

Short-term vegetation shifts in an alpine grassland under current and simulated climate change

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Abstract

Questions: Recent years have been characterised by extreme climate conditions. Given that high elevations are undergoing enhanced warming and alpine ecosystems provide important services, we ask: Have alpine grasslands experienced rapid vegetation changes over the last five years? Which species are more sensitive to warmer and/or drier conditions?

Location: *Carex curvula* grassland in the southern Alps (Italy).

Methods: Species cover was visually estimated in 20 permanent plots, including both control and climate-manipulated plots, during the period 2017–2022. Climate manipulations, that is, increased temperature and/or reduced precipitation during the snow-free period, started from 2018. Principal component analysis, redundancy analysis and generalised least-squares or linear mixed-effect models were employed to investigate variations in species assemblage and species-specific responses.

Results: Detectable changes were found in species cover over time and between climate manipulations, with warmed plots experiencing greater shifts in species composition compared to controls. At the species level, however, both increases and decreases in cover were observed over time, with only two non-dominant forbs, *Phyteuma hemisphaericum* and *Leucanthemopsis alpina*, showing either increased cover in warmed plots or lower cover values under drier conditions. No treatment effects and the lowest variation across years were found for the two dominant species (the sedge *Carex curvula* and the forb *Alchemilla pentaphyllea*) which together make up more than 70% of vascular plant cover. Despite the short time period investigated, a major cover reduction was observed in all treatments for some snowbed species.

Conclusions: The plant species assemblage of the target alpine grassland was found to be sensitive to short-term manipulations simulating future climate changes, with individual species exhibiting idiosyncratic responses to manipulations and different cover dynamics over time. A decline in some snowbed specialists already seems to be taking place even in these late-successional grasslands – at a rate likely to increase in

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the future—with the majority of other vascular species exhibiting greater resistance to changing environmental conditions.

KEYWORDS

Carex curvula, climate change, climate manipulations, drought, grassland, high elevation, vegetation, warming

1 | INTRODUCTION

The last 10 years have been characterised by some of the warmest years on record (World Meteorological Association, 2023), with warming levels so high that the last year the United Nations has declared that the world is entering an era of 'global boiling' (United Nations, 2023). In this scenario, more attention is being paid to high-elevation areas, regarded as important 'climate hotspots' where analyses of paired stations within the same region show enhanced elevation-dependent warming (Pepin et al., 2022). Advanced flowering and altered length of phenological stages (Jabis et al., 2020; Kudo, 2020; Körner, 2021; Vorkauf et al., 2021), growth enhancement (Elmendorf et al., 2012; Bjorkman et al., 2018), upward shifts in range limits and optima (Rumpf et al., 2018), and evident 'shrubification' (Myers-Smith et al., 2011) are some of the most important changes evidencing that climate-driven alterations are already affecting alpine species and communities (De Boeck et al., 2019). In terms of vegetation composition, however, not all high-elevation communities respond to changes in climate to the same extent (Rosbakh et al., 2014; Gritsch et al., 2016; Matteodo et al., 2016) which is probably the result of differences in microclimate, biotic interactions and natural disturbance regimes (Gritsch et al., 2016).

On numerous mountain summits, for instance, plant communities have been reported as undergoing increasing richness (Grabherr et al., 1994; Pauli et al., 2012; Steinbauer et al., 2018) and vegetation thermophilisation (Gottfried et al., 2012; Wipf et al., 2013) as a result of upward migration and/or species range shifts. On the other hand, small compositional changes have been found in dense, closed alpine grasslands (Vittoz et al., 2009; Windmaier & Reisch, 2013; Gritsch et al., 2016; Matteodo et al., 2016). In detail, weak changes (Matteodo et al., 2016) or no modifications (Windmaier & Reisch, 2013) in species richness and the Shannon–Wiener diversity index were detected in surveys of over 20–30 years for late-successional acidophilous alpine grasslands, leading to the conclusion that these densely vegetated communities, dominated by long-lived plant species, exhibit slow (if any) changes in composition under warming (Körner, 2021). However, another 50-year long resurvey in the European Alps in similar alpine grasslands detected an increase in richness, decreasing cover trends of abundant species and the highest number of extinct species compared with other alpine communities (Cannone & Pignatti, 2014)—a result hypothesised as being mainly driven by anthropogenic changes in climate. Moreover, studies in other alpine meadows in the Tibetan Plateau have reported increases in

the relative abundance of grasses and decreases in that of forbs in response to short-term (four years) experimental warming (Liu et al., 2018; Hu et al., 2021). These apparently contrasting outcomes, together with the increasing frequency and intensity of heat waves and drought (Naumann et al., 2018; Hari et al., 2020; IPCC, 2021) and a 20% summer precipitation reduction predicted for the Southern Alps (Gobiet et al., 2014) could, therefore, make generalisations and long-term predictions on late-successional alpine communities difficult to ascertain. Further studies are needed which also include reduced precipitation, as well as its interaction with warmer temperatures.

Precipitation manipulations have, in fact, revealed that late-successional alpine grasslands may be sensitive to drought, in some cases exhibiting shifts in plant community composition (Liu et al., 2018; Möhl et al., 2023) and in others a decrease in above-ground biomass in response to complete (Gilgen & Buchmann, 2009; Möhl et al., 2023) or partial rainfall exclusion (Zhang et al., 2017) during the growing season. Negative effects on plant growth were greater when water shortage was coupled with simulated heat waves (De Boeck et al., 2016) highlighting how low water availability may interact with higher temperatures, dampening or nullifying the enhancing effects of warming on alpine plant growth. In a meta-analysis on experimental warming studies in Arctic and alpine ecosystems, it has already been reported that plant growth in response to increased temperatures was lower in warmer, drier sites compared to colder, moister ones (Elmendorf et al., 2012). Even at a landscape-level, after four years of experimental warming, it was found that community composition in a Mongolian steppe exhibited greater changes in the moister, lower slope of the study site, which was dominated by *Carex* species (Ronk et al., 2020).

Different responses of alpine species and plant functional groups to drought alone, or coupled with warming, have also been detected (Peterson & Billings, 1982; Winkler et al., 2016; Liu et al., 2018), highlighting differences in drought sensitivity which may lead to altered vegetation composition (Möhl et al., 2023). In addition, Matteodo et al. (2016) concluded that results from long-term studies still leave a large measure of uncertainty about how constant the rate of changes will be in the future (i.e., will remain slow) since accelerated changes in community composition may take place even in dense plant communities if exceptionally dry events take place (Stampfli & Zeiter, 2004; Vittoz et al., 2009; Stanik et al., 2021). Such extreme episodes are already affecting alpine communities, with alpine plant wilting being reported in recent years in various



high-elevation sites in the European Alps (Körner, 2021; Vorkauf et al., 2021; pers. obs.). There is a chance, therefore, that changes in vegetation composition and species abundance may have occurred in alpine grasslands over recent years.

Field experiments enable researchers to assess the effects of climate change on plant communities by simulating future climate scenarios and integrating results with those from observational studies (Smith, 2011; Beier et al., 2012; Hollister et al., 2022). In the present study, we aimed to assess if and how current climate conditions, together with simulated summer warming (ca +1.5 K) and/or precipitation reduction (ca -40%), changed vegetation composition of a *Carex curvula* grassland between 2017 and 2022—a period including some of the hottest and driest years on record (World Meteorological Association, 2023). Investigations were performed using species cover data collected annually in 20 permanent plots, with response variables including community composition, the Shannon–Wiener diversity index and percentage cover of vascular species, mosses and lichens. The main aims of the study were to: (1) assess whether any compositional change took place after five years and, if so, towards which ‘floristic direction’ the target grassland is shifting; (2) determine whether climate manipulations affected vegetation diversity and composition and, if so, test how the magnitude of this change compared with the natural, interannual variation; and (3) investigate cover variation over time of the vascular species, mosses and lichens, identifying those taxa whose dynamics were influenced by climate manipulations. On the basis of the literature reported above, we hypothesised that warming would produce only small (if any) changes in vegetation composition and species diversity of this densely and relatively stable alpine grassland, potentially affecting only those species typical of snowbed communities which have already been found to be more sensitive to climate change. We also expected precipitation reduction to reduce the abundance of some species, in particular affecting snowbed specialists that are usually less drought-resistant, with drought effects exacerbated with the co-occurrence of drier and warmer conditions as a result of increased evapotranspiration and consequent drought-stress.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the Stelvio National Park (Rhaetian Alps), in an alpine grassland located at ca 2700 m a.s.l. (46°21′14″ N, 10°29′24″ E). The snow-free period (June–September) is characterised by a mean air temperature and precipitation of 7.5°C and 380 mm, respectively (Forte et al., 2023). The target ecosystem is a *Carex curvula* All. primary alpine grassland, highly diffuse in the main mountain chains in central Europe and representing the climax vegetation on acidic soils within the alpine vegetation belt above 2400 m (Reisigl & Keller, 1990). The sedge *C. curvula* and the

forb *Alchemilla pentaphyllea* L. are the two dominant taxa (48% and 39% mean relative cover measured in 2017) with only a few other species (all perennial) characterised by high cover values and/or high frequency (occurrence in more than 80% of plots), such as the grasses *Agrostis rupestris* All. and *Poa alpina* L., and the forbs *Leontodon helveticus* Mérat, *Leucanthemopsis alpina* (L.) Heywood, *Ligusticum mutellina* (L.) Crantz, *Phyteuma hemisphaericum* L., and *Soldanella pusilla* Baumg. (see Appendix S1). The only annual species growing in the grassland is *Euphrasia minima* Schlecht. Mosses and lichens are also present throughout the grassland, with *Polytrichum juniperinum* Hedw. and *Cetraria islandica* (L.) Ach. being the most common species for each group, respectively. The community develops on acidic soil (pH 4.3 in the 0–15 cm layer) reaching a mean depth of 31 cm. Wild and domestic herbivores are present in the site—e.g., grasshoppers, ibex, chamois, marmots, cattle and sheep.

2.2 | Experimental design

In summer 2017 (pre-treatment year), twenty permanent plots of 1 × 1 m² were identified at the site, within an area ca 250 m long and 50 m wide located on an east-facing slope of Mt Gavia (3223 m). In 2018, following a randomised block-design consisting of five replicates, plots were randomly assigned to one of the following treatments: no manipulation (C, control), drought (D), warming (W), and drought combined with warming (DW) (Appendix S2). Temperature was passively increased by means of open-top chambers (OTCs) following the International Tundra Experiment guidelines (Hollister et al., 2022), whereas precipitation was reduced using partial rain-out shelters (modified infrastructures of Yahdjian & Sala, 2002) following the International Drought Experiment protocol for short-statured vegetation (Smith et al., 2024). In particular, the imposed ‘drought’ simulated a rainfall reduction equal to the statistically extreme deviation in precipitation relative to long-term, site-specific records (Knapp et al., 2015, 2017). Shelters were, therefore, built so as to reduce the rainfall by ca 43% during the growing season (June–September)—a percentage based on the first percentile of a long-term climate record gathered by two nearby weather stations: Careser Diga (46°25′21.5″ N, 10°41′56.1″ E; 2600 m a.s.l.) and Passo Tonale (46°15′47.9″ N, 10°36′39.8″ E; 1780 m a.s.l.). Shelters consisted of aluminium frames sustaining ten rows of 3 mm thick, V-shaped, UV-transparent sheets of polymethyl methacrylate (PMMA), 12 cm apart and placed at ca 1 m above the canopy surface. Precipitation reduction and increased temperature (DW treatment) were simulated concurrently by placing OTCs under the shelters. Manipulations were carried out exclusively during the growing season, with the experimental setup taking place from 1 to 10 days after snowmelt and the area being entirely fenced to prevent large-herbivore grazing. Exact dates of snowmelt, experimental setup and removal, and plant cover estimation for each year are reported in Appendix S3.



2.3 | Microclimate

To estimate manipulation effects on microclimate, hourly measurements of air temperature (AT, °C) and relative humidity (RH, %) were taken 5 cm above the soil surface during the snow-free period, with two replicates per treatment for the summers of 2018, 2019 and 2021 and one replicate for 2020 (EHT Temperature/RH Sensor, Decagon Devices, Inc., Pullman, WA, USA) and 2022 (ATMOS-14, Decagon Devices, Inc.). Hourly records of soil temperature (ST, °C) were also taken at 5 cm depth in two replicates per treatment (HOBO Pendant® Temperature/Light 64K Data Logger, Part # UA-002-64, HOBO Data Loggers, Burne, MA, USA). In addition, soil moisture expressed as volumetric water content (VWC, %) was measured for the 0–3.8 cm and 0–7.6 cm soil layers using a portable instrument (TDR 100; Spectrum Technologies Inc., Chicago, IL, USA), with records consisting of four measurements per plot taken on 1–9 different dates, depending on the year, during the period between experimental setup and vegetation cover estimates. To quantify shelter performance two precipitation gauges were installed, one under and one outside the rain-out shelters (mm, Rain Collector, Decagon Devices, Inc.). Site-specific climate characterisation was carried out by logging the following additional climate data hourly: AT and RH at ca 20 cm above the ground (Spectrum WD1650) and solar radiation (SR, $W\ m^{-2}$) (Spectrum Technologies, Inc.). Snowmelt time was recorded through direct observations. Mean daily vapour pressure deficit (VPD, hPa) was also calculated from mean daily AT and RH, following Jones (1992) – R package *plantecophys* (Duursma, 2015).

2.4 | Vegetation measurements

Data was recorded annually at the peak of the growing season (ca mid-August) during the pre-treatment year (2017) and the experimental period 2018–2022. To estimate vegetation dynamics in response to treatments and during the experimental period, the cover percentage of vascular species, mosses and lichens was visually estimated in each permanent plot using a 1-m² frame with a 10-cm-mesh grid. Species cover was also used to calculate the Shannon–Wiener diversity index.

2.5 | Data analysis

To explore possible plot compositional shifts at the end of the five years, a principal component analysis (PCA) was performed on Hellinger-transformed cover data, recorded in the pre-treatment year (2017) and in 2022. To assess if temporal shifts represented random interannual variation or directional trends, a PCA on mean species abundances at the treatment level was also performed on Hellinger-transformed data, including all years in the period 2017–2022 (Appendix S4).

To assess whether the Shannon–Wiener index differed across climate manipulations and years, a linear mixed-effect model was fitted to the data, with the fixed component including treatments

(four-level factor), years (numerical variable) and their interaction, together with the Shannon index pre-treatment (2017) value as a covariate; 'plot' was included in the random structure of the model (20-level random intercept term).

Partial redundancy analysis (RDA) was carried out to investigate the influence of climate manipulations and interannual variation on species cover change compared to the pre-treatment year, that is, difference between the cover percentage of each taxon measured in 2017 and the values measured in each experimental year (2018–2022). To compare both the magnitude of species cover variation, and response similarities to manipulations and trends over time, two separate RDAs were performed: the first based on raw cover changes of species cover, and the second based on changes in cover scaled at zero mean and unit variance at species level. In both RDAs, the constrained component included treatment (four-level factor) and year (five-level factor), whereas the conditional component included the block of plots.

Finally, to investigate cover variation at the taxon level over time and under simulated climate change, generalised least-squares (GLS) or linear mixed-effect models (LMMs) were performed for the eight species occurring in all monitored plots (Appendix S1). In these models, the response variable was the species cover, while the fixed component included the year (five-level factor: 2018 to 2022), drought (two-level factor: yes and no), warming (two-level factor: yes and no), and their two- and three-way interactions. In order to account for spatial heterogeneity among plots prior to the experiment, 2017 pre-treatment cover values were also included as a covariate (numerical variable). A top-down model selection was carried out, maintaining only the highly significant interaction terms ($p < 0.01$) in order to obtain conservative results. To cope with repeated surveys within the same plots and heterogeneous variance, for each species alternative random effect and variance structures were tested and compared by means of the Akaike information criterion, with models fitted with restricted maximum likelihood. On the other hand, the fixed-effect selection was carried out with models fitted using maximum likelihood. Models were carried out for vascular species occurring in all the plots, for mosses and lichens, and for the four other vascular species with an uneven distribution but present in more than three plots for each of the two climate factors, drought and warming.

All analyses were performed in R version 4.1.3 (R Core Team, 2022), with the packages *nlme* (Pinheiro et al., 2022) and *vegan* (Oksanen et al., 2022). The graphical output of GLS and LMMs was produced using the package *ggeffects* (Lüdtke, 2018).

3 | RESULTS

3.1 | Climate features

Compared to the 1988–2017 period, the five years of our manipulations (2018–2022) were characterised by higher air temperatures (+1.2 K) and lower precipitation ($-0.22\ mm\ d^{-1}$, corresponding to -6%



precipitation) during the June to August period, as well as lower precipitation occurring in days with sub-zero mean temperatures during the October to May period (-106mm , which corresponds to -26% precipitation) (Appendix S5). There were also differences in climate conditions within the five growing seasons (Figure 1 and Appendix S6). The first principal component (PC1) explained 65.0% of the climate variability, while PC2 explained 17.5%, with the 2021 and 2022 growing seasons situated at the extremes of PC1. The former growing season (2021) was characterised by the highest RH, coupled with the highest rainfall and the coldest AT, whereas in the following year (2022) the maximum proportion of days without rainfall was recorded, together with the highest levels of VPD and SR. This latter variable was negatively correlated with snowmelt time, with a more-than-one-month variation between 2019 (17 June) and 2022 (17 May). The first and most important ordination axis was mainly correlated with variables indicating weather-related moisture (e.g., days without precipitation and vapour pressure deficit), which showed higher yearly variation compared to heat-related variables (i.e., solar radiation and air temperature) (Appendix S6).

Over the study period, shelters reduced precipitation by 40.5% on average. Compared to controls, OTCs increased mean air and soil temperature by 1.5 K and 0.9 K, respectively, in the W treatment, and by 1.9 K and 0.9 K, respectively, in DW. When drought was combined with warming, the VPD was higher ($+0.8\text{hPa}$ in DW compared to C) whereas similar values to controls were recorded in D and W. Compared to controls, soil moisture was lower both under shelters and in OTCs in the 0–3.8 cm and 0–7.6 cm profiles. In the topsoil layer (0–3.8 cm) VWC was reduced by 2.4% and 5.4% in D and W, respectively; the strongest reduction was in DW (-6.2%). In the deeper soil layer (0–7.6 cm) differences in soil moisture were lower compared to controls: -2.3% in D, -4.3% in W and -3.9% in DW. Climate variable mean values measured in treatments are reported in Table 1.

FIGURE 1 PCA correlation biplot of microclimate variables across the experimental period (2018–2022). For each year, data correspond to the period between snowmelt and plant cover estimation date. Microclimate variables: cumulative precipitation (P); proportion of days without precipitation (DWP); solar radiation (SR); air temperature (AT), relative humidity (RH) and vapour pressure deficit (VPD) at ca 20 cm above-ground; snowmelt time (SMT).

3.2 | Compositional change over time

Principal component analysis performed on Hellinger-transformed cover data recorded in the pre-treatment year and after five years (Figure 2) showed that most plots shifted over time to lower scores on the first axis and positive scores on the second axis (details of species abbreviations, frequency and cover percentage recorded in each treatment and growing season are reported in Appendix S1). When compared with climatically manipulated plots, controls appeared to undergo smaller shifts, in particular along the second ordination axis. The first axis, explaining 43.5% of the variation in species cover, correlated positively with *Soldanella pusilla* and negatively with *Ligusticum mutellina*, whereas the second axis, explaining 17.4% of the variance, revealed a difference between plots with a high abundance of *Alchemilla pentaphyllea* (positive scores) and those with a high cover of mosses and lichens (negative scores). This indicates a general trend between 2017 and 2022 characterised by an increase in *L. mutellina* cover and/or decrease in *S. pusilla*, often coupled with an expansion of *A. pentaphyllea* and/or reduction of mosses. Such shifts in the floristic composition did not appear to result from random, interannual variations, but exhibited a directional trend over time, as highlighted by a further PCA showing the complete temporal sequence in the different treatments (Appendix S4).

3.3 | Vegetation responses to climate manipulations: Diversity and composition

Despite this variation in vegetation composition, the Shannon–Wiener diversity index did not significantly differ ($p > 0.05$), either between climate manipulations or across years (Appendix S7), with

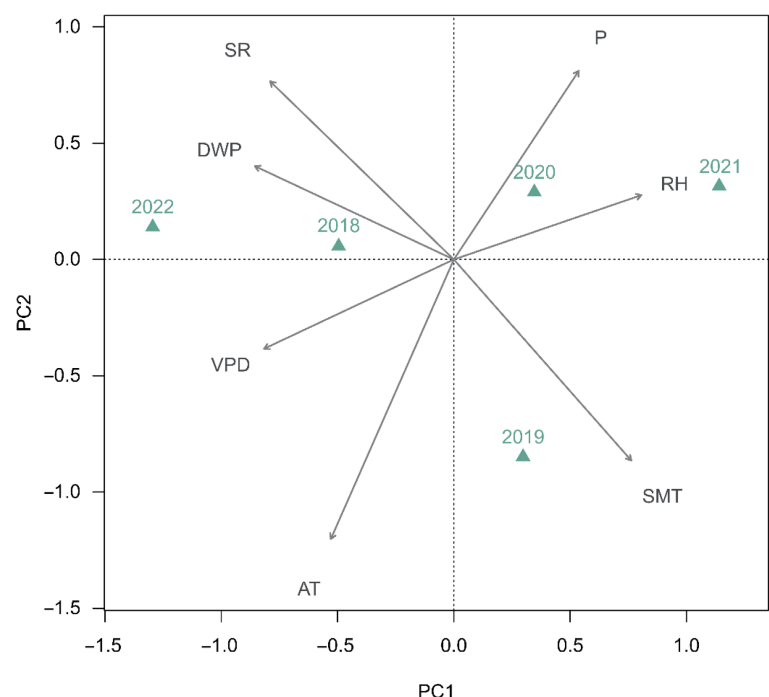


TABLE 1 Mean values (standard error) of environmental variables in the four climate treatments. Values were obtained by averaging seasonal means of daily values (24 hr) gathered during the experimental period 2018–2022 (for each year, from setup of experimental structures until cover estimation date).

	Control	Drought	Warming	Drought + Warming
Precipitation (mm cumulative)	291 (19)	173 (23)	–	–
Air temperature (°C)	10.4 (0.2)	10.8 (0.4)	11.9 (0.3)	12.3 (0.2)
Relative humidity (%)	77.5 (0.6)	77.3 (0.2)	78.1 (0.9)	74.8 (1.8)
Vapour pressure deficit (hPa)	2.9 (0.1)	3.0 (0.1)	3.2 (0.1)	3.8 (0.3)
Soil temperature (°C)	11.1 (0.4)	11.5 (0.3)	12.0 (0.3)	12.0 (0.3)
Volumetric water content 0–3.8 cm (%)	29.8 (2.0)	27.3 (1.9)	24.4 (1.5)	23.6 (1.2)
Volumetric water content 0–7.6 cm (%)	33.0 (2.4)	30.7 (2.2)	28.8 (1.9)	29.1 (2.0)

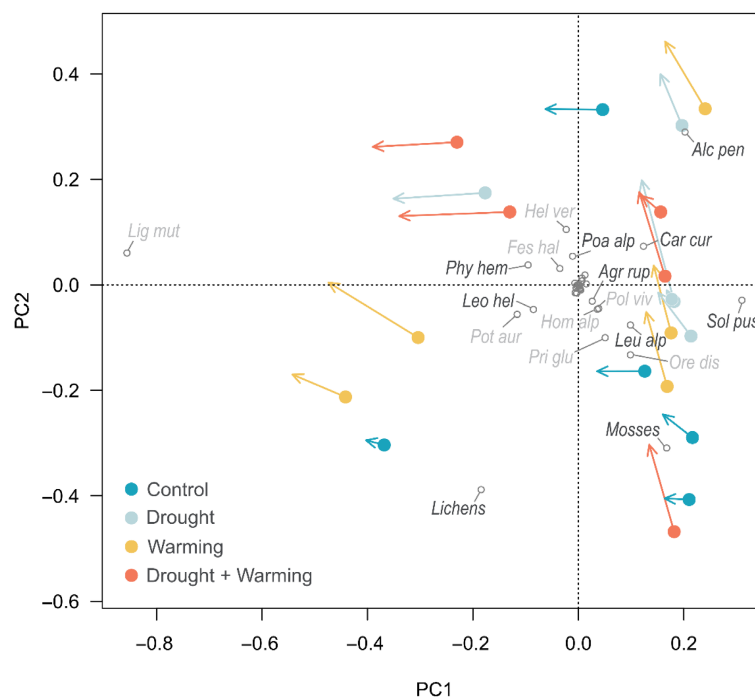


FIGURE 2 PCA correlation biplot of cover data in the pre-treatment year (2017) and the final experimental year (2022). Arrows indicate compositional shifts over time (i.e., the five-year period). The four treatments are reported. Dark grey identifies taxa present in more than 80% of plots. For visual clarity, abbreviations are reported only for the taxa with the most variation. Alc pen, *Alchemilla pentaphyllea*; Agr rup, *Agrostis rupestris*; Car cur, *Carex curvula* subsp. *curvula*; Fes hal, *Festuca halleri* subsp. *halleri*; Hel ver, *Helictotrichon versicolor*; Hom alp, *Homogyne alpina*; Leo hel, *Leontodon helveticus*; Leu alp, *Leucanthemopsis alpina*; Lig mut, *Ligusticum mutellina*; Ore dis, *Oreochloa disticha*; Phy hem, *Phyteuma hemisphaericum*; Poa alp, *Poa alpina*; Pol viv, *Polygonum viviparum*; Pot aur, *Potentilla aurea*; Pri glu, *Primula glutinosa*; Sol pus, *Soldanella pusilla*.

only a significant positive effect of the pre-treatment 2017 value over that of the following years ($F_{1,18} = 120.96$, $p < 0.001$) (Figure 3).

Partial redundancy analysis performed on species cover change compared to the pre-treatment year (Figure 4a) revealed significant variation related to both climate manipulations (pseudo- $F_{3,88} = 6.13$, $p < 0.001$) and time (pseudo- $F_{4,88} = 5.32$, $p < 0.001$). However, the variance explained by this constrained component was not particularly high (20.9% based on adjusted R^2) and similar to that due to spatial variation among blocks (20.5%). Consequently, there was a large unexplained variation (60.9%), suggesting the occurrence of correlated responses of species residuals, likely due to the presence of other relevant environmental drivers not considered in the

present study. When considering raw cover changes (Figure 4a), the ordination was strongly influenced by the variation of the two most abundant species, that is, *Carex curvula*, which exhibited the slightest decrease in control plots, and *Alchemilla pentaphyllea*, which increased the most in warmed plots. Overall, the dominant sedge did not show a consistent trend over time, indicating a fluctuation in its cover during the period investigated. However, giving equal weight to all species (i.e., scaling species data, Figure 4b), the five years are represented by a straight line on the first two canonical axes, suggesting that vegetation is naturally experiencing compositional shifts towards an increase in some taxa (such as *Phyteuma hemisphaericum* and *Agrostis rupestris*) and a decrease in others (such as

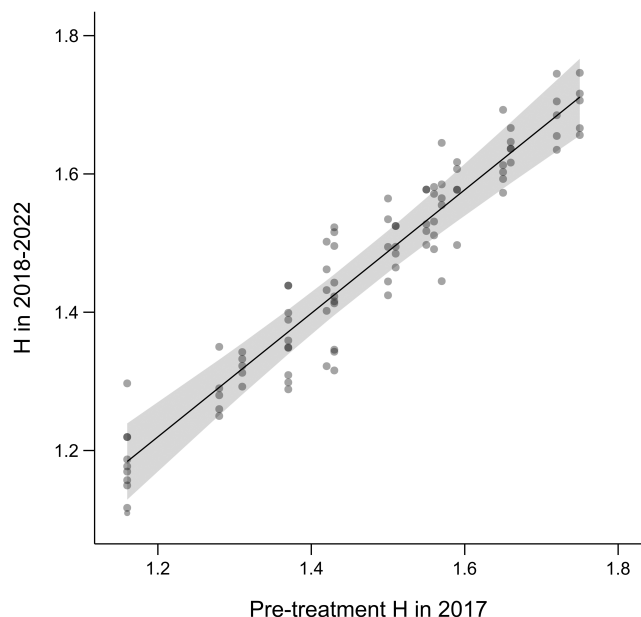


FIGURE 3 Relationship between the Shannon–Wiener index (H) values estimated during the experimental years (2018–2022) and pre-treatment year (2017) values ($p < 0.001$). Dots represent the partial residuals of the model, whereas the grey band the 95% confidence interval.

mosses, *Soldanella pusilla* and *Gnaphalium supinum*). Both ordinations were consistent in revealing a slight but significant role of both treatments and interannual variation, arranged orthogonally, indicating an absence of correlation between climate manipulations and temporal dynamics.

3.4 | Responses of vascular species, mosses and lichens

During the study period, a total of 31 vascular species were monitored within the plots, together with mosses and lichens (Appendix S1). Five vascular species were already present in some plots in 2017 but were then found in new ones during the study period (*Anthoxanthum alpinum*, *Helictotrichon versicolor*, *Polygonum viviparum*, *Potentilla aurea* and *Taraxacum alpinum*); four species were absent in the pre-treatment year, entering the plots during the experiment (*Avenella flexuosa*, *Diphysastrum alpinum*, *Lotus alpinus* and *Veronica bellidioides*); two species present at the beginning disappeared from the study plots during the experimental period (*Hieracium piliferum* and *Pedicularis kernerii*); and, finally, one species was observed during only one year (*Luzula spicata*).

For the eight vascular species present in all plots, most of the variation in cover values during the treatment period (2018–2022) was significantly explained (i.e., positively correlated) by pre-treatment values recorded in 2017 (Table 2, Appendix S8). Only *Phyteuma hemisphaericum* and *Leucanthemopsis alpina*, each with an individual cover below 3%, showed significant responses to climate

manipulations (Table 2, Figure 5): the former exhibited a greater cover increase over time under warmer temperatures compared to ambient conditions (warming $\times$ year interaction $p < 0.001$), while the latter species showed overall lower cover values under drier conditions (drought treatment $p = 0.005$). For the other common species, increased temperature and reduced precipitation did not affect cover values which, instead, significantly differed across years. The three most abundant species (total cover more than 80%, individual relative cover more than 15%) exhibited different trends (Figure 5): *Carex curvula* showed a pronounced oscillation over time, with the lowest values in 2020 and 2021; *Alchemilla pentaphyllea* showed a constant increase over time, whereas *Soldanella pusilla* exhibited a constant reduction. The remaining three species (total cover ca 6%, individual relative cover less than 3%), exhibited either interannual fluctuations (*Leontodon helveticus*) and a cover increase over time (*Agrostis rupestris*) (Figure 5) or no differences between years (*Poa alpina*).

Further analyses performed on four other species, which were unevenly distributed and with low cover values, also revealed a positive correlation between pre-treatment values and those recorded in the following years (with the exception of *Gnaphalium supinum*) and idiosyncratic responses to manipulations and over time (Appendix S8–S10). Significant effects of treatments were detected for the annual *Euphrasia minima* and the dwarf shrub *Salix herbacea*, with the first showing greater interannual fluctuations in warmed plots (warming $\times$ year interaction, $p = 0.004$) and the shrub exhibiting similar cover values in all plots, with the exception of warmer and drier ones, where the lowest cover was recorded (warming $\times$ drought interaction, $p < 0.001$). Cover of the remaining two vascular species, *Gnaphalium supinum* and *Primula glutinosa*, significantly differed across years, exhibiting a constant, declining trend over time.

Finally, mosses and lichens exhibited no significant differences in cover either across treatments or years, with only the 2017 pre-treatment values positively correlated with values observed in the following years (Appendix S8, S9).

The model estimates on the controlling factors of species cover variation for all the analysed taxa are reported in Appendix S11.

4 | DISCUSSION

4.1 | Short-term changes in floristic composition

The first aim of this study was to assess whether vegetation composition changed over the study period (2017–2022) since some of the hottest, driest years were recorded globally during this time frame—a climate trend confirmed at our site with regard to warming (Appendix S5). We found that all 20 plots underwent some degree of compositional change during this period, mainly related to an increase and/or decrease of a small number of species. In particular, between pre-treatment year (2017) and 2022, plots showed an increase in *Ligusticum mutellina* cover and/or a decrease in *Soldanella pusilla*, often coupled with an expansion of *Alchemilla pentaphyllea*

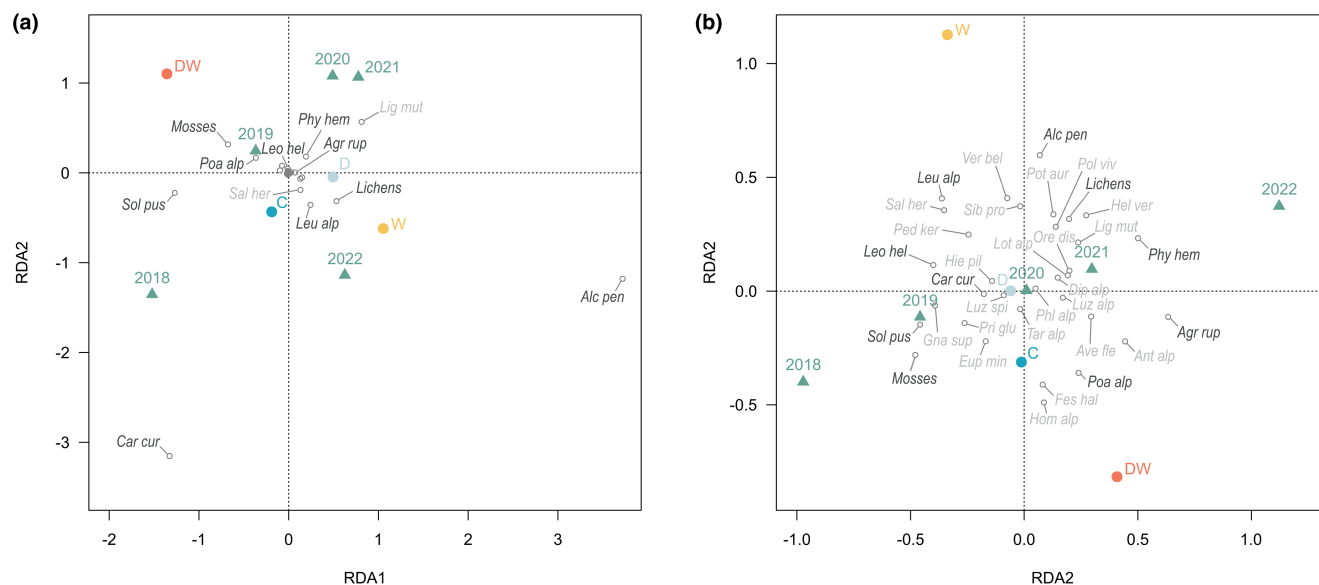


FIGURE 4 Partial RDA correlation biplot of cover variation of vascular species, mosses and lichens across years (2018–2022) and climate manipulations (control, C; drought, D; warming, W; drought + warming, DW). (a) Cover changes compared to pre-treatment, providing abbreviations only for the taxa which vary the most. (b) Scaled cover changes. Dark grey identifies taxa present in more than 80% of plots. *Alc pen*, *Alchemilla pentaphyllea*; *Agr rup*, *Agrostis rupestris*; *Ant alp*, *Anthoxanthum alpinum*; *Ave fle*, *Avenella flexuosa*; *Car cur*, *Carex curvula* subsp. *curvula*; *Dip alp*, *Diphysastrum alpinum*; *Eup min*, *Euphrasia minima*; *Fes hal*, *Festuca halleri* subsp. *halleri*; *Gna sup*, *Gnaphalium supinum*; *Hel ver*, *Helictotrichon versicolor*; *Hie pil*, *Hieracium piliferum*; *Hom alp*, *Homogyne alpina*; *Leo hel*, *Leontodon helveticus*; *Leu alp*, *Leucantheropsis alpina*; *Lig mut*, *Ligusticum mutellina*; *Lot alp*, *Lotus alpinus*; *Luz alp*, *Luzula alpinopilosa* subsp. *alpinopilosa*; *Luz spi*, *Luzula spicata* subsp. *mutabilis*; *Ore dis*, *Oreochloa disticha*; *Ped ker*, *Pedicularis kernerii*; *Phl alp*, *Phleum alpinum*; *Phy hem*, *Phyteuma hemisphaericum*; *Poa alp*, *Poa alpina*; *Pol viv*, *Polygonum viviparum*; *Pot aur*, *Potentilla aurea*; *Pri glu*, *Primula glutinosa*; *Sal her*, *Salix herbacea*; *Sib pro*, *Sibbaldia procumbens*; *Sol pus*, *Soldanella pusilla*; *Tar alp*, *Taraxacum alpinum*; *Ver bel*, *Veronica bellidioides*.

TABLE 2 Results of generalised least-squares or linear mixed-effect models on the controlling factors of species cover variation.

Species	Fixed term	df (N, D)	F-value	p-value	Random intercept	Variance structure
<i>Carex curvula</i>	Year (Y)	4,76	20.31	<0.001	Plot	Ide(Y)
	Pre-treatment	1,18	44.51	<0.001		
<i>Alchemilla pentaphyllea</i>	Year (Y)	4,76	3.76	0.008	Block/Plot	Ide(Y)
	Pre-treatment	1,14	57.87	<0.001		
<i>Soldanella pusilla</i>	Year (Y)	4,76	8.57	<0.001	Plot	Ide(Y) + Pow(Fitted)
	Pre-treatment	1,18	69.80	<0.001		
<i>Poa alpina</i>	Pre-treatment	1,18	4.56	0.047	Plot	–
	Year	4,76	5.05	0.001	Plot	Pow(Pre-treatment)
<i>Phyteuma hemisphaericum</i>	Pre-treatment	1,18	99.48	<0.001		
	Warming (W)	1,17	2.00	0.175	Plot	Ide(Y) + Pow(Fitted)
	Year (Y)	4,72	3.50	0.011		
	Pre-treatment	1,17	22.61	<0.001		
<i>Leucantheropsis alpina</i>	W × Y	4,72	7.02	<0.001		
	Drought	1,93	8.22	0.005	Block	Exp(Fitted)
	Pre-treatment	1,93	17.56	<0.001		
<i>Agrostis rupestris</i>	Year (Y)	4,76	5.54	<0.001	Plot	Ide(Y) + Pow(Fitted)
	Pre-treatment	1,18	49.36	<0.001		

Note: Fixed effects with associated degrees of freedom (df), F- and p-values are shown, as well as random and variance structures. For random intercept, 'I' refers to nested factors, whereas variance structures are coded as follows: 'Ide' indicates that the variance of residuals is allowed to have different spread among the levels of a categorical variable, 'Pow' that the residual variance is a function of the power of the absolute values of a numerical variance covariate, 'Exp' that the residual variance is an exponential function of a numerical variance covariate, and 'ConPow' that the variance of residuals is a function of a constant plus the power function of a variance covariate.

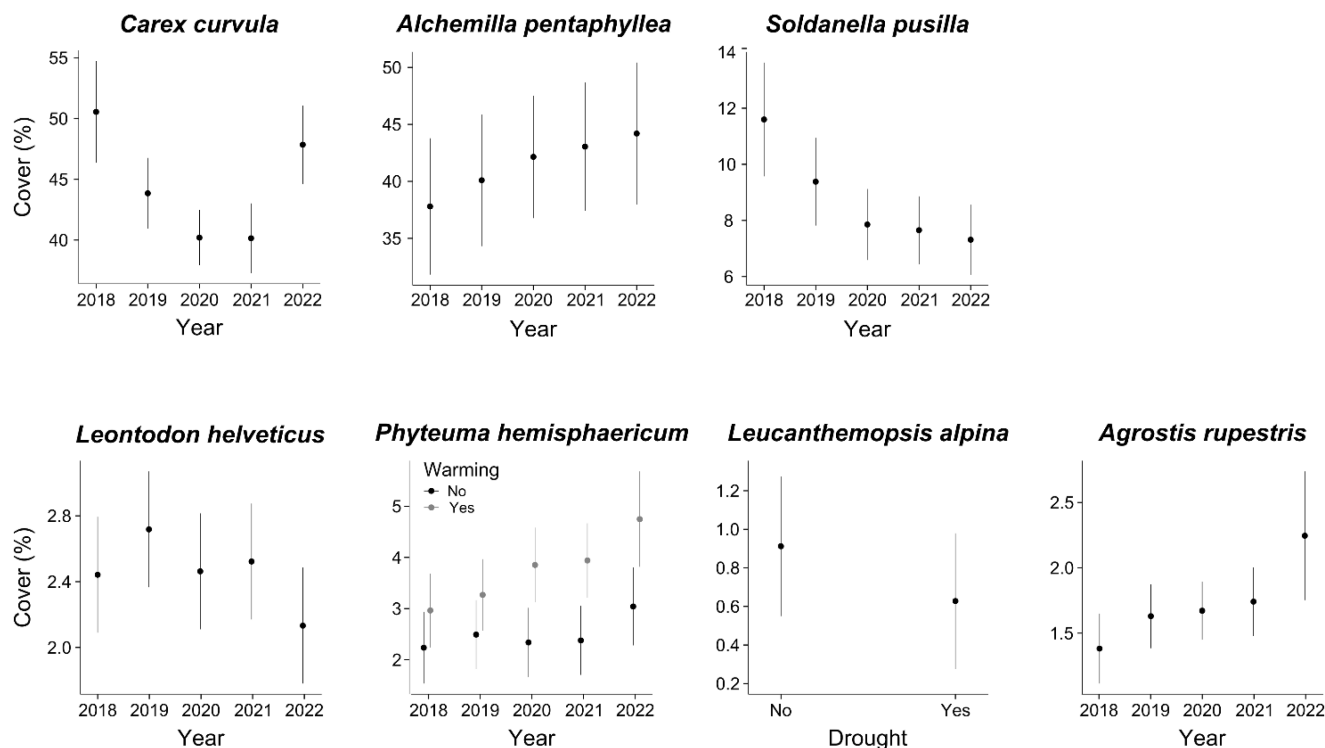


FIGURE 5 Cover percentage of vascular species present in all plots. Results are reported only for significant controlling factors of species cover variation ($p < 0.05$ for single factors, $p < 0.01$ for interactions). Error bars represent 95% confidence intervals.

and/or a reduction of mosses. For all treatments, temporal change trajectories in vegetation composition seemed to be characterised by a consistent directionality over time (Appendix S4), with similar shifts in direction seen in both controls and climate manipulations. This suggests that ongoing, long-term climate change could be driving this phenomenon, as previously observed in alpine plant communities in both the study area (Carbognani et al., 2014) and a nearby site (Cannone & Pignatti, 2014). Results are also in line with observational studies reporting decreased abundance of some chionophilous species (Carbognani et al., 2014), arctic-alpine species (Lesica, 2014), and cryptogams (Elmendorf et al., 2012). In addition, an increased abundance of tall species or species with lateral-shoot spread following warming and/or fertilisation have been found in experimental studies (Klanderud, 2008) – two traits which characterise *Ligusticum mutellina* and *Alchemilla pentaphyllea* on our site, respectively. Notably, the absence of a substantial directional difference among climate manipulations seemed, nevertheless, to be accompanied by greater compositional change for those plots experiencing experimental warmer and/or drier conditions (Figure 2, Appendix S4). A higher rate of change in alpine plant communities with increased warming has, in fact, already been measured for high-elevation sites located on European summits, indicating not only an overall increased richness (five-fold increase in 2007–2016 compared with 1957–1966; Steinbauer et al., 2018) but also a faster transition towards more warmth-demanding, drought-adapted vegetation (Lamprecht et al., 2018). It would appear, therefore, that compositional shifts are already taking place in the short term in response to natural climate change, with induced warmer scenarios

(with or without drought) potentially accelerating ongoing changes in the target alpine grassland. However, it should be noted that when responses to treatments were assessed at the species level, no manipulation effects were observed for the majority of species.

4.2 | Effects of climate manipulations and interannual climate variability on vegetation

The second research aim was to assess the effect of climate manipulations on vegetation and compare this with changes produced by natural, interannual variation in environmental conditions. We found that experimental warming and reduced precipitation coupled with warming significantly affected the abundance of vascular species and cryptogams – a result which partially contrasts with our initial hypothesis of negligible effects of warming on the target alpine grassland. Overall, vegetation change was mainly driven by the two dominant species within the community, that is, the sedge *Carex curvula* and the forb *Alchemilla pentaphyllea* (Figure 3a). Such an outcome is not surprising, since these species exhibit the highest cover values within the plots (Appendix S1) and have, therefore, a higher potential for variation compared to other taxa. Interestingly, *C. curvula* showed lower cover values in all climate manipulations compared to controls, while *A. pentaphyllea* had the highest cover values in the warmed plots. At first this may suggest that warmer, drier conditions in some years could hamper the performance of the dominant sedge. In fact, in a five-year warming experiment, a decreased number of *C. curvula* shoots was detected over time and in OTCs



(Erschbamer, 2001). Liu et al. (2018) also observed a lower growth of the sedges *Kobresia humilis* and *Carex przewalskii* in response to a four-year experiment including active warming and partial precipitation exclusion. However, a recent study by Möhl et al. (2023) reported no significant effects of a five- and 10-week full precipitation exclusion on *C. curvula* cover, suggesting that treatments may not necessarily be driving the trend observed in our study. The dominant forb, on the other hand, appears to have been positively affected by increased temperature in the absence of water limitation, which is in line with the general increasing cover trend found over the five-year study period and which could be related to naturally warmer growing seasons. It is important to note, however, that the effect of climate manipulations did not emerge when the two dominant species were analysed separately, meaning that the effect of climate manipulations at the community-level reflects changes in the overall, multi-species vegetation composition. Nevertheless, the high level of unexplained variance that emerged from canonical ordinations indicates that some other structure in the data, which was not considered in this study, is driving vegetation responses. One such driver could be species associations (either positive or negative) produced by biotic interactions or by other environmental factors (e.g., edaphic ones).

Interestingly, the first canonical ordination, performed on raw cover changes over time, did not show a clear or consistent temporal trend (Figure 4a), which only later emerged when scaled cover values were analysed (Figure 4b). In fact, giving equal weight to all species through scaling produced results suggesting that vegetation is naturally experiencing compositional changes towards an increase of some taxa (i.e., the forb *Phyteuma hemisphaericum* and the grass *Agrostis rupestris*) and a decrease of others (i.e., mosses and the snowbed forbs *Soldanella pusilla* and *Gnaphalium supinum*)—a result consistent with individual analysis for each species.

Outcomes also show that species cover variation due to climate manipulations was slightly lower than that occurring over time, with treatments and years arranged orthogonally in the RDA plot. There was no correlation, therefore, between climate manipulations and temporal dynamics—a result also found in a partial-exclusion precipitation experiment conducted in a *Nardus stricta* mountain grassland (Stanik et al., 2021). Such a response may be explained in the short term by the role played by internal vegetation dynamics, which may be changing in a different direction (in the multidimensional space deriving from species cover changes) as opposed to that induced by simulated climate change. In other words, the abundance of species in these communities depends, to a large extent, on other factors outside the brief of this study, such as biotic interactions or, considering the response of the more chionophilous species, the length of the snow cover period in alpine tundra (Rixen et al., 2022), which might have triggered intrinsic vegetation dynamics. Such changes may occur on a much longer time scale than the one under investigation and could, thus, determine a degree of inertia in the dynamic compositional structure of the vegetation which, in the short term, produces only minor changes in response to warmer temperatures and drought during the short alpine growing season. Elmendorf

et al. (2015) effectively found that vegetation thermophilisation was greater along natural temperature gradients than under experimental warming, with the lower response in treatments explained by the lag in species' biological response to climate change and the slower changes in edaphic conditions.

Finally, no significant effect of either climate manipulations or years was found on the Shannon–Wiener diversity index, a result in line with previous studies on similar alpine grasslands (Windmaier & Reisch, 2013; Matteodo et al., 2016; Hu et al., 2021; Möhl et al., 2023). Overall, findings from our study confirm that plant diversity in these dense, late-successional grasslands is particularly stable in the face of increased summer temperatures, with no short-term effects even when summer precipitation is reduced by 40%. Such a result is probably driven by the absence of above- and below-ground free growing space, together with the presence of long-lived, clonal species (Grabherr, 1989; Körner, 2021). With regard to precipitation reduction, however, it should be noted that the imposed drought treatment was probably not 'extreme' from a physiological point of view (Smith, 2011). This is in line with findings from a meta-analysis assessing effects of extreme experimental drought on gross primary production, where only ca 15% of extreme drought events (i.e., years with precipitation below the fifth percentile of the historical probability distribution of annual precipitation) were found to produce extremely low GPP (Zhang et al., 2019). Moreover, a recent mesocosm study carried out on the same grassland has demonstrated that extreme dry events (i.e., one-month zero precipitation) could potentially boost species composition shifts in these grasslands if soil moisture is reduced below a threshold of 15% (volumetric water content) during the peak production period, determining species-specific plant death (Forte et al., 2023). During the period investigated in our study, such levels of VWC were only reached in the field on one date in July 2022 (see Appendix S1 in Forte et al., 2023). Furthermore, the precipitation reduction treatment produced only minor reductions in mean soil moisture compared to controls (−2.4% and −6.2% in D and DW, respectively, in the 0–3.8 cm layer) and values were always above 20%. When taking into account the entire study period, ambient soil moisture variation was greater than that produced by shelters (Table 1). We conclude, therefore, that no severe water limitation occurred under the drought treatments carried out in our study.

4.3 | Species-specific responses to treatments and over time

The last aim of our study was to identify cover variation for vascular species, mosses and lichens and identify the taxa which were influenced by climate manipulations. No response to enforced warming and/or drought was observed for cryptogams and the majority of species analysed, including the dominant sedge *Carex curvula* and forb *Alchemilla pentaphyllea*. The only species affected by treatments were the forbs *Phyteuma hemisphaericum* and *Leucanthemopsis alpina*, present in all plots but with low relative cover values (<3%),



and the unevenly distributed annual forb *Euphrasia minima* and shrub *Salix herbacea*. Concerning *P. hemisphaericum*, this species exhibited a significant cover increase over time in plots where warming was simulated either singly or combined with drought, while *L. alpina* showed overall lower cover values in plots where precipitation was reduced. These results partially differ from the outcome of a 50-year resurvey conducted in a nearby area, which reported a declining trend for both species under a period of natural warming (Cannone & Pignatti, 2014). The differences observed may be explained by the use, in the present study, of permanent plots which allow cover trend detection of non-dominant species to be more precise, as opposed to semi-permanent plots used by Cannone and Pignatti. Furthermore, Cannone and Pignatti's research dates from 1953 to 2003, with resurveys carried out in a year (2003) in which both a heat wave and drought occurred in Europe (Ciais et al., 2005). With regard to *E. minima*, the species showed greater interannual fluctuations under warming due to higher cover values recorded in warmed plots in 2018, 2019 and 2022. Considering these three summers were the hottest of our five-year record, it is possible that such conditions may have favoured the annual species of our community—a hypothesis supported by results observed on the same species or on co-generic species in other resurvey studies in alpine grasslands and snowbeds (Klanderud, 2008; Carbone et al., 2014; Matteodo et al., 2016). Finally, *S. herbacea* was the only species for which a significant warming $\times$ drought interaction was detected, with the lowest cover in plots where increased temperature and precipitation reduction were combined. Such an outcome is in line not only with the general knowledge that the dwarf shrub is intolerant to prolonged soil drying (Beerling, 1998), but also with recent findings from a dendrochronological study in the Arctic showing a positive correlation between *S. herbacea* ring growth and summer precipitation following analyses of a 65-year-long record (Opała-Owczarek et al., 2024).

With regard to the other vascular species present in the community, significant cover variations were observed among years (2018–2022) with the exception of *Poa alpina*, the cover of which was explained exclusively by initial, pre-treatment values recorded in 2017. The same result was found for mosses and lichens, with differences in cover mainly driven by the initial spatial distribution of the two groups within plots. In contrast, the rest of vascular species exhibited either significant cover oscillations, an increasing trend or a progressive decline.

Interannual cover fluctuations were found for the dominant sedge (*Carex curvula*) and one of the most abundant forbs (*Leontodon helveticus*). Interestingly, *C. curvula* showed a declining trend in the period 2018–2021 (cover drop from 50.5% to 40.1%), but almost regained its initial cover values in 2022 (47.9%). The species appears, therefore, to have a high recovery capacity in the face of environmental changes—a pattern once again highlighting the conservative growth control of this particular sedge. This was recently evidenced by Möhl et al. (2023), with results proving that *C. curvula* above-ground biomass and cover were not reduced by a five- and 10-week summer drought over a six-year study period. A large proportion of

phytomass allocated below-ground, coupled with below-ground apical meristems able to continuously produce new tissue, could enable *C. curvula* to compensate, in the short term, for low rates of above-ground production induced by unfavourable conditions during the growing season (Erschbamer & Winkler, 1995).

Increasing cover trends during the observation period were exhibited by only two out of the eight species present in all plots, that is, the dominant forb *Alchemilla pentaphyllea* (from 37.8% to 44.2%) and the grass *Agrostis rupestris* (from 1.3% to 2.5%), with the latter confirming the positive trends already identified by Windmaier and Reisch (2013) in a similar *C. curvula* sward between 1980 and 2012. With regard to *A. pentaphyllea*, cover increase may be explained by its ability to produce stolons, a trait which could favour species growth under warmer, non-water-limited conditions (Klanderud, 2008). Another species sharing this trait (*Potentilla aurea*) exhibited a similar pattern in our study (from 2.2% to 2.7%). Additionally, a high SLA and N concentration were reported for *A. pentaphyllea*, indicating a high resource acquisition capacity (Choler, 2005) possibly allowing this forb to profit in the short term from potentially higher nutrient concentrations in the soil as a result of naturally warmer conditions.

On the other hand, marked decreasing trends over time were exhibited by snowbed specialists, such as the common *Soldanella pusilla* (from 12.5% to 6.6%) and the unevenly distributed *Gnaphalium supinum* (from 0.12% to 0.02%) and *Salix herbacea* (from 1.04% to 0.17%). Such trends are in line with the already recorded decline of snowbed species in the Alps under global warming (Matteodo et al., 2016). As already evidenced by Carbone et al. (2014), this pattern may result from the balance between potential positive and negative effects of climate and vegetation changes. Longer growing seasons, due to warmer temperatures coupled with reduced snowfall observed in our site (Appendix S5), probably determined an increase in negative plant–plant interactions, as suggested by responses to early-snowmelt and warming experiments in alpine snowbeds (Carbone et al., 2014). This hypothesis is also supported by results in a grazing-exclusion experiment carried out on a *C. curvula* grassland, where snowbed species (including *Gnaphalium supinum*) and short-statured taxa were found to be the species most negatively affected by herbivore removal, which produced increased competition (Kaufmann et al., 2021).

These findings, therefore, confirm once more that idiosyncratic responses to environmental conditions occur even within the same plant functional group (Hu et al., 2021). However, it is interesting to note that when the coefficient of variation (CV) over time was calculated for each species (Appendix S11), not only the direction of change but also the amount of variability was not the same across species. In particular, the two dominant species (*C. curvula* and *A. pentaphyllea*) exhibited a high temporal stability, showing the lowest CV, that is, low interannual variation relative to their own cover. In contrast, the snowbed specialists *Gnaphalium supinum* and *Salix herbacea* were among the species with the highest CV, indicating that the degree of change over time (i.e., decline) was stronger compared to the other species.

Overall, results from this study highlight how shifts in vegetation are currently taking place in response to climate change, although

no detrimental effect of experimental drought was found on cryptogams and on the majority of vascular species. Our results, therefore, partially contradict the initial hypotheses, where no effects of warming or detrimental effects of extreme precipitation reduction on these alpine primary grasslands were envisaged. Results also reconfirm that responses to climate manipulations and environmental changes are species-specific in these particular grasslands, with the local species pool determining the impacts of altered climate conditions (Möhl et al., 2023).

We acknowledge that predictions of long-term changes based on the five-year record analysed are limited, reflecting short-term responses which depend on the sampling baseline and time frame analysed (Körner, 2018). This means that, even given the same experimental setup, outcomes may differ in the long term (Alatalo et al., 2020). For instance, the cover increase for the forbs *A. pentaphyllea* and *P. hemisphaericum* recorded in this study might be counterbalanced in the long term by increased competition from taller species (e.g., *Ligusticum mutellina*). Furthermore, climate change effects on vegetation are obviously contingent on several factors, such as changes in land use (Körner, 2021), how OTCs affect herbivores (Hollister et al., 2022) and how grazers themselves will be affected by climate change (Spence et al., 2014). Despite this, it was interesting to find that changes were effectively detected after 'only' five years in this late-successional grassland—potentially an early sign that vegetation is already responding to increasingly longer, warmer and drier growing seasons. Finally, considering that recent summers have been characterised by generally warmer, drier conditions compared to the climate mean, this may have led to an underestimation of climate manipulation effects.

5 | CONCLUSIONS

Results from this study show that vegetation composition in the target *Carex curvula* grassland exhibited small, natural shifts over a five-year period, a dynamic which appears to have been amplified by forced warming and/or precipitation reduction. Climate manipulations and years significantly explained the variation of the community composition, although analysis suggests that temporal variations are strongest, with vegetation naturally experiencing compositional changes towards an increase of some species and a decrease of others. The species investigated, whether dominant or rare, exhibited either cover fluctuations, reductions, or increases over time, with idiosyncratic responses even within the same plant functional group. The increase of some species under simulated warming (either singly or combined with drought) suggests that future climate scenarios could alter the trajectory of current vegetation dynamics. Plant diversity remained stable over time and was not influenced by climate manipulations. Results from this study highlight, once again, that an overall decline of some chionophilous species is already taking place, probably as a result of ongoing climate warming and naturally occurring climate extremes. Further

monitoring is, however, necessary to assess whether such findings are the result of either transient or permanent species responses to environmental change.

AUTHOR CONTRIBUTIONS

Alessandro Petraglia and Michele Carbognani conceived the project and designed the experiment. All authors planned the research and led the field sampling. T'ai Gladys Whittingham Forte and Michele Carbognani conducted data analysis and interpretation. T'ai Gladys Whittingham Forte wrote the manuscript, which was subsequently critically revised by all the authors.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Appendix S1-S5 and Figures S1-S6.

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