







# Stabilization versus decomposition in alpine ecosystems of the Northwestern Caucasus: The results of a tea bag burial experiment

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**Abstract:** Mountainous areas exhibit highly variable decomposition rates as a result of strong local differences in climate and vegetation type. This paper describes the effect of these factors on two major determinants of the local carbon cycle: litter decomposition and carbon stabilization. In order to adequately reflect local heterogeneity, we have sampled 12 typical plant communities of the Russian Caucasus. In order to minimize confounding effects and encourage comparative studies, we have adapted the widely used tea bag index (TBI) that is typically used in areas with low decomposition. By incubating standardized tea litter for a year, we investigated whether (1) initial litter decomposition rate ( $k$ ) is negatively correlated with litter stabilization ( $S$ ) and (2) whether  $k$  or  $S$  exhibit correlations with altitude

and other environmental conditions. Our results show that  $S$  and  $k$  are not correlated. Altitude, pH, and water content significantly influenced the stabilization factor  $S$ , while soil-freezing had no influence. In contrast, none of these factors predicted the decomposition rate  $k$ . Based on our data, we argue that collection of decomposition rates alone, as is now common practice, is not sufficient to understand carbon input to soils and can potentially lead to misleading results. Our data on community-specific decomposition and stabilization rates further constrain estimates of litter accumulation in subalpine communities and the potential effects of climate change.

**Keywords:** Litter decomposition; Alpine communities; Tea bag index; Carbon cycle

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## Introduction

Litter decomposition is a crucial component of the biospheric nutrient cycle. The main factors determining decomposition rates are climate, soil properties, litter quality, and microbial community structure (Trofymow et al. 2002; Prescott 2010; Creamer et al. 2015). The impacts of litter quality, environmental factors (Prescott 2010), and plant traits on the decomposition rate have been well studied (Freschet et al. 2012). Significantly less is known about how these factors influence the stabilization of litter. The stabilization process is driven by the production of complex, decay resistant compounds during decomposition, and it determines how much carbon is sequestered in the soil.

In alpine ecosystems, variation in altitude, slope, and aspect can cause large differences in the abiotic factors that determine decomposition within rather short distances. As a result of lower temperatures, biological processes in the alpine belt are generally slower than in lowland areas (Körner 2003). Large concentrations of carbon in alpine soils and conservation of the organic material suggest that microbial activity disproportionally decreases with altitude (Makarov et al. 2001). Slope steepness and position towards the main wind direction affect snow accumulation. Thin snow cover on ridges reduce decomposers activity during winter, but deep snow with temperatures at the soil level close to zero promotes decomposition in winter. However, deep snow retards decomposition in summer due to late snow melt (O'Lear and Seastedt 1994).

Despite a number of studies on decomposition that used a standard material in alpine soils (Schinner 1983; Leinsoo et al. 2004; Drewnik 2006), little is known about carbon stabilization. Keuskamp et al. (2013) introduced a novel approach for standardized estimation of decomposition rates and litter stabilization that is based on decomposition of labile (green tea) and recalcitrant (rooibos) litter. This method is referred to as the tea bag index (TBI), and the standard material exhibits similar responses to temperature and precipitation as native litter (Didion et al. 2016). The TBI approach allows comparison of decomposition constants among plant communities without the confounding effects

associated with using native litter. For this reason, TBI is increasingly popular in comparative ecological research (e.g., Fujii et al. 2017; Mayer et al. 2017; Whigham et al. 2017). Generally, stabilization decreases with temperature and precipitation, and stabilization is negatively correlated with decomposition (Keuskamp et al. 2013). For example, across the elevation gradient of Mt. Kilimanjaro, the decomposition constant decreases logarithmically with increasing stabilization (Becker 2017).

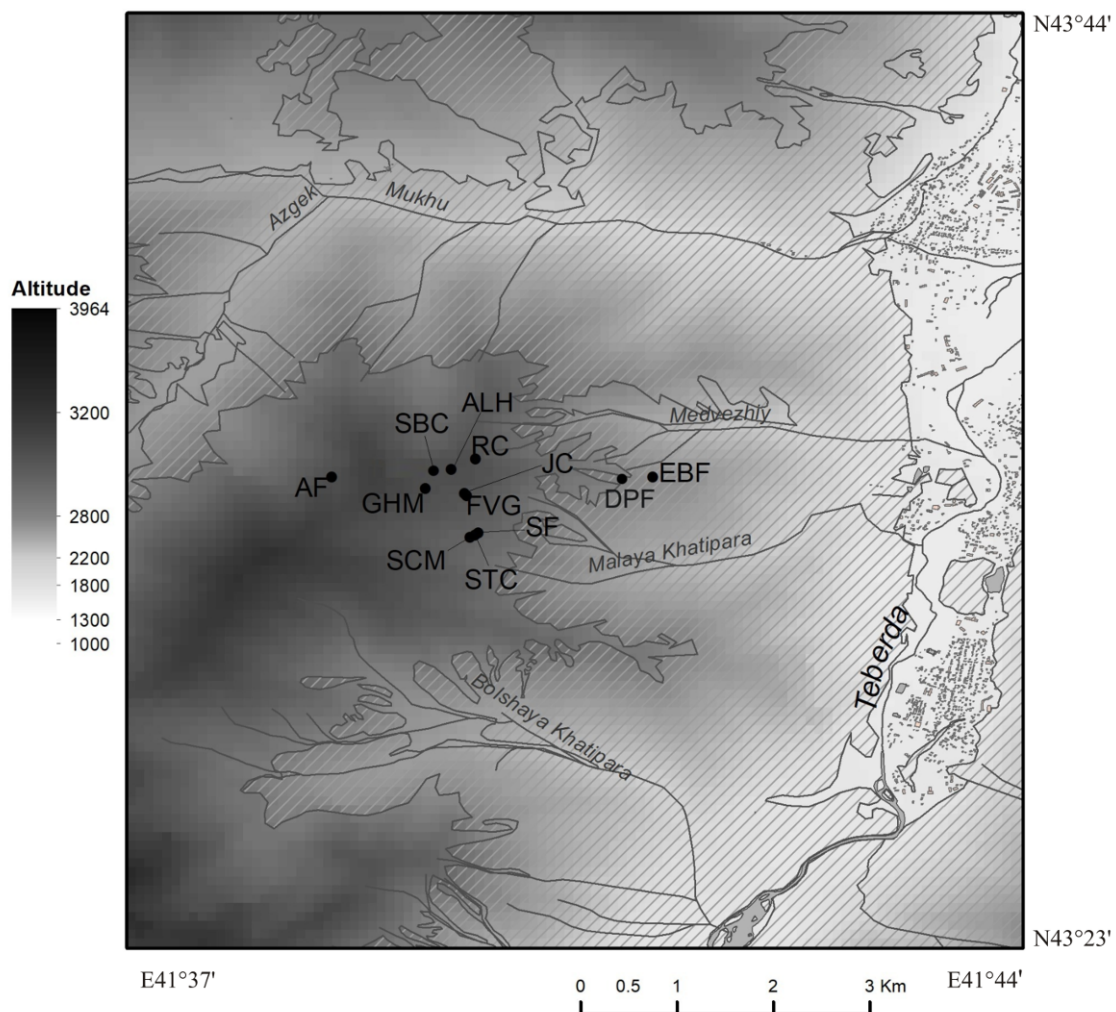
In the present study, we tailored the TBI protocol for use in a low-decomposition environment to compare decomposition in 12 typical alpine and subalpine communities of the Northwestern Caucasus. We investigated whether (1) initial litter decomposition rate ( $k$ ) is negatively correlated with litter stabilization ( $S$ ) and (2) whether  $k$  or  $S$  is correlated with altitude and other environmental conditions.

## 1 Materials and Methods

### 1.1 Study area

The study site is located in the subalpine and alpine belt of the Teberda State Biosphere Reserve (Northwestern Caucasus, Russia) on Mt. Malaya Khatipara Mountain. The climate of this region is a typical temperate mountain climate. The mean annual temperature is approximately  $-1.2^{\circ}\text{C}$  and the mean annual precipitation is 1400 mm (Onipchenko 2004a). Soils are classified as Umbric Leptosols according to the World Reference Base for Soil Resources (2006). The timberline is at approximately 2500 m above mean sea level.

The decomposition study included plots in 12 typical alpine and subalpine plant communities in the altitudinal range from 2540 to 2800 m above mean sea level (Figure 1): elfin birch forest, dry pine forest, subalpine fen, a subalpine tall grass community, subalpine *Calamagrostis* meadow, a *Juniperus* community, *Festuca varia* grassland, a *Rhododendron* community, *Geranium-Hedysarum* meadow, alpine lichen heath, an alpine snowbed, and alpine fen. They occupy various positions in the relief ranging from windward ridges to flat bases of slopes, and they are differentiated by snow cover duration and



**Figure 1** The map of the study site. EBF – elfin birch forest, DPF – dry pine forest, SF – subalpine fen, STC – subalpine tallgrass community, SCM – subalpine *Calamagrostis* meadow, JC – *Juniperus* community, FVG – *Festuca varia* grassland, RC – *Rhododendron* community, GHM – *Geranium-Hedysarum* meadow, ALH – alpine lichen heath, SBC – alpine snowbed, and AF – alpine fen. Striped pattern shows afforested area, and area that is not striped indicates woodless area. Grey shading pattern shows the elevation gradient from below 1000 m a.s.l. (white) to 3964 m a.s.l. (dark grey).

depth. The main characteristics of the studied communities are shown in [Appendix 1](#), and a full description of alpine vegetation in the Teberda reserve can be found in [Onipchenko 2002](#).

## 1.2 Decomposition experiment

The decomposition experiment was performed with standard Lipton pyramid tea bags of green tea (*Camellia sinensis*) and rooibos (*Aspalathus linearis*) according to the modified TBI protocol of [Keuskamp et al. \(2013\)](#). To accommodate for the low decomposition rates, we incubated for an entire year instead of using the recommended

three-month incubation period. Five replicate pairs of a green tea bag and a rooibos tea bag were buried into the soil at a depth of 8 cm in sites representative of the studied communities during 18-19 September 2011, and they were retrieved after one year of incubation during 20-21 September 2012. The distance between the green tea and rooibos bags and between replicate pairs was ~25 cm in every site. After incubation, mass loss was determined by subtracting the litter mass of each bag from their initial mass. Prior to measuring litter mass, we removed root ingrowth and dried samples at 80°C for 24 hours. After weighing, the samples were incinerated at 500°C

and ash mass was subtracted from dry mass to eliminate soil contamination of the samples.

### 1.3 Determination of environmental factors influencing decomposition

To characterize the decomposition environment, we used volumetric soil moisture, soil pH, and altitude as a proxy for temperature at the incubation sites. We used snow depth and snow cover as estimated in Onipchenko (2002) as a proxy for freezing. Freezing was assumed to occur when the soil was only covered during part of the winter or when snow cover exhibited a thickness less than 0.5 m. Snow cover characteristics were not linked with elevation in our altitudinal range, because snow accumulation in the alpine belt is strongly influenced by relief and winds (Onipchenko 2004).

Volumetric soil moisture was measured on 10 September 2014 with a TRIME-EZ sensor (IMKO Micromodultechnik GmbH, Ettlingen, Germany) during the same day to control for precipitation. At this time, snow cover had completely disappeared at all sites and soil was not receiving snowmelt water. Therefore, the measurements show differences in moisture due to precipitation and soil properties across the sites. Soil pH was measured by Hanna Instruments pH-meter 213 in three replicates, with samples taken from tea bag sites in the summer of 2015. For measurements, the slurry of soil and deionized water was mixed for one hour. The mass of the soil sample and dilution depended on the soil carbon content under the studied communities (Makarov et al. 2001) and it was 2.5 g (ratio 1:15) for subalpine fen; 2.5 g (ratio 1:10) for elfin birch forest, the *Rhododendron* community, and alpine fen; 5 g (ratio 1:5) for alpine snowbed, alpine lichen heath, *Juniperus* community, and subalpine *Calamagrostis* meadow; and 10 g (ratio 1:2.5) for dry pine forest, *Geranium-Hedysarum* meadow, *F. varia* grassland, and the subalpine tall grass community.

### 1.4 Weather conditions during the observation time

Air temperature in the alpine belt was measured by the iButton DS 1923 temperature data logger (Dallas semiconductor, USA) from October

2011 to September 2012 at the alpine lichen heath site. To compare weather conditions during the observation time with average values for past decades (from 1980 to 2017), we used data on temperature and precipitation derived from the nearby weather station “Teberda” located at 1313 m a.s.l. This is the nearest station to our study region with a distance of 4.5 km. Despite the fact that subalpine and alpine climates are very different from conditions at the base of the mountain, the temperature parameters at particular altitudes are highly correlated and reflect the same interannual trends (Appendixes 2 and 3).

Soil temperature at the depth of 10 cm was measured via iButton DS 1921Z loggers from October 2011 to September 2012 in four alpine communities: alpine lichen heath, *F. varia* grassland, *Geranium-Hedysarum* meadow, and alpine snowbed (Appendix 4).

### 1.5 Data analysis

The decomposition constant  $k$  and litter stabilization factor  $S$  were calculated from the mass loss of green and rooibos tea as described in Keuskamp et al. (2013). Briefly,  $S$  is quantified as the difference between measured and predicted mass loss of green tea. The decomposition constant  $k$  is calculated from the mass loss of rooibos using an exponential decomposition model with the assumption that only labile material decomposes over the course of one year of incubation. As we exceeded the recommended incubation time of three months, we made sure that  $k$  could still be adequately estimated by assuring that rooibos mass loss was significantly smaller than its labile fraction. See Keuskamp et al. (2013) for further details.

To link  $S$  and  $k$  to environmental factors we used mixed effect models using the “lme” function in the *nlme* package (Pinheiro et al. 2015) of Section 3.2.2. Statistical Environment (R Core Team 2015). Decomposition data were fitted to mixed models with altitude, pH, soil water content, and extent of soil freezing as fixed factors as well as location as a random factor to accommodate within-site replication. Prior to the analysis, we checked for collinearity by calculating Pearson’s correlation coefficients between explanatory variables using Hmisc 4.0-3 (Harrell 2017). We checked the models for normality of residuals using



quantile-quantile plots. The *p*-values of fixed effects were estimated by the analysis of deviance (Type II sum of squares) via the function “Anova” in the *car* package of *R* (Fox and Weisberg 2011). The coefficients of determination for variance explained by fixed effects (marginal *R*<sup>2</sup>) were obtained in the *MuMIn* package (Bartoń 2017) via the algorithm of Nakagawa and Schielzeth (2013).

## 2 Results

The soils of the studied communities exhibited highly variable pH and water content (Table 1). Strongly acidic soil was observed in the elfin birch forest with *Rhododendron* (pH 3.89 ± 0.02, Mean±SE) and in the *Rhododendron* community (4.09 ± 0.06). The highest pH values were found in the subalpine fen (6.08±0.03), the subalpine tallgrass community (5.29 ± 0.13), and the dry pine forest (5.29 ± 0.13). The most water saturated soils were in the subalpine and alpine fens (88% and 57%, respectively). During the exposure time, February and March were colder and the end of the growing season was warmer than average; low precipitation was observed in November, December, and February; and high precipitation occurred in August towards the end of observations (Appendixes 3 and 4). Among the four alpine communities where soil temperatures were measured, the soil of the alpine lichen heath was frozen during winter at 10 cm deep. The alpine snowbed exhibited the shortest growing season,

but its mean temperatures in July and August were higher than in the three other communities (Appendix 4).

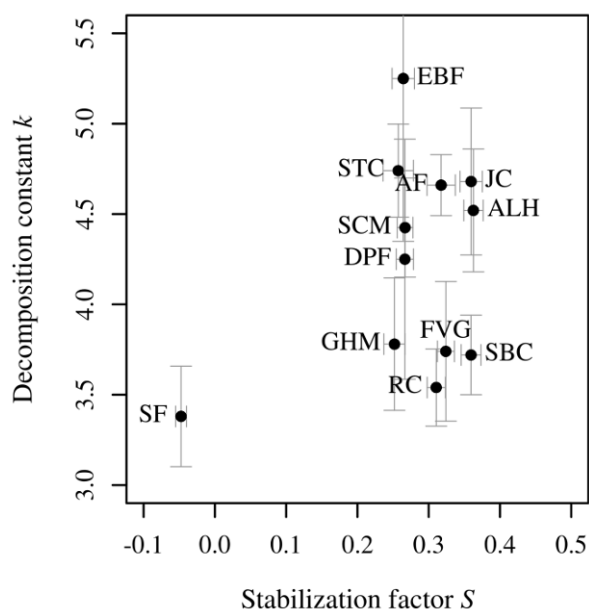
The highest stabilization factor (*S*) was observed in the alpine lichen heath (0.363±0.014) and the *Juniperus* community (0.360±0.016; Table 1). The lowest stabilization factor was observed in the subalpine fen, which was the only community that exhibited a negative value of *S* (-0.047±0.008). The stabilization level in this community significantly differed from the values in all other communities (Table 1). The other communities can be divided into three groups: relatively low stabilization (*Geranium-Hedysarum* meadow, subalpine *Calamagrostis* meadow, subalpine tallgrass community, elfin birch forest, and dry pine forest), high stabilization (alpine lichen heath, *Juniperus* community, and alpine snowbed) and communities with intermediate levels (the subalpine fen, *F. varia* grassland, the *Rhododendron* community, and alpine fen, Table 1).

The lowest value of the decomposition constant *k* was observed in the *Rhododendron* community (3.54 mg·g<sup>-1</sup>·day<sup>-1</sup>), and the highest values were found in the subalpine tallgrass community (4.74 mg·g<sup>-1</sup>·day<sup>-1</sup>).

The stabilization factor and decomposition constant were not correlated in the studied alpine communities (*r*=-0.24; *p*=0.5) (Figure 2). Altitude, pH, and water content significantly influenced the stabilization factor *S*, while soil freezing did not influence the stabilization factor (Table 2). In

**Table 1** Soil characteristics, stabilization factor (*S*) and decomposition constant (*k*, mg·g<sup>-1</sup>·day<sup>-1</sup>) in alpine communities. EBF – elfin birch forest, DPF – dry pine forest, SF – subalpine fen, STC – subalpine tallgrass community, SCM – subalpine *Calamagrostis* meadow, JC – *Juniperus* community, FVG – *Festuca varia* grassland, RC – *Rhododendron* community, GHM – *Geranium-Hedysarum* meadow, ALH – alpine lichen heath, SBC – alpine snowbed, AF – alpine fen. Letters show differences between community means at *p*<0.05 (results of Mann-Whitney U tests of pairs of communities). When *n*<5, tea bags were damaged during exposition.

Community	pH (Mean±SE, <i>n</i> =3)	Volumetric soil moisture (%)	<i>S</i>		<i>k</i> (mg·g <sup>-1</sup> ·day <sup>-1</sup> )	
			<i>n</i>	(Mean±SE)	<i>n</i>	Mean±SE
EBF	3.89±0.02	20.3	5	0.264±0.016 <sup>b</sup>	3	4.33±0.34
DPF	5.29±0.13	8.0	5	0.267±0.012 <sup>b</sup>	2	4.25
SF	6.08±0.03	88.5	5	-0.047±0.008 <sup>d</sup>	5	3.38±0.28 <sup>c</sup>
STC	5.29±0.13	17.1	5	0.257±0.021 <sup>b</sup>	5	4.74±0.26 <sup>b</sup>
SCM	4.89±0.02	31.1	5	0.267±0.011 <sup>b</sup>	4	4.43±0.31 <sup>ac</sup>
JC	4.71±0.06	31.4	5	0.360±0.016 <sup>a</sup>	5	4.68±0.41 <sup>ab</sup>
FVG	4.60±0.03	33.3	5	0.324±0.012 <sup>c</sup>	5	3.74±0.39 <sup>ac</sup>
RC	4.09±0.06	22.0	4	0.311±0.014 <sup>ac</sup>	5	3.54±0.23 <sup>ac</sup>
GHM	4.61±0.03	29.8	5	0.252±0.015 <sup>b</sup>	5	3.78±0.37 <sup>ac</sup>
ALH	4.96±0.04	32.9	5	0.363±0.014 <sup>a</sup>	5	4.52±0.34 <sup>b</sup>
SBC	4.64±0.05	30.7	5	0.359±0.014 <sup>ac</sup>	5	3.72±0.22 <sup>ac</sup>
AF	4.83±0.07	57.3	5	0.317±0.020 <sup>ac</sup>	5	4.66±0.17 <sup>b</sup>



**Figure 2** Links between stabilization factor (*S*) and decomposition constant (*k*) in subalpine and alpine communities of the Teberda reserve (Mean and SE). EBF – elfin birch forest, DPF – dry pine forest, SF – subalpine fen, STC – subalpine tallgrass community, SCM – subalpine *Calamagrostis* meadow, JC – *Juniperus* community, FVG – *Festuca varia* grassland, RC – *Rhododendron* community, GHM – *Geranium-Hedysarum* meadow, ALH – alpine lichen heath, SBC – alpine snowbed, AF – alpine fen.

contrast, none of these factors predicted the decomposition rate *k*. In accordance with this result, variation in *S* was largely explained by soil conditions (marginal  $R^2=0.72$ ), while this was not the case for *k* (marginal  $R^2=0.08$ ).

### 3 Discussion

This work is the first attempt to relate both litter decomposition and stabilization to environmental conditions in alpine and subalpine soils. Following the TBI method, we estimated both litter decomposition rate, which results from microbial activity and shows short-term dynamics,

and litter stabilization, which results from microbial ability to transform organic matter and is indicative of long-term carbon storage (Keuskamp et al. 2013; Fujii et al. 2017).

The leading factors for determination of *S* in our study were elevation above sea level, soil pH, and water content, while the decomposition constant *k* was not significantly linked with measured factors. Overall, the stabilization factor *S* was lower in the subalpine belt than in the alpine belt, but other environmental factors also influenced its value within belts. Stabilization decreased with increases in pH and soil moisture. The slightly acidic wet soils of the subalpine fen exhibited a low decomposition constant with the lowest stabilization factor, and even the non-hydrolyzable fraction of green tea began to decompose in the first year of exposure. However, the observed mass loss could also occur due to rapid leaching from running water.

In a previous study, cellulose and wood decomposition were measured in four of the alpine communities considered in the current study (Leinsoo et al. 2004). Based on mass loss, the authors reported a decrease in decomposition rate in the sequence: *Geranium-Hedysarum* meadow, *F. varia* grassland, alpine snowbed, and alpine lichen heath. Interestingly, we cannot reproduce this result for the decomposition rate as values are not significantly different. However, our estimates of litter stabilization show the inverse pattern with increasing stabilization rates. Based on this observation, it seems likely that the pattern reported by (Leinsoo et al. 2004) resulted from confounding a low decomposition rate with high litter stabilization. This confounding of decomposition and stabilization rate cannot be ruled out in any decomposition study which only uses one litter type and timepoint. Estimating decomposition rates from single data points without explicitly considering stabilization should be avoided in decomposition studies, as this

**Table 2** Results of the models, linking stabilization factor *S* and decomposition constant *k* with environmental factors. n.s. – not significant.

Environmental factors	Stabilization factor <i>S</i>				Decomposition factor <i>k</i>				
	Effect	$\chi^2$	<i>Df</i>	<i>p</i>	Effect	$\chi^2$	<i>Df</i>	<i>p</i>	
Altitude	+	9.144	1	0.002**	n.s.	0.103	1	0.749	
pH	-	5.667	1	0.017*	n.s.	0.038	1	0.846	
Soil moisture	-	4.802	1	0.028*	n.s.	0.370	1	0.543	
Soil frost	n.s.	2.162	1	0.141	n.s.	1.057	1	0.304	

potentially leads to a misinterpretation of results. Nevertheless, low stabilization rates are typical for productive subalpine communities, such as tallgrass meadows or *Calamagrostis* meadows, with rather high decomposition constants as well as productive alpine *Geranium-Hedysarum* meadows with a low decomposition constant (Figure 1). The altitudinal temperature gradient influences the decomposition rate by changing the composition of microbial communities and their activity (Margesin et al. 2009). A decrease in decomposition rate with altitude is consistently found in mountainous areas (Schinner 1982, Drewnik 2006). However, several studies report decrease or no change in decomposition rate with elevation (Murphy et al. 1998, Withington and Sanford Jr. 2007). Along the elevation gradient at Mt. Kilimanjaro, decomposition rates are limited by temperature only at altitudes above 2850 m a.s.l. (Becker 2017). In lowlands, the effects of temperature on decomposition rates are shown experimentally, e.g., warming between 4°C and 10°C increases the litter decomposition rate of tundra plants (Hobbie 1996). In the Northwestern Caucasus, altitude mostly enhanced stabilization processes but did not enhance decomposition. It is possible that the studied gradient (2184-2800 m a.s.l.) is not wide enough to reveal the influence of elevation on the decomposition constant, and local factors play a more important role in its determination.

Another predictor of the stabilization factor was soil water content at the time of sampling. This reflects the small-scale relief of the communities. For example, soils on ridges and slopes are much drier than soils in depressions with prolonged melting times of deep snow cover. In addition, water content increases in the vicinity of water fluxes, which are usually located near depressions. In the forest–alpine tundra ecotone of the Colorado Front Range, soil moisture was the primary factor influencing cellulose decomposition (Withington and Sanford Jr. 2007). In the arid landscapes of Arizona, decomposition is limited by moisture but not by temperature, and decomposition increases with altitude (Murphy et al. 1998). However, aerobic microorganisms are hampered by oxygen limitation if conditions are too wet (Skopp et al. 1990). In the relatively moist soils under alpine and subalpine communities of the Northwestern

Caucasus, decomposition rates are not influenced by moisture, and the stabilization factor tends to decrease with excess soil moisture. The subalpine fens are supplied by oxygen-rich flowing water. In these areas, initially labile fractions of litter are not stabilized due to rapid decomposition or leaching, while initially stable fractions show the lowest decomposition constant (Table 1). Moisture and soil pH are also closely linked with microbial activity and community composition. Typically, soil moisture decreases the potential activity of enzymes and increases microbial biomass (Brockett et al. 2012). In experimental studies of forest soils, soil moisture was more important for cellulose and lignin decomposition than temperature and pH (Donnelly et al. 1990). Microbial diversity and richness are low in acidic soils (Fierer and Jackson 2006; Lauber et al. 2009), and microbial activity usually decreases at low pH values and increases at high pH (Djukic et al. 2010). The positive correlation between soil pH and decomposition rate of cellulose has been established (Drewnik 2006). In our study, the most acidic soils were found under the *Rhododendron* community and the *Betula* forest with *Rhododendron*. In these sites, pH could be maintained by vegetation. Leaching of organic acids from litter, generation of carbonic acid by roots, and imbalances in the uptake of ions from soil could result in reduced soil pH (Ehrenfeld et al. 2005). In the southern Appalachian hardwood forests, soil pH was lower in areas where *Rhododendron maximum* was present in the understory (Wurzburger and Hendric 2007). It has also been shown that *Rhododendron ponticum* litter amendment reduced the decomposition rate of other litter types (Sariyildiz and Küçük 2009). Thus, plants such as *Rhododendron* reduce pH and form conditions that increase the recalcitrance of organic compounds and increase stabilization.

#### 4 Conclusion

Throughout the wide range of habitats of the alpine and subalpine belts of the Caucasus, stabilization (but not decomposition) of dead plant material depends on the elevation, soil properties that are caused by the mineral base and current vegetation, as well as the small-scale relief of the

location. The collected data on the community-specified decomposition and stabilization rates further constrain estimates and predictions of potential litter accumulation in the alpine and subalpine communities, and the potential effect of climate change on these rates. Furthermore, our study highlights the importance of explicitly

considering the stabilization factor when measuring decomposition to avoid misinterpretation of the data. In the alpine belt, a rather high stabilization rate of litter under relatively productive plant communities illustrates the importance of litter stabilization for carbon sequestration in alpine soils.

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**Electronic supplementary material:** Supplementary material (Appendixes 1-4) is available in the online version of this article at <https://doi.org/10.1007/s11629-018-4960-z>

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