ORIGINAL PAPER

Long-term vegetation dynamic in the Northwestern Caucasus: which communities are more affected by upward shifts of plant species?

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Abstract We studied long-term (25–31 years) dynamics of alpine communities at the Teberda Reserve, NW Caucasus, Russia, to test the following hypotheses: (1) lower altitude species increase and high altitude species decrease their abundance as a consequence of climate warming; (2) such changes in abundance are more significant in communities with short growth season (due to persistent snow cover) compared to exposed communities; (3) species with similar changes in abundance have similar functional traits. Four alpine communities with different positions in relief were considered in order of winter snow cover: alpine lichen heaths (ALH), *Festuca varia* grasslands (FVG), *Geranium-Hedysarum* meadows (GHM), and snowbed communities (SBC).

The altitudinal distribution of species significantly predicted the direction and degree of changes in species abundance in GHM ($p < 0.001$), SBC ($p < 0.02$) and FVG ($p < 0.05$) with high altitude species decreasing and low altitude species increasing their abundance. Mean altitudes of significantly decreasing species exceeded that of increasing species by ca. 100–130 m in FVG, GHM and SBC. There were no species traits or trait combinations that consistently predicted their changing abundance in ALH, FVG and SBC. In GHM increasing species tended to have leaves with higher SLA (i.e. softer leaves) and lower root nitrogen content. The observed dynamic processes may be caused partly by recent climate warming, although slow recovery from historic grazing pressure may also play a role. Regardless of the causes driving the plant species' upward shift, communities experiencing high snow accumulation (SBC, GHM) seem to be more vulnerable to changes in structure and composition.

Keywords Climate change · Alpine community · Altitude · Functional traits

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Introduction

The impact of recent climate changes on vegetation of cold biomes, such as the tundra and alpine belts, is observed worldwide (Wookey et al. 2009; Elmendorf et al. 2012). The most important recent trend in the dynamics of natural alpine vegetation of Europe is an upward shift of altitudinal ranges of plant species, which will eventually lead to shifts in alpine belts (Gottfried et al. 2012; Pauli et al. 2012). For example, the upper limits of several tree species in the Western Caucasus have risen recently (Akatov 2009). The enrichment of the alpine belt with species invasions from the lower altitudes is observed in various regions of the Alps both at short (Erschbamer et al. 2009) and long time scale, but newcomers have not yet replaced high alpine specialist

species (Walther et al. 2005). In mountains of central Norway the abundance of lowland species, dwarf shrubs and species with wide altitudinal and ecological ranges increased over the recent 68 years, while some high altitude species disappeared from habitats in lower parts of their range and increased in abundance in upper parts (Klanderud and Birks 2003). Usually changes in floristic composition within alpine belts are considered, and changes in species abundance within communities have been less studied. However, the recent study of Windmaißer and Reisch (2013) revealed no considerable changes in structure and composition of the alpine grassland in the central Alps during 1980–2012, even though a few species increased in abundance.

The upward shift in plant distribution has often been linked with climate warming in recent decades (Elmendorf et al. 2012; Gottfried et al. 2012; Pauli et al. 2012). However, usually plant species have quite broad amplitude to mean temperature. For example, it was expected that 2 °C increase in summer temperature and 4 °C in winter temperature should not have a direct effect on most mountain plant species of Norway (Sætersdal and Birks 1997).

In mountains the impact of climatic factors, including snow accumulation and length of growing season, depends on relief (Körner 2003), and temperature within the alpine belt varies strongly among plant communities due to microtopographic heterogeneity (Scherrer et al. 2011). Besides climate effects, distribution shifts in some species may be the result of the disturbance history (Schwilk and Keeley 2012) or land use history (Bodin et al. 2013) and mediated by herbivory (Speed et al. 2012).

Few studies have analyzed functional traits of species as determinants of their upper limit of altitudinal distribution. Traits thought to be linked with plant response to climate changes, are, for example, growth form, life form, specific leaf area, leaf dry matter content, leaf N and P content, size and leaf life span, specific root length and diameter of fine roots (Cornelissen et al. 2003). An analysis of global variation of leaf functional traits worldwide revealed that leaf life span, leaf mass per area and nitrogen content per leaf mass are positively correlated with mean annual temperature (Wright et al. 2005). Due to their ecological plasticity, plant species may change their trait parameters while persisting in the same habitat, as has been shown for responses to additional mineral nutrition (Akhmetzhanova et al. 2012a). Regenerative traits, such as seed mass or dispersal mode, have less obvious associations with climatic variation than vegetative traits, even though correlations between seed mass and altitude have been recorded (Pluess et al. 2005; Zhao et al. 2006; Guo et al. 2010). Also, Holzinger et al. (2008) observed more anemochorous species migrating upward than zoochorous and autochorous species in the alpine-

nival ecotone of the Alps. Thus, to relate traits of species to clear trends in their natural dynamics is of great potential importance for modeling and prediction of vegetation changes. This objective requires a set of long-term fine-scale observations on permanent plots. Such raw data are available from the Teberda reserve, NW Caucasus, Russia, where, over a period of about 30 years, shoot numbers of vascular plants have been recorded on permanent plots every year in four typical alpine plant communities varying in their topographic position and corresponding snow accumulation intensity. Earlier the detailed analysis of their dynamics revealed some species with directional changes in shoot number over the observation period (Onipchenko et al. 2004; Elumeeva and Onipchenko 2006; Cherednichenko 2001). Functional traits of leaves and roots were also studied for a wide range of typical alpine species (Shidakov and Onipchenko 2007; Salpagarova et al. 2012).

In the current study, we estimate the significance of changes in abundance of the most common alpine species of the Northwestern Caucasus and link these changes in abundance with plant functional traits. We test the following hypotheses:

1. lower altitude species have increased and high altitude species decreased their abundance in Caucasian alpine communities in response to recent climate warming;
2. such changes in abundance are more significant in communities with a short growth season (due to possible changes in duration of persistent snow cover) compared to exposed communities;
3. species with similar changes in abundance are similar in their functional traits.

Materials and methods

Study area

Long-term natural dynamics of alpine plant communities were studied in the Teberda State Biosphere Reserve in the Northwestern Caucasus (Karachaevo-Cherkessian Republic, Russia). Permanent plots were established in 1981–1987 at Mt. Malaya Khatipara at ca. 2,750 m a.s.l.

This alpine belt has a temperate-zone mountain climate. The mean annual temperature is about −1.2 °C and the mean annual precipitation is 1,400 mm. The warmest month is August with a mean monthly temperature of +8.3 °C, but frost can occur throughout summer (Onipchenko 2004).

Four typical alpine communities were studied: alpine lichen heath (ALH), *Festuca varia* grassland (FVG), *Geranium-Hedysarum* meadow (GHM), and alpine snowbed (SBC).

ALH occupies windward crests and slopes without snow accumulation or with thin (up to 20–30 cm) snow cover. The growing season lasts about 5 months. Fruticose lichens are the main dominants. Among vascular plants the most abundant species are *Festuca ovina, Carex sempervirens, C. umbrosa, Trifolium polyphyllum, Anemone speciosa, Antennaria dioica, Campanula tridentata.* For nomenclature see Onipchenko et al. (2011).

FVG occupies slopes with little snow accumulation (about 0.5–1 m), and the growing season lasts about 4 months. Dense tussock narrow-leaved grasses *Festuca varia* and *Nardus stricta* are the main dominants.

GHM occurs on lower parts of slopes and small depressions with typical snow depth of 2–3 m. The growing season lasts 2.5–3.5 months. The main dominants are *Geranium gymnocaulon* and *Hedysarum caucasicum.*

SBC occupies deep depressions with heavy winter snow accumulation more than 4 m. Growing season lasts 2–2.5 months. Low stature plants, such as *Sibbaldia procumbens, Minuartia aizoides* and *Taraxacum stevenii* are the main dominants here.

Data sampling

We used total shoot number (including vegetative and reproductive shoots as well as juvenile plants) of vascular plants species to estimate each species' abundance during long-term observations on permanent plots. These square plots of 0.0625 m^2 were arranged in transects (ALH and SBC) or in square clusters with four plots in each (FVG and GHM), located close to each other in sites that had been identified as typical for the target plant communities in the larger alpine belt in this region. The total area used for shoot counting was 5 m^2 in ALH and SBC, and 2.5 m^2 in FVG and GHM, and number of plots was 80 in ALH and SBC and 40 in FVG and GHM.

The period of observations was 31 years (1981–2011) in ALH, 26 years (1986–2011) in GHM and SBC, and 25 years (1987–2011) in FVG. The shoots were counted annually in the middle of the growing season: late July-early August in ALH, middle August in FVG and GHM, and late August in SBC.

The following functional traits were included in the analysis:

– leaf traits: dry weight (g), leaf area (cm^2), specific leaf area (SLA, cm^2 g^{-1}), thickness (mm), dry matter content (DMC, mg g^{-1}), nitrogen and carbon content, and C:N ratio (Shidakov and Onipchenko 2007);
– root traits: specific root length (SRL, m g^{-1}), nitrogen and carbon content, and C:N ratio (Salpagarova et al. 2012, 2013); intensity of mycorrhizal infection (Onipchenko and Zobel 2000; Akhmetzhanova et al. 2012b).
– seed traits: mass of 100 seeds (g).

Data analysis

We selected plant species that formed at least 15 shoots per year on average. In total 48 species were included in the entire analysis. To estimate the direction and significance of trends in their interannual dynamics of the initial 50 species we used generalized linear model with a Poisson distribution with year as a predictor and shoot number as a response variable. After applying this procedure we excluded from the subsequent analysis *Euphrasia ossica* in FVG and ALH, and *Rumex alpestris* in GHM, because the shoots of these species were absent on plots in the first years of observations, which made outliers of the regression coefficients of these species in the GLM with Poisson distribution.

Mean altitude of species distribution (m a.s.l.) was derived from the authors' unpublished database of 1,206 vegetation relevés from the Teberda reserve and adjacent areas (mostly from 1,200 to 3,500 m a.s.l.) and calculated as the mean of altitudes where species was recorded in the relevés. Thus, the altitude where a species occurs in more relevés reflects its weighted altitudinal distribution.

For functional trait analysis we combined traits of *Carex umbrosa* and *C. sempervirens* and of *Pedicularis comosa* and *P. caucasica* in ALH, which are difficult to distinguish in the field without reproductive shoots. Mean trait values of these species pairs were used. Two species, *Festuca brunnescens* and *F. ovina,* were excluded from analysis in SBC because of possible inconsistency of shoot counting in some years.

To link the regression coefficients of shoot number against years with plant functional traits and altitudinal distribution, respectively, we ran ordinary least squares (OLS) regressions in an R statistical environment (R Development Core Team, 2011). Subsequently we tested how a complex of plant functional traits predicts the increase or decrease of species abundance in multiple regressions. This procedure was done separately for every community (ALH, FVG, GHM, SBC).

All data on leaf, root, and seed functional traits were log$_{10}$-transformed to comply with normality assumptions for analysis. Percent mycorrhizal infection was arcsine-transformed. AIC statistic was used for selection of the best model (combination of predictors and their interactions). Data included in these models were centered and scaled.

To compare mean altitudinal distribution of significantly increasing and decreasing species (with directional changes and regression coefficient of shoot number over the years highly significant at $p < 0.005$) within every community, we used t test.

Results

A number of species by community combinations (87 %) showed significant ($p < 0.005$) increase or decrease in shoot

Table 1 Regression coefficients of shoot numbers over years for alpine species (R)

Species	Initial number of shoots (Mean ± SE)	Final number of shoots (Mean ± SE)	R	SE	p
ALH					
Agrostis vinealis	12 ± 7	93 ± 14	0.047	0.003	<0.001
Anemone speciosa	177 ± 8	227 ± 4	0.006	0.001	<0.001
Antennaria dioica	294 ± 18	379 ± 10	0.010	0.001	<0.001
Arenaria lychnidea	89 ± 11	145 ± 9	0.014	0.002	<0.001
Campanula tridentata	1,080 ± 95	1,930 ± 170	0.018	0.001	<0.001
Carex spp.	1,660 ± 120	926 ± 59	−0.023	0.001	<0.001
Carum caucasicum	300 ± 63	621 ± 107	0.018	0.001	<0.001
Erigeron alpinus	10 ± 2	33 ± 4	0.038	0.005	<0.001
Eritrichium caucasicum	315 ± 36	272 ± 22	−0.016	0.001	<0.001
Festuca ovina	5,850 ± 560	8,440 ± 430	0.018	0.000	<0.001
Gentiana pyrenaica	389 ± 54	781 ± 115	0.001	0.001	n.s.
Helictotrichon versicolor	730 ± 44	1,470 ± 100	0.027	0.001	<0.001
Luzula spicata	100 ± 15	149 ± 14	0.012	0.002	<0.001
Minuartia circassica	25 ± 1	91 ± 8	0.054	0.003	<0.001
Pedicularis spp.	39 ± 3	59 ± 6	0.001	0.003	n.s.
Trifolium polyphyllum	397 ± 13	255 ± 9	−0.017	0.001	<0.001
Veronica gentianoides	21 ± 6	18 ± 3	−0.010	0.005	n.s.
FVG					
Anthemis cretica	37 ± 4	63 ± 3	0.023	0.004	<0.001
Anthoxanthum odoratum	124 ± 19	295 ± 60	0.034	0.002	<0.001
Calamagrostis arundinacea	268 ± 23	536 ± 42	0.034	0.001	<0.001
Campanula collina	29 ± 2	83 ± 4	0.054	0.004	<0.001
Campanula tridentata	26 ± 3	5 ± 1	−0.074	0.007	<0.001
Carex atrata	49 ± 6	21 ± 1	−0.049	0.005	<0.001
Carex umbrosa	34 ± 3	25 ± 2	−0.019	0.004	<0.001
Deschampsia flexuosa	904 ± 148	2,000 ± 80	0.005	0.001	<0.001
Erigeron caucasicus	63 ± 9	23 ± 3	−0.055	0.004	<0.001
Festuca brunnescens	182 ± 30	112 ± 10	−0.033	0.002	<0.005
Festuca ovina	229 ± 87	78 ± 8	−0.042	0.002	<0.001
Festuca varia	5,300 ± 490	6,280 ± 240	0.002	0.000	<0.001
Galium verum	28 ± 7	32 ± 3	0.017	0.004	<0.001
Gentiana pyrenaica	19 ± 5	181 ± 12	0.127	0.004	<0.001
Leontodon hispidus	235 ± 11	353 ± 22	0.016	0.002	<0.001
Matricaria caucasica	41 ± 2	10 ± 2	−0.089	0.006	<0.001
Minuartia aizoides	233 ± 11	3 ± 2	−0.138	0.004	<0.001
Nardus stricta	5,540 ± 590	3,370 ± 390	−0.028	0.000	<0.001
Ranunculus oreophilus	14 ± 2	41 ± 5	0.066	0.007	<0.001
Scorzonera cana	61 ± 7	77 ± 9	0.009	0.003	<0.001
Sibbaldia procumbens	110 ± 9	118 ± 5	0.001	0.002	n.s.
Veronica gentianoides	40 ± 7	37 ± 3	−0.011	0.004	<0.05
Viola altaica	123 ± 26	86 ± 9	−0.022	0.004	<0.001
GHM					
Agrostis vinealis	24 ± 6	198 ± 48	0.100	0.004	<0.001
Anthemis cretica	28 ± 2	19 ± 8	−0.010	0.005	<0.05
Anthoxanthum odoratum	719 ± 83	886 ± 57	−0.002	0.001	n.s.
Campanula tridentata	47 ± 3	15 ± 2	−0.050	0.005	<0.001

Table 1 continued

Species	Initial number of shoots (Mean ± SE)	Final number of shoots (Mean ± SE)	R	SE	p
Carex atrata	72 ± 8	107 ± 7	0.018	0.003	<0.001
Carum meifolium	361 ± 80	963 ± 137	0.047	0.001	<0.001
Catabrosella variegata	98 ± 16	25 ± 4	−0.070	0.004	<0.001
Deschampsia flexuosa	1,050 ± 130	1,470 ± 240	0.011	0.001	<0.001
Festuca brunnescens	1,680 ± 170	569 ± 55	−0.038	0.001	<0.001
Festuca ovina	549 ± 226	110 ± 56	−0.044	0.001	<0.001
Gentiana pyrenaica	38 ± 8	43 ± 11	−0.003	0.003	n.s.
Geranium gymnocaulon	414 ± 38	585 ± 41	0.013	0.001	<0.005
Hedysarum caucasicum	272 ± 58	299 ± 13	0.004	0.001	<0.01
Leontodon hispidus	1 ± 1	64 ± 12	0.174	0.008	<0.001
Luzula multiflora	32 ± 13	291 ± 50	0.093	0.003	<0.001
Matricaria caucasica	515 ± 48	295 ± 14	−0.016	0.001	<0.001
Minuartia aizoides	356 ± 36	171 ± 28	−0.024	0.002	<0.001
Nardus stricta	6,420 ± 580	5,950 ± 920	−0.007	0.000	<0.001
Phleum alpinum	427 ± 77	665 ± 79	0.021	0.001	<0.001
Ranunculus oreophilus	24 ± 5	58 ± 10	0.040	0.004	<0.01
Scorzonera cana	107 ± 20	111 ± 18	0.008	0.002	<0.01
Sibbaldia procumbens	39 ± 8	6 ± 2	−0.062	0.006	<0.001
Veronica gentianoides	128 ± 10	267 ± 48	0.032	0.002	<0.005
SBC					
Agrostis vinealis	675 ± 79	654 ± 107	0.006	0.001	<0.001
Anthoxanthum odoratum	324 ± 39	1,399 ± 131	0.055	0.001	<0.001
Carex atrata	112 ± 8	133 ± 33	0.001	0.002	n.s.
Carex oreophila	1,480 ± 140	895 ± 93	−0.012	0.001	n.s.
Carum meifolium	149 ± 7	1,200 ± 140	0.066	0.001	<0.001
Catabrosella variegata	1,980 ± 150	929 ± 96	−0.033	0.001	<0.001
Corydalis conorhiza	136 ± 21	426 ± 300	0.020	0.001	<0.001
Gentiana pyrenaica	4 ± 0	19 ± 6	0.039	0.005	<0.001
Gnaphalium supinum	2,720 ± 260	145 ± 30	−0.087	0.001	<0.001
Hyalopoa pontica	8 ± 5	5 ± 3	−0.011	0.006	n.s.
Luzula multiflora	165 ± 15	235 ± 40	0.016	0.002	<0.001
Minuartia aizoides	6,010 ± 380	3,900 ± 490	−0.014	0.000	<0.001
Nardus stricta	6,230 ± 1,080	13,200 ± 1,900	0.029	0.000	<0.001
Pedicularis nordmanniana	382 ± 42	302 ± 48	−0.013	0.001	<0.001
Phleum alpinum	412 ± 31	1,081 ± 159	0.031	0.001	<0.001
Potentilla verna	968 ± 100	315 ± 46	−0.037	0.001	<0.001
Sibbaldia procumbens	6,030 ± 520	4,570 ± 600	−0.007	0.000	<0.001
Taraxacum stevenii	2,580 ± 110	1,420 ± 170	−0.022	0.001	<0.001

$n = 31$ years in ALH, 25 years in FVG, 26 years in GHM, and 26 years in SBC. Initial number of shoots – mean number of shoots in the first 5 years of observations (1981–1985 in ALH, 1986–1990 in GHM and SBC, 1987–1991 in FVG). Final number of shoots – mean number of shoots in the last 5 years (2007–2011 in all communities). The data on shoot number in intermediate years (1986–2006 in ALH, 1991–2006 in GHM and SBC, and 1992–2006 in FVG) are omitted

number during the period of observations; 29 out of 42 species (69 %) showed a positive trend at least in one of communities where they occur, indicating an overall trend of increase in shoot numbers over 25–31 years (Table 1).

The altitudinal distribution of species significantly predicted the direction and degree of trends in GHM ($p < 0.001$), SBC ($p < 0.02$) and FVG ($p < 0.05$) with high altitude species decreasing and low altitude species

Table 2 Relationships between mean of altitudinal range, plant functional traits and regression coefficients of shoot number vs. year (R, presented here as R^2, see Table 1) over years across species in alpine communities (only significant models included)

Community	Predictor	n	B	SE B	R^2	p value
ALH	Altitude	17	−0.270	0.249	0.073	n.s.
FVG	Altitude	23	−0.456	0.194	0.208	<0.05
GHM	Altitude	23	−0.638	0.168	0.407	<0.001
	SLA	23	0.453	0.195	0.205	<0.05
	Root N	23	−0.473	0.192	0.224	<0.05
	Root C:N ratio	23	0.496	0.189	0.246	<0.02
	SLA + Root N + Root C	23	0.506;	0.155;	0.547	<0.005;
			−0.575;	0.158;		<0.005; n.s.
			−0.258	0.157		
SBC	Altitude	18	−0.543	0.210	0.295	<0.02

For multiple regressions significance is displayed for each parameter

n number of species included into analysis, B OLS regressions coefficients
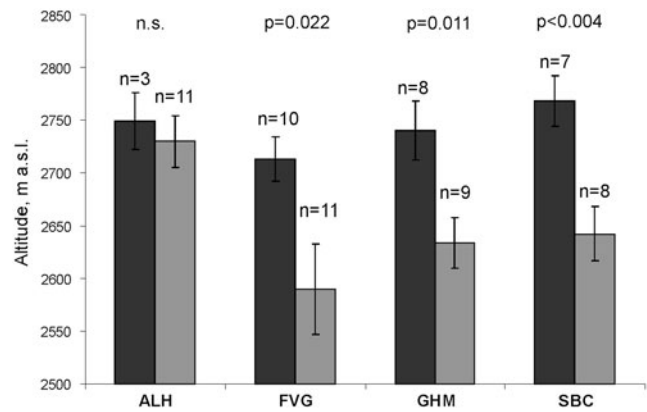

Fig. 2 Altitudinal distribution of species with significant ($p < 0.005$) trends in Teberda Reserve (mean and standard error). *Dark bars* species decreasing their abundance, *light bars* species increasing in abundance. *ALH* alpine lichen heaths, *FVG Festuca varia* grasslands, *GHM Geranium-Hedysarum* meadows, *SBC* snowbed communities. n number of species with significant trends. p significance of differences between groups of decreasing and increasing species by results of t test
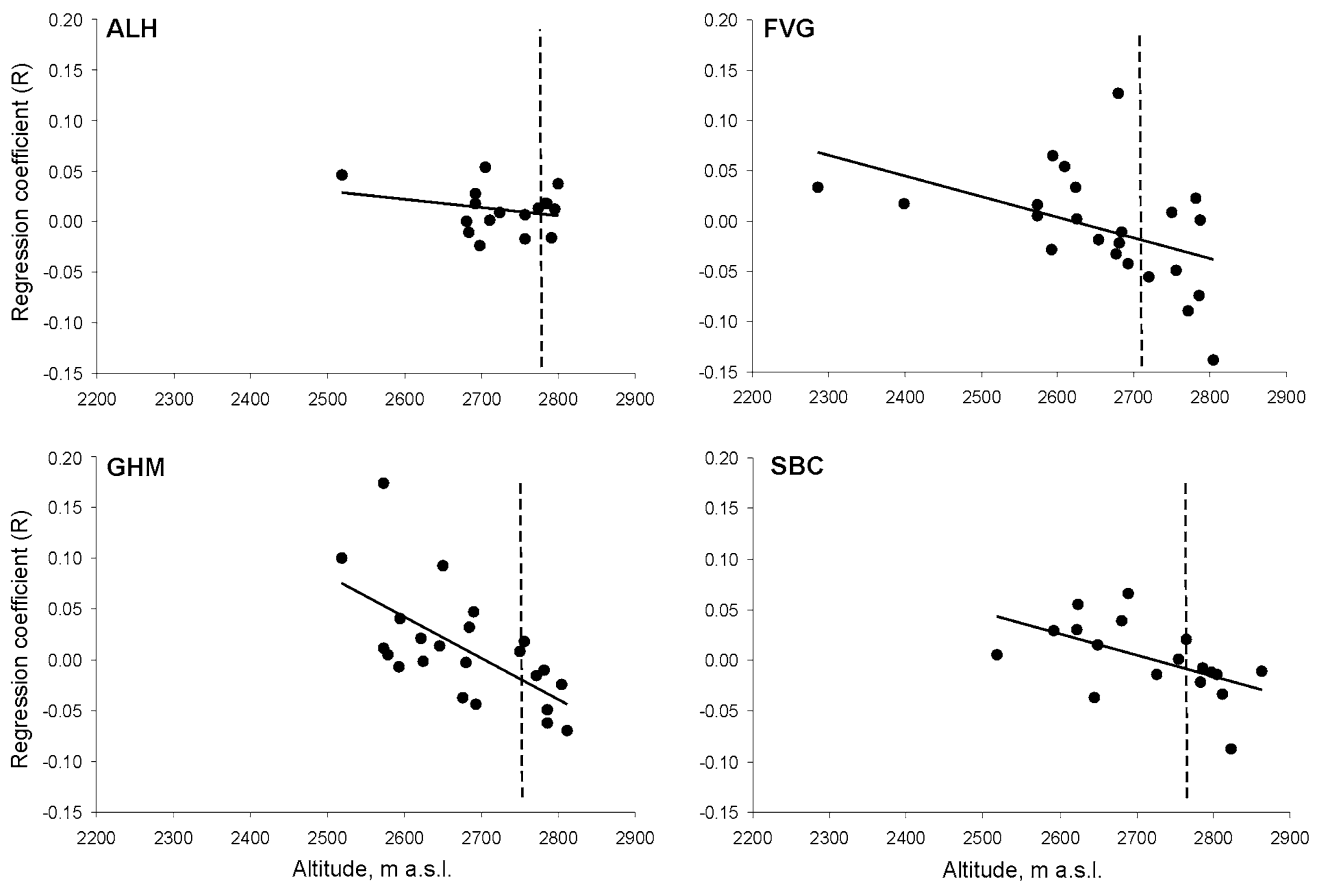

Fig. 1 The relationships between altitude and regression coefficients of shoot number over years in alpine communities of the Teberda Reserve. *Vertical dashed lines* altitudinal position of observation plots on Mt. Malaya Khatipara

increasing their abundance (Table 2; Fig. 1). Mean altitudes of significantly (at $p < 0.005$) decreasing species exceeded that of increasing species by ca. 100–130 m in FVG, GHM and SBC. Mean altitudes of increasing and decreasing species of ALH did not differ (Fig. 2).

Only in GHM we revealed a set of traits that could be attributed to species abundance over years. The single traits associated with species increasing their abundance were SLA, root nitrogen content and root C:N ratio (Table 2), however, the relationships were weak. The best model, based on both leaf and root traits of GHM plants, explained 54.7 % of variance and included as predictors, root nitrogen (27.0 %), SLA (22.9 %) and root carbon content (4.8 %). The increasing species of GHM tended to have leaves with higher SLA and roots with lower content of both nitrogen and carbon. There were no specific traits or trait combinations associated with increasing and decreasing species of ALH, FVG or SBC.

Discussion

Our results are consistent with numerous reports from alpine sites of Europe on an upward shift of the upper limit of species distributions and their increasing abundance in communities of upper alpine zones (Gottfried et al. 2012). However, within the range of the Northwestern Caucasus, we reveal that such trends are context dependent. Specifically, we observed different patterns of change among alpine communities occupying different positions in relief, with concomitant differences in snow accumulation in winter. Communities with no or low snow cover (ALH) were less subjected to expansion of species from low altitudes than communities with deep snow cover (GHM and SBC); FVG held an intermediate position both in terms of snow cover and its weak, only marginally significant relationship between species trends over time and their altitudinal distributions. This suggests that a possible extension of the snow-free growing season due to increasing temperatures is more important for plants of habitats with high snow accumulation. But can we consider temperature increase as the most important driving factor of recent vegetation dynamics of the studied communities?

The observed changes in species abundance in only one community, i.e. GHM, could be weakly linked with traits: specific leaf area and root nitrogen content. So the plants with higher SLA increased and plants with lower SLA decreased their abundance in our study. In contrast, Soudzilovskaia et al. (2013), who analyzed which traits are good predictors of alpine plant abundance response to temperature per se, found that alpine plants with smaller SLA and thicker leaves increase in abundance due to temperature increase. This suggests that increase in abundance of broad-leaved GHM plants in the last decades could not be associated solely with warming climate. Moreover, at global scale across species, SLA is negatively correlated with temperature (Wright et al. 2005). Thus, we can not simply conclude from our findings that temperature regime is the major driver of long-term alpine community dynamics in the Northwestern Caucasus. Speed et al. (2012) revealed that upward shift of plant species in southern Norway occurred only in sites where herbivores had been excluded, while at high sheep density a downward shift was observed and no changes were registered in sites with unchanged grazing activity. In our study site grazing of alpine communities by cattle was ended ∼70 years ago when Teberda became a nature reserve. Moreover, the impact of wild ungulates, such as the Caucasian ibex (*Capra caucasica* Guldenst.), seems to be insignificant. The cessation of grazing in the alpine communities of Teberda coincided with the upward shift of mostly those species with higher SLA. In an extended set of Caucasian alpine species SLA was positively correlated with leaf area (Shidakov and Onipchenko 2007). So, it is not inconceivable that plants with high SLA at the Teberda reserve have gradually been outcompeted by species with low SLA and thus more sclerophyllous leaves with structurally reinforcement that presumably makes them less palatable. Thus, the positive link of SLA with shoot number trends would also be consistent with an environmental regime of reduced grazing pressure.

Directional changes in abundance of species within permanent plots with limited area may also be caused by various other factors, like other forms of land use or (extreme) climatic events. We also have to be aware that population processes and spatio-temporal dynamics, as for instance related to population cycles of rodent herbivores, may obscure long-term linear trends in species dynamics, especially in GHM and SBC, where pine voles (*Pitymys majori* Thom.) are abundant (Fomin et al. 2004; Zibrov and Gerasimova 2007).

The use of separate functional traits or combinations of them does not have strong explanatory power for understanding the causes of altitudinal shifts of plant species in the Caucasus. In plant communities species with low abundance may be analogues of dominants in terms of functional traits and differ only in terms of their capability to respond to environmental factors, and the presence of such species is very important for ecosystem maintenance under changed conditions (Grime 1998; Walker et al. 1999). In this case ecosystem function on average would not change, as increasing and decreasing species would be relatively similar in their effects on biogeochemical cycles and production (Suding et al. 2008).

In conclusion, whilst we do not yet understand the (interacting) factors driving the upward shift of alpine plant species, communities experiencing high snow accumulation

and short growing season seem to have been more sensitive to recent changes in vegetation structure and composition. Our study has provided some support for the more widely reported notion that species' altitudinal shifts in alpine regions may be associated with climate warming (Gottfried et al. 2012; Pauli et al. 2012). However, it also highlights the potential pitfalls of interpreting correlation as causality, as in our study the same species' altitudinal shifts would also be consistent with the slow recovery from a historic grazing regime.

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