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Temporal beta diversity patterns reveal global change impacts in closed mountain grasslands

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ABSTRACT

Global changes are recognized as one of the main drivers of biodiversity changes over time, especially in mountain ecosystems. A key approach to detect and investigate the effect of climate and land use change on these ecosystems is represented by vegetation surveys. In this study, based on the resurvey of historical vegetation data, we assessed temporal beta-diversity patterns within and between subalpine and alpine vegetation types in the Dolomiti Bellunesi National Park. Resurvey was focussed on plots sampled in four main vegetation types: 1 and 2) Mesophytic and xerophytic grasslands on neutral or base-rich soils respectively dominated by *Sesleria caerulea* and *Carex sempervirens* and by *Sesleria caerulea* and *Helictotrichon parlatorei*; 3) Acidophytic grasslands dominated by *Nardus stricta*; 4) Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*. Our results revealed a pattern of floristic homogenization in grasslands and snowbeds indicating a decreasing heterogeneity, both within and between different vegetation types that can be associated with different components of global change. The highest temporal beta diversity and floristic homogenization were detected in snowbeds. In general, the magnitude of temporal changes differ between communities, thus claiming for conservation activities that are tailored to each vegetation type.

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1. Introduction

European alpine ecosystems cover only 2% of the global alpine area (Testolin et al. 2020) and about 3% of the European territory, but host 20% of the European vascular plant flora (Väre et al. 2003; Jiménez-Alfaro et al. 2021), being an important spot of biodiversity that is increasingly threatened by global change (Dirnbock et al. 2003; Stevens et al. 2010; Carbognani et al. 2014; Baatar et al. 2019). In the last decades, the effects of climate change were investigated on the alpine communities and mountain summits across Europe, revealing a steep increase in plant species richness over the last century (Steinbauer et al. 2018) in connection with an upward shift of thermophilous species from lowlands and range size reduction for several cold-adapted species (Dullinger et al. 2012; Elsen and Tingley 2015; Rumpf et al. 2018; Porro et al. 2019). These dynamics lead both to floristic thermophylization (Gottfried et al. 2012) and homogenization of summit vegetation on the European mountains (Jurasinski and Kreyling 2007).

Floristic homogenization, due to the spread of ubiquitous species with large temperate distributions that out-compete habitat specialists (Britton et al. 2009), is among the main

negative impacts of climate change on biodiversity of natural vegetation. It reduces compositional heterogeneity both within and between plant communities (e.g. Olden and Rooney 2006), thus undermining habitat distinctiveness and heterogeneity conservation (Baatar et al. 2019). Therefore, exploring how the entity and magnitude of temporal changes may differ between communities coexisting in the same area is crucial for planning conservation activities (Ross et al. 2012; Baatar et al. 2019).

In this perspective, resurvey studies based on historical vegetation data coupled with the analysis of beta-diversity patterns may provide a powerful tool to detect changes in species composition and diversity over time (Vittoz et al. 2009; Ross et al. 2012; Windmaißer and Reisch 2013; Carbognani et al. 2014; Socolar et al. 2016; Liberati et al. 2019; Lelli et al. 2021). Beta diversity analyses may help to detect temporal changes both within a given community and among coexisting plant communities, as in most resurvey studies on Alpine vegetation (e.g. Ross et al. 2012; Liberati et al. 2019).

In the Alps, several studies are shedding light on the magnitude and direction of compositional changes occurring in high elevation open communities, characterized by small

vegetated patches in rocky environments (Vittoz et al. 2008), while temporal dynamics in closed grasslands are less investigated (Cannone and Pignatti 2014; Gritsch et al. 2016), especially in the subalpine vegetation belt (Vittoz et al. 2009). Closed grasslands, characterised by a continuous canopy coverage in space, are expected to be more stable than high elevation open communities, due to a higher inertia in species composition related to the slow growth rates and longevity of the extant species, and low rates of disturbance, hindering the availability of open niches for new colonisations (Grabherr 2003; Körner 2003; Bürli et al. 2021). While the regional pool of species is largely dependent on historical biogeography (Jiménez-Alfaro et al. 2021), significant changes in both species richness and composition have been recently observed over a relatively short timescale at the community level (Carbognani et al. 2014; Matteodo et al. 2016; Liberati et al. 2019), suggesting that changes may be more rapid and less predictable than was previously thought (Cannone et al. 2007).

This situation poses concern for biodiversity conservation since alpine grasslands represent an important fraction of the vegetation in the alpine life zone as defined by Körner (2003). In this environment, they are among the species-richest habitats (Onipchenko and Semenova 1995; Vonlanthen et al. 2006), and provide multiple ecosystem services such as nutrient cycling, carbon sequestration, biomass production, habitat for pollinators, soil formation and protection, water flow and climate regulation, and recreation (Tomaselli et al. 2019). Moreover, they host several species of biogeographical interest, including many endemics (Jiménez-Alfaro et al. 2021) and populations of species at their distributional edge. This particularly applies to peripheral areas on the southern slope of the Alps that are of exceptional evolutionary history since they provided refugia during the last glaciation period (Schönswetter et al. 2005). Under these circumstances, temporal dynamics may be exacerbated by a strong species response to climate change due to the fact that in these range-edge environments climate is considered harsher than in species' core environments (Rehm et al. 2015). Besides climate change, also land use change may affect vegetation patterns in closed alpine grasslands. In particular, during the 20th century alpine grasslands were prone to abandonment of grazing activities due to decreasing economic profitability of raising living stock (MacDonald et al. 2000). In several European mountain areas, this led to decrease pasturing and many previously grazed pastures were abandoned. At higher altitudes, they gave way to subalpine dwarf shrub heaths in many places (Gennai et al. 2014), whereas at lower altitudes land abandonments have been connected to the expansion of mountain tree species and the loss of grassland habitat in the Pyrenees and in the Alps (Gehrig-Fasel et al. 2007; Ameztegui et al. 2010; Carlson et al. 2014).

In this study, based on the resurvey of historical vegetation data, we aim at assessing temporal beta-diversity patterns within and between alpine vegetation types in the Dolomiti Bellunesi National Park that is a keystone area for biodiversity, being one of the most distinctive region of the South-Eastern Alps in terms of floristic composition (Pignatti and Pignatti 2016) and at interpreting these patterns in the

light of climate and landuse changes. Our analysis was focussed on three widespread grassland types in this area, including primary and secondary communities occurring from lime-rich to lime-poor substrates and with soils ranging from alkaline to neutral and acidic. We included in the analysis also snowbeds that occur very sporadically as isolated small patches, acting as refugial sites for many chionophilous species, that are close to their southernmost distribution border in the South-Eastern Alps (see Lasen 1982; Tomaselli et al. 2005). Specifically, we address the following questions:

- i. Is there any variation in terms of species richness over time and is it similar across the four vegetation types?
- ii. Is the magnitude of temporal beta-diversity comparable across the four vegetation types?
- iii. Are there signals of floristic convergence and homogenization among and within the vegetation types?

2. Materials and methods

2.1. Study area

The study was carried out in the Dolomiti Bellunesi National Park (Site Code: IT3230083) covering a surface of 31.000 ha, located in the South-Eastern Italian Alps (Figure 1), spanning a steep elevational gradient between 412 and 2565 m asl. The average annual temperature is 10-11°C at the bottom of the valley, 4-5°C at 1500m and 2-3°C at 2000m. These mountains are a barrier against the humid winds coming from the Adriatic Sea that is reflected in abundant rainfall (over 2000mm/year) with a seasonal trend of a sub-equinoctial type, with an autumn maximum and a winter minimum. In this area, the bedrock is mainly composed of several Mesozoic sedimentary stratified formations. The geological diversity of the Park is reflected by a mosaic of morphological landscapes, often with distinctive and unique features, like high-mountain karst-nival environments shaped by the glaciers, and subsequently by snow and karst phenomena. During the last glaciation period this area provided refugia to both cold- and warm-adapted species, thus hosting several glacial and Cenozoic relicts (Tribsch and Schönswetter 2003; Tribsch 2004). Overall, the vascular flora includes about 1750 species, while the landscape is dominated by forests (60% of the total surface), rocky environments (25%), and meadows, pastures and primary grasslands (12%).

2.2. Vegetation data and relocation process

This resurvey study was based on the historical plot data stored in the vegetation database of the Dolomiti Bellunesi National Park that includes 350 phytosociological relevés collected in grasslands and snowbeds between 1975 and 2003. For this study, we focussed only on the plots sampled in four main vegetation types: 1) Primary mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* (L.) Ard. and *Carex sempervirens* Vill. (**SC**); 2) Primary xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei* (J. Woods) Pilg. (**SH**); 3)

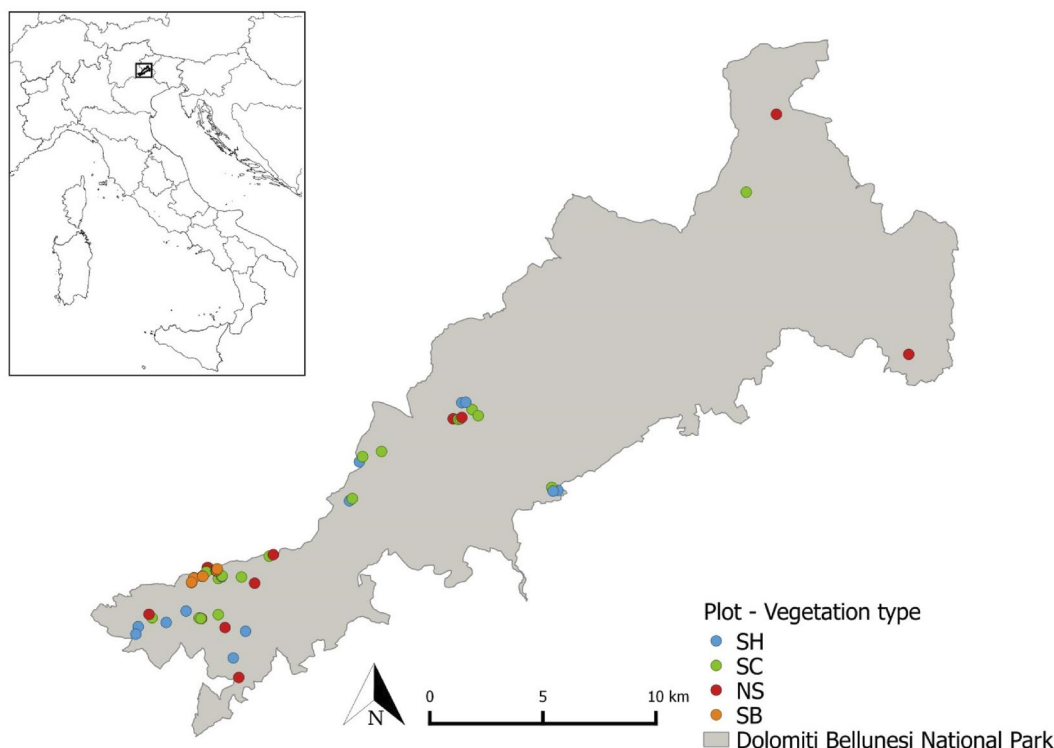


Figure 1. Location of the 59 plots in the Dolomiti Bellunesi National Park (South-Eastern Alps; Veneto, Italy): SH=Xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei*; SC=Mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens*; NS=Alpine and subalpine acidophytic grasslands dominated by *Nardus stricta*; SB=Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*. The rectangle in the inset shows the location of the National Park in Italy.

Secondary alpine and subalpine acidophytic grasslands dominated by *Nardus stricta* L. (**NS**); 4) Snowbeds with dominance of dwarf willows (*Salix herbacea* L. or *S. retusa* L.) or *Luzula alpinopilosa* (Chaix) Breistr. (**SB**).

For these vegetation types, a pool of 164 plots was available. Among them, we selected all those that met the criterion of reliability and accuracy of relocation accuracy following the precautions in order to reduce the inherent sources of error in resurvey suggested by Kapfer et al. (2017). The assessment of this criterion was based on information available from the historical field books (site description, elevation, surface, slope, and aspect), direct indications by the original surveyors that are among the co-authors of this work, and using a DTM with 20m grid resolution (QGIS Development Team) and the vegetation maps. This selection yielded a total of 76 plots.

To avoid seasonality biases, the resampling was performed in the period of the year phenologically more similar and comparable to the historical survey. In the field, once the plot was approximately located, the area with a species composition most similar to the historical relevé was selected, according to a conservative approach (Liberati et al. 2019). When no correspondence to the historical plot (in terms of vegetation or site description) was found, the site was discarded. For several plots, including all the snowbeds, the relocation accuracy was extremely high thanks to the direct collaboration of the original surveyors (MT for snowbeds, CL for several other plots), that contributed to the relocation process and to the resurvey, thus minimizing

also the surveyor bias (Chytrý et al. 2014) and the risk of pseudo-turnover associated to quasi-permanent plots (*sensu* Kapfer et al. 2017). To avoid oversampling, we removed historical plots < 10 metres distant considered as minimum distance to ensure plot distinctiveness (Matteodo et al. 2016).

A total of 76 plots were resurveyed from July to August 2018 and 2019. In order to reduce the wide temporal range in which the original plots were collected, in this study we considered only the original plots sampled from 1998 to 2003. Thus a total of 59 plots were retained for the analysis: 15 in snowbeds, 12 in *Nardus* grasslands, 19 in mesophytic *Sesleria* grasslands, 13 in xerophytic *Sesleria* grasslands. These plots were scattered between 1320 and 2190m, with an average elevation of 1400m (± 198 m SD). Most of the resurveyed plots are located inside the alpine life zone including the areas above the natural or anthropic tree-line (Körner 2003). They were, hence, scarcely or not at all influenced by human activities, except for *Nardus* grassland plots and 5 plots in mesophytic *Sesleria* grasslands. Several plots of the xerophytic *Sesleria* grasslands were indeed located at lower elevations below the tree line, but they occurred on rocky steep slopes at high distance from rural buildings, being definitely referable to primary formations.

The plot area was selected according to the main standard for our vegetation types and it was identical between the current and the historical surveys being 10m x 10m for *Nardus* grasslands, mesophytic *Sesleria* grasslands and xerophytic *Sesleria* grasslands and 1m x 1m for snowbeds. Each resurveyed plot was marked with aluminium plates in the

soil at two corners and coordinates of these two points were recorded (± 3 m GPS Garmin Oregon 450t) for future inventories. Within each plot, all vascular plant species were recorded with visual cover estimation according to percent of species cover. Taxonomical nomenclature harmonisation between historical and current species lists was based on the check-list of the Italian flora (Bartolucci et al. 2018). Information on the elevational range of the species was drawn from Aeschimann et al. (2004) and Pignatti et al. (2017), while that on species ecology (temperature, soil reaction, and nutrient availability) were derived by Landolt et al. (2010).

2.3. Data analyses

Prior to analyses, species occurring in only one plot in each survey were excluded to avoid pseudo-absence or pseudo-presence signals (Pauli et al. 2012). Moreover, in order to avoid bias due to conversion of data from the ordinal Braun-Blanquet scale (original survey) to the continuous percentage cover scale (resurvey) or viceversa (Podani 2006), we used presence-absence data. Changes over time in beta diversity were analysed using both pairwise temporal beta diversity and multiple-site dissimilarities within historical and resurveyed vegetation types.

Pairwise Beta - To detect temporal changes within each vegetation type, a pairwise beta diversity was calculated by comparing each historical plot with its current counterpart (function `beta.temp`, Jaccard index, `betapart` R package; Baselga et al. 2017). Analysis on beta diversity partitioning was performed both for turnover and nestedness component.

Multiple-site dissimilarities - To estimate overall beta diversity the mean Jaccard dissimilarity (particularly well suited for binary data analysis with species lists derived from field observations) was calculated within each historical and resurveyed vegetation types (function `beta.pair`, `betapart` R package). To assess whether the data were normally distributed we used Shapiro-Wilk test. To detect compositional homogenization, the difference between historical and current dissimilarities was tested with the nonparametric test, Wilcoxon-Mann-Whitney, `vegan` R package (Liberati et al. 2019).

A NMDS ordination based on Jaccard dissimilarity index was performed to visualize changes in species composition both within and between vegetation types (500 runs, 3 dimension). The length of the vector joining the coordinates of the historical and current points for each plot in the NMDS was used to represent the magnitude and direction of species composition change in the plot between the two surveys and to highlight systematic changes in community composition.

To identify species changes over time, we performed an analysis based on the frequency (i.e. number of plots in which the species occurred) of each species for the four vegetation types separately. For each species, we considered a minimum conservative threshold of 18% in variation (increase or decrease at least in 2 plots) on the total number of plots for each vegetation type, thus considering as winners those species with a frequency increase greater than 18%

and losers those species with a frequency decrease greater than 18% (losers). All analyses were performed with the numerical software R version 3.4.2 (R Core Team 2018).

3. Results

A total of 416 species were recorded, 334 already listed in the historical survey and 360 in the current resurvey. A general increase in species richness, from the historical to the current survey, was detected in all the vegetation types. Specifically, significant increase was observed only for mesophytic subalpine and alpine grasslands (SC, Figure 2a). A similar pattern across all the vegetation type was observed by partitioning species richness variation into gained and lost species (Figure 2b). The median value of gained species ranges from 9 species in snow beds (SB) to 14 species in the mesophytic subalpine and alpine grasslands (SC), while lost species range between 3 species to 5.

Pairwise Beta - The four vegetation types displayed different amplitude of change over time, with snowbeds (SB) showing the highest mean beta diversity between historical and current surveys. The nestedness-resultant dissimilarity across time shows similar pattern across vegetation types, while as observed for beta diversity the spatial turnover was highest in snowbeds (Figure 3).

Multiple-site dissimilarities - A marginal trend of increasing floristic homogenization (i.e. decreasing beta-diversity over time) within three vegetation types (SB, SC, SH) was detected, but significant decrease of beta-diversity was observed only for the mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens* (SC, Figure 4). In contrast, an increase of beta diversity within vegetation was detected only for acidophytic grasslands dominated by *Nardus stricta* (NS).

A general floristic convergence among vegetation types was detected. Mean vectors of composition change on axes 1 and 2 of the NMDS plot (Figure 5; number of dimensions = 3, stress = 0.11) showed similar trends which are on average shifting towards the centre of the diagram.

Considering changes in frequency of each species within the four vegetation types, we detected a high number of winners and only a few losers (Figure 6). The number of winners is especially relevant in SC, whereas it is negligible in SH. Some winners are species locally spanning a wide altitudinal range, from the low-montane to the subalpine belt, such as *Carex ornithopoda* Willd., *Dactylorhiza maculata* L., *Daphne mezereum* L., and *Leontodon hispidus* L. They presumably represent newcomers in the subalpine grasslands as a consequence of an upward migration. The majority of winners are, however, species that are mainly related to the subalpine and alpine vegetation belts. Their occurrence in our vegetation types could derive from a 'transversal' migration from adjacent habitats. Losers were detected only in SB, NS and SC. In all cases, they mainly include species typically adapted to these habitats such as *Taraxacum* sect. *alpina* and *Veronica alpina* L. in SB, *Gentiana acaulis* L. in NS and *Erigeron glabratus* Bluff & Fingerh in SC. Among losers, it is included also *Silene acaulis* L., an arctic-alpine species that in the historical surveys was confined to SB.

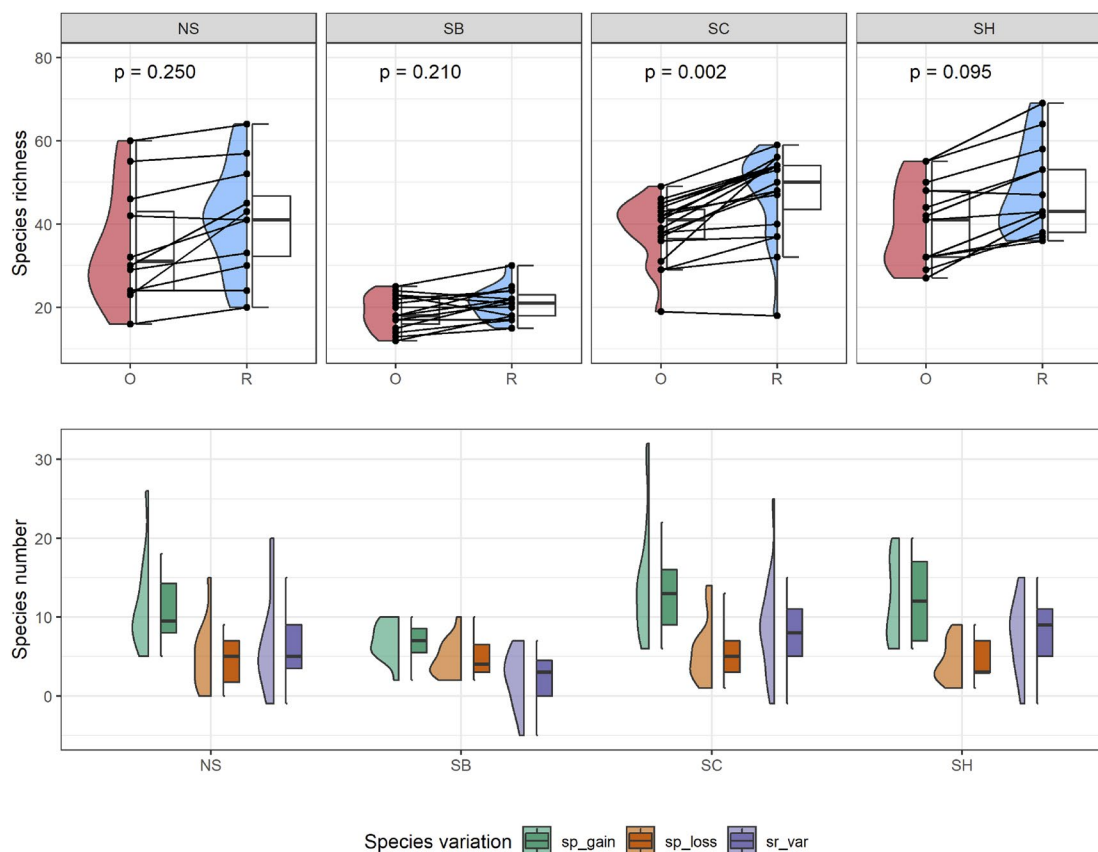


Figure 2. Species richness variation from the historical (O) to the current survey (R) (2a). Partitioning species richness variation into gained and lost species for each vegetation type (2b). Boxes show values between the first and the third quartiles, whiskers encompass 1.5 inter quartile range. SH=Xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei*; SC=Mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens*; NS=Alpine and subalpine acidophytic grasslands dominated by *Nardus stricta*; SB=Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*.

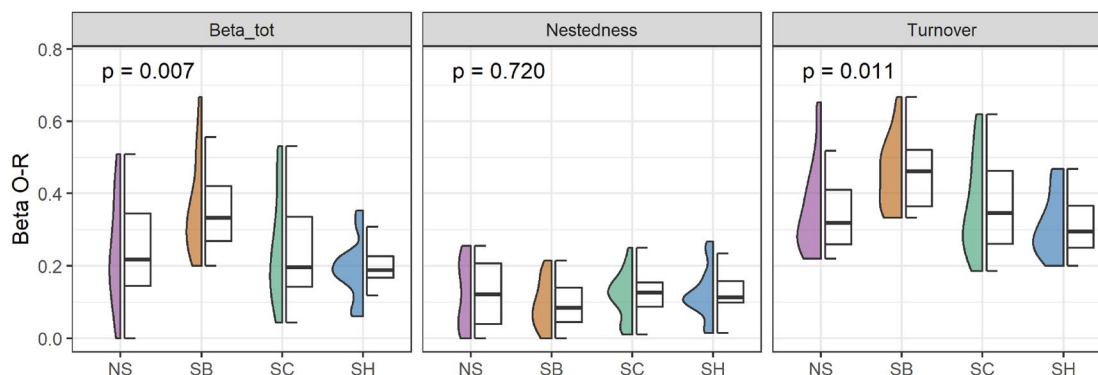


Figure 3. Pairwise beta diversity calculated by comparing each historical plot (O) with its current counterpart (R), total and partitioned into nestedness and turnover components. Violin plots represent the density distribution of the values. Boxes show values between the first and the third quartiles, whiskers encompass 1.5 inter quartile range. **SH=Xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei*; SC=Mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens*; NS=Alpine and subalpine acidophytic grasslands dominated by *Nardus stricta*; SB=Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*.**

4. Discussion

Our results, based on the analysis of temporal beta diversity, reveal a pattern of floristic homogenization in plant communities of closed grasslands and snowbeds of the South-Eastern Alps indicating a tendency towards decreasing heterogeneity, both within and between different vegetation types. These

dynamics are triggered by floristic shifts related to the increase (winners) or decrease (losers) of several species.

This situation mainly applies to snowbeds, where higher temporal beta diversity and floristic homogenization were detected. Similarly to results of other studies (e.g. Carbognani et al. 2014; Matteodo et al. 2016; Liberati et al. 2019), this pattern in snowbeds is associated with the decrease of some

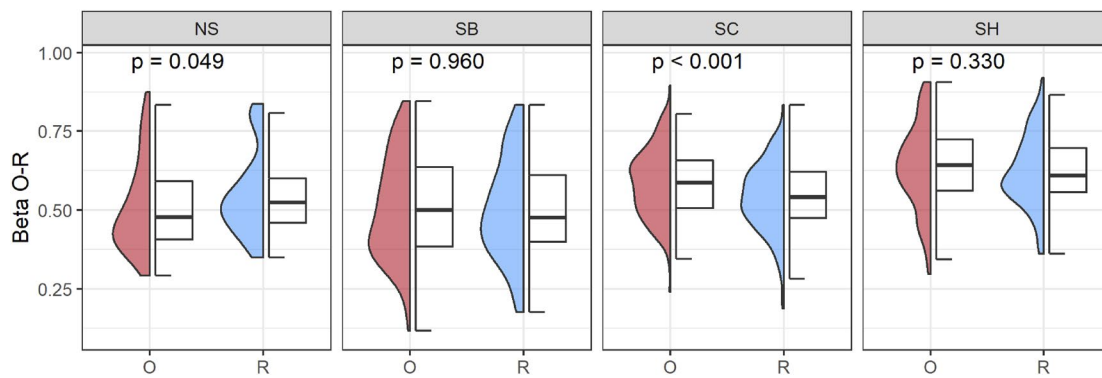


Figure 4. Multiple-site dissimilarities calculated as mean Jaccard dissimilarity within each historical (O) and resurveyed vegetation types (R). Difference between historical and current dissimilarities was tested with the Wilcoxon–Mann–Whitney test. Boxes show values between the first and the third quartiles, whiskers encompass 1.5 inter quartile range. SH=Xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei*; SC=Mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens*; NS=Alpine and subalpine acidophytic grasslands dominated by *Nardus stricta*; SB=Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*.

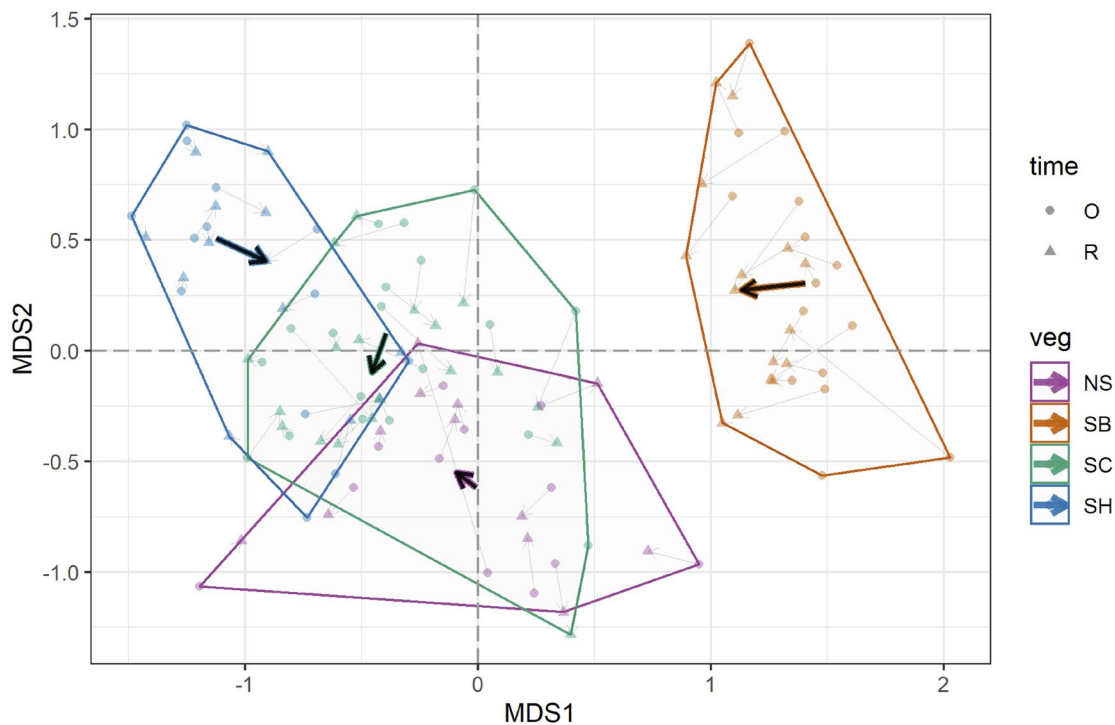


Figure 5. NMDS (number of dimensions = 3, stress = 0.11) performed on abundance data. Grey arrows show the change composition of each plot. The coloured arrows represent changes of median centroids from historical to recent composition of each vegetation types. SH=Xerophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Helictotrichon parlatorei*; SC=Mesophytic subalpine and alpine grasslands on neutral or base-rich soils dominated by *Sesleria caerulea* and *Carex sempervirens*; NS=Alpine and subalpine acidophytic grasslands dominated by *Nardus stricta*; SB=Snowbeds with dominance of dwarf willows (*Salix herbacea* or *S. retusa*) or *Luzula alpinopilosa*.

specialists (chionophilous) species, and the increase of more generalist species (e.g. *Anthoxanthum nipponicum* Honda) that may benefit of more favourable conditions induced by the reduction of snow cover duration and growth season prolonging (e.g. Virtanen et al. 2003; Carbognani et al. 2012). Results also suggest that in this vegetation type compositional changes may be accelerating since their magnitude in our study is comparable to that of previous studies in the Swiss Alps (Matteodo et al. 2016; Liberati et al. 2019) that, however, considered a larger timespan between the original and the resurveyed data. These faster compositional shifts may be aligned with a general accelerating increase in

species richness in high elevation areas of the Alps (Steinbauer et al. 2018), and could be exacerbated in peripheral areas, as in the case of the Dolomiti Bellunesi National Park, where this vegetation type is intrinsically relictual and reduced to scattered fragments where microclimatic, refugial conditions are suitable.

However, also in less extreme vegetation types, as in the case of the closed subalpine and alpine grasslands, a pattern of floristic homogenization can be detected, even if with some differences among types. While an increase in similarity of floristic composition within each vegetation type was clearly found only for mesophytic grasslands, compositional

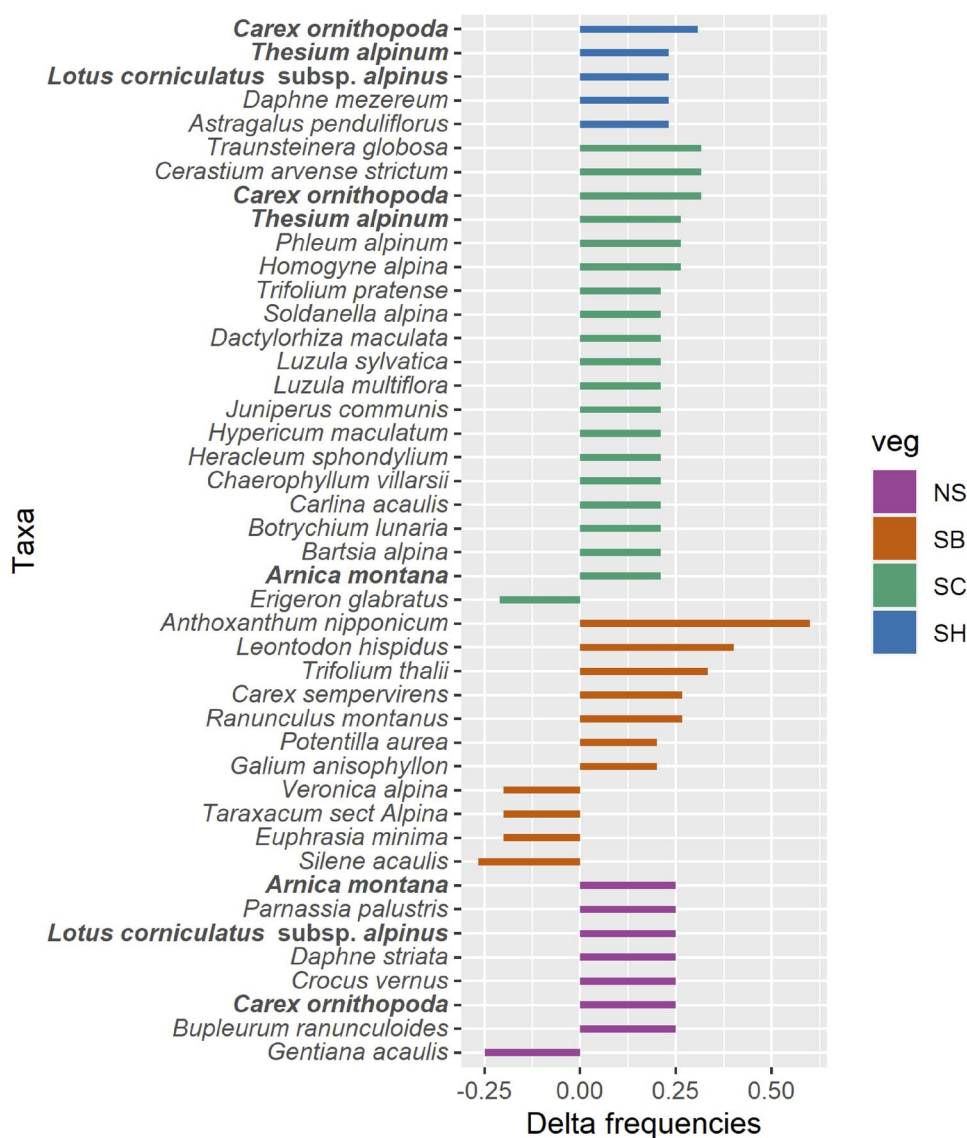


Figure 6. Changes in species occurrences (delta frequency) for each vegetation type. For each species, we considered a minimum conservative threshold of 18% in variation (increase or decrease at least in 2 plots) on the total number of plots for each vegetation type, thus considering as winners those species with a frequency increase greater than 18% and losers those species with a frequency decrease greater than 18% (losers).

similarity is increasing between different vegetation types. This pattern seems to be only partially associated with the spread of thermophilous species coming from lower elevations, as in the emblematic case of *Carex ornithopoda* that increased its frequency in all the three grassland types. A similar pattern of upward migration for this European-Caucasian species was found also by Erschbamer et al. (2008) for the South Tyrolean Dolomites, little further north of the study area, and by Vittoz et al. (2009) for the Swiss Alps. Among these vegetation types, xerophytic subalpine and alpine calcareous grasslands seem to be less prone to temporal floristic shifts, as indicated by the very low values of temporal beta diversity, the lack of a clear direction of floristic change and the very low amount of winners. A similar pattern was reported by Baatar et al. (2019) and may be related to the extreme site conditions of this vegetation type, mainly establishing in steep, south-facing slopes with scarcely developed soil that is strongly influenced by the carbonatic matrix of the rocky substrate. Under these selective conditions,

specialized species are hardly outcompeted by generalists. In this perspective, xerophytic grasslands that are particularly rich in endemics and late Tertiary relicts (Pignatti and Pignatti 1983) are probably more resistant to global change and their slow dynamics still leave a chance for effective local conservation in the long-term.

Differently from xerophytic calcareous grasslands, mesophytic grasslands dominated by *Sesleria caerulea* and *Carex sempervirens* show higher amplitude of change over time, a significant trend of increasing floristic homogenization, a clear direction of floristic change and a higher amount of winners. Among the latter, the relevant increase of the acidophilous *Homogyne alpina* (L.) Cass., *Luzula sylvatica* (Huds.) Gaudin, *L. multiflora* (Ehrh.) Lej. and *Traunsteinera globosa* (L.) Rchb. could be explained by the humus accumulation and soil acidification normally occurring in the mature stages of this community (Pignatti and Pignatti 2016). In addition, the thermophilous *Carex ornithopoda* and *Cerastium arvense* L. subsp. *strictum* (W.D.J. Koch) Greml. show a substantial increase that is a

possible consequence of their upward shift. Less relevant, but still significant, is the frequency increase of several mesophilous and nutrient demanding species such as *Chaerophyllum villarsii* W.D.J. Koch and *Hypericum maculatum* Crantz. suggesting a potential dynamic trend in these grasslands depending from more eutrophic conditions. In absence of data on the nitrogen deposition in the study area (at our best knowledge), eutrophication trend in these grasslands could be explained considering that the warmer temperatures increase decomposition rates stimulating the mineralization of nitrogen in the soil, and increasing nutrient availability for plant growth (Djukic et al. 2018; Rumpf et al. 2018). In conclusion, it sounds plausible that the effects of climate warming on the floristic composition of this community, determined by species upward migration and accelerated nitrogen mineralisation, could overlap and, in the long-term, interplay with the evolution of the mesophytic *Sesleria* grasslands, normally leading to humus accumulation and soil acidification.

In contrast with other vegetation types, beta diversity over time increased in *Nardus* grasslands. This pattern may be associated with a strong floristic convergence towards other vegetation types triggered by a 'transversal' migration of species from adjacent vegetation types. About half of the winners in *Nardus* grasslands is represented by species occurring on neutral to alkaline soils (*Parnassia palustris* L., *Crocus vernus* (L.) Hill, *Carex ornithopoda*, *Thesium alpinum* L., and *Bupleurum ranunculoides* L.). The increase of these species is accompanied by a decline of acidophilous specialists, typical of this vegetation type. This combined floristic pattern of winners and losers could be interpreted as a consequence of eutrophication, inducing less acidic conditions within the *Nardus stricta* grasslands (Kurtogullari et al. 2020). Besides other potential eutrophication sources, we can hypothesize also a role of auto-eutrophication, a process triggered by the insufficient nutrient removal consequent to the subalpine and alpine pasture abandonment or to reduced grazing intensity (Peppler-Lisbach et al. 2020). Actually, in our study area Lasen (1983) already forty years ago indicated a trend of abandonment of several *Nardus* pastures that enhanced species of neutral to alkaline soils, as in the case of *Festuca nigricans* (Hack.) K. Richt. Auto-eutrophication provides also advantage to the tall and tussock species outcompeting the small-growing *Nardus* grassland specialists. However, across our sampling sites there are contrasting management/abandonment patterns in the timespan considered in our study, suggesting that the complex dynamics of *Nardus* grasslands should be investigated more in detail.

5. Conclusions

Compositional changes observed in this study are likely influenced by both climate and land use change. The former seems to play a major role in snowbeds that are rapidly losing several peculiar elements, especially among specialist species. This vegetation type should be mapped in detail and submitted to strict protection (e.g. reducing the touristic use) and constant monitoring and re-evaluation of habitat identity (Baatar et al. 2019), even outside of areas already designated as

integral natural reserves. The latter seems to play a major role in secondary vegetation types, such as *Nardus* grasslands, where auto-eutrophication may strongly impact on species composition. Moderate grazing could be the best management option for the conservation of this vegetation type and should be extended also to mesophytic grasslands dominated by *Sesleria caerulea* and *Carex sempervirens* to prevent similar auto-eutrophication process. In contrast, xerophytic calcareous grasslands would not require any active conservation, being relatively stable and conserving their peculiar plant diversity over the last decades.

Availability of data and material

The data used for the analyses are permanently stored in Zenodo (<https://zenodo.org/record/6901578#.Yt6aOHZBw2w>) under a regime of restricted access and can be obtained upon reasonable request.

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References

- Aeschmann P, Lauber K, Moser DM, Theurillat JP. 2004. Flora Alpina [Flora of the Alps]. Bologna (IT): Zanichelli.
- Ametztegui A, Brotons L, Coll L. 2010. Land-use changes as major drivers of mountain pine (*Pinus uncinata*) expansion in the Pyrenees. *Global Ecol Biogeogr.* 19:632–641.
- Baatar U-O, Dirnböck T, Essl F, Moser D, Wessely J, Willner W, Jiménez-Alfaro B, Agrillo E, Csiky J, Indreica A, et al. 2019. Evaluating climatic threats to habitat types based on co-occurrence patterns of characteristic species. *Basic Appl Ecol.* 38:23–35. <https://doi.org/10.1016/j.baae.2019.06.002>.
- Bartolucci F, Peruzzi L, Galasso G, Albano A, Alessandrini A, Ardenghi NMG, Astuti G, Bacchetta G, Ballelli S, Banfi E, et al. 2018. An updated checklist of the vascular flora native to Italy. *Plant Biosyst.* 152(2):179–303. <https://doi.org/10.1080/11263504.2017.1419996>.
- Baselga A, Orme D, Villeger S, Bortoli J, De Leprieur F. 2017. "Package betapart" partitioning beta diversity into turnover and nestedness. [accessed 2022 Jan 3]. <https://search.r-project.org/CRAN/refmans/betapart/html/betapart-package.html>.
- Britton AJ, Beale CM, Towers W, Hewison RL. 2009. Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. *Biol Conserv.* 142(8):1728–1739. <http://dx.doi.org/10.1016/j.biocon.2009.03.0102>.
- Bürli S, Theurillat J-P, Winkler M, Lamprecht A, Pauli H, Rixen C, Steinbauer K, Wipf S, Abdaladze O, Andrews C, et al. 2021. A common soil tem-

- perature threshold for the upper limit of alpine grasslands in European mountains 2021. *Alp Botany*. 131(1):41–52. <https://doi.org/10.1007/s00035-021-00250-1>.
- Cannone N, Pignatti S. 2014. Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? *Clim Change*. 123(2):201–214. <https://doi.org/10.1007/s10584-014-1065-8>.
- Cannone N, Sgorbati S, Guglielmin M. 2007. Unexpected impacts of climate change on alpine vegetation. *Front Ecol Environ*. 5(7):360–364. [https://doi.org/10.1890/1540-9295\(2007\)5\[360:UOCCO\]2.0.CO;2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[360:UOCCO]2.0.CO;2.0.CO;2)
- Carbognani M, Petraglia A, Tomaselli M. 2012. Influence of snowmelt time on species richness, density and production in a late snowbed community. *Acta Oecol*. 43:113–120. <https://doi.org/10.1016/j.actao.2012.06.003>.
- Carbognani M, Tomaselli M, Petraglia A. 2014. Current vegetation changes in an alpine late snowbed community in the south-eastern Alps (N-Italy). *Alp Botany*. 124(2):105–113. <https://doi.org/10.1007/s00035-014-0135-x>.
- Carlson BZ, Renaud J, Biron PE, Choler P. 2014. Long-term modelling of the forest grassland ecotone in the French Alps: implications for conservation and pasture management. *Ecol Appl*. 24(5):1213–1225.
- Chytrý M, Tichý L, Hennekens SM, Schaminée JHJ. 2014. Assessing vegetation change using vegetation-plot databases: a risky business. *Appl Veg Sci*. 17(1):32–41. <https://doi.org/10.1111/avsc.12050>.
- Dirnböck T, Dullinger S, Grabherr G. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *J Biogeogr*. 30(3):401–417. <https://doi.org/10.1046/j.1365-2699.2003.00839.x>.
- Djukic I, Kepfer-Rojas S, Schmidt IK, Larsen KS, Beier C, Berg B, Verheyen K, Caliman A, Paquette A, Gutiérrez-Girón A, et al. 2018. Early stages of litter decomposition across biomes. *Sci Total Environ*. 628-629:1369–1394.
- Dullinger S, Gatteringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzer C, Leitner M, Mang T, et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Clim Change*. 2(8):619–622. <https://doi.org/10.1038/nclimate1514>.
- Elsen PR, Tingley MW. 2015. Global mountain topography and the fate of montane species under climate change. *Nat Clim Change*. 5:5–10. <https://doi.org/10.1038/nclimate2656>.
- Erschbamer B, Schlag RN, Winkler E. 2008. Colonization processes on a central Alpine glacier foreland. *J Veg Sci*. 19(6):855–862. <https://doi.org/10.3170/2008-8-18464>.
- Gehrig-Fasel J, Guisan A, Zimmermann NE. 2007. Treeline shifts in the Swiss Alps: climate change or land abandonment? *J Veg Sci*. 18(4):571–582. <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>.
- Gennai M, Foggi B, Viciani D, Carbognani M, Tomaselli M. 2014. The *Nardus*-rich communities in the northern Apennines (N-Italy): a phytosociological, ecological and phytogeographical study. *phyto*. 44(1–2):55–80.
- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, et al. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Clim Change*. 2(2):111–115. <https://doi.org/10.1038/nclimate1329>.
- Grabherr G. 2003. Alpine vegetation dynamics and climate change – a synthesis of long-term studies and observations. In: Nagy L, Grabherr G, Körner C, Thompson DBA, editors. *Alpine biodiversity in Europe. Ecological studies*. Vol.167. Berlin (DE): Springer; p. 399–409.
- Gritsch A, Dirnböck T, Dullinger S. 2016. Recent changes in alpine vegetation differ among plant communities. *J Veg Sci*. 27(6):1177–1186. <https://doi.org/10.1111/jvs.12447>.
- Jiménez-Alfaro B, Abdulhak S, Attorre F, Bergamini A, Carranza ML, Chiarucci A, Čušterevska R, Dullinger S, Gavilán RG, Giusso del Galdo G, et al. 2021. Post-glacial determinants of regional species pools in alpine grasslands. *Global Ecol Biogeogr*. 30(5):1101–1115. <https://doi.org/10.1111/geb.13274>.
- Jurasinski G, Kreyling J. 2007. Upward shift of alpine plants increases floristic similarity of mountain summits. *J Veg Sci*. 18(5):711–718. <https://doi.org/10.1111/j.1654-1103.2007.tb02585.x>.
- Kapfer J, Hédl R, Jurasinski G, Kopecký M, Schei FH, Grytnes JA. 2017. Resurveying historical vegetation data – opportunities and challenges. *Appl Veg Sci*. 20(2):164–171. <https://doi.org/10.1111/avsc.12269>.
- Körner C. 2003. *Alpine plant life - Functional plant ecology of high mountain ecosystems*. Berlin (DE): Springer.
- Kurtogullari Y, Rieder NS, Arletta R, Humbert J. 2020. Conservation and restoration of *Nardus* grasslands in the Swiss northern Alps. *Appl Veg Sci*. 23(1):26–38. <https://doi.org/10.1111/avsc.12462>.
- Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli FA, Lämmler W, Nobis M, Rudmann-Maurer K, Schweingruber FH, Theurillat JP. 2010. *Flora indicativa: Ecological indicator values and biological attributes of the flora of Switzerland and the Alps*. Bern (CH): Haupt.
- Lasen C. 1982. Vegetazione nivale a *Luzula alpinopilosa* nelle Alpi Feltrine [*Luzula alpinopilosa* snow-bed vegetation in the Alps close to Feltre]. *Stud Trent Sci Nat Acta Biol*. 59:31–40.
- Lasen C. 1983. La vegetazione di Erera-Brendol-Camporotondo [The vegetation of Erera-Brendol-Camporotondo]. *Stud Geobot*. 3:127–169.
- Lelli C, Nascimbene J, Alberti D, Agostini N, Zoccola A, Piovesan G, Chiarucci A. 2021. Long term changes in Italian mountain forests detected by resurvey of historical vegetation data. *J Veg Sci*. 32:e12939. <https://doi.org/10.1111/jvs.12939>.
- Liberati L, Messerli S, Matteodo M, Vittoz P. 2019. Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps. *Alp Bot*. 129(2):95–105. <https://doi.org/10.1007/s00035-019-00223-5>.
- MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A. 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J Env Manag*. 59(1):47–69.
- Matteodo M, Ammann K, Verrecchia EP, Vittoz P. 2016. Snowbeds are more affected than other subalpine – alpine plant communities by climate change in the Swiss Alps. *Ecol Evol*. 6(19):6969–6982. <https://doi.org/10.1002/ece3.2354>.
- Olden JD, Rooney TP. 2006. On defining and quantifying biotic homogenisation. *Global Ecol Biogeogr*. 15(2):113–120. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>.
- Onipchenko VG, Semenova GV. 1995. Comparative analysis of the floristic richness of alpine communities in the Caucasus and the Central Alps. *J Veg Sci*. 6(2):299–304. <https://doi.org/10.2307/3236225>.
- Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernández Calzado R, et al. 2012. Recent plant diversity changes on Europe's mountain summits. *Science*. 336(6079):353–355.
- Peppler-Lisbach C, Stanik L, Könitz N, Rosenthal G. 2020. Long-term vegetation changes in *Nardus* grasslands indicate eutrophication, recovery from acidification, and management change as the main drivers. *Appl Veg Sci*. 23(4):508–521. <https://doi.org/10.1111/avsc.12513>.
- Pignatti E, Pignatti S. 1983. La vegetazione delle Vette di Feltre al di sopra del limite degli alberi [The Vette di Feltre vegetation above tree line]. *Stud Geobot*. 3:7–47.
- Pignatti E, Pignatti S. 2016. *Plant Life of the Dolomites. Vegetation tables*. Heidelberg, Germany: Springer.
- Pignatti S, Guarino R, La Rosa M. 2017. *Flora d'Italia [Flora of Italy]*. 2nd ed. Bologna (IT): Edagricole.
- Podani J. 2006. Braun-Blanquet's legacy and data analysis in vegetation science. *J Veg Sci*. 17(1):113–117. <https://doi.org/10.1111/j.1654-1103.2006.tb02429.x>.
- Porro F, Tomaselli M, Abeli T, Gandini M, Gualmini M, Orsenigo S, Petraglia A, Rossi G, Carbognani M. 2019. Could plant diversity metrics explain climate-driven vegetation changes on mountain summits of the GLORIA network? *Biodivers Conserv*. 28(13):3575–3596. <https://doi.org/10.1007/s10531-019-01837-1>.

- QGIS Development Team. QGIS Geographic Information System. Open Source Geospatial Foundation Project. [accessed 2022 January 3]. <http://qgis.osgeo.org>.
- R Core Team. 2018. R: a language and environment for statistical computing. Vienna (AT): R Foundation for Statistical Computing.
- Rehm EM, Olivas P, Stroud J, Feeley KJ. 2015. Losing your edge: climate change and the conservation value of range-edge populations. *Ecol Evol.* 5(19):4315–4326. <https://doi.org/10.1002/ece3.1645>.
- Ross LC, Woodin SJ, Hester AJ, Thompson DBA, Birks HJB. 2012. Biotic homogenization of upland vegetation: patterns and drivers at multiple spatial scales over five decades. *J Veg Sci.* 23(4):755–770.
- Rumpf SB, Hülber K, Klöner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger S. 2018. Range dynamics of mountain plants decrease with elevation. *Proc Natl Acad Sci U S A.* 115(8):1848–1853. <https://doi.org/10.1073/pnas.1713936115>.
- Schönswetter P, Stehlik I, Holderegger R, Tribsch A. 2005. Molecular evidence for glacial refugia of mountain plants in the European Alps. *Mol Ecol.* 14(11):3547–3555.
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. 2016. How should beta-diversity inform biodiversity conservation? *Trends Ecol Evol.* 31(1):67–80. <https://doi.org/10.1016/j.tree.2015.11.005>.
- Steinbauer MJ, Grytnes J, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E, et al. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature.* 556(7700):231–234. <https://doi.org/10.1038/s41586-018-0005-6>.
- Stevens CJ, Thompson K, Grime JP, Long CJ, Gowing DJG. 2010. Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Funct Ecol.* 24(2):478–484. <https://doi.org/10.1111/j.1365-2435.2009.01663.x>.
- Testolin R, Attorre F, Jiménez-Alfaro B. 2020. Global distribution and bioclimatic characterization of alpine biomes. *Ecography.* 43(6):779–788. <https://doi.org/10.1111/ecog.05012>.
- Tomaselli M, Carbognani M, Foggi B, Petraglia A, Rossi G, Lombardi L, Gennai M. 2019. The primary grasslands of the northern Apennine summits (N-Italy): a phytosociological and ecological survey. *Tuexenia.* 39:181–213.
- Tomaselli M, Petraglia A, Lasen C. 2005. Flora briologica e vegetazione delle vallette nivali nelle Vette di Feltre (Parco Nazionale Dolomiti Bellunesi, Italia settentrionale) [Snow-bed bryological flora and vegetation in the Vette di Feltre Dolomiti Bellunesi National Park, northern Italy]. *Gortania.* 26:111–136.
- Tribsch A. 2004. Areas of endemism of vascular plants in the Eastern Alps in relation to Pleistocene glaciation. *J Biogeogr.* 31(5):747–760. <https://doi.org/10.1111/j.1365-2699.2004.01065.x>.
- Tribsch A, Schönswetter P. 2003. Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. *Taxon.* 52(3):477–497.
- Väre H, Lampinen R, Humphries C, Williams P. 2003. Taxonomic diversity of vascular plants in the European alpine areas. In: Nagy L, Grabherr G, Körner Ch, Thompson DBA, editors. *Alpine biodiversity in Europe. Ecological studies.* Vol.167. Berlin (DE): Springer; p. 133–148.
- Virtanen R, Eskelinen A, Gaare E. 2003. Long-term changes in alpine plant communities in Norway and Finland. In: Nagy L, Grabherr G, Körner C, Thompson DBA, editors. *Alpine biodiversity in Europe.* Berlin (DE): Springer; p. 411–422.
- Vittoz P, Bodin J, Ungricht S, Burga C, Walther GR. 2008. One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *J Veg Sci.* 19(5):671–680. <https://doi.org/10.3170/2008-8-18434>.
- Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O. 2009. Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Glob Change Biol.* 15(1):209–220. <https://doi.org/10.1111/j.1365-2486.2008.01707.x>.
- Vonlanthen CM, Kammer PM, Eugster W, Bühler A, Veit H. 2006. Alpine vascular plant species richness: the importance of daily maximum temperature and pH. *Plant Ecol.* 184(1):13–25. <https://doi.org/10.1007/s11258-005-9048-5>.
- Windmaïßer T, Reisch C. 2013. Long-term study of an alpine grassland: local constancy in times of global change. *Alp Botany.* 123(1):1–6. <https://doi.org/10.1007/s00035-013-0112-9>.