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# Effects of Climate Change vs. Grazing Exclusion on Species Diversity Over 18 Years Along an Elevation Gradient in the European Alps

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Climate change was already shown to increase species numbers in high elevations. In contrast, grazing might interfere with climate change effects. To disentangle both the effects remains a major challenge of alpine ecology. The present study investigated both the effects on species diversity along an elevation gradient in the Austrian Central Alps. We aimed to answer the following questions: How do species diversity and frequency of subalpine–alpine–subnival plant communities change in grazed sites with time? Do competitive plant species increase in the communities? How does grazing exclusion affect species diversity, functional groups, and strategy types? Are environmental changes (temperature, sunshine duration, precipitation) responsible for diversity changes or does grazing override climate effects? The study was carried out for 18 years along an elevation gradient from 1,958 to 2,778 m a.s.l. at Obergurgl (Tyrol, Austria), including six different plant communities. A total of 11 grazing exclusions were established. At each community, the frequency of the species was counted in 1 $m^2$ plots yearly or at least every 3–4 years. Environmental data were obtained from the weather station Obergurgl. Changes of the community parameters and the species composition were analyzed by partial redundancy analyses and mixed-effect models. Species diversity increased with time at all grazed sites, but this increase was suppressed under grazing exclusion. Grazing exclusion effects became pronounced after 5 years. The most consistent result was the increase of bryophytes throughout. At the subalpine grassland, tall-growing species expanded in the exclosures; at the upper alpine *Carex curvula* grassland, snow bed species decreased with grazing exclusion. Among the environmental factors, sunshine duration of the previous year's autumn quartal was found to be the essential variable for the changes. We concluded that diversity increases in grazed communities of the Austrian Central Alps can be attributed to climate change. An indication of slightly reduced and altered weather effects under grazing exclusion was found.

**Keywords: diversity, environmental factors, exclosures, long term monitoring, plant community**

## INTRODUCTION

In view of the ongoing climate warming (Gobiet et al., 2014), biodiversity changes in high elevations are one of the central topics in today's ecological research (Winkler et al., 2019). A severe biodiversity loss is expected worldwide (Un Report, 2019) with major impacts also in high elevations, although probably with some time lags in the alpine zone (Dullinger et al., 2012; Alexander et al., 2018). Data comparing new and old relevés or data from long-term monitoring projects revealed increases in alpine plant species diversity (Grabherr et al., 1994; Holzinger et al., 2008; Pauli et al., 2012; Wipf et al., 2013) with striking accelerations during the last decades (Steinbauer et al., 2018). However, these studies focused on diversity changes of upper summit areas. Plant communities in the alpine zone were less investigated (e.g., Vittoz et al., 2009; Gritsch et al., 2016; Matteodo et al., 2016). Responses to climate change were found to be weak or even missing (Windmaißer and Reisch, 2013) or they were rather heterogeneous (Gritsch et al., 2016). Only snow bed communities seem to be an exception, showing significant changes with time (Matteodo et al., 2016; Liberati et al., 2019).

Especially in the Austrian Central Alps, a long tradition of grazing prevails in high elevations (Vorren et al., 1993; Bortenschlager, 2000). More or less all landscapes from the subalpine to the subnival zone are grazed—even today—by sheep at higher elevations and cattle/horses at the subalpine zone. Cessation of grazing may cause severe changes in community composition (Tasser and Tappeiner, 2002; Dullinger et al., 2003) as shown recently in the Tatra Mts (Czortek et al., 2018), although also accessibility of the sites has to be considered. Mayer and Erschbamer (2017) reported that alpine plant communities exhibit an individualistic reaction to grazing exclusion, depending on the kind of grazers. Abandonment of livestock grazing might decrease short-statured plants and promote competitive species (Vittoz et al., 2009) such as trees (Gehrig-Fasel et al., 2007; Vittoz et al., 2008; Wieser et al., 2019). Generally, the literature shows rather inconsistent results on the effects of grazing in high elevations (review in Pardo et al., 2015), the slow reaction of alpine species to grazing exclusion causing interpretation problems and aggravating predictions (Evju et al., 2009; Pardo et al., 2015).

All in all, alpine ecology has to deal with two major drivers governing diversity and abundance of species. On the one hand, the ongoing warming with mean temperature increases of 1.2°C during the last 55 years in the Austrian Central Alps (Fischer, 2010) might continuously enhance species numbers. On the other hand, permanent grazing activity might reduce species diversity (Song et al., 2020); however, it may also interact with climate change in the way that community changes are decelerated or avoided (Speed et al., 2012; Vowles et al., 2017; Wang et al., 2019) or enhanced during warm and dry periods (Pardo et al., 2015). In the Southern Scandes, Norway, alpine grasslands were found to shift upward by 3 m over 8 years of grazing exclusion (Speed et al., 2012). Such striking effects were never seen in the Alps. However, machine-based models predicted that alpine calcareous pastures with *Carex firma* will be reduced by future climate while *Nardus stricta* and *Carex curvula* pastures will gain distribution area in the Italian mountains (Dibari et al., 2020).

With our study, we aimed to assess ongoing climate change effects in grazed and ungrazed plant communities along an elevation gradient from the subalpine to the alpine and subnival zone in the Austrian Central Alps. We selected seven widespread plant communities and followed the changes in species number, frequency, and composition over time (up to 18 years of monitoring). We expected significant changes in species diversity depending on community type. In order to evaluate the impact of climate change on vegetation structure (Pardo et al., 2015), we classified the species according to functional groups in graminoids, herbs, dwarf shrubs, mosses, and lichens.

Climate change scenarios outline a migration of lowland species toward higher elevations (Pauli et al., 2007, 2012; Lamprecht et al., 2018). Alpine species are known as strictly adapted to the harsh conditions (Körner, 2003), having a limited plasticity compared to species from lower elevations (Gugger et al., 2015). Due to their higher growth rate, competitive species are particularly benefiting from warming (Farrer et al., 2015; Winkler et al., 2019) and the low-statured alpine species are threatened by competitive displacement (Alexander et al., 2015, 2018). Finally, new communities could evolve (Alexander et al., 2015). We expected that such tendencies should be observable with our long-term investigations. We grouped the species by means of the C-S-R strategy concept of Grime (1979), differentiating between competitive, stress-tolerant, and ruderal species. By this, we will be able to answer the question if competitive species tend to increase in the studied communities. However, not only may competitive species increase due to invasions from lower elevations (direct climate change effect, Farrer et al., 2015) but also predominant resident species may inhibit companion species due to their increased growth intensity and competitive ability, provoking "indirect effects" of climate change (Farrer et al., 2015). Consequently, an increase of the competitive species group might be attributed to invasion of new competitive species or by enhanced growth and competition of predominant resident species. In addition to functional attributes, we used also ecological indicator values (Landolt et al., 2010) to detect if increases in temperature values and nitrogen values occurred with time. Calculating indicator values for each studied plant community, we expected to gain information on shifts of community composition and thermophilization tendencies (Pauli et al., 2007, 2012; Gottfried et al., 2012).

Moreover, using regional weather data (temperature, sunshine duration, precipitation) for the whole study period, we aimed to analyze the environmental effects on grazed and ungrazed sites. By this, we tried to disentangle climate and grazing effects and to evaluate if grazing had the power to modify climate-induced changes in diversity (Speed et al., 2013).

Altogether, our objectives were (i) to study changes and environmental effects in species diversity, functional groups, strategy types, and ecological indicator values of all grazed and ungrazed communities; (ii) to investigate the dynamics of species composition; and (iii) to highlight grazing effects on alpine species. The overall goal of this paper was to unravel

environmental vs. grazing effects. The following hypotheses were tested:

H1 Species diversity and frequency of all functional groups (graminoids, herbs, dwarf shrubs, mosses, lichens) will be enhanced with time at all grazed sites.

H2 Competitive strategists and species with high Landolt temperature values (i.e., species from lower elevations or species with wide distribution ranges) as well as species with high nitrogen values will increase at all grazed sites.

H3 Diversity will decrease in grazing exclusion plots.

H4 Changes in temperature, sunshine duration, and precipitation are responsible for diversity changes. Grazing will not override environmental effects.

# MATERIALS AND METHODS

## Study Sites

The investigated sites (**Table 1** and **Supplementary Material 1**) are located along an elevation gradient, from the subalpine to subnival zone at Obergurgl in the inner Ötztal (Tyrol, Austria). The study sites belong to the Long-Term Ecosystem Research Network (LTER) within the Long-Term Socio-Ecological Research (LTSER) platform Tyrolean Alps[1] and LTER-Austria[2]. The subalpine zone (1,960–2,200 m a.s.l.) is grazed by cattle during summer; the alpine and subnival zone (2,300–2,900 m a.s.l.) by sheep; and the area of the sites S03–S05, S06, and S13 by sheep, Haflinger horses, and partly also by goats. Details on number of grazers and stocking rates are given in Mayer et al. (2009).

## Field Work

Permanent plots of 1 $m^2$ were marked at S01–S04, S07–S09, S12, and S14–S16 in 2000; at S06 in 2001; S13 in 2003; and at S05, S10, and S11 in 2005 (**Table 1**). Within fenced exclosures (**Table 1**), three ungrazed × 1 $m^2$ plots were established per exclosure site together with three × 1 $m^2$ plots as controls outside the fence. At the grazed sites without exclosures (**Table 1**), six × 1 $m^2$ plots were installed. The sites were monitored regularly (except 2007 when monitoring was restricted to S05, S10, and S11) till 2018 (**Table 1**) by means of a frequency frame, divided into 100 subplots of 1 $dm^2$. Within each subplot, presence/absence of the species and the functional groups (graminoids, herbs, dwarf shrubs, mosses, lichens) were recorded. The total frequency per 1 $m^2$ was given as percentage of the 100 subplots.

The nomenclature of vascular plant species follows Fischer et al. (2008); bryophytes (with exception of *Polytrichum* species, which were identified at the genus level) and lichens were treated as functional groups. Some lichens were identified at the species level (*Cetraria islandica*, *Peltigera aphthosa*) and integrated in the species analyses. Vascular species not present at the first monitoring but present in 2018 were defined as newcomers. The frequency sum of each species/functional group per plot was calculated for each sampling year.

## Statistical Analyses

Statistical analyses and graphs were done using PRIMER 7 with the PERMANOVA + add-on (Anderson et al., 2008; Clarke and Gorley, 2015), CANOCO 5.12 (Ter Braak and Šmilauer, 2018), and R 3.6 (R Core Team, 2019) with packages lme4, lmerTest, effects, ggplot2, and grid.

The plant communities were grouped by means of a principal coordinate ordination (PCO, PRIMER) with Bray–Curtis similarity of square-root-transformed species data (**Table 1** and **Supplementary Material 2**). Seven communities were distinguished: siliceous subalpine *Agrostis–Festuca* grassland (one exclosure, one control, S01), siliceous lower alpine *Nardus stricta* grassland (three exclosures, three controls, S02–S04), siliceous upper alpine *Carex curvula* grassland (three exclosures, three controls, S07–S09), siliceous lower alpine peat bog (three exclosures, three controls, S05, S10, S11), calcareous upper alpine *Kobresia* grassland (one exclosure, one control, located at the Rotmoos glacier foreland, S06; one grazed subnival site, no exclosure, S14), siliceous lower alpine *Festuca nigrescens* grassland (one grazed site, no exclosure, S13), and siliceous subalpine dwarf shrub communities (S12, S15, S16, all of them grazed, no exclosure, **Table 1**). Dominant species per site are shown in **Table 1** and more comprehensively in **Supplementary Material 3**. In total, 33 × 1 $m^2$ plots were monitored inside the exclosures and 33 × 1 $m^2$ outside the exclosures (controls). These plots were analyzed to detect exclosure effects. To detect climate change effects, a total of 63 × 1 $m^2$ grazed plots were analyzed.

For the functional groups, frequency sums (graminoids, herbs, dwarf shrubs, mosses, and lichens) and frequency fractions were calculated. C-S-R strategies were extracted from Flora Indicativa (Landolt et al., 2010) and converted to numeric indicators (values 1/3, 2/3, 1 according to the number of letters per strategy type; for instance, CCS was converted to 2/3 value C). For further calculations, weighted sums and fractions of total sum were used. Landolt indicator values temperature, light, nitrogen, and soil reaction were checked in Flora Indicativa (Landolt et al., 2010) and calculated as weighted means of species frequencies (omitting species without indicator values).

The temporal changes of all grazed communities (**Table 1**) and their species composition were analyzed by partial redundancy analyses (pRDA on correlations, CANOCO) testing for linear trends (year as metric variable) and for additional non-linear fluctuations around this trend (year as categorical variable). To isolate these effects, and to account for repeated measures, the large differences between plots were partialed out. Species frequencies were square-root transformed and species with $< 5$ presences excluded. All significance tests were done with 4,999 Monte-Carlo permutations (giving minimal $p$-values of 0.0002).

Univariate analyses of the diversity parameters [total frequency N, species number S, Pielou evenness J, and Shannon diversity $H'$ ($\log_2$)] and all species (bryophytes were regarded as species, though being a functional group; the functional group containing bryophytes and *Polytrichum* spp. was called "mosses") were done for a screening of the same effects (year as metric

[1]http://www.lter-austria.at/ta-tyrolean-alps

[2]https://www.lter-austria.at/

**TABLE 1 |** Overview on the sites and their elevation (m above sea level, a.s.l.), description of the plant communities and the dominant species, number of grazed and ungrazed plots per community, size of the fence in m, and sampling years.

| Site | Ma.s.l. | Description | Dominant species | Plot no. | Fence size (m) | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2011 | 2014 | 2018 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S01 | 1,958 | Subalpine ***Agrostis-Festuca*** grassland | *Agrostis capillaris*<br>*Festuca rubra* | 3 grazed<br>3 ungrazed | 12 × 12 | + | | | + | + | + | + | | + | + | + | + |
| S02 | 2,292 | Lower alpine ***Nardus stricta*** grassland | *Nardus stricta*<br>*Potentilla aurea* | 3 grazed<br>3 ungrazed | 6 × 6 | + | + | + | + | + | + | + | | + | + | + | + |
| S03 | 2,310 | Lower alpine ***Nardus stricta*** grassland | *Nardus stricta*<br>*Scorzoneroides helvetica* | 3 grazed<br>3 ungrazed | 12 × 12 | + | + | + | + | + | + | + | | + | + | + | + |
| S04 | 2,320 | Lower alpine ***Nardus stricta*** grassland | *Nardus stricta*<br>*Geum montanum* | 3 grazed<br>3 ungrazed | 6 × 6 | + | + | + | + | + | + | + | | + | + | + | + |
| S07 | 2,576 | Upper alpine ***Carex curvula*** grassland | *Carex curvula*<br>*Gnaphalium supinum* | 3 grazed<br>3 ungrazed | 6 × 6 | + | + | + | + | + | + | + | | + | + | + | + |
| S08 | 2,592 | Upper alpine ***Carex curvula*** grassland | *Carex curvula*<br>*Avenula versicolor* | 3 grazed<br>3 ungrazed | 12 × 12 | + | + | + | + | + | + | + | | + | + | + | + |
| S09 | 2,590 | Upper alpine ***Carex curvula*** grassland | *Carex curvula*<br>*Geum montanum* | 3 grazed<br>3 ungrazed | 6 × 6 | + | + | + | + | + | + | + | | + | + | + | + |
| S05 | 2,265 | Lower alpine **peat bog** | *Carex nigra*<br>*Eriophorum angustifolium* | 3 grazed<br>3 ungrazed | 12 × 12 | | | | | | + | + | + | | + | + | + |
| S10 | 2,270 | Lower alpine **peat bog** | *Nardus stricta*<br>*Carex nigra* | 3 grazed<br>3 ungrazed | 12 × 12 | | | | | | + | + | + | | + | + | + |
| S11 | 2,261 | Lower alpine **peat bog** | *Trichophorum cespitosum*<br>*Carex rostrata* | 3 grazed<br>3 ungrazed | 12 × 12 | | | | | | + | + | + | | + | + | + |
| S06 | 2,289 | Upper alpine ***Kobresia*** grassland | *Kobresia myosuroides*<br>*Poa alpina* | 3 grazed<br>3 ungrazed | 12 × 12 | | + | | + | + | + | + | | + | + | + | + |
| S14 | 2,778 | Upper alpine ***Kobresia*** grassland | *Festuca pumila*<br>*Kobresia myosuroides* | 6 grazed | | + | | | + | + | | | | + | + | + | + |
| S13 | 2,292 | ***Festuca nigrescens*** grassland | *Festuca nigrescens*<br>*Nardus stricta* | 6 grazed | | | | | + | + | | | | + | + | + | + |
| S12 | 2,040 | Subalpine **dwarf shrub** (tall) | *Rhododendron ferrugineum*<br>*Vaccinium* spp. | 6 grazed | | + | | | + | + | | | | + | + | + | + |
| S15 | 2,250 | Subalpine **dwarf shrub** (prostrate) | *Loiseleuria procumbens*<br>*lichens* | 6 grazed | | + | | | + | + | | | | + | + | + | + |
| S16P | 2,334 | Potentially **dwarf shrub** (ski piste) | *Festuca nigrescens,*<br>*Achillea millefolium* agg. | 3 grazed | | + | | | + | + | | | | + | + | + | + |
| S16H | 2,335 | **Dwarf shrub** (close to the ski piste) | *Vaccinium* spp.<br>*Potentilla aurea* | 3 grazed | | + | | | + | + | | | | + | + | + | + |

*For further explanation, see text. Community names are given in bold.*

variable and year as categorical variable) by linear mixed-effect models with plot as random factor (done in R). Significances were Bonferroni-corrected for the number of species tested. The strength of time trends of all community parameters (diversity, functional group, C-S-R strategy, Landolt indicator values) was shown graphically, using the loadings of axis 1 from pRDA.

Exclosure effects on species composition were tested by PERMANOVA (also with plot as random factor, 4,999 permutations) using Bray–Curtis distances of square-root-transformed species frequencies. Effects should appear as differences in the changes over time between the fenced and grazed plots, therefore, the interaction "exclosure × years (categorical)" was the target effect for this analysis. Also for the exclosure effects, univariate analyses were performed for diversity parameters and single species, again using mixed-effect models but now with the focus on the interaction "exclosure × years."

Data from the weather station Obergurgl (1,938 m a.s.l.) were obtained by © ZAMG (Christian Posch 18/02/2020), spanning the years 1999–2018. Quartal means of air temperature in 200 cm height, sunshine duration, and precipitation sums were calculated for months 1–3 (Q1 winter), 4–6 (Q2 spring), 7–9 (Q3 summer), and 10–12 (Q4 autumn). Two quartals of the previous year (*_Q3p, *_Q4p) were included to allow analysis of delayed weather effects. The weather data were used as explanatory variables for the community parameters of all samples in a pRDA and tested for simple and conditional effects (using CANOCO's summarize-effects option).

In all analyses, the repeated measures of plots were taken into account, as covariates in partial analyses or as random factor in mixed-effect models.

# RESULTS

## Changes in Grazed Communities Over Time

All grazed communities showed more or less pronounced changes over time. Variation partitioning (**Table 2**) revealed that across all sites a common linear trend of change accounted for 27.3% of the variation (Yr, range for communities 17.4–35.5%) and another 13.2% were due to synchronous fluctuations between years (Yrc, range for communities 7.9–42.3%). These fractions refer to the variation remaining after accounting for the very large plot (and site) differences (86.2% of the total variation, range for communities 26.3–81.4%). The time effects were highly significant throughout ($p < 0.001$, except effect of Yrc in the peat bog). The diversity parameters species number S, frequency N, Pielou evenness J, and Shannon index H′ increased at all grazed communities (**Figure 1**). The increases of S and H′ were lowest at the peat bog and highest at the subalpine *Agrostis–Festuca* grassland. Also J increased with time with exception of the *Festuca nigrescens* grassland. Lowest changes per site occurred at S15 and S11. Details on diversity changes per site are reported in **Supplementary Material 4**.

Among the functional groups, clear linear increases resulted in all grazed communities for mosses (**Figure 1**). All other functional groups exhibited divergent increasing/decreasing patterns especially when considering the relative values. Small changes occurred in dwarf shrubs and in lichens (**Figure 1**). The competitive strategists decreased mainly at the *Carex curvula* and *Kobresia* grassland while stress tolerators decreased at the *Agrostis–Festuca* and *Nardus stricta* grassland (**Figure 1**). Temperature values decreased at the *Agrostis–Festuca* and *Festuca nigrescens* grassland, light values at the *Nardus stricta* grassland, the peat bog, and the *Festuca nigrescens* grassland. Nitrogen and soil reaction showed minor changes with exception of the *Agrostis–Festuca* grassland where these values remarkably increased (**Figure 1**).

Changes at the grazed sites did not follow a straight trajectory even if the main change occurred along axis 1 of the pRDA (**Figure 2**). There were remarkable fluctuations between the years 2000 and 2003, and also 2005 and 2008. The most relevant species/species groups for the changes were bryophytes, *Polytrichum* spp., *Phyteuma hemisphaericum*, *Pinus cembra* (newcomer), *Luzula multiflora*, *Pseudorchis albida*, and one species which disappeared during the second half of the study period (*Diphasiastrum alpinum*, **Figure 2**).

Bryophyte frequencies linearly increased throughout the years ($p < 0.001$, 17 plots, **Table 3**) with steepest increases at S01, S10–S12, and S16P (**Supplementary Material 5**). A broad variety of herbs (*Phyteuma hemisphaericum*, *Scorzoneroides helvetica*, *Homogyne alpina*, *Geum montanum*, *Campanula scheuchzeri*, *Leucanthemopsis alpina*, *Veronica alpina*) and graminoids (*Nardus stricta*, *Anthoxanthum odoratum* agg., *Carex curvula*, *Poa alpina*, *Festuca halleri*, *F. nigrescens*) had significant linear increases together with one lichen (*Cetraria islandica*, **Table 3**). Only one species (*Salix herbacea*, **Table 3**) showed significant decreases over time.

## Grazing Exclusion Effects

Across all sites (without the peat bog because of later installation of the exclosure fences), diversity was significantly lower within the fences than in the controls outside (species number S and Shannon index H′: $p < 0.001$, mixed effect models), and the effect started to appear after 5 years of exclosure (**Figure 3**).

Regarding functional groups, only at the *Agrostis–Festuca* grassland was the exclusion effect strong with responses of both graminoids ($p < 0.001$) and herbs ($p = 0.012$). At the *Nardus stricta* grassland, there was a decrease in graminoids ($p = 0.018$) and at the *Carex curvula* grassland in herbs ($p < 0.001$), while none of the functional groups were significantly affected by grazing exclusion at the peat bog and the *Kobresia* grassland.

Grazing exclusion effects on species composition were not consistent across the plant communities. PERMANOVA results revealed that 8 out of 11 sites were significantly affected by grazing exclusion (**Table 4**). Two of the three sites at the *Nardus stricta* grassland (S03, S04) and the *Carex curvula* grassland (S07, S09), respectively, showed significant exclusion effects. Also at the peat bog only two sites had significant exclosure effects (S05, S10) while on the wettest site S11 weakest changes occurred ($p = 0.07$). Exclosure plots diverged also at the *Agrostis–Festuca* grassland (S01) and the *Kobresia* grassland (S06) from the control plots ($p = 0.0002$, **Table 4**). Within the exclosures, different species were significantly affected by grazing exclusion; some

**TABLE 2 |** Results of the pRDA (of all diversity parameters, total frequency, C-S-R strategies, and Landolt indicator values): changes over time for all grazed sites and grazed communities separately.

| | All sites | *Nardus stricta* | *Carex curvula* | Peat bog | Dwarf shrub | *Kobresia* | *Agrostis-Festuca* | *Festuca nigrescens* |
|---|---|---|---|---|---|---|---|---|
| Number of sites | 17 | 3 | 3 | 3 | 4 | 2 | 1 | 1 |
| Samples | 510 | 99 | 99 | 54 | 126 | 69 | 27 | 36 |
| EV pRDA1 | 0.0527 | 0.1148 | 0.1834 | 0.0343 | 0.0782 | 0.2069 | 0.3545 | 0.1956 |
| Correlation Yr-pRDA1 | 0.6876 | 0.6483 | 0.7446 | 0.8392 | 0.794 | 0.5802 | 0.8255 | 0.7158 |
| **Variation partitioning (of partial variation after accounting for plot differences)** | | | | | | | | |
| Linear trend (Yr) | 27.3% | 17.4% | 35.5% | 17.4% | 35.0% | 20.7% | 35.4% | 26.1% |
| Non-linearity (additional by Yrc) | 13.2% | 15.4% | 24.1% | 11.4% | 7.9% | 42.3% | 31.2% | 29.4% |
| **Variation partitioning (of total variation)** | | | | | | | | |
| Plot | 86.2% | 52.3% | 66.1% | 81.4% | 80.5% | 56.4% | 26.3% | 54.7% |
| Linear trend (Yr) | 3.8% | 8.3% | 12.0% | 3.2% | 6.8% | 9.0% | 26.1% | 11.8% |
| Non-linearity (additional by Yrc) | 1.8% | 7.3% | 8.2% | 2.1% | 1.5% | 18.4% | 23.0% | 13.3% |
| Unexplained | 8.2% | 32.0% | 13.7% | 13.3% | 11.1% | 16.1% | 24.6% | 20.2% |
| **Significances of explanatory variables** | | | | | | | | |
| p (Yr) | 0.0002 | 0.0002 | 0.0002 | 0.0002 | 0.0002 | 0.0002 | 0.0002 | 0.0002 |
| p (Yrc \| Yr) additional non-linearity | 0.0002 | 0.0006 | 0.0002 | 0.0516 | 0.0004 | 0.0002 | 0.0008 | 0.0010 |

*Test of linear time changes (variable Yr) and superimposed non-linearity (variable Yrc), after partialing out plot differences. Variation partitioning is given with respect to total variation and to partial variation (after accounting for plot differences).*

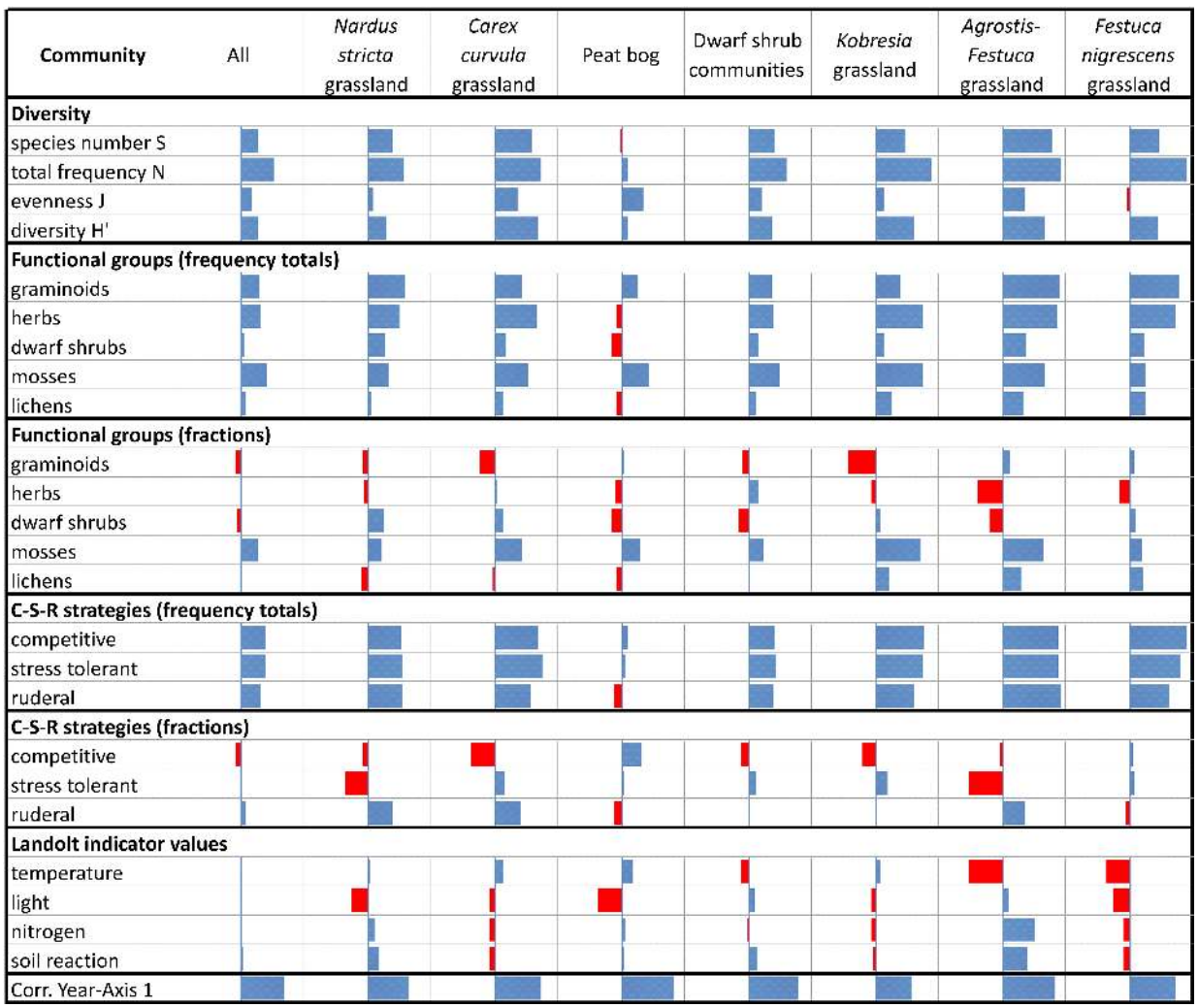



**FIGURE 1 |** Strength of time trend of community parameters (grazed sites): loadings on axis 1 (correlations) from pRDA representing the linear increase or decrease over time (range of bars −1 to +1). Bottom line shows correlation of explanatory variable Yr with pRDA axis 1. Results shown for the seven communities and for all communities together.

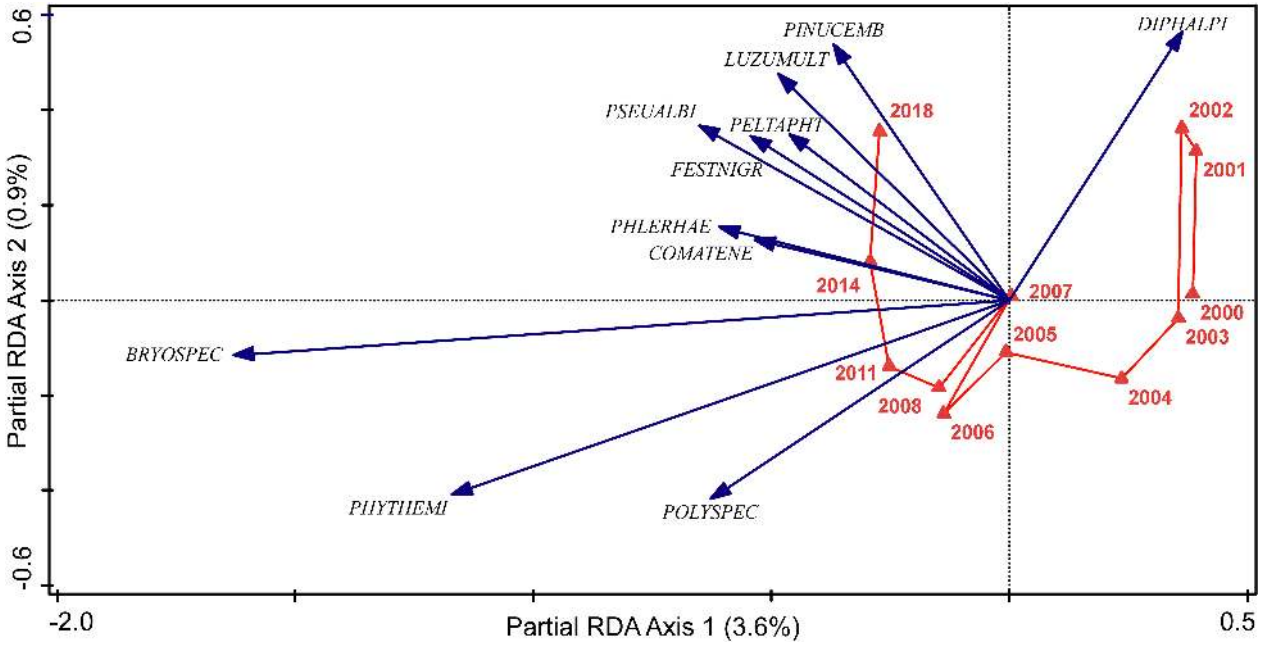



**FIGURE 2 |** Changes of the grazed sites from 2000 to 2018. The most relevant species (fit > 2%) are plotted as vectors (POLYSPEC = *Polytrichum* species, PHYTHEMI = *Phyteuma hemisphaericum*, BRYOSPEC = brophyte species, COMATENE = *Comastoma tenellum*, PHLERHAE = *Phleum rhaeticum*, FESTNIGR = *Festuca nigrescens*, PSEUALBI = *Pseudorchis albida*, PELTAPHT = *Peltigera aphthosa*, LUZUMULT = *Luzula multiflora*, PINUCEMB = *Pinus cembra*, DIPHALPI = *Diphasiastrum alpinum*). Partial RDA with plot as covariate, Monte-Carlo p = 0.0002, explained variation of axes indicated.

enhanced their frequency, and some decreased considerably with respect to the controls. At the *Nardus stricta* grassland, within the exclosures bryophytes increased after 10 years and *Geum montanum* from the beginning; *Anthoxanthum odoratum* agg. first increased more than in the controls but decreased in the end (**Figure 4**). At the *Carex curvula* grassland, snow bed species (*Sibbaldia procumbens*, *Gnaphalium supinum*) decreased in the exclosures while the dominating *Carex curvula* was not affected (the species showed parallel changes of exclosures and controls, **Figure 4**). At the peat bog, only *Carex rostrata* increased in the exclosures. At the *Agrostis–Festuca* grassland, increasing species were *Geranium sylvaticum* (in the last years) and *Potentilla aurea* (only temporarily over 10 years), whereas some graminoids (*Nardus stricta*, *Poa alpina*) and other herbs decreased (*Trifolium pratense* ssp. *nivale*, *Galium anisophyllon*, *Leontodon hispidus*) (not all species shown in **Figure 4**). At the *Kobresia* grassland, the dominant *Kobresia myosuroides* further increased, *Minuartia gerardii* increased temporarily during the first 10 years, and *Sedum atratum* reacted unclearly, because it was initially present only in the exclosure plots where it rapidly decreased toward the controls.

**TABLE 3 |** Selection of species with significant increase/decrease (only *Salix herbacea*) over time (linear trend), number of grazed plots with presences, slope for Yr ± S.E., and Bonferroni-corrected *p*-values (*p*).

| Species | No. plots | Slope Yr ± S.E. | *p* |
|---|---|---|---|
| Bryophyta | 17 | 2.07 ± 0.14 | <0.000001 |
| *Cetraria islandica* | 13 | 0.87 ± 0.11 | <0.000001 |
| *Potentilla aurea* | 13 | 0.75 ± 0.10 | <0.000001 |
| *Phyteuma hemisphaericum* | 12 | 0.61 ± 0.07 | <0.000001 |
| *Nardus stricta* | 11 | 0.57 ± 0.11 | 0.000038 |
| *Polytrichum* spp. | 11 | 1.09 ± 0.15 | <0.000001 |
| *Scorzoneroides helvetica* | 11 | 1.30 ± 0.11 | <0.000001 |
| *Anthoxanthum odoratum* agg. | 10 | 1.53 ± 0.17 | <0.000001 |
| *Carex curvula* | 10 | 0.36 ± 0.06 | 0.000004 |
| *Homogyne alpina* | 10 | 1.91 ± 0.14 | <0.000001 |
| *Geum montanum* | 9 | 0.61 ± 0.09 | <0.000001 |
| *Poa alpina* | 9 | 0.69 ± 0.15 | 0.000717 |
| *Campanula scheuchzeri* | 8 | 1.18 ± 0.16 | <0.000001 |
| *Festuca halleri* | 8 | 1.08 ± 0.18 | <0.000001 |
| *Festuca nigrescens* | 8 | 1.76 ± 0.21 | <0.000001 |
| *Leucanthemopsis alpina* | 8 | 0.61 ± 0.12 | 0.000076 |
| *Salix herbacea* | 8 | −0.71 ± 0.19 | 0.032456 |
| *Veronica alpina* | 8 | 0.42 ± 0.10 | 0.002640 |

## Environmental Effects

Increases of temperature at Obergurgl from 1999 till 2018 ranged from 0.03 to 0.08°C per year for the different quartals. The weather effects on the community parameters proved to be highly significant and mostly consistent across the communities (pRDA with site as covariate, $p = 0.0002$). Interestingly, the sunshine duration of the previous autumn quartal ($p = 0.003$) had by far the highest explanatory power (11.8% explained variation) and defined the first pRDA axis, which was highly correlated with total frequency, bryophytes, competitive and stress-tolerant species, and to a lesser degree diversity (**Figure 5**;

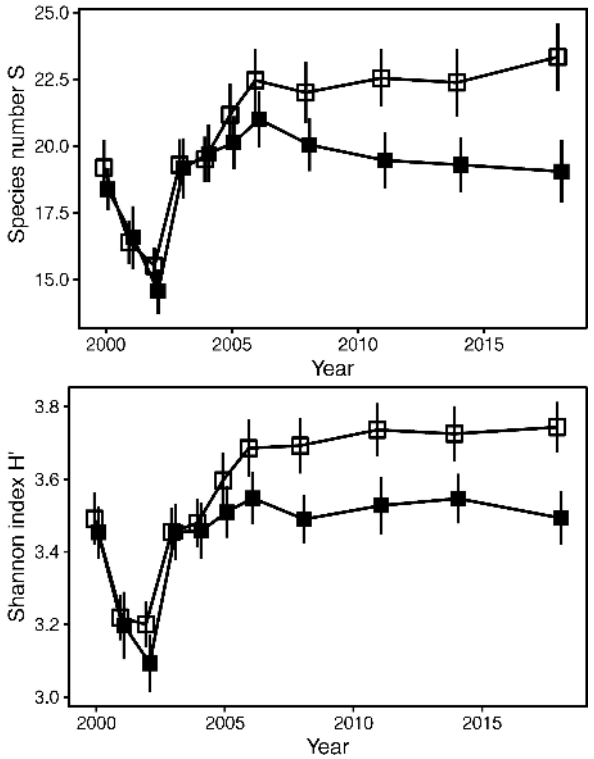



**FIGURE 3 |** Grazing effects on diversity [species number S and Shannon index H′ ($log_2$)]: time courses for exclosure and control plots diverging after 5 years. Means ± S.E. for exclosure plots (filled squares) and grazed control plots (open squares). Sites with later installation of fences excluded (peat bog: fences in 2005).

**TABLE 4 |** Exclosure effects (exclosure × year interaction) on species composition of the communities and single sites.

| Community | Site | df | SS | MS | Pseudo-F | p |
|---|---|---|---|---|---|---|
| *Nardus stricta* grassland | All | 10 | 1928 | 192.8 | 2.04 | **0.0030** |
| | S02 | 10 | 738.2 | 73.82 | 1.18 | 0.2116 |
| | S03 | 10 | 1493.8 | 149.38 | 1.58 | **0.0066** |
| | S04 | 10 | 1584.9 | 158.49 | 1.79 | **0.0008** |
| *Carex curvula* grassland | All | 10 | 1315.4 | 131.54 | 1.01 | 0.475 |
| | S07 | 10 | 1684.1 | 168.41 | 3.57 | **0.0002** |
| | S08 | 10 | 418.6 | 41.86 | 1.78 | 0.0808 |
| | S09 | 10 | 1818.4 | 181.84 | 2.55 | **0.0002** |
| Peat bog | All | 5 | 326.4 | 65.28 | 0.51 | 0.8498 |
| | S05 | 5 | 833.4 | 166.67 | 6.76 | **0.0002** |
| | S10 | 5 | 560.9 | 112.19 | 3.02 | **0.0026** |
| | S11 | 5 | 222.8 | 44.57 | 1.62 | 0.0726 |
| *Agrostis-Festuca* grassland | S01 | 8 | 4048.9 | 506.11 | 4.02 | **0.0002** |
| *Kobresia*-grassland | S06 | 8 | 1579.7 | 197.46 | 3.98 | **0.0002** |

*PERMANOVA results on Bray–Curtis distances of square-root transformed species frequencies. Fixed factors = exclosure, year; random factor = plot (and community for analyses All). Significant p-values in bold.*

see also **Supplementary Material 6**). Summer precipitation of the previous year and spring/summer temperatures were also positively correlated with this axis. Precipitation and temperature of the previous autumn quartal ($p$ = 0.003) were negatively correlated. For the exclosure sites, we also tested if the weather response was affected by grazing exclusion. Indeed, there was a small but significant ($p$ = 0.0002) effect, with a slightly attenuated (and altered) response to sunshine duration of the previous autumn quartal in the fenced plots (**Supplementary Material 7**).

# DISCUSSION

## Diversity Changes in Grazed Communities

The most consistent result was that species diversity (species number, Shannon index) and species frequencies increased significantly with time at all grazed communities. Thus, hypothesis 1 can be confirmed. Primarily, bryophytes increased significantly in the course of 18 years (however, they increased also in the exclosures, see section "Discussion" below). This is in line with long-term observations in the alpine vegetation of Dovrefjell, Norway (Vanneste et al., 2017). The benefit for bryophytes from grazing was already highlighted by several other authors (Väre et al., 1996; Austrheim and Eriksson, 2001; Takala et al., 2014), showing that grazers promote certain bryophytes by creation of gaps.

Lichens—as a functional group—were not affected throughout the years in our study area, maybe due to a rather low importance in most of the investigated communities. This holds also for dwarf shrubs. At arctic sites, lichen richness was found to decline due to increased shading by dwarf shrubs and shrubs (Elmendorf et al., 2012; Vanneste et al., 2017) and litter increase (Cornelissen et al., 2001) as a consequence of climate warming.

The overall increase in species numbers in the grazed plots is in line with the accelerated species increase at high elevations in Europe (Steinbauer et al., 2018), as an effect of the ongoing climate warming. The lowest changes in diversity throughout the years occurred at S15 (prostrate dwarf shrub) and S11 (wettest site of the peat bog). At the prostrate dwarf shrub, obviously hardly any microsites for seedling recruitment (Graae et al., 2011) are present and sheep grazing also seems to have no influence on this *Loiseleuria procumbens* lichen heath, the dense carpet obviously preventing invasions of other species. This might be an example of "community-level resistance," defined by Hudson and Henry (2010). Similarly, also the calcareous *Kobresia* grasslands showed low diversity changes. This result is comparable to the low effects in subalpine calcareous grasslands in the Apennines found by Frate et al. (2018). At the peat bog site S11, the canopy of very few species remained stable throughout time. Grazers almost avoid this site due to the high water level and unpalatable species.

## No Increase of Competitive Species

Hypothesis 2 suggested that competitive strategists and species with high temperature and/or nitrogen values should increase at the grazed sites due to climate change effects. Although the absolute frequency number of all the three C-S-R strategy types increased at all grazed communities, the relative changes did not really support our hypothesis. The fraction of competitors slightly decreased at most of the grazed communities (except the

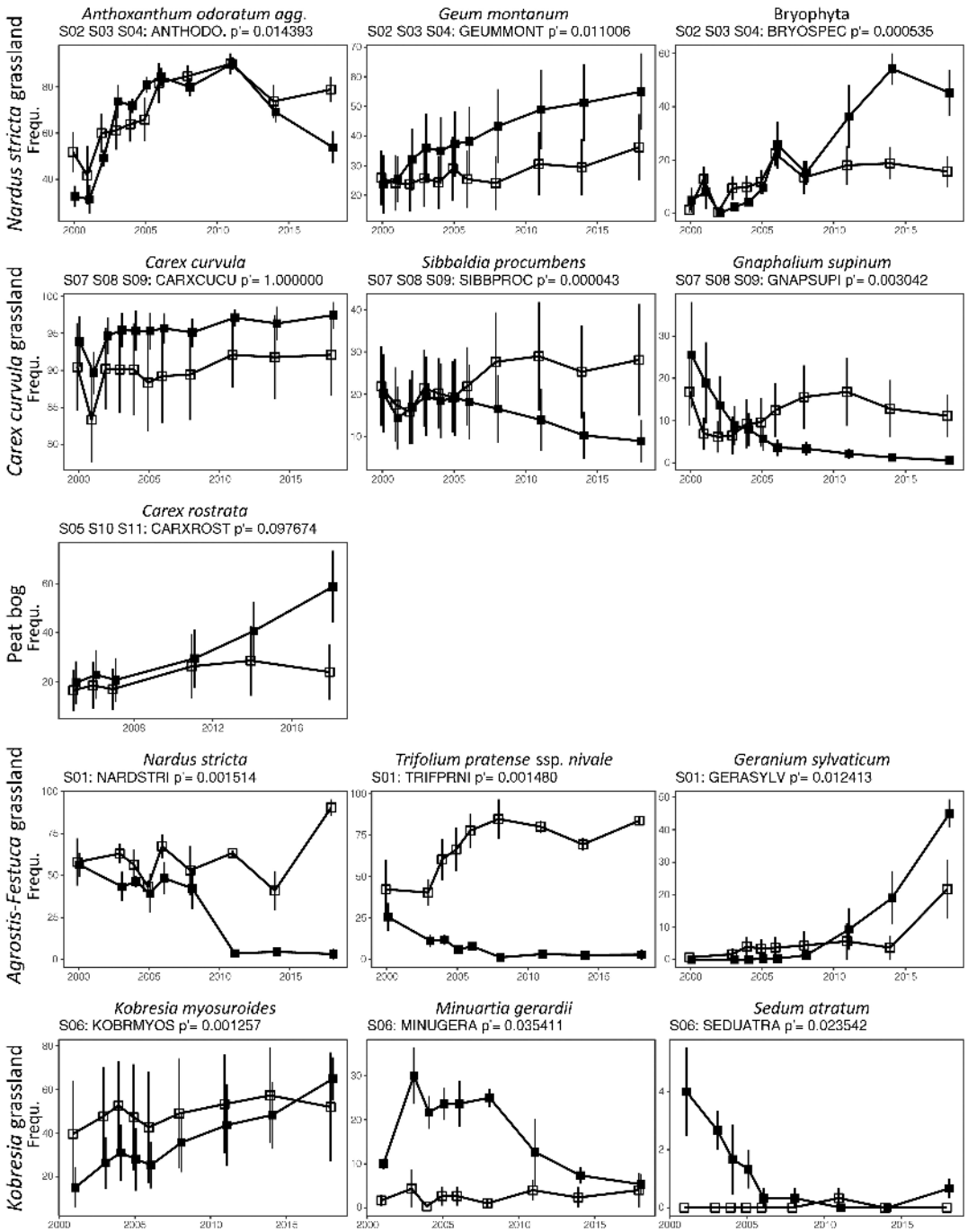



**FIGURE 4 |** Grazing effects on species frequency (tested by mixed-effect models, Bonferroni-corrected $p < 0.05$ for the exclosure × year interaction) for the different communities. Means ± S.E. for exclosure plots (filled squares) and grazed control plots (open squares).

peat bog, **Figure 1**) or did not change at all. The climate change scenarios suggest an increase of competitive, tall-growing species. This was not the case on our grazed communities. Similar to the competitors, the stress tolerators showed no uniform response in our study; only at the *Agrostis–Festuca* and the *Nardus stricta* grassland was this group reduced. In contrast, ruderals increased slightly, though not significantly. Our finding may be a clear indication of rather stable species composition and vegetation structure, probably due to long-term evolution of grazing in the area, grazing lasting already more than 6,000 years (Vorren et al., 1993; Bortenschlager, 2000).

For the Landolt temperature values, an increase was predicted due to the ongoing climate warming. However, also here rather divergent results were obtained. The findings suggest that hardly

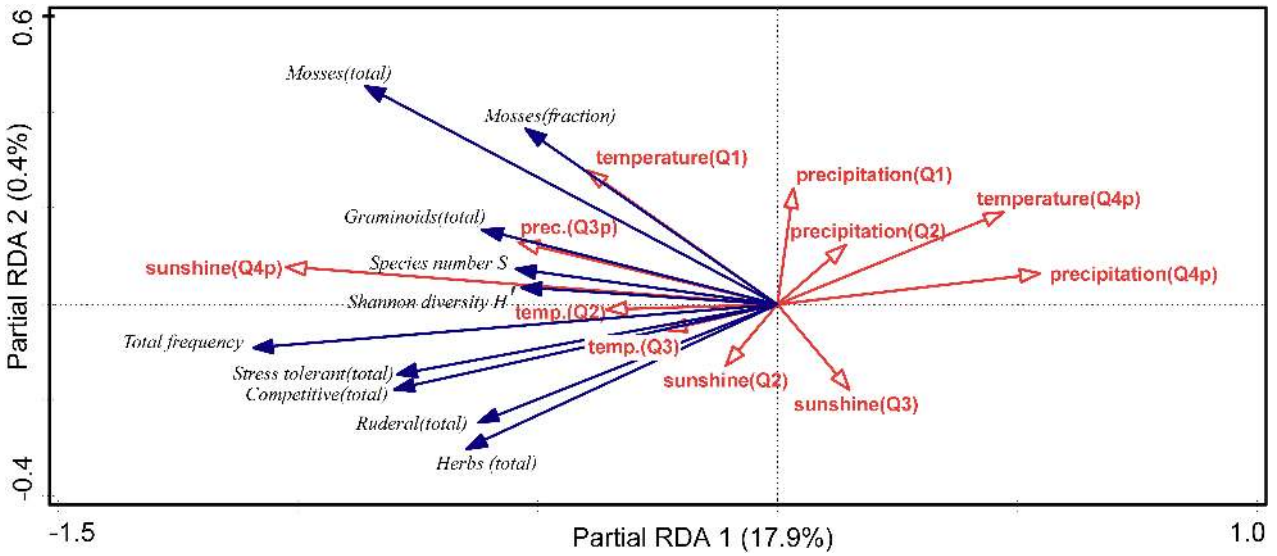



**FIGURE 5 |** pRDA showing the environmental effects on diversity (S, H′), total frequency, functional groups, and strategy types of the grazed sites (total frequencies and fractions indicated for the latter). Explanatory weather variables (sunshine duration, temperature, precipitation) shown with quartals in brackets (Q1 Jan–Mar, Q2 Apr–Jun, Q3 Jul–Sep, Q3p Jul–Sep previous year, Q4p Oct–Dec previous year). Partial RDA (site as covariate) on all community parameters (variables with fit > 5% shown), explained variation of axes indicated, $p = 0.0002$.

any species from lower elevations (having higher temperature values) invaded the grazed areas of the lower and upper alpine grasslands. The reaction of the light values seems to follow a decreasing trend (except at the dwarf shrub communities and *Kobresia* grasslands). This might be explained by the increasing cover and canopy height in the plots (Mayer and Erschbamer, 2014, 2017), promoting shade-tolerant species. Remarkable was the increasing amount of nitrogen-demanding species at the subalpine *Agrostis–Festuca* grassland and the changes in soil reaction values. Here, the grazed control plots were fertilized during the first years of the monitoring period, without our knowledge, by the owner of the cattle (Mayer et al., 2009). This might explain the surprising increases of nitrogen and soil reaction values. Unfortunately, we have no data on atmospheric N-deposition and amount of fertilizers spread. On the other hand, Evangelista et al. (2016) also found an increase in N-demanding species in the Apennines at 2,400–2,790 m a.s.l. after four decades.

## Decreasing Diversity in Grazing Exclusions

With hypothesis 3, we predicted a decreasing diversity in grazing exclusion plots. While this can clearly be confirmed (i.e., species number S and Shannon index H′) when analyzed across the communities, the effect did not consistently occur at all sites. However, at 8 sites out of 11 there was a strong response of the entire species community (**Table 4**). This is by far a higher response compared to the results of the long-term study by Pardo et al. (2015) in the Pyrenees. There, two decades of grazing exclusion did not result either in diversity changes or in changes of the community structure. The authors explained the missing response mainly by (i) the absence of dwarf shrubs and trees in the surrounding, (ii) the predominance of long-lived alpine species, and (iii) possibly depletion of the species pool due to intensive grazing throughout the last centuries.

Considering the functional groups at our study sites, the communities showed a rather heterogeneous behavior: at the *Nardus stricta* grassland, mostly graminoids were negatively affected, at the *Carex curvula* grasslands mostly herbs, and at the *Agrostis–Festuca* grassland both. Contrasting responses of functional groups were highlighted also by Austrheim et al. (2008) in southern Norway, and the authors suggested that individual plant life histories should be known to evaluate the results. *Nardus stricta* is more or less avoided by grazers and may largely extend in extensively grazed areas at the treeline and in the lower alpine zone (e.g., Schaminée and Meertens, 1992). This resulted also by modeling future conditions (Dibari et al., 2020). In our sites, *Nardus stricta* significantly increased in most of the grazed plots, but decreased in the subalpine *Agrostis–Festuca* exclosure as well as at its typical grassland exclosures.

Graminoids were not affected in the *Carex curvula* grassland. *Carex curvula* is known to be highly persistent (Grabherr, 1989), lacking moderate grazing effects (Schneiter, 1977; Cernusca, 1989; Erschbamer et al., 2003). Here, the most striking indicator species for the grazing exclusion effects were snow bed species (*Sibbaldia procumbens*, *Gnaphalium supinum*). This might be an alarming signal, as snow bed species are also among the highest threatened species due to climate warming (Matteodo et al., 2016; Liberati et al., 2019). Also in the arctic tundra, herbivore removal caused increasing losses of 'short-statured' species (Kaarlejärvi et al., 2017).

At the subalpine *Agrostis–Festuca* grassland, *Geranium sylvaticum* became dominant throughout the years in the

exclosure. The species is known as tall herb, selectively grazed by sheep (Evju et al., 2006). The developing dominance of tall-growing herbs following grazing exclusion parallels mowing cessation effects (Bohner et al., 2020), i.e., land-use abandonment in general provokes a remarkable decrease in species richness and Shannon index. This conclusion is not new: several authors highlighted the role of grazing (or mowing) in preserving grasslands and enhancing species diversity (Olff and Ritchie, 1998; Adler et al., 2001; Austrheim and Eriksson, 2001; Dupré and Diekmann, 2001; Pavlu et al., 2005; Sebastià et al., 2008; Mayer and Erschbamer, 2017 and citations therein; Wang et al., 2017; Perotti et al., 2018). With the selection of tall-growing species and their biomass accumulation, microsites for seedling recruitment may become rare on such sites (Graae et al., 2011).

The increase of bryophytes also within the exclosure plots may be attributed to enhanced shading effects by a remarkably increased canopy height due to grazing exclusion (Mayer and Erschbamer, 2017). Generally, bryophytes benefit from grazing (as mentioned above); however, canopy structure changes due to grazing exclusion led to similar frequency increases as in the grazed plots.

## Environmental Factors Govern Diversity Changes

Hypothesis 4 postulated that environmental factors drive diversity changes. At our study site, a steady increase in temperature was observed (Fischer, 2010; Kuhn et al., 2013). Generally, temperature was identified as the major climatic factor, driving vegetation changes in high elevations (Körner, 2003; Gottfried et al., 2012). Indeed, temperatures of the spring and summer quartals were positively correlated with total frequency, species number, and Shannon index, while precipitation of the winter and spring quartals as well as precipitation and temperature of the autumn quartals of the previous year were negatively correlated. Additionally, water deficit in warmer summers might increase, and together with elevated N deposition, these factors might be responsible for shifts of grassland communities (Wüst-Galley et al., 2020). Sunshine during winter (quartal 4) was the weather variable with the strongest steady increase, making it the dominating predictor in our study. We had expected more influence of the variables temperature and precipitation, but this could not be confirmed.

## Interaction of Climate Warming and Grazing Effects

According to Speed et al. (2011, 2012), grazing exclusion may provoke upward shifts of species, especially advances of the treeline. Such signals were hardly detected at our study area. Only one tree sapling—*Pinus cembra*—newly appeared at one plot (**Figure 2**), although not within an exclosure. The distribution range of this tree is highly depending on the bird *Nucifraga caryocatactes* (spotted nutcracker) and its caching activity (Neuschulz et al., 2017). The nutcrackers hardly perform seed caching above the actual treeline due to deep snow (Mattes, 1982) or the lack of landmarks at high elevations (Neuschulz et al., 2017). Our results, showing missing shrub and tree invasions within exclosures are comparable to land-use changes in the Eastern Alps: formerly mown grasslands exhibited no invasion of shrubs and trees even after 60 years of abandonment (Bohner et al., 2020). Missing effects despite climate warming and grazing such as in our study area are known also from the LTER site Niwot Ridge (Scharnagl et al., 2019). In contrast, experiments (Alexander et al., 2015) demonstrated that lowland competitors might outperform alpine plants. At our study site, no montane or colline-centered species were recorded throughout the 18 years of observation. All newcomers and species with increasing frequency belonged to the treeline and alpine species pool.

Long-term processes caused by climate warming and/or grazing exclusion may interact and are difficult to disentangle. Major changes due to climate warming can be weakened or completely overruled by high grazing intensity (Speed et al., 2012, 2013; Jäschke et al., 2018). In contrast, continuous low-intensity grazing may retard or even inhibit community changes (Speed et al., 2013; Wang et al., 2019). Pardo et al. (2015) recorded low impacts of grazing exclusion on species richness but highlighted synergistic effects with extreme weather events such as dry and warm periods. Our study was not conclusive in this respect, but we found an indication of slightly reduced and altered weather effects under grazing exclusion. Our sites generally exhibited a relatively low grazing intensity, as the grazers forage large areas with exception of the subalpine *Agrostis–Festuca* grassland, where six cattle per 1 ha graze from the beginning of July to the end of August each year, provoking a higher grazing pressure (Mayer et al., 2009; Mayer and Erschbamer, 2017).

The problem of disentangling climate change and grazing exclusion effects is an aspect which certainly has to be analyzed in more detail. For a more stringent interpretation, data of the local conditions per individual site would be helpful and a much higher sampling intensity would be necessary.

## Shortcomings of the Study

Long-term monitoring studies are expected to give comprehensive answers to research questions such as effects of climate or land-use changes (Evangelista et al., 2016; Frate et al., 2018; Scharnagl et al., 2019). However, even in long-term studies we have to deal with directional and non-directional changes over time as well as plot variability (Spasojevic et al., 2013), exacerbating a clear interpretation. Initial differences between exclosure and control plots often aggravated the interpretation, the effects being very small in comparison to general changes over time and to site differences.

Moreover, we are aware of several limitations of the study design. First, replications of exclosures at the subalpine *Agrostis–Festuca* grassland and the upper alpine *Kobresia* grassland as well as at the grazed *Festuca nigrescens* grassland are missing due to local circumstances. Second, due to technical and financial problems, monitoring was not equal for all sites and years. Third, the uneven number of replicated permanent plots in the grazed and exclosure/control sites, respectively, might limit the strength of our results for species numbers.

## CONCLUSION

Diversity increases in grazed subalpine–alpine–subnival plant communities in the Central Austrian Alps were attributed to the ongoing climate change. During the 18 years of investigation, the communities were not invaded by species from low elevations; the newcomers mainly belonged to the treeline and alpine species pool. The investigated sites were not affected by the increase of competitive species with exception of the subalpine *Agrostis–Festuca* exclosure. Here, grazing exclusion lead toward a tall-forb community. The missing increase of competitive species in all other sites may be attributed to the typical vegetation structure of alpine communities where already highly competitive species predominate as residents, such as *Kobresia myosuroides* in the subnival grasslands, *Carex curvula* in the upper alpine grassland, *Nardus stricta* in the lower alpine grassland, *Vaccinium* spp. in the tall dwarf shrub, or *Loiseleuria procumbens* in the prostrate dwarf shrub. In the *Carex curvula* grasslands, snow bed species decreased within the exclosures. Cessation of grazing might multiply the threat of this species group as it was found to be also endangered by climate warming.

An indication of slightly reduced and altered weather effects under grazing exclusion was found. The interaction of climate change and grazing is not easy to disentangle. However, this topic definitely should be considered for predictions of community shifts in the future.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s. The raw data are included in the GRASSPLOT database (https://edgg.org/databases/Grassplot).

## AUTHOR CONTRIBUTIONS

RK and BE designed the study. RM set up the exclosures and carried out the field work. NS provided equipment and set up the exclosures during the last years. RK analyzed the data. BE wrote the drafts of the manuscript. All authors contributed to the final version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.640103/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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