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Jumping the barrier: does a glacier tongue affect species distribution along the elevation gradient in the subnival and nival belts? A case study on Mt. Kazbegi, Georgia, Central Great Caucasus Mountains

Zaal Kikvidze[1,2], Tamar Jolokhava[3,4,5]*, Arsen Bakhia[2,3] and Otar Abdaladze[3]

1 Ilia State University, Institute of Ethnobiology and Socio-ecology, K. Cholokashvili Ave. 3/5, Tbilisi 0162, Georgia
2 Ilia State University, Institute of Botany, Botanikuri Str. 1, Tbilisi 0105, Georgia
3 School of Natural Sciences and Medicine, Institute of Ecology, Ilia State University, K. Cholokashvili Ave. 3/5, Tbilisi 0162, Georgia
4 Ivane Javakhishvili Tbilisi State University, Faculty of Exact and Natural Sciences, I. Chavchavadze Ave. 3, Tbilisi 0179, Georgia
5 Ministry of Environmental Protection and Agriculture of Georgia, Science-Research Centre of Agriculture, Soil Fertility Division, Marshal Gelovani Ave. 6, Tbilisi 0160, Georgia
* correspondence: tamar.jolokhava.1@iliauni.edu.ge

ABSTRACT:

Glaciers are a prominent feature in high mountains and can affect plant distribution along the gradients. However, the possible effect of glaciers on plant community structure at landscape scale has been little studied. We asked: if a glacier tongue crosses a slope laterally and potentially blocks dispersal and migrations, how can this affect vegetation structure and species composition below and above this barrier? A suitable study system is offered by slopes on Mt. Kazbegi, where we established a transect through the subnival and nival belts. We sampled vegetation below and above the glacier tongue and conducted direct gradient analyses to reveal possible effects of the glacier on patterns of species distribution and vegetation structure such as the ratio of solitary plants in vegetation patches. The obtained results indicate that the glacier tongue in our study does not cause a "vegetation switch" in the usual sense of this phrase. However, it might contribute to an abrupt change in the share of solitary plants, as well as to a very rapid decline of plant abundance and species numbers above the glacier.

INTRODUCTION

Throughout the world, glaciers are an important feature of cold landscapes, including high mountains (Pfeffer *et al.* 2014). There are 2020 glaciers in the Great Caucasus Mountains, with a surface of 1193.2 ± 54.0 km² and mean elevation of 3506 m a.s.l. (Tielidze & Wheate 2018). Glaciers can affect plant distributions along the gradients in mountains in various ways. Because glaciers are retreating owing to the ongoing climate warming, most current research is focused on the revegetation of glacier forelands (see Malanson *et al.* 2020 for the lat-

est contribution). Another line of research is focused on topographic heterogeneity created by existing or retreating glaciers to reveal important drivers of plant distribution at a rather microtopographic scale (ca. 1 to 10 m): temperature (Scherrer & Körner 2011), high soil moisture (Litaor *et al.* 2008), disturbance (Bruun *et al.* 2006) and convex *versus* concave topography (Choler *et al.* 2001). However, glaciers, as landscape features, can be important at larger scales too (10 to 100 m and greater), and the possible effect of glaciers on plant community structure at these scales has been little studied. In fact, glaciers and snow-covered areas often are excluded from

vegetation sampling on large-scale gradients such as the elevation gradient (Cuesta *et al.* 2017). Vegetation in the subnival and nival zones is patchy, and patches can contain several species at lower elevations, and yet the share of single-species patches (solitary plants) becomes higher with increasing elevation (Kikvidze & Nakhutsrishvili 1998; Körner & Paulsen 2017; Nakhutsrishvili & Abdaladze 2017a). A glacier could affect this trend too, with implications for the stress-gradient hypothesis (SGH), an important model in plant community ecology (Brooker *et al.* 2008). The SGH states that interspecific plant interactions – competition and facilitation – are in dynamic tension in plant communities. In productive communities, competition prevails, while facilitation is prevalent in stressful communities. The SGH has received much experimental support from alpine systems, where strong competition was documented in alpine meadows, but interactions appeared to become facilitative in subnival environments (Callaway *et al.* 2002). The current version of this hypothesis, however, suggests that facilitative interactions can collapse because of too strong environmental stress factors in very harsh habitats such as the nival belt (Michalet *et al.* 2006), where facilitation loses its importance to community structure (Kikvidze *et al.* 2011). Assume that above a certain elevation, the vegetation is represented only by monospecific patches, which would mean that interspecific effects become impossible and thereby no facilitation can occur. In other words, we would see a collapse of interspecific facilitation. Variation of the share of solitary plants in subnival and nival patches has been rarely examined quantitatively on elevation gradients, and we included this question in our study. Finally, we know little about pH and available nutrients in subnival and nival belts of the Central Caucasus, although works conducted in other mountains point to the importance of soil processes (Hofmann *et al.* 2016; Praeg *et al.* 2019). Knowing the patterns of soil properties along the elevation gradient would allow us to look at how the observed changes in vegetation structure and species composition are associated with soil processes (Chapin & Körner 1994; Walker *et al.* 2001; Körner 2003).

The aim of our study was to address the above questions. In particular, a glacier tongue can cross a slope laterally and potentially block dispersal and migrations. How can this affect vegetation structure and species composition below and above this barrier? Can it create a "vegetation switch" (sensu Wilson & Agnew 1992; Lloyd *et al.* 2000)? Or is this barrier permeable and relatively less important to the patterns of plant species distributions on the elevation gradient? To obtain answers, we collected data on the abundance and identity of species along the elevation gradient below and above the glacier barrier on the transect, analysed soil samples and conducted direct gradient analyses to reveal possible effects of the glacier on the patterns of species distribution

Fig. 1. Location of the Kazbegi region, central Great Caucasus Mountains (marked in green tones).

and vegetation structure, including the ratio of solitary plants in vegetation patches.

MATERIALS AND METHODS

Study area. Our study was conducted on the slopes of Mt. Kazbegi in the Central Great Caucasus Mountains (Fig. 1). The exact coordinates for the lowest and highest points of the transect are as follows: the north slope - from N 42°39'39.50", E 44°33'32.14" to N 42°41'06.63", E 44°31'51.83"; south slope - from N 42°39'38.42", E 44°33'33.43" to N 42°41'.05.94", E 44°31'50.36". This is the most elevated and geomorphologically complex part of the Great Caucasus Mountains. The dominant soil types are: leptic, folic, alumic and humic umbrisols (Abdaladze *et al.* 2015). The topography is characterised by high bare sharp-ridged rocky ranges divided by large depressions and narrow ravines of erosive and tectonic origin (Abdaladze *et al.* 2015). The summit of Mt. Kazbegi reaches 5054 m (Fig. 1).

The climate of Mt. Kazbegi is humid with short cold summers and long severe winters (Table 1). At 3650 m a.s.l., the mean annual air temperature is -6.1°C and morning frosts are frequent during summers. The number of windstorms is 12 per month and the number of snowy days is 170 per year. Weather can change dramatically during a day (Nakhutsrishvili *et al.* 2005; Abdaladze *et al.* 2015).

Vegetation zones are clearly pronounced in the Caucasus, and the potential tree line in the Kazbegi region occurs at an elevation of ca. 2650 m, with well-developed alpine grasslands (meadows) higher up. These meadows form a continuous cover up to ca. 3000 m a.s.l., above which the vegetation becomes patchy (subnival and nival zones) (Nakhutsrishvili 2013; Nakhutsrishvili & Abdaladze 2017b). The vegetation patches are formed mostly by growth forms adapted to the harsh conditions of high elevations: cushions, prostrate plants, etc. (Nakhutsrishvili & Gamtsemlidze 1984; Körner & Larcher 1988; Körner 2003, 2011; Nakhutsrishvili

Table 1. Climate characteristics of subnival and nival belts of the Kazbegi region (taken from Nakhutsrishvili 2003). Max. = Maximum.

Vegetation zone	Temperature of summer (July-August) months		Temperature of winter (January-February) months		Duration of snow cover	Max. depth of snow cover	Ave. annual precipitation
	(ºC)		(ºC)		(months)	(cm)	(mm)
	Ave.	Max.	Ave.	Max.			
Subnival	6.1	16	-12.0	-30.0	7-8	<200	800-1000
Nival	2.2	14	-14.0	-33.0	12	>200	1000-1200

& Abdaladze 2017a). These growth forms can be found growing in a solitary form (monospecific patches) or in association with grasses and forbs (multispecific patches) (Kikvidze 1993; Kikvidze & Nakhutsrishvili 1998). Plant abundance declines rapidly with increasing elevation, although some plants can reach the snow line, which occurs here at ca. 4000 m a.s.l. – the upper limit of vascular plant distribution in the region, only one species – *Cerastium kasbek* – occurring at this limit (Nakhutsrishvili & Abdaladze 2017a).

Sampling design and data collection. We set a transect on the slopes of Mt. Kazbegi in the Central Great Caucasus Mountains (Fig. 1). The range of this transect was from 3000 to 3900 m a.s.l., i.e., from the alpine-nival ecotone to almost the snowline (Nakhutsrishvili 2013), including the subnival and nival zones (sensu Nagy & Grabherr 2009; Gottfried et al. 2011). At an elevation of 3400-3500 m, the transect is crossed by a tongue of glacier (Fig. 2), which provides an opportunity to observe the effects of this barrier on vegetation structure and species distribution patterns along the transect. The transect (Fig. 2) was set along a ridge where the slopes have well-pronounced north and south aspects. Study plots were established on two slopes of these opposite aspects, at the following elevations: 3000 m, 3100 m, 3200 m, 3300 m, 3600 m, 3700 m and 3900 m. No sampling was conducted at 3400 m and 3500 m because the transect here was crossed by the glacier; 3800 m also appeared to be covered entirely with ice, so sampling at this elevation was not possible. Elevation and slope aspects were determined using a GPS device (Etrex Summit, Garmin, Switzerland). At each plot (area approximately 200 m²), we randomly established 20 sampling quadrats of 1 m × 1 m in size (Fig. 3). The distance between the quadrats was at least 4-5 m.

Within each plot, all plant species were recorded, and their abundance was measured by the frequency of occurrence of countable shoots in the patches (Kent 2011). We also separately counted monospecific patches (solitary plants) to analyse their percent share among the patches. For plant species names, we followed the
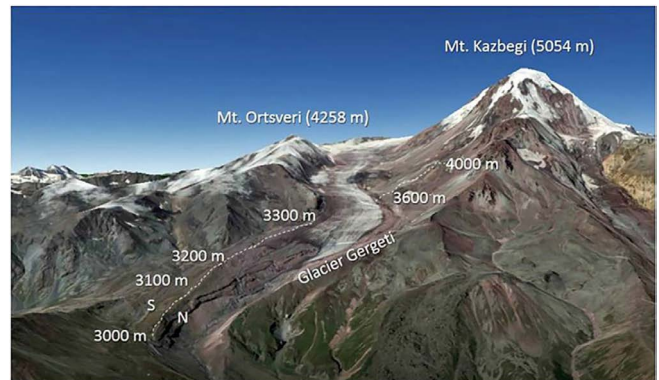

Fig. 2. Study transect on the slopes of Mt. Kazbegi (Central Great Caucasus Mountains); N – north slope, S – south slope. The glacier prevents sampling at elevations of 3400 m and 3500 m.

Fig. 3. 1-m² quadrat for vegetation sampling: recording all species and counting the number of their stems.

Checklist of Vascular Plants of Georgia by Gagnidze (2005).

Soil samples were taken at a depth of 0-20 cm using a gouge auger (Tan 2005). From each quadrat, five samples of soil were taken from five randomly chosen points and

Table 2. Distribution of species abundances (countable stems) along elevation gradient on the north slope of Mt. Kazbegi.

Elevation, m a.s.l. / Species	3000	3100	3200	3300	3600	3700	3900
Saxifraga sibirica	67	80	72	31	5	3	
Tripleurospermum subnivale	45	110	55	7			
Alopecurus glacialis	84	21	8	18			
Cerastium kasbek					20	16	13
Poa alpina	62	44	24				
Saxifraga moschata	41	5	3			2	
Antennaraia caucasica	81	15	1				
Erigeron uniflorus	15	21					
Sibbaldia parviflora	53	1					
Saxifraga flagellaris	19	11	1				
Senecio sosnovskyi		30	17	2			
Carex tristis	48						
Eunomia rotundifolia				27			
Colpodium versicolor	17	8	3				
Sedum tenellum	31	9	5				
Veronica telephiifolia	6	20	21	1			
Festuca supina	1						
Campanula ciliata	28	4					
Delphinium caucasicum	3		1				
Draba siliquosa		9	14				
Taraxacum porphiranthum	9	3					
Alchemilla caucasica	12						
Minuartia oreina	13	3					
Minuartia inamoena							
Tephroseris karjaginii			1				
Scrophularia minima		3					
Nardus stricta	3						
Saxifraga juniperifolia	12						

Table 3. Distribution of species abundances (countable stems) along elevation gradient on the south slope of Mt. Kazbegi.

| Elevation, m a.s.l. / Species	3000	3100	3200	3300	3600	3700	3900
Saxifraga sibirica	19	38	32	39	6	5	
Tripleurospermum subnivale	11	44	39	8			
Alopecurus glacialis	62	12	4	5			
Cerastium kasbek					60	33	22
Poa alpina	7	12	10	1			
Saxifraga moschata	40	15	34	2		3	
Antennaraia caucasica	9	11					
Erigeron uniflorus	16	10	29				
Sibbaldia parviflora	9						
Saxifraga flagellaris	11	16	4				
Senecio sosnovskyi	5			2	2		
Carex tristis	1	4					
Eunomia rotundifolia		1		25			
Colpodium versicolor		13	10				
Sedum tenellum		6					
Veronica telephiifolia							
Festuca supina	43		1				
Campanula ciliata		9					
Delphinium caucasicum	25	10					
Draba siliquosa		4	11				
Taraxacum porphiranthum	7	1	2				
Alchemilla caucasica	6	1					
Minuartia oreina	1	2					
Minuartia inamoena	18						
Tephroseris karjaginii	11	1	4				
Scrophularia minima	8	4					
Nardus stricta			9				
Saxifraga juniperifolia							
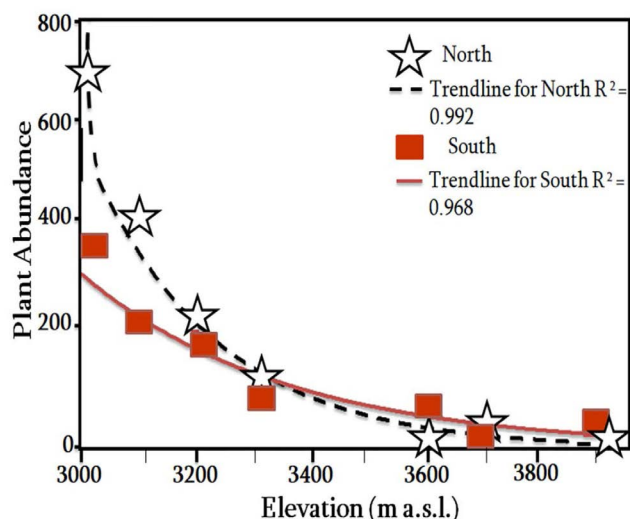
Fig. 4. Exponential model describing the decline of plant abundance along an elevation gradient on Mt. Kazbegi, Central Great Caucasus Mountains.

Fig. 6. Semivariogram of floristic similarity of sampling sites on an elevation gradient on Mt. Kazbegi, Central Great Caucasus Mountains.
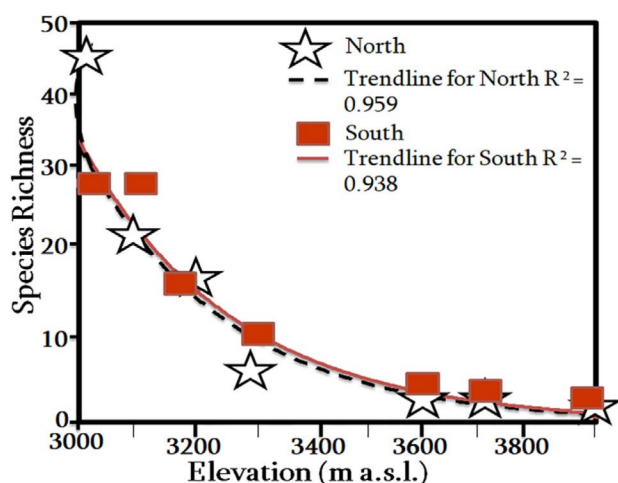

Fig. 5. Exponential model describing the decline of plant species richness along an elevation gradient on Mt. Kazbegi, Central Great Caucasus Mountains.

Fig. 7. Percent share of solitary plants in subnival-nival patches along elevation gradient on Mt. Kazbegi, Central Great Caucasus Mountains. Hill's sigmoidal model describes the change accurately (adjusted R^2>0.95).

mixed. The mixed samples (7 elevations × 2 expositions = 14) were collected in paper bags and transferred to the laboratory. From each mixed sample, two replicates were analysed chemically: the samples were oven-dried at 35°C, ground and sieved through a 2-mm sieve. Soil pH was determined in a 1:2.5 soil/water suspension using a pH meter (WTW Benchtop pH Meter InoLab® Multi 9310 IDS, Xylem Analytics, Germany) with a glass electrode (Jackson 2005). Mobile forms of nitrogen were measured in potassium chloride extracts (Norman & Stucki 1981), followed by ultraviolet spectrophotometry. Plant- available phosphorus was extracted with a so-
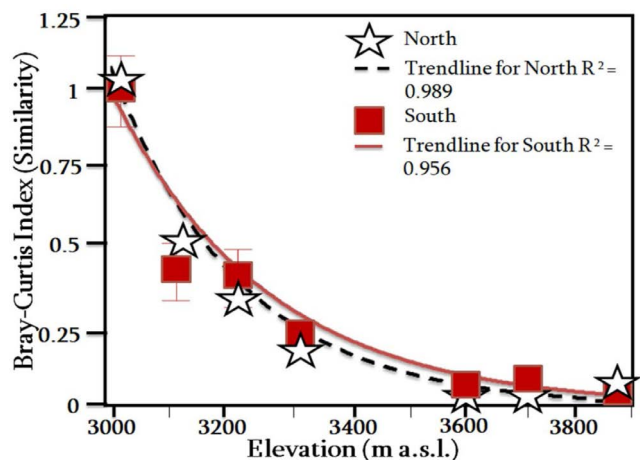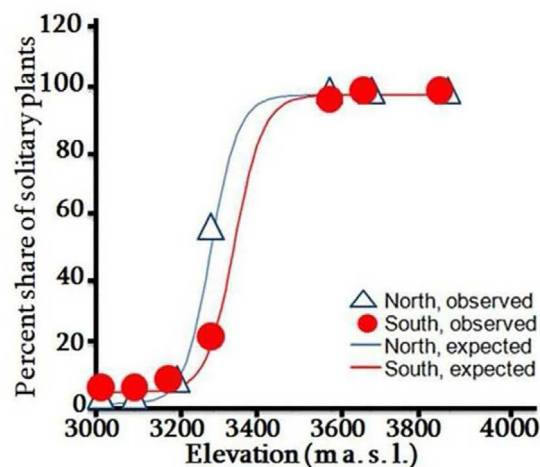
dium bicarbonate solution as described by Olsen (1954) with final photometric determination using the molybdenum blue method (Pansu & Gautheyrou 2007) on a UV/VIS spectrophotometer (Specord 210 Plus, Analytik Jena, Germany). Plant-available potassium was determined in an ammonium nitrate extract (Stuanes *et al.* 1984) using a flame atomic absorption spectrometer (Zeenit 700p, Analytik Jena, Germany).

Data analyses. We constructed a community matrix, which included environmental data (elevation, exposition, soil pH, plant available N, P and K) and plant community data (plant species occurrence and abundance at sites). We used linear and non-linear regression anal-
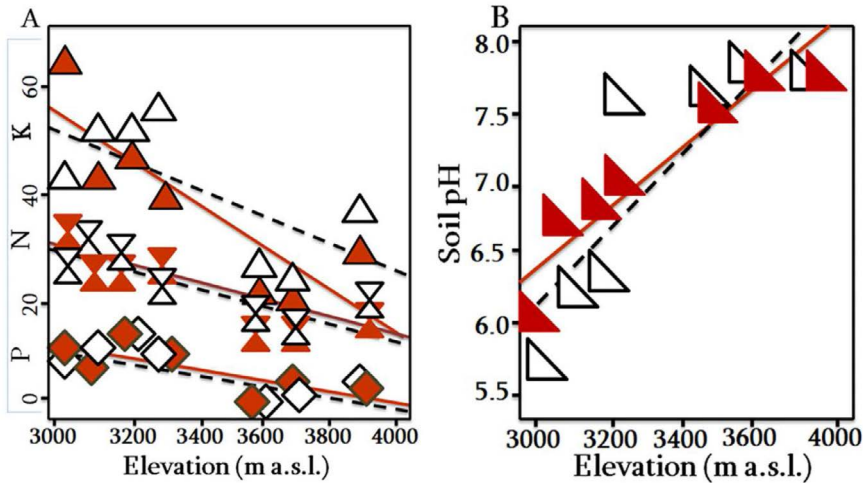
Fig. 8. Soil nutrients and pH along an elevation gradient on Mt. Kazbegi, Central Great Caucasus Mountains (3000 to 3900 m a.s.l.). A: Plant-available N (squares), P (pentagons) and K (circles); B: soil pH (triangles). Solid and empty symbols show north and south slopes, respectively.

yses to examine the dependence of soil properties (pH, N, P and K), plant abundance (measured as the number of countable stems within the quadrats in the plot, see above) and species richness (number of species recorded per plot) on elevation. We also calculated the Bray-Curtis Similarity Index and built a variogram to show how floristic similarity changes along the elevation gradient. Finally, we analysed dependence of the percent share of solitary plants on elevation. To select the best model for describing the dependence of the above variables on elevation, we used Akaike's information. The quality of fit of the models was assessed by the determination coefficient (R^2). We conducted these analyses separately for the north and south slopes. Among the best models were exponential regression and Hill's equation.

We used IBM SPSS Statistics for Windows, Version 21.0 (IBM Corp 2012) and PAST 3.20 (Hammer *et al.* 2001) software.

RESULTS

Plant abundance, as measured by the countable stems, decreased sharply with increasing elevation (Fig. 4). This decrease could be accurately modeled with an exponential equation, on both the north and south slopes, with high values of the determination coefficient ($R^2 <$ 0.95). Similarly, species richness also decreased sharply with increasing elevation (Fig. 5) and was accurately described by an exponential equation on both the north and south slopes. Even though the observed decreasing patterns in plant abundance and species richness were very sharp, they were monotonic and seemingly continuous. Another observation was that vegetation abundance and species richness on the north slope at lower elevations was higher than that on south slopes.

The patterns of species distribution explained the decreasing species richness along the elevation gradient:

almost all major species were more abundant at lower elevations and were gradually but rapidly excluded as elevation increased (Tables 2 and 3) (for north and south slopes, respectively). A minor process of species turnover – replacing of dropped-out species by "typical" subnival and nival species--could also be noticed, yet only a few such replacements were observed: the most prominent was *Cerastium kasbek*, which entered at the highest elevations. Then came species that entered at middle elevations but dropped out again at higher elevations: *Draba siliquosa* and *Eunomia rotundifolia* on both northern and southern expositions, *Senecio sosnowskyi* on north slopes and *Campanula ciliata, Colpodium versicolor, Nardus stricta* and *Sedum tenellum* on south slopes (Tables 2 and 3). There could therefore be only a very limited species turnover observed, so almost all changes in species composition along the elevation gradient could be accounted for by the exclusion of species. This pattern can be described by a semivariogram of floristic similarity that with reference to the lowest communities declined exponentially along the elevation gradient (Fig. 6).

Analysis of vegetation patch membership revealed a strongly sigmoid shape of dependence of the solitary plant percent share in total vegetation patches on the elevation gradient and was accurately described by Hill's function (Fig. 7).

Finally, while available N, P and K decreased (Fig. 8A), pH increased (Fig. 8B) with increasing elevation.

DISCUSSION

Our results show that at the spatial scale of our study, the glacier tongue did not noticeably affect the patterns of distribution of plant abundance, species richness, species composition, soil pH and nutrient contents. However, the glacier tongue's location coincided

with sharp changes in the share of solitary plants. This might be a coincidence, the tongue lying exactly in the zone where multi-species patches give way to solitary plants (Kikvidze & Nakhutsrishvili 1998; Körner & Paulsen 2017; Nakhutsrishvili & Abdaladze 2017a), or the glacier could somewhat contribute to the abruptness of this change. The described sharp shift from multi-species to solitary plant patches also also implications for the Stress-Gradient Hypothesis (SGH), which states that interspecific plant interactions – competition and facilitation – are in dynamic tension in plant communities (Brooker et al. 2008). The current version of this hypothesis suggests that facilitative interactions can collapse because of too strong environmental stress factors in very harsh habitats such as the nival belt (Michalet et al. 2006), where facilitation can lose its importance to community structure (Kikvidze et al. 2011). Because interspecific relationships are impossible in monospecific patches, the abrupt transition from multi-specific patches to solitary plants can indicate a line above which facilitation collapses. This might support the theory behind the SGH, but further studies are required to look at the variation in the ratio of solitary plants to the number of patches and see whether or not its abrupt change along elevation is a common feature.

Overall, we observed a very rapid decline in plant abundance and soil nutrients along the elevation gradient through the subnival and nival belts. This is perhaps a very steep gradient, along which plant abundance and species richness decline exponentially to quite low values, mirrored by sharply decreasing available nutrients. Rapidly reducing plant abundance apparently fails to stabilise soils at higher elevations (Legros 1992; Baruck et al. 2016). The decline of species composition was also very steep: direct gradient analysis showed that plant species dropped out quite rapidly along the gradient, and only very few species replaced them, and they dropped out again at the highest elevations to leave a single remaining species – *Cerastium kasbek*. The glacier tongue might actually contribute to steepness of the observed changes. In other words, without the glacier tongue's influence, the exponential curves might run less steeply, and species turnover could be more tangible. Indeed, only three species could be found both below and above the glacier tongue – *Saxifraga sibirica*, a species with a remarkably wide elevation range, *Saxifraga moschata* and *Senecio sosnowskyi*, but without the glacier tongue there might be more such species. It is noteworthy that these three species are wind-dispersed. This type of dispersal is important to colonising subnival habitats (Tovar et al. 2012; Matteodo et al. 2013), and the dominance of wind-dispersed species early after glacial retreat is commonly observed (Zimmer et al. 2018). Glaciers worldwide are shrinking, Mt. Kazbegi is no exception and the presence of the above three species on both sides of the glacier might simply reflect strong abil-ity of these species to colonise emerging ice-free habitats. Wind dispersal can become even more important in the nival belt close to the snowline (Cuesta et al. 2017): traits related to wind dispersion might help make possible the uppermost distribution of *Cerastium kasbek* – a species particularly specialised in coldest habitats near the snowline. However, at this stage these assumptions are impossible to assess, as a large data set is required to enable comparing multiple slopes with and without glaciers and conduct a robust quantitative analysis.

Finally, we observed that vegetation abundance and species richness on the north slope at lower elevations was higher than that on south slopes – a phenomenon commonly found in temperate alpine gradients (Vittoz et al. 2010; Winkler et al. 2016).

CONCLUSIONS

At this stage, it can be concluded that the glacier tongue in our study does not cause a "vegetation switch" in the usual sense of this phrase. However, it might contribute to abrupt changes in some characteristics (the share of solitary plants) and also might affect the distribution of plants along the elevation gradient.

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REZIME

Botanica SERBICA

Preskakanje barijere: da li kraj lednika utiče na distribuciju vrsta duž visinskog gradijenta u subnivalnom i nivalnom pojasu? Studija slučaja planine Kazbegi, Gruzija, Centralni Veliki Kavkaz

Zaal Kikvidze, Tamar Jolokhava, Arsen Bakhia i Otar Abdaladze

Glečeri predstavljaju upadljivu karakteristiku visokih planina i mogu uticati na distribuciju biljnih vrsta duž gradijenta. Međutim, mogući efekti glečera na biljne zajednice nisu dovoljno istraživani. Mi smo se pitali: ako jezičak lednika pređe nagib bočno i potencijalno blokira širenje i migracije, kako to može uticati na strukturu vegetacije i sastav vrsta ispod i iznad ove barijere? Pogodan sistem za proučavanje su padine planine Kazbegi, gde smo uspostavili transekt kroz subnivalni i nivalni pojas. Sakupili smo vegetaciju ispod i iznad jezička glečera i napravili direktne analize gradijenta, sa ciljem otkrivanja mogućih efekata glečera na distribuciju biljnih vrsta i strukturu vegetacije kao što je odnos pojedinačnih vrsta u delovima vegetacije. Naši rezultati su pokazali da jezičci glečera u našoj studiji ne uzrokuju "promenu vegetacije" u uobičajenom smislu te reči. Međutim, to može doprineti promeni udela pojedinačnih biljaka, kao i veoma brzom smanjenju gustine biljaka i broja vrsta iznad glečera.

Ključne reči: visinski gradijent; nutrijenti dostupni biljakama; diverzitet vrsta; subnivalno-nivalni delovi.