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Do patterns of intra-specific variability and community weighted-means of leaf traits correspond? An example from alpine plants

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ABSTRACT

Intraspecific variability of the traits is usually less than interspecific, but directions of inter- and intraspecific variation along environmental gradients are not well studied. For 17 alpine species we test a hypothesis that the direction of intraspecific variation in leaf traits among different communities along an environmental gradient coincides consistently with community weighted mean (CWM) trait variation at the community level along the same gradient. We obtained two groups of leaf traits according to their response to CWM and topographic (snow depth and snow melt) gradients. For leaf mass and area intraspecific variation corresponded to CWM variation among communities. SLA, water content and leaf thickness patterns within species changed directly among communities according to the toposequence (snowmelt gradient). These results are well expressed for forbs, but mostly they were not significant for graminoids. For leaf area we obtained opposite response of forbs and graminoids to snowmelt gradient. Forbs increased, but graminoids decreased leaf area when snow depth increased. Intraspecific trait variation across natural gradients does not necessarily follow that for interspecific or community-level variation.

Keywords: leaf functional traits, alpine plant communities, specific leaf area, community weighted mean, Caucasus

РЕЗЮМЕ

Онипченко В.Г., Рожин А.О., Смирнов В.Э., Ахметжанова А.А., Елумеева Т.Г., Хубиева О.П., Дудова К.В., Судзиловская Н.А., Корнелиссен Х.Г. Согласуются ли внутривидовая изменчивость и средневзвешенные значения признаков листа в сообществе (на примере альпийских растений)? Внутривидовое варьирование признаков, как правило, меньше, чем межвидовое, однако направления меж- и внутривидового варьирования по градиентам среды изучены недостаточно. Для 17 альпийских видов мы проверили гипотезу о том, что направление внутривидовой изменчивости по признакам листа между разными сообществами по градиенту среды последовательно совпадает со средневзвешенными значениями признаков в сообществах (CWM) по тому же градиенту. Мы выделили две группы признаков листа на основе выявленных связей с CWM и топографическими (глубина снежного покрова и время схода снега) градиентами. Для массы листа и его площади внутривидовое варьирование соответствует варьированию CWM среди сообществ. Удельная листовая поверхность, обводненность листа и его толщина внутри видов изменяются в соответствии с расположением сообществ на склоне (градиент времени снеготаяния). Эти результаты хорошо выражены для видов разнотравья, но в большинстве случаев не значимы для злаковых. Для площади листа мы показали противоположную реакцию этих двух групп (разнотравье и злаки) по градиенту снегонакопления. Площадь листа у видов разнотравья увеличивается, а злаков уменьшается при увеличении глубины снежного покрова. Таким образом, внутривидовое варьирование признаков по естественным градиентам не обязательно согласуется с изменчивостью межвидовой и варьированием на уровне сообществ.

Ключевые слова: функциональные признаки листа, альпийские растительные сообщества, удельная листовая поверхность, взвешенное среднее сообщества, Кавказ

Functional leaf traits (FLT) are important parameters for plant fitness as well as many ecological functions of plants including their role in carbon, nutrient and water cycling. These traits include dry leaf mass, leaf (lamina) area, leaf thickness, leaf water contents and specific leaf area (SLA; leaf area per mass unit; also used in its inversed form as leaf mass per area). Traits based on the leaf mass, area and water content are the best predictors for quantitative identification of plant strategies (Pierce et al. 2017). SLA is one of the best predictors to estimate relative growth rate (RGR) (Poorter & Remkes 1990, Poorter & van der Werf 1998, Cornelissen et al. 1998, Shipley 2006; Metcalf et al. 2006, Rees et al. 2010) and it is very sensitive to ecological conditions, such as temperature, water availability, light regime

and nutrient regime (Garnier et al. 2004, Suding & Goldstein 2008, Poorter et al. 2009, Scheepens et al. 2010, Ordonez et al. 2010, Hodgson et al. 2011, Venn et al. 2011, Read et al. 2014), as well as growing season length (Borgy et al. 2017).

Most plant traits, including the mentioned leaf traits, vary most strongly and consistently in their mean values among species (Kattge et al. 2011), when compared to intraspecific variation of the same traits. However, this does not exclude the possibility that mean values for these traits are not strongly determined genetically and have low heritability, even though low genetic variability can decrease the range of their variation (Donovan et al. 2011). Genotypically driven variation is lower than environment-driven variation in SLA (Scheepens et al. 2010). Environmental factors govern the traits significantly (Poorter et al. 2009), but other factors, such as ontogenetic stage and allometry, may also have pronounced effects on leaf trait variability (Cornelissen 1999, Niinemets 2004). Relative role of intraspecific variability is higher for species-poor communities (Hulshof et al. 2013). Plant and leaf size as well as nutrient regime have meaningful effects on SLA (Milla et al. 2008, Rees et al. 2010, Akhmetzhanova et al. 2012). As mentioned above, while intraspecific variability of plant traits can be remarkably high (Mitchell & Bakker 2014, Andrade et al. 2014, Albert 2015, Carlucci et al. 2015, Siefert et al. 2015, Siefert & Ritchie 2016), it is usually significantly lower than interspecific for a given species set (Albert et al. 2010, Jung et al. 2010, Auger & Shipley 2013, Dwyer et al. 2014, Messier et al. 2017, but see Jung et al. 2014). Many species may have similar mean SLA values, but differ in SLA responses to environmental variation (Dwyer et al. 2014). He et al. (2018) shown that there is a positive relationship between intraspecific variation of SLA and species habitat range with respect to soil carbon and nitrogen. Siefert (2012:767) noted that including intraspecific variation "provides a more complete view of communities and the processes driving their assembly". Bagousse-Pinguet et al. (2014) showed that intra-specific variation of plant traits may be an important factor of species coexistence and a possible mechanism of diversity maintenance.

To compare plant traits among different plant communities or even small plots of given communities, many authors use community weighted means (CWM) (Garnier et al. 2004, Suding & Goldstein 2008, Lavorel et al. 2008, Jung et al. 2010). CWM is an integrative value of plant trait for the whole plant community where species "weight" depends on species abundance, such as cover, density or biomass (more abundant species contribute more than rare species). CWM trait values based on plant biomass are useful parameters for functional structure comparison between communities with different floristic composition. Changes in trait CWM depend mainly on floristic and dominance structure (Kichenin et al. 2013). CWM trait values are usually good indicators of environmental gradients (Jung et al. 2010, de Bello et al. 2013). The impact of interspecific variation in CWM was studied in many papers (Cornwell & Ackerly 2009, Kamiyama et al. 2014, Lajoie & Vellend 2015, Siefert et al. 2015), but the direction of this variation is much less known. Namely, it is not yet clear whether direction of intraspecific variation of plant traits among dif-

ferent communities coincides consistently with CWM variation at the community level, the latter of which should be largely driven by interspecific variation. In some cases interspecific (based on CWM) and intraspecific trait variations coinside, but there some examples of opposite cases (Lajoie & Vellend 2015). Within vs. across species trait correlations may have opposite signs (Anderegg et al. 2018) and intraspecific FLT variations of different species were not coincided (Pakeman 2013).

There are several types of intraspecific variation: variation within individual (ontogenetic, seasonal etc.), within community (plot) variation and between communities variation (Siefert et al. 2015). Only last one is reasonable to use for studding directions of intraspecific variation between communities and we used only this level in our study.

Key factors for community's structure and function can be considered as (primary) abiotic and (secondary) biotic (Belyea & Lancaster 1999). Abiotic factors (e.g. climate) select adapted species for a site, biotic factors (e.g. competition) form community structure. CWM of functional traits are parameters of community functional structure. So there is an interesting question, which factors are more important for trait intraspecific variation – abiotic or community functional structure per se. We can expect that for different functional traits different factors are more important.

In temperate alpine areas depth and duration of winter snow cover is one of the main local factors responsible for plant community's patterns (Kudo & Ito 1992, Onipchenko 1994, Körner 2003, Choler 2005, Carlson et al. 2015). Different plant communities change at short distances according to "snowmelt" gradient. The communities have various functional structure and differ according to their CWM of plant functional traits (Shidakov & Onipchenko 2007, Venn et al. 2011). Variability of functional leaf traits (including intraspecific variation) depends on abiotic and biotic (e.g. competition) factors (Grime 2006, Mouillot et al. 2007) and influence of biotic factors often dominates (Burns & Strauss 2012). In case of alpine communities, abiotic and biotic gradients do not coincide. Usually more wet depressions with significant snow accumulations are inhabited by plants with thinner leaves and high SLA than that for plants from snowfree ridges and slopes (Choler 2005). But CWM do not linearly change according snowmelt gradient (Shidakov & Onipchenko 2007), so the alpine communities represent useful object to study directions of intraspecific functional trait variation.

Our null hypothesis is that, for a set of traits widely studied for their important association with plant environmental response and impact, the direction of intraspecific variation in leaf traits among different communities coincides consistently with CWM trait variation at the community level. As an alternative hypothesis, we may postulate that abiotic filter (here snowmelt gradient) may have more important influence on the direction of intraspecific variation than the functional structure (CWM) of the communities. So our paper will be narrowly restricted to study directions of intraspecific leaf trait variation between alpine communities along abiotic (snowdepth) and WM gradients.

We tested this hypothesis for 17 plant species belonging to four native alpine communities in the Caucasus Mts.

MATERIAL AND METHODS
Site description

Plant traits were studied in four 1.5 by 1.5 m plots for each of four alpine communities in the Teberda Reserve, North-West Caucasus, Russia (43°26.8'N 41°41.5'E). The communities represent a toposequence from ridges to depressions: alpine lichen heaths (ALH), *Festuca varia* grasslands (FVG), *Geranium–Hedysarum* meadows (GHM) and snowbed communities (SBC) at the elevation of about 2750 m a.s.l. Winter snow depth increases and growing season length decreases along the toposequence from ALH to SBC. Productivity follows the order ALH < FVG < GHM > SBC. Detailed descriptions of the communities are given in our earlier publications (Onipchenko 1994, 2002, 2004).

Leaf traits

Leaf traits (leaf blade thickness, wet and dry mass of a leaf, water content at saturation, and SLA) were measured for 120 plant species in the four communities, together representing nearly all vascular plant species richness (Shidakov & Onipchenko 2007). We used standard protocols to measure the traits (Cornelissen et al. 2003). We collected 12 well developed leaves without signs of damage, pathogenic infection or senescence. Each leaf was collected from separate plants which growing at distances more than 1 m, but within one type of community. When leaves were small (e.g., *Minuartia aizoides*), one sample from one plant included 10 leaves, but in all cases total number of samples was 12. Cutoff leaves were placed in plastic bags with water and were kept in fridge for 5-10 hours to get water-saturated status. Leaf blade thickness was measured by micrometer with precision 0.01 mm for water saturated leaves. Before weighting surface water was removed by filter paper. We used balances with 0.0001g precision. Then leaves were scanned with resolution 300 dpi (600 dpi for small leaves). ImageJ software was used for leaf area measurement. After scanning leaves were dried in individual paper bags during 8–10 hours at 80°C in drying oven. Dry mass was measured with 0.0001 g precision as well. Next leaf traits were analyzed:

1) LA – leaf area (cm²) without petioles;

2) Leaf dry mass (g) without petioles;

3) Leaf saturated water content, calculated as w=(mw-md) * 100 %/mw, where mw – water saturated fresh leaf mass, md – dry leaf mass;

4) Leaf thickness (mm);

5) SLA – specific leaf area (cm²/g), calculated as LA/md.

Seventeen common species were studied in two or more communities each (Table 1). There were 10 forb species and 7 graminoids. We made statistical tests for the whole set of species and separately for forbs and graminoids to study possible difference between these functional groups in directions of inraspecific variability changes.

Aboveground biomass estimation

To calculate CWM trait values we measured aboveground plant biomass for all studied communities on 0.25×0.25 m subplots in the second half (August) of short alpine growth season during several years. Plants were clipped at ground level, sorted by species, dried (8 hours, 105°C) and weighed.

Biomass was measured during 3–5 years at different places within the communities; total replications were 104 in ALH and 92 in each of FVG, GHM and SBC.

Statistics

Basic statistics and community weighted means. For each of 17 species we calculated mean values and their standard errors for the plants from each studied community. The values were used for subsequent meta-analysis, they are represented in Table S1 (Supplemental materials).

CWMs for each leaf trait were calculated based on species mean values and aboveground biomass:

$$CWM = \frac{\sum_{i=1}^{n}(B_i \times C_i)}{\sum_{i=1}^{n} B_i}$$

where C_i = the trait value for species i, B_i = the weight (aboveground biomass) of species i, n = the number of species. For each plant trait, CWM were calculated for each small subplot and then used to calculate the mean for the community. To compare CWM between communities one-way ANOVA was applied for individual plot's CWM values.

Check of the weighted mean model. The studied communities are very dissimilar according to species composition (for example, floristic similarity between ALH and SBC is about 7 % – Sørensen Index – Onipchenko & Semenova 1995), they differ completely according dominant composition, so it was not possible to find many abundant species shared several communities. Differences in CWM between communities were mainly depended on differences in species composition than intraspecific trait variation due to low representation of common species. In such conditions it was very interesting to estimate the direction of intraspecific trait variation. Meta-analysis looks the most appropriate method to combine responses of different species with very different trait values.

Table 1. Species studied in different communities (+ a species was measured in the community) Nomenclature follows Onipchenko et al. 2011. Functional groups: G – graminoids (grasses and sedges), F – forbs (herbaceous eudicots). Communities: ALH – alpine lichen heath, FVG – *Festuca varia* grassland, GHM – *Geranium-Hedysarum* meadow, SBC – snowbed community.

| Species | Func. group | Community | | | |
		ALH	FVG	GHM	SBC
Agrostis vinealis	G			+	+
Campanula collina	F	+	+		
Campanula tridentata	F	+		+	
Carex atrata	G		+	+	
Catabrosella variegata	G			+	+
Festuca brunnescens	G		+	+	
Festuca varia	G		+	+	
Gentiana septemfida	F	+	+		
Leontodon hispidus	F		+	+	
Minuartia aizoides	F			+	+
Nardus stricta	G		+	+	+
Phleum alpinum	G			+	+
Polygonum bistorta	F	+	+		
Ranunculus oreophilus	F	+	+		
Scorzonera cana	F	+	+		
Sibbaldia procumbens	F			+	+
Veronica gentianoides	F	+	+	+	

To check for statistical differences between communities for each trait we used the approximate Games-Howell test because the data were heteroscedastic and no transformations proved to be helpful.

Then, for each trait, communities were ordinated from lowest to highest values of CWM. For example, CWM-SLA followed the sequence:

FVG (93 cm²/g) < ALH (140) < GHM (170) < SBC (192)

Then we analyzed the concordance in the direction of the transition of intraspecific variation in SLA (or any other trait) among communities versus the direction of the transition of CWM–SLA among communities. For the study we employed meta-analysis approach. In the frame of this approach we used random effects models and Hedge's g as the effect measure – that is, the standardized mean difference adjusted for small sample bias (Hedges 1981). g was computed on the exact formulae (White & Thomas 2005). Values of g above 0 indicate that the transition had a positive effect on the variable; values below 0 indicate a negative effect. The analysis was conducted for all studied species occurring in more than one community (17) as well as for two functional groups (forbs – 10 species and graminoids – 7 species) separately. For each of the analyses we calculated a number of statistics associated with g (Tables S2, S3).

All statistical calculations were run in the R environment (R Core Team 2017) using the package 'userfriendlyscience' for the Games-Howell test and the package 'meta' for the meta-analysis, both of which are in concordance with recommendations of Sokal and Rohlf (2012).

Check of toposequence model. Our four studied communities build a monotonic gradient of several environmental parameters in the sequence: ALH < FVG < GHM < SBC for snow depth and snowmelt date, and ALH > FVG > GHM > SBC for length of growth season (Onipchenko 1994, 2004). Because of the broadly known environmental response of plant traits with elevation (Read et al. 2014), we checked for directional changes of plant traits for each species and transition using the same meta-analysis approach. As previous analysis this one was conducted for all studied species (17), as well as for two functional groups separately.

RESULTS

Community weighted means

The factor "community" had a significant effect on all studied CWM traits. All CWM differed significantly between all studied communities except leaf area between ALH and FVG (Fig. 1, 2).

We can recognize three types of CWM change along the toposequence. From snow-free ridges to depressions (ALH–FM–GHM–SBC) CWM of leaf size related parameters (wet and dry mass, area) generally increased from ALH and FVG to GHM and decreased from GHM to SBC. SLA CWM decreased from ALH to FVG and then increased to GHM and SBC. Water content had its lowest CWM in FVG, but generally increased along the snow depth gradient. Leaf thickness had the opposite pattern – it had the highest CWM in FVG, but generally decreased from ridges to depressions (Fig. 2).

CWM gradient and intraspecific variation

The leaf traits of the target species changed very differently along the gradient compared to the pattern for CWM. Generally, only size parameters (dry mass, leaf area) for most of the species had significant concordance in trend with CWM (Fig. 3, Table 2 Supplement). This concordance was mostly due to significant forb response (Fig. 3), whereas graminoid reaction was not significant. But general direction of graminoid leaf size variability was similar to forbs. However, some species had opposite behavior: e.g. low, mainly rosette plants (*Campanula tridentata*, *Minuartia aizoides*) had smaller leaves in the highly productive GHM, against the trend for CWM. All other functional traits showed significant deviation from correspondence between CWM patterns and changes at the level of species. The highest value for CWM leaf thickness was noted for FVG, the lowest for GHM and SBC. Most of the studied species, except dominant *Festuca varia*, did not follow this pattern; they often had thinner leaves in FVG than in other communities. Thus, CWM of leaf thickness depends on the dominant species and does not correspond to the pattern for intra-specific variability of subordinate species.

Toposequence model

The intraspecific trait changes along the toposequence (i.e. snowmelt gradient) were very variable (Table 3). When
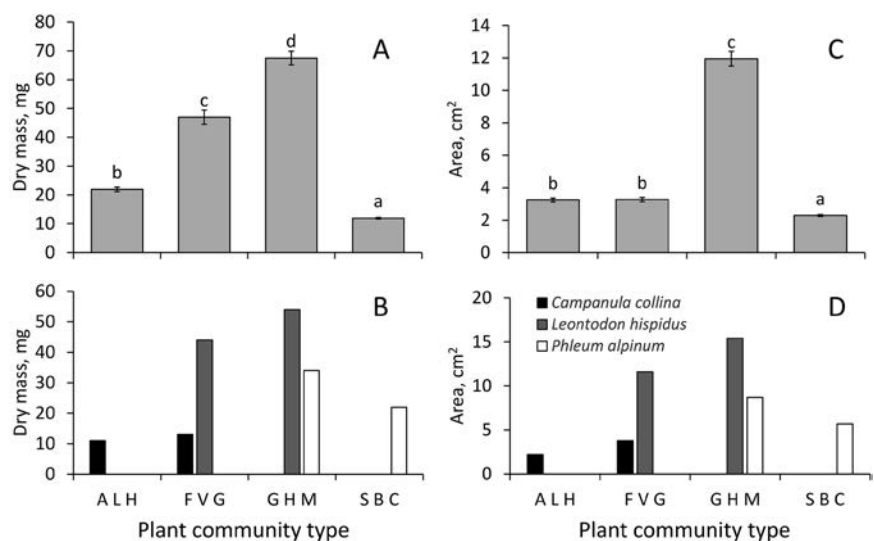

Figure 1 Community weighted mean values and their standard errors for leaf dry mass (A) and leaf area (C) and those trait interspecific response for 3 alpine species (B, D). Communities: ALH – alpine lichen heath FVG – *Festuca varia* grassland GHM – *Geranium-Hedysarum* meadow SBC – snow bed community. Significant (p < 005) differences between CWMs are shown by different letters

considered all species three traits showed significant g values in this case. SLA and water content increased and leaf thickness decreased according snowmelt gradient (toposequence) from snow free ALH to snow-rich SBC. These species responses was determined by forbs, the responses of graminoids had various directions and were not significant (Fig 4). So, generally these three related traits followed the environmental gradient but not the CMW gradient. There were some examples that do not follow this general tendency, e.g. *Nardus stricta* leaf thickness was higher in GHM than in FVG (Table S1, Appendix).

The most interesting response was obtained for the leaf area. Generally, this trait did nor show significant response to snowmelt gradient, but this was due to significant, but opposite response of forbs and graminoids. Forbs increased, but graminoids decreased leaf area when snow depth increased (Fig 4). This was the only one case with significant opposite reactions of plants belonging to different functional groups.

DISCUSSION

CWM and snowmelt gradient

Among five studied leaf traits no one trait showed linear change CWM according to snowmelt gradient. We suggest that the absence of monotonic CWM response this gradient deals with principal different structure-forming mechanisms of the communities. They are 1) shallow poor soils in ALH leading to low production and sparse vascular plant cover (Onipchenko 1985, 2004), 2) strong dominant (*Festuca varia*) influence on subordinate species by accumulation of great amount of recalcitrant litter in FVG (Pokarzhevskaya 1998), 3) intensive zoogenic disturbances within the most productive GHM (Fomin et al. 1989), 4) snow depth and short growth season in SBC (Zakharov et al. 2002). These factors may have important influence on CWM leaf traits, e.g. low water content and high leaf thickness in FVG (due

to rough leaves of the dominant) or high leaf mass and area in productive GHM with relatively large leaves of dominants (*Geranium gymnocaulon* and *Hedysarum caucasicum*).

CWM and size-related leaf traits

All studied communities differed significantly in their CWM for practically all studied functional leaf traits. There were no monotonic changes of CWM along one of the most important alpine environmental gradients – depth of winter snow and snowmelt date. Instead we showed the highest leaf size values for GHM – the most productive alpine community halfway down the toposequence (Onipchenko 1990, 1994). The GHM has relatively nutrient rich soil and intensive decomposition processes (Grishina et al. 1993, Elumeeva et al. 2018). Thus, CWM for leaf size related traits are in good correspondence with annual productivity (e.g. Pearson correlation coefficient between productivity and CWM leaf dry mass $r = 0.963$, $p < 0.001$, n=4). For these traits a good correspondence was obtained between means based on individual species and CWM (Shidakov & Onipchenko 2007). Hump-backed patterns of size traits and production deal with different constrain factors at the ends of snowmelt gradient. Production on snowfree ridges and slopes (ALH) is restricted by poor shallow soils with deep winter freezing (Onipchenko 1985, 1994). On the other hand, production of snowbed communities constrains by short growth season (about 2 months, Onipchenko 2004). In our study we have shown that intraspecific variation in size related traits (leaf mass, leaf area) generally corresponds with CWM and production variations. In contrast, we found deviation in pattern between species level and CMW-based values among communities for leaf quality related traits.

CWM for several leaf quality traits, namely SLA and saturated water content, depends mainly on the specific dominance structure of the communities. The values are lowest for FVG, a community dominated by narrow-leaved
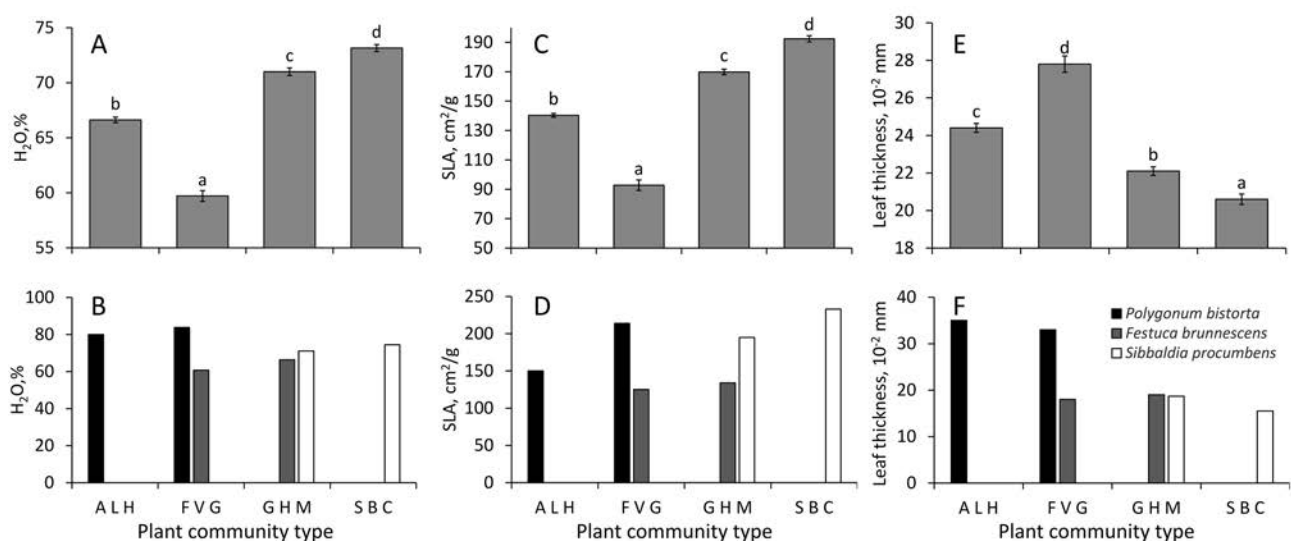

Figure 2 Community weighted mean values and their standard errors for water content (A), SLA (C) and leaf thickness (E) and those trait interspecific response for 3 alpine species B, D, F). Communities as in Fig 1. Significant (p < 005) differences between CWMs are shown by different letters
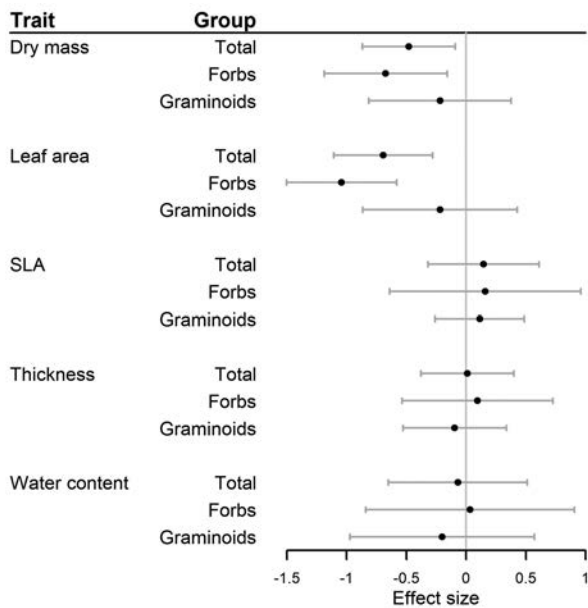
Figure 3 Results of analysis of the correspondence in trend for leaf traits between species-based and CWM based pattern among alpine communities (the CWM gradient). Group effect sizes (dots) and their 95% confidence intervals (error bars) are shown. Statistic details are presented in Table S2 (Supplemental material). SLA – specific leaf area
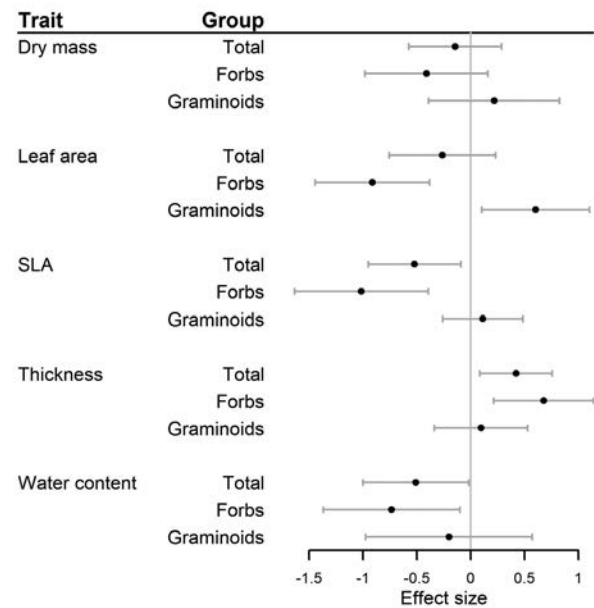

Figure 4 Results of analysis of the correspondence in trend for leaf traits between species-based and CWM based pattern among alpine communities according to the toposequence model (the snowmelt gradient). Group effect sizes (dots) and their 95 % confidence intervals (error bars) are shown. Statistic details are presented in Table S3 (Supplemental material). SLA – specific leaf area

bunch grasses (mainly *Festuca varia* and *Nardus stricta*). These grasses have tough leaves with low SLA and low water content. In contrast, leaves of many other species in FVG have different features (mostly high SLA and leaf water content) and do not correspond with those of the dominants (Shidakov & Onipchenko 2007). Our results thus demonstrate various deviations in pattern among communities between intraspecific variation of the traits and CWM-based variation; the leaf trait values of the dominant species mainly determine CWM values, which can follow opposite patterns among communities than values based on the individual responses of the subordinate species.

Snowmelt gradient

Three leaf traits (SLA, water content, and leaf thickness) within all studied species followed a pattern directly according to the toposequence, i.e the snowmelt gradient. Leaf thickness decreased, but SLA and water content increased from ALH on ridges and upper slopes to SBC in deep mesorelief depressions. Forbs are responsible for these regular trends while graminoids did not show significant changes. These results are in good correspondence with several published results about SLA pattern along alpine toposequences (Choler 2005). Indeed, similar and concurrent changes of CWM and intraspecific SLA were shown for a valley toposequence (Jung et al. 2010). In that case CWM-SLA decreased monotonically from low to upper parts of the toposequence.

Leaf area of graminoids and forbs showed opposite direction of response to snowmelt gradient: forbs increased, but graminoids decreased this with increasing snow depth. Venn et al. (2011) noted leaf area decreasing with increasing snow depth along an Australian alpine snowmelt

gradient. This is a good correspondence with our results for Caucasian graminoids, but opposite to leaf area change of forbs. We suggest that such differences in response to snowmelt gradients may be due to overall differences in leaf lifespan and structure of the alpine floras involved: evergreens in Australia (and partly winter green graminoids in Caucasus) versus mostly summer green forbs in the Caucasus.

CONCLUSIONS

In spite of great variation in leaf traits among and within species in a Caucasian alpine flora, we obtained two groups of leaf traits according to community weighted means and topographic (snow depth and snow melt) gradients. For leaf mass and area (i.e. size related leaf traits) intraspecific variation corresponded to CWM variation among communities; these patterns followed those for plant community productivity, which had a hump-back pattern along the toposequence. In contrast SLA, water content and leaf thickness patterns within species changed directly among communities according to the toposequence (snowmelt gradient), contrary to the community level pattern strongly driven by dominant species that had relatively low SLA halfway along the toposequence. An important take home message from our work is that intraspecific trait variation does not necessarily follow that for interspecific or community-level variation (see the conceptual model in Yang et al. 2015). This has important implications for predicting the consequences of environmental (e.g. climatic) changes; plastic or genotypic trait responses of extant species in communities should be disentangled from community-level responses due to species replacements in order to optimize such predictions.

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LITERATURE CITED

Akhmetzhanova, A.A., V.G. Onipchenko, M.Kh. El'kanova, A.V. Stogova & D.K. Tekeev 2012. Changes in ecologo-morphological parameters of alpine plant leaves upon application of mineral nutrients. *Biology Bulletin Review* 2(1): 1–12.

Andrade, B.O., G.E. Overbeck, G.E. Pilger, J-M. Hermann, T. Conradi, I.I. Boldrini & J. Kollmann 2014. Intraspecific trait variation and allocation strategies of calcareous grassland species: results from a restoration experiment. *Basic and Applied Ecology* 15(7):590–598.

Albert, C.H. 2015. Intraspecific trait variability matters. *Journal of Vegetation Science* 26(1):7–8.

Albert, C.H., W. Thuiller, N.G. Yoccoz, R. Douzet, S. Aubert & S. Lavorel 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology* 24(6):1192–1201.

Anderegg, L.D.L., L.T. Berner, G. Badgley, M.L. Sethi, B.E. Law & J. HilleRisLambers 2018. Within species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* 21(5):734–744.

Auger, S & B. Shipley 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science* 24(3):419–428.

Bagousse-Pinguet, Y.L., F. de Bello, M. Vandewalle, J. Leps & M.T. Sykes 2014. Species richness of limestone grasslands increases with trait overlap : evidence from within- and between-species functional diversity partitioning. *Journal of Ecology* 102(2):466–474 .

Belyea, L.R. & J. Lancaster 1999. Assembly rules within a contingent ecology. *Oikos* 86(3):402–416.

Carlson, B.Z., P. Choler, J. Renaud, J-P. Dedieu & W. Thuiller 2015. Modelling snow duration improves predictions of functional and taxonomic diversity for alpine plant communities. *Annals of Botany* 116(6):1023–1034.

Borgy, B., C. Violle, P. Choler, P. Denelle, F. Munoz, J. Kattge, S. Lavorel et al. 2017. Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. *Global Ecology and Biogeography* 26(10):1138–1152.

Burns, J.H. & S.Y. Strauss 2012. Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits. *Ecology* 93(8):S126–S137.

Carlucci, M., V. Debastiani, V. Pillar & L. Duarte 2015. Between- and within-species trait variability and the assembly of sapling communities in forest patches. *Journal of Vegetation Science* 26(1):21–31.

Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research* 37(4):444–453.

Cornelissen, J.H.C. 1999. A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118(2):248–255.

Cornelissen, J.H.C., P. Castro-Diez & A.L. Carnelli 1998. Variation in relative growth rate among woody species. In: *Inherent variation in plant growth. Physiological Mechanisms and Ecological Consequenses* (H. Lamberts, H. Poorter & M.M.I. Van Vuuren, eds), pp. 363–392, Backhuys, Leiden.

Cornelissen, J.H.C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D.E. Gurvich, P.B. Reich et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51(4):335–380.

Cornwell, W.K. & D.D. Ackerly 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79(1):109–126.

de Bello, F., S. Lavorel, S. Lavergne, C.H. Albert, I. Boulangeat, F. Mazel & W. Thuiller 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* 36(3):393–402.

Donovan, L.A., H. Maherali, C.M. Caruso, H. Huber & H. de Kroon 2011. The evolution of the worldwide leaf economics spectrum. *Trends in Ecology and Evolution* 26(2): 88–95.

Dwyer, J.M., R.J. Hobbs & M.M. Mayfield 2014. Specific leaf area responses to environmental gradients through space and time. *Ecology* 95(2):399–410.

Elumeeva, T.G., V.G. Onipchenko, A.A. Akhmetzhanova, M.I. Makarov and J.A. Keuskamp 2018. Stabilization versus decomposition in alpine ecosystems of the Northwestern Caucasus: the results of tea bag burial experiment. *Journal of Mountain Science* 15(8):1633–1641.

Fomin, S.V., V.G. Onipchenko & A.V. Sennov 1989. Feeding and digging activities of the pine vole *Pitymys majori* Thom. in alpine cenoses of the Northwestern Caucasus. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologicheskii* 94(3):6–13 (in Russian). [Фомин С.В., Онипченко В.Г., Сеннов А.В. 1989. Питание и роющая деятельность кустарниковой полевки (*Pitymys majori* Thos.) в альпийских сообществах северо-западного Кавказа // Бюллетень МОИП, отдел биологический. Т. 94, № 1. С. 6–13].

Garnier, E., J. Cortez, G. Billes, M–L. Navas, C. Roumet, M. Debussche, G. Laurent et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85(9):2630–2637.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17(2):255–260.

Grishina, L.A., V.G. Onipchenko, M.I. Makarov & V.A. Vanyasin 1993. Changes in properties of mountain-meadow alpine soils of the northwestern Caucasus under different ecological conditions. *Eurasian Soil Science* 25(9):1–12.

Gurevitch, J. & L.V. Hedges 1999. Statistical issues in ecological meta-analyses. *Ecology* 80(4):1142–1149

He, D., Y. Chen, K. Zhao, J.H.C. Cornelissen & C. Chu 2018. Intra- and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest. *Annals of Botany* 121(6): 1173–1182.

Hedges, L.V. 1981. Distribution theory for Glass's estimator of effect size and related estimators. *Journal of Educational and Behavioral Statistics* 6(2):107–128.

Hulshof, C.M., C. Violle, M.J. Spasojevic, B. McGill, E. Damschen, S. Harrison & B.J. Enquist 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science* 24(5):921–931.

Jung, V., C.H. Albert, C. Violle, G. Kunstler, G. Loucougaray & T. Spiegelberger 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology* 102(1): 45–53.

Botanica Pacifica. A journal of plant science and conservation. 2020. 9(1):53–61

59

Jung, V., C. Violle, C. Mondy, L. Hoffmann & S. Muller 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98(5):1134–1140.

Kamiyama, C., M. Katabuchi, T. Sasaki, M. Shimazaki, T. Nakashizuka & K. Hikosaka 2014. Leaf-trait responses to environmental gradients in moorland communities: contribution of intraspecific variation, species replacement and functional group replacement. *Ecological Research* 29(4):607–617.

Kattge, J., S. Diaz, S. Lavorel, I.C. Prentice, P. Leadley, G. Bönisch, E. Garnier et al. 2011. TRY – a global database of plant traits. *Global Change Biology* 17(9):2905–2935.

Kichenin, E., D.A. Wardle, D.A. Peltzer, C.W. Morse, G.T. Freschet 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradients. *Functional Ecology* 27(5):1254–1261.

Körner, C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems.* 2nd ed. Springer, Berlin, 345 pp.

Kudo, G. & K. Ito 1992. Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, Northern Japan. *Vegetatio* 98(2):165–174.

Lajoie, G. & M. Velend 2015. Understanding context dependence in the contribution of intraspecific variation to community trait-environment matching. *Ecology* 96(11): 2912–2922.

Lavorel, S., K. Grigulis, S. McIntyre, N.S.G. Williams, D. Garden, J. Dorrough, S. Berman et al. 2008. Assessing functional diversity in the field-methodology matters! *Functional Ecology* 22(1):134–147.

Messier, J., B.J. McGill, B.J. Enquist & M.J. Lechowicz 2017. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography* 40(6):685–697.

Metcalf, C.J.E., M. Rees & J.M. Alexander 2006. Growth-survival trade-offs and allometrics in rosette-forming perennials. *Functional Ecology* 20(2):217–225.

Milla, R, P.B. Reich, Ü. Niinemets & P. Castro Diez 2008. Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional Ecology* 22(4):565–576.

Mitchell, R.M. & J.D. Bakker 2014. Quantifying and comparing intraspecific functional trait variability: a case study with *Hypochaeris radicata*. *Functional Ecology* 28(1):258–269.

Mouillot, D., N.W.H. Mason & J.B. Wilson 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia* 152(4):729–737.

Niinemets, U. 2004. Adaptive adjustments to light in foliage and whole–plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. *New Phytologist* 162(3): 683–696.

Onipchenko, V.G. 1985. Structure, phytomass and production of alpine lichen heaths. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* 90(1):59–66 (in Russian). [Онипченко В.Г. 1985. Структура, фитомасса и продуктивность альпийских лишайниковых пустошей // Бюллетень МОИП, отдел биологический. Т. 90, № 1. С. 59–66].

Onipchenko, V.G. 1990. Phytomass of the alpine communities in the Northwestern Caucasus, Russian SFSR USSR. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* 95 (6):52–62 (in Russian). [Онипченко В.Г. 1990. Фитомасса альпийских сообществ северо-

западного Кавказа // Бюллетень МОИП, отдел биологический. Т. 95, № 6. С. 52–62].

Onipchenko, V.G. 1994. The structure and dynamics of alpine plant communities in the Teberda Reserve, the Northwestern Caucasus. *Oecologia Montana* 3(1–2):40–50.

Onipchenko, V.G. 2002. *Alpine vegetation of the Teberda Reserve, the Northwest Caucasus.* Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich, 168 pp.

Onipchenko, V.G. ed. 2004. *Alpine ecosystems in the Northwest Caucasus.* Kluwer, Dordrecht, 410 pp.

Onipchenko, V.G. & G.V. Semenova 1995. Comparative analysis of the floristic richness of alpine communities in the Caucasus and the Central Alps. *Journal of Vegetation Science* 6(2):299–304.

Onipchenko, V.G., A.S. Zernov & F.M. Vorob'eva 2011. *Vascular plants of Teberda Reserve annotated list of species.* 2nd ed. MAKS Press, Moscow, 144 pp. (in Russian). [Онипченко В.Г., Зернов А.С., Воробьева Ф.М. 2011. Сосудистые растения Тебердинского заповедника (аннотированный список видов). М.: МАКС-Пресс. 144 с.].

Ordonez, J.C., P.M. van Bodegom, J.–P.M. Witte, R.P. Bartholomeus, H.F. van Dobben & Aerts 2010. Leaf habit and woodiness regulate different leaf economy traits at a given nutrient supply. *Ecology* 91(11):3218–3228.

Pakeman, R.J. 2013. Intra-specific leaf trait variation: management and fertility matter more than the climate at continental scales. *Folia Geobotanica* 48(3):355–371.

Pierce, S., D. Negreiros, B.E.L. Cerabolini, J. Kattge, S. Diaz, M. Kleyer, B. Shipley et al. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31(2):444–457.

Pokarzhevskaya, G.A. 1998. Influence of the dominant grass *Festuca varia* Haenke on the spatial pattern of alpine grasslands in the northwestern Caucasus, Russia. *Arctic and Alpine Research* 30(1):11–18.

Poorter, H. & C. Remkes 1990. Leaf area ratio and net assimilation rate of 24 species differing in relative growth rate. *Oecologia* 83(4):553–559.

Poorter, H. & A. van der Werf 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: *Inherent variation in plant growth. Physiological Mechanisms and Ecological Consequenses.* (H. Lamberts, H. Poorter & M.M.I. Van Vuuren, eds), pp 309–336. Backhuys, Leiden.

Poorter, H., U. Niinemets, L. Poorter, I.J. Wright & R. Villar 2009. Causes and consequences of variation in leaf mass per area LMA: a meta-analysis. *New Phytologist* 182(3): 565–588.

R Core Team 2017. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R–project.org.

Read, Q.D., L.C. Moorhead, N.G. Swenson, J.K. Bailey & N.J. Sanders 2014. Convergent effects of elevation on functional traits within and among species. *Functional Ecology* 28(1):37–45.

Rees, M., C.P. Osborne, F.I. Woodward, S.P. Hulme, L.A. Turnbull & S.H. Taylor 2010. Partitioning the components of relative growth rate: how important is plant size variation? *American Naturalist* 176(6):E152–E161.

Scheepens, J.F., E.S. Frei & J. Stocklin 2010. Genotypic and environmental variation in specific leaf area in a widespread alpine plant after transplantation to different altitudes. *Oecologia* 164(1):141–150.

Shidakov, I.I. & V.G. Onipchenko 2007. Comparative analysis of alpine plant leaf traits in the Teberda Reserve. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 112(4):42–50 (in Russian). [Шидаков И.И., Онипченко В.Г. 2007. Сравнение параметров листового аппарата растений альпийского пояса Тебердинского заповедника // Бюллетень МОИП, отдел биологический. Т. 11, № 4. С. 42–50].

Shipley, B. 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Functional Ecology* 20(4):565–574.

Siefert, A. 2012. Incorporating intraspecific variation in tests of trait–based community assembly. *Oecologia* 170(3): 767–775.

Siefert, A. & M.E. Ritchie 2016. Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia* 181(1):245–255.

Siefert, A., C. Violle, L. Chalmandrier, C.H. Albert, A. Taudiere, A. Fajardo, L.W. Aarssen, C. Baraloto et al. 2015. A global meta–analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18(12):1406–1419.

Sokal, R.R. & F.J. Rohlf 2012. *Biometry: the principles and practice of statistics in biological research.* 4th ed. WH Freeman, New York, 915 pp.

Suding, K.N. & L.J. Goldstein 2008. Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytologist* 180(3):559–562.

Venn, S.E., K. Green, C.M. Pickering & J.W. Morgan 2011. Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecology* 212(9):1491–1499.

White, I.R. & J. Thomas 2005. Standardized mean differences in individually-randomized and cluster-randomized trials, with applications to meta-analysis. *Clinical Trials* 2(2): 141–151.

Yang, X.J., Z.Y. Huang, K.L. Zhang & J.H.C. Cornelissen 2015. C:N:P stoichiometry of *Artemisia* species and close relatives across northern China: unraveling effects of climate, soil and taxonomy. *Journal of Ecology* 103(4):1020–1031.

Zakharov, A.A., M.A. Gerasimova & V.G. Onipchenko 2002. Relationship between plant distribution and snow depth in an alpine snowbed community. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* 107(5): 80–83 (in Russian).[Захаров А.А., Герасимова М.А., Онипченко В.Г. Зависимость распределения растений альпийских ковров от мощности снежного покрова // Бюллетень МОИП, отдел биологический. Т.107, №5. С. 80–83].