedlich auf Temperaturveränderungen reagieren: Zwölf Arten, darunter Zwergsträucher und Einjährige, gehören zu den Gewinnern, acht Arten zählen zu den Verlierern und 31 Arten zeigen keine signifikanten oder klaren Veränderungen auf den lokal analysierten GLORIA-Standorten. Zusätzlich haben Gewinner auf regionaler Ebene ihre obere Verbreitungsgrenze signifikant nach oben verschoben, während Verlierer dort nach unten wanderten. Insbesondere *Luzula spicata*, *Erigeron uniflorus*, *Poa alpina* und *Gentiana bavarica* zeigen nicht nur lokale Rückgänge in ihrer Häufigkeit, sondern reduzierten auch ihre regionalen Verbreitungsgebiete, was auf ihre Vulnerabilität hinweist. Außerdem betont die Studie, dass von lokalen Häufigkeitsveränderungen, auf regionale Veränderungen in den Verbreitungsgebieten geschlossen werden kann. Diese Ergebnisse zeigen, dass Zwergsträucher und Einjährige mit unterschiedlichen Lebenszyklusstrategien (lang oder kurz) einen Vorteil bei der Anpassung an den Klimawandel haben. Die Gewinner, welche in der Lage sind, neue Lebensräume an ihrer oberen Verbreitungsgrenze zu besiedeln, folgen ihrer Temperaturnische, während Verlierer aufgrund sich ändernder Umweltbedingungen dort partiell zurückgehen. Um das ökologische Gleichgewicht in alpinen Umgebungen zu bewahren, ist die Erhaltung der vom Klimawandel betroffenen Arten von entscheidender Bedeutung.

Table of contents

1. Introduction

Throughout history, the environmental conditions for plants worldwide have undergone constant change, which is a natural and gradual phenomenon (Körner, 2021). Nonetheless, the climate is now changing at a unprecedentedly fast rate due to human activity. Since the 1980s, every decade has been warmer than the previous one. Notably, the seven warmest years globally have all occurred since 2015, with 2016, 2019 and 2020 taking the lead (MeteoSchweiz, 2016). The acceleration of climate warming presents a substantial threat to numerous species, raising the likelihood of extinction within a short period (Thomas *et al.*, 2004). Particularly, alpine habitats are experiencing the effects of warming to a greater extent than the average in the northern hemisphere (Rebetez and Reinhard, 2008) or in the lowlands (Pepin *et al.*, 2015). Due to their adaptation to cold temperatures (Körner, 2021; Vanneste *et al.*, 2017), alpine biota are among the most vulnerable ecosystems to climate change (Nicklas *et al.*, 2021).

Several studies have already demonstrated the responsiveness of vascular plants in mountain regions to rapidly changing environmental conditions. The effects observed include changes in local abundance, shifts in range distributions and local extinctions (Auld *et al.*, 2022; Dirnböck *et al.*, 2011; Dullinger *et al.*, 2012; Felde *et al.*, 2012; Rumpf *et al.*, 2018; Walther, 2003). However, the response varies between plant species, with some benefiting from a warming climate (referred to as 'winner species') and others suffering from it (referred to as 'loser species') (Rumpf *et al.*, 2018). For winner species, the concept of 'thermophilisation' is of central importance, referring to the shift of plant species composition towards an increase in species that are better adapted to warmer and drier conditions (Lamprecht *et al.*, 2018; Oldfather and Ackerly, 2019; Vanneste *et al.*, 2017). The shift in plant communities towards species with higher nutrient requirements is also widely accepted in the scientific literature (Rumpf *et al.*, 2018; Staude *et al.*, 2022). Given that competitive species with faster growth rates particularly benefit from warming conditions, high-altitude, cold-adapted and low-nutrient species are expected to face the greatest challenges and suffer the most in this changing environmental landscape (Alexander *et al.*, 2015).

In addition, species migrate to higher and cooler elevations in response to raising temperatures in search of more favourable growing conditions (Hackett *et al.*, 2008; Pauli *et al.*, 2012; Rumpf *et al.*, 2018; Zu *et al.*, 2021). This phenomenon has led to an increase in plant species richness on summits (Alexander *et al.*, 2015; Nicklas *et al.*, 2021), which has become more pronounced with accelerated global warming in recent decades (Steinbauer *et al.*, 2018). The movement to higher elevations is strongly influenced by elevation-dependent processes, whereas the upper range limits, often referred to as leading edges, and the lower range limits, often referred to as rear edges, are subject to different processes. Rising temperatures provide more favourable growing conditions at the 'leading edges' where species were previously constrained by harsh environmental conditions. This has led to upward shifts as species take advantage of new opportunities to establish themselves at higher elevations (Auld *et al.*, 2022). High alpine plant species located at the 'rear edges' may encounter less favourable growing conditions as a result of increased competition from more competitive species within communities or a general increase in productivity of neighbours. This could ultimately result in extinctions at the rear edge, shifting these species upwards. However, the scientific literature focuses predominantly on shifts of the leading edge or the mean range limit, while shifts of the less studied rear edge are rather rare (Auld *et al.*, 2022; Rumpf *et al.*, 2018).

Another significant deficiency in the present literature is the frequent disregard on the existing downward migration phenomena of species to lower altitudes, albeit this plays a noteworthy role in certain regions (Crimmins *et al.*, 2011; Zu *et al.*, 2021). A downward shift is predominate for species subject to intense competition. These species have realised distributions that do not fully occupy their potential ranges along the gradient. Concurrently, climate warming is likely to induce shifts in the distribution of competing species towards higher elevations, creating a warming-induced competitive release that allows range shifts towards lower elevations (Lenoir *et al.*, 2010).

Leading and rear edges do not necessarily shift synchronously, nor do they always move in the same direction (Rumpf *et al.*, 2018). Thus, only a combined evaluation of both range edges enables assessing whether species are expanding or contracting their elevational distributions in the face of climate change. This is particularly important, as contraction of elevational distributions can serve as an indicator of high extinction risk (Zu *et al.*, 2021). Unfortunately, data on species' rear edges are often scarce (Auld *et al.*, 2022; Rumpf *et al.*, 2018). Focusing on this aspect of species' distributions, future research can provide valuable insights into the underlying mechanisms operating at the rear edges.

Due to environmental warming, alpine plants could experience changes in their abundance and distribution. Changes in abundance are predicted to emerge locally, whereas distribution changes are expected to occur on a more regional scale. In particular, species exhibiting an increase in local abundance are deemed well-adapted to changing temperature conditions, may possess enhanced competitive abilities, and therefore are likely to be able to colonise habitats beyond their former range limits. This indicates a potential correlation between an increase in local abundance and range expansion due to the mechanistic relationship between local and regional processes (Leibold *et al.*, 2004; Lynn *et al.*, 2021; Sporbert *et al.*, 2020). In contrast, declining local abundance may lead to adverse effects on species distribution as a result of environmental changes and an increased likelihood of range contraction leading to extinction. However, it remains unclear how changes in species abundance and altitudinal range shifts are linked, and whether there is a relationship between these two types of responses. Providing evidence that local-scale changes in abundance can serve as predictors of regional-scale range shifts could make a significant contribution to understanding changes in the distribution of individual species.

Understanding the impact of climate change on high alpine plant species at both local and regional scales is an important task, as climate change poses a risk of extinction for numerous species. Using different data sets, I have quantified and compared the responses of 51 alpine plant species over a 20-year period in and around the Swiss National Park to obtain insight into how individual species have responded at different spatial scales. The species were classified into 'winners' and 'losers' based on a compound index considering their abundance and occurrence. To explore general differences between winners and losers, I employed morphological, ecological, and dispersal indicator values established by Landolt *et al.* (2010) and identified the characteristics of winner and loser species based on their leading and rear edge shifts on a regional scale (over a century, across the entire canton of Grisons, Switzerland). As information on rear edge shifts is restricted, I outlined my fieldwork methods and experiences from 2022, seeking to generate valuable rear edge data. Ultimately, I examined how changes in abundance at various elevations relate to range shifts, exploring whether local-scale changes in abundance can forecast regional-scale range area shifts.

Analyses were conducted to test the following hypotheses:

H1. Changes in abundance and occurrence in response to rising temperatures varies among species, as some benefit (= winners) from climate change and others suffer (= losers).

H2. Whether a species is a winner or a loser under climate change depends on their morphological, ecological, and dispersal traits.

H3. On average, winners exhibit an upward shift at their leading edge, aligning with their optimal temperature range. Simultaneously, they establish resilience at their rear edge by withstanding increased competition. In contrast, losers tend to remain at their leading edge due to limitations in colonizing higher elevations. However, they experience an upward shift in their rear edge, contributing to their vulnerability and heightened risk of local extinction, primarily driven by intensified competition.

H4. Changes in local abundance can serve as a predictor for regional range area shifts, due to a mechanistic relationship between local and regional processes.

2. Material and Methods

2.1. GLORIA approach and study area

In times of a rapidly changing environment, the preservation of sensitive alpine ecosystems has become a pressing concern. Initiatives like the Global Observation Research Initiative in Alpine Environments (GLORIA) have taken up the challenge to document ecological changes in mountains worldwide and their drivers. To achieve this, GLORIA has established a worldwide network dedicated to analyzing the changes taking place in fragile alpine landscapes above the treeline in mountain ranges on all continents (except Antarctica). There, GLORIA places a particular focus on studying changes in vascular plant composition of summits in the context of climate change.

The Multi-Summit Approach is the key methodology employed by the GLORIA initiative (Fig. 1). It involves establishing monitoring plots at multiple summits within a particular mountain region (target region), capturing the ecological diversity and variability across different elevations. Typically, the summits are located in high-mountain regions, usually from the treeline to highest occurrence of vegetation. This ensures the covering of the entire gradient from alpine to nival ecosystems.

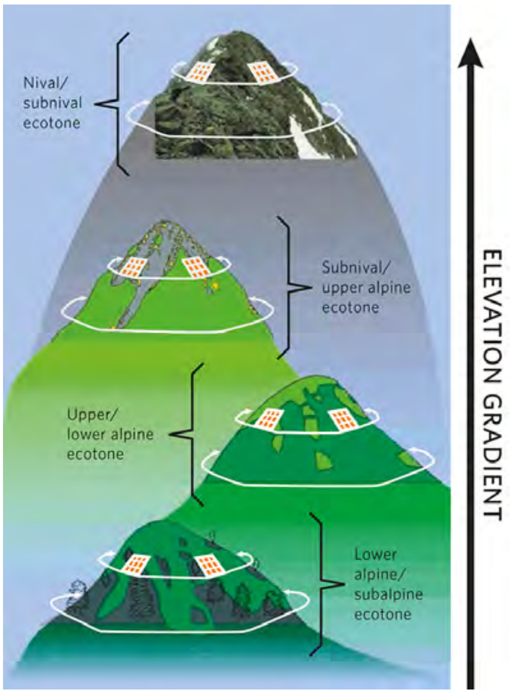


Figure 1 Multi-Summit Approach of Global Observation Research Initiative in Alpine Environments (GLORIA) of one target region (GLORIA, 2023).

My study was conducted in two GLORA target regions in and around the Swiss National Park (SNP) located in the east of Switzerland in the canton of Grisons (Fig. 2). The two target regions, CH-SN1 and CH-SN2, are characterized by varying geological features and their respective plant species spectra. SN1 is dominated by siliceous bedrock, represented in blue, while SN2 is composed of calcareous bedrocks, represented in red. The summit *Muot sper la Chamanna Sesvenna* (MCS) is composed of both siliceous and the more dominant calcareous bedrock and therefore hosts species of both.

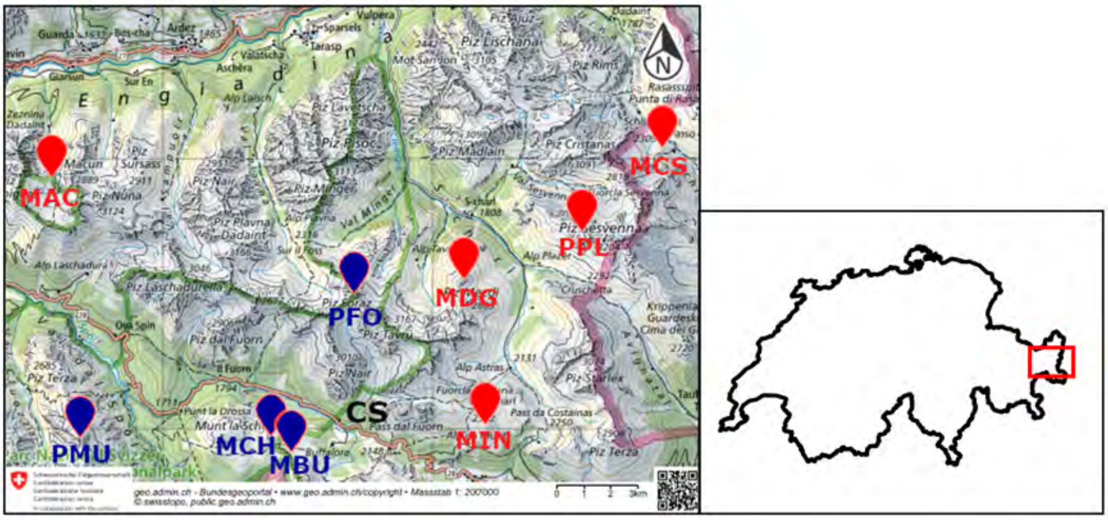


Figure 2 Location of GLORIA summits of the target regions SN1 (blue) and SN2 (red) in and around the Swiss National Park, indicated by a green border, in the canton of Grisons. SN1 is on siliceous and SN2 on calcareous bedrock. CS: Climate station Buffalora (© by Bundesamt für Landestopografie).

Table 1 Selected summits based on the Multi-Summit Approach of the target regions SN1 and SN2 in and around the Swiss National Park.

Target region	Summit code	Summit name	Altitude (m asl)	Longitude (WGS84)	Latitude (WGS84)
CH-SN1	MBU	Munt Buffalora	2438	10° 14’ 37”	46° 38’ 19”
CH-SN1	MCH	Munt Chavagl	2542	10° 14’ 03”	46° 38’ 39”
CH-SN1	PMU	Piz Murtèr	2836	10° 08’ 30”	46° 38’ 45”
CH-SN1	PFO	Piz Foraz	3092	10° 16’ 36”	46° 41’ 27”
CH-SN2	MCS	Muot sper Chamana Sesvenna	2424	10° 25’ 43”	46° 44’ 08”
CH-SN2	MIN	Minschuns	2519	10° 20’ 17”	46° 38’ 44”
CH-SN2	MAC	Macun Chavagliet	2642	10°13’22’	46° 73’ 32’
CH-SN2	MDG	Mot dal Gajer	2797	10° 19’ 52”	46° 41’ 40”
CH-SN2	PPL	Piz Plazèr	3104	10° 23’ 17”	46° 42’ 31”

The summits of each target region were selected using the Multi-Summit approach, resulting in four summits per target region at different elevations (Table 1). Specifically, SN1 spans an elevation gradient from 2438 to 3092 m a. s. l., while SN2 ranges from 2424 to 3104 m a. s. l.. The selected summits are situated within or in close proximity to the Swiss National Park. The park provides a natural buffer against extensive human impact. One additional summit, *Macun Chavagliet* (MAC), was included in the study later. MAC is located within the protected boundaries of the Swiss National Park. Monitoring at this summit started in 2016 (i.e. after the third of four surveys). Nevertheless, MAC was equally treated in the data analyses as the other summits. However, the time period for monitoring changes at MAC is relatively shorter than that of the other summits. Consequently, for abundance change analysis, where the time period holds utmost importance, MAC was excluded from the data set (chapter 2.3.4.).

The study region in and around the Swiss National park experiences distinctive seasonal temperature variations. Winters are long and harsh, with temperatures frequently dropping far below freezing, especially at higher elevations. In contrast, summers are relatively short, with mild to warm temperatures during the day and cool nights. This continental climate result in a mean annual air temperature of 0.4℃ (9.64 ℃ in June/July/August), a precipitation total of 75 mm (110 mm in June/July/August) and 190 snow cover days. This was measured from 1917 to 2022 at the climate station Buffalora (46° 38' 54" N and 10° 16' 02" E) laying at 1968 m a.s.l. at the eastern border of the Swiss National Park (MeteoSchweiz, 2016). Within the study area, the exact location is shown visually in figure 2, denoted by the label 'CS' for climate station. The proximity of this climate station to the target regions allows me to observe temperature changes dating back to 1917. Notably, from 1992 onward, an distinct increase in the mean annual temperature for the summer months of June, July, and August has been observed (see Fig. 3, blue dashed line).

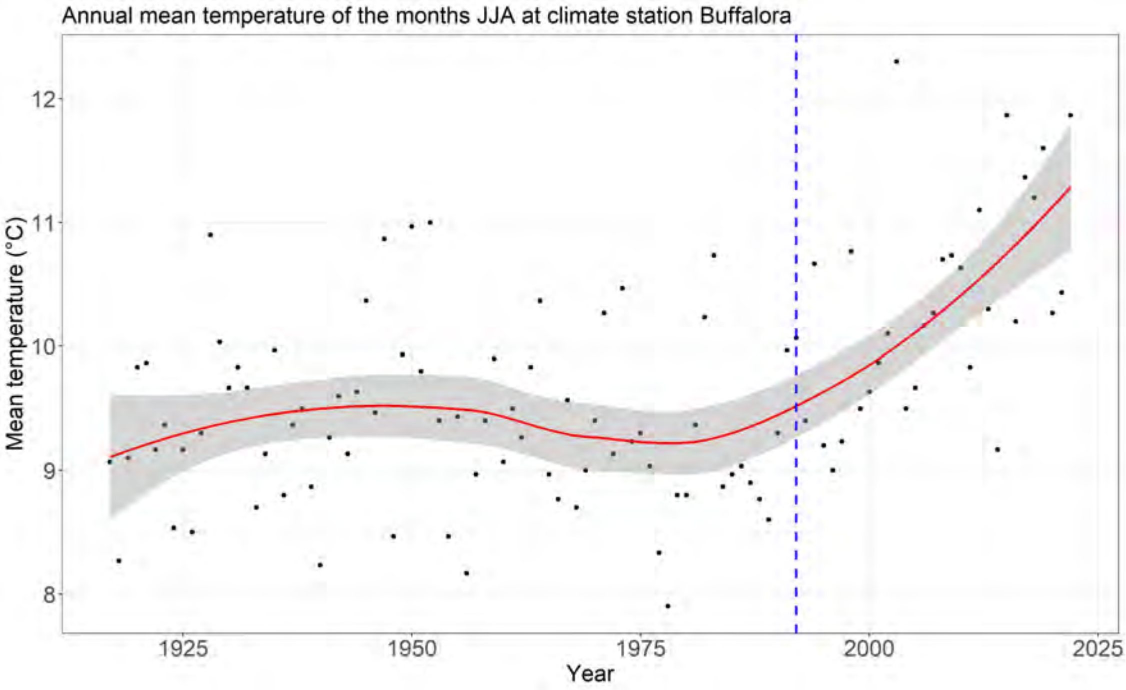


Figure 3 Annual temperature of the summer month June, July and August from 1917 to 2022 at climate station Buffalora (46° 38' 54" N and 10° 16' 02" E). Within the study area, the exact location is shown visually in figure 2, denoted by the label 'CS' for climate station. Since 1992 there has been an increase in mean annual temperature (blue dashed line).

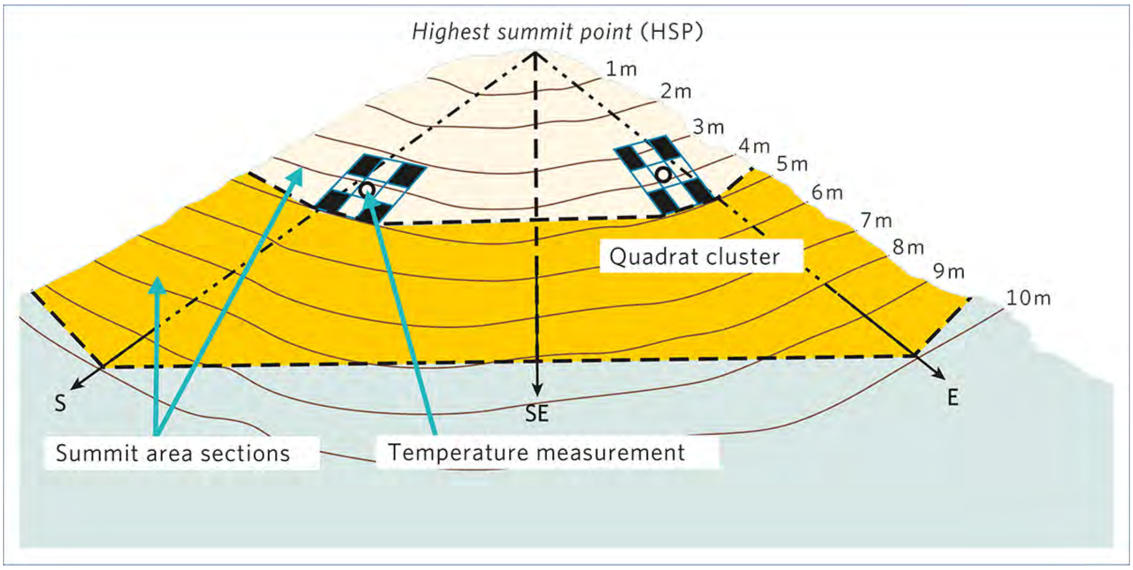


Figure 4 Oblique view of a GLORIA summit with schematic contour lines (GLORIA, 2023).

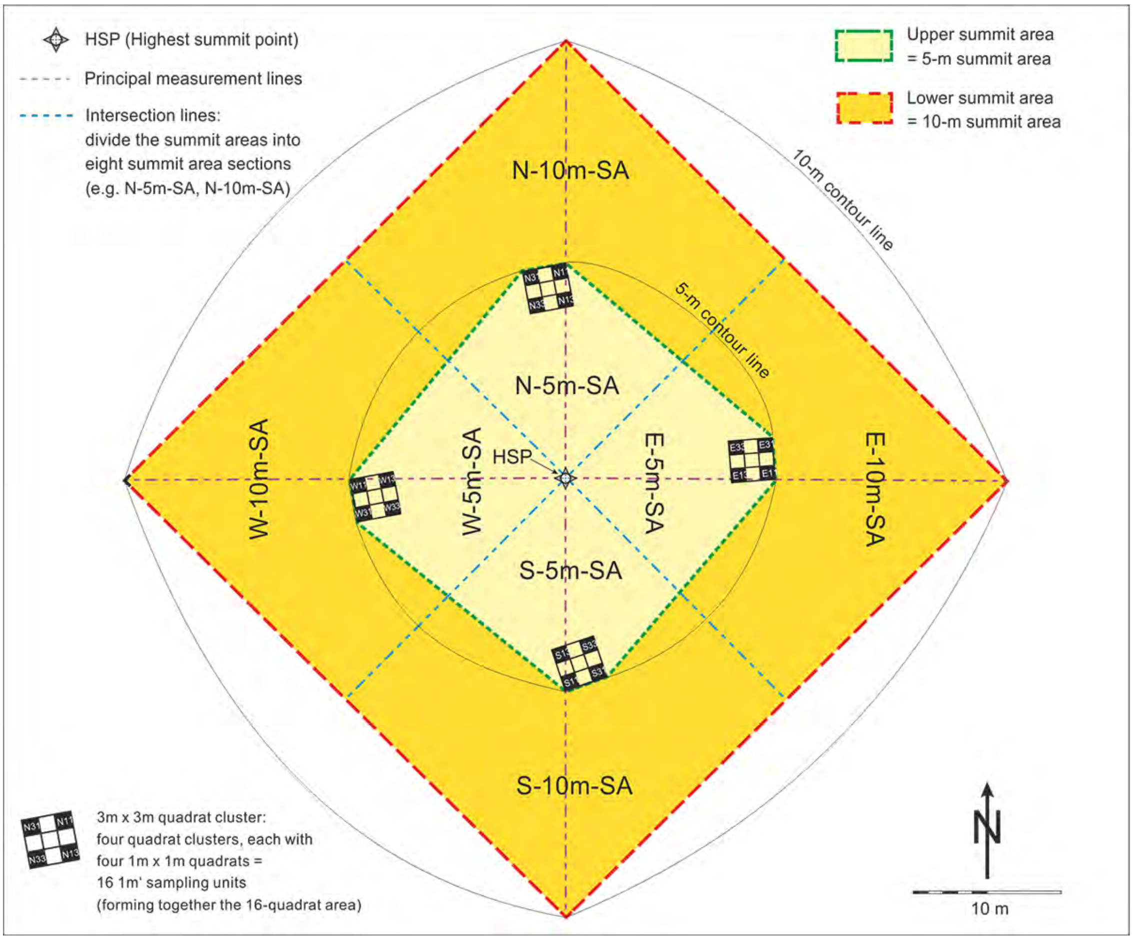


Figure 5 Scheme of the sampling design of a GLORIA summit in top view. The standard sampling design comprises 16 1-m² quadrats and eight summit area sections (SASs) (GLORIA, 2023).

2.2. Data collection

2.2.1. Vegetation survey

According to the GLORIA protocol, comprehensive vegetation surveys on the target summits have to be carried out every five to seven years. In the target region, surveys were conducted in the years 2002/2003, 2009/2010, and 2015/2016, and 2022, i.e. fourth repetitions in total. In the following, ’survey 1’ refers to the evaluations from the years 2002/2003, ’survey 2’ to those from the years 2009/2010, ’survey 3’ to the evaluations from the year 2015/2016 and ’survey 4’ to the surveys from the year 2022. It is essential to note that all surveys were carried out using the same methodology at the same locations.

In 2022, field work started on 05.07.2022 at Munt Buffalora (MBU) and ended on 23.08.2022 at Piz Murtèr (PMU). The sampling design followed the standard protocol of the Multi-Summit approach according to the GLORIA Field Manual (Pauli *et al.*, 2015). At a larger spatial scale, so-called Summit Area Sections (SAS) were mapped. Each summit was divided into an upper (5 meter) and lower summit area (10 meter) below the highest summit point as well as into the four cardinal directions (Fig. 4). This results in eight SAS per summit. In each SAS, the abundance of each occurring species was estimated in five classes ranging from very rare to dominant. Surveying large areas with minimal observer effort and accuracy enables the detection of all species, allowing to observe general changes, such as species turnover.

At a smaller spatial scale, quadrat clusters were established located five metres below the highest summit point, one in each cardinal direction (north, east, south, and west). Each quadrat cluster measured 3x3 meters, and the four corner 1x1 meter quadrats of each quadrat cluster served as permanent quadrats for vegetation surveys. Thus, in total, each summit was equipped with a total of four quadrat clusters, and vegetation was surveyed in 16 quadrats per summit (Fig. 5). Surveying small areas offers the advantage of precise species detection and cover estimation, providing insights into species-specific changes like abundance change.

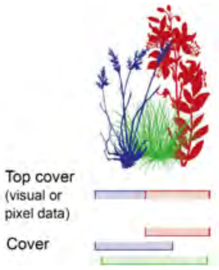


Figure 6 Estimated vegetation cover based on the ’cover’ approach instead of the ’top cover’ approach. As a result, the sum of vegetation cover in a quadrat may exceed 100 % (Damgaard and Irvine, 2019).

For every surveyed quadrat, a comprehensive list of vascular plants was compiled, and their coverage was evaluated on a percentage scale. The smallest cover value recorded was 0.005 %. Plant cover refers to the proportional area occupied by a particular species when projected onto the surface (Wilson, 2011). It is essential not to confuse this with top cover (Fig. 6). Since plants often grow under one another, the cumulative cover values of all species in a quadrant could exceed 100 %.

The species identification process consulted authoritative sources including Flora Helvetica (Lauber *et al.*, 2012) and Flora Vegetativa (Eggenberg and Möhl, 2013). Taxa were identified to the species level, and when possible, even to the subspecies level. Cases where the identification remained uncertain were labeled in the species list with “cf.” (confer). After the fieldwork was completed, the species names were translated to those in the Flora Europaea as GLORIA follows their nomenclature (Tutin, 2010).

2.2.2. Microclimate

Temperature data from 2015 (except for MAC: 2017) to 2022 were collected for each quadrat cluster. To achieve this, wireless temperature loggers (Model M-Log5W (433/915 MHz), produced by GeoPrecision) were employed and placed approximately 10 cm below the ground in the center of each quadrat cluster (MIN-S and MAC-West loggers have been lost). These loggers continuously recorded soil temperatures at hourly intervals throughout the summer periods. The microclimatic conditions for the four quadrats, denoted as for example S11, S13, S31, and S33, were derived from the corresponding temperature logger positioned at the center of the quadrat cluster (Fig. 7). This data collection method allowed us to obtain detailed and accurate temperature information per quadrat cluster.

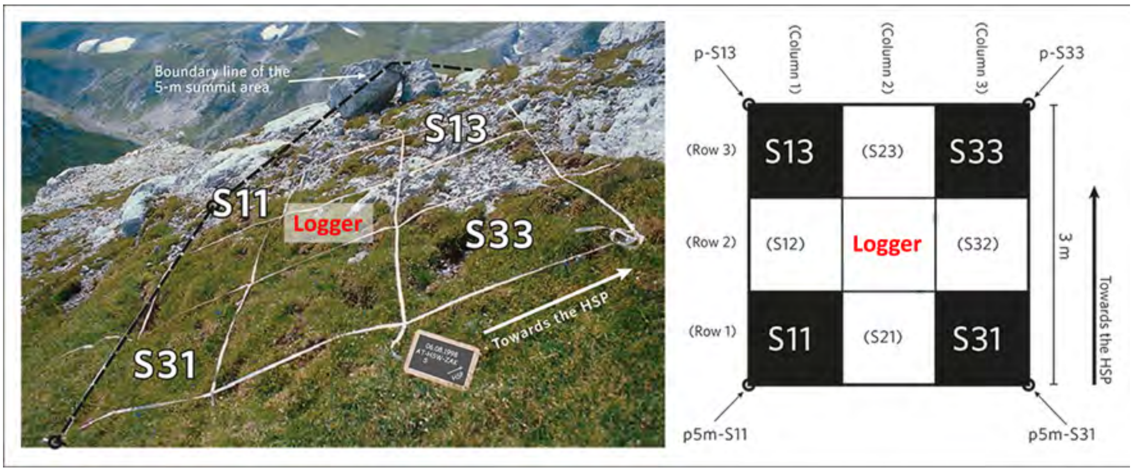


Figure 7 A 3 m × 3 m quadrat cluster with location of temperature logger. **Left:** example from the NE-Alps (2250 m), quadrat cluster in the S-direction. **Right:** scheme of the quadrat cluster with the quadrat codes. Note the location of the temperature logger in the center of the quadrat cluster (red) (GLORIA, 2023).

2.3. Data analysis

All calculations, figures and statistical analyses were conducted with R Statistical Software version 4.0.5 (2021-03-31) using RStudio version 2022.07.2. For further plotting and data processing, the following packages were used: betareg (v. 3.1-4), broom (v. 1.0.4), dplyr (v. 1.1.4), ggplot2 (v. 3.4.1), glmmTMB (v. 1.1.7), graphics (v. 4.0.5), gridExtra (v. 2.3), lme4 (v. 1.1-32), reshape2 (v. 1.4.4), tibble (v. 3.2.0), tidyr (v. 1.3.0), viridis (v. 0.6.2).

2.3.1. Species selection

As the standard GLORIA protocol provides data on different spatial scales, consideration was given to which data type best suited my research hypothesis. Abundance estimates within the SAS are coarser than within the 1x1 m quadrats. However, data are available for fewer species within the quadrats than within the SAS, as only a fraction of the total SAS species are present in the quadrats. The more accurate coverage estimates on the quadrat lever, due to the smaller scales, were the reason for selecting the quadrat plot data for further analysis. Therefore, SAS were not examined in this study. To ensure consistency and accuracy, differences at species/subspecies level or uncertainties between the four surveys were manually harmonised for each quadrat. Within certain quadrats, there existed species for which cover data were absent. To address this issue, I consulted the concerned manual field sheets. If cover data remained incomplete, the respective species on a quadrat were excluded from analysis. In addition, records for unknown seedlings were removed.

In order to obtain a set of target species with sufficient data, species occurring on less than three summits were omitted. Moreover, species characterized by ambiguous or difficult taxonomic identification, namely *Hieracium alpinum*, *Hieracium glanduliferum*, *Leontodon hispidus*, *Leontodon pyrenaicus*, and *Taraxacum apenninum agg.*, were omitted to ensure a correct comparison over time. After this selection process, I was left with a total of 51 species out of the initial 195 (please refer Table A1 in the appendix).

2.3.2. Microclimate

The raw data of each temperature logger were cleaned from outliers. However, due to technical issues, not all loggers recorded temperature for the entire study period. I selected the year yielding the most comprehensive data set, which was the year 2018. This year's data was used to characterize the soil temperature of each quadrat cluster and the differences between clusters, assuming that the temperature differences between quadrat clusters does not change significantly between years.

The few missing data points were replaced by a gap-filling algorithm: up to three continuous hours with missing data were replaced by the mean value of the nearest neighbor temperatures. Regression model assumptions (independent and normally distributed errors, constant error variance, errors with mean zero) were checked visually with residual plots.

2.3.3. Time-dependent cover trend

Cover percentages were estimated on quadrats at GLORIA sites to analyse the relationship between cover and time for target species. In the original data frame I only had presence data, absence data was missing. In order to show a time-dependent cover trend, I added a cover score of 0 if a species was not detected in one survey, but was present in the same plot in at least one out of the four surveys. Thus, this resulted in four data points for each species x quadrat combination, when a species was found at least once in the four surveys, with the following exceptions:

As I only have data from surveys 3 and 4 for the MAC summit, a coverage of 0 was only added for surveys 3 or 4, as surveys 1 and 2 had not been not conducted . Similarly, all East-exposed quadrats on the MCH summit were disregarded, as this quadrat cluster was destroyed by erosion and thus, monitoring had to be given up after the third survey in 2015. In this scenario, a cover value of 0 was only introduced if the species was not recorded in surveys 1, 2 or 3, but had occurred in one of the other surveys.

In the realm of data analysis and modeling, selecting appropriate statistical distributions is a fundamental step in accurately representing the inherent characteristics of the data. Delving into the 'cover data set,' much like in numerous ecological datasets, I encountered a deviation from the normal distribution assumption. This assumption, which implies that data can take any value between negative infinity and positive infinity, including non-integer values and that the data is symmetrically distributed around the mean, did not hold in this data set (Fig. 8, A). Notably, data representations like percent cover demonstrate a closer alignment with the attributes of a beta distribution, as highlighted in studies by Knight, Nicole (2022) and Damgaard and Irvine (2019).

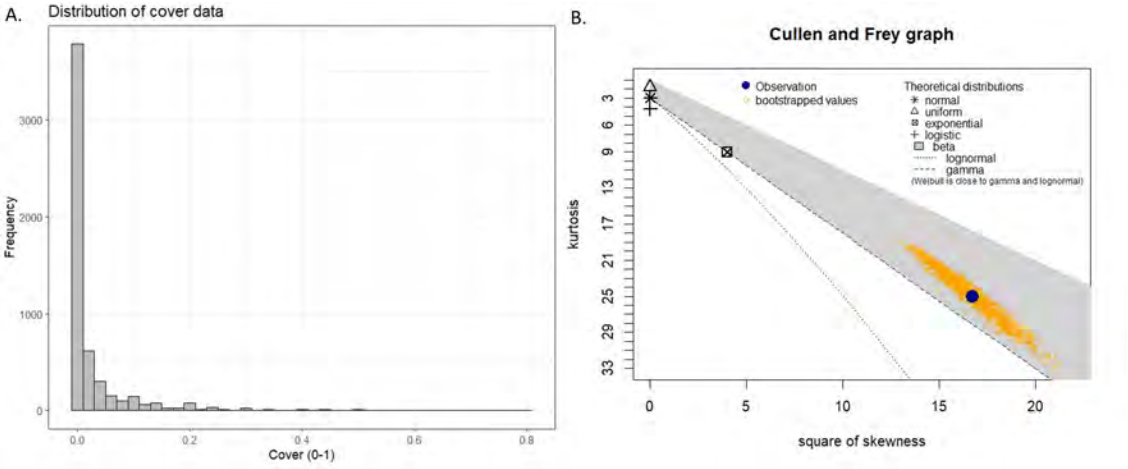


Figure 8 Surveyed cover data on GLORIA quadrats. **A.**: Distribution of cover data in quadrats; **B.**: Cullen–Frey graph (kurtosis versus square of skewness). The data set of cover data (observation), indicated in orange, is located in the grey area covered by the beta distribution function.

To determine the most suitable distribution for the cover data, the Cullen and Frey plot emerged as an valuable tool. By examining the position of the data within this plot, I could discern whether it conforms to a specific theoretical distribution. In my case, the Cullen and Frey graph supports the hypothesis that the distribution of cover percentages closely followed a beta distribution (Fig. 8, B).

The complexity of the GLORIA study design introduced an additional layer of intricacy due to its hierarchical structure. The design comprises four quadrats arranged along a cardinal direction, nested within a summit. This nested structure necessitates the incorporation of a random effect into the modeling framework, as the observations within the quadrats are not independent.

Employing the Generalized Linear Mixed Model (GLMM), with its proficiency in handling beta-distributed data and accommodating random effects, equipped me with the means to effectively account for the non-independence of observations. This enabled me to accurately model the relationship between the year and the cover percentages, all while considering the nested structure of the plots along the cardinal direction within the summit. I performed these calculations separately for each species to ensure a comprehensive and species-specific analysis:

```
glmmTMB(cover_percentage ~ year + (1 | plot_on_summit),
         ziformula = ~1, data = data_spe, family = 'beta_family')
```

To analyze how different species responded to climate change, the outcomes of this model offer insights into the first of three key variables 'time-dependent cover trend' as discussed in chapter 2.4.

2.3.4. Abundance change in relation to temperature and elevation

To compute the abundance change for each target species, I conducted a comprehensive regression analysis across all quadrats (Fig. A1 in the appendix). As the intervals between surveys were slightly variable, the estimated regression coefficient (beta) from the linear model was multiplied by the difference in survey years between survey 4 and survey 1. Offering an illustrative example, Fig. 9 shows all quadrats containing *Agrostis alpina* and elucidates my approach to calculating abundance change. The grey dashed line represent the abundance change, and its slope is shown as a number in the upper right corner of each quadrat. To ensure robust comparability, any quadrants with fewer than four surveys, encompassing all 'Macun' (MAC) and 'Minschuns east' (MCH_E) quadrats, were removed from the data set.

Considering the abundance change values for each species x quadrat combination, the assumption of a normal distribution does not hold true (Fig. 10 & 11A). The Normal Q-Q plot demonstrates a trend where the data points in the center of the graph align with the reference

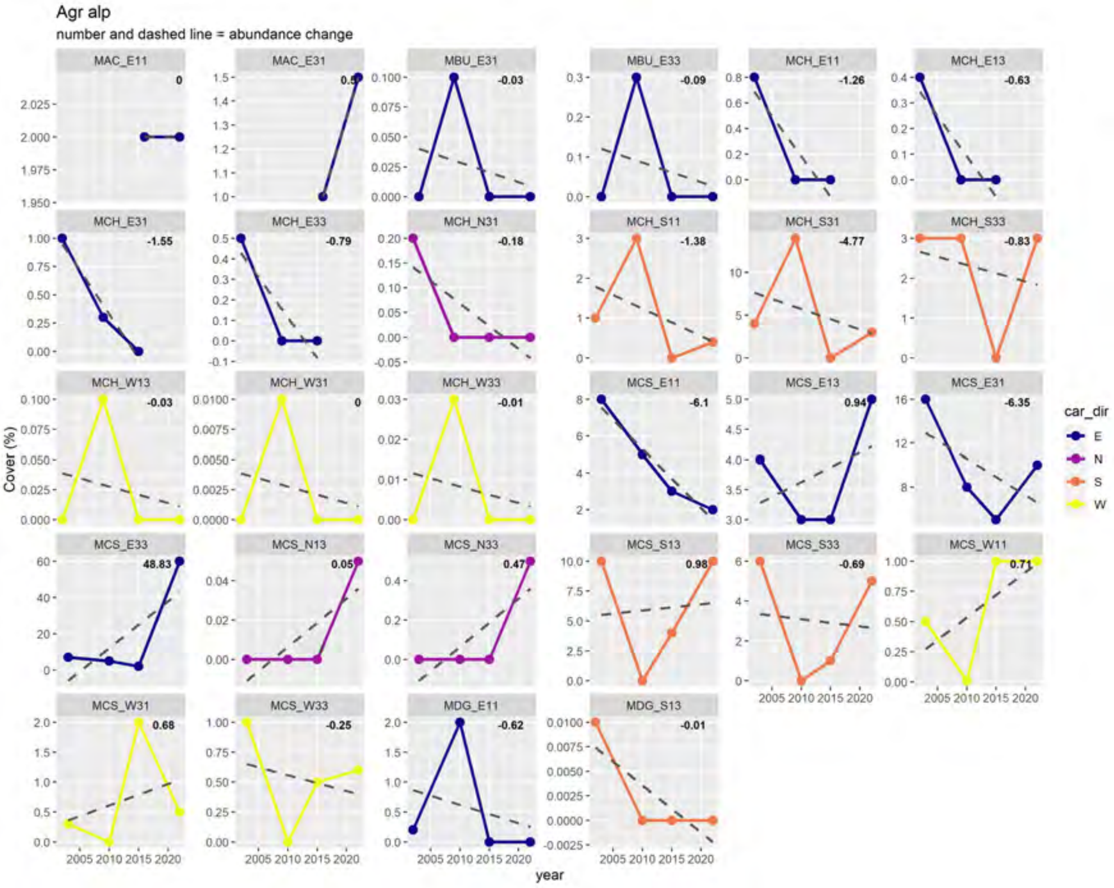


Figure 9 Abundance change calculation per quadrat for example species *Agrostis alpina*. Note that the Macun summit only has two surveys (3 and 4) and Minschuns east only have three (erosion of the quadrat cluster at survey 4) and were deleted from the data set. Car. dir. is an abbreviation for cardinal direction. Calculations for target species are shown in Fig. A1 in the appendix.

line, but deviate at the extremes. Such behavior typically indicates the presence of more extreme values than expected in a truly normal distribution. Furthermore, the P-P plot underscores the presence of long-tailed data, suggesting a greater variance than what is typically anticipated in a normal distribution.

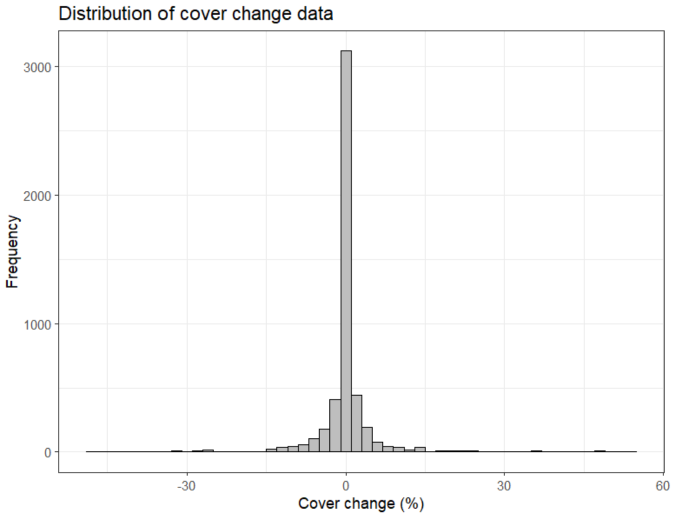


Figure 10 Distribution of abundance change data in quadrats at GLORIA sites.

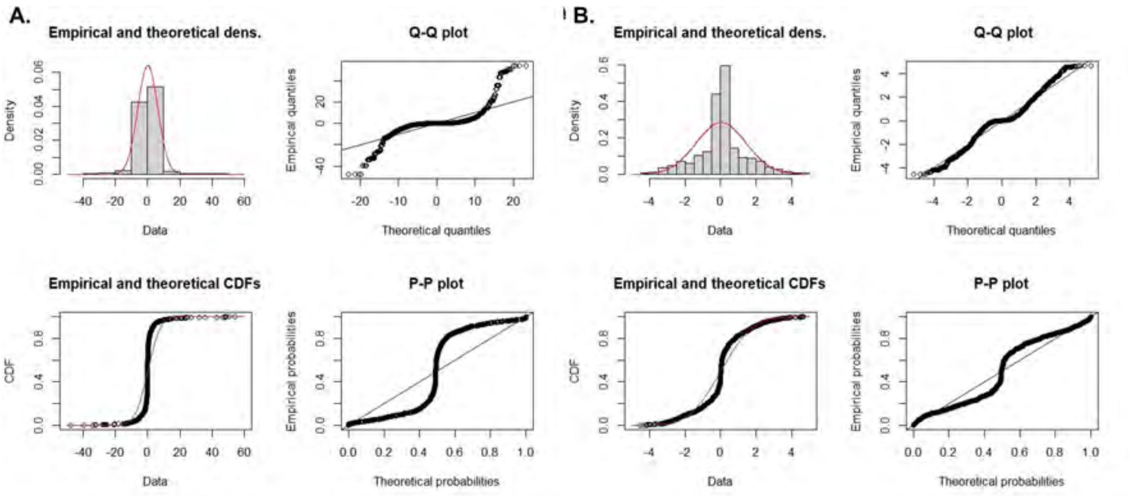


Figure 11 Analysis plots of abundance change data in quadrats at GLORIA sites. **A.** without transformation, **B.** with arcsin transformation.

To address this deviation from normality, an 'arcsin' transformation was applied (Fig. 11B). This transformation led to a notable improvement in both the Q-Q and P-P plots. As a result, the assumption of a normal distribution could be maintained, allowing for the utilization of a linear model. Acknowledging the hierarchical data structure previously mentioned, it was decided to implement a linear mixed-effect model, introducing a random factor. The model analyzes the relationship between species' abundance change (transformed using the 'arcsine' function) and the fixed effects 'temperature in 2018' and 'species name':

```
lmer(asinh_abundance_change ~ temperatur_2018 * short_name +
    (1 | plot_on_summit), data = data)
```

To revert the data to its original scale after running the linear mixed-effect model, the estimates of the fixed effects were back transformed by a 'sinh' function. To analyze how different species responded to climate change, the outcomes of this model offer insights into the second of three key variables 'temperature-dependent abundance change' as discussed in chapter 2.4..

2.3.5. Time-dependent number of occurrences

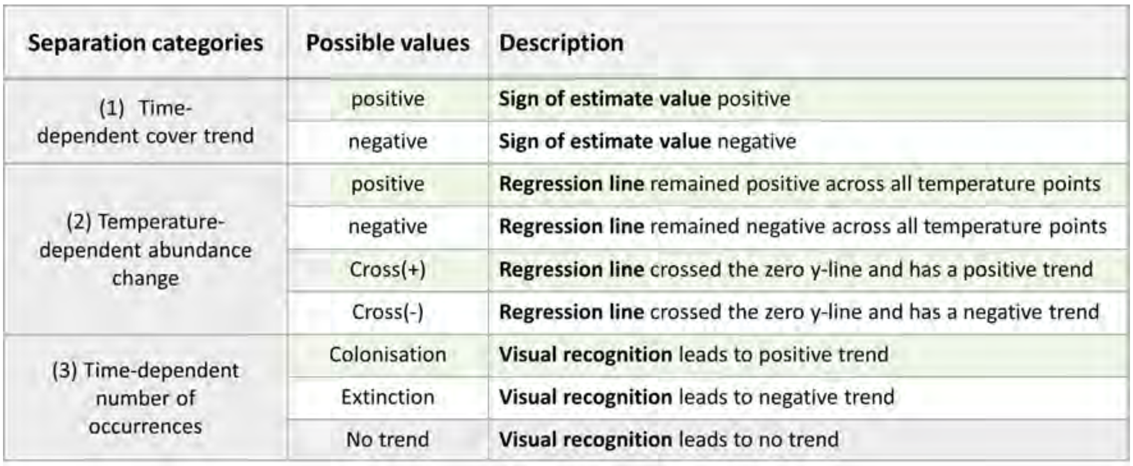
In addition to quantifying changes in vegetation abundance, I evaluated whether species have colonized new quadrats or, conversely, faced local extinction. Understanding these colonization and extinction patterns provides valuable insights into the ability to adapt and persist within the changing environment. Therefore, I plotted species occurrence counts per quadrat across the surveys. This approach allows me to visualize the processes of colonization and extinction events for each target species. It was not tested for significance but examined using visualizations. The results obtained through this visual examination served as the third of three key variables, which I referred to as 'time-dependent number of occurrences' in chapter 2.4..

2.4. Classification into winner and loser species

A method has been devised to classify species' responses into winners, losers, inconsistent responding, or not responding species. To accomplish this categorisation, three variables were taken into account: (1) time-dependent cover trend, (2) temperature-dependent abundance change, and (3) time-dependent number of occurrences. Initially, two models were executed, as described above, to determine estimates of the dependent factors for the first two variables, evaluating the presence of statistically significant estimates. For cases where both factors yielded non-significant estimates, the species were classified as 'not responding' species.

For species not falling into the 'not responding' category, the first two variables were treated differently (Table 2, (1) and (2)). While it is possible to read directly from the (1) 'time-dependent cover trend' whether trends are positive or negative, the interpretation of the (2) 'temperature-dependent abundance change' variable required a more complex interpretation: abundance-temperature relationship was assessed by analyzing the behavior of the regression line. If it remained positive across all temperature points, it was labeled 'positive'. If it remained negative across all temperature points, it was labeled 'negative'.

Table 2 Method to classify species' responses into winners, losers, inconsistent responding, or not responding species based on three separation categories: (1) time-dependent cover trend, (2) temperature-dependent abundance change, and (3) time-dependent number of occurrences. Winners categories are highlighted in green (or grey for the third category), while those from losers are highlighted in white (or grey for the third category). Species responses containing both green and white background colour are designated as 'inconsistent-reacting' species.



Separation categories	Possible values	Description
(1) Time-dependent cover trend	positive	**Sign of estimate value** positive
	negative	**Sign of estimate value** negative
(2) Temperature-dependent abundance change	positive	**Regression line** remained positive across all temperature points
	negative	**Regression line** remained negative across all temperature points
	Cross(+)	**Regression line** crossed the zero y-line and has a positive trend
	Cross(-)	**Regression line** crossed the zero y-line and has a negative trend
(3) Time-dependent number of occurrences	Colonisation	**Visual recognition** leads to positive trend
	Extinction	**Visual recognition** leads to negative trend
	No trend	**Visual recognition** leads to no trend

Further complexity arose when the regression line crossed the zero y-line. Here, it was labeled 'Cross(+)' for a positive and 'Cross(-)' for a negative trend. The reason for this was that 'Cross(+)' indicates increasing cover with warmer temperatures, which is a signal of benefit from climate change. Conversely, a 'Cross(-)' indicates that cover will decrease with rising temperatures, which is a signal of suffering from climate change.

The regression line may have a negative trend, but if it still remains positive over all temperature points, it is labeled as 'positive'. This phenomenon can be exemplified by referencing Fig. 16 featuring *Phyteuma hemisphaericum*, panel B. Conversely, a scenario could also arise in which the regression line exhibited a positive trend, despite which it managed to maintain an overall negative disposition across all temperature points. This scenario is illustrated in Fig. 16 depicting *Luzula lutea*, panel B.

To classify species into winners and losers, all three separation categories should go in the same direction. Winners exhibit (1) increasing time-dependent cover trend (positive sign), (2) positive change of temperature-dependent abundance (positive regression line throughout the gradient) or increased abundance at higher elevations (positive trend of the regression line crossing the zero y-line), and (3) increasing time-dependent number of occurrences (referred to as colonisation) or displayed no distinct trend. These criteria are highlighted with a green background in table 2.

Conversely, losers exhibit (1) declining time-dependent cover trend (negative sign), (2) negative changing temperature-dependent abundance (negative regression line across the entire gradient) or reduced cover at higher elevations (negative trend with the regression line crossing the zero y-line), and (3) declining time-dependent number of occurrences (referred to as local extinctions) or no discernible trend. These characteristics are represented with a white background in table 2. Species demonstrating opposing trends, such as (1) increased time-dependent cover trend, (2) positive changing temperature-dependent abundance, but (3) declining time-dependent number of occurrences, are identified as 'inconsistent-reactors'.

In order to weight and display the severity of a species' positive (winners) or negative (losers) response characteristics, the species were arranged and marked with a winner-to-loser gradient bar with a specific order of arrangement (as show in the result section in table 4). Among the winner species, the first group comprises those where all characteristics exhibited consistent trends. This indicates that these species (1) increased their time-dependent cover, (2) positively changed their temperature-dependent abundance (positive) or changed their abundance in high elevations (Cross+), and (3) increased their time-dependent number of occurrences. Within this group, species with significant trends in both characteristics (1 and 2) were listed first, followed by those with the greatest (1) increase in time-dependent cover. This arrangement creates a winner-to-loser gradient from red to yellow colours (Table 4). The next group includes winner species that exhibited 'no trend' in their (3) time-dependent number of occurrences, implying that these species were unable to colonize new quadrats. These species are represented in light green on the winner-to-loser gradient.

Within the loser species, first the ones with weaker declining trend were listed before those with higher decline rates. The first species to be listed were those with (1) declining time-dependent cover, (2) negative changing temperature-dependent abundance, and no clear trend in their (3) time-dependent number of occurrences. These species are shown in blue in the winner-to-loser gradient. Towards the end of the Table 4, loser species were listed for which all characteristics showed consistent declining trends. Among these species, those with the smallest estimated beta-values for their (1) time-dependent cover trend were listed first, and those with two significant estimates of (1) and (2) were listed last. These species are represented in purple.

2.5. Characterization of winner and loser species

A variety of sources have been used to characterize the winner and loser species. First, the species were characterized based on their indicator values and morphological, ecological, and dispersal traits. Second, the focus shifted to a regional scale within the canton of Grisons of a time span of a century. This research focused on identifying disparities between winners and losers in regional range shifts at their leading and rear edges as well at their range area.

2.5.1. Indicator values

For characterization of the winner and loser species, indicator values from the 'Flora Indicativa' book were used (Landolt *et al.*, 2010). It provides insights into ecological characteristics using indicator values for plant species' niche spaces along a variety of ecological gradients. While Landolt values are developed and used for Swiss plant species, a similar system called Ellenberg Indicator Values is common in Germany. Moreover, alongside, a number of morphological and ecological traits listed in Landolt *et al.* (2010) were selected and analyzed for differences between winners and losers. I visualized all available indicator values and selected those displaying changes between winners and losers. This selection was divided into morphological, ecological, and dispersal traits resulting in a total of twelve analyzed traits. Data transformation steps were executed to enhance clarity and facilitate a more straightforward analysis:

When faced with the presence of multiple values within a single species, a transformation step was implemented to manage this variability and streamline the data. In this systematic approach, all variables for each species were multiplied (each value received one row), creating a comprehensive representation. As a result, one species can yield multiple data points in the analysis, leading to certain traits having more data points than the number of species analyzed. This approach was employed for the 'Reserve And Storage Organs' (RO), 'Vegetative Dispersal' (VA), 'Pollination System' (BS), and 'Diaspore Dispersal' (DA) traits. For both the 'Pollination System' (BS) and 'Diaspore Dispersal' (DA) traits any values enclosed within brackets, which held subordinate meaning, were removed from the dataset.

Another transformation step involved the consolidation of different values into more general categories. These data transformations were carried out to enhance clarity and simplify the analysis across various species in my study. Within the 'Reserve And Storage Organs trait' (RO), distinct values were aggregated into 'roots,' 'rhizomes,' and 'no such organs.' In our examination of 'Vegetative Dispersal Traits' (VA), the diverse values were classified into four distinct groups: 'above ground,' 'underground,' 'bulbils,' and 'no vegetative dispersal.' For the 'Pollination System' (BS), the categories were amalgamated into 'wind dispersal,' 'animal dispersal,' and 'water dispersal.' Similarly, in the case of 'Diaspore Dispersal' (DA), the diverse values were reduced into the three categories of 'wind dispersal,' 'animal dispersal,' and 'water dispersal.

Root depth (WT) is a categorical variable, but some species had intermediate values. To reduce the number of different possible categories, species bearing intermediate values were categorized with the next lower category. I encountered species with values such as 1.5 and 2.5, which can be somewhat cumbersome to work with. To simplify my analysis, these species have been given labels corresponding to their root depth values. For example, species with a root depth value of 1.5 were labelled '1'. Similarly, species with a root depth value of 2.5 were labelled '2'. This labelling system streamlines the data and allows for easier reference and interpretation.

To assess potential differences in traits between winner and loser species, I conducted a Chi-square test in combination with a Fisher's test. The Fisher's test was employed due to the presence of many values in the Chi-square table being smaller than five. In such instances, I calculated the exact p-value using the Fisher's test, which was used to determine the significance of my findings.

2.5.2. Range shifts

To gain a general overview of elevational range limit changes on a regional scale and over the period of one century, I used data of historical and recent upper and lower distribution limits from literature and data base records across the canton of Grisons.

Historical elevation limits

As historical elevation distribution data, I used the work 'Flora von Graubünden' (Braun-Blanquet and Rübel, 1932). It was published between 1932 and 1934 and contains data on the then lowest and highest sites of all plant species in different regions of Grisons, as known from publications, own research, and herbaria records at the time. To ensure the comparability with the GLORIA data set, some species were renamed with the Flora Europaea nomenclature, as listed in Table 3.

Table 3 Replacement of species names with Flora Europaea nomenclature in the data sets 'Flora von Graubünden' and 'InfoFlora'.

Source	**Species name at source**	**Flora Europaea nomenclature**
Flora von Graubünden; InfoFlora	*Sesleria caerulea*	*Sesleria albicans*
Flora von Graubünden	*Anemone vernalis*	*Pulsatilla vernalis*
Flora von Graubünden	*Chrysanthemum alpinum*	*Leucanthemopsis alpina*
Flora von Graubünden	*Kobresia bipartita*	*Kobresia myosuroides*
Flora von Graubünden	*Sesleria disticha*	*Oreochloa disticha*
InfoFlora	*Chrysanthemum alpinum*	*Leucanthemopsis alpina*
InfoFlora	*Elyna myosuroides*	*Kobresia myosuroides*
InfoFlora	*Helictotrichon versicolor*	*Avenula versicolor*
InfoFlora	*Saxifraga exarata subsp. moschata*	*Saxifraga moschata*

The book 'Flora von Graubünden' had organized the Grisons region into eleven distinct areas, referred to as 'Bezirk' in German, such as Upper Engadin, Lower Engadin, and Prättigau. These divisions were established according to the natural geographical separation of mountain ranges. However, these historical regions did not align with the recent administrative divisions of Grisons. To address this discrepancy, I utilized QGIS 3.26 Buenos Aires to digitize the boundaries of the historical regions using a map from 'Flora von Graubünden' as template (Fig. 12).

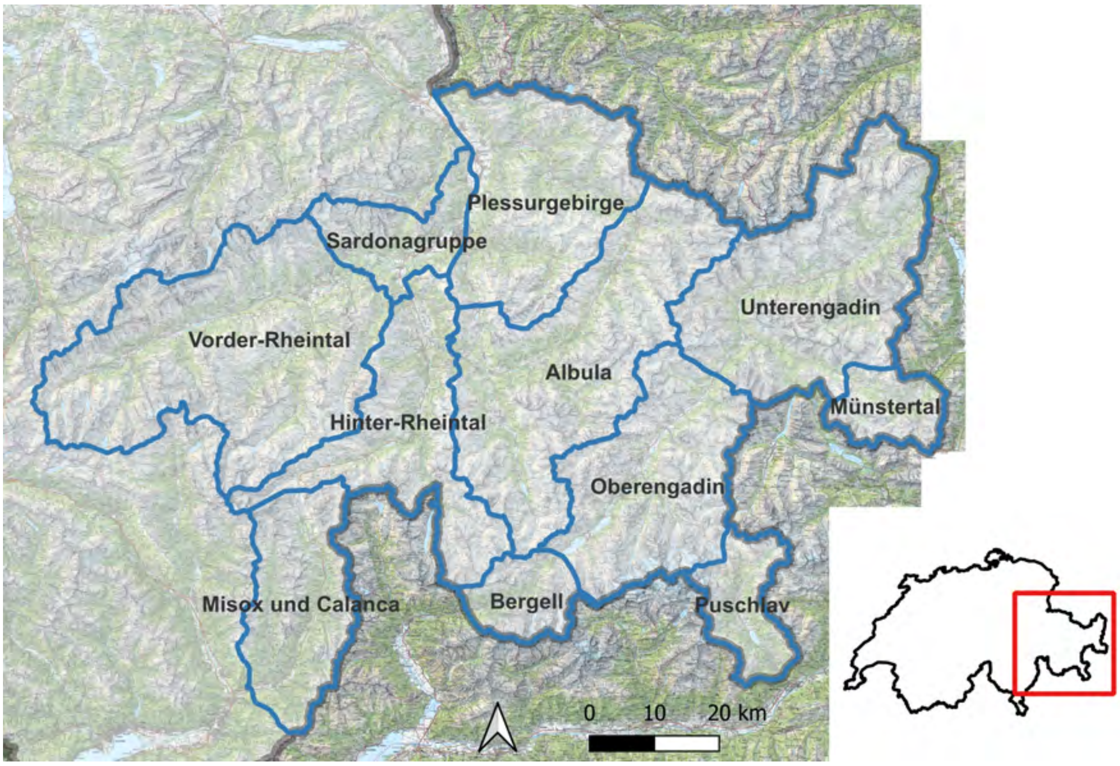


Figure 12 Historical regions of the canton of Grisons, Switzerland following the natural geographical division of mountain ranges. A map from Braun-Blanquet and Rübel (1932) served as template.

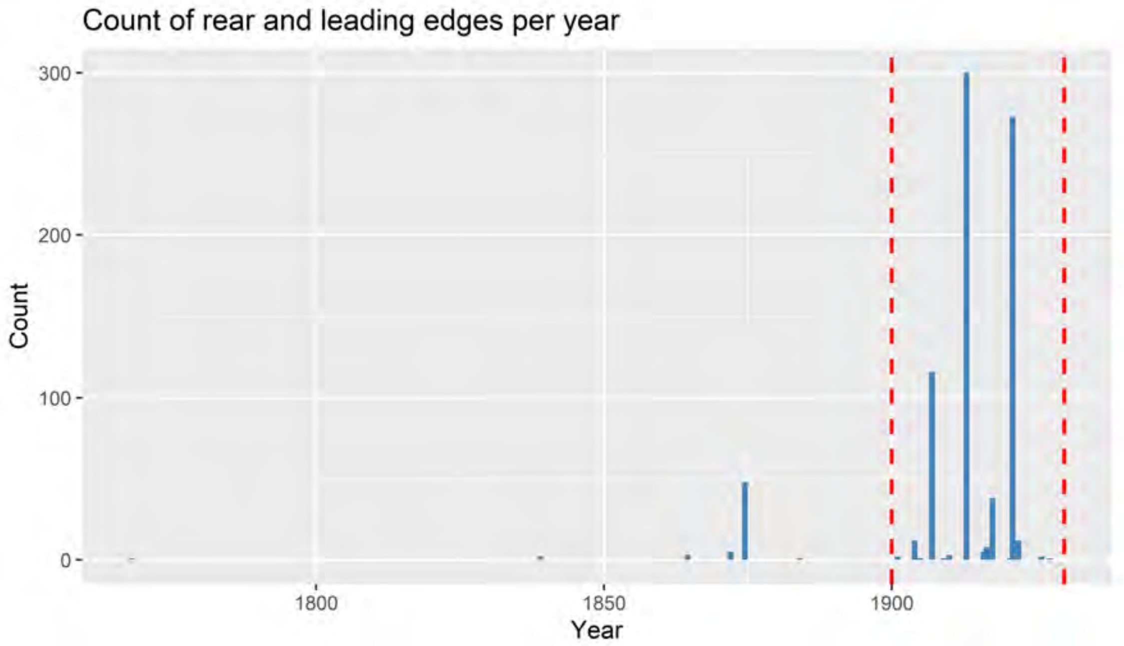


Figure 13 Number of highest and lowest locations per historical region in Grisons, Switzerland, of the target species per year. Information has been extracted from the book 'Flora von Graubünden' (Braun-Blanquet and Rübel, 1932). The area between the red dashed lines symbolises the data set used for subsequent analyses, ranging from 1900 to 1930 (30 years).

For each target species, I identified the highest and lowest locations within each of these historical regions. I also consulted the respective original data sources to assign a year to each location. If the time reference of one location covered a period of time, the mean value was used. These data sources covered a wide time frame, ranging from 1573 to 1930. The majority of the data points are concentrated from 1900 onward, as shown in Fig. 13.

To ensure data precision and comparability with recent data (see below), a deliberate decision was made to exclude sources originating before 1900 from the data set. In contrast, sources not relating to a year were left in the data set. This strategic inclusion of such sources ensures a diverse range of data points.

Recent elevation limits

To determine the current lowest and highest range limits of the target species, I used data of the central plant species database of Switzerland 'InfoFlora', which collects all observations of the Swiss flora with coordinates and altitudes and contains data both from professional monitoring projects as well from citizen scientists.

I requested locations of target species throughout Grisons with their specific elevation information. Even in the cases where the locations were only available at a 1x1-kilometer resolution, I was able to obtain the original elevation data. As most of the data is available from 1992 onward (Fig. 14), I excluded data prior to this year to ensure a consistent comparative analysis with the historical data covering a 30-year period. This deliberate decision ensures a time span of recent data that is consistent with the historical data.

In QGIS, recent data points between 1992 and 2022 were linked with their respective historical regions (Fig. 12). For each target species within each region, the highest and lowest surveys were determined and compared with the respective historical value from 1900 to 1930, 92 years prior.

In my detailed analysis at the leading edge, I counted all regions where recent elevations were higher compared to historical data. I also calculated regions with recent elevations lower than historic ones, and determined the differences. As a result, I obtained a single value for each species. Positive values indicated an upward shift of the leading edge, while negative values indicated a downward shift.

Similarly, I applied the same methodology to the rear edge. I calculated regions with lower recent elevations and regions with higher recent elevations, and again computed the difference between these values. Positive values indicated a downward shift, while negative values indicated an upward shift in the species' rear edge.

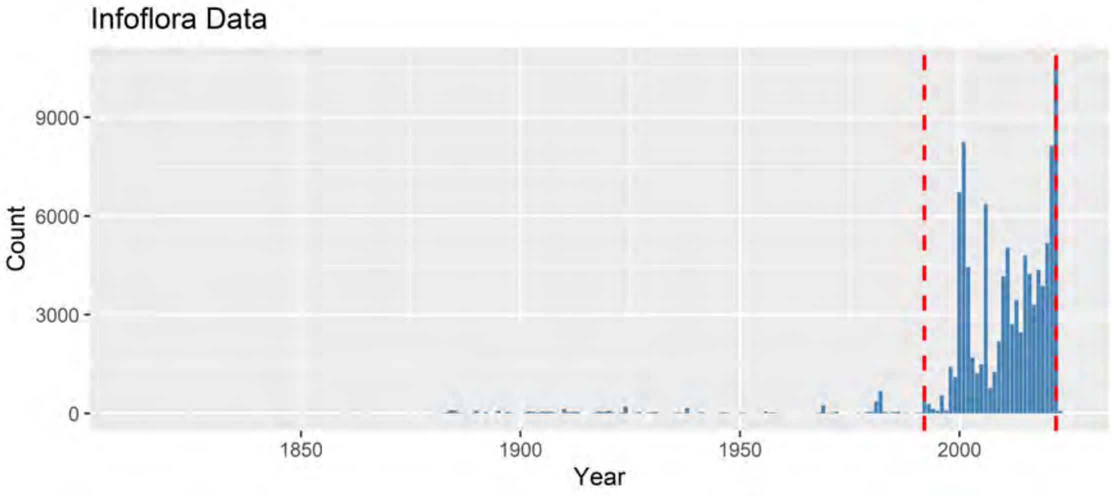


Figure 14 Number of available recent data points of target species locations per year. Data were used from the central plant species database of Switzerland 'InfoFlora'. The area between the red dashed lines symbolises the data set used for my subsequent analyses, ranging from 1992 to 2022 (30 years).

Classification of range area shifts

When considering changes in the distribution area of a species, the movement of its leading and rear edge plays a crucial role (Fig. 15). If the leading edge moves downward while the rear edge moves upward, the result is a reduction in the species' distribution range. In other words, the species is retreating or becoming less prevalent in this area. Conversely, when both the leading and rear edges move downward, this indicates a downward shift in the distribution range. The species is still present, but its habitat has shifted towards lower altitudes. On the contrary, if both edges move upward, the species is undergoing an upward shift. This implies that the species is now found at higher altitudes than before. In the case where the leading edge moves upward while the rear edge moves downward, the species is expanding its distribution range. This indicates that the species is now being detected in locations it formerly did not occupy.

Figure 15 Possible reactions of target species between historical (from 1900 to 1930) and recent distribution ranges (from 1992 to 2022). Orange arrows indicating range edge reduction, blue arrows range edge expansion.

In summary, monitoring the movements of both the leading and rear edges provides valuable insights about how a species responded to changing environment and whether its distribution area is contracting, shifting, or expanding. Therefore each target species was assigned to one possible value (reduction, downward shift, upward shift or expansion) based on there behavior on there leading and rear edges (Fig. 15).

2.6. Excursus: Shift of rear edges

To comprehensively understand distribution shifts of high alpine plant species, it is essential to study both the leading and the rear edge. However, obtaining valuable data for the rear edge presents unique challenges. Determining the lowest location of a species from existing data sets, i.e. InfoFlora as described in chapter 2.5.2, can be challenging due to uncertainty over whether botanists actively searched for the lowest point or randomly sampled sites, which is more probable. In contrast, data collection at the leading edge is more obvious, as summits have a natural limit to their highest point.

Extreme habitats such as rocks, riverbeds, and avalanche channels add complexity, as high alpine plant species often grow much lower than expected due to unique (climatic) conditions. For example, rocky environments can experience more extreme temperature variations, and riverbed dynamics can lead to high alpine plants growing much lower, where floods and associated disturbances keep competitors away. Therefore, it is crucial to distinguish between the lowest points within the expected distribution area and extreme habitats such as rocks, riverbeds, and avalanche channels, as extreme habitats strongly influence the rear edges.

To address the problem of often not having reliable data on rear edges, I would like to present a method I used in the summer of 2022 to generate reliable data on the rear edges. Vegetation surveys on rear edges were carried out simultaneously to surveys on GLORIA summits. Therefore, during the survey, it was uncertain which target species on the GLORIA summits would be selected for the vegetation change analysis. As a result, the species of the rear edge project do not align with target species of GLORIA summits, preventing the integration of my results into the main study. Nevertheless, I would like to include it as an excursus to encourage further research on rear edges.

2.6.1. Data collection

To assess the rear edge shift over long time periods, 22 high-alpine plant species that are easily recognisable in the field were chosen. The historically lowest populations in the area of the Swiss National park were located and resurveyed whether they were still present, or had shifted in elevation. To locate the lowest populations, data from the ’Flora des Schweizerischen Nationalparks und seiner Umgebung’ by Heinrich Zoller (Zoller, 1964) was used. In this flora, many lower distribution limits are listed with altitude and location. Mostly, however, an entire valley or mountain is indicated without very precise location information. Assuming that H. Zoller surveyed easily accessible places such as near hiking trails at the time, the resurveys were limited to such places. Maps were created in ArcGIS, using the available information, to mark the potential historical lower range limit.

In the summer 2022, the estimated sites of plant populations at their lower range limit were resurveyed and their current altitude of the lowest occurrence recorded (if the species was found at all). To achieve this, I searched for the specific plant species within a predefined search range (often along paths) from approx. 100 m below the historical occurrence until approx. 200 m above that site. Within that range, all suitable habitats were surveyed. However, when multiple target species were searched within the same region but at different elevations, it could happen that a species was relocated further away from the historical limit than these predefined search areas.

For each location, a determination was made to identify extreme habitats such as rocks, riverbeds, and avalanche channels. In cases where these extreme habitats were confirmed, data was used only if I could ascertain that these habitats have remained nearly unchanged since the historical surveys. For example, if a species had its lowest historical location in an avalanche channel that no longer exists, its recent occurrence is not predominantly influenced by shifts in temperature but rather by the disturbance regimes. These locations were not considered for the analysis.

To ensure accurate data collection, I employed the FlorApp developed by InfoFlora. This technology enabled us to document the precise coordinates and abundance levels of the target species at each location.

2.6.2. Data analysis

The locations were digitized and the difference of relocated and historical elevation was calculated. Additionally the data from InfoFlora was used to get additional information about recent locations. Locations deviating more than 500 meters in elevation from the historic elevation were not used.

2.7. Relationship between local abundance change and regional range area shift

In an effort to understand whether changes in a species' abundance on a local scale (measured over 20 years at the GLORIA sites) can serve as a predictor for the shift in its range on a regional scale (spanning a century in the Grisons region), I employed regression analysis. Specifically, I conducted an analysis to explore the relationship between changes in species abundance and elevation. Furthermore, I compared these results to range area shifts observed for each species.

The regression based on abundance change and elevation was not used to classify target species as winners or losers; the classification relied on the relationship between abundance change and temperature (as discussed in chapter 2.4.). For the purpose of comparing range shifts associated with elevation, it is more meaningful to evaluate the elevation-dependent abundance change (for this please also see Fig. A2 in the appendix).

To enable a meaningful comparison between the local changes in abundance and the regional shifts in range area, I divided the elevation-based regression results for the target species into three distinct groups: ’positive’, ’cross’, and ’negative’ (Table 5).

’Positive’ indicated the regression line stayed positive for all elevations, regardless of the trend direction. Conversely, ’negative’ indicated that the regression line stayed negative across all elevations. I added ’(+)’ and ’(-)’ labels to specify the trend of the regression line. ’(+)’ signified an increase in abundance with rising elevation, while ’(-)’ indicated the opposite trend. ’Cross’ signaled the regression line crossed the y-axis at zero, indicating a change in the direction of abundance change within the elevation gradient. In terms of ecological interpretation, both ’positive’ (whether labeled ’(+)’ or ’(-)’) and ’cross(+)’ suggested that species benefited from higher temperatures at a local scale. Conversely, ’negative’ and ’cross(-)’ implied that species were negatively impacted by rising temperatures. This classification allowed us to better understand how temperature changes influenced species abundance at different elevations. Afterwards, I compared the categorization of local elevation-dependent abundance change with the regional area shifts for each species.

3. Results

3.1. Individual species reaction to rising temperatures

Half of the target species, a total of 25 out of 51 species, exhibited no significant time- or temperature-dependent changes in cover within the 1x1 metre quadrats on GLORIA sites (see Table A1 in the appendix, species in bold). In the effort to decipher the dynamics of species responses in changing cover and occurrences, Fig. 16 presents a comprehensive overview of the species that exhibit significant changes in their cover patterns (Fig. 16, A and B). The time-dependent number of occurrences (Fig. 16, C) did not undergo significance testing.

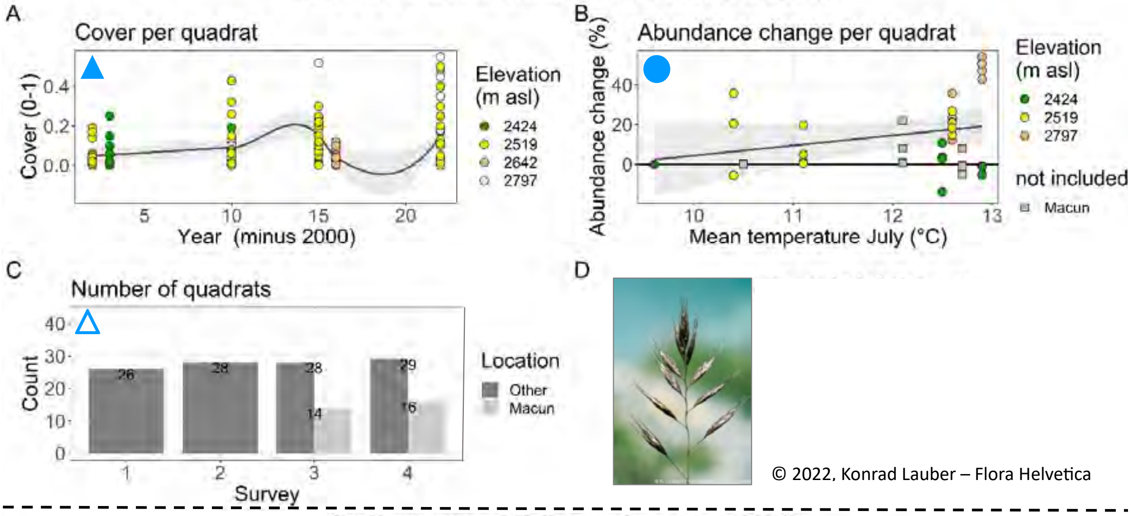
A total of 26 species demonstrated significant trends in at least one category (Fig. 16, A and/or B). Notably, *Avenula versicolor* and *Saxifraga oppositifolia* emerged as major beneficiaries of rising temperatures, with their (A) significant increase in time-dependent cover and (B) significant positive change of temperature-dependent abundance. In contrast, *Potentilla aurea* experienced the greatest challenge, with significant negative trends evident in categories A and B.

Species that consistently shifted in the same direction across all categories (A, B, and C) while only displaying significance in either category A or B, providing a clear indication of their response to rising temperatures. *Vaccinium vitis-idaea*, *Phyteuma hemisphaericum*, *Veronica bellidioides*, *Poa laxa* and *Euphrasia salisburgensis*, showed (A) increases in their time-dependent cover trend, (B) positive changes in temperature-dependence abundance, and (C) increases in their time-dependent number of occurrences, showing a clear tendency to spread under warmer conditions. Conversely, *Minuartia sedoides* and *Arenaria ciliata* experienced a (A) decrease in their time-dependent cover trend, a (B) negative change in their temperature-dependence abundance, and (C) a decrease their time-dependent number of occurrences, highlighting their vulnerability to the effects of climate change.

In several cases, the time-dependent number of occurrences (Fig. 16, C) did not exhibit a discernible trend, while the other categories moved consistently in the same direction. Notably, this pattern is evident in species such as *Campanula scheuchzeri*, *Sesleria albicans*, *Ligusticum mutellina*, *Euphrasia minima*, and *Dryas octopetala*, which clearly benefit from rising temperatures, and in *Luzula spicata*, *Erigeron uniflorus*, *Antenaria carpathica*, and *Poa alpina*, which fall under the category of suffering species.

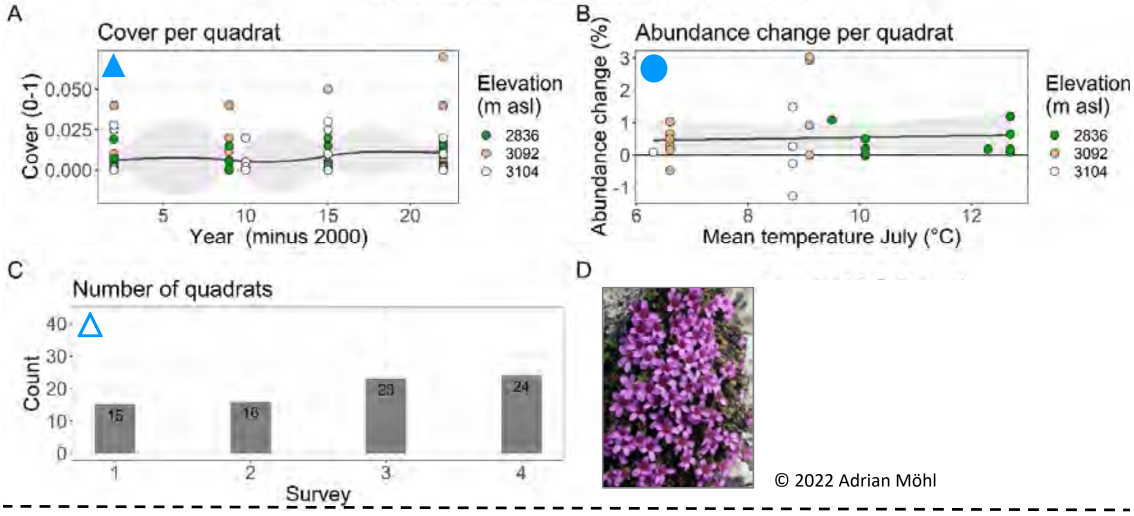
The species *Carex ericetorum*, *Gentiana nivalis*, *Saxifraga bryoides*, *Festuca quadriflora*, *Geum montanum*, and *Luzula lutea* displayed variable responses across the three characteristics and were classified as species with a ’inconsistent response’ (Table A2).

Avenula versicolor (Vill.) M.Laínz subsp. versicolor



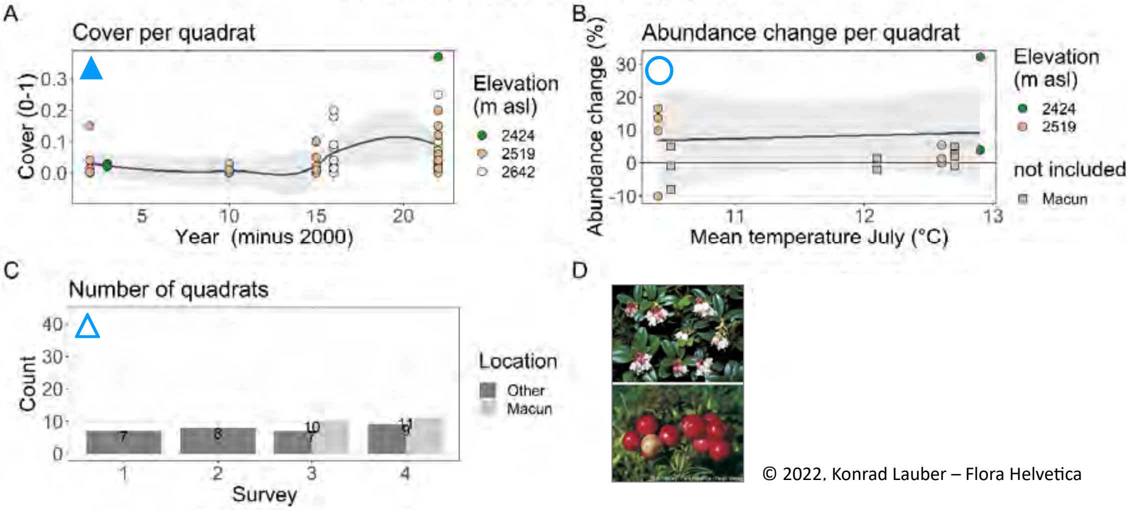
© 2022, Konrad Lauber – Flora Helvetica

Saxifraga oppositifolia L. subsp. oppositifolia



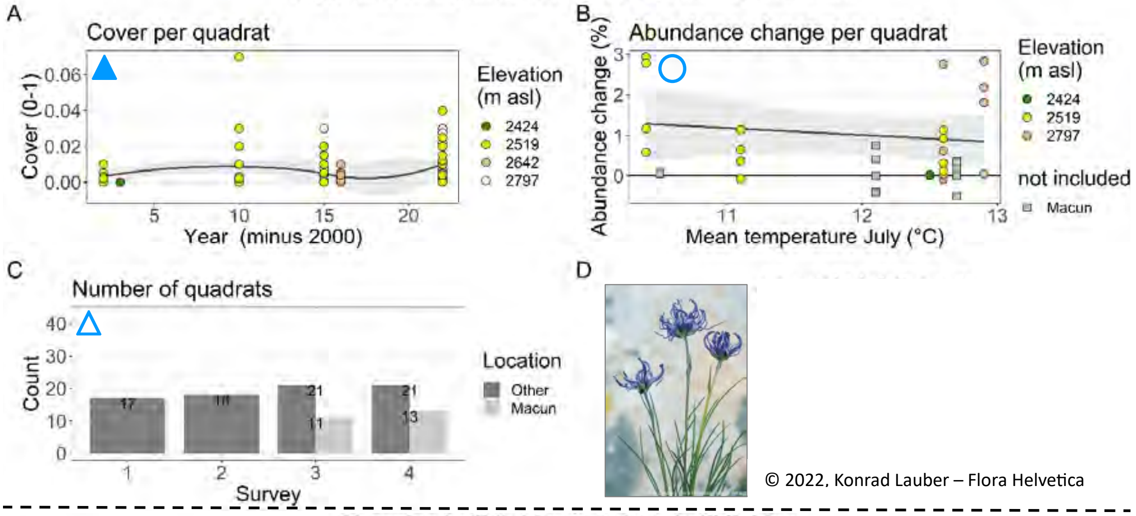
© 2022 Adrian Möhl

Vaccinium vitis-idaea L. subsp. vitis-idaea



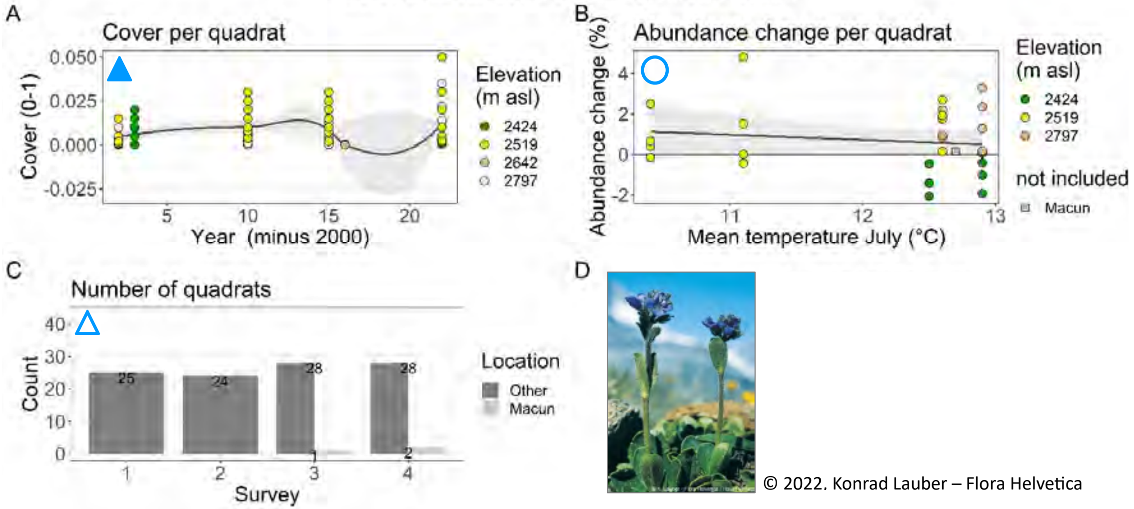
© 2022. Konrad Lauber – Flora Helvetica

Phyteuma hemisphaericum L. subsp. hemisphaericum



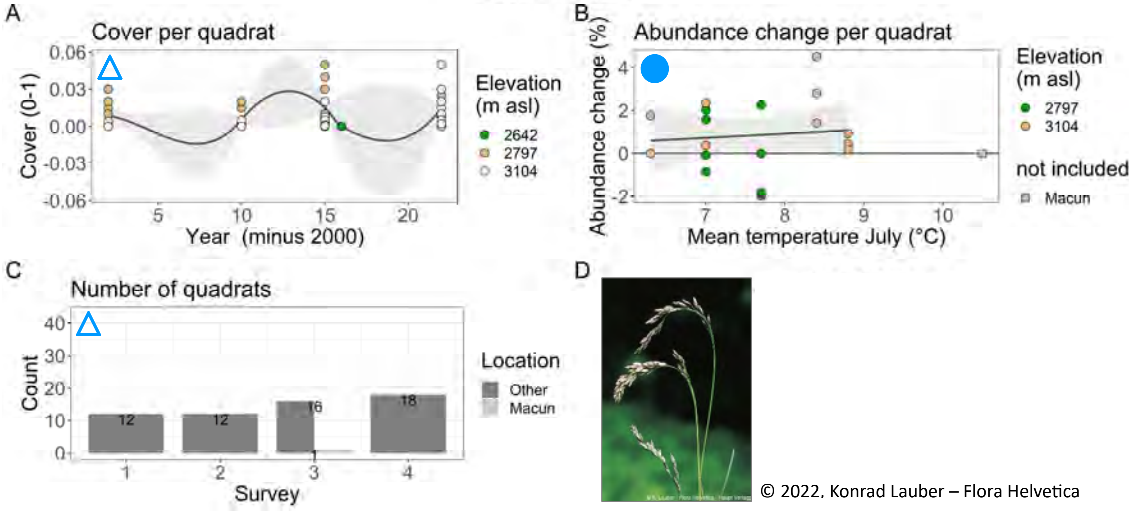
© 2022, Konrad Lauber – Flora Helvetica

Veronica bellidioides L. subsp. bellidioides



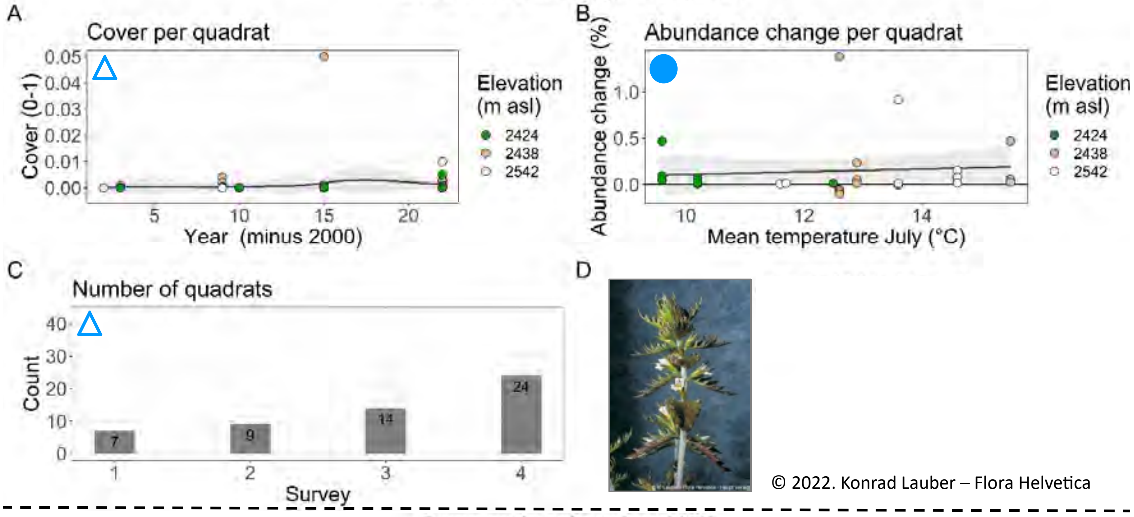
© 2022, Konrad Lauber – Flora Helvetica

Poa laxa Haenke



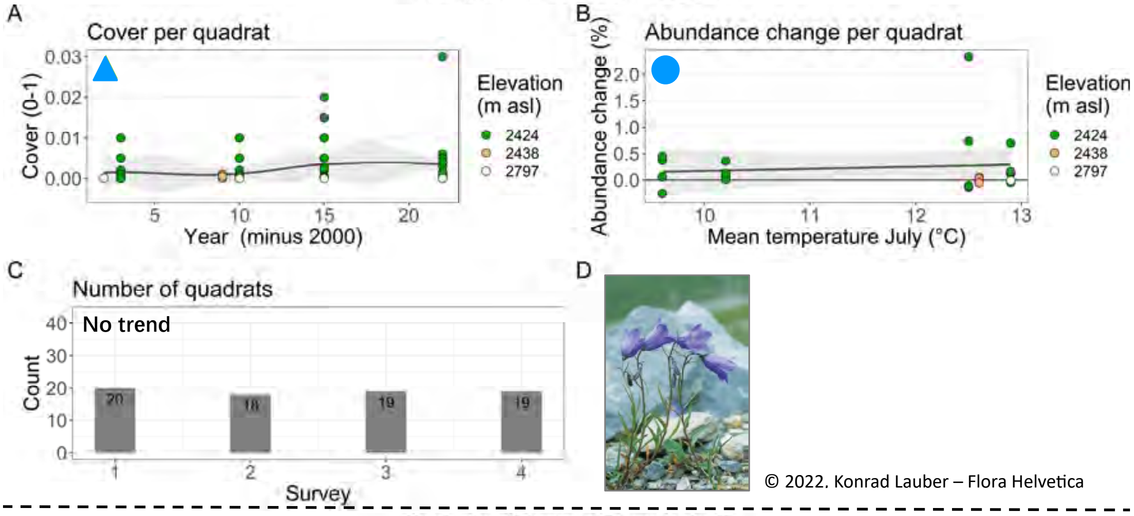
© 2022, Konrad Lauber – Flora Helvetica

Euphrasia salisburgensis Funck



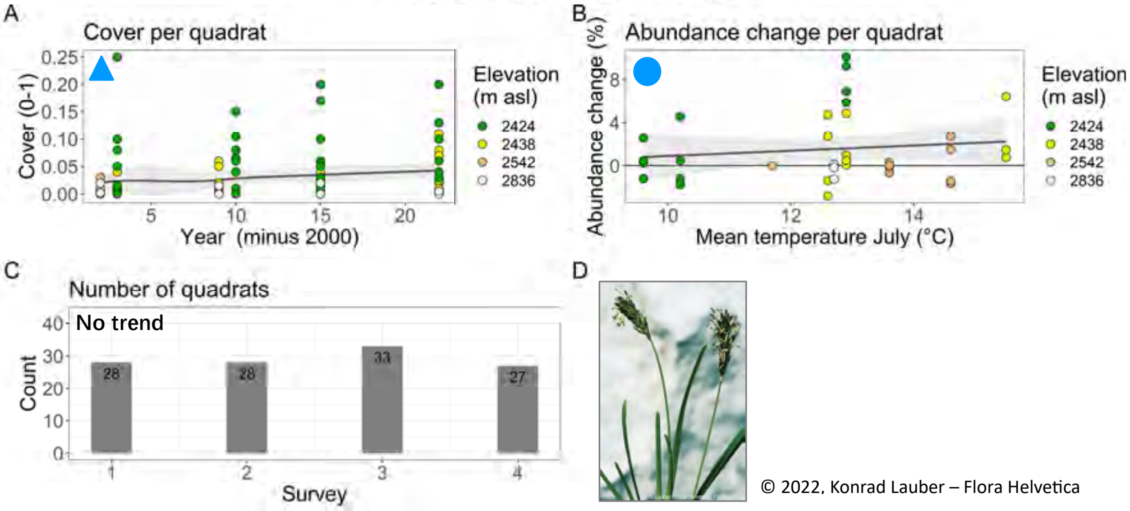
© 2022. Konrad Lauber – Flora Helvetica

Campanula scheuchzeri Vill.



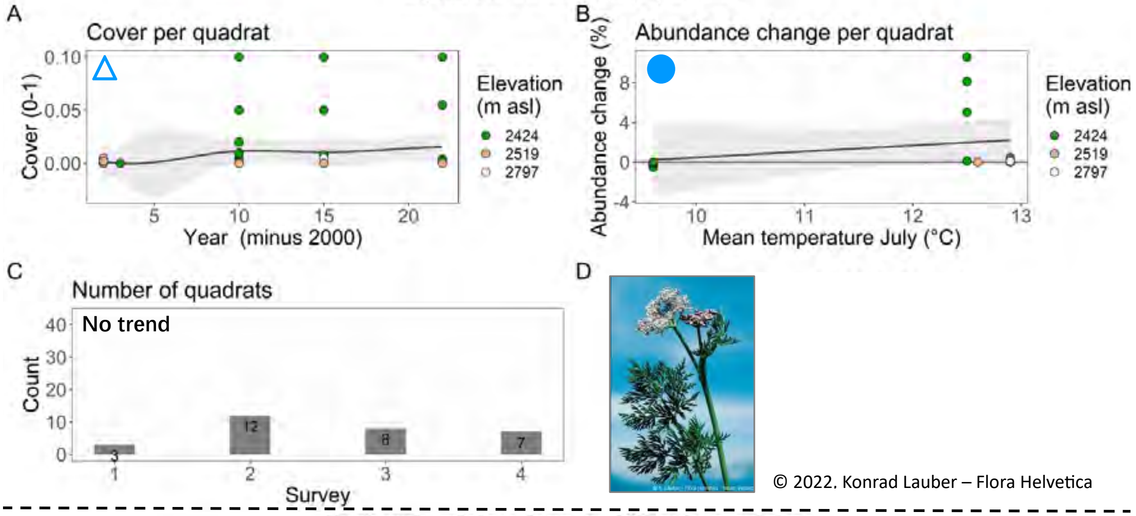
© 2022. Konrad Lauber – Flora Helvetica

Sesleria albicans Kit. ex Schult.



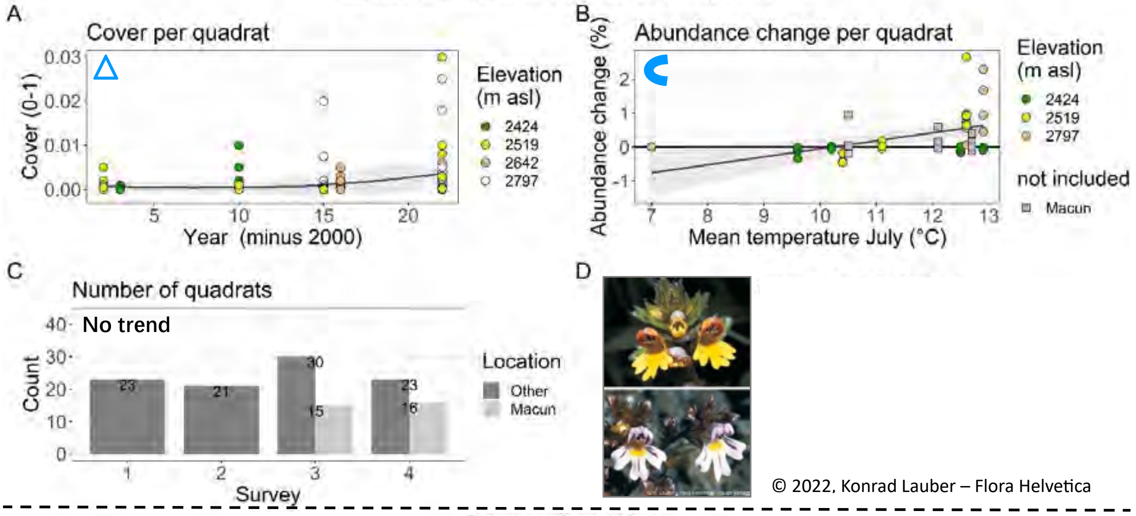
© 2022. Konrad Lauber – Flora Helvetica

Ligusticum mutellina (L.) Crantz



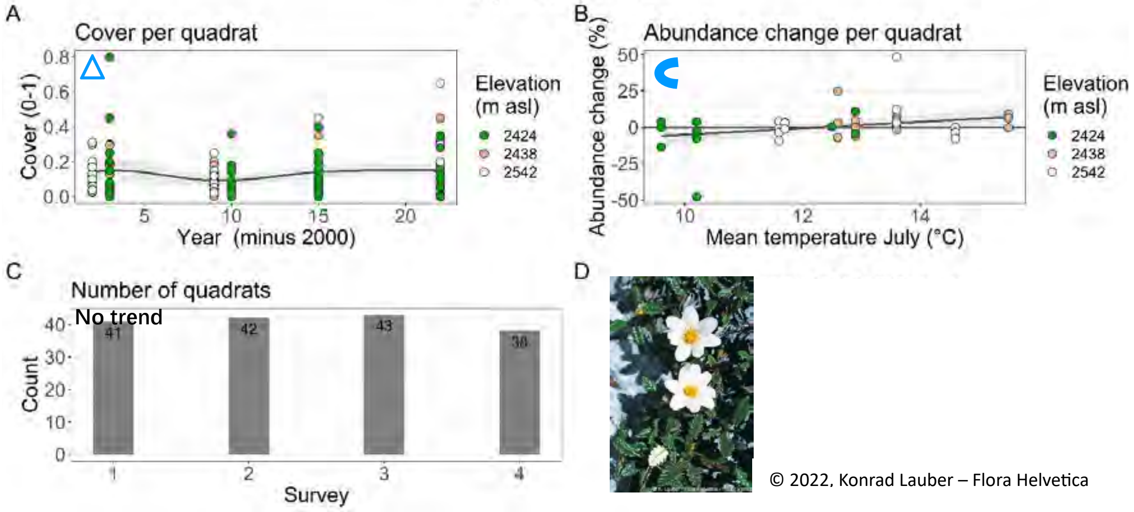
© 2022. Konrad Lauber – Flora Helvetica

Euphrasia minima Jacq. ex DC. subsp. minima



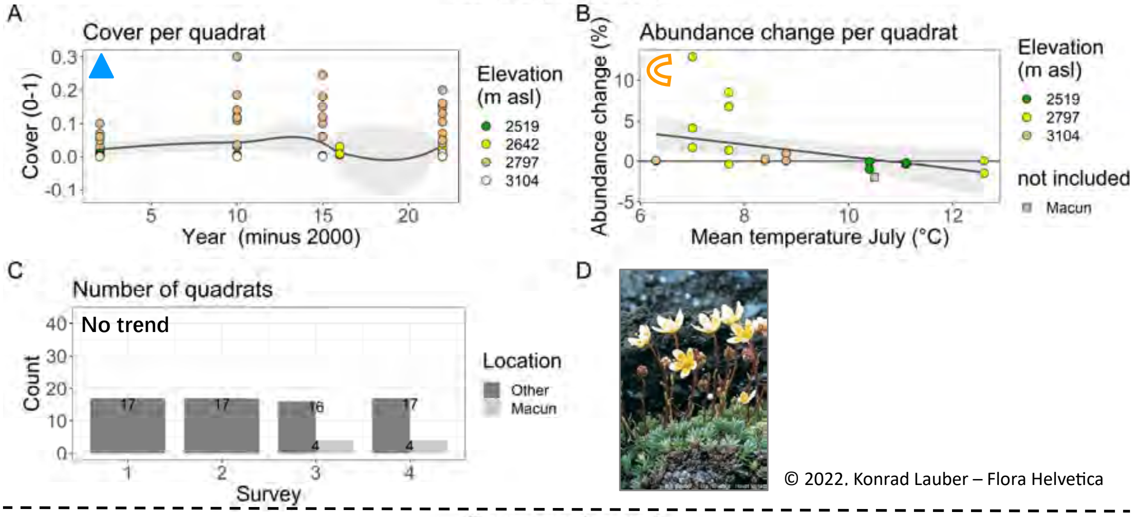
© 2022. Konrad Lauber – Flora Helvetica

Dryas octopetala L.



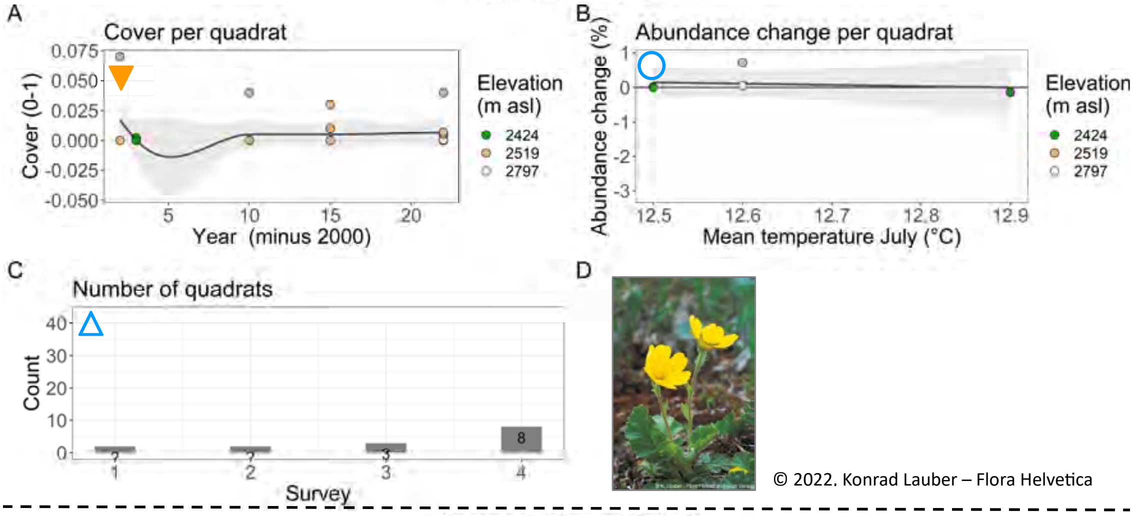
© 2022. Konrad Lauber – Flora Helvetica

Saxifraga bryoides L.



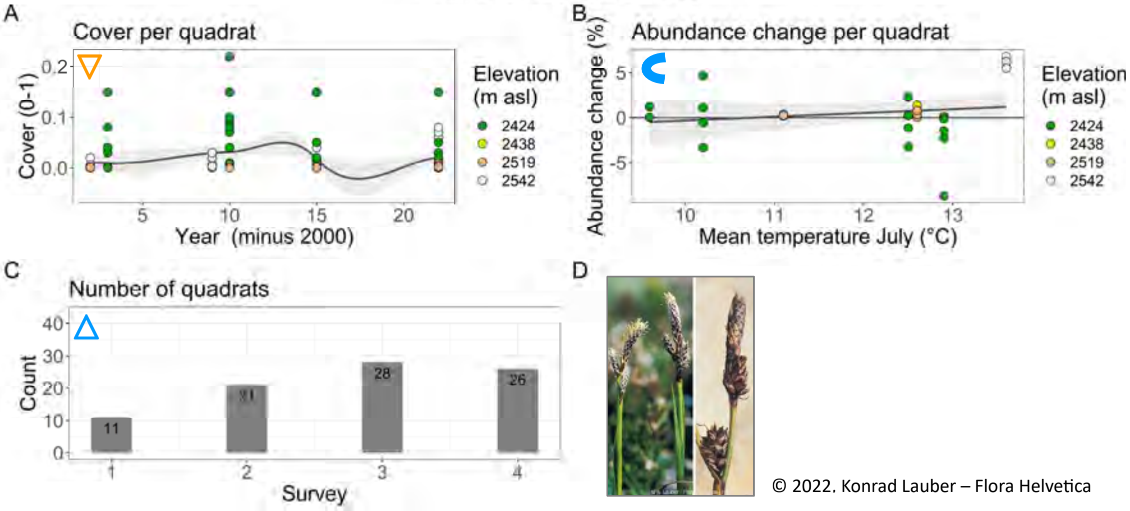
© 2022. Konrad Lauber – Flora Helvetica

Geum montanum L.



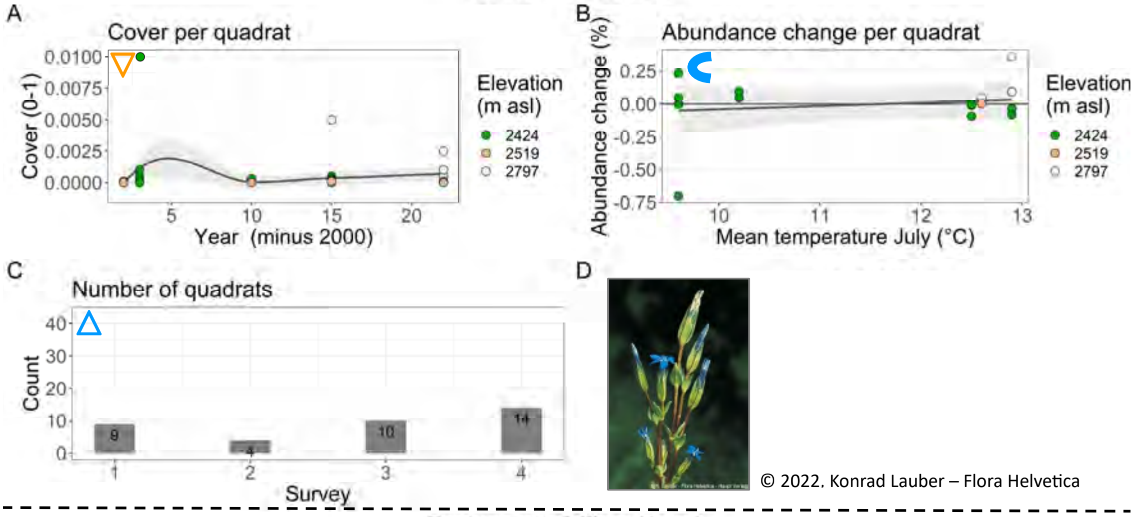
© 2022. Konrad Lauber – Flora Helvetica

Carex ericetorum Pollich



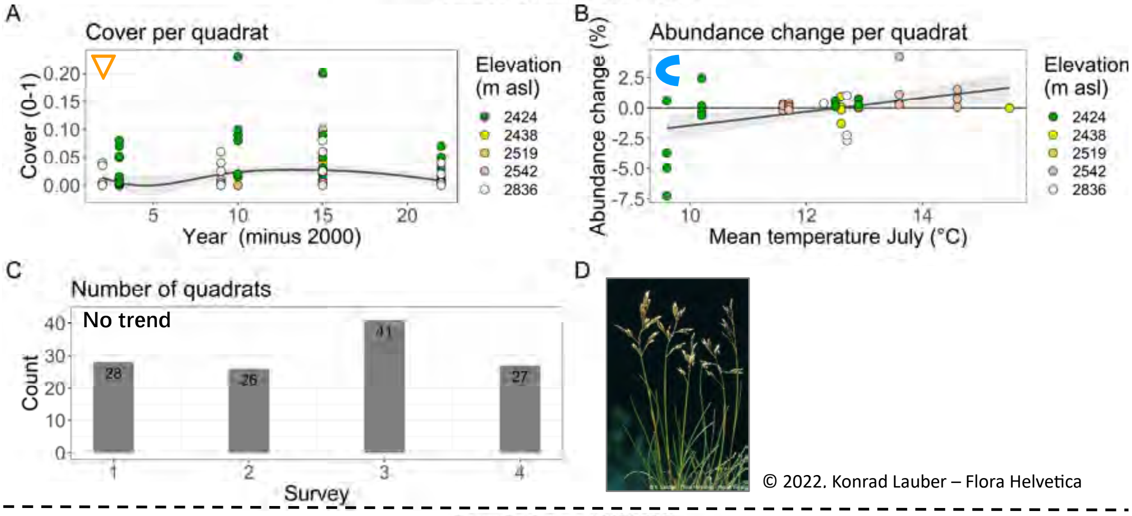
© 2022. Konrad Lauber – Flora Helvetica

Gentiana nivalis L.



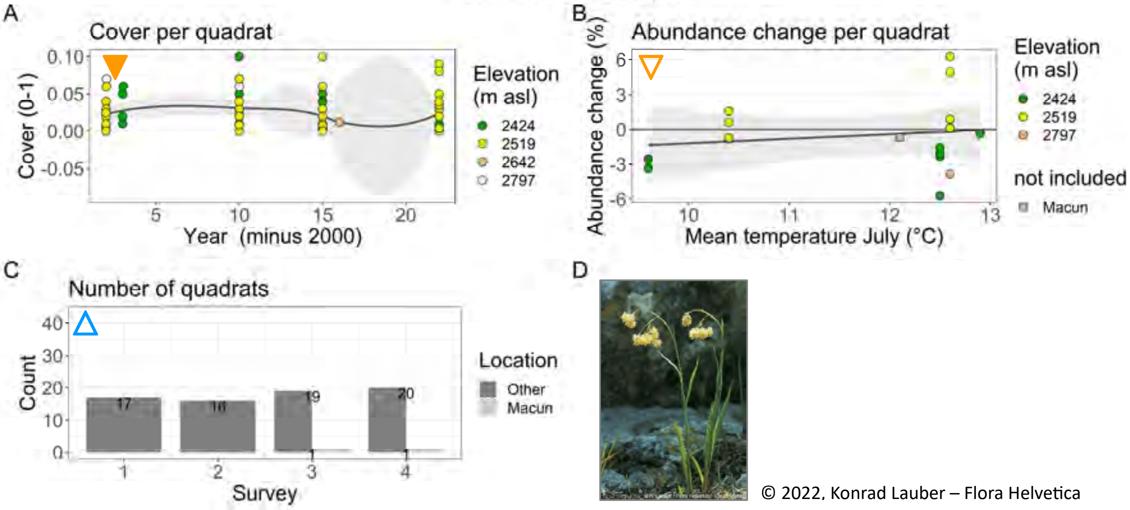
© 2022. Konrad Lauber – Flora Helvetica

Festuca quadriflora Honck.



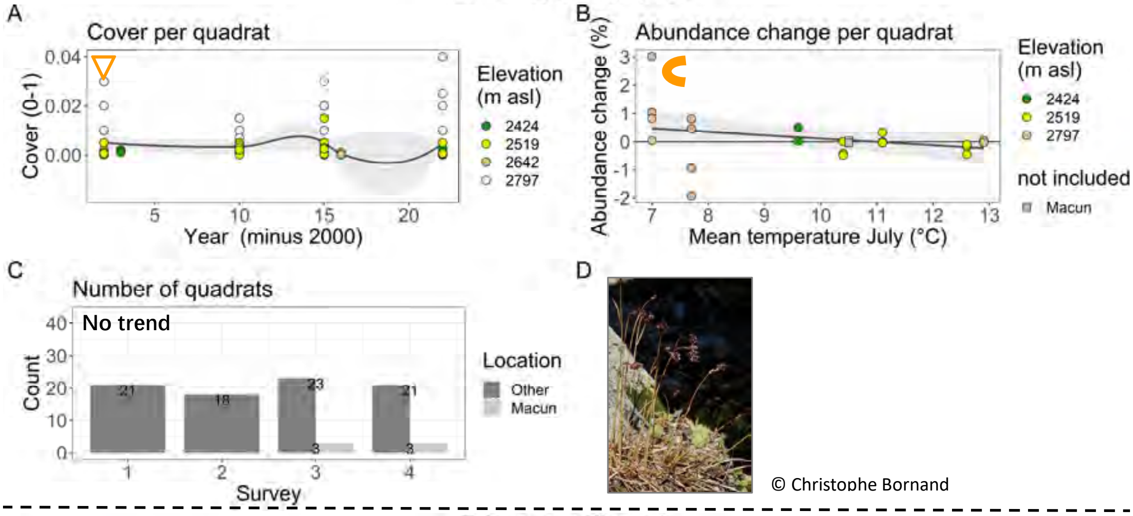
© 2022. Konrad Lauber – Flora Helvetica

Luzula lutea (All.) DC.



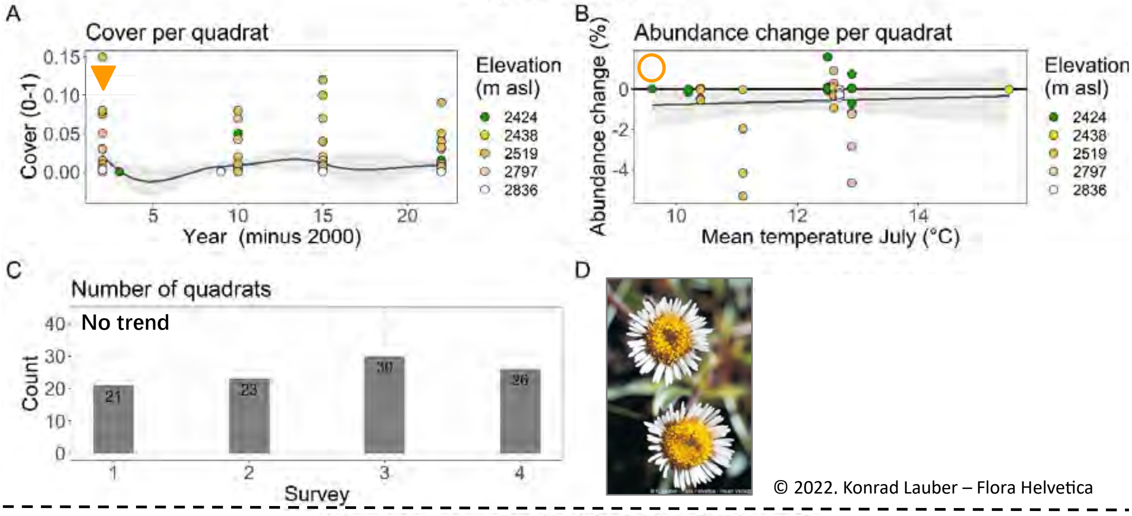
© 2022. Konrad Lauber – Flora Helvetica

Luzula spicata (L.) DC.



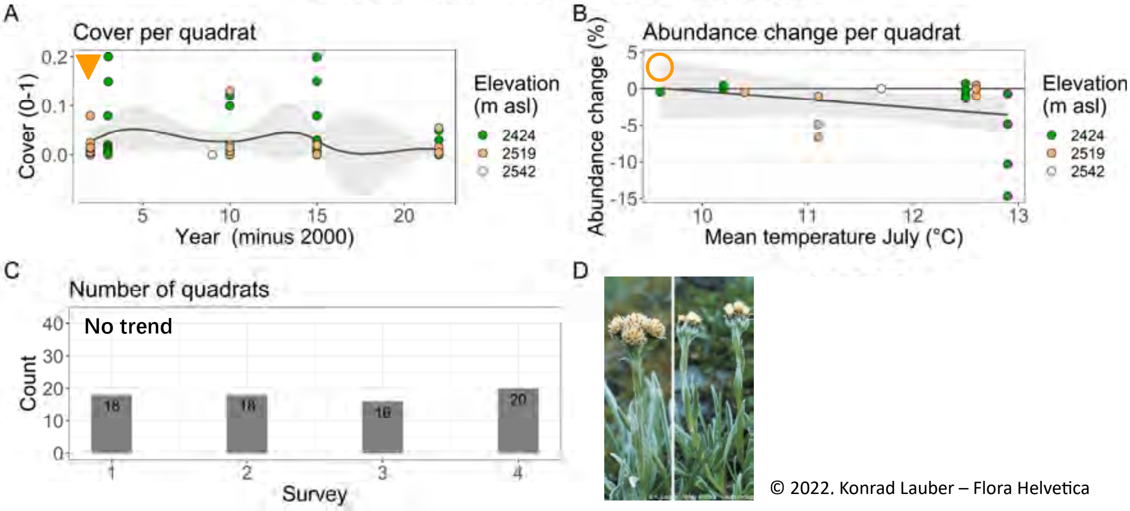
© Christophe Bornand

Erigeron uniflorus L.



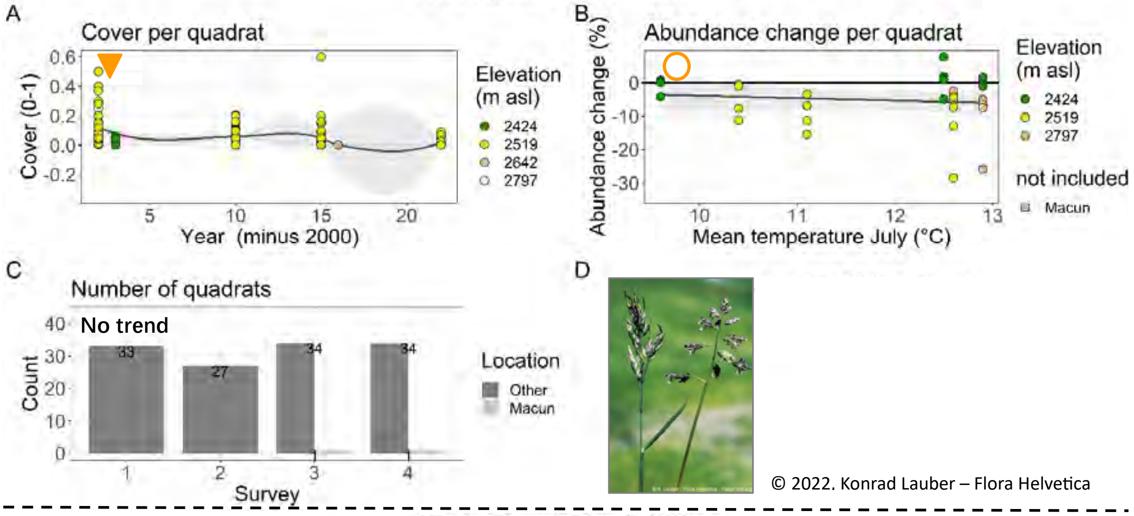
© 2022. Konrad Lauber – Flora Helvetica

Antennaria carpatica (Wahlenb.) Bluff & Fingerh.



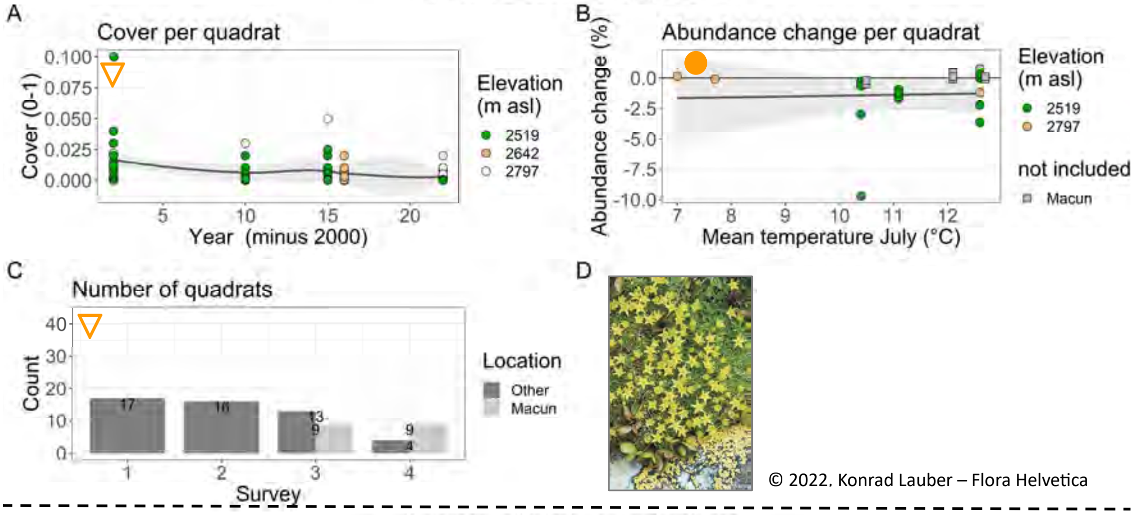
© 2022. Konrad Lauber – Flora Helvetica

Poa alpina L. subsp. alpina



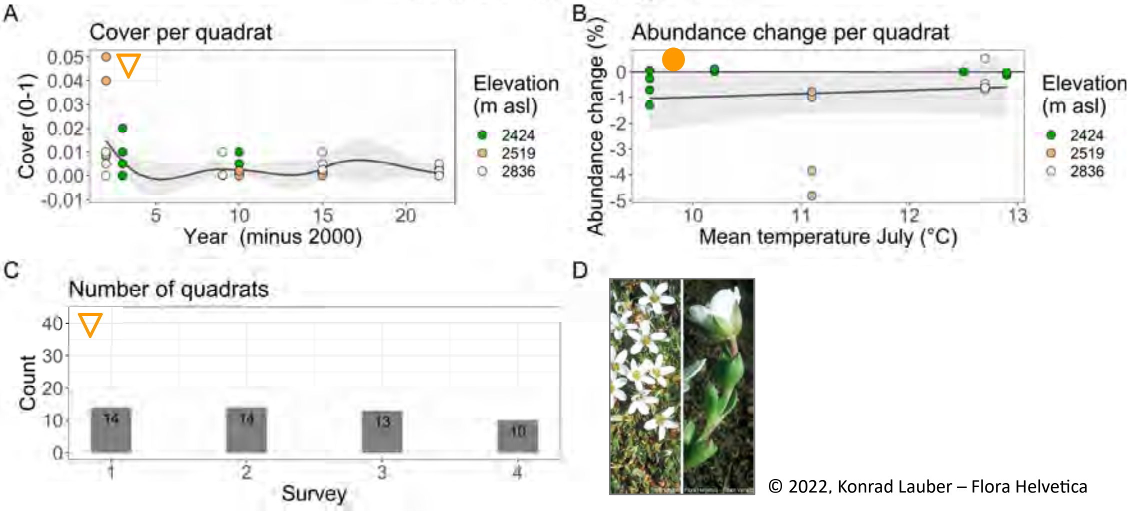
© 2022, Konrad Lauber – Flora Helvetica

Minuartia sedoides (L.) Hiern



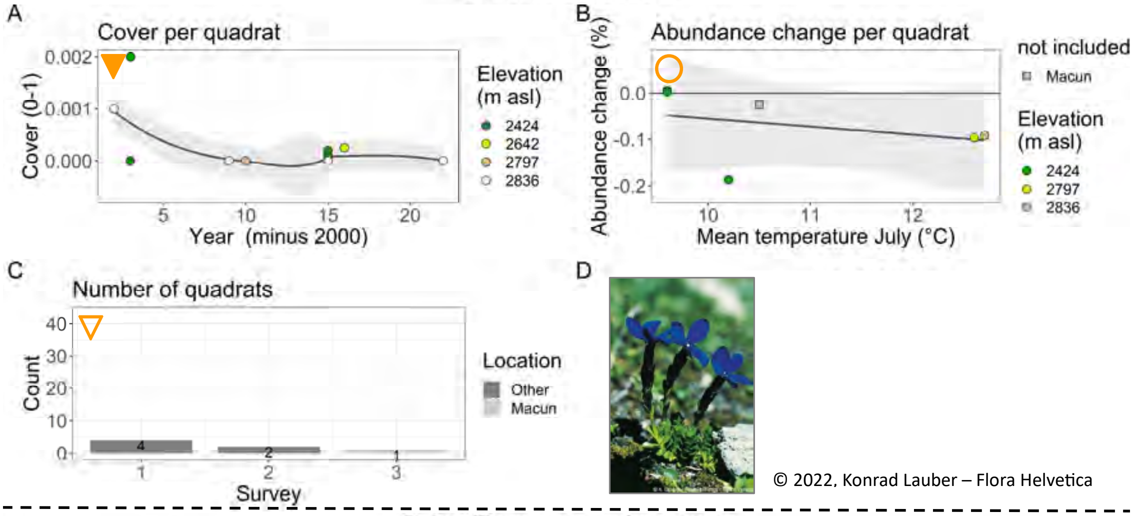
© 2022, Konrad Lauber – Flora Helvetica

Arenaria ciliata L. subsp. ciliata



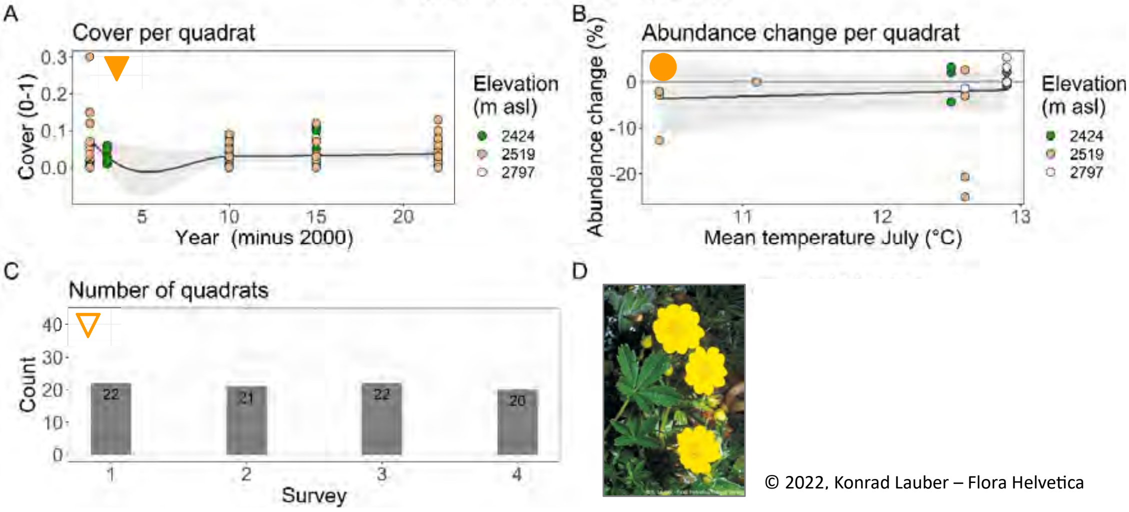
© 2022, Konrad Lauber – Flora Helvetica

Gentiana bavarica L.



© 2022, Konrad Lauber – Flora Helvetica

Potentilla aurea L. subsp. aurea

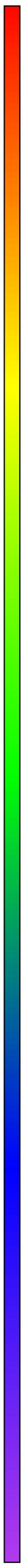


© 2022, Konrad Lauber – Flora Helvetica

Figure 16 Overview of the species showing significant changes in their cover patterns in response to changing environmental conditions. **A:** Time-dependent cover trend. Triangles represent trends, with blue icons indicating increasing cover in relation to time, and orange icons indicating decreasing cover in relation to time. Filled triangles denote statistically significant values. **B:** Temperature-dependent abundance change. Circles denote the location of the regression line, where blue indicates a positive relationship across all temperatures, orange indicates a negative relationship, and 'C' signifies a crossing regression line. The colour of 'C' corresponds to the direction: blue for positive abundance change with rising temperatures and orange for negative. Filled icons represent statistically significant values. The summit Macun, excluded due to a different time period, is depicted as gray squares out but was not included in the model estimates. **C:** Time-dependent number of occurrences. Triangles indicate colonization (blue) and extinction (orange) trends of species. If no trend is visible, it has been labelled as 'no change'. The Macun summit is shown separately because it has fewer surveys than the other summits. **D:** Species morphology. The arrangement of species begins with those that clearly benefit from changing conditions by showing increasing cover patterns, followed by species exhibiting more nuanced and controversial responses, and finally, those that suffer by showing declining cover and occurrence patterns.

Table 4 Classification into winner and loser species due to the three categories (1) time-dependent cover trend, (2) temperature-dependent abundance change, and (3) time-dependent number of occurrences. Only value 1 and 2 were tested statistically. The values in bold were significant. **(1) Time-dependent cover trend:** numbers are the estimates from the generalized mixed model. **(2) Temperature-dependent abundance change:** Positive values indicate that the regression line remains positive over the whole temperature gradient, independently whether it rises or falls. Same with the value 'negative'. 'Cross' is indicating the regression line crosses the zero y-line. **(3) Time-dependent number of occurrences:** Evaluation was made visually. Increasing numbers indicate colonisation, decreasing numbers extinction events. The species *Carex ericetorum*, *Gentian nivalis*, *Saxifraga bryoides*, *Festuca quadriflora*, *Geum montanum* and *Luzula lutea* exhibited different responses within three specific traits. These species are not depicted here. A winners-to losers-gradient was added to assess the extent of the species' responses. To assess the magnitude of species' responses, a winner-to-loser gradient bar was added.

Short name	(1) Time-dependent cover trend	(2) Temp.-dependent abundance change	(3) Time-dependent number of occurrences	Classification
Ave ver	**0.0530**	**positive**	colonisation	winner
Sax opp	**0.0242**	**positive**	colonisation	winner
Vac vit	**0.0558**	positive	colonisation	winner
Phy hem	**0.0309**	positive	colonisation	winner
Ver bel	**0.0236**	positive	colonisation	winner
Poa lax	0.0193	**positive**	colonisation	winner
Eup sal	0.0034	**positive**	colonisation	winner
Cam sch	**0.0366**	**positive**	no trend	winner
Ses alb	**0.0174**	**positive**	no trend	winner
Lig mut	0.0429	**positive**	no trend	winner
Eup min	0.0250	**Cross (+)**	no trend	winner
Dry oct	0.0040	**Cross (+)**	no trend	winner
Luz spi	-0.0030	**Cross (-)**	no trend	loser
Eri uni	**-0.0313**	negative	no trend	loser
Ant car	**-0.0481**	negative	no trend	loser
Poa alp	**-0.0670**	negative	no trend	loser
Min sed	-0.0281	**negative**	extinction	loser
Are cil	-0.0326	**negative**	extinction	loser
Gen bav	**-0.1247**	negative	extinction	loser
Pot aur	**-0.0257**	**negative**	extinction	loser



In summary, the target species are very variable in their response to climate change and can be classified into three categories: 'no response' (25 species), 'consistent response' (20 species) and 'inconsistent response' (six species).

3.2. Classification into winner and loser species

Of the 20 species with 'consistent response', twelve species could be categorized as winners in response to rising temperatures, while eight were identified as losers (Table 4). Across all categories, the winner species *Avenula versicolor*, *Saxifraga oppositifolia*, *Vaccinium-vitis-idea*, *Phytheuma hemisphaericum*, *Veronica bellidioides*, *Poa laxa* and *Euphrasia salisburgensis* demonstrated a consistent (1) increase of time-dependent cover, a (2) positive change in temperature-dependent abundance, and (3) increase of time-dependent number of occurrences on GLORIA sites (Table 4; winners above dashed line).

In contrast, the loser species, namely *Minuartia sedoides*, *Arenaria ciliata*, *Gentiana bavarica* and *Potentilla aurea* experienced a (1) decrease of time-dependent cover, a (2) negative change in temperature-dependent abundance, and (3) decrease of time-dependent number of occurrences (Table 4; losers below dashed line). The remaining species exhibited a consistent response in categories (1) and (2) but did not display a specific trend in the third category.

3.3. Characterization of winner and loser species

In order to examine whether winner and loser species could be distinguished based on particular attributes, I characterized these species using the morphological, ecological, and dispersal traits outlined in the Flora Indicativa book (Landolt *et al.*, 2010). All the target species in this study belong to the ecological group of alpine plants and are considered indigenous, meaning they either immigrated without human influence or have survived since the last ice age.

In the analysis of these species, no significant differences were observed in their morphological, ecological, and dispersal traits. These traits were systematically arranged within their respective groups (morphological, ecological, and dispersal) in ascending order, based on the p-values obtained from the Fisher Test, ranging from the smallest to the largest. Subsequently, winner and loser species were further characterized by examining range shift traits, which included considerations of leading edge, rear edge, and range area shifts. These assessments were conducted on a regional scale, specifically within the canton of Grisons, and over an extended time period spanning a century.

3.3.1. Morphological traits

Reserve and storage organs (RO)

Most winner and loser species usually possesses storage organs (Fig. 17). However, while among loser species rhizomes were the only type of such organs, among the winners there were several species with storage in roots (e.g. *Dryas octopetala* and *Vaccinium vitis-idaea*) and two species (*Euphrasia minima* and *E. salisburgensis*) without such organs. The reserve and storage organs trait achieves a p-value of 0.068, falling just short of reaching statistical significance.

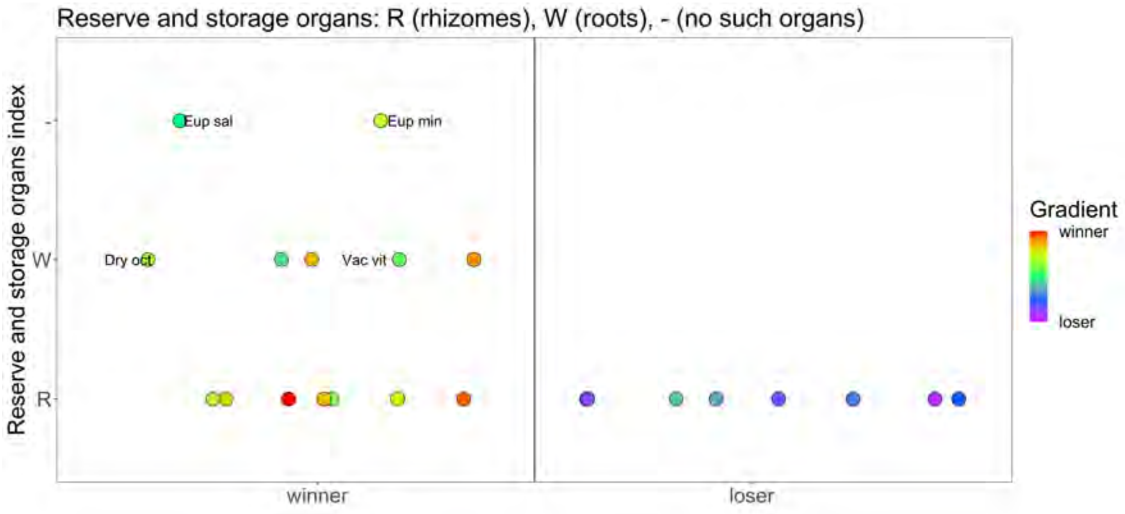


Figure 17 Reserve and storage organs trait (RO) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Leaf duration (BD)

Species exhibit variations in their leaf duration throughout the year. Winner and loser species can be characterized by the presence of either wintergreen (Fig. 18; value 'w') or semi-wintergreen (value 't' with a p-value of 0.2) leaves. Wintergreen species produce leaves during the growing season in summer, which endure until the following spring. On the other hand, semi-wintergreen species retain the vitality of up to 70% of their leaves during the winter months, with the remaining leaves shedding in the autumn.

However, a higher diversity in leaf duration types is observed in winner than in loser species, as summer-green (value 's') or evergreen (value 'i') were practically absent in loser species. The summer-green species, such as *Euprasia salisburgensis* and *E. minima*, have leaves only during the growing season, from spring to autumn, whereas the evergreen species *Vaccinium vitis-idaea* and *Dryas octopetala* retain their leaves throughout the year, enabling year-round photosynthesis. *Luzula spicata*, the sole loser species with summer-green leaves is marked in green, indicating its close proximity to the winner species within the winner-to-loser gradient.

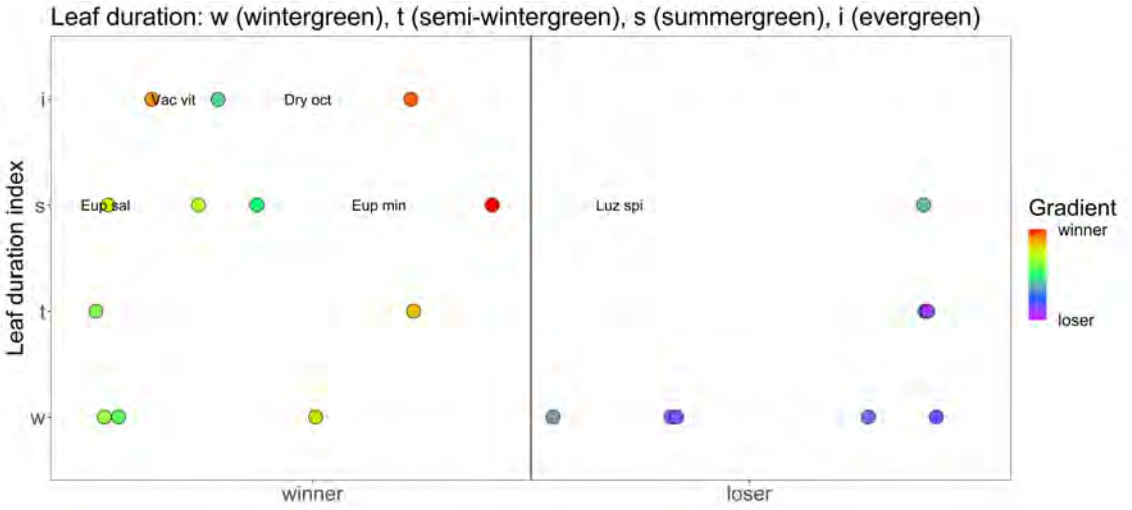


Figure 18 Leave duration trait (BD) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Life form (LF)

Winner and loser species are primarily hemikryptophytes (value ’h’), which are plants that overwinter with buds either on or just below the surface of the ground, often forming rosettes or clumps (Fig. 19; p value of 0.3). These plants continue to flower and fruit for multiple years.

However, among the winners, in contrast to the losers, there are also therophytes (value ’t’) and woody chamaephytes (value ’z’). Therophytes, like *Euphrasia salisburgensis* and *E. minima*, are species growing only for a single vegetation period, wilting after flowering, and they endure the cold season as either summer annuals in the form of seeds or as rosettes in the case of winter annuals. They often produce a large number of seeds, which increases their reproduction rates.

The woody chamaephytes *Vaccinium vitis-idaea* and *Dryas octopetala*, on the other hand, are dwarf shrubs that overwinter with buds above the surface of the ground, typically having woody parts less than 0.4 mm in height. These dwarf shrubs often grow in tight, clonal clusters, creating dense canopies that raise temperatures considerably above the surrounding air, and they commonly find protection from the harsh winter conditions under snow (Körner, 2021).

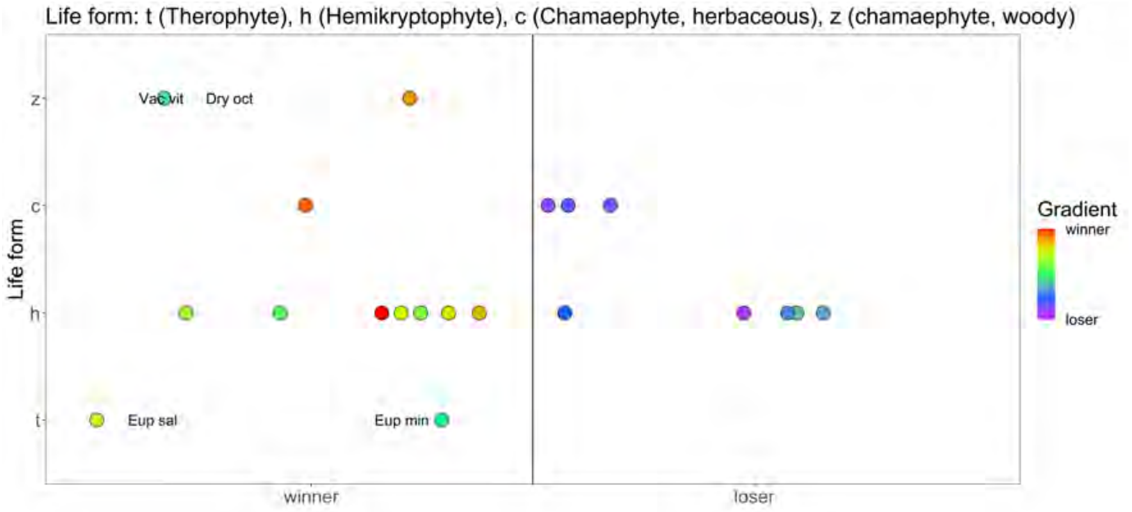


Figure 19 Life form trait (LF) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Root depth (WT)

Most of the winners and losers have roots barely penetrate the soil surface, remaining below 25 centimetres. However, while loser species only have root depths of less than 25 cm, some winner species, such as *Campanula scheuchzeri*, *Dryas octopetala*, *Ligusticum mutellina*, and *Sesleria albicans* have roots penetrating deep into the soil, reaching a depth of between 25 and 100 centimetres (Fig. 20, p-value of 0.6).

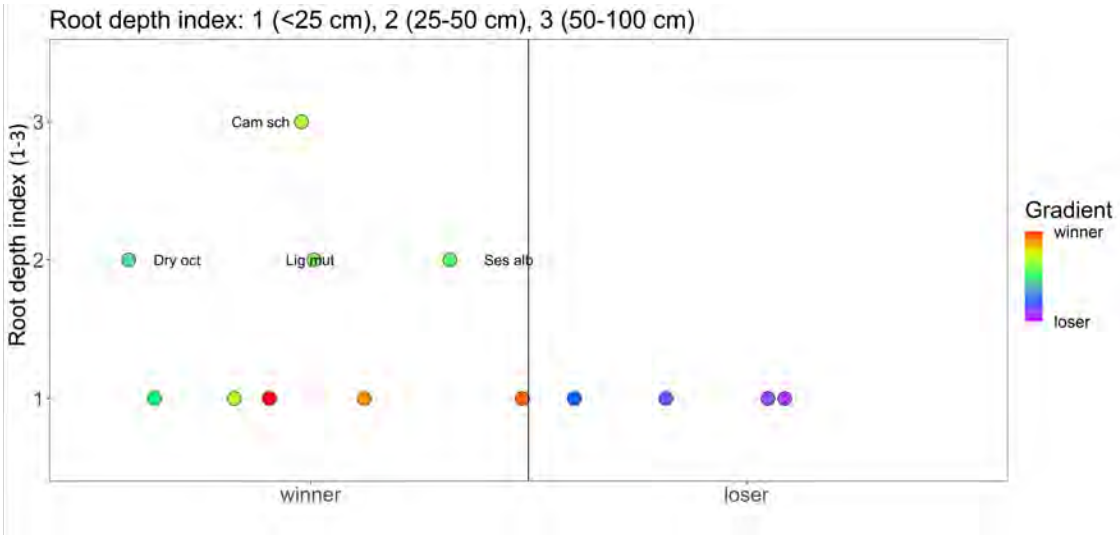


Figure 20 Root depth trait (WT) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

3.3.2. Ecological traits

Dominance in field (DG)

Dominance in the context of plant ecology pertains to the relative frequency or abundance of plant individuals within a given area of occurrence (Landolt *et al.*, 2010). Specifically, winners tend to exhibit a higher level of dominance in the field compared to losers (Fig. 21, p-value of 0.09). This trend is evident in the fact that winners are more commonly found in larger groups (value 3), such as *Vaccinium vitis-idaea*, *Dryas octopetala*, and *Euphrasia minima*, or even in more extensive colonies (value 4), such as *Sesleria albicans*, while losers are less densely distributed and tend to have a lower dominance value (value 1). The greatest loser in terms of the winner-to-loser gradient, *Potentilla aurea*, which is rarely found in great density in the field (value 1).

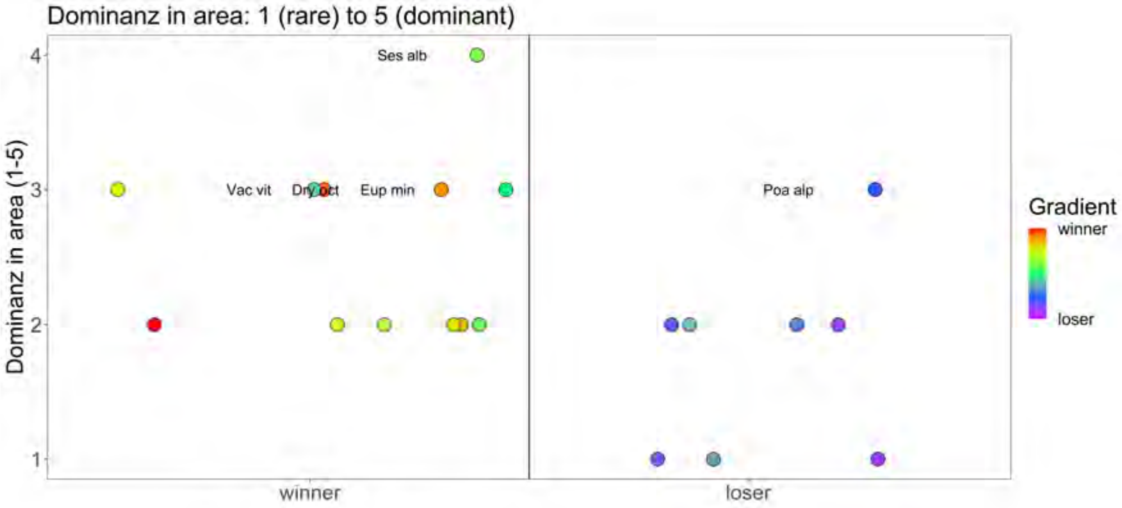


Figure 21 Dominance in the field (DG) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Nutrient value (N)

The indicator value for nutrient (N) serves as an indication of a species' preference for the level of nutrient availability in the soil. In this context, lower values suggest an affinity for nutrient-poor, while higher values indicate a preference for nutrient-rich conditions. It was observed that most species prefer low nutrient levels (value 2). However, losers tend to grow on soils with very low nutrient levels as exemplified by *Luzula spicata* and *Minuartia sedoides* (Fig. 22; value 1), while winners display a preference for soils with medium to medium-rich nutrient content as evidenced by *Campanula scheuchzeri* and *Ligusticum mutellina* (value 3; p-value of 0.1). *Poa alpina* deviates from this pattern. Despite being categorized as a loser in the context of rising temperatures, *Poa alpina* grows on nutrient-rich soils (value 4).

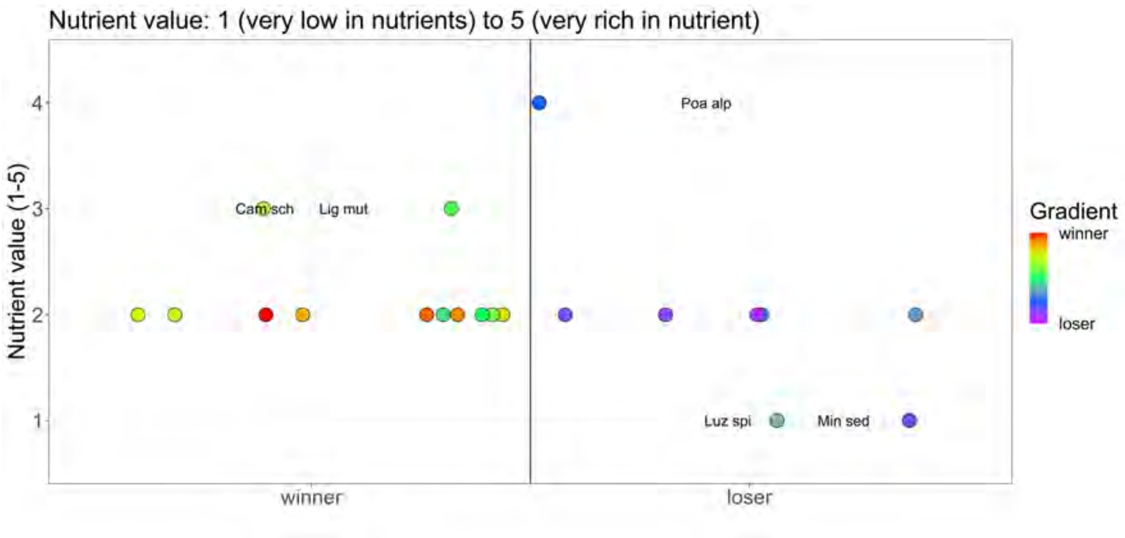


Figure 22 Nutrient value trait (BD) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Reaction value of the soil (R)

Certain winner species grow at the extremes of the pH scale, in both strongly acidic (Fig. 23; value 1; *Vaccinium vitis-idaea*, *Phyteuma hemisphaericum* and *Veronica bellidioides*) and basic (value 5; *Dryas octopetala* and *Euphrasia salisburgensis*) soil environments, while the losers are confined exclusively to the middle range of the pH scale (p-value of 0.1).

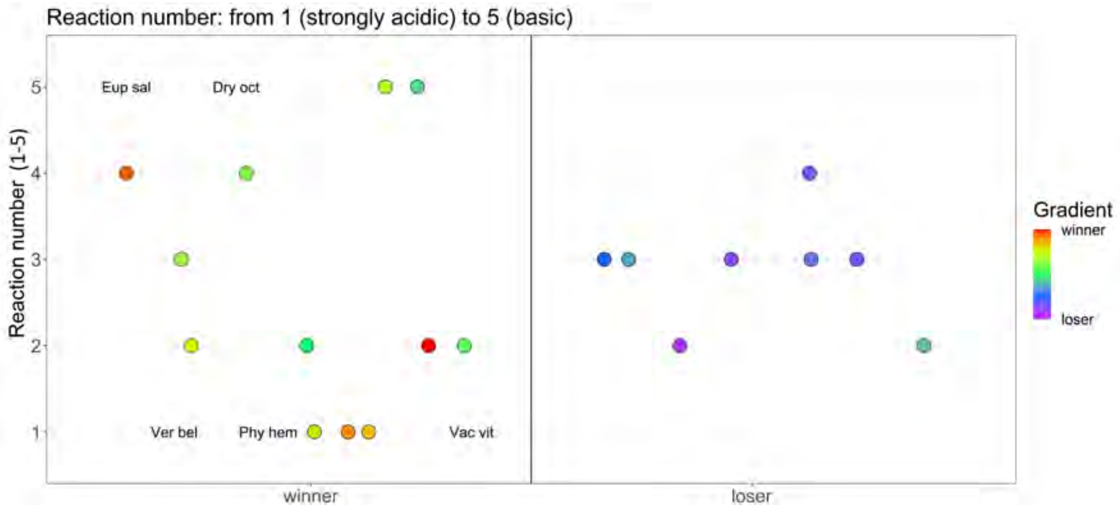


Figure 23 Reaction value of the soil (R) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Organic matter content in the soil (H)

The organic matter content indicator reflects the levels of organic matter present in the soil. Higher numerical values signify a greater presence of organic matter, while lower values indicate lower levels. In this context, all loser species consistently exhibit a preference for medium organic matter content (Fig. 24; value 3), while winners spread more. Some can grow in conditions with minimal organic matter content (value 1), as exemplified by species like *Poa laxa*, *Dryas octopetala*, and *Saxifraga oppositifolia*. Other winners thrive in environments with higher levels of organic matter (value 5), as observed in species such as *Vaccinium vitis-idaea*. However, the organic matter content in the soil did not yield significant results, as indicated by a p-value of 0.2.

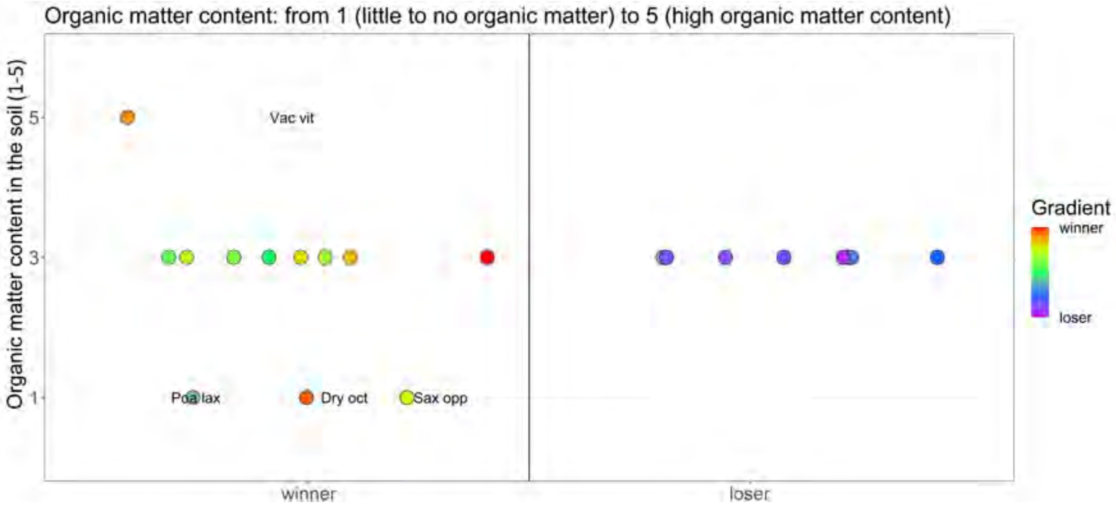


Figure 24 Organic matter content in the soil (H) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

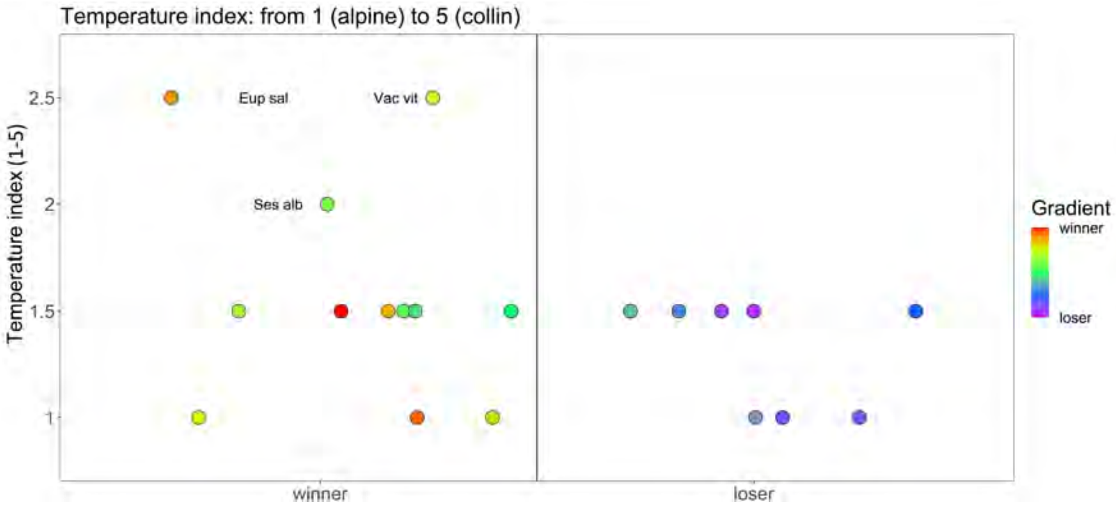


Figure 25 Temperature index trait (T) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Temperature index (T)

Winners and losers in the study predominantly inhabit nival/alpine environments, as illustrated in 25 (value 1 and 1.5). However, only among winners there are species from subalpine (value 2) and upper-montane (value 2.5) locations, as evidenced by species such as *Sesleria albicans*, *Euphrasia salisburgensis*, and *Vaccinium vitis- idaea*. Despite this observation this particular trend did not reach statistical significance (p-value of 0.7).

3.3.3. Dispersal traits

Vegetative dispersal (VA)

Vegetative dispersal of plant species is a complex process involving a variety of mechanisms. One of the critical aspects of vegetative dispersal is whether it occurs above or below ground (Fig. 26). While winners and losers show both above- and below-ground dispersal, among the winners there are also species with no vegetative dispersal (*Euphrasia minima* and *E. salisburgensis*) (p-value 0.3).

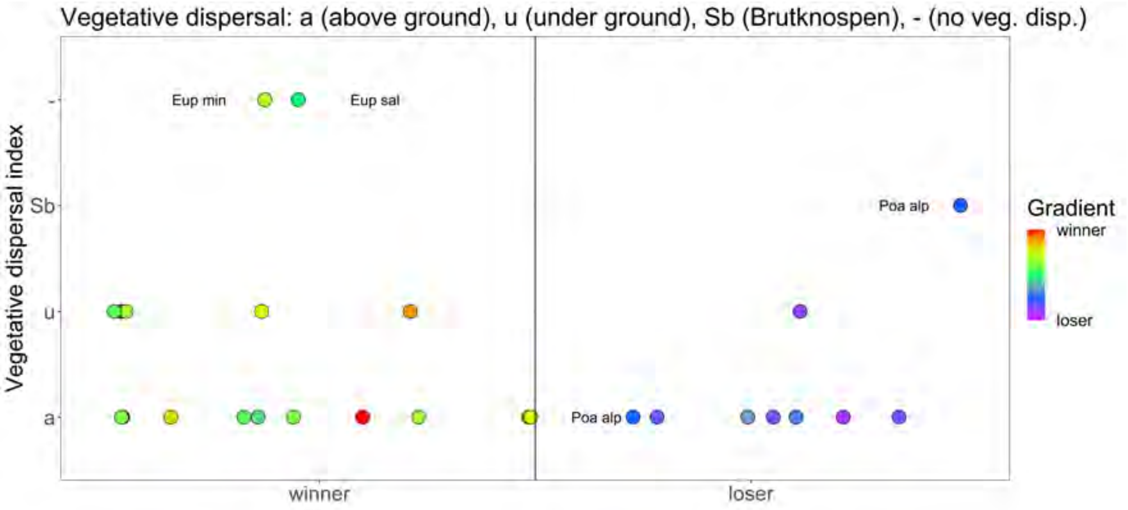


Figure 26 Vegetative dispersal (VA) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Pollinators (BS)

Both winner and loser species are insect- (value 'i') or wind- (value 'w') pollinated (Fig. 27). However, several winner species, such as *Dryas octopetala*, *Phytheuma hemisphaericum*, *Euphrasia minima*, and *E. salisburgensis*, are self-pollinated (value 's', p-value of 0.5), while none of the loser species have this ability. The greatest losers are pollinated by insects, as indicated by the winner-to-loser gradient used in the analysis.

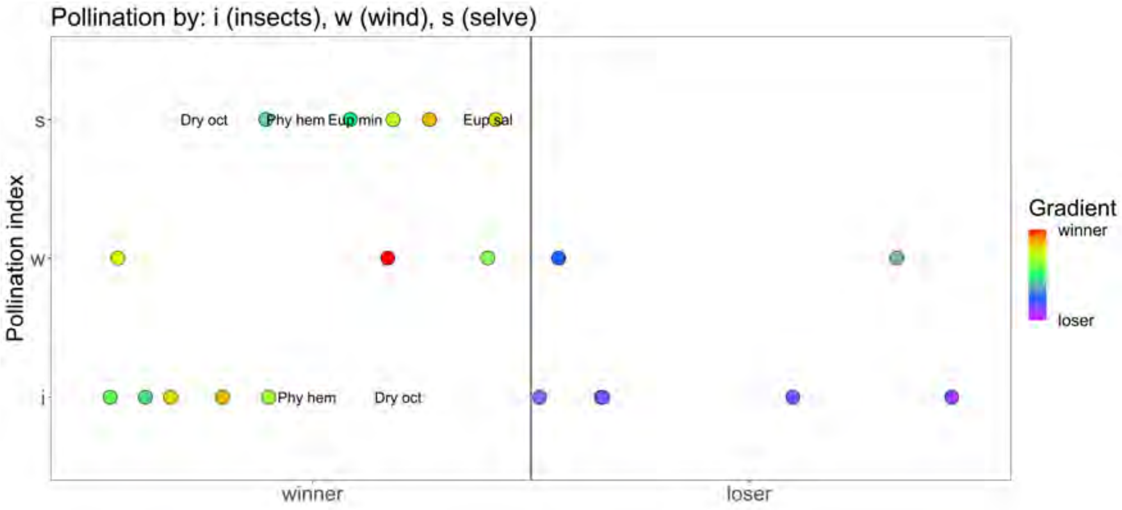


Figure 27 Pollinators trait (BS) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Disapore dispersal (DA)

Regarding diaspore dispersal, the study reveals no differences between winner and loser species (Fig. 28, p-value of 0.8). The winner species *Dryas octopetala* is the only exception showing dispersal by water.

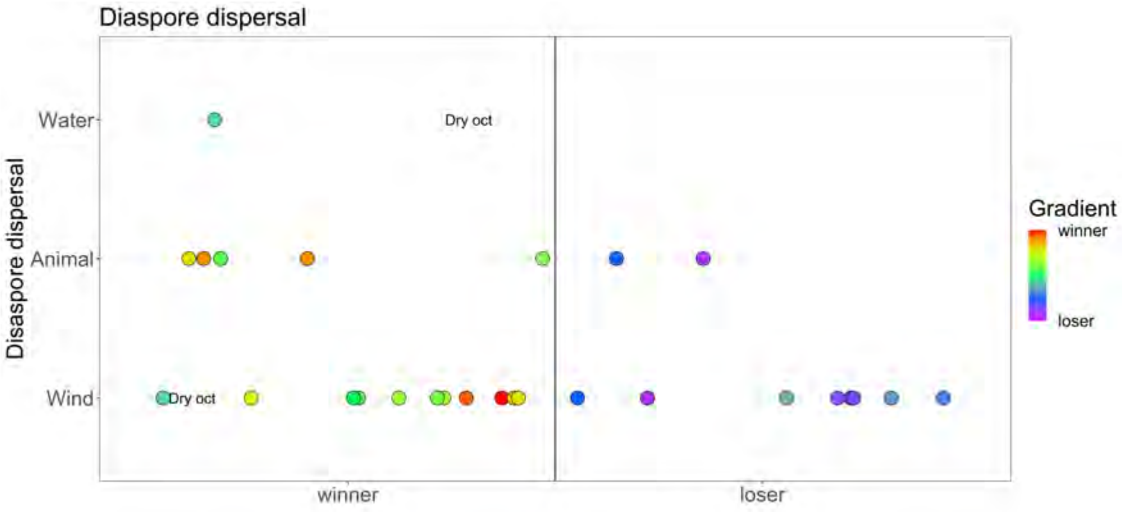


Figure 28 Disapore dispersal trait (DA) of winner and loser species according to Landolt *et al.* (2010). Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

Table 5 Range edge shift of leading and rear edges of winner and loser species. Winner species are listed above, loser species below the line. **Leading edge shift**: Number of leading edge were generated by calculating the difference between the number of regions with colonization events minus number of regions of extinction events. Positive numbers indicate an upward shift, negative numbers indicate a downward shift (Fig. A2, A). **Rear edge shift**: Number of rear edge were generated by calculating the difference between the number of regions with colonization minus extinction events. Positive numbers indicating downward shift, negative numbers indicate an upward shift (Fig. A2, A). **Range area shift**: Depending on both leading and rear edge, range area shifts were defined. For more details see chapter 2.5.2. **Abundance change trend**: to determine whether conclusions about regional range area shifts can be drawn from local abundance changes, I examined the relationship of abundance changes per quadrat at the GLORIA sites and elevation (Fig. A2, B). The term 'positive' signifies that the regression line remains positive across the entire elevation range. The same applies to 'negative'. '(+)' and '(-)' indicate the trend of the regression line. The regression line intersects the 0 line of the y-axis '(Cross)', indicating a change in sign.

Short name	Leading edge sift	Rear edge shift	Range area shift	Abundance change trend
Ave ver	3	-1	upward shift	positive (+)
Sax opp	-5	-4	reduction	positive (+)
Vac vit	2	-2	upward shift	positive (-)
Phy hem	-6	1	downward shift	positive (+)
Ver bel	1	-2	upward shift	Cross (+)
Poa lax	0	3	expansion	positive (+)
Eup sal	0	-1	reduction	positive (+)
Cam sch	3	2	expansion	no valid data
Ses alb	0	1	expansion	Cross (-)
Lig mut	0	0	no change	Cross(-)
Eup min	2	0	expansion	positive (+)
Dry oct	5	0	expansion	Cross(+)
Luz spi	-4	-2	reduction	Cross(+)
Eri uni	-1	-7	reduction	negative (-)
Ant car	1	0	expansion	negative (+)
Poa alp	-2	-2	reduction	negative (-)
Min sed	-4	2	downward shift	negative (+)
Are cil	-5	1	downward shift	negative (+)
Gen bav	-5	-2	reduction	negative (-)
Pot aur	0	0	no change	negative (+)

3.3.4. Range shifts

To ascertain whether there are discernible differences in range shifts between species classified as winners and losers, I analyzed a dataset containing historical upper and lower ranges spanning the period from 1900 to 1930, alongside recent data covering the years from 1992 to 2022 (Table 5). The first three columns of this table 'leading edge', 'rear edge' and 'area shifts' were analyzed separately.

Leading edge

In the context of the leading edge (Fig. 29), the analysis reveals a notable pattern: on average, winner species exhibit a significant upward shift, while loser species shifted downwards over the past century. This pattern attains statistical significance with a p-value of 0.04.

Notably, the winner species *Saxifraga oppositifolia* and *Phyteuma hemispharicum* defied this trend by shifting their leading edge downward, whereas the loser species *Antennaria capatica* shifted its edge upward. All other target species confirm the above pattern.

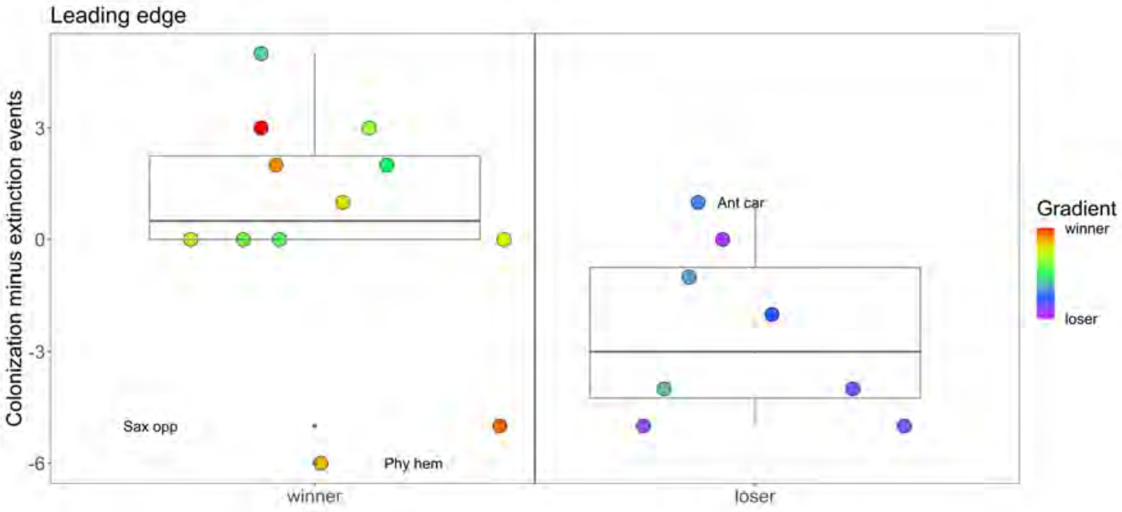


Figure 29 Difference in leading edge shifts between winner and loser species. Colonisation/extinction events were generated by calculating the difference between the number of historical regions of Grisons with colonization minus extinction events. Colours indicating location of each species in the winner-to-loser gradient (see also Table 4)

Rear edge

At the rear edge, a slight difference between winners and losers becomes evident (Fig. 30). Specifically, for winners the rear edges remained stable, indicated by a median value of 0 (value unit is 'median of colonisation minus extinction events of eleven regions of Grisons, Switzerland'). However, for the loser species, there has been a slight upward shift, with a median value of -0.8.

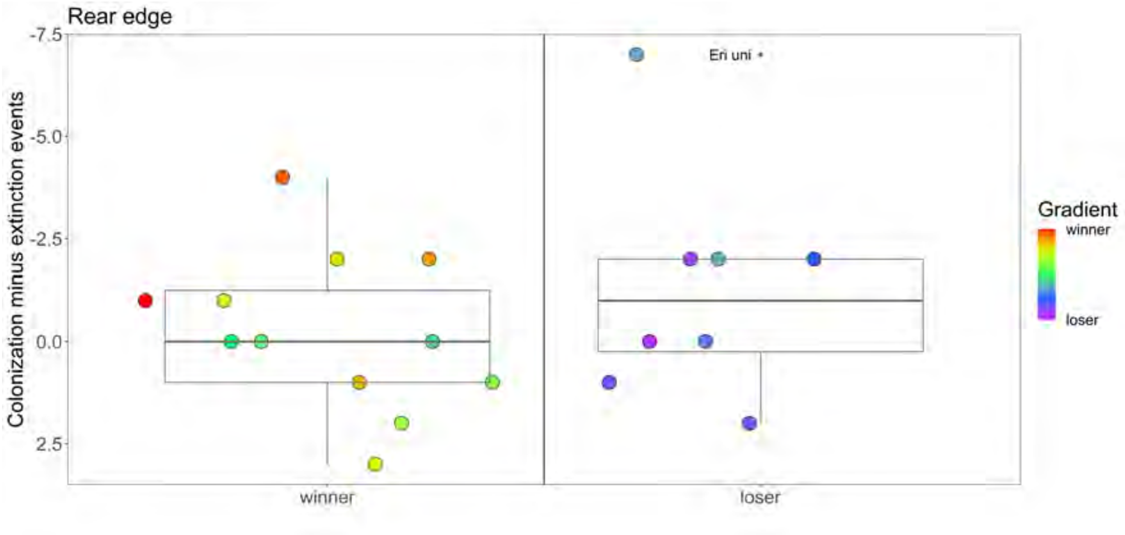


Figure 30 Difference in rear edge shifts between winner and loser species. Colours indicating location of each species in the winner-to-loser gradient (see also Table 4). Colonisation/extinction events were generated by calculating the difference between the number of historical regions in Grisons with colonization minus extinction events. Note the inverted Y-axis. This is due to the fact that negative values indicate an upward shift and positive values indicate a downward shift at the rear edge

Range area shift

Comparing the range area shifts of winners and losers, it becomes evident that winner species predominantly expanded (Fig. 31, value 'e') or shifted their ranges upward (value 'us', p-value of 0.2). In contrast, loser species primarily exhibited reductions (value r) or downward shifts (value 'ds') in their ranges. However, certain species, such as *Antennaria carpatica*, *Phyteuma hemisphaericum*, *Euphrasia salisburgensis*, and *Saxifraga oppositifolia*, deviated from this pattern.

Figure 31 Difference in range area shifts between winner and loser species. Colours indicating location of each species in the winner-to-loser gradient (see also Table 4).

3.4. Excursus: Shift of rear edges

By resurveying the historical sites of rear edge populations of selected species, I was able to find again 12 out of 17 species at 20 out of 30 sites (Fig. 32, orange dots). At five additional sites, recent records from the InfoFlora database were available. Most of the species in the resurveyed areas were found at a higher elevation than they were previously recorded. A small number of species were discovered at a lower elevation than historically recorded. Only *Saxifraga seguerii* showed both up- and downwards shifts at different locations. I excluded one location in 'Val Nuna' from the dataset due to the absence of the historically described avalanche channel. However, all riverbed locations are viable for use, as changes in river management have been accounted for and ruled out.

The species shifted their rare edges on average 52 metres upwards over a period of 58 years. Across all species and sites, the difference between historical and recent locations was negatively correlated with the elevation of the historical location, i.e. the upwards shift of the rear edge location (probably caused by the disappearance of the lowest populations) was greatest at lowest altitudes and virtually absent at high altitudes (Fig. 33).

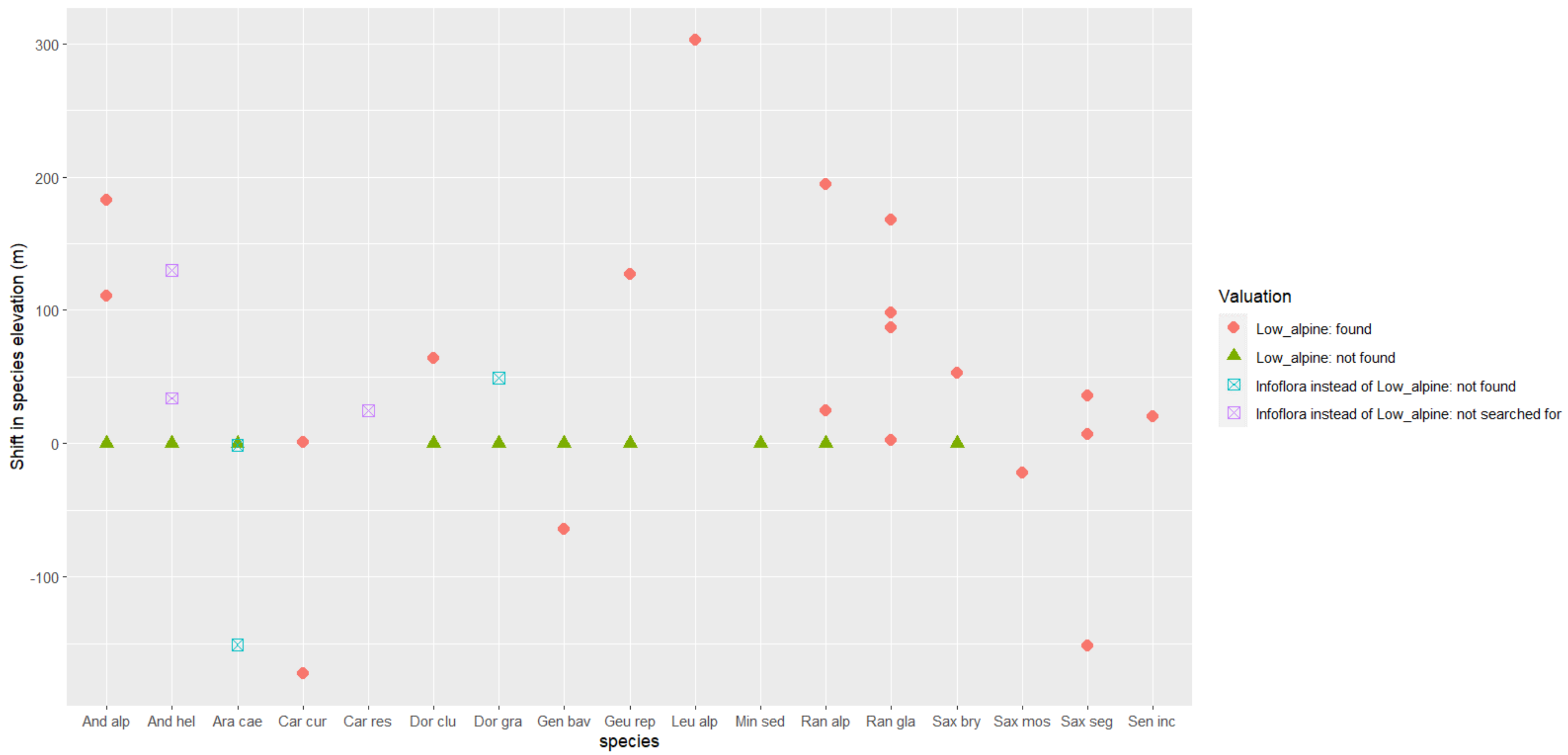


Figure 32 Rear edge shift of target species in and around the Swiss National Park. Historical locations originate from Zoller (1964), whereas recent data has been collected by revisiting the historical sites. Filled orange dots signify the presence of the target species, whereas green triangles represent locations where the target species were not found. Unfilled squares indicate elevation information originate from recent sites in the Info Flora database.

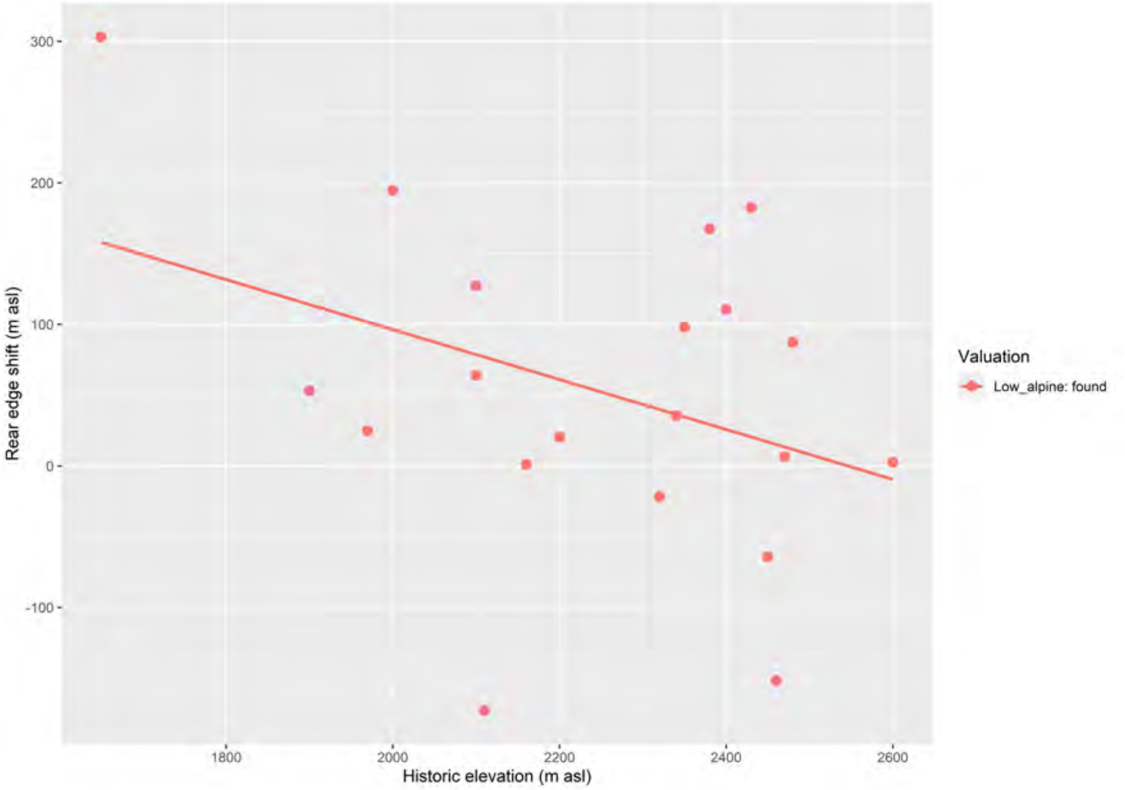


Figure 33 Rear edge shift at historical elevations of target species in and around the Swiss National Park. The historical places originate from Zoller (1964).

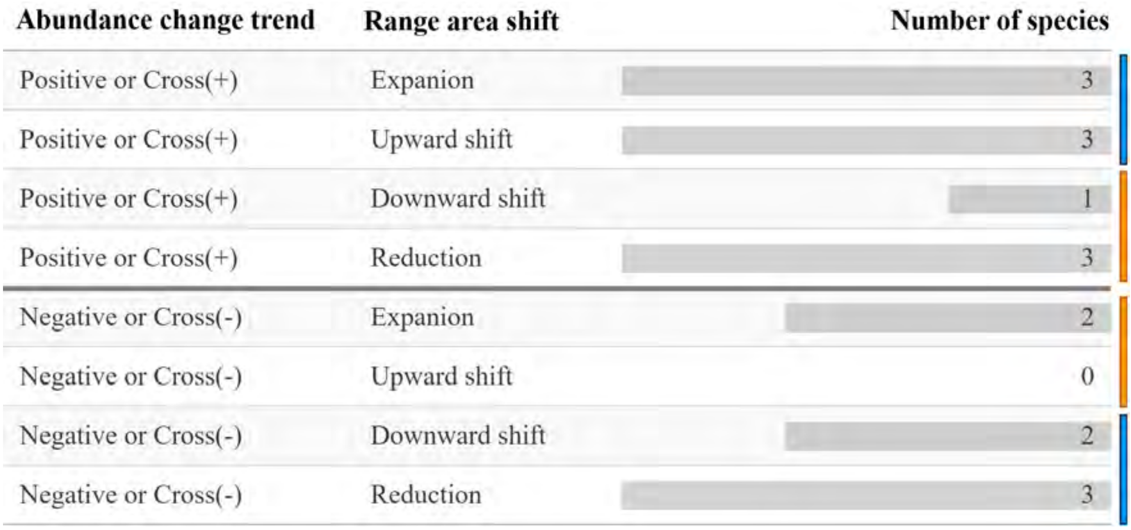
3.5. Relationship of local abundance change and regional range shift

To assess whether changes in abundance at local-scaled GLORIA sites can serve as predictors of range area shifts at regional scales in Grisons, I compiled data on both range area shifts and abundance changes, as shown in Table 5, columns ’Abundance change trend’ and ’Range area shift’.

Within this context, species with a ’positive’ or ’Cross(+)’ abundance change trend benefited from rising temperatures at a local scale (Table 6). This group of species predominantly experiences an expansion or an upward shift in their range areas at a regional scale (refer to Table 6, rows 1 and 2 highlighted with a blue bar). Only four out of the ten species in this category show a reduction or a downward shift in their ranges (Table 6, rows 3 and 4 highlighted with a orange bar).

Conversely, species demonstrating decreased abundances (’negative’) or reduced abundances at high elevations (’Cross(-)’) are likely to continue to suffer from rising temperatures. These species primarily showed range reductions or even experienced downward shifts at a regional scale (Table 6, rows 7 and 8 highlighted with a blue bar). Notably, only two species out of seven, *Antenaria carpatica* and *Sesleria albicans*, experienced an expansion of their ranges (Table 6, row 5 highlighted with a orange bar).

Table 6 Relationship between regional-scaled range area shift and local-scaled abundance change. Bars on the right side of the table show expected (blue) and unexpected (orange) relationships between abundance change and range area shifts.



Abundance change trend	Range area shift	Number of species
Positive or Cross(+)	Expanion	3
Positive or Cross(+)	Upward shift	3
Positive or Cross(+)	Downward shift	1
Positive or Cross(+)	Reduction	3
Negative or Cross(-)	Expanion	2
Negative or Cross(-)	Upward shift	0
Negative or Cross(-)	Downward shift	2
Negative or Cross(-)	Reduction	3

To summarise, of the 17 target species with analysable data, only six demonstrated local-scale changes that contradicted the direction of their regional-scale range shifts (Table 6, rows 3, 4, and 5). This leads me to conclude that, for the majority of species, changes in abundance at local-scale permanent plots indeed provide valuable insights into which direction their range edges will shift. Species demonstrating increased local abundances predominantly tended to expand or shift their range edges upwards on a regional scale, while species with reduced local abundances tended to contract their range edges or undergo downward shifts on a regional scale. This connection between local-scale abundance changes and regional-scale range shifts underscores the potential utility of these localized data for predicting broader ecological responses to changing environmental conditions.

4. Discussion

After a 20-year observational study of climate warming effects on the vegetation composition of nine GLORIA monitoring summits in Grisons, Switzerland, my research reveal several key findings:

1. I identified and classified changes in alpine plant species' abundance and occurrence in response to rising temperatures. Among 51 target species, twelve emerged as winners and eight as losers of climate warming, while 31 did not show a significant or constant trend.
2. Dwarf shrubs and annual species are among the winners in a changing climate.
3. Over the past century, on average the winners have shifted their leading edge upwards, while the losers have shifted theirs downwards.
4. There is a general relationship between local abundance change and regional range area shifts. Species with increased local abundance over 20 years tended either to expand their range areas or shift them upwards on a regional scale during a 100-year period. Conversely, species whose abundance decreased tended either to reduce their range areas or shift them downwards.

4.1. Diverse responses to climate change

Species are responding with abundance and occurrence shifts to rapidly changing environmental conditions caused by human activities (Auld *et al.*, 2022; Dirnböck *et al.*, 2011). This presents a substantial threat to numerous species, raising the likelihood of extinction within a short period (Thomas *et al.*, 2004). The hypothesis (H1) therefore claims 'changes in abundance and occurrence at GLORIA summits vary between species, as some benefit and others suffer from climate induced warming'.

My analyses revealed a spectrum of responses within the 51 target species over a 20-year period. In particular, twelve emerged as winners and eight as losers of climate change (Table 4). However, the majority of species, a total of 31 species, did not show a significant or consistent trend in their responses. This observation is consistent with previous research, such as the work presented in Rumpf *et al.* (2018), where the largest group of species does not allow a clear classification as winners or losers. The lack of significant responses for most species may be due to the relatively short observation period of 20 years. Closed vegetation in alpine regions tends to change very slowly, making short-term responses less pronounced (Körner, 2021; Windmaißer and Reisch, 2013). The variability and complexity of species specific responses to climate change, as well as the lack of significant responses of half of the target species, underscores the need for long-term monitoring to fully comprehend the impacts of climate change on alpine plant species.

Moreover, a larger number of species can be classified as winners than losers in climate change, aligning with the outcomes of Rumpf *et al.* (2018). In their study, 51 species were classified as winners, while a smaller number of species, 33 in total, were classified as losers in the face of changing environmental conditions. As most species benefit from rising temperatures by increasing their abundance and occurrence, species diversity on summits has increased (Rixen and Wipf, 2017; Steinbauer *et al.*, 2018).

4.2. Dwarf shrubs and annuals benefiting in the changing climate

To better understand the impact of environmental changes on species and develop proactive conservation strategies, it is critical to analyse the traits of both winner and loser species (Soudzilovskaia *et al.*, 2013). Therefore, I tested my hypothesis (H2) 'whether a species is a winner or a loser under climate change depends on its ecological, morphological and dispersal traits'.

Unfortunately, although several patterns emerged, no trait showed significant differences between winners and losers. This can be attributed to the relatively small number of species available for statistical analysis. This limited species pool is due to the research approach of the GLORIA sites, where only four summits per target region were designated. In order to meet the requirements for robust statistical analysis - specifically, the use of species occurring on at least three summits at different altitudes - the majority of species (116 out of 167) were excluded from consideration. I applied a strict criterion of retaining only those species showing significant changes in abundance. This resulted in the exclusion of a further 25 species. In addition, the three-component separation method containing (1) time-dependent cover trend, (2) temperature-dependent abundance change, and (3) time-dependent number of occurrences and the consistent trends of species in all categories resulted in the removal of a further six species from consideration. This left us with a relatively small sample size of 20 species for testing, whether traits and indicator values differed between the two groups of species. It might therefore be better to use more summits to increase the number of species, or to weaken the separation method by using only one or two categories instead of three. However, the rigorous methodology provides a high level of confidence in identifying winners and losers. This enabled me to identify the most noticeable distinction between winner and loser species.

The winner species, *Dryas octopetala*, and *Vaccinium vitis-idaea*, are the sole members among the targeted species to demonstrate dwarf shrub characteristics, leading to the conclusion that climate change has a favourable impact on dwarf shrubs. Furthermore, two (*Euphrasia minima*, and *E. salisburgensis*) out of three species with annual characteristics were identified as winner species. The residual species, *Gentiana nivalis*, exhibited inconsistent responses; nevertheless, a increase in its occurrence suggests that annual species also benefit from higher temperatures. Remarkably, the losers do not display any noticeable differences when compared to the winners.

Benefits of dwarf shrubs life form in warming climate

Recent studies suggest that dwarf shrubs respond more positively to warming conditions compared to herbs and grasses, indicating a potential shift in favor of dwarf shrubs in the future (Dawes *et al.*, 2011; Körner, 2021; Vanneste *et al.*, 2017; Wilson and Nilsson, 2009). This trend, known as shrubification, is contributing to increased shrub dominance in alpine tundra, a consequence of rapid climate warming (Malfasi and Cannone, 2020; Myers-Smith *et al.*, 2015). Additionally, specific dwarf shrub species, such as *Rhododendron ferrugineum* (Francon *et al.*, 2017) and *Vaccinium myrtillus* (Rixen *et al.*, 2010), are exhibiting enhanced growth as a result of climate change. The positive reaction of dwarf shrubs to rising temperatures can be credited to various features of their morphology, ecology, and dispersal characteristics.

Morphological traits

The first morphological characteristic is their life form as 'woody chamaephytes' (Fig. 19). During the winter months, they maintain buds close to the ground and typically possess woody stems less than 0.4 mm in height (Landolt *et al.*, 2010). These woody parts provide insulation and protect the plant from extreme temperature fluctuations, which are increasing with climate change. Furthermore, woody plants often have a longer lifespan than herbaceous plants (Körner, 2021). This longevity emphasises the idea that investing in costly structures increases resistance to climatic extremes and various forms of mechanical disturbance, including snow and erosion (Körner, 2021).

Secondly, the evergreen nature of the leaves of some dwarf shrub species (Fig. 18) is a crucial adaptation allowing them to prolong photosynthetic activity from early spring to late autumn. Just two weeks after the snow melts, the evergreen leaves allow them to reach their full photosynthetic rate (Körner, 2021). A time when other plant species are still dormant. This strategy is even more advantageous in environments where the snow melts even earlier, such as in alpine regions. There, the ability to take advantage of the extended growing season and use available resources can be a key factor in the success of dwarf shrubs.

Thirdly, dwarf shrubs use roots as a storage strategy, whereas losers have to rely on rhizomes as their primary storage organ (Fig. 17). Roots therefore play a vital role in the dwarf shrub's arsenal, often living as long as the plant itself (Körner, 2021). Long-lived and stable roots have the distinct advantage of being able to access water and nutrients from deeper layers of the soil than short-lived rhizomes, ensuring survival in situations where resource availability fluctuates due to changing environmental conditions.

Ecological traits

The findings suggest that dwarf shrubs tend to exhibit greater dominance in the field compared to losers (Fig. 21). Being a more dominant plant species in a field confers several advantages in the face of rising temperatures. Dominant species typically have a stronger presence, greater resource access, and competitive advantages over others and can therefore adapt more effectively to changing environmental conditions (Collins *et al.*, 2022). In contrast, rare or less dominant species may struggle in a changing climate. They might face increased competition and reduced access to resources. As a result, they are often more vulnerable to the impacts of rising temperatures.

Dispersal traits

In addition to insect pollination, *Vaccinium vitis-idaea* and *Dryas octopetala* possess the capacity for self-pollination (Fig. 27). High alpine environments can be characterized by extreme conditions, including low temperatures, short growing seasons, and limited pollinator activity. Self-pollination can provide reproductive assurance in harsh conditions, where pollinators may be scarce. Additionally self-pollination can be a more resource-efficient reproductive strategy, as it does not require the allocation of energy to attract pollinators or produce copious nectar.

Benefits of annual life form in warming climate

Surprisingly, the short-lived annuals *Euphrasia salisburgensis*, and *E. minima*, which have a completely opposite strategy to long-lived dwarf shrubs, also benefit from rising temperatures. These plants, which rarely constitute more than 2% of the alpine flora and become rarer at higher altitudes (Grabherr *et al.*, 2010; Körner, 2021), have received less attention in recent literature. However, there is evidence to suggest that annual plants can benefit from the effects of climate change. For instance, *Euphrasia minima* has been observed to establish in the Arctic region due to warming caused by climate change (Gussarova *et al.*, 2012). Additionally, annual plants have been found to be more dominant in regions with longer growing seasons, such as the Mediterranean Alps and the Californian Sierras, compared to the Alps (Körner, 2021). These observations suggest that alpine annuals may benefit from the warming temperatures and longer growing seasons expected in the future.

Morphological traits

The benefit that annuals gain in a warming climate is the result of particular morphological and dispersal characteristics. The life form of annual plants is classified as therophytes (Fig. 19). These plants have a short life cycle ending within a single growing season. During the cold season they persist either as summer annuals in the form of seeds or as rosettes in the case of winter annuals (Landolt *et al.*, 2010). Due to their rapid life cycle, therophytes can adapt quickly to environmental changes by germinating and reproducing when conditions are suitable.

Annuals show an adaptation by having leaves only during the summer growing season (Fig. 18). They concentrate their energy and resources on leaf production when conditions are ideal for photosynthesis, typically during the summer months. This strategy of efficient resource allocation can result in reduced energy expenditure compared to evergreen or wintergreen species.

In addition, annuals do not have reserve or storage organs such as roots or rhizomes, as they complete their entire life cycle within a single growing season (Fig. 17). This lack of storage organs is advantageous in times of climate change, as it increases flexibility in resource allocation and reduces maintenance costs. The maintenance of storage organs can be resource intensive, requiring energy and nutrients. By not investing in reserve or storage organs, annuals can conserve resources being redirected to immediate survival and reproduction (Körner, 2021).

Dispersal traits

Although no ecological traits have been identified for annuals, they possess dispersal traits characterizing them. Their high reproductive output, resulting in the production of numerous seeds, enhances their chances of successful reproduction and colonisation, which is especially beneficial in dynamic environments (Körner, 2021). Additionally, similar to the dwarf shrubs *Vaccinium vitis-idaea* and *Dryas octopetala*, annuals like *Euphrasia salisburgensis* and *E. minima* exhibit efficient self-pollination capabilities (Fig. 27).

The absence of a vegetative dispersal mechanism is another distinctive characteristic of annuals (Fig. 26). Unlike dwarf shrubs, which use below-ground dispersal, annuals depend largely on seed dispersal. This emphasises the importance of high seed production as the principal means by which annuals spread and establish themselves in diverse ecological niches.

Beneficial traits in times of climate change

The scientific literature investigates further traits differentiating winners from losers in warming environments. One of the central traits is 'thermophilization', which reflects the shift in plant species towards those better adapted to warmer and drier conditions (Lamprecht *et al.*, 2018; Oldfather and Ackerly, 2019; Vanneste *et al.*, 2017). The investigations reveal a weak trend indicating that winner species favour warmer conditions compared to loser species, which suggests thermophilization processes (Fig. 25).

Furthermore, the ongoing trend in plant communities to favour species with higher nutrient requirements is a well-established agreement amongst the scientific literature (Rumpf *et al.*, 2018; Staude *et al.*, 2022). With the exception of *Poa alpina*, this pattern was confirmed in this study, however not significantly (Fig. 22). The success of nutrient-demanding species could be attributed to previously scarce resources, such as nutrients, becoming more accessible due to transformations in the global environment (Staude *et al.*, 2022).

4.3. Winners shifted leading edge up and losers down

In a warming climate, species are responding by shifting their elevation ranges as a result of the colonisation of new habitats and the occurrence of local extinction (Pauli *et al.*, 2012; Rumpf *et al.*, 2018; Zu *et al.*, 2021). Hence, I aimed to test my third hypothesis (H3), which suggests that ‘on average, winners exhibit an upward shift at their leading edge, aligning with their optimal temperature range. Simultaneously, they establish resilience at their rear edge by withstanding increased competition. In contrast, losers tend to remain at their leading edge due to limitations in colonizing higher elevations. However, they experience an upward shift in their rear edge, contributing to their vulnerability and heightened risk of extinction, primarily driven by intensified competition’. The impacts of warmer temperatures are therefore determinate by increased competition on the rear edges, while the leading edges may be constrained by the scarcity of suitable soil substrates or nutrients (Callaway *et al.*, 2002; Rumpf *et al.*, 2018).

Range shifts at the leading edge

As global temperatures rise, new habitats are becoming available at higher elevations. In response, numerous species are moving to higher elevations to follow their temperature niche (Zu *et al.*, 2021). My research reveals a significant upward movement of winners at their leading edge in response to this possibility of colonizing new habitats in higher elevations. Losers were unable to colonise new habitats at higher elevations and, in fact, exhibited on average an unexpected downward shift at their leading edge (Fig. 29). As range edges are heavily influenced by climate (Zimmermann *et al.*, 2009), it is possible that environmental changes could cause unexpected downward shifts. Higher temperatures, for example, might reduce the duration of winter snow coverage and cause frost damage at a species leading edge, potentially leading to local extinctions and downward shifts of loser species (Lenoir *et al.*, 2010). The results provides evidence for H3, indicating that the winning species have shifted their leading edge upwards on average but contradicts H3 as loser species shifted their rear edge downwards instead of staying on the same elevation.

Range shifts at the rear edge

In contrast to the leading edge, where abiotic conditions primarily determine the upper limit, competitive effects play a key role in determining the lower limit of species’ elevational ranges (Lenoir *et al.*, 2010). My results indicate that loser species slightly shifted their rear edge upwards, while winners remained at the same elevation, confirming H3.

Several factors may explain why winners remain at their rear edge without shifting. First, increased disturbance in response to climate warming could reduce the importance of competition in structuring communities (Lenoir *et al.*, 2010). Higher levels of disturbance may reduce competitive pressure to some extent, allowing winners to persist in their current locations (Chardon *et al.*, 2018). Secondly, winners are able to defend their established positions against competitors due to the microclimatic variability of mountainous terrain. This creates diverse abiotic conditions over short distances (Scherrer and Körner, 2011). This allows the coexistence of 'subalpine', 'alpine' and 'nival' species at the same elevation. Alpine terrain therefore provides a safe refuge for many species under changing climatic conditions due to its short distance escape from novel thermal regimes (Scherrer and Körner, 2011). Applying this to my results, winner species may find more favourable climatic conditions nearby at the same elevation, reducing the need for elevational shifts (Rumpf *et al.*, 2018). In contrast, loser species are unable to defend their established sites against increased competition, leading to their local extinction in these habitats and the subsequent upward shift of their rear edge. Thirdly, high alpine plant species can grow in extreme low-elevated outposts, such as rocks or riverbeds, with very different climatic conditions compared to their surroundings. For example, alpine species can occasionally be found at scattered cold microsites far below the treeline (Rumpf *et al.*, 2018). These unique microhabitats may be especially vulnerable to a warming climate.

Excursus: Selecting data for rear edges

To ensure reliable data on the rarely studied rear edge (Auld *et al.*, 2022; Rumpf *et al.*, 2018), I suggest conducting resurveys of historical rear edge sites outlined in chapter 2.6 of my methods section. This approach has proven successful in providing results at the species level, showing species have, on average, shifted their rare edges 52 metres upwards over a period of 58 years. Advancement in rear edge research will generate more reliable outcomes in the future, leading to a more comprehensive understanding of how species range areas changed during climate change.

Range area shifts

An evaluation of both the leading and rear edge, indicates changes of species range area, including expansion, upward movement, reduction, and downward movement. Winner species predominantly expand or shift their range upwards (Fig. 31), using the ability to colonise new habitats at higher elevations, following their temperature niche. Expanding to higher altitudes equips them to deal with the challenges of climate change.

In contrast, loser species primarily experienced downward shifts or reduction of range areas, primly caused by local extinction. When a species reduces its range area, it usually encounters a decrease in its population size, hence raising the threat of extinction, as specified by the IUCN Red List of Threatened Species (Zu *et al.*, 2021). My research findings indicate that the species *Luzula spicata*, *Erigeron uniflorus*, *Poa alpina*, and *Gentiana bavarica* are not only experiencing a decline in abundance but also a reduction in range. Therefore, it is highly recommended that all four species are taken into account for future conservation planning efforts.

Factors driving distribution edge shifts beyond temperature

Some species, such as the winners *Euphrasia salisburgensis*, and *Saxifraga oppositifolia*, exhibit a contrary pattern by decreasing their range area. This divergence suggests that factors beyond temperature, such as precipitation patterns, snow cover duration, water balance, and seasonal climate variations, play significant roles in influencing species range areas (Lenoir *et al.*, 2010). Moreover, distribution changes are not solely driven by climatic factors; external factors like land use change also contribute (Rumpf *et al.*, 2018; Zu *et al.*, 2021). The complex interplay of these various factors suggests that there may be unexpected shifts in the distribution areas of species.

4.4. Local abundance changes forecast regional range shifts

Ecological processes at both local and regional levels are known to be mechanistically connected (Leibold *et al.*, 2004; Lynn *et al.*, 2021; Sporbert *et al.*, 2020). Therefore, my research aimed to test the fourth hypothesis (H4) that 'changes in abundance at a local scale can predict range area shifts at a regional scale'. In my study, I define 'local' as permanent GLORIA quadrats, as descried in chapter 2.1. Meanwhile, 'regional' refers specifically to the Grisons region of Switzerland, as descried in chapter 2.5.2.

My results indicates that species with an increase in local abundance primarily expanded or shifted their range area upwards on a regional scale. Species with increasing local abundance are generally well adapted to changing temperature conditions as they have increased competitive ability. Consequently, they have been able to colonize new habitats to following their temperature niche on a regional scale. In contrast, species experiencing a local decline in abundance resulted in a regional reduction in range area or a downward shift. Species with reduced local abundance are considered to be negatively impacted by rising temperatures as less favourable conditions can lead to reduced competitive ability. Therefore, these species encounter challenges, including heightened competition pressure. Species may respond to these challenges by reducing their range areas or shifting their range edges downward, typically following local extinctions. The findings emphasize the correlation between local changes in abundance and regional range area shifts and thus confirm H4. Therefore, it is plausible to deduce the responses of species from the local to the regional level in relation to climate warming.

4.5. Conclusions

The high alpine environment is experiencing the effects of climate change due to higher temperatures, and various species are responding differently, resulting in winners and losers based on their abundance and occurrence change on local GLORIA summits. Notably, all dwarf shrubs of the target species emerges as winners of climate change as well as two out of three annuals, suggesting that diverse strategies, such as long and short life cycles, can positively influence adaptation to climate change. Additionally on a regional scale, winners have significantly shifted their leading edge upwards, while the losers have moved downwards, indicating that winners have the potential to colonize new habitats at higher altitudes, following their temperature niche. However, the losers are facing challenges leading to local extinctions at both leading and rear edge. In particular, *Luzula spicata*, *Erigeron uniflorus*, *Poa alpina*, and *Gentiana bavarica*, not only decreased their local abundance but also reduced their regional range areas, making them particularly vulnerable to extinction. Therefore, it is imperative to consider conservation efforts for these species, both within the Swiss National Park and in the Grisons region. Protecting and preserving these vulnerable species is essential to maintaining the ecological balance in these high alpine environments as they continue to respond to the ongoing effects of climate change.

In addition to these observations, this study underscores the significance of carefully selecting and preserving data related to the rear edges of species. This involves revisiting historical sites at lower elevations, where such information is currently lacking but holds immense importance for future research on range area shifts. Furthermore, the study underscores the critical role of local monitoring projects, such as GLORIA. These initiatives possess the potential to forecast regional range area shifts, such as for Grisons, Switzerland. Specifically, species demonstrating increased local abundance are considered to be well adapted to changing temperature conditions and possessing enhanced competitive abilities, allowing them to colonize new habitats at higher elevations and, consequently, expand or shift their range upwards regionally. In contrast, species experiencing a decrease in local abundance are negatively affected by the changing environment and face regionally range contraction and downward shifts due to the possibility of extinctions.

As global change intensifies, it is expected that alpine plants will continue to respond in the future (Rumpf *et al.*, 2018). This situation is concerning since it may lead to the extinction of several species (Thomas *et al.*, 2004). In this regard, research studies such as this one provide insights into the reaction of high alpine plant species to the effects of global warming. This enables the development of preservation strategies to mitigate the risk of species extinction. As high alpine environments are particularly vulnerable to the impacts of climate change, they often display signs of change before other terrestrial ecosystems begin to respond (Winkler *et al.*, 2019). Studying these early indicators in alpine ecosystems can provide insights beyond their immediate context and enable the development of more comprehensive strategies to address the impacts of climate change on ecosystems worldwide.

Acknowledgements

I would like to thank all the people who have supported me in the process of writing this thesis. In particular, I would like to extend my special thanks to Sonja Wipf, whose generosity in inviting me to be part of the incredible GLORIA team of 2022 has had a profound impact on my academic and personal growth. Her invaluable scientific guidance and warm-hearted nature not only enriched my research experience, but also made the whole journey incredibly enjoyable. I would also like to thank Christian Rixen, Anja Rammig, Raphael von Büren and Sandra Djabarow for their helpful, kind and uncomplicated support. Many thanks to the SNP GLORIA fieldwork team of 2022 for this unforgettable summer and instructive hours in alpine botany. I also would like to thank my family for their support and encouragement in every situation during my master's thesis.

Bibliography

Alexander, J. M., Diez, J. M. and Levine, J. M. (2015): Novel competitors shape species' responses to climate change. *Nature*, 525(7570):515–518. doi:10.1038/nature14952.

Auld, J., Everingham, S. E., Hemmings, F. A. and Moles, A. T. (2022): Alpine plants are on the move: Quantifying distribution shifts of australian alpine plants through time. *Diversity and Distributions*, 28(5):943–955. doi:10.1111/ddi.13494.

Braun-Blanquet, J. and Rübel, E. (1932): Flora von Graubünden: Vorkommen, Verbreitung und ökologisch-soziologisches Verhalten der wildwachsenden Gefässpflanzen Graubündens und seiner Grenzgebiete. Gedruckt mit Unterstützung der Stiftung Dr. Joachim de Giacomi der Schweiz. Naturforschenden Gesellschaft. *Geobot. Inst. ETH Stiftung Rübel Zürich*, 7(4).

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C., Michalet, R., Paolini, L., Pugnair, F., Newingham, B., Aschnehoug, C., Kikodze, D. and Cook, B. (2002): Positive interactions among alpine plants increase with stress. *Nature*, 417(6891):841–844. doi: 10.1038/nature00805.

Chardon, N. I., Wipf, S., Rixen, C., Beilstein, A. and Doak, D. F. (2018): Local trampling disturbance effects on alpine plant populations and communities: Negative implications for climate change vulnerability. *Ecology and evolution*, 8(16):7921–7935. doi:10.1002/ece3.4276.

Collins, C. G., Elmendorf, S. C., Smith, J. G., Shoemaker, L., Szojka, M., Swift, M. and Suding, K. N. (2022): Global change re-structures alpine plant communities through interacting abiotic and biotic effects. *Ecology letters*, 25(8):1813–1826. doi:10.1111/ele.14060.

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T. and Mynsberge, A. R. (2011): Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science (New York, N.Y.)*, 331(6015):324–327. doi:10.1126/science.1199040.

Damgaard, C. F. and Irvine, K. M. (2019): Using the beta distribution to analyse plant cover data. *Journal of Ecology*, 107(6):2747–2759. doi:10.1111/1365-2745.13200.

Dawes, M. A., Hagedorn, F., Zumbrunn, T., Handa, I. T., Hättenschwiler, S., Wipf, S. and Rixen, C. (2011): Growth and community responses of alpine dwarf shrubs to in situ co_2 enrichment and soil warming. *The New phytologist*, 191(3):806–818. doi: 10.1111/j.1469-8137.2011.03722.x.

Dirnböck, T., Essl, F. and Rabitsch, W. (2011): Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17(2):990–996. doi:10.1111/j.1365-2486.2010.02266.x.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D. R., Silc, U., Vittoz, P. and Hülber, K. (2012): Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2(8):619–622. doi:10.1038/nclimate1514.

Felde, V. A., Kapfer, J. and Grytnes, J.-A. (2012): Upward shift in elevational plant species ranges in sikkilsdalen, central norway. *Ecography*, 35(10):922–932. doi:10.1111/j.1600-0587.2011.07057.x.

Francon, L., Corona, C., Roussel, E., Lopez Saez, J. and Stoffel, M. (2017): Warm summers and moderate winter precipitation boost rhododendron ferrugineum l. growth in the taillefer massif (french alps). *The Science of the total environment*, 586:1020–1031. doi:10.1016/j.scitotenv.2017.02.083.

GLORIA (2023): Methods: The gloria multi-summit approach. URL: https://gloria.ac.at/methods/multi–summits, last checked on 11.04.2023.

Grabherr, G., Gottfried, M. and Pauli, H. (2010): Climate change impacts in alpine environments. *Geography Compass*, 4(8):1133–1153. doi:10.1111/j.1749-8198.2010.00356.x.

Gussarova, G., Alsos, I. G. and Brochmann, C. (2012): Annual plants colonizing the arctic? phylogeography and genetic variation in the euphrasia minima complex (orobanchaceae). *TAXON*, 61(1):146–160. doi:10.1002/tax.611011.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K.-L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C. and Yuri, T. (2008): A phylogenomic study of birds reveals their evolutionary history. *Science (New York, N.Y.)*, 320(5884):1763–1768. doi:10.1126/science.1157704.

Knight, Nicole (2022): Using the beta distribution to model ecological data. *RPubs*, URL: https://rpubs.com/nicoleknight/936037, last checked on 02.08.2022.

Körner, C. (2021): *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer eBook Collection. Springer International Publishing and Imprint Springer, Cham, 3rd ed. 2021 edition. doi:10.1007/978-3-030-59538-8.

Lamprecht, A., Semenchuk, P. R., Steinbauer, K., Winkler, M. and Pauli, H. (2018): Climate change leads to accelerated transformation of high-elevation vegetation in the central alps. *The New phytologist*, 220(2):447–459. doi:10.1111/nph.15290.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W. and Wolgemuth, T. (2010): *Flora indicativa: Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Editions des Conservatoire et Jardin botanique de la Ville de Genève and Haupt, Geneve and Bern and Stuttgart and Wien, 2., völlig neu bearb. u. erw. aufl. der "Ökologischen Zeigerwerte zur Flora der Schweiz" (1977) edition.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. (2004): The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, 7(7):601–613. doi:10.1111/j.1461-0248.2004.00608.x.

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W. and Svenning, J.-C. (2010): Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33:295–303. doi:10.1111/j.1600-0587.2010.06279.x.

Lynn, J. S., Klanderud, K., Telford, R. J., Goldberg, D. E. and Vandvik, V. (2021): Macroecological context predicts species' responses to climate warming. *Global Change Biology*, 27(10):2088–2101. doi:10.1111/gcb.15532.

Malfasi, F. and Cannone, N. (2020): Climate warming persistence triggered tree ingression after shrub encroachment in a high alpine tundra. *Ecosystems*, 23(8):1657–1675. doi:10.1007/s10021-020-00495-7.

MeteoSchweiz (2016): Idaweb. URL: https://gate.meteoswiss.ch/idaweb/system/welcome.do, last checked on 01.08.2023.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., Dawes, M. A., Lantz, T. C., Weijers, S., Jørgensen, R. H., Buchwal, A., Buras, A., Naito, A. T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J. A., Wipf, S., Guay, K. C., Hik, D. S. and Vellend, M. (2015): Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, 5(9):887–891. ISSN 1758-6798. doi:10.1038/nclimate2697.

Nicklas, L., Walde, J., Wipf, S., Lamprecht, A., Mallaun, M., Rixen, C., Steinbauer, K., Theurillat, J.-P., Unterluggauer, P., Vittoz, P., Moser, D., Gattringer, A., Wessely, J. and Erschbamer, B. (2021): Climate change affects vegetation differently on siliceous and calcareous summits of the european alps. *Frontiers in Ecology and Evolution*, 9. doi:10.3389/fevo.2021.642309.

Oldfather, M. F. and Ackerly, D. D. (2019): Increases in thermophilus plants in an arid alpine community in response to experimental warming. *Arctic, Antarctic, and Alpine Research*, 51(1):201–214. doi:10.1080/15230430.2019.1618148.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, R., Ghosn, D., Holten, J. I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., Molero Mesa, J., Nagy, L., Pelino, G., Puşcaş, M., Rossi, G., Stanisci, A., Syverhuset, A. O., Theurillat, J.-P., Tomaselli, M., Unterluggauer, P., Villar, L., Vittoz, P. and Grabherr, G. (2012): Recent plant diversity changes on europe's mountain summits. *Science (New York, N.Y.)*, 336(6079):353–355. doi:10.1126/science.1219033.

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., Williamson, S. N., Yang, D. Q. and Mountain Research Initiative EDW Working Group (2015): Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5):424–430. doi:10.1038/nclimate2563.

Rebetez, M. and Reinhard, M. (2008): Monthly air temperature trends in switzerland 1901–2000 and 1975–2004. *Theoretical and Applied Climatology*, 91(1-4):27–34. doi:10.1007/s00704-007-0296-2.

Rixen, C., Schwoerer, C. and Wipf, S. (2010): Winter climate change at different temporal scales in vaccinium myrtillus, an arctic and alpine dwarf shrub. *Polar Research*, 29(1):85–94. doi:10.1111/j.1751-8369.2010.00155.x.

Rixen, C. and Wipf, S. (2017): Non-equilibrium in alpine plant assemblages: shifts in europe's summit floras. *High mountain conservation in a changing world*, 62:285–303. doi:10.1007/978-3-319-55982-7_12.

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E. and Dullinger, S. (2018): Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 115(8):1848–1853. doi:10.1073/pnas.1713936115.

Scherrer, D. and Körner, C. (2011): Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38(2):406–416. doi:10.1111/j.1365-2699.2010.02407.x.

Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K. and Cornelissen, J. H. C. (2013): Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 110(45):18180–18184. doi:10.1073/pnas.1310700110.

Sporbert, M., Keil, P., Seidler, G., Bruelheide, H., Jandt, U., Aćić, S., Biurrun, I., Campos, J. A., Čarni, A., Chytrý, M., Ćušterevska, R., Dengler, J., Golub, V., Jansen, F., Kuzemko, A., Lenoir, J., Marcenò, C., Moeslund, J. E., Pérez-Haase, A., Rūsiņa, S., Šilc, U., Tsiripidris, I., Vandvik, V., Vasilev, K., Virtanen, R. and Welk, E. (2020): Testing macroecological abundance patterns: The relationship between local abundance and range size, range position and climatic suitability among european vascular plants. *Journal of Biogeography*, 47(10):2210–2222. doi:10.1111/jbi.13926.

Staude, I. R., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., van Calster, H., Vellend, M., Bjorkman, A. D., Brunet, J., de Frenne, P., Hédl, R., Jandt, U., Lenoir, J., Myers-Smith, I. H., Verheyen, K., Wipf, S., Wulf, M., Andrews, C., Barančok, P., Barni, E., Benito-Alonso, J.-L., Bennie, J., Berki, I., Blüml, V., Chudomelová, M., Decocq, G., Dick, J., Dirnböck, T., Durak, T., Eriksson, O., Erschbamer, B., Graae, B. J., Heinken, T., Schei, F. H., Jaroszewicz, B., Kopecký, M., Kudernatsch, T., Macek, M., Malicki, M., Máliš, F., Michelsen, O., Naaf, T., Nagel, T. A., Newton, A. C., Nicklas, L., Oddi, L., Ortmann-Ajkai, A., Palaj, A., Petraglia, A., Petřík, P., Pielech, R., Porro, F., Puşcaş, M., Reczyńska, K., Rixen, C., Schmidt, W., Standovár, T., Steinbauer, K., Świerkosz, K., Teleki, B., Theurillat, J.-P., Turtureanu, P. D., Ursu, T.-M., Vanneste, T., Vergeer, P., Vild, O., Villar, L., Vittoz, P., Winkler, M. and Baeten, L. (2022): Directional turnover towards larger-ranged plants over time and across habitats. *Ecology letters*, 25(2):466–482. doi: 10.1111/ele.13937.

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., Fernández-Arberas, O., Fossheim, K. F., Gómez-García, D., Georges, D., Grindrud, E. T., Haider, S., Haugum, S. V., Henriksen, H., Herreros, M. J., Jaroszewicz, B., Jaroszynska, F., Kanka, R., Kapfer, J., Klanderud, K., Kühn, I., Lamprecht, A., Matteodo, M., Di Cella, U. M., Normand, S., Odland, A., Olsen, S. L., Palacio, S., Petey, M., Piscová, V., Sedlakova, B., Steinbauer, K., Stöckli, V., Svenning, J.-C., Teppa, G., Theurillat, J.-P., Vittoz, P., Woodin, S. J., Zimmermann, N. E. and Wipf, S. (2018): Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556(7700):231–234. doi:10.1038/s41586-018-0005-6.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. and Williams, S. E. (2004): Extinction risk from climate change. *Nature*, 427(6970):145–148. doi:10.1038/nature02121.

Vanneste, T., Michelsen, O., Graae, B. J., Kyrkjeeide, M. O., Holien, H., Hassel, K., Lindmo, S., Kapás, R. E. and de Frenne, P. (2017): Impact of climate change on alpine vegetation of mountain summits in norway. *Ecological Research*, 32(4):579–593. doi: 10.1007/s11284-017-1472-1.

Walther, G.-R. (2003): Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(3):169–185. doi:10.1078/1433-8319-00076.

Wilson, D., Scott and Nilsson, C. (2009): Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15(7):1676–1684. doi:10.1111/j.1365-2486.2009.01896.x.

Wilson, J. B. (2011): Cover plus: ways of measuring plant canopies and the terms used for them. *Journal of Vegetation Science*, 22(2):197–206. doi:10.1111/j.1654-1103.2010.01238.x.

Windmaißer, T. and Reisch, C. (2013): Long-term study of an alpine grassland: local constancy in times of global change. *Alpine Botany*, 123(1):1–6. ISSN 1664-2201. doi: 10.1007/s00035-013-0112-9.

Winkler, D. E., Lubetkin, K. C., Carrell, A. A., Jabis, M. D., Yang, Y. and Kueppers, L. M. (2019): Chapter 12 - responses of alpine plant communities to climate warming. In J. E. Mohan, editor, *Ecosystem Consequences of Soil Warming*, 297–346. Academic Press. doi:https://doi.org/10.1016/B978-0-12-813493-1.00013-2.

Zimmermann, N. E., Yoccoz, N. G., Edwards Jr, T. C., Meier, E. S., Thuiller, W., Guisan, A., Schmatz, D. R. and Pearman, P. B. (2009): Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences*, 106(2):19723–19728. doi:10.1073/pnas.0901643106.

Zoller, H. (1964): *Flora des schweizerischen Nationalparks und seiner Umgebung*. Impr. P. Attinger.

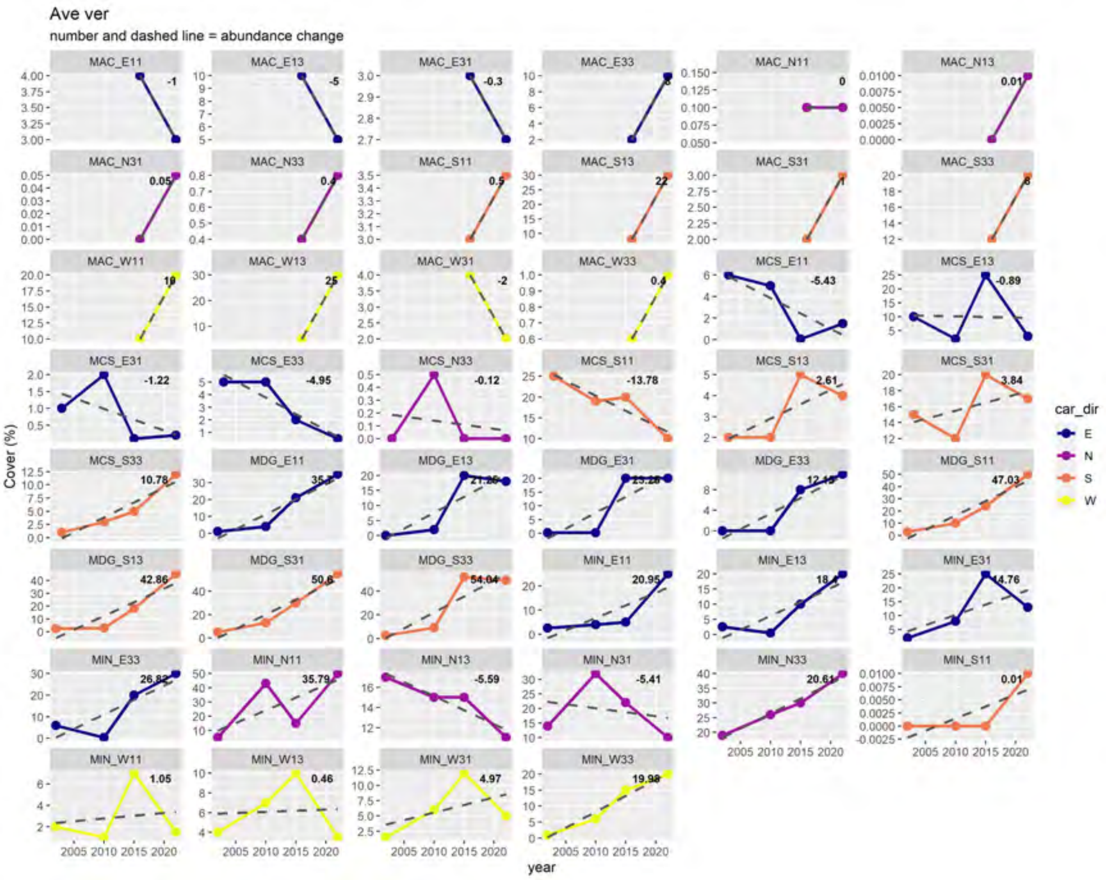
Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., Luo, A., Li, Y., Ji, C., Peng, S., Meng, J. and Zhou, J. (2021): Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *The Science of the total environment*, 783:146896. doi:10.1016/j.scitotenv.2021.146896.

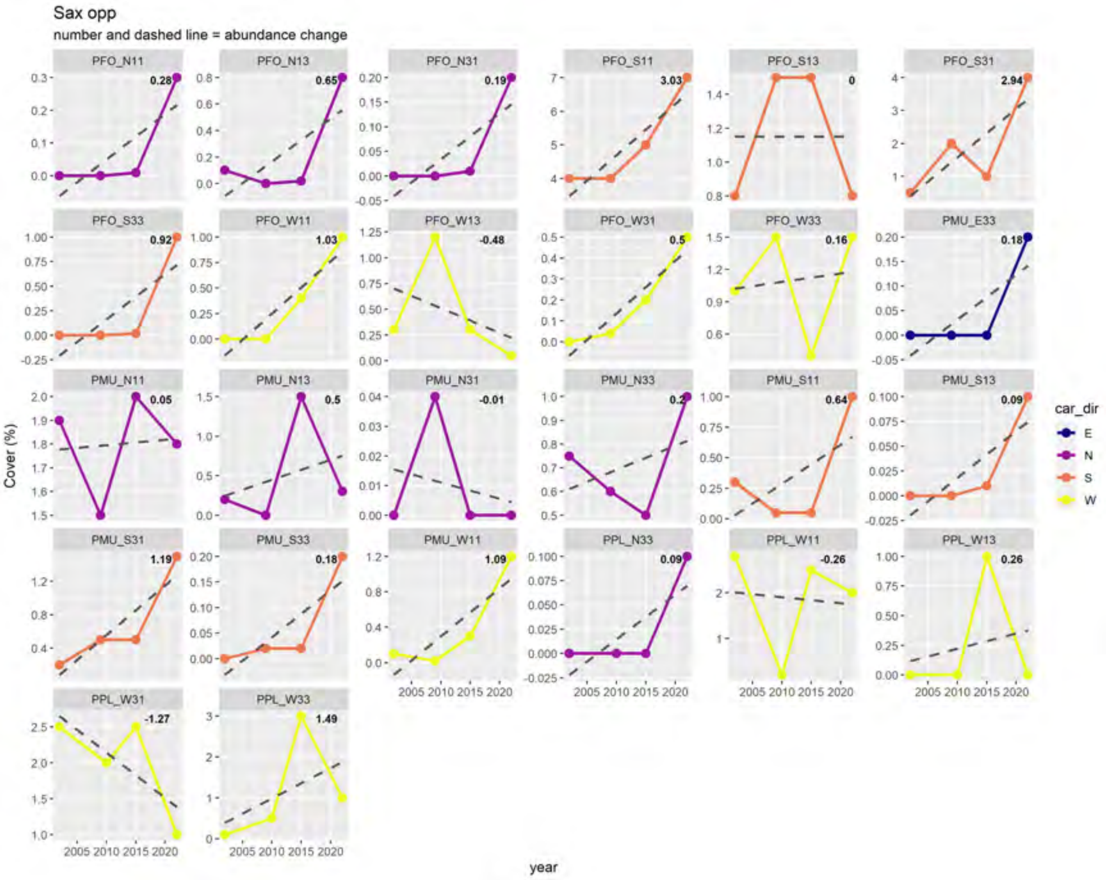
5. Appendix

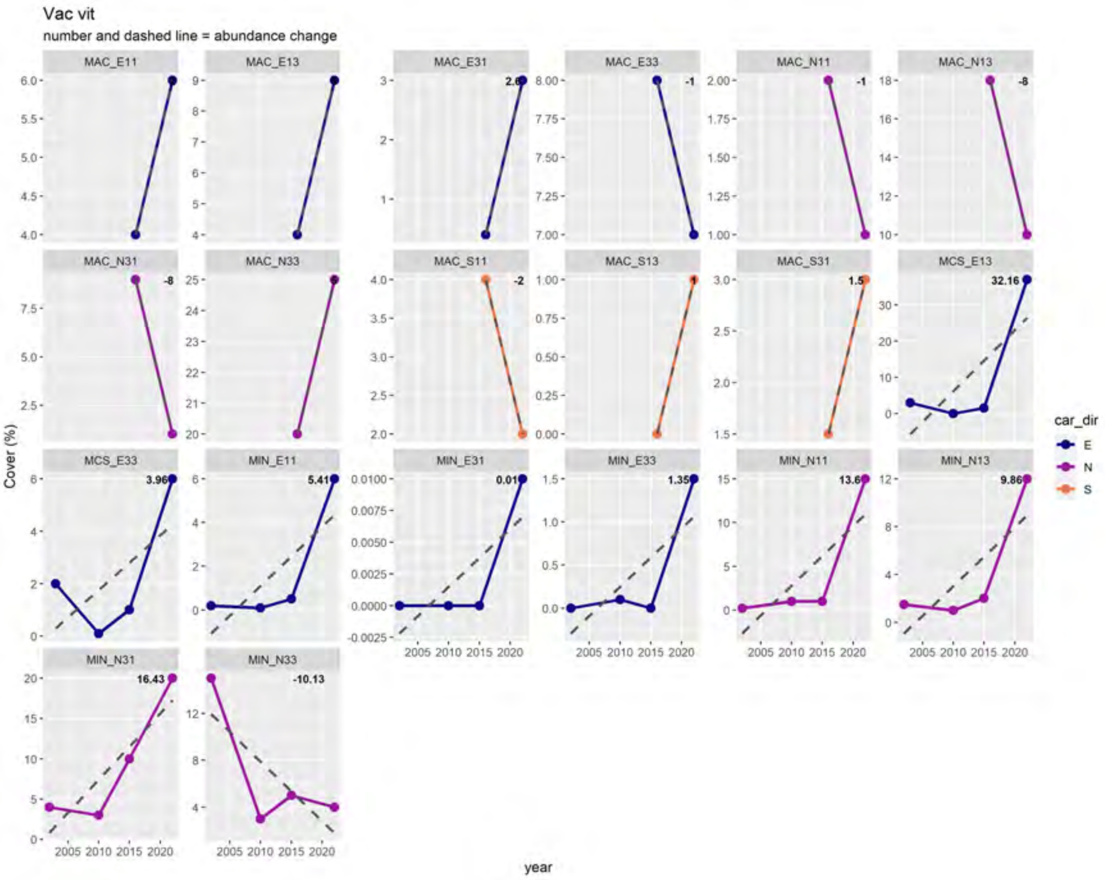
Table A1 Target species on GLORIA sites occurring on more than two summits. The change in abundance was significant for the species highlighted in bold. Species in bracket were deleted from further analysis due to inconsistencies in the nomenclature. 'Car dir' is a abbreviation for 'cardinal direction'. Some species names were labeled with abbreviated forms using dots.

Target species	**Numb. summits**	**Numb. car. dir.**	**Numb. quadrats**
Agrostis alpina	5	12	15
Agrostis rupestris	5	14	16
Antennaria carpatica	3	8	14
Anthoxanthum odoratum	3	7	11
Anthyllis vulneraria	3	10	16
Arenaria ciliata	3	6	14
Avenula versicolor	4	13	16
Campanula cochlearifolia	4	6	10
Campanula scheuchzeri	3	6	16
Carex curvula	4	11	16
Carex ericetorum	4	9	16
Carex firma	3	8	15
Carex rupestris	4	10	16
Cerastium uniflorum	3	6	14
Draba aizoides	4	6	12
Dryas octopetala	3	12	16
Erigeron uniflorus	5	12	16
Euphrasia minima	4	14	16
Euphrasia salisburgensis	3	11	16
Festuca halleri	4	14	16
Festuca quadriflora	6	15	16
Gentiana bavarica	4	5	6
Gentiana brachyphylla	3	8	13
Gentiana nivalis	3	8	13
Gentiana verna	3	7	12
Geum montanum	3	5	6
(Hieracium alpinum)	4	12	13

Target species	**Numb. summits**	**Numb. car dir**	**Numb. quadrats**
(Hieracium glanduliferum)	3	9	15
Homogyne alpina	5	6	7
Kobresia myosuroides	3	10	16
(Leontodon hispidus)	4	8	11
(Leontodon pyrenaicus)	4	11	15
Leucanthemopsis alpina	5	15	16
Ligusticum mutellina	3	7	12
Luzula lutea	4	8	12
Luzula spicata	4	10	15
Minuartia sedoides	3	10	15
Minuartia verna subsp. ver.	5	12	16
Oreochloa disticha	4	12	16
Phy. hemisphaericum	4	11	16
Poa alpina	4	10	16
Poa laxa	3	7	13
Polygonum viviparum	3	10	16
Pot. aurea subsp. aur.	3	8	13
Potentilla crantzii	3	6	12
Pulsatilla vernalis	4	8	12
Saxifraga bryoides	4	10	12
Sax. opp. subsp. opp.	3	9	13
Selaginella selaginoides	3	6	14
Sempervivum. montanum	3	4	7
Sesleria albicans	4	12	16
Sibbaldia procumbens	3	6	8
Silene acaulis subsp. bry.	3	9	15
(Taraxacum ape. agg.)	3	6	9
Vac. vitis-idaea	3	6	11
Veronica bellidioides	4	9	16

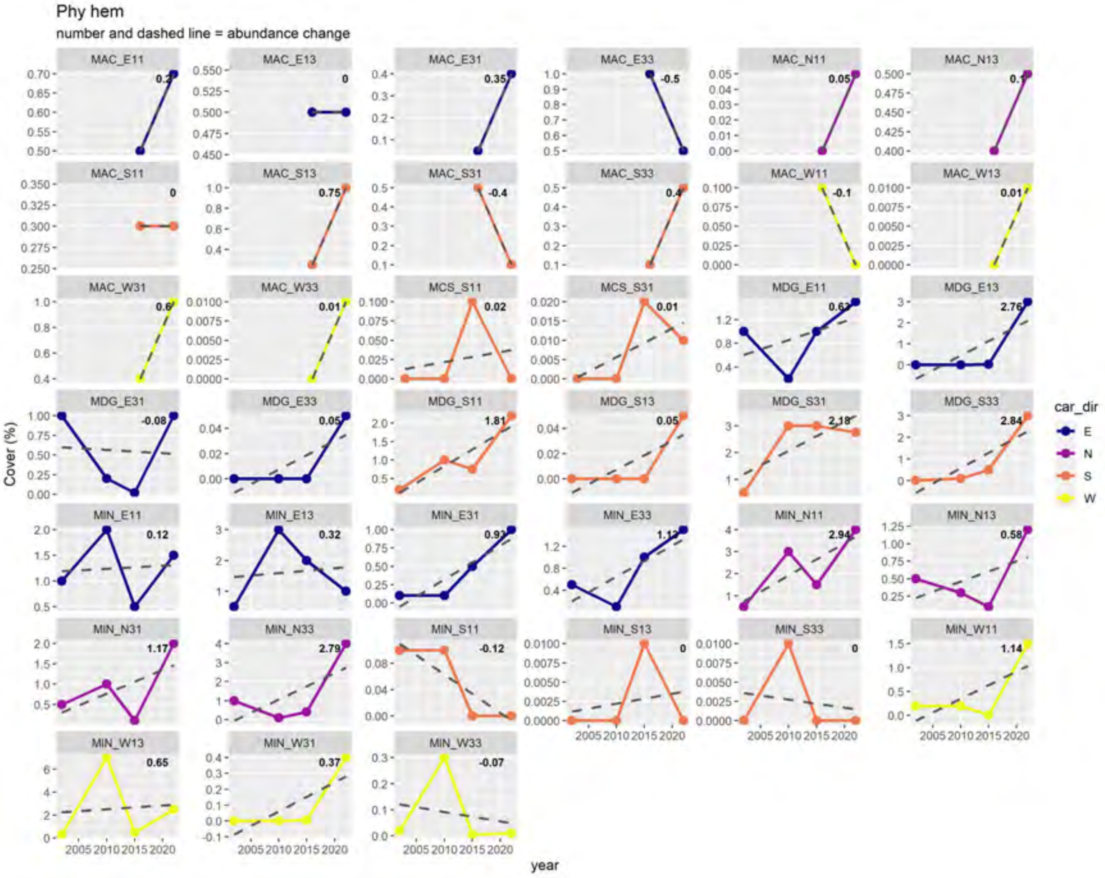

Ave ver
number and dashed line = abundance change
MAC_E11 -1
MAC_E13 -5
MAC_E31 -0.3
MAC_E33 8
MAC_N11 0
MAC_N13 0.01
MAC_N31 0.05
MAC_N33 0.4
MAC_S11 0.5
MAC_S13 22
MAC_S31 1
MAC_S33 8
MAC_W11 10
MAC_W13 25
MAC_W31 -2
MAC_W33 0.4
MCS_E11 -5.43
MCS_E13 -0.89
MCS_E31 -1.22
MCS_E33 -4.95
MCS_N33 -0.12
MCS_S11 -13.78
MCS_S13 2.61
MCS_S31 3.84
MCS_S33 10.78
MDG_E11 35.3
MDG_E13 21.26
MDG_E31 23.26
MDG_E33 12.15
MDG_S11 47.03
MDG_S13 42.86
MDG_S31 50.6
MDG_S33 54.04
MIN_E11 20.95
MIN_E13 18.4
MIN_E31 14.76
MIN_E33 26.82
MIN_N11 35.79
MIN_N13 -5.59
MIN_N31 -5.41
MIN_N33 20.61
MIN_S11 0.01
MIN_W11 1.05
MIN_W13 0.46
MIN_W31 4.97
MIN_W33 19.98
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Sax opp
number and dashed line = abundance change
PFO_N11 0.28
PFO_N13 0.65
PFO_N31 0.19
PFO_S11 3.03
PFO_S13 0
PFO_S31 2.94
PFO_S33 0.92
PFO_W11 1.03
PFO_W13 -0.48
PFO_W31 0.5
PFO_W33 0.16
PMU_E33 0.18
PMU_N11 0.05
PMU_N13 0.5
PMU_N31 -0.01
PMU_N33 0.2
PMU_S11 0.64
PMU_S13 0.09
PMU_S31 1.19
PMU_S33 0.18
PMU_W11 1.09
PPL_N33 0.09
PPL_W11 -0.26
PPL_W13 0.26
PPL_W31 -1.27
PPL_W33 1.49
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W



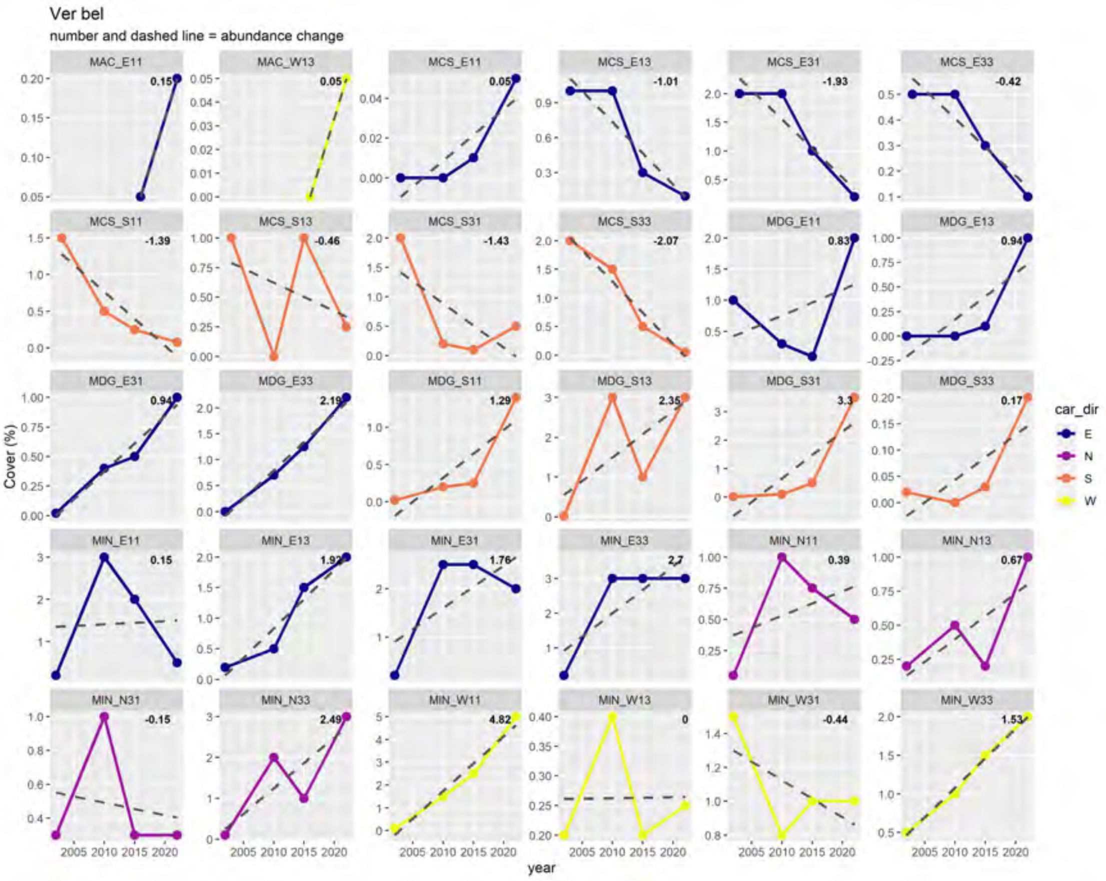
Vac vit

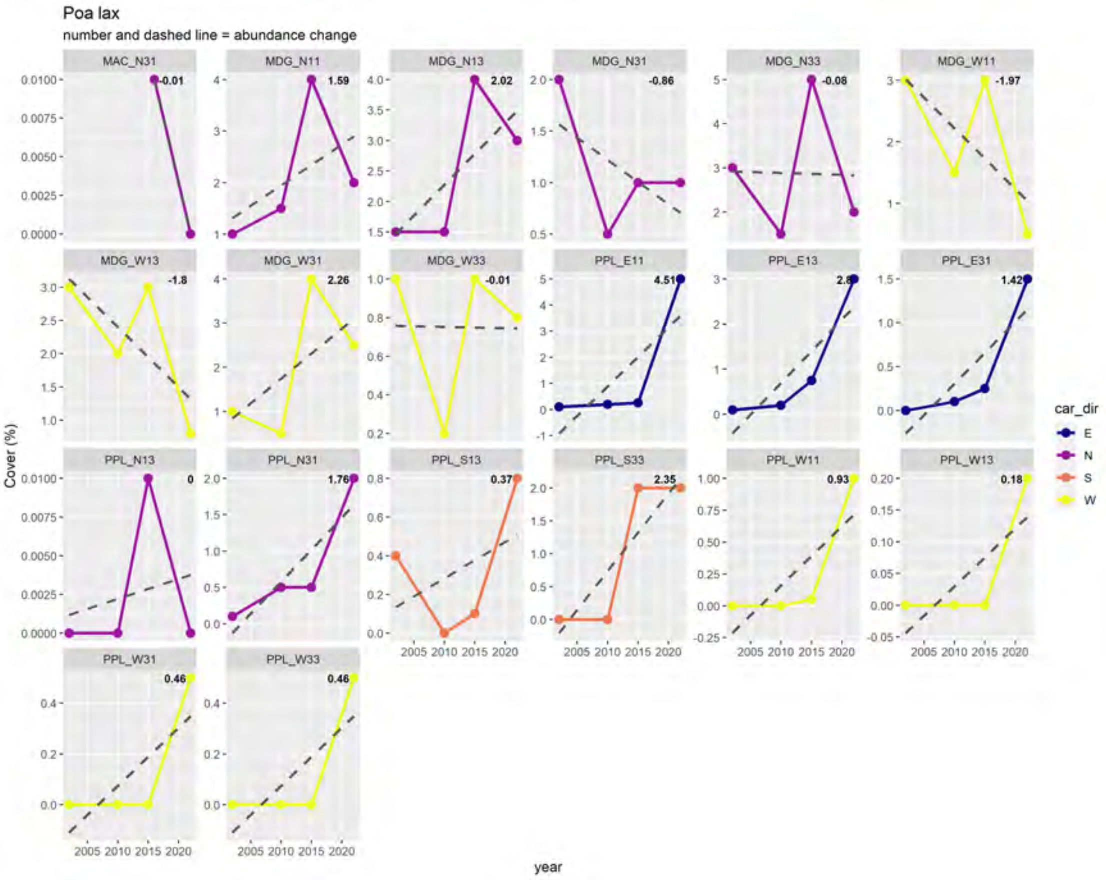
number and dashed line = abundance change

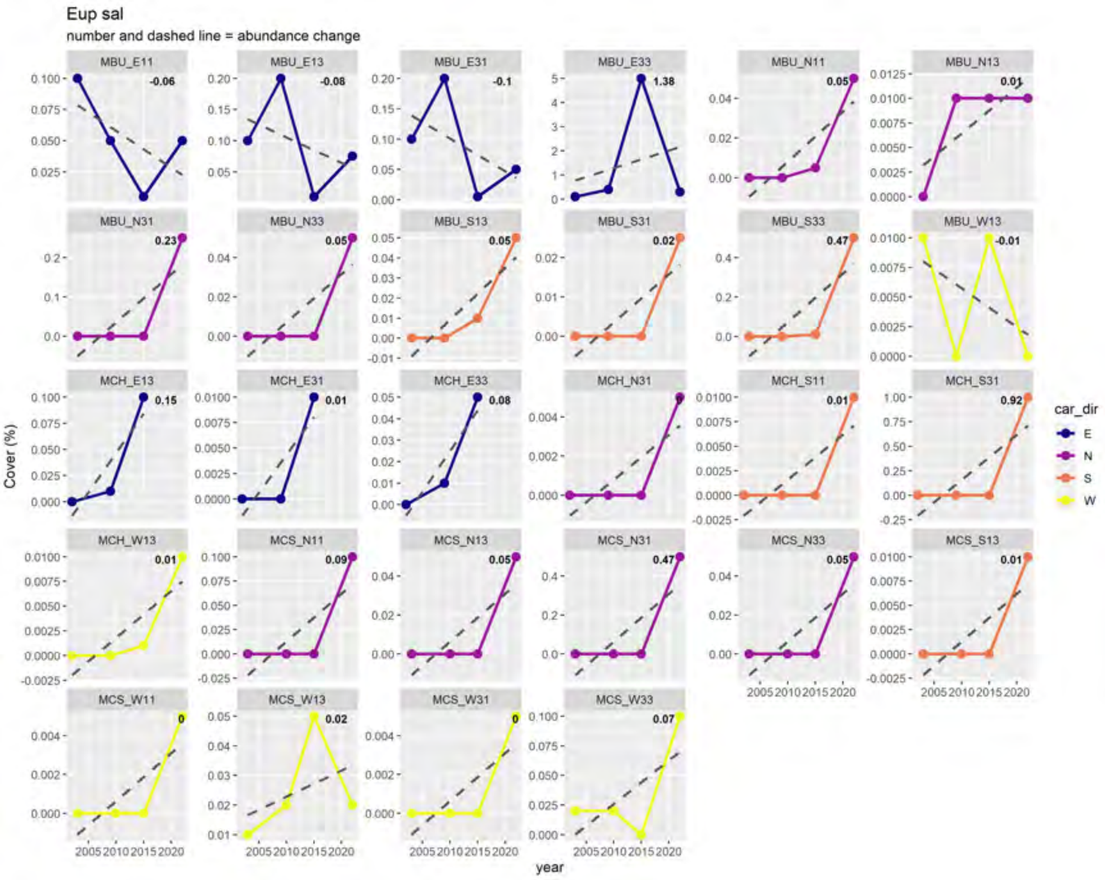


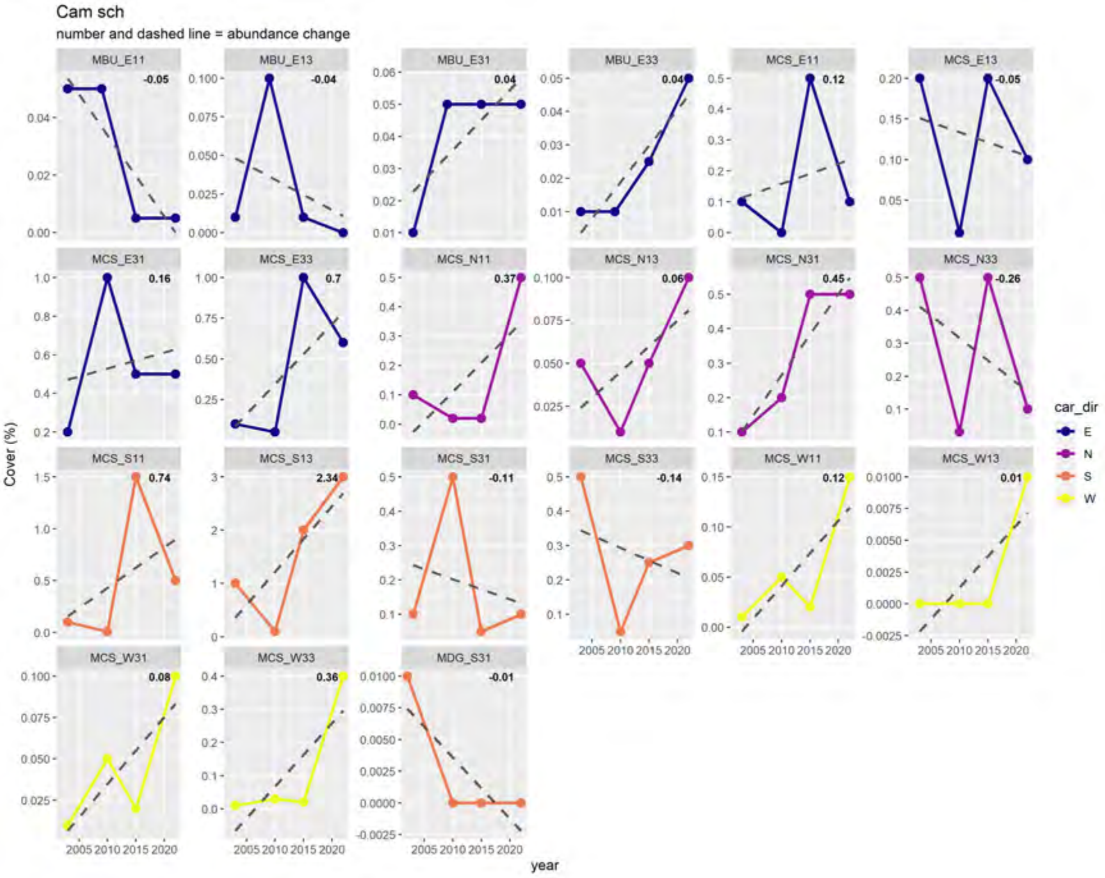
Phy hem

number and dashed line = abundance change


Ver bel
number and dashed line = abundance change
MAC_E11 0.15
MAC_W13 0.05
MCS_E11 0.05
MCS_E13 -1.01
MCS_E31 -1.93
MCS_E33 -0.42
MCS_S11 -1.39
MCS_S13 -0.46
MCS_S31 -1.43
MCS_S33 -2.07
MDG_E11 0.83
MDG_E13 0.94
MDG_E31 0.94
MDG_E33 2.19
MDG_S11 1.29
MDG_S13 2.35
MDG_S31 3.3
MDG_S33 0.17
MIN_E11 0.15
MIN_E13 1.92
MIN_E31 1.76
MIN_E33 2.7
MIN_N11 0.39
MIN_N13 0.67
MIN_N31 -0.15
MIN_N33 2.49
MIN_W11 4.82
MIN_W13 0
MIN_W31 -0.44
MIN_W33 1.53
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W

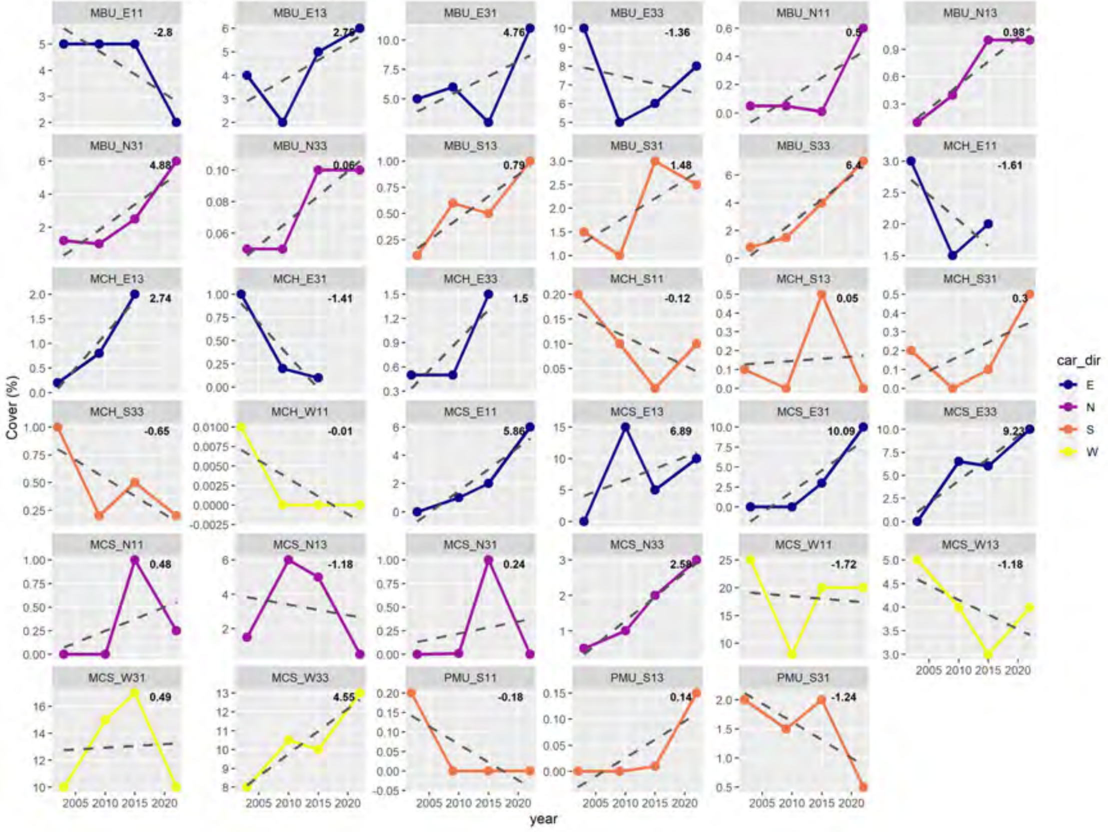

Poa lax
number and dashed line = abundance change
MAC_N31 -0.01
MDG_N11 1.59
MDG_N13 2.02
MDG_N31 -0.86
MDG_N33 -0.08
MDG_W11 -1.97
MDG_W13 -1.8
MDG_W31 2.26
MDG_W33 -0.01
PPL_E11 4.51
PPL_E13 2.8
PPL_E31 1.42
PPL_N13 0
PPL_N31 1.76
PPL_S13 0.37
PPL_S33 2.35
PPL_W11 0.93
PPL_W13 0.18
PPL_W31 0.46
PPL_W33 0.46
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Eup sal
number and dashed line = abundance change
MBU_E11 -0.06
MBU_E13 -0.08
MBU_E31 -0.1
MBU_E33 1.38
MBU_N11 0.05
MBU_N13 0.01
MBU_N31 0.23
MBU_N33 0.05
MBU_S13 0.05
MBU_S31 0.02
MBU_S33 0.47
MBU_W13 -0.01
MCH_E13 0.15
MCH_E31 0.01
MCH_E33 0.08
MCH_N31 0
MCH_S11 0.01
MCH_S31 0.92
MCH_W13 0.01
MCS_N11 0.09
MCS_N13 0.05
MCS_N31 0.47
MCS_N33 0.05
MCS_S13 0.01
MCS_W11 0
MCS_W13 0.02
MCS_W31 0
MCS_W33 0.07
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Cam sch
number and dashed line = abundance change
MBU_E11 -0.05
MBU_E13 -0.04
MBU_E31 0.04
MBU_E33 0.04
MCS_E11 0.12
MCS_E13 -0.05
MCS_E31 0.16
MCS_E33 0.7
MCS_N11 0.37
MCS_N13 0.06
MCS_N31 0.45
MCS_N33 -0.26
MCS_S11 0.74
MCS_S13 2.34
MCS_S31 -0.11
MCS_S33 -0.14
MCS_W11 0.12
MCS_W13 0.01
MCS_W31 0.08
MCS_W33 0.36
MDG_S31 -0.01
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W

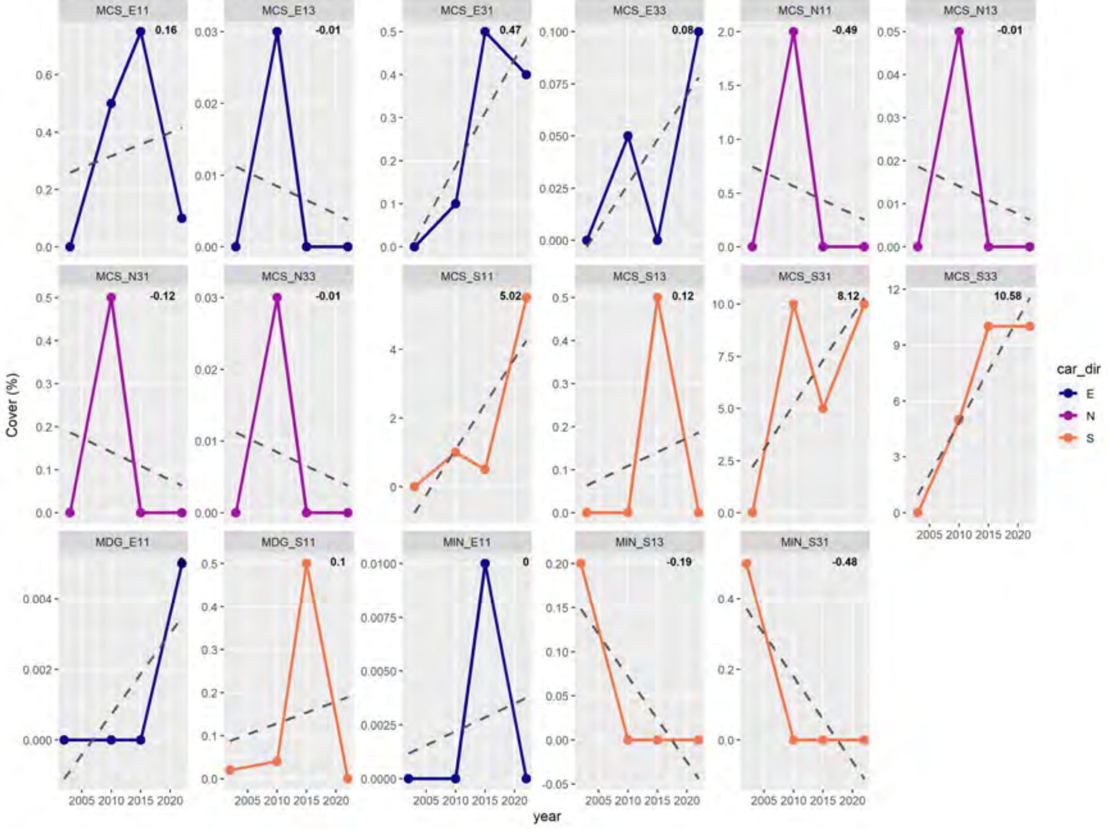
Ses alb

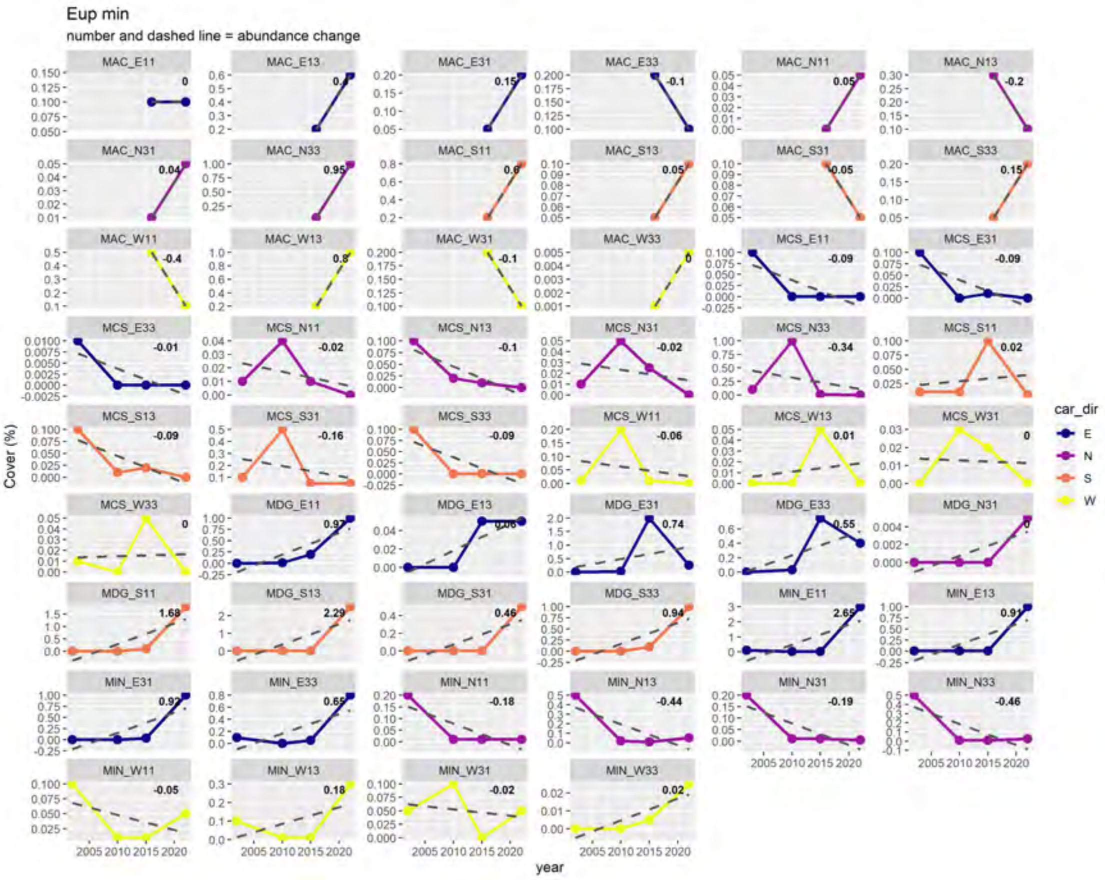
number and dashed line = abundance change

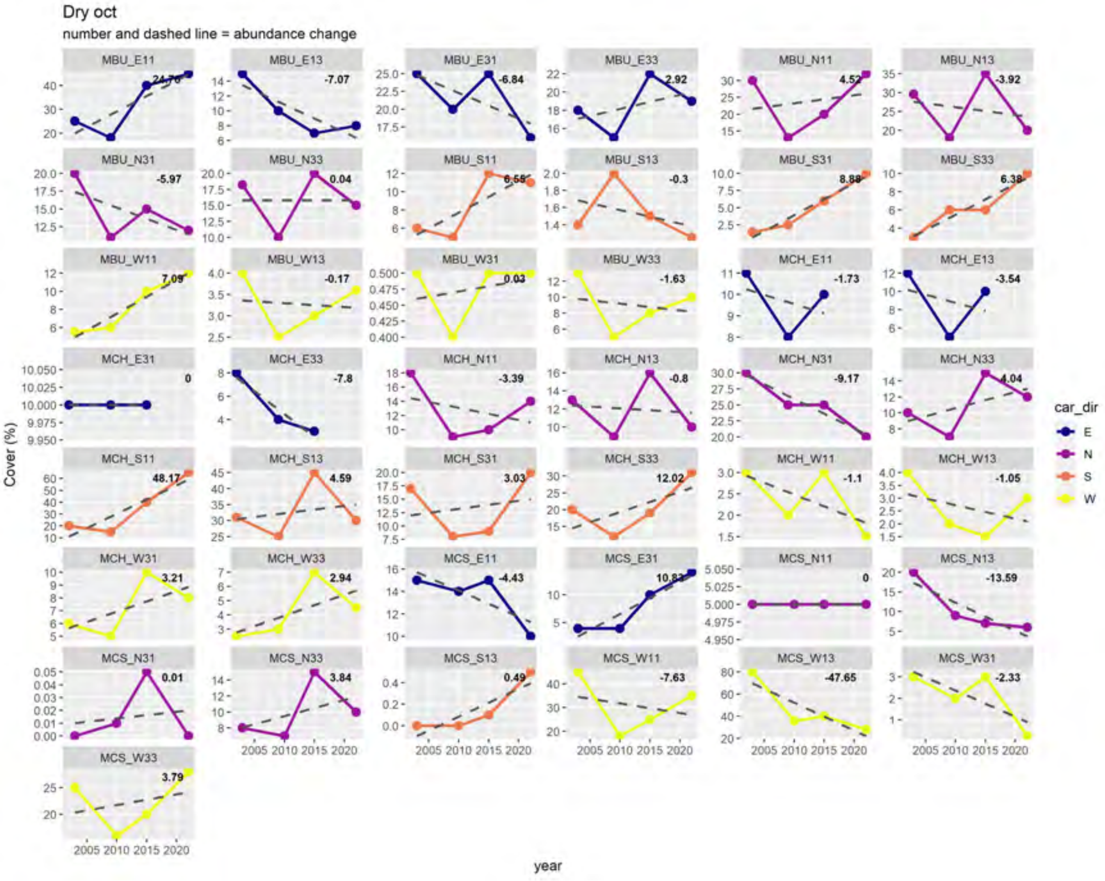


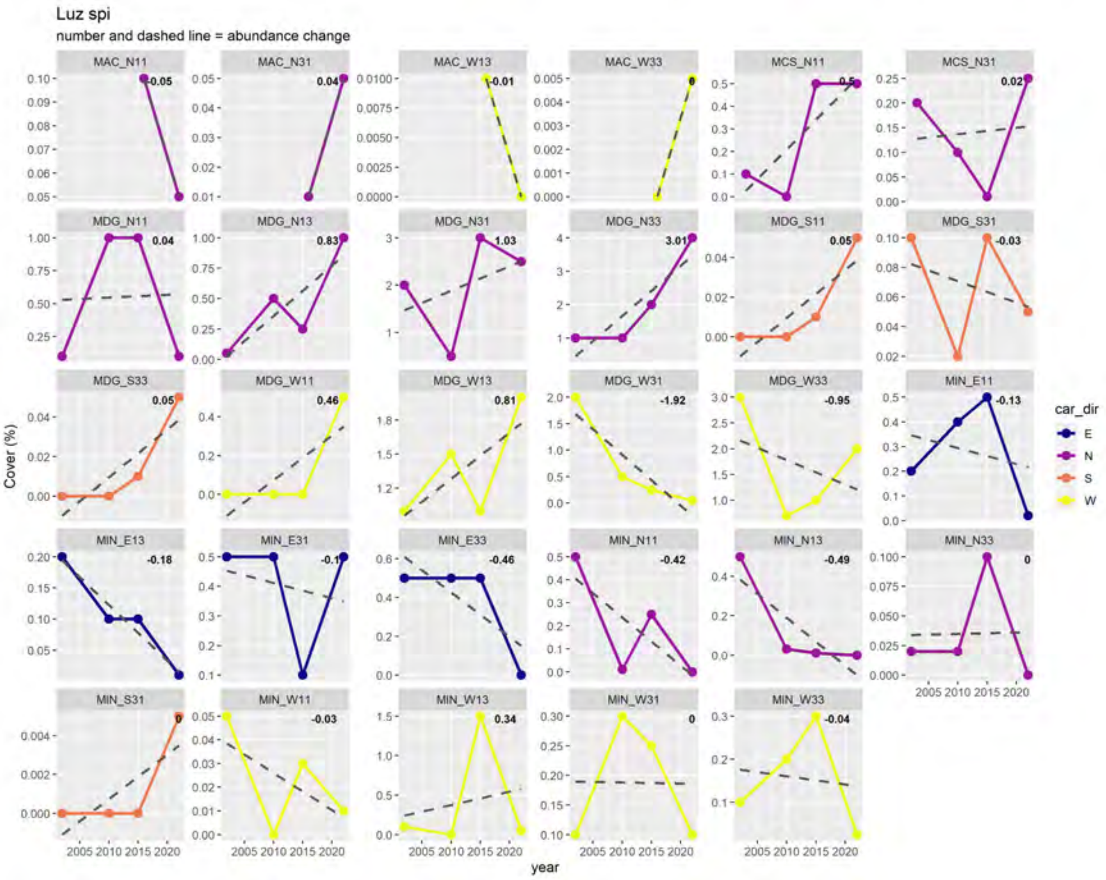
Lig mut

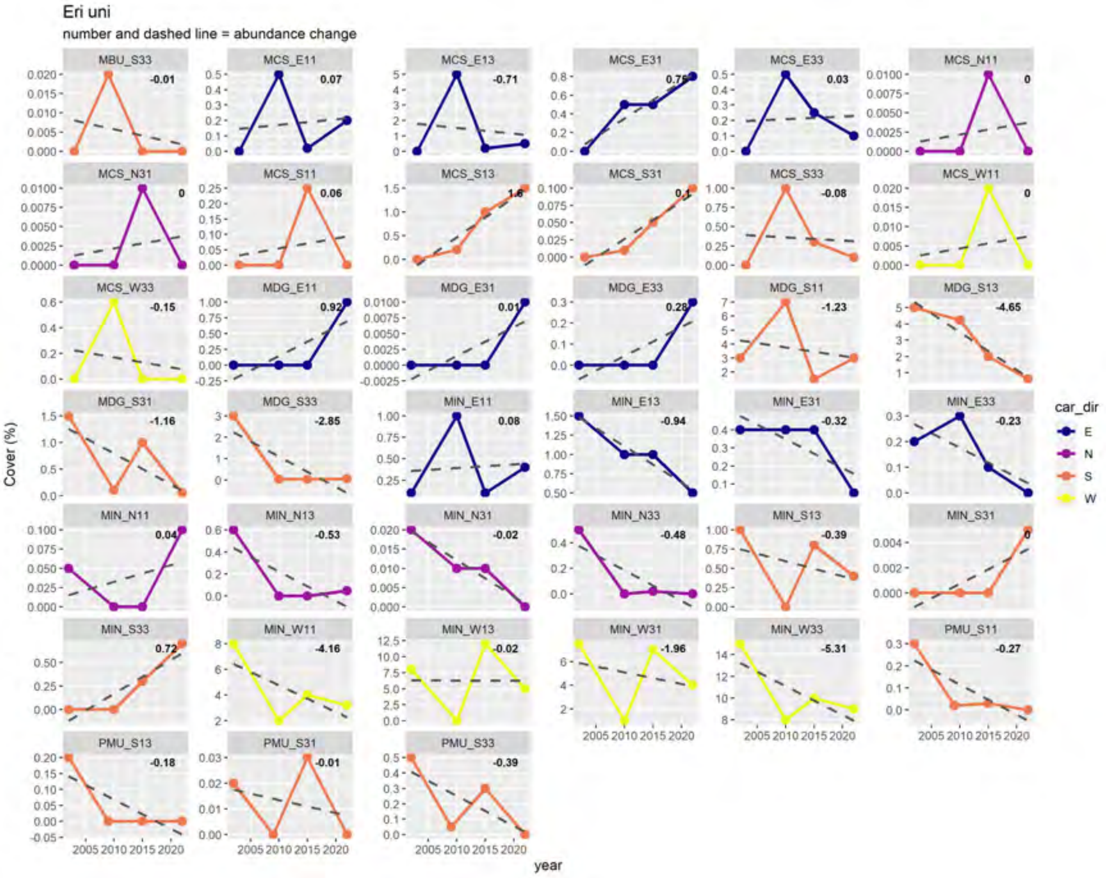
number and dashed line = abundance change

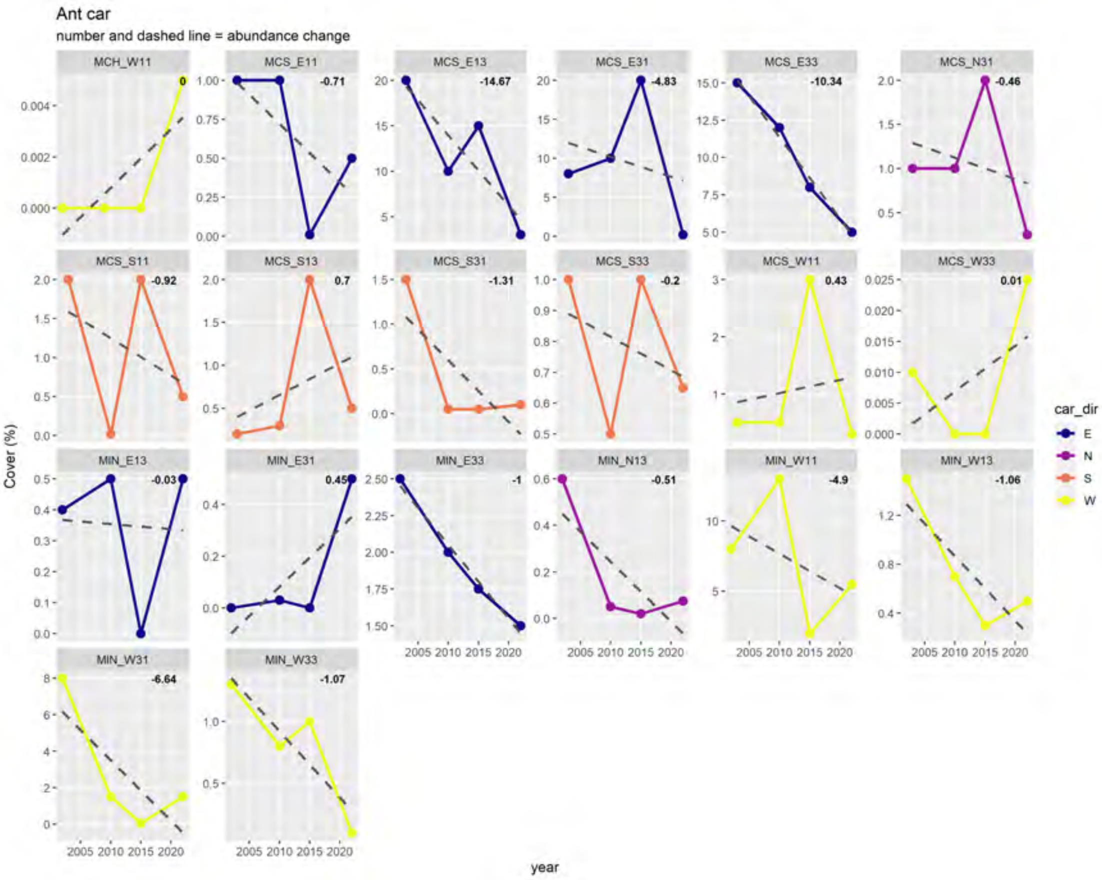


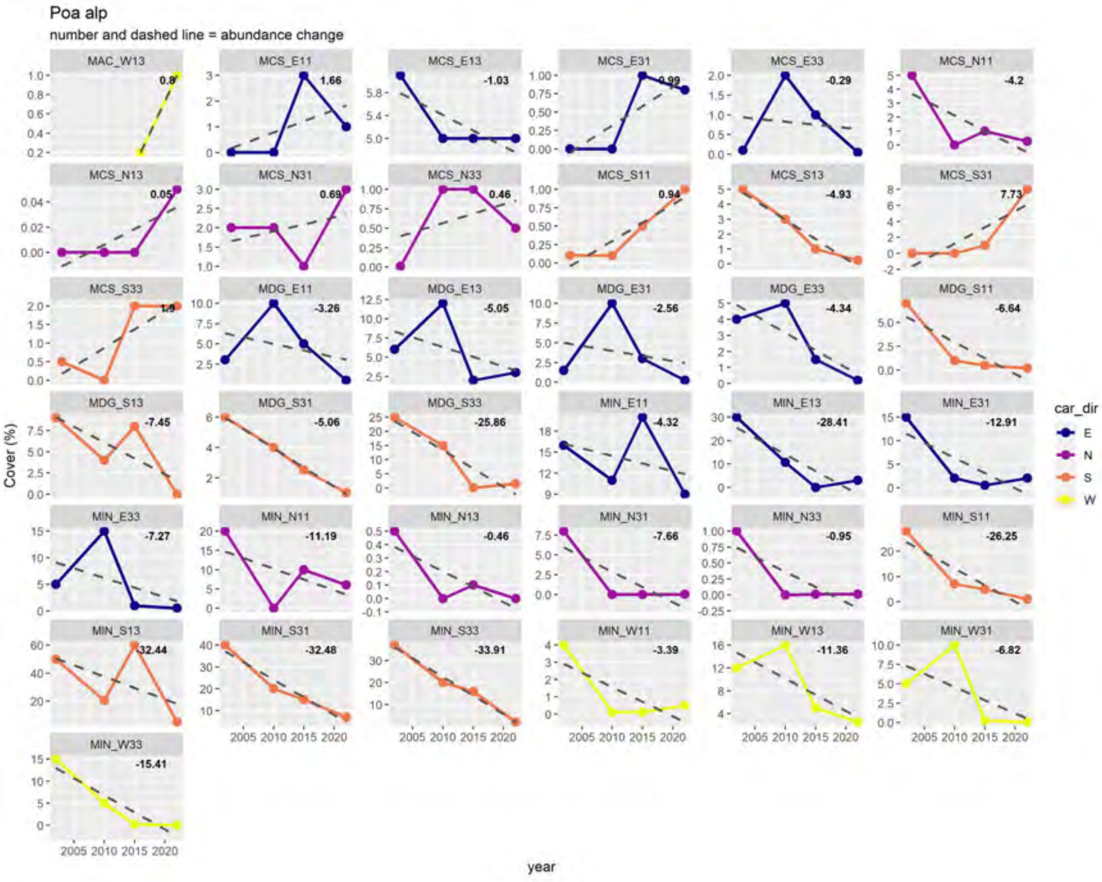

Eup min
number and dashed line = abundance change
MAC_E11 0
MAC_E13 0.4
MAC_E31 0.15
MAC_E33 -0.1
MAC_N11 0.05
MAC_N13 -0.2
MAC_N31 0.04
MAC_N33 0.95
MAC_S11 0.6
MAC_S13 0.05
MAC_S31 -0.05
MAC_S33 0.15
MAC_W11 -0.4
MAC_W13 0.8
MAC_W31 -0.1
MAC_W33 0
MCS_E11 -0.09
MCS_E31 -0.09
MCS_E33 -0.01
MCS_N11 -0.02
MCS_N13 -0.1
MCS_N31 -0.02
MCS_N33 -0.34
MCS_S11 0.02
MCS_S13 -0.09
MCS_S31 -0.16
MCS_S33 -0.09
MCS_W11 -0.06
MCS_W13 0.01
MCS_W31 0
MCS_W33 0
MDG_E11 0.97
MDG_E13 0.06
MDG_E31 0.74
MDG_E33 0.55
MDG_N31 0
MDG_S11 1.68
MDG_S13 2.29
MDG_S31 0.46
MDG_S33 0.94
MIN_E11 2.65
MIN_E13 0.91
MIN_E31 0.92
MIN_E33 0.65
MIN_N11 -0.18
MIN_N13 -0.44
MIN_N31 -0.19
MIN_N33 -0.46
MIN_W11 -0.05
MIN_W13 0.18
MIN_W31 -0.02
MIN_W33 0.02
Cover (%)
2005 2010 2015 2020
year
car_dir
E
N
S
W

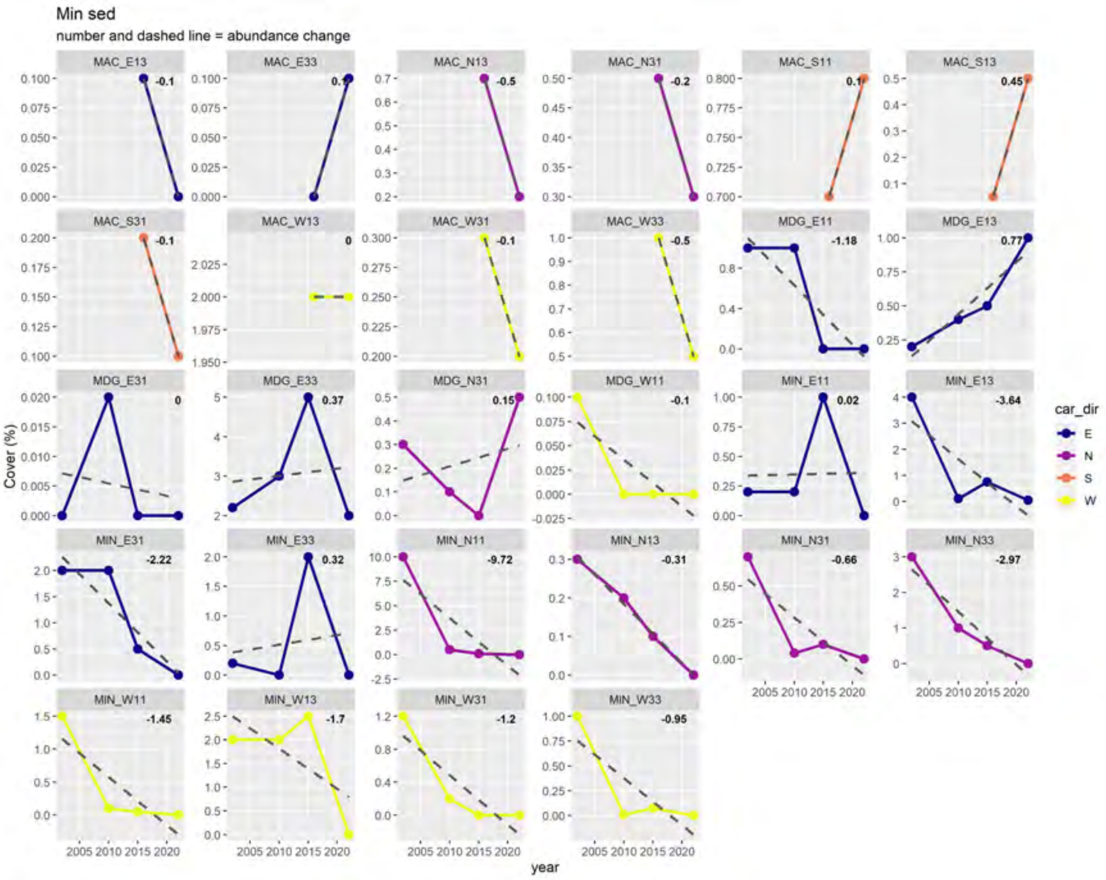

Dry oct
number and dashed line = abundance change
MBU_E11 24.76
MBU_E13 -7.07
MBU_E31 -6.84
MBU_E33 2.92
MBU_N11 4.52
MBU_N13 -3.92
MBU_N31 -5.97
MBU_N33 0.04
MBU_S11 6.55
MBU_S13 -0.3
MBU_S31 8.88
MBU_S33 6.38
MBU_W11 7.09
MBU_W13 -0.17
MBU_W31 0.03
MBU_W33 -1.63
MCH_E11 -1.73
MCH_E13 -3.54
MCH_E31 0
MCH_E33 -7.8
MCH_N11 -3.39
MCH_N13 -0.8
MCH_N31 -9.17
MCH_N33 4.04
MCH_S11 48.17
MCH_S13 4.59
MCH_S31 3.03
MCH_S33 12.02
MCH_W11 -1.1
MCH_W13 -1.05
MCH_W31 3.21
MCH_W33 2.94
MCS_E11 -4.43
MCS_E31 10.83
MCS_N11 0
MCS_N13 -13.59
MCS_N31 0.01
MCS_N33 3.84
MCS_S13 0.49
MCS_W11 -7.63
MCS_W13 -47.65
MCS_W31 -2.33
MCS_W33 3.79
Cover (%)
2005 2010 2015 2020
year
car_dir
E
N
S
W

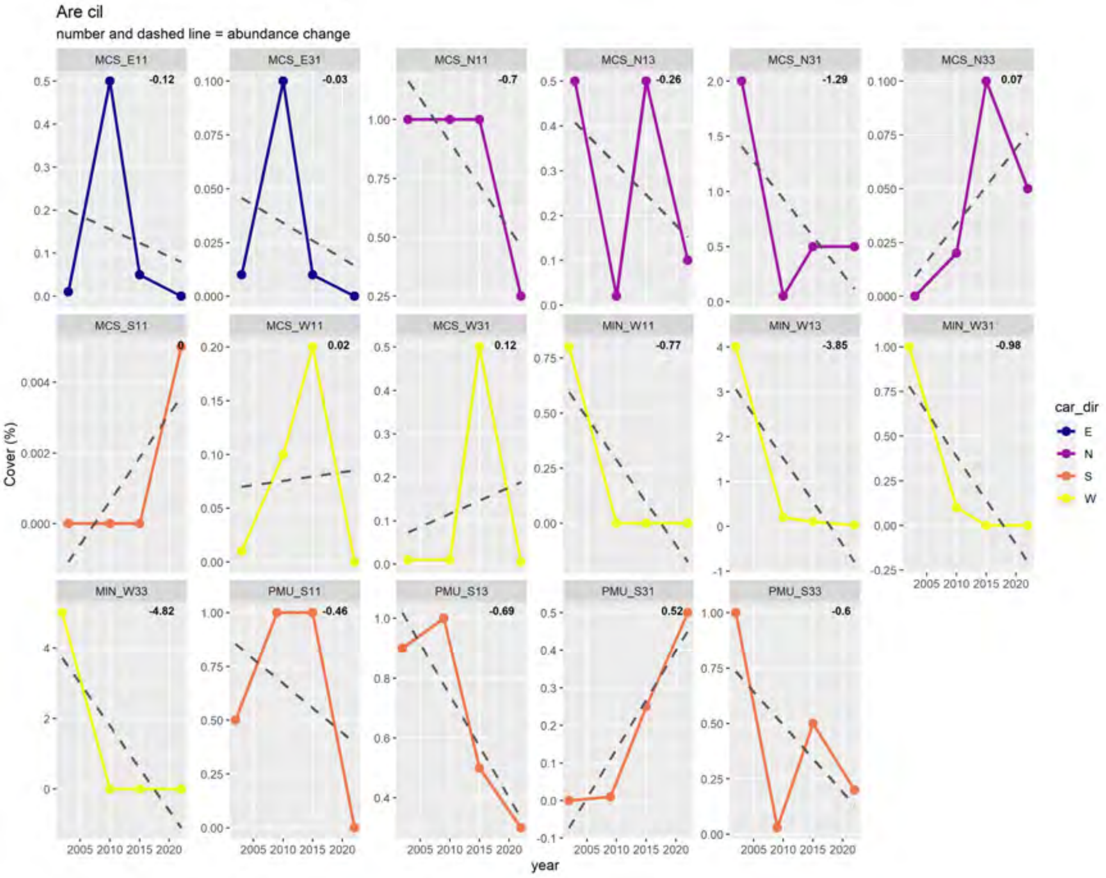

Luz spi
number and dashed line = abundance change
MAC_N11 -0.05
MAC_N31 0.04
MAC_W13 -0.01
MAC_W33 0
MCS_N11 0.5
MCS_N31 0.02
MDG_N11 0.04
MDG_N13 0.83
MDG_N31 1.03
MDG_N33 3.01
MDG_S11 0.05
MDG_S31 -0.03
MDG_S33 0.05
MDG_W11 0.46
MDG_W13 0.81
MDG_W31 -1.92
MDG_W33 -0.95
MIN_E11 -0.13
MIN_E13 -0.18
MIN_E31 -0.1
MIN_E33 -0.46
MIN_N11 -0.42
MIN_N13 -0.49
MIN_N33 0
MIN_S31 0
MIN_W11 -0.03
MIN_W13 0.34
MIN_W31 0
MIN_W33 -0.04
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W

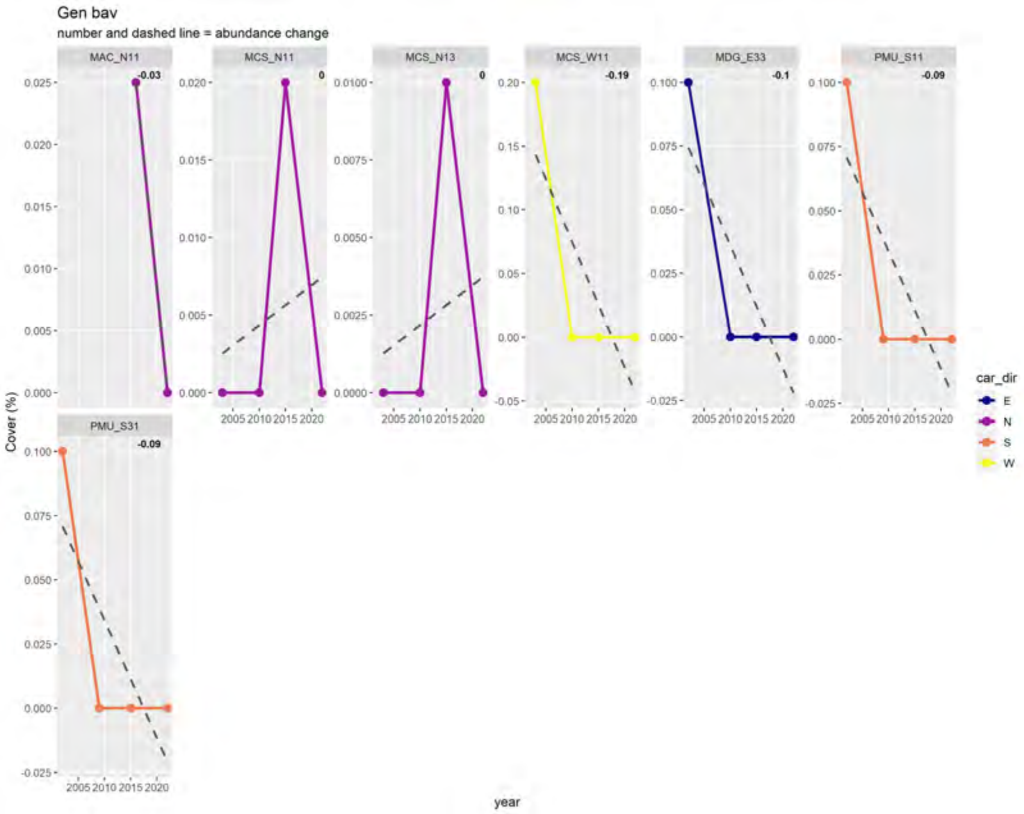

Eri uni
number and dashed line = abundance change
MBU_S33 -0.01
MCS_E11 0.07
MCS_E13 -0.71
MCS_E31 0.76
MCS_E33 0.03
MCS_N11 0
MCS_N31 0
MCS_S11 0.06
MCS_S13 1.6
MCS_S31 0.1
MCS_S33 -0.08
MCS_W11 0
MCS_W33 -0.15
MDG_E11 0.92
MDG_E31 0.01
MDG_E33 0.28
MDG_S11 -1.23
MDG_S13 -4.65
MDG_S31 -1.16
MDG_S33 -2.85
MIN_E11 0.08
MIN_E13 -0.94
MIN_E31 -0.32
MIN_E33 -0.23
MIN_N11 0.04
MIN_N13 -0.53
MIN_N31 -0.02
MIN_N33 -0.48
MIN_S13 -0.39
MIN_S31 0
MIN_S33 0.72
MIN_W11 -4.16
MIN_W13 -0.02
MIN_W31 -1.96
MIN_W33 -5.31
PMU_S11 -0.27
PMU_S13 -0.18
PMU_S31 -0.01
PMU_S33 -0.39
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Ant car
number and dashed line = abundance change
MCH_W11 0
MCS_E11 -0.71
MCS_E13 -14.67
MCS_E31 -4.83
MCS_E33 -10.34
MCS_N31 -0.46
MCS_S11 -0.92
MCS_S13 0.7
MCS_S31 -1.31
MCS_S33 -0.2
MCS_W11 0.43
MCS_W33 0.01
MIN_E13 -0.03
MIN_E31 0.45
MIN_E33 -1
MIN_N13 -0.51
MIN_W11 -4.9
MIN_W13 -1.06
MIN_W31 -6.64
MIN_W33 -1.07
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Poa alp
number and dashed line = abundance change
MAC_W13 0.8
MCS_E11 1.66
MCS_E13 -1.03
MCS_E31 0.99
MCS_E33 -0.29
MCS_N11 -4.2
MCS_N13 0.05
MCS_N31 0.69
MCS_N33 0.46
MCS_S11 0.94
MCS_S13 -4.93
MCS_S31 7.73
MCS_S33 1.9
MDG_E11 -3.26
MDG_E13 -5.05
MDG_E31 -2.56
MDG_E33 -4.34
MDG_S11 -6.64
MDG_S13 -7.45
MDG_S31 -5.06
MDG_S33 -25.86
MIN_E11 -4.32
MIN_E13 -28.41
MIN_E31 -12.91
MIN_E33 -7.27
MIN_N11 -11.19
MIN_N13 -0.46
MIN_N31 -7.66
MIN_N33 -0.95
MIN_S11 -26.25
MIN_S13 -32.44
MIN_S31 -32.48
MIN_S33 -33.91
MIN_W11 -3.39
MIN_W13 -11.36
MIN_W31 -6.82
MIN_W33 -15.41
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Min sed
number and dashed line = abundance change
MAC_E13 -0.1
MAC_E33 0.1
MAC_N13 -0.5
MAC_N31 -0.2
MAC_S11 0.1
MAC_S13 0.45
MAC_S31 -0.1
MAC_W13 0
MAC_W31 -0.1
MAC_W33 -0.5
MDG_E11 -1.18
MDG_E13 0.77
MDG_E31 0
MDG_E33 0.37
MDG_N31 0.15
MDG_W11 -0.1
MIN_E11 0.02
MIN_E13 -3.64
MIN_E31 -2.22
MIN_E33 0.32
MIN_N11 -9.72
MIN_N13 -0.31
MIN_N31 -0.66
MIN_N33 -2.97
MIN_W11 -1.45
MIN_W13 -1.7
MIN_W31 -1.2
MIN_W33 -0.95
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W


Are cil
number and dashed line = abundance change
MCS_E11 -0.12
MCS_E31 -0.03
MCS_N11 -0.7
MCS_N13 -0.26
MCS_N31 -1.29
MCS_N33 0.07
MCS_S11 0
MCS_W11 0.02
MCS_W31 0.12
MIN_W11 -0.77
MIN_W13 -3.85
MIN_W31 -0.98
MIN_W33 -4.82
PMU_S11 -0.46
PMU_S13 -0.69
PMU_S31 0.52
PMU_S33 -0.6
Cover (%)
year
2005 2010 2015 2020
car_dir
E
N
S
W



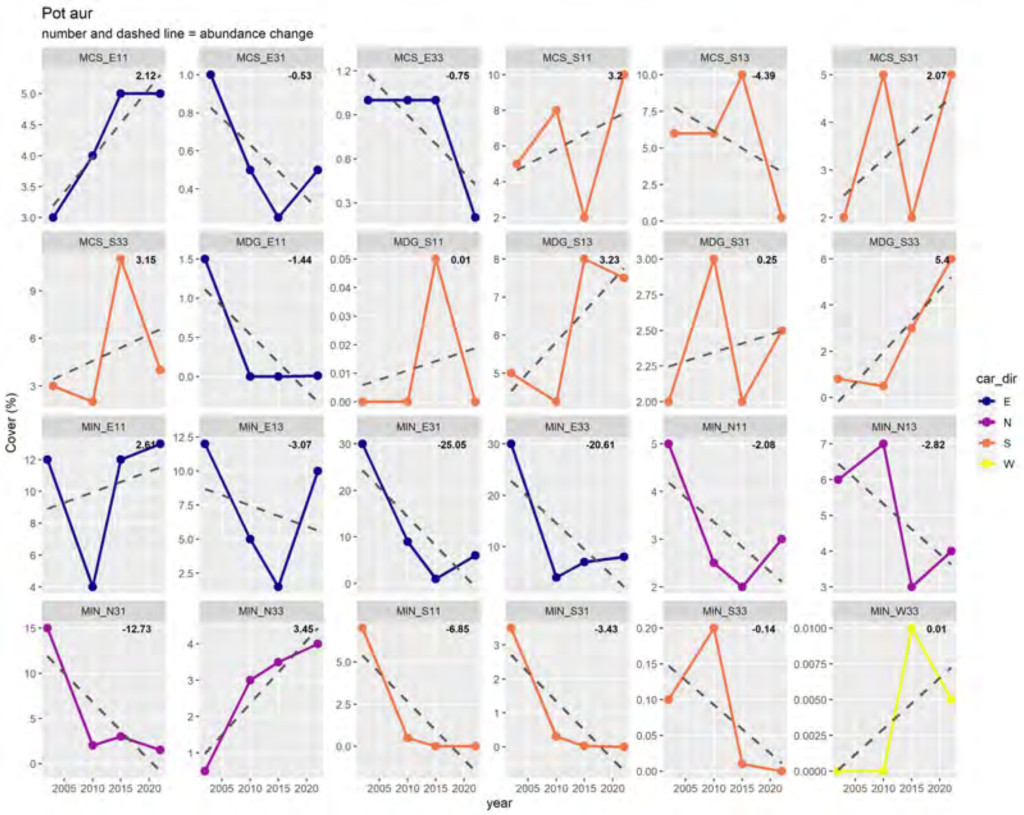
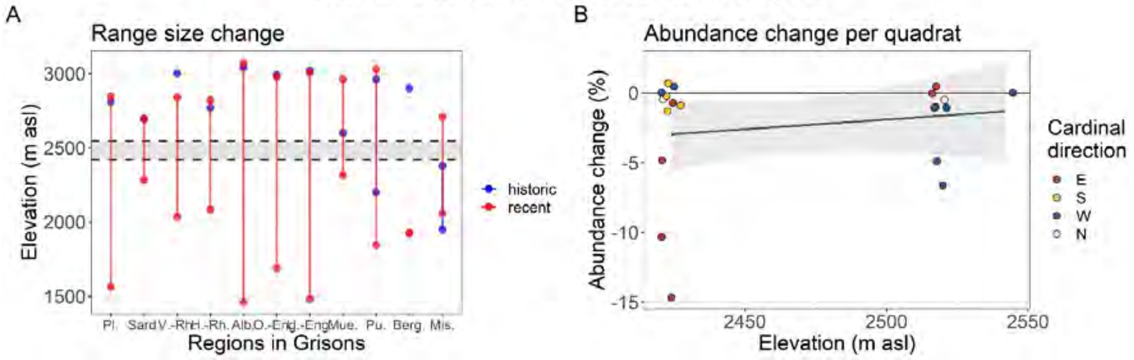


Figure A1 Abundance change of species showing significant changes per quadrat (e.g. MAC_E11). See the methodology section for quadrat designations. The change in abundance is calculated from the slope of the regression line (dashed grey line) and given a number in the upper right corner. Colours indicate the cardinal direction (car_dir) of quadrats.

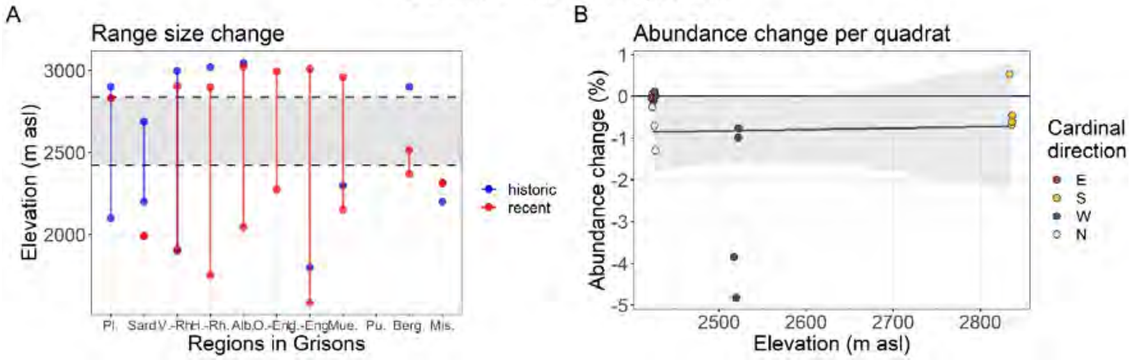
Table A2 Inconsistent-reacting species due to the three categories (1) time-dependent cover trend, (2) temperature-dependent abundance change, and (3) time-dependent number of occurrences. Only value (1) and (2) were tested statistically. The values in bold were significant. **Time-dependent cover trend**: numbers are the estimates from a generalized mixed model. **Temperature-dependent abundance change**: positive values meaning the regression line remains positive over the whole temperature gradient, independently whether it rises or falls. Same with the value 'negative'. 'Cross' is indicating the regression line crosses the zero y-line. **Time-dependent number of occurrences**: Increasing numbers indicate colonisation. Evaluation was made visually.

Short name	(1) Time-dependent cover trend	(2) Temp.-dependent abundance change	(3) Time-dependent number of occurrences
Car eri	-0.0102	**Cross (+)**	colonisation
Gen niv	-0.0007	**Cross (+)**	colonisation
Sax bry	**0.0221**	Cross (-)	no trend
Fes qua	-0.0055	**Cross (+)**	no trend
Geu mon	**-0.0421**	positive	colonisation
Luz lut	**-0.0263**	**negative**	colonisation

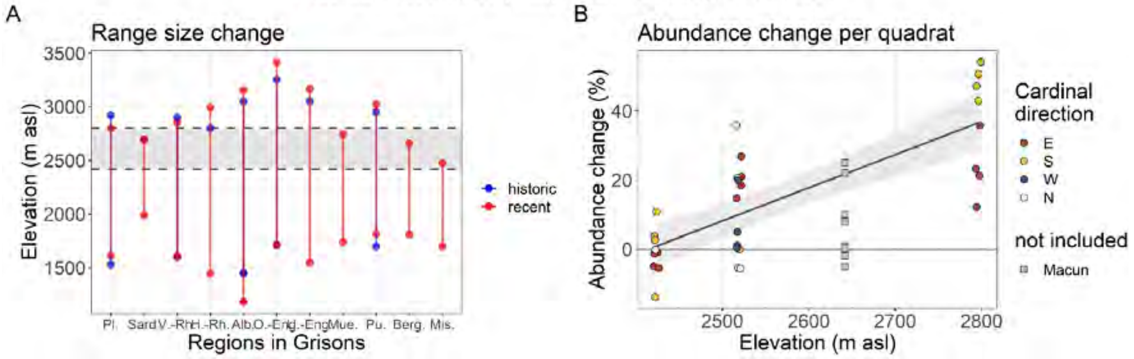
Antennaria carpatica (Wahlenb.) Bluff & Fingerh.



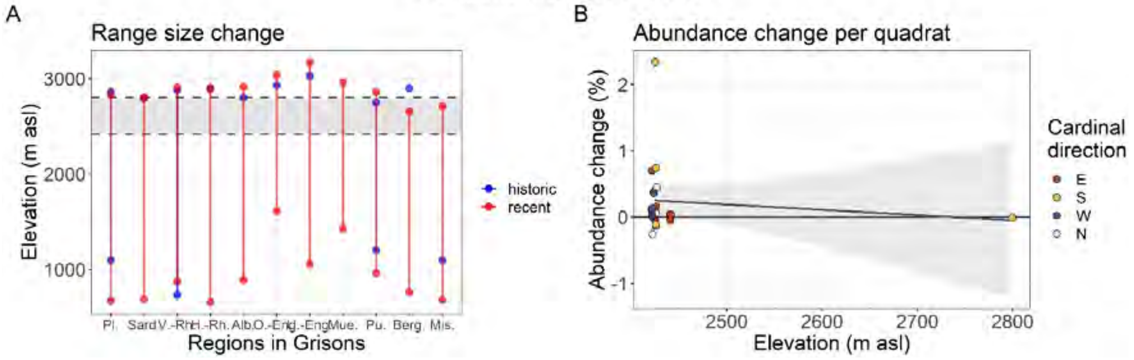
Arenaria ciliata L. subsp. ciliata



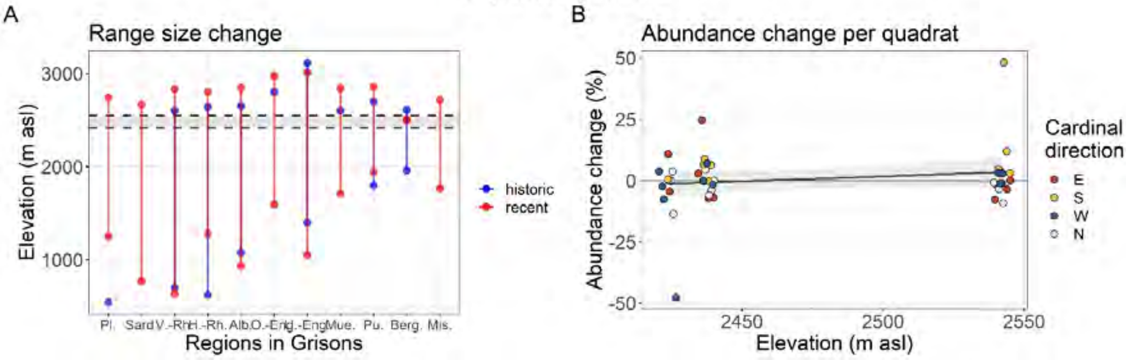
Avenula versicolor (Vill.) M.Laínz subsp. versicolor



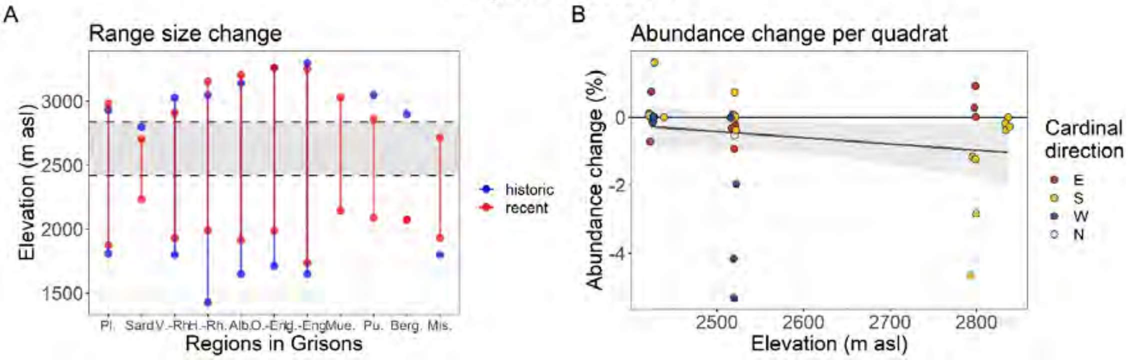
Campanula scheuchzeri Vill.



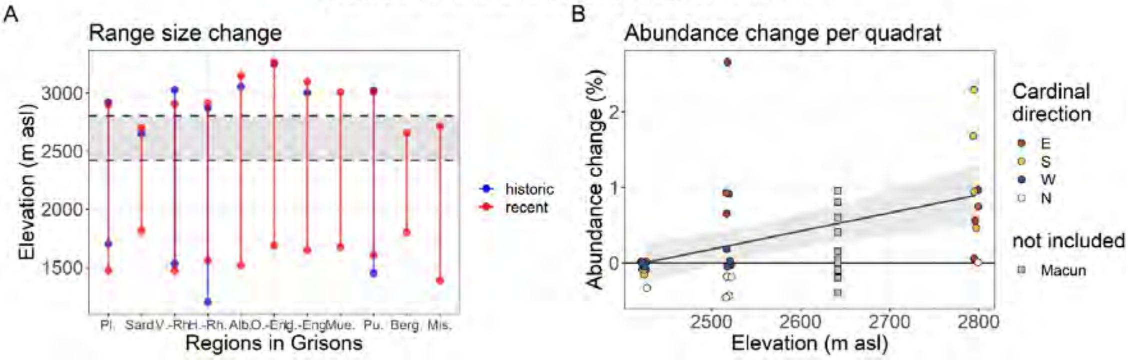
Dryas octopetala L.



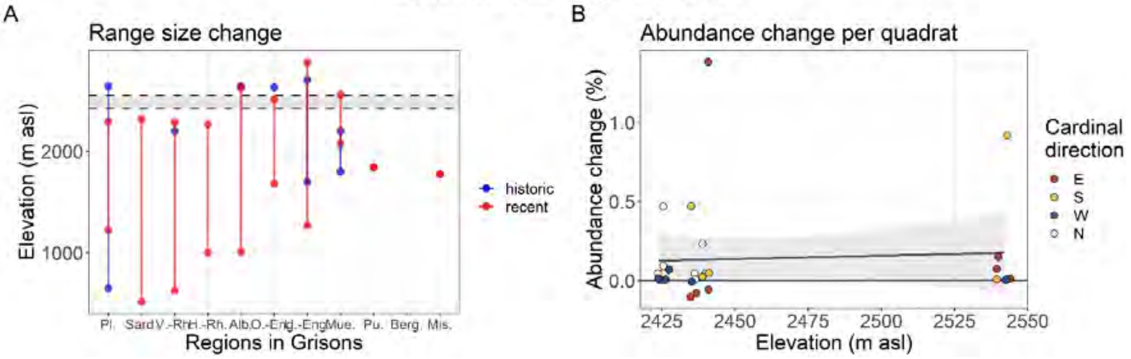
Erigeron uniflorus L.



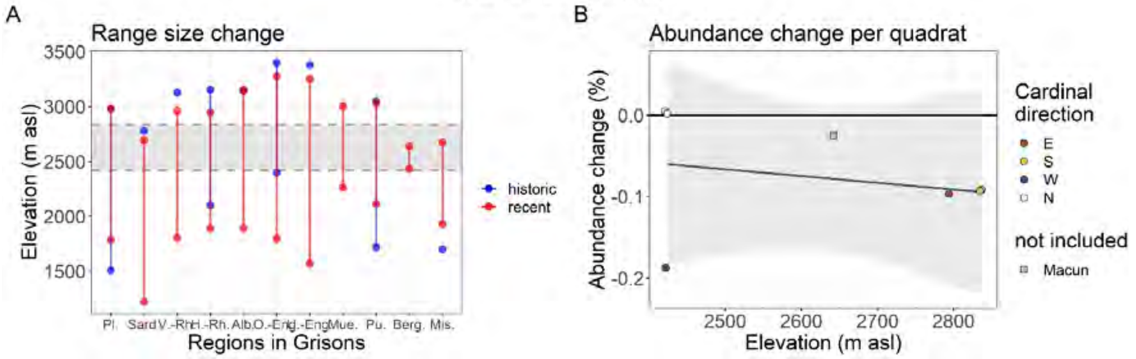
Euphrasia minima Jacq. ex DC. subsp. minima



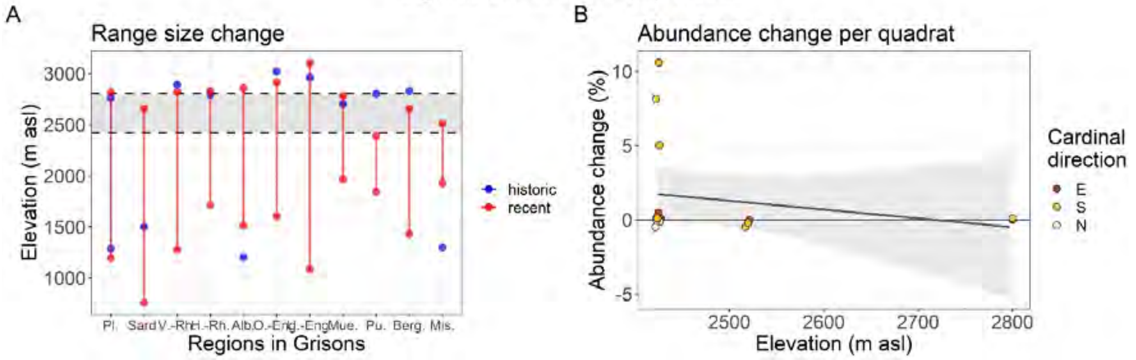
Euphrasia salisburgensis Funck



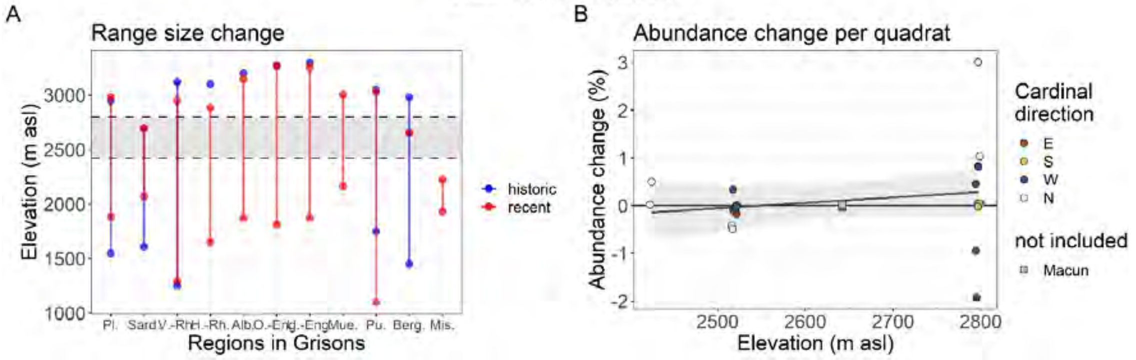
Gentiana bavarica L.



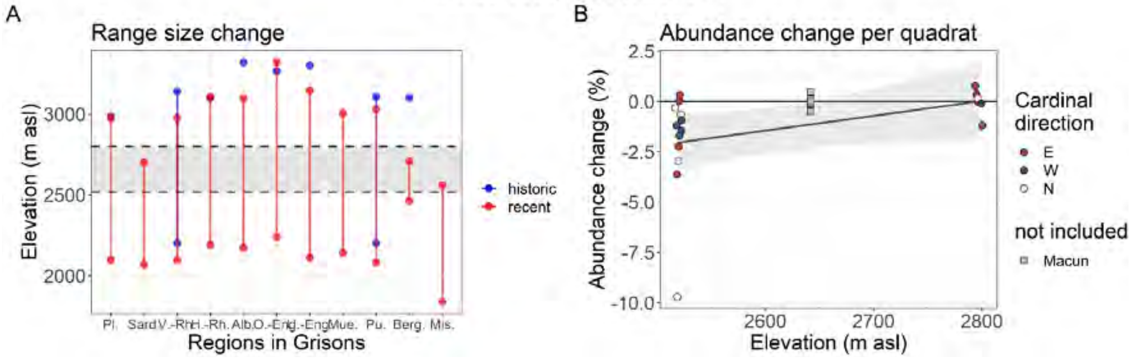
Ligusticum mutellina (L.) Crantz



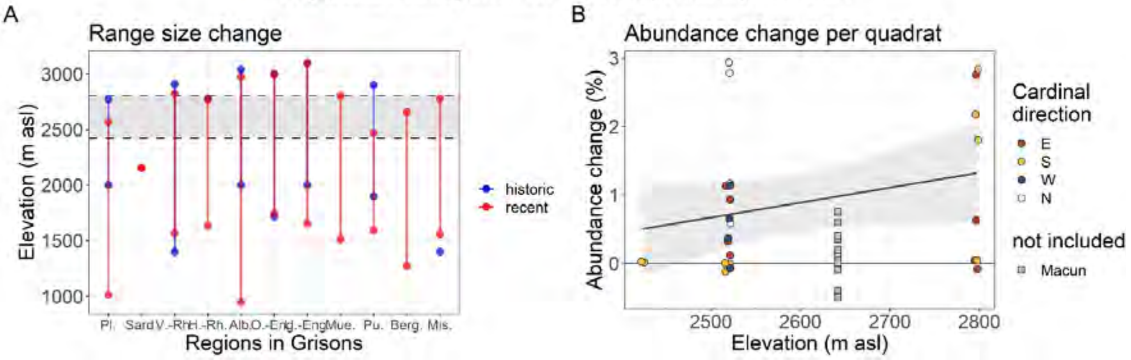
Luzula spicata (L.) DC.



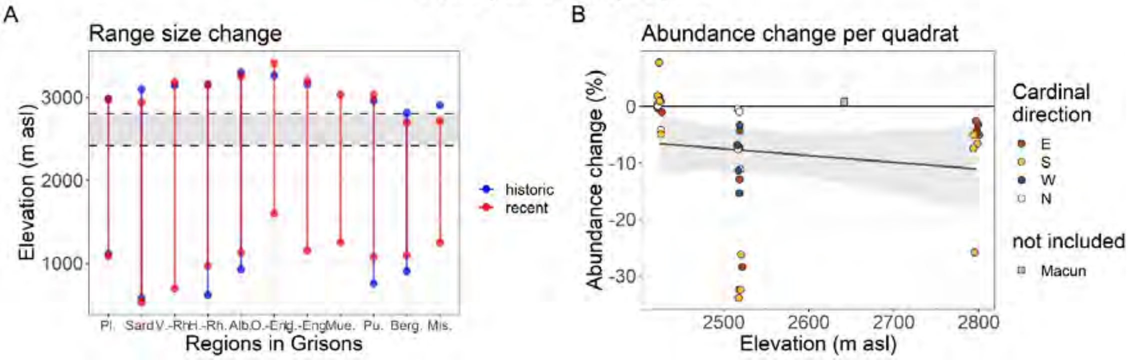
Minuartia sedoides (L.) Hiern



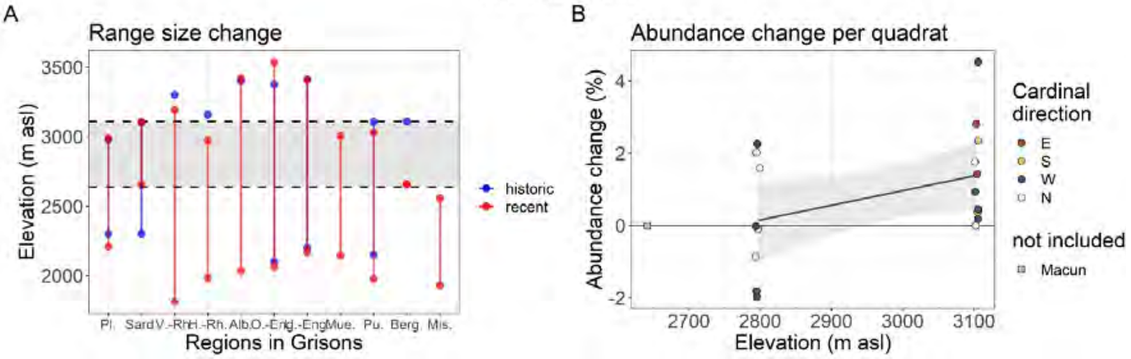
Phyteuma hemisphaericum L. subsp. hemisphaericum



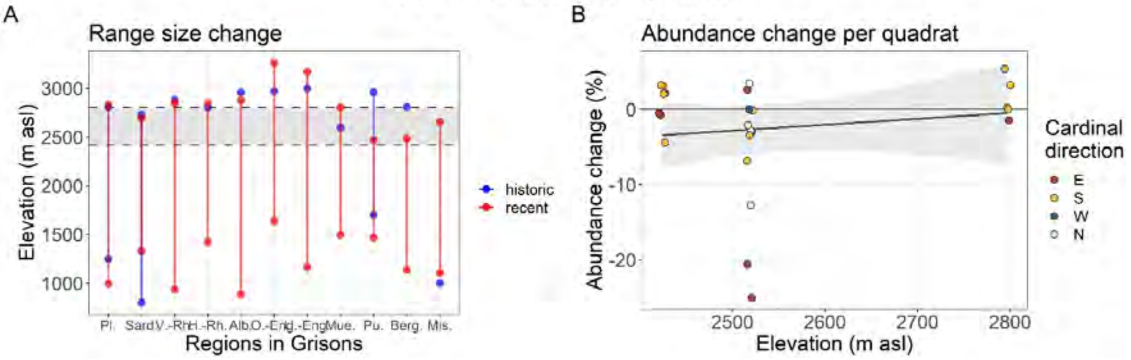
Poa alpina L. subsp. alpina



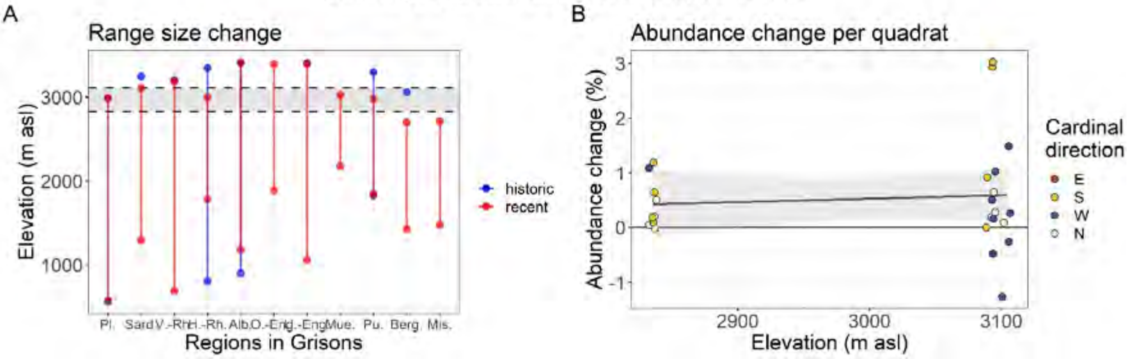
Poa laxa Haenke



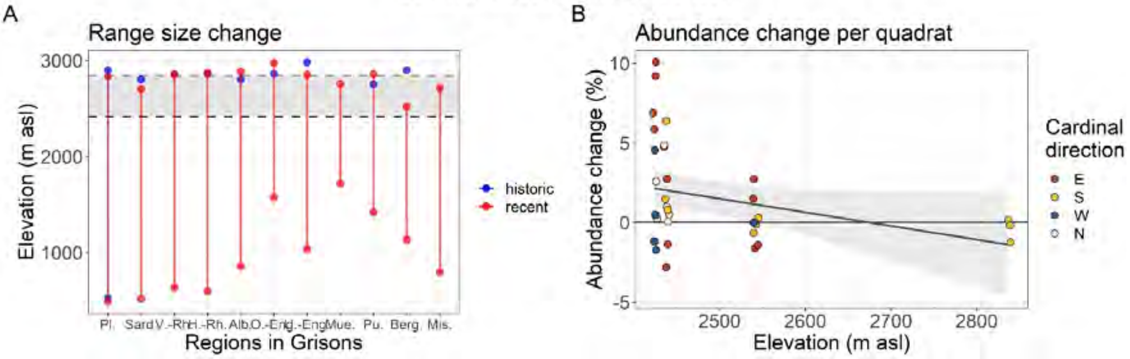
Potentilla aurea L. subsp. aurea



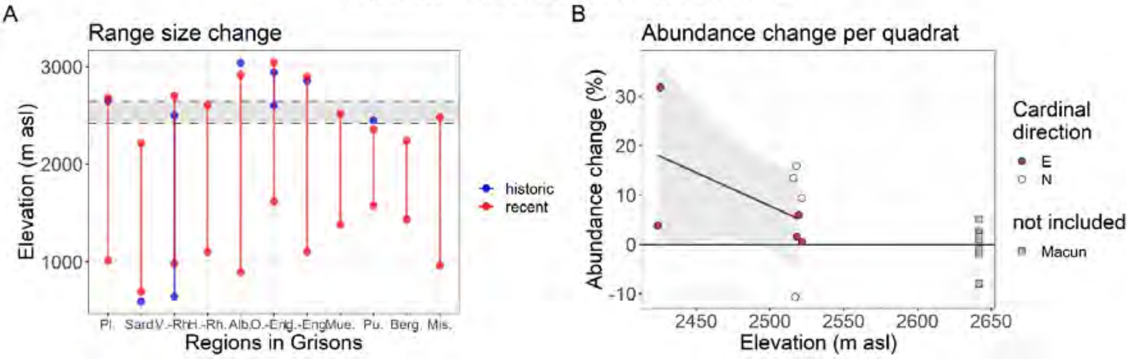
Saxifraga oppositifolia L. subsp. oppositifolia



Sesleria albicans Kit. ex Schult.



Vaccinium vitis-idaea L. subsp. vitis-idaea



Veronica bellidioides L. subsp. bellidioides

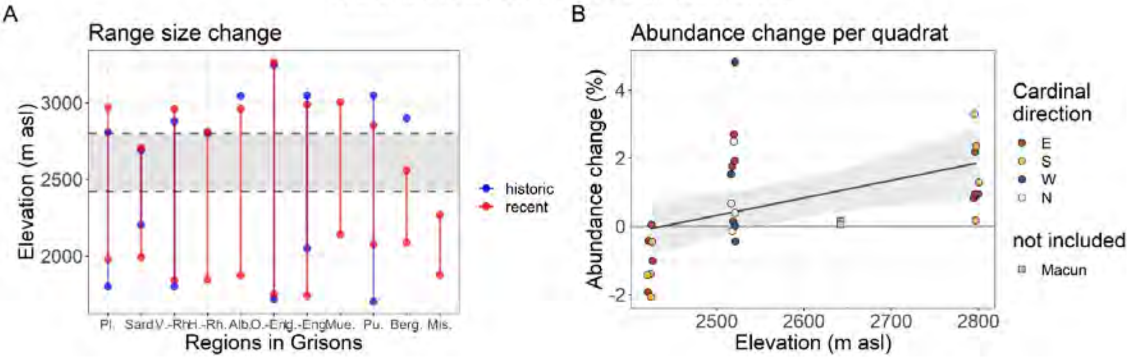


Figure A2 Relationship of (A) regional-scaled range shift at leading and rear edge in historical regions of Grisons, Switzerland and (B) local-scaled abundance change in relation to elevation **A.** Comparison of highest historical/recent and lowest historical/recent location per region. Grey area is indicating elevation range of GLORIA sites on local scales. **B.** Regression line of abundance change on quadrats on GLORIA sites in relation to elevation. Grey area indicates confidence interval. Position of regression line define characterisation. For further information please see chapter 2.7.

Declaration of Authorship

I hereby declare that the paper submitted is my own unaided work. All direct or indirect sources used are acknowledged as references.

Munich, November 22, 2023

C. Altmiks

Corinna Altmiks