

Drivers of carbon stabilization in surface horizons of mineral forest soils in Switzerland

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Summary

Soil organic matter (SOM) consists of a continuum of compounds in different decomposition stages. One of the most slowly decomposing compounds, and therefore contributing to the stability of SOM, is lignin. Using the Klason method, we extracted the lignin compounds of the organic layer (L-F-H horizons) and, using density fractionation, we separated the uppermost 20 cm of the mineral soil into light and heavy fractions. The light fraction responds faster to changes and cycles more rapidly, whereas the heavy one is considered to be the more stable fraction.

We studied the organic layers and the surface mineral soil (0-20cm) of 14 forest soils sites, located throughout the territory of Switzerland. The sites are part of a long-term forest ecosystem research program, ensuring the availability of additional climatic, vegetational, and soil data. To estimate the effect of temperature, we further selected two elevational transects (Schänis and Beatenberg) with three sub-stations each. The selected transects covered an elevational range between 540 and 1800 m a.s.l. We examined the effect of different climatic variables, tree species composition and, soil chemistry on total lignin, carbon (C), and nitrogen (N) contents, as well as, on C:N ratios.

Our results show that mean annual temperature and precipitation are important drivers of C and N concentrations, but also of total lignin contents. Possibly, this has implications on SOM decomposition. Furthermore, soil temperature was an important factor when examining the two elevational transects, as it had a negative effect on C concentrations at both Schänis and Beatenberg. N concentrations and C:N ratios were higher under conifer forests as compared to broadleaf ones. Finally, soil chemistry (pH) was found to be important for N concentration both in the organic layer and the surface mineral soils. These results contribute to the improvement of the carbon decomposition model Yasso07, which is used in Switzerland to simulate changes in soil organic carbon stocks in Swiss forests.

1. Introduction

Soils represent the largest terrestrial carbon (C) pool (Lehmann and Kleber 2015, Bradford et al. 2016), storing twice to three times as much C compared to either the atmosphere or vegetation (Batjes 1996). The surface horizons of soils consist of a continuum of compounds in different stages of decomposition. These can range from fresh plant and animal residues to entirely degraded organic matter (Blume et al. 2016). An important component of soil organic matter (SOM) is the aromatic plant compound lignin, known to decompose slower compared to other soil compounds. Decomposition rates and mean residence time of SOM depend on various chemical, biological and physical processes (Schmidt et al. 2011, Blume et al. 2016). Decomposition processes are the key to determining what remains in the soil. The quality of the litter (inputs) further is considered an important determinant of litter decomposition and eventually for SOC stocks.

Forest soils are very carbon-rich (Lorenz and Lal 2010, Lal and Lorenz 2012) with high diversity of dead organic matter of different chemical quality (Merilä et al. 2010). Mainly as a result of improved management practices and forest expansion taking place in Europe since the 1950s, forest soils are currently considered to represent an enormous carbon-sink (Luyssaert et al. 2010, Pan et al. 2011). This development has also occurred in Switzerland (Rigling and Schaffer 2015, Gosheva 2017) where soil organic carbon (SOC) stocks are particularly high (Nussbaum et al. 2014). Furthermore, in the Southern part of Switzerland, soils rich in aluminium and iron oxides and fire-derived C have contributed to exceptionally high SOC stocks (Eckmeier et al. 2010).

A map of forest SOC stocks in Switzerland was produced by Nussbaum et al. (2014), which is the basis for the forest SOC stocks reported in the Swiss Greenhouse Gas Inventory (FOEN 2017). Changes in SOC stocks in Swiss forests are estimated based on simulations with the carbon decomposition model Yasso07 (Didion and Thürig 2016, FOEN 2017). The model was found to accurately reproduce C loss during litter decomposition (Didion et al. 2014) and changes in SOC stocks in Europe (Hernández et al. 2017). However, based on a comparison between SOC stock measurements and simulated C stocks during the PhD project of Sia Gosheva (Gosheva 2017), it was found that the Yasso model tends to underestimate SOC stocks in some regions of Switzerland (particularly in the areas of the Southern Alps and the Jura).

2. Goals

The goal of this study was to investigate drivers of SOC storage in Swiss forest soils and to deliver additional knowledge to studies examining the comparatively high SOC stocks in Switzerland (NFP68, “Soil as a resource”). The results of this research were intended to explain differences in measured and simulated C stocks in Swiss forests (cf. Gosheva 2017) and to contribute to the further development of existing soil C models such as the Yasso model.

3. Materials and methods

Fourteen long-term forest ecosystem research (LWF) sites in Switzerland were selected and examined in this study (LWF 2017). The sites were chosen in a way as to ensure a wide variety in soil type, pH, mean annual temperature (MAT), and mean annual precipitation (MAP, see *Table 1*). Additionally, elevational transects were included in Beatenberg and Schänis (*Table 2*) to study particularly the effect of temperature. The locations of all examined sites are shown in *Figure 1*.



Figure 1: Location of examined long-term forest ecosystem research sites in Switzerland including elevation transects in Beatenberg and Schänis (indicated in yellow).

3.1. Field sampling and measurements

At each site, a minimum of eight samples of the organic layer were collected and separated into the corresponding horizons (L-F-H). Furthermore, the top mineral soil (at soil depth 0-20 cm) was sampled and separated into heavy and light fractions. Per site, three composites were selected (40 x 40 m²) and for each composite, eight soil cores were sampled and mixed together to diminish spatial variability (González Domínguez In prep.).

3.1.1. Elevational transects

Since SOC stocks tend to increase with an increasing elevation mainly due to changes in climatic conditions (Hagedorn et al. 2010), elevational transects were included in the analysis to study the effect of temperature on SOC stocks in the organic layer. Transects were established at the sites Schänis and Beatenberg (Figure 1), which are dominated by *Fagus sylvatica* and *Picea abies*, respectively, the two dominant tree species in Switzerland. The two transects were used in a previous litterbag study (Frey 2011). The selected elevational transects ranged from 540 to 1150 m a.s.l. (Schänis) and from 1200 to 1800 m a.s.l. (Beatenberg, see Table 1).

Table 1. Main properties of LWF sites.

Site	Elevation (m a.s.l.)	MAT* (°C)	MAP* (mm)	pH	Region	Soil type	Forest type
Alpthal	1154	6.0	2216	5.19	Pre-Alps	GLEYSOL	spruce-fir
Beatenberg	1500	4.9	1447	3.47	Pre-Alps	PODZOL	spruce-fir
Chironico	1319	5.1	1668	4.19	S. Alps	PODZOL	spruce-fir
Davos	1650	2.5	1009	3.63	Alps	PODZOL	spruce-fir
Jussy	500	10.2	1001	6.83	Plateau	STAGNOSOL	mixed deciduous
Lausanne	792	7.6	1264	4.02	Plateau	CAMBISOL	beech
Lens	1031	8.0	796	6.21	Alps	CALCISOL	pine
Lägern	645	8.9	1158	4.19	Plateau	LUVISOL	mixed deciduous
Nationalpark	1885	1.1	866	7.52	Alps	CALCISOL	pine
Neunkirch	521	8.8	951	7.25	Jura	CALCISOL	beech
Novaggio	937	8.5	2097	4.08	S. Alps	UMBRISOL	mixed deciduous
Othmarsingen	465	9.4	1112	3.79	Plateau	CAMBISOL	beech
Schänis	720	8.1	1833	4.63	Pre-Alps	CAMBISOL	beech
Vordemwald	470	9.1	1153	3.88	Plateau	STAGNOSOL	spruce-fir

* Mean annual temperature (MAT) and precipitation (MAP) for the period 1981-2010 were provided by Meteotest (Remund et al. 2014).

Table 2. Elevation transects in Beatenberg and Schänis including annual mean soil temperature between 2001 and 2010 based on (Frey 2011); see also Table 1 for site details.

Site	Elevation (m a.s.l.)	Soil Temperature (annual mean 2001-2010 at 5 cm depth [°C])
Beatenberg H1	1800	3.9
Beatenberg Meteo	1520	5.5
Beatenberg H4	1200	6.4
Schänis H1	1150	6.9
Schänis H3	800	8.2
Schänis H4	540	9.0

3.2. Laboratory analysis – lignin extractions

Concentrations of C and N were measured at the central lab of the WSL (Zentrallabor 2017). Lab analyses included lignin extractions according to the Klason method (Dence 1992). This analysis followed a similar procedure as the one used by the Yasso developers (Heinonsalo personal communication) to ensure methodological consistency for further model development and possible comparisons.

In a five-step process, first water soluble compounds were extracted, followed by the extraction of ethanol soluble compounds. In a third step, the samples were treated with sulfuric acid (H₂SO₄), autoclaved, and in a next step filtrated. Finally, the absorption ranges of the samples were measured photometrically. The single steps of the process are described in detail below.

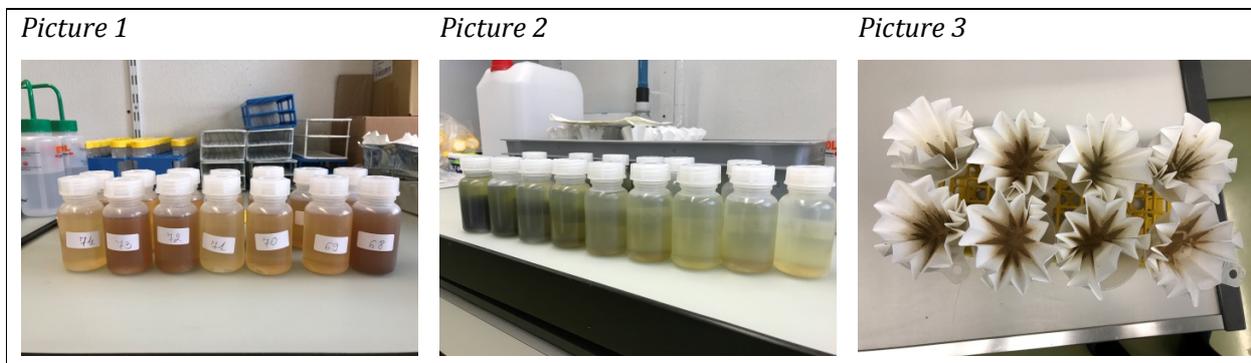
3.2.1. Extraction of water soluble compounds

Very finely grinded samples were extracted via hot ultrapure water (80°C, *Picture 1*) and shaken in a water bath, followed by a centrifuging of the samples for 10 minutes at 4500 rpm. This procedure was repeated three times. During the fourth time, room temperature ultrapure water (25 ml) was added to the samples, instead of hot water, before centrifuging these. Finally the samples were dried over night at 80°C.

3.2.2. Extraction of ethanol soluble compounds

The dried samples were weighted in order to calculate how much water soluble material has been lost after the water extractions. Ethanol was added to all samples, then these were shaken in a horizontal shaker for 15 min at 250 rpm and centrifuged for 10 minutes at 4500 rpm. This

procedure was repeated three times. Finally the samples were filtrated into paper filters and dried over night at 60°C (*Pictures 2 and 3*).



3.2.3. Extraction of acidic soluble compounds

After the dried filters were weighted (in order to calculate how much material had been lost after the ethanol treatment), 300 mg from each sample were weighted in Schott-bottles and 72% H₂SO₄ was added to them, after which, these were put in a 30°C water bath for one hour. Ultrapure water (84 ml) was added to the samples and these were inserted in an autoclave for one hour at 120°C.

3.2.4. Filtration of samples and incineration

For the filtration, we used a custom made filtration apperature with a vacuum pump and hoses, available at the WSL. After the samples were autoclaved, the content of these was filtrated in a two-step process: firstly, the acidic contents of the samples (both liquid and particles) were poured into porcelain filter crucibles and filtered, and secondly, to ensure that the entire content had been emptied, the samples were rinsed twice with 25 ml ultrapure water and filtered. Finally, the crucibles were dried over night at 105°C and weighted the next morning to calculate how much material had been lost after the acidic treatment. Then, the crucibles were incinerated for four hours at 550°C and weighted in. This represents the amount of Klason lignin.

3.2.5. Photometer measurements

A diluted solution (called matrix solution) was created by mixing ultrapure water with 72% H₂SO₄ at a ratio 84:3 (482.76 ml H₂O with 17.24 ml H₂SO₄, respectively). The filtered liquid samples from the previous day (0.3 ml) were mixed with 10 ml of the matrix. The adsorption of the solution was then measured with a photometer at 205 nm. This represents the amount of acid soluble lignin (ASL). Total amount of lignin is represented as the sum of Klason lignin and ASL.

3.3. Laboratory analysis - density fractionation

During a cooperation with the University of Zurich within the PhD thesis of Sia Gosheva, samples from the top 20 cm of the mineral soil were separated via density fractionation into light and heavy fractions (Gosheva 2017). The bulk soil was divided according to the method of (Griepentrog et al. 2014) into two light fractions: a free light fraction and an occluded light fraction, whereas heavy fractions were separated into a fine heavy fraction and a coarse heavy fraction (*Figure 2*). The two light fractions represent the particulate organic matter (POM), considered to be more easily decomposable; the two heavy fractions characterize the mineral-associated organic matter (MOM), considered to be more stable and resistant to decomposition.

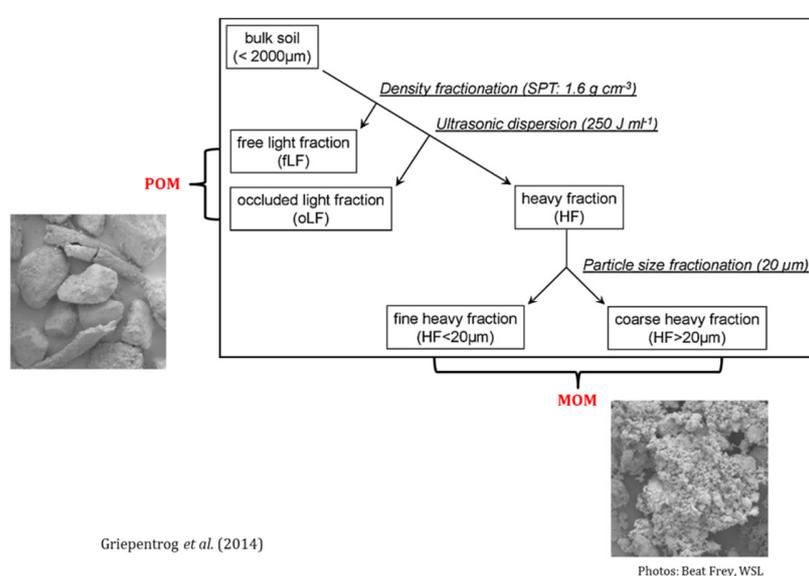


Figure 2. Process of density fractionation after the method of Griepentrog et al. (2014)

3.4. Statistical analysis

In this study, elevation was used as an environmental proxy since it correlates to a variety of factors, which are of importance for C contents. The variables used for the statistical analyses in this study were the following: mean annual temperature (MAT), mean annual precipitation (MAP), forest type, pH, clay content, aspect, forest age, base cation content (BC) and cation exchange capacity (CEC), root depth. Furthermore, the following factors were included: organic layer horizon, LWF site, and for the subsets of the two elevational transects – the three subsites (Beatenberg: H1, Meteo, H4; Schänis: H1, H3, H4). For the additional analysis of the two elevational transects, soil temperature information was available (*Table 2*) and included in the analysis. The data was not normally

distributed; therefore, we used log-transformation to approximate normality. The normality of the residuals was tested using histograms and Shapiro-Wilk Normality test. Simple ANOVA tests were used to examine the controlling factors of C and N contents, C:N ratio, and total lignin. Throughout the protocol, data is presented as means \pm standard errors.

3.5. Yasso decomposition compound groups

The Yasso model describes decomposition of organic matter and the resulting C flows between different C pools (i.e. litter and soil) and to the atmosphere based on four different compound groups with different rates in mass loss (Tuomi et al. 2009, 2011). These are soluble in water (W), in ethanol (E), in acid (A), or are insoluble (N). These compound groups are assumed to correspond to the different types of lignin extractions since these represent the degree of extraction of compounds from fastest to slowest (water extraction towards insoluble).

The simulated decomposition is thus dependent on the distribution of the four compounds in the fresh litter which is entering the model in each time step (Tuomi et al. 2009). Liski et al. (2009) provide examples of the proportions of the four lignin compounds of fresh litter. The chemical composition of fresh foliage litter was analyzed in the litterbag study at Schänis and Beatenberg (Frey 2011 reproduced in Didion et al. 2014). A comparison of the measured data by Frey (2011) and the results of the lignin extraction from this study can be used to verify the assumed decomposition dynamics in the model.

4. Results

Below, results of the different analyses are presented with reference to the 14 LWF sites and the two elevational transects (Beatenberg and Schänis).

4.1. Lignin extractions: all LWF sites

Though lignin compound extractions of the L-F-H horizons of the organic layer differed among the individual LWF sites, regional distribution did not reveal a particular trend on total lignin. The highest contents of extracted lignin in litter were observed in Novaggio, Beatenberg, and Vordemwald (all above 50% of total lignin), whereas, the lowest rates of total lignin were detected in Jussy, Alpthal, and Lausanne (see *Table 3*). However, the three LWF sites with the highest total lignin values are sites with a lower pH (values ranging between 3.47 and 4.08, see *Table 1*). This relationship seems to be supported also by the comparatively high lignin values in Davos and

Otmarsingen (see *Table 3*) – both acidic sites (pH= 3.5 and 3.8, respectively). High pH values (above 5.0) were found at two out of the three sites with the lowest total lignin (except for Lausanne). Furthermore, total lignin differed according to tree species: spruce-fir sites had higher total lignin values as compared to beech sites (52.4±1.3 vs. 43.7±1.4, respectively). The organic layer horizons explained 12.4% of the statistical model variance, whereas MAT and MAP, explained 6.3% and 5.8%, respectively.

Table 3. Average lignin extraction values for all LWF sites and all organic layer horizons

Type of extraction (in %) LWF area	Water extractable compounds	Ethanol extractable compounds	Klason Lignin	Acid Soluble Lignin (ASL)	Total Lignin **
Alpthal	16.9±NA*	3.1±NA	39.8±NA	0.9±NA	40.8±NA
Beatenberg	9.3±0.9	3.8±0.7	52.7±1.5	0.8±0.1	53.6±1.5
Chironico	12.9±0.7	4.6±0.1	46.1±2.1	0.9±0.3	47.1±2.2
Davos	13.3±0.4	4.2±0.2	48.7±3.3	0.5±0.2	49.2±3.5
Jussy	14.3±NA	20.1±NA	38.0±NA	1.5±NA	39.5±NA
Lägern	15.4±3.3	0.2±0.5	41.1±1.6	0.7±0.4	41.8±2.1
Lausanne	11.7±1.4	0.5±0.4	40.2±2.1	1.1±0.3	41.2±2.4
Lens	13.8±NA	6.5±NA	47.6±NA	0.7±NA	48.3±NA
Nationalpark	13.4±NA	4.3±NA	46.8±NA	0.3±NA	47.1±NA
Neunkirch	18.9±NA	3.9±NA	46.9±NA	1.5±NA	48.5±NA
Novaggio	15.5±NA	1.8±NA	57.5±NA	1.5±NA	58.9±NA
Othmarsingen	14.8±0.9	4.1±1.9	48.6±1.0	1.2±0.4	49.8±1.5
Schänis	8.6±0.4	0.3±0.2	42.4±1.5	0.9±0.1	43.3±1.6
Vordemwald	14.9±0.6	6.2±0.8	48.7±0.5	1.6±0.5	50.3±0.8

* NA sign denotes that there is only one sample per site, therefore no standard error can be calculated. Values in bold demonstrate the highest and the lowest values for every lignin extraction phase.
 ** Total lignin is formed by the sum of Klason lignin and ASL

4.2. Lignin extractions: elevation transects Beatenberg and Schänis

At the beech-dominated transect in Schänis, we observed a lower total extracted lignin at higher elevations for all organic layer horizons (*Figure 3*). The difference in total lignin furthermore increased from L through F to H horizons (from easily decomposable to less easily decomposable fractions). In particular, in the H horizon the lignin was the lowest with an increase in elevation (difference of 16.2% between 540 and 1150 m a.s.l., see *Table 4*). At the higher situated spruce-dominated transect in Beatenberg (examined areas ranged in elevation between 1200-1800 m a.s.l.), we did not observe an univocal change in total lignin. However, for the F and H horizons, there was a larger change in total lignin with an increase in elevation (e.g. in the F horizon, total lignin at 1200 m a.s.l. (H4) was 44.9%, whereas it increased to a 57.8% at 1800 m a.s.l. (H1), see *Figure 3*).

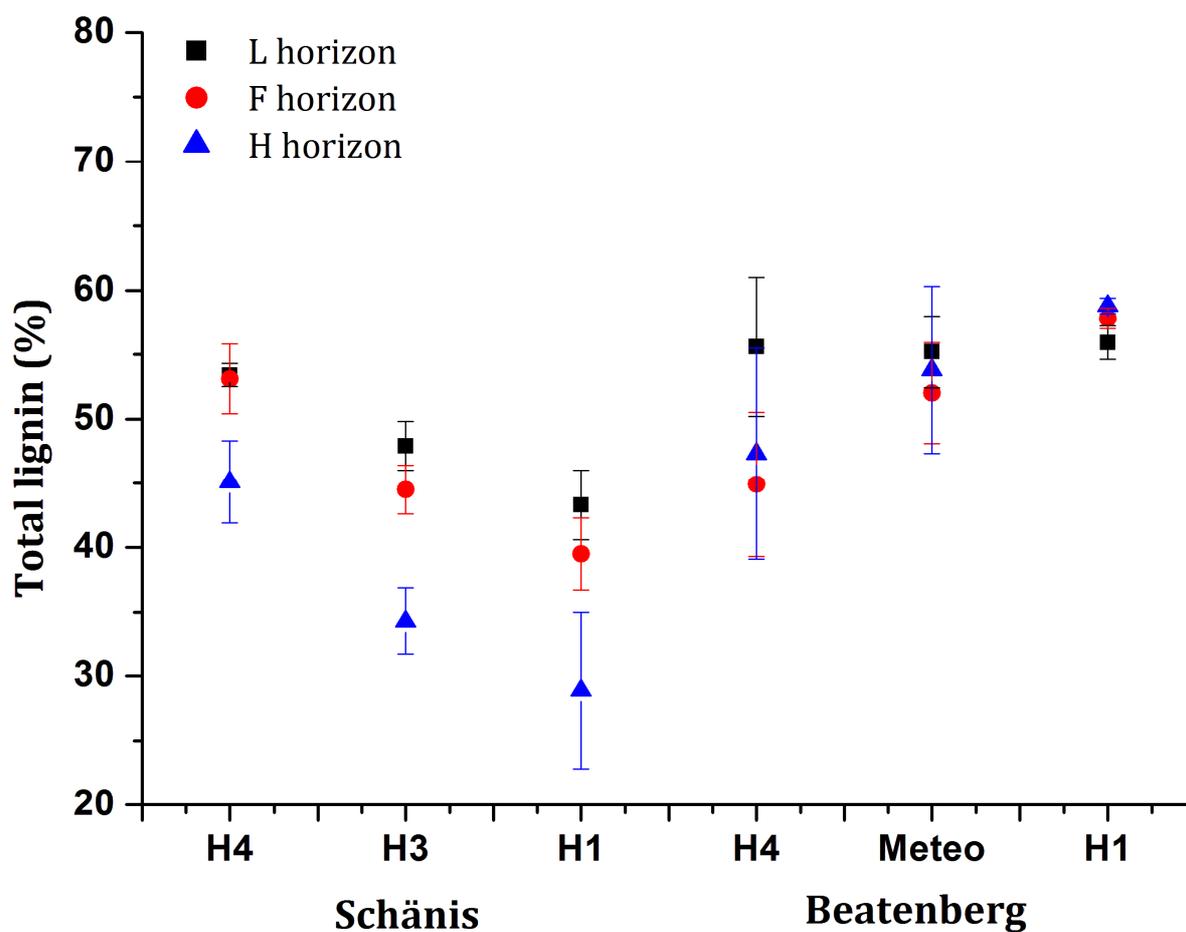


Figure 3. Total lignin (in %) according to organic layer horizons (L-F-H) and elevational transects (Schänis sites: 540 (H4), 800 (H3), and 1150 (H1) m a.s.l., Beatenberg sites: 1200 (H4), 1520 (Meteo), and 1800 (H1) m a.s.l.). Data is represented as means \pm standard errors.

The statistical analysis showed the degree of total lignin between sites to significantly differ with changes in elevation. Changes in elevation represent particularly changes in the MAT, which is a known driver of lignin decomposition (Thevenot et al. 2010) as well as of litter quality.

Table 4. Lignin extractions according to elevation transects and horizons for Beatenberg and Schänis.

Type of extraction (in %)	Elevational transect	Horizons		
		L	F	H
Schänis				
Water extractable compounds	540 m a.s.l. (H4)	11.8±0.9	11.9±1.1	8.5±0.8
	800 m a.s.l. (H3)	7.9±0.5	10.2±1.4	6.5±0.6
	1150 m a.s.l. (H1)	8.3±0.4	7.3±0.8	5.2±1.0
Ethanol extractable compounds	540 m a.s.l. (H4)	0.7±1.3	0.9±0.2	0.2±0.2
	800 m a.s.l. (H3)	NA±NA	NA±NA	0.2±NA
	1150 m a.s.l. (H1)	1.8±NA	0.9±0.1	0.4±0.2
Klason lignin	540 m a.s.l. (H4)	52.3±0.9	51.8±2.8	44.2±3.3
	800 m a.s.l. (H3)	46.9±1.9	43.6±2.1	33.5±2.4
	1150 m a.s.l. (H1)	42.3±2.4	38.6±2.7	28.3±6.1
ASL	540 m a.s.l. (H4)	1.2±0.2	1.3±0.3	0.9±0.3
	800 m a.s.l. (H3)	0.9±0.1	0.9±0.3	0.8±0.2
	1150 m a.s.l. (H1)	1.0±0.4	0.9±0.4	0.6±0.1
Total lignin	540 m a.s.l. (H4)	53.4±0.9	53.1±2.7	45.1±3.2
	800 m a.s.l. (H3)	47.9±1.9	44.5±1.9	34.3±2.6
	1150 m a.s.l. (H1)	43.3±2.7	39.5±2.8	28.9±6.1
Beatenberg				
Water extractable compounds	1200m a.s.l. (H4)	9.9±1.0	7.3±0.3	6.6±1.3
	1520 m a.s.l. (Meteo)	11.4±0.7	8.2±0.2	5.6±0.3
	1800 m a.s.l. (H1)	13.5±0.6	12.9±0.3	13.1±0.9
Ethanol extractable compounds	1200m a.s.l. (H4)	0.3±1.0	8.5±4.3	4.1±1.6
	1520 m a.s.l. (Meteo)	2.6±0.5	3.9±1.1	6.7±2.1
	1800 m a.s.l. (H1)	2.7±0.8	3.2±1.3	2.8±0.3
Klason lignin	1200m a.s.l. (H4)	54.7±5.3	44.4±5.6	46.6±8.3
	1520 m a.s.l. (Meteo)	54.6±2.8	51.2±3.8	52.8±6.5
	1800 m a.s.l. (H1)	55.0±1.4	56.8±0.7	57.9±0.5
ASL	1200m a.s.l. (H4)	0.8±0.3	0.6±0.1	0.7±0.2
	1520 m a.s.l. (Meteo)	0.7±0.1	0.8±0.2	1.0±0.1
	1800 m a.s.l. (H1)	0.9±0.1	0.9±0.2	0.9±0.2
Total lignin	1200m a.s.l. (H4)	55.6±5.4	44.9±5.6	47.3±8.2
	1520 m a.s.l. (Meteo)	55.2±2.8	52.0±3.9	53.8±6.5
	1800 m a.s.l. (H1)	55.9±1.3	57.8±0.8	58.8±0.6

4.3. Lignin extractions according to organic layer horizons

We observed a decrease in lignin from L towards H horizons during the extraction of the water soluble compounds, the Klason lignin, and, though to a lesser extent, the acid soluble lignin (ASL, see *Figure 4*). The highest means (\pm standard errors) for extracted lignin were observed for the Klason lignin (49.2±1.1, 47.2±1.4, and 43.1±2.4 for L, F, and H, respectively), whereas the lowest means

were observed for the ASL extraction (for L, F, and H: 1.1 ± 0.1 , 0.9 ± 0.1 , and 0.8 ± 0.1 , respectively). In the ethanol soluble extraction, we observed no univocal direction of change in lignin, possibly due to two outliers in the F horizon. The differing amounts of extracted lignin compounds suggest that, firstly, decomposition rates differ between individual components (from more easily to less easily soluble ones), and secondly, that the amount of decomposed material varies between organic layer horizons. Since SOM decomposition and stability advances from the organic layer towards the mineral soil (Schrumpf et al. 2013, Gunina and Kuzyakov 2014) the implementation of such information in models will contribute to improved model simulations.

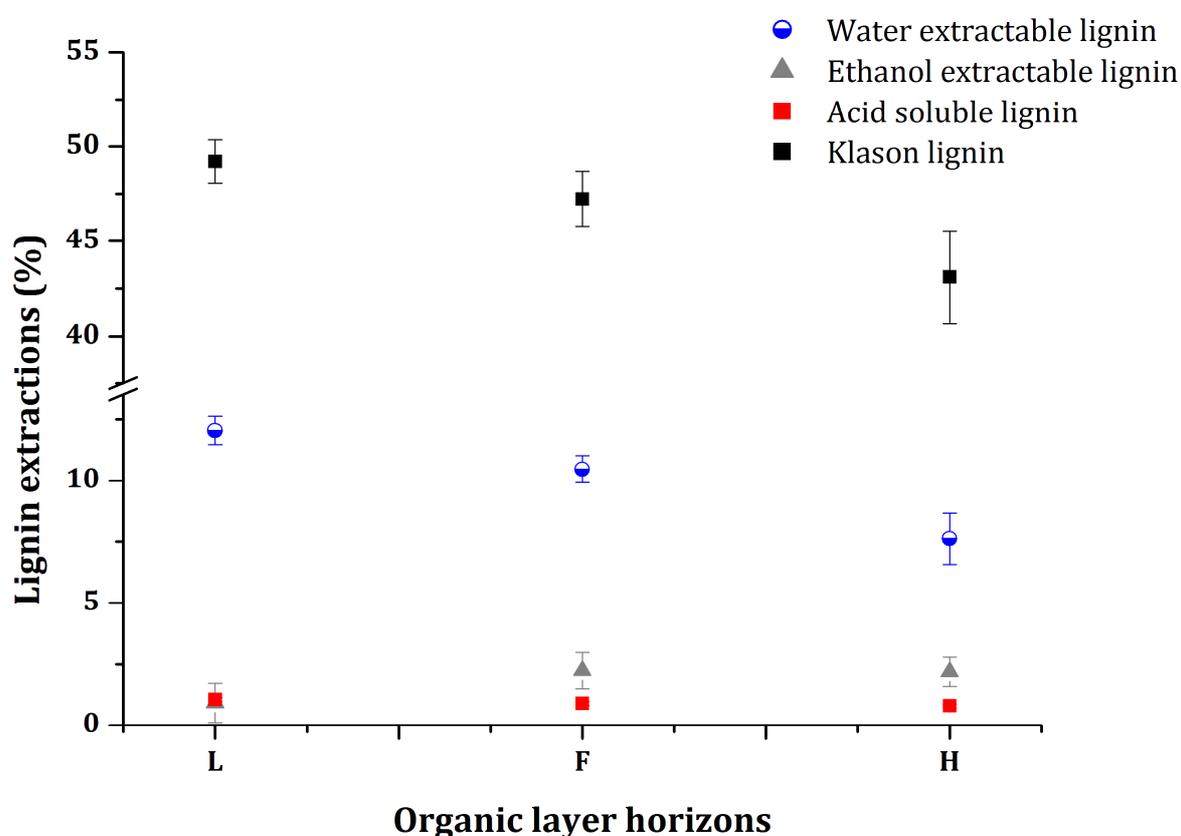


Figure 4. Lignin extractions for the organic layer horizons from all 14 sites. Data is presented as means \pm standard errors. Please note the break on the y-axis (break between 13.5% and 37.5%).

Litter quality, an important determinant of SOM decomposition (Wang et al. 2015), varies according to tree species (Liu et al. 2016, Wang et al. 2016). The mean proportions of the four lignin compounds in fresh needle and leaf litter measured by Frey (2011) were 29.4% water extractable, 6.5% ethanol extractable, 40.1% acid soluble, and 23.5% Klason lignin for coniferous foliage litter and 13.2%, 5.5%, 48.2%, and 33.0% for broadleaf litter (Tab. 3 in Didion et al. 2014). These

represent proportions relative to the total lignin. Compared to the measured data at the transects, we find 15.7% water extractable, 3.3% ethanol extractable, 1.7% acid soluble, and 79.3% Klason lignin at the broadleaf-dominated site Schänis, and 16.9% water extractable, 3.3% ethanol extractable, 1.2% acid extractable, and 78.6% Klason lignin at the conifer-dominated site Beatenberg (relative proportions for the L horizon). We observed decomposition from the L towards the H horizons in Schänis (but not in Beatenberg) when examining Klason lignin values (*Supplementary table 1*). The differences in the proportions between the fresh litter and our data can probably be attributed to rapid loss of soluble lignin components during initial litter decomposition (Klotzbücher et al. 2011).

4.4. Lignin extractions – influential factors

4.4.1. All LWF sites

Our analysis indicates that total lignin significantly differed between organic layer horizons; total lignin content decreased with horizons (mean values: 50.3, 48.1, and 43.9 for L, F, and H horizons, respectively). Mean annual precipitation (MAP) had a strong negative effect on total lignin (*Figure 5*), that seemed to increase with horizons. Another important explanatory variable was mean annual temperature (MAT), which was negatively related to total lignin as well. Furthermore, total lignin was found to increase with elevation in all horizons, but predominantly strong in the H horizon (figure not shown). Elevation was excluded from the analysis due to proof of multicollinearity (vif function, HH package; Heiberger, R. M. 2017) . However, in general MAP and MAT correlate with elevation (Henry 1919). Forest type had no significant effect on total lignin content.

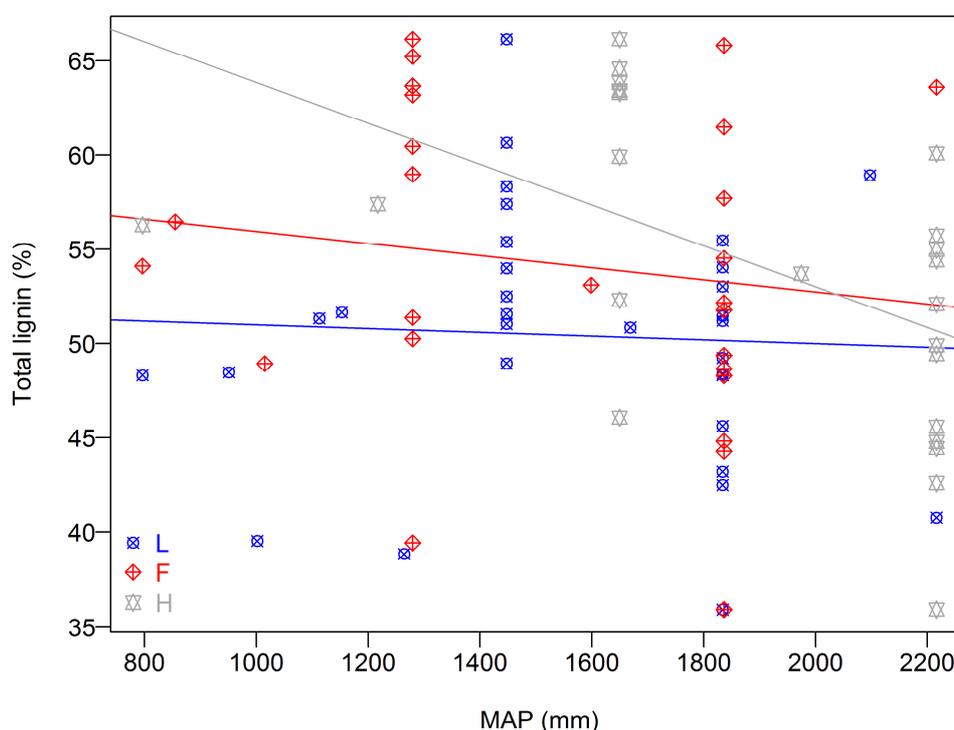


Figure 5. Total lignin contents (in %) according to MAP (in mm) for organic layer horizons (L-blue, F-red, and H-grey). Lines represent robust linear regressions. Data is based on the 14 LWF sites.

4.4.2. Elevational transects

Also for the two elevational transects, total lignin was significantly different between organic layer horizons. In general, total lignin decreased with horizon depth, corresponding to a higher degree of C decomposition (*Table 4*). For the two transects, information on soil temperature was available and included in the statistical analyses. In Beatenberg and in Schänis, the factor with the greatest influence on total lignin, and therefore decomposition, was be mean soil temperature (explaining 10.6% of the statistical model variance, $R^2=0.50$). Though total lignin values differed among horizons in Beatenberg (especially in F and H horizons, see *Table 4*), the results do not show significance. In Schänis, however, we found a significant decrease in total lignin content from L towards H horizon. Interestingly, neither forest type nor MAT had any effect on total lignin at the two transects.

4.5. Total carbon (C), nitrogen (N) contents, and C:N ratios – influential factors

4.5.1. All LWF sites

As mentioned in the Material and Methods section (cf 3.2), total amounts of C and N of the samples were measured, and the factors influencing these were examined. Carbon concentrations were higher with increasing elevation. C contents decreased significantly from L towards H horizons ($P < 0.05$) decreased significantly with increase in MAT ($P = 0.01$). Nitrogen contents were significantly affected by forest type ($P = 0.01$) - we observed higher N contents under conifer forests, with highest contents found in spruce-fir forests. C:N ratios differed significantly according to organic layer horizons ($P < 0.05$) and declined from L towards H horizons. Furthermore, C:N ratios were highest under pine forest sites (Lens and Nationalpark) and lowest under mixed deciduous ones (Jussy, Lägern, and Novaggio). C:N ratios increased with altitude and slope (*Supplementary figure 3*).

4.5.1. Elevational transects

Considering the two elevational transects, there were significant differences between the organic layer horizons ($P < 0.05$). C concentrations in both Beatenberg and Schänis decreased from L towards H horizons; concurrently, these increased along the elevational transect (*Table 5*). Soil temperature was negatively correlated with C concentrations in both examined transects ($P < 0.05$). MAP had a strong negative effect on N concentrations ($P = 0.01$). Though N contents in the spruce-fir dominated Beatenberg were higher compared to beech-dominated Schänis (1.6 vs. 1.4, respectively), forest type did not show a significant effect in the analyses. Forest type, furthermore, did not have an effect on C:N ratios (29.8 and 28.1 for Beatenberg and Schänis, respectively). Soil temperature had a strong negative effect, with lower C:N ratios in Schänis and higher ones in Beatenberg. Finally, differences between organic layer horizons ($P < 0.05$) and along the elevational transects ($p = n.s.$) were detected (*Table 5*).

Table 5. Cross-comparison of C and N contents, and C:N ratio values for the two elevational transects and according to organic layer horizons.

Site Horizon Station (Elevation m a.s.l.)	Carbon (%C) (mean ± st. error)			Nitrogen (%N) (mean ± st. error)			C:N ratio (mean ± st. error)		
	L	F	H	L	F	H	L	F	H
Beatenberg									
H1 (1800)	50.2±0.3	50.6±0.6	49.8±0.3	1.4±0.1	1.5±0.1	1.7±0.1	35.1±1.6	33.2±1.4	29.3±1.3
Meteo (1520)	48.2±1.1	47.9±1.7	40.1±9.6	1.4±0.1	1.6±0.2	1.3±0.3	33.6±0.8	31.0±2.6	29.8±2.2
H4 (1200)	47.2±1.5	38.3±5.3	39.2±7.9	1.6±0.1	1.8±0.1	1.7±0.2	29.6±2.8	21.4±1.4	23.2±1.8
Schänis									
H1 (1150)	44.8±1.4	36.5±3.4	26.1±5.9	1.3±0.0	1.3±0.1	1.1±0.2	33.4±1.3	28.6±1.5	22.9±1.1
H3 (800)	45.9±1.7	43.0±1.3	30.3±0.7	1.4±0.1	1.5±0.1	1.3±0.1	34.4±2.4	28.8±0.9	22.2±0.7
H5 (540)	42.7±3.8	44.7±0.9	29.4±2.3	1.6±0.1	1.6±0.1	1.2±0.2	26.7±3.6	29.5±2.8	26.1±2.8

As demonstrated in *Figure 6*, the relationship lignin:C ratio vs. C:N ratio indicate a decrease of C:N ratio with increasing lignin:C ratio in the L and F horizons, whereas we observed an increase in the H horizon. This observation can hint towards a depletion of more easily decomposable C sources, leading to an impairment in the lignin decomposition (Duboc et al. 2014). However, it is not possible to make an univocal conclusion based on the data presented here.

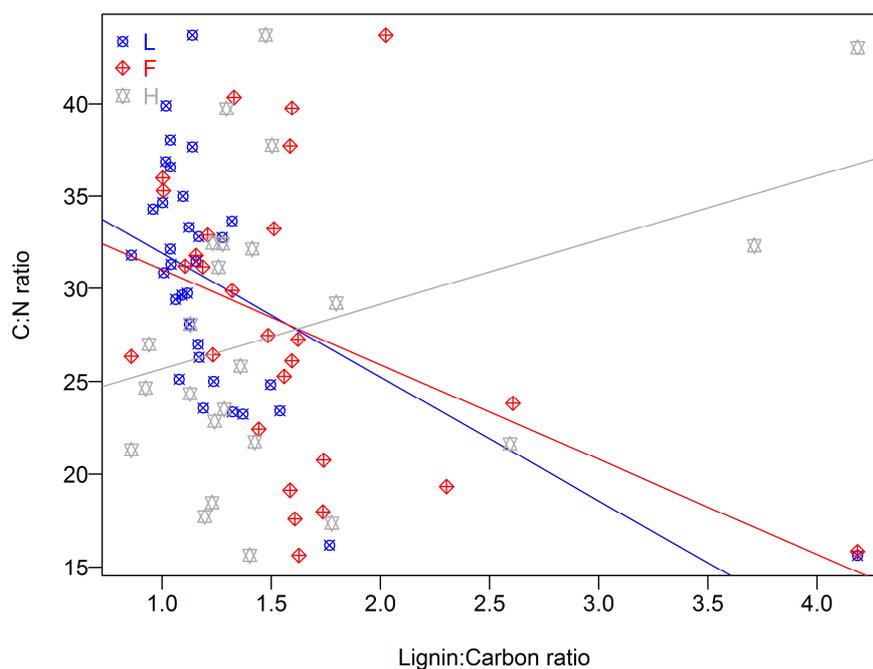


Figure 6. Relationship between lignin:C ratio and C:N ratio according to organic layer horizons (L-blue, F-red, and H-grey). Lines represent robust linear regressions.

4.6. Density fractionation: all LWF sites

In the mineral soil, the POM fraction is considered a more labile carbon fraction compared to the more stable MOM fraction (Schrumpf et al. 2013). Therefore, the density fractionation of the uppermost 20 cm of the mineral soil aimed at contributing to a better understanding to the rates of C decomposition and SOM stabilization. The results presented below represent data from the 14 LWF areas and include the organic layer horizons (L-F-H and including roots found in the organic layer), as well as, the top 20 cm of the mineral soil, separated into two light fractions (POM) and two heavy fractions (MOM).

4.6.1. Density fractionation: C and N contents

C concentration was highest in roots found in the organic layer (mean: 46.6%). The C content decreased substantially between POM and MOM (33.1% vs. 4.2%, respectively). For all fractions, N concentration was closely correlated with MAP, whereas precipitation was only related to C concentrations in the MOM fraction (*Figure 7*). N contents differed significantly between fractions and decreased in the following order: org. layer (1.4) > POM (1.3) > MOM (0.5). N content decreased

with an increasing pH, with N contents being lower in calcareous soils as compared to acidic and water-logged ones.

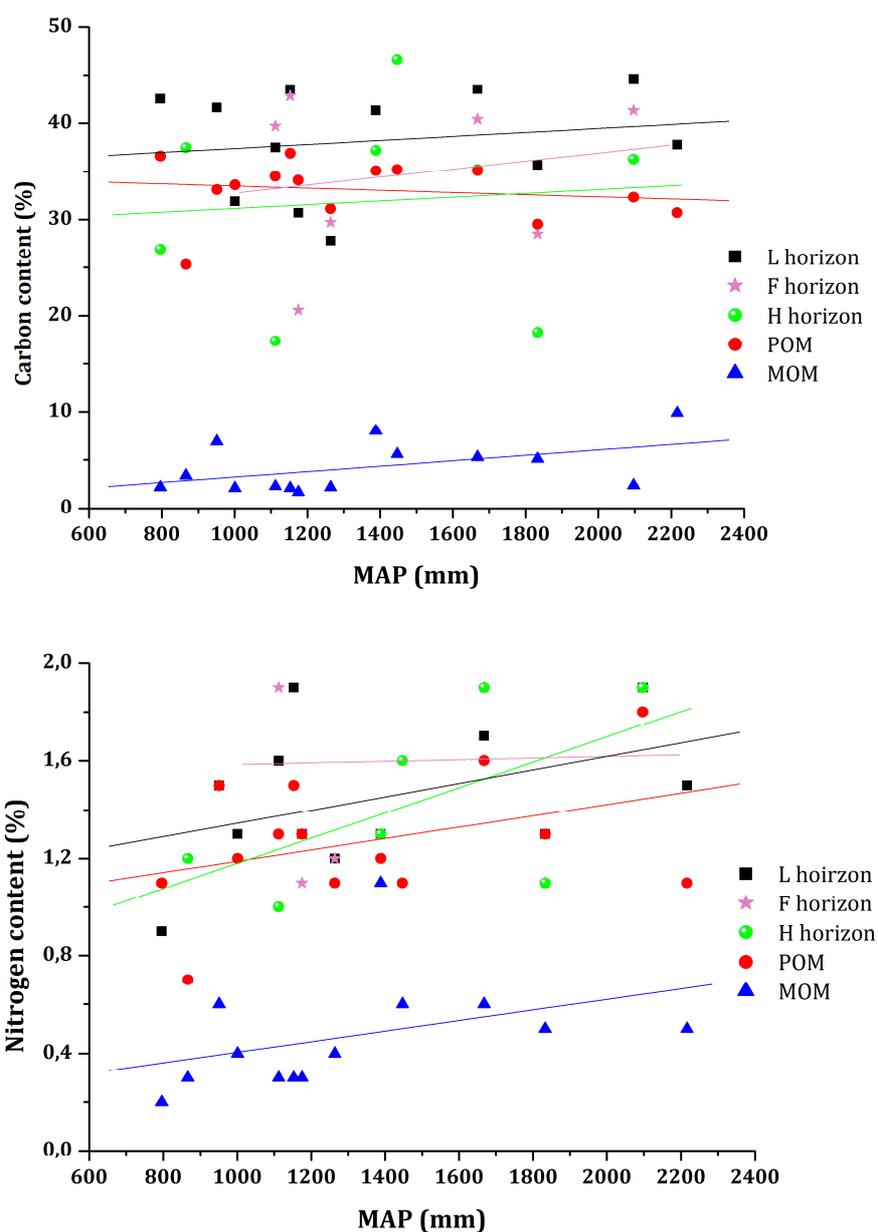


Figure 7. The impact of MAP (in mm) on C content (top) and N content (bottom, both in %) according to organic layer horizons: L (black), F (magenta), and H (green), as well as POM (red), and MOM (blue). Lines represent individual linear regressions.

4.6.2. Density fractionation: C:N ratio

Whereas C:N ratios of the organic layer and the POM fraction were almost identical (26.0 and 26.9, respectively), the C:N ratio of the MOM fraction had significantly lower values (13.8). This demonstrates advancing of SOM decomposition from the organic layer towards the mineral soil (Gosheva 2017), and it is furthermore an indicator for a higher contribution of microbial residues during in decomposed SOM (Conen et al. 2008). C:N ratios strongly increased with elevation (for e.g., C:N ratio was around 22.0 at 600 m a.s.l. whereas forests above 1500 m a.s.l., C:N ratio values were around 30.0). We further observed a small decrease in C:N ratios in the organic layer and POM at areas with higher precipitation.

5. Conclusions

In our study, we observed different climatic variables, tree species composition and, to some extent, soil chemistry to exert effect on total lignin, C, and N contents, as well as, on C:N ratios. It has previously been shown that MAT plays an important role for C and N concentrations in the organic layer (Gosheva 2017, Gosheva et al. 2017). However, in this study, we also found that MAT affects the contents of total lignin (in all LWF areas), which can have implications on SOM decomposition. Soil temperature information was available for the two elevational transects (Beatenberg and Schänis) and used in the analysis, showing a very strong negative effect on total lignin for all organic layer horizons (*Supplementary figure 1*). Furthermore, soil temperature had a negative impact on C contents at the two transects. The effect of soil temperature was not examined at other LWF areas. Previous studies have also confirmed the effect of soil temperature (Frey 2011, Heim and Frey 2004, Didion et al. 2014); therefore, one could expect that similar results would be observed at the other LWF areas.

Mean annual precipitation was another very important variable, both for lignin and for C and N contents. While MAP had a strong negative impact on lignin and N contents in all organic layer horizons, as well as on C:N ratios at the two transects, its effect on C contents was only significant in the MOM fraction but not in the POM fraction or the organic layer. In temperate forests, such as the ones in Switzerland, a substantial fraction of labile carbon is stored in the organic layer, making it potentially vulnerable to disturbances, such as changes in climate or the chemical composition of soils. Soil chemistry (e.g. pH) was related to N concentrations in the organic layer and in the top mineral soil of the selected LWF plots, which are located throughout the entire area of Switzerland.

Tree species can be an important determinant for C and N contents, particularly in the organic layer. In our study, we observed no direct effect of tree species composition on total lignin contents. However, N contents and C:N ratio were higher under conifer forests as compared to broadleaf ones. This was especially visible at the elevational transects, where higher values were observed at the spruce-fir dominated Beatenberg compared to the beech-dominated Schänis (which is also the warmer site). Litter from conifer forests contains compounds, such as phenols, which are known to be more difficult to decompose than broadleaf tree-litter (Jacob et al. 2010). This can contribute to a larger accumulation of the more labile organic layer at conifer sites (such as Beatenberg), making the accumulated carbon also more vulnerable, possibly resulting in C source (loss of carbon). Many studies (mostly temperate forest studies but not limited to, such as (Vesterdal et al. 2013, Wiesmeier et al. 2013, Schleuß et al. 2014) suggest that the management of tree species composition can contribute to an increase of SOC storage (by mixing broadleaf trees in conifer forests, since broadleaf trees store most of its carbon in the more stable mineral soil). However, in our study, it cannot be distinguished whether the observed changes with elevation in C and N contents and in total extracted lignin are due to changes in climate or due to changes in the tree species, or even the physico-chemical composition of the soils.

However, what does this mean for the Yasso model simulations?

A great advantage of the Yasso model is that it only needs climate data and litter input for the model simulations. However, this could possibly contribute to underestimation of SOC stocks, due to lack of consideration of additional parameters, such as soil chemical parameters (we observed that pH has an effect on N content). In addition, the PhD thesis of Sia Gosheva suggests that further soil chemical characteristics (which are pH-dependent), such as iron, aluminum, and calcium contents, exert a strong impact on SOC stocks in Swiss forest soils and that these parameters should be considered in Yasso simulations (Gosheva 2017). Moreover, it was demonstrated in this study, but also in other ones (Yuste et al. 2003, Thuille and Schulze 2006, Meier and Leuschner 2010, Prietzel and Christophel 2014), that precipitation is an important factor for carbon storage and for soil decomposition. It is known that Yasso underestimates SOC stocks at areas with high precipitation (de Wit et al. 2006, Didion and Thürig 2012). Therefore, areas receiving high precipitation rates (such as the Southern Alps in Switzerland) should be considered separately, possibly with a correction logarithm to account for potential inconsistencies. Finally, the included elevational transect of this study revealed differences in total extracted lignin content (total extracted lignin decreased with an increase in elevations in Schänis, but not in Beatenberg). This could be linked to

changing climatic conditions at both sites; therefore, we suggest that climatic conditions at different elevations need to be considered separately.

In conclusion, the inclusion of additional parameters to Yasso would improve the precision of future model simulations.

6. Acknowledgements

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7. References

- Batjes, N. H. 1996. Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science*:151–163.
- Blume, H.-P., G. W. Brümmer, H. Fleige, R. Horn, E. Kandeler, I. Kögel-Knabner, R. Kretschmar, K. Stahr, and B.-M. Wilke. 2016. *Scheffer/Schachtschabel Soil Science*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Bradford, M. A., W. R. Wieder, G. B. Bonan, N. Fierer, P. A. Raymond, and T. W. Crowther. 2016. Managing uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change* 6:751–758.
- Conen, F., M. Zimmermann, J. Leifeld, B. Seth, and C. Alewell. 2008. Relative stability of soil carbon revealed by shifts in delta 15N and C:N ratio. *Biogeosciences* 5:123–128.
- Dence, C. W. 1992. *Methods in Lignin Chemistry*.
- Didion, M., B. Frey, N. Rogiers, and E. Thürig. 2014. Validating tree litter decomposition in the Yasso07 carbon model. *Ecological Modelling* 291:58–68.

- Didion, M., and E. Thürig. 2012. Estimation of carbon stocks and stock changes in soil, LFH layer and deadwood in Swiss forests with Yasso07. Birmensdorf.
- Didion, M., and E. Thürig. 2016. Data on soil carbon stock change, carbon stock and stock change in surface litter and in coarse dead wood prepared for the Swiss GHGI. Swiss Federal Institute for Forest, Snow and Landscape Research WSL / Federal Office for the Environment FOEN, Birmensdorf / Bern.
- Duboc, O., M.-F. Dignac, I. Djukic, F. Zehetner, M. H. Gerzabek, and C. Rumpel. 2014. Lignin decomposition along an Alpine elevation gradient in relation to physicochemical and soil microbial parameters. *Global Change Biology* 20:2272–2285.
- Eckmeier, E., M. Egli, M. W. I. Schmidt, N. Schlumpf, M. Nötzli, N. Minikus-Stary, and F. Hagedorn. 2010. Preservation of fire-derived carbon compounds and sorptive stabilisation promote the accumulation of organic matter in black soils of the Southern Alps. *Geoderma* 159:147–155.
- FOEN. 2017. Emissionen von Treibhausgasen nach revidiertem CO₂-Gesetz und Kyoto-Protokoll, 2. Verpflichtungsperiode (2013–2020). Bundesamt für Umwelt BAFU.
- Frey, B. 2011. Langfristige Streuabbauexperimente auf LWF-Flächen – Daten zur Validierung von Bodenkohlenstoffmodellierungen im Schweizer Wald. Abschlussbericht, Eidgenössische Forschungsanstalt WSL, Zürcherstr. 111, 8903 Birmensdorf.
- González Domínguez, B. R. G. In prep. Climate influence on SOC dynamics overridden by soil and landform properties.
- Gosheva, S. 2017. The Drivers of SOC Storage: the Effect of Climate, Forest Age, and Physicochemical Soil Properties in Swiss Forest Soils. Kumulativ, Universität Zürich, Zürich.

Gosheva, S., L. Walthert, P. A. Niklaus, S. Zimmermann, U. Gimmi, and F. Hagedorn. 2017.

Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils. *Ecosystems*.

Griepentrog, M., S. Bodí, P. Boeckx, F. Hagedorn, A. Heim, and M. W. I. Schmidt. 2014.

Nitrogen deposition promotes the production of new fungal residues but retards the decomposition of old residues in forest soil fractions. *Global Change Biology* 20:327–340.

Gunina, A., and Y. Kuzyakov. 2014. Pathways of litter C by formation of aggregates and SOM

density fractions: Implications from ¹³C natural abundance. *Soil Biology and Biochemistry* 71:95–104.

Hagedorn, F., A. Moeri, L. Walthert, and S. Zimmermann. 2010. Kohlenstoff in Schweizer

Waldböden - bei Klimaerwärmung eine potenzielle CO₂-Quelle | Soil organic carbon in Swiss forest soils - a potential CO₂ source in a warming climate. *Schweizerische Zeitschrift für Forstwesen* 161:530–535.

Heiberger, R. M. 2017. *HH: Statistical Analysis and Data Display: Heiberger and Holland*. R

package version 3.1-34.

Heim, A., and B. Frey. 2004. Early stage litter decomposition rates for Swiss forests.

Biogeochemistry:299–313.

Heinonsalo, J. personal communication. Jussi Heinonsalo, University of Helsinki, personal communication.

Henry, A. J. 1919. Increase of precipitation with altitude.

Hernández, L., R. Jandl, V. N. B. Blujdea, A. Lehtonen, K. Kriiska, I. Alberdi, V. Adermann, I.

Cañellas, G. Marin, D. Moreno-Fernández, I. Ostonen, M. Varik, and M. Didion. 2017. Towards complete and harmonized assessment of soil carbon stocks and balance in

- forests: The ability of the Yasso07 model across a wide gradient of climatic and forest conditions in Europe. *Science of The Total Environment* 599–600:1171–1180.
- Jacob, M., K. Viedenz, A. Polle, and F. M. Thomas. 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). *Oecologia* 164:1083–1094.
- Klotzbücher, T., K. Kaiser, G. Guggenberger, C. Gatzek, and K. Kalbitz. 2011. A new conceptual model for the fate of lignin in decomposing plant litter. *Ecology* 92:1052–1062.
- Lal, R., and K. Lorenz. 2012. Carbon Sequestration in Temperate Forests. *Page Recarbonization of the Biosphere*. Springer Netherlands, Dordrecht.
- Lehmann, J., and M. Kleber. 2015. The contentious nature of soil organic matter. *Nature*.
- Liski, J., M. Tuomi, and J. Rasinmäki. 2009. Yasso07 user-interface manual.
- Liu, Y., S. Li, X. Sun, and X. Yu. 2016. Variations of forest soil organic carbon and its influencing factors in east China. *Annals of Forest Science* 73:501–511.
- Lorenz, K., and R. Lal. 2010. *Carbon Sequestration in Forest Ecosystems*. Springer Netherlands, Dordrecht.
- Luyssaert, S., P. Ciais, S. L. Piao, E.-D. Schulze, M. Jung, S. Zaehle, M. J. Schelhaas, M. Reichstein, G. Churkina, D. Papale, G. Abril, C. Beer, J. Grace, D. Loustau, G. Matteucci, F. Magnani, G. J. Nabuurs, H. Verbeeck, M. Sulkava, G. R. van der WERF, I. A. Janssens, and members of the CARBOEUROPE-IP SYNTHESIS TEAM. 2010. The European carbon balance. Part 3: forests. *Global Change Biology* 16:1429–1450.
- LWF. 2017. . <https://www.wsl.ch/en/forest/forest-development-and-monitoring/long-term-forest-ecosystem-research-lwf.html>.
- Meier, I. C., and C. Leuschner. 2010. Variation of soil and biomass carbon pools in beech forests across a precipitation gradient. *Global Change Biology* 16:1035–1045.

- Merilä, P., M. Malmivaara-Lämsä, P. Spetz, S. Stark, K. Vierikko, J. Derome, and H. Fritze. 2010. Soil organic matter quality as a link between microbial community structure and vegetation composition along a successional gradient in a boreal forest. *Applied Soil Ecology* 46:259–267.
- Nussbaum, M., A. Papritz, A. Baltensweiler, and L. Walthert. 2014. Estimating soil organic carbon stocks of Swiss forest soils by robust external-drift kriging. *Geosci. Model Dev.*:1197–1210.
- Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. I. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science* 333:988–993.
- Prietzl, J., and D. Christophel. 2014. Organic carbon stocks in forest soils of the German Alps. *Geoderma* 221–222:28–39.
- Remund, J., B. Rihm, and B. Huguenin-Landl. 2014. Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert Schlussbericht. Bundesamtes für Umwelt BAFU, Bern.
- Rigling, A., and H.-P. Schaffer. 2015. Forest Report. Federal Office of the Environment FOEN and Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Bern.
- Schleuß, P.-M., F. Heitkamp, C. Leuschner, A.-C. Fender, and H. F. Jungkunst. 2014. Higher subsoil carbon storage in species-rich than species-poor temperate forests. *Environmental Research Letters* 9:014007.
- Schmidt, M. W. I., M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, M. Kleber, I. Kögel-Knabner, J. Lehmann, D. A. C. Manning, P. Nannipieri, D. P. Rasse, S. Weiner, and S. E. Trumbore. 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478:49–56.

- Schrumpf, M., K. Kaiser, G. Guggenberger, T. Persson, I. Kögel-Knabner, and E.-D. Schulze. 2013. Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. *Biogeosciences* 10:1675–1691.
- Thevenot, M., M.-F. Dignac, and C. Rumpel. 2010. Fate of lignins in soils: a review *Soil Biology and Biochemistry*:1200–1211.
- Thuille, A., and E.-D. Schulze. 2006. Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. *Global Change Biology* 12:325–342.
- Tuomi, M., J. Rasinmäki, A. Repo, P. Vanhala, and J. Liski. 2011. Soil carbon model Yasso07 graphical user interface. *Environmental Modelling & Software* 26:1358–1362.
- Tuomi, M., T. Thum, H. Järvinen, S. Fronzek, B. Berg, M. Harmon, J. A. Trofymow, S. Sevanto, and J. Liski. 2009. Leaf litter decomposition? Estimates of global variability based on Yasso07 model. *Ecological Modelling* 220:3362–3371.
- Vesterdal, L., N. Clarke, B. D. Sigurdsson, and P. Gundersen. 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecology and Management* 309:4–18.
- Wang, G., Y. Jia, and W. Li. 2015. Effects of environmental and biotic factors on carbon isotopic fractionation during decomposition of soil organic matter. *Scientific Reports* 5.
- Wang, H., S.-R. Liu, J.-X. Wang, Z.-M. Shi, J. Xu, P.-Z. Hong, A.-G. Ming, H.-L. Yu, L. Chen, L.-H. Lu, and D.-X. Cai. 2016. Differential effects of conifer and broadleaf litter inputs on soil organic carbon chemical composition through altered soil microbial community composition. *Scientific Reports* 6.
- Wiesmeier, M., J. Prietzel, F. Barthold, P. Spörrlein, U. Geu?, E. Hangen, A. Reischl, B. Schilling, M. von Lütow, and I. Kögel-Knabner. 2013. Storage and drivers of organic carbon in

forest soils of southeast Germany (Bavaria) ? Implications for carbon sequestration.

Forest Ecology and Management 295:162–172.

de Wit, H. A., T. Palosuo, G. Hysten, and J. Liski. 2006. A carbon budget of forest biomass and soils in southeast Norway calculated using a widely applicable method. Forest Ecology and Management 225:15–26.

Yuste, J. C., I. A. Janssens, A. Carrara, L. Meiresonne, and R. Ceulemans. 2003. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. Tree Physiology:1263–1270.

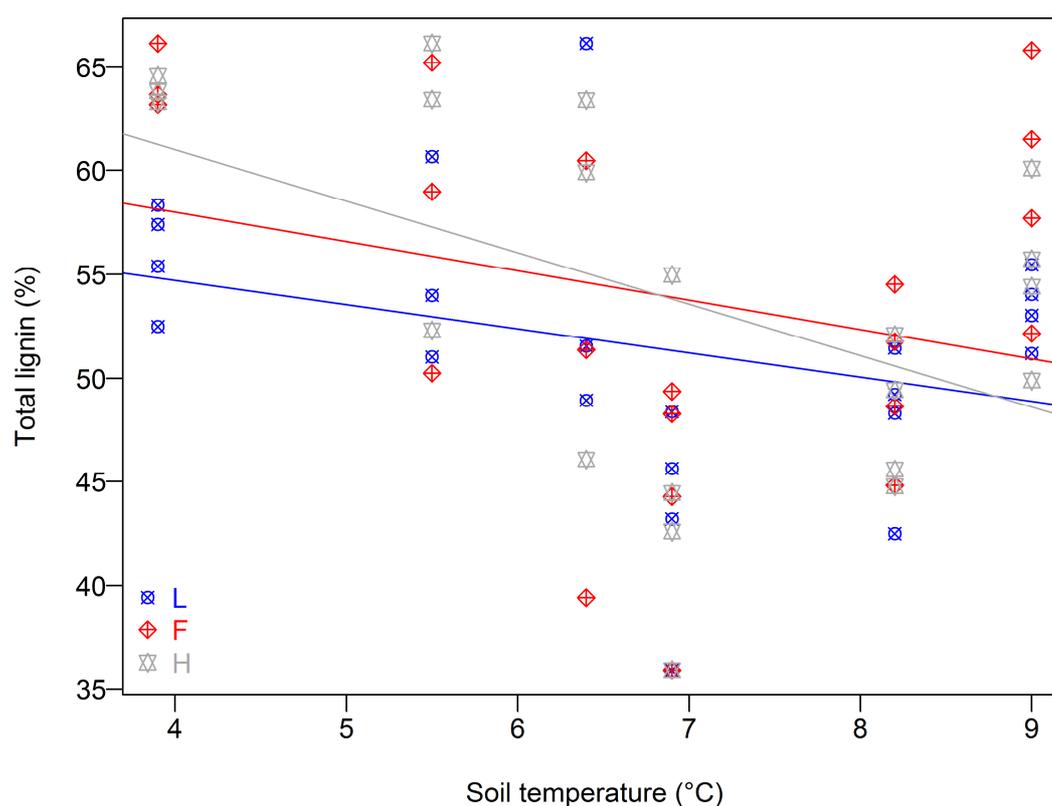
Zentrallabor, W. 2017. Zentrallabor WSL. <https://www.wsl.ch/de/ueber-die-wsl/organisation/facheinheiten/support/zentrallabor.html>.

8. Supplementary data

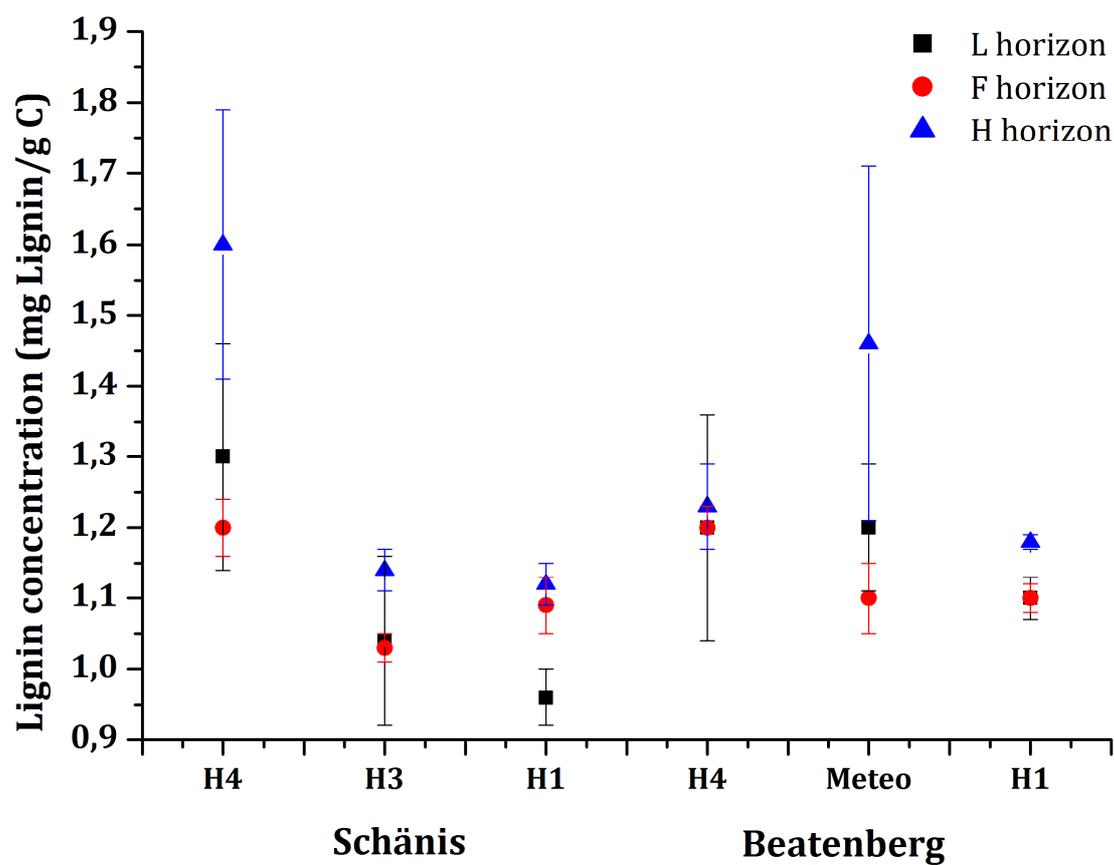
Supplementary Table 1: Relative proportions of lignin extraction compounds in the two elevational transects separated according to organic layer horizons.

Org. layer horizon	Beatenberg				Schänis			
	W	E	A	K	W	E	A	K
L	16.9	3.3	1.2	78.6	15.7	3.3	1.7	79.3
F	14.3	7.9	1.2	76.7	17.3	1.6	1.9	79.1
H	13.2	6.8	1.4	78.7	15.6	0.8	1.8	81.7

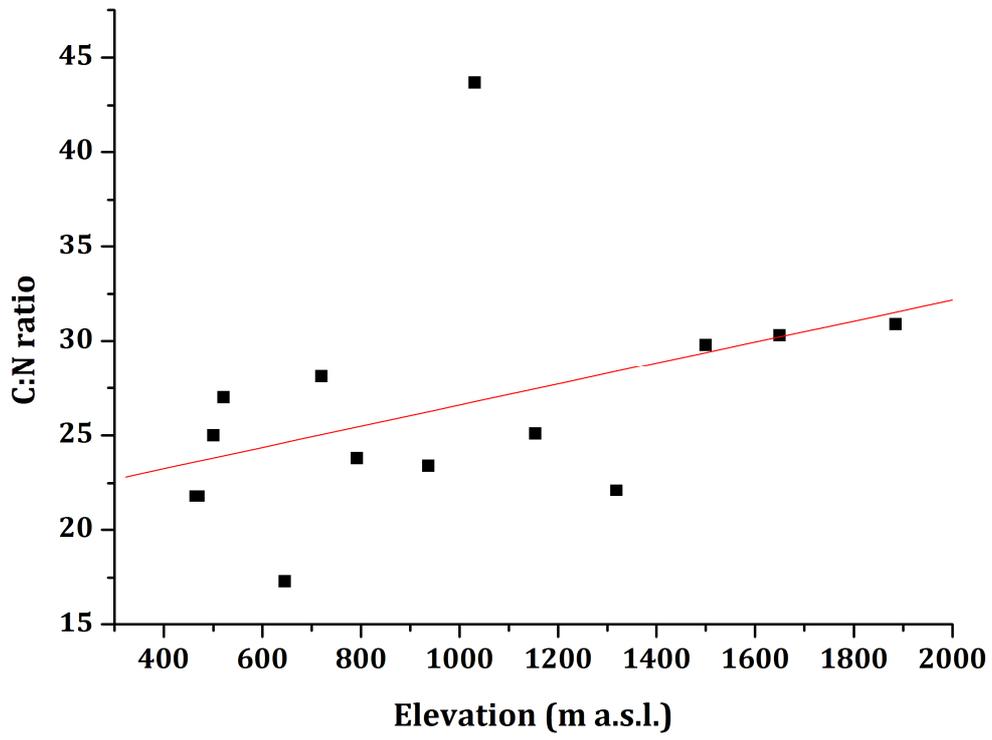
*W: Water-soluble compound, E: Ethanol-soluble compound, A: Acid-soluble lignin (ASL), K: Klason lignin



Supplementary Figure 1: Relationship between soil temperature (in °C) and total lignin content (in %) at the two elevational transects (Beatenberg and Schänis) according to organic layer horizons (L: blue, F: red, and H: grey). Lines represent robust linear regressions.



Supplementary Figure 2: Lignin:C ratio according to organic layer horizons (L-F-H) and elevational transects (Schänis sites: 540 (H4), 800 (H3), and 1150 (H1) m a.s.l., Beatenberg sites: 1200 (H4), 1520 (Meteo), and 1800 (H1) m a.s.l.). Data is represented as means \pm standard errors.



Supplementary Figure 3: Relationship C:N ratios according to elevation (in m. a.s.l.). Red line represents a linear fit.