

Eberhard Karls Universität Tübingen
Mathematisch-Naturwissenschaftliche Fakultät
Fachbereich Geowissenschaften
Fachbereich Biologie

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**Tea Time On the Summits:
Leaf Litter Decomposition in the Alpine Environment**

Jonathan von Oppen

Prüfer:
Prof. Dr. Oliver Bossdorf
Dr. Sonja Wipf

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Abstract

Decomposition processes control carbon and nutrient turnover in terrestrial ecosystems and essentially influence ecosystem structures by interacting with above- and belowground biota. Effective nutrient cycling is of great importance in cold and low-productivity biomes such as alpine regions. Here, soils are characterised by high heterogeneity in both abiotic and biotic conditions depending on local topography, bedrock or vegetation effects. Currently, alpine regions are facing substantial changes in response to a rapidly warming climate, including plant species distribution shifts and acceleration of biogeochemical processes, probably also altering decay of leaf litter. This study aimed to (i) quantify litter decomposition in a variable alpine setting, to (ii) increase availability of comparable decomposition data from cold environments using the Tea Bag Index (Keuskamp et al. 2013) and to (iii) facilitate assessments on the future development of decomposition as well as its impact on alpine plant communities.

Nylon bags containing litter of four contrasting resource qualities (2× tea, 2× local leaf litter) were buried in all main aspects on six high-alpine summits on different altitudes and parent materials. In addition, mesocosms containing single litterbags as well as soil inoculated with suspensions of summit soil were installed at two contrasting elevations to test for temperature as well as site-specific microbial effects.

Generally, decomposition was significantly stronger for N-rich compared to relatively more C-rich litter types, and overall comparison verified the adequacy of tea as a model for local litter. Moreover, decomposition in the field was constantly higher on gneiss than on dolomite bedrock and well related with vegetation parameters, while, against initial expectations, mass loss in all litter types responded less strongly and rather inconsistently to temperature variations between altitudes or aspects. Decay in mesocosms was significantly higher in the warmer low-elevation site but did not differ between inoculum types, though the process might have been stunted by anoxia during incubation.

Along with the projected relative decrease in litter decomposability, these findings point toward a certain resilience of alpine decomposition processes to warming and emphasise the importance of plant-soil interactions. Long-term studies could valuably add to this picture by incorporating winter or physical decay processes.

Zusammenfassung

Zersetzungsprozesse regulieren Kohlenstoff- und Nährstoffumsetzung in terrestrischen Ökosystemen und beeinflussen deren Strukturen durch Interaktionen mit ober- und unterirdischen Lebewesen entscheidend. In kühlen und wenig produktiven Lebensräumen wie alpinen Regionen sind effektive Nährstoffkreisläufe von besonderer Bedeutung. Allerdings sind abiotische und biotische Verhältnisse in alpinen Bodenstrukturen sehr heterogen, je nach lokalen Auswirkungen von Topographie, Untergrundgestein oder Vegetation. Zusätzlich sind alpine Regionen gegenwärtig mit großen Veränderungen als Reaktion auf rasche Klimaerwärmung konfrontiert, etwa Verschiebungen des Ausbreitungsraumes von Pflanzenarten oder Beschleunigung biogeochemischer Prozesse, was sich voraussichtlich auch auf den Abbau von Laubstreu auswirken wird. Mit dieser Studie soll (i) Abbau von Laubstreu im variablen alpinen Raum quantifiziert, (ii) durch den Einbezug des „Tea Bag Index“ (Keuskamp et al. 2013) zu einer größeren Verfügbarkeit leicht vergleichbarer Daten aus Abbauxperimenten in kühlen Lebensräumen beigetragen, und (iii) die Vorhersage zukünftiger Entwicklungen von alpinen Zersetzungs Vorgängen ermöglicht sowie deren Auswirkungen auf alpine Pflanzengemeinschaften untersucht werden.

Vier unterschiedliche Arten von Streu (2× Tee, 2× lokale Laubstreu) wurden jeweils an nach den vier Haupthimmelsrichtungen ausgerichteten Standorten auf sechs Berggipfeln vergraben, die sich in Höhe und Untergrundgestein unterschieden. Zusätzlich wurde ein Experiment mit Mesokosmen an zwei unterschiedlich hoch gelegenen Standorten eingerichtet. Die Behälter enthielten jeweils eine einzelne Streuprobe sowie Boden, der mit einer Suspension aus Boden von einem der Gipfel geimpft worden war. So sollte der Einfluss von Temperatur sowie standortspezifischen Gemeinschaften von Mikroorganismen untersucht werden.

Stickstoffreiche Streu wurde durchgehend stärker abgebaut als Streu mit hohem relativen Kohlenstoffgehalt. Dabei bestätigte sich die Repräsentativität von Tee als Modell für lokale Streu. Der Abbau war zudem stärker auf Gneis- als auf Dolomitgestein und zeigte Parallelen mit Vegetationsparametern. Hingegen wirkten sich

Temperaturunterschiede zwischen Höhenstufen oder Expositionen unerwartet gering und in hohem Maße ungleichmäßig auf die Zersetzung der verschiedenen Streutypen aus. Der Abbau in den Mesokosmen war am tiefer gelegenen Standort signifikant stärker, unterschied sich jedoch nicht zwischen den Bodenbehandlungen, wobei dies durch anoxische Verhältnisse verfälscht worden sein könnte.

Mit Blick auf die insgesamt vorhergesagte Abnahme der Zersetzbarkeit mit der Erwärmung des Klimas weisen diese Ergebnisse auf eine gewisse Resilienz alpiner Abbauprozesse hin und unterstreichen die Bedeutung von Pflanze-Boden-Interaktionen. Langzeitstudien, die Zersetzung im Winter oder durch physikalische Vorgänge einbeziehen, könnten diesen Eindruck weiter vertiefen.

Introduction

Plant growth, and consequently any buildup of organic tissues, initially requires the supply with inorganic carbon – particularly carbon dioxide, CO₂ – for photosynthesis. The ultimate source for CO₂ is the biosphere itself by providing organic material of animal carcasses, faeces and non-living plant tissues, like leaf litter. Thus, the crucial step in the cycling of carbon and nutrients is to interlink the carbon pools of living organisms and the atmosphere by transforming dead organic material from soils into plant-available CO₂. As such, the decomposition process holds a key role in ecosystem functioning (Swift et al. 1979), especially in low-productivity environments, and ultimately in enabling a diverse and productive plant life under unfavourable conditions (Gavazov 2010).

THE ALPINE ENVIRONMENT

Starting above the treeline (*sensu* Körner 2003), the alpine life zone stretches over several hundred meters of altitude. Towards higher elevations, the initially closed vegetation cover becomes increasingly fragmented as favourable sites for plant growth decrease in frequency, again limiting resource availability for higher trophic levels. Nevertheless, alpine vegetation occurs on all continents, covering about 3% of global land area (Körner 1995). High altitude ecosystems generally pose many challenges to their inhabiting biota. Among others, these include extreme climatic conditions (e.g. cold temperatures, variable moisture conditions, and high wind exposure) as well as short growing seasons. Thus, organic material turnover is usually slow and soil genesis processes as well as nutrient availability are generally limited (Körner 2003).

Nevertheless, insights into nutrient cycling processes in low-productivity ecosystems are still crucial to understand the mechanisms of plant survival and growth under unfavourable conditions (Gavazov 2010). Alpine regions provide a good framework for

such research, being under relatively low anthropogenic impact and featuring sharp distinctions between neighbouring ecotones (Pauli et al. 2005). As such, alpine environments also show high diversity on both habitat and species level (Beniston 2003), consequently holding approximately one third of terrestrial plant species (Barthlott et al. 1996). Further, temperature limitation on most processes makes alpine ecosystems very sensitive to climate change (Pauli et al. 2005), enabling scientists to effectively study ecosystem process responses to warming. In this context, altitudinal gradients have served as a powerful and effective tool to compare responses of plants and ecosystem processes to present and potential future conditions in higher elevations (Normand et al. 2009; Sundqvist et al. 2011). However, the unique diversity of alpine environments is inherently threatened due to low abundances of species and limited spatial extent of their habitats (e.g. Spehn & Körner 2005; Rixen et al. 2014). Therefore, insights into nutrient cycling can serve to understand how such diverse plant life could evolve and what changes it might be subject to in the course of climate change.

One of the most distinctive features of the alpine life zone is the high variability of environmental conditions on extremely small spatial and temporal scales (Gavazov 2010). For instance, surface and soil temperatures as well as moisture levels are highly dependent on slope aspect or local relief characteristics due to variations in solar irradiation and precipitation amounts, respectively (Kerner 1891; Geiger et al. 1995). As a consequence, previous studies found more advanced stages in soil genesis on south- compared to north-facing slopes due to higher soil microbial activity (e.g. Cooper 1960). As such, other belowground processes like decomposition are probably likewise subject to strong small-scale variation in response to local topography (Bradford et al. 2016).

THE DECOMPOSITION PROCESS

In general, decomposition involves transformation of organic matter by chemical, physical and biotic agents, thus gradually increasing organic matter stability and lowering its energy content (Chapin et al. 2012; Berg & McClaugherty 2014). Plant litter

represents the largest part of that organic matter, accounting for around 70% of the global annual carbon (C) flux, which is estimated at 68×10^{15} g C / yr (Raich & Schlesinger 1992). Its decay mostly takes place underground, where dead organic material is exposed to various chemical and physical processes.

These processes influence decomposition rates directly, for instance by leaching of soluble components, abrasion, fragmentation, photodegradation, and the impact of thermal cycles like freeze-thaw, shrink-swell and wet-dry events (Anderson 1973; Swift et al. 1979; Gavazov et al. 2014; Berg & McLaugherty 2014). The leaching process has been assigned particular importance since it represents the dominant process in the initial phase of the decay progression (Swift et al. 1979; Gallardo & Merino 1993; Joffre & Ågren 2001). As sugars and other easily soluble substances are removed by the water flow, fiber concentration and subsequently recalcitrance of the remaining litter is gradually increased, resulting in a maximum mass loss rate in the first three months of incubation (Schinner 1982) and fundamentally reduced decay rates towards the later stages of decomposition (Joffre & Ågren 2001).

Environmental conditions also act indirectly via their effect on decomposing organisms, controlling their activity by alterations of temperature, moisture, aeration and pH in the soil (Waksman & Gerretsen 1931; Swift et al. 1979; Kardol et al. 2010). For instance, following classical kinetic models, activity of decomposing organisms can generally be expected to increase along with warming (Eliasson et al. 2005; Davidson & Janssens 2006), and especially so in cold regions (Lloyd & Taylor 1994). Indeed, higher decomposition rates have been found at warmer sites in an alpine setting (Djukic et al. 2013), and this relationship can be estimated to be particularly strong in the first phase of decomposition (Berger et al. 2015). Besides, positive correlations between moisture availability and decay rates have been observed in various natural systems due to water limitation of decomposers at low moisture levels (e.g. O'Lear & Seastedt 1994; Bryant et al. 1998; Murphy et al. 1998; Seastedt et al. 2001). However, too high amounts of soil moisture may cause waterlogging and subsequently lower decomposer activity because of insufficient supply with oxygen (Schinner 1983). Furthermore, soil pH is mainly

influenced by the underlying parent material, with alkaline soils developing on calcareous bedrocks and more acid soils being found on siliceous bedrock types. It controls the availability of many important nutrients and thus shapes the living conditions of both soil organisms and vegetation (Anderson 1988). However, while some plant species strongly depend on specific soil chemical conditions to persist (e.g. Landolt et al. 2010), soil chemistry is regarded to rather impact the composition of the decomposer community than directly their activity. Nevertheless, decomposition rates might be substantially affected.

Another highly influential parameter in the decomposition process is the quality, i.e. the specific chemical composition, of the organic material being decomposed (e.g. Swift et al. 1979; Aerts 1997; Wardle 2002; Zhang et al. 2008). Litter quality thus determines the nutritional value for decomposer organisms (Vos et al. 2013). To quantify litter chemistry, various measures have been used, including concentrations of nitrogen (N), diverse groups of carbohydrates and several different ratios of these (Swift et al. 1979; Wardle 2002; Parton et al. 2007). Due to varying concentrations of such compounds, different types of tissues generally show largely dissimilar turnover rates. To provide here only a rough classification, reproductive organs decompose faster than leaf material, which is in turn processed at a rate more than five times higher than for woody parts (Swift et al. 1979). Moreover, leaf litter is estimated to account for 64% of total annual plant litter production (Meentemeyer et al. 1982), and leaves are usually available in much higher quantities than reproductive organs. These facts combined have made them an expedient and popular study object for decomposition experiments over almost one century (Tenney & Waksman 1929; Berg & McClaugherty 2014). Perhaps the best-established method involves litter incubation in litter bags (Berg et al. 1993). However, leaf litter quality varies largely between plant species and functional groups (e.g. Gillon et al. 1994), implicating substantial differences in decomposability (Cornelissen 1996; Shaw & Harte 2001; Zhang et al. 2008; Makkonen et al. 2012). For instance, enhanced recalcitrance has been related to high leaf content ratios of C:N (Taylor et al. 1989; Cotrufo et al. 1995; Perez-Harguindeguy et al. 2000) as well as physical toughness of leaves (Gallardo & Merino 1993). Additionally, with regard to functional groups, Cornelissen (1996) found

increasing decomposability in the following order: evergreen shrubs < deciduous shrubs ≤ graminoids < forbs. Overall, it has been demonstrated that litter chemistry represents the most distinctive criterion for decomposition rates over a wide variety of biomes (Parton et al. 2007).

Not only dead plant material but also the living community has been shown to affect litter decay processes (see Van der Putten et al. 2013). Depending on plant species composition, plant root exudates alter soil abiotic properties like nutritional and pH values in the rhizosphere (Anderson 1988), thereby attracting or excluding specific groups of detritivores. Similarly, belowground conditions are affected by the amount and type of mycorrhizal associations as well as the input of secondary metabolites, and species-specific above- and belowground growth patterns affect microclimate as well as physical and chemical soil properties (Ward et al. 2015). Moreover, decomposer organisms have been found to adapt to litter properties of particular plant species (Ayres et al. 2009), causing accelerated decay of litter in closer vicinity to individuals of the respective species (Veen, Freschet, et al. 2015). This plant-decomposer interaction effect has been repeatedly referred to as the ‘Home Field Advantage’ (HFA; e.g. Gholz et al. 2000), but its applicability beyond forest ecosystems has yet been rarely studied (Veen, Freschet, et al. 2015; but see Veen, Sundqvist, et al. 2015).

Besides vegetation, composition of the decomposer community poses another crucial control of decomposition processes (Hättenschwiler et al. 2005), although it is regarded to be of minor importance compared to the abiotic environment and litter quality characteristics (Coûteaux et al. 1995; Aerts 1997; Gavazov 2010). Soil organisms of numerous size classes and phylogenetic groups break down dead material in a cascading system. Microorganisms, i.e. fungi and bacteria, representing the most abundant group of decomposers in alpine regions (Schinner 1982), use extracellular enzymes either released into their surroundings or attached to the cell surface to access carbohydrates from organic matter (Burns 1982; Berg & McClaugherty 2014). However, microbial community composition is highly variable between sites in response to local abiotic conditions and soil properties. For instance, Sundqvist et al. (2011) showed substantial differences in

both the ratio of fungal:bacterial abundance as well as the composition of both groups separately between differing vegetation types, moisture and temperature conditions in subarctic tundra. Thus, both small- and large-scale environmental variation may substantially alter decomposer communities and decomposition patterns.

ALPINE DECOMPOSITION IN A CHANGING CLIMATE

The likely positive feedback of decomposition processes to global atmospheric warming, which is mainly caused by rising concentrations of greenhouse gases (GHG) like CO₂ or methane (CH₄) (IPCC 2014), has even more raised the scientific community's interest in decomposition processes over the past decades. Increased decomposer activity results in elevated carbon effluxes from soils to the atmosphere (Schleser 1982; Raich & Schlesinger 1992; Davidson & Janssens 2006; Bond-Lamberty & Thomson 2010; Hagedorn et al. 2010), thereby inducing a self-enhancing loop by accumulation of GHG in the atmosphere. This development might turn out especially strong in high-altitude regions as cold ecosystems are expected to face comparatively high rates of warming (Lloyd & Taylor 1994; Pauli et al. 2005; Pepin et al. 2015). However, besides the observed rapid warming in alpine areas (e.g. Rebetez & Reinhard 2008), also profound alterations in hydrological regimes are expected. For the European Alps, this is likely to result in an overall decrease of soil moisture availability (Beniston 2009), leading to a reduction of decomposition rates which might at least partly counteract accelerating warming effects (Aerts 2006; Gavazov 2010). Thus, projections on the overall outcome of the changing alpine environment on decomposition processes are still uncertain due to the lack of empirical data.

In addition to these abiotic influences, also changes in plant community composition and vegetation structure will most likely alter alpine decomposition regimes, and shifts in belowground processes are likewise expected to feed back on vegetation. Uphill migration with rising temperatures has been detected in numerous alpine species (e.g. Grabherr et al. 1995; Keller et al. 2000; Gottfried et al. 2012). However, shifts are not appearing uniformly across communities but rather depend on species-specific tolerance,

resistance, adaptive potential, and interactions, thus substantial changes might occur in community structures and composition as well as ecosystem processes (Pauli et al. 2005; Kardol et al. 2010). Specifically, reptant deciduous shrubs have been assigned a key role under warmer alpine temperatures (Gavazov 2010), and observations in the European Alps have recorded an increase in relative abundance of deciduous shrubs compared to other functional groups (Cannone et al. 2007). This is likely to result in retarded leaf litter turnover (Cornelissen et al. 2007; Cornwell et al. 2008). A similar effect has been proposed for the relative expansion of graminoids at the expense of forb vegetation in alpine regions (Gavazov 2010, A. Kulonen unpubl.), again slowing decomposition rates due to lower relative decomposability (Cornelissen 1996). Along with such denser vegetation structure, increased shading might lower soil temperatures (Myers-Smith et al. 2011), adding to the negative feedback on decomposition rates. This might in turn further decelerate nutrient cycling and retard transition of species adapted to warmer climate and higher nutrient levels. On the other hand, during winter, higher shrub densities are likely to increase snow depth and subsequently soil temperatures, thus intensifying soil microbial and decomposer activity (Sturm et al. 2005). However, on the whole, empirical knowledge on species shift effects on alpine decay processes as well as plant-soil interaction effects on plant communities in general is still scarce (Van der Putten et al. 2013).

TOWARDS A LARGE-SCALE DECOMPOSITION PICTURE

Despite litter decomposition being a process of major ecological relevance, so far only few studies have examined decomposition patterns on an inter-continental and/or inter-biome scale within the same experimental framework (Berg et al. 1993; Parton et al. 2007). In addition, litter bags have been a widely used and acknowledged method in leaf litter decay experiments for decades (e.g. Wieder & Lang 1982), but a standardised and high-resolution approach has long been missing (Bonan et al. 2013).

Aiming to fill this gap, Keuskamp et al. (2013) introduced the Tea Bag Index (TBI) method based on commercially available tea packed in nylon mesh bags. This cost-efficient, low-effort and ubiquitously applicable approach follows an easy protocol and can potentially serve to create a global and precise set of decomposition data from all biomes. Specifically, green and rooibos tea are being used as model labile and recalcitrant litter fractions, respectively, and decomposition is assumed to follow a negative exponential decay function with the labile fraction decomposing at higher rate over shorter time and the recalcitrant fraction decomposing at lower rate over a longer period of time (Wieder & Lang 1982). Hydrolysable fractions of both tea types are constant and determined via laboratory analyses as the sum of non-polar extractable fraction, water and acid soluble fraction. After incubation, decomposition rates of a pair of green/ rooibos tea are being related to their respective potentially decomposable fraction as well as length of incubation period, resulting in a stabilisation factor S defined by

$$S = 1 - \frac{a_g}{H_g}$$

with decomposed fraction a_g and hydrolysable fraction H_g of green tea. The stabilization factor thus represents the relative amount of the labile litter fraction having decomposed under the influence of environmental factors. From here, predicted labile fraction of rooibos tea a_r can be calculated as

$$a_r = H_r \cdot (1 - S) = H_r \cdot \frac{a_g}{H_g}$$

with hydrolysable fraction of rooibos tea H_r , assuming that environment is the only factor influencing the relation of potentially (H) and actually (a) decomposed fractions. Incorporating the remaining fraction of rooibos tea $W(t)$ after incubation time t , decomposition rate k can be calculated from the negative exponential decay function

$$W(t) = a_r e^{-kt} + (1 - a_r)$$

as

$$k = -\ln\left(\frac{W(t) - (1 - a_r)}{a_r}\right) \cdot t^{-1}.$$

Keuskamp et al. (2013) already demonstrated applicability of the method in a variety of biomes. By applying TBI, the TEACOMPOSITION network aims to acquire comparable decomposition data from mountain summits all over the world, so far involving researchers from 15 countries on four continents. It builds on the GLORIA initiative, a global-scale program for long-term monitoring of alpine summit flora (Pauli et al. 2005), and includes incubation of tea over time periods of one, two, and three years following a standardised protocol. The initiative thus assesses mid- and long-term decomposition patterns in order to (i) shape the picture of both large-scale C dynamics and storage, and (ii) quantify the impact of climatic and site-specific drivers of litter decay (I. Djukic, pers. comm.).

HYPOTHESES

The present study aimed at quantifying decomposition processes in a high-alpine environment over a single growing season, taking into account variation in several abiotic and biotic parameters. Slightly modifying the TEACOMPOSITION method, litter bags were buried in the eastern Swiss Alps on six summits each representing a unique combination of one out of two bedrock types (gneiss or dolomite) and one out of three altitudinal levels (between approx. 2400 and 2800 m.a.s.l.). Incubation time was between approx. two and three months depending on elevation, resembling shorter growing season length in high-elevation sites. On every summit, one plot was established in each of the four main aspects. To evaluate representativeness of the tea bag approach for natural decomposition in the high-alpine zone (Keuskamp et al. 2013), leaf litter of two local species (*Anthyllis vulneraria subsp. alpestris* and *Dryas octopetala*) was incubated alongside green and rooibos tea bags. Decomposition impact was measured as the remaining fraction of initial litter mass, hypothesising that (i) warmer (i.e. eastern and southern) aspects or low-elevation summits, respectively, would show lower remaining litter mass and higher k values than colder sites, (ii) gneiss bedrock sites would have lower remaining litter mass and higher k values than dolomitic sites, (iii) remaining litter mass would be lower for *Anthyllis* and green tea than for *Dryas* and rooibos tea, and (iv) remaining litter mass

would be lower for *Anthyllis* and *Dryas*, respectively, in closer vicinity of individuals from the same species.

In addition, looking more closely at the influence of temperature and microflora composition on the decomposition process, a mesocosm experiment was conducted incubating litter bags in standard soil inoculated with extracts of soil from the six summits to enable microflora transfer at two sites of contrasting elevation, and a control treatment. Remaining litter mass was expected to be (v) generally lower in inoculated compared to control treatments, (vi) lower in the warmer (low-elevation) site, and (vii) less different between soil treatments at the high- compared to the low-elevation site.

Material and Methods

LITTER PREPARATION

Four types of litter were used in the study. Firstly, as potential 'standard' litter, commercially available green tea and rooibos tea (Lipton, Unilever) were employed. Green tea consists of 89 % green tea and 11 % natural flavouring; rooibos tea consists of 93 % rooibos needles and 7 % flavouring (Keuskamp et al. 2013). Both were packed in synthetic bags of tetrahedron shape with 250 µm mesh size. These two types of tea have been shown to differ in litter quality, as green tea was decomposed relatively fast while rooibos tea proved rather slow decomposition rates (Keuskamp et al. 2013). In addition, autochthonous litter was incubated to provide a 'realistic' comparison to the artificial substrate, since local decomposing organisms are likely to be more familiar with litter of species native to the study area. Thus, leaves of two alpine species were collected from local populations in the Sertig valley near Davos, Grisons, Switzerland. Litter species were chosen based on their leaf traits in order to represent a strong contrast in decomposability, similar to green tea and rooibos (Keuskamp et al. 2013). Specifically, fresh leaves of *Anthyllis vulneraria* subsp. *alpestris* (SCHULT.) ASCH. & GRAEBN. (further referred to as *Anthyllis*) are expected to decompose rather easily, while senesced, previous-year leaves of *Dryas octopetala* L. (from here referred to as *Dryas*) should represent a rather recalcitrant type of litter. After collection, leaves were dried to constant weight and filled into original Lipton tea bags which had been cut open and emptied before. Finally, the synthetic tea bags were re-sealed using a soldering iron. All litter bags were then dried at 70 °C for 48 hours and weighed individually prior to incubation. In addition, three subsamples were taken from every litter type for analysis of C and N content.

STUDY SITES

The field study was conducted on six summits in the Engadin area in the Swiss and Italian Alps (Table 1), five of which have been monitored within the GLORIA research network (Pauli et al. 2005; Scheurer et al. 2013). Litter bags were buried between approx. 2400 and 2800 m.a.s.l. in the alpine tundra zone in sites with treeless vegetation and shallow soils featuring low organic matter content. The summits each combined one out of three elevation levels (low \approx 2430 m / mid \approx 2530 m / high \approx 2800 m) and one out of two bedrock types (dolomite or gneiss). To explore the influence of aspect-related, local-scale microclimatic differences on the decomposition process, plots were established in all main aspects of the summits, i.e. east, south, west, and north, approx. 10 altitudinal meters below the mountaintop. Exact plot position varied in some cases due to local relief structures.

Table 1: Location, elevation, and predominant bedrock characteristics of the study sites around the Engadin valley in the South-Eastern Swiss Alps and Northern Italy.

<i>Name</i>	<i>Position</i>	<i>Elevation [m.a.s.l.]</i>	<i>Elevation level</i>	<i>Bedrock type</i>
Mot sper la Chamonna Sesvenna	46°44' 07.845"N 10°25' 42.499"E	2424	low	gneiss
Munt Buffalora	46°38' 26.271"N 10°14' 17.473"E	2437	low	dolomite
Minschuns	46°38' 43.301"N 10°20' 16.080"E	2519	mid	gneiss
Munt Chavagl	46°38' 38.797"N 10°14' 02.243"E	2542	mid	dolomite
Mot dal Gajer	46°41' 39.939"N 10°19' 51.215"E	2797	high	gneiss
Ils Cuogns (secondary)	46°42' 55.777"N 10°10' 15.499"E	2812	high	dolomite

PLOT DESIGN AND BURIAL OF SAMPLES

In each main aspect of the six summits a plot of 1×0.3 m was established in a patch with vegetation that was largely homogenous and representative for the local situation. Three bags of each litter type were buried within each plot, summing up to 12 bags per plot and, over all summits, a total of 288 samples. The litter bags were arranged in a 4×3 grid with approx. 10 cm vertical and 30 cm horizontal distance from each other. Positioning was randomized within the grid, with no litter type occurring twice in the same line or column. Bags were installed in 2 cm depth to ensure biotic activity and also impact of abiotic decomposition agents. Moreover, leaf litter represents a substrate from the early stages of decomposition which is naturally processed close to the surface. Positioning of litter bags was noted and GPS coordinates were recorded for the plots.

ABIOTIC AND BIOTIC FACTORS

Soil temperature was recorded every three hours throughout the incubation phase using iButton temperature loggers (Maxim Integrated Inc., San Jose, CA, USA), one of which was buried between two columns of litter bags within a plot (i.e., three loggers in a plot). Slope angle was recorded in each plot since it has profound impact on water runoff dynamics, and soil depth was measured to assess the extent of soil formation history and site underground activity using a 30 cm iron nail. Signs of anthropogenic or animal disturbance were noted down both at installation and retrieval of the experiment.

In addition, vegetation type and plant community composition were recorded within a 1.7×1 m square around each plot (i.e., in 0.35 m distance to the plot boundaries). This should assist in determining possible presence or absence effects of particular species, especially of the two that are being used as autochthonous litter. Vegetation surveys were conducted before the start of incubations and verified upon retrieval of the litter bags, including determination of the species present and cover estimations of species as well as total vascular plants. Moreover, canopy height was measured at 5 random locations within the plot and averaged.

To assess potential HFA patterns in decomposition of *Anthyllis* and *Dryas* litter, distance of individuals of the respective species from the plot was recorded on a 5-level ranking scale (1 – species occurring within the plot; 2 – species present within 2 m distance from the plot centre; 3 – species occurring within 10 m distance from the plot centre; 4 – species occurring in the summit area, but outside a 10 m radius around the plot; 5 – species not present in the summit area).

CHEMICAL ANALYSES OF LITTER AND SOIL

To obtain litter C and N contents, 3 dried samples of every litter type were ground in a pebble mill and transferred into zinc saggars (approx. 4 mg per sample). For soil analyses, three soil samples per plot were taken at installation of the bags to determine soil moisture as well as physical and chemical site properties. Samples were stored in plastic bags at 3 °C until further processing. For determination of gravimetric soil moisture and bulk density, small cubic subsamples were cut out and dimensions of cubes were noted. Fresh weight was recorded before drying at 105 °C for 48 hours, and finally dry weight was measured directly after retrieval from the drying oven. To obtain soil N and C content, plant parts and stones were sorted out from the original samples which were then homogenized, sieved through a 2 mm mesh and dried at 60 °C for 10 hours. The soil was then ground with a pebble mill and approx. 25 mg of ground soil per sample were transferred into zinc saggars. C and N content of both litter and soil samples was determined separately with a NC2500 Elemental Analyser (CE Instruments Ltd, Wigan, U.K.).

POST-INCUBATION PHASE

Litter bags were retrieved between 72 and 85 days after the start of incubation. Six bags were lost during the incubation period, presumably due to animal activity, e.g. of foxes or chamois (C. Rixen, pers. comm.). Bags were transferred to the lab, cleaned from remaining soil with a paintbrush, and dried at 70 °C for 48 hours. One paper bag per

sample was prepared, labelled and weighed empty. After drying, litter bags were cut open and the remaining litter was transferred to the paper bag which was then weighed again. Since some bags had been heavily penetrated by roots, root penetration was recorded on a four-level ranking scale (0 – no roots; 1 – few, small roots on the outside or easy to remove; 2 – many roots, also inside the bag, but probably all removable; 3 – heavy presence of roots on the outside and inside, some small fragments might have remained between the remaining litter). The surface of empty nylon bags was scratched clean using a razorblade to remove roots and soil before weighing the bag including string and label in order to finally obtain the amount of litter mass lost during incubation. In case a bag's string or label had been lost during the incubation phase, a mean weight of string + label of other tea bags was instead added to the empty bag weight. Data of two *Dryas* samples was removed from analyses because values for remaining litter mass exceeded initial weight. In addition, data of one *Anthyllis* sample was removed because of heavy infection with larvae.

MESOCOSM EXPERIMENT

In order to test for the effect of temperature and microbial community composition on decomposition dynamics, additional litter bags were incubated in transparent 250 ml polyethylene bottles buried at two altitudinal belts in Flüela valley near Davos, Grisons, Switzerland. The lower site was located in a flat grassland patch in Davos (1560 m.a.s.l.). The high-elevation site was set up on a gently inclined, east-facing ridge with alpine heath vegetation close to Flüela Pass (2390 m.a.s.l.).

There were seven different treatments of soils, six of which had been inoculated with an aqueous suspension of soil from one of the field study summits, following the protocol of van de Voorde et al. (2012), and one control treatment that had received the same amount of deionised water instead. Three replicates of each of the four litter species were combined with every inoculum type, resulting in 84 containers per elevation. Each container received 125 g of soil, then one litter bag and finally another 125 g of soil were

added. In addition, three randomly selected bottles per elevation received one iButton temperature logger for hourly temperature recording. Soils were watered to field capacity before the containers were sealed in order to avoid contamination and buried in a 14×6 grid with approx. 10 cm distance between bottles. Positioning of bottles was randomised and recorded as a potentially obscuring factor due to e.g. higher irradiation influence towards the edges. Each container was assigned a category of either 'edge' (outermost position, 36 bottles per plot), 'outer' (one-bottle distance to the edge, 28 bottles per plot), or 'centre' (innermost position, 20 bottles per plot). Lids remained above ground level so during the incubation period they could be removed for a short time once a week in order to enable gas exchange and supply with fresh air. Between opening events, all bottles were covered with a thin white fleece to enhance reflectivity and prevent extreme heating by solar irradiation. In the lower site, vegetation between containers was removed twice over the course of the experiment to avoid irregular shading effects and damage of the cover. In the upper plot, the fleece was removed once by grazing cattle, but no other impact was observed and the plot was fenced electrically hereafter.

71 days after burial, all containers were transferred back to the lab and stored at 3 °C until further analyses. Pre- and post-incubation processing of litter and bags were analogue to the field incubation study.

STATISTICAL ANALYSES

All data processing, exploration and analyses was conducted using R v3.3.1 (R Core Team 2016).

Temperature data for every logger was averaged over the growing season, excluding the respective days of burial and retrieval. From these, mean plot temperatures were calculated, which were then used for determination of mean temperatures per aspect and summit. A three-way Analysis Of Variance (ANOVA) was applied to test for differences and interaction patterns between aspects, elevation levels, and bedrock types. Temperature data from the mesocosm experiment was treated similarly, calculating mean

temperatures over the burial period for loggers at both sites and testing for differences using a two-sample t-test. Data from one logger in the lower site could not be extracted.

Litter chemical composition (i.e., carbon to nitrogen content ratio) was averaged by litter type and analysed using a one-way ANOVA.

Magnitude of decomposition was generally measured as remaining litter mass relative to initial litter mass of each bag. Since the summits used for the experiment represent a subsample of all the mountain tops theoretically available in the area, summit was treated as a random factor. Thus, a Linear Mixed Effect Model (*lme* function from the *nlme* package; Pinheiro et al. 2016) was applied, with bedrock, aspect, level of elevation, and litter type as fixed factors (in order of ascending importance according to hypotheses) to explain decomposition patterns. Site- and plot-specific measurements describing abiotic and biotic influences were tested for correlation patterns. As a result, soil depth and root penetration were included into the model as additional covariates since they were expected to explain additional parts of the model variance.

To increase model simplicity, a model selection process was applied based on minimum AIC and using the *stepAIC* function of the *MASS* package (Venables & Ripley 2002) which excluded the covariates soil depth and root penetration from the model. Specific effects of factors and interactions were tested using a full-factorial Type III ANOVA (*Anova* function from the *car* package; Fox & Weisberg 2011).

For rooibos and green tea litter from the field study, tea bag index (TBI) values were calculated following the method presented by Keuskamp et al. (2013) to enable straight comparison of the experiment results with previous studies as well as evaluation of the experimental setup. Regarding the model, tea bag index values were analysed analogous to decomposition data, with litter type being redundant in this case. Model selection removed the interaction term between aspect and bedrock.

For the mesocosm experiment, random positioning in the plots was corrected for by performing a One-way ANOVA with position as fixed factor. Residuals from this model

were then used for a Three-way ANOVA testing for effects of soil treatment, incubation site, and litter type.

Plant community composition of the plots was compared using a Non-Metric Multidimensional Scaling (NMDS) analysis based on Raup-Crick dissimilarity index (Raup & Crick 1979). NMDS was applied by the *metaMDS* function from *vegan* package (Oksanen et al. 2016). Statistical comparison of vegetation composition between plots was conducted by a permutational multivariate ANOVA (PERMANOVA, (Anderson 2001), applying the *adonis* function from *vegan*. Bedrock type, level of elevation and aspect were used as fixed factors.

In order to obtain a measurement for specific vegetation characteristics within each plot, indicator values extracted from Landolt et al. (2010) were assigned to each species. Representative indicator values *R* (reaction number) and *T* (temperature number) were then calculated for each plant community using weighted averages based on relative species cover within a plot. Linear regressions were performed to look for immediate influence of vegetation on decomposition patterns.

To test for a potential Home Field Advantage effect (*sensu* Gholz et al. 2000), decomposition data of *Anthyllis* and *Dryas* litter were analysed for each species in two separate Linear Mixed Effect Models with distance class as fixed and summit as random factor.

Post-hoc tests on ANOVAs were performed using pairwise t-test comparisons with p-value adjustment for reduction of Type I-error following Benjamini & Hochberg (1995). Significance level was defined as $\alpha = 0.05$.

Results

All relative and percentage values in the results section refer to relative and not absolute differences between response mean values, one of them serving as baseline, in order to point out the effect of the respective treatment or factor.

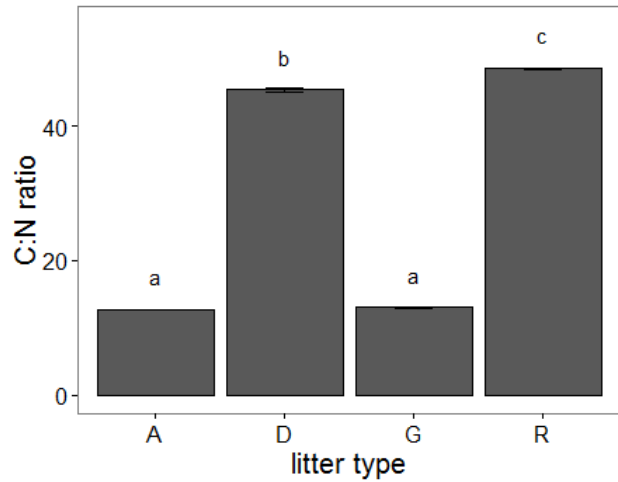


Figure 1: Mean (± 1 SE) C:N content ratios in different litter types (A: Anthyllis, D: Dryas, G: green tea, R: rooibos tea).. Different letters over bars indicate significant differences as reported by One-way ANOVA.

LITTER CHEMICAL COMPOSITION

Litter types differed greatly in C:N ratio, with lowest mean value for *Anthyllis*, a similarly small value for green tea, more than a 3.5-fold value for rooibos tea and an even higher ratio for *Dryas* litter (One-way ANOVA, $df=3$, $F=22037$, $p<0.001$; Fig. 1).

Table 2: Results of Three-way ANOVA testing on temperature differences between levels of experiment factors. Bold values indicate significant differences.

source of variation	df	MSQ	F	p
aspect	3	29.8	332.1	< 0.001
elevation level	2	24.7	275.1	< 0.001
bedrock	1	4.6	50.7	< 0.001
aspect \times elevation	6	0.5	5.7	< 0.001
aspect \times bedrock	3	2.6	29.4	< 0.001
elevation \times bedrock	2	4.0	45.0	< 0.001
aspect \times elevation \times bedrock	6	1.0	11.6	< 0.001
Residuals	44	0.1		

FIELD INCUBATION EXPERIMENT

Environmental and site-specific covariates

Mean growing season soil temperatures were highest at low elevation, slightly lower in mid- and significantly lower in high altitudes (Table 2, Fig. 2) resulting in a difference of 1.9 °C between low- and high-elevation mean

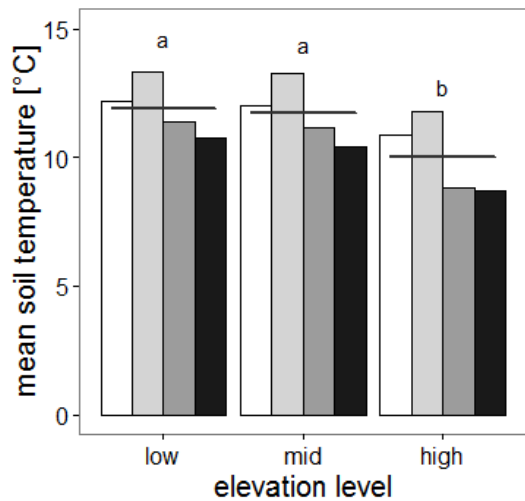


Figure 2: Mean soil temperatures over incubation period in response to elevation (horizontal lines) and slope aspect (bars). Different letters over bars indicate significant differences as reported by One-way ANOVA.

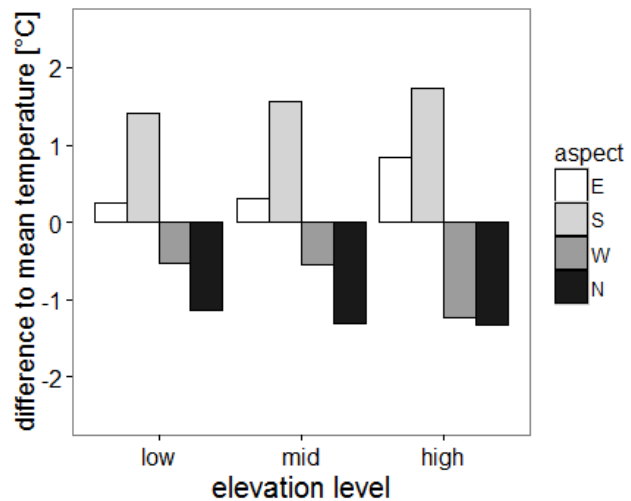


Figure 3: Mean differences in soil temperatures between aspects on each elevation level.

values and an average lapse rate of $0.51\text{ }^{\circ}\text{C} / 100\text{ m}$ elevation. Temperature varied even stronger between aspects (Fig. 2), with southern plots being generally between $2.54\text{ }^{\circ}\text{C}$ and $3.07\text{ }^{\circ}\text{C}$ warmer than northern sites and largest variation at high altitudes (Table 2, Fig. 3). Sites on gneiss bedrock were on average $0.48\text{ }^{\circ}\text{C}$ colder than on dolomitic substrate, this difference being largest between low-elevation summits (Table 2, Fig. S1). Additionally, variation between individual exposures was less pronounced on gneissic substrates, and, as indicated by the significant three-way interaction, temperature variation between aspects differed considerably between summits (Table 2).

On gneissic summits, significantly steeper slopes, higher soil moisture as well as lower C:N ratio, higher canopy, and higher vascular plant cover were observed than at sites with dolomite bedrock (Table 3). Also, soils were slightly, though not significantly, shallower on dolomitic summits (Table 3). South exposed plots had significantly higher canopy than northern sites, with east- and west-exposed plots ranging in between (Table 3), but other covariates did not differ significantly between aspects (Table 3). Finally, soil moisture and depth as well as vascular plant cover decreased significantly towards higher elevations, yet other covariates did not show significant differences between altitude levels (Table 3).

Table 3: Results of ANOVA testing for factor influences on abiotic and vegetation characteristics in plots. Different superscript letters indicate significant differences. Bold values indicate significant differences.

factor	level	plot parameters								vegetation parameters					
		slope [°]		soil depth [cm]		soil moisture [g / g soil]		soil C:N		canopy height [cm]		vascular plant cover [%]		species number	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
bedrock type	gneiss	28.88^A	2.03	16.79 ^A	2.17	0.82^A	0.11	13.66^A	0.31	6.67^A	0.86	75.03^A	6.61	22.92^A	3.02
	dolomite	20.17^B	1.56	14.38 ^A	1.68	0.34^B	0.03	44.81^B	8.83	2.93^B	0.60	49.55^B	9.41	8.58^B	1.02
aspect	E	25.67 ^A	3.55	18.83 ^A	3.35	0.48 ^A	0.04	26.09 ^A	6.72	5.30^{AB}	1.54	25.67 ^A	3.55	18.33 ^A	4.67
	S	25.50 ^A	3.68	16.42 ^A	2.11	0.56 ^A	0.06	17.46 ^A	1.52	7.37^A	1.04	25.50 ^A	3.68	18.33 ^A	5.74
	W	26.25 ^A	3.02	12.58 ^A	1.94	0.51 ^A	0.12	22.96 ^A	6.07	3.88^{AB}	1.09	26.25 ^A	3.02	12.67 ^A	3.69
	N	20.67 ^A	2.17	14.50 ^A	3.25	0.73 ^A	0.21	28.13 ^A	6.02	2.65^B	0.73	20.67 ^A	2.17	13.67 ^A	3.46
elevation level	low	22.75 ^A	2.59	16.50^{AB}	2.10	0.92^A	0.15	19.54 ^A	2.37	4.71 ^A	0.81	81.29^A	5.61	22.25^A	4.32
	mid	24.00 ^A	2.44	19.13^A	2.27	0.50^B	0.07	45.51 ^A	12.65	5.16 ^A	1.12	65.29^{AB}	9.86	15.88^{AB}	3.53
	high	26.81 ^A	3.11	11.13^B	2.01	0.32^B	0.04	22.65 ^A	5.17	4.53 ^A	1.46	40.30^B	11.44	9.13^B	1.60

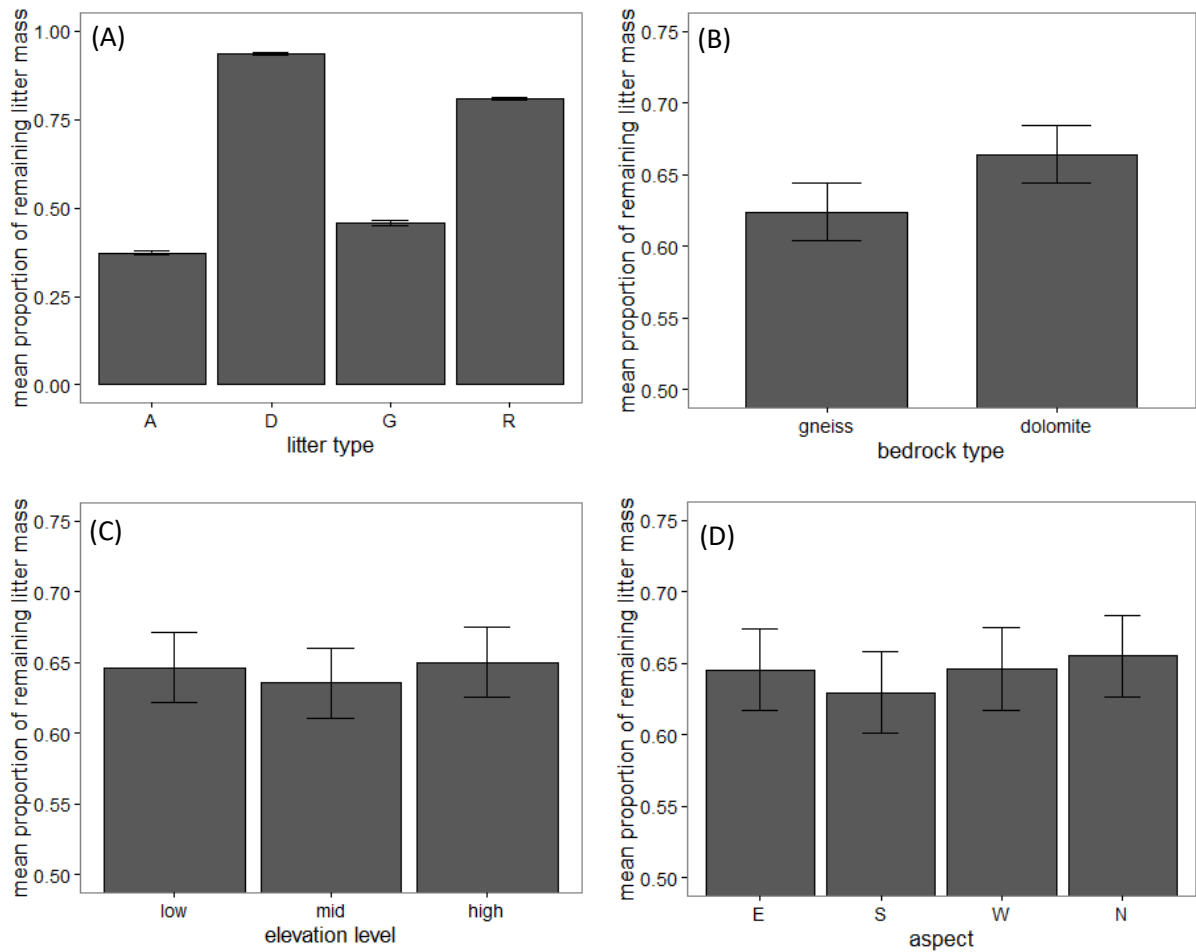


Figure 4: Mean (± 1 SE) proportional remaining litter mass (A) in litter types (A: Anthyllis, D: Dryas, G: green tea, R: rooibos tea), (B) between contrasting bedrock types, (C) on different elevation levels (low \approx 2430m, mid \approx 2530m, high \approx 2800m), and (D) in response to slope aspects.

Table 4: ANOVA results of a Linear Mixed-effects Model testing on differences in decomposition between levels of experiment factors in summit-soil incubations. Bold *p* values indicate significant differences.

source of variation	df	X^2	<i>p</i>	source of variation	df	X^2	<i>p</i>
bedrock	1	4.12	0.042	litter type \times bedrock	3	8.48	0.037
aspect	3	3.75	0.290	litter type \times aspect	9	18.13	0.033
elevation level	2	5.76	0.056	litter type \times elevation	6	23.85	< 0.001
litter type	3	1042.96	< 0.001	litter type \times aspect \times bedrock	9	23.90	< 0.01
bedrock \times aspect	3	12.45	< 0.01	litter type \times aspect \times elevation	18	48.76	< 0.001
aspect \times elevation	6	9.98	0.125				

Decomposition patterns

Overall litter mass loss was highly different between litter types (Table 4, Fig. 4A). Decomposition was most intense for *Anthyllis* leaves, with remaining litter mass being 23 % higher for green tea, 117 % higher for rooibos tea, and 152 % higher for *Dryas* leaves (Fig. 4A). Consequently, remaining litter mass was on average 110 % higher for recalcitrant litter species (rooibos tea, *Dryas*) than for easily decomposable types (green tea, *Anthyllis*; Fig. 4A). In addition, mean decomposition was significantly and by 6 % faster at sites with gneiss bedrock than with dolomitic parent material (Table 4, Fig. 4B). There was also a trend of slower decomposition at high altitudes compared to mid-elevation sites, with no considerable difference to low-altitude summits (Table 4, Fig. 4C). Overall decomposition patterns did not differ significantly between aspects (Table 4, Fig. 4D). Litter mass loss did, however, vary differently between aspects on the two bedrocks, with dolomite plots showing relatively higher remaining litter mass in eastern plots and lower remaining mass in western plots compared to their respective gneissic equivalents (Table 4, Fig. S2). In addition, the effects of aspect, bedrock and elevation

Table 5: ANOVA results of four Linear Mixed-effects Model testing on differences in decomposition between levels of experiment factors for four litter types separately. Bold *p* values indicate significant differences between factor levels.

source of variation	<i>Anthyllis</i>			<i>Dryas</i>			green tea			rooibos tea		
	<i>df</i>	<i>X</i> ²	<i>p</i>	<i>df</i>	<i>X</i> ²	<i>p</i>	<i>df</i>	<i>X</i> ²	<i>p</i>	<i>df</i>	<i>X</i> ²	<i>p</i>
bedrock	1	3.79	0.052	1	9.60	< 0.01	1	7.60	< 0.01	1	23.68	< 0.001
aspect	3	3.34	0.342	3	2.39	0.495	3	9.68	0.021	3	11.44	< 0.01
elevation level	2	5.65	0.059	2	17.74	< 0.001	2	1.54	0.464	2	6.92	0.031
aspect × bedrock	3	11.24	0.011	3	1.57	0.666	3	9.59	0.022	3	1.96	0.580
aspect × elevation	6	9.15	0.165	6	7.90	0.245	6	25.58	< 0.001	6	20.34	< 0.01

differed significantly between litter types (Table 4). Therefore, separate models for each litter type were performed.

Consequentially, decomposition responses of individual litter types to factors were largely divergent. Though all decomposed at least marginally significantly slower on dolomitic than gneissic bedrock (Table 5, Fig. 5A), the average difference was larger for tea (9.3 %) than local litter types (7.6 %). Furthermore, despite decreasing temperatures, decomposition of litter types also reacted unequally to increasing elevation, with a trend of faster decomposition in local litter types but a slowing trend in tea (Fig. 5B), though no significant differences between elevation levels were detected for green tea (Table 5). Overall following the observed temperature patterns, decomposition was most intense in southern aspects for all litter types (Fig. 5C), but green tea was decomposed most slowly in western aspects in contrast to northern aspects for the others, and significant differences were detected for tea only (Table 5, Fig. 5C). Further, effects of aspect on litter types varied differently between bedrock types (Table 5). Specifically, decomposition in

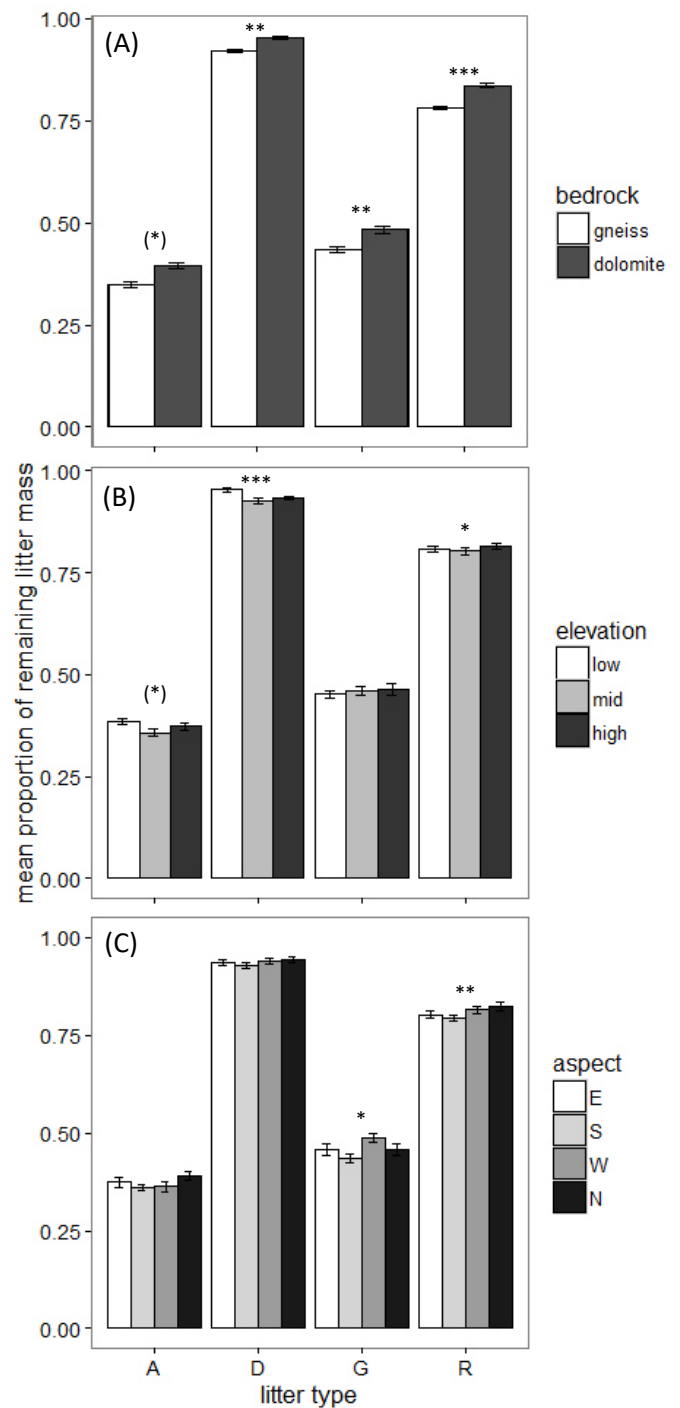


Figure 5: Mean (± 1 SE) proportional remaining litter mass in four litter types (A: Anthyllis, D: Dryas, G: green tea, R: rooibos tea) in response to (A) contrasting bedrock types, (B) elevation levels, and (C) slope aspects. Stars above bars indicate significant variation to factors as reported by ANOVAs of a separate Linear Mixed Model for each litter type as following: $p=0.05$ [(*)], $p<0.05$ [*], $p<0.01$ [**], $p<0.001$ [***].

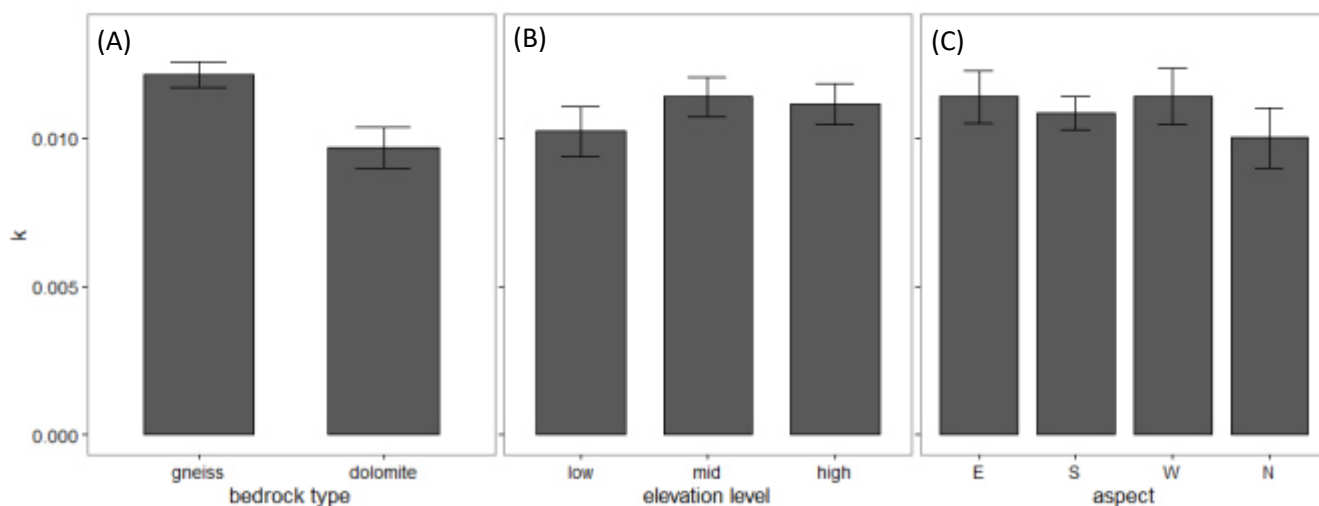


Figure 6: Mean (± 1 SE) Tea Bag Index decomposition rates k in response to (A) contrasting bedrock types, (B) elevation levels, and (C) slope aspects. ANOVA of a Linear Mixed Model testing for factor effects on decomposition rates revealed significant influence of all three factors (Table 6).

western plots on gneiss and dolomite, respectively, differed most for *Anthyllis* but least for green tea, and there was no significant difference in response for both *Dryas* and rooibos tea (Fig. S3). Moreover, decomposition of individual litter types in the four aspects did not change uniformly with elevation (Table 5). For instance, green tea mass loss in southern aspects was intensified with altitude while the opposite trend occurred for rooibos tea, and no major changes were detected for both *Anthyllis* and *Dryas* litter (Fig. S4).

Tea Bag Index

Conforming to general litter mass loss patterns, TBI values for decomposition rates k were significantly and by 25.4 % higher on summits with gneiss than dolomitic bedrock (Table 6, Fig. 6A). However, inconsistently with temperature observations, mid- and high-altitude summits had

Table 6: ANOVA results of a Linear Mixed-effects Model testing on differences in Tea Bag Index decomposition rates between levels of experiment factors. Bold p values indicate significant differences between respective factor levels.

source of variation	df	X^2	p
bedrock	1	4.45	0.035
aspect	3	7.99	0.046
elevation level	2	6.10	0.047
aspect \times elevation	6	20.76	< 0.01

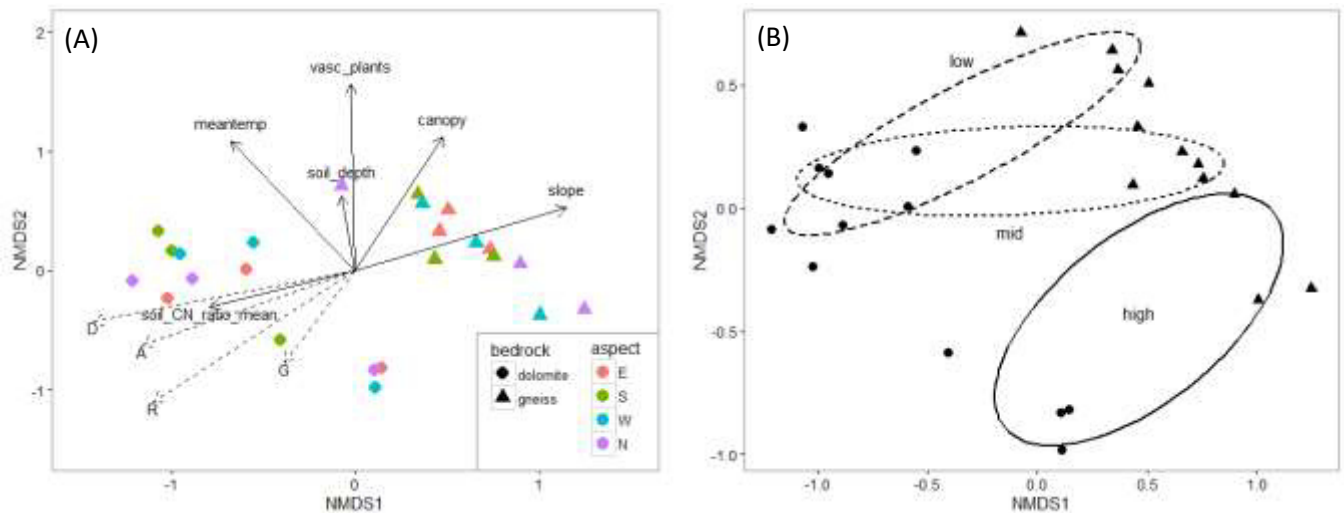


Figure 7: Results of NMDS analysis on plant community composition, displayed in relation to (A) bedrock, aspect, environmental variables and decomposition rates of the four litter types, and to (B) bedrock and elevational level.

significantly higher k values than low-elevation peaks, and same was the case for west and east plots compared to northern sites (Table 6, Fig. 6B,C). Decomposition in the four aspects also varied considerably between elevation levels (Table 6). While strongly increasing with elevation in southern aspect plots, the opposite trend was visible in northern sites, and maximum k was observed on mid-elevation summits for both east and west-aspect plots, however with high variation in the data (Fig. S5). Aspect effects did not differ between bedrock types as the interaction term was excluded in the model selection process.

Vegetation patterns

Plant community composition was strongly influenced by bedrock and elevation level, though not by aspect (Table 7, Fig. 7A,B). NMDS axis 1 was well explained by bedrock, increasing slope and decreasing soil C:N ratio as well as low decomposition impact, while NMDS

Table 7: Results of a PERMANOVA testing for differences in species composition of plant communities between levels of experiment factors. *Bold p values indicate significant differences between respective factor levels.*

<i>source of variation</i>	<i>df</i>	<i>SSQ</i>	<i>F</i>	<i>p</i>
bedrock	1	3.209	104.38	< 0.001
aspect	3	0.117	1.265	0.307
elevation level	2	1.905	30.97	< 0.001
Residuals	17	0.523		

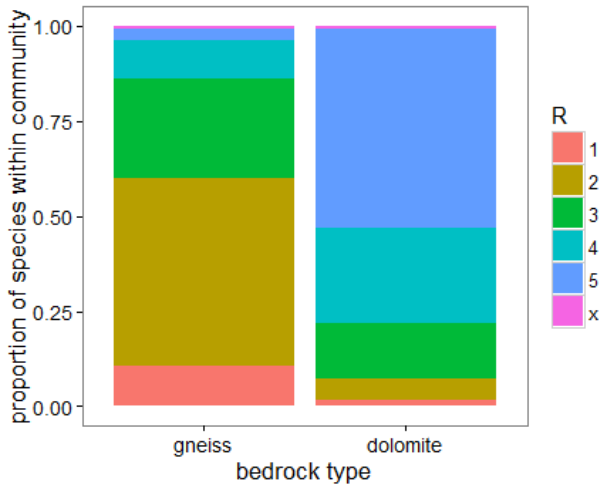


Figure 8: Summit plant community composition as indicated by occurrence of indicator values R on summits with contrasting parent material. Low R values indicate species favouring acidic conditions, high values represent more alkaline species.

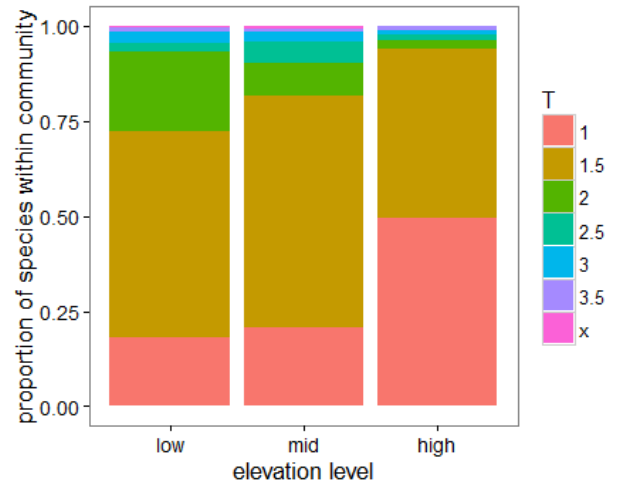


Figure 9: Summit plant community composition as indicated by occurrence of indicator values T along different altitudes. Low T values indicate alpine taxa, high values represent more thermophilous species.

axis 2 was best explained by increasing vascular plant cover and soil depth (Fig. 7A). Gneiss bedrock favoured acidophilic species ($F = 1$ or 2) while a substantially differing predominance of alkaline species ($F = 4$ or 5) was found on dolomitic parent material (Fig. 8). Also, plant community composition differed along the altitudinal gradient, especially on gneissic parent material (Fig. 7B), with increasing relative abundance of alpine plant species ($T = 1$ or 1.5) while proportion of subalpine species ($T \geq 2$) was considerably reduced with elevation (Fig. 9).

However, direct influence of vegetation on decomposition was subordinate to bedrock influence. Decomposition was significantly faster with more acidic species in the community (Fig. 10A), but this effect was neither significant nor uniform across bedrock types (Fig. 10B). Moreover, there was a slight trend of faster decomposition with less alpine species in the communities (Fig. 11A). Such a tendency was visible both on dolomitic and on gneissic summits, but differences between bedrock types largely exceeded effects of temperature-related community composition (Fig. 11B). However, for all cases there was great uncertainty in the data (Fig. 10,11).

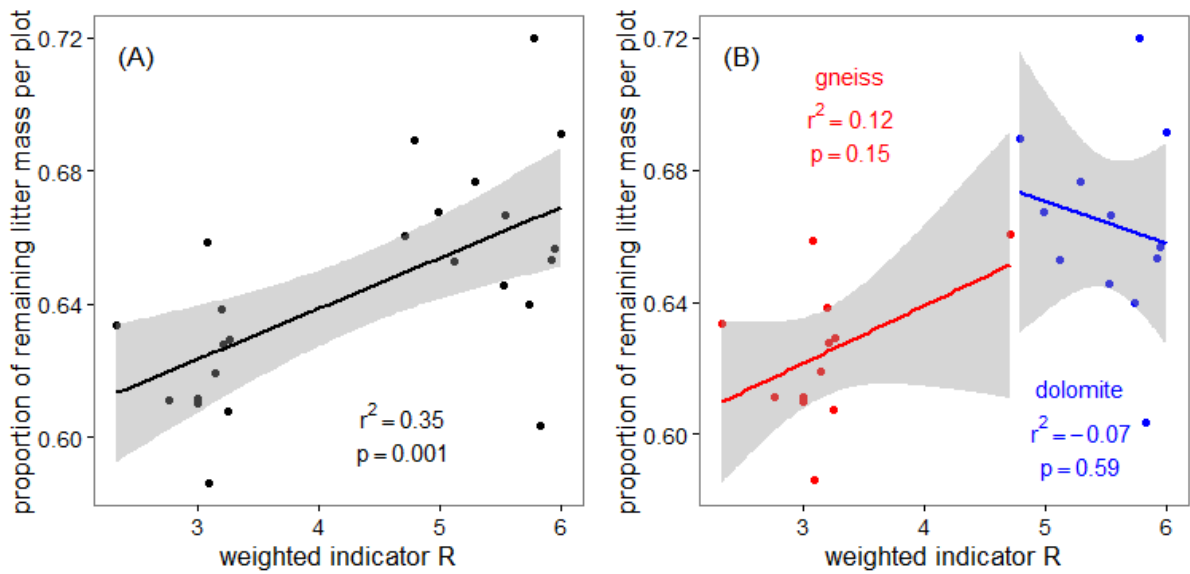


Figure 10: Linear regression analysis on the effect of plant community composition (as represented by species' reaction number R weighted by relative cover) on mean remaining litter mass in each plot ($N=24$). Analysis was conducted (A) for all plots combined, and (B) separately for plots with gneissic (red) or dolomitic (blue) bedrock. Grey areas indicate standard errors.

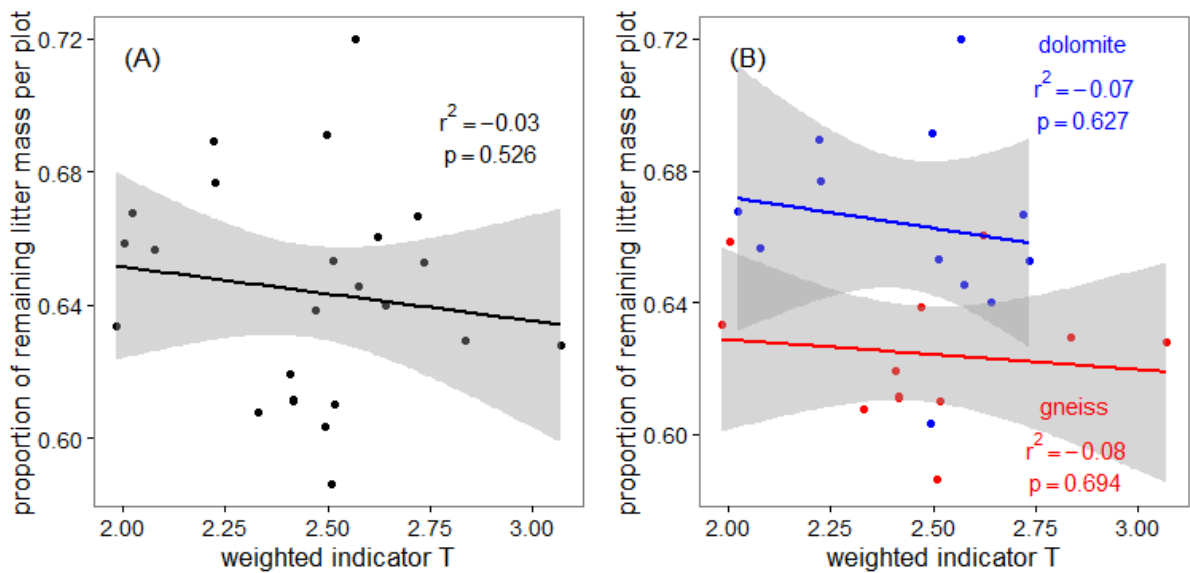


Figure 11: Linear regression analysis on the effect of plant community composition (as represented by species' reaction number T weighted by relative cover) on mean remaining litter mass in each plot ($n=24$). Analysis was conducted (A) for all plots combined, and (B) separately for plots with gneissic (red) or dolomitic (blue) bedrock. Grey areas indicate standard errors.

Home Field Advantage

Strongly contrasting HFA theory and our expectations, *Anthyllis* litter decomposition increased significantly with higher distance to individuals of the same species, and was intermediate if no *A. vulneraria* plants were around (Linear mixed-effects model, $df=4$, $F=5.079$, $p<0.01$; Fig. 12). A similar, though weaker trend was observed for *Dryas* (Fig. 12), but distance did not decrease remaining litter mass significantly (Linear mixed-effects model, $df=3$, $F=1.812$, $p=0.19$).

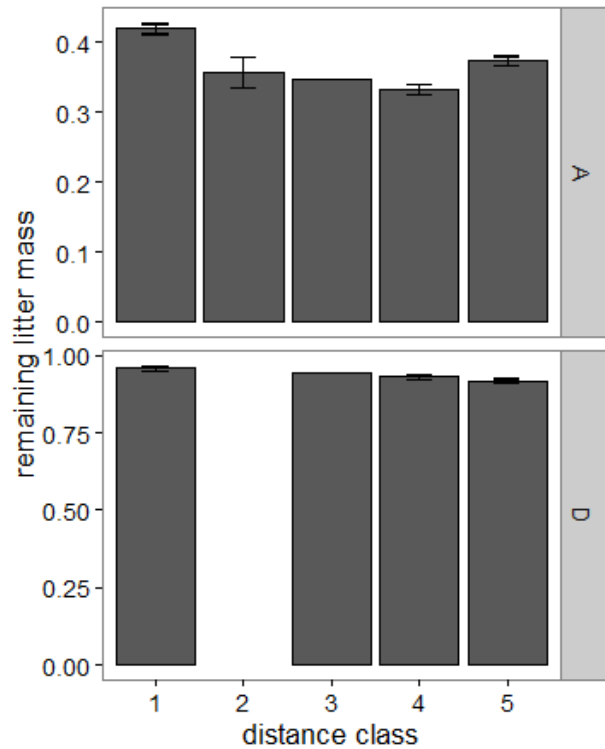


Figure 12: Mean (± 1 SE) mass loss in *Anthyllis* (A) and *Dryas* (D) litter in relation to distance of living individuals of the same species (from 1 – very close to 5 – species not present). No plot with *D. octopetala* in class 2 distance occurred.

MESOCOSM EXPERIMENT

Mean temperature over the burial period was significantly and by 4.6°C (39 %) higher at the lower site (mean: 16.3°C) than at the high-elevation location (mean: 11.7°C; Two-sample t-test, $df=3$, $t=8.88$, $p<0.01$).

Again, overall decomposition strongly differed between litter types (Table 8, Fig. 13A). Again, *Anthyllis* litter was decomposed most intensely, with remaining litter mass being 104 % higher for green tea, 150 % higher for rooibos tea and 169 % higher for *Dryas* litter. Hence, unlike in the field experiment, green tea decomposition was more similar to that of rooibos tea than of *Anthyllis* litter (Fig. 13A). Moreover, reflecting the temperature gap, remaining litter mass was significantly and by 5.6 % higher in the high-elevation site (Table 8, Fig. 13B). This difference was considerably greater for *Anthyllis*

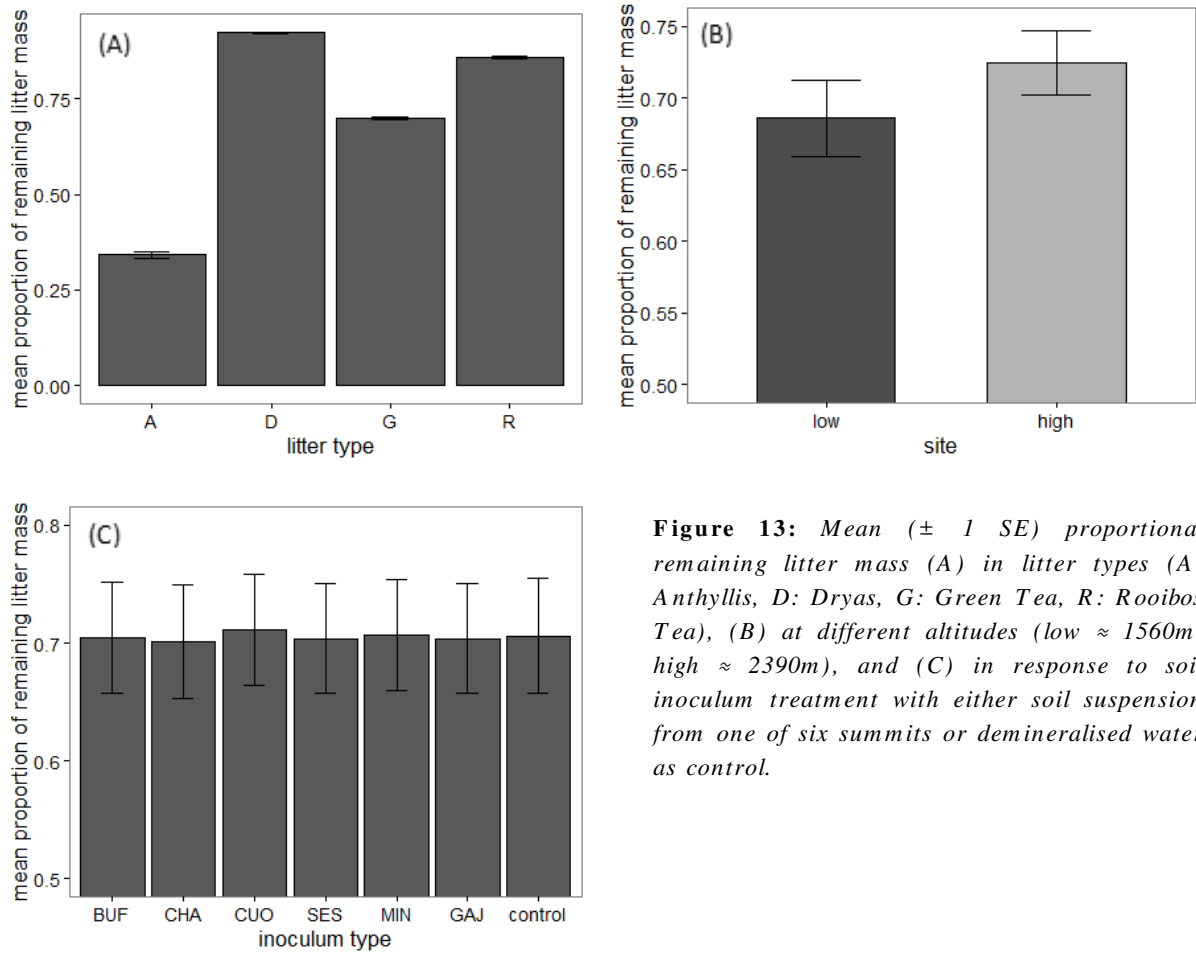


Figure 13: Mean (± 1 SE) proportional remaining litter mass (A) in litter types (A: Anthyllis, D: Dryas, G: Green Tea, R: Rooibos Tea), (B) at different altitudes (low $\approx 1560m$, high $\approx 2390m$), and (C) in response to soil inoculum treatment with either soil suspension from one of six summits or demineralised water as control.

than for other litter types (Table 8, Fig. S6). In contrast, there was no effect of soil inoculum type on the decomposition process (Table 8, Fig. 13C).

Table 8: ANOVA results of a LMM testing on differences in decomposition between levels of factors in mesocosm incubations. Bold *p* values indicate significant effects.

source of variation	df	SSQ	F	<i>p</i>
soil treatment	6	0.003	0.72	0.633
incubation site	1	0.062	100.05	< 0.001
litter type	3	8.339	4451.54	< 0.001
treatment \times site	6	0.003	0.91	0.492
treatment \times litter type	18	0.011	0.964	0.505
site \times litter type	3	0.088	46.83	< 0.001
treatment \times site \times litter type	18	0.007	0.598	0.895
Residuals	112	0.070		

Discussion

Decomposition impact in this alpine setting was most dependent on litter composition, indicating sensitivity towards warming-induced species shifts. Further, between-summit variation in soil and vegetation parameters was apparently more influential on litter decay than small-scale temperature variation, highlighting also the impact of plant communities on belowground processes via plant-soil feedbacks. Yet, in combination with expected shifts in plant community composition towards enhanced leaf litter recalcitrance, overall acceleration of decay processes in response to rising temperatures appears an unlikely scenario.

LITTER QUALITY AS THE CONSISTENT MAIN DRIVER OF DECOMPOSITION

Generally, decomposition patterns of the four litter types were highly dissimilar, and these differences largely exceeded the effects of other factors in the experiment. Mass loss was highest for relatively N-rich litter types (*Anthyllis* and green tea) and decreased with lower relative N content in rooibos tea and finally *Dryas*, conforming to previously reported findings (Taylor et al. 1989; Cotrufo et al. 1995; Perez-Harguindeguy et al. 2000). Differences in decay patterns between the two labile types might be due to the fact that fresh *Anthyllis* leaves were collected from natural populations and immediately dried thereafter. In contrast, green tea leaves are usually steamed or roasted after harvesting to enhance stability of the product for storage (Wang et al. 2000), and some polyphenolic compounds have been assigned antimicrobial properties (Hamilton-Miller 1995), thus potentially lowering decomposability. Similarly, *Dryas* litter dated from the previous growing season and plants had already resorbed valuable N-rich compounds into perennial tissues (Thomas & Stoddart 1980), decreasing attractiveness for detritivores. Resultantly,

higher mass loss in rooibos tea was probably due to rooibos containing slightly higher relative N amounts than *Dryas*.

Despite large similarities, decomposition patterns differed between field and mesocosm incubations. Most importantly, remaining mass in green tea and slightly also in rooibos tea was greater in mesocosms than after burial on the summits. These differences might be caused by a lack of water flow in the mesocosms and thus a vast reduction of leaching effects. Green and rooibos tea contain 11 % and 7 % flavouring substances, respectively (Keuskamp et al. 2013), which are highly water-soluble and were probably washed out quickly by the water flow in the field. Thus, the use of *in situ* experiments in decomposition experiments is strongly recommended.

RELATING ALPINE TO LARGE-SCALE DECOMPOSITION

For future field studies on decomposition, the TBI approach using green and rooibos tea generally seems a reasonable approach to model decay of alpine species. Decomposition of both types of tea varied stronger in response to differences between aspects and bedrock types than decay of local litter types. However, overall applicability of the method is suggested by the much larger difference in litter mass loss between easily decomposable and recalcitrant type in both groups than within tea and local litter types, respectively, as well as by similarity of litter C:N content ratios within groups. Moreover, the extreme difference in ‘freshness’ between the two allochthonous materials of *Anthyllis* (freshly sprouted) and *Dryas* (senesced from the last growing season) might even have caused a slight overestimation of realistic discrepancies in decay rates. Thus, if comparing freshly senesced material of both species, decomposition patterns are likely to even better resemble the decay pictures of the two tea varieties.

On a larger scale, despite minor deficiencies in the alpine context, the TBI method may still serve for comparing decay data from different biomes. Since litter decomposition represents a complex process that is highly variable in space and time and depends upon a vast number of influencing factors, standardising it is a challenging task and necessarily

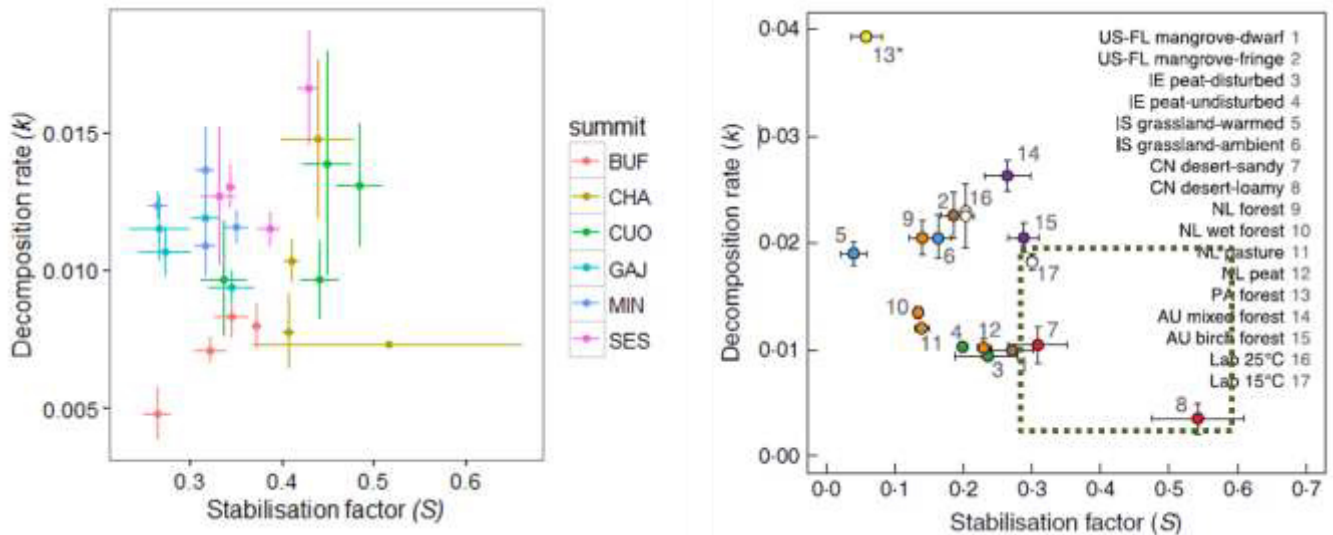


Figure 14: Mean (± 1 SE) Tea Bag Index decomposition rates k and stabilisation factors S , (A) as measured in situ on six alpine mountain summits in Switzerland, and (B) showing the same range of values (dashed rectangle) in comparison to different sites in low-elevation ecosystems. For site codes in (B) and study details, see Fig. 3 in Keuskamp et al., 2013.

involves simplifications. For instance, accounting for incubation time as duration in days might be questioned if similar shares of growing season length are represented. This might have provoked overestimation of observed decomposition rates k (Fig. 14A), though the overall comparison appropriately reveals lower k values than in numerous low-altitude ecosystems (Fig. 14B; see Keuskamp et al. 2013). Also, stabilisation factors were relatively high, indicating rather slow decay of green tea or the labile litter fraction, respectively, but still conforming to the generally low nutrient turnover in cold biomes (Körner 2003).

LITTER CONTROLLING ECOSYSTEM RESPONSE TO WARMING

Our findings strongly emphasise the importance of litter quality in decomposition processes (Swift et al. 1979; Wardle 2002; Parton et al. 2007; Zhang et al. 2008), highlighting also the considerable potential for shifts in high-alpine decomposition rates in the context of global environmental change. Upward shifts have been observed particularly in shrub species in response to warming (Myers-Smith et al. 2011) and land-use change (Tasser et al. 2005; Brandt et al. 2013) and also predicted for graminoids at

the expense of forb-rich specialised alpine vegetation (Zhang & Welker 1996; Schöb et al. 2009; Pickering et al. 2014). However, litter of both groups has been shown to decompose at slower rates than in forbs (Seastedt et al. 2001; Shaw & Harte 2001), which was confirmed for shrub litter by the results of this study. This could potentially result in considerable reductions of litter turnover rates in warmer alpine environments, at least partly counteracting assumed warming-induced increases in decomposer activity (Cornelissen et al. 2007; Gavazov 2010).

THE IMPORTANCE OF BEDROCK AND VEGETATION-DECOMPOSER RELATIONS

Our results question the assumed dominant and generally positive influence of temperature on decay rates, but rather stress the complex interplay of influencing factors in this alpine setting. As expected, soil temperatures were higher towards lower altitudes as well as south- and east-exposed sites but varied less between parent materials. However, these patterns could not explain variations in decomposition observed between levels of either aspect, elevation, or bedrock. Specifically, decay differed most between parent materials and also responded slightly stronger to elevation than different aspects although temperature variation was most pronounced between the latter. Interestingly, these findings contrast the results from our mesocosm incubations as well as general predictions (Lloyd & Taylor 1994; Davidson & Janssens 2006) and previous experimental findings (Hobbie 1996). In their review, von Lützow & Kögel-Knabner (2009) also found inconsistent temperature effects on decomposition and related this to various biological and physico-chemical constraints that soil organic matter is exposed to. Thus, and especially in the generally temperature-limited high-alpine setting, it can be expected that temperature is indeed not the primary driver of decomposition intensity.

Instead, of all controlled factors in the experiment, bedrock type rather than exposure or elevation was the most consistent influence on most environmental variables as well as on vegetation structure, and resultantly also the main driver of decomposition patterns. Specifically, and over all litter types, litter mass loss was higher on gneissic summits even

though temperatures were slightly lower in comparison to dolomitic sites. The underlying parent material is the basis for soil formation and thus influences greatly the supply with moisture and nutrients to organisms living in and on the substrate (Anderson 1988). Soils on dolomitic bedrock had lower soil moisture than on gneiss, demonstrating more effective drainage of surface water on calcareous substrates. Correspondingly, previous studies have repeatedly demonstrated a positive relationship between soil moisture content and decomposition intensity (e.g. Bryant et al. 1998; Murphy et al. 1998; Withington & Sanford 2007; Gavazov et al. 2014). However, in contrast to bedrock, decomposition patterns did not correlate consistently with variations in soil moisture between altitudes, which declined steadily towards higher elevation while remaining litter mass was lowest in intermediate altitude. Similarly, north-exposed plots showed highest soil moisture but lowest decomposition intensity, though differences in moisture between aspects were smaller than between bedrock types or along the elevational gradient. Nevertheless, both soil chemical composition and moisture can be expected to influence alpine decomposition rates to a higher extent than temperature does.

Although being under strong influence of parent material themselves, changes in vegetation may actively account for part of the bedrock effect on decomposition patterns. Along with higher soil water content, plant growth as well as diversity was promoted on gneissic rather than dolomitic parent material and towards lower altitudes, crucially altering plant community structure and composition along these gradients, this effect also exceeding the direct influence of plant communities on decomposition. However, no such major changes in vegetation were visible between aspects. These findings well mirror the observed decomposition patterns, especially in recalcitrant litter species which varied in decay intensity between elevation levels but not aspects, suggesting a close relationship between vegetation structure and decomposition processes. With higher canopy, cover, and species number, vegetation impact on belowground processes can therefore be expected to increase and crucially influence decomposition processes (Van der Putten et al. 2013). For example, in a boreal setting, De Long et al. (2016) found higher rates of litter mass loss with shrub removal, demonstrating an important controlling effect of vegetation structure and composition on decay processes. Such control is mainly being

exerted by effects on decomposing organisms and has been shown to influence decomposition rates in general as well as C, N, and phosphorous cycling specifically (see Wardle 2002).

Further, this above-belowground link once more emphasises the central role of the decomposing community which, besides abiotic environmental variables and litter quality, represents the third major control on decomposition processes (Robinson 2002). In cold and nutrient-poor ecosystems, microbes represent the largest fraction of decomposers (Schinner 1982), being of higher importance for ecosystem productivity than in more fertile biomes (Van Der Heijden et al. 2008). Heterogeneous spatial distribution is a common phenomenon observed in soil (micro)organisms (Ettema & Wardle 2002), and is especially likely to occur in low-productivity ecosystems due to local variation in nutrient availability (Sundqvist et al. 2011; Roy et al. 2013). Therefore, also speed and characteristics of decomposition processes might vary considerably between different sites, and, due to the large control on microbes by plant communities, especially in case of large differences in vegetation. In this study system, microbial communities differ probably more between than within summits given the smaller variation in environmental parameters among aspects relative to elevations and parent materials.

However, this assumption is challenged by the absent effect of inoculum type in the mesocosm experiment. Yet, due to the consistent response as well as variation over all treatments, success of microorganism transfer to mesocosms by soil inoculation is highly questionable. Further, even if transfer was successful, microflora might have suffered from anoxia because of insufficient aeration during the incubation period, decelerating decomposition processes (e.g. Neckles & Neill 1994). Resultantly, this again highlights the importance of *in situ* decomposition experiments.

In contrast to HFA theory, which predicts faster decomposition of litter in closer vicinity to individuals of the originating plant species due to specific adaptation of detritivores (Gholz et al. 2000; Veen et al. 2015a), decomposition of *Anthyllis* litter was weaker if *A. vulneraria* individuals were nearby, and a similar trend was visible for *Dryas*. The latter is even more surprising as numerous saprophyte fungi have been shown to

associate with alpine *D. octopetala* (Lamoure 1972), which should be especially used to decompose *Dryas* litter and thus increase decay impact. However, patterns for both litter varieties were largely overridden by summit identity and thus site-specific effects, as both species showed much higher abundance on dolomitic summits. Thus, presumably, the decelerating effect of calcareous parent material slowed down decomposition in proximity of both *Anthyllis* and *Dryas* rather than impacts of plant individuals on soil biota. Adding to that, findings of Veen et al. (2015b) in subarctic tundra suggest that conditioning of soil organisms towards decay of certain litter types may not occur in cold biomes to a comparable degree like observed in more productive ecosystems (e.g. Keiser et al. 2011).

OUTLOOK: WARMING FEEDBACKS BETWEEN PLANT AND SOIL SUBSYSTEMS

Considerable shifts in species richness and community composition in alpine regions have been reported with climate warming (Walther et al. 2005; Pauli et al. 2005, 2012; Gottfried et al. 2012; Wipf et al. 2013), but their consequences for important ecosystem processes like decomposition have not yet been identified (Wookey et al. 2009). Given the low relative importance of temperature and the high impact of litter identity as well as soil abiotic properties observed in this study, decomposition in high-alpine environments seems somewhat inert towards warming-induced changes. Similarly, based on theory of both positive (soil warming) and negative (species shift-related increase in litter recalcitrance) feedbacks, Gavazov (2010) proposed the existence of an inherent buffering mechanism on decomposition rates in alpine environments, resulting in little alteration or even retardation of decomposition processes along with climatic changes. Even with the reported high rates of warming, and in contrast to rapid changes in vegetation, many belowground processes are likely to be altered much more slowly due to slow adjustment of nutrient stocks (Wookey et al. 2009). However, experiments focusing explicitly on plant community effects on decomposition dynamics would be helpful to more closely explore the role of plant-soil feedbacks.

Moreover, also the question of how belowground processes influence the structure and dynamics of alpine vegetation will have to be addressed more specifically in future research. However, due to complex interplay of ecosystem processes, long-term and large-scale investigations are needed to increase both reliability and resolution of results (Bradford et al. 2016), underlining the potential of the TEACOMPOSITION study network. Such experiments will also be able to assess the influence of processes during winter season, which are commonly of high importance for high-alpine ecosystem dynamics both with regard to plant community regulation (e.g. Walker et al. 1993) and directly affecting decomposition rates (Baptist et al. 2010) as well as nutrient cycling (Fisk et al. 1998; Sturm et al. 2005). Additionally, physical decomposition processes, which were not subject of this study but are generally of high importance in cold environments, might contribute essentially to ecosystem functioning (Gavazov 2010) and should be included in future studies. Further, closer insights into structuring and controls of decomposer communities could enhance understanding of above-belowground relationships and the role of decomposition processes in shaping changing alpine plant communities.

Conclusion

Decay intensity differed between leaf litter of contrasting qualities in combination with a consistent effect of bedrock-related soil properties like moisture content, but decomposition response to temperature variations was limited and highly inconsistent between litter types. Although high-alpine ecosystems are predicted face major changes with the rapidly warming climate (IPCC 2014), these results suggest relative resilience of high-alpine decomposition rates as generally a relative increase of recalcitrant litter types is expected (Cornelissen et al. 2007; Gavazov 2010). Nevertheless, parallel variation in decomposition and vegetation patterns suggests a close relationship via plant-soil feedbacks (Van der Putten et al. 2013) and indicates the potential of belowground processes to shape aboveground community structure and diversity. In contrast, small-scale (i.e., within-summit) site parameters seem to be of minor importance for litter mass loss compared to abiotic and biotic variation over larger distances, stressing the remarkable versatility of the alpine region. Simultaneously, our findings highlight the dependence of ecosystem processes such as decomposition on the local environment (e.g. Bryant et al. 1998; Fisk et al. 1998), which however ultimately impedes general predictions on the ecosystem scale. Long-term investigations incorporating winter season impact and physical decay as well as detailed studies of decomposer communities could potentially improve our understanding of the functioning of decomposition processes and their role in shaping high-alpine ecosystems.

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Supplementary materials

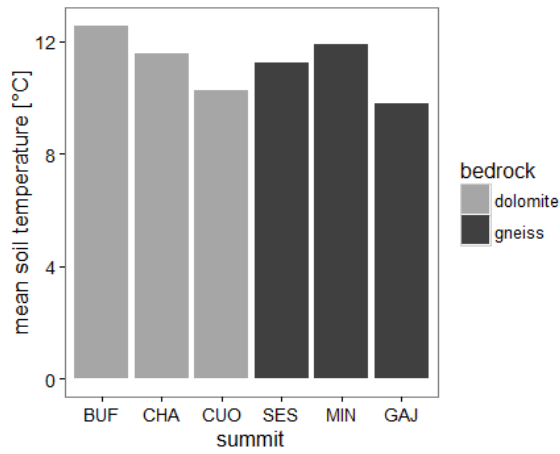


Figure S1: Mean soil temperatures over incubation period on summits.

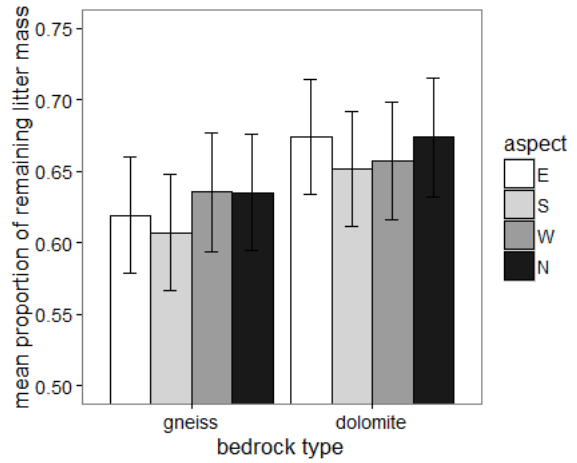


Figure S2: Mean (± 1 SE) remaining litter mass in slope aspects of summits with contrasting bedrock.

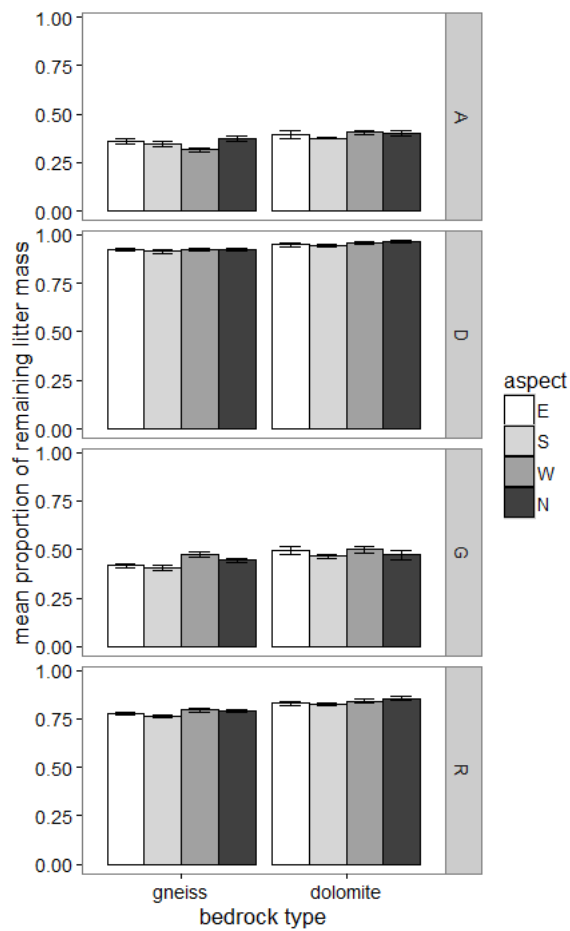


Figure S3: Mean (± 1 SE) remaining litter mass in four litter types (A: Anthyllis, D: Dryas, G: green tea, R: rooibos tea) in response to slope aspects on contrasting bedrock types.

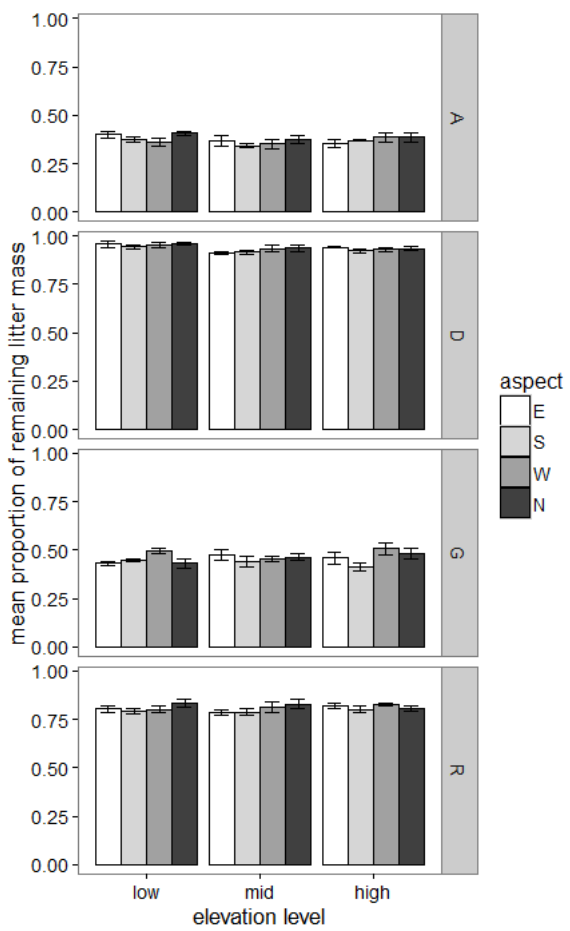


Figure S4: Mean (± 1 SE) remaining litter mass in four litter types (A: Anthyllis, D: Dryas, G: Green Tea, R: Rooibos Tea) in response to slope aspects on different elevation levels.

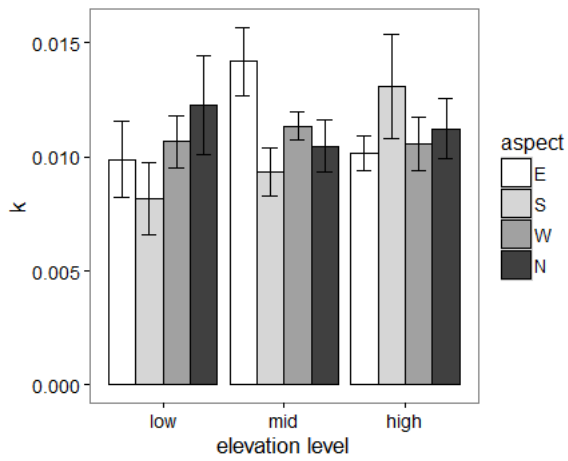


Figure S5: Mean (± 1 SE) Tea Bag Index decomposition rates k in slope aspects of summits on different elevation levels.

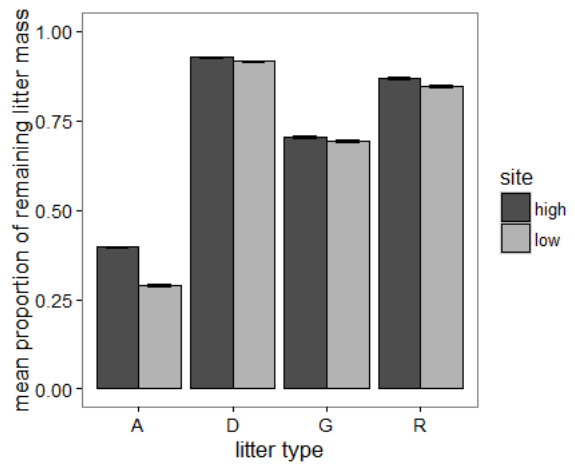


Figure S6: Mean (± 1 SE) remaining litter mass for litter types in response to incubation in sites at contrasting altitude.

Eigenständigkeitserklärung:

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig verfasst, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und wörtlich sowie inhaltlich übernommenen Stellen eindeutig gekennzeichnet habe.

Diese Arbeit war weder vollständig noch in wesentlichen Teilen Gegenstand eines anderen Prüfungsverfahrens.

Tübingen, den 16.01.2017

Unterschrift: