Microtopography on Mountains: complex terrain augments heterogeneity of belowground carbon and nitrogen in the Swiss Central Alps.

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i. Abstract

Mountain ecosystems are experiencing accelerated climate change and more frequent climatic extremes. Mountain soils play a critical role in local and regional biogeochemistry, while underpinning ecological stability and ecosystem multifunctionality. In the European Alps, mountain soils represent a critical carbon pool with the potential to modulate climate change through the sequestration of atmospheric carbon dioxide (CO_2). However, climate warming may exacerbate soil carbon (C) and nitrous oxide (N_2O) fluxes to the atmosphere. Consequently, European mountain ecosystems may become strong sources of atmospheric greenhouse gases, however, the environmental factors controlling the distribution of belowground C and N in mountain ecosystems and their relative importance across different spatial scales are largely unexplored. I aim to demonstrate that heterogeneity in the distribution of total soil C and N, and total organic C and N in microbial biomass, would occur with elevation and be augmented by microtopography. I explore elevation gradients stratified by life zone, underlying geology, parent material, vegetation composition and land-use type, differing only in proxy variables for microtopography.

Heterogeneity in belowground C and N occurred with elevation and between sites of the same altitude for all transects. Slope angle was the most important topographic variable at lower elevations, likely due to the relationship with aboveground vegetation. Heterogeneity was constrained across the treeline ecotone, likely due to the overarching effect of declining temperature with increasing elevation on aboveground vegetation and second-order soil physicochemical drivers. The effect of slope was closely linked to response values at higher altitudes but was augmented by the effects of microtopography which became more pronounced with elevation. Overall, it emerged that the macro-scale effects of elevation-dependent factors may control belowground C and N in a general way, and site-specific conditions as a consequence of microtopographic and microclimatic dynamics may augment their heterogeneity at smaller scales.

ii. Declarations

I hereby declare that this work is original in its entirety and has never before been submitted for any form of assessment. The practical work, data analysis, presentation and written work presented are all my own unless otherwise stated.

I grant the Lancaster University institutional repository permission with respect to online access of this work.

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Iv. Abbreviations

A = aspect
ANOVA = analysis of variance
C = carbon
cb = control blank
cdsm = control sample dry soil mass
$CHCl_3$ = chloroform
CI = confidence interval
CO_2 = carbon dioxide
cTOC = control total organic carbon
cTN = control total nitrogen
DW = dry weight
E = elevation
EDTA = ethylenediaminetetraacetate
fb = fumigated blank
FEAST = Functional Ecology of Alpine Systems
fTOC = fumigated total organic carbon
fTN = fumigated total nitrogen
K_2SO_4 = potassium sulphate
LEC = Lancaster Environment Centre
LOESS = local estimated scatterplot smoothing
m asl = meters above sea level
MAP = mean annual precipitation
MAT = mean annual temperature
MBC = total organic carbon in microbial biomass
MBN = total nitrogen in microbial biomass
MilliQ = water purified using Millipore system
mv = matrix volume
N = nitrogen
N_2O = nitrous oxide
PCA = principal component analysis
PERMANOVA = permutational multivariate analysis of variance
S = slope
SFG = Swiss Federal Geoportal
SMC = soil moisture content
SOC = soil organic carbon
SOM = soil organic matter
TC = total carbon
TN = total nitrogen
TOC = total organic carbon
Tr = transect
vc = volume of chloroform
vm = volume of MilliQ

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1. Introduction

Mountain ecosystems occupy over 24% of the Earths land area and provide ecosystem services that extend beyond their geographical boundaries (Körner, 2004; Nogués-Bravo et al, 2007; Körner, 2007b; Yang et al., 2018). The most extensive mountain areas are located in the Holarctic temperate zone, including the mountains of the European Alps (Ohmura, 2012; Rubel et al, 2017), which are experiencing accelerated climate change and more frequent climatic extremes compared to ecosystems at lower elevations (Pauli, 2016; Rangwala et al, 2013; Rebetez and Reinhard, 2007; Gavin et al, 2018). These ecosystems are among the most vulnerable to rapid climate change (Ernakovich et al, 2014) and are sensitive indicators of its consequences (Pauli, 2016). Pronounced altitudinal zonation combined with steep meteorological and topographical gradients in mountain ecosystems are great challenges for spatiotemporal investigations (Löffler and Finch, 2005). However, the study of these environmental gradients can be implemented to capture nonlinearities of ecological responses to interacting environmental drivers, while simultaneously detecting ecologically important thresholds (Kreyling et al, 2018).

Mountain soils and their microbiota are critical to local and regional belowground biogeochemistry (Hagedorn et al, 2009; Bing et al, 2015; Xu et al, 2014; Nannipieri et al, 2003) and are the interface for biogeochemical interactions across the Earths spheres (Bardgett, 2005; Martin and Johnson, 2012; Whitton, 2012). Mountain soils represent a critical carbon pool with the potential to modulate climate change through the sequestration of atmospheric carbon dioxide (CO_2) (Georgiou et al, 2019; Hagedorn et al, 2009; Scharlemann et al, 2014). In the European Alps, over 92% of ecosystem carbon (C) is sequestered in mountain soils (Körner, 2003). Disturbed and liberated C can accelerate C loss from the ecosystem, increase atmospheric CO_2 levels and exacerbate soil carbon fluxes to the C cycle (Wang et al, 2018; Bardgett et al, 2008; Kardol et al, 2010). In this context, European mountain ecosystems may become increasingly strong sources of atmospheric C (Leifield et al, 2009). The decomposition of below ground nitrogen (N) pools may also increase atmospheric nitrous oxide (N_2O) levels due to increased net N mineralization, nitrification and soil inorganic processing of N as a result of climate warming (Bai et al, 2013). However, the environmental factors controlling the distribution of belowground C and N in mountain ecosystems and their relative importance across different spatial scales are largely unexplored (Murugan et al, 2019; Bhople et al, 2019; Hu et al, 2019).

Across elevation gradients in mountain ecosystems, the adiabatic lapse of atmospheric temperature is approximately -0.6°K per 100m elevation increase (Körner, 2012; Mayor et al, 2017; Nagy and Grabherr, 2009), representing an equivalent isothermic change otherwise encountered over a distance of 111 km latitude. This lapse rate change in isothermal temperature causes vegetation assemblages to form in distinct belts characterised by functional life-forms (Körner et al, 2011; Nagy and Grabherr, 2009). In the European Alps, this change is characterised by a transition from lowland forest belts into high montane forest, the sub-alpine and the treeline ecotone. The treeline is an inexact transitional zone of life-form dominance, forming within a globally consistent isotherm (Körner, 2003; Mayor et al, 2017; Hoch and Körner, 2011). Above the treeline, a gradual decline in tree size and the opening of the canopy signifies the transition into the treeless alpine zone, defined as the position between the natural climatic treeline and the non-seasonal snowline (Gottfried et al, 2011; Körner, 2003), occurring at equal temperatures on a global scale and at progressively lower elevations along a northward latitudinal gradient (Körner et al, 2003; Britton et al, 2011; Edwards et al, 2007). In the European Alps, this transition occurs at approximately 2000 meters above sea level (m asl) and is characterised by low stature vegetation, graminoids, herbaceous perennials and cushion plants. The persistence of these function life forms becomes increasingly sparser into the sub-nival, beyond which, into the true nival zone, life is restricted to favourable microclimatological refugia in a landscape dominated by snow and ice (Körner, 2003; Nagy and Grabherr, 2009; Keppel et al, 2011; Körner, 2011).

Climatic dynamics across elevation gradients exert a powerful control over ecosystem functions. Soil C concentrations generally increase with increasing elevation, increasing mean annual precipitation (MAP) and decreasing mean annual temperature (MAT) (Körner, 2003; Leifield et al, 2009). These dynamics are linked to the higher accumulation of soil organic matter (SOM) at higher altitudes due to the constraints of cold temperatures on decomposition (Li et al, 2010; Siles et al, 2016; Djukic et al, 2010). Soil N generally decreases with increasing elevation and decreasing annual biomass production (Körner, 2003), and lower soil temperatures at high elevations reduce rates of ecosystem N turnover and accumulation (Huber et al, 2007; Hiltbrunner et al, 2005). Soil nutrient decomposition and mineralisation is suppressed by low temperatures at high elevations (Li et al, 2010; Wang et al, 2019) and is linked to decreased C and N in microbial biomass (Bhople et al, 2019; Whitaker et al, 2014; Siles et al, 2016).

Complex topography on mountainsides creates microtopographic features (Garcia-Pausas et al, 2007; Makarov et al, 2003; Kotas et al, 2018; Mastrotheodoros et al, 2019; Frindte et al, 2019) that modulate microclimate conditions differing significantly from those at the macro-scale (Sun et al, 2015; Bennie et al, 2008). Microclimate conditions are the synergistic effects of the thermal climate experienced, the stature of vegetation, surface structure and complex topography (Körner, 2003; Fang et al, 2004; Nagy and Grabherr, 2009; Pepin et al, 2015; Lozano-García et al, 2016; Mastrotheodoros et al, 2019). The influence of these physico-environmental variations and ecosystem constraints are more pronounced in mountain ecosystems (Garcia-Pausas et al, 2007; Körner, 2003) where a legacy of glacial and periglacial dynamics drives spatial heterogeneity in the soil environment and topographic-linked gradients of exposure to abiotic controls (Garcia-Pausas et al, 2007; Kirkpatrick et al, 2014). Complex microtopography controls the partitioning of climatic inputs, such as water and energy, via connections to regional climatic processes. These processes are further modulated by orographic precipitation gradients and exposure to radiative forcing, driving interactions between energy fluxes and moisture transport across the landscape (Mastrotheodoros et al, 2019). Atmospheric and radiative processes interacting with microtopographic linked gradients modify fine-scale environmental conditions to create microclimates over scales of tens of meters to <1 meter, occurring at localised areas across the soil-atmosphere interface (Zhu et al, 2017; Zhu et al, 2018; Mastrotheodoros et al, 2019). The microclimate experienced within the upper surface of the vegetation down to the deepest roots in the soil may effectively be decoupled from free-air temperatures (Larcher and Wagner, 2010); within microtopographic features at high elevations, the MAT of mountain soils may be up to 7°C warmer than free-air synoptic temperatures (Scherrer and Körner, 2010b).

Steep mountain ecosystems are influenced by the effects of gravity and high kinetic potential which manifests in high-energy mass movement and erosion events developing over long periods. Rockfalls and landslides radically alter the landscape and ecological conditions over short timescales (Bales et al, 2006; Hasan et al, 2008; Mourey et al, 2019). In the absence of stabilising vegetation, soils on steep slopes are highly susceptible to erosion (Egli et al, 2006). The intensity of weathering, parent material and substrate age control the release of inorganic elements and soil formation (Poulenard and Podwojewski, 2006; Reich and Oleksyn, 2004; Kirkpatrick et al, 2014; Tian et al, 2009). As a result of more intensive chemical weathering and steeper slopes, soils in the alpine are generally shallower, coarser textured, horizons are poorly developed and in are in a constant process of rejuvenation relative to soils of the sub-alpine and montane forests (Kirkpatrick et al, 2014; Poulenard and Podwojewski, 2006).

Slope gradient controls soil moisture and soil temperature due to the relative exposure to leeward and western winds and the effect of convective heat loss at the aerodynamic boundary layer resulting from the interaction of wind with relief (Körner, 2003). Slope gradient further modulates incoming solar radiation, precipitation, soil moisture, soil temperature, above ground biomass (Zhu et al, 2018) and the capacity to accumulate or retain snow (Litaor et al, 2005). Slope aspect is an important modifier of climatological conditions (Sharma et al, 2009; Kunkel et al, 2011) and the amount of solar radiation microtopographic features are exposed to (Zhu et al, 2018). Slope aspect can cause angles of solar incidence equivalent to equatorial levels, permanent shade or all possible intermediate sun-surface angles and their seasonal and diurnal variation (Körner, 2003; Scherrer and Körner, 2010a). Microtopographic modification of incoming incident solar radiation determines the delivery of energy into the ecosystem (Ernakovich et al, 2014), and more or less insulation or insolation controls pedogenic processes linked with below ground C and N content (Tsui et al, 2013; Yimer et al, 2006a/b; Lozano-García et al, 2016). Solar radiation influences soil biogeochemical processes, snow accumulation and persistence, freeze-thaw cycles, soil temperature and soil moisture regimes, microbial activity and vegetation structure (Lozano-García et al, 2016; Löffler and Finch, 2005; Garcia-Pausas et al, 2007).

To make inferences on the fluxes and feedbacks of mountain soils to the climate, the spatial distribution of belowground C and N must be understood (Khan et al, 2016; Joergensen and Wichern, 2018). In this study I aim to demonstrate that heterogeneity in the distribution of total soil C and N, and total organic C and N in microbial biomass, with elevation, would be augmented horizontally by the effect of microtopography. My objectives were to explore the relationship between multiple samples from the same site, and between sites at the same altitude across three transects. These elevation gradient transects share the same isothermally driven, bioclimatic life zones their respective ecotones, including the treeline ecotone occurring at approximately 1900-2100m; share overall similar macro scale aspect; start and finish at the same altitudes; share similar bedrock, parent material, vegetation composition and land-use type across the gradient. However, they differ in proxy variables for microtopography. Firstly, I hypothesised that the response of TC, TN, MBC, MBN and their stoichiometric ratios across the elevation gradient, would be non-linear for each transect. Secondly, I hypothesised that variation would occur between sites of the same altitude, on different transects covering the same elevation gradient, due to the augmenting effect of site-specific microtopography which would become more pronounced at higher altitudes.

2. Materials and Methods

2.1. Study sites and Sampling Locations

Study sites were located in the upper Goms valley in the canton of Valais, Swiss Central Alps (appendix 1a/b). The region experiences a temperate-continental climate, though the mountains have considerable orographic influence (Herwegh et al, 2017). Precipitation in the high mountains exceeds 4,000 mm per year (Keller et al, 2000) and the regional climate at 2,500m is characterised by a growing season mean temperature of 9.0°C (min -8.2°C, max 19.2°C). August is the warmest month and the average growing season is 126 days duration (Körner et al, 2003). In the valley, the mean annual temperature is 3.7°C and annual precipitation is 1212 mm, distributed regularly throughout the year (Strebel et al, 2015). The underlying geology of the study sites is comprised of gneiss, amphibolite and metagranite in the lower-middle reaches, and granite, granodionite and quartz-diorite in the upper (Federal Office of Topography, 2020). Forest stands in the high-montane and sub-alpine are largely composed of *Larix decidua* (Mill.) and *Picea abies* (L.). Vegetation above the treeline is dominated by *Ericaceae* (Juss.), *Asteraceae* (L.), grasslands of *Nardus stricta* (L.) and *Carex curvula* (L.), as well as low stature, prostrate woody shrubs. Graminoids, herbaceous perennials, rosettes, cushion plants cryptograms and lichens are present in the upper realms of the sub-nival zone (Stöcklin and Hefel, 2010; Körner, 2003).

2.2. Sampling Protocol

Three transects were established from Selkingen to Stockflesch (Fig. 1a/1b); Biine (Münster) to Chly Chastelhorn (Fig. 2a/b); and Geschinen to Unnere Stock (Fig. 3a/b). These transects began in the montane forest, extending into the sub-alpine forest and the treeline ecotone (1900-2100 m asl), the alpine zone and terminated in the sub-nival. Transects consisted of 10 sampling points, reproduced every 100m, within each altitudinal zone and ecotone and represented an adiabatic lapse rate change of approximately -5.4°K from the lowest to highest sampling point. I used a sampling design based on the Fibonacci sequence of numbers to avoid problems and bias associated with trend and directionality (Fortin and Dale, 2005; Chagnan et al, 2017) (appendix 2). Six, 10 x 5cm soil cores were extracted at each altitude following this method. Site coordinates were recorded using a Garmin GPSMAP 64S (Garmin, 2019). Measurements were recorded for slope gradient and slope aspect using a field compass, steel angle protractor rule and magnetic spirit level. Soils were stored in an air-tight cooler in shaded, ambient temperatures and transferred to a fridge (4°C) in Lausanne within a week. Upon completion, soils were transported to the UK in an air-tight cooler and placed immediately into cold storage (4°C) at the Lancaster Environment Centre (LEC).

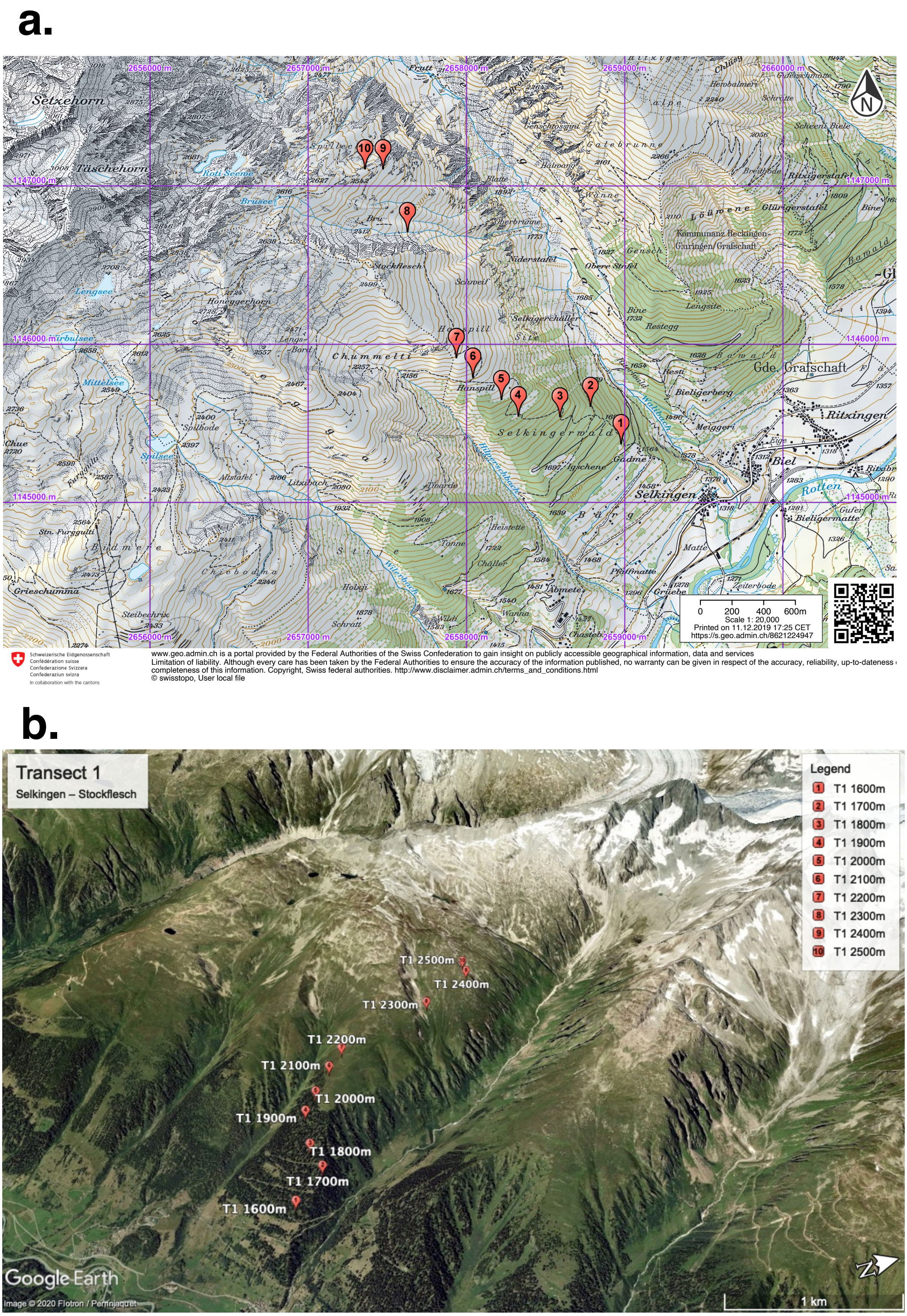
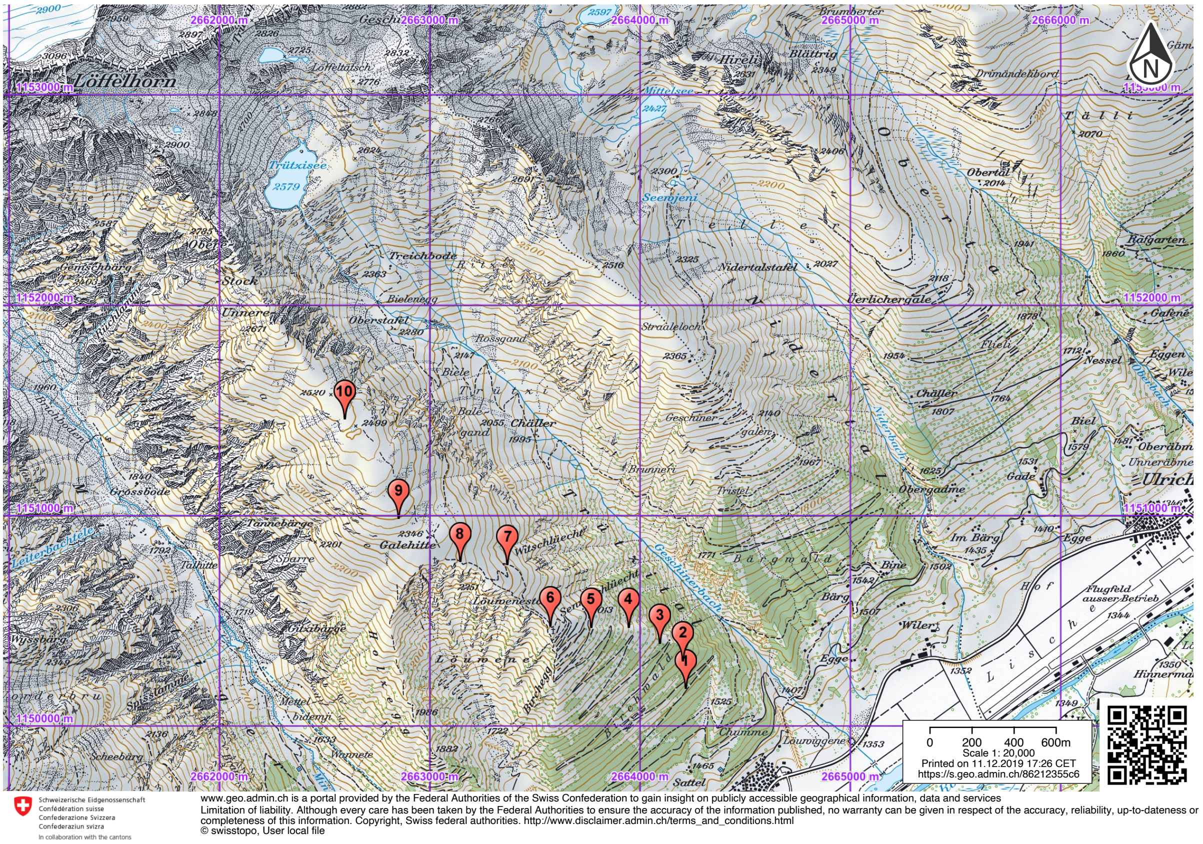


Figure 4a. Transect 1 (Selkingen – Stockflesch), Southern Bernese Alps, Switzerland from the Swiss Federal Geoportal (SFG, 2020). **Figure 1b.** 3D illustration of Transect 1 in Google Earth Pro (2019).

a.



b.

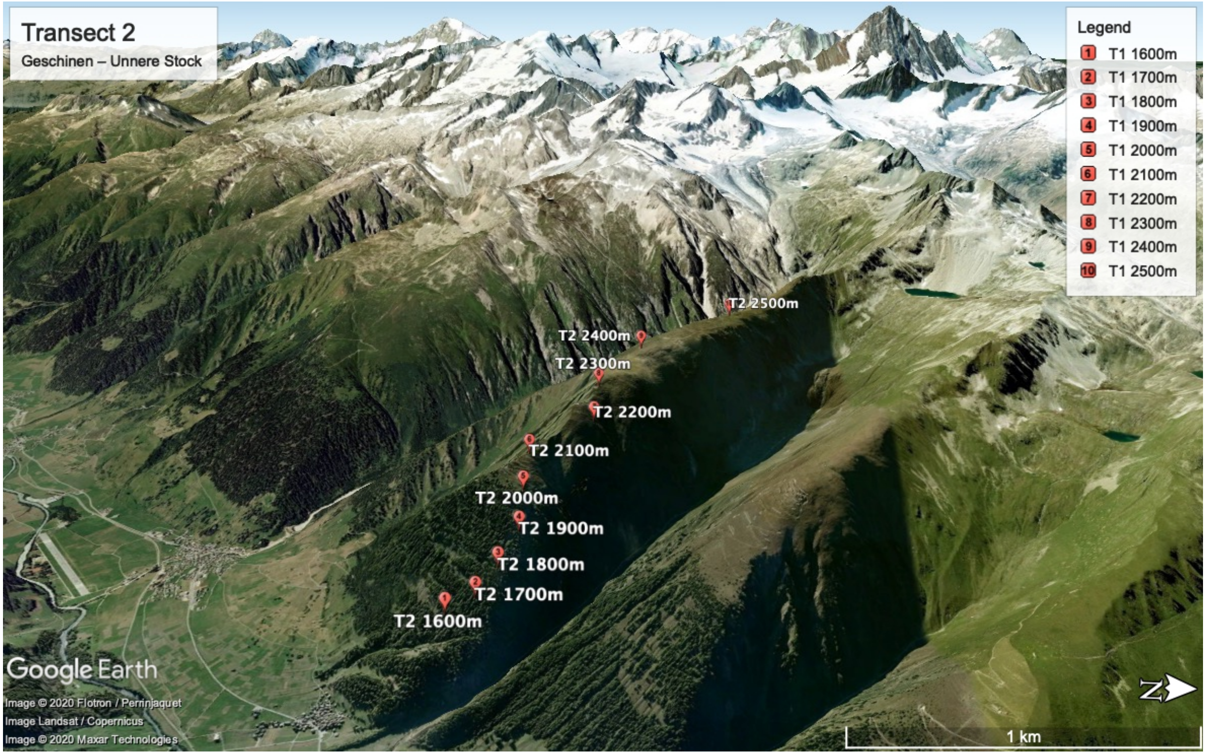
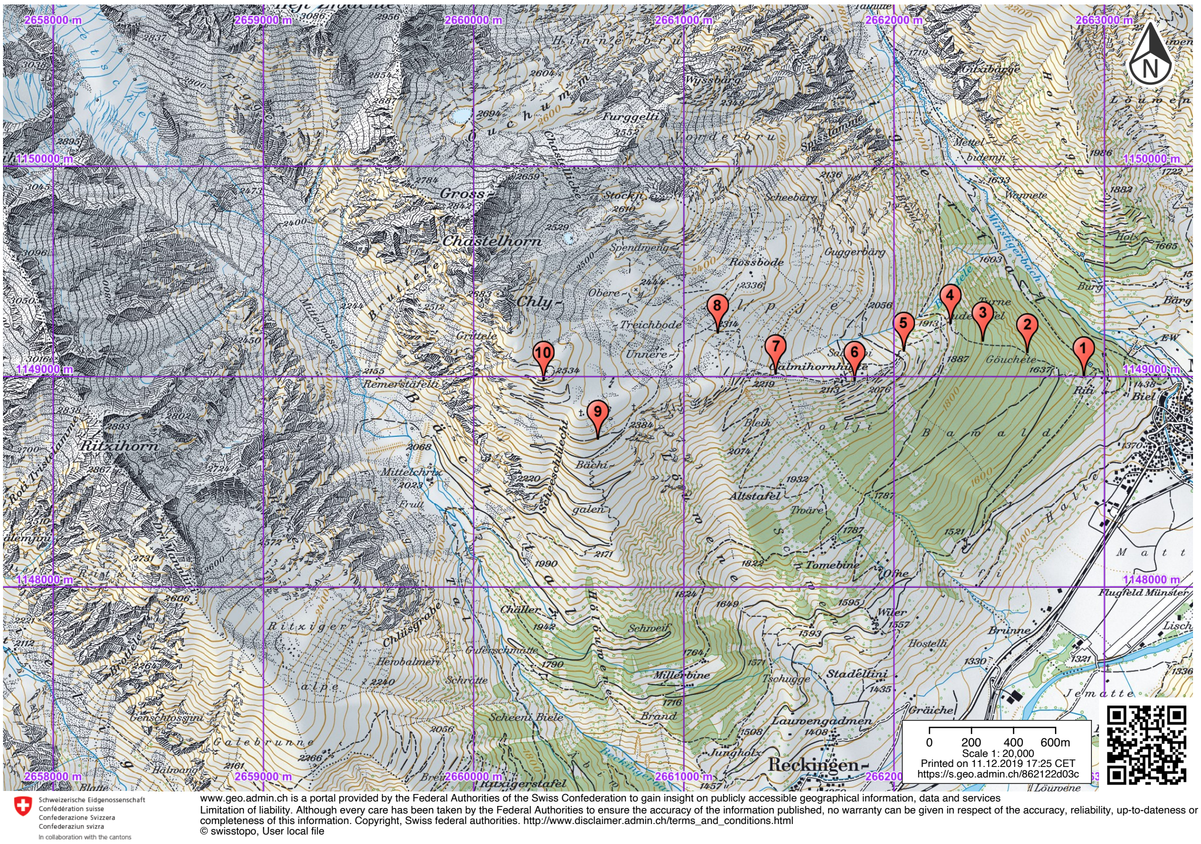


Figure 2a. Transect 2 (Geschinen – Unnere Stock), Southern Bernese Alps, Switzerland in SFG (2020).
Figure 5b. 3D illustration of Transect 2 in Google Earth Pro (2019).

a.



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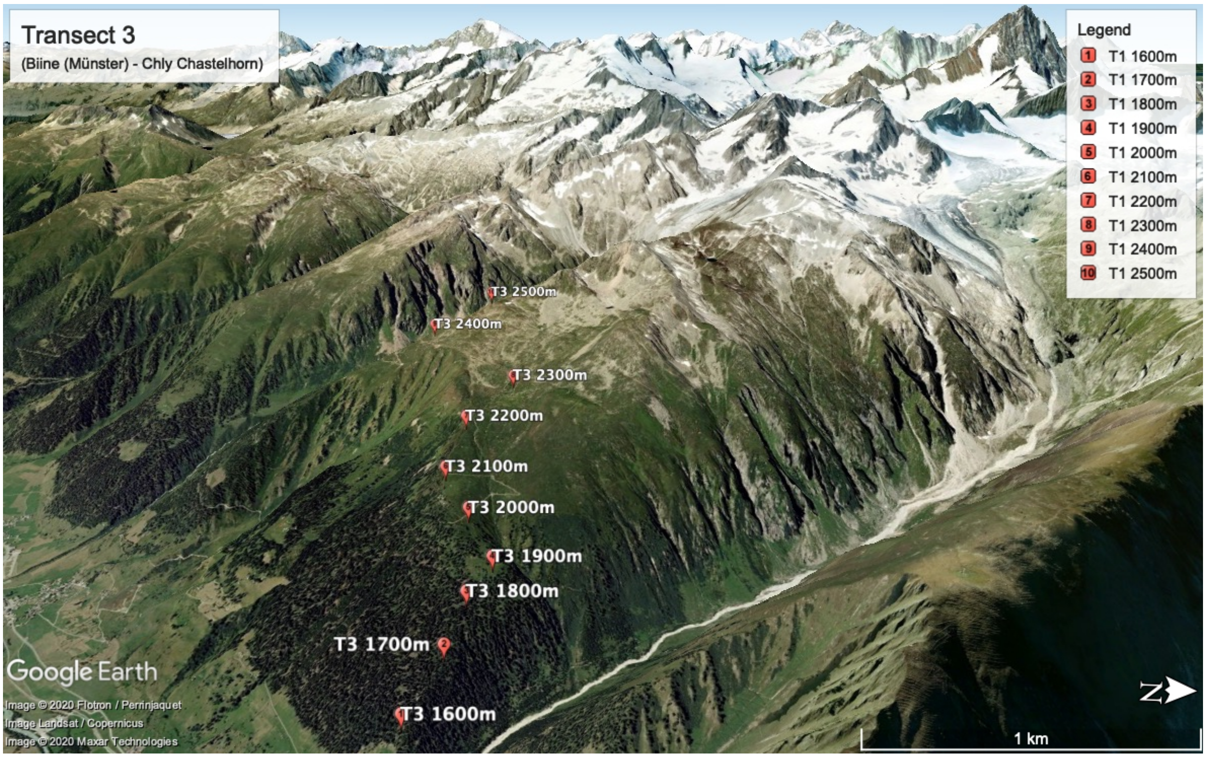


Figure 6a. Transect 3 (Biine (Münster) - Chly Chastelhorn), Southern Bernese Alps, Switzerland in SFG (2020). **Figure 3b.** 3D illustration of Transect 3 in Google Earth Pro (2019).

2.3. Laboratory Analysis

2.3.1. Total Carbon and Total Nitrogen

Sub-samples (5.0g (± 0.5g)) frozen at -80°C were freeze-dried, milled and further sub-samples of 0.1000g (± 0.0010g) prepared. Total carbon (TC) and total nitrogen (TN) content was measured using a Truspec C:N Analyser (LECO, 2019). Three standards were used for calibration and drift correction: Soil Lot 1000 (C – 3.82%, N – 0.323%), Soil Lot 1011 (C – 12.25%, N – 1.03%), and ethylenediaminetetraacetate (EDTA) Lot 1056 (C – 41.08%, N – 9.56%). TC and TN values were calculated and provided for through the Truspec software. The ratio of TC to TN was calculated as $TC(mg) \div TN(mg)$.

2.3.2. Total Organic Carbon and Total Nitrogen in Microbial Biomass

Total organic carbon (TOC) and total nitrogen (TN) in microbial biomass was determined using the chloroform fumigation-extraction method (Woloszczyk et al, 2020; Brookes et al, 1985; Vance et al, 1987) and analysed on a Shimadzu TOC-L Analyser (Shimadzu Global and Analytical Measuring Instruments, 2019). TOC and TN in microbial biomass (µg C or N per gram DW soil) was calculated as:

$$cTOC - \bar{x}\,(cb + fb)\;x\;(mv + vm)\;x\;(1\;\div cdsm)$$

$$cTN - \bar{x}\,(cb + fb)\;x\;(mv + vm)\;x\;(1\;\div cdsm)$$

cTOC and c*TN* = control TOC and TN; $\bar{x}$ = mean of control blanks (*cb*) and fumigated blanks (*fb*); *mv* = matrix (potassium sulphate (K_2SO_4)) volume (ml); *vm* = volume of MilliQ added (ml) and *cdsm* = control sample dry soil mass.

Fumigated TOC and TN (µg C or N per gram dry weight (DW) soil) was calculated as:

$$fTOC - \bar{x}\,(cb + fb)\;x\;(mv + vc)\;x\;(1\;\div cdsm)$$

$$fTN - \bar{x}\,(cb + fb)\;x\;(mv + vc)\;x\;(1\;\div cdsm)$$

fTC and *fTN* = fumigated TC and TN, and *vc* = volume of chloroform ($CHCl_3$) added (ml).

MBC or MBN (µg C or N per gram DW soil) was calculated as:

$$fTOC\ (\mathrm{\mu g\ C/g\ DW\ soil}) - \ cTOC\ (\mathrm{\mu g\ C/g\ DW\ soil})$$

$$fTN\ (\mathrm{\mu g\ N/g\ DW\ soil}) - \ cTN\ (\mathrm{\mu g\ N/g\ DW\ soil})$$

MBC:MBN was calculated as $MBC \div MBN$. Soil moisture content as a percentage of dry weight (SMC (% DW)) was calculated to express the values of total organic carbon and nitrogen in microbial biomass:

$$SMC\ (\%\,DW) = \left(\frac{(wet\ soil\ mass - dry\ soil\ mass)}{dry\ soil\ mass}\right) x\ 100$$

2.4. Data Analysis

Data were transformed prior to analysis using package *rcompanion* (Mangiafico, 2020) following Tukey's Ladder of Powers. Tukey's transformation performs iterative Shapiro–Wilk tests, finds the lambda value that maximises the W statistic and identifies the power transformation which brings the data closest to normal distribution.

2.4.1. Unconstrained Ordination with Principal Component Analysis (PCA)

PCA explored relationships between sites, samples and topography. PCA was carried out in RStudio (2019) using packages *vegan* (Oksanen et al, 2019) and *MASS* (Ripley et al, 2017) following methods adapted from Oksanen (2013) and Borcard et al (2018). Analysis was performed on transformed data standardised to unit variance using correlation coefficients. Response variables were dimensionless after Tukey's transformation.

2.4.2. Response of Belowground Carbon and Nitrogen with Elevation

TC, TN, MBC, MBN and their stoichiometric ratios were plotted using package *ggplot2* (Wickham et al, 2019) in RStudio (2019) using raw values to illustrate responses with elevation. Smoothed lines were fitted to plots corresponding to local polynomial regression following local estimated scatterplot smoothing (LOESS).

2.4.3. Permutational Multivariate Analysis of Variance (PERMANOVA)

PERMANOVA identified significant singular and interactive effects of microtopographic covariances with response variables. Non-parametric PERMANOVA using distance matrices was carried out using package *vegan* (Oksanen et al, 2019) in RStudio (2019) on transformed data. Matrices were calculated using the Bray-Curtis dissimilarity index for TC, TN, MBC and MBN, and the Gower similarity coefficient for stoichiometric ratios. Models analysed singular and interactive effects between response and microtopographic variables. Terms were added sequentially with unconstrained permutations. Results were considered significant at the 95% confidence interval (CI).

2.4.4. Analysis of Variance (ANOVA) and Post-hoc Tests

ANOVA was carried out on transformed data using package *car* (Fox et al, 2019) in RStudio (2019). Models were analysed using Games-Howell post-hoc tests using package *userfriendlyscience* (Peters et al, 2018) to confirm where differences occurred between the groups in PERMANOVA and ANOVA tests that yielded statistically significant results. Statistical tests were considered significant at the 95% CI.

3. Results

3.1. Heterogeneity in Response Variables with Transect, Elevation and Topography

Transect (*Tr*) ($R^2 = 0.14$), elevation (*E*) ($R^2 = 0.08$) and slope (*S*) ($R^2 = 0.22$) were significant ($p = \leq 0.001$) in principal component analysis (PCA) of all response variables (fig. 4). PCA of TC, TN and TC:TN (appendix 3a/b) explained 99.7% variance. *Tr* ($R^2 = 0.10$) *S* ($R^2 = 0.30$) and *E* ($R^2 = 0.30$) were highly significant ($p = \leq 0.001$). Aspect (*A*) was significant to the 0.05 confidence interval (CI) ($R^2 = 0.03$, $p = 0.035$). The effect of *S* was strongest between angles of 10-25° and high values of TC and TN, and weakest with steep slopes $\geq$ 25° and low values. The effect of *E* was strongest at 2300 – 2500m and lowest TC and TN values. The effect of *A* was strongest at higher elevations. PCA of MBC, MBN and MBC:MBN (appendix 4) explained 99.7% variance. Highly significant ($p = \leq 0.001$) variables were *Tr* ($R^2 = 0.16$) and *S* ($R^2 = 0.14$). Response values decreased with increasing elevation and correlated with increasing slope steepness. The effect of *A* increased with elevation and correlated with decreasing responses at elevations $\geq$2300m.

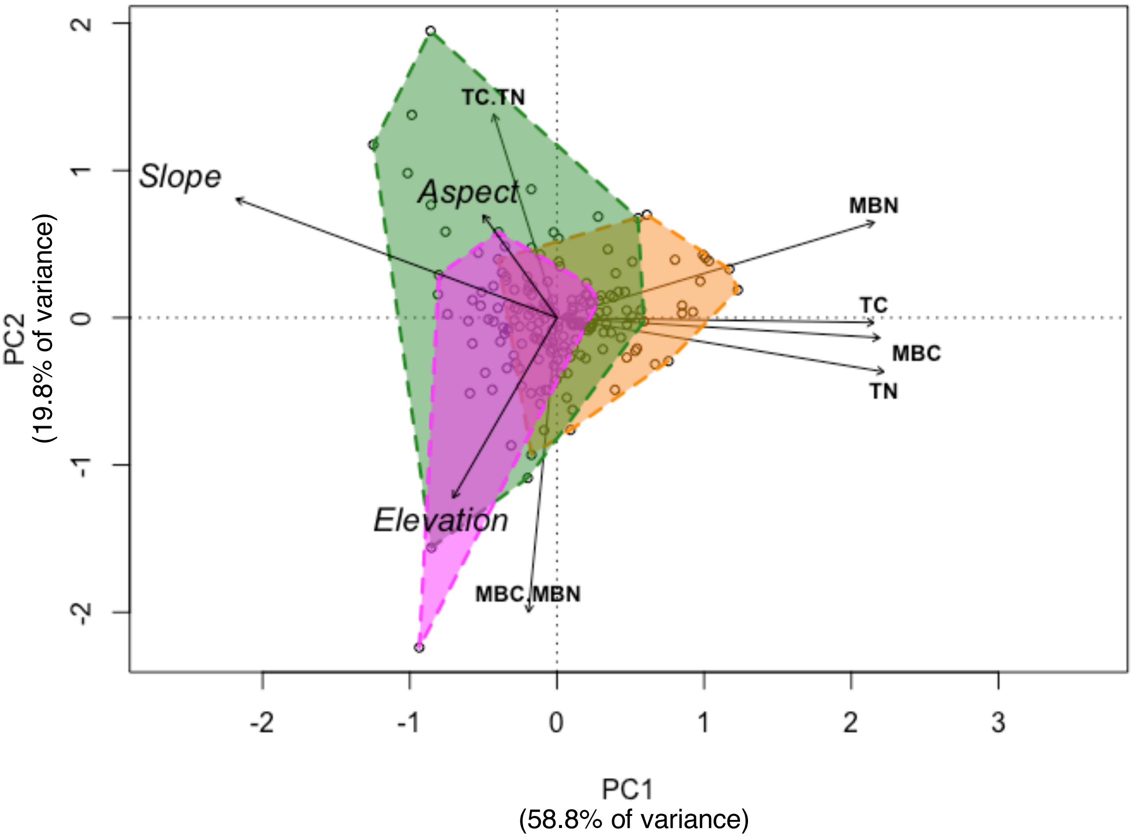


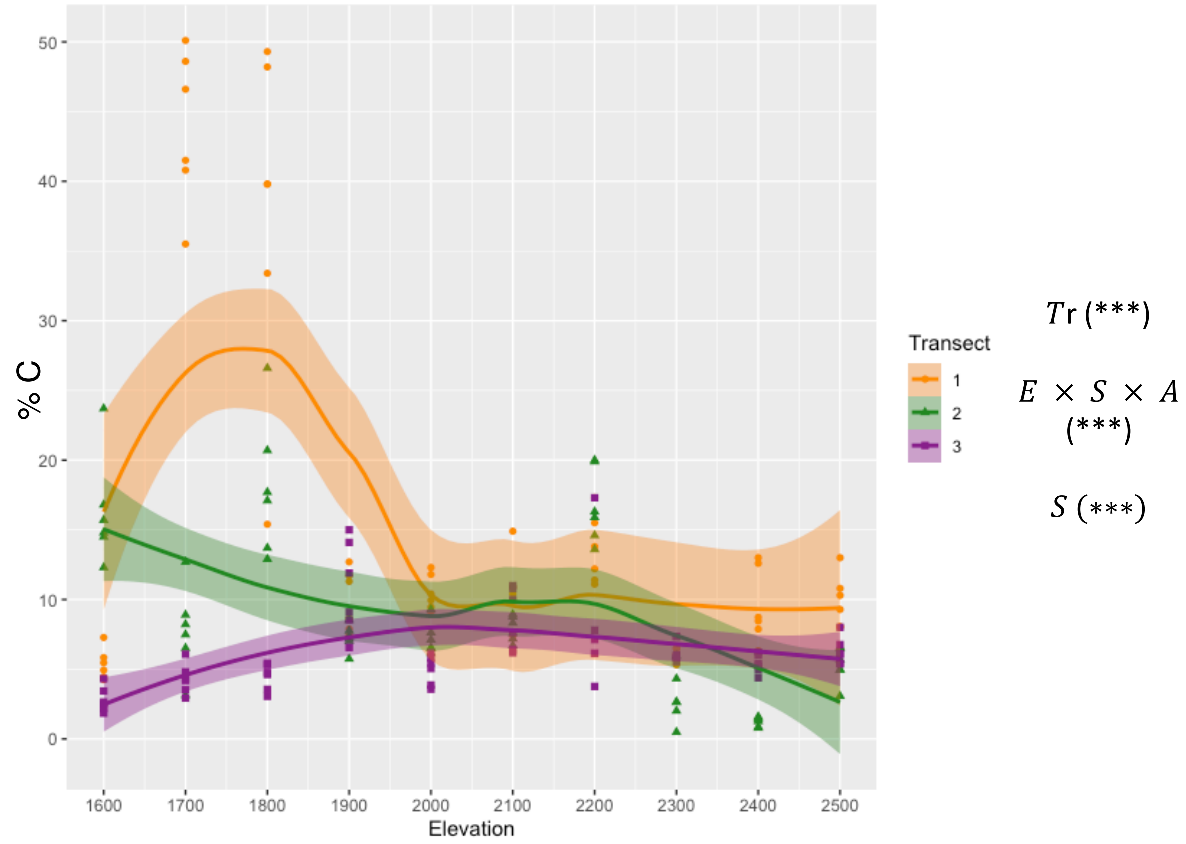
Figure 4. PCA biplot of TC, TN, MBC, MBN and their stoichiometric ratios. Black circles are samples and black arrows point to samples with the highest response value, the most rapid change in that variable and is proportional to the correlation between sample and variable. Topographic variables (elevation, slope and aspect) are vectors. Convex hulls enclose the samples from transect 1 (orange), transect 2 (green) and transect 3 (magenta).

3.2. Inter-Transect Variability and Microtopographic Heterogeneity

In PERMANOVA, significant variables in the response of TC were *Tr* (F = 102.5, R^2 = 0.16), the interactive effect of $E \times S \times A$ (F = 99.3, R^2 = 0.15) and *S* (F = 90.2, R^2 = 0.14) (fig. 5). *Tr* was the most significant variable for TC in ANOVA and post-hoc tests (F = 18.2, *p* = <0.001) and the greatest variation occurred between Tr1 and Tr3 (*t* = 5.26, *p* = <0.001). Elevation (*E*) was significant (*p* = <0.001) and important groups were 2300 × 2200m (*t* = 6.12, *p* = <0.001), 2300 × 2100m (*t* = 5.66, *p* = <0.001) and 2300 × 1900m (*t* = 5.36, *p* = <0.001). Slope (*S*) was significant (F = 11.1, *p* = <0.001) and significant group combinations were 10-19° × 0-9° (*t* = 5.16, *p* = <0.001) and 40-49° × 10-19° (*t* = 5.61, *p* = <0.001). Aspect (*A*) was not significant in PERMANOVA, but group combinations SSE × E in post-hoc tests were (*t* = 2.63, *p* = 0.049).

The highest explanatory variables in PERMANOVA of TN were *S* (F = 103.5, R^2 = 0.19), *Tr* (F = 86.9, R^2 = 0.16) and the interactive effect of $E \times S \times A$ (F = 63.6, R^2 = 0.11) (fig. 6). *Tr* was significant in ANOVA and post-hoc tests (F = 25.8, *p* = <0.001) and greatest variance was exhibited between *Tr1* and *Tr3* (*t* = 6.46, *p* = <0.001). *E* was significant (F = 4.9, *p* = <0.001) and group-combinations 2300 × 1900m (*t* = 5.76, *p* = <0.001) and 2300 × 2100m (*t* = 5.23, *p* = <0.001) were the most variable. *S* was second only to the effect of *Tr* in magnitude (F = 18.1, *p* = <0.001). Group combinations of 40-49° × 30-39° (*t* = 9.02, *p* = <0.001) and 40-49° × 10-19° (*t* = 8.59, *p* = <0.001) were significant.

The highest explanatory variables in PERMANOVA of MBC were *Tr* (F = 85.083, R^2 = 0.20), *S* (F = 43.7, R^2 = 0.10), and the interactive effect of $E \times S \times A$ (F = 38.2, R^2 = 0.09) (fig. 7). *Tr* had the greatest influence on MBC in the ANOVA model (F = 31, *p* = <0.001) and variance was greatest between *Tr1* and *Tr3* (*t* = 6.72, *p* = <0.001). *E* was significant (F = 4.4, *p* = <0.001) and the most significant group-combinations were 2400 × 2200 (*t* = 5.46, *p* = 0.001) and 2300 × 2200 (*t* = 5.08, *p* = 0.001). *S* was significant (F = 14.5, *p* = <0.001) and group-combinations 10-19° × 0-9° (*t* = 6.15, *p* = <0.001); 40-49° × 10-19° (*t* = 6.01, *p* = <0.001) and 30-39° × 10-19° (*t* = 4.97, *p* = <0.001) were significant.



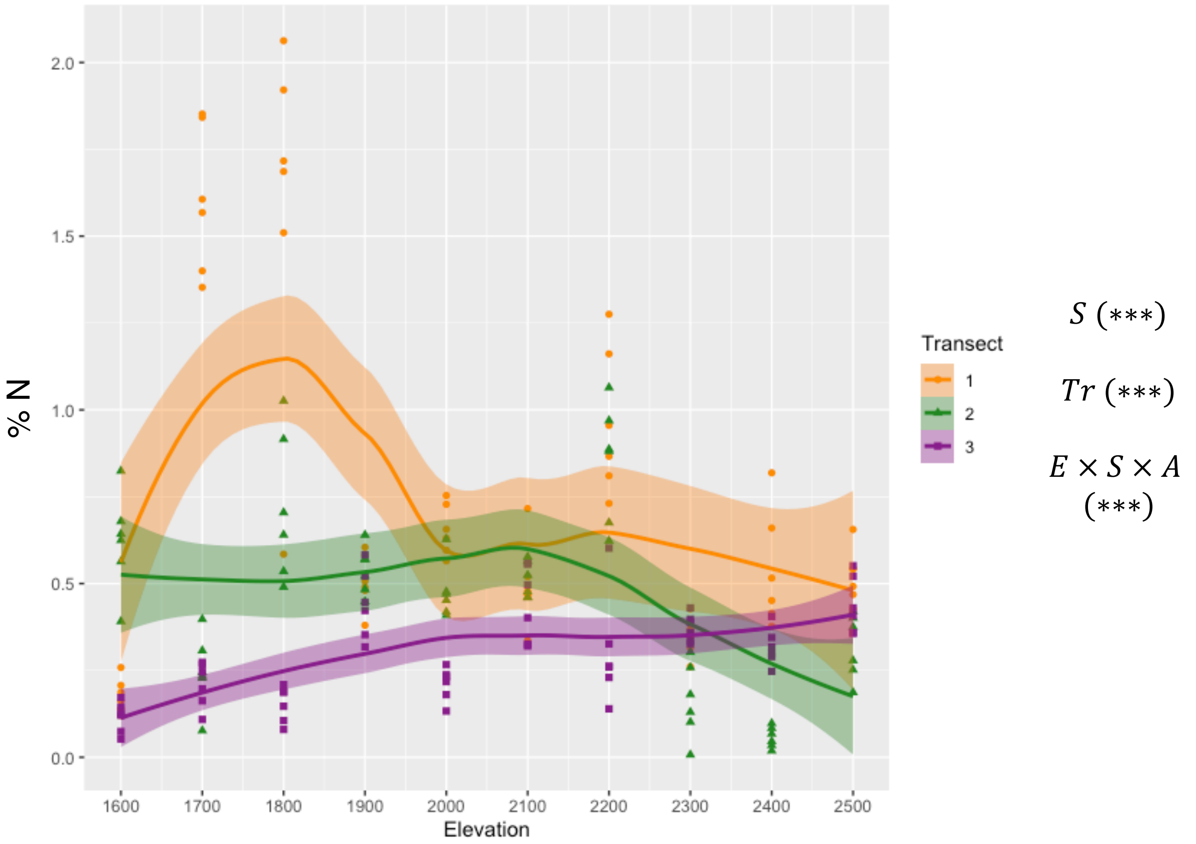
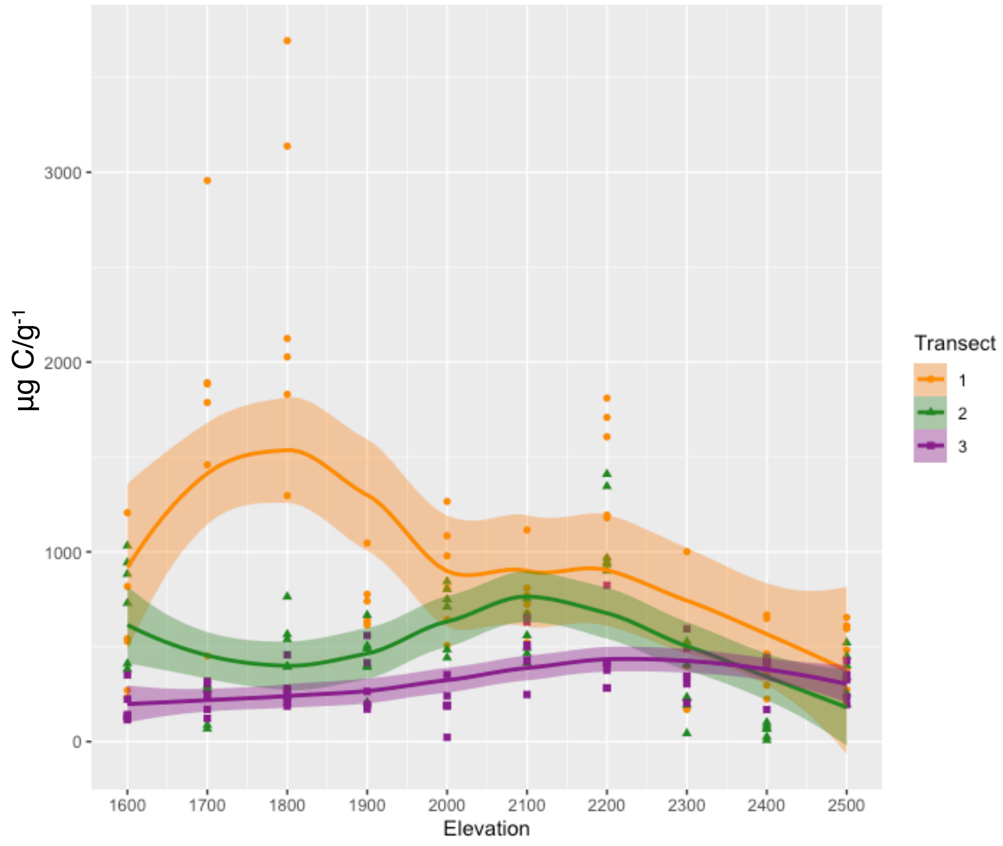


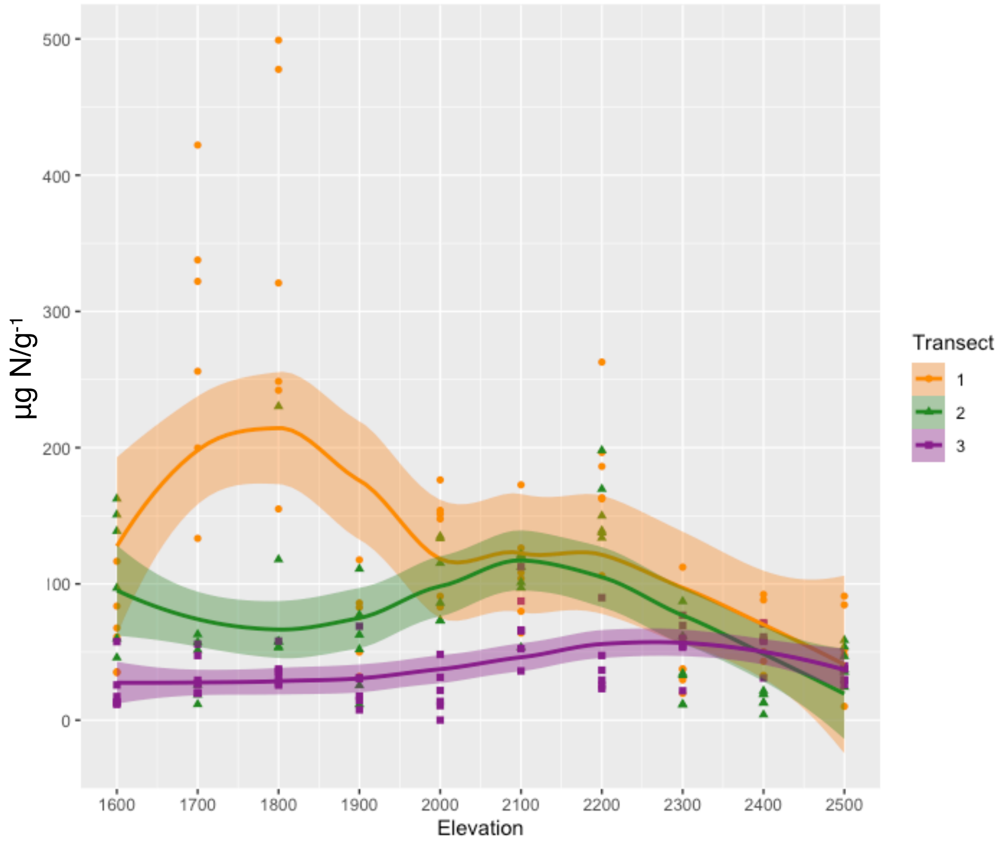
Figure 5 (above). Response of total carbon (TC) with elevation. **Figure 6 (below).** Response of total nitrogen (TN) with elevation. Smoothed lines correspond to LOESS regression and illustrate responses across the elevation gradient. Confidence bands around regression lines represent the 95% CI. Topographic variables significant to ≤0.001 (***) in PERMANOVA are listed to the right of their figure.



$Tr\ (***)$

$S\ (***)$

$E \times S \times A$
$(***)$

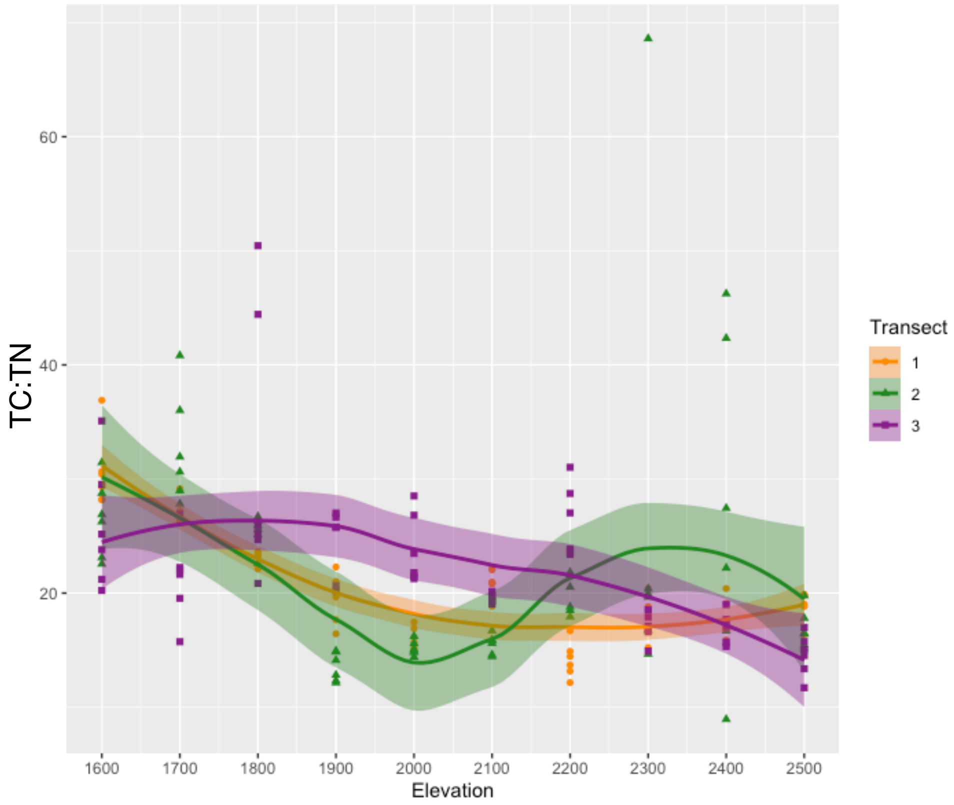


$Tr\ (***)$

S
$(***)$

$E \times S \times A$
$(***)$

Figure 7 (above). Response of total organic carbon in microbial biomass (MBC) with elevation. **Figure 8 (below).** Response of total nitrogen in microbial biomass (MBN) with elevation. Smoothed lines correspond to LOESS regression and illustrate responses across the elevation gradient. Confidence bands around regression lines represent the 95% CI. Topographic variables significant to ≤0.001 (***) in PERMANOVA are listed to the right of their figure.

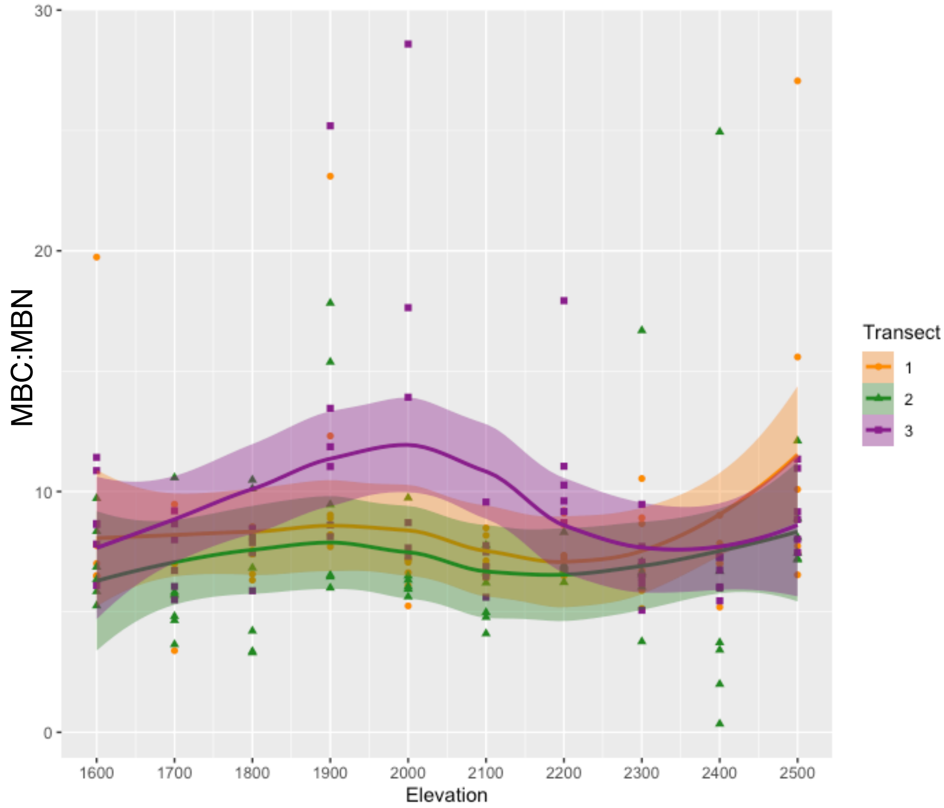


$E\ (***)$

$S\ (***)$

$S \times A$
$(***)$

$Tr \times S \times A$
$(***)$



$E \times Tr \times S \times A$
$(*)$

$E \times Tr \times A$
$(*)$

$E \times Tr \times A$
$(*)$

$Tr \times A\ (*)$

Figure 9 (above). Response in the ratio of total carbon to total nitrogen (TC:TN) with elevation. **Figure 10 (below).** Response in the ratio of total organic carbon to total nitrogen in microbial biomass (MBC:MBN) with elevation. Smoothed lines correspond to LOESS regression and illustrate responses across the elevation gradient. Confidence bands around regression lines represent the 95% CI. Topographic variables significant to ≤0.001 (***) or ≤0.05 (*) in PERMANOVA are listed to the right of their figure.

IN PERMANOVA for MBN, the highest explanatory variables were *Tr* (F = 68.4, R^2 = 0.20), *S* (F = 28.9, R^2 = 0.08) and the interactive effect of $E \times S \times A$ (F = 23.2, R^2 = 0.06) (fig. 8). *Tr* (F = 25.1, *p* = <0.001) was the most significant in the ANOVA model. Group-combinations *Tr1* × *Tr3* (*t* = 6.32) and *Tr3* × *Tr2* (*t* = 4.76) were significant (*p* = <0.001). *E* was significant (F = 4.8, *p* = <0.001), as were group-combination 2500 × 2100m (*t* = 5.43, *p* = <0.001) and 2400 × 2100m (*t* = 4.79, *p* = <0.001), 2300 × 2100m (*t* = 4.55, *p* = 0.002) and 2500 × 2200m (*t* = 4.77, *p* = 0.004). *S* was significant (F = 14.1, *p* = <0.001) as were group combinations 10-19° × 0-9° (*t* = 6.77, *p* = <0.001), 40-49° × 10-19° (*t* = 6.29, *p* = <0.001), 30-39° × 0-9° (*t* = 6.17, *p* = <0.001) and 30-39° × 10-19° (*t* = 5.01, *p* = <0.001).

The TC:TN PERMANOVA identified *E* (F = 71.9, R^2 = 0.24), *S* (F = 21.3, R^2 = 0.07), the interactive effect of $Tr \times S \times A$ (F = 17.3, R^2 = 0.05) and of $S \times A$ (F = 14.9, R^2 = 0.05) as significant variables (fig. 9). *Tr* was not significant in ANOVA for TC:TN, however *E* (F = 6.9, *p* = <0.001) had more significant group-combinations in the TC:TN model than any other. *S* was significant (F = 11.1, *p* = <0.001), and group-combinations 40-49° × 0-9° (*t* = 10.22, *p* = <0.001), 40-49 × 10-19 (*t* = 6.61, *p* = <0.001) and 40-49 × 30-19 were significant (*t* = 6.34, *p* = <0.001). Aspect was significant (F = 5.3, *p* = 0.002) and group-combinations SSE × SE (*t* = 4.71, *p* = <0.001), SSE-ESE (*t* = 4.17, *p* = <0.001) and SE × E were significant (*t* = 2.74, *p* = 0.002).

Significant variables in the MBC:MBN PERMANOVA model were the interactive effects of $Tr \times A$ (F = 6.3, R^2 = 0.03), $E \times Tr \times S \times A$ (F = 6.1, R^2 = 0.03), $E \times Tr \times A$ (F = 6.1, R^2 = 0.03) and, $E \times A$ (F = 4.1, R^2 = 0.02) (fig. 10). ANOVA and post-hoc tests indicated that *Tr* was the most significant factor in the response ratios of MBC:MBN (F = 3.69, *p* = 0.027). *Tr2* and *Tr3* were significant at the 0.05 CI (*t* = 2.69, *p* = 0.022). *E* was significant (F = 3.3, *p* = 0.001), as were group-combinations 1900 × 1700 (*t* = 3.72, *p* = 0.033) and 2100 × 1900 (*t* = 3.60, *p* = 0.046), though fewer relative to all other models. Aspect was not identified as a significant overall, although the group-combination SSE × E was (*t* = 2.76, *p* = 0.038).

4. Discussion and Conclusions

The response of TC, TN, MBC, MBN and their stoichiometry was non-linear with elevation, agreeing with my first hypothesis. The effect of site-specificity was a significant factor in the response of TC, TN, MBC, MBN, and in the interactive models for the stoichiometric ratios. The greatest variance was exhibited between sites on Tr1 and Tr3, and occurred at 1700, 1800 and 2200m (figures 5-8). Tr1 and Tr3 differed in underlying geology only (Swiss Federal Geoportal, 2020), however, granite (Tr1) and gneiss (Tr2) share the same chemistry, mineralogy and did not account for differences in soil properties in Liptzin and Seastedt (2010). Alternatively, slope angles for Tr1 were 23° at 1700m and 18° at 1800m, but 36° at 1700m and 38° at 1800m for Tr3. Responses at slope angles <24° and >30° were significantly different, and the effect of slope was significant for TC, TN, MBC and MBN; overall, angles ≤24° correlated with high response values and angles ≥30° correlated with low values. Therefore, variability between the two transects may be explained by significant differences in slope steepness at sites of the same altitude. The interactive effect of $E \times S \times A$ was significant for TC, TN, MBC and MBN. Elevation was, singularly, the most significant variable in the response of TC:TN. The interaction of $Tr \times E \times S \times A$ was significant in the stoichiometry of MBC:MBN. Significant differences for all response variables occurred above (2500-2100m), at (2100-1900m) and below (1900-1600m) below the treeline. Elevation correlated positively with slope steepness, and with decreasing response values. The effect of elevation and of aspect was strongest at altitudes ≥2300m. Significant differences occurred between aspects of SSE – SE and ESE – E. Overall, variation occurred between response variables at sites of the same altitude, and were augmented by the effect of site-specific microtopography which appeared to become more pronounced at higher altitudes, consistent with my second hypothesis.

The greatest heterogeneity in the response of TC, TN, MBC and MBN at sites of the same altitude, between transects, occurred below the treeline. TC was constrained at the treeline (fig. 5), though values on Tr1 and Tr2 rose at 2200m where slope angles were <24°, and the response between transects followed a relatively similar trend through the alpine into the sub-nival. TN was more variable at the treeline, through the alpine into the sub-nival, with greater intra-site variability than for TC, though the response between transects was more closely linked above the treeline than below (fig. 6). MBC and MBN did not always follow TC and TN, were generally constrained at and above the treeline (fig. 7/8) and converged at 2500m. The TC:TN ratio was variable across the elevation gradient and did not describe a clear trend due to variability in TC and TN. The MBC and MBN responses were relatively similar with elevation and the MBC:MBN ratio was closely linked across the elevation gradient. The relationship between response variables and slope was significant and linear across the gradient; shallow slopes correlated with high values, and steep slopes corresponded with low values. Slope angle was the most important topographic variable at lower elevations and appeared to be an accurate general predictor of response values. For all response variables below the treeline, where slope angles were ≥30°, responses values were low, and where slopes were ≤24°, values were high. At higher elevations, the effect of slope was closely linked to response values but was augmented by the effects of elevation and aspect which were strongest ≥2300. The effects of microtopography appeared to become more important and pronounced at higher altitudes.

Topographic features were poor predictors of belowground C and N compared to climate in Li et al (2010) and Dieleman et al (2013), though the opposite has been shown (Prichard et al, 2000; Thompson and Kolka, 2005; Yimer et al, 2006a/b; Zhu et al, 2017; Hu et al, 2019). A possible resolution to these contradictions is the synergistic controls of elevation, climate and topography on vegetation assemblages across elevation gradients (Körner et al, 2011; Nagy and Grabherr, 2009). Below the treeline in temperate forests, greater soil and microbial biomass C and N occurs on gentle to moderate slopes and is linked to aboveground vegetation (Martin et al, 2010; Nahidan et al, 2014). Landforms with lesser slope angles are associated with greater aboveground biomass, as less-steep slopes enable more intensive vegetation cover, which leads to greater inputs of C and N into the soil (Bastida et al, 2006; Bhople et al, 2019; Djukic et al, 2010; Li et al, 2010; Tashi et al, 2016). Well-established vegetation also prevents slope failure (Segadelli et al, 2020) and enables more stable edaphic conditions. Stable soil properties, including available C and N content, pH and soil temperature and moisture (Zhang et al, 2013) facilitate greater microbial decomposition of SOM into MBC and MBN (Siles et al, 2016; Zhou et al, 2015; Knoepp et al, 2018). In mountain ecosystems characterised by high microtopographic heterogeneity, soil temperature and moisture regimes play a major role in microbial activity, and microtopography-affected microbial taxa under stable edaphic conditions are more resilient (Frindte et al, 2019).

The response of TC was constrained across the treeline ecotone. Current understanding posits that the formation of treelines on mountainsides represents an overarching effect of declining temperature with increasing elevation on aboveground vegetation due to the direct effect of low temperatures on metabolic processes and declining carbon sink strength, rather than declining photosynthetic capacity (Mayor et al, 2017). There is no evidence that trees are carbon limited at high elevation (Körner, 2007). Due to their upright architecture, trees are exposed to free atmospheric convection and air temperatures, whereas smaller plants profit more from aerodynamic decoupling and periodic canopy warming (Körner, 2007; Hoch and Körner, 2011). Extensive areas of krummholz (stunted, deformed) vegetation occur in the upper reaches of the treeline ecotone (Wielgolaski et al, 2017; Körner, 2003) and the effects of temperature on the quality and quantity of C and N in SOM are mediated by the cascading influence of tree cover on soil and microbial properties (Mayor et al, 2017). The gradual decline in tree size corresponds to a gradual decline in aboveground biomass, correlating with declining TC and TN, which are significantly positively correlated with MBC and MBN, respectively (Ravindran and Yang, 2015). The ratio of MBC:MBN (fig. 10) was tightly linked between transects, increasing up to the lower-reaches of the treeline ecotone (1900m) and decreasing across the upper-reaches of ecotone into the alpine (2000~2300m). TC:TN for all transects was <30:1 across the treeline ecotone, indicating that soils were C limited from the approximate centre of the treeline into the alpine (Thébault et al, 2014). Plant physiological traits and associated nutrient properties are systematically driven by declining temperature with increasing elevation. Soils at the treeline are predominantly colder than in the high montane forest and exhibit reduced quality and quantity of C and N in SOM (Loomis et al, 2006). Soil nutrients are tightly coupled across the treeline ecotone because cold temperatures reduce microbial mineralisation, and the local effects of soil moisture and soil organic matter quality have stronger effects on variation in nutrient cycling than temperature alone (Loomis et al, 2006). Hence, the decrease in MBC:MBN may reflect second-order soil physicochemical drivers of nutrient stoichiometry at the treeline, after the influence of climate on the physiognomic properties of vegetation is considered (Mayor et al, 2017).

The transition from the treeline ecotone to the low stature vegetation of the treeless alpine zone is one of the most conspicuous climate-driven ecological boundaries (Holtmeier, 2009; Liu et al, 2013; Duan et al, 2010). Here, slope position and angle are important in structuring the physical and chemical environment (Zhang et al, 2013). In the Swiss Central Alps, the mountain slopes became broader and gentler in the lower alpine, similar to that in Han et al (2017). They report that soils in low slope positions with a gradual slope gradient and trees sparsely distributed with krummholz morphology had the highest soil organic carbon (SOC) and soil C:N ratios. Soil C:N ratios typically increase with elevation (Leifeld et al, 2005; Leifield et al, 2009), reaching the highest values at the middle-upper elevations of the alpine, before decreasing at the uppermost reaches (Li et al, 2017). A similar unimodal pattern was observed in this study, and in Ohtsuka et al (2008) and Lit et al (2017). Accordingly, percentage plant cover typically decreases systematically with elevation and is reflected in the quality and quantity of SOM (Kotas et al, 2018). SOM tends to accumulate with elevation up to the high montane forest, gradually decreasing above the tree line, reaching almost zero in un-vegetated substrates of the upper alpine zone (Thébault et al, 2014; Garcia-Pausas et al, 2007). Soil C:N may be lower at the lowest elevations of the alpine zone than in the forest due to the absence of coarse woody debris and a lower input of carbon from litter, and highest at mid-elevations under alpine vegetation where the decomposition of soil C is slowed as a consequence of the colder climate (Yimer et al, 2006a/b; Garcia-Pausas et al, 2007; Thébault et al, 2014). Large amounts of N in its organic and inorganic forms is stored in SOM, therefore TN stocks may also appear to increase correspondingly (Loomis et al, 2006).

A positive relationship between TC and MBC, and between TN and MBN across elevation gradients into the alpine is observed, irrespective of the combination of low temperature and high precipitation on microbial decomposition (Bhople et al, 2019). The relationship between total soil C:N and microbial biomass C:N has been reported as non-significant elsewhere (Chu and Grogan, 2009) because MBC and MBN can be strongly correlated to soil C and N, but not necessarily in their ratios (Thébault et al, 2014). This is consistent with my results here, where the response of MBC:MBN was consistent across transects above the treeline, whereas TC:TN was not; however, TC and MBC, and TN and MBN exhibited similar patterns with elevation above the treeline.

The soil C pool in an ecosystem represents the balance between litter inputs to the soil and carbon loss through microbial activity and decreases with altitude due to the effects of temperature on decomposition (Ohtsuka et al, 2008). The chemical composition of soil C and physical protection from microbes regulates decomposition over short timescales, whereas environmental variables relating to lateral and vertical mobilization of soil C through erosion and leaching (Schaub and Alewell, 2009), such as slope steepness, are more important controls on longer time scales (Doetterl et al, 2016). Soil C pools should be greatest towards higher altitudes under steady-state conditions but can be expected to be lower in the sub-nival than the alpine due to sparser vegetation cover (Ohtsuka et al, 2008). Lower TC:TN ratios generally indicate easily decomposable, high quality SOM, and indicate a direct correlation between SOM and ecosystem productivity (Chu and Grogan, 2009). Above-ground biomass is a major source of soil C in the alpine zone, and a larger input is positively correlated with soil C concentrations (Li et al, 2017). Across alpine meadows or grasslands, litter input to the soil decreases with declining NPP and biomass (Ohtsuka et al, 2008), which is in part also due to shorted growing seasons at higher elevations (Leifield et al, 2009). The shift from shrubs and higher plants to lower plants, mosses, graminoids and lichens at higher elevations indicates a reduction in aboveground biomass and decreased C and N inputs to the soil (Britton et al, 2011; Bolliger et al, 2008; Bühlmann et al, 2015). Indeed, TC, TN, MBC and MBN for all transects was lowest at the sub-nival (2500m), with the one exception of TN on Tr3 which increased slightly. TC:TN for all transects was low at 2500m, whereas MBC:MBN increased. Reduced TC:TN and higher MBC:MBN may occur where ecosystem C is dominated by soil C rather than above ground biomass at higher elevations (Devi and Sherpa, 2019), or due to competition between aboveground vegetation and soil microbiota for limited soil N (Thébault et al, 2014).

Climate, vegetation and topography are important in influencing alpine soil characteristics (Kirkpatrick et al, 2014; Garcia-Pausas et al, 2007), and gradients in soil moisture and nutrient availability associated with microtopography are important for inter- and intra-site variability across elevation gradients (Britton et al, 2011). Slope angle and aspect may vary considerably over distances of a few metres, and the exposure of a slope to solar radiation is the dominant component of the surface energy balance. The positive surface energy balance has been shown to gradually decrease with increasing altitude (Kotas et al, 2018) and decreasing atmospheric temperature which leads to increased SOC in the alpine, reducing thermal conductivity and enhancing soil water holding capacity. These conditions affect the microclimatic components of soil moisture content, near-surface temperatures and the exposure of vegetation to photosynthetically active and ultra-violet wavelengths (Luo et al, 2020; Bennie et al, 2008). In Garcia-Pausas et al (2007), similar values of SOC on southern aspects occurred across the elevation gradient, with the lowest values at the highest elevations alongside a slight increase towards ESE aspects, which is consistent with my findings. Differences in soil nutrients may be further modulated by the effect of eastern and western aspects, relating to increased precipitation on windward slopes relative to leeward (Singh, 2018). Wind and water are major agents of erosion and nutrient redistribution within alpine habitats (Britton et al, 2011). The extreme exposure of windward slopes to erosion is associated with lower rates of accumulated organic matter and the downslope movement of fine material important for soil development and nutrient stabilisation (Kirkpatrick et al, 2014). Soil physico-chemical properties are strongly related to microbial biomass and activity (Bardelli et al, 2017), and the milder edaphic conditions of southern-aspects enables higher microbial diversity, the coexistence of more taxa in competition and greater microbial growth (Carletti et al, 2008). Site-specific effects of nutrient availability exert a greater control on soil microbial activity than the general effect of decreasing soil temperature with altitude (Siles et al, 2016), and local-scale differences in microtopography and microclimate regulate the availability of energy and water essential for soil nutrient cycling (Knoepp et al, 2018). Biasi et al (2005) also report that microtopography was more important than temperature in controlling soil C and N due to the partitioning of soil physicochemical parameters such as soil moisture and temperature. Complex toposequences promote the flow of water away from higher ground to lower situated areas of relief, and the combination of low temperatures and high water-content restricts microbial activity.

There is a clear disparity in the response of belowground C and N between north and south aspects in the literature (Yimer et al, 2006a/b; Bangroo et al, 2017; Måren et al, 2015; Kunkel et al, 2011; Nahidan et al, 2014; Zhao and Li, 2017). Therefore, future studies would benefit from the sampling of a northern facing mountainside. I had originally planned for this on the opposing side of the Valley (Lepotine Alps) but omitted the idea due to time and safety constraints of working on my own. Snow cover is another important factor in belowground C and N dynamics, the distribution and depth of which is modulated by the steepness of the terrain. Accumulations of up to 4m can occur on slopes $\leq 50°$ (Draebing et al, 2016), which includes all the sites in this study. Aspect is another primary driver in snow cover and timing of melt, especially in complex terrain in which slope angle and aspect differences occur on scales <100m (Schirmer and Pomeroy, 2020). Aspect was a significant predictor of snow depth in Maxwell et al (2019). Snow cover directly controls pedospheric temperatures, insulating soil from free atmospheric conditions (Edwards et al, 2007); 30-40cm of snow effectively decouples soil temperatures from free-air temperatures (Cline, 1997). Under moderate snow cover, the combination of moist and insulated conditions drives increased mineralisation, decomposition and subsequently higher TC, TN, MBC and MBN concentrations (Freppaz et al, 2012). At sites with very short durations of snow cover, soils remain frozen for much of the winter, heterotrophic activity is low, leading to low soil C and N (Brooks and Williams, 1999). Factoring in an understanding of snow dynamics at the study sites in analysis would be useful in elucidating the effects of seasonal snow cover on belowground C and N dynamics.

Furthermore, this study relies on the assumptions that the regional climate of the Swiss Central Alps exerts the same climatic influence across the three transects, and that the vegetation assemblages are roughly the same across the bioclimatic zones of each transect. The current literature indicates that the interactive effect of elevation, slope and aspect drive distinct microclimatological conditions and microhabitats for aboveground vegetation. To address these limitation, future studies should include climatological measures at the same fine scales as the microtopographic proxies in this study. During sampling, I instrumented Tr1 with 10 aboveground and 60 belowground microclimate loggers to support the Functional Ecology of Alpine Systems (FEAST) project. One years-worth of data will be available from August 2020 and will contribute site specific microclimate measurements to future studies. Site-specific vegetation surveys for community composition, vegetation height, forest stand basal area and aboveground biomass would also be valuable. I suggest that future work would benefit from a hierarchical approach towards capturing the multifactorial environmental variation driving heterogeneity in belowground C and N. This would begin with capturing the same elevation gradient from the montane to the sub-nival, incorporating macro- and micro-scale climatic data, snow dynamics, vegetation surveys and the microtopographic proxies. This could then be complimented by measurements of soil-physicochemical properties and microbial community composition, then comparing these between systems at different latitudes to elucidate mechanistic determinants for the distribution of response variables.

This work validates the utility of elevation as a general, mechanistic predictor of the distribution of belowground C and N due to the overarching effects of the adiabatic lapse rate change in atmospheric temperature on vegetation assemblages, SOM decomposition and mineralisation. However, non-linearity in response variables occurring with elevation and between sites of the same altitude also demonstrates a significant augmenting effect of fine-scale topographic heterogeneity. Slope angle was the most important topographical variable at lower elevations, likely due to the relationship with aboveground vegetation. Heterogeneity was constrained across the treeline ecotone, which was likely due to the overarching effect of declining temperature with increasing elevation on aboveground vegetation and second-order soil physicochemical drivers. The effect of slope was closely linked to response values at higher altitudes; however, this was augmented by the effects of microtopographic complexity which became more pronounced with elevation. Thus, it appears that macro-scale effects of elevation-dependency may control belowground C and N in a general way, whereas site-specific conditions as a consequence of microtopographic and microclimatic dynamics may augment heterogeneity at smaller scales. These findings will hopefully catalyse novel approaches to capturing spatial heterogeneity in high-altitude mountains, enabling a deeper understanding of how these ecosystems may respond to climate change, and how they may be safeguarded to sustainably provide for biodiversity, ecosystem services, natural resources and livelihoods.

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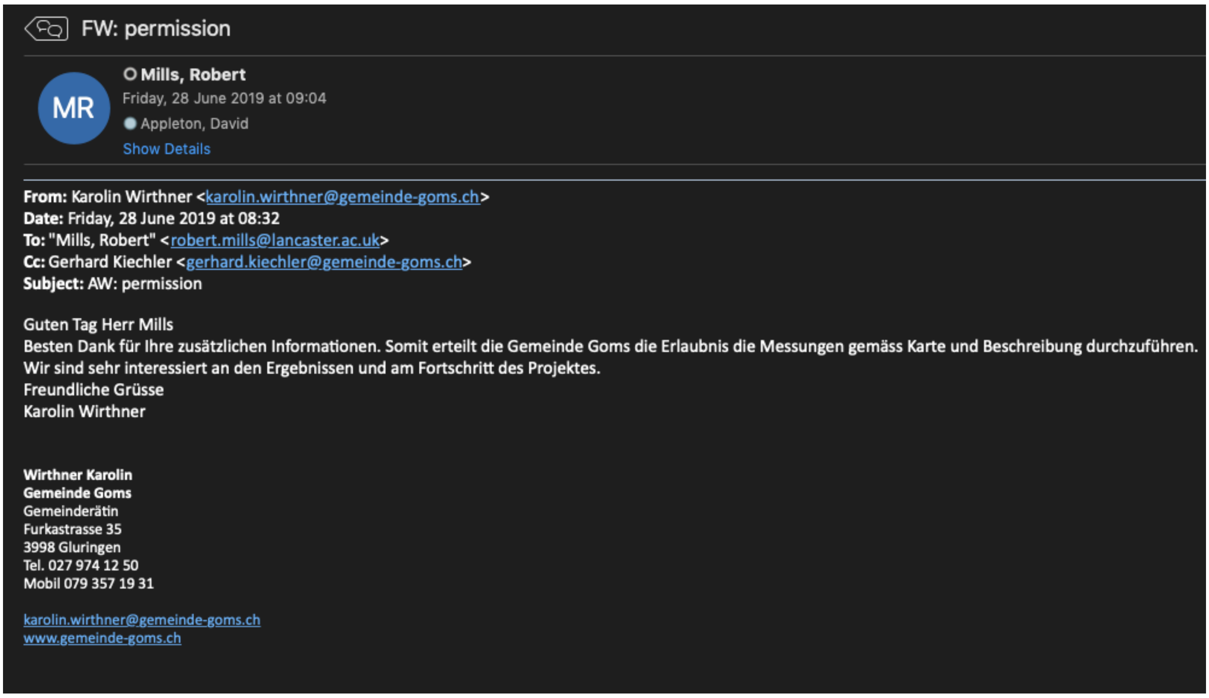
6. Appendices

a.



Mills, Robert
Friday, 28 June 2019 at 09:04
Appleton, David
Show Details

From: Karolin Wirthner <karolin.wirthner@gemeinde-goms.ch>
Date: Friday, 28 June 2019 at 08:32
To: "Mills, Robert" <robert.mills@lancaster.ac.uk>
Cc: Gerhard Kiechler <gerhard.kiechler@gemeinde-goms.ch>
Subject: AW: permission

Guten Tag Herr Mills
Besten Dank für Ihre zusätzlichen Informationen. Somit erteilt die Gemeinde Goms die Erlaubnis die Messungen gemäss Karte und Beschreibung durchzuführen.
Wir sind sehr interessiert an den Ergebnissen und am Fortschritt des Projektes.
Freundliche Grüsse
Karolin Wirthner

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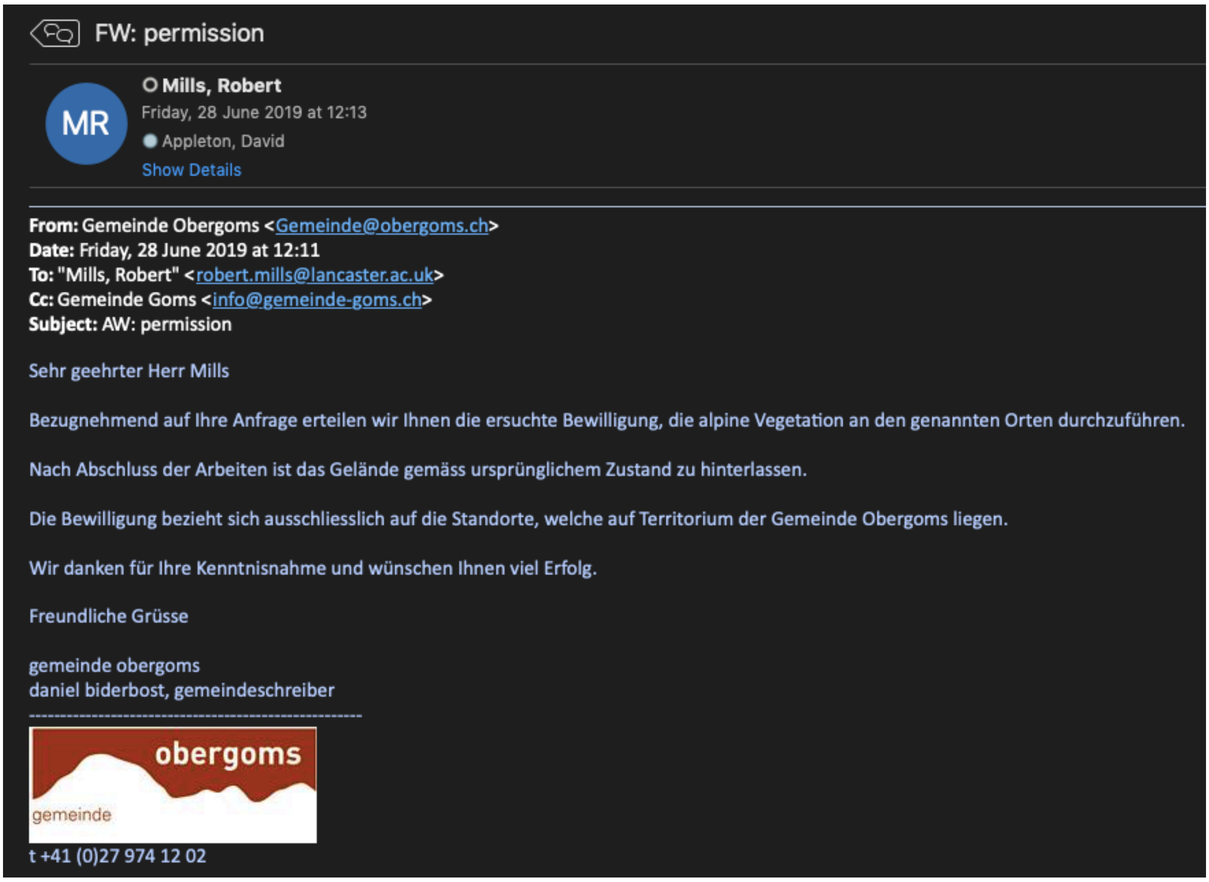
b.



Mills, Robert
Friday, 28 June 2019 at 12:13
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From: Gemeinde Obergoms <Gemeinde@obergoms.ch>
Date: Friday, 28 June 2019 at 12:11
To: "Mills, Robert" <robert.mills@lancaster.ac.uk>
Cc: Gemeinde Goms <info@gemeinde-goms.ch>
Subject: AW: permission

Sehr geehrter Herr Mills

Bezugnehmend auf Ihre Anfrage erteilen wir Ihnen die ersuchte Bewilligung, die alpine Vegetation an den genannten Orten durchzuführen.

Nach Abschluss der Arbeiten ist das Gelände gemäss ursprünglichem Zustand zu hinterlassen.

Die Bewilligung bezieht sich ausschliesslich auf die Standorte, welche auf Territorium der Gemeinde Obergoms liegen.

Wir danken für Ihre Kenntnisnahme und wünschen Ihnen viel Erfolg.

Freundliche Grüsse

gemeinde obergoms
daniel biderbost, gemeindeschreiber

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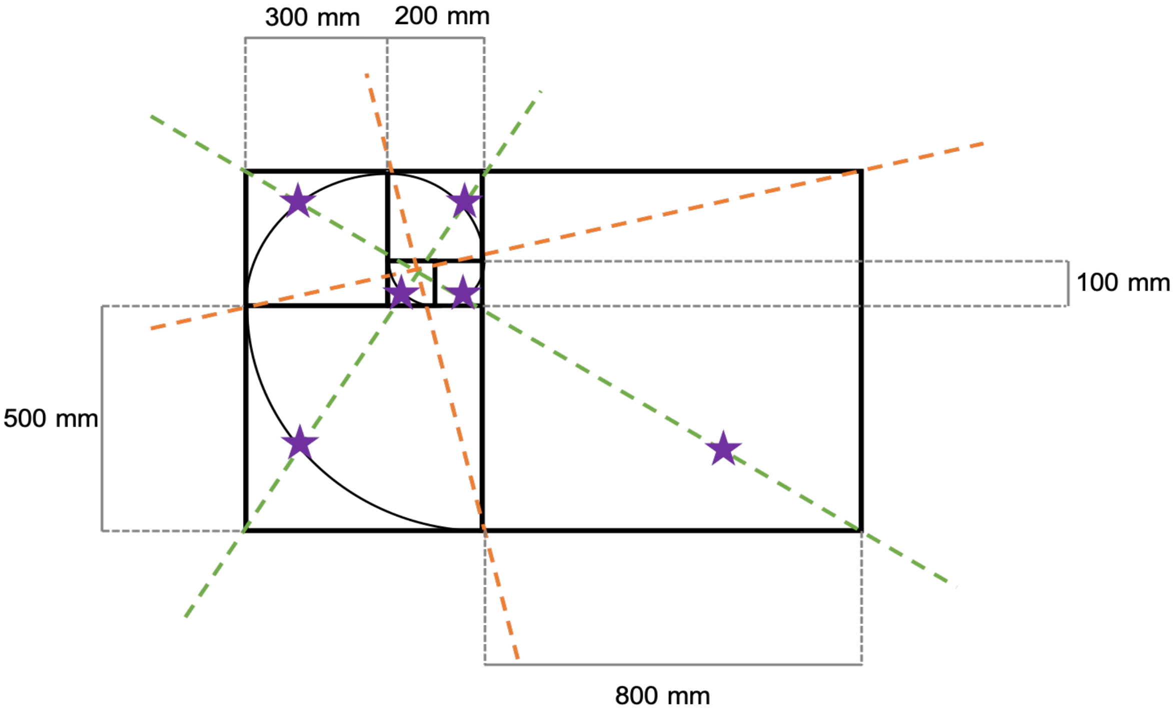
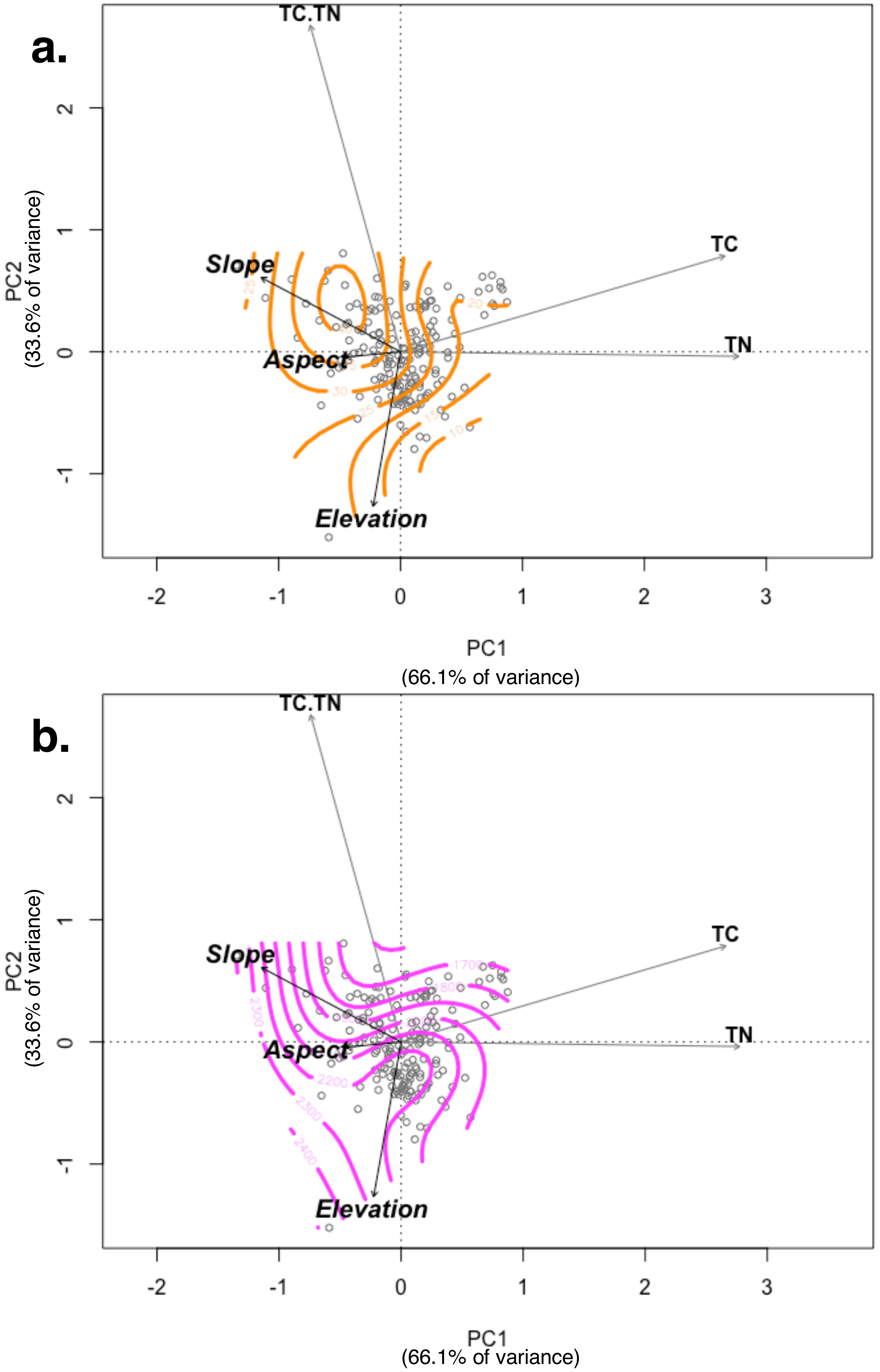
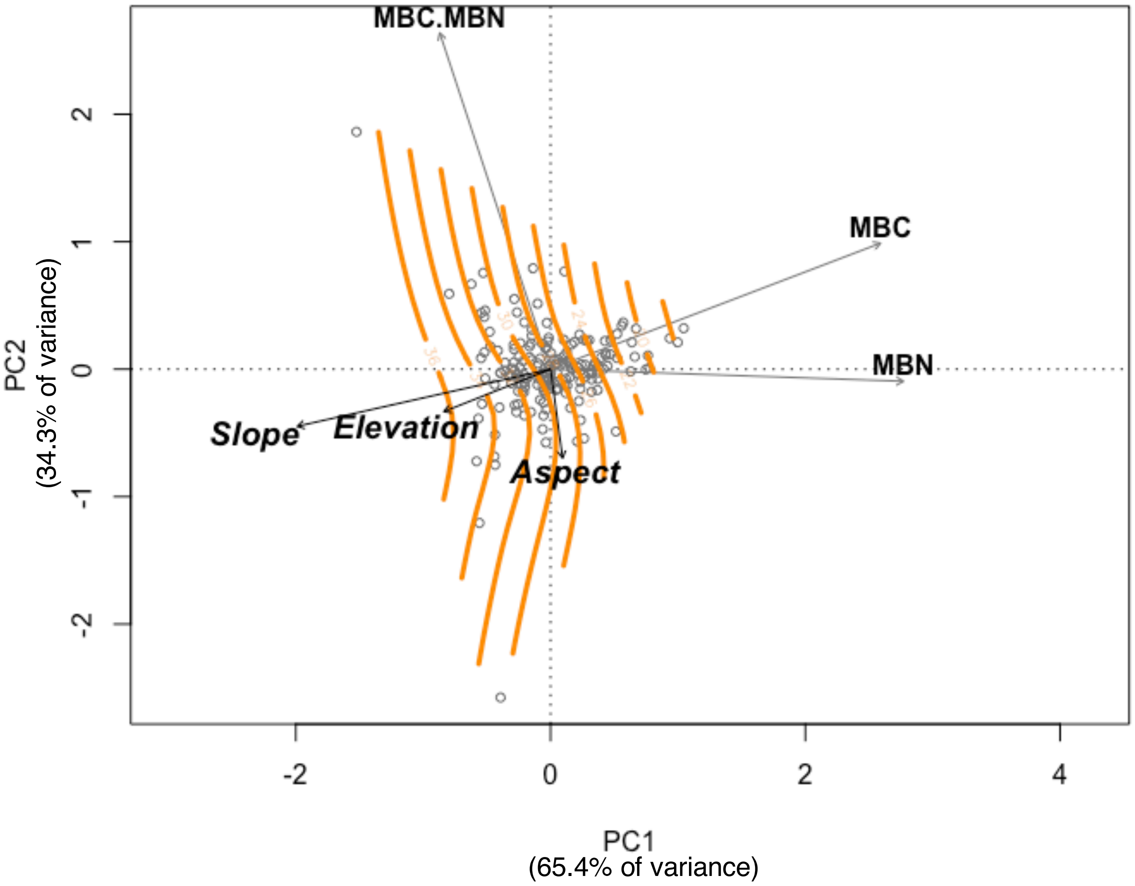
Appendix 1a. Permission letter from the Goms municipal authority to carry out fieldwork; **1b.** Permission from the Obergoms municipal authority to carry out fieldwork.



Appendix 2. Sampling design based on the Fibonacci sequence of numbers. The sampling area is divided into six rectangles with areas following the Fibonacci numbers (1, 1, 2, 3, 5, 8), with the starting position (origin) at the intersection of the axes (dotted lines) from each corner (0, 0). All axes are separated by 45˚. A spiral travelling anti-clockwise from the origin using the sequence to determines its trigonometry, increases proportionally and determines the sampling point where the curve meets the axis bisecting the respective square. All of these sampling points (magenta stars) are then at an angle of 122˚ relative to the origin (first sample). Thus, the Fibonacci sequence determines hierarchically where the soil core is extracted, with the position of each core maintained at a consistent angle to the first, whilst increasing proportionally in distance according to the sequence.



Appendix 3 (a/b). PCA of total carbon, total nitrogen, and their stoichiometric ratios. Significant variables are thin-plate spline surfaces a. (above) = slope (orange) and b. (below) = elevation (magenta). The response is linear where the surface gradient is parallel to the arrow and contours are equally spaced.



Appendix 4. PCA of total organic carbon, nitrogen and their stoichiometric ratios. Slope had the most significant *p-value* in the model and is fitted as an orange thin-plate spline. The response is linear where the surface plane gradient is parallel to the arrow and the contours are equally spaced.

Appendix 5 (above left). The high montane forest at Transect 2 (Geschinen – Unnere Stock).
Appendix 6 (above right). An alpine meadow along Transect 3 (Biine (Münster)).

Appendix 7 (above left). The upper alpine of Transect 1 (Selkingen – Stockflesch). **Appendix 8 (above right).** The sub-nival on Transect 3 (Biine (Münster)).

Appendix 9 (above left). Late season snowpack on Transect 2 (Geschinen – Unnere Stock). **Appendix 10 (above right).** Elevation gradient of Transect 3 (Biine (Münster)) from Transect 2.

Appendix 11/12 (above). Sampling at 2500m on Transect 1 (Selkingen – Stockflesch).

Appendix 13 (above left). Steep sampling at 2300m on Transect 1 (Selkingen – Stockflesch).
Appendix 14 (above right). The upper treeline ecotone at around 2100m on Transect 1.

Declaration of word length, as agreed with supervisors: 9,174.
I confirm that this thesis does not exceed the permitted maximum word length.