

## Monitoring of vascular plant diversity in a changing climate in the alpine zone of the Central Greater Caucasus

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**Abstract:** Short-term changes in plant species number, cover, frequency, and composition were studied along an altitudinal gradient crossing 4 GLORIA summits (from 2240 m to 3024 m a.s.l.) from the treeline ecotone to the subnival zone in the Central Caucasus. Large-scale (summit area) and small-scale (16 plots of 1 m<sup>2</sup>/summit) patterns were monitored in 2001. Recording was repeated in 2008. During the monitoring period, the average soil temperature and growing-degree days did not significantly increase. After 7 years, a revisit of the summit area revealed a considerable increase of species richness, especially at the lower alpine zone (CP1 and CP2 summits). At a small scale (1 m<sup>2</sup>), species richness also increased at the lower summit (from 12.5 ± 2.87 to 15.5 ± 3.12 species on the CP1 summit). The cover of 17 species significantly decreased, while that of 5 increased. There were significant linear relationships between species richness and altitude and climatic variables. The main newcomers were species from the lower altitudinal zones and their percentage was highest on the southern slope. Endemics and cold-adapted species were not seriously endangered. In the Central Caucasus we do not consider climate warming as the primary driver of the changes of plant richness and competition.

**Key words:** Alpine plant diversity, global climate change, GLORIA-Europe, richness, species cover

### 1. Introduction

High mountains of the temperate zone are among the most sensitive areas in terms of environmental impacts of climate change (Körner, 2002; Nagy and Grabherr, 2009). Development and normal functioning of alpine ecosystems are largely determined by the low temperature conditions, frequency and intensity of wind, and the distributional character of precipitation (Larcher, 2012; Larcher et al., 2012). Changing of these limiting effects will have an impact on the diversity of the vegetation: migration of species from low altitudes to high altitudes will start and the species adapted to high altitude conditions will gradually disappear (Körner, 1992; Nagy and Grabherr, 2009). According to the recent data (IPCC, 2007; Erschbamer et al., 2009), the minimum temperatures in the Alps have increased by 1.1–2 K during the past century. It is expected that climate warming of 1–2 °C will cause small changes in alpine vegetation, but even greater warming of the climate will cause more significant changes (Theurillat and Guisan, 2001). Climate change will likely lead to increased stress from drought and warm winters (St. Clair and Howe, 2011). As single species have individual responses to environmental changes, creation of a new plant community is more feasible than migration of already existed species (Pauli et al., 2007).

Many observations, e.g., in the Alps (Gottfried et al., 1998; Keller et al., 2000; Grabherr et al., 2001; Walther et al., 2005), Scandinavian mountains (Klanderud and Birks, 2003), Rocky Mountains, and the Central Greater Caucasus (Nakhutsrishvili et al., 2004, 2009), have shown that climate warming leads to the changes of habitats, distribution peculiarities, and viability of some vegetation types. In particular, the investigations conducted in the South and Central Alps (Erschbamer et al., 2006) have shown the change in the diversity of vegetation from the treeline to the alpine zone, invasion of forest elements in alpine meadows that represents a certain danger to the prior ones. Vertical shifting of the treeline has been shown for several mountain systems of the world (Moiseev and Shiyatov, 2003; Kullman, 2007) and in particular in the Central Greater Caucasus (Nakhutsrishvili, 2003; Akhalkatsi et al., 2006; Hughes et al., 2009). Studies in the high mountains of the Kazbegi region (the Central Greater Caucasus) revealed enhancement of seed formation process in birch forests, with individuals of *Betula litwinowii* Doluch. of 6–8 years old found at the altitude of 2200–2550 m (Akhalkatsi et al., 2006; Hughes et al., 2009). Subalpine forests have been shifted upwards by 60–80 m in the South Urals during the last 70 years (Moiseev and Shiyatov, 2003). In Scandinavia the observed treeline

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advances of up to 150–165 m during the 20th century reflected the 1 °C summer warming during that period (Kullman, 2007).

Climate change in Georgia has a mosaic character reflected in the temperature rises in East Georgia in recent decades. In West Georgia, on the contrary, the temperature is reducing. During the 2 equal 40-year periods of 1921–1960 and 1961–2000, it was determined that the frequency of warm months in the second period compared to the first decreased over the glaciers of the West and Central Caucasus by 6.6% and 7.2%, respectively (Elizbarashvili et al., 2009, 2010). During the last 70–80 years the permanent backward movement of the glaciers on the south slopes of the Greater Caucasus range is apparent and its speed (1.5 m/year on average) is the same as in the Alps in Europe (Gobejishvili and Kotlyakov, 2006).

The impact of climate change on transformation of the alpine plant diversity has been monitored in the Central Greater Caucasus in the framework of the EU-funded project GLORIA-Europe (Global Observation Research Initiative in Alpine Environments). The project GLORIA-Worldwide established a high mountain monitoring network of permanent plots on summits from the treeline ecotone to subnival/nival zone (Pauli et al., 2004). One of the strengths of the GLORIA network is its focus on the alpine zone, i.e. the zone above the treeline. The main idea of the monitoring project was to investigate species richness in a first monitoring round in 2001 and to observe changes in diversity and plant migrations after 7 years in 2008. The overall evaluation of existing plant species richness revealed quite a large diversity and was relevant to the background of global climate change that is evident in the Caucasus mountain range, especially in the Central Caucasus region during the last 15–20 years (Nakhutsrishvili et al., 2006, 2009; Dullinger et al., 2007;

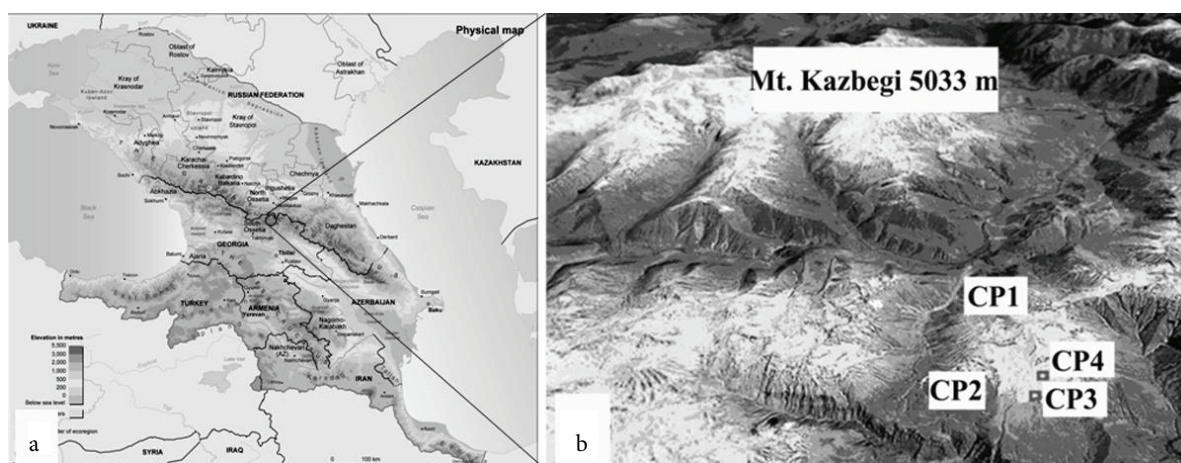
Erschbamer et al., 2010; Pauli et al., 2012). The aim of this study was to determine if there have been any changes in the vegetation on the permanent plots of the GLORIA network in the Central Greater Caucasus from 2001 to 2008 and whether such changes can be related to change in the climate in the same period.

## 2. Materials and methods

### 2.1. Study sites

In 2001 and 2008, field monitoring was carried out on the main watershed range of the Central Greater Caucasus in the Cross Pass (CP) of the Kazbegi district of Georgia (Figures 1a and 1b). The topography of this area is formed by Jurassic rocks, Paleozoic and even older gray granites, younger lava, and moraines, washed out in some places as a result of erosion activity of the Tergi River. Mountain massifs of the Kazbegi volcanic area are overlain by Quaternary glacial or river deposits and rock falls as well as major accumulations of calcareous tuffs and travertine. Glacial deposits occur in many places. Deposits of the Jurassic period, in particular Leas, are most widespread in the region. The rocks are composed of slates and quartzite. Sandy loams and diabasic veins are also found. The relief of the Kazbegi region is formed by ascending, bare, sharp ridges; isolated peaks; very steep rocky slopes; narrow gorges; and caves of erosion-tectonic origin (Nakhutsrishvili et al., 2005, 2006).

According to the GLORIA protocol (Pauli et al., 2004), in each target mountain region 4 summits were chosen along the vertical vegetation zones. In the Central Greater Caucasus region the following summits were selected (Table 1). Summit 1 (CP1: 2240 m a.s.l.) is located in the treeline ecotone with birch (*Betula litwinowii*) krummholz forest predominately with dwarf birch trees and alpine *Rhododendron caucasicum* Pall. shrubs. The birch forest



**Figure 1.** a- Study regions of GLORIA-Europe projects. b- Study summits in Cross Pass on the main watershed range of the Central Greater Caucasus: CP1 - 2240 m a.s.l.; CP2 - 2477 m a.s.l.; CP3 - 2815 m a.s.l.; CP4 - 3024 m a.s.l.

**Table 1.** Characteristics of study sites. Four summits at the Cross Pass (CP) of the main range of the Central Greater Caucasus.

Study summits	Elevation (m a.s.l.)	Coordinates	Summit area (m <sup>2</sup> )	Vegetation zone
CP1	2240	44°29'35"N, 42°32'22"E	1085.77	Treeline ecotone
CP2	2477	44°27'23"N, 42°29'57"E	9628.81	Lower alpine
CP3	2815	44°30'04"N, 42°29'44"E	14974.31	Upper alpine
CP4	3024	44°30'36"N, 42°29'49"E	3429.60	Subnival

was degraded in the past centuries and a small number of trees remained. The summit has no current human impacts by land use and grazing seldom takes place. Summit 2 (CP2: 2477 m a.s.l.) is located in the lower alpine zone and represents an area between the treeline ecotone and alpine grassland, which was used as a hay meadow in the past and currently has no impacts. Summit 3 (CP3: 2815 m a.s.l.), in the upper alpine zone, is covered by alpine grassland and used as cattle pasture with lower grazing impact. Summit 4 (CP4: 3024 m a.s.l.) is located in the subnival zone and has no human impact. The CP3 and CP4 summits are located in the vicinity of the alpine ski resort Gudauri.

## 2.2. Field work

The summits were monitored in 2001 and 2008. The sampling design developed by the GLORIA-EU project protocol (Pauli et al., 2004) was used in all study sites on each summit. Square clusters of 3 × 3 m were marked in all 4 main compass directions at the 5-m contour line below each highest summit point. Four corner plots (1-m<sup>2</sup> permanent plots; total of 64 plots) of each square cluster were used to monitor plant composition and frequency. In the central plot of the 3-m<sup>2</sup> cluster, temperature data loggers (Onset StowAway Tidbit –20 to +50 Model, USA) were buried at a soil depth of 10 cm. Soil temperatures were monitored in 2002, 2005, and 2008 using Onset Computer Corporation software BoxCar 4. Growing-degree day (GDD) index was calculated using temperature data logger information on the number of days per year when soil upper layer mean temperatures were above 2 °C (Molau and Mølgaard, 1996).

Species nomenclatures are given according to Sakhokia and Khutsishvili (1975). The species nomenclature fits with the international nomenclature. We used The Plant List ([www.theplantlist.org](http://www.theplantlist.org)) and Pan-European Species Directories Infrastructure ([www.eu-nomen.eu/portal/search.php](http://www.eu-nomen.eu/portal/search.php)).

Plant species were classified into 1 of 6 ranges: 1) (colline) montane-treeline, (*co*)-*mo-tl* - species from lower altitudes growing up to the treeline but 'normally' not occurring in the alpine zone; 2) montane-treeline-alpine, *mo-tl-al* - species with a wide altitudinal range from the montane to the alpine zone; 3) treeline-alpine, *tl-al* - species occurring from the treeline to the alpine zone; 4)

alpine, *al* - species typical of the alpine zone; (5) alpine-subnival, *al-sn* - species of the alpine and subnival zones; 6) subnival/nival, *sn* - species exclusively growing in the subnival up to the nival zone.

The top cover of surface types (vascular plant cover, solid rock, scree, etc.) and species cover of each vascular plant species were recorded in each 1 m<sup>2</sup> of 64 permanent plots at the 4 summits. The cover value of each vascular plant species was visually determined and was estimated on the percentage scale (e.g., an area of 10 × 10 cm equals 1%, while 1 × 1 cm equals 0.01%) (Frey and Lösch, 2004). The frequency of species was determined using a frame divided into 100 subplots of all 1-m<sup>2</sup> permanent plots. The data were registered in electronic format with the MSAccess program (Pauli et al., 2004).

In 2008 the reinvestigation contained 2 steps: 1) redescription of the plant species richness and cover conducted in 2001; 2) use of the 2001 species data and photos for comparison. We observed changes of the species richness and cover in this period of time.

## 2.3. Data analysis

Mean, median, and standard error were calculated for each quantitative data set. Means were compared using one-way ANOVA ( $P < 0.05$ ) post hoc range tests. The difference in the number of 1-m<sup>2</sup> plots occupied by a species in 2001 versus 2008 was examined using a binomial test. Species that occurred in only 1 plot in 2001 were excluded from the list.

To analyze the changes of the species cover at the 4 summits in 2001–2008, we picked out only species that occupied 3 or more 1-m<sup>2</sup> permanent plots, and their altitudinal distributions were treeline-alpine, alpine, alpine-subnival, and subnival. For testing changes in species cover, we used Wilcoxon's signed-rank test. We compared the 2 groups of significantly increasing and significantly decreasing species. To test the relation between these altitudinal classes and the 2 groups of species with increasing and decreasing cover, we applied a Fisher–Freeman–Halton exact test (Freeman and Halton, 1951). The analysis was performed using the SPSS 13.0 for Windows (SPSS Inc., 2004). Linear regression on the different measures of species richness with altitude and the different soil temperature-derived variables was also

performed in SPSS. Polynomial regression by cubic effect was used for each graphic to fit a nonlinear relationship between the value of  $x$  (year and summits) and the corresponding conditional mean of  $y$  (temperature and number of days).

The definition of indicator species was done as keystone species: species whose strong interactions with other species generate effects that are large relative to their abundance. We used indicator species analysis (ISA) (Dufrene and Legendre, 1997) to describe the value of different species for indicating environmental condition. We performed a detrended correspondence analysis with the species data (main matrix) of all 64 permanent plots of the summit elevation classes (CP1, CP2, CP3, and CP4) using PC-ORD 5.32 software (McCune and Mefford, 1999). We used ISA to contrast the species present in the 4 topographic positions.

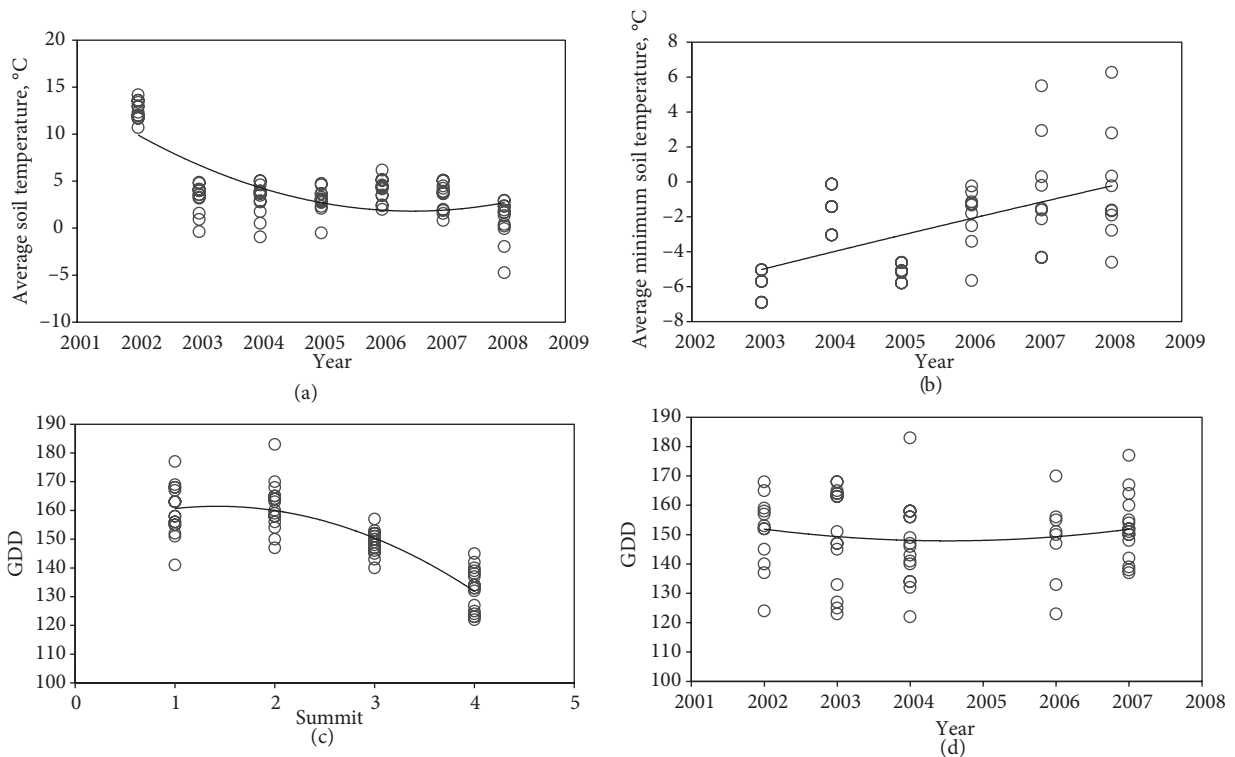
### 3. Results

#### 3.1. Soil temperature

Temperature recording by the data loggers allowed the analyzing of the temperature gradient in the soil's upper layer (10-cm depth) from 2002 to 2008. The average annual temperatures of the soil varied very significantly ( $P$

$< 0.0001$ ) between the years with the highest temperature in 2002 on all 4 summits, and it showed a decline ( $R^2 = 0.8$ ) among the monitoring years (Figure 2a). The changes of the annual minimum temperature for the study period showed a significant trend only in winter on the CP1 summit ( $P < 0.001$ ; Figure 2b). From the lowest (CP1 = 2240 m) to the highest (CP4 = 3024 m) summit in the hottest year, 2002, there was only a  $0.04^\circ\text{C}$  average annual temperature difference. In the colder year of 2005, the same value reached  $3.1^\circ\text{C}$ .

Calculation of GDD index (defined as the period with mean daily soil temperature above  $2^\circ\text{C}$ ) revealed significant differences among the summits ( $P < 0.001$ ), differing along the altitudinal gradient (Figure 2c). The defrosting period on the lowest summit, CP1, starts in April, and the mean daily temperatures persisted for the whole spring, summer, and part of autumn, falling below  $2^\circ\text{C}$  in early November and thus lasting, on average,  $213.25 \pm 20.18$  days for the monitoring period. On the highest summit, CP4, the frost-free period was shorter:  $175.8 \pm 11.64$  days from the end of April through early October, more than 1 month less than that on the lowest summit. GDD varied during the study period (2002–2008;  $P < 0.001$ ), but there was not increasing trend from 2002 to 2008 (Figure 2d).



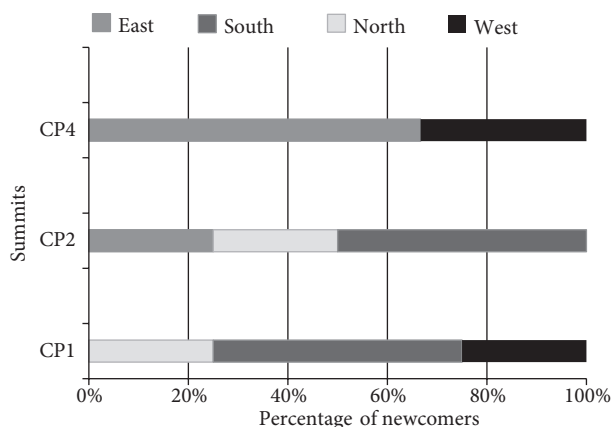
**Figure 2.** a- Average annual soil temperature (10-cm depth) in monitoring years 2002–2008 at all 4 summits; b- average annual minimum soil temperature in winter during monitoring years 2002–2008 on CP1 summit; c- GDD (growing-degree days) at 4 studied summits (1. CP1 - 2240 m a.s.l.; 2. CP2 - 2477 m a.s.l.; 3. CP3 - 2815 m a.s.l.; 4. CP4 - 3024 m a.s.l.); d- GDD at all 4 studied summits in different monitoring years of 2002–2007.

Results of Pearson's correlation test (Table 2) showed that the average temperature and GDD correlated with altitude in 2002 and 2008, and the linear relationship between these variables was significant.

### 3.2. Changes of species richness in the summit areas

The absolute number of vascular plant species observed increased on 3 summits (CP1, CP2, CP4) from 2001 to 2008 (Table 3). Only 2 species each were not refound on CP2 (*Alchemilla chlorosericea* Juz. and *Euphrasia minima* Jacq. ex DC.) and on CP3 (*Alchemilla sericata* Rchb. and *Anthoxantum odoratum* L.). The increase was highest on the CP2 summit and lowest on the CP4 summit. The percentage of newcomer species was highest on the southern slope, except the subnival zone, with the highest number of newcomer species toward the western compass direction (Figure 3). The altitudinal distribution of the newcomers was mainly of the montane-treeline-alpine classes, while only one species [*Scrophularia minima* (M.Bieb.) A.P.Khokhr.] belonging to the alpine-subnival classes appeared on the western slope of the CP4 summit.

Species richness per 1 m<sup>2</sup> increased during the monitoring period (2001–2008) by 6.9 on the lowest (CP1) summit and by 1.5 on the upper (CP4) summit. There was a significant linear relationship between species richness and altitude in both years (Table 2). Species richness also correlated with annual average daily soil temperature and GDD.



**Figure 3.** Percentage of newcomers after 7 years along the main expositions at the tree summits: CP1 - 2240 m a.s.l.; CP2 - 2477 m a.s.l.; CP4 - 3024 m a.s.l.

Changes in the number of 1-m<sup>2</sup> plots occupied by a species in 2001 versus 2008 revealed 2 directions: increased and decreased frequency of species distributed in these areas (Table 4). Eight species showed a significant expansion to new plots, whereas only 3 species reduced their plot occupancy. The expanding species included mostly treeline-alpine plants.

### 3.3. Species cover

Only 68 species from a total 143 vascular plant species described on the 4 summits revealed at least 3 plot

**Table 2.** Results for Pearson's correlation tests for species richness in 1 m<sup>2</sup> in 2001 and 2008.

	Species richness in 1 m <sup>2</sup>				Altitude				Average temperature			
	2001		2008		2001		2008		2001		2008	
	Per. cor.	P	Per. cor.	P	Per. cor.	P	Per. cor.	P	Per. cor.	P	Per. cor.	P
Altitude	-0.675	<0.001	-0.701	0.001								
Av. temp	0.389	0.002	0.465	<0.001	-0.191	0.31	-0.719	0.001				
GDD	0.747	<0.001	0.646	<0.001	-0.811	0.001	-0.722	0.001	0.438	0.001	0.775	0.001

**Table 3.** Total number of vascular plant taxa at the 4 study summits and in 1 m<sup>2</sup> for each summit (mean number with standard deviation) in 2001 and in 2008, and number of new and lost species.

Summits	Altitude	Number of species		Number of species in 1 m <sup>2</sup>		New sp.	Lost sp.
		2001	2008	2001	2008		
CP1	2240	59	63	12.5 ± 2.87	15.5 ± 3.12	4	0
CP2	2477	71	77	17.6 ± 3.29	21.06 ± 3.17	8	2
CP3	2815	15	13	9.12 ± 1.2	10.8 ± 1.68	0	2
CP4	3024	29	32	5.25 ± 2.5	6.65 ± 3.2	3	0

**Table 4.** Significant changes of species occurrences in the 1-m<sup>2</sup> plots (*tl-al* - treeline to alpine species; *al*-alpine species; *al-sn* - alpine to subnival species; *sn* - subnival to nival species).

Species	Altitudinal distribution	Number of plots occupied		Std. deviation	Std. error of mean	P
		2001	2008			
Increasing						
<i>Campanula collina</i>	<i>tl-al</i>	15	17	1.414214	1	0.039
<i>Festuca woronowii</i>	<i>tl-al</i>	18	19	0.707107	0.5	0.017
<i>Poa alpina</i>	<i>tl-al</i>	33	37	2.828427	2	0.039
<i>Ranunculus oreophilus</i>	<i>tl-al</i>	12	14	1.414214	1	0.048
<i>Rhododendron caucasicum</i>	<i>tl-al</i>	2	6	2.828427	2	0.029
<i>Taraxacum confusum</i>	<i>tl-al</i>	7	8	0.707107	0.5	0.042
<i>Sibbaldia procumbens</i>	<i>al-sn</i>	20	26	0.707107	0.5	0.015
<i>Taraxacum stevenii</i>	<i>al-sn</i>	24	21	1.414214	1	0.025
Decreasing						
<i>Deschampsia flexuosa</i>	<i>mo-tl-al</i>	8	7	0.707107	0.5	0.042
<i>Alchemilla sericata</i>	<i>tl-al</i>	29	17	2.485181	2	0.026
<i>Alchemilla chlorosericea</i>	<i>sn</i>	13	12	0.707107	0.5	0.025

preferences in both 2001 and 2008. Among them, the cover percentage of 17 species significantly decreased, while 5 others increased in cover (Table 5). The highest decrease in cover was seen for treeline-alpine species *Alchemilla sericata* (-58.83%), and the other species decreasing in cover were alpine-subnival species such as *Luzula spicata* L. DC. (-29.17%), *Saxifraga exarata* Vill. (-27.63%), *Sibbaldia procumbens* L. (-19.18%), and *Taraxacum stevenii* DC. (-7.28%), and subnival species such as *Matricaria brevifolia* (Lebed.) Rauschert (-41.4%) and *Veronica telephifolia* Vahl (-14.27%). The species with increased cover percentage were predominantly taxa with a distribution center in the treeline-alpine zone, such as *Anthoxanthum odoratum* L. (20.3%), and alpine *Carum caucasicum* (M.Bieb.) Boiss. (18.11%). Only 1 was an alpine-subnival species, *Alchemilla caucasica* Buser (1.6%), and 1 was a subnival species, *Alchemilla chlorosericea* (7.2%).

### 3.4. Indicator species

According to the ISA, we found some significant indicator species of particular exposition on the 4 summits (Table 6). In 2001 on the CP1 summit, 3 species (*Empetrum nigrum* subsp. *caucasicum* (Juz.) Kuvae, *Vaccinium vitis-idaea* L., *Hieracium pilosella* L.) were significant indicators of the north slope and 1 species (*Vicia cracca* subsp. *cracca* L.) indicated the west slope. All of its occurrences were only in north (3 species) and west (1 species) exposition. Three species (*Empetrum nigrum*, *Vaccinium vitis-idaea*, *Vicia cracca*) occurred on 100% of plots and *Hieracium pilosella* occurred on 75% of the plots. The randomization test showed that the probability of an indicator value of

75 or 100, given this species' distribution of abundances, was significant ( $P < 0.05$ ). On the CP2 summit, 4 species (*Carex atrata* L., *Matricaria braviradiata*, *Sibbaldia procumbens*, and *Luzula stenophylla* Steud.) indicated the north exposition and 2 species (*Geranium ibericum* Cav. and *Trifolium trichocephalum* M.Bieb.) were significant indicators of the south slope. On CP3 we did not find the significant indicator species. On CP4 only one species, *Veronica telephifolia*, indicated the west exposition. In 2008 the indicator value (IV) of the indicator species did not change, but on the CP2 summit we found a new indicator species of the west exposition: *Campanula tridentata* subsp. *biebersteiniana* (Schult.) Ogan.

### 4. Discussion

In 2001–2008, studies conducted in the framework of the GLORIA project at 4 different altitudes of the Central Greater Caucasus clearly showed the changes in species richness and cover. In 2008, 15 new species were recorded in comparison with 2001 on the permanent research plots.

In 2002 and 2003, the average soil annual temperature was especially high. In the following years, the temperature decreased. This was confirmed by the data recorded by the used loggers as well as findings of a large-scale survey conducted throughout Georgia (Elizbarashvili et al., 2009). The fact that in the warmest year, 2002, the average annual soil temperatures from the 2240 m a.s.l. treeline zone to 3024 m a.s.l. became almost the same confirms the hypothesis that global climate warming is expected to shift ranges of plant species adapted to concrete climatic

**Table 5.** Significant changes of species cover between 2001 and 2008.

Species	Altitudinal distribution	Mean $\pm$ std. deviation in 2001	Mean $\pm$ std. deviation in 2008	Mean percentage change	P
Decreasing					
<i>Alchemilla sericata</i>	<i>tl-al</i>	10.14 $\pm$ 6.798	4.18 $\pm$ 3.244	-58.83	0.002
<i>Deschampsia flexuosa</i>	<i>tl-al</i>	8.01 $\pm$ 4.334	5.97 $\pm$ 0.75	-25.47	0.01
<i>Festuca airoides</i>	<i>tl-al</i>	7.4 $\pm$ 5.372	5.94 $\pm$ 0.355	-19.86	<0.001
<i>Festuca ovina</i>	<i>tl-al</i>	25.44 $\pm$ 11.856	24.53 $\pm$ 11.167	-3.61	<0.001
<i>Potentilla crantzii</i>	<i>tl-al</i>	2.9 $\pm$ 4.006	2.25 $\pm$ 3.591	-12.17	<0.001
<i>Rhododendron caucasicum</i>	<i>tl-al</i>	2.1 $\pm$ 2.001	1.4 $\pm$ 1.259	-28.5	0.02
<i>Cerastium purpurascens</i>	<i>tl-al</i>	1.01 $\pm$ 0.023	0.9 $\pm$ 0.244	-10.9	0.001
<i>Antennaria caucasica</i>	<i>al</i>	2.27 $\pm$ 2.051	2.09 $\pm$ 1.48	-7.6	<0.001
<i>Fritillaria lutea</i>	<i>al</i>	1.1 $\pm$ 0.452	0.48 $\pm$ 0.303	-52	0.004
<i>Kobresia capilliformis</i>	<i>al</i>	8.25 $\pm$ 6.396	4.6 $\pm$ 3.507	-44.25	0.03
<i>Leontodon hispidus</i>	<i>al</i>	3.3 $\pm$ 1.861	2.82 $\pm$ 1.099	-14.55	0.015
<i>Luzula spicata</i>	<i>al-sn</i>	3.1 $\pm$ 2.309	2.12 $\pm$ 1.866	-29.17	0.01
<i>Saxifraga exarata</i>	<i>al-sn</i>	3 $\pm$ 2.898	2.17 $\pm$ 2.001	-27.63	0.03
<i>Sibbaldia procumbens</i>	<i>al-sn</i>	24.15 $\pm$ 9.926	19.52 $\pm$ 8.318	-19.18	<0.001
<i>Taraxacum stevenii</i>	<i>al-sn</i>	3.62 $\pm$ 2.901	3.36 $\pm$ 2.704	-7.28	0.006
<i>Matricaria brevifida</i>	<i>sn</i>	2.1 $\pm$ 1.673	1.17 $\pm$ 1.099	-41.4	0.01
<i>Veronica telephifolia</i>	<i>sn</i>	2.33 $\pm$ 0.577	2.1 $\pm$ 0.816	-14.27	0.007
Increasing					
<i>Anthoxanthum odoratum</i>	<i>tl-al</i>	8.1 $\pm$ 8.701	9.75 $\pm$ 7.908	20.3	0.021
<i>Gentiana septemfida</i>	<i>tl-al</i>	2.29 $\pm$ 2.563	2.32 $\pm$ 2.373	1.75	0.005
<i>Carum caucasicum</i>	<i>al</i>	2.76 $\pm$ 2.605	3.27 $\pm$ 3.510	18.47	<0.001
<i>Alchemilla caucasica</i>	<i>al-sn</i>	3.6 $\pm$ 1.673	4.2 $\pm$ 2.564	16	0.04
<i>Alchemilla chlorosericea</i>	<i>sn</i>	5.87 $\pm$ 2.525	6.25 $\pm$ 2.361	7.02	0.027

$\alpha = 0.05$ ; *tl-al* - treeline-alpine species; *al* - alpine species; *al-sn* - alpine to subnival species; *sn* - subnival-nival species.

conditions to higher altitudes (Körner, 2009; Gottfried et al., 2012). During the monitoring period the changes of GDD did not show an increasing trend, and average soil temperature significantly increased ( $P < 0.001$ ) only in winter on the CP1 summit.

Species number per summit was increased on all 4 summit areas during the 7 years, as was the case in most of the boreal-temperate mountain regions (Pauli et al., 2012). The increase of the species number was highest at the treeline and on lower alpine summits CP1 and CP2. Decrease in species number was rarely recorded

during the monitoring of the Central Alps (Gottfried et al., 1998; Grabherr et al., 2001; Walther et al., 2005), with the exception of the decline of nival and subnival species resulting from the expanding growth of alpine species (Klanderud and Birks, 2003; Pauli et al., 2007). Increase of species richness at lower altitudes was also recorded (Michelsen et al., 2011). The percentage of newcomer species was highest on the southern slope, except for the subnival zone, with the highest number of newcomer species toward the western compass direction (Figure 3). New species preferred the southern and eastern slopes,

**Table 6.** Relative abundance (%), frequency (%) and indicator value (IV) of the species of the 3 summits (CP1, CP2, CP4) in the 4 expositions. Significant indicators are shown in bold.

Species	Relative abundance (%)					Relative frequency (%)					Monte Carlo test			
	Exposition					Exposition					IV from randomized groups			
CP1	Max	East	North	South	West	Max	East	North	South	West	Indicator Value(IV)	Mean	S.Dev	P
<i>Deschapsia flexuosa</i>	80	80	20	0	0	100	100	50	0	0	79.9	30/8	13.23	0.0086
<i>Trifolium ambiguum</i>	66	66	17	17	0	100	100	100	75	0	66.1	40.5	12.33	0.0462
<i>Taraxacum confusum</i>	81	81	0	19	0	75	75	0	25	0	61.1	29	15.08	0.0888
<b><i>Empetrum nigrum</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>28.2</b>	<b>14.95</b>	<b>0.0034</b>
<b><i>Vaccinium vitis-idaea</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>28</b>	<b>14.71</b>	<b>0.0034</b>
<b><i>Hieracium pilosella</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>25.2</b>	<b>14.19</b>	<b>0.0276</b>
<i>Euphrasia hirtella</i>	91	0	5	91	5	100	0	25	100	25	90.9	31.9	13.88	0.001
<i>Bromus variegatus</i>	61	0	2	61	36	100	0	25	100	50	61.4	30.4	11.73	0.028
<i>Potentilla crantzii</i>	83	0	0	83	17	75	0	0	75	25	62.5	27.5	13.92	0.0788
<b><i>Vicia cracca</i></b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>100</b>	<b>26.6</b>	<b>13.01</b>	<b>0.0034</b>
CP1														
<i>Carex tristis</i>	50	3	17	30	50	100	25	100	100	100	50.5	35	6.85	0.026
<i>Alchemilla caucasica</i>	100	0	0	0	100	75	0	0	0	75	75	25.6	14.14	0.0304
CP2														
<i>Potentilla crantzii</i>	85	85	0	0	15	100	100	0	0	50	84.7	35.7	15.87	0.0176
<b><i>Carex atrata</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>28.7</b>	<b>14.74</b>	<b>0.0026</b>
<b><i>Matricaria breviradiata</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>32.8</b>	<b>15.59</b>	<b>0.0026</b>
<b><i>Sibbaldia procumbens</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>26.2</b>	<b>12.61</b>	<b>0.0026</b>
<i>Anthoxanthum odoratum</i>	80	20	80	0	0	100	75	100	0	0	80.3	32.9	13.29	0.0126
<i>Festuca airoides</i>	68	21	68	0	11	100	50	100	0	50	68.2	32.8	12.05	0.0136
<i>Veronica gentianoides</i>	64	12	64	0	24	100	25	100	0	25	64.3	29.2	12.28	0.0254
CP2														
<b><i>Luzula stenophylla</i></b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>26</b>	<b>14.51</b>	<b>0.0266</b>
<i>Agrostis capillaris</i>	85	0	85	0	15	75	0	75	0	25	63.6	26.5	12.77	0.0294
<b><i>Geranium ibericum</i></b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>28.3</b>	<b>14.09</b>	<b>0.0024</b>
<b><i>Trifolium trichocephalum</i></b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>0</b>	<b>75</b>	<b>29.1</b>	<b>14.03</b>	<b>0.0272</b>
<i>Fritillaria lutea</i>	79	21	0	0	79	100	25		0	100	79.2	28.7	13.02	0.0078
<i>Carex tristis</i>	44	29	8	19	44	100	100	75	75	100	43.5	33.9	5.14	0.0446
CP4														
<i>Alchemilla retinervis</i>	97	97	0	3	0	75	75	0	25	0	73.1	27.4	14.67	0.0284
<b><i>Veronica telephifolia</i></b>	<b>100</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>100</b>	<b>75</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>75</b>	<b>75</b>	<b>25</b>	<b>14.27</b>	<b>0.0288</b>
<i>Festuca woronowii</i>	65	65	11	24	0	100	100	25	75	0	65.5	35.2	13.35	0.0498



i.e. the directions with the higher temperature and longer growing season (Erschbamer et al., 2009). Invasion of species on the south slopes, resulting from climate warming, was predicted by a number of researchers (Stanisci et al., 2005; Kazakis et al., 2006). On the eastern and southern slopes the soil is better developed and the substrate is more stable (Nadelhoffer et al., 1996), but the northern slopes are more conservative for distribution of the vegetation. Increasing temperatures and prolonged growing season have important effects on mineralization activity (Chapin et al., 2005). Over the 7 years 8 (5.6%) species out of the total of 143 species showed a significant expansion to new plots. The species of the treeline-alpine range predominated among them and only 4 species were alpine and subnival.

The observed increase in species richness in the studied plots in the Central Caucasus mostly reflects a filling process of species that were already present in the alpine ecotone, rather than colonization of species immigrating from lower altitudes. In high mountains, local colonization or filling processes by new species appear to be more rapid than local extirpations (Grabherr et al., 2001; Walther et al., 2005). In the upper alpine and subnival zones, the scattered vegetation provides space for new plants, and thus invasion should be easier than on the lowest summit (Holzinger et al., 2006). However, potential immigrants from lower elevations would have to cross the upper alpine grassland belt, which may act as an effective barrier to invasion due to the predominantly closed, long-lived grassland communities (Pauli et al., 2007).

In the Central Caucasus in 2001 and 2008, species richness was related to altitude with a trend of decreasing richness with increasing altitude. This is a common pattern in mountain regions (Körner, 2002). Species richness in the Caucasian summits was not only correlated with altitude; it was also correlated with climatic variables such as annual average daily soil temperature and GDD, with fewer species as the growing season became shorter and temperatures declined. This result supports the basis of the GLORIA protocol, where climate is considered an important factor affecting the composition and species richness of plants on summits (Pauli et al., 2004).

The given data show that among the species with reduced cover, the share of grasses is less than the share of forbs. The grasses in general are species with very high competitiveness, and they are able to suppress the invasion of new species (Grabherr, 1989; Abd El-Chany et al., 2013). The monitoring carried out in tundra regions showed that the grasses appear to be able to get more benefit from the climate change than forbs (Klanderud and Totland, 2005; Walker et al., 2006). The decreasing number of some species in the permanent plots of the treeline ecotone can probably be explained

by ongoing changes in the competitive balance. In the mentioned plots of the Central Greater Caucasus, the grasses experienced less change. Only one grass species reduced its plots occupancy (*Deschampsia flexuosa* (L.) Trin.). This process is particularly evident at CP1's altitude. Meanwhile, the decreased cover of some species, especially at CP2's altitude, cannot be explained only by competition. Change of average annual soil temperature is a normal phenomenon and plants are generally able to tolerate short-term fluctuations through phenotypic plasticity. Gottfried et al. (2002) showed that alpine and nival species responded differently to night-time temperature during the growing season and to the snow cover duration in early summer. The changes of some species' cover in our plots may be caused by different responses of species. The other potential drivers of vegetation changes may be also seldom grazing by domestic ungulates and human activities. Such activities change the community structure, species diversity, and plant cover (Abdel Khalik et al., 2013), but this effect must be minor in our particular study area, which lies outside the main grazing land.

In the permanent plots of the Central Caucasus, 51 (37%) species out of the total of 143 species were Caucasus endemics (Schatz et al., 2013). Seven of them were recorded on the highest summit. When habitats of the endemic species are damaged by human activities or by other factors, the distribution range and population sizes of the species will be reduced (Işık, 2011). During study period, Caucasus endemics were not seriously endangered. Only one species, *Alchemilla chlorosericea*, disappeared from the CP2 summit. This consideration proves the revealing test of indicator species. Among the indicator species (ISA), 5 are Caucasus endemics, and they significantly indicated the particular exposition. Their IV did not change during the monitoring period.

Thus, the results of this study confirm the hypothesis that high mountains of temperate zones are one of the most sensitive areas in terms of environmental impacts of climate change, which already has influence on the diversity of vegetation and migration of species from low to high altitudes. The tendency of occupation of new plots by plants of lower altitude is obvious in the Central Greater Caucasus. The species of the treeline-alpine range predominate among them. We suppose that since the Central Greater Caucasus faced little climate warming, the changes of species richness, cover, and competition at the permanent plots may be caused by filling processes and interannual climate oscillations. The most cold-adapted species and endemics were not seriously endangered. It should be mentioned that in a variable environment, such as the alpine areas, it is difficult to ascertain change based on just 2 time periods and so these observations should be continued in the future.

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