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Doctoral Thesis

Responses of alpine plant species to anthropogenic global changes across contrasting European biomes: Alps and Mediterranean mountains

submitted by

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I hereby declare that I made the available work independently and without use of others than the indicated aids. Ideas and quotes taken directly or indirectly from other sources are identified as such.

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> *'Das Artenverzeichnis mag einen, wenn auch kleinen Zuwachs erhalten, dagegen ist vorauszusetzen, dass die Höhengrenzen der Arten eine Verschiebung erleiden werden. Dies zu verfolgen wird, wie ich hoffe, in späteren Jahren eine anregende Aufgabe darstellen.'*
>
> Josias Braun-Blanquet, 1958

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ABSTRACT

The global decline of biodiversity presents one of the greatest challenges in human history. Consequently, investigating the current biodiversity patterns, their changes and processes behind these changes is essential. Opportunities for long-term observations in natural habitats are rare. Precisely for this reason, the *Global Observation Research Initiative in Alpine Environments* (GLORIA), a global long-term monitoring programme, was established to discern trends in vegetation changes, and to assess and predict losses in biodiversity in these sensitive alpine ecosystems which are under accelerating global change pressures.

This thesis used vascular plant species diversity and abundance data from permanent plots of three surveys of GLORIA mountain sites in the climatically contrasting temperate (represented by the Alps) and Mediterranean biomes. Generalized linear mixed-effects models were used to examine temporal and spatial trends in species composition and their relationship to climate factors (ERA5 temperature and precipitation data; snow cover durations, derived from *in situ* soil temperature data), and to species and plot specific characteristics. Furthermore, human activities and land-use changes were assessed in the regions.

In the Alps, with a summer-humid temperate climate, ongoing species richness increase and simultaneous cover decrease, primarily through decline of all cold-adapted specialists, were leading to an accelerating transformation towards a more warmth-demanding and more drought-adapted vegetation. On Mediterranean summits, species richness and cover changes switched direction between surveys, with a slight net increase over the entire period of almost two decades. This was not the case for endemic species, which almost exclusively occur in the upper vegetation belts. While endemics underwent cover losses compared to non-endemics, more widespread shrub species increased. In addition, the results of correlations underpin the implication of climate change impacts on changes of biodiversity patterns of high-mountain vegetation in both biomes. Nevertheless, divergent responses of contrasting biomes suggest that direct warming effects are the primary causes of the observed patterns in the Alps, whereas on Mediterranean summits, changing water availability appears to play the key role. Influences through direct human activities cannot fully explain currently observed vegetation changes, but a certain regional influence cannot be ruled out.

The observed decreases in cryophilic species in both biomes could imply a period of reinforced species declines and losses. Only partly filled vegetation gaps in temperate mountains arising from population dieback of cold-adapted specialists, indicates that species decreases have occurred not exclusively because of competition pressure. High mountain vegetation in Mediterranean areas seems to be even more sensitive to climate fluctuations, especially to water availability. This strengthens concerns about biodiversity losses, if projections of rising temperature in combination with decreasing precipitation in Europe's South hold true.

Key words: Alpine plant diversity; Alps; climate change impact indicator; GLORIA programme; long-term monitoring; Mediterranean mountains; land-use changes; species composition changes.

KURZFASSUNG

Die aktuelle globale Biodiversitätskrise ist eine der größten Herausforderungen der Menschheit. Die Kenntnis rezenter Biodiversitätsmuster, sowie ihrer Veränderungen und zugrundeliegender Prozesse ist daher von immenser Bedeutung. Präzise Langzeitbeobachtungen in natürlichen Lebensräumen sind jedoch rar. Aus diesem Grund wurde das globale Langzeitbeobachtungsprogramm GLORIA (*Global Observation Research Initiative in Alpine Environments*) ins Leben gerufen, um Veränderungen der Vegetationszusammensetzung in hochsensiblen alpinen Ökosystemen sowie ihre Ursachen zu erkennen und den Verlust an biologischer Vielfalt einschätzen und voraussagen zu können.

Im Rahmen der vorliegenden Dissertation wurden Vegetationsdaten (Anzahl und Deckung von Gefäßpflanzenarten) in Dauerbeobachtungsflächen in klimatisch kontrastierenden Regionen, den Alpen und mediterranen Gebieten, in drei Aufnahmezyklen erhoben. Untersucht wurden zeitliche und räumliche Entwicklungen der Artenzusammensetzung und die Beziehung zu Klimafaktoren (ERA5 Temperatur- und Niederschlagsdaten; Schneebedeckungsdauer, errechnet aus lokalen Bodentemperaturdaten), sowie zu art- und flächenspezifischen Merkmalen. Darüber hinaus wurden direkte anthropogene Einflüsse und Landnutzungsänderungen in den Bergregionen erhoben und bewertet.

In temperaten Dauerbeobachtungsflächen führten die fortschreitende Zunahme der Artenanzahlen und die gleichzeitige Abnahme der Vegetationsdeckung, die vor allem auf den Rückgang von Kältespezialisten zurückzuführen ist, zu einer beschleunigten Transformation hin zu einer wärmeliebenderen und an mehr Trockenheit angepassten Vegetation. Auf den mediterranen Gipfeln schwankten die Änderungen der Artenanzahlen und Deckungen zwischen den Erhebungen, über den gesamten Zeitraum von fast zwei Dekaden nahmen sie jedoch leicht zu. Endemischen Arten, die fast ausschließlich in den oberen Vegetationszonen vorkommen, verzeichneten hingegen proportional zu Nicht-Endemiten Deckungsverluste, während verbreitete Straucharten zunahmen. Weiters bestätigen die vorliegenden Ergebnisse in beiden Biomen den vorherrschenden Klimawandel als starken Einflussfaktor für Veränderungen der Biodiversitätsmuster. Die unterschiedlichen Reaktionen in den gegensätzlichen Biomen deuten jedoch darauf hin, dass direkte Erwärmungseffekte die Hauptursachen für die beobachteten Veränderungen in temperaten Hochgebirgen sind, während auf den mediterranen Gipfeln die Wasserverfügbarkeit die Schlüsselrolle zu spielen scheint. Einflüsse durch direkte menschliche Aktivitäten können die aktuell beobachteten Vegetationsveränderungen nicht vollständig erklären, ein gewisser regionaler Einfluss kann jedoch nicht ausgeschlossen werden.

Die beobachteten Rückgänge von Kältespezialisten in beiden Biomen könnten den Beginn von verstärkten Artenverlusten andeuten. Dass die durch das Absterben von Arten entstandenen Lücken in temperaten Flächen nur teilweise von neuen Arten besiedelt wurden, weist darauf hin, dass der Artenrückgang nicht allein auf den Druck durch Höherwandern konkurrenzstärkerer Arten aus tieferen Lagen zurückzuführen ist. Hochgebirgsarten mediterraner Lebensräume scheinen noch sensibler auf Klimaschwankungen zu reagieren, vor allem auf die Niederschlagsmengen. Wenn sich die Klimaprognosen bewahrheiten, die für den Süden Europas eine Kombination aus steigenden Temperaturen und sinkenden Niederschlägen voraussagen, stellt das für die einzigartige biologische Vielfalt in diesem Lebensraum eine starke Bedrohung dar.

Schlagwörter: Alpen; Diversität alpiner Pflanzen; GLORIA Programm; Indikatoren für den Einfluss des Klimawandels; Landnutzungsänderungen; Langzeitbeobachtung; Mediterranes Gebirge; Veränderungen der Artenzusammensetzung

Contents

1. *GENERAL INTRODUCTION*

High mountain ecosystems and their biota are governed by low-temperature conditions, a short growing season, high habitat diversity, and a generally higher degree of naturalness and fewer direct anthropogenic influences than lowlands. Thus, they are particularly suitable as 'natural laboratories' for climate change impacts on natural systems (Barry, 1994; Pauli *et al.*, 2015), provided that appropriate long-term data exist. Indeed, re-visitations of historical vegetation surveys in Europe already showed climate-induced increase of species numbers on temperate, boreal and Artic summits (Grabherr *et al.*, 1994; Klanderud & Birks, 2003; Holzinger *et al.*, 2008; Parolo & Rossi, 2008; Vittoz *et al.*, 2008; Wipf *et al.*, 2013). Steinbauer *et al.* (2018) highlighted not only an acceleration in the rate of increase across all major temperate, boreal and Arctic European mountain regions with 302 summits in the 21st century, but also showed a clear correlation between this acceleration and accelerated global warming. This was not or only locally the case for other global change factors such as nitrogen deposition or land-use changes. The effect of precipitation changes over time differed strongly among regions and thus did not show a consistent pattern across the continent, compared to the effect of temperature changes (Steinbauer *et al.*, 2018). A similar trend of richness increase could not be confirmed for southern Europe, the Mediterranean high mountains. Observational studies in semi-arid mountains are still underrepresented in the context of climate change (Giménez-Benavides *et al.*, 2018). However, increase of species richness is the result of upward shifts of species from lower elevations, which were also detected in the Mediterranean mountains by re-visiting historical survey sites (Evangelista *et al.*, 2016). As a consequence of such range expansions of relatively warmth-demanding plants, cold-adapted species with an optimum zone in the upper bioclimatic belts are expected to suffer habitat lost or even to go (locally) extinct. This is especially crucial in small scaled and scattered mountain ranges, which commonly is the case for Mediterranean mountains. Furthermore, isolated mountains often harbour high numbers of endemic species (Flantua *et al.*, 2020), enhancing the risk of biodiversity losses. However, studies incorporating distribution values of species are comparatively rare, and even rarer in Mediterranean mountains (Giménez-Benavides *et al.*, 2018), which may also reflect the scarcity of vegetation data from precisely located plots, including information not only on species occurrence, but also species abundance.

To fill this gap and investigate the magnitudes and velocities of vegetation changes and the potential risk on biodiversity, an extensive set of permanent plots and summit area sections on mountain summits were established within the long-term monitoring network GLORIA (Global Observation Research in Alpine Environments; www.gloria.ac.at). Already in 1994, more than 1000 permanent plots were installed at the GLORIA master site Schrankogel in the Central Alps, aided by the use of continuously advanced high precision global positioning systems and high-resolution cameras. By using a globally applicable and comparable standardised summit approach (Pauli *et al.*, 2015), long-term monitoring sites were established on mountain summits across all climate zones on Earth, beginning in 2001. A baseline survey alone represents a major contribution to the evaluation of the current status of biodiversity on mountain ranges of the world. Every resurvey contributes to improve the knowledge about changes, trends and developments of high mountain ecosystems and their biota, including differences among mountain systems, given the use of a common protocol in the growing international monitoring network.

So far, it was possible to highlight differences and concordances between contrasting biomes by including Mediterranean summits in European studies. An over-representation of more-warmth-demanding plants among colonising species were found in all biomes in Europe, leading to a so called thermophilisation (Gottfried *et al.*, 2012; Fernández Calzado & Molero, 2013; Stanisci *et al.*, 2014; Unterluggauer *et al.*, 2016; Vanneste *et al.*, 2017). Furthermore, cover increases of alpine pioneer species were documented, but also significant cover declines of cold-adapted species (Pauli *et al.*, 2007). On temperate, boreal and Arctic mountains with increasing air temperature, an ongoing increase of species richness was affirmed (Erschbamer *et al.*, 2009; Pauli *et al.*, 2012), whereas on Mediterranean mountains a decline of species numbers was detected despite increasing air temperatures (Pauli *et al.*, 2012; Fernández Calzado & Molero, 2013; Kazakis *et al.*, 2021). On boreal mountains without a warming trend in the last decades, species richness stagnated (Vanneste *et al.*, 2017). The congruence of ongoing warming and species accumulation rates reinforces the hypothesis, that warming is the primary driver of increasing species numbers in mountains where water supply is not a limiting factor so far. On mountains with a climate regime characterised by dry summers, however, increased water stress was suggested as a reason for decreasing species richness (Pauli *et al.*, 2012).

Global mean surface temperature has been strongly rising in the last decades, accelerating in the 21st century with 19 warmest years on record taking place since 2000 (Earth Science Communications Team, 2021). This global trend is even more pronounced at higher latitudes and higher elevations (Ohmura, 2012; Mountain Research Initiative E. D. W. Working Group, 2015; Wang *et al.*, 2016), e.g., the European Alps are experiencing a 3.5 times larger temperature increase than the northern hemisphere (Marty & Meister, 2012). Besides direct effects, increased temperature leads to a reduction of water availability in summer, due to enhanced rates of evapotranspiration, more rain instead of snow and earlier snowmelt.

Precipitation patterns over time and space showed large variability within and across European mountains (Kovats *et al.*, 2014). In the Mediterranean mountain range Sierra Nevada in Spain, for instance, the average annual rainfall is ranging between 400 and well over 1000 mm (Polo *et al.*, 2019), depending mostly on elevation and topography. The comparison of six high-altitude observatories in the European Alps showed high inter-annual variability in precipitation sum for all stations (e.g., Sonnblick at 3109 msl. ranged between 1400 and 2300 mm in the period 1991–2014; Marty & Meister, 2012). For realistic assessments of ongoing processes and the risk on biodiversity temperature alone is considered as insufficient and data about water availability are crucial (Crimmins *et al.*, 2011; Engler *et al.*, 2011; McCain & Colwell, 2011), especially in mountains where aridity during summer is already a restraining factor. Nevertheless, even for water-limited environments little is known about the complex interaction of different climate factors and their effects on vegetation changes.

Furthermore, species responses to climate change might be masked or influenced by coincidental land-use changes, e.g., resulting in nitrogen accumulation, fragmentation or destruction of habitats (Honnay *et al.*, 2002). These global effects are least pronounced in high mountain ecosystems, where agriculture is not feasible and population density and accessibility is low (Bender *et al.*, 2011). More than half of the mountain areas worldwide are categorized as not or only little influenced by direct human activities (Rodríguez-Rodríguez & Bomhard, 2012), which is one criterion for the establishment of a GLORIA site (Pauli *et al.*, 2015). However, it is of paramount importance to not ignore that human activities, such as pastoralism, tourism, gathering and hunting are widely distributed in mountain regions all over the world (Yager *et al.*, 2008; Patty *et al.*, 2010), and these impacts are subjected to changes. Investigations of possible human activities in areas where vegetation is monitored are definitely desirable, in a best case finding none and consequently excluding them as impact factor for vegetation changes. Such extensive interdisciplinary studies, however, are difficult to conduct and the quantification of relationships between vegetation changes and different types of land-use is challenging. Therefore, knowledge about the complex effects of global change drivers on diversity patterns is still limited in many respects.

Preserving diversity is not only a question of conserving unique species and landscapes, high biodiversity ensures higher stability of ecosystems and their services by buffering them against functional losses (Mace *et al.*, 2012; Isbell *et al.*, 2015). However, the magnitude and velocity of ongoing global changes may even exceed the resilience of well-buffered highly diverse ecosystems (Mooney *et al.*, 2009; IPCC, 2018). Changes in biodiversity distribution imply strong consequences for ecosystem health, for closely related human well-being, and for the dynamics of climate change itself (Pecl *et al.*, 2017; IPBES, 2019). Thus, assessments of recent biodiversity changes and the processes behind are crucial.

2. *OBJECTIVES*

The focus of the thesis was to disentangle global change impacts on high mountain plant species responses across contrasting European biomes, the temperate biome represented by the Alps and the Mediterranean biome. In the light of the currently alarming poor state of biodiversity, the driving force was not only the sincere desire for knowledge about the most recent developments of high mountain flora, but also providing new field survey data and accurate analyses to contribute to the current and future dialogue on biodiversity loss and other global changes.

In particular, actual species compositions, their temporal changes and the processes behind were investigated in two contrasting biomes, in (a) temperate mountains within the Alps, where water is not a limited factor so far, and (b) Mediterranean mountains, where water supply is known as limited factor for plant growth. So far, long-term monitoring has mainly focused on changes in temperature and snow cover duration as undisputed important drivers of changes in plant species composition in the alpine life zone (e.g., Gottfried *et al.*, 2012; Pauli *et al.*, 2012). In the present thesis, an additional focus was lying on the second key climatic factor water supply. In order to additionally assess direct anthropogenic influences in the alpine life zones, an extended socioecological approach was implemented.

In this context, the present thesis primarily focused on the

(1) Identification of ongoing changes in vascular plant species diversity and composition:

Do the previously found patterns of change in species richness, species gains and losses, and species' abundances on GLORIA sites in contrasting biomes, the Alps and Mediterranean mountains (Pauli *et al.*, 2007; Pauli *et al.*, 2012; Fernández Calzado & Molero, 2013), constitute ongoing trends in terms of direction and magnitude?

(2) Identification of main drivers responsible for observed vegetation changes:

Can the observed changes be attributed to key climatic factors, i.e., rising temperatures and water-related factors (precipitation, snow cover duration), or both? Are there identifiable influences from land-use, which have to be considered in the discourse of biodiversity changes?

(3) Identification of interdependencies between vegetation changes and species and plot characteristics:

Do vegetation changes reflect homogenous tendencies within species groups (with similar distribution pattern, same morphological characteristics or species preferences) or similar habitats (regarding topography, elevation and thermic situation)?

3. MATERIALS AND METHODS

To cover the targeted topics, different approaches on different levels were combined. On the first level, extensive field studies were conducted, in order to acquire data on (a) species composition of high-mountain vegetation, (b) *in situ* soil temperature, (c) discernible anthropogenic influences, and (d) socio-ecological information. On the second level, data on (e) climate parameters and (f) species characteristics and distribution were compiled from available open access databases.

(a) The first approach is based on repeated systematic observations of natural plant assemblages between the treeline ecotone and the upper elevation zones where plants still occur. In this respect, the GLORIA network provides a unique dataset on changes in occurrence and abundance of alpine plants, firstly on the GLORIA master site Mount Schrankogel in the Central Alpes (Pauli *et al.*, 2007), and secondly, in all other GLORIA regions all over the world, based on a standardized monitoring, the GLORIA multi-summit approach (Pauli *et al.*, 2015). The present thesis included the third survey on Mount Schrankogel in 2014, as well as the third surveys on six European GLORIA regions in 2015, representing the geographically and climatically strongly differing regions of the Mediterranean regions and the Alps, as well as different substrate types. The Mediterranean biome is represented by Sierra Nevada – West (ES-SNE, silicate bedrock), Majella/Central Apennines (IT-CAM, limestone) and Lefka Ori/Crete (GR-LEO; limestone); and the Alps by Entremont/Valais (CH-VAL, silicate bedrock), Latemar-Sella/Dolomites (IT-ADO, dolomite) and Hochschwab/NE-Alps (AT-HSW, limestone). The recording of the six GLORIA regions were conducted within the framework of the project MediAlps (see Lamprecht *et al.*, 2019b). To strengthen the Mediterranean dataset, the three surveys of Sierra Nevada – Northeast (ES-SNN, silicate bedrock) were included as well.

(b) On each GLORIA summit, data loggers buried at 10 cm soil depth, have been measuring soil temperatures at hourly intervals since the setup of the permanent plots.

(c) To identify and compare discernible anthropogenic influences, systematic observations were conducted in each region.

(d) To additionally assess the spatial and temporal dimension of land use and other direct anthropogenic influences in the high mountain areas, qualitative semi-structured interviews were conducted in six regions.

(e) For air temperature and precipitation data, ERA5 data were compiled for relevant summits (https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5). Hourly values are provided on a 30 km grid at 700 hPa which is equivalent to an elevation of 3000 m a.s.l. ERA5 combines available observation data from satellites and *in situ* stations, which are assimilated and processed using ECMWF's Integrated Forecast System (IFS) Cycle 41r2.

(f) As an additional approach for measuring climate related indices, altitudinal ranks as a proxy for the thermal preferences of species were used after Gottfried *et al.* (2012) and expert judgment of regional partners, and soil moisture indicator values according to Landolt *et al.* (2010). For completing information about morphological characteristics of species in the Sierra Nevada, data according to Lorite *et al.* (2020) were used.

4. SCIENTIFIC RELEVANCE

The thesis incorporated repeated surveys of GLORIA Europe sites and the master site Schrankogel, thus contributing to the advancement of the GLORIA Europe network. Furthermore, new methods for additional and interdisciplinary monitoring approaches (i.e., systematic land-use observations and semi-structured interviews) were designed and tested, with the aim to apply the same approaches at other existing GLORIA sites.

On a temperate mountain (Mount Schrankogel), changes of species compositions of high-mountain vegetation followed a steady trend in terms of direction but not magnitude (Article 1 and 2: Lamprecht *et al.*, 2018; Steinbauer *et al.*, 2020), whereas on Mediterranean mountains (in the Sierra Nevada) even the directions changed (Article 3: Lamprecht *et al.*, 2021).

On Mount Schrankogel an ongoing increase in species richness was confirmed, although the increase in species numbers slowed down due to species disappearances from the permanent plots, which were almost exclusively observed in the recent decade (Article 1: Lamprecht *et al.*, 2018). We could also show that these changes were strongly driven by a continued decrease in cover of all cryophilic, cold-adapted species (Article 2: Steinbauer *et al.*, 2020). The resulting gaps were only partly filled by species from lower elevations. On the Mediterranean summits, species richness and cover were decreasing until 2008 (cf. Pauli *et al.*, 2012; Fernández Calzado & Molero, 2013), and increasing thereafter, resulting in an overall significant increase in richness and cover between 2001 and 2019 (Article 3: Lamprecht *et al.*, 2021). The proportion of shrub species in relation to the total cover increased, indicating a consistent expansion of their upper distribution ranges to higher vegetation zones (cf. Fernández Calzado & Molero, 2013), leading to a 'shrubification' of high-elevation habitats of the Sierra Nevada. At the same time, the proportion of endemic species decreased and endemic species disappeared significantly more often than more widespread species (Article 3: Lamprecht *et al.*, 2021). The majority of the assessed endemic species occurs almost exclusively in the upper vegetation belt (Fernández Calzado *et al.*, 2012) and thus, most of them are low-temperature specialist species.

Temperature was confirmed as an important driver for biodiversity changes in the Alps, but of subordinate importance in the Mediterranean area, where water supply seemed to be the key factor. The repeated survey on Mount Schrankogel showed thermophilisation effects of the same magnitude as the European average (cf. Gottfried *et al.*, 2012) after the first decade, which significantly accelerated in the recent decade (Article 1: Lamprecht *et al.*, 2018). In addition, an ongoing transformation of the community composition towards more drought-tolerant species was found on this temperate mountain with no obvious water limitation (Article 1: Lamprecht *et al.*, 2018). In the Mediterranean mountains, the thermic indicator did not change over the whole period of almost two decades. The increasing air temperature was only positively related to changes in species richness, whereas increasing precipitation sums were highly positively related to not only changes in species richness, but also colonisations and changes in cover sums, and negatively with disappearances (Article 3: Lamprecht *et al.*, 2021).

Changes in land use, including reductions in livestock density and growing tourism, have been evaluated and deemed unlikely as explanation for the current observed vegetation changes (Article 3 and Report Chapter: Lamprecht *et al.*, 2019a; Lamprecht *et al.*, 2021). It was not possible to exclude any interference through human activities and associated impacts, but missing correlations and trends suggested, that the influences were not the driving factors on the GLORIA summits.

5. CONCLUSIONS

With regard to the current global biodiversity crisis (IPBES, 2019), mountains play a decisive role, as they harbour half of the world's biodiversity hotspots and a high number of endemic species on only about one quarter of the global terrestrial surface (Kollmair *et al.*, 2005; Körner *et al.*, 2011). In Europe, for instance, about 20 % of all native European vascular plant species may be found in alpine environments which cover only 3 % of the continent's area (Väre *et al.*, 2003).

Ongoing climate changes and socioeconomic developments (e.g., population growth, competition for land, water and other natural resources) will continue to influence ecosystems and their functions and services, for instance through more frequent droughts or migration of people and livestock to or from mountain habitats (Hoegh-Guldberg *et al.*, 2018; IPBES, 2019). Generally, Europe's biomes are projected to be exposed to different climate change scenarios: Most warming in northern Europe is projected in winter, whereas southern Europe maxima of warming are expected in summer. Mean precipitation is projected to rise in northern Europe, especially in winter, whereas for Mediterranean areas a marked decline is anticipated by the end of the 21st century (Nogués Bravo *et al.*, 2008; Fronzek *et al.*, 2012; Gobiet *et al.*, 2014; Pérez-Palazón *et al.*, 2018), which may have significant effects on the performance of high-mountain plants.

In this context, empirical evidence on recent plant diversity trends in mountain systems is urgently needed, and a better understanding of their interdependencies with climatic and socioecological key-drivers under global changes is essential (McCain & Colwell, 2011; Rodríguez-Rodríguez & Bomhard, 2012; Pecl *et al.*, 2017).

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7. PUBLICATIONS

The following part presents three published articles and one report chapter.

7.1 *ARTICLE 1:*

ANDREA LAMPRECHT, PHILIPP ROBERT SEMENCHUK, KLAUS STEINBAUER, MANUELA WINKLER & HARALD PAULI (2018):

Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps.

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New
Phytologist

Research

Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps

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Key words: alpine–nival ecotone, climate change impact indicator, GLORIA, high mountain plants, long-term monitoring, species composition change, species richness, thermophilisation.

Summary

- High mountain ecosystems and their biota are governed by low-temperature conditions and thus can be used as indicators for climate warming impacts on natural ecosystems, provided that long-term data exist.
- We used data from the largest alpine to nival permanent plot site in the Alps, established in the frame of the *Global Observation Research Initiative in Alpine Environments* (GLORIA) on Schrankogel in the Tyrolean Alps, Austria, in 1994, and resurveyed in 2004 and 2014.
- Vascular plant species richness per plot increased over the entire period, albeit to a lesser extent in the second decade, because disappearance events increased markedly in the latter period. Although presence/absence data could only marginally explain range shift dynamics, changes in species cover and plant community composition indicate an accelerating transformation towards a more warmth-demanding and more drought-adapted vegetation, which is strongest at the lowest, least rugged subsite.
- Divergent responses of vertical distribution groups of species suggest that direct warming effects, rather than competitive displacement, are the primary causes of the observed patterns. The continued decrease in cryophilic species could imply that trailing edge dynamics proceed more rapidly than successful colonisation, which would favour a period of accelerated species declines.

Introduction

High mountain plants are adapted to low-temperature conditions (Körner & Larcher, 1988) and, apart from low latitudes, to a short growing season, which makes them sensitive to increasingly warmer climates. Alpine and subnival plants, however, may respond only little to short-term climatic oscillations, but rather to longer lasting climatic trends, because most species are persistent, slow growing and long lived; annual and short-lived species are rare above the treeline (Billings & Mooney, 1968; Körner, 2003; de Witte & Stöcklin, 2010). High mountain ecosystems, especially above the alpine grassland zone, are governed by climatic factors, whereas the importance of biotic factors, such as competition among species for light and nutrient resources and direct human impacts, for example through farming and livestock grazing, decreases with elevation. Therefore, changes in the occurrence of alpine and subnival plant species and in the composition of their assemblages are highly relevant as indicators of ecological impacts of climate change (Theurillat & Guisan, 2001; Grabherr *et al.*, 2010; Malanson *et al.*, 2011).

The last three decades were globally the warmest on record and, in the northern hemisphere, the period from 1983 to 2012 was probably the warmest of the last 1400 years (Hartmann *et al.*, 2013; Luterbacher *et al.*, 2013). Moreover, global climate warming tends to amplify in high-elevation areas, compared with lowland areas (Barry, 2008; Ohmura, 2012; Mountain Research Initiative EDW Working Group, 2015), with a *c.* 1.2 times faster rise in annual mean temperatures at high-elevation stations (> 500 m above sea level, asl) over the period 1961–2010 (Wang *et al.*, 2016). Across the European Alps, high-elevation stations show uniform warming trends of 0.8°C annual mean between 1981 and 2010, and 2.5°C mean from April to June, which is 3.5 times larger than the corresponding northern hemisphere temperature rise (Marty & Meister, 2012). Changes in precipitation show a larger regional and seasonal variability, especially in Europe (Kovats *et al.*, 2014). Nevertheless, increases in evaporation and atmospheric humidity, as well as reductions in snow amount and snowpack period, are corresponding consequences of climate warming (Jiménez Cisneros *et al.*, 2014). Although the spatial patterns of snow are determined by topography and the prevailing wind direction, the temporal patterns of snowmelt are directly linked to temperature change (Friedel, 1961; Kirkpatrick *et al.*, 2017), and snow cover duration in the Alps showed a declining trend during the last decades (Gottfried *et al.*, 2011; Cramer *et al.*, 2014). Future scenarios predict a continued shift from snow to rain in mountainous regions, which alone could

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*These authors contributed equally to this work.

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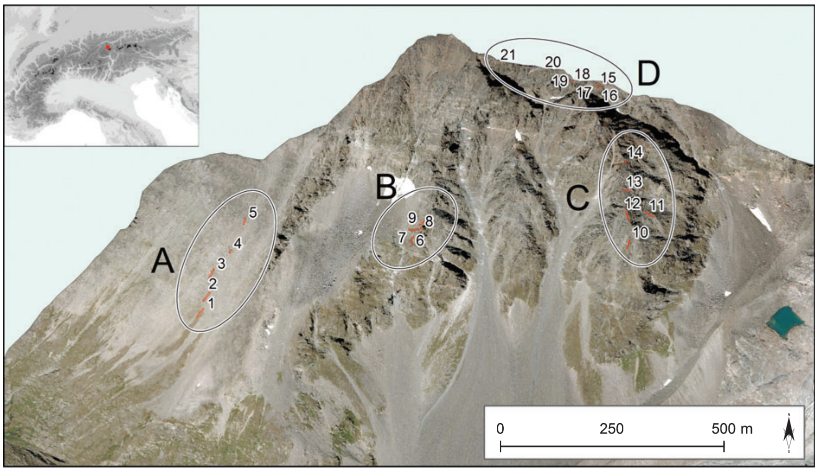

Fig. 1 Location of permanent plots on Mount Schrankogel. Plots are grouped in transects clustered into four topographic blocks: (A) uniformly shaped southwest slope, rich in scree; (B) rugged south-facing ridge; (C) rugged south–southeast-facing ridge; and (D) south-facing, high-elevation plots along the east ridge. Orthophotos (© Land Tirol) modified with ArcGIS 10.3. for Desktop, Esri Inc. Details of transects are shown in Supporting Information Fig. S1.

lead to a significant decrease in snow cover duration in central Europe (Steger *et al.*, 2013; Jiménez Cisneros *et al.*, 2014). This would result in an increase in the length of the growing seasons, and hence in a potential threat to high-elevation plant species through the opening of immigration pathways for competitors from lower elevations (Dullinger *et al.*, 2007; Steger *et al.*, 2013). Increased drought risk has already been detected in central Europe over the past century, with surface warming as the primary cause after the mid-1980s, and can be expected for the region of the Alps in the future (Dai *et al.*, 2004; Gobiet *et al.*, 2014). The climatically suitable area of alpine habitats is therefore successively shrinking. Depending on the climate change scenario, model projections suggest a loss of > 80% of habitats in some European mountains, including parts of the Alps, for up to 55% of the alpine species studied, until the end of the century (Engler *et al.*, 2011).

Habitat loss, however, may not be immediately accompanied by a rapid species decline, which could lag behind for several decades, because of the long-lived nature of most alpine plants (Dullinger *et al.*, 2012b). A topographically diverse habitat situation may further buffer against the loss of climatically suitable habitats (Scherrer & Körner, 2011; Opedal *et al.*, 2015). Upwardly advancing treelines, however, have been repeatedly observed (Kullman, 2002; Harsch *et al.*, 2009; Hagedorn *et al.*, 2014), as well as increasing numbers of vascular plant species at alpine to nival sites (Grabherr *et al.*, 1994, 2001; Bahn & Körner, 2003; Klanderud & Birks, 2003; Holzinger *et al.*, 2008; Vittoz *et al.*, 2008; Stöckli *et al.*, 2011; Pauli *et al.*, 2012; Wipf *et al.*, 2013; Steinbauer *et al.*, 2018). Among the colonising species, an over-representation of more warm-demanding (i.e. thermophilic) species was found on summits distributed across the alpine life zone from the Mediterranean to boreal Europe (i.e. thermophilisation; Gottfried *et al.*, 2012), which was primarily caused by an upward shift of plant species ranges (Pauli *et al.*, 2012).

In order to determine climate-driven changes in species distribution, an extensive setting of permanent plot transects was established in 1994 across the alpine–nival ecotone of Schrankogel in the central Tyrolean Alps as part of the *Global Observation Research Initiative in Alpine Environments* (GLORIA, www.gloria.ac.at; Pauli *et al.*, 2015). This ecotone is the transition zone between closed alpine grassland and open subnival plant assemblages (Gottfried *et al.*, 1998; Pauli *et al.*, 1999). The elevation of the ecotone on Schrankogel was found to strongly coincide with that of the median summer snow duration (i.e. where the probability of snow cover is 50% during the period June to August) derived from data across the Alps (Gottfried *et al.*, 2011). Changes in species composition can be expected to be discernible earlier at the alpine–nival ecotone, where the upper range limits of the more thermophilic alpine grassland species and the lower margins of cold-adapted (i.e. cryophilic) subnival–nival species coincide (Gottfried *et al.*, 1999, 2011). The GLORIA master site Schrankogel is the largest permanent plot site close to the elevation limits of vascular plant life in the Alps, with four spatially separated subsites (blocks), representing elevations and different topographic complexity of the mountain's southerly oriented slope system (Fig. 1). Resurveys were undertaken in 2004 and 2014, thus spanning the period of amplified anthropogenic climate warming (Böhm *et al.*, 2001; Marty & Meister, 2012; Hartmann *et al.*, 2013).

After the first decade, an increase in species richness, resulting from colonisations of species into the plots, but hardly any disappearances from the plots, was observed. The novel aspect, however, was the evidence of decreasing abundance of all subnival–nival, i.e. outstandingly cold-adapted, species (Pauli *et al.*, 2007). Through the third survey in 2014, we assess whether the observed changes in species distribution patterns constitute ongoing trends in relation to recent climate warming by addressing the following four topics and inherent hypotheses. (1) Changes in vascular plant species diversity: (1a) species richness continues to increase, but (1b) the ratio of colonisations vs disappearances shifts towards the latter. (2) Changes in vascular plant cover: (2a) the total cover of vascular plants is increasing because (2b) the continued expansion of more thermophilic alpine and alpine–subnival pioneer species exceeds the ongoing decline of cryophilic high-elevation species. (3) Changes in community-weighted ecological indicators: the composition of species and their abundances change directionally in relation to climate trends, resulting in (3a) a thermophilisation of plant communities (Gottfried *et al.*, 2012) and (3b) a more drought-tolerant species composition. (4) Topography and elevation: plots in rugged habitats and in high elevations show lower rates of change, because habitat complexity in rocky terrain as well as low-temperature conditions buffer against colonisation events and the expansion of established species.

Materials and Methods

Study area and design

The GLORIA master site Schrankogel (3497 m) is located in the Stubaier Alps, Tyrol, Austria. The bedrock mainly consists of gneiss (Hammer *et al.*, 1929; Purtscheller, 1978); typical soil types are leptosols and cambisols (Hofmann *et al.*, 2016). Characteristic plant communities of the upper alpine zone are grassland with *Carex curvula* and *Oreochloa disticha* (Caricion curvulae) and subnival to nival plant assemblages on siliceous screes (Androsacion alpinae; Grabherr, 1993; Abrate, 1998; Dullinger, 1998). Schrankogel is part of the protected area 'Ruhegebiet Stubaier Alpen', ranked in the International Union for Conservation of Nature (IUCN) category IV (UNEP-WCMC & IUCN, 2018), and of the Long-Term Socio-economic and Ecosystem Research (LTSER) platform Tyrolean Alps (Mirtl *et al.*, 2015).

In 1994, *c.* 1000 plots of 1 × 1 m^2 were established as permanent plots across and above the alpine–nival ecotone (2911–3457 m), arranged in transects in order to cover the main habitat types of the alpine–nival ecotone of Schrankogel's southwest- to southeast-facing slope system (Gottfried *et al.*, 1998). Transects were grouped into four blocks (A, B, C and D), where (A) encompasses the uniformly shaped southwest slope which extends uninterruptedly from the alpine grassland belt to the alpine–nival ecotone, (B) encompasses the rugged south-facing middle, (C) encompasses the rugged south–southeast-facing eastern part within the ecotone and (D) encompasses the south-facing, high-elevation outposts in the nival zone along the east ridge (Fig. 1, Supporting Information Fig. S1; Table S1). The steep, mostly unvegetated, northern face and gullies and cliffs on the southern side had to be excluded, because of inaccessibility, unstable material and a high rockfall frequency.

In 2004, a representative subset of 362 plots was resurveyed in order to include all predominant plant communities (Pauli *et al.*, 2007) distinguished by Pauli *et al.* (1999) and, in 2014, a larger subset of 661 plots was reinvestigated.

In each of the three survey campaigns, all vascular plant species were recorded and the percentage cover of each vascular plant species was estimated visually in each plot. At both resurvey campaigns, only data recorded without the aid of previous survey data were used.

Data analyses

After removing plots in which disturbances (through rockfalls and substrate movements) had occurred, the dataset involving all three surveys (1994–2004–2014; Table S1) included 355 plots. A second dataset was constructed, only involving the first and third surveys (1994–2014), with a total of 654 plots (results are shown only in Supporting Information). Two annual species (*Euphrasia minima* and *Gentianella tenella*; Table S2) were removed from the datasets because of high inter-annual fluctuation, which can strongly influence colonisation and disappearance rates.

Analyses were carried out using the entire dataset and also separately for each topographic block (A, B, C and D). As a result of the spatial arrangement of plots in transects, clustered in blocks, and the temporal dimension of the data (resurveys of the same plots at decadal intervals), all statistical models included a random intercept term with the structure: plot nested in transect (except for block D, where transects consisted of too few plots; Table S1), nested in block (the latter only for analyses over the entire study area).

All statistical analyses were performed in R v.3.1.3 (R Core Team, 2015). The significance of the effects of the predictor variables of all models was tested with the lsmeans function; for pairwise comparison, the cld function was used (package LSMEANS; Tukey's honestly significant difference (HSD); Lenth, 2016). Table 1 gives an overview of the statistical models employed and the hypotheses they address.

Changes in vascular plant species diversity

For the response variables species richness, colonisation and disappearance, here treated as counts, the appropriate distribution for the models was determined by building two generalised mixed-effects models (GLMMs), one assuming a Poisson distribution and one assuming a negative binomial distribution, which better fits many zero values (zero inflation; glmer and glmer.nb from LME4 package, respectively; Bates *et al.*, 2015). A likelihood ratio test between these two models was performed (ANOVA function from STATS package) to determine the appropriate model in each case ($P < 0.05$). For both models, over-dispersion was tested with the overdisp.glmer function from the RVAIDEMEMOIRE package (Hervé, 2016). In cases of over-dispersion, the function glmmPQL from the MASS package (Venables & Ripley, 2002) was used, which employs penalised quasi-likelihood and takes an over-dispersion parameter into account.

Species richness was calculated as the number of species per plot and survey, and was analysed as Poisson distributed counts with year (i.e. survey) as predictor. Species richness data within the blocks were over-dispersed (over-dispersion parameter of the glmer model > 1.2), and therefore the function glmmPQL was used.

Colonisations were defined as the number of species per plot present at the time of the resurvey, which were absent in the respective plot at the previous survey, and disappearances were defined as the number of species per plot absent at the time of the resurvey, which were present at the previous survey. These counts were analysed with GLMMs with a negative binomial distribution, with type (colonisation or disappearance) and decade as fixed effects.

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Table 1 Overview of the statistical models employed

Hypotheses	Response	Fixed effects	Random effects	Model type (function)	Error distribution	Results shown in
1, 4	Species richness per plot	Year	Block/transect/plot	GLMM (glmmPQL)	Poisson	Fig. 2(a); Supporting Information Tables S4, S5
1	Species richness per plot and AR	Year × AR	Block/transect/plot	GLMM (glmmPQL)	Negative binomial	Fig. S3(b); Tables S6, S7
1, 4	Number of colonisation or disappearance events per plot	Decade × Type (Colon. or Disapp.)	Block/transect/plot	GLMM (glmer)	Negative binomial	Fig. 2(b); Tables S8, S9
1	Colonisation success per AR	Decade × AR	Block/transect/plot, Species	GLMM (glmmadmb)	Binomial	Fig. S4(a); Tables S10, S11
1	Disappearance success per AR	Decade × AR	Block/transect/plot, Species	GLMM (glmmadmb)	Binomial	Fig. S4(b); Tables S10, S11
2, 4	Cover sum per plot	Year	Block/transect/plot	LMM (lmer)	Gaussian	Fig. 3; Tables S12, S13
2	Cover sum per species and AR	Year × AR	Species	LMM (lmer)	Gaussian	Fig. S5(b); Tables S14, S15
3, 4	Thermic indicator per plot	Year	Block/transect/plot	LMM (lmer)	Gaussian	Fig. 4(a); Tables S16–S18
3, 4	Soil moisture indicator per plot	Year	Block/transect/plot	LMM (lmer)	Gaussian	Fig. 4(b); Tables S19–S21
4	Topographic differences among blocks	Block	Transect	LMM (lmer)	Gaussian	Figs S7, S8; Table S22

Given are the hypotheses addressed, model type (GLMM, generalised linear mixed-effects model; LMM, linear mixed-effects model) and corresponding R function used, error distribution, response variables, fixed and random effects, and figures and tables in which the results are shown. AR, altitudinal rank.

As a proxy for the thermal preferences of species, species with different distributions along the elevation gradient were assigned to species groups of different altitudinal ranks (ARs) after Gottfried *et al.* (2012) (Table S3). To determine which AR species group drives the observed changes, species richness and relative colonisation and disappearance events (the proportion of the number of plots not yet occupied in the case of colonisation, and of previously occupied plots in the case of disappearance) were calculated for each AR separately, and the above analyses on species richness were repeated with AR included in the fixed effects. Colonisation and disappearance events were treated as Bernoulli trials (1, successful colonisation of an empty plot or disappearance from an occupied plot of a given species; 0, plot not colonised or species not disappeared from a plot) and modelled as binomial GLMMs (function glmmadmb in package GLMMADMB; Fournier *et al.*, 2012).

Changes in vascular plant cover

Changes in cover sums (i.e. cumulative cover of all species present in a plot) were modelled using linear mixed-effect models (LMMs, function lmer of package LME4) with survey year as the only fixed effect, and, additionally, with AR as another fixed effect.

Changes in community-weighted ecological indicators

To investigate directional changes in plant species composition, the following ecological indicator values of the species occurring in a plot were used: AR (Table S3) and the soil moisture indicator values in Landolt *et al.* (2010), which were available for all species. All other available indicators by Landolt *et al.* (2010) were not present in a sufficient dispersion along their gradients to enable a reasonable statistical analysis (e.g. temperature T), did not indicate any significant effects (e.g. continentality K, nutrients N) or were not meaningful in the context of this study (e.g. soil reaction R). Each rank was given a number which represents the position along an environmental gradient; for AR: 1 = subnival–nival, 2 = alpine–subnival, 3 = alpine, 4 = (montane–)treeline–alpine species; for soil moisture: 1 = very dry to 4 = very moist. The thermic and soil moisture indicators were calculated after Gottfried *et al.* (2012) for each plot, and survey as an averaged composite score of the AR and the soil moisture indicator values, respectively, weighted by the cover of the occurring species:

$$\text{Indicator} = \left(\sum \text{rank}(\text{species}_i) \times \text{cover}(\text{species}_i)\right) / \sum \text{cover}(\text{species}_i)$$

The thermic indicator was significantly positively correlated with temperature sums derived from *in situ* soil temperature measurements (Fig. S2). Each indicator was analysed after tests for normal distribution with survey year as fixed effect with LMMs. To indicate any direction of changes in community-weighted ecological indicators between surveys, the effect size of the predictor year and its associated confidence interval were used as Δ indicator:

$$\Delta\,\text{indicator} = \text{Indicator}_{t+1} - \text{Indicator}_t$$

The correlation between Δ thermic indicator and Δ soil moisture indicator per plot was modelled using LMMs with plot

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(nested in transect nested in block) and decades as random intercept terms.

Topography and elevation

To assess the topographic similarity among the four blocks, nonmetric multidimensional scaling (NMDS) was used (function METAMDS, R package VEGAN; Oksanen *et al.*, 2018). A matrix was built with rescaled parameters for each plot, that is, estimated top cover of surface types (rock, scree, bare soil and vegetation) and topographic parameters (altitude, aspect, slope and ruggedness) derived from a digital elevation model (© Land Tirol). Ruggedness was calculated as the standard deviation of elevation with a $100 \times 100\,\mathrm{m}^2$ raster per plot using ARCGIS 10.3. for Desktop, Esri Inc. Plotting was performed using the package GGPLOT (Wickham, 2009). To analyse differences among blocks, an LMM with the first NMDS axis as response, block as fixed effect and transect as random effect was fitted.

Results

Changes in species richness, colonisation, disappearances and community-weighted ecological indicators showed equal trends in dataset 1994–2004–2014 (involving three surveys with 355 plots, see below) and 1994–2014 (involving only the first and third surveys with 654 plots). Therefore, only the former is reported here (Figs 2–4, S3–S8; Tables S4–S22) and the latter is provided in Supporting Information (Tables S23–S30).

(1) Changes in vascular plant species diversity

Species richness The total number of species increased from 51 species in 1994 to 54 in 2004 and 61 in 2014.

The mean species number per plot increased from 10.84 species in 1994 to 12.61 in 2004 and 13.08 in 2014 (Fig. 2a; Table S4), and was significantly higher at the later surveys than at the preceding ones (GLMMs, $P < 0.001$ in all cases; Table S5).

Within ARs, the total number of species was stable with six and 20 species in each survey at AR1 and AR2, respectively, whereas species numbers increased slightly in AR3 (18, 19 and 20 species in 1994, 2004 and 2014, respectively), and more than doubled in AR4 between 1994 and 2014 (six, eight and 13 species; Table S3). Species richness summed over all plots (Fig. S3a) and mean species numbers per plot (Fig. S3b) were highest in AR2, followed by AR1, and increased significantly only between 1994 and 2004 within AR2 and AR3 (GLMMs, $P < 0.0001$; Tables S6, S7).

Colonisations and disappearances The mean number of colonisations decreased significantly from 2.08 species per plot between 1994 and 2004 to 1.76 between 2004 and 2014. The mean number of disappearances increased significantly from 0.31 species per plot in the first decade to 1.29 in the second decade (means calculated from raw data; effect sizes from GLMMs, $P < 0.05$; Fig. 2b; Tables S8, S9). No species, however, disappeared completely from the whole area. By contrast, four and seven species were recorded for the first time in 2004 and 2014, respectively (Fig. S3). These new species belonged exclusively to AR3 (one and two new species in 2004 and 2014, respectively) and AR4 (three and five species). Colonisation in relation to previously unoccupied plots was highest among AR1 species (Fig. S4a; Table S10), but decreased significantly from the first to the second decade (GLMMs, $P = 0.01$; Table S11), whereas there was no change among AR2–4 species. Relative disappearance was fairly low (2–3%) in AR1–3 in the first decade, whereas AR4 species disappeared from almost a quarter of their formerly occupied plots (Fig. S4b; Table S10). In the second decade, however, relative disappearance increased sharply and significantly by factors of 3.23, 2.65 and 6.9 in species of AR1–3, respectively, whereas AR4 remained stable (GLMMs; Table S11).

Exotic species and woody plants did not occur in or colonise the permanent plots during the study period.

(2) Changes in vascular plant cover

(2a) The mean cover sum of all vascular plant species per plot decreased significantly from 24.33 dm² in 1994 to 21.9 dm² and 20.83 dm² in 2004 and 2014, respectively (LMMs, $P < 0.05$; Fig. 3; Tables S12, S13).

(2b) Cover sums over all plots for each AR were initially highest in AR1 and AR2, followed by AR3 and AR4 (Fig. S5a). Over time, cover sums of AR1 showed a pronounced linear decrease, whereas those of AR2 increased. The mean cover sums per species were highest in AR1 in all 3 years, but decreased significantly over time, whereas there was no change in the other ARs (GLMMs; Fig. S5b; Tables S14, S15).

(3) Changes in community-weighted ecological indicators

Thermic indicator of plant communities The thermic indicator increased significantly over successive surveys from 1.61 in 1994 to 1.67 in 2004 and 1.76 in 2014, with a Δ thermic indicator of 0.06 in the first decade and 0.09 in the second decade (GLMMs, $P < 0.001$; Fig. 4a; Tables S16–S18).

Soil moisture indicator of plant communities The soil moisture indicator decreased significantly over successive surveys from 2.95 in 1994 to 2.89 in 2004 and 2.79 in 2014, with a Δ soil moisture indicator of -0.05 for the first decade and -0.11 for the second decade (GLMMs, $P < 0.001$; Fig. 4b; Tables S19–S21).

ARs and the Landolt soil moisture indicator were not correlated at the species level (Spearman rank correlation, $\mathrm{rho} = -0.196$, $P = 0.134$). At the plot level, however, Δ soil moisture indicator decreased significantly with increasing Δ thermic indicator (LMM, $P < 0.0001$; Fig. S6).

(4) Topography and elevation

Plots in the lowest block A had, on average, the largest proportion of scree and vegetation cover, and the lowest proportion of

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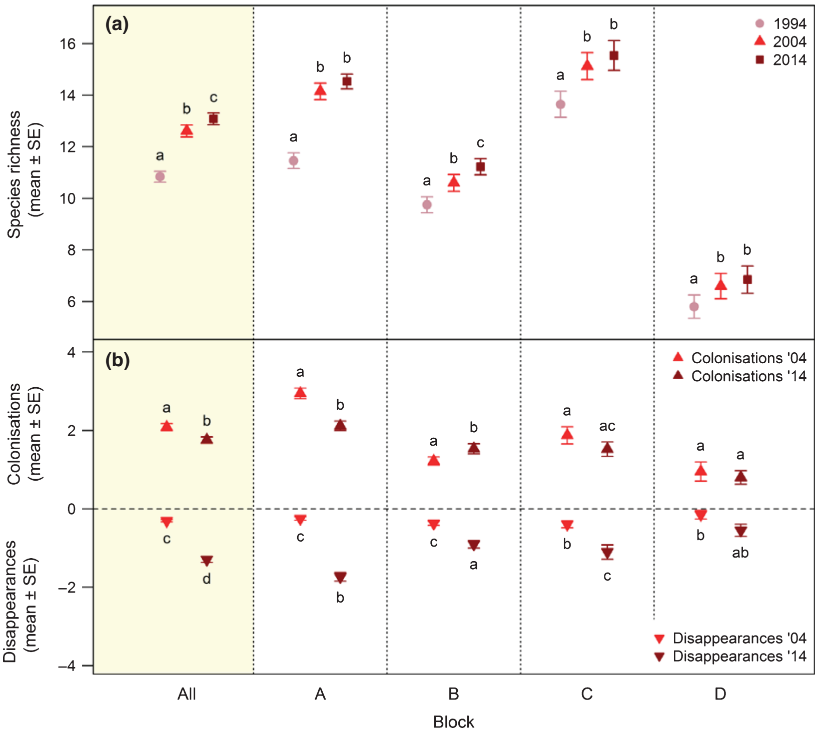

Fig. 2 Changes in vascular plant species diversity on Mount Schrankogel. Mean ± SE of raw data of (a) species richness (Supporting Information Table S4) and (b) numbers of colonising and disappearing species (Table S8) per plot on Mount Schrankogel in the survey years 1994, 2004 and 2014. Mean values over the entire study area (All, shaded) and for each block (A, B, C, D) are shown. For plot numbers per block, see Table S1. Different lowercase letters denote significant differences: (a) between the survey years within each block based on generalised mixed-effects models using penalised quasi-likelihood with a negative binomial distribution (Table S5); and (b) between the survey years and types (colonisations, disappearances) within each block based on generalised mixed-effects models with a negative binomial distribution (Table S9).

solid rock (Fig. S7). Further, they showed the lowest degree of ruggedness and steepness. The nival, that is, highest, block D was the most rugged and steepest block. The topographic parameters (first axis of NMDS; Fig. S8) of block A differed significantly from those of blocks B and D; block D differed significantly from all other blocks, whereas blocks B and C were not significantly different (Table S22).

Changes in species richness in individual blocks showed the same tendencies as in the entire dataset (Fig. 2a; Table S4), even though the increase in richness stagnated in all blocks, except in block B in the second decade (Table S5). The number of colonisations decreased significantly in block A as over the whole study area, whereas there was no significant change in blocks C and D, and, in block B, colonisations even increased in the second decade. The number of disappearances increased significantly in all blocks as in the entire dataset, except in block D, where no significant change was observed (Fig. 2b; Tables S8, S9).

Vascular plant cover decreased significantly over time in all blocks, except D, where no significant change in cover sums was observed. In block A, however, the decrease stopped in the second decade (Fig. 3; Tables S12, S13).

Changes in community-weighted ecological indicators per block did not fundamentally deviate from the results over all plots. A significant overall increase in the thermic indicator, however, was only reached in block B (Fig. 4a; Tables S16–S18), whereas a significant overall decrease in the soil moisture indicator was also found in blocks A and B (Fig. 4b; Tables S19–S21).

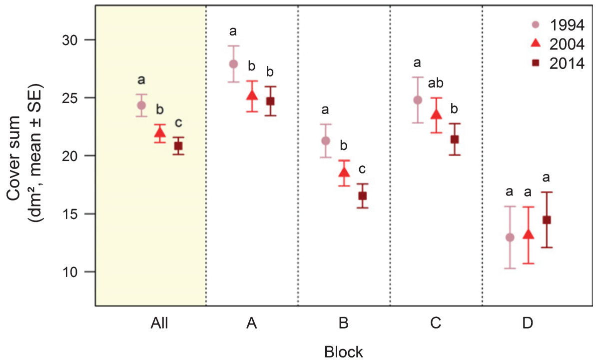

Fig. 3 Changes in vegetation cover of vascular plants on Mount Schrankogel. Mean ± SE of raw data of cover sum (Supporting Information Table S12) per plot on Mount Schrankogel in the survey years 1994, 2004 and 2014. Mean values over the entire study area (All, shaded) and for each block (A, B, C, D) are shown. For plot numbers per block, see Table S1. Different lowercase letters denote significant differences between the survey years within each block based on linear mixed-effects models (Table S13).

Discussion

Over a decade ago, the first repeated survey of the 10-yr-old permanent plots in the alpine–nival ecotone of Schrankogel showed an increase in species numbers similar to other studies, but, most noteworthy, also a divergent change in species abundance, providing the first consistent evidence of population declines of cryophilic species (Pauli *et al.*, 2007). After 20 yr of progressing

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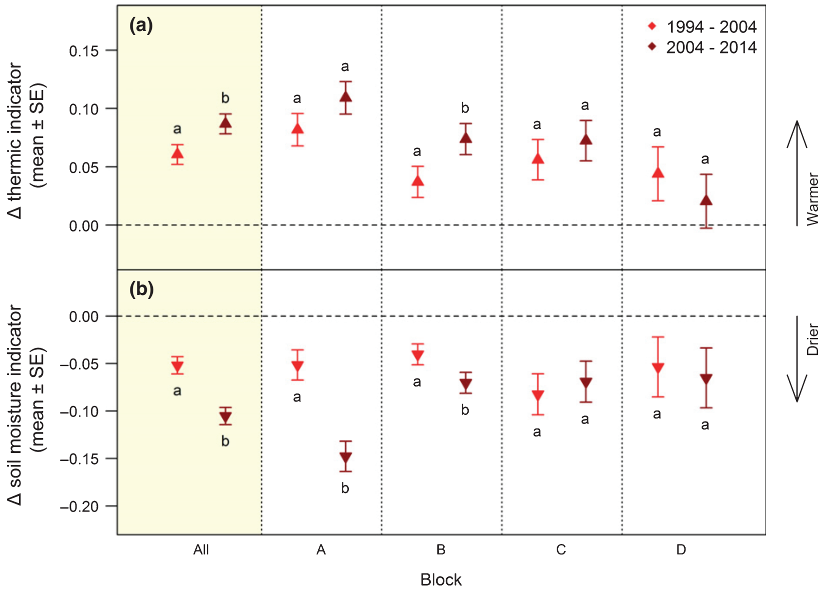

Fig. 4 Changes in community-weighted ecological indicators. Changes in (a) thermic indicator (Gottfried *et al.*, 2012) and (b) soil moisture indicator in the periods 1994–2004 and 2004–2014 (Supporting Information Tables S16, S19). Modelled effect sizes and ± SE over the entire study area (All, shaded) and for each block (A, B, C, D) are shown (Tables S17, S20). For plot numbers per block, see Table S1. Different lowercase letters denote significant differences between the changes in indicators from the first to the second decade within each block based on linear mixed-effects models (Tables S18, S21).

climate warming, we find that (1) species turnover involves the disappearances of species almost exclusively in the second decade, (2) the decrease in vegetation cover constitutes an ongoing trend over both decades, (3) the plant community transformation towards more thermophilous species assemblages, which are increasingly adapted to drier soil conditions, has accelerated, and (4) differences among the blocks reflect the temperature gradient, topography and connectivity to lower elevation species pools.

Changes in vascular plant species diversity

The prevailing net gain in vascular plant species richness found on Schrankogel (Fig. 2a) confirms the ample evidence from other parts of the Alps (Grabherr *et al.*, 1994; Stöckli *et al.*, 2011; Matteodo *et al.*, 2013), temperate to boreal mountains across Europe (Britton *et al.*, 2009; Pauli *et al.*, 2012; Grytnes *et al.*, 2014; Steinbauer *et al.*, 2018) and in parts of temperate–continental North America (Lesica, 2014). There is little doubt that the increase in species numbers has been caused by an upward shift of species previously occurring at lower elevations (Odland *et al.*, 2010; Pauli *et al.*, 2012). Range shifts towards higher elevation are commonly driven by climate warming (Chen *et al.*, 2011), which has been pronounced in the Alps during recent decades (Marty & Meister, 2012), whereas stagnating species numbers over a 14-yr period of rather stable temperature conditions have been found in southern Norway (Vanneste *et al.*, 2017). In the Alps, increases in species numbers have even been observed to accelerate at century-old study sites on high-alpine to nival summits during recent decades (Walther *et al.*, 2005; Wipf *et al.*, 2013; Steinbauer *et al.*, 2018).

The increase in species richness in our plots was smaller in the second decade (Fig. 2a), suggesting a slowing down of species upward shifts. The separate consideration of colonisation and disappearance of species, however, showed that the number of colonisations decreased only slightly, whereas the number of disappearances increased markedly (Fig. 2b). Species disappearances at the alpine–nival ecotone can indicate retracting lower range margins, as expected through warming-driven competitive displacements (Engler *et al.*, 2011; Lenoir & Svenning, 2013). In particular, cold-adapted species have been found recently to have experienced range contractions in the Alps (Rumpf *et al.*, 2018) and alpine Mediterranean species have been shown to decline, possibly as a result of the combined effects of warming and a reduction in precipitation (Pauli *et al.*, 2012). Species disappearances on Schrankogel, however, did not only concern subnival–nival species (AR1), but also alpine–subnival pioneer species (AR2) and alpine species (AR3) in similar proportions (Fig. S4b). Species colonisation numbers remained stable in all altitudinal species groups, except for AR1, where they dropped significantly (Fig. S4a). We therefore cannot unequivocally attribute the observed species turnover to warming-driven range dynamics. The detection of leading edge shifts driven by climate warming is hampered by the stochastic nature of processes, such as the propagation of diaspores, germination and establishment of seedlings. Similarly, the disappearance of species may either be the final stage of a population decline or the result of an unsuccessful species establishment, which are difficult to disentangle (Grytnes *et al.*, 2014). Further, projected directional range shifts and associated local species extinctions in temperate and boreal mountains (Engler *et al.*, 2011) may still require longer periods for the usually long-lived perennial alpine plants. Species dwelling in cold environments may persist even in climatically unsuitable habitats, and thereby accumulate an extinction debt (Dullinger *et al.*, 2012a). Yet, the increase in richness in our plots was mainly driven by alpine–subnival pioneer species (AR2), whereas the number of subnival–nival species (AR1) decreased slightly (Fig. S3), which could already be an indication of warming-driven range shift dynamics. This also accounts for the fact that

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newly appearing species all belong to the lower elevation groups (AR3 and AR4; Table S3), which is in line with increasingly rising species numbers on mountain summits in Europe (Steinbauer *et al.*, 2018).

Changes in vascular plant cover

In contrast with increasing species numbers, cover sums of vascular plant species showed a decreasing trend (Fig. 3). This was mainly driven by a strong continued population decline of all subnival–nival species (AR1), which could not be compensated by the ongoing increase in alpine–subnival species (AR2; Fig. S5).

The strongly divergent cover change of altitudinal species groups clearly depicts a shift in habitat suitability at the range margins of species, and is consistent with Cotto *et al.* (2017) and Rumpf *et al.* (2018), suggesting that population declines are occurring more rapidly than range shifts. This could lead, at least transitionally, to a disruption of distribution patterns, rather than to a rapid greening of the alpine–nival ecotone. The importance of directional changes in species cover was also shown in alpine permanent plots in the Montana Rocky Mountains by Lesica (2014), who noted that changes in species abundance can reveal far more sensitive responses to climate change effects than presence/absence data.

The most relevant potential mechanisms underlying the observed patterns are, first, a successive competitive displacement of the high-elevation species (AR1) through expansion of lower elevation species (AR2, AR3) and, second, direct climatic effects which may deteriorate the performance of cryophilic species. Competition effects, as were verified experimentally (Elmendorf *et al.*, 2012; Alexander *et al.*, 2015), are potentially relevant; however, conspicuous signs of competition pressure, such as for light through taller growing species, are not common at the alpine–nival ecotone, as all species are dwarf-stature plants. Further, the typical habitats at the alpine–nival ecotone do not have a closed vegetation cover (*c.* 10–25% of the plot surface; Fig. S7). Although species of different elevational distribution preferences can grow in the direct neighbourhood, habitats at the alpine–nival ecotone are governed by abiotic, mostly climatic, factors, where the stress gradient hypothesis (Bertness & Callaway, 1994; Callaway *et al.*, 2002) would posit that facilitative interspecific interactions outweigh competitive effects.

Overall, however, vascular plant cover is decreasing, which suggests that advancing alpine–subnival species (AR2) cannot fill the space released by AR1 species. We therefore assume that direct climatic effects may be of superior relevance for an increasing maladaptation and population decline of cryophilic species. Ecophysiological studies of cryophilic species have not been conducted often, but some species, including several of our AR1 group, have been found to show high heat sensitivity and low ability to acclimate respiration rates to higher temperatures, causing detrimentally high respiration rates, and thus the plants rapidly attain a negative carbon balance (Larigauderie & Körner, 1995; Larcher *et al.*, 1997; Cooper, 2004). Such metabolic disadvantages may explain the continued population decline even in the absence of competition through higher temperatures alone. Drier conditions, through earlier snowmelt and stronger evapotranspiration, can further deteriorate the situation by leading to lower soil moisture levels, and thus to warmer soils, which could cause detrimentally high root respiration rates (Cooper, 2004; Lesica, 2014).

Changes in community-weighted ecological indicators

Changes in plant community composition in our plots show a transformation towards a more thermophilic vegetation in both decades (Fig. 4a), in congruence with Gottfried *et al.* (2012). Most noteworthy, the thermophilisation signal, already significant in the first decade of observation 1994–2004 (Table S17), was significantly stronger during the second decade 2004–2014 (Table S18).

Thermophilisation effects have substantial consequences for subnival plant communities in the alpine–nival ecotone, where AR1 species have the centre of their distribution close to their rear edge (Gottfried *et al.*, 1999). This ecotone was found to strongly coincide with the altitude of the summer snow line (Gottfried *et al.*, 2011). Plant assemblages at the ecotone should therefore respond sensitively to warming and associated shifts in temporal patterns of snow duration. High-altitude weather stations distributed over the central and northern Alps show a uniform temperature increase in annual mean temperatures of 0.8°C during the last three decades (Marty & Meister, 2012), which would correspond to 0.53°C in the period 1994–2014. Using the environmental lapse rate of −0.65°C per 100 m elevation, a temperature increase of 0.53°C corresponds to a difference of *c.* 80 m in elevation. As an approximation, one unit of the thermic indicator translates roughly to the elevation range of an entire vegetation belt, for example, the alpine belt on Schrankogel ranges from *c.* 2300 to 2800 m (Dullinger, 1998). The observed thermophilisation values of 0.06, 0.09 and 0.15 units during the first and second decade, and the 20-yr period, respectively, thus approximate to 6%, 9% and 15% of a vegetation belt. This is within the same magnitude of change as observed by Gottfried *et al.* (2012) on the European level (i.e. 5% of one vegetation belt after 7 yr). Given a vegetation belt of a vertical extent of 500 m, the observed change of 0.15 units in the thermic vegetation indicator corresponds to 75 m in elevation. Thus, the vegetation at the alpine–nival ecotone seems to be largely tracking recent climate warming.

An even stronger amplification effect was detected for the soil moisture indicator (Table S21). Our results show a shift of the species composition towards more drought-tolerant plant compositions, that is, an aridisation (Fig. 4b). Delta values of the community-level soil moisture and thermic indicators were highly negatively correlated (Fig. S6), and hence mainly reflect changes in the same species. Yet, this does not necessarily mean that all species experiencing a disadvantage through warmer conditions effectively suffer from drought stress.

Higher temperatures, however, cause greater evapotranspiration, leading to reduced water availability, which alone can increase the probability of drought stress (Beniston, 2003).

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Regional scenarios on precipitation change are inconsistent; however, projections for central Europe show that mean precipitation tends to decrease in summer and increase in winter (Schmidli *et al.*, 2007), with increasingly more rain instead of snow in mountainous regions (Steger *et al.*, 2013). Snow cover is generally declining in the Alps, although patterns of changes in the amount of snowfall are also rather patchy (Gobiet *et al.*, 2014). Moreover, the significant trend towards a longer annual snow-free period has been shown to be consistent with reported trends of longer growing seasons (Dye, 2002; Giménez-Benavides *et al.*, 2007). Combined effects of higher temperatures and concomitant drier conditions can result in strong transforming forces on cold-adapted plant communities (Lesica, 2014), which was also experimentally confirmed (De Boeck *et al.*, 2016).

Topography and elevation

Despite the deviating habitat situations among the four spatially separated blocks (Figs S7, S8), which may lead to different response patterns (Scherrer & Körner, 2011), changes in species occurrence, cover and composition were generally consistent, especially across the blocks in the ecotone (Figs 2–4). The observed deviations from the common trends, however, can contribute to a better understanding of possible causes and mechanisms behind the observed changes.

Contrary to the others, species patterns in the nival block D were rather stable over the 20-yr period, which could be explained by the larger distance to the alpine species pool. Obviously, low-temperature conditions suitable for cryophilic species still prevailed, that is, these populations occurred well above their lower range margin and above the upper margins of alpine species. Block D, however, consisted of fewer plots with fewer species, compared with the others. The results should therefore be treated with some caution.

The higher numbers of both colonising and disappearing species (Fig. 2b) and the stronger thermophilisation and aridisation signals (Fig. 4) at the uniform slope in the ecotone (block A) conform with the lowest elevation and closest connection to the alpine grassland zone. The different magnitudes of change among the four blocks reflect a gradient of increasing low-temperature conditions and a thinning of species pools, and thus the importance of the particular position along the thermal gradient for the velocity of warming-driven vegetation dynamics. This corresponds to recently observed effects over larger elevation ranges, where both species ranges and abundances changed more rapidly the lower a species was situated historically (Rumpf *et al.*, 2018). In the alpine–nival ecotone on Schrankogel, vascular plant species cover decreased in general (Fig. 3). Interestingly, however, the cover remained stable in block A in the second decade, which could signal an early stage of infilling processes. Combined with the strong thermophilisation signal, this is likely to indicate an enhanced expansion of the more thermophilous species. By contrast, cover continued to decrease in the rugged blocks B and C, together with a significant thermophilisation (Table S17), and thus was mainly driven by the dieback of subnival–nival species. Rugged terrain did not restrain the decline of cryophilic species, but may have provided a barrier to the expansion of potential competitors. We therefore suggest that factors other than competition, such as direct temperature effects on plant metabolism, have strongly contributed to the decrease in cover of the cold-adapted, high-elevation species.

In conclusion, we argue that a combination of continued temperature rise and decreased snow cover duration has a major impact on the composition, performance and persistence of plant species in subnival communities. This is manifested by an accelerating loss of subnival plant communities in the central Alps. The longevity and persistence abilities of high-elevation plants may have delayed the disappearance of species from habitats which have become climatically unsuitable (Dullinger *et al.*, 2012a). Increasing maladaptation of cryophilic high-elevation species to warmer and longer growing seasons, however, has led to their continued retraction, even in the absence of competitive displacement. An incomplete infilling through succeeding species from lower elevation further suggests that trailing edge dynamics proceed faster than leading edge advances in environments above the alpine grassland zone. If this holds true in further progress, it could imply that the pay-off of a rising extinction debt (Kuussaari *et al.*, 2009; Cotto *et al.*, 2017) enters into force before colder habitats, if available, can be reached.

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Author contributions

H.P., M.W., A.L. and K.S. designed the study and were part of the recording team. P.R.S., A.L., K.S. and M.W. analysed the output data. H.P. managed the study. A.L., P.R.S. and H.P. wrote the manuscript. All authors discussed the results and implications, and commented on the manuscript at all stages. A.L. and K.S. contributed equally to this work.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Location of permanent plots on Mount Schrankogel with transect details.

Fig. S2 Correlation between thermic indicator and temperature sum on Mount Schrankogel.

Fig. S3 Vascular plant species richness per altitudinal rank in the survey years 1994, 2004 and 2014.

Fig. S4 Relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014.

Fig. S5 Cover sum of vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014.

Fig. S6 Correlation between the changes in thermic indicator and changes in soil moisture indicator per plot in the periods 1994–2004 and 2004–2014.

Fig. S7 Topographic parameters per block on Mount Schrankogel.

Fig. S8 Non-metric multidimensional scaling (NMDS) of topographic parameters of plots.

Table S1 Setup of permanent plots for the monitoring of vascular plant species on Mount Schrankogel

Table S2 Frequency of annual plant species

Table S3 Vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014

Table S4 Vascular plant species richness in the survey years 1994, 2004 and 2014

Table S5 Changes in vascular plant species richness in the periods 1994–2004, 1994–2014 and 2004–2014

Table S6 Vascular plant species richness per altitudinal rank in the survey years 1994, 2004 and 2014

Table S7 Changes in vascular plant species richness per altitudinal rank in the periods 1994–2004, 1994–2014 and 2004–2014

Table S8 Number of colonising and disappearing species at the end of periods 1994–2004 and 2004–2014

Table S9 Differences between numbers of colonising and disappearing species within and among the periods 1994–2004 and 2004–2014

Table S10 Relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014

Table S11 Changes in relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014

Table S12 Cover sum of species in the survey years 1994, 2004 and 2014

Table S13 Changes in cover sum of species in the periods 1994–2004, 1994–2014 and 2004–2014

Table S14 Cover sum of vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014

Table S15 Changes in mean cover sum of vascular plant species per altitudinal rank in the periods 1994–2004, 1994–2014 and 2004–2014

Table S16 Thermic indicator in the survey years 1994, 2004 and 2014

Table S17 Thermophilisation in the periods 1994–2004, 1994–2014 and 2004–2014

Table S18 Changes in thermophilisation between the periods 1994–2004 and 2004–2014

Table S19 Soil moisture indicator in the survey years 1994, 2004 and 2014

Table S20 Change in soil moisture indicator in the periods 1994–2004, 1994–2014 and 2004–2014

Table S21 Changes in Δ soil moisture indicator between the periods 1994–2004 and 2004–2014

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Table S22 Differences in abiotic factors between blocks on Mount Schrankogel

Table S23 Vascular plant species richness in the survey years 1994 and 2014

Table S24 Changes in vascular plant species richness in the period 1994–2014

Table S25 Number of colonising and disappearing species in the period 1994–2014

Table S26 Differences between numbers of colonising and disappearing species in the period 1994–2014

Table S27 Thermic indicator in the survey years 1994 and 2014

Table S28 Thermophilisation in the period 1994–2014

Table S29 Soil moisture indicator in the survey years 1994 and 2014

Table S30 Changes in soil moisture in the period 1994–2014

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New Phytologist Supporting Information

Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps

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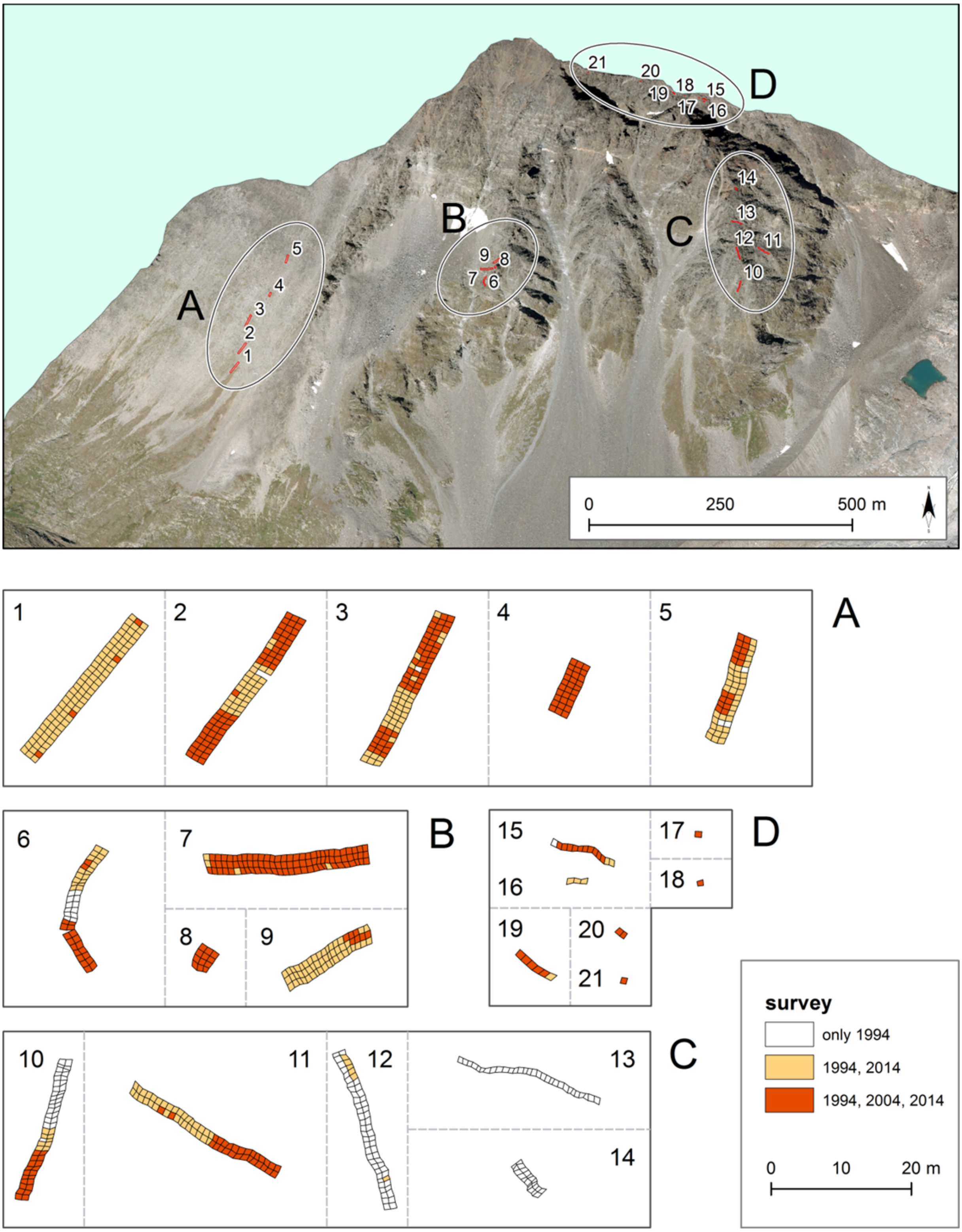

Fig. S1 *Location of permanent plots on Mount Schrankogel with transect details. Plots are grouped in transects clustered in four topographic blocks: A) uniformly shaped SW- slope, rich in scree; B) rugged S-facing ridge, C) rugged S-SE facing ridge and D) S-facing high-elevation plots along the E-ridge. Orthophotos (© Land Tirol) modified with ArcGIS 10.3. for Desktop, Esri Inc. Inserts show a detailed view of each transect.*

Table S1 *Setup of permanent plots for monitoring of vascular plant species on Mount Schrankogel. Within four blocks (A, B, C, D), 21 transects are situated, each consisting of 1 up to 90 1-m² permanent plots. The number of plots surveyed in all three survey-years 1994, 2004 and 2014 and the number of plots of an additional dataset including only plots from 1994 and 2014 (data only given in supplementary; Tables S23 – S30), as well as the altitudinal range of each transect are given. Transects 12-14 were not resurveyed.*

Block	Transect	Number of plots	Number of plots of additional dataset (1994 – 2014)	Altitude [m]
A	1	4	90	2911-2927
A	2	59	88	2936-2952
A	3	52	89	2970-2987
A	4	30	30	3022-3028
A	5	18	51	3074-3084
	sum A	163	348	2911-3084
B	6	20	38	3072-3086
B	7	85	89	3088-3105
B	8	12	12	3108-3109
B	9	7	56	3109-3120
	sum B	124	195	3072-3120
C	10	20	29	3084-3094
C	11	28	56	3100-3115
	sum C	48	85	3084-3115
D	15	10	12	3348-3354
D	16	0	3	3348-3349
D	17	1	1	3360
D	18	1	1	3382
D	19	5	6	3392-3349
D	20	2	2	3418-3420
D	21	1	1	3457
	sum D	20	26	3348-3457
	total	355	654	2911-3457

Table S2 *Frequency of annual plant species. Number of plots where annual species occurred in the survey years 1994, 2004 and 2014 in the permanent plots on Mount Schrankogel.*

Year	*Euphrasia minima*	*Gentianella tenella*
1994	37	0
2004	14	0
2014	166	6

Table S3 *Vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014 over the whole study area on Mount Schrankogel. The altitudinal rank (AR) denotes a species' distribution centre along the elevation gradient (range; after Gottfried et al. 2012). Shown are the total number of species over the whole study area in all three study years, the number of species over the whole study area present in 1994, 2004 and 2014, respectively, and all vascular plant species per altitudinal rank. Species present in all three surveys are given in bold. Species which occure for the first time in the whole study area in a survey year are marked with *, which disappeared completely in one survey year with †, in each case with the corresponding year.*

Altitudinal rank	Range	Number of species All	 1994	 2004	 2014	Species
AR1	Subnival – nival	6	6	6	6	***Androsace alpina; Cerastium uniflorum; Poa laxa; Ranunculus glacialis; Saxifraga bryoides; Saxifraga oppositifolia*** **subsp.** ***oppositifolia***
AR2	Alpine – subnival	20	20	20	20	***Arenaria ciliata*** **subsp.** ***ciliata; Cardamine resedifolia; Draba fladnizensis; Erigeron uniflorus; Festuca intercedens; Gentiana bavarica; Geum reptans; Leucanthemopsis alpina*** **subsp.** ***alpina; Linaria alpina; Luzula spicata; Oreochloa disticha; Pedicularis aspleniifolia; Potentilla frigida; Primula glutinosa; Saxifraga androsacea; Saxifraga exarata*** **subsp.** ***exarata; Saxifraga seguieri; Silene acaulis*** **subsp.** ***bryoides; Trisetum spicatum*** **subsp.** ***spicatum; Veronica alpina***
AR3	Alpine	21	18	19	20	*Agrostis alpina*^{*14}***; Agrostis rupestris; Antennaria carpatica; Carex curvula*** **subsp.** ***curvula; Cerastium cerastoides;*** *Cerastium pedunculatum*^{*14}***; Gentiana brachyphylla*** **subsp.** ***brachyphylla; Juncus jacquinii; Minuartia sedoides; Minuartia verna*** **subsp.** ***verna; Omalotheca supina;*** *Oxyria digyna*$^{*04, †14}$***; Phyteuma hemisphaericum; Poa alpina; Primula minima; Sagina saginoides*** **subsp.** ***saginoides; Salix herbacea; Sedum alpestre; Senecio carniolicus; Sibbaldia procumbens; Veronica bellidioides***
AR4	(Montane -) treeline – alpine	14	6	8	13	*Alchemilla vulgaris* agg.^{*14}; *Anthoxanthum odoratum* subsp. *alpinum*^{*04}***; Avenula versicolor*** **subsp.** ***versicolor;*** *Botrychium lunaria*^{*04}***; Festuca halleri*** **subsp.** ***halleri; Geum montanum;*** *Homogyne alpina*^{*14}***; Leontodon pyrenaicus*** **subsp.** ***helveticus; Polygonum viviparum;*** *Potentilla aurea* subsp. *aurea*^{*14}; *Potentilla crantzii*^{*14}; *Primula hirsuta*^{*14}; *Ranunculus grenieranus*^{†04}; *Taraxacum apenninum* agg.^{*04}

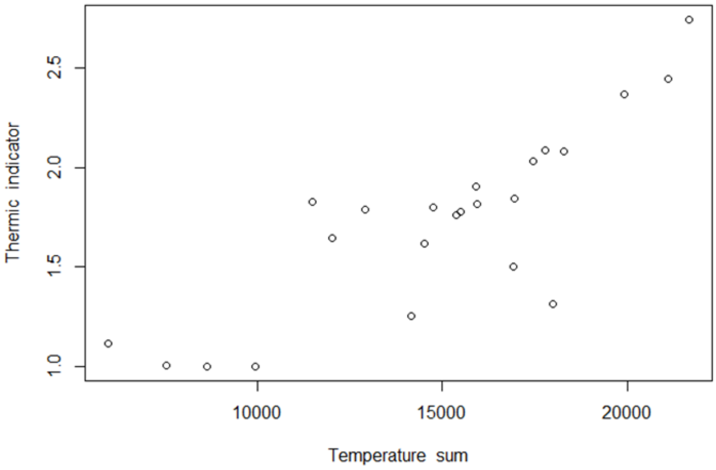

Fig. S2 *Correlation between thermic indicator and temperature sum on Mount Schrankogel. The thermic indicator per plot was calculated as the mean altitudinal rank (1 = subnival-nival, 2 = alpine-subnival, 3 = alpine, 4 = treeline-alpine species) weighted with the respective species' cover (Gottfried et al., 2012). The shown thermic indicator values are means from five plots in the vicinity of each temperature logger. Temperature sums represent annual mean values of hourly measurements from soil temperature loggers (n=23) summed up above a threshold of 3 °C in the period 01.08.2012 – 31.07.2014. The correlation was highly significant (linear mixed effect model; $p < 0.0001$; df = 21; marginal $R^2 = 0.66$, conditional $R^2 = 0.7$: calculated using the function r.squaredGLMM from the R-package MuMIn; Burnham & Anderson, 2002).*

Vascular plant species richness

Table S4 *Vascular plant species richness in the survey years 1994, 2004 and 2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE), degrees of freedom (df) and 95% confidence interval (LCL and UCL), derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a Poisson distribution, of the species richness per plot in the three survey years For plot numbers per block see Table S1.*

		(a) Raw data		(b) Model				
Year	Block	mean	SE	lsmean	SE	df	LCL	UCL
1994	All	10.84	0.21	8.81	1.26	3	5.59	13.90
2004	All	12.61	0.23	10.26	1.47	3	6.50	16.17
2014	All	13.08	0.22	10.64	1.52	3	6.74	16.77
1994	A	11.46	0.30	10.07	1.26	4	7.11	14.26
2004	A	14.15	0.32	12.43	1.56	4	8.78	17.60
2014	A	14.53	0.29	12.77	1.60	4	9.02	18.08
1994	B	9.75	0.31	8.75	1.15	3	5.76	13.28
2004	B	10.60	0.33	9.51	1.25	3	6.26	14.43
2014	B	11.23	0.31	10.07	1.32	3	6.63	15.29
1994	C	13.65	0.51	13.32	0.47	1	8.47	20.94
2004	C	15.13	0.52	14.76	0.52	1	9.42	23.13
2014	C	15.54	0.58	15.17	0.54	1	9.69	23.75
1994	D	5.80	0.46	5.54	0.45	19	4.68	6.56
2004	D	6.60	0.49	6.31	0.50	19	5.34	7.45
2014	D	6.85	0.53	6.55	0.52	19	5.55	7.73

Table S5 *Changes in vascular plant species richness in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of the species richness per plot between the initial survey 1994 and the resurveys 2004 and 2014, derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a Poisson distribution. For plot numbers per block see Table S1.*

Block	Hypothesis	Estimate	LCL	UCL	p-value
All	2004 - 1994 == 0	0.15	0.13	0.18	<0.001
All	2014 - 1994 == 0	0.19	0.16	0.21	<0.001
All	2014 - 2004 == 0	0.04	0.01	0.06	<0.001
A	2004 - 1994 == 0	0.21	0.17	0.25	<0.001
A	2014 - 1994 == 0	0.24	0.20	0.27	<0.001
A	2014 - 2004 == 0	0.03	-0.01	0.06	0.152
B	2004 - 1994 == 0	0.08	0.04	0.12	<0.001
B	2014 - 1994 == 0	0.14	0.10	0.18	<0.001
B	2014 - 2004 == 0	0.06	0.02	0.10	0.001
C	2004 - 1994 == 0	0.10	0.06	0.15	<0.001
C	2014 - 1994 == 0	0.13	0.09	0.17	<0.001
C	2014 - 2004 == 0	0.03	-0.02	0.07	0.300
D	2004 - 1994 == 0	0.13	0.02	0.24	0.014
D	2014 - 1994 == 0	0.17	0.06	0.27	0.001
D	2014 - 2004 == 0	0.04	-0.07	0.14	0.676

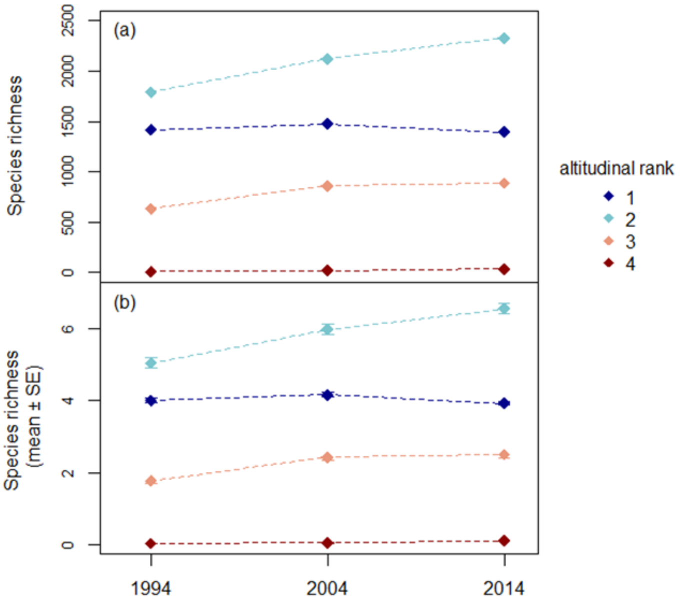

Fig. S3 *Vascular plant species richness per altitudinal rank in the survey years 1994, 2004 and 2014 on Mount Schrankogel. a) Sum of species counts over all 355 plots and b) mean and standard error of raw data of species richness per plot in each altitudinal rank. 1994-2004 and 1994-2014 were significantly different within altitudinal rank 2 and 3, respectively (generalized mixed effects models using penalized quasi likelihood and a negative binomial distribution; Tables S6, S7). For species numbers per altitudinal rank and year see Table S3.*

Table S6 *Vascular plant species richness per altitudinal rank (AR) in the survey years 1994, 2004 and 2014 on Mount Schrankogel.* ***a)*** *Sum of species counts over all plots, mean and standard error (SE) of raw data and* **b)** *least-square mean (lsmean), standard error (SE), degrees of freedom (df) and 95% confidence interval (LCL and UCL), derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a negative binomial distribution, of the species richness per plot and altitudinal rank in the three survey years. For species numbers per altitudinal rank and year see Table S3.*

		(a) Raw data			(b) Model				
Year	AR	sum	mean	SE	lsmean	SE	df	LCL	UCL
1994	1	1418	3.99	0.06	3.65	0.32	3	2.77	4.81
2004	1	1478	4.16	0.06	3.82	0.33	3	2.90	5.05
2014	1	1394	3.93	0.06	3.62	0.32	3	2.74	4.77
1994	2	1790	5.04	0.14	4.62	0.40	3	3.50	6.09
2004	2	2122	5.98	0.14	5.36	0.47	3	4.06	7.06
2014	2	2329	6.56	0.14	5.83	0.51	3	4.42	7.69
1994	3	630	1.77	0.08	1.83	0.16	3	1.38	2.43
2004	3	860	2.42	0.10	2.33	0.20	3	1.76	3.08
2014	3	887	2.50	0.10	2.39	0.21	3	1.81	3.16
1994	4	10	0.03	0.01	1.09	0.20	3	0.60	1.98
2004	4	18	0.05	0.02	1.05	0.16	3	0.66	1.69
2014	4	34	0.10	0.02	1.14	0.14	3	0.77	1.69

Table S7 *Changes in vascular plant species richness per altitudinal rank (AR) in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of the species richness per plot between the initial survey 1994 and the resurveys 2004 and 2014, derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a negative binomial distribution. For species numbers per altitudinal rank and year see Table S3.*

AR	Hypothesis	Estimate	LCL	UCL	p-value
1	2004 - 1994 == 0	1.05	1.02	1.08	0.863
1	2014 - 1994 == 0	1.01	0.98	1.04	1.000
1	2014 - 2004 == 0	1.06	1.03	1.09	0.684
2	2004 - 1994 == 0	1.16	1.13	1.19	<.0001
2	2014 - 1994 == 0	1.26	1.23	1.30	<.0001
2	2014 - 2004 == 0	1.09	1.06	1.12	0.070
3	2004 - 1994 == 0	1.27	1.23	1.31	<.0001
3	2014 - 1994 == 0	1.30	1.26	1.35	<.0001
3	2014 - 2004 == 0	1.03	0.99	1.06	1.000
4	2004 - 1994 == 0	1.04	0.85	1.24	1.000
4	2014 - 1994 == 0	1.04	0.83	1.25	1.000
4	2014 - 2004 == 0	1.08	0.92	1.24	1.000

Colonisations and disappearances

Table S8 *Number of colonising and disappearing vascular plant species at the end of the periods 1994-2004 and 2004-2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE) and asymptotic confidence interval (LCL and UCL), derived from negative binomial generalized linear mixed-effects models, of numbers of colonising and disappearing species per plot between the initial survey 1994 and the resurveys 2004 and 2014. For plot numbers per block see Table S1.*

			(a) Raw data		(b) Model			
Type	Year	Block	mean	SE	lsmean	SE	LCL	UCL
Colonisations	2004	All	2.08	0.09	1.58	0.31	1.07	2.33
Disappearances	2004	All	0.31	0.03	0.23	0.05	0.15	0.36
Colonisations	2014	All	1.76	0.08	1.34	0.27	0.91	1.99
Disappearances	2014	All	1.29	0.07	0.98	0.20	0.66	1.45
Colonisations	2004	A	2.94	0.14	2.90	0.17	2.58	3.27
Disappearances	2004	A	0.25	0.04	0.25	0.04	0.18	0.34
Colonisations	2014	A	2.12	0.12	2.09	0.14	1.83	2.38
Disappearances	2014	A	1.73	0.12	1.71	0.12	1.49	1.96
Colonisations	2004	B	1.22	0.10	1.06	0.21	0.71	1.57
Disappearances	2004	B	0.37	0.05	0.32	0.08	0.20	0.51
Colonisations	2014	B	1.53	0.13	1.33	0.26	0.90	1.97
Disappearances	2014	B	0.90	0.10	0.79	0.16	0.52	1.18
Colonisations	2004	C	1.88	0.22	1.84	0.21	1.48	2.29
Disappearances	2004	C	0.40	0.09	0.39	0.09	0.25	0.61
Colonisations	2014	C	1.52	0.18	1.49	0.18	1.17	1.90
Disappearances	2014	C	1.10	0.18	1.08	0.15	0.82	1.43
Colonisations	2004	D	0.95	0.25	0.95	0.22	0.61	1.49
Disappearances	2004	D	0.15	0.11	0.15	0.09	0.05	0.47
Colonisations	2014	D	0.80	0.17	0.80	0.20	0.49	1.31
Disappearances	2014	D	0.55	0.15	0.55	0.17	0.30	0.99

Table S9 *Differences between numbers of colonising and disappearing vascular plant species within and among the periods 1994-2004 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of differences of numbers of colonising and disappearing species per plot over the entire study area and for each block between 1994, 2004 and 2014, derived from negative binomial generalized linear mixed-effects models with an ANOVA likelihood ratio test. For plot numbers per block see Table S1.*

Block	Hypothesis	Estimate	LCL	UCL	p-value
All	colonisations 2004 - colonisations 2014 == 0	0.16	0.01	0.31	0.03
All	disappearances 2004 - disappearances 2014 == 0	-1.43	-1.71	-1.15	0.001
All	disappearances 2004 - colonisations 2004 == 0	-1.91	-2.17	-1.64	0.001
All	disappearances 2014 - colonisations 2014 == 0	-0.32	-0.48	-0.15	0.001
All	colonisations 2004 - disappearances 2014 == 0	0.48	0.31	0.64	0.001
All	disappearances 2004 - colonisations 2014 == 0	-1.75	-2.02	-1.48	0.001
A	colonisations 2004 - colonisations 2014 == 0	0.33	0.15	0.51	0.001
A	disappearances 2004 - disappearances 2014 == 0	-1.93	-2.35	-1.51	0.001
A	disappearances 2004 - colonisations 2004 == 0	-2.46	-2.87	-2.05	0.001
A	disappearances 2014 - colonisations 2014 == 0	-0.2	-0.4	0	0.052
A	colonisations 2004 - disappearances 2014 == 0	0.53	0.34	0.72	0.001
A	disappearances 2004 - colonisations 2014 == 0	-2.13	-2.55	-1.71	0.001
B	colonisations 2004 - colonisations 2014 == 0	-0.23	-0.5	0.05	0.138
B	disappearances 2004 - disappearances 2014 == 0	-0.89	-1.33	-0.45	0.001
B	disappearances 2004 - colonisations 2004 == 0	-1.19	-1.61	-0.76	0.001
B	disappearances 2014 - colonisations 2014 == 0	-0.53	-0.83	-0.23	0.001
B	colonisations 2004 - disappearances 2014 == 0	0.3	-0.02	0.61	0.07
B	disappearances 2004 - colonisations 2014 == 0	-1.42	-1.83	-1	0.001
C	colonisations 2004 - colonisations 2014 == 0	0.21	-0.19	0.61	0.534
C	disappearances 2004 - disappearances 2014 == 0	-1.03	-1.71	-0.34	0.001
C	disappearances 2004 - colonisations 2004 == 0	-1.56	-2.2	-0.91	0.001
C	disappearances 2014 - colonisations 2014 == 0	-0.32	-0.78	0.14	0.276
C	colonisations 2004 - disappearances 2014 == 0	0.53	0.09	0.97	0.011
C	disappearances 2004 - colonisations 2014 == 0	-1.35	-2	-0.69	0.001
D	colonisations 2004 - colonisations 2014 == 0	0.17	-0.69	1.04	0.956
D	disappearances 2004 - disappearances 2014 == 0	-1.3	-2.96	0.36	0.181
D	disappearances 2004 - colonisations 2004 == 0	-1.85	-3.43	-0.26	0.015
D	disappearances 2014 - colonisations 2014 == 0	-0.37	-1.37	0.62	0.765
D	colonisations 2004 - disappearances 2014 == 0	0.55	-0.42	1.51	0.46
D	disappearances 2004 - colonisations 2014 == 0	-1.67	-3.28	-0.07	0.036

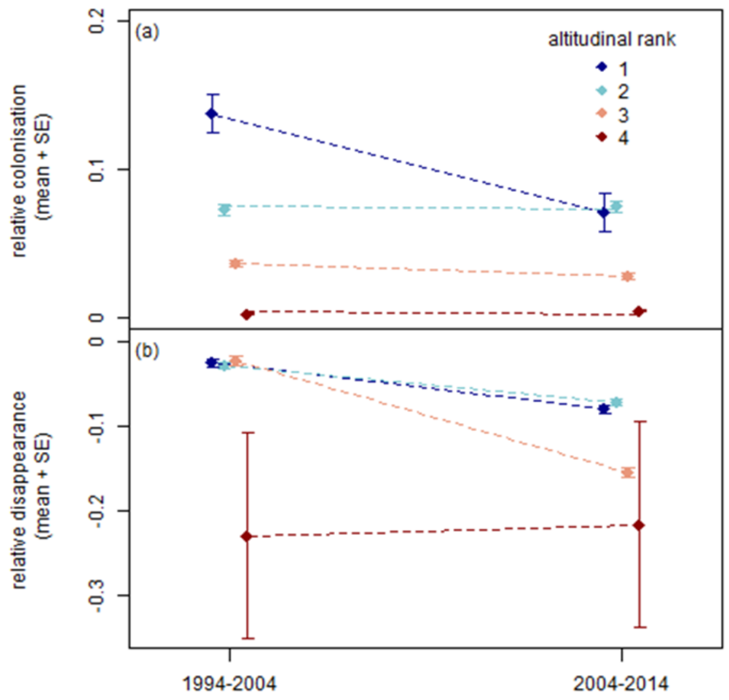

Fig. S4 *Relative colonisation and disappearance per altitudinal rank (AR) in the periods 1994–2004 and 2004-2014 on Mount Schrankogel. Shown are mean and standard error (SE) per species in each AR for a) relative colonisations and b) relative disappearances (Table S10). Relative colonisations of AR1 were significantly different between 1994-2004 and 2004-2014. Relative disappearances were all significantly different between both periods except for AR4 (Table S11). For species numbers per altitudinal rank see Table S3.*

Table S10 *Relative colonisation and disappearance per altitudinal rank (AR) in the periods 1994-2004 and 2004-2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE) and 95% confidence interval (LCL and UCL), derived from generalized linear mixed effect models with function glmmadmb and a binomial distribution, of relative colonisation events per unoccupied plot and relative disappearance events per occupied plot for each species in different altitudinal ranks during two periods. For species numbers per altitudinal rank see Table S3.*

			(a) Raw data		(b) Model			
Period	Type	AR	mean	SE	lsmean	SE	LCL	UCL
1994-2004	Colonisation	1	0.14	0.01	0.17	2.23	0.03	0.82
2004-2014	Colonisation	1	0.07	0.01	0.08	2.16	0.02	0.37
1994-2004	Colonisation	2	0.07	0.00	0.03	2.84	0.00	0.25
2004-2014	Colonisation	2	0.07	0.00	0.04	2.81	0.01	0.31
1994-2004	Colonisation	3	0.04	0.00	0.01	2.93	0.00	0.06
2004-2014	Colonisation	3	0.03	0.00	0.01	2.90	0.00	0.05
1994-2004	Colonisation	4	0.00	0.00	0.00	4.13	0.00	0.01
2004-2014	Colonisation	4	0.00	0.00	0.00	3.49	0.00	0.01
1994-2004	Disappearance	1	-0.03	0.00	-0.02	1.64	-0.05	-0.01
2004-2014	Disappearance	1	-0.08	0.01	-0.06	1.55	-0.15	-0.03
1994-2004	Disappearance	2	-0.03	0.00	-0.04	2.00	-0.15	-0.01
2004-2014	Disappearance	2	-0.07	0.01	-0.10	1.78	-0.32	-0.03
1994-2004	Disappearance	3	-0.02	0.01	-0.02	2.07	-0.10	-0.01
2004-2014	Disappearance	3	-0.16	0.01	-0.17	1.70	-0.49	-0.06
1994-2004	Disappearance	4	-0.23	0.12	-0.22	3.31	-2.27	-0.02
2004-2014	Disappearance	4	-0.22	0.09	-0.19	2.16	-0.87	-0.04

Table S11 *Changes in relative colonisation and disappearance per altitudinal rank (AR) in the periods 1994-2004 and 2004-2014 on Mount Schrankogel. Mean changes (Odds ratio) in relative colonisation and disappearance events between the periods 1994 -2004 and 2004 -2014 with standard error (SE), z-ratio and p-value, derived from generalized linear mixed-effects models with the function glmmadmb and likelihood ratio tests. For species numbers per altitudinal rank see Table S3.*

AR	Type	Contrast	Odds ratio	SE	z-ratio	p-value
1	Colonisation	1994 – 2004 == 2004 – 2014	2.05	0.42	3.50	0.01
2	Colonisation	2004 – 2014 == 1994 – 2004	1.27	0.18	1.70	0.69
3	Colonisation	1994 – 2004 == 2004 – 2014	1.06	0.16	0.40	1.00
4	Colonisation	2004 – 2014 == 1994 – 2004	1.93	1.16	1.10	0.96
1	Disappearance	2004 – 2014 == 1994 – 2004	3.23	0.62	6.15	<.0001
2	Disappearance	2004 – 2014 == 1994 – 2004	2.65	0.84	3.08	0.04
3	Disappearance	2004 – 2014 == 1994 – 2004	6.90	2.73	4.88	<.0001
4	Disappearance	1994 – 2004 == 2004 – 2014	1.12	1.04	0.13	1.00

Vascular plant cover

Table S12 *Cover sum of vascular plant species in the survey years 1994, 2004 and 2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE), degrees of freedom (df) and 95% confidence interval (LCL and UCL) derived from linear mixed effects models, of the cover sum of the vascular plant species per plot in the three survey years. For plot numbers per block see Table S1.*

		(a) Raw data		(b) Model				
Year	Block	mean	SE	lsmean	SE	df	LCL	UCL
1994	All	24.33	0.95	25.28	2.76	13.90	19.36	31.19
2004	All	21.90	0.78	22.79	2.76	13.90	16.88	28.71
2014	All	20.83	0.74	21.78	2.76	13.90	15.86	27.70
1994	A	27.91	1.56	29.93	4.95	2.95	14.03	45.83
2004	A	25.11	1.32	27.00	4.95	2.95	11.10	42.90
2014	A	24.70	1.25	26.72	4.95	2.95	10.82	42.62
1994	B	21.27	1.43	24.19	5.71	3.03	6.10	42.28
2004	B	18.50	1.09	21.42	5.71	3.03	3.33	39.50
2014	B	16.55	1.04	19.46	5.71	3.03	1.38	37.55
1994	C	24.79	1.96	23.86	5.91	1.01	-48.61	96.33
2004	C	23.46	1.51	22.53	5.91	1.01	-49.94	95.01
2014	C	21.40	1.36	20.47	5.91	1.01	-52.01	92.94
1994	D	12.96	2.68	21.54	5.73	5.22	7.00	36.09
2004	D	13.15	2.44	21.73	5.73	5.22	7.19	36.28
2014	D	14.47	2.39	23.06	5.73	5.22	8.51	37.60

Table S13 *Changes in cover sum of vascular plant species in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of the cover sum of the vascular plant species per plot between the initial survey 1994 and the resurveys 2004 and 2014, derived from linear mixed effects models. For plot numbers per block see Table S1.*

Block	Hypothesis	Estimate	LCL	UCL	p-value
All	2004 - 1994 == 0	-2.48	-2.91	-2.05	0.000
All	2014 - 1994 == 0	-3.50	-3.92	-3.07	0.000
All	2014 - 2004 == 0	-1.01	-1.44	-0.59	0.047
A	2004 - 1994 == 0	-2.94	-3.66	-2.21	0.000
A	2014 - 1994 == 0	-3.21	-3.93	-2.49	0.000
A	2014 - 2004 == 0	-0.27	-1.00	0.45	0.924
B	2004 - 1994 == 0	-2.77	-3.40	-2.14	0.000
B	2014 - 1994 == 0	-4.72	-5.35	-4.09	0.000
B	2014 - 2004 == 0	-1.95	-2.58	-1.32	0.006
C	2004 - 1994 == 0	-1.33	-2.21	-0.44	0.295
C	2014 - 1994 == 0	-3.39	-4.28	-2.51	0.001
C	2014 - 2004 == 0	-2.07	-2.95	-1.18	0.055
D	2004 - 1994 == 0	0.19	-1.31	1.68	0.991
D	2014 - 1994 == 0	1.51	0.02	3.01	0.574
D	2014 - 2004 == 0	1.32	-0.17	2.82	0.652

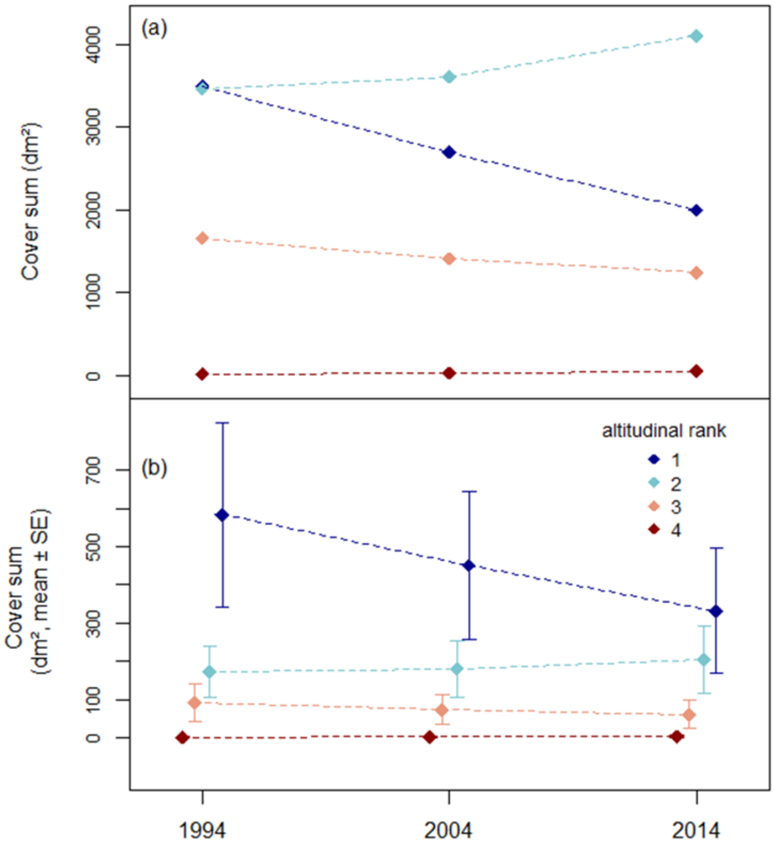

Fig. S5 *Cover sum of vascular plant species per altitudinal rank (AR) in the survey years 1994, 2004 and 2014 on Mount Schrankogel. a) Cover sum over all 355 plots for all species combined in each AR group, and b) mean and standard error of raw data of cover sum per species in each altitudinal rank (Table S14). In b) only the three years within altitudinal rank 1 were significantly different (linear mixed effects models; Table S15). For species numbers per altitudinal rank and year see Table S3.*

Table S14 *Cover sum of vascular plant species per altitudinal rank (AR) in the survey years 1994, 2004 and 2014 on Mount Schrankogel.* ***a)*** *Cover sum (dm²) over all plots, mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE), degrees of freedom (df) and 95% confidence interval (LCL and UCL) derived from linear mixed effects models, of the cover sum per vascular plant species in the three survey years. For species numbers per altitudinal rank and year see Table S3.*

		(a) Raw data			(b) Model				
Year	AR	sum	mean	SE	lsmean	SE	df	LCL	UCL
1994	1	3496.73	582.79	240.35	582.79	109.56	60	363.66	801.92
2004	1	2704.51	450.75	194.68	450.75	109.56	60	231.62	669.88
2014	1	1995.14	332.52	163.36	332.52	109.56	60	113.39	551.65
1994	2	3465.12	173.26	67.70	173.26	60.01	60	53.23	293.28
2004	2	3611.52	180.58	73.72	180.58	60.01	60	60.55	300.60
2014	2	4107.83	205.39	87.19	205.39	60.01	60	85.37	325.41
1994	3	1659.93	92.22	50.82	82.35	58.95	62	-35.50	200.19
2004	3	1409.16	74.17	39.33	68.25	58.82	61	-49.35	185.85
2014	3	1243.54	62.18	35.64	58.91	58.68	61	-58.44	176.26
1994	4	13.76	2.29	1.14	-1.81	75.35	72	-152.00	148.38
2004	4	26.50	3.31	1.71	1.30	73.79	67	-145.98	148.59
2014	4	47.87	3.68	2.48	3.83	71.97	61	-140.08	147.74

Table S15 *Changes in mean cover sum of vascular plant species per altitudinal rank (AR) in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of the mean cover sum (dm²) of the vascular plant species per AR between the initial survey 1994 and the resurveys 2004 and 2014, derived from linear mixed effects models. For species numbers per altitudinal rank and year see Table S3.*

AR	Hypothesis	Estimate	LCL	UCL	p-value
1	2004 - 1994 == 0	-132.04	-163.79	-100.28	0.004
1	2014 - 1994 == 0	-250.26	-282.02	-218.51	<.0001
1	2014 - 2004 == 0	-118.23	-149.99	-86.47	0.017
2	2004 - 1994 == 0	7.32	-10.07	24.71	1.000
2	2014 - 1994 == 0	32.14	14.74	49.53	0.787
2	2014 - 2004 == 0	24.82	7.42	42.21	0.955
3	2004 - 1994 == 0	-14.09	-32.42	4.23	1.000
3	2014 - 1994 == 0	-23.44	-41.75	-5.12	0.980
3	2014 - 2004 == 0	-9.34	-27.65	8.96	1.000
4	2004 - 1994 == 0	3.11	-29.87	36.09	1.000
4	2014 - 1994 == 0	5.64	-27.21	38.48	1.000
4	2014 - 2004 == 0	2.53	-24.86	29.91	1.000

Changes in community-based ecological indicators

Thermic indicator

Table S16 *Thermic indicator in the survey years 1994, 2004 and 2014 on Mount Schrankogel. Least-square mean (lsmean), standard error (SE), degrees of freedom (df, rounded to the nearest integer) and 95% confidence interval (LCL and UCL) of the thermic indicator per plot in the three survey years. As a proxy for the thermal preferences of a species the altitudinal rank (1 = subnival-nival, 2 = alpine-subnival, 3 = alpine, 4 = treeline-alpine species; Gottfried et al., 2012) was used. Data were analysed with linear mixed-effects models. For plot numbers per block see Table S1.*

Year	Block	lsmean	SE	df	LCL	UCL
1994	All	1.61	0.15	5	1.23	1.99
2004	All	1.67	0.15	5	1.29	2.06
2014	All	1.76	0.15	5	1.38	2.14
1994	A	1.61	0.19	4	1.08	2.14
2004	A	1.69	0.19	4	1.16	2.22
2014	A	1.80	0.19	4	1.27	2.33
1994	B	1.90	0.14	3	1.44	2.35
2004	B	1.94	0.14	3	1.48	2.39
2014	B	2.01	0.14	3	1.55	2.46
1994	C	1.79	0.27	1	-1.61	5.19
2004	C	1.85	0.27	1	-1.56	5.25
2014	C	1.92	0.27	1	-1.48	5.32
1994	D	1.19	0.06	21	1.05	1.32
2004	D	1.23	0.06	21	1.09	1.37
2014	D	1.25	0.06	21	1.12	1.39

Table S17 *Thermophilisation in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Mean changes (estimate) in thermic indicator (Δ thermic indicator = thermophilisation) between 1994 and 2004, 1994 and 2014, and 2004 and 2014, with standard error (SE), 95% confidence interval (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio tests. For plot numbers per block see Table S1.*

Block	Hypothesis	Estimate	SE	LCL	UCL	p-value
All	2004 - 1994 == 0	0.06	0.01	0.04	0.08	<0.001
All	2014 - 1994 == 0	0.15	0.01	0.13	0.17	<0.001
All	2014 - 2004 == 0	0.09	0.01	0.07	0.11	<0.001
A	2004 - 1994 == 0	0.08	0.01	0.05	0.11	<0.001
A	2014 - 1994 == 0	0.19	0.01	0.16	0.22	<0.001
A	2014 - 2004 == 0	0.11	0.01	0.08	0.14	<0.001
B	2004 - 1994 == 0	0.04	0.01	0.01	0.07	0.015
B	2014 - 1994 == 0	0.11	0.01	0.08	0.14	0.001
B	2014 - 2004 == 0	0.07	0.01	0.04	0.11	0.001
C	2004 - 1994 == 0	0.06	0.02	0.02	0.10	0.003
C	2014 - 1994 == 0	0.13	0.02	0.09	0.17	0.001
C	2014 - 2004 == 0	0.07	0.02	0.03	0.11	0.001
D	2004 - 1994 == 0	0.04	0.02	-0.01	0.10	0.138
D	2014 - 1994 == 0	0.06	0.02	0.01	0.12	0.015
D	2014 - 2004 == 0	0.02	0.02	-0.03	0.07	0.651

Table S18 *Changes in thermophilisation between the periods 1994-2004 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate) of changes in thermophilisation (Δ thermic indicator) from the first (1994-2004) to the second (2004-2014) decade of survey, with 95% confidence interval (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio test. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	0.03	0.01	0.05	0.009
A	0.03	-0.01	0.06	0.108
B	0.04	0.01	0.07	0.020
C	0.02	-0.02	0.06	0.429
D	-0.02	-0.07	0.03	0.344

Soil moisture indicator

Table S19 *Soil moisture indicator in the survey years 1994, 2004 and 2014 on Mount Schrankogel. Least-square mean (lsmean), standard error (SE), rounded degrees of freedom (df) and 95% confidence interval (LCL and UCL) of the soil moisture indicator per plot in the three survey years. As a proxy for the soil moisture preferences of a species the indicator value for soil moisture (1 = very dry to 4 = very moist; Landolt et al., 2010) was used. Data were analysed with linear mixed-effects models. For plot numbers per block see Table S1.*

Year	Block	lsmean	SE	df	LCL	UCL
1994	All	2.95	0.13	5	2.62	3.27
2004	All	2.89	0.13	5	2.57	3.22
2014	All	2.79	0.13	5	2.46	3.12
1994	A	2.97	0.10	4	2.68	3.26
2004	A	2.92	0.10	4	2.63	3.21
2014	A	2.77	0.10	4	2.49	3.06
1994	B	2.79	0.14	3	2.35	3.24
2004	B	2.75	0.14	3	2.31	3.20
2014	B	2.68	0.14	3	2.24	3.12
1994	C	2.68	0.14	1	1.01	4.36
2004	C	2.60	0.14	1	0.92	4.27
2014	C	2.53	0.14	1	0.86	4.20
1994	D	3.32	0.06	23	3.20	3.44
2004	D	3.27	0.06	23	3.15	3.39
2014	D	3.20	0.06	23	3.08	3.32

Table S20 *Change in soil moisture indicator in the periods 1994-2004, 1994-2014 and 2004-2014 on Mount Schrankogel. Least-square mean changes (estimate) in soil moisture indicator between 1994 and 2004, 1994 and 2014, and 2004 and 2014, with standard error (SE), 95% confidence interval (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio test. For plot numbers per block see Table S1.*

Block	Hypothesis	Estimate	SE	LCL	UCL	p-value
All	2004 - 1994 == 0	-0.05	0.01	-0.07	-0.03	<0.001
All	2014 - 1994 == 0	-0.16	0.01	-0.18	-0.14	<0.001
All	2014 - 2004 == 0	-0.11	0.01	-0.13	-0.08	<0.001
A	2004 - 1994 == 0	-0.05	0.02	-0.09	-0.01	0.003
A	2014 - 1994 == 0	-0.20	0.02	-0.24	-0.16	0.001
A	2014 - 2004 == 0	-0.15	0.02	-0.19	-0.11	0.001
B	2004 - 1994 == 0	-0.04	0.01	-0.07	-0.01	0.001
B	2014 - 1994 == 0	-0.11	0.01	-0.14	-0.08	<0.001
B	2014 - 2004 == 0	-0.07	0.01	-0.10	-0.04	<0.001
C	2004 - 1994 == 0	-0.08	0.02	-0.13	-0.03	0.001
C	2014 - 1994 == 0	-0.15	0.02	-0.20	-0.10	0.001
C	2014 - 2004 == 0	-0.07	0.02	-0.12	-0.02	0.004
D	2004 - 1994 == 0	-0.05	0.03	-0.13	0.02	0.206
D	2014 - 1994 == 0	-0.12	0.03	-0.19	-0.04	<0.001
D	2014 - 2004 == 0	-0.07	0.03	-0.14	0.01	0.098

Table S21 *Changes in Δ soil moisture indicator between the periods 1994-2004 and 2004-2014 on Mount Schrankogel. Effect sizes (estimate) of Δ soil moisture indicator from the first (1994-2004) to the second (2004-2014) decade of survey, with 95% confidence intervals (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio test. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	-0.05	-0.07	-0.03	<0.001
A	-0.10	-0.13	-0.06	<0.001
B	-0.03	-0.05	-0.01	0.016
C	0.01	-0.03	0.06	0.543
D	-0.01	-0.06	0.04	0.638

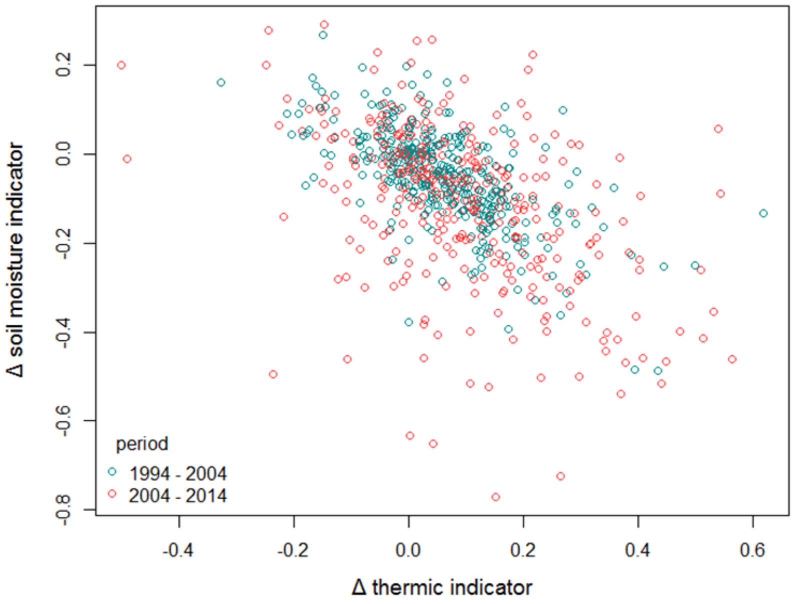

Fig. S6 *Correlation between the changes of thermic indicator and changes of soil moisture indicator per plot in the periods 1994-2004 and 2004-2014 on Mount Schrankogel. The thermic indicator per plot was calculated as the mean altitudinal rank (1 = subnival-nival, 2 = alpine-subnival, 3 = alpine, 4 = treeline-alpine species) weighted with the respective species' cover (Gottfried et al., 2012). The soil moisture indicator per plot was calculated as the mean of indicator values for soil moisture (1 = very dry to 4 = very moist; Landolt et al., 2010) weighted with the respective species' cover. The correlation was highly significant (linear mixed effect model; p <0.0001).*

Topography and elevation

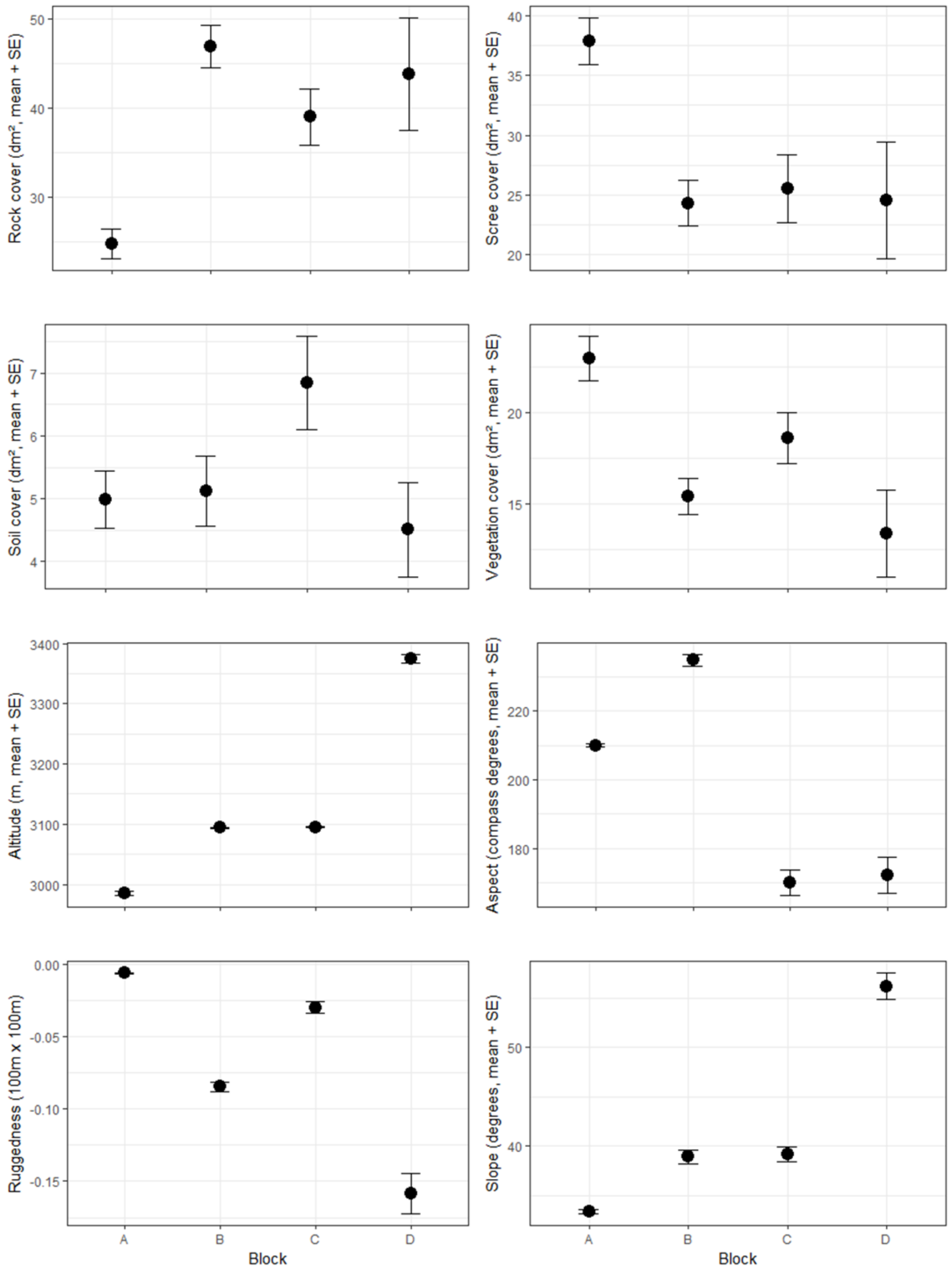

Fig. S7 *Topographic parameters per block on Mount Schrankogel. Means of estimated top cover of surface types per plot (rock, scree, bare soil and vegetation) and topographic parameters (altitude, aspect, slope and ruggedness) derived from a digital elevation model (© Land Tirol). Ruggedness was calculated as standard deviation of elevation with a 100 m x 100 m raster per plot by using ArcGIS 10.3. for Desktop, Esri Inc. For plot numbers per block see Table S1.*

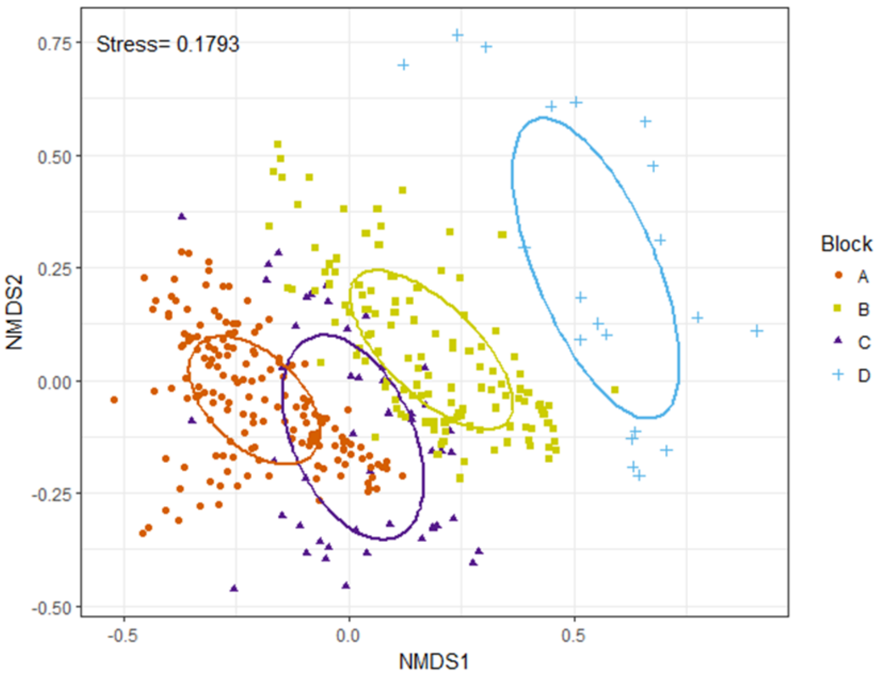

Fig. S8 *Non-metric multidimensional scaling (NMDS) of permanent plots on Mount Schrankogel, which was fitted using rescaled topographic parameters (altitude, aspect, slope, ruggedness) derived from a digital elevation model (© Land Tirol) and estimated cover of main surface types per plot (rock, scree, bare soil and vegetation). Ellipses represent the standard deviations of each plot score within each block. For plot numbers per block see Table S1.*

Table S22 *Differences among blocks on Mount Schrankogel. Differences (estimate*) among *blocks (contrast), standard error (SE), degrees of freedom (df) and p-values derived from linear mixed effect models with the first axis of a non-metric multidimensional scaling of topographic parameters (Fig. S8) as response, block as fixed effect and transect as random effect.* For plot *numbers per block see Table S1.*

Contrast	Estimate	SE	df	p.value
A – B	0.44	0.08	8.87	0.001
A – C	0.25	0.09	8.46	0.099
A – D	0.81	0.08	13.50	<0.001
B – C	0.19	0.10	8.56	0.274
B – D	0.37	0.08	13.10	0.003
C – D	0.56	0.10	11.01	<0.001

Dataset 1994 – 2014 (n_{plot} = 654)

Vascular plant species richness

Table S23 *Vascular plant species richness in the survey years 1994 and 2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE), degrees of freedom (df) and 95% confidence interval (LCL and UCL), derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a Poisson distribution, of the species richness per plot in the two survey years. For plot numbers per block see Table S1.*

		(a) Raw data		(b) Model				
Year	Block	mean	SE	lsmean	SE	df	LCL	UCL
1994	All	9.95	0.17	8.02	1.08	3	5.22	12.32
2014	All	12.64	0.19	10.19	1.37	3	6.64	15.65
1994	A	10.58	0.22	9.47	1.63	4	5.88	15.25
2014	A	14.18	0.24	12.69	2.18	4	7.88	20.43
1994	B	8.36	0.27	7.83	1.12	3	4.97	12.33
2014	B	9.75	0.28	9.13	1.30	3	5.80	14.37
1994	C	12.27	0.43	11.82	0.44	1	7.33	19.07
2014	C	14.80	0.47	14.26	0.53	1	8.92	22.81
1994	D	5.69	0.43	5.21	0.58	25	4.14	6.54
2014	D	6.54	0.49	5.98	0.66	25	4.77	7.50

Table S24 *Changes in vascular plant species richness in the period 1994-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of the species richness per plot between the initial survey 1994 and the resurvey 2014, derived from generalized linear mixed effect models with a penalized quasi-likelihood estimation and a Poisson distribution. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	0.24	0.22	0.26	<0.001
A	0.29	0.26	0.32	<0.001
B	0.15	0.12	0.19	<0.001
C	0.19	0.14	0.23	<0.001
D	0.14	0.04	0.24	0.011

Colonisations and disappearances

Table S25 *Number of colonising and disappearing vascular plant species in the period 1994-2014 on Mount Schrankogel.* ***a)*** *Mean and standard error (SE) of raw data and* ***b)*** *least-square mean (lsmean), standard error (SE) and asymptotic 95% confidence interval (LCL and UCL), derived from negative binomial generalized linear mixed-effects models, of numbers of colonising and disappearing species per plot between the initial survey 1994 and the resurvey 2014. For plot numbers per block see Table S1.*

		(a) Raw data		(b) Model			
Type	Block	mean	SE	lsmean	SE	LCL	UCL
Colonisations	All	3.57	0.10	2.54	0.58	1.624	3.984
Disappearances	All	0.88	0.04	0.63	0.15	0.401	0.995
Colonisations	A	4.51	0.14	4.39	0.34	3.765	5.121
Disappearances	A	0.91	0.06	0.89	0.08	0.743	1.070
Colonisations	B	2.20	0.12	2.08	0.32	1.532	2.817
Disappearances	B	0.82	0.08	0.77	0.13	0.553	1.067
Colonisations	C	3.53	0.24	3.23	0.56	2.296	4.550
Disappearances	C	1.00	0.13	0.92	0.18	0.623	1.350
Colonisations	D	1.31	0.22	1.30	0.25	0.890	1.902
Disappearances	D	0.46	0.14	0.46	0.14	0.255	0.826

Table S26 *Differences between numbers of colonising and disappearing vascular plant species in the period 1994-2014 on Mount Schrankogel. Effect sizes (estimate), 95% confidence interval (LCL and UCL) and p-values of differences of numbers of colonising and disappearing species per plot over the entire study area and for each block between 1994 and 2014, derived from negative binomial generalized linear mixed-effects models with an ANOVA likelihood ratio test. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	1.39	1.28	1.51	<0.001
A	1.59	1.45	1.74	<0.001
B	1.00	0.77	1.22	<0.001
C	1.26	0.97	1.55	<0.001
D	1.04	0.32	1.76	0.001

Changes in community-based ecological indicators

Thermic indicator

Table S27 *Thermic indicator in the survey years 1994 and 2014 on Mount Schrankogel. Least-square mean (lsmean), standard error (SE), degrees of freedom (df, rounded to the nearest integer) and 95% confidence interval (LCL and UCL) of the thermic indicator per plot of the years 1994 and 2014. As a proxy for the thermal preferences of a species the altitudinal rank (1 = subnival-nival, 2 = alpine-subnival, 3 = alpine, 4 = treeline-alpine species; Gottfried et al., 2012) was used. Data were analysed with linear mixed-effects models. For plot numbers per block see Table S1.*

Year	Block	lsmean	SE	df	LCL	UCL
1994	All	1.56	0.13	4	1.21	1.90
2014	All	1.71	0.13	4	1.37	2.05
1994	A	1.60	0.18	4	1.11	2.09
2014	A	1.77	0.18	4	1.27	2.26
1994	B	1.80	0.08	3	1.53	2.07
2014	B	1.93	0.08	3	1.66	2.20
1994	C	1.60	0.09	1	0.51	2.70
2014	C	1.79	0.09	1	0.70	2.89
1994	D	1.29	0.13	6	0.98	1.60
2014	D	1.36	0.13	6	1.05	1.67

Table S28 *Thermophilisation in the period 1994-2014 on Mount Schrankogel. Mean changes (estimate) in thermic indicator (Δ indicator = thermophilisation) between 1994 and 2014, with 95% confidence interval (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio tests. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	0.15	0.14	0.17	<0.001
A	0.17	0.14	0.19	<0.001
B	0.12	0.09	0.16	<0.001
C	0.19	0.15	0.23	<0.001
D	0.07	0.02	0.12	0.009

Soil moisture indicator

Table S29 *Soil moisture indicator in the survey years 1994 and 2014 on Mount Schrankogel. Least-square mean (lsmean), standard error (SE), rounded degrees of freedom (df) and 95% confidence interval (LCL and UCL) of the soil moisture indicator per plot in the three survey years. As a proxy for the soil moisture preferences of a species the indicator value for soil moisture (1 = very dry to 4 = very moist; Landolt et al., 2010) was used. Data were analysed with linear mixed-effects models. For plot numbers per block see Table S1.*

Year	Block	lsmean	SE	df	LCL	UCL
1994	All	2.97	0.10	4	2.68	3.26
2014	All	2.83	0.10	4	2.55	3.12
1994	A	2.97	0.10	4	2.69	3.24
2014	A	2.83	0.10	4	2.55	3.10
1994	B	2.82	0.09	3	2.53	3.12
2014	B	2.71	0.09	3	2.41	3.01
1994	C	2.82	0.04	1	1.94	3.69
2014	C	2.64	0.04	1	1.76	3.51
1994	D	3.22	0.14	6	2.88	3.55
2014	D	3.10	0.14	6	2.76	3.43

Table S30 *Changes in soil moisture in the period 1994-2014 on Mount Schrankogel. Mean changes (estimate) in soil moisture indicator between 1994 and 2014, with 95% confidence interval (LCL and UCL) and p-value, derived from linear mixed-effects models and likelihood ratio test. For plot numbers per block see Table S1.*

Block	Estimate	LCL	UCL	p-value
All	-0.14	-0.16	-0.12	<0.001
A	-0.14	-0.17	-0.11	<0.001
B	-0.12	-0.14	-0.09	<0.001
C	-0.18	-0.23	-0.14	<0.001
D	-0.12	-0.19	-0.05	0.002

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7.2 ARTICLE 2:

KLAUS STEINBAUER, ANDREA LAMPRECHT, PHILIPP ROBERT SEMENCHUK, MANUELA WINKLER & HARALD PAULI (2020):

Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps.

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ORIGINAL ARTICLE

Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps

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Abstract

The largest alpine–nival vegetation permanent plot site in the Alps, the GLORIA mastersite Schrankogel (Tirol, Austria), provided evidence of warming-driven vegetation changes already 10 years after its establishment in 1994. Another decade later, in 2014, substantial compositional changes with increasing ratios of warmth-demanding to cold-adapted species have been found. The current study deals with species-specific responses involved in an ongoing vegetation transformation across the alpine–nival ecotone on Schrankogel by using presence/absence as well as cover data from permanent plots, situated between 2900 and 3400 masl. The number of occupied plots per species remained constant or even increased during the first decade, whereas disappearance events became more frequent during the second one, especially for cold-adapted specialists (subnival–nival species). Remarkably, the latter was accompanied by continued strong losses in cover of all subnival–nival species. These losses were more frequent in plots with a more thermophilous species composition, suggesting an increasing maladaptation of subnival–nival species to warmer habitat conditions and a successive trailing-edge decline. Several species with a distribution centre at lower elevations (alpine–subnival) markedly increased in cover, comparatively more so in colder plots, indicating a leading-edge expansion. Moreover, our findings show an increase in occupied plots and cover of almost all snowbed species, suggesting that areas previously with a too long snowpack period are now becoming suitable snowbed habitats. Vegetation gaps arising from population dieback of cold-adapted species, however, could only be partly filled by advancing species, indicating that species declines have occurred already before the onset of strong competition pressure.

Keywords Alpine · Biodiversity · Climate change · Ecotone · Migration · Nival · Schrankogel · Species

Introduction

Cold-adapted mountain plant species are expected to suffer severe area losses because of warming-driven upward range shifts into high-elevation zones where space is limited (Engler et al. 2011; Freeman et al. 2018; Lenoir and Svenning 2015). However, revisitation studies of historical sites most commonly show increases in species numbers (Erschbamer et al. 2011; Grabherr et al. 1994; Grytnes et al. 2014; Walther et al. 2005; Wipf et al. 2013). A pan-European study found that the increase in species richness on summits was highly synchronous with warming trends and was related to climate-sensitive plant functional traits of alpine to subnival species in all European study regions. In contrast, changes in patterns of precipitation and nitrogen deposition did not or only regionally coincide with increasing plant diversity (Steinbauer et al. 2018). The congruency of the acceleration of warming with species accumulation rates thus reinforced the hypothesis that warming is the primary driver of upward

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shifting leading range margins of species. This finding is remarkable, however, with respect to the known slow growth rates of most high mountain plants (Körner 2003). Although model projections forecast reductions of suitable alpine habitats (Engler et al. 2011), refined models suggested delayed responses to warming due to the capability of long-lived alpine species to persist even in unsuitable habitats until life spans of resident individuals are reached (Cotto et al. 2017; Dullinger et al. 2012). This might explain why evidence of increasing species numbers through colonisation events, so far, outweighs observations of species declines. Alternatively, however, this imbalance may also reflect the scarcity of data from old enough permanent plots with information on species' abundances and/or their distribution across their entire vertical ranges.

A study comparing vegetation relevés dating back at least 45 years with recent surveys across the Eastern Alps showed that trailing edges are shifting at least as fast as leading edges and that both are ascending faster the lower they are situated (Rumpf et al. 2018). Given the conical shape of mountain summits, this could lead to a rapid narrowing of species ranges (Bertuzzo et al. 2016). Changes in the abundance of species even showed stronger signals compared to range shifts (Rumpf et al. 2018). Indeed, shifting abundances, such as in-filling or declines of resident populations, should be more immediate responses than actual shifts of their distribution ranges, given the high stochasticity involved in dispersal and recruitment of plant species (Giménez-Benavides et al. 2018) and the commonly rather long time until populations of perennial alpine species will have disappeared completely.

High-elevation plant assemblages above the closed grassland of the alpine zone should be especially useful for elucidating species-specific climate change effects, because they are less affected by biotic interactions and human land use, and species are highly adapted to low-temperature conditions. Data from the largest high-alpine to nival permanent plot site in the Alps (Schrankogel in the central Tyrolean Alps), comprising several hundred 1 m^2 permanent plots, provided one of the first evidence of declining species covers already a decade after its setup in 1994 (Pauli et al. 2007). A repeated survey in 2014 showed thermophilisation effects of the same magnitude as the European average (Gottfried et al. 2012), which significantly accelerated in the recent decade (Lamprecht et al. 2018). Although this shift was accompanied by a net increase in species richness, the gain in species numbers slowed down due to species disappearances from the permanent plots, which were almost exclusively observed in the recent decade (Lamprecht et al. 2018).

In the light of the observed alteration of community composition and shifting balances of species gains and losses, we here focus on responses on the species level, i.e. we evaluate whether species adapted to high-elevation climates (subnival–nival species) respond consistently differently from species with lower distribution optima (alpine–subnival species). The focus on the level of individual species should enable to discern if species of similar vertical distribution show consistent response patterns and to contribute to a vulnerability assessment of high mountain plant species in the context of future conservation strategies.

Specifically, we ask:

(i) Do the dynamics of colonisation and disappearance events reflect homogenous tendencies within each species group (i.e. predominantly alpine–subnival species and subnival–nival species)?
(ii) Do cover increases of alpine–subnival species and cover decreases of subnival–nival species constitute to ongoing trends?
(iii) Do subnival–nival species decrease more pronouncedly in warmer plots and less in colder plots and vice versa for alpine–subnival species and therefore indicate gains at leading edges and losses at trailing edges?

Methods

The study site Schrankogel (3497 m; Stubaier Alpen, Tyrol, Austria) is located in the eastern central Alps within the protected area "Ruhegebiet Stubaier Alpen" (IUCN category IV). It is part of the Long-Term Socio-economic and Ecosystem Research (LTSER) platform Tyrolean Alps (Mirtl et al. 2015) and the Global Observation Research Initiative in Alpine Environments (GLORIA, http://www.gloria.ac.at). The bedrock is composed of siliceous material, mostly amphibolite and gneiss (Hammer et al. 1929). Annual precipitation sum at the closest nival observatory (Sonnblick 3109 msl, 200 km east of Schrankogel) ranged between 1400 and 2300 mm in the period 1991–2014. Mean monthly air temperature of June, July and August at Brunnenkogel (3440 msl, located 30 km southwest of Schrankogel) varied roughly between − 2.9 and 3.9 °C between 2004 and 2014 (Zentralanstalt für Meteorologie und Geodynamik, http://www.zamg.ac.at).

Vegetation sampling and dataset

With the intention of detecting climate-driven vegetation changes, around 1000 1 m^2 permanent plots were established along the southwest to east facing slope system of Schrankogel in 1994 (Lamprecht et al. 2018). Plots were arranged in transects which were grouped in four spatially divided blocks (Fig. S1). Field sampling comprised the visual estimation of the percentage cover of surface types (solid rock, scree, bare ground and vegetation) and of each vascular plant species present in a permanent plot, where a cover of 1% refers to 1 dm^2. Resurveys of the permanent plots were conducted in 2004 (362) and 2014 (661 plots). Plots with high disturbance due to rockfall were excluded, leaving 355 plots in 2004 and 654 in 2014. Two datasets were compiled for further analysis: (1) A dataset comprising 654 permanent plots for changes across a time span of 20 years (1994 to 2014; dataset-2s), and (2) a smaller subset of 355 permanent plots, where data available from all three surveys (1994, 2004 and 2014; dataset-3s) allowed for the comparison among the two decades. Species names follow Fischer et al. (2008) except for *Senecio incanus* subsp. *carniolicus* where we used *Senecio carniolicus* agg. (Flatscher et al. 2015).

Statistical analyses

All statistical analyses were performed using the statistic software R version 3.5.0 (R Core Team 2018) and figures were created with *ggplot2* (Wickham 2016). Generalised linear mixed effects models (GLMMs) were fitted to analyse changes in the number of occupied plots (presence/absence) and cover across the surveys in both datasets and colonisations and disappearances in dataset-3s in the two decades for each species. To reflect the spatial structure of the dataset, plot nested in transect nested in block was included as random intercept term in all models. Only species present in at least 30 plots and with at least ten colonisations or disappearance events were analysed individually. Hypothesis testing of all models was conducted by a simultaneous inference procedure implemented in function *glht* from the *multcomp* package (Hothorn et al. 2008). Model diagnostic graphs were checked visually for outliers, homogeneity of variance and independence of residuals. Outliers were subsequently removed. The annual *Euphrasia minima* was excluded from analysis, because it shows high inter-annual fluctuations both in occurrence and abundance (Table S1), which may reflect shorter-term weather conditions over one or two seasons rather than longer-term climatic changes (Lamprecht et al. 2018).

To analyse differences in the number of occupied plots (presence/absence) between the surveys and differences in colonisations and disappearances between the decades 1994–2004 and 2004–2014 for each species, GLMMs (function *glmer* from package *lme4*) assuming a binomial error distribution were used (Bates et al. 2015; Kuznetsova et al. 2016; Mangiafico 2018). A species' presence (1)/absence (0) in each plot was used as response and year as fixed. For colonisations and disappearances, the binary response variable was set to 1 if a species had colonised or disappeared from a plot, respectively, and to 0 if this was not the case. Decade was used as fixed effect. A colonisation event is defined as absence in year_t and presence in year_{t+10} of a given species in a given permanent plot. A disappearance event occurs when a species was present in a given permanent plot in year_t and absent in year_{t+10}. Only plots which could potentially be colonised (i.e. where a species was not present in year_t) or from which a species could potentially disappear (i.e. where a species was present in year_t), respectively, were used. For *Gnaphalium supinum* and *Sagina saginoides* with no disappearance events in one decade, a negative binomial distribution was assumed, as the binomial GLMM did not converge due to a singular fit.

To analyse differences in species cover, all plots with a species present in at least one survey year were considered. Absent species were assigned a cover value of zero. As both datasets were heteroscedastic and asymmetric, we used GLMMs (function *glmmTMB*; Brooks et al. 2017) with a standard beta distribution (Cribari-Neto and Zeileis 2010) and year as fixed effect. Percentage cover of each species (y) within an interval of zero and one, where one represented the maximal possible value of 100%, was subsequently compressed to bound data away from zeros and ones. This was conducted according to Smithson and Verkuilen (2006) by

$$y' = \frac{(y(N-1) + 0.5)}{N},$$

where N is the sample size. In dataset-2s, the assumption of independence in the residuals was violated in the case of *Arenaria ciliata*, *Minuartia sedoides* and *Poa alpina* and a negative binomial distribution was chosen instead.

Altitudinal ranks (ARs) are classifications of species according to their distributions along an altitudinal gradient ranging from subnival–nival (AR = 1) to subalpine–alpine (AR = 4). A community-weighted thermic indicator (TI) for each plot and survey year was calculated based on each species' AR classification and weighted by its relative cover:

$$\text{TI} = \left(\sum \text{AR}(\text{species}_i) \times \text{cover}(\text{species}_i)\right) \Big/ \sum \text{cover}(\text{species}_i).$$

The TI of the permanent plots on Schrankogel was shown to be highly correlated with soil temperature (Lamprecht et al. 2018) and was previously used as an indicator of temperature conditions (e.g. Gottfried et al. 2012).

To show changes in cover sum of AR species groups and of individual species across a temperature gradient between 1994 and 2014, the TI of the baseline year 1994 (TI_{94}) of each permanent plot in dataset-2s was used as a proxy for thermal conditions where $\text{TI}_{94} = 1$ refers to subnival–nival and $\text{TI}_{94=}3$ to alpine conditions. Differences in cover between 1994 and 2014 across the TI_{94}-gradient for each AR were analysed using GLMMs assuming a beta distribution. Cover was used as response, the interaction of TI_{94} and year as fixed effect and species as second random effect. Function *ggpredict* was used to plot model predictions (Lüdecke 2018).

Results

In dataset-2s (654 plots) and dataset-3s (355 plots), 72 and 63 vascular plant species were present, respectively, during the study period (Table S1). Eighteen species were recorded only in 2014 and two species only in 1994.

Changes in the number of occupied plots

The number of occupied plots increased for most of the species between 1994 and 2014 (dataset-2s). Thirty out of 40 modelled species increased significantly, including 1 AR1 ($P < 0.0001$), 15 AR2 ($P < 0.02$), 11 AR3 ($P < 0.01$) and 3 AR4 species ($P < 0.0001$; GLMMs, Table 1, Tables S1, S2). The number of occupied plots decreased only in the AR1 species *Poa laxa* ($P < 0.0001$). Five out of nine snowbed species, associated with AR2 and AR3, showed an increasing tendency ($P < 0.0001$). Six AR3 and 12 AR4 species, respectively, were found for the first time in the plots in 2014. Significant changes in the number of occupied plots were increases in both decades for almost all AR2 and AR3 species, whereas AR1 species showed increases only in the first and decreases in the second decade (dataset-3s; Table S3).

Changes in colonisations and disappearances (dataset-3s)

Colonisation rates increased significantly for *Festuca intercedens* ($P = 0.001$; AR2) and *Sibbaldia procumbens* ($P = 0.001$; AR3) between 1994–2004 and 2004–2014 (Table S4). In contrast, *Androsace alpina* and *Ranunculus glacialis* ($P < 0.03$; AR1), as well as *Gnaphalium supinum*, *Sagina saginoides* and *Sedum alpestre* ($P < 0.03$; AR3) showed significantly fewer colonisation events in the period 2004–2014. In the second decade, significantly more disappearances were recorded in four AR1 ($P < 0.01$), five AR2 ($P < 0.01$) and six AR3 species ($P < 0.03$; Table S5).

Changes in species cover

The cumulative cover of 13 species, including all 6 AR1 species ($P < 0.0001$), 3 AR2 ($P < 0.01$) and 4 AR3 species ($P < 0.02$) decreased significantly between 1994 and 2014 (datatset-2s; GLMMs; Table 1, Table S6). In contrast, none of the AR4 species decreased significantly. A significant increase in cover was observed in 16 species including 10 AR2 ($P < 0.03$), 4 AR3 ($P < 0.0001$) and 2 AR4 species ($P < 0.0001$). Six snowbed species increased their cover significantly, only *Sedum alpestre* declined ($P < 0.0001$). Overall, *Cerastium uniflorum*, *Poa laxa*, *Saxifraga bryoides* (AR1) and *Carex curvula (*AR3) showed the strongest decrease and *Pedicularis aspleniifolia*, *Silene exscapa* and *Veronica alpina* (AR2) the strongest increase in total cover during the study period ($P < 0.0001$).

All AR1 species declined in both decades ($P < 0.0001$), except *Saxifraga oppositifolia* with a significant decrease only in the period 2004–2014 ($P = 0.001$; dataset-3s, GLMMs, Fig. 1a, d; Table S7). Two AR2 species (*Pedicularis aspleniifolia* and *Silene exscapa*) increased in both decades ($P < 0.03$), and three (*Festuca intercedens*, *Saxifraga exarata* and *Trisetum spicatum*) in only one decade ($P < 0.04$; Fig. 1b, e; Table S7). In contrast, *Gentiana bavarica* decreased in both decades and *Primula glutinosa* only in the second decade ($P < 0.04$). The graminoid AR3 species *Carex curvula* and *Poa alpina* declined in one of the decades ($P < 0.0001$; Fig. 1c, f, Table S7). The snowbed species *Veronica alpina* and *Sibbaldia procumbens* increased in both decades ($P < 0.04$), while *Sedum alpestre* decreased in both decades ($P < 0.01$), and *Sagina saginoides* increased in cover between 1994 and 2004 and decreased between 2004 and 2014 *(*$P < 0.0001$; Fig. 1b, c, e, f; Table S7).

Species cover changes across a community-weighted thermic indicator gradient

Cover sums of individual species (Fig. S2) and of AR species groups (Fig. 2) revealed considerable differences when comparing the patterns of 1994 and 2014 along the TI gradient of the baseline year (TI_{94}; Fig. 2; Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI_{94} gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8). In contrast, AR2 species became more abundant in colder (subnival–nival) plots with a $TI_{94} < 2$ ($P < 0.0001$; Fig. 2f; Table S8). Species of AR3 were initially more abundant in plots with a $TI_{94} > 2.4$, but changed significantly towards higher cover in colder and less cover in warmer plots in 2014 ($P < 0.001$; Fig. 2g; Table S8). The latter was mainly driven by cover losses of *Carex curvula* and *Poa alpina* (Fig. S2). AR4 species, on the contrary, expanded significantly, but uniformly in abundance over the entire TI_{94}-gradient ($P = 0.048$; Fig. 2d, h, Fig. S2; Table S8).

Discussion

Data from permanent plots distributed across the alpine–nival ecotone on Schrankogel provided an early signal of climate change-driven plant species declines, already 10 years after the baseline was set in 1994 (Pauli et al. 2007). After adding the data from 2014, another decade later, the previously observed cover declines could be confirmed, along with a continued increase in species richness, although

Table 1 Vascular plant species per altitudinal rank (AR) and their occurrences in 654 permanent plots across the alpine–nival ecotone on Schrankogel in 1994 and 2014 (dataset-2 s)

Altitudinal rank	Species	Occupied plots		Colonisation/ disappearance	Cover	
		N	*P* value	*N*	Sum (dm^2)	*P* value
		1994/2014	1994–2014	1994–2014	1994/2014	1994–2014
AR1	*Androsace alpina*	247/228	↘	51/70	111.8/27.8	↓↓↓
	Cerastium uniflorum	440/444	ns	51/47	1401.8/643.4	↓↓↓
	Poa laxa	614/581	↓↓↓	15/48	1125.6/605.1	↓↓↓
	Ranunculus glacialis	478/479	ns	54/53	278.3/143.6	↓↓↓
	Saxifraga bryoides	540/590	↑↑↑	61/11	2229.3/1650.3	↓↓↓
	Saxifraga oppositifolia	66/68	ns	12/10	193.3/127.4	↓↓↓
AR2	*Arenaria ciliata*	32/37	↗	7/2	21.0/19.2	ns
	Cardamine resedifolia$^{\text{sn}}$	17/63	↑↑↑	50/4	2/7.4	↑↑↑
	Draba fladnizensis	41/37	ns	13/17	2.6/1.4	↓↓
	Erigeron uniflorus	192/317	↑↑↑	133/8	245.5/273.8	↑↑↑
	Festuca intercedens	124/218	↑↑↑	107/13	161.3/212.2	↑↑↑
	Gentiana bavarica var. *subacaulis*	298/335	↑↑↑	56/19	145.3/57.3	↓↓↓
	Leucanthemopsis alpina	504/577	↑↑↑	81/8	1171.9/1116.1	ns
	Luzula spicata	445/523	↑↑↑	101/23	647.3/689.9	↑
	Oreochloa disticha	210/277	↑↑↑	81/14	515.5/532.4	↑
	Pedicularis aspleniifolia	32/92	↑↑↑	63/3	12.9/71.4	↑↑↑
	Primula glutinosa	281/306	↑	50/25	471.8/421.5	↓↓
	Saxifraga androsacea	17/41	↑↑	34/10	3.1/9.8	ns
	Saxifraga exarata s.str.	122/193	↑↑↑	93/22	70.8/113.1	↑↑↑
	Saxifraga seguieri	16/26	↑↑	19/9	3.6/6.3	ns
	Silene exscapa	382/478	↑↑↑	108/12	1750.7/2418.6	↑↑↑
	Trisetum spicatum	27/79	↑↑↑	57/5	12.3/28.0	↑↑↑
	Veronica alpina$^{\text{sn}}$	113/235	↑↑↑	122/0	46.9/173.8	↑↑↑
AR3	*Carex curvula*	109/122	↑↑	15/2	1985.7/1381.1	↓↓↓
	Cerastium cerastoides$^{\text{sn}}$	18/21	ns	16/13	2.4/9.7	↗
	Gnaphalium supinum$^{\text{sn}}$	69/227	↑↑↑	161/3	8.2/34	↑↑↑
	Minuartia gerardii	75/99	↑↑	41/17	30.7/35.2	ns
	Minuartia sedoides	368/456	↑↑↑	104/16	1033.4/1028.9	ns
	Phyteuma hemisphaericum	47/59	↑↑	15/3	92.5/47.4	↓
	Poa alpina	176/244	↑↑↑	90/22	325.5/174.0	↓
	Sagina saginoides$^{\text{sn}}$	40/117	↑↑↑	90/13	7.3/11.1	↑↑↑
	Sedum alpestre$^{\text{sn}}$	191/241	↑↑↑	71/21	48.9/31.3	↓↓↓
	Senecio carniolicus agg.	20/34	↑↑↑	16/2	4.4/4.1	ns
	Sibbaldia procumbens$^{\text{sn}}$	12/52	↑↑↑	40/0	4.8/22.6	↑↑↑
	Veronica bellidioides	25/55	↑↑	34/4	23.8/58.1	↑↑↑
AR4	*Avenula versicolor*	18/45	↑↑↑	29/2	48.5/118.7	↑↑↑
	Potentilla aurea	0/31	↑↑↑	31/0	0/4.1	↑↑↑

AR denotes a species' distribution range along the elevation gradient (after Gottfried et al. 2012). Shown are vascular plant species with significant differences either in the number of occupied plots or cover. *P* values were derived from generalised linear mixed effects model with the number of occupied plots or cover as response, year or decade as fixed effect and plot nested in transect nested in block as random effect. For further details and all study species see Tab S1-S2, S6

NA, model not available; ns, not significant; ↑, increase; ↓, decrease; ↗/↘, $P=0.05$–0.1; ↑/↓, $P=0.01$–0.05; ↑↑/↓↓, $P=0.01$–0.001; ↑↑↑/↓↓↓, $P<0.001$; AR1, subnival–nival; AR2, alpine–subnival; AR3, alpine; AR4, subalpine–alpine; sn, refers to snowbed species

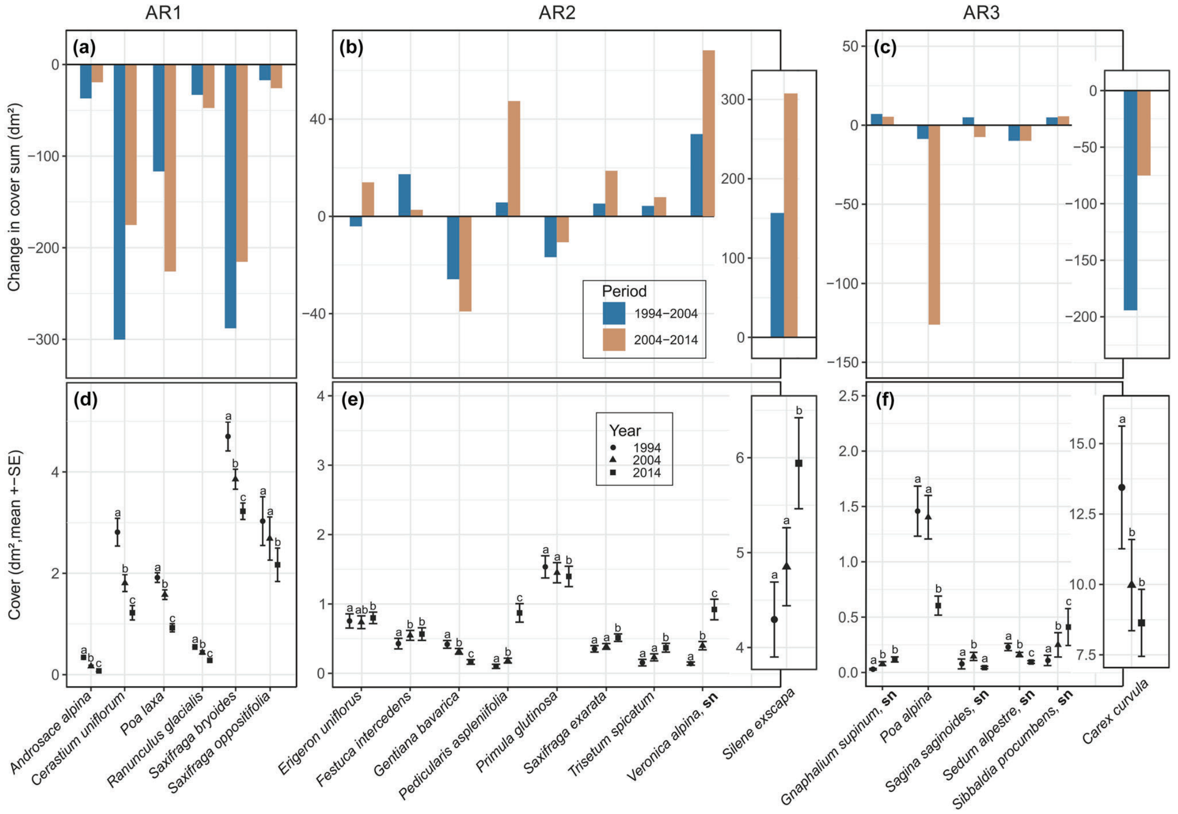

Fig. 1 Changes in cover values of vascular plant species on Schrankogel from 1994–2004–2014 (dataset-3s). Shown are changes in cover sum between the periods 1994–2004 and 2004–2014 (**a**–**c**) and mean cover values per plot ± standard error (SE) in the years 1994, 2004 and 2014 (**d**–**f**). Only vascular plant species with significant differences grouped in altitudinal ranks (ARs) are shown. The AR denotes a species' distribution range along the elevation gradient (after Gottfried et al. 2012). AR1 (**a**, **d**) are subnival–nival, AR2 (**b**, **e**) alpine–subnival, and AR3 (**c**, **f**) alpine species. Lower-case letters denote significant differences between survey years. Note different scales for each AR as well as for *Carex curvula* and *Silene exscapa*. Snowbed species are indicated by sn. For details on raw data and significant differences see Tables S1 and S7

less pronounced in the second decade, and a progressing transformation of the community composition towards more warmth-demanding and drought-tolerant species (Lamprecht et al. 2018). Here, we show that these changes were strongly driven by a continued decrease in cover of all cryophilic AR1 species. The resulting gaps were only partly filled by species from lower elevations (mainly AR2 species). In addition, AR1 species showed declining numbers of successful colonisations and growing numbers of disappearances from the plots.

Trailing-edge contraction of crypophilic species and leading-edge expansion of lower-elevation species

The majority of species have expanded their distribution over the alpine–nival permanent plots on Schrankogel during the 20 years of observation (Table 1, Tables S1–S5), corroborating recently found increases in species richness in other parts of the Alps (Erschbamer et al. 2011; Wipf et al. 2013) and on more than 300 mountain summits distributed across Europe (Grytnes et al. 2014; Pauli et al. 2012; Steinbauer et al. 2018).

Even though the high-elevation species group (AR1) showed both colonisations and disappearances (Table 1, Tables S1, S4, S5), colonisations became rarer and disappearances more frequent in the second decade. Such a decrease in the gain/loss ratio signals a trailing-edge contraction (i.e. trailing edge moving closer to the leading edge; Lamprecht et al. 2018). Propagation capabilities of at least some AR1 species, however, should be sufficient for reaching new habitats. Tackenberg and Stöcklin (2008) reported that seeds of *Saxifraga bryoides* can be transported more than 1000 m by wind. At the same time, observations of

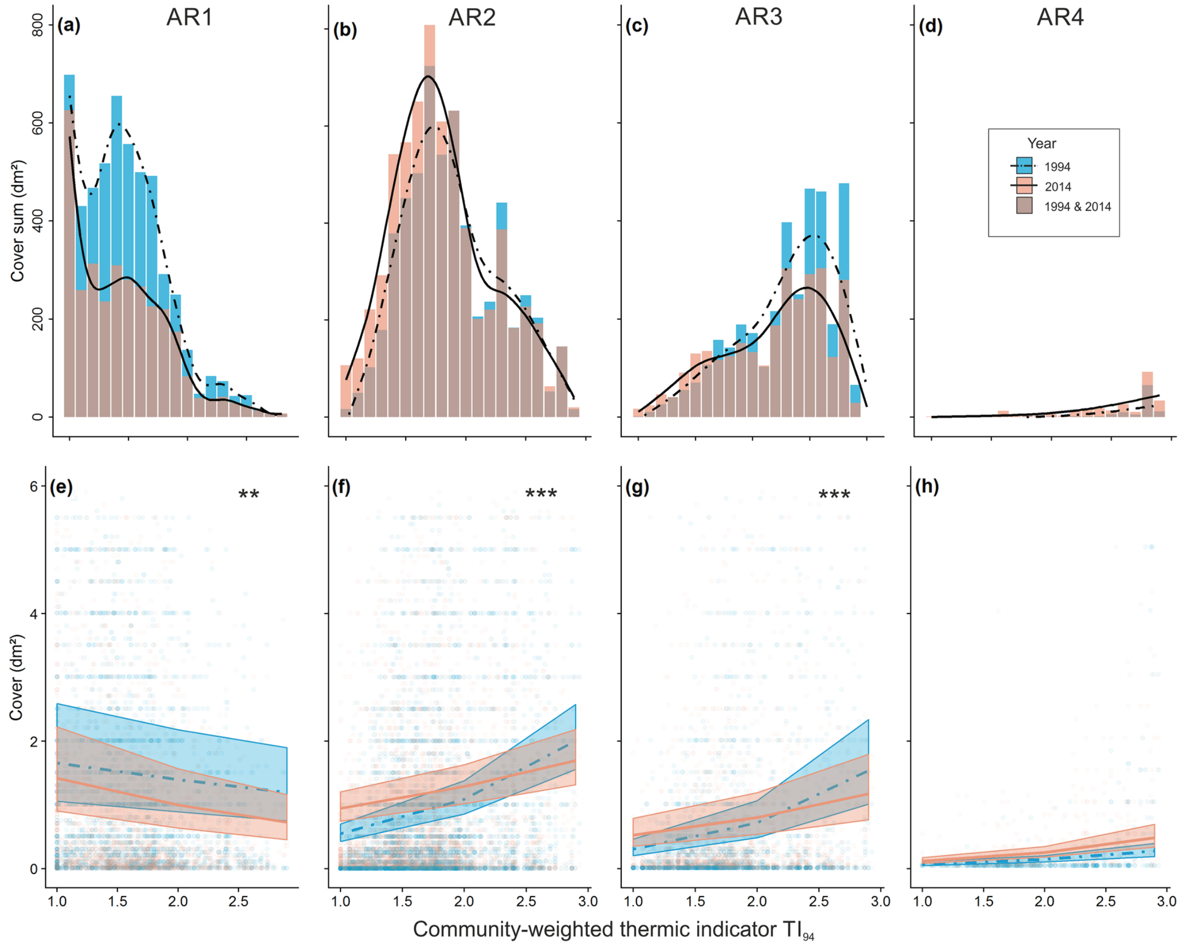

Fig. 2 Cover sum and cover per permanent plot of vascular plant species in different altitudinal ranks (AR) between 1994 and 2014 on 654 permanent plots on Schrankogel (dataset 2-s). The AR denotes a species' distribution range along the elevation gradient (after Gottfried et al. 2012). AR1 (**a**, **e**; $n=6$) denotes subnival–nival, AR2 (**b**, **f**; $n=21$) alpine–subnival, AR3 (**c**, **g**; $n=23$) alpine and AR4 (**d**, **h**; $n=22$) subalpine–alpine species. All permanent plots were grouped following their community-weighted thermic indicator values of the baseline year 1994 (TI_{94}). These TI_{94}-values ranged between 1.0 (subnival–nival plots) and 3.0 (alpine plots). A generalised additive model was used to fit smooth splines with cover sum as response and TI_{94} as explanatory variable in each year (**a**–**d**). Cover of each AR in every plot and year was analysed using a generalised linear mixed effects model assuming a beta distribution (**e**–**f**). The interaction of TI_{94} and year was used as a fixed effect and plot nested in transect, nested in block as well as species were used as random effects. Shown are predicted values with a 95% confidence interval (lines) and raw data (points). *Significant differences between interaction of TI_{94} with year. For model details see Table S8. For details of cover sum of single species across the TI_{94}-gradient, cf. Fig.S2. AR1 (**a**, **e**; $n=6$) denotes subnival–nival, AR2 (**b**, **f**; $n=21$) alpine–subnival, AR3 (c, g; n=23) alpine and AR4 (**d**, **h**; $n=22$) subalpine–alpine species

colonisation events are fairly unlikely, as most AR1 species already occupy a large number of plots, rendering the interpretation of decreasing colonisation events difficult (e.g. *Cerastium uniflorum*, *Poa laxa*, *Ranunculus glacialis* and *Saxifraga bryoides* are present in more than two-thirds of all plots; Table 1, Table S1).

Most of the AR2 species show a clear prevalence of colonisations over disappearances (Table 1, Tables S1, S4, S5), suggesting a leading-edge expansion of this species group, similar to previous observations of elevational and latitudinal range shifts (Carilla et al. 2018; Parmesan and Yohe 2003; Rumpf et al. 2018). Among the common AR2 species, *Silene exscapa* exhibited a moderate but steady increase and hardly any losses, whereas others like *Festuca intercedens* showed contrasting changes with both numbers of colonisations and disappearances significantly increasing from the first to the second decade (Tables S1, S4, S5). Such varied fluctuations presumably reflect different ratios of successful/failed establishments, rather than trends in range expansion or contraction. Despite overall warming, late frost events or cold spells during summer continue to occur and can affect temperature-sensitive seedlings and young plants (Ladinig et al. 2013), which may have contributed to the observed variation in species occurrences.

Furthermore, 18 of the colonising species were new, i.e. not observed previously in any of the plots, whereas only 2 disappeared from the single plot they had previously occupied (Table S1). All newcomers were alpine or species from lower elevations (AR3, AR4), having shifted their upper ranges to the alpine–nival ecotone during two decades (1994–2014), most likely driven by strongly rising temperatures within this period (Chen et al. 2011; Marty and Meister 2012).

Generally, all common AR3 species show more colonisation than disappearance events, however, with some fluctuations among decades, e.g. for the short-lived *Sagina saginoides*, which exhibits annual behaviour and plentiful seed production (Tables S1, S5, S6; Cannone et al. 2008). The same was true within the AR4 group, which showed a strong increase in the number of occupied plots, although this group is so far rather negligible concerning the total number of plots.

Regarding research question *i*, we cannot confirm a consistent response pattern within ARs. While an overall increase of alpine–subnival (AR2) and lower elevational species could be detected, some species reacted in other ways. In contrast, although a decline of subnival–nival (AR1) species is visible most notably in the second decade, the overall signal obtained by presence/absence data is weak.

The dieback of the cryophiles

In contrast to presence/absence data, almost all high-elevation specialist species (AR1) showed a clear signal of cover reduction. This decrease in abundance was already found 10 years after the baseline survey (Pauli et al. 2007) and remained unbroken during the second decade across all AR1 species (Fig. 1 a, Table 1, Tables S1, S6, S7). This negative abundance change of resident species was to be expected as a first response to climate warming, as it reflects changes in growth performance. Range shifts, in contrast, do not only depend on climatic factors but also involve uncertainties of successful establishment. Evidence of abundance declines in alpine plants is scarce in the literature compared to the ample evidence of changing species numbers, as suitable long-term data series are lacking.

The few studies involving abundance records, indeed, found significant decreases of cold-adapted species: Lesica (2014) reported that species restricted to high elevations declined more than species with broader elevation amplitudes in the Montana Rocky Mountains between 1988 and 2011. In the alpine zone of the central Appenines, a revisitation study found decreasing abundances of cryophilic species after 42 years (Evangelista et al. 2016). A comparison of old plots (before 1970) with resurveys at nearby locations with similar habitat conditions showed that changes in abundance were stronger than shifts of lower and upper range margins, with above-average declines found for the high-elevation species (Rumpf et al. 2018).

Given that all AR1 species are perennial plants, the compelling evidence of their cover decrease suggests a response to increasingly unsuitable climate at their present habitats, rather than responses to short-term weather events. While several studies proposed an extinction debt associated with the persistence of high-elevation species, which delays species-specific responses to climate warming (Alexander et al. 2018; Dullinger et al. 2012) until their life spans are reached (Cotto et al. 2017), our findings indicate the onset of debt repayment through a progressing dieback at their lower range margins. Considering the second research question *ii,* a consistent decrease in cover of each AR1 species reflects a continued trend also in the second decade, whereas such a pattern is less homogenous for species advancing from lower elevations.

The continued cover declines of the high-elevation specialists may have been caused either by direct climatic factors or by competitive displacement through advancing species from lower down. The overall decrease of vegetation cover, however, suggests that the shrinkage of AR1 species was faster than the expansion of other species (Fig. 2; Lamprecht et al. 2018). The majority of permanent plots on Schrankogel are located on raw soils, rock and scree, where species were found to be less exposed to competitive pressure, compared to habitats with developed soils rich on organic material (Kulonen et al. 2018). In turn, direct negative effects of warmer temperatures on cryophilic species through respiratory losses of carbohydrates are probable, if their limited capability to adapt respiration rates to higher temperatures, as reported for *Cerastium uniflorum* and *Ranunculus glacialis* (Cooper 2004; Körner 2003; Larigauderie and Körner 1995), holds true for the majority of AR1 species. Another more recent study found that higher temperatures cause increasing drought stress with negative effects on annual growth for *Saxifraga oppositifolia* in Spitsbergen (Opala-Owczarek et al. 2018). On Schrankogel, an increasing transformation towards a community composition adapted to drier soil conditions was indicated for the 20-year study period (Lamprecht et al. 2018).

High topographic variation of adjacent microhabitats was suggested to buffer effects of rising temperatures on local species survival (Scherrer and Körner 2011). The observed continued decrease in cover of all AR1 species in a large number of permanent plots, however, does not confirm this hypothesis. Thus, referring to research question *iii*, cold-adapted AR1 species tend to decrease slightly more in warmer plots, while species of AR2 and AR3 showed higher cover increases in colder plots (Fig. 2). Although the latter increase could not keep pace with an overall decrease of AR1 species, some common advancing species, such as *Silene exscapa* (AR2), may have exerted competitive pressure on AR1 species. In the baseline year 1994, its total cover was well below that of the then most dominant species *Saxifraga bryoides* (AR1), but only 20 years later *Silene exscapa* was undisputedly the number one in terms of total cover (Fig. 1; Table 1, Tables S1, S6, S7). Several other AR2 species showed gains in cover, such as *Festuca intercedens*, *Trisetum spicatum*, *Pedicularis aspleniifolia*, and *Erigeron uniflorus*, but they are far less abundant than *Silene exscapa*.

The pronounced expansion and/or filling of six out of nine species associated with snowbed habitats was surprising, since higher temperatures should lead to earlier snow melt and, thus, to a shrinkage of snowbed habitats (Fig. 1; Table 1, Tables S1, S6, S7). Alpine snowbed species and communities are thought to be highly vulnerable to climate change effects (Björk and Molau 2007). They have been found to be affected by competition through encroaching taller-growing species from neighbouring communities in the subalpine to lower alpine zone in the Swiss Alps (Matteodo et al. 2016) and showed rapid reduction in growth performance when transplanted to alpine ridge habitats in New Zealand (Lord et al. 2018). In turn, increases of snowbed species' abundances were found in southern Norway in combination with increasing snow cover (Felde et al. 2012). A pan-European study, comparing historical and new alpine–subnival summit flora inventories, found an above-average increase in the number of snowbed species on the summits (Grytnes et al. 2014), where an enforced melting of ice and snow patches, which liberates new habitats for colonisation, was suggested as explanation for the advance of snowbed species. Given that many of their summits were situated at the alpine–nival ecotone, our observations on Schrankogel could likely be additional evidence supporting their hypothesis. Subnival and nival environments, formerly mostly providing habitats for AR1 species only, which are capable of dealing with both low-temperature conditions and short growing seasons (Gottfried et al. 2002), are increasingly suitable for the less cold-adapted snowbed species.

An ongoing decline in cover of two AR3 graminoids, *Carex curvula* and *Poa alpina* was unexpected as well (Fig. 1, Fig. S2, Table 1, Tables S1, S6, S7), as both are common elements of alpine grassland vegetation, which should have shifted their distributions higher up. A similar decline of *Carex curvula* was observed by Cannone et al. (2007) and Cannone and Pignatti (2014) in the Italian Alps, who suggested negative effects of increased disturbance through permafrost degradation. We cannot test this hypothesis, although we observed an increasing surface destabilisation on Schrankogel.

Limitations of the study

While we are confident that our results are representative for ongoing vegetation changes across the alpine–nival ecotone, a number of limitations might have biased the observed species-specific changes. Such are a non-random study design, with permanent plots organised in transects. These were not homogenously distributed, which might have caused over- or underrepresentation of certain habitat types and species, but we accounted for the spatial structure inherent in the dataset by using permanent plots as random term in the GLMMs. Influences of ungulate herbivory by *Capra ibex* and additionally by sheep and goats in the lowermost plots cannot be excluded, but grazing signs were minor and impacts would not cause a directional change of plant species. Interference with concurrently changing patterns of soil microorganisms, micro- and mesofauna might have an influence on plant performance, but requires further studies. Another source of error might arise from inter-annual species fluctuation in phenology, which we attempted to minimise by resurveys in the same month in the peak growing season. Finally, observer errors unavoidably occur when using visual cover estimations. A recent study on observer variability, which included data from the Schrankogel permanent plots, indicated that observer errors did not exceed changes over time in cover, species turnover and the TI for observation periods ≥ 10 years (Futschik et al. 2019).

Conclusions

The current study provides evidence of severe species-specific vegetation changes in permanent plots across the alpine–nival ecotone during the period 1994–2014 on Schrankogel. An overall increase in colonisations and a more pronounced increase in cover of most AR2 and lower elevational species in colder plots suggest a continued leading-edge expansion. The surprisingly prolific performance of most of the snowbed species may indicate the liberation of new microhabitats through an elongated snow-free period.

All subnival–nival AR1 species provide evidence of a rear-edge decline by showing the highest rates of disappearances combined with a consistent and strong decrease in cover, which was more pronounced in warmer plots. AR2 to AR4 species could not compensate these decreases, which points towards low levels of competition, but a continued maladaptation of high-elevation specialists to the current climate. Notably, this study revealed substantial differences between presence/absence and cover data. While, for example, only *Poa laxa* decreased in the number of occupied plots, all AR1 species declined consistently in cover. This underpins the importance of including species abundance data in studies analysing climate-driven vegetation changes.

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Author contributions HP, MW, AL and KS designed the study and were part of the recording team. KS, AL, PS and MW analysed the output data. HP managed the study. KS, AL and HP wrote the manuscript. All authors discussed the results and implications and commented on the manuscript at all stages.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study does not involve research on human participants or animals.

Informed consent Informed consent was obtained from all individual participants included in the study.

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Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps, Alpine Botany

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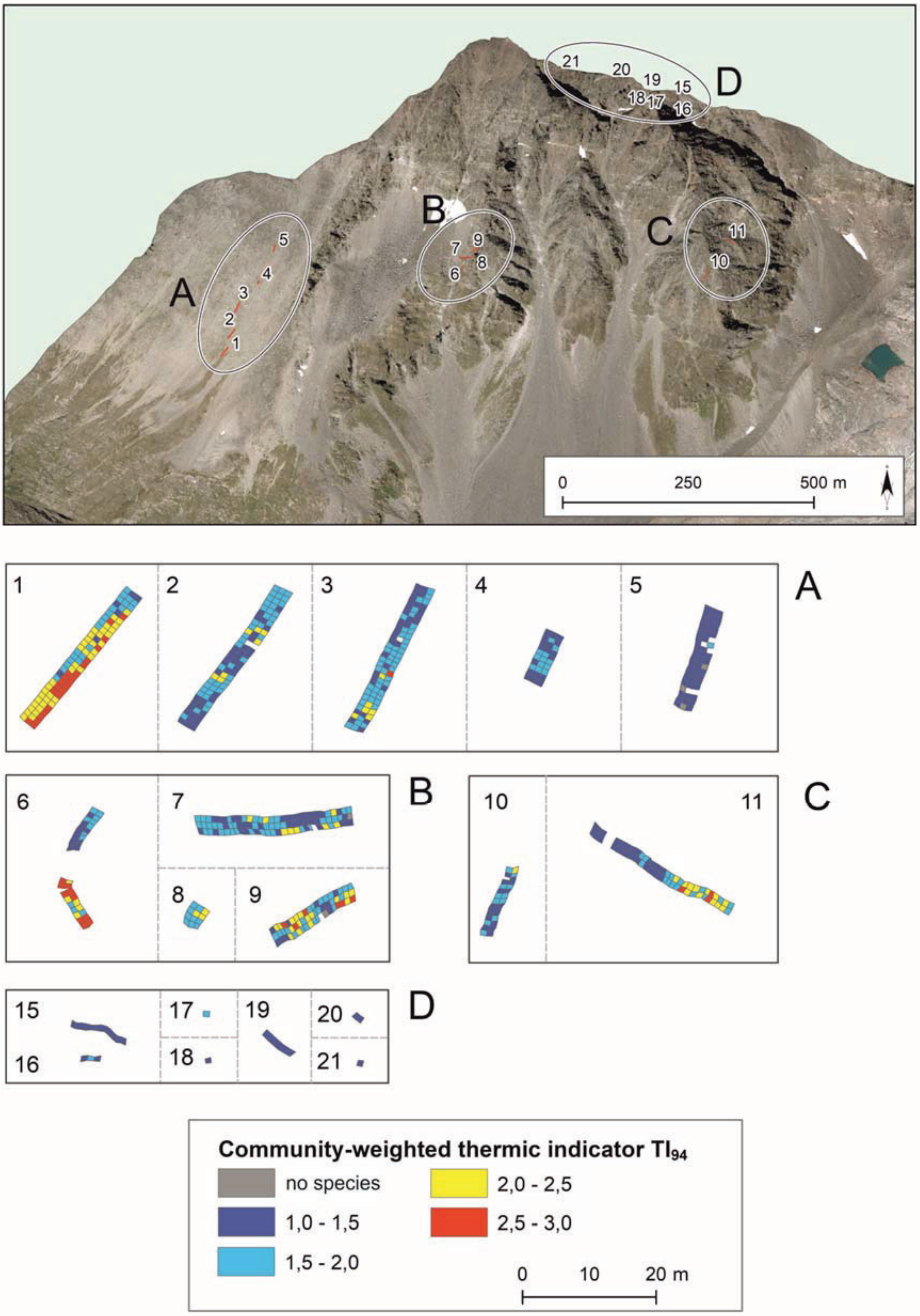

Figure S1 Location of 654 permanent plots (dataset-2s) on Schrankogel with transect details, changed after Lamprecht et al. (2018). Plots are grouped in transects clustered in four topographic blocks: A) uniformly shaped SW- slope, rich in scree; B) rugged S-facing ridge, C) rugged S-SE facing ridge and D) S-facing high-elevation plots along the E-ridge. Inserts show the community-weighted thermic vegetation indicator in 1994 (*TI_{94}*) of each plot. Orthophotos (© Land Tirol) modified with ArcGIS 10.3. for Desktop, Esri Inc

Table S1 Vascular plant species per altitudinal rank (AR) in permanent plots on Schrankogel. Number of occupied plots, colonisations, disappearances and cover sum of raw data in 654 permanent plots across the alpine-nivale ecotone on Schrankogel in 1994 and 2014 (dataset-2s) as well as 355 permanent plots surveyed in 1994, 2004 and 2014 (dataset-3s). Colonisations give number of plots with a species being not present in the prior survey year, but present in the following year; Disappearances give the number of plots with a species present in the prior, but missing in the following survey year

		Dataset-2s			Dataset-3s			
		Occupied plots	Colonisation / Disappearance	Cover	Occupied plots	Colonisation	Disappearance	Cover
		N	N	Sum (dm²)	N	N	N	Sum (dm²)
Altitudinal Rank	Species	1994 / 2004	1994-2014	1994 / 2014	1994 / 2004 / 2014	1994-2004 / 2004-2014	1994-2004 / 2004-2014	1994 / 2004 / 2014
AR1	*Androsace alpina*	247 / 228	51 / 70	111.82 / 27.76	172 / 190 / 150	30 / 13	12 / 53	72.36 / 35.34 / 15.87
	Cerastium uniflorum	440 / 444	51 / 47	1401.83 / 643.41	277 / 284 / 264	17 / 8	10 / 28	840.64 / 540.38 / 365.17
	Poa laxa	614 / 581	15 / 48	1125.59 / 605.06	339 / 336 / 321	4 / 6	7 / 21	662.82 / 546.12 / 320.18
	Ranunculus glacialis	478 / 479	54 / 53	278.31 / 143.61	268 / 287 / 274	27 / 10	8 / 23	166.69 / 133.58 / 86.09
	Saxifraga bryoides	540 / 590	61 / 11	2229.33 / 1650.3	319 / 334 / 339	15 / 7	0 / 2	1602.77 / 1314.81 / 1099.45
	Saxifraga oppositifolia	66 / 68	12 / 10	193.27 / 127.38	45 / 47 / 46	5 / 2	1 / 3	151.45 / 134.29 / 108.4
AR2	*Arenaria ciliata*	32 / 37	7 / 2	20.98 / 19.23	28 / 33 / 31	6 / 2	1 / 4	14.68 / 16.45 / 18.28
	Cardamine resedifolia ^{sn}	22 / 63	50 / 4	2.01 / 7.37	7 / 13 / 22	7 / 13	1 / 4	1 / 1.12 / 1.28
	Draba fladnizensis	41 / 37	13 / 17	2.62 / 1.41	34 / 38 / 32	9 / 7	5 / 13	2.24 / 1.26 / 1.33
	Kobresia myosuroides	4 / 4	133 / 8	7.6 / 3.55	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Erigeron uniflorus	192 / 317	107 / 13	245.49 / 273.76	132 / 182 / 206	54 / 38	4 / 14	167.6 / 163.48 / 177.48
	Festuca intercedens	124 / 218	56 / 19	161.25 / 212.18	68 / 93 / 131	26 / 52	1 / 14	62.55 / 79.9 / 82.59
	Gentiana bavarica var. *subacaulis*	298 / 335	9 / 0	145.27 / 57.29	209 / 236 / 240	28 / 19	1 / 15	106.95 / 81.1 / 42
	Geum reptans	4 / 22	1 / 1	11.4 / 11.22	3 / 7 / 10	4 / 3	0 / 0	10.6 / 8.58 / 10.64
	Leucanthemopsis alpina	504 / 577	81 / 8	1171.93 / 1116.14	260 / 296 / 311	41 / 26	5 / 11	538.38 / 554.36 / 556.5
	Linaria alpina	25 / 21	8 / 12	4.64 / 2.11	13 / 6 / 4	0 / 2	7 / 4	0.75 / 0.36 / 0.32
	Luzula spicata	445 / 523	101 / 23	647.32 / 689.94	271 / 293 / 302	25 / 23	3 / 14	422.81 / 371.05 / 435.35
	Oreochloa disticha	210 / 277	81 / 14	515.5 / 532.37	120 / 120 / 146	18 / 20	4 / 8	515.5 / 520.79 / 532.37
	Pedicularis aspleniifolia	32 / 92	63 / 3	12.87 / 71.4	20 / 39 / 66	22 / 30	3 / 3	6.95 / 12.67 / 60.09
	Potentilla frigida	25 / 27	7 / 5	14.49 / 11.48	23 / 25 / 24	5 / 4	3 / 5	13.99 / 11.44 / 11.15
	Primula glutinosa	281 / 306	50 / 25	471.82 / 421.49	173 / 182 / 185	11 / 15	2 / 12	305.36 / 288.58 / 277.94
	Saxifraga androsacea	17 / 41	34 / 10	3.06 / 9.75	10 / 23 / 17	13 / 7	0 / 13	2.21 / 2.8 / 1.72
	Saxifraga exarata s.str.	122 / 193	93 / 22	70.83 / 113.07	93 / 114 / 124	30 / 27	9 / 17	52.57 / 57.83 / 76.58
	Saxifraga seguieri	16 / 26	19 / 9	3.61 / 6.3	9 / 14 / 19	7 / 9	2 / 4	2.33 / 6.42 / 5.04
	Silene exscapa	382 / 478	108 / 12	1750.68 / 2418.56	236 / 256 / 277	22 / 25	2 / 4	1211.17 / 1368 / 1675.55
	Trisetum spicatum	27 / 79	57 / 5	12.25 / 28.04	18 / 31 / 54	16 / 23	0 / 3	8.8 / 13.11 / 21.03
	Veronica alpina ^{sn}	113 / 235	122 / 0	46.91 / 173.78	63 / 104 / 128	41 / 27	0 / 3	18.39 / 52.24 / 120.54
AR3	*Agrostis alpina*	0 / 2	2 / 0	0 / 0.55	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.35
	Agrostis rupestris	2 / 25	23 / 0	0.85 / 7.57	1 / 4 / 9	4 / 8	1 / 3	0.6 / 0.55 / 2.28
	Antennaria carpatica	3 / 5	3 / 1	1.05 / 2.63	3 / 4 / 2	1 / 0	0 / 2	1.05 / 1.04 / 1.11
	Arenaria biflora ^{sn}	0 / 8	8 / 0	0 / 3.52	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Carex curvula	109 / 122	15 / 2	1985.68 / 1381.13	46 / 49 / 55	4 / 6	1 / 0	752.92 / 558.68 / 483.6
	Cerastium cerastoides ^{sn}	18 / 21	16 / 13	2.38 / 9.7	11 / 19 / 4	10 / 1	2 / 16	1.77 / 2.11 / 0.16
	Cerastium pedunculatum	0 / 1	1 / 0	0 / 0.2	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.2
	Comastoma tenellum ^{an}	0 / 10	10 / 0	0 / 0.3	0 / 0 / 6	0 / 6	0 / 0	0 / 0 / 0.2

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine, sn...snowbed species, an…annual species

Table S1 continued

		Dataset-2s			Dataset-3s			
		Occupied plots	Colonisation / Disappearance	Cover	Occupied plots	Colonisation	Disappearance	Cover
		N	N	Sum (dm²)	N	N	N	Sum (dm²)
Altitudinal Rank	Species	1994 / 2004	1994-2014	1994 / 2014	1994 / 2004 / 2014	1994-2004 / 2004-2014	1994-2004 / 2004-2014	1994 / 2004 / 2014
AR4	*Gentiana brachyphylla*	1 / 3	3 / 1	0.01 / 0.03	1 / 2 / 3	1 / 3	0 / 2	0.01 / 0.12 / 0.03
	Gnaphalium supinum ^{sn}	69 / 227	161 / 3	8.21 / 33.97	29 / 112 / 117	83 / 29	0 / 24	4.16 / 11.26 / 16.61
	Juncus jacquinii	1 / 2	1 / 0	5.5 / 1.4	1 / 2 / 2	1 / 0	0 / 0	5.5 / 3.4 / 1.4
	Minuartia gerardii	75 / 99	41 / 17	30.73 / 35.15	61 / 68 / 70	11 / 16	4 / 14	22.46 / 27.51 / 27.37
	Minuartia sedoides	368 / 456	104 / 16	1033.35 / 1028.88	204 / 234 / 249	31 / 29	1 / 14	566.62 / 520.1 / 561.57
	Oxyria digyna	0 / 8	8 / 0	0 / 1.71	0 / 1 / 0	1 / 0	0 / 1	0 / 0.05 / 0
	Phyteuma hemisphaericum	47 / 59	15 / 3	92.45 / 47.41	7 / 9 / 8	2 / 1	0 / 2	25.15 / 11.55 / 11.1
	Poa alpina	176 / 244	90 / 22	325.49 / 174.01	114 / 127 / 129	18 / 27	4 / 26	230.33 / 221.64 / 95.46
	Primula minima	1 / 4	3 / 0	0.02 / 0.98	1 / 2 / 4	1 / 2	0 / 0	0.02 / 0.25 / 0.98
	Sagina saginoides ^{sn}	40 / 117	90 / 13	7.27 / 11.13	24 / 61 / 46	37 / 13	0 / 28	5.78 / 10.74 / 3.25
	Salix herbacea ^{sn}	7 / 7	0 / 0	17.95 / 13.6	1 / 1 / 1	0 / 0	0 / 0	0.5 / 0.8 / 1.6
	Sedum alpestre ^{sn}	191 / 241	71 / 21	48.89 / 31.27	104 / 132 / 119	29 / 13	1 / 26	33.57 / 23.69 / 13.79
	Senecio carniolicus agg.	20 / 34	16 / 2	4.4 / 4.1	13 / 15 / 22	3 / 7	1 / 0	2.45 / 2.36 / 2.56
	Sibbaldia procumbens ^{sn}	12 / 52	40 / 0	4.83 / 22.57	6 / 12 / 35	6 / 23	0 / 0	3.8 / 8.73 / 14.37
	Veronica bellidioides	25 / 55	34 / 4	23.76 / 58.07	3 / 5 / 10	2 / 5	0 / 0	3.25 / 4.57 / 5.77
	Alchemilla vulgaris agg.	0 / 1	1 / 0	0 / 0.06	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.06
	Antennaria dioica	1 / 0	0 / 1	0.5 / 0	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Anthoxanthum alpinum	0 / 21	21 / 0	0 / 10.24	0 / 1 / 1	1 / 0	0 / 0	0 / 0.4 / 0.25
	Atocion rupestre	0 / 1	1 / 0	0 / 0.07	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Avenula versicolor	18 / 45	29 / 2	48.5 / 118.74	3 / 6 / 6	4 / 2	1 / 2	7.61 / 14.55 / 32.7
	Botrychium lunaria	0 / 1	1 / 0	0 / 0.06	0 / 1 / 1	1 / 0	0 / 0	0 / 0.1 / 0.06
	Campanula barbata	0 / 2	2 / 0	0 / 0.23	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Campanula scheuchzeri	0 / 5	5 / 0	0 / 1.25	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Deschampsia cespitosa	0 / 6	6 / 0	0 / 2.22	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Euphrasia minima ^{an}	71 / 299	232 / 4	24.08 / 90.82	37 / 14 / 166	5 / 153	28 / 1	9.38 / 2.24 / 27.39
	Festuca halleri	1 / 14	13 / 0	0.6 / 11.48	1 / 1 / 6	0 / 5	0 / 0	0.6 / 2 / 7.03
	Festuca violacea	0 / 2	2 / 0	0 / 0.24	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Geum montanum	1 / 2	1 / 0	1 / 2.9	0 / 0 / 1	0 / 0	0 / 0	1 / 1.8 / 2.2
	Homogyne alpina	1 / 3	2 / 0	0.05 / 0.17	0 / 0 / 2	0 / 2	0 / 0	0 / 0 / 0.02
	Lotus corniculatus	0 / 4	4 / 0	0 / 0.4	0 / 0 / 0	0 / 0	0 / 0	0 / 0 / 0
	Persicaria vivipara	17 / 19	3 / 1	30 / 18.06	1 / 1 / 1	0 / 0	0 / 0	3 / 5.5 / 2
	Potentilla aurea	0 / 31	31 / 0	0 / 4.13	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.2
	Potentilla crantzii	0 / 3	3 / 0	0 / 0.28	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.1
	Primula hirsuta	0 / 1	1 / 0	0 / 0.01	0 / 0 / 1	0 / 1	0 / 0	0 / 0 / 0.01
	Ranunculus villarsii	1 / 0	0 / 1	0.15 / 0	1 / 0 / 0	0 / 0	1 / 0	0.15 / 0 / 0
	Scorzoneroides helvetica	4 / 19	15 / 0	1.65 / 4.11	3 / 5 / 10	3 / 6	1 / 1	1.4 / 1.55 / 2.88
	Taraxacum alpinum agg.	0 / 3	3 / 0	0 / 0.4	0 / 2 / 2	2 / 2	0 / 2	0 / 0.6 / 0.37

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine, sn...snowbed species, an…annual species

Table S2 Differences in the number of occupied plots on Schrankogel between 1994 and 2014 (dataset-2s). Only species present in at least 30 plots are considered. Estimate, 95% confidence interval (*CI*) and *p-values* were derived from generalized linear mixed effects models assuming a binomial error distribution with occurrence as response, year as fixed effect and plot nested in transect nested in block as random effect. Significant *p-values* bold. For number of occupied plots per year see Tab. S1

Altitudinal Rank	Species	Linear Hypothesis: 2014-1994=0			
		Estimate	Lower CI	Upper CI	p-value
AR1	*Androsace alpina*	-0.27	-0.58	0.03	0.081
	Cerastium uniflorum	0.07	-0.24	0.38	0.668
	Poa laxa	-3.45	-4.75	-2.15	**0.000**
	Ranunculus glacialis	0.02	-0.34	0.37	0.928
	Saxifraga bryoides	2.68	2.4	2.95	**0.000**
	Saxifraga oppositifolia	0.14	-0.59	0.86	0.712
AR2	*Arenaria ciliata*	2	-0.2	4.19	0.075
	Cardamine resedifolia ^{sn}	9.61	9.6	9.61	**0.000**
	Draba fladnizensis	-0.58	-1.66	0.49	0.288
	Erigeron uniflorus	2.25	1.72	2.78	**0.000**
	Festuca intercedens	1.67	1.22	2.12	**0.000**
	Gentiana bavarica var. *subacaulis*	0.82	0.39	1.25	**0.000**
	Leucanthemopsis alpina	1.89	1.33	2.45	**0.000**
	Linaria alpina	-0.95	-2.36	0.46	0.185
	Luzula spicata	1.24	0.85	1.64	**0.000**
	Oreochloa disticha	1.35	0.91	1.8	**0.000**
	Pedicularis aspleniifolia	11.41	10.78	12.04	**0.000**
	Potentilla frigida	0.66	-0.97	2.29	0.427
	Primula glutinosa	0.49	0.1	0.88	**0.015**
	Saxifraga androsacea	1.14	0.48	1.8	**0.001**
	Saxifraga exarata s.str	1.26	0.85	1.68	**0.000**
	Saxifraga seguieri	2.05	0.58	3.53	**0.006**
	Silene exscapa	1.71	1.25	2.16	**0.000**
	Trisetum spicatum	9.5	7.86	11.15	**0.000**
	Veronica alpina ^{sn}	16.55	14.51	18.59	**0.000**
AR3	*Carex curvula*	2.71	0.75	4.67	**0.007**
	Cerastium cerastoides ^{sn}	0.18	-0.5	0.87	0.600
	Gnaphalium supinum ^{sn}	3.11	2.29	3.94	**0.000**
	Minuartia gerardii	0.75	0.24	1.26	**0.004**
	Minuartia sedoides	1.46	1.05	1.87	**0.000**
	Phyteuma hemisphaericum	1.8	0.47	3.14	**0.008**
	Poa alpina	1.2	0.79	1.61	**0.000**
	Sagina saginoides ^{sn}	1.71	1.2	2.22	**0.000**
	Sedum alpestre ^{sn}	1.06	0.62	1.5	**0.000**
	Senecio carniolicus agg	9.32	6.43	12.21	**0.000**
	Sibbaldia procumbens ^{sn}	16.13	11.18	21.08	**0.000**
	Veronica bellidioides	5.9	2.36	9.45	**0.001**
AR4	*Avenula versicolor*	10.65	8.24	13.06	**0.000**
	Potentilla aurea	6.29	6.26	6.33	**0.000**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine, sn...snowbed species

Table S3 Differences in the number of occupied plots of vascular plant species on Schrankogel in the years 1994, 2004 and 2014 (dataset-3s). Only species present in at least 30 plots are considered. Estimate, 95% confidence interval (*CI*) and *p-values* were derived from generalized linear mixed effects models assuming a binomial error distribution with occurrence as response, year as fixed effect and plot nested in transect nested in block as random effect. Significant *p-values* bold. For details on the number of occupied plots per species in each year see Tab. S1

	Linear Hypothesis:	2004-1994=0			2014-2004=0			2014-1994=0			p-value		
Altitudinal rank	Species	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	1994-2004	2004-2014	1994-2014
AR1	*Androsace alpina*	0.56	-0.03	1.15	-1.20	-1.85	-0.62	-0.70	-1.27	-0.09	0.069	**0.001**	**0.020**
	Cerastium uniflorum	0.37	-0.39	1.13	-1.00	-1.74	-0.22	-0.60	-1.35	0.12	0.497	**0.007**	0.119
	Poa laxa	-0.60	-2.00	0.88	-2.40	-3.92	-0.82	-2.90	-4.55	-1.31	0.633	**0.001**	**0.000**
	Ranunculus glacialis	0.86	0.14	1.59	-0.60	-1.33	0.12	0.25	-0.43	0.94	**0.015**	0.121	0.657
	Saxifraga bryoides	8.09	4.87	11.30	2.43	-0.55	5.41	10.5	6.01	15.00	**0.001**	0.134	**0.001**
	Saxifraga oppositifolia	0.69	-0.71	2.09	-0.20	-1.50	1.18	0.53	-0.88	1.93	0.481	0.956	0.653
AR2	*Arenaria ciliata*	1.55	-0.46	3.56	-0.50	-2.26	1.20	1.01	-0.99	3.01	0.169	0.751	0.459
	Draba fladnizensis	0.39	-0.65	1.42	-0.60	-1.65	0.46	-0.20	-1.28	0.86	0.657	0.386	0.891
	Erigeron uniflorus	1.81	1.10	2.52	0.89	0.23	1.55	2.70	1.89	3.51	**0.001**	**0.004**	**0.001**
	Festuca intercedens	1.08	0.36	1.80	1.31	0.65	1.97	2.39	1.59	3.18	**0.001**	**0.000**	**0.000**
	Gentiana bavarica var. *subacaulis*	1.26	1.26	1.26	0.21	0.20	0.21	1.46	1.46	1.46	**0.000**	0.680	**0.000**
	Leucanthemopsis alpina	1.60	0.82	2.38	0.89	0.06	1.72	2.49	1.58	3.41	**0.001**	**0.032**	**0.001**
	Luzula spicata	0.97	0.25	1.69	0.49	-0.29	1.27	1.46	0.68	2.24	**0.005**	0.306	**0.000**
	Oreochloa disticha	0.85	0.01	1.69	0.68	-0.12	1.49	1.54	0.66	2.41	**0.045**	0.114	**0.000**
	Pedicularis aspleniifolia	6.59	6.59	6.59	8.15	8.15	8.16	14.70	14.74	14.80	**0.000**	**0.000**	**0.000**
	Potentilla frigida	0.62	-1.24	2.49	-0.30	-2.14	1.53	0.32	-1.56	2.20	0.714	0.920	0.916
	Primula glutinosa	0.52	-0.29	1.32	0.17	-0.62	0.97	0.69	-0.12	1.50	0.287	0.867	0.113
	Saxifraga androsacea	2.79	1.02	4.57	-1.10	-2.63	0.37	1.66	-0.04	3.36	**0.001**	0.183	0.057
	Saxifraga exarata s. str.	0.85	0.17	1.54	0.38	-0.27	1.03	1.23	0.53	1.93	**0.010**	0.358	**0.001**
	Silene exscapa	1.10	0.52	1.67	1.40	0.69	2.11	2.50	1.76	3.24	**0.000**	**0.000**	**0.000**
	Trisetum spicatum	11.20	7.27	15.20	10.20	7.48	12.90	21.40	15.78	27.00	**0.000**	**0.000**	**0.000**
	Veronica alpina ^{sn}	3.79	1.42	6.15	2.37	0.88	3.85	6.15	2.81	9.49	**0.001**	**0.001**	**0.001**
AR3	*Carex curvula*	1.37	-1.02	3.76	2.81	-0.29	5.92	4.19	0.73	7.64	0.368	0.086	**0.013**
	Gnaphalium supinum ^{sn}	3.91	2.70	5.11	0.18	-0.44	0.81	4.09	2.86	5.32	**0.000**	0.770	**0.000**
	Minuartia gerardii	0.47	-0.40	1.33	0.12	-0.70	0.95	0.59	-0.27	1.45	0.412	0.934	0.241
	Minuartia sedoides	1.25	0.71	1.80	0.69	0.12	1.26	1.94	1.35	2.54	**0.001**	**0.014**	**0.001**
	Poa alpina	0.59	-0.10	1.28	0.04	-0.63	0.72	0.63	-0.06	1.32	0.111	0.989	0.082
	Sagina saginoides ^{sn}	2.21	1.24	3.18	-0.80	-1.54	0	1.44	0.52	2.36	**0.000**	**0.050**	**0.001**
	Sedum alpestre ^{sn}	1.58	0.72	2.44	-0.70	-1.55	0.07	0.84	0.04	1.65	**0.001**	0.081	**0.038**
	Sibbaldia procumbens ^{sn}	14.90	6.07	23.80	16.70	9.86	23.6	31.60	19.00	44.30	**0.000**	**0.000**	**0.000**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, sn…snowbed species

Table S4 Differences in colonisation events of vascular plant species on Schrankogel between the periods 1994-2004 and 2004-2014 (dataset-3s). Estimate, standard error (*SE*), *z-value*, 95% confidence interval (*CI*) and *p-values* were derived from binomial generalized linear mixed effects models with year as fixed effect and plot nested in transect nested in block as random effect. Only species showing ≥ 10 events in one or both decades were considered. Significant *p-values* bold. For details on number of colonisations per decade see Tab. S1

Altitudinal Rank	Species	Linear Hypothesis: 2004-2014 – 1994-2004=0					
		Estimate	SE	z-value	Lower CI	Upper CI	p-value
AR1	*Androsace alpina*	-0.76	0.33	-2.30	-1.41	-0.11	**0.022**
	Cerastium uniflorum	-0.73	0.41	-1.76	-1.53	0.08	0.078
	Poa laxa	0.83	0.63	1.32	-0.41	2.07	0.188
	Ranunculus glacialis	-0.99	0.38	-2.59	-1.73	-0.24	**0.010**
	Saxifraga bryoides	-0.69	0.46	-1.49	-1.73	0.22	0.137
AR2	*Draba fladnizensis*	-0.21	0.45	-0.45	-1.59	0.69	0.651
	Erigeron uniflorus	-0.24	0.23	-1.07	-0.69	0.20	0.284
	Festuca intercedens	0.87	0.26	3.40	0.37	1.38	**0.001**
	Gentiana bavarica var. *subacaulis*	-0.23	0.31	-0.72	-0.84	0.39	0.470
	Leucanthemopsis alpina	-0.24	0.28	-0.86	-0.80	0.31	0.391
	Luzula spicata	0.13	0.32	0.42	-0.80	0.76	0.676
	Oreochloa disticha	0.27	0.34	0.78	-0.40	0.94	0.434
	Pedicularis aspleniifolia	0.47	0.29	1.63	-0.10	1.05	0.103
	Primula glutinosa	0.40	0.38	1.07	-0.33	1.14	0.284
	Saxifraga androsacea	-0.56	0.43	-1.30	-0.33	0.28	0.193
	Saxifraga exarata s. str.	-0.03	0.27	-0.11	-0.56	0.50	0.909
	Silene exscapa	0.31	0.31	1.01	-0.30	0.92	0.314
	Trisetum spicatum	0.46	0.32	1.42	-0.17	1.09	0.156
	Veronica alpina ^{sn}	-0.07	0.30	-0.23	-0.67	0.53	0.820
AR3	*Carex curvula*	0.41	0.65	0.64	-0.86	1.68	0.523
	Gnaphalium supinum ^{sn}	-0.83	0.24	-3.44	-1.31	-0.36	**0.001**
	Minuartia gerardii	0.48	0.36	1.34	-0.22	1.18	0.179
	Minuartia sedoides	0.09	0.27	0.34	-0.44	0.63	0.730
	Poa alpina	0.59	0.31	1.90	-0.02	1.19	0.057
	Sagina saginoides ^{sn}	-0.83	0.34	-2.41	-1.50	-0.15	**0.016**
	Sedum alpestre ^{sn}	-0.76	0.34	-2.25	-1.42	-0.10	**0.024**
	Sibbaldia procumbens ^{sn}	1.52	0.46	3.32	0.62	2.42	**0.001**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, sn...snowbed species

Table S5 Differences in disappearance events of vascular plant species on Schrankogel between the periods 1994-2004 and 2004-2014 (dataset-3s). Estimate, standard error (*SE*), *z-value*, 95% confidence interval (*CI*) and *p-value* were derived from binomial generalized linear mixed effects models with year as fixed effect and plot nested in transect nested in block as random effect. Only species showing ≥ 10 events in one or both decades were considered. Underlined species were analysed using a negative binomial error distribution. Significant *p-values* bold. For details on number of disappearances per decade see Tab. S1

Altitudinal Rank	Species	Linear Hypothesis: 2004-2014 – 1994-2004=0					
		Estimate	SE	z-value	Lower CI	Upper CI	p-value
AR1	*Androsace alpina*	1.67	0.39	4.23	0.90	2.44	**0.000**
	Cerastium uniflorum	1.23	0.39	3.14	0.46	2.00	**0.002**
	Poa laxa	1.26	0.39	3.22	0.49	2.03	**0.001**
	Ranunculus glacialis	14.35	0	8383.09	14.34	14.35	**0.000**
AR2	*Draba fladnizensis*	1.31	0.77	1.70	-0.20	2.82	0.090
	Erigeron uniflorus	1.12	0.62	1.79	-0.11	2.34	0.074
	Festuca intercedens	2.52	0	812.17	2.52	2.53	**0.000**
	Gentiana bavarica var. *subacaulis*	14.34	0	7224.13	14.33	14.34	**0.000**
	Leucanthemopsis alpina	3.45	2.68	1.29	-1.80	8.69	0.198
	Luzula spicata	1.51	0.53	2.87	0.48	2.54	**0.004**
	Oreochloa disticha	13.70	1.57	8.70	10.62	16.79	**0.000**
	Primula glutinosa	12.97	0	11216.29	12.97	12.97	**0.000**
	Saxifraga exarata s. str.	0.68	0.57	1.21	-0.42	1.79	0.226
AR3	*Gnaphalium supinum* ^{sn}	23.88	0.05	506.00	23.78	23.97	**0.000**
	Minuartia gerardii	1.53	0.67	2.28	0.22	2.85	**0.023**
	Minuartia sedoides	15.41	1.55	9.96	12.38	18.44	**0.000**
	Poa alpina	2.18	0.58	3.77	1.04	3.31	**0.000**
	Sagina saginoides ^{sn}	26.70	0.05	535.70	26.60	26.80	**0.000**
	Sedum alpestre ^{sn}	3.33	1.04	3.19	1.28	5.37	**0.001**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, sn...snowbed species

Table S6 Differences in cover of vascular plant species on Schrankogel in the period 1994-2014 (dataset-2s). Only species present in at least 30 plots are considered. Estimate, 95% confidence interval (*CI*) and *p-values* were derived from generalized linear mixed effects models assuming a beta distribution, using year as fixed effect and plot nested in transect nested in block as random effect. Underlined species were analysed, assuming a negative-binomial distribution. Significant *p-values* bold. For species total cover in each year see Tab. S1

Altitudinal rank	Species	Linear Hypothesis: 2014-1994=0			
		Estimate	Lower CI	Upper CI	p-value
AR1	*Androsace alpina*	-0.48	-0.59	-0.37	**0.000**
	Cerastium uniflorum	-0.59	-0.70	-0.48	**0.000**
	Poa laxa	-0.52	-0.60	-0.43	**0.000**
	Ranunculus glacialis	-0.51	-0.59	-0.44	**0.000**
	Saxifraga bryoides	-0.18	-0.26	-0.10	**0.000**
	Saxifraga oppositifolia	-0.31	-0.43	-0.19	**0.000**
AR2	*Arenaria ciliata*	0.09	-1.24	1.43	0.889
	Cardamine resedifolia ^{sn}	1.05	0.73	1.37	**0.000**
	Draba fladnizensis	-0.01	-0.02	0	**0.009**
	Erigeron uniflorus	0.29	0.19	0.38	**0.000**
	Festuca intercedens	0.31	0.18	0.44	**0.000**
	Gentiana bavarica var. *subacaulis*	-0.55	-0.65	-0.45	**0.000**
	Leucanthemopsis alpina	0.02	-0.05	0.09	0.517
	Linaria alpina	4.71	-1.81	11.22	0.157
	Luzula spicata	0.10	0.02	0.18	**0.015**
	Oreochloa disticha	0.10	0.02	0.18	**0.020**
	Pedicularis aspleniifolia	0.62	0.44	0.81	**0.000**
	Potentilla frigida	-0.08	-0.17	0.02	0.127
	Primula glutinosa	-0.10	-0.17	-0.03	**0.006**
	Saxifraga androsacea	0.06	-0.01	0.13	0.103
	Saxifraga exarata s. str.	0.31	0.18	0.45	**0.000**
	Saxifraga seguieri	0	-0.07	0.06	0.947
	Silene exscapa	0.41	0.33	0.50	**0.000**
	Trisetum spicatum	0.34	0.23	0.45	**0.000**
	Veronica alpina ^{sn}	0.84	0.70	0.97	**0.000**
AR3	*Carex curvula*	-0.39	-0.51	-0.27	**0.000**
	Cerastium cerastoides ^{sn}	0.05	0	0.09	0.053
	Gnaphalium supinum ^{sn}	0.41	0.32	0.50	**0.000**
	Minuartia gerardii	0.07	-0.06	0.20	0.282
	Minuartia sedoides	0.01	-0.08	0.10	0.829
	Phyteuma hemisphaericum	-0.26	-0.46	-0.06	**0.012**
	Poa alpina	-0.52	-0.76	-0.28	**0.000**
	Sagina saginoides ^{sn}	0.18	0.11	0.25	**0.000**
	Sedum alpestre ^{sn}	-0.22	-0.32	-0.12	**0.000**
	Sencecio carniolicus agg.	0.02	-0.02	0.07	0.330
	Sibbaldia procumbens ^{sn}	0.32	0.23	0.41	**0.000**
	Veronica bellidiodes	0.49	0.34	0.60	**0.000**
AR4	*Avenula versicolor*	0.19	0.13	0.24	**0.000**
	Potentilla aurea	0.12	0.08	0.15	**0.000**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine, sn...snowbed species

Table S7 Differences in cover of vascular plant species on Schrankogel between the years 1994, 2004 and 2014 (dataset-3s). Only species present in at least 30 plots were considered. Estimate, 95% confidence interval (*CI*) and *p-values* were derived from generalized linear mixed effects models assuming a beta distribution, using year as fixed effect and plot nested in transect nested in block as random effect. Significant *p-values* bold. For species total cover in each year see Tab. S1

	Linear Hypothesis:	2004-1994=0			2014-2004=0			2014-1994=0			p-value		
Altitudinal rank	Species	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	1994-2004	2004-2014	1994-2014
AR1	*Androsace alpina*	-0.30	-0.41	-0.20	-0.42	-0.85	-0.60	-0.73	-1.26	-0.81	**0.000**	**0.000**	**0.000**
	Cerastium uniflorum	-0.32	-0.41	-0.23	-0.59	-1.02	-0.80	-0.91	-1.44	-1.03	**0.000**	**0.000**	**0.000**
	Poa laxa	-0.17	-0.24	-0.10	-0.65	-0.91	-0.73	-0.82	-1.15	-0.83	**0.000**	**0.000**	**0.000**
	Ranunculus glacialis	-0.15	-0.22	-0.08	-0.39	-0.63	-0.46	-0.54	-0.85	-0.54	**0.000**	**0.000**	**0.000**
	Saxifraga bryoides	-0.13	-0.20	-0.06	-0.27	-0.48	-0.32	-0.40	-0.68	-0.38	**0.001**	**0.000**	**0.000**
	Saxifraga oppositifolia	-0.10	-0.19	0	-0.20	-0.40	-0.19	-0.30	-0.59	-0.20	0.099	**0.001**	**0.000**
AR2	*Arenaria ciliata*	0.07	-0.05	0.19	0.03	-0.02	0.22	0.10	-0.07	0.41	0.498	0.846	0.218
	Draba fladnizensis	-0.06	-0.39	0.26	-0.13	-0.52	0.13	-0.20	-0.91	0.39	0.920	0.699	0.469
	Erigeron uniflorus	0.09	-0.02	0.20	0.06	0.04	0.27	0.15	0.02	0.47	0.258	0.485	**0.025**
	Festuca intercedens	0.29	0.16	0.43	-0.03	0.12	0.40	0.26	0.28	0.83	**0.000**	0.862	**0.001**
	Gentiana bavarica var. *subacaulis*	-0.12	-0.22	-0.03	-0.45	-0.68	-0.46	-0.57	-0.90	-0.49	**0.030**	**0.000**	**0.000**
	Leucanthemopsis alpina	0.09	0.01	0.16	-0.07	-0.06	0.10	0.02	-0.05	0.26	0.059	0.178	0.886
	Luzula spicata	-0.06	-0.14	0.02	0.01	-0.13	0.03	-0.05	-0.27	0.06	0.333	0.975	0.476
	Oreochloa disticha	0.01	-0.05	0.08	0.01	-0.04	0.09	0.02	-0.09	0.17	0.895	0.968	0.772
	Pedicularis aspleniifolia	0.23	0.05	0.41	0.72	0.78	1.12	0.95	0.84	1.53	**0.027**	**0.000**	**0.000**
	Potentilla frigida	-0.08	-0.18	0.02	-0.02	-0.21	0	-0.10	-0.39	0.02	0.283	0.900	0.127
	Primula glutinosa	-0.02	-0.09	0.05	-0.11	-0.21	-0.05	-0.13	-0.30	0	0.821	**0.014**	**0.002**
	Saxifraga androsacea	0.03	-0.04	0.11	-0.06	-0.10	0.05	-0.02	-0.14	0.16	0.648	0.290	0.811
	Saxifraga exarata s. str.	0.14	0.02	0.26	0.14	0.16	0.41	0.28	0.18	0.67	0.063	**0.037**	**0.000**
	Silene exscapa	0.20	0.12	0.28	0.16	0.28	0.45	0.36	0.40	0.73	**0.000**	**0.000**	**0.000**
	Trisetum spicatum	0.14	-0.01	0.30	0.21	0.21	0.50	0.35	0.20	0.80	0.150	**0.011**	**0.000**
	Veronica alpina ^{sn}	0.52	0.37	0.66	0.54	0.91	1.20	1.06	1.29	1.86	**0.000**	**0.000**	**0.000**
AR3	*Carex curvula*	-0.32	-0.41	-0.23	-0.12	-0.54	-0.34	-0.44	-0.95	-0.57	**0.000**	0.060	**0.000**
	Gnaphalium supinum ^{sn}	0.17	0.10	0.24	0.07	0.18	0.31	0.24	0.28	0.55	**0.000**	0.071	**0.000**
	Minuartia gerardii	0.11	-0.02	0.23	-0.07	-0.09	0.16	0.04	-0.10	0.39	0.203	0.531	0.813
	Minuartia sedoides	-0.02	-0.11	0.06	-0.01	-0.12	0.05	-0.03	-0.23	0.11	0.847	0.963	0.713
	Poa alpina	0.04	-0.08	0.16	-0.97	-1.11	-0.75	-0.93	-1.19	-0.58	0.797	**0.000**	**0.000**
	Sagina saginoides ^{sn}	0.19	0.12	0.26	-0.14	-0.02	0.11	0.05	0.10	0.37	**0.000**	**0.000**	0.380
	Sedum alpestre ^{sn}	-0.15	-0.25	-0.06	-0.16	-0.40	-0.21	-0.31	-0.65	-0.28	**0.003**	**0.004**	**0.000**
	Sibbaldia procumbens ^{sn}	0.05	0.02	0.08	0.03	0.05	0.11	0.08	0.08	0.18	**0.001**	**0.034**	**0.000**

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine, sn…snowbed species

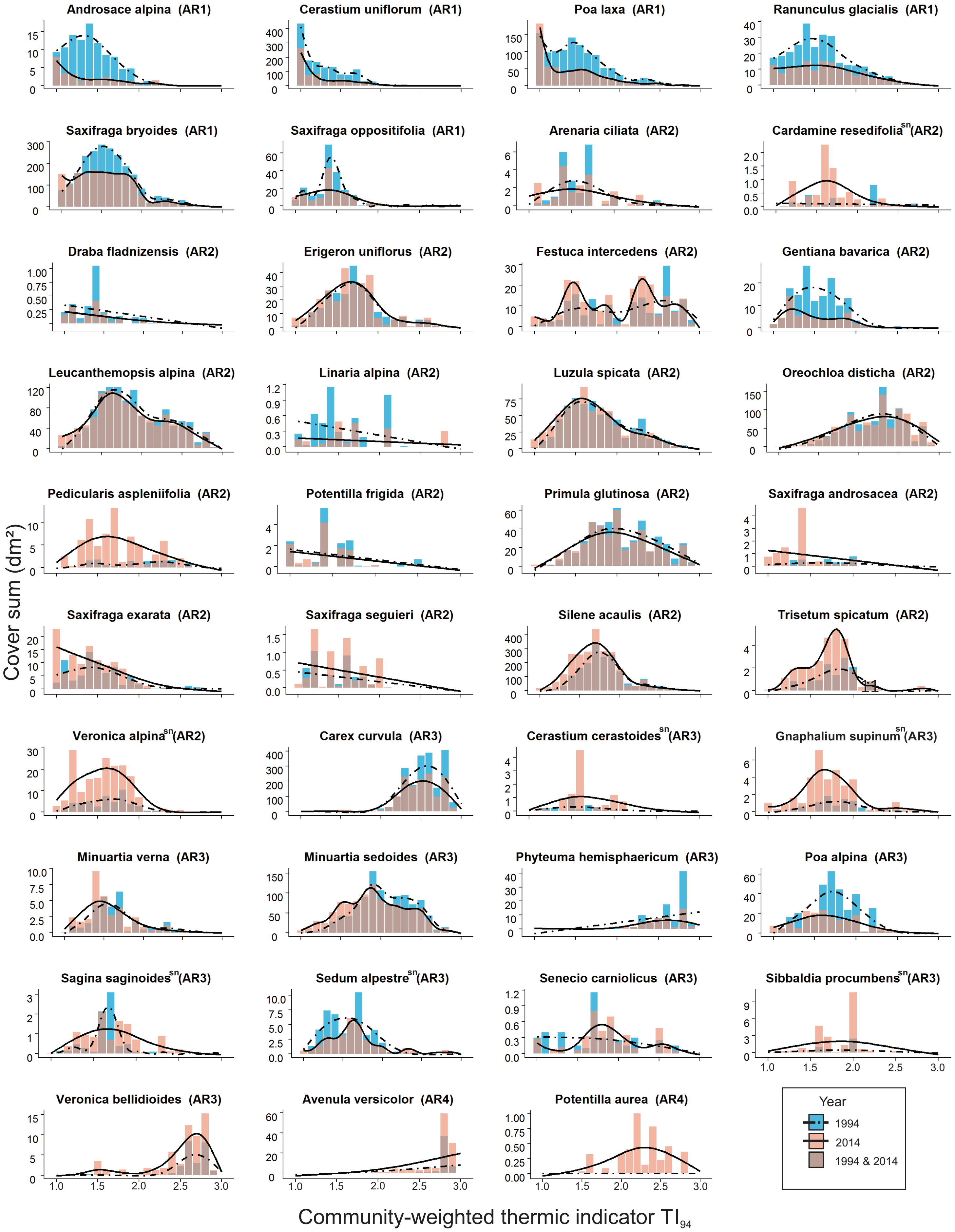

Figure S2 Cover sum of vascular plant species in permanent plots across a thermic indicator gradient (*TI_{94}*) on Schrankogel between 1994 and 2014 (dataset-2s). All permanent plots were grouped following their community-weighted thermic indicator values of the baseline year 1994 (*TI_{94}*). These *TI_{94}*-values ranged between 1.0 (subnival-nival plots) and 3.0 (alpine plots). A generalized additive model was used to fit smooth splines with total cover as response and *TI_{94}* as explanatory variable in each year. Notice differing scales of the y-axis, which might mislead interpretations of species cover. Species arranged in alphabetical order within each altitudinal rank (AR). The AR denotes a species' distribution range along the elevation gradient (after Gottfried et al. 2012). AR1 denotes subnival-nival, AR2 alpine-subnival, Ar3 alpine and AR4 subalpine-alpine species. Snowbed species indicated by sn

Table S8 Differences in cover of vascular plant species in different altitudinal ranks (ARs) across a thermic indicator gradient (TI_{94}) on Schrankogel for the period 1994-2014 (dataset-2s). The AR denotes a species' distribution range along the elevation gradient (after Gottfried et al. 2012). Estimate, standard error (*SE*), *z-value*, 95% confidence interval (*CI*) and *p-value* of the cover per plot of each AR as response and the interaction of the TI_{94} and year as fixed effect were derived from generalized linear mixed effects models. TI_{94} represents the *TI* value of each plot in 1994. Plot nested in transect nested in block was used as first and species as second random effect. Significant *p-values* in bold

Altitudinal Rank		Estimate	SE	z-value	Lower-CI	Upper-CI	p-value
AR1	(Intercept)	-3.91	0.24	11.19	-4.39	-3.43	**0.000**
	TI_{94}	-0.17	0.05	-4.87	-0.27	-0.08	**0.000**
	year2014	0.03	0.09	0.38	-0.16	0.21	0.787
	TI_{94}:year2014	-0.18	0.06	-3.21	-0.29	-0.07	**0.001**
AR2	(Intercept)	-5.89	0.14	-0.06	-6.16	-5.61	**0.000**
	TI_{94}	0.69	0.04	19.80	0.61	0.77	**0.000**
	year2014	0.93	0.08	18.64	0.77	1.08	**0.000**
	TI_{94}:year2014	-0.38	0.04	-13.46	-0.46	-0.29	**0.000**
AR3	(Intercept)	-6.63	0.24	45.41	-7.10	-6.17	**0.000**
	TI_{94}	0.85	0.07	16.00	0.72	0.99	**0.000**
	year2014	0.97	0.11	5.12	0.75	1.19	**0.000**
	TI_{94}:year2014	-0.43	0.06	-4.99	-0.54	-0.32	**0.000**
AR4	(Intercept)	-7.88	0.27	-6.27	-8.42	-7.35	**0.000**
	TI_{94}	0.69	0.10	9.37	0.48	0.89	**0.000**
	year2014	0.45	0.23	9.38	0	0.89	**0.048**
	TI_{94}:year2014	0.04	0.10	-1.95	-0.16	0.24	0.690

AR1…subnival-nival, AR2…alpine-subnival, AR3…alpine, AR4…subalpine-alpine

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7.3 ARTICLE 3:

ANDREA LAMPRECHT, HARALD PAULI, MARIA ROSA FERNÁNDEZ CALZADO, JUAN LORITE, JOAQUÍN MOLERO MESA, KLAUS STEINBAUER & MANUELA WINKLER (2021):

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ORIGINAL ARTICLE

Changes in plant diversity in a water-limited and isolated high-mountain range (Sierra Nevada, Spain)

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Abstract

Climate change impacts are of a particular concern in small mountain ranges, where cold-adapted plant species have their optimum zone in the upper bioclimatic belts. This is commonly the case in Mediterranean mountains, which often harbour high numbers of endemic species, enhancing the risk of biodiversity losses. This study deals with shifts in vascular plant diversity in the upper zones of the Sierra Nevada, Spain, in relation with climatic parameters during the past two decades. We used vegetation data from permanent plots of three surveys of two GLORIA study regions, spanning a period of 18 years (2001–2019); ERA5 temperature and precipitation data; and snow cover durations, derived from on-site soil temperature data. Relationships between diversity patterns and climate factors were analysed using GLMMs. Species richness showed a decline between 2001 and 2008, and increased thereafter. Species cover increased slightly but significantly, although not for endemic species. While endemics underwent cover losses proportional to non-endemics, more widespread shrub species increased. Precipitation tended to increase during the last decade, after a downward trend since 1960. Precipitation was positively related to species richness, colonisation events, and cover, and negatively to disappearance events. Longer snow cover duration and rising temperatures were also related to increasing species numbers, but not to cover changes. The rapid biotic responses of Mediterranean alpine plants indicate a tight synchronisation with climate fluctuations, especially with water availability. Thus, it rather confirms concerns about biodiversity losses, if projections of increasing temperature in combination with decreasing precipitation hold true.

Keywords Alpine plant diversity · Climate change · GLORIA programme · Local endemic species · Mediterranean mountains · Water-limited ecosystem

Introduction

High mountain environments generally reach higher degrees of naturalness and are exposed to fewer direct human impacts than lowlands (Rodríguez-Rodríguez and Bomhard 2012), show high habitat variation over short distances (Scherrer and Körner 2010), but are often strongly fragmented (Antonelli et al. 2018). A number of studies in European mountain ranges found rapid directional shifts in plant species compositions of alpine communities and increasing species numbers in synchrony with rising temperatures (e.g. Gottfried et al. 2012; Pauli et al. 2012; Steinbauer et al. 2018), thus corroborating the expectation of a high sensitivity of mountain floras to climatic changes (Lenoir and Svenning 2015). These local increases in species richness are the result of an upward shift of species' distribution ranges (McCain and Colwell 2011), where their lower range

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margins were reported to move at least at similar velocities as the upper ones in the Eastern Alps (Rumpf et al. 2018). Of particular concern is the situation in small mountain ranges with a limited vertical extent, where suitable cold-enough habitats are expected to rapidly become scarce in the usually cone-shaped mountain topographies. This applies to most of the Mediterranean mountain ranges (Jiménez-Alfaro et al. 2014). Owing to the orographic isolation of their alpine refugia, which were even ice-free during Pleistocene glacial periods (Flantua et al. 2020; Gomez-Ortiz et al. 2013), Mediterranean mountains host an exceptionally high number of cold-adapted endemic plants (Fernández Calzado et al. 2012; Kazakis et al. 2007; Noroozi et al. 2018; Stanisci et al. 2005), and, thus, they are exposed to a high risk of climate change-induced biodiversity loss on the species level. Although observational studies in high-mountain vegetation in the context of climate change are still underrepresented in semi-arid areas (Giménez-Benavides et al. 2018), upward shifts of species including drought-tolerant shrub species were found in Mediterranean mountains by re-visiting historical survey sites (Evangelista et al. 2016).

A prominent example of a small-scaled isolated Mediterranean high-mountain range is the Sierra Nevada of southern Spain, exhibiting the only true alpine region between the North African Atlas mountains, the Sistema Central, and the Pyrenees, all being several hundreds of kilometers away. The Sierra Nevada marks the southernmost limit of the influence of the Quaternary glaciations in Europe, when it was covered with glaciers only in areas above 2500 m a.s.l., while large areas remained free of permanent ice even at higher elevations (Gomez-Ortiz et al. 2013). This has promoted speciation, resulting in the highest level of vascular plant endemism on the Iberian Peninsula (Buira et al. 2020), and probably in Europe (Lorite et al. 2020). For the Sierra Nevada, a mean temperature increase of 4.8 °C at the end of the twenty-first century was simulated, indicating a vertical shift of the suitable habitats for Sierra Nevada key species at a rate of 12 m/year (Benito et al. 2011). If this holds true, extinction events may occur within a few decades, because many of the endemic species are concentrated in the uppermost bioclimatic belts. A pan-European study (including Sierra Nevada) detected widespread thermophilisation of alpine vegetation, i.e. a plant community transformation towards more thermophilous species assemblages, after a period of only seven years (2001–2008; Gottfried et al. 2012). Contrary to temperate and boreal high mountains, a decline in the overall species number per summit was found for all assessed Mediterranean sites (Pauli et al. 2012), suggesting increasing water stress as explanation. For the simple reason that plants are not only constrained by energy input but also by water supply, temperature changes alone will not be sufficient to understand biodiversity changes (Crimmins et al. 2011), especially not in water-limited environments (Cowles et al. 2018). For example, McCain and Colwell (2011) predicted a tenfold increase in extinction risk for vertebrates in mountain areas, when considering combined effects of warming and decrease in precipitation, which also may be relevant for plants as sessile organisms. For the Mediterranean high mountains, a general warming trend coupled with a reduction in the average annual rainfall is projected, resulting in longer periods with drought stress (Nogués Bravo et al. 2008; Sillmann et al. 2013). As a consequence, a higher vulnerability of alpine Mediterranean vegetation is expected through declines in snow cover duration (Beniston 2003), and shifts from snowfall to rainfall (Pérez-Palazón et al. 2018). To assess relationships between plant diversity and the two most vital aspects of climatic changes, we used permanent plot data sets of plant assemblages on Sierra Nevada summits of the international GLORIA monitoring network (Global Observation Research in Alpine Environments; www.gloria.ac.at) with three surveys spanning a total period of 18 years (2001–2019). Combined with continuous measurements of soil temperature at the plot locations and large-scaled temperature and precipitation data, we address the following questions:

Do the previously found patterns (Fernández Calzado and Molero 2013; Pauli et al. 2012) of change in species richness, species gains and losses, and species' abundances constitute ongoing trends?

Have the observed changes been driven by particular growth forms or vertical species distribution types?—i.e., can processes of 'thermophilisation', 'shrubification' and/or loss of endemic species be observed?

Can the observed changes be attributed to either rising temperatures, to water-related factors (precipitation, snow cover duration), or both?

Methods

Site description

The Sierra Nevada is a European and Mediterranean biodiversity hotspot (Blanca et al. 1998; Cañadas et al. 2014) located in southern Spain, extending from 36° 50′ 24″ to 37° 15′ 0″ N in latitude and 3° 44′ 24″ to 2° 35′ 24″ W in longitude. Within its limited surface area of 2100 km^2, it has a complex orography with a wide altitudinal range from 200 to 3482 m a.s.l. (Fig. 1a). The climate is Mediterranean, characterized by cold and wet winters and hot and dry summers (pronounced summer drought in July–August; Gómez 2002). Average temperatures are below 0 °C during winter with a snow cover that can persist up to 8 months in the highest areas (occasionally up to 10 months in small patches of snowbeds). The average annual rainfall is highly irregular,

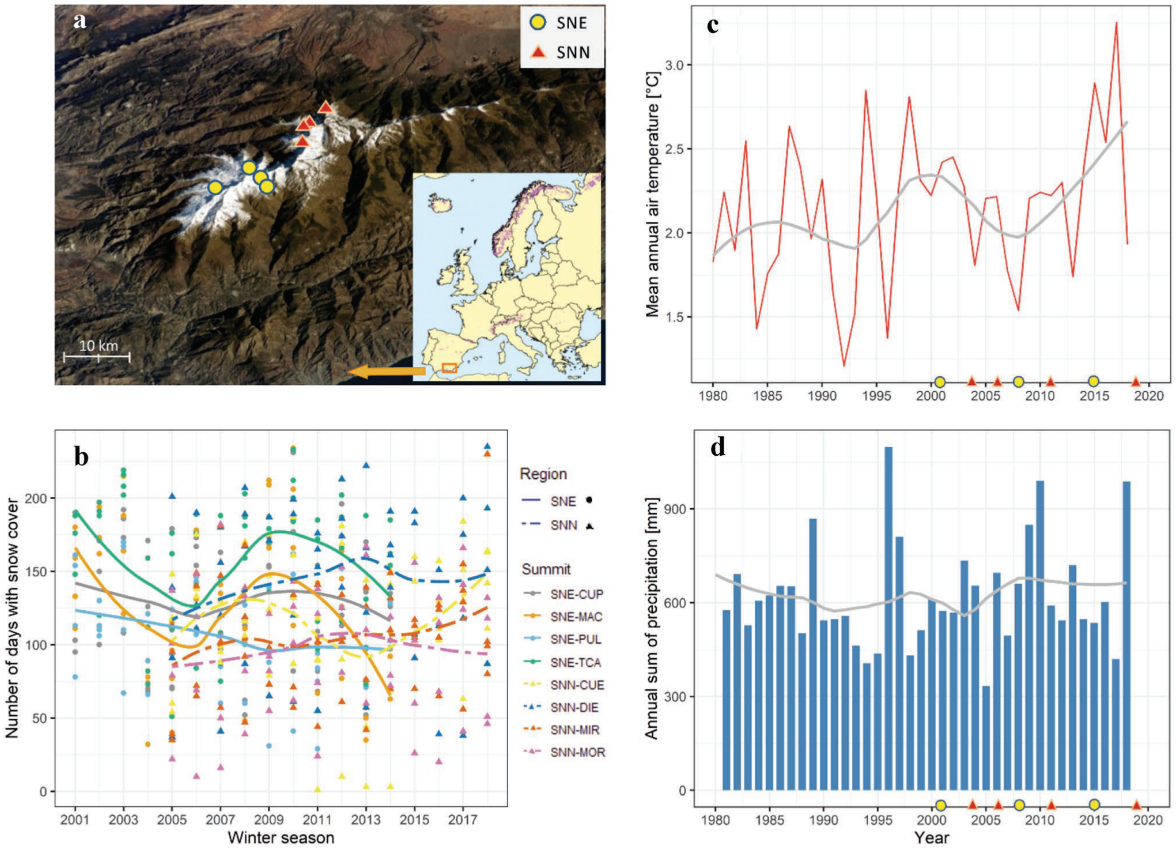

Fig. 1 Location of the GLORIA summits in Sierra Nevada, Spain, and the climatic conditions during the recent decades. **a** Geographic location of eight GLORIA summits of the two study regions Sierra Nevada—West (SNE) and Sierra Nevada—Northeast (SNN). Map source: modified after Esri et al. (2019). **b** Days with snow cover, i.e., days with a maximum of 0.5 °C and a minimum of − 5 °C and a maximum daily difference of 2 °C (after Liberati et al. 2019; Teubner et al. 2015), derived from soil temperature measurements in each cardinal direction on each summit (dots and triangles), as well as the loess local weighted regression (lines). **c** Mean annual air temperature and **d** annual precipitation of the Sierra Nevada, derived from ERA5 data. The grey line represents the 20-year Gaussian low-pass filter smooth trend. On the *x*-axis, vegetation survey years in the two study regions are shown (dots and triangles)

with values ranging between 400 and well over 1000 mm in areas above 2500 m (Polo et al. 2019), depending mostly on elevation and the topographic position. Precipitation is mainly in the form of snow above 2500 m a.s.l. The core area is composed of siliceous rocks, mainly mica-schists, surrounded by limestone and dolomite at lower elevations (Jabaloy et al. 2008).

Site design

The two GLORIA study regions of the Sierra Nevada (SNE: Sierra Nevada—West, SNN: Sierra Nevada—Northeast) include eight summits, arranged along an elevation gradient between 2668 and 3327 m (Fig. 1a, Table 1). On each summit, eight summit area sections (SAS), and four 3 m × 3 m quadrat clusters (in each cardinal direction) were established following the standardized protocol of the GLORIA Multi-Summit approach (Pauli et al. 2015). The presence of vascular plant species was recorded for each SAS and the four corner quadrats of each quadrat cluster (i.e., per summit 16 quadrats of 1 × 1 m). The percentage cover of each vascular plant species was estimated visually only in the quadrats. The summits of SNE were surveyed in 2001, 2008 and 2015, those of SNN in 2004, 2011 and 2019, except summit MIR, where the baseline survey was in 2006.

Climate data

In the centre of each quadrat cluster, a data logger (Onset TidbiT and later GeoPrecision M-Log5W) was buried at 10 cm soil depth, measuring soil temperature at hourly intervals since the setup of the permanent plots. Measurements

Table 1 Number of vascular plant species per summit and survey in the Sierra Nevada, Spain

Region	Summit name	Summit code	Elevation (m)	Number of species in survey 1	2	3
SNE	Pulpitito	PUL	2778	45 (2)	41 (4)	44 (4)
SNE	Cúpula	CUP	2968	51 (1)	47 (2)	51 (1)
SNE	Pico del Tosal Cartujo	TCA	3150	39 (1)	37 (1)	43 (2)
SNE	Cerro de los Machos	MAC	3327	18 (0)	16 (0)	18 (1)
SNN	Monte Rosa	MOR	2668	36 (4)	40 (4)	40 (4)
SNN	Miron	MIR	2717	55 (8)	61 (7)	62 (5)
SNN	Diegisa	DIE	2800	41 (5)	49 (7)	55 (5)
SNN	Cuervo	CUE	3144	20 (5)	23 (5)	27 (5)

Shown are the number of perennial species (annuals in brackets) recorded per summit in the two study regions Sierra Nevada—West (SNE) and Sierra Nevada—Northeast (SNN) for each of three surveys (SNE: 2001, 2008, 2015; SNN: 2004 (2006 on MIR), 2011, 2019)

24 h before and after each logger change were discarded. All temperature values outside the 0.05–99.95 percentile, temperature differences between two subsequent measurements exceeding a threshold of 4 °C and plotted time series were checked for plausibility. Obvious inconsistencies, most likely deriving from logger failure, were excluded. Gaps were imputed based on the measurements of the remaining loggers on the same summit using the function *amelia* (R-package Amelia II; Honaker et al. 2011) which applies an EM (expectation–maximisation)—algorithm on multiple bootstrapped samples of the incomplete original dataset. Imputation of missing values was repeated 30 times. Soil temperature data were used to calculate days with snow cover, i.e., days with a maximum of 0.5 °C and a minimum of − 5 °C and a maximum daily difference of 2 °C (after Teubner et al. 2015).

For longer time series of climate-related indices, we used ERA5 data which provide hourly estimates of air temperature and precipitation on a 30 km grid at different elevation levels (from 1979 to 2019 for the coordinates 37° 2′ 44.988″ N, 3° 21′ 7.9992″ W; https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5). We used temperature at 700 hPa which is equivalent to an elevation of 3000 m a.s.l. ERA5 combines available observation data from satellites and in situ stations, which are assimilated and processed using ECMWF's Integrated Forecast System (IFS) Cycle 41r2. Despite the low spatial resolution of ERA5, the time series patterns are consistent with those of local soil temperatures (Fig. S1).

Analyses were conducted with prior periods of one, five and seven years (i.e., means of mean annual air temperature, annual precipitation and mean number of days with snow cover per year over a given period prior to the vegetation record). For the concept of prior periods, see Gottfried et al. (2011) and Gottfried et al. (2012). Yearly means were calculated from June to May of the following year to incorporate climate factors until the onset of a growing season and, thus, the period immediately preceding a vegetation survey, as well as the entire winter season (e.g., for mean precipitation of a period of five years prior to survey year 2001 ($\mathrm{Prec01}_{p(5)}$) = sums from June 1996 to May 2001 divided by five). The model with the best performance was selected using the Akaike Information Criteria (AIC; Burnham and Anderson 2002).

Vegetation data

All thirteen annual species were removed from the dataset (Table S1, Table 1) because of high inter-annual fluctuation, which can influence the results in a random way. Thirty records identified only to the genus level (3 in SNE and 27 in SNN) were also removed from the data, however, these cases only represented poorly developed individuals with low cover (median = 0.1%) which may well belong to a determined species.

All statistical analyses were performed using R (v. 3.6.1; R Core Team 2019). Generalized linear mixed models were derived using template model builder (R-package glmmTMB; Brooks et al. 2017). Table S2 gives an overview of the statistical models employed, including the response variable, fixed effects, random intercept terms and distribution family.

For the response variables, the appropriate distribution was determined by building a histogram (package lattice; Deepayan 2008) and performing likelihood ratio tests (anova function from stats package; R Core Team 2019) between models using different distribution families. To avoid multicollinearity between predictors, the Variance Inflation Factor (VIF) of the function *corvif* (Zuur et al. 2009) was tested (VIF > 2: concerned predictor was removed). Model assumptions were checked visually by plotting fitted values and residuals of model data (plot function from base; R Core Team 2019) and for small sample sizes additionally with simulated residuals (function simulateResiduals from package DHARMa; Hartig 2019). Correlations between raw data and predicted model data were tested with the function *simulate* (package glmmTMB; Brooks et al. 2017) and visualised with *ggplot*. If required, overdispersion was tested with the functions *check_overdispersion* (package performance; Lüdecke et al. 2020) and *testDispersion* (package DHARMa; Hartig 2019). Significance of the predictor variables' effects of all models was extracted with the function *summary* (R Core Team 2019) and for pairwise comparisons the function *emmeans* was used (package emmeans; Lenth 2019). All graphs were generated with *ggplot* (package tidyverse; Wickham 2017).

Species richness was calculated as the number of species per SAS and survey year. Colonisation events were defined as the number of species per SAS present at the time of the resurvey, which were absent in the respective SAS at the previous survey. Disappearance events were defined as the number of species per SAS absent at the time of the resurvey, which were present at the previous survey. Colonisation and disappearance events per species were treated as Bernoulli trials from a local species pool, i.e., all species ever found on a given summit (1: successful colonisation of a species into a not-occupied SAS or disappearance from an occupied SAS; 0: species not colonised SAS or not disappeared from a SAS).

Species cover sum per quadrat was calculated as the cumulative cover of all species present in a quadrat. Cover per species and quadrat was used for species-specific analyses.

The thermic indicator was calculated after Gottfried et al. (2012) for each quadrat and survey as an averaged composite score of the species-specific altitudinal distribution values (altitudinal ranks (ARs): a proxy for the thermal preferences of species and their distribution along the elevation gradients after Gottfried et al. (2012) and expert judgment of authors for new species), weighted by the cover of the respective species.

Species characteristics were used according to expert judgment of authors: growth form (gr: graminoid; he: forb-hemicryptophyte; cu: cushion; sh: shrub (including dwarf-shrubs and matorral species); su: succulent), and according to Lorite et al. (2020): endemic restricted to Sierra Nevada (yes/no), spinescence (yes/no) and hygrophilous (yes/no). For the change of the proportional cover sums per species group (shrubs, spiny, endemic), the proportional cover sums per quadrat c within an interval of zero and one were compressed to avoid zeros and ones after Smithson and Verkuilen (2006) by $c' = \frac{c \times (n-1) + 0.5}{n}$, where n is the number of observations.

To investigate the effects of climatic drivers, the average vegetation change per year (i.e., divided by the number of years between the respective surveys) was related to the change of climatic factors in the prior periods (e.g., for change of precipitation from 2001 to 2008 ($\Delta \mathrm{Prec08}_{p(5)} = \mathrm{Prec08}_{p(5)} - \mathrm{Prec01}_{p(5)}$).

Results

Climate data

Snow cover duration on study summits changed considerable, most pronounced on the two higher summits of the SNE with a strong decrease between 2001 and 2006 followed by an increase until around 2010 and again decrease thereafter (Fig. 1b). The highest summit of SNN fitted into this pattern, and showed an increase again after 2013. All lower summits showed less pronounced changes in snow cover duration. Annual precipitation varied between ~ 350 and 1100 mm over the past forty years, with a peak in 1996 followed by years with lower values, and further peaks in 2010 and 2018 (Fig. 1d). Mean annual air temperature ranged from ~ 1.2 to ~ 3.25 °C (Fig. 1c). The years prior to the baseline survey showed stronger inter-annual fluctuation than in the following years, but a maximum in 2018.

Vegetation changes with time and space

The total number of species in Sierra Nevada—West (SNE) dropped from 76 in 2001 to 71 species in 2008 and increased to 75 in 2015. In Sierra Nevada—Northeast (SNN), the total number of species increased from 67 species in the first survey (2004, 2006) to 73 in 2011 and to 77 in 2019. For numbers of species per summit and survey, see Table 1; for species' presence/absence over all SASs per study region, see Table S1. In total, 13 woody plant species occurred on the summits (shrubs in Table S1). Neophytes did not occur on nor colonised the summits.

In the study region SNE, mean species richness per SAS decreased significantly on three of the four summits and overall from 2001 to 2008, and increased significantly between 2008 and 2015 on all four summits. In SNN, the study region and its individual summits (except MIR) showed significant increases in mean species richness over the entire observation period, but the increase over the periods 2004–2011 and 2011–2019 was only significant on DIE (Fig. 2a, b, Tables S3a, S4a). Over all eight summits, the species richness per SAS increased slightly but significantly by 0.01 species per year (GLMM, $p = 0.006$, Table S5a). Irrespective of time, species richness decreased significantly by 0.2 species per 100 m of altitudinal gain (GLMM, $p < 0.0001$, Table S5a) over the eight summits. They showed, however, no significant differences between the upper and the lower sections of a summit (i.e. the SASs 0–5 m versus

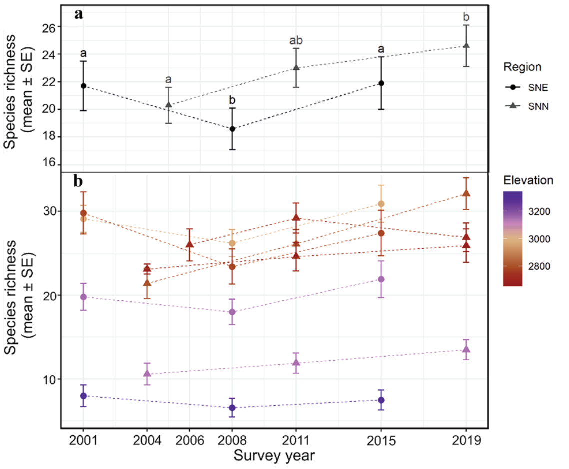

Fig. 2 Vascular plant species richness on GLORIA summits in the Sierra Nevada, Spain. Mean richness (± standard error SE) per **a** study region (SNE: Sierra Nevada—West and SNN: Sierra Nevada—Northeast), each including four summits consisting of eight summit area sections, respectively, and **b** per summit. Summit elevation (m) is colour-coded. Different lowercase letters in (**a**) denote significant differences between the survey years within a study region based on generalised mixed-effects models (glmmTMB; Brooks et al. 2017). In SNN the first survey took place in 2004 and 2006 and was therefore set to the year in-between (2005) in (**a**). For further details see Tables S3a, S4a and S5a

5–10 m below the highest summit point, Table S5a), nor between the aspects (N, E, S, W; Tables S5a, S6a).

The mean number of colonisation events per SAS increased significantly on each of the four summits in SNE from the first to the second period. In SNN, colonisations remained constant, except on summit MIR, which showed a significant decrease from the first to the second period (Fig. 3a, b, Tables S3b, S7a). Over all eight summits, colonisations per SAS decreased significantly with increasing elevation with − 0.14 species per 100 m of altitudinal gain (GLMM, $p = 0.042$), but did not change over the entire timespan (2001–2019), aspects or position of SAS (Tables S5b, S6b).

The mean number of disappearance events per SAS decreased significantly from the first to the second period on three summits in SNE (except on the highest summit MAC with the lowest number of disappearances in both periods) and in the whole study region. In SNN, there was no change in disappearances from the first to the second period (Fig. 3c, d, Tables S3c, S7b). Over all eight summits, disappearances per SAS decreased significantly with increasing elevation with -0.15 species per 100 m of altitudinal gain (GLMM, $p = 0.042$), but did not change over the entire timespan (2001–2019), aspects or position of SAS (Tables S5c, S6c).

The mean species cover sum per quadrat in SNE was 11.89 dm^2 in 2001, 10.01 dm^2 in 2008, and increased

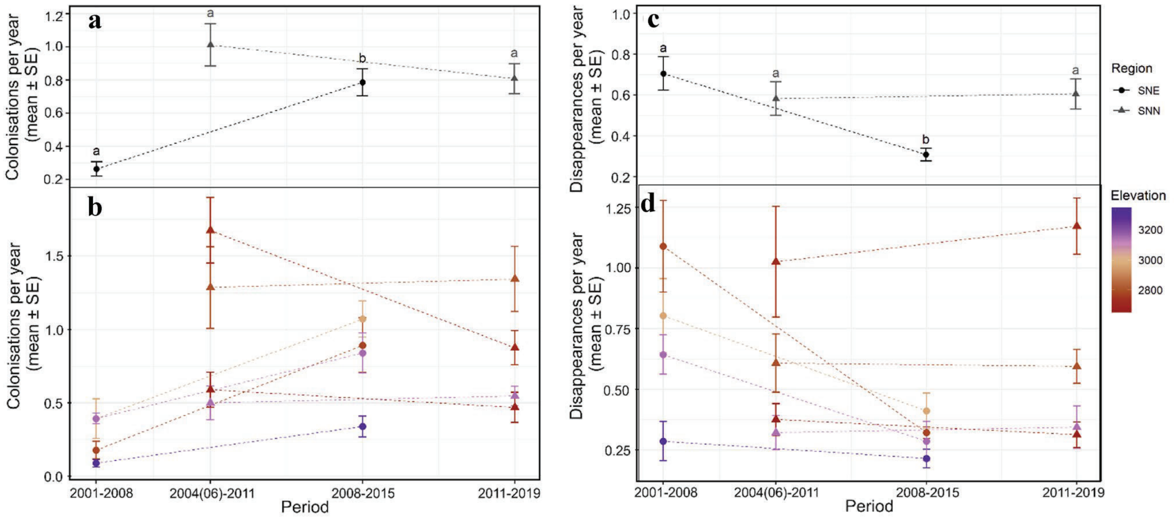

Fig. 3 Colonisation and disappearance events of vascular plant species on the GLORIA summits in the Sierra Nevada, Spain. Mean values (± standard error SE) of (**a**, **b**) colonisation and (**c**, **d**) disappearance events per year for each (**a**, **c**) study region (SNE: Sierra Nevada—West and SNN: Sierra Nevada—Northeast) and (**b**, **d**) summit, calculated over eight summit area sections per summit of the four summits per study region. The number of colonisation and disappearance events is calculated for each period between subsequent surveys, and divided by the number of years between surveys to account for different lengths of periods. Summit elevation (m) is colour-coded. Different lowercase letters in (**a**) and (**c**) denote significant differences between the periods within a study region, based on generalised mixed-effects models (glmmTMB; Brooks et al. 2017). For further details see Tables S3b, c, S5b, c, and S7

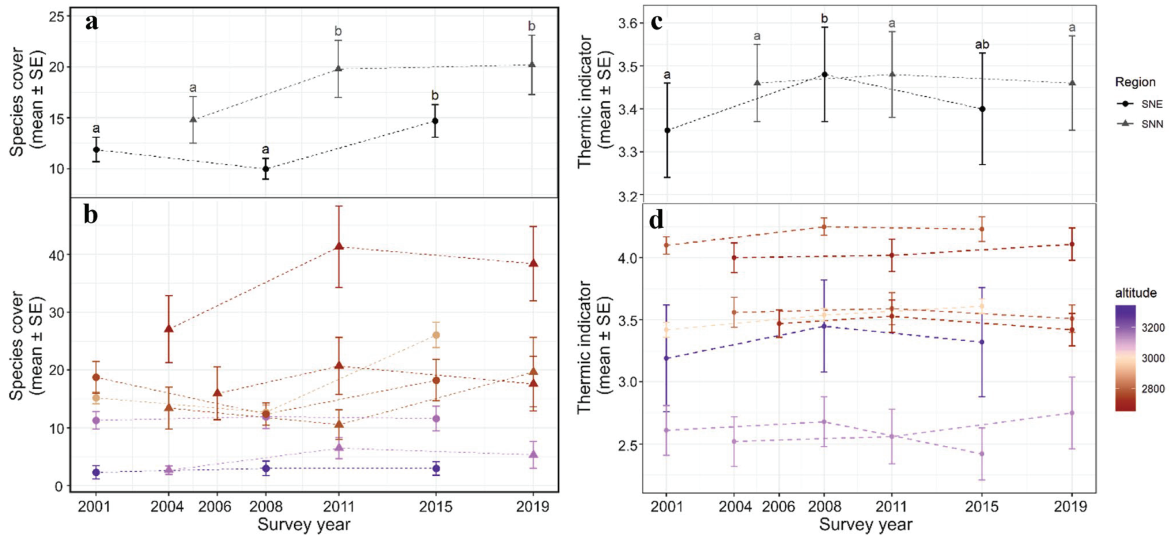

Fig. 4 Vascular plant cover and thermic indicator on GLORIA summits in the Sierra Nevada, Spain. Mean (±standard error SE) of (**a**, **b**) cover sums (dm^2) and (**c**, **d**) thermic indicator (Gottfried et al. 2012) for each (**a**, **c**) study region (SNE: Sierra Nevada—West and SNN: Sierra Nevada—Northeast) and (**b**, **d**) summit, calculated over 64.1 m × 1 m quadrats per study region (16 per summit). Summit elevation (m) is colour-coded. Different lowercase letters in (**a**) and (**c**) denote significant differences between the survey years within a study region, based on generalised mixed-effects models (glmmTMB; Brooks et al. 2017). In SNN the first survey took place in 2004 and 2006 and was therefore set to the year in-between (2005) in (**a**) and (**c**). For details see Tables S3d, e and S4b, c

significantly to 14.73 dm^2 in 2015. In SNN, the mean species cover sum per quadrat increased significantly from 14.79 dm^2 at the first survey (2004, 2006) to 19.78 dm^2 in 2011, and to 20.25 dm^2 in 2019 (Fig. 4a, b, Tables S3d, S4b). Over all eight summits, the mean species cover sum per quadrat increased slightly but significantly with 0.02 dm^2 per year (GLMM, $p < 0.0001$, Table S8a). Along the elevation gradient, the mean species cover sum per quadrat decreased significantly with 0.4 dm^2 per 100 m of altitudinal gain (GLMM, $p < 0.001$, Table S8a), without significant differences among aspects (Table S6d).

The thermic indicator per quadrat in SNE increased significantly from 2001 to 2008. In 2015, the thermic indicator was intermediate between the values of the two preceding surveys. In SNN, the thermic indicator per quadrat remained constant over all surveys (Fig. 4c, d, Tables S3e, S4c). Along the elevation gradient over all eight summits, the thermic indicator decreased significantly with − 0.18 per 100 m of altitudinal gain (GLMM, $p < 0.001$, Table S8b). The thermic indicator did not change among the aspects (Table S6e) and not over time (2001–2019; Table S8b).

Species groups

Forb-hemicryptophytes represented the highest number of species in each survey, followed by graminoids and shrubs (Table S1, Fig. S2a). The number of colonisations of shrub species was not different to other growth forms (Table S9a), whereas the number of disappearances of shrub species was significantly lower than that of hemicryptophytes (Table S9b). Shrubs had the highest total cover in all surveys, followed by graminoids and hemicryptophytes (Table S1, Fig. S2b). The average cover of shrub species was significantly higher than the cover of other growth forms (Table S9c) and increased slightly but significantly with 0.02 dm^2 per quadrat and year (GLMM, $p = 0.002$). The proportion of shrub species of the total cover sum increased marginally significantly with 1.6% per year (GLMM, $p = 0.064$).

Twelve species out of the species pool of 103 species were spiny. Spiny species colonised (Table S9a) and disappeared (Table S9b) significantly less often than non-spiny ones, but, over time, their cover significantly exceeded that of non-spiny species (Table S9c). The significant increase of the cover of spiny species was 0.03 dm^2 per quadrat and year (GLMM, $p < 0.001$). However, the proportion of spiny species of the total cover sum did not change significantly (GLMM, + 1% per year, $p = 0.203$).

In total, 40 Sierra Nevada endemics and 63 non-endemic species occurred on the summits. In SNE, the mean cover of endemic species per quadrat decreased from 5.1 dm^2 in 2001 to 4.3 dm^2 in 2008 and increased to 5.6 dm^2 in 2015. In SNN, the mean cover of endemic species per quadrat increased from 3.0 to 4.4 dm^2 in 2011, and decreased slightly to 4.0 dm^2 in 2019 (Table S1, Fig. S3). Over all eight summits, there were significantly more disappearance events of endemic species than of non-endemic species (Table S9b), but no difference in the number of colonisations (Table S9a), nor in species cover (Table S9c). The cover of endemics did not change over the entire time span (GLMM, 0.005, $p=0.24$). However, the proportion of endemic species of the total cover sum decreased significantly by 2.4% per year (GLMM, $p=0.002$).

Nine out of 103 species were hygrophilous. There were no differences in colonisations, disappearances and cover between hygrophilous/non-hygrophilous species (Table S9).

Relationship with climatic factors

In all cases, models using a 5-year or a 7-year period prior to the surveys had the lowest AIC (Table S10).

Rising mean annual air temperatures between the periods prior to the surveys were highly positively related to changes in species richness (GLMM, estimate = 0.88, $p < 0.0001$), but there was no significant relationship with colonisation, disappearance or changes in cover sums (Table S10).

Increasing mean annual precipitation sums between the periods prior to the surveys were highly significantly and positively related to changes in species richness (GLMM, estimate = 0.005, $p < 0.0001$), colonisations (GLMM, estimate = 0.003, $p < 0.0001$), and changes in cover sums (GLMM, estimate = 0.005; $p < 0.0001$), and negatively with disappearances, i.e. increasing precipitation led to a decrease in species losses (GLMM, estimate = − 0.002, $p < 0.0001$; Table S10).

An increasing number of days with snow cover per year of the periods prior to the surveys were positively related to changes in species richness (GLMM, estimate = 0.005, $p = 0.001$), and colonisations of species (GLMM, estimate = 0.003, $p < 0.0001$). Changes in disappearances and in cover sums of species did not show significant relationship with increasing snow cover duration (Table S10).

Discussion

Contrary to previous findings (Fernández Calzado and Molero 2013; Pauli et al. 2012), we found an increase in vascular plant species richness and vegetation cover on alpine summits of the Sierra Nevada in Spain. Generally, in European mountain systems, rising species numbers were found far more often than decreasing ones. Repeated surveys of historical vascular plant species inventories on alpine to subnival summits of temperate, boreal and arctic Europe even showed an acceleration of increase in species richness during the last decades in synchrony with rapid warming (Steinbauer et al. 2018). Increases in species numbers were mainly attributed to upward range shifts of species, which were found to be greatest where the highest levels of warming were observed in a global study across different organism groups (Chen et al. 2011). Upward species shifts as response to climate warming were also reported for Mediterranean alpine grassland communities in Sierra de Guadarrama, Spain, resulting in a general increase in species richness (historical surveys from 1962, 1977 and 1983 resurveyed in 2012; Jiménez-Alfaro et al. 2014). However, on Mediterranean summits of Europe (including Sierra Nevada), species numbers decreased from 2001 to 2008. Combined effects of warming and a reduction in precipitation in Mediterranean areas were hypothesized to be the main drivers of species losses (Fernández Calzado and Molero 2013; Pauli et al. 2012). Our study shows not only an increase in species richness after 2008, but a significant relationship between increasing species richness and rising temperatures, increasing precipitation, and more days with snow cover. Previous studies suggested that temperature alone is insufficient to explain diversity changes in a water-limited environment (Crimmins et al. 2011). For instance, consistent and negative relationships between drought stress and species richness (Giménez-Benavides et al. 2007; Walck et al. 2011), and positive effects of snow cover duration (Niittynen et al. 2018; Wipf and Rixen 2010) have been reported. After a general downward trend of precipitation during the second half of the twentieth century (Sinoga et al. 2011), precipitation tended to rise in the Sierra Nevada during the last decade according to ERA5 data used in this study. However, this has to be treated with caution, because (1) the rather coarse resolution of our precipitation data must be taken into account, (2) we could not evaluate the actual increase in precipitation with local data because the available high-elevation station data showed gaps, measuring errors or did not cover the recent years, and (3) a considerable inter-annual variability of precipitation patterns has been reported (Norrant and Douguedroit 2006; Polo et al. 2019). Published time series do not extend to 2019, however, data in Polo et al. (2019) at least indicate a precipitation increase between the two survey periods of SNE (2001–2008 and 2008–2015). As an additional measure of water availability, we used the number of days with snow cover, derived from temperature loggers, positioned at our plots. Both, coarse precipitation data and the duration of snow cover, clearly indicate a significant positive relationship between species numbers and water supply in the Sierra Nevada.

Colonisation and disappearance events

Increasing number of colonisation events, combined with a decreasing number of disappearances were found more often on the lower summits. The lower alpine belt of Sierra Nevada is populated by more species (Fernández Calzado et al. 2012) and thus the species pool for upwards migration is larger, similar to the situation in other European mountains (Bruun et al. 2006; Vittoz et al. 2010). Colonisation showed a highly significant positive relation to the variables for water supply: precipitation and duration of snow cover. While longer growing seasons were suggested as one of the main factors for higher community productivity and associated species distribution changes under climate change, and at the same time implicate an increased risk of frost damage (Bueno de Mesquita et al. 2020; Wipf and Rixen 2010), a higher snowpack generates an increased water supply during the vegetation period, which is especially relevant in water-limited environments. Seed dormancy, germination and establishment are mainly driven by temperature and water supply (Bernareggi et al. 2016; Walck et al. 2011), so that in water-limited environments climate change may have an immediate effect on seedling success, in addition to a higher probability of a reduced reproductive success (Giménez-Benavides et al. 2018). The high seedling mortality due to summer drought is considered a primary constraint for recruitment in Mediterranean mountains (Cavieres et al. 2005; Giménez-Benavides et al. 2018). In turn, Crimmins et al. (2011) documented a significant downward shift in the optimum elevation of mountain plants in Mediterranean California, following increasing water availability that outpaces evaporative demands. In line with this, species colonisation on our summits in Sierra Nevada could represent horizontal shifts from microrefugia (Scherrer and Körner 2010) in response to ameliorating climatic water-deficit. Besides, colonisations could also result from upper range shifts of lower-elevation species (Jiménez-Alfaro et al. 2014; Rumpf et al. 2019).

Species disappearances were highly significantly negatively related to an increasing amount of precipitation, i.e., the number of disappearances decreased with increasing precipitation. However, disappearance events were not related to changes in temperature or days with snow cover. Disappearance events in high-mountain areas can indicate retracting lower range margins, as expected through warming-driven range shifts (Giménez-Benavides et al. 2018; Ugarte et al. 2019) or competitive displacements (Lenoir and Svenning 2015). Rumpf et al. (2018) reported from the Alps that the trailing lower margins of species ranges are contracting at least as rapidly as the leading edges are expanding towards higher elevations. In the central Alps, cold-adapted species, being restricted to the high-elevation zones, have experienced strong losses in cover in the lower part of their distribution range (Lamprecht et al. 2018; Steinbauer et al. 2020). In the Sierra Nevada, endemic species disappeared significantly more often than more widespread species. The majority of the Sierra Nevada endemics almost exclusively occurs in the upper vegetation belts (Fernández Calzado et al. 2012) and thus most of them are low-temperature specialist species. The relative contributions of different processes leading to disappearances were probably different in the climatically contrasting mountains of the Alps and the Sierra Nevada, even though apparently driven by climatic changes in both. Water supply, however, is confirmed to be a crucial component for the survival or disappearance of species in periods of drought.

Changes in cover and community-weighted thermic indicator

A thermophilisation of alpine vegetation, i.e. an increase of the ratio of warmth-demanding to cold-adapted species, was detected on the SNE summits only during the first seven-year period (2001–2008; Gottfried et al. 2012), accompanied by an insignificant decrease in the mean total species cover. Similar to the situation in the central Alps, where accelerating thermophilisation occurred with progressing losses of vegetation cover over a 20-year period (Lamprecht et al. 2018), thermophilisation in Sierra Nevada resulted from slightly stronger losses of cold-adapted than gains of warmth-demanding species. In the high central Alps, however, this was far more pronounced with strong and consistent losses of all subnival–nival species (Steinbauer et al. 2020). Periods without signals of thermophilisation (2004/2006–2011 in SNN; 2008–2015 in SNE), in contrast, showed increases of total species cover. Species cover did not show a relation to temperature, which generally was rising in the Sierra Nevada (Pérez-Luque et al. 2016), but a significant positive relationship with increasing annual precipitation. This would indicate a high sensitivity of plant growth to changes of water availability, however, an increase of days with snow cover was not related with an increase in species cover. Impacts of different snow cover durations are only little studied in Mediterranean mountain environments, but positive effects of meltwater on plant growth can hardly be negated (Giménez-Benavides et al. 2018; Ugarte et al. 2019). In temperate and boreal mountains, an earlier snowmelt extends the humid growing season, whereas in Mediterranean mountains, it would expand the dry summer period and thus the period of potential drought stress. Besides, positive effects of an extended growing season are hypothesised to be counteracted by the detrimental effects of an increasing frequency and intensity of frost (Choler 2018; Klein et al. 2018).

Changes in endemic species and shrubification

The cover of endemic species did not change over time, however, the proportion of endemics of the total cover sum decreased significantly by 2.4% per year. This is in line with declines in endemic dry alpine grassland specialists in alpine vegetation assemblages of central Spain, where also an ongoing colonisation of shrubs into alpine areas was found (Jiménez-Alfaro et al. 2014). Similarly, we found not only a continued increase in shrub cover, but also an increase of their proportion of the total cover sum. This increase of either locally common but endemic shrub species dominating the vegetation zone between the treeline and high-mountain dry grasslands (i.e., *Cytisus galianoi, Genista versicolor, Thymus serpylloides* subsp. s*erpylloides*), or generally widespread shrub species (i.e., *Hormathophylla spinosa, Juniperus sabina*) indicates a consistent expansion of their upper distribution ranges to higher vegetation zones (cf. Fernández Calzado and Molero 2013), leading to a 'shrubification' of high-elevation habitats of the Sierra Nevada. Shrub advances are known from the alpine belt of the central Apennines and the southwestern Alps (Stanisci et al. 2014). Unfortunately, studies on changes in the abundance of high-mountain species are far rarer than on species numbers, and even more underrepresented in Mediterranean ecosystems (Giménez-Benavides et al. 2018), which is particularly unfortunate, since Mediterranean high-mountain regions host many locally endemic and at the same time cold-adapted species (Blanca et al. 1998; Pauli et al. 2012). The vulnerability of these species through climate warming increases with the growing risk of summer drought, caused by the rise in average summer air temperature and a reduction in annual rainfall (Nogués Bravo et al. 2008).

Land use changes

Change in land use, including reductions in livestock density or abandonment, which may have significant effects on the performance of high-mountain plants, is unlikely as an explanation for the current observed vegetation changes. While livestock grazing in Sierra Nevada, based on traditionally established rights and thus tolerated even in the core zone of the national park, tends to be more relevant in lower areas and in depressions with snowbed vegetation and shows slight declining tendencies (National park staff personal communication), the population of wild ungulates (in particular Iberian ibex, *Capra pyrenaica hispanica*) increased tenfold between 1960 and 2012, but individual numbers are considered to be more or less stable over the last twenty years (Granados et al. 2020). This may imply an overall pressure on the vegetation, yet, less so for spiny species, such as abundantly occurring *Hormathophylla spinosa*, *Arenaria pungens* and *Festuca indigesta*, having xeromorphic leafs with spiny stems or tips. Indeed, over time the cover sum of spiny species increased more than the cover sum of non-spiny species and they disappeared significant less than non-spiny species. We therefore cannot exclude any interference through ibexes, but positive trends also of the non-spiny species during the supposedly less dry periods, as well as stable numbers of ungulates over the last twenty years, suggests, that the influence was not a dominant factor. By the way, there were no obvious impacts of ibex grazing discernible in the plots. Tourism was also rapidly growing, with the number of visitors tripled since the establishing of the national park in 1999 (MITECO 2020). However, trampling is expected to reduce cover of most species and only may promote some trampling-resistant graminoids (Barros and Pickering 2015). A new phenomenon of touristic donkey or horse riding in the national park is noticed with concern, as this activity not only damages alpine vegetation, but also supports eutrophication of high-mountain areas as well as the dispersal of low-land plant seeds (Barros et al. 2020); for example, *Urtica dioica* grows on the summit of Mulhacén, the highest peak of the Sierra Nevada (pers. obs. Lamprecht and Pauli 2016). However, the GLORIA summits are less attractive secondary peaks situated off the main riding trails.

Limitations

Limitations of the datasets and results discussed above are mainly associated with the poor availability of local climate data, in particular indicators for water supply. This study therefore had to be based on rather large-scaled climate data, thus, we must be cautious with interpretations of the underlying mechanisms behind the observed plant diversity changes. New well-managed weather stations in the higher areas are required for a better understanding of the impacts of both temperature and precipitation, as suggested by Pérez-Palazón et al. (2018). Further, investigations in stress physiology of alpine plant species, using experimental studies (e.g., warming manipulation and irrigation; Pugnaire et al. 2020) or biotic proxies, such as dendrochronology (e.g., Juniperus sabina; García-Cervigón Morales et al. 2012), would help to assess and interprete vegetation changes in relation to key climate components.

Conclusion

Plant species composition and diversity on Sierra Nevada summits are strongly influenced by climate change, where both warming and water supply are crucial components for understanding and predicting biodiversity losses and gains. Between 2001 and 2008, the retreat of low-temperature specialist species, which are to a great proportion Sierra Nevada endemic, was rapidly leading to a thermophilisation of the summit vegetation. Vice versa, in periods with more precipitation, vegetation seems to 'recover', since it increased in cover, but to the disadvantage of the endemics. For the twenty-first century, not only a pronounced warming is projected (Pérez-Palazón et al. 2018), but also a severe decrease in mean precipitation and an increase in interannual variability for most Mediterranean regions (Nogués Bravo et al.

2008). Giorgi (2006) considered the Mediterranean region to be the largest 'climate change hot-spot' in the world. If these climate projections come true, our results suggest that detrimental effects on this water-limited high-mountain flora of the Sierra Nevada are to be expected. Linked to that, Mediterranean ecosystems are among the 'hyper-hot candidates' for conservation support (Myers et al. 2000). In this context, continued vegetation monitoring and in situ climate measurements are of high priority for an effective evaluation of the status of ecosystems and their biodiversity, of changing processes and their relevance for conservation. Rapid responses of Mediterranean alpine species indicate a tight synchronisation with climate changes, notably with water availability, which reinfores concerns of endemic biodiveristy losses in the view of regional climate projections.

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Author contributions MRFC, JL and JMM conducted the field work. AL prepared vegetation and temperature data, did the analyses and prepared the manuscript. HP and MW supervised the manuscript preparation, MW the analyses. KS provided statistical advice. All authors contributed to the text of the manuscript.

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Data availability Supplementary material is appended and data and codes can be obtained from the authors on request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Field work was conducted in a non-destructive way. No plants were collected for this study.

Informed consent Informed consent was obtained from all individual participants included in the study.

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Alpine Botany **Supplementary Material**

Changes in plant diversity in a water-limited and isolated high-mountain range (Sierra Nevada, Spain)

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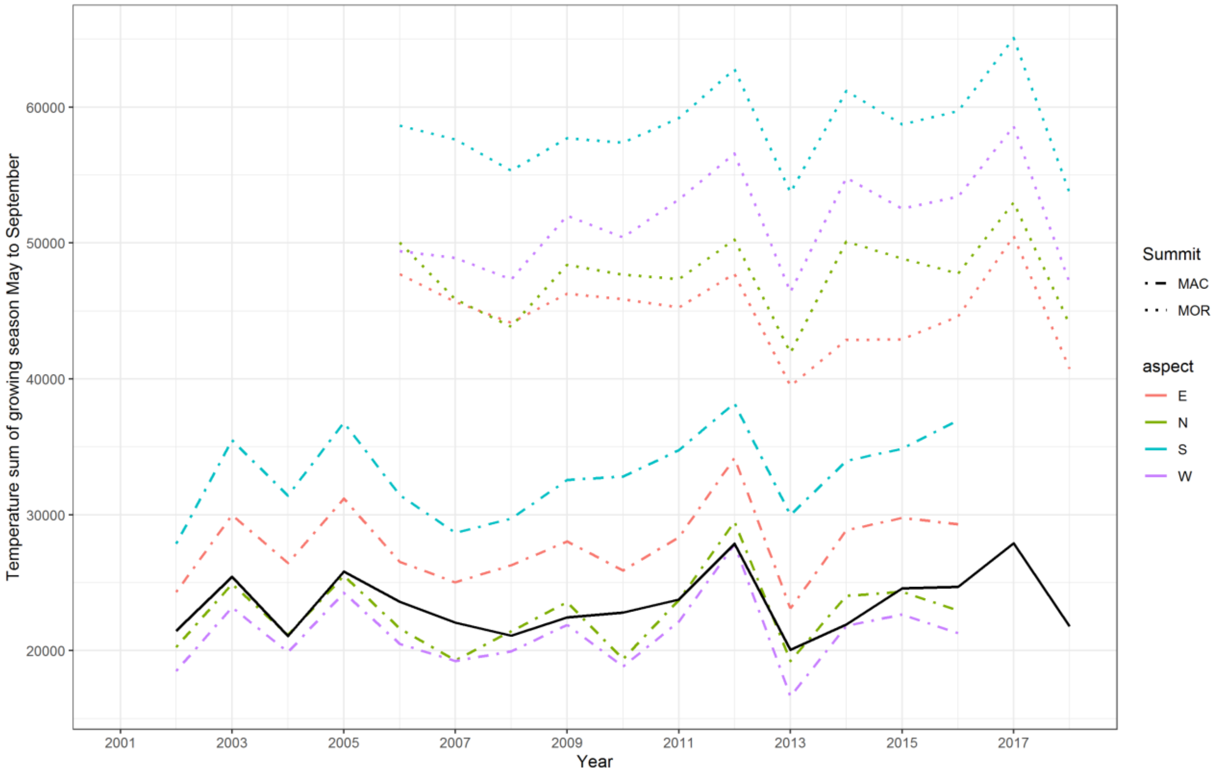

Fig. S1 Comparison of air and soil temperature sums in the Sierra Nevada, Spain.
Temperature sums of the growing season from May to September with a threshold of 1°C calculated from ERA5 data (black solid line; 700hPa, equivalent to an elevation of 3000m; https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5) and measured soil temperature May to September (10 cm below surface) of the four cardinal directions on the highest (MAC, 3327m) and lowest (MOR, 2668m) summit of the GLORIA study regions in the Sierra Nevada.

Table S1 Vascular plant species in two GLORIA study regions in the Sierra Nevada, Spain
Shown are all vascular plant species occurring in at least one of the two study regions (SNE: Sierra Nevada – West and SNN: Sierra Nevada – Northeast) and survey years[1]. For each species, growth form (GR)[2], status of endemism (EN)[3], altitudinal ranks (AR)[4], as well as (a) number of occurrences in summit area sections (SAS)[5] and (b) cover sum [dm²] of the species over all 1m x 1m-quadrats[6] are given per study region and survey year.

				(a) Number of occurrences in SASs						(b) Cover sum over all quadrats [dm²]					
				SNE			SNN			SNE			SNN		
Species name	GR	EN	AR	2001	2008	2015	2004/06	2011	2019	2001	2008	2015	2004/06	2011	2019
Acinos alpinus (L.) Moench subsp. meridionalis (Nyman) P.W.Ball	he	0	5	5	3	6	0	0	0	0.07	0	0	0	0	0
Aethionema marginatum (Lapeyr.) Montemurro	he	0	5	8	5	7	0	2	0	0.82	1.1	1.51	0	0	0
Agrostis nevadensis Boiss.$^{\Delta}$	gr	1	3	5	6	8	9	11	13	0	0	0	0	0	0.2
Alyssum nevadense Wilmott ex P.W.Ball & T.R.Dudley	he	1	4	0	0	0	10	4	1	0	0	0	0.41	0.05	0
Alyssum purpureum Lag. & Rodr.	cu	1	1	20	18	20	5	7	12	7.62	6.41	8.4	1.12	0.5	0.1
Alyssum serpyllifolium Desf.	he	0	6	0	0	0	0	0	3	0	0	0	0	0	0.5
Anarrhinum laxiflorum Boiss.	he	0	6	0	0	0	0	0	1	0	0	0	0	0	0
Androsace vitaliana subsp. nevadensis (Chiarugi) Luceño	cu	1	2	1	0	1	11	13	14	0	0	0	4.02	5.52	3.6
Andryala agardhii Haens. ex DC.	he	0	5	7	7	7	0	0	0	2	4	3.5	0	0	0
Anthyllis vulneraria L. subsp. pseudoarundana H.Lindb.	he	0	3	14	12	14	15	19	17	1.98	1.8	5.5	10.01	17.91	5.15
Arabis auriculata Lam.	an	0	NA	0	0	0	0	2	2	0	0	0	0	0.1	0.1
Arenaria armerina Bory	cu	0	4	2	1	6	18	17	24	0.25	0	0	13.29	21.55	17.8
Arenaria grandiflora L.	he	0	4	0	0	0	8	11	7	0	0	0	7.24	31.9	10.8
*Arenaria pungens Clemente ex Lag.**	sh	0	3	13	13	14	18	20	19	14.6	10.5	21.5	166.61	174.9	250.4
Arenaria tetraquetra L. subsp. amabilis (Bory) H.Lindb.	cu	1	3	20	19	19	16	15	15	32.3	36.4	17.5	23.11	15.5	16.35
Artemisia granatensis Boiss.	cu	1	2	4	1	4	0	0	1	0	0	0	0	0	0
Asperula aristata L.f. subsp. scabra (J.Presl & C.Presl) Nyman	he	0	6	7	7	6	0	0	0	2.82	3.41	4.8	0	0	0
Asplenium septentrionale (L.) Hoffm.	he	0	5	0	0	0	1	2	1	0	0	0	0.1	0.3	0
*Astragalus nevadensis Boiss. subsp. nevadensis**	sh	0	6	0	0	0	8	8	9	0	0	0	2.8	5.4	6.81
Avenula levis (Hack.) Holub	gr	1	3	0	0	0	0	0	1	0	0	0	0	0	0
Biscutella glacialis (Boiss. & Reut.) Jord.	he	0	4	16	14	16	3	5	4	2.5	1.76	3.2	0.11	0.9	0.6
Bromus tectorum L.	an	0	6	0	0	0	7	12	13	0	0	0	44.72	10.21	2.95
Campanula rotundifolia L. subsp. willkommii (Witasek.) Blanca	he	1	3	4	4	5	5	5	4	0.45	0.5	0.5	0	0.01	0

				(a) Number of occurrences in SASs						(b) Cover sum over all quadrats [dm²]					
					SNE			SNN			SNE			SNN	
Species name	GR	EN	AR	2001	2008	2015	2004/06	2011	2019	2001	2008	2015	2004/06	2011	2019
*Carduus carlinoides Gouan subsp. hispanicus (Kazmi) Franco**	he	1	3	10	8	5	13	13	13	8.3	0.4	1.15	7.74	31.5	4.2
Cerastium gibraltaricum Boiss.	he	0	6	0	0	0	0	0	2	0	0	0	0	0	0
Cerastium ramosissimum Boiss.	an	0	4	2	3	1	5	4	1	0.02	0.31	0	1.2	10.4	0.3
Chaenorhinum glareosum (Boiss.) Willk.	he	1	2	19	17	20	10	13	15	0.3	0.62	0.3	0.22	0.91	1.3
*Cirsium acaule Scop. subsp. gregarium (Boiss. ex DC.) H.Werner**$^{\Delta}$	he	0	3	2	3	3	5	8	7	0	0	0	1.2	9.5	0.8
Coincya monensis (L.) Greuter & Burdet subsp. nevadensis (Willk.) Leadlay	he	1	2	1	0	0	0	0	0	0	0	0	0	0	0
Crepis oporinoides Boiss. ex Froel.	he	0	3	16	15	17	8	10	13	13.8	9.6	18	6.4	24.75	12.9
Cryptogramma crispa (L.) R.Br. ex Hook.	he	0	4	0	0	1	0	0	0	0	0	0	0	0	0
Cuscuta epithymum (L.) L. subsp. epithymum	an	0	6	0	0	2	0	0	0	0	0	0	0	0	0
Cuscuta planiflora Ten.	an	0	6	0	0	1	3	4	2	0	0	0	0	0	0
Cystopteris fragilis (L.) Bernh.	he	0	5	2	1	4	2	2	1	0	0	0	0	0	0
Cytisus galianoi Talavera & P.E. Gibbs	sh	1	5	7	7	7	0	0	0	79.7	71.7	110.5	0	0	0
Dactylis glomerata L. subsp. juncinella (Bory) Stebbins & Zohary	gr	0	3	13	12	15	13	15	15	17.7	32.4	65.45	31.65	29.4	29.7
Deschampsia flexuosa (L.) Trin. subsp. iberica Rivas Martínez	gr	0	4	9	10	11	8	10	10	9.8	4.4	9.5	0.2	1.3	0.4
Dianthus brachyanthus Boiss.	cu	0	4	8	8	7	9	11	10	4.05	5.5	11.25	4.32	3.4	3.9
Digitalis purpurea L. subsp. purpurea	he	0	6	0	0	0	6	5	6	0	0	0	0.92	0.9	0.5
Draba hispanica Boiss. subsp. laderoi Rivas Martínez, M.E. García & Penas	cu	1	3	15	13	14	18	20	21	1.82	2.5	5.65	1.5	2.96	1.75
Erigeron frigidus Boiss. ex DC.	he	1	1	6	7	6	0	0	2	0.53	0.5	0.2	0	0	1
Erigeron major (Boiss.) Vierh.	he	0	3	11	10	10	14	16	17	3.61	7	9.3	0.61	1.3	3.7
Erodium cheilanthifolium Boiss.	cu	0	4	7	8	7	12	13	13	40.25	20.3	47.5	21.2	16.95	15.7
Erophila verna (L.) Chevall.	an	0	6	0	5	2	6	3	10	0	0.86	0	0	0	0.76
*Eryngium glaciale Boiss.**	he	0	3	15	13	13	15	16	22	1.3	0.43	0.01	15.31	31.85	27.55
Erysimum nevadense Reut. subsp. nevadense	he	1	5	7	1	4	0	0	0	0.14	0	0.3	0	0	0
Euphorbia nevadensis Boiss. &	he	0	4	7	6	7	20	19	22	0.3	0.02	0.2	2.13	3.92	4.95

				(a) Number of occurrences in SASs						(b) Cover sum over all quadrats [dm²]					
				SNE			SNN			SNE			SNN		
Species name	GR	EN	AR	2001	2008	2015	2004/06	2011	2019	2001	2008	2015	2004/06	2011	2019
Reut.															
Euphrasia willkommii Freyn	an	0	3	2	2	2	7	13	6	0	0	0	0	3.1	0
Festuca baetica subsp. moleroi Cebolla & Rivas Ponce	gr	1	6	0	0	0	0	0	1	0	0	0	0	0	0
Festuca clementei Boiss.	gr	1	1	14	14	18	7	8	7	35.3	30.5	49.18	7.7	14.6	16.6
*Festuca indigesta Boiss. subsp. indigesta**	gr	0	4	16	15	16	23	22	24	153.1	98.1	156	186.75	208.5	300.95
*Festuca pseudeskia Boiss.**	gr	1	3	11	8	9	1	1	4	0.8	0	0.1	0.6	0.2	3.4
Galium nevadense Boiss. & Reut.	he	0	4	0	0	0	1	4	5	0	0	0	0	0	0.3
Galium pyrenaicum Gouan	he	0	4	15	12	14	21	18	27	4.92	2.8	2.2	4.04	4.4	2.15
Galium rosellum (Boiss.) Boiss. & Reut.	he	0	3	5	0	3	0	1	0	0.11	0	0.1	0	0	0
*Genista versicolor Boiss.**	sh	1	5	0	0	0	0	0	1	0	0	0	0	0	0
Helictotrichon sedenense (DC.) Holub	gr	0	4	0	0	0	6	5	3	0	0	0	0	4.8	0
Herniaria boissieri J.Gay	he	1	3	9	6	9	9	11	11	0.42	2.3	0.9	0.39	2.3	2.3
Holcus caespitosus Boiss.	gr	1	1	2	2	6	4	5	7	0	0	0	0	0.1	1.9
*Hormathophylla spinosa (L.) Küpfer**	sh	0	4	28	28	30	4	4	6	74.56	107.65	114.41	0	0	0
Iberis carnosa Willd. subsp. embergeri (Serve) Moreno	he	1	2	6	3	0	0	2	0	0.13	0.2	0	0	0	0
Jasione amethystina Lag. & Rodr.	he	1	3	20	19	19	21	18	16	34.28	14.1	20.65	2.35	6.86	3.05
*Juniperus communis L. subsp. hemisphaerica (J.Presl & C.Presl) Nyman**	sh	0	5	7	6	7	2	5	7	0	0	0	0	0	0
Juniperus sabina L.	sh	0	5	6	6	6	11	12	11	0	0	0	216.2	288.5	267.5
Jurinea humilis (Desf.) DC.	he	0	5	10	8	12	8	8	11	0	0	0.3	0.91	3	2.1
*Koeleria crassipes Lange**	gr	0	6	0	0	0	7	8	7	0	0	0	5.7	17	15.95
Lactuca perennis L. subsp. granatensis Charpin & Fernández. Casas	he	0	4	6	6	6	0	0	0	0.3	0	0.2	0	0	0
Leontodon boryi Boiss. ex DC.	he	0	3	20	21	21	17	16	18	16.1	11.1	22.9	5.01	7.1	6
Lepidium stylatum Lag. & Rodr.	he	1	2	6	4	4	0	0	0	4.6	0.3	6.3	0	0	0
Leucanthemopsis pectinata (L.) G.López & C.E.Jarvis	he	1	3	6	3	7	0	1	0	0	0	0	0	0	0
Linaria aeruginea subsp. nevadensis (Boiss.) Malag.	he	1	3	12	4	17	10	13	5	1.51	0.2	0.65	0.22	0.8	0.4
Linaria glacialis Boiss.	he	1	1	0	2	3	0	1	0	0	0	0	0	0	0
Logfia arvensis (L.) Holub	an	0	6	0	0	6	10	8	6	0	0	0	0.52	1.22	0.5

				(a) Number of occurrences in SASs						(b) Cover sum over all quadrats [dm²]					
				SNE			SNN			SNE			SNN		
Species name	GR	EN	AR	2001	2008	2015	2004/06	2011	2019	2001	2008	2015	2004/06	2011	2019
Lotus corniculatus L. subsp. glacialis (Boiss.) Valdés$^{\Delta}$	he	1	2	7	8	9	6	13	14	3.9	0.9	0.5	0	0.1	8
Luzula spicata DC.$^{\Delta}$	gr	0	3	2	0	0	1	2	5	0	0	0	0	0.8	0.95
Myosotis minutiflora Boiss. & Reut.	an	0	5	1	1	2	10	14	6	0	0.01	0	0.98	4.66	0.7
Nepeta nepetella subsp. laciniata (Willk.) Aedo$^{\Delta}$	he	1	4	1	1	1	0	0	0	0	0	0	0	0	0
Omalotheca supina (L.) DC.	he	0	3	0	0	1	0	0	1	0	0	0	0	0	0
Paronychia polygonifolia (Vill.) DC.	he	0	4	6	3	10	5	10	12	1.55	0.9	1.7	1.4	6.91	3.35
Pilosella castellana (Boiss. & Reut.) F.W.Schultz & Sch.Bip.	he	0	5	6	2	9	11	9	18	0.26	0.3	0.05	3.21	4.3	5.2
Pimpinella procumbens (Boiss.) H.Wolff	he	1	3	9	8	11	0	0	0	4.17	2.24	3.1	0	0	0
Plantago holosteum Scop.	cu	0	4	1	1	4	6	9	11	0	0	0.5	1.51	1.7	1.8
Plantago nivalis Boiss.$^{\Delta}$	he	1	3	1	0	0	0	0	0	0	0	0	0	0	0
Poa ligulata Boiss.	gr	0	4	16	14	14	16	21	21	7.79	8.9	12.8	9.01	14.05	17.25
Poa minor Gaudin subsp. nevadensis Nannfeldt$^{\Delta}$	gr	1	2	1	0	0	0	0	0	0	0	0	0	0	0
Poa nemoralis L.	gr	0	6	3	2	4	2	5	5	0	0	0	0	0.31	0
Polygonum aviculare L.	an	0	6	0	0	0	1	4	0	0	0	0	1.9	9.4	0
Polystichum lonchitis (L.) Roth	he	0	6	0	0	1	0	3	2	0	0	0	0	0	0
Potentilla nevadensis Boiss.$^{\Delta}$	he	1	4	0	0	0	0	0	3	0	0	0	0	0	0
Potentilla reuteri Boiss.	he	0	5	0	0	0	2	3	0	0	0	0	0	0	0
Prunus prostrata Labill.	sh	0	4	2	2	2	0	0	0	0	0	0	0	0	0
Ranunculus demissus DC.$^{\Delta}$	he	0	4	5	5	5	0	0	0	21.1	4.1	8	0	0	0
Reseda complicata Bory	sh	1	4	10	11	8	9	11	12	50.7	44.5	39.35	1.21	0.4	0
Rhamnus pumilus Turra	sh	0	5	1	0	0	0	0	0	0	0	0	0	0	0
Rumex angiocarpus Murb.	he	0	6	0	0	0	0	1	2	0	0	0	0	0	0
Saxifraga granulata L.	he	0	5	0	0	0	4	2	8	0	0	0	0	1.5	0.3
Saxifraga nevadensis Boiss.	cu	1	1	9	5	7	2	3	0	0.4	0.4	0	0	0	0
Scutellaria alpina L. subsp. alpina	he	0	4	0	0	0	4	3	3	0	0	0	0	0	0
Sedum amplexicaule DC.	su	0	4	9	8	12	21	21	20	6.57	4.82	6.6	11.55	23.47	7.6
Sedum dasyphyllum L.	su	0	5	8	7	7	0	0	0	0	0	0.2	0	0	0
Sempervivum minutum (Willk.) Pau	su	1	3	18	17	18	15	14	16	11.55	8.12	23.2	12.1	10	7.3
Senecio boissieri DC.	he	0	3	13	12	11	11	18	15	1	1	1.5	8.01	11.5	4.8
Senecio nebrodensis L.	he	0	5	0	0	0	8	10	7	0	0	0	1.02	1.01	1.95

				(a) Number of occurrences in SASs						(b) Cover sum over all quadrats [dm²]					
				SNE			SNN			SNE			SNN		
Species name	GR	EN	AR	2001	2008	2015	2004/06	2011	2019	2001	2008	2015	2004/06	2011	2019
Senecio nevadensis Boiss. & Reut.	he	1	2	0	2	1	0	0	0	0	0	0	0	0	0
Senecio pyrenaicus Loefl. subsp. granatensis (Boiss. ex DC) Rivas Martínez	he	0	3	3	1	1	3	0	1	0	0	0	0.11	0	0
*Sideritis glacialis Boiss.**	sh	0	3	16	14	15	22	25	26	25.95	15.1	27.1	14.31	24.61	17.75
Silene boryi Boiss.	he	0	5	15	15	13	14	19	15	7.2	8.6	35	13.03	17.95	4
Solidago virgaurea L.	he	0	5	0	0	0	3	1	5	0	0	0	0.22	4.6	0
Teucrium lerrouxii Sennen	sh	0	4	8	5	8	16	20	19	2.1	0.8	2	15.01	14.3	21.8
Thymus serpylloides Bory subsp. serpylloides	sh	1	3	16	15	16	22	24	22	27.87	41.7	43.05	99.01	129.4	146.85
Trisetum glaciale (Bory) Boiss.	gr	1	2	18	16	16	13	14	15	15.8	9.7	17.1	3.91	7.7	3.6
Urtica dioica L.	he	0	6	0	0	0	1	1	3	0	0	0	0	0	0
Veronica arvensis L.	an	0	6	0	0	0	0	1	0	0	0	0	0	0.8	0
Veronica verna L.	an	0	5	0	0	0	8	1	0	0	0	0	1	0	0
Viola arvensis Murray	an	0	6	0	0	0	0	2	0	0	0	0	0	0.31	0
Viola crassiuscula Bory	he	1	2	9	4	6	0	0	0	0.2	0	1.15	0	0	0

*spiny

[Δ] hygrophilous

[1] Survey years of SNE: all four summits in 2001, 2008, 2015; SNN: three summits in 2004, one summit in 2006, all four in 2011, 2019

[2] Growth form (GR) according to expert judgment of authors: an = annual; cu = cushion; gr = graminoid; he = forb-hemicryptophyte; sh = shrub (including dwarf-shrubs and matorral species); su = succulent

[3] Status of endemism (EN) according to Lorite et al. (2020): 1 = endemic to Sierra Nevada, 0 = non-endemic

[4] Altitudinal ranks (AR) as a proxy for the thermal preferences of species and their distribution along the elevation gradients after Gottfried et al. (2012), based on regional flora (Molero Mesa and Pérez-Raya 1987), and expert judgment of authors for new species: 1 = cryoro-mediterranean, 2 = oro – cryoro-med., 3 = oro (– cryoro-med.), 4 = (supra –) oro-med., 5 = supra (– oro-med.), 6 = meso (– oro-med.). Vegetation belts in the Sierra Nevada after Molero Mesa and Pérez-Raya (1987) and Molero Mesa et al. (1996).

[5] Eight summit area sections (SAS) per summit, four summits per study region, i.e. 32 SASs per study region

[6] From a total of 16 quadrats per summit, i.e. 64 quadrats per study region

Table S2 Overview of statistical models employed to analyse changes in vascular plant species richness and composition on GLORIA summits in the Sierra Nevada, Spain.
Given are the question addressed, response variables, fixed effects, random intercept terms, and distribution family of (a) richness, (b) colonisation and (c) disappearance events per summit area section (SAS), and (d) cover and (e) thermic indicator (Gottfried et al. 2012) per 1m x 1m-quadrat. For study design see Pauli et al. (2015) For all models generalised mixed-effects models using template model builder were used (R-package glmmTMB; Brooks et al. 2017).

	Question	Response variable	Fixed effect(s)	Random intercept term(s)	Distribution family
(a) Richness per SAS	(1) Change with time and space	Species richness (overall)	Survey year[n] + aspect + elevation[s] + position of SAS[m]	Summit / SAS	Poisson
	(2) Difference among surveys within a summit	Species richness (per summit)	Survey year	SAS	Gaussian
	(3) Difference among surveys within a study region	Species richness (per study region)	Survey year	Summit / SAS	Gaussian
	(4) Effects of climatic factors	Change of species richness[y] (overall)	Change of mean annual precipitation sum[p(5)] + change of mean annual air temperature[p(5)] + mean number of snow days[y]	SAS + survey year	Gaussian
(b) Colonisation events per SAS	(1) Change with time and space	Colonisation events[y] (overall)	Survey year[n] + aspect + elevation[s] + position of SAS[m]	Summit / SAS	Poisson
	(2) Difference among surveys within a summit	Colonisation events[t,y] (per summit)	Survey year	SAS	Gaussian
	(3) Difference among surveys within a study region	Colonisation events[t,y] (per study region)	Survey year	Summit / SAS	Gaussian
	(4) Effects of species characteristics (Growth form, Spinescence, Endemic, Hygrophilous)	Colonisations as Bernoulli trial (overall)	Species characteristic	Summit / SAS + species	Binomial
	(5) Effects of climatic factors	Colonisation events[t,y] (overall)	Change of mean annual precipitation sum[p(5)] + change of mean annual air temperature[p(5)] + mean number of snow days[y]	Summit / SAS + survey year	Gaussian
(c) Disappearance events per SAS	(1) Change with time and space	Disappearance events[y] (overall)	Survey year[n] + aspect + elevation[s] + position of SAS[m]	Summit / SAS	Poisson
	(2) Difference among surveys within a summit	Disappearance events[t,y] (per summit)	Survey year	SAS	Gaussian
	(3) Difference among surveys within a study region	Disappearance events[t,y] (per study region)	Survey year	Summit / SAS	Gaussian
	(4) Effects of species characteristics (Growth form, Spinescence, Endemic, Hygrophilous)	Disappearances as Bernoulli trial (over all)	Species characteristic	Summit / SAS + species	Binomial
	(5) Effects of climatic factors	Disappearance events[t,y] (overall)	Change of mean annual precipitation sum[p(5)] + change of mean annual air temperature[p(5)] + mean number of snow days[y]	Summit / SAS	Gaussian

	Question	Response variable	Fixed effect(s)	Random intercept term(s)	Distribution family
(d) Cover per 1x1m quadrat	(1) Change with time and space	Cover sum (overall)	Survey year[n] + aspect + elevation	Summit / quadrat	Negative binomial (quadratic parameterization)
	(2) Difference among surveys within a summit	Cover sum[t] (per summit)	Survey year	Quadrat	Gaussian
	(3) Difference among surveys within a study region	Cover sum[t] (per study region)	Survey year	Summit / quadrat	Gaussian
	(4) Effects of species characteristics (Growth form, Spinescence, Endemic, Hygrophilous)	Cover per species[t] (overall)	Species characteristic * survey year[n]	Summit / quadrat + species	Gaussian
	(5) Change with time	Cover sum of species group (shrubs, spiny, endemic)	Survey year[n]	Summit / quadrat	Negative binomial (quadratic parameterization)
	(6) Change with time	Proportion of cover sum of species group (shrubs, spiny, endemic) from total cover sum[c]	Survey year[n]	Summit / quadrat	Beta
	(7) Effects of climatic factors	Change of cover sum[y] (overall)	Change of mean annual precipitation sum[p(7)] + change of mean annual air temperature[p(7)] + mean number of snow days[y]	Summit + survey year	Gaussian
(e) Thermic indicator per 1x1m quadrat	(1) Change with time and space	Thermic indicator (overall)	Survey year[n] + aspect + elevation	Summit / quadrat	Gaussian
	(2) Difference among surveys within a summit	Thermic indicator[t] (per summit)	Survey year	Quadrat	Gaussian
	(3) Difference between surveys within a study region	Thermic indicator (per study region)	Survey year	Summit / quadrat	Gaussian

[c] Compressed to avoid zeros and ones after Smithson and Verkuilen (2006)

[n] Numeric (in all other cases as factor variable)

[m] Position of SAS was divided into two groups (lower = 10m, upper = 5m below the highest summit point)

[p] Calculated for prior periods (Gottfried et al. 2012) of one, five and seven years (June_{y-1} to May_{y}) prior to the survey years (y). The model with the best performance was selected using the Akaike Information Criteria (AIC; Burnham and Anderson 2002; year in brackets).

[s] Scaled, because of model convergence problems. To obtain a rescaled estimated value, the estimated value was divided by the standard deviation of the value.

[t] Tukey-transformed, because of heteroscedasticity (transformTukey function from R-package rcompanion; Mangiafico 2020)

[y] Per year, *i.e.*, divided by number of years between subsequent surveys

Table S3 Vascular plant species richness, colonisations, disappearances, cover and thermic indicator on GLORIA summits in the Sierra Nevada, Spain.

Mean and standard error (SE) of raw data of (a) richness, (b) colonisation and (c) disappearance events[1] in summit area sections[2] and (d) species cover sum[3] and (e) thermic indicator (TI; Gottfried et al. 2012) of 1m x 1m-quadrats[4] per study region (SNE: Sierra Nevada - West and SNN: Sierra Nevada – Northeast) and per summit[5] for each survey year. For TI, number of involved quadrats (N) is also shown because quadrats without vegetation had to be removed from analyses.

			(a) Richness		(b) Colonisation		(c) Disappearance		(d) Cover [dm²]		(e) TI		
Study region	Summit	Year	mean	SE	mean a^{-1}	SE	mean a^{-1}	SE	mean	SE	mean	SE	N
SNE	all	2001	21.66	1.8					11.89	1.2	3.35	0.1	56
SNE	all	2008	18.56	1.6	0.26	0.0	0.71	0.1	10.01	1.0	3.48	0.1	56
SNE	all	2015	21.91	1.9	0.79	0.1	0.31	0.0	14.73	1.6	3.40	0.1	57
SNE	PUL	2001	29.8	2.5					18.7	2.8	4.10	0.1	16
SNE	PUL	2008	23.4	2.1	0.18	0.1	1.09	0.2	12.4	2.0	4.25	0.1	16
SNE	PUL	2015	27.4	2.7	0.89	0.2	0.32	0.0	18.3	3.6	4.23	0.1	16
SNE	CUP	2001	29.1	1.6					15.2	1.0	3.42	0.1	16
SNE	CUP	2008	26.2	1.6	0.39	0.1	0.80	0.2	12.7	1.2	3.54	0.1	16
SNE	CUP	2015	30.9	2.2	1.07	0.1	0.41	0.1	26.1	2.2	3.61	0.1	16
SNE	TCA	2001	19.8	1.6					11.3	1.5	2.61	0.2	16
SNE	TCA	2008	18.0	1.5	0.39	0.0	0.64	0.1	11.9	2.0	2.68	0.2	16
SNE	TCA	2015	21.9	2.2	0.84	0.1	0.29	0.1	11.6	2.1	2.42	0.2	16
SNE	MAC	2001	8.0	1.3					2.3	1.1	3.19	0.4	8
SNE	MAC	2008	6.6	1.1	0.09	0.0	0.29	0.1	3.0	1.3	3.45	0.4	8
SNE	MAC	2015	7.5	1.2	0.34	0.1	0.21	0.0	3.0	1.2	3.32	0.4	9
SNN	all	2004/06	20.28	1.3					14.79	2.3	3.46	0.1	58
SNN	all	2011	22.97	1.4	1.01	0.1	0.58	0.1	19.78	2.8	3.48	0.1	58
SNN	all	2019	24.59	1.5	0.81	0.1	0.61	0.1	20.25	2.9	3.46	0.1	62
SNN	MOR	2004	23.1	0.6					27.1	5.8	4.00	0.1	16
SNN	MOR	2011	24.6	1.7	0.59	0.1	0.38	0.1	41.3	7.1	4.02	0.1	16
SNN	MOR	2019	25.9	2.0	0.47	0.1	0.31	0.1	38.4	6.4	4.11	0.1	16
SNN	MIR	2006	26.0	1.9					16.0	4.6	3.47	0.1	16
SNN	MIR	2011	29.2	1.8	1.68	0.2	1.03	0.2	20.7	4.9	3.53	0.1	16
SNN	MIR	2019	26.9	1.7	0.88	0.1	1.17	0.1	17.6	4.7	3.42	0.1	16
SNN	DIE	2004	21.4	1.8					13.4	3.6	3.56	0.1	15
SNN	DIE	2011	26.1	1.7	1.29	0.3	0.61	0.1	10.6	2.6	3.59	0.1	14
SNN	DIE	2019	32.1	1.9	1.34	0.2	0.59	0.1	19.7	6.0	3.51	0.1	15
SNN	CUE	2004	10.6	1.3					2.7	0.7	2.52	0.2	11
SNN	CUE	2011	11.9	1.2	0.50	0.1	0.32	0.1	6.5	1.8	2.56	0.2	12
SNN	CUE	2019	13.5	1.2	0.55	0.1	0.34	0.1	5.3	2.3	2.75	0.3	15

[1] Colonisations and disappearances were calculated per year to make different time spans between survey years comparable.

[2] Eight summit area sections (SAS) per summit, four summits per study region, i.e. 32 SASs per study region

[3] Cover sum: cover of all species per quadrat

[4] 16 quadrats per summit, i.e. 64 quadrats per study region

[5] Given are the summit codes. For summit names see Table 1

Table S4 Changes of vascular plant species richness, cover and thermic indicator on GLORIA summits in the Sierra Nevada, Spain.

Mean, standard error (SE) and p-values of differences between two subsequent surveys (*i.e.*, in a period) in (a) species richness in summit area sections[1], (b) species cover sum[2] and (c) thermic indicator (TI; Gottfried et al. 2012) of 1m x 1m-quadrats[3] per study region (SNE: Sierra Nevada - West and SNN: Sierra Nevada – Northeast) and per summit[4], based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al., 2017)[5]. Pairwise significance tested with the emmean function (Lenth 2019).

			(a) Richness			(b) Cover [dm^2]			(c) TI		
Study region	Summit	Period	mean	SE	p-value	mean	SE	p-value	mean	SE	p-value
SNE	all	2001-08	-3.09	0.6	**<0.0001**	-0.44	0.2	0.149	0.13	0.1	**0.022**
SNE	all	2008-15	3.34	0.6	**<0.0001**	1.08	0.2	**<0.0001**	-0.06	0.1	0.491
SNE	all	2001-15	0.25	0.6	0.905	0.64	0.2	**0.020**	0.08	0.1	0.279
SNE	PUL	2001-08	-6.38	1.4	**<0.0001**	-1.21	0.4	**0.012**	0.13	0.1	0.071
SNE	PUL	2008-15	4.00	1.4	**0.022**	0.98	0.4	0.048	-0.02	0.1	0.949
SNE	PUL	2001-15	-2.38	1.4	0.213	-0.22	0.4	0.843	0.11	0.1	0.135
SNE	CUP	2001-08	-2.88	1.0	**0.024**	-0.21	0.1	**0.045**	0.03	0.0	**0.002**
SNE	CUP	2008-15	4.62	1.0	**<0.0001**	0.72	0.1	**<0.0001**	0.02	0.0	0.126
SNE	CUP	2001-15	1.75	1.0	0.207	0.52	0.1	**<0.0001**	0.04	0.0	**<0.0001**
SNE	TCA	2001-08	-1.75	1.0	0.215	0.00	0.0	0.991	0.05	0.1	0.781
SNE	TCA	2008-15	3.88	1.0	**0.003**	-0.01	0.0	0.896	-0.19	0.1	**0.040**
SNE	TCA	2001-15	2.13	1.0	0.113	-0.01	0.0	0.833	-0.14	0.1	0.164
SNE	MAC	2001-08	-1.37	0.4	**0.007**	0.15	0.1	0.435	0.26	0.2	0.450
SNE	MAC	2008-15	0.87	0.4	0.099	0.10	0.1	0.702	0.03	0.2	0.989
SNE	MAC	2001-15	-0.50	0.4	0.440	0.25	0.1	0.113	0.29	0.2	0.403
SNN	all	2004/06-11	0.12	0.1	0.059	0.28	0.1	**0.008**	0.00	0.1	0.998
SNN	all	2011-19	0.07	0.1	0.381	0.00	0.1	1.000	0.02	0.1	0.938
SNN	all	2004/06-19	0.19	0.1	**0.001**	0.28	0.1	**0.007**	0.01	0.1	0.960
SNN	MOR	2004-11	1.50	1.1	0.355	0.04	0.0	**<0.0001**	0.00	0.0	0.996
SNN	MOR	2011-19	1.25	1.1	0.481	-0.01	0.0	0.411	0.00	0.0	0.710
SNN	MOR	2004-19	2.75	1.1	**0.046**	0.03	0.0	**0.001**	0.01	0.0	0.658
SNN	MIR	2006-11	3.25	1.3	0.063	0.11	0.1	0.446	0.00	0.0	0.858
SNN	MIR	2011-19	-2.37	1.3	0.205	-0.08	0.1	0.646	-0.01	0.0	0.371
SNN	MIR	2006-19	0.87	1.3	0.793	0.03	0.1	0.943	0.00	0.0	0.686
SNN	DIE	2004-11	4.75	1.9	**0.048**	-0.17	0.1	0.487	0.00	0.0	0.973
SNN	DIE	2011-19	6.00	1.9	**0.011**	0.50	0.1	**0.005**	0.00	0.0	0.777
SNN	DIE	2004-19	10.75	1.9	**<0.0001**	0.33	0.1	0.083	0.00	0.0	0.887
SNN	CUE	2004-11	1.25	0.9	0.326	0.43	0.1	**0.007**	-0.05	0.1	0.702
SNN	CUE	2011-19	1.62	0.9	0.162	-0.14	0.1	0.538	-0.02	0.1	0.954
SNN	CUE	2004-19	2.87	0.9	**0.008**	0.29	0.1	0.096	-0.06	0.1	0.529

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[1] Eight summit area sections (SAS) per summit, four summits per study region, i.e. 32 SASs per study region

[2] Cover sum: cover of all species per quadrat

[3] 16 quadrats per summit, i.e. 64 quadrats per study region

[4] Given are the summit codes. For summit names see Table 1

[5] Fixed effect: Survey year (as factor); for random intercept term(s) and distribution family see Table S2(a2,3, d2,3, e2,3)

Table S5 Effects of temporal and spatial variables on vascular plant species (a) richness, (b) colonisation and (c) disappearances in summit area sections (SAS)[1] of the Sierra Nevada, Spain.
Given are estimate, standard error (SE) and p-values of the fixed effects year[2], aspect[3], position of SAS[4] and elevation of summit (scaled)[5], based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al., 2017)[6].

	(a) Richness			(b) Colonisation			(c) Disappearance		
	estimate	SE	p-value	estimate	SE	p-value	estimate	SE	p-value
Intercept	2.91	0.1	**< 0.0001**	-0.54	0.4	0.211	0.09	0.5	0.844
year	0.01	0.0	**0.006**	0.03	0.0	0.269	-0.04	0.0	0.155
aspect North	0.09	0.1	0.204	-0.04	0.3	0.895	0.01	0.3	0.967
aspect South	0.04	0.1	0.553	-0.16	0.3	0.576	-0.01	0.3	0.976
aspect West	-0.10	0.1	0.195	-0.41	0.3	0.187	-0.17	0.3	0.630
upper SAS	-0.04	0.1	0.437	-0.28	0.2	0.178	-0.33	0.2	0.174
scale (elevation)	-0.38	0.1	**< 0.0001**	-0.31	0.2	**0.042**	-0.34	0.1	**0.017**

[1] Eight SAS per summit, four summits per study region, two study regions, i.e. in total 64 SASs
[2] Survey years as numeric: 1 for 2001, 4 for 2004, etc. For survey years see Table S1.
[3] Base level: aspect East
[4] Lower SAS = 10m, upper SAS = 5m below the highest summit point, base level: lower SAS
[5] For elevation of summits see Table 1.
[6] Random intercept term: Summit / SAS; for distribution family see Table S2(a1, b1, c1)

Table S6 Comparison of vegetation performance on aspects in the Sierra Nevada, Spain.
Comparison of (a) richness, (b) colonisation events and (c) disappearance events[1] per summit area section (SAS)[2], and (d) cover sums[3] and (e) thermic indicator (Gottfried et al. 2012) per 1m x 1m-quadrats[4] on aspects (E: East, N: North, S: South, W: West), based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al. 2017)[5]. Pairwise contrasts were tested with the emmean function (Lenth 2019).

	(a) Richness			(b) Colonisation			(c) Disappearance			(d) Cover [dm^2]			(e) Thermic indicator		
contrast	est.	SE	p-val.	est.	SE	p-val.	est.	SE	p-val.	est.	SE	p-val.	est.	SE	p-val.
E - N	-0.09	0.1	0.583	0.04	0.3	0.999	-0.01	0.3	1.000	-0.31	0.3	0.663	0.11	0.2	0.896
E - S	-0.04	0.1	0.934	0.16	0.3	0.944	0.01	0.3	1.000	-0.11	0.3	0.977	-0.21	0.2	0.555
E - W	0.10	0.1	0.566	0.41	0.3	0.553	0.17	0.3	0.963	-0.12	0.3	0.971	0.15	0.2	0.790
N - S	0.05	0.1	0.908	0.12	0.3	0.974	0.02	0.3	1.000	0.20	0.3	0.886	-0.32	0.2	0.181
N - W	0.19	0.1	0.053	0.37	0.3	0.634	0.18	0.3	0.954	0.19	0.3	0.898	0.04	0.2	0.996
S - W	0.14	0.1	0.244	0.25	0.3	0.867	0.16	0.3	0.969	-0.01	0.3	1.000	0.36	0.2	0.112

[1] Colonisations and disappearances were calculated per year to make different time spans between survey years comparable.
[2] Eight SAS per summit, four summits per study region, two study regions, i.e. in total 64 SASs
[3] Cover sum: cover of all species per quadrat
[4] 16 quadrats per summit, four summits per study region, two study regions, i.e. in total 128 quadrats
[5] For fixed effect, random intercept term(s) and distribution family see Table S2(1)

Table S7 Changes of colonisation and disappearance events between study periods in the Sierra Nevada, Spain. Mean, standard error (SE) and p-values of differences between two periods[1] of (a) colonisation and (b) disappearance events[2] in summit area sections[3] per study region (SNE: Sierra Nevada - West and SNN: Sierra Nevada – Northeast) and per summit, based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al., 2017)[4]. Pairwise contrasts were tested with the *emmean* function (Lenth 2019).

			(a) Colonisation			(b) Disappearance		
Study region	Summit	Contrast periods	mean a^{-1}	SE	p-value	mean a^{-1}	SE	p-value
SNE	all	2001/08 – 2008/15	0.43	0.1	**<0.0001**	-0.27	0.1	**<0.0001**
SNE	PUL	2001/08 – 2008/15	0.57	0.1	**0.001**	-0.15	0.0	**<0.001**
SNE	CUP	2001/08 – 2008/15	0.59	0.1	**<0.001**	-0.06	0.0	**0.019**
SNE	TCA	2001/08 – 2008/15	0.31	0.1	**<0.001**	-0.35	0.1	**<0.001**
SNE	MAC	2001/08 – 2008/15	0.28	0.1	**0.003**	-0.06	0.1	0.319
SNN	all	2004(06)/11 – 2011/19	-0.03	0.0	0.259	0.03	0.1	0.577
SNN	MOR	2004/11 – 2011/19	-0.06	0.0	0.214	-0.05	0.1	0.371
SNN	MIR	2006/11 – 2011/19	-0.35	0.1	**0.009**	0.15	0.3	0.577
SNN	DIE	2004/11 – 2011/19	0.09	0.1	0.440	0.02	0.0	0.680
SNN	CUE	2004/11 – 2011/19	0.06	0.1	0.628	0.03	0.1	0.786

[1] Period: between subsequent survey years

[2] Colonisations and disappearances were calculated per year to make different time spans between survey years comparable.

[3] Eight summit area sections (SAS) per summit, four summits per study region, i.e. 32 SASs per study region

[4] Fixed effect: Survey year = last year in a period (as factor); for random intercept term(s) and distribution family see Table S2(b2,3, c2,3)

Table S8 Effects of temporal and spatial variables on (a) vascular plant cover and (b) thermic indicator (Gottfried et al. 2012) on summits in 1m x 1m-quadrats[1] of the Sierra Nevada, Spain. Given are estimate, standard error (SE) and p-values of the fixed effects year[2], aspect[3] and elevation of summit (scaled)[4], based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al., 2017)[5].

	(a) Cover [dm²]			(b) Thermic indicator		
	estimate	SE	p-value	estimate	SE	p-value
Intercept	12.20	3.0	**< 0.0001**	8.70	1.6	**< 0.0001**
year	0.02	0.0	**< 0.0001**	0.00	0.0	0.474
aspect North	0.31	0.3	0.253	-0.11	0.2	0.482
aspect South	0.11	0.3	0.683	0.21	0.2	0.189
aspect West	0.12	0.3	0.659	-0.15	0.2	0.354
elevation	-0.004	0.0	**< 0.001**	-0.002	0.0	**< 0.001**

[1] 16 quadrats per summit, four summits per study region, two study regions, i.e. in total 128 quadrats

[2] Survey years as numeric: 1 for 2001, 4 for 2004, etc. For survey years see Table S1.

[3] Base level: aspect East

[4] For elevation of summits see Table 1.

[5] Random intercept term: Summit / SAS; for distribution family see Table S2(d1, e1)

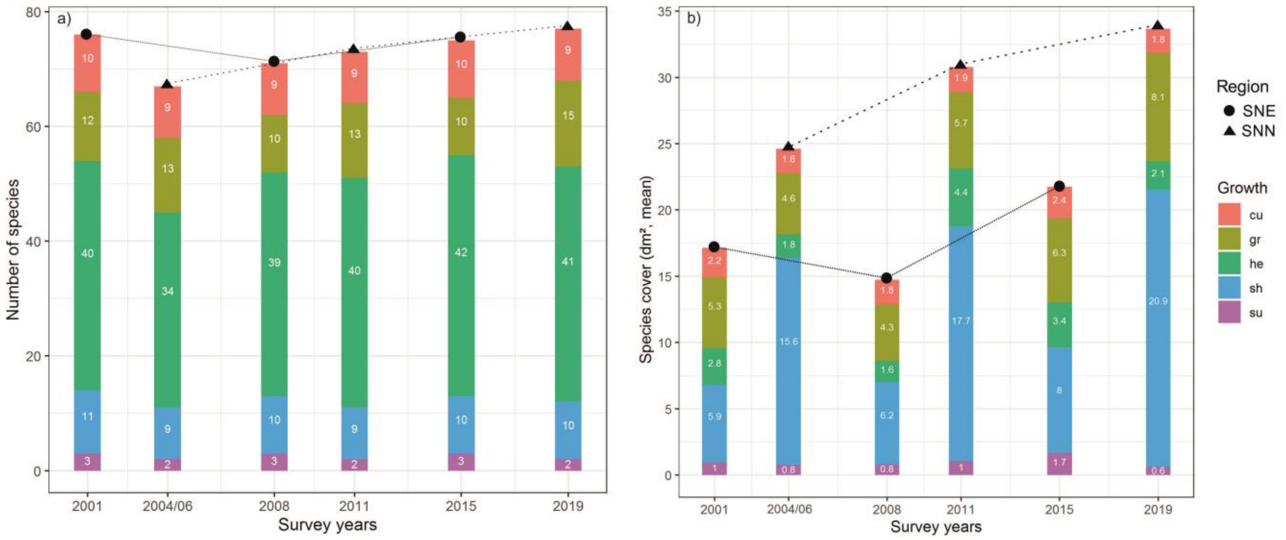

Fig. S2 Number of species and cover of different growth forms on GLORIA summits in the Sierra Nevada, Spain. (a) Total number of species per growth form of 32 summit area sections of the four summits per study region and (b) mean of species cover sums [dm²] per growth form per quadrat (64 quadrats per study region; *i.e.*, 16 on each of four summits). Growth forms: cu: cushion; gr: graminoid; he: herbaceous hemicryptophyte; sh: shrub; su: succulent), study region (SNE: Sierra Nevada - West and SNN: Sierra Nevada - Northeast). For details on species per growth form see Table S1, for details on study regions and survey years see Table 1.

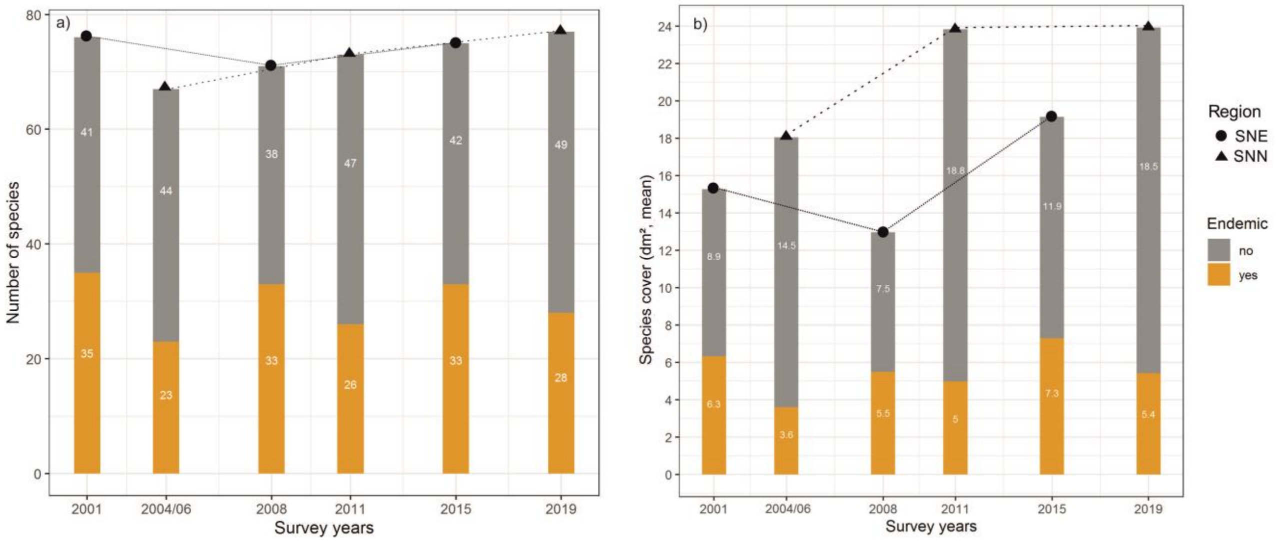

Fig. S3 Number and cover of Sierra Nevada endemics and more widespread species occurring on the GLORIA summits in the Sierra Nevada, Spain. (a) The total number of endemic and non-endemic species (Lorite et al. 2020) in the 32 summit area sections per study region (SNE: Sierra Nevada - West and SNN: Sierra Nevada - Northeast) and (b) their mean species cover sums [dm²] per quadrat in 64 quadrats per study region and survey year. For details to species within the two groups see Table S1, for details to study regions and survey years see Table 1.

Table S9 Comparison of performance of species groups with different characteristics in the Sierra Nevada, Spain. (a) Colonisation events and (b) disappearance events[1] per summit area section[2], and (c) cover sums[3] per quadrat[4], based on generalised mixed-effects models using template model builder (glmmTMB; Brooks et al. 2017)[5], separately for each species group (characteristic). Pairwise contrasts were tested with the emmean function (Lenth 2019). For details on species within the groups see Table S1.

		(a) Colonisation			(b) Disappearance			(c) Cover [dm2]		
Characteristic	contrast	estimate	SE	p-value	estimate	SE	p-value	estimate	SE	p-value
Growth forms[6]	cu - gr	0.28	0.2	0.625	0.11	0.3	0.996	-0.11	0.1	0.404
	cu - he	0.12	0.2	0.946	-0.32	0.2	0.638	0.05	0.1	0.906
	cu - sh	0.59	0.2	0.074	0.80	0.3	0.093	-0.33	0.1	**< 0.0001**
	cu - su	0.44	0.4	0.750	0.46	0.5	0.860	-0.02	0.1	1.000
	gr - he	-0.16	0.2	0.834	-0.43	0.2	0.267	0.16	0.0	**0.011**
	gr - sh	0.31	0.2	0.624	0.69	0.3	0.159	-0.22	0.1	**0.004**
	gr - su	0.16	0.4	0.993	0.36	0.5	0.936	0.09	0.1	0.878
	he - sh	0.47	0.2	0.089	1.12	0.3	**< 0.001**	-0.38	0.1	**< 0.0001**
	he - su	0.31	0.3	0.887	0.78	0.4	0.349	-0.06	0.1	0.957
	sh - su	-0.15	0.4	0.994	-0.34	0.5	0.956	0.31	0.1	**0.014**
Spinescence[7]	yes - no	-0.41	0.2	**0.017**	-0.73	0.3	**0.004**	0.18	0.1	**0.003**
Endemic[7]	yes - no	0.10	0.1	0.408	0.49	0.2	**0.003**	-0.06	0.0	0.164
Hygrophilous[7]	yes - no	0.01	0.2	0.957	0.18	0.3	0.599	0.08	0.1	0.437

[1] Colonisations and disappearances were calculated as Bernoulli trial

[2] Eight SAS per summit, four summits per study region, two study regions, i.e. in total 64 SASs

[3] Cover sum (cover of all species per quadrat) transformed (transformTukey function from R-package rcompanion; Mangiafico 2020)

[4] 16 quadrats per summit, four summits per study region, two study regions, i.e. in total 128 quadrats

[5] For fixed effect, random intercept term(s) and distribution family see Table S2(b4, c4, d4)

[6] Growth forms after expert judgment of authors (sh: shrub; cu: cushion; gr: graminoid; he: herbaceous hemicryptophyte; su: succulent)

[7] Spinescence, Sierra Nevada endemics, and hygrophilous species after Lorite et al. (2020)

Table S10 Relationships between change in vegetation and climate variables on summits of the Sierra Nevada, Spain. Changes in climate variables (fixed effects) were calculated with different periods prior to the surveys[1] in order to select the model with the best performance for their effects on (a) changes in richness, (b) colonisation, and (d) disappearance per summit area section[2] and (e) changes in cover per 1m x 1m-quadrats[3]. Therefore generalised mixed-effects models using template model builder (glmmTMB; Brooks et al. 2017) were used[4] and the Akaike Information Criteria (AIC; Burnham and Anderson 2002) was compared. The order of models is set with the period performing best on top.

Response	AIC	Period	Fixed effects	estimate	SE	p-value
(a) Richness	221.3	5	temperature	0.882	0.18	**<0.0001**
			precipitation	0.005	0.00	**<0.0001**
			days with snow cover	0.005	0.00	**0.001**
	222.6	1	temperature	0.853	0.19	**<0.0001**
			precipitation	0.002	0.00	**<0.0001**
			days with snow cover	0.005	0.00	**0.001**
	229.1	7	temperature	0.485	0.41	0.232
			precipitation	0.006	0.00	**0.004**
			days with snow cover	0.005	0.00	**0.002**
(b) Colonisation	25.9	7	temperature	0.103	0.07	0.136
			precipitation	0.003	0.00	**<0.0001**
			days with snow cover	0.003	0.00	**<0.0001**
	44.4	1	temperature	0.497	0.23	**0.031**
			precipitation	0.002	0.00	**<0.0001**
			days with snow cover	0.004	0.00	**<0.0001**
	48.0	5	temperature	0.720	0.29	**0.013**
			precipitation	0.004	0.00	**0.003**
			days with snow cover	0.004	0.00	**<0.0001**
(c) Disappearance	-15.3	7	temperature	-0.116	0.06	0.063
			precipitation	-0.002	0.00	**<0.0001**
			days with snow cover	0.000	0.00	0.559
	29.1	1	temperature	-0.139	0.29	0.628
			precipitation	0.001	0.00	0.078
			days with snow cover	0.000	0.001	0.595
	30.4	5	temperature	-0.118	0.12	0.308
			precipitation	-0.001	0.00	0.199
			days with snow cover	0.000	0.00	0.788
(d) Cover	985.7	5	temperature	0.546	0.32	0.089
			precipitation	0.005	0.00	**<0.0001**
			days with snow cover	-0.003	0.00	0.370
	986.6	1	temperature	0.467	0.32	0.148
			precipitation	0.003	0.00	**<0.001**
			days with snow cover	-0.003	0.00	0.324
	988.4	7	temperature	-0.090	0.35	0.795
			precipitation	0.006	0.00	**<0.001**
			days with snow cover	-0.004	0.00	0.220

[1] Analyses were conducted with prior periods of one, five and seven years (i.e., means of mean annual air temperature, annual precipitation and mean number of days with snow cover per year over a given period prior to the vegetation record). For the concept of prior periods see Gottfried et al. (2012) and Gottfried et al. (2011). Yearly means were calculated from June to May of the following year.

[2] Vegetation changes per year between subsequent surveys, on eight SAS per summit, four summits per study region, i.e. in total 64 SASs

[3] Changes in cover sum (cover of all species per quadrat) per year between subsequent survey years, for 16 quadrats per summit, four summits per study region, two study regions, i.e. in total 128 quadrats

[4] For random intercept term(s) and distribution family see Table S2(a4, b5, c5, d7)

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7.4 REPORT CHAPTER

ANDREA LAMPRECHT, HARALD PAULI & MANUELA WINKLER (2019)

Potential drivers of changes in biodiversity and plant species composition: Land use.

In:

ANDREA LAMPRECHT, MARTIN RUTZINGER, HARALD PAULI, MANFRED BARDY-DURCHHALTER, KATRIN EULLER, ROBERT NIEDERHEISER, KLAUS STEINBAUER, KATRIN WILFING, BRIGITTA ERSCHBAMER, ROSA FERNÁNDEZ CALZADO, VALTER DI CECCO, ANDREAS GATTRINGER, GEORGE KAZAKIS, MARTIN MALLAUN, JOAQUÍN MOLERO MESA, DIETMAR MOSER, HLEKTRA REMOUNDOU, ANGELA STANISCI, JEAN-PAUL THEURILLAT, PASCAL VITTOZ, JOHANNES WESSELY & MANUELA WINKLER:

Disentangling anthropogenic drivers of climate change impacts on alpine plant species: Alps vs. Mediterranean mountains.

Final report of the project MediAlps (Research Program “Earth System Sciences (ESS)”); Austrian Academy of Sciences Press, Vienna

doi: 10.1553/ESS-MEDIALPSs1

ABSTRACT OF THE PROJECT MEDIALPS

Global warming has been strongly accelerating in the last decades. Climate models tell us that this trend will continue in the future, accompanied by a marked decline in precipitation in Southern Europe, whereas the Alps will likely receive more winter and less summer precipitation. Climate factors and additionally nitrogen deposition and land-use changes have been identified as global change factors posing threats on high-mountain biodiversity, ecosystem stability and services. On the other hand, the characteristic micro-topographic variability of high mountain ecosystems may buffer them against global change impacts. Monitoring data from European mountain peaks show that changes in biodiversity patterns are closely related to rising temperatures. However, the effects of climate change on plant biodiversity differ significantly between temperate and Mediterranean biomes with species richness increases synchronously with warming in the former and richness decreases in the latter.

The MediAlps project aimed at disentangling anthropogenic and natural factors underlying differential changes in plant species composition and richness observed on mountain summits in the European Alps and the Mediterranean biome at the local and regional spatial scale. Changes in plant species richness and composition and present land-use impact based on systematic field observations were recorded on long-term monitoring plots on 23 summits. Soil temperature, water potential and local dry nitrogen deposition were measured in situ. Topographic parameters were recorded with photogrammetric methods. At the regional level, climate data and regional nitrogen deposition data from online resources (CHELSA, EMEP) were used and past land-use impact was assessed via guideline-aided semi-structured interviews. (Generalized) linear mixed-effects models and structural equation models (SEM) were employed to assess the impact of these drivers on biodiversity changes. Furthermore, spatio-temporal analyses based on satellite images were conducted.

Climate change is and will probably continue to be the main driver of plant biodiversity, species composition and their changes on mountain summits in both biomes. However, there are biome-specific differences with precipitation playing an important role in the Mediterranean biome in addition to temperature, which clearly is the most important single factor in the temperate biome. These changes will likely lead to a further thermophilisation in both biomes. The upwards movement of species from lower elevations will likely also result in a biotic homogenization of the vegetation, exacerbated by the decline of high-elevation endemic species. Species richness will likely continue to increase in the temperate biome until the “pay-off” of extinction debts or threshold effects of population size on extinction risks set in. With decreasing precipitation species richness in the Mediterranean biome will probably decline in the long run, too.

Nevertheless, other anthropogenic drivers have to be considered as well, although their influence is arguably much smaller than that of climate variables, namely nitrogen deposition with a negative influence on species richness change in the temperate biome and present land-use with a positive one in the Mediterranean biome.

In addition to MediAlps’ main focus on comparing multiple anthropogenic ecological drivers in the Alps with the Mediterranean mountains, the project substantially contributed to a spatially larger scaled long-term observation effort in the frame of the GLORIA (Global Observation Research Initiative in Alpine Environments) program.

In the present thesis, only the chapter ‘POTENTIAL DRIVERS OF CHANGES IN BIODIVERSITY AND PLANT SPECIES COMPOSITION: LAND USE’ is included.

3.2 LAND-USE

3.2.1 *GRAZING INDICES IN THE 1M² QUADRATS AND SUMMIT AREA SECTIONS*

The frequency of signs indicating the presence of grazing mammals (faeces/droppings, browsing damage, trampling) were recorded for each of the hundred 10cm x 10cm subplot of the corner quadrats of the 3m x 3m quadrat clusters at the summits in 2001 and 2008. In 2015, the frequency of each grazing impact category (faeces/droppings, browsing damage and trampling) was estimated as percentage cover in each 1m² plot. In the SASs, comments on grazing impact were noted in all three survey years.

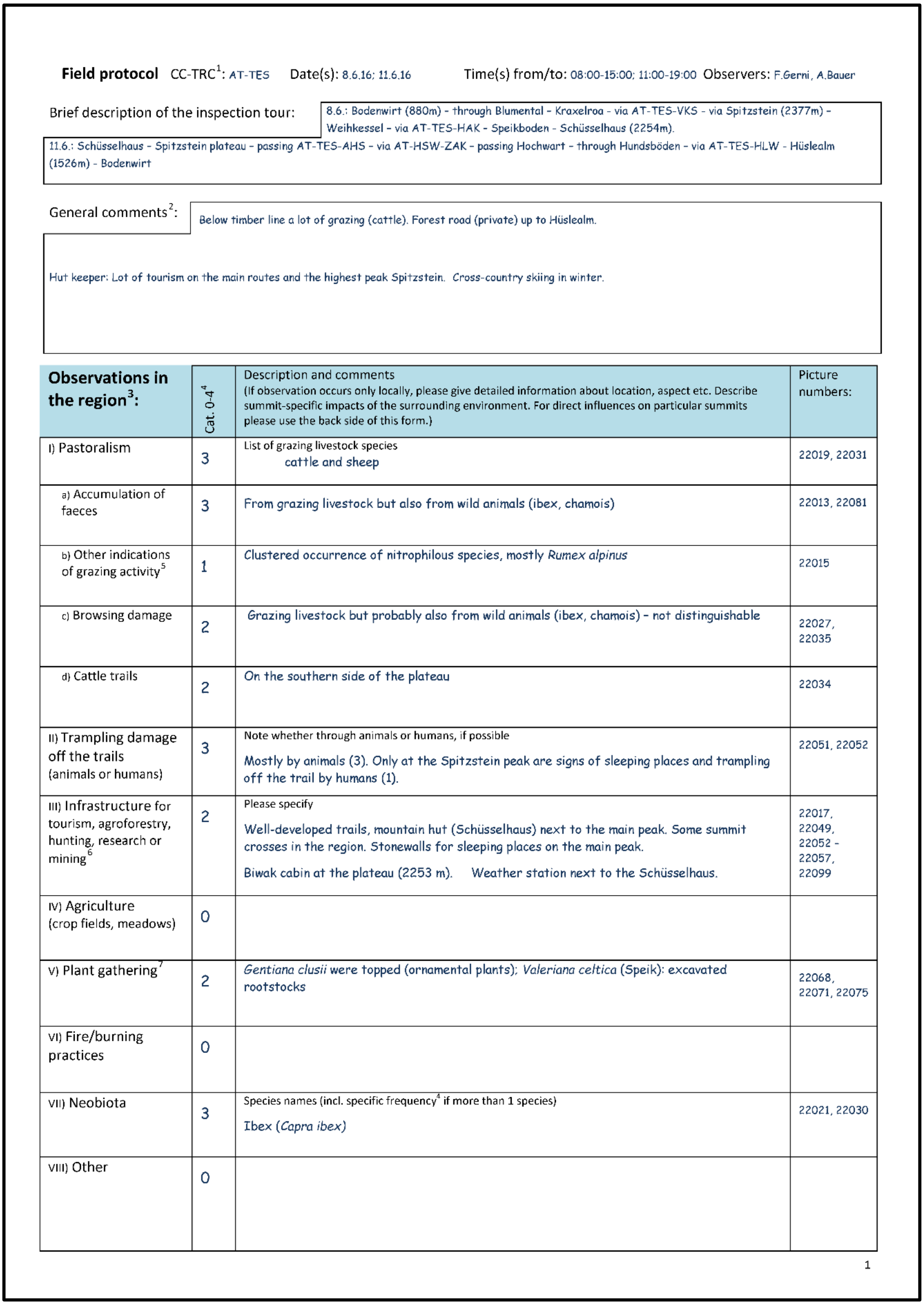
3.2.2 *SYSTEMATIC OBSERVATIONS*

To identify and compare discernible anthropogenic influences, systematic observations were conducted in each of the six selected target region throughout the alpine life zone. Standardised field sheets were developed (Fig. 11), accompanied by a photo-documentation. Recorded key-indications of human impact were grouped in eight categories: pastoralism (e.g., browsing damage, faeces accumulation, eutrophication indicators), trampling damage, infrastructure (e.g., for summer and winter tourism), agriculture, plant gathering, fire, neobiota and other human land-use. Systematic observations were conducted by members of the GLORIA coordination team in each region and additionally by the local teams between June 2016 and August 2018. The added impact scores (0 … no impact to 4… high impact) of the eight categories represent the "Present Land-Use Score" (Table 1).

3.2.3 *HISTORICAL DIMENSIONS: QUALITATIVE INTERVIEWS*

To assess types of anthropogenic activities as well as spatial and temporal dimension of land use and anthropogenic influences in our target sites we carried out qualitative semi-structured, guideline-aided interviews (Fig. 12). Depending on the specific influencing factors of a region, different interviewees, such as regional land-use experts or stakeholders, were interviewed (Table 2). Durations of interviews took between one to more than five hours. Used languages were English, German, French (with translation in English) and Spanish (with translation in English).

The information gathered in the interviews were grouped in three main categories (grazing, tourism, plant gathering) and their added impact scores (0 … no impact to 4… high impact) represent the region-specific "Past Land-Use Score" (Table 1).



Field protocol CC-TRC[1]: AT-TES Date(s): 8.6.16; 11.6.16 Time(s) from/to: 08:00-15:00; 11:00-19:00 Observers: F.Gerni, A.Bauer

Brief description of the inspection tour: 8.6.: Bodenwirt (880m) - through Blumental - Kraxelroa - via AT-TES-VKS - via Spitzstein (2377m) - Weihkessel - via AT-TES-HAK - Speikboden - Schüsselhaus (2254m).
11.6.: Schüsselhaus - Spitzstein plateau - passing AT-TES-AHS - via AT-HSW-ZAK - passing Hochwart - through Hundsböden - via AT-TES-HLW - Hüslealm (1526m) - Bodenwirt

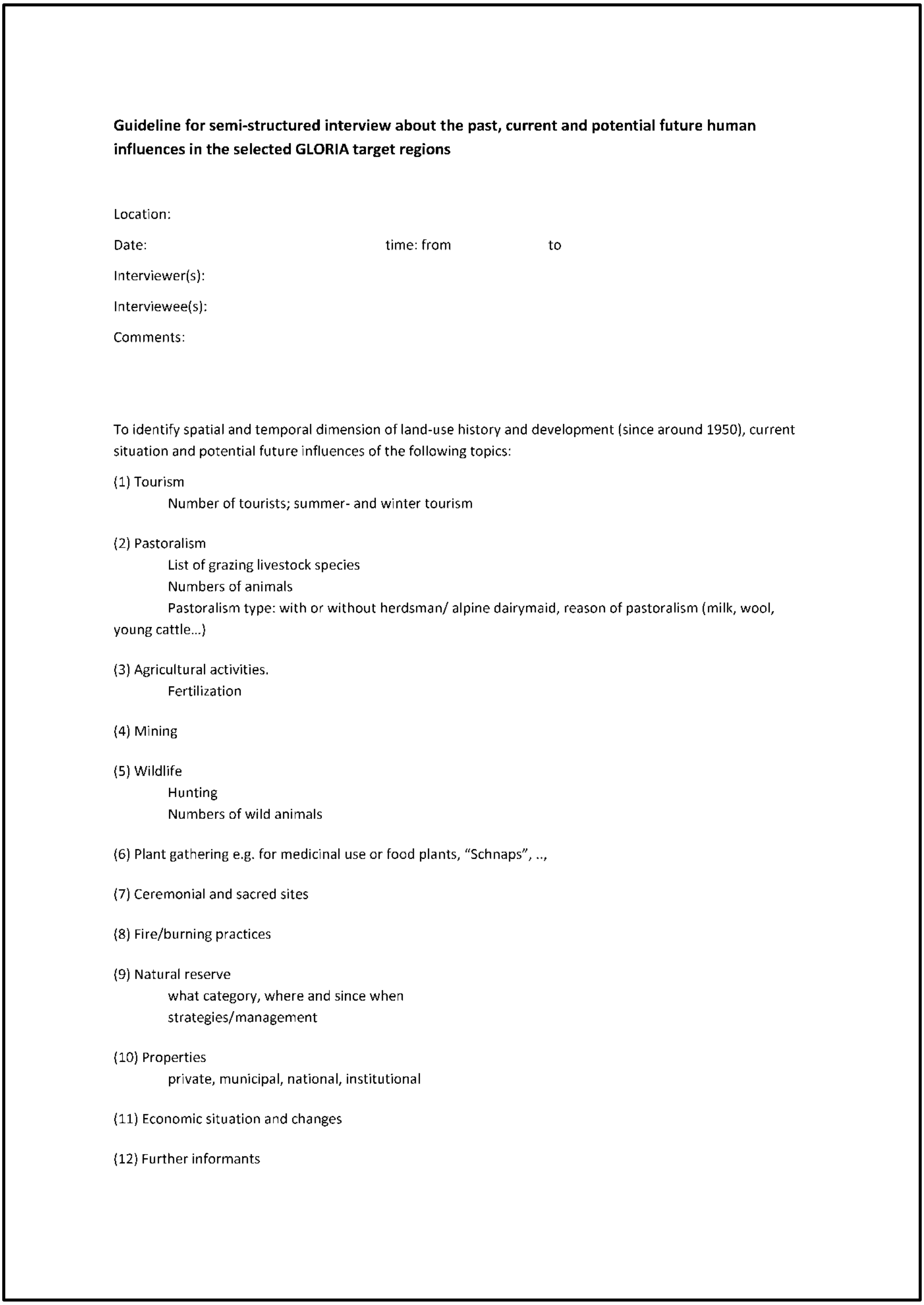
General comments[2]: Below timber line a lot of grazing (cattle). Forest road (private) up to Hüslealm.

Hut keeper: Lot of tourism on the main routes and the highest peak Spitzstein. Cross-country skiing in winter.

Observations in the region[3]:	Cat. 0-4[4]	Description and comments (If observation occurs only locally, please give detailed information about location, aspect etc. Describe summit-specific impacts of the surrounding environment. For direct influences on particular summits please use the back side of this form.)	Picture numbers:
I) Pastoralism	3	List of grazing livestock species cattle and sheep	22019, 22031
a) Accumulation of faeces	3	From grazing livestock but also from wild animals (ibex, chamois)	22013, 22081
b) Other indications of grazing activity[5]	1	Clustered occurrence of nitrophilous species, mostly *Rumex alpinus*	22015
c) Browsing damage	2	Grazing livestock but probably also from wild animals (ibex, chamois) – not distinguishable	22027, 22035
d) Cattle trails	2	On the southern side of the plateau	22034
II) Trampling damage off the trails (animals or humans)	3	Note whether through animals or humans, if possible Mostly by animals (3). Only at the Spitzstein peak are signs of sleeping places and trampling off the trail by humans (1).	22051, 22052
III) Infrastructure for tourism, agroforestry, hunting, research or mining[6]	2	Please specify Well-developed trails, mountain hut (Schüsselhaus) next to the main peak. Some summit crosses in the region. Stonewalls for sleeping places on the main peak. Biwak cabin at the plateau (2253 m). Weather station next to the Schüsselhaus.	22017, 22049, 22052 - 22057, 22099
IV) Agriculture (crop fields, meadows)	0		
V) Plant gathering[7]	2	*Gentiana clusii* were topped (ornamental plants); *Valeriana celtica* (Speik): excavated rootstocks	22068, 22071, 22075
VI) Fire/burning practices	0		
VII) Neobiota	3	Species names (incl. specific frequency[4] if more than 1 species) Ibex (*Capra ibex*)	22021, 22030
VIII) Other	0		

1

Figure 11. Standardised field sheets for systematic observation of present land-use.



Guideline for semi-structured interview about the past, current and potential future human influences in the selected GLORIA target regions

Location:

Date: time: from to

Interviewer(s):

Interviewee(s):

Comments:

To identify spatial and temporal dimension of land-use history and development (since around 1950), current situation and potential future influences of the following topics:

(1) Tourism
  Number of tourists; summer- and winter tourism

(2) Pastoralism
  List of grazing livestock species
  Numbers of animals
  Pastoralism type: with or without herdsman/ alpine dairymaid, reason of pastoralism (milk, wool, young cattle…)

(3) Agricultural activities.
  Fertilization

(4) Mining

(5) Wildlife
  Hunting
  Numbers of wild animals

(6) Plant gathering e.g. for medicinal use or food plants, "Schnaps", ..,

(7) Ceremonial and sacred sites

(8) Fire/burning practices

(9) Natural reserve
  what category, where and since when
  strategies/management

(10) Properties
  private, municipal, national, institutional

(11) Economic situation and changes

(12) Further informants

Figure 12. Guideline for land-use interviews.

Table 2: Overview of land-use interviews.

Region	Date	Position/Role	Interviewee[a]	Interviewer	Language	Translator
SNE	26.07.2016	Staff of the Sierra Nevada national park & the Botanical garden (Jardín Botánico Hoya de Pedraza)	A	AL, HP	Spanish	RF, HP, (JM)
SNE	26.07.2016	Retired park ranger	B	AL, HP	Spanish	RF, HP, (JM)
SNE	01.08.2016	Forestry staff	C	AL, HP	Spanish	RF, HP, (JM)
SNE	01.08.2016	Expert for ibex	D	AL, HP	Spanish	RF, HP, (JM)
CAM *	13.01.2019	Member of GLORIA IT-CAM	VC	AL	English	-
CAM *	13.01.2019	Head of GLORIA IT-CAM	AS	AL	English	-
LEO **	12.12.2018	Head of GLORIA GR-LEO	GK	AL	English	-
VAL	29.08.2018	Farmer, member of bourgeoisie[b] of Bagnes	E	AL	French	JT
VAL	29.08.2018	Farmer, member of bourgeoisie[b] of Liddes	F	AL	French	JT
VAL	30.08.2018	Farmer, member of bourgeoisie[b] of Liddes	G	AL	French	JT
VAL	30.08.2018	Farmer, member of bourgeoisie[b] of d´Orsières	H	AL	French	JT
ADO	06.08.2017	Functionary of fraction Eggen	I	AL	German	-
HSW	26.10.2016	Manager of a mountain hut	J	MW	German	-
HSW	20.08.2018	Local herbalist	K	AL	German	-

[a] interviewees who are not co-authors of this report (A-K) are anonymised
[b] statutory corporation
AL … Andrea Lamprecht, AS … Angela Stanisci, GK … George Kazakis, HP … Harald Pauli, JM … Joaquín Molero Mesa, JT … Jean-Paul Theurillat, MW … Manuela Winkler, RF … Rosa M. Fernández Calzado, VC …Valter Di Cecco
* written interview, ** via Skype

In the study regions the two main forms of land-use are pastoralism and tourism. Where pastoralism is present, shepherds are increasingly rare and absent. The number of free ranging domestic animals tends to increase in some regions (see below). Tourism is increasing in most regions.

3.2.4 *LAND-USE IN THE MEDIALPS REGIONS*

3.2.4.1 ***ES-SNE***

Since 1989, the area of the Sierra Nevada in Spain is a natural park (IUCN cat. V) and parts of it were upgraded into a national park (IUCN cat. II) in 1999. Traditionally it was used as animal husbandry and agriculture (subsistence farming) was realized up to 1600m, but this changed, when it became a hunting reserve in 1960.

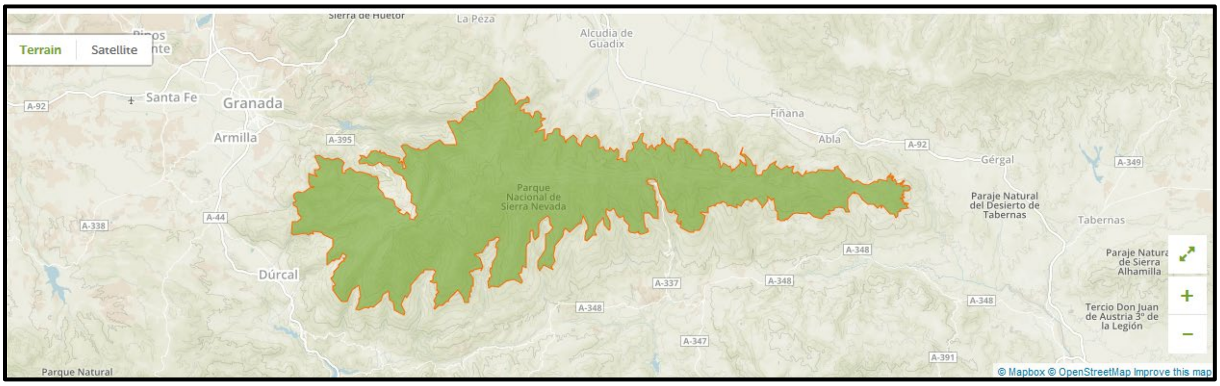


Figure13. Map of the area of the national park Sierra Nevada in Spain[4].

Actually, there are still many cattle and other livestock inside the national park, also in the core zone. From April until around October, there are about 2000-3000 cattle in the park area, however, the real number is stated as certainly higher than the official number. Local politics, rather than the national park administration, is responsible for allocations of grazing areas on the public land, which differ every year. The animals are kept free and are checked only once or twice a week. While the number of cattle is increasing, sheep and goats are decreasing because shepherds or dogs are needed to protect them. In the lower regions there are still goat herds with shepherds, however, overall, there are rarely any shepherds. The main reason for the utilisation is meat. Instead, in the Alpujarras dairy products, including cheese are produced, but wool and leather are not used. Sheep have been found to climb up to the highest peak Mulhacén repeatedly. Cows could be sighted close to the lower GLORIA summits during systematic observations. However, even if the impact of pastoralism in the region was documented as moderate, mainly exemplified through faeces accumulation, the impact by livestock on the GLORIA summits was not observed. Observed resting places and faeces were most likely from ibex (*Capra pyrenaica* subsp. *hispanica*). At the same time, it is hard to distinguish between impact from livestock and wildlife. Further, neglected animals become wild repeatedly. According to ibex specialists, *Capra pyrenaica* subsp. *hispanica* (Iberian Ibex) is

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[4] Source: https://www.protectedplanet.net/sierra-nevada-nacional-park

immigrating from neighbouring areas, after the population was reduced to 200 to 400 individuals during Spanish Civil War (1936 – 1939). Hunting was allowed until the 1950s. Since the 1960s the area above 3000m in the Sierra Nevada is a hunting reserve (Reserva Nacional de Caza). Currently, there are between 14,000 and 15,000 individuals in the national park area, resulting in discussions about changes of management strategies. Additionally, animals like horses and mules are more and more used for touristic purposes. Agencies offer horse trips into the national park, which leads not only to increased trampling but also to droppings on the highest peaks of the Sierra Nevada. During systematic observations *Urtica dioica* could be determined as one of the highest growing plants of Spain, found on the summit zone on 3474m (Fig. 14).

Figure 14. *Urtica dioica* on the Mulhacén at 3480m, July 2016.

As a whole, tourism in the Sierra Nevada is strongly increasing since the designation as national park. Road infrastructure up to 3100m and numerous hiking trails make accessibility to the area easy, even of the highest peaks Mulhacén and Veleta. Since 2010, a ski lift is operating also during summer as it is suggested a more ecological transport system. Another reason for rising popularity of hiking in the Sierra Nevada the financial crisis has been stated, as it forced local people (which are most of the visitors) to search for cheaper holiday alternatives in the region. The introduction of the camino integral is a famous trekking tour over all 3000m peaks of the Sierra Nevada and was followed by an invasion of active sports fans. During the systematic observations, touristic infrastructure was documented as moderate in the region and as low impact on the highest GLORIA summit, although camino integral is passing through. As a further identifiable influence, the use of *Artemisia granatensis* was specified, which is used as tea. Considering the low numbers of individuals (~5000) of this local endemic, gathering is problematic. However, controls and fines are not executed, due to a low number of national park rangers. Because only little examples of *A. granatensis* were found during the systematic observation, with no signs of disturbance, impact by plant gathering was documented as not observed.

3.2.4.2 *IT-CAM*

The National Park of Majella was established in 1991 with the aim to strictly protect high elevation areas.

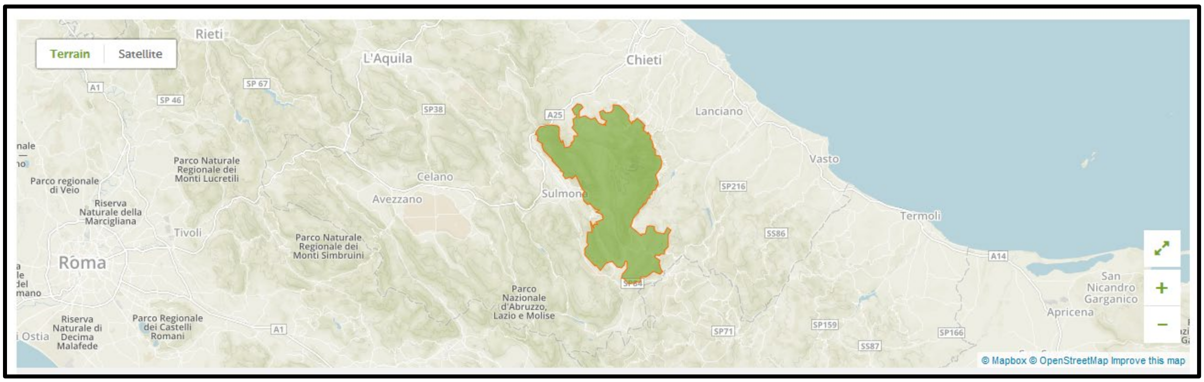

Figure 15. Map of the area of the national park Majella (Parco nazionale della Majella)[5].

Nature-related and hiking tourism in summer has recently increased in the national park. However, the number of tourists is low. According to our informants it is no mass tourism but “niche tourism”. The GLORIA summits are far-off from indicated pathways so they are not visited by hikers. Just a “hardly noticeable” trail was documented during the systematic observation for one summit (MAM).

More direct impact seems to come from pastoralism. Between 500 – 1000 grazing livestock are reported by the GLORIA partners to graze in the national park area. Among them are sheep, goats, cows, horses and mules. Sheep and goats are mainly used for milk and are guided by shepherds at altitudes that rarely exceed 2200 m a.s.l. during summer. According to our partners fewer and fewer shepherds are available, which results in a decreasing number of sheep and goats. Cows and horses are used for meat and are kept without shepherds from July to September, leading to an increase in numbers. Only the lowest GLORIA summit, Femmina Morta, is near to the grazing area. According to the observation protocol, there is no impact observed directly on Femmina Morta but approximately 40 m below the summit. In the region, pastoralism was only observed in the southern parts of the national park up to 2300m. Wild animals are increasing as a result of protection activities and re-introduction actions of endangered species (e.g. chamois). Around 3000-5000 ungulates live perennially or occasionally at the high altitudes of the national park, most of them are chamois. Hunting and gathering is forbidden in the national park, yet, historical records for the usage of some species (*Gentiana lutea*, *Chenopodium bonus-henricus* and *Artemisia umbelliformis* subsp. *eriantha)* by the local population exist.

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[5] Source: https://www.protectedplanet.net/parco-nazionale-della-maiella-national-park

3.2.4.3 *GR-LEO*

The area of Lefka Ori belongs to the Natura 2000 network. Since 2000 it was declared as “Site of Community Importance” (SCI) and since 2011 it is characterized as “Special Area of Conservation” (SAC). The area is managed by the Management Body of Samaria National Park. A Special Environmental Study and a Management Plan were developed, but the necessary presidential degrees for their ratification, are still missing. Thus, an actual management plan doesn’t exist (see also Natura 2000, 2019, 6. site management).

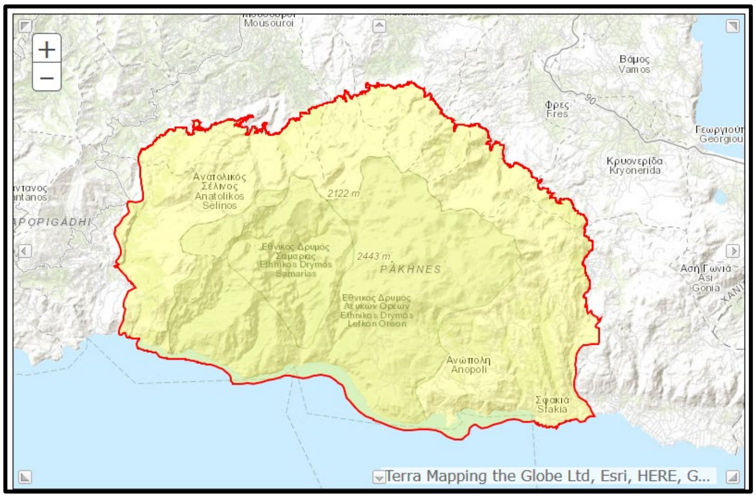

Figure 16. Map of the Special Area of Conservation Lefka Ori Kai Paraktia Zoni (ΛΕΥΚΑ ΟΡΗ ΚΑΙ ΠΑΡΑΚΤΙΑ ΖΩΝΗ)[6].

Pastoralism and apiculture is an old tradition in the region. According to the interviewee pastoralism is traditional for thousands of years in the region, which assumes a preadaptation of the vegetation to grazing. Sheep are the most important livestock with the latest official number of 13.250 animals in 2010 in the whole area of Anopoli. The number of sheep increased from 6.000 to 12.000 to 18.000 in 1970, 1990 and 2000 respectively and is associated with European subsidies. Also important are goats which numbers increased from 3.000 in 1970 to 8.250 in 2010.

Livestock is utilised for milk and meat, sheep are sheared once a year without using the wool. Nowadays there are two to three dairy maids/dairyman in the region making cheese. The number of shepherds was higher in former times, but since a road was built up to 2000m, a permanent residence at higher elevations became redundant. Livestock is more or less free grazing, in higher areas mainly between June and August. In the last 20 years the grazing pressure has been decreasing on the summits and will further decrease in the future, because trade-off between money raised

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[6] Source: http://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=GR4340008

from pastoring and the low efforts (“Not so many young people want to do that.”). However, during systematic observations, a high impact of pastoralism for the region was observed. For the summits (in average), a moderate impact was documented which was visible through browsing damage and a low frequency of faeces accumulation.

Above 600m apiculture has always been the main agricultural activity. It is a very old tradition which is still popular and even increasing. Nowadays, there are around 1,000 bee hives in the region of Anopoli. Some of them are close to the lowest GLORIA summit. Since 20 years also a soft tourism is increasing. In summer, between May and September, around 1,000 people are hiking from Anopoli to the highest peak Pachnes (2454 m). Locals try to establish agrotourism in the area. The GLORIA summits are not affected by visitors at present. During observation days in the region, three to five visitors were documented per day. All of them stayed on the paths.

Additionally, worth mentioning for the Lefka Ori region is plant gathering of *Sideritis syriaca*, which is endemic for Crete and very famous for the region. It is used as the Greek mountain tea, also available in Austria. Special collection rules for the gatherers are respected, e.g. they just cut the branches. Allowed areas and quantity are under the control of the Forest Directorate of Chania. According to the interviewee, the type of collection is traditional and there’s no danger for the species because of gathering. According to Natura 2000 (2019), *Sideritis syriaca* subsp. *syriaca* is listed as important species of the flora but common in abundance. *Origanum microphyllum*, is gathered in high elevations as well. *Origanum vulgare* and *Salvia fruticosa* are only gathered at low elevations in the area around the village of Anopoli. *Origanum vulgare* is cultivated as well. Directly on the GLORIA summits no impact was apparent through plant gathering.

Further anthropogenic impact, such as hunting of rabbits and partridges, are negligible for the region.

3.2.4.4 ***CH-VAL***

The region around the GLORIA summits of CH-VAL is a traditional grazing area. According to a farmer of the region, the oldest written record about grazing dates back to 1287. The GLORIA summits are located in three different communes (municipalities; are the lowest level of administrative division in Switzerland): commune de Bagne, c. de Liddes and c. d'Orsières. The Bourgeoisie is a parallel system within a commune, which combines property of land as well as easement of wood. These rights can also be leased by non-bourgeoisie members. The infrastructure (streets, huts, …) on this land, however, belongs to the commune. Membership in a bourgeoisie is inheritable and more or less patrilineal. All farmers close to GLORIA summits are hired by the bourgeoisies, although the size of their farms, technical development and management strategies are very different. One thing they have in common is the possession of Hérens (Fig. 17), a special cattle breed from the Val d'Hérens, a region in the Valais, which are aggressive and prone to fight between themselves (to define the hierarchy of the females in the herd). The Hérens fights are very popular and famous for the region, as can be seen on many mural paintings on houses in the Valais.

Figure 17. Hérens on a mountain pasture in the Valais, August 2018.

All four interviewed farmers predominantly have cows. Three of them are producing cheese, especially raclette. One farmer is using his livestock only for meat because of low quality of the grazing area. The livestock density, which should be kept per area, was calculated by the government in the 80's. For a full subvention by the state, farmers have to fulfil the requirements, which include a mixture of landscape quality (inclusive biodiversity), combined with a predefined livestock density (±20%) and diversity of animals (different species and breeds). Some of the farmers use fences and confirmed that they never included the GLORIA summits by showing the exact grazing areas on a map. They couldn't exclude, however, that young cows or sheep go up to the two lower summits occasionally when they are free. During the systematic observations of the area, on one of the summits a low frequency of faeces from cows could be documented. The other summits seemed unaffected.

An unpaid duty of the bourgeoisie is called corvée and includes cleaning and clearing of the grazing area. The most important species they cut to prevent from spreading are *Alnus viridis, Larix decidua,*

Juniperus nana and sometimes *Veratrum album*, which is invading since ten to 15 years because of warmer climate. At the lower parts of the grazing areas they spread the liquid manure which is collected in the stable at the Alp.

Plant gathering is popular among people of elder generations but younger people are not interested anymore. Two plant species were mentioned for production of schnapps. While *Artemisia genipi* is used for the famous Génépy, a distilled alcoholic drink, a schnapps of *Arnica montana* is used externally for smaller injuries like sprains. Further, the use of *Euphrasia s.l.* was mentioned for problems with the eyes and *Vaccinium myrillus* as well as *Vaccinium vitis-idea* are collected for making jam. One of the interviewees is the founder of Valplantes (http://www.valplantes.ch/), a company cultivating medicinal plants for cosmetics, pharmacy and drinks in the lower region, instead of gathering wild plants. They also have a very small culture of *Artemisia genipi*.

Wild animals are very rare in the area, e.g. chamois diminished quite a lot over the last decades. Ibex (*Capra ibex*) can only be found in the higher regions. Marmots almost disappeared because of overhunting. Only eagles recolonized the whole area since hunting is forbidden.

The study region in Switzerland is located in one of the less touristic regions of the Valais. During the last 15 years, an increase of “easy” hiking with good paths for families was noticed. The hikers stay mostly on the paths and are more sensitive to nature and leave much less litter in environment compared to earlier times. Some of the farmers try to introduce ecotourism by organising some trips and selling their products.

3.2.4.5 ***IT-ADO***

Since 1996, both parts of the study site in the Dolomites, the Latemar and the Sella massif, are Sites of Community Importance (Nodo del Latemar) and as part of the Dolomites also a World Heritage Site since 2009.

As most parts of the Dolomites the study sites are touristy. The Latemar round trip is very popular among hikers and mountain bikers. Mainly limited to the western and southwestern parts, winter tourism is as important as summer tourism. First ski lifts were built in 1973. Currently, there are 14 lifts up to 2300m (at Mount Zanggen) and 2150m at the Latemar and tourism is the number one source of income of the valley. The skiing area belongs to the provinces Trento and Bolzano/Bozen. Two of four GLORIA summits are at the north-eastern part of the Latemar massif in a surprisingly little touristy area without infrastructure, neither for summer nor winter tourism. One summit is close to the ski area at the south-eastern part. The fourth one is in a remote part on the Sella plateau, which is really touristic in most parts, due to a powerful cable car and easy tracks. All four summits seem to be unaffected from tourism (proved by interview and systematic observation), which is not easy to find in the Dolomites.

This does not apply for pastoralism. The area around the Latemar has been used for grazing at least since the Second World War, when Karakul sheep were kept for their fell. According to our informant this led to massive overgrazing and was quitted immediately after the end of the war. Since then, the area has been used as commonage grazing for cows and sheep. Number of animals and management differ between the provinces Trento and Bolzano/Bozen. The impact by grazing is moderate on the summits in the Latemar area, noticeable by faeces, browsing and trampling damages. The impact is caused mainly by cows on the lowest summit and by sheep on the higher ones, but also goats occur. There is no information about pastoralism at the high plateau of the Sella massif. Even through the systematic observation no signs of pastoralism could be observed there.

Moreover, meadows up to 2000 m are mown once a year at the end of July, and are used for grazing in autumn.

Wild ungulates are rare in the area. Ibex could not be found and chamois have been decimated by scabies. Red deer is common in lower areas and sometimes mouflons are appearing. Hunting is allowed and managed by an annual shooting plan. Plant gathering is forbidden, nevertheless, you can find regional “Zirbenschnaps” from *Pinus cembra* and *Artemisia* spp. (one of the species known as “Edelraute”) were historically used for tea. During the systematic observations no signs of collecting activities were noticed.

3.2.4.6 ***AT-HSW***

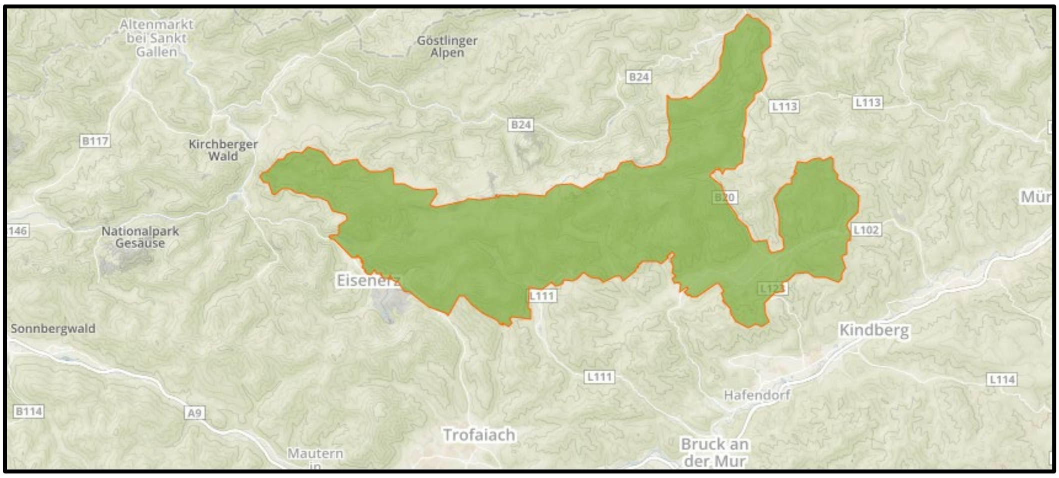

Figure 18. Map of the area of the landscape protection area Hochschwab - Staritzen[7].

Since 1981, the area of the Hochschwab massif is a Landscape Protection Area (IUCN cat. V).

Mountaineering has a long tradition in this easily accessible and well developed region and popularity is still rising. Since 2005 the number of overnight stays at the highest hut has doubled and would be even higher, if more beds would be available, commented the hut keeper. Nevertheless, according to the interviewees hikers are disciplined and do not leave the paths. During the systematic observations, impact through tourism was designated as hardly noticeable, just small cairns on the highest points were documented.

Grazing concentrates on areas below the timberline. Especially in the western and eastern parts there are distributed mountain pastures. The high plateau has always been unsuitable for grazing due to the absence of water. All four GLORIA summits were found to be unaffected by pasturing. Faeces on the summits originate from wild ungulates, mainly from the re-introduced ibex, whose population seems to be fairly stable (or even increasing) on Mt. Hochschwab (Fig. 19). Hunting has played a very important role already since the second half of the 19th century when hunting grounds were massively extended at the expense of alpine grazing grounds (Nevole 1908 in Dirnböck *et al.* 1999)

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[7] Source: https://www.protectedplanet.net/hochschwab-staritzen-landscape-protection-area

Figure 19. Ibex on Mt. Hochschwab, August 2015.

8. PUBLICATIONS NOT INCLUDED IN THE THESIS

Bürli, S., Theurillat, J.-P., Winkler, M., Lamprecht, A., Pauli, H., Rixen, C., et al. A common soil temperature threshold for the upper limit of alpine grasslands in European mountains. *Alpine Botany* (under revision).

Futschik, A., Winkler, M., Steinbauer, K., Lamprecht, A., Rumpf, S. B., Barančok, P., et al. (2020). Disentangling observer error and climate change effects in long-term monitoring of alpine plant species composition and cover. *Journal of Vegetation Science*, *31*, 14-25. https://doi.org/10.1111/jvs.12822

Hofmann, K., Lamprecht, A., Pauli, H. and Illmer, P. (2016). Distribution of Prokaryotic Abundance and Microbial Nutrient Cycling Across a High-Alpine Altitudinal Gradient in the Austrian Central Alps is Affected by Vegetation, Temperature, and Soil Nutrients. *Microb Ecol.*, *72*(3): 704-716. https://doi.org/10.1007/s00248-016-0803-z

Kattge, J., Boenisch, G., Diaz, S., …, Lamprecht, A., … et al. (2020). TRY plant trait database - enhanced coverage and open access. *Global Change Biology*, 26(1): 119-188. https://doi.org/10.1111/gcb.14904

Lembrechts, J.J., Aalto, J., Ashcroft, M.B., …, Lamprecht, A., … et al. (2020). SoilTemp: A global database of near-surface temperature. *Global Change Biology*, 26(11): 6616-6629. https://doi.org/10.1111/gcb.15123

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Niederheiser, R., Winkler, M., Di Cecco, V., …, Lamprecht, A., … et al. (2021): Using automated vegetation cover estimation from close-range photogrammetric point clouds to compare vegetation location properties in mountain terrain. *GIScience & Remote Sensing.* https://doi.org/10.1080/15481603.2020.1859264

Niederheiser, R., Rutzinger, M. Lamprecht, A., Steinbauer, K. Winkler, M. and Pauli H. (2016): Mapping Alpine Vegetation Location Properties by Dense Matching. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives.* Vol. XLI-B5. https://doi.org/doi:10.5194/isprsarchives-XLI-B5-881-2016

Pauli, H., Gottfried, M., Lamprecht, A., Nießner, S., Rumpf, S., Winkler, M., et al. (2015). *The GLORIA field manual – standard Multi-Summit approach, supplementary methods and extra approaches*. 5th edn. GLORIA-Coordination, Austrian Academy of Sciences & University of Natural Resources and Life Sciences, Vienna. https://doi.org/10.2777/095439; Published also in Spanish, Chinese and Russian.

Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., … Lamprecht, A., … et al. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*, 231–234. https://doi.org/10.1038/s41586-018-0005-6

Winkler, M., Lamprecht, A., Steinbauer, K., Hülber, K., Theurillat, J. P., Breiner, F., et al. (2016). The rich sides of mountain summits–a pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*, *43*, 2261–2273. https://doi.org/10.1111/jbi.12835

Winkler, M., Illmer, P., Querner, P., Fischer, B. M., Hofmann, K., Lamprecht, A., et al. (2018). Side by side? Vascular Plant, invertebrate, and microorganism distribution patterns along an alpine to nival elevation gradient. *Arctic, Antarctic, And Alpine Research*, *50*, 1-13. https://doi.org/10.1080/15230430.2018.1475951

9. CURRICULUM VITAE

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Education

Since 2015	*Doctoral studies of 'Natural Resources and Life Sciences' at the University of Natural Resources and Life Sciences, Vienna.*
2005 - 2012	*Diploma program 'Cultural and Social anthropology' at the University of Vienna.*
2005 - 2012	*Diploma program 'Conservation biology, Vegetation ecology and Landscape ecology' at the University of Vienna.*
2002 - 2005	*Bachelor's program 'Biodiversity and Ecology' at the Karl-Franzens-University, Graz.*

Scientific research related to high mountain ecology

Since 2011	*Scientific and administrative staff member of the coordination of The Global Observation Research Initiative in Alpine Environments (GLORIA), Vienna. Employed by the University of Vienna (2011 - 2014), University of Natural Resources and Life Sciences, Vienna (2011 -) and Austrian Academy of Sciences (project-based).*
2018	*Researcher in the project MEDIALPS: field work in the Alps of Valais-Entremont, Switzerland (CH-VAL) and Hochschwab (AT-HSW).*
2017	*Method training and site selection in Eastern Carpathians, Rodnei Mts., Romania (RO-CRO), in Pirin and Rila mountains, Bulgaria (BG-RIL) and in Olympus and Pindos, Greece.* *Researcher in the project MEDIALPS: field work in Central Apennines, Majella, Italy (IT-CAM) and Dolomites, Italy (IT-ADO).*
2016	*Researcher in the project MEDIALPS: field work in Sierra Nevada, Spain (ES-SNE, ES-SNN).* *Exploring trip to Alborz and Zagros mountain ranges in Iran.*
2015	*Co-organisation and implementation of the third survey of Hochschwab (AT-HSW).* *Researcher in the project MEDIALPS, incl. field work in Crete, Lefka Ori, Greece (GR-LEO).* *Method training and site selection in Eastern Pamir, Kokuibel Tajikistan (TJ-EPK) and Tian Shan, Terskey Alatoo Ak Shyrak, Kyrgyzstan (KG-TTA).*
2014	*Co-organisation and implementation of the third survey of the master site Schrankogel within ACRP project SCHRANKOGEL_20YEARS, incl. setup and management of a high-altitude camp at 2600m for five weeks. Method training and site selection in Daxue Shan, Gongga Shan, Sichuan, China (CN-GON).*
2013	*Co-organisation of the GLORIA - West Glacier Summit meeting in Montana, USA.*
2011	*Method training and site selection in the High Atlas West, Marokko (MA-ATW).*
2010	*Member of the organisation committee of 5th International GLORIA conference in Perth, Scotland, UK. Resurvey of monitoring plots of dynamic areas in the national park Gesäuse.*
2009	*Co-organisation and implementation of a new GLORIA target region in the national park Gesäuse (AT-XEI). Establishing of monitoring plots of dynamic areas in the national park Gesäuse.*