

Plant communities along elevational and temporal gradients at the GLORIA sites in the Dolomites

Abstract

Climate warming can be regarded as the main factor for changes occurring in alpine ecosystems. As high elevation species in the Alps are considered to be particularly sensitive to climate change, long term monitoring projects are important to determine amount and direction of biodiversity changes. This study extended the monitoring of the GLORIA sites in the Dolomites, started in 2001. According to previous studies, eastern and southern aspects are those with the most notable changes. We focused, therefore, on the identification and distribution of plant communities and the phytosociological differences between the summits and their southern slopes from the treeline upward. Ecological differences should be unravelled by the analysis of LANDOLT indicator values temperature and soil nutrients as well as by the competitive and non-competitive species. Four plant communities were identified on the south-facing slopes. Three of them were alpine grassland communities, while scree vegetation was only found on the higher plots of the highest summit. At the summits, additionally, two pioneer grassland communities were identified. This study gives further evidences of the ongoing thermophilisation at the summits. From our results it seems that on one summit changes in the plant communities are more likely to happen in the near future, while on the other two summits topographical barriers should prevent imminent changes.

Introduction

Biotic factors and human impacts decline with elevation (THEURILLAT & GUISAN 2001; CALLAWAY et al. 2002), thus, climate warming can be regarded as the main factor for changes occurring in alpine ecosystems (GRABHERR et al. 2010). Mountain ranges like the European Alps are strongly affected by climate change (GRITSCH et al. 2016; LAMPRECHT et al. 2018) as high-elevation areas show faster warming trends than lowland areas (MARTY & MEISTER 2012; MOUNTAIN RESEARCH INITIATIVE EDW WORKING GROUP 2015). The average warming for the European Alpine region is expected to reach up to +3.3 °C for the second half of the 21st century (GOBIET et al. 2014). Plant species at high elevations are adapted to special conditions and are therefore particularly sensitive to changes in temperature and growing conditions (KÖRNER & LARCHER 1988; GRABHERR et al. 1994; LAMPRECHT et al. 2018; ROGORA et al. 2018). Projections showed that until the end of the century half of the investigated alpine species are at risk of being displaced by invading low-elevation species (ENGLER et al. 2011; DULLINGER et al. 2012). Due to these migration events, new plant communities could evolve in the future (ALEXANDER et al. 2015; 2018). On European mountains, plant species were found to move from lower elevations upwards due to rising temperatures (GOTTFRIED et al. 2012; PAULI et al. 2012; WIPF et al. 2013; GRITSCH et al. 2016; UNTERLUUGAUER et al. 2016) and alpine species were increasing at higher elevations (PAULI et al. 2007). Increases in species richness on mountain tops

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were found to be highly accelerated during the last decades (STEINBAUER et al. 2018). At a first glance, in the temperate zone of Europe, the predicted decline of cold-adapted species seems to occur at a slow rate. However, at highest elevations (e.g., Mt Schrankogel, Stubai Alps, Tyrol; STEINBAUER et al. 2020), a remarkable decline of subnival-nival species was already recorded during the last study decade.

In order to determine amount and direction of biodiversity changes and to follow the fate of species across elevation and habitats, long term projects are necessary. A worldwide operating initiative to investigate these topics is the project GLORIA (Global Observation Research Initiative in Alpine Environments, www.gloria.ac.at). In the Western Dolomites, Trentino-South Tyrol, Northern Italy, a GLORIA site was established in 2001 as part of the European GLORIA project. Here, four summits along an elevational gradient were sampled in 2001 and resampled in 2006, 2008 and 2015 (ERSCHBAMER et al. 2003; 2011; UNTERLUGGAUER et al. 2016). The results of the European GLORIA surveys showed that the increase of species occurred mainly on the southern and eastern aspects due to the availability of climatically favoured microsites (WINKLER et al. 2016). Further studies indicate that the potential newcomers at higher elevations should be already present on the slopes below the summits or at the same elevation on other mountains of the same region (GOTTFRIED et al. 1998; KAMMER et al. 2007; GRITSCH et al. 2016). Therefore, the analysis of the slopes should give good indications about potential species migrating upwards due to climate warming.

The process of increasing thermophilic species and declining cold adapted species on high summits was called thermophilisation (GOTTFRIED et al. 2012; LAMPRECHT et al. 2018). Various studies (e.g., GOTTFRIED et al. 2012; ALEXANDER et al. 2015; GRITSCH et al. 2016; NICKLAS et al. 2021a) showed that the migrating species from lower elevations were more thermophilic, more nutrient-demanding and more competitive. UNTERLUGGAUER et al. (2016) already detected that the newly arrived species on the GLORIA summits of the Western Dolomites were of more thermophilic character compared to the resident alpine species. In a similar study, performed on the GLORIA summits and its southern slopes in the Texelgruppe, South Tyrol, NICKLAS et al. (2021a) suggested that the invasion of thermophilic species might limit cryophilic species in the near future on the lowest summit at the treeline and the entire subalpine ecotone. The ecological indicator value temperature (LANDOLT et al. 2010) should therefore be a good indicator for the changes induced by climate warming on alpine environments (GRITSCH et al. 2016).

The present study aimed to sample the elevational gradients on the southern slopes from the treeline to the GLORIA summits in the Western Dolomites. We are aware that also the eastern slopes would be interesting in this context, however, due to logistic and financial problems it was not possible to consider them. We therefore focused on the identification and distribution of plant communities and the phytosociological connection between the summits and their southern slopes. Ecological differences should be unravelled by the analysis of LANDOLT indicator values of the species (LANDOLT et al. 2010). Specifically, we were interested in the distribution of thermophilic and nutrient-demanding species, which are characteristically occurring at lower elevations. These species can be regarded as potential migrators towards the summits. We therefore discriminated cryophilic versus thermophilic species and oligophilous versus nitrophilous species (EVANGELISTA et al. 2016) along the southern elevational gradients of the summits.

Migrating species from lower elevation might be considered to be more competitive compared to the alpine resident species (ALEXANDER et al. 2015), originating from nutrient-richer sites and having larger range sizes (STAUDE et al. 2022). In order to contribute to this hypothesis, a classification of the sampled species according to competitive versus non-competitive was intended. We used therefore the CSR strategies defined by GRIME (1979) and determined by LANDOLT et al. (2010). These strategies have already been applied successfully within community analysis (ZANZOTTERA et al. 2020).

Furthermore, we checked whether the vegetation change in the permanent plots on the summits already goes in the direction of warmer demanding communities and whether the proportion of thermophilic, nitrophilous and competitive species increased over the past 14 years of GLORIA monitoring (ERSCHBAMER et al. 2003; UNTERLUGGAUER et al. 2016).

The following questions were addressed:

1. Which plant communities occur along the south-facing slopes below the GLORIA-summits in the Western Dolomites and how do they diverge ecologically?
2. Are the plant communities of the summits (i.e., all the permanent plots per summit) phytosociologically and ecologically connected to the communities on the south-facing slopes?
3. Is the proportion of thermophilic, nitrophilous or competitive species increasing at the summits?
4. Which predictions can be drawn from the results?

Material and Methods

Study area

The study area GLORIA target region IT_ADO lies in the Western Dolomites (Trentino-South Tyrol region, Northern Italy). In 2001, four summits were chosen according to the GLORIA protocol (PAULI et al. 2015). Three of these summits are located in the Latemar group (N46°19'-N46°23', E11°33'), while the fourth and highest summit lies in the Sella group (N46°31', E11°49'). Due to the lack of topographical names for these summits, fictional names were given: ‚Grasmugl‘ (GRM 2199 m a.s.l.), ‚Do Peniola‘ (official name, PNL 2463 m a.s.l.), ‚Ragnarok‘ (RNK 2757 m a.s.l.) and ‚Monte Schutto‘ (MTS 2893 m a.s.l., ERSCHBAMER et al. 2003). As GRM lies next to the tree line, no transect records were made at this summit and no data from this summit was used in the analyses.

Geologically, PNL and RNK consist of Latemar limestone with characteristic intrusions of volcanic rocks, mainly augite-porphry close-by or on lower elevations of the summits (BOSELLINI 1998; STINGL & MAIR 2005). The south-facing slopes below these summits are medium to very steep and covered by grassland, scree and rocks. MTS is made of dolomitic rocks (Hauptdolomit, BOSELLINI 1998). The summit lies on the Mesules plateau which presents a moon-like appearance with scarce vegetation. This plateau is separated by a vertical wall from the Val Lasties underneath where scree, pioneer vegetation and more developed sward can be found. The transect followed this valley up to the vertical wall and continued from the top of the wall on the plateau.

Field work

The transect surveys were made from the actual treeline up to the 10 m contour lines of the three IT_ADO summits PNL, RNK and MTS. The vegetation was recorded in clusters of 3×3 m every 50 m of elevation (Fig. 1), similar to the GLORIA summit method (i.e., a cluster of 3×3 m was established 5 m below the highest summit point in each cardinal direction, the four corner squares being sampled; PAULI et al. 2015). The position of the transects and the plots was determined prior to field work with the help of orthophotos and terrain models to find a directional line from the summit down, fulfilling the following criteria: 1) best exposed to the southern and/or eastern aspect as possible to have higher temperatures; 2) going down to the treeline as far as possible; 3) avoiding inaccessible terrain; 4) checking the presence of rocks or scree to detect all vegetation patches in between in order to sample the best developed communities with the highest diversity and highest probability to identify migrating species from lower elevations. Due to inaccessible terrain the transects needed to be partially deviated from the exact southern orientation.

Within each of the four 1×1 m corner squares (Fig. 1) the occurring vascular plant species were recorded and the percentage cover of each species was estimated (NICKLAS et al. 2021a). Furthermore, the percentage cover of vascular plants, lichens on soil, bryophytes on soil, litter, bare ground, scree and solid rock per 1 m² was recorded. Additionally, the data from the 1 m² permanent plots of the GLORIA summit survey 2001 and 2015 were used (UNTERLUGGAUER et al. 2016).

The nomenclature followed FISCHER et al. (2008) with exceptions of *Achillea millefolium* agg. and *Alchemilla vulgaris* agg.. Aggregates were further employed for species impos-

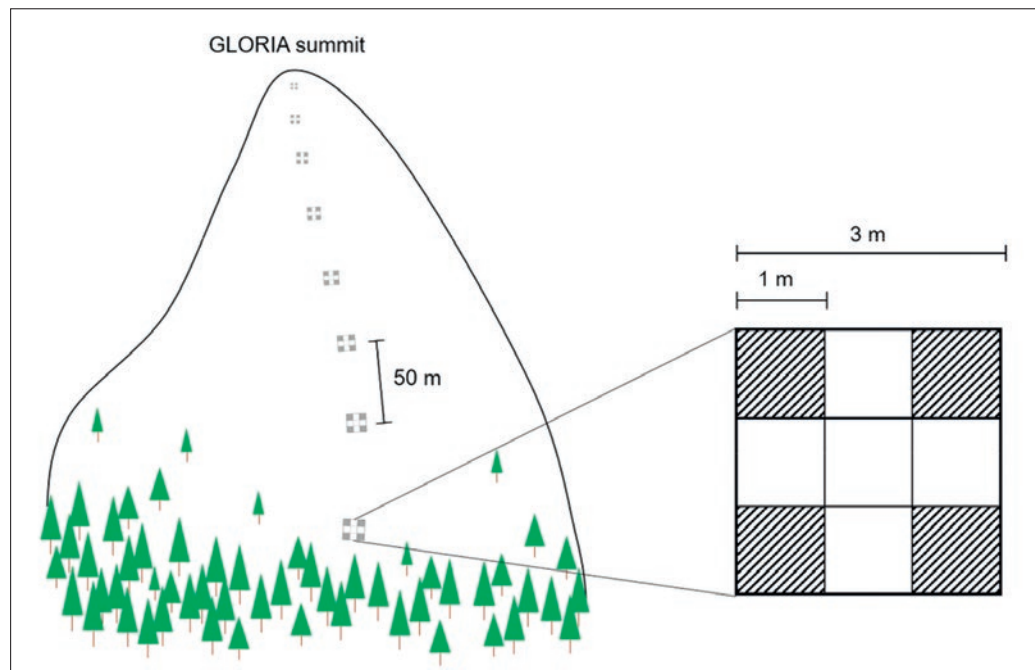


Fig. 1: Field work setup. The vegetation was recorded every 50 m of elevation from the actual treeline to the GLORIA-summits' 10 m contour line. Percentage cover was estimated for every occurring vascular plant species in the filled squares (graph from Nicklas et al. 2021a).

sible to determine in detail (*Euphrasia minima* agg., *Erigeron alpinus* agg., *Hieracium murorum* agg., *Ranunculus montanus* agg.). Due to determination problems, *Laserpitium siler* includes also *Laserpitium peucedanoides*.

Data analyses

Arithmetical means of the cover estimates (species and surface cover types) were calculated per cluster (i.e., per $4 \times 1 \text{ m}^2$) and used for all following analyses. For classification of the samples, Two Way Indicator Species Analyses (TWINSPAN) and ordinations (Nonmetric MultiDimensional Scaling, NMDS) were performed: (1) for the transect data set only and (2) for the combined dataset including transect data and summit data from the surveys 2001 and 2015 (i.e., all 1 m^2 permanent plots per summit at the 5 m contour line). Bray-Curtis dissimilarity metric was used and species scores were Wisconsin double standardized. The community groups obtained by the TWINSPAN analyses were implemented in the ordination graphs. All environmental factors with a significant influence on the structure of the data ($p < 0.05$; field data: elevation, scree, solid rock, species number, vascular plant cover; LANDOLT indicator values: continentality, light, moisture, soil nutrients, temperature; competition value) were fitted to the NMDS. The LANDOLT indicator values and competition values were used as arithmetical means from all occurring species per cluster. The competition value per species was calculated as the number of 'c' (Table 1) from the CSR strategy by GRIME (1979), determined by LANDOLT et al. (2010), reaching from 0 (sss) to 3 (ccc).

To compare the communities ecologically, for each cluster the mean proportion of cryophilic versus thermophilic, of oligophilous versus meso- to nitrophilous, and of competitive versus non-competitive species was calculated. Therefore, species were classified according to the LANDOLT indicator values temperature and soil nutrients (EVANGELISTA et al. 2016) and their competition strategy (Table 1).

The differences in the proportion of these species groups between the communities were tested by an Analysis of Variance (ANOVA). The heteroskedasticity was mitigated with the calculation of robust standard errors and their corresponding t values. At the

Table 1: Classification of the indicator values temperature and soil nutrients (EVANGELISTA et al. 2016) as well as that for the competition values.

| Factor | Description |
|--|---|
| <i>Temperature [1 = nival to 5 = colline]</i> | |
| Cryophilic species | temperature values 1 and 1.5 |
| Thermophilic species | temperature values 2 and higher |
| <i>Soil nutrients [1 = oligophilous to 4 = nitrophilous]</i> | |
| Oligophilous species | nutrient values 1 and 2 |
| Meso- to nitrophilous species | nutrient values 3 and 4 |
| <i>Competition</i> | |
| Competitive species | including competitive CSR strategies: ccc, ccs, ccr |
| Not competitive species | all other CSR strategies |

summit clusters, changes in the proportions between the two surveys (2001, 2015) were tested by paired t-tests.

All statistical analyses were done in R 3.6.3 (R CORE TEAM 2020) using the package tidyverse (WICKHAM et al. 2019). The twinspanR-package (ZELENY et al. 2016) was used for the TWINSpan analyses. The NMDS ordinations were performed with the R-package vegan, using the envfit-function for the fitting of the environmental factors. For all statistical tests, normality and heteroskedasticity of the residuals was tested by a Kolmogorov-Smirnov test and a Breusch-Pagan test, respectively. Due to heteroskedasticity ANOVAs were performed with robust standard errors using the function vcovHC from the sandwich-package (ZEILEIS et al. 2019).

Results

Plant communities along the transects

Along the south-facing slopes, three alpine grassland communities – *Festuca nigrescens* community, Seslerio-Caricetum sempervirentis, and Festucetum pumilae – and the scree community Saxifragetum sedoidis could be discriminated. The NMDS ordination (Appendix I) showed a clear segregation of the plant communities along the elevational gradient. At lower elevations more competitive species as well as species with a higher temperature value were present. The number of species with higher light values increased with elevation. At the summit plots of PNL, more species with high soil reaction values were present. In contrast, the lowest soil reaction values were assigned to the *Festuca nigrescens* community.

The only species present in all four communities were *Poa alpina* and *Persicaria vivipara*. The three alpine grasslands included the following species with a high constancy: *Carex sempervirens*, *Sesleria caerulea*, *Festuca norica*, *Campanula scheuchzeri*, *Galium anisophyllum*, *Ranunculus montanus* agg., *Scabiosa lucida*, *Soldanella alpina*, and *Thymus praecox* subsp. *polytrichus*.

On lower elevations, the *Festuca nigrescens* community and the Seslerio-Caricetum sempervirentis Berger 1922 em. Br.-Bl. 1926 (Seslerietum from now on) were determined. They were partially found next to each other. The first was found on PNL and RNK ranging from 2050 to 2250 m a.s.l. and the latter on MTS and PNL from 2150 to 2400 m a.s.l. as well as on RNK at 2150, 2300 and 2350 m a.s.l. The *Festuca nigrescens* community was characterized by a high presence of acidophilic and nitrophilous species. Its mean cover of vascular plants was $75.6\% \pm 8.5$ (mean \pm standard deviation) and its mean species number was 32 ± 3.5 . The Seslerietum showed a mean vascular plant cover of $63\% \pm 8.6$ and a mean species number of 27 ± 3.9 .

The dominant species for both associations were *Carex sempervirens*, *Sesleria caerulea* and *Festuca norica*, while *Festuca nigrescens*, *Anthoxanthum alpinum*, *Carex ornithopoda*, *Crocus albiflorus*, *Lotus corniculatus*, and *Potentilla crantzii* distinguished the *Festuca nigrescens* community from the Seslerietum. Also, *Festuca varia* and *Nardus stricta* were

found in some plots of the *Festuca nigrescens* community with a high cover. Species found only in the Seslerietum and in the *Festuca nigrescens* community were: *Avenula praeusta*, *Coeloglossum viride*, *Daphne striata*, *Nigritella rhellicani*, *Ranunculus hybridus*, and *Polygala chamaebuxus*.

The transect plots on RNK between 2400 and 2700 m a.s.l. and the plot on MTS 2450 m a.s.l. were assigned to the Festucetum pumilae Gams 1927 with a mean vascular plant cover of $55.8\% \pm 4.7$ and a mean species number of 30 ± 3.7 . Species with a high constancy were *Festuca pumila*, *Minuartia sedoides*, *Draba aizoides*, *Kobresia myosuroides*, *Salix serpyllifolia*, *Silene acaulis*, *Anemone baldensis*, *Gentiana brachyphylla*, *Homogyne alpina*, and *Carex ornithopodioides*.

Species found with a high constancy in both the Festucetum pumilae and the Seslerietum were: *Gentianella anisodonta*, *Helianthemum alpestre*, *Agrostis alpina*, *Anthyllis vulneraria* subsp. *alpicola*, *Achillea clavennae*, and *Festuca pumila*.

The Saxifragetum sedoidis Pign. E. et S. 1995 was only found on the Mesules plateau on MTS between 2700 and 2850 m a.s.l. and just before the vertical wall separating Val Lasties and the Mesules plateau on 2500 m a.s.l. These records had a mean vascular plant cover of $5.5\% \pm 4.4$ and a mean species number of 8 ± 4.4 . Characteristic species with a high constancy were *Saxifraga sedoides*, *Carex parviflora*, *Cerastium uniflorum*, and *Hornungia alpina*. Species occurring in the Saxifragetum sedoidis as well as in the Festucetum pumilae were *Achillea oxyloba*, *Draba hoppeana*, and *Solidago virgaurea*. The plot on MTS 2700 m a.s.l. was classified as an isolated sample by TWINSPAN. However, due to the presence of *Saxifraga sedoides* and several scree species it was grouped to the Saxifragetum sedoidis.

The four communities were considerably different regarding the proportion of thermophilic, meso- to nitrophilous and competitive species (Fig. 2). The grasslands on lower elevations (*Festuca nigrescens* community and Seslerietum) had a significantly higher proportion ($P < 0.001$) of thermophilic, meso- to nitrophilous and competitive species compared to the communities on higher elevations (Festucetum pumilae and Saxifragetum sedoidis, Fig. 2). At the *Festuca nigrescens* community and the Seslerietum 63% and 51% thermophilic species were recorded, respectively, while at the Festucetum pumilae the percentage was only 31.4%. The Saxifragetum sedoidis had a considerably lower proportion of thermophilic and competitive species than the other communities of the transects, with only few thermophilic species, such as *Cystopteris fragilis*, *Minuartia gerardii* and *Salix cf. waldsteiniana* found in its plots. Among all the species occurring in the Saxifragetum sedoidis, only one (*Salix cf. waldsteiniana*) had a competitive strategy (Fig. 2).

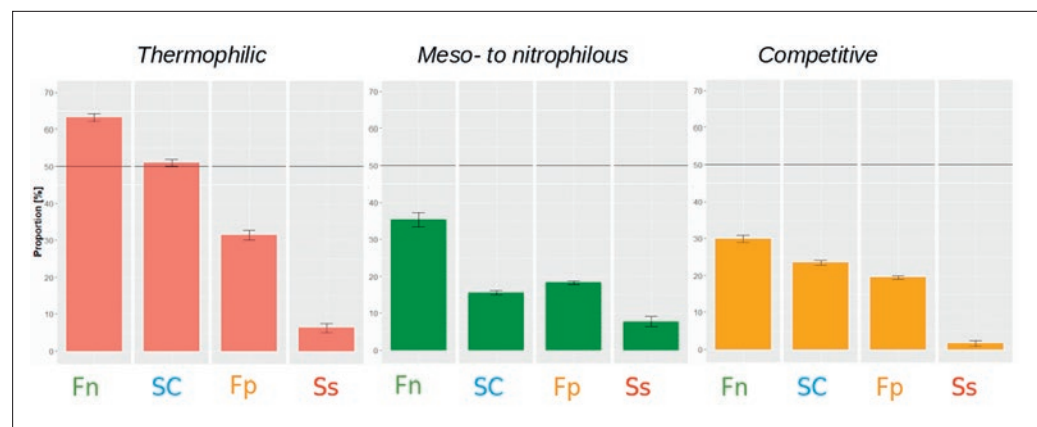


Fig. 2: Ecological comparison between the plant communities occurring along the south-facing slopes. The bars show the proportion of thermophilic (red), meso- to nitrophilous (green) and competitive (orange) species for each community with the standard error. Fn: *Festuca nigrescens* community, SC: Seslerio-Caricetum sempervirentis, Fp: Festucetum pumilae, Ss: Saxifragetum sedoidis. The proportion of thermophilic, meso- to nitrophilous and competitive species differed significantly between communities (Analyses of variance, $P < 0.001$). The remaining portion on 100% can be filled by the counter species category i.e., cryophilic species (for classification see Table 1).

Comparison of transects and summits

The TWINSPLAN classification (Appendix II and III) and the NMDS of the combined data set (Fig. 3) resulted in six plant communities: beside the already defined four communities, also a *Caricetum firmae* on PNL and a *Caricetum rupestris* on RNK were described. Furthermore, the plots on RNK at 2400 m and 2450 m a.s.l., which were identified as *Festucetum pumilae* (Appendix I) were now included in the *Seslerietum* (Fig. 3).

On PNL, the summit plots of the surveys 2001 and 2015 were assigned to the *Caricetum firmae* Br.-Bl. 1926, subassociation with *Dryas octopetala* (GRABHERR et al. 1993; PIGNATTI & PIGNATTI 2014b), i.e., a community not present on the southern slopes of the three analysed summits. This community had a mean vascular plant cover of $21.4\% \pm 7.3$ and a mean species number of 16 ± 1.2 . Constant and abundant species were *Carex firma*, *Euphrasia minima* agg., *Potentilla nitida*, *Oxytropis montana*, *Phyteuma sieberi*, *Saxifraga caesia*, *Festuca pumila*, and *Helianthemum alpestre*. While *Dryas octopetala* was not present in all plots, it had a high cover, where it occurred.

Species that occurred in the *Caricetum firmae* as well as in the *Seslerietum* and *Festucetum pumilae* were: *Carex firma*, *Euphrasia minima* agg., *Anthyllus vulneraria* subsp. *alpicola*, and *Dryas octopetala*. However, the PNL summit plots with the pioneer grassland *Caricetum firmae* were clearly separated from the more developed grasslands found on the southern transect of this summit (Fig. 3).

On RNK, the *Festucetum pumilae* was found at the southern summit plots of both surveys (2001, 2015), representing the same community as on its southern slope (Fig. 3). At the northern and eastern plots of the RNK summit, the *Caricetum rupestris* Pign. E. et S. 1985 (GRABHERR 1993; PIGNATTI & PIGNATTI 2014a) was found and also the transect site MTS 2700 was grouped to this community. The mean vascular plant cover for this community was $12.6\% \pm 6.6$ and the mean species number 15 ± 5.7 . The presence of *Carex rupestris* and the higher abundance of *Draba aizoides*, *Salix serpyllifolia*, *Sesleria sphaerocephala*, and *Silene acaulis* differentiated the *Caricetum rupestris* from the *Saxifragetum sedoidis*, even though *Saxifraga sedoides* had a high constancy also here.

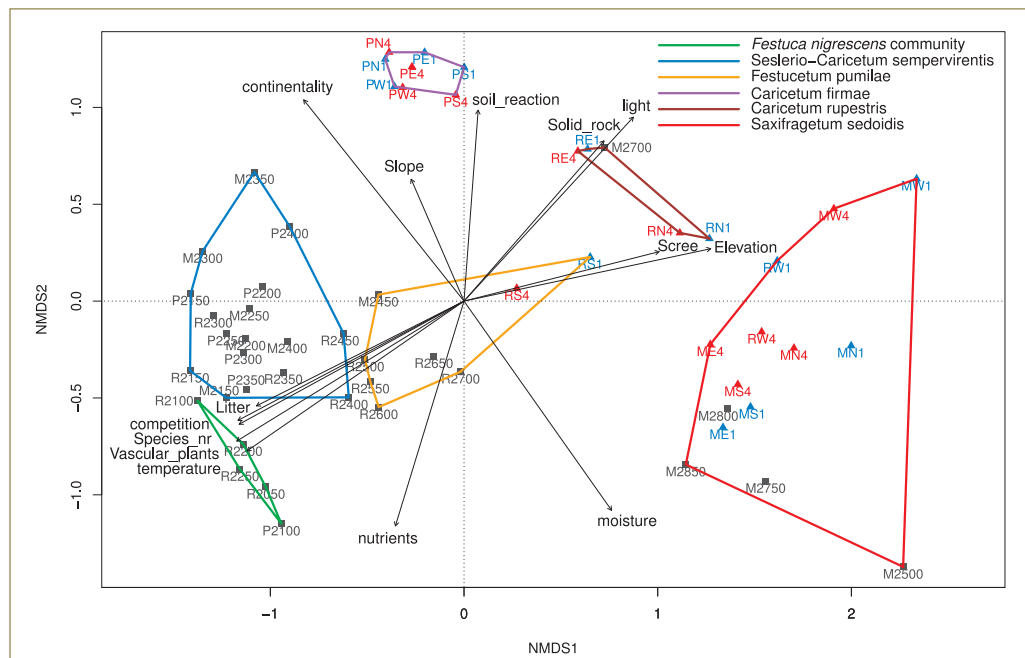


Fig. 3: NMDS ordination showing the cluster plots of the transects (squares) together with the summit cluster plots (triangles) per aspect from the first survey 2001 (blue) and the resurvey 2015 (red). The polygons represent the plant communities found by the TWINSPLAN analysis. Summit abbreviations: M: MTS, P: PNL, R: RNK. For the transect clusters (squares) the numbers after the letter denote the elevation; the summit clusters (triangles) include the first letter of the summit with the cardinal direction (E = east, S = south, W = west, N = north) of the cluster and the chronological number of the survey (1 = 2001, blue; 4 = 2015, red). Ecological variables (see Data analyses) were fitted and shown as arrows.

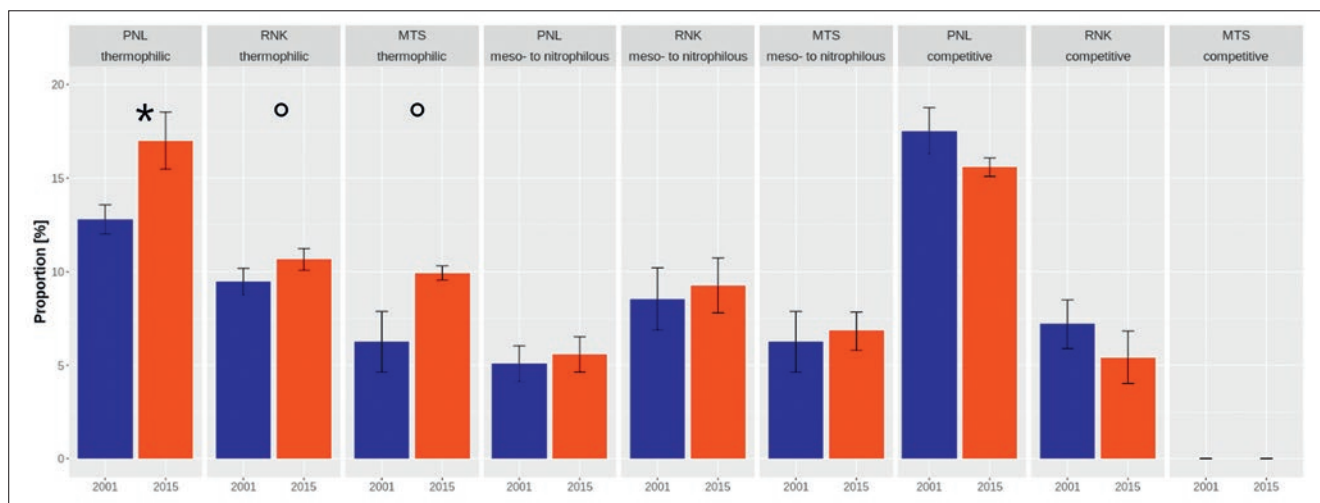


Fig. 4: Proportion of thermophilic, meso- to nitrophilous and competitive species at the three GLORIA summits, comparing the surveys of 2001 and 2015. Significance levels: '*' denotes $P < 0.05$; 'o' denotes $P < 0.1$.

The following species occurred in the *Caricetum rupestris* as well as in the *Festucetum pumilae*: *Draba aizoides*, *Silene acaulis*, *Salix serpyllifolia*, *Erigeron uniflorus*, and *Carex rupestris*. *Arenaria ciliata* was found not only in these two communities, but also in the *Caricetum firmiae* with a high constancy.

The summit plots of MTS as well as the western summit plots of RNK were grouped to the *Saxifragetum sedoidis*. *Minuartia sedoides* and *Saxifraga oppositifolia* occurred in the *Saxifragetum sedoidis* as well as in the *Caricetum rupestris* and in the *Festucetum pumilae*. The following species had a high constancy in the *Caricetum rupestris* as well as in the *Saxifragetum sedoidis*: *Saxifraga sedoides*, *Cerastium uniflorum*, and *Hornungia alpina*. All the MTS-plots from the Mesules plateau and the summit plots were clearly separated from the grassland communities found at the Val Lasties (Fig. 3).

Changes at the summit clusters from 2001 to 2015

In the course of 14 years, several summit clusters showed a development of the species composition into the direction of the lower and more thermophilic plant communities (Fig. 3). Especially the southern cluster of RNK and the western and the northern cluster of MTS exhibited directional changes. Contrastingly, western and northern clusters of PNL did not change at all.

From the first to the last survey, the mean proportion of thermophilic species on the three summits increased by +3.3 % (Fig. 4). The increase on PNL amounted to +4.2 %, on RNK +1.2 %, and on MTS +3.7 %. Only on PNL, this increment was significant ($P < 0.05$). The changes in nutrient-demanding and competitive species were not significant, however, trends were visible. Meso- to nitrophilous species slightly increased on all summits. On PNL and RNK competitive species decreased. On MTS competitive species were completely missing, in 2001 as well as in 2015 (Fig. 4).

Discussion

Plant communities on the south-facing slopes

The plant communities identified along the southern transects include the typical associations found in the Eastern Alps on limestone and dolomite, such as the grassland association *Seslerietum* as well as the pioneer grassland community *Festucetum pumilae* (GRABHERR et al. 1993; PIGNATTI & PIGNATTI 2014a). In contrast, the *Festuca nigrescens* community found on lower elevations of PNL and RNK next to the *Seslerietum*, is characterised by the presence of acidophilic and nitrophilous species, which can be explained by the existence of deeper soils. The community is comparable to *Nardion*

strictae communities, studied on the Eggentaler Alm at the southern region of the Latemar group (VORHAUSER & ERSCHBAMER 2000), where *Festuca nigrescens* also appeared with high constancy. For these communities, pH values of 4.9 were determined.

The Saxifragetum sedoidis identified on the Mesules plateau on MTS is a typical scree vegetation of the Dolomites with dwarf chamaephytes found between the scree, in contact with rocky, overhanging walls, growing only in patches which cover small parts of the surface (see also PIGNATTI & PIGNATTI 2014b).

The communities along the southern slopes reflect the elevational gradient from thermophilic to cryophilic communities as well as the ecological differences. The high proportion of thermophilic species in the communities of lower elevation indicates an important source of potential upward migrants with warmer climatic conditions.

Phytosociological and ecological connection between slopes and summits

Differences between most of the summit communities and the communities along the southern slopes were clearly shown in our analyses. Two associations restricted to the summits underline the specific characteristics of alpine/subnival summit vegetation. Interestingly, in the siliceous Central Alps of the Texelgruppe similar analyses showed a stronger connection and similarity between summit communities and their southern slope communities (NICKLAS et al. 2021a). This might emphasize the special condition on calcareous summits, probably related to the higher proportion of rock, acting as topographical barrier for species migration along the slopes.

The Caricetum firmae subassociation with *Dryas octopetala* at the PNL summit clusters included only few species from the communities found on the southern slope. This could partly be explained by the presence of a secondary summit, separating the southern slope from the real GLORIA summit, acting probably as advanced catchment area of migrating species. Therefore, on the PNL summit, the typical pioneer grassland Caricetum firmae still did not change towards a Seslerietum, although it was the only summit community with a significant increase of thermophilic species. It seems that here the Caricetum firmae has a permanent status ('Dauergesellschaft'). This may be underlined by the fact that neither the number of nutrient-demanding nor the competitive species number changed significantly.

The Caricetum rupestris at the northern and eastern clusters of RNK and at the upper MTS transect can be clearly discriminated from all other communities. PIGNATTI & PIGNATTI (1985) described this community as being endemic for the southeastern calcareous Alps, however, later the authors (PIGNATTI & PIGNATTI 2014c) suggested a wider distribution in other areas of the Alps and in Northern Europe. Based on descriptions of PITSCHMANN et al. (1980) and on his own unpublished data, GRABHERR (1993) also suggested a wider occurrence for this association. Close connections seem to exist to the Saxifragetum sedoidis. However, our sample data are too few to clarify the status of these two syntaxa. While PIGNATTI & PIGNATTI (2014c) predicted a possible succession towards a Caricetum firmae for this community, we suggest that a development towards a pioneer grassland or a closed alpine grasslands will hardly occur in the near future on the northern and eastern summit clusters of RNK due to the rough rocky terrain. The Caricetum firmae of PNL and the Caricetum rupestris of RNK differ in terms of ecological as well as phytosociological characteristics (Fig. 3). Possible explanations are differences in elevation, topography, soil- and community evolution.

Various studies highlighted the variation on species numbers and composition on temperate mountains depending on aspect (WINKLER et al. 2016; NICKLAS et al. 2021b). We found no remarkable differences on PNL and MTS, however, on RNK the southern summit plots were assigned to the Festucetum pumilae, found also on the transect clusters. These similarities between transect and summit underline the observations made by WINKLER et al. (2016), indicating that on the warmer southern aspects colonization and community development is enhanced. Thus, on the southern RNK summit cluster a development towards a climax calcareous grassland such as a Seslerietum can be suggested for the middle-term future with a strong increase in vegetation cover and a

possible loss of pioneer plant species such as *Draba aizoides* and *Saxifraga oppositifolia* (see Appendix II).

On MTS, the differences between the grasslands of the Val Lasties (transect clusters) and the scree vegetation on the Mesules plateau (uppermost transect and summit clusters) were highlighted by the identification of two very different associations: the Seslerietum as developed grassland on lower positions and the Saxifragetum sedoidis as scree vegetation. The high wall separating the Val Lasties with the developed grasslands from the moon-like Mesules plateau with scree vegetation should be the reason for this difference. Phytosociologically, the Saxifragetum sedoidis has some similarities to the Papaveretum rhaetici Wikus 1959 (ENGLISCH et al. 1993), i.e., the southern alpine scree community.

Nevertheless, we should not forget, that the investigated transects only represent a sample of the most likely best developed plant communities below the summits. Sampling approaches on the other aspects or entire transects across the slopes might have resulted in a more comprehensive description of the communities.

Future development and predictions

Our results showed an increase of the proportion of thermophilic species on the three analysed summits and give further evidence of the ongoing thermophilisation trend already observed at these summits (UNTERLUGGAUER et al. 2016). This is in line with changes observed on various European mountain ranges (GOTTFRIED et al. 2012; PAULI et al. 2012; WIPF et al. 2013; STEINBAUER et al. 2018). Several studies on alpine summits showed that the frequency of thermophilic species is increasing, while the abundance of cryophilic species is declining (GOTTFRIED et al. 2012; PAULI et al. 2012; WIPF et al. 2013; LAMPRECHT et al. 2018; STEINBAUER et al. 2018). This increment of thermophilic species at the expense of cryophilic species was clearly related to the effects of climate warming (ENGLER et al. 2011; GOTTFRIED et al. 2012; FERNÁNDEZ CALZADO & MESA 2013; STEINBAUER et al. 2018).

For the near future, only for the southern summit cluster RNK a prediction of the future development seems to be plausible, as it appears to change towards more developed grasslands. The consequences should be an increase of the total species number in the short-term (PAULI et al. 2012), but in the long-term alpine specialists such as scree and rock crevice species could lose their habitat to the more competitive species immigrating from lower elevations (WINKLER et al. 2019). However, from our results, spanning a survey of 14 years, the number of competitive species did not increase at the three summits.

On PNL and MTS, the short-term future should not bring remarkable changes of the summit floras due to the ecological distinction and topographical barriers between the slopes and the summits. This applies especially for MTS, as the Mesules plateau is clearly separated from the vegetation growing at lower elevations by vertical walls and boulder on all sides. However, especially on the summit MTS a strong increase in species richness was already observed (UNTERLUGGAUER et al. 2016). Species of the Mesules plateau, 25 to 50 m below the summit clusters, invaded. According to our results, no competitive species were found, neither in 2001 nor in 2015. In addition, mean temperature values (LANDOLT et al. 2010) of the species did not significantly change during that period (BERTOL 2021). Furthermore, the presence of climatic microrefugia at the summit should prevent the disappearance of the already present high alpine/subnival and less competitive species (ROTA et al. 2022).

The results clearly suggest that long term investigations are necessary to refine the predictions. Therefore, the ongoing of the monitoring at the GLORIA summits (next census 2022) is crucial. Additionally, analysing finer categories of the ecological species groups with an additional category between thermophilic and cryophilic species might improve the relevance and information content of the results.

Finally, this study underlines the suggestions from other researchers (GOTTFRIED et al. 1998; KAMMER et al. 2007; ENGLER et al. 2011; GRITSCH et al. 2016), that the potential newcomers are already occurring on the slopes below the summits. This applies not only to the southern aspects analysed in this study but also to the eastern slopes (WINKLER et

al. 2016). As the future development of the vegetation on summits is strongly linked to the vegetation on the slopes below them, all cardinal aspects should ideally be included in future studies and predictions.

Zusammenfassung

Klimaerwärmung kann als der wichtigste Faktor für Veränderungen in alpinen Ökosystemen angesehen werden. Da Pflanzen aus größeren Höhenlagen in den Alpen als sehr sensibel gegenüber der Klimaerwärmung gelten, sind Langzeit-Monitoring-Programme wichtig, um Richtung und Grad der Diversitätsänderung zu ermitteln. Diese Studie erweitert das 2001 begonnene Monitoring in der GLORIA-Region Dolomiten. Laut vorangehender Untersuchungen sind die östlichen und südlichen Hänge am stärksten vom Klimawandel betroffen. Wir konzentrierten uns daher auf die Pflanzengesellschaften an den Südhängen von der Baumgrenze aufwärts und untersuchten die Unterschiede zur jeweiligen Gipfelvegetation. Ökologische Unterschiede sollten durch die Analyse der LANDOLT-Indikatorwerte Temperatur und Bodennährstoffe sowie die Differenzierung von konkurrenzstarken und konkurrenzschwachen Arten aufgedeckt werden. An den Südhängen wurden vier Pflanzengesellschaften bestimmt. Drei davon waren alpine Rasen, während nur auf den höheren Flächen des höchsten Gipfels Schutzvegetation vorkam. Auf den Gipfeln wurden außerdem zwei alpine Pionierasen ausgewiesen. Diese Studie gibt weitere Hinweise über die fortlaufende Thermophilisierung auf den Gipfeln. Die Ergebnisse lassen nur auf einem Gipfel eine Veränderung in naher Zukunft vorhersagen, während auf den beiden anderen Gipfeln topographische Hürden kurzfristige Veränderungen verhindern sollten.

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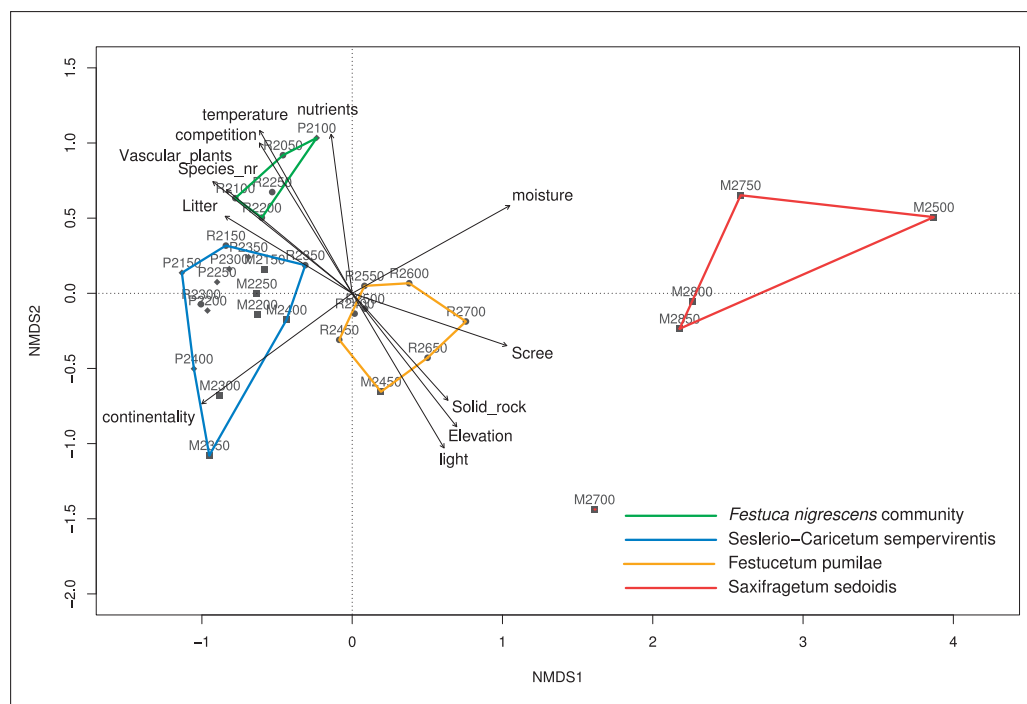
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Appendix

Appendix I – NMDS ordination of the 2019 dataset (transects on the southern slopes of the GLORIA summits in the Dolomites)

NMDS ordination showing the four communities as polygons (based on the results of the TWINSpan analysis) together with the fitted variables as arrows (see Data analyses). Summit abbreviations: M: MTS, P: PNL, R: RNK; the numbers after the letter denote the elevation of the plot cluster. Significant environmental parameters ($p < 0.05$, permutation test 999) were fitted.



Appendix II – Community table of the transects and summits (2001, 2015 and 2019 datasets)

Constancy table of the species for the six communities determined at the southern slopes of the three GLORIA summits MTS, PNL and RNK in the Dolomites from the treeline upward as well as in the permanent summit clusters on the 5 m contour line below the highest summit point of these summits. Data refer to the summit sampling of 2001 and 2015 and to the transect sampling of 2019 at the southern slopes. Different colours show species with highest constancy in the specific communities.

The six communities were: *Festuca nigrescens* community on the southern slopes of PNL and RNK, Seslerio-Caricetum sempervirentis on the southern slopes of PNL and RNK, Festucetum pumilae on the southern slopes of RNK and MTS as well as on the summit plots of RNK, Caricetum rupestris on the southern slopes of MTS as well as on the summit plots of RNK, Saxifragetum sedoidis on the southern slopes of MTS as well as on the summit plots of RNK and MTS, Caricetum firmiae on the summit plots of PNL. Six constancy classes were used: '-': 0%, I: species present in > 0–20% of the samples, II: > 20–40%, III: > 40–60%, IV: > 60–80%, V: > 80–100%. Only the characterising species of the communities are shown. For additional species see Appendix III.

| | <i>Festuca nigrescens</i> community | Seslerio-Caricetum semper-virentis | <i>Festucetum pumilae</i> | <i>Caricetum rupestris</i> | <i>Saxifragetum sedoidis</i> | <i>Caricetum firmae</i> |
|---|-------------------------------------|------------------------------------|---------------------------|----------------------------|------------------------------|-------------------------|
| <i>Festuca nigrescens</i> | V | – | – | – | – | – |
| <i>Crocus albiflorus</i> | V | – | – | – | – | – |
| <i>Carex ornithopoda</i> | V | II | – | – | – | – |
| <i>Anthoxanthum alpinum</i> | V | I | II | – | – | – |
| <i>Lotus corniculatus</i> | V | III | III | – | – | – |
| <i>Potentilla crantzii</i> | V | II | V | I | – | – |
| <i>Botrychium lunaria</i> | IV | I | III | – | – | – |
| <i>Daphne striata</i> | IV | III | – | – | – | – |
| <i>Coeloglossum viride</i> | IV | II | – | – | – | – |
| <i>Scorzoneroideis helvetica</i> | IV | II | IV | – | – | – |
| <i>Nigritella rhellicani</i> | IV | II | – | – | – | – |
| <i>Carlina acaulis</i> | IV | II | I | – | – | – |
| <i>Trifolium pratense</i> subsp. <i>nivale</i> | IV | I | – | – | – | – |
| <i>Trollius europaeus</i> | IV | II | – | – | – | – |
| <i>Luzula multiflora</i> | IV | – | I | – | – | – |
| <i>Festuca varia</i> | II | I | I | – | – | – |
| <i>Nardus stricta</i> | II | – | – | – | – | – |
| <i>Biscutella laevigata</i> subsp. <i>laevigata</i> | IV | V | – | – | – | – |
| <i>Avenula praeusta</i> | IV | IV | – | – | – | – |
| <i>Carduus defloratus</i> | IV | IV | II | – | – | – |
| <i>Campanula scheuchzeri</i> | V | V | V | I | – | – |
| <i>Ranunculus montanus</i> agg. | V | V | V | – | – | – |
| <i>Festuca norica</i> | V | V | III | – | – | – |
| <i>Galium anisophyllum</i> | V | V | V | – | – | – |
| <i>Soldanella alpina</i> | V | IV | IV | – | – | – |
| <i>Thymus praecox</i> subsp. <i>polytrichus</i> | V | V | V | I | – | – |
| <i>Scabiosa lucida</i> | IV | IV | III | – | – | – |
| <i>Hippocrepis comosa</i> | IV | III | III | – | – | – |
| <i>Homogyne alpina</i> | III | III | V | – | – | – |
| <i>Polygala alpestris</i> | III | III | III | – | – | – |
| <i>Sesleria caerulea</i> | IV | V | V | I | – | II |
| <i>Carex sempervirens</i> | V | V | IV | – | – | – |
| <i>Ranunculus hybridus</i> | II | IV | – | – | – | – |
| <i>Festuca pumila</i> | – | V | V | I | – | V |
| <i>Helianthemum alpestre</i> | III | V | V | – | – | V |
| <i>Gentianella anisodonta</i> | III | V | V | I | – | – |
| <i>Agrostis alpina</i> | II | V | V | – | – | – |
| <i>Achillea clavennae</i> | – | V | III | – | – | II |
| <i>Kobresia myosuroides</i> | II | IV | V | – | – | – |
| <i>Anemone baldensis</i> | – | II | V | – | – | – |
| <i>Gentiana brachyphylla</i> | – | II | V | – | – | – |
| <i>Veronica aphylla</i> | – | I | IV | I | – | – |
| <i>Myosotis alpestris</i> | II | II | IV | – | – | – |
| <i>Minuartia gerardii</i> | – | III | IV | II | III | IV |
| <i>Minuartia sedoides</i> | – | I | V | V | III | II |
| <i>Draba aizoides</i> | – | – | V | V | – | I |
| <i>Silene acaulis</i> agg. | – | III | V | IV | II | IV |
| <i>Salix serpyllifolia</i> | – | II | V | IV | I | II |

| | <i>Festuca nigrescens</i> community | Seslerio-Caricetum sempervirentis | Festucetum pumilae | Caricetum rupestris | Saxifragetum sedoidis | Caricetum firmae |
|--|-------------------------------------|-----------------------------------|--------------------|---------------------|-----------------------|------------------|
| <i>Erigeron uniflorus</i> | – | I | V | IV | II | – |
| <i>Carex rupestris</i> | I | I | III | III | – | V |
| <i>Sesleria sphaerocephala</i> | – | I | I | V | I | V |
| <i>Asplenium ruta-muraria</i> | – | – | I | V | I | – |
| <i>Saxifraga oppositifolia</i> | – | – | III | V | III | – |
| <i>Arabis stellulata</i> | – | – | – | IV | I | II |
| <i>Festuca alpina</i> | – | – | I | IV | – | II |
| <i>Persicaria vivipara</i> | IV | V | V | IV | – | V |
| <i>Poa alpina</i> | IV | II | V | IV | IV | I |
| <i>Saxifraga sedoides</i> | – | – | – | V | V | – |
| <i>Cerastium uniflorum</i> | – | – | I | V | V | – |
| <i>Hornungia alpina</i> | – | – | I | V | V | – |
| <i>Draba hoppeana</i> | – | – | – | – | IV | – |
| <i>Carex firma</i> | – | III | II | – | – | V |
| <i>Euphrasia minima</i> agg. | – | IV | III | – | – | V |
| <i>Potentilla nitida</i> | – | I | I | I | – | V |
| <i>Oxytropis montana</i> | I | II | I | I | – | V |
| <i>Phyteuma sieberi</i> | – | III | – | – | – | V |
| <i>Saxifraga caesia</i> | – | I | II | II | – | V |
| <i>Arenaria ciliata</i> | – | – | III | III | I | V |
| <i>Anthyllis vulneraria</i> subsp. <i>alpicola</i> | I | V | III | – | – | V |
| <i>Dryas octopetala</i> | – | III | I | – | – | IV |
| <i>Hedysarum hedysaroides</i> | – | I | – | – | – | IV |
| <i>Saxifraga squarrosa</i> | – | I | – | I | – | IV |
| <i>Gentiana terglouensis</i> | – | – | I | III | – | IV |
| <i>Crepis jacquinii</i> subsp. <i>kernerii</i> | – | I | – | – | – | III |

Appendix III – Companion species of the transect and summit communities (2001, 2015 and 2019 datasets)

Additional species occurring at the southern slopes from the treeline upward of the three GLORIA summits MTS, PNL and RNK in the Dolomites as well as at the permanent plots on the 5 m contour line below the highest summit point of these summits. Data refer to the summit sampling of 2001 and 2015 and to the transect sampling of 2019 at the southern slopes.

The following species also occurred in the *Festuca nigrescens* community on the southern slopes of PNL and RNK:

Achillea millefolium, *Ajuga pyramidalis*, *Alchemilla vulgaris* agg., *Antennaria dioica*, *Arnica montana*, *Astragalus australis*, *Avenula versicolor*, *Bartsia alpina*, *Briza media*, *Carex ericetorum*, *Centaurea triumfetti*, *Cerastium holosteoides*, *Deschampsia cespitosa*, *Erica carnea*, *Gentiana acaulis*, *Gentiana clusii*, *Gentiana verna*, *Geum montanum*, *Gymnadenia conopsea*, *Helianthemum nummularium* subsp. *grandiflorum*, *Hieracium angustifolium*, *Hieracium murorum* agg., *Hieracium pilosella*, *Hieracium villosum*, *Horminum pyrenaicum*, *Juncus trifidus*, *Knautia longifolia*, *Leontodon hispidus*, *Oxytropis campestris*, *Parnassia palustris*, *Pedicularis elongata*, *Phleum rhaeticum*, *Polygala chamaebuxus*, *Potentilla aurea*, *Primula elatior*, *Pulsatilla alpina* subsp. *alpina*, *Pulsatilla vernalis*, *Senecio abrotanifolius*, *Senecio doronicum*, *Solidago virgaurea*, *Thesium alpinum*, *Traunsteinera globosa*, *Trifolium repens*, *Veronica chamaedrys*, *Viola biflora*

The following species also occurred in the Seslerio-Caricetum sempervirentis on the southern slopes of PNL and RNK:

Achillea oxyloba, *Asplenium viride*, *Aster alpinus*, *Astragalus australis*, *Athamanta cretensis*, *Bartsia alpina*, *Bellidiastrum michelii*, *Carex ericetorum*, *Carex humilis*, *Carex mucronata*, *Carex ornithopodioides*, *Cerastium holosteoides*, *Chamorchis alpina*, *Cirsium spinosissimum*, *Clinopodium alpinum*, *Crepis froelichiana* subsp. *froelichiana*, *Dianthus sylvestris*, *Erica carnea*, *Festuca pulchella*, *Gentiana clusii*, *Gentiana verna*, *Geum reptans*, *Gnaphalium hoppeanum*, *Gymnadenia conopsea*, *Gymnadenia odoratissima*, *Gypsophila repens*, *Hieracium bifidum* agg., *Hieracium* cf. *lactucella*, *Hieracium pilosum*, *Hieracium villosum*, *Horminum pyrenaicum*, *Juncus monanthos*, *Larix decidua*, *Laserpitium siler*, *Leontodon hispidus*, *Leontodon hispidus*, *Leontopodium alpinum*, *Luzula sylvatica*, *Mutellina adonidifolia*, *Oxytropis campestris*, *Paederota bonarota*, *Parnassia palustris*, *Pedicularis rostratocapitata*, *Pedicularis verticillata*, *Phyteuma hemisphaericum*, *Phyteuma orbiculare*, *Pinus cembra*, *Polygala chamaebuxus*, *Primula auricula*, *Primula halleri*, *Pulmonaria angustifolia*, *Pulsatilla vernalis*, *Ranunculus seguieri*, *Rhododendron hirsutum*, *Salix alpina*, *Salix breviserrata*, *Salix reticulata*, *Saxifraga aizoides*, *Selaginella selaginoides*, *Senecio abrotanifolius*, *Senecio doronicum*, *Silene vulgaris* subsp. *glareosa*, *Soldanella minima*, *Solidago virgaurea*

The following species also occurred in the Festucetum pumilae on the southern slopes of RNK and MTS as well as on the summit plots of RNK:

Achillea oxyloba, *Androsace obtusifolia*, *Antennaria carpatica*, *Armeria alpina*, *Bartsia alpina*, *Bellidiastrum michelii*, *Carex curvula* subsp. *rosae*, *Carex ericetorum*, *Carex ornithopodioides*, *Cerastium holosteoides*, *Cirsium spinosissimum*, *Clinopodium alpinum*, *Festuca intercedens*, *Gentiana clusii*, *Gentiana clusii*, *Gentiana verna*, *Geum montanum*, *Gnaphalium hoppeanum*, *Hieracium bifidum* agg., *Hieracium pilosella*, *Hieracium villosum*, *Horminum pyrenaicum*, *Leontodon hispidus*, *Leontodon hispidus*, *Luzula spicata*, *Pachypleurum mutellinoides*, *Pedicularis verticillata*, *Poa minor*, *Potentilla aurea*, *Pulsatilla vernalis*, *Sagina saginoides*, *Saussurea alpina*, *Saxifraga aizoides*, *Saxifraga caesia*, *Sedum atratum*, *Selaginella selaginoides*, *Soldanella minima*, *Solidago virgaurea*, *Valeriana supina*, *Veronica alpina*, *Veronica fruticans*

The following species also occurred in the Caricetum rupestris on the southern slopes of MTS as well as on the summit plots of RNK:

Achillea oxyloba, *Arabis alpina* subsp. *alpina*, *Armeria alpina*, *Carex ornithopodioides*, *Carex parviflora*, *Draba dolomitica*, *Geum reptans*, *Minuartia cherleroides* subsp. *cherleroides*, *Saxifraga caesia*, *Solidago virgaurea*

The following species also occurred in the Saxifragetum sedoidis on the southern slopes of MTS as well as on the summit plots of RNK and MTS:

Achillea oxyloba, *Arabis alpina* subsp. *alpina*, *Arabis caerulea*, *Carex parviflora*, *Cystopteris fragilis*, *Draba dolomitica*, *Draba tomentosa*, *Gnaphalium hoppeanum*, *Linaria alpina* subsp. *alpina*, *Noccaea rotundifolia* subsp. *rotundifolia*, *Papaver alpinum* subsp. *rhaeticum*, *Sagina saginoides*, *Salix* cf. *waldsteiniana*, *Saxifraga androsacea*, *Saxifraga caesia*, *Solidago virgaurea*, *Veronica alpina*

The following species also occurred in the Caricetum firmae on the summit plots of PNL:

Bartsia alpina, *Campanula barbata*, *Juniperus communis* subsp. *nana*, *Minuartia cherleroides* subsp. *cherleroides*, *Pedicularis rosea*, *Pedicularis rostratocapitata*

