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## Shift in plant-soil interactions along a lakeshore hydrological gradient

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► **To cite this version:**

Wenjuan Feng, Mathieu Santonja, Luca Bragazza, Alexandre Buttler. Shift in plant-soil interactions along a lakeshore hydrological gradient. *Science of the Total Environment*, 2020, 742, pp.140254. 10.1016/j.scitotenv.2020.140254 . hal-02892088

**HAL Id: hal-02892088**

**<https://amu.hal.science/hal-02892088>**

Submitted on 17 Sep 2020

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1 **Title: Shift in plant-soil interactions along a lakeshore hydrological gradient**

2

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24

25 **Abstract**

26 Wetlands occupy the transitional zone between aquatic and terrestrial systems.  
27 Hydrological conditions have significant influence on wetland plant communities and soil  
28 biogeochemistry. However, our knowledge about plant-soil interactions in wetlands along  
29 hydrological gradients is still limited, although it is crucial to guide wetland management  
30 decisions and to adapt, whenever possible, hydrological conditions to the different plant  
31 communities. To this aim, we related vegetation composition, plant functional traits, soil  
32 physicochemical properties, soil microbial biomass, and soil enzymatic activities in wetlands  
33 on the southeastern shore of Neuchâtel lake, Switzerland, a lake whose level is partly regulated.  
34 Aboveground and belowground plant biomass and correspondent C, N and P concentrations  
35 remained constant or decreased moving from the vegetation community subjected to more  
36 frequent flooding events to the community with almost no flooding. The soil organic layer  
37 exhibited always higher nutrient concentrations and greater enzymatic activities than the  
38 organo-mineral and mineral layers. The chemical and biological characteristics of the soil  
39 organic layer showed decreasing values for most of the parameters along the hydrological  
40 gradient from lakeshore to upland wetland communities. On the basis of nutrient stoichiometry,  
41 plant-soil system in the plant community with most flooding events had no-nutrient limitation,  
42 while there was a N limitation in the transitional community. In the upland plant community  
43 where there was no flooding effect, the plant-soil system was characterized by N and P co-  
44 limitation. These findings are important because they provide a threshold for flooding regime  
45 by the lake in the context of optimization of lake level regulation under various stakeholders  
46 needs.

47

48 **Keywords:** wetland; flooding; plant biomass; biogeochemistry; nutrient stoichiometry

49

## 50 **1. Introduction**

51 Wetlands are important ecosystems supporting biodiversity by providing habitats for  
52 numerous plants and animals (Neckles et al., 1990; Gibbs, 2000). Furthermore, they ensure  
53 several key ecosystem services such as flood control, groundwater replenishment, water  
54 purification, carbon (C) sequestration and they provide livelihoods for local populations  
55 (Ramsar, 2013). Extreme climate events such as flooding and drought, as well as anthropogenic  
56 activities such as sand mining and agriculture intensification (Lai et al., 2014; Xu et al., 2019)  
57 are likely to change the hydrological conditions of wetlands (Hingray et al., 2007; Sarneel et  
58 al., 2019) and their habitats (Dawson et al., 2003). In particular, variation in frequency and  
59 duration of soil flooding and dryness can profoundly affect biogeochemical cycles of C,  
60 nitrogen (N) and phosphorous (P) with cascading effects on wetland plant community  
61 composition (Baldwin and Mitchell, 2000; Wang et al., 2015b; Swanson et al., 2017).

62 Flooding regime affects soil organic C and nutrient content and availability by controlling  
63 microbial mineralization (Wolf et al., 2013; Wang et al., 2015a; Swanson et al., 2017).  
64 Accumulation of degraded organic compounds in water saturated soils and under oxygen  
65 deficiency (Hopkinson, 1992; Swanson et al., 2017) leads to increasing dissolved soil organic  
66 carbon (DOC) and nutrients, resulting partly from C, N and P leaching from leaf litter under  
67 rewetting conditions (Baldwin and Mitchell, 2000; Shrestha et al., 2014). Extracellular  
68 degrading enzymes are produced by microorganisms in response to environmental signals or  
69 through cell lysis (Sinsabaugh et al., 2009; Cui et al., 2018). It has been proved that their higher  
70 activities in wet conditions can accelerate organic C, N and P mineralization rates by breaking  
71 down large organic molecules for microbial consumption (Wilson et al., 2011; Heuck et al.,  
72 2015). Soil organic carbon (SOC) and nutrient concentrations were shown to be relatively  
73 higher in the wetter as compared to the drier part in both river and lake wetlands (Bai et al.,  
74 2005; Wang et al., 2016) and this increase of nutrient pool promoted microbial activity and

75 nutrient cycling (Baldwin and Mitchell, 2000; Heuck et al., 2015). Thus, microbial biomass is  
76 both a source and a sink for nutrients and participates to nutrient transformation (Gil-Sotres et  
77 al., 2005). However, drying of formerly inundated wetlands may cause a severe C limitation  
78 and consequently a decrease in the rate of nutrient cycling because of C being lost (Baldwin  
79 and Mitchell, 2000) and microbial die-off (Qiu and McComb, 1995).

80 Hydrological conditions in wetlands can have strong impact on plant-soil interactions (Fu  
81 et al., 2018; Wang et al., 2018) through changing both organic matter accumulation and  
82 mineralization processes (Wilson et al., 2011; Swanson et al., 2017). Plant C, N, P  
83 concentrations and their stoichiometric ratios may reflect nutrient availability from substrate  
84 and plant nutrient uptake (Demars and Edwards, 2007; Agren, 2008; Elser et al., 2010),  
85 Furthermore, the above- and belowground nutrient content and stoichiometry are tightly linked  
86 (Bell et al., 2014) and therefore represent important indicators of ecosystem structure and  
87 nutrient cycling (Zechmeister-Boltenstern et al., 2015; Sardans et al., 2017). Plant nutrient  
88 content and stoichiometry have been studied to detect tissue nutrient allocation (Wang et al.,  
89 2015b; Hu et al., 2018), seasonal nutrient variation (Fu et al., 2018), nutrient limitation (Bedford  
90 et al., 1999; Demars and Edwards, 2007) or variation between plant functional types (Wang  
91 and Moore, 2014; Hu et al., 2018). For example, Li et al. (2017) and Li et al. (2018b) showed  
92 that soil nutrient content and stoichiometry are changing along hydrological gradients, and that  
93 plant nutrient content and stoichiometry are regulated rather by flooding duration than by soil  
94 nutrient content.

95 Different plant species and their abundances can also cause variation in soil and microbial  
96 nutrient stoichiometry (De Graaff et al., 2010; Bell et al., 2014) and modulate ecosystem  
97 functions through ecological processes affecting microbial and enzymatic activities (Bever et  
98 al., 2010; Kardol et al., 2010). There are ample evidences of the close relationships among plant  
99 species and soil stoichiometry (Hobbie et al., 2006; Bell et al., 2014; Wang et al., 2018). Pattern

100 of nutrient availability varies among plant species (Bedford et al., 1999; Güsewell and  
101 Koerselman, 2002) and conversely, plants apply some control over nutrient availability by  
102 driving soil microbial and enzymatic activities (Richardson et al., 2009; Sardans and Peñuelas,  
103 2012; Bragazza et al., 2015). Along hydrological gradients, the relationship between plant  
104 functional traits and soil properties has been explored in wetlands, revealing potential plant-soil  
105 relationships (Liu et al., 2015; Wang et al., 2015b; Hu et al., 2018).

106 In the present study, we investigated soil physico-chemical characteristics (including C,  
107 N, P stock and availability), soil microbial biomass nutrients (C, N, P), soil enzymatic activities,  
108 and nutrient content in plant and moss biomass (C, N, P) in three plant communities along a  
109 hydrological gradient from lakeshore to upland. Investigations took place at the beginning and  
110 at peak of the growing season in a wetland along the southern shore of Lake Neuchâtel,  
111 Switzerland. We hypothesized that: (i) soil nutrient content, microbial biomass and enzymatic  
112 activities, and plant nutrient content are higher in the flooded areas near the lakeshore as  
113 compared to the upland area; (ii) the nutrient stoichiometry of plant and soil components can  
114 reveal contrasted ecosystem functioning along the hydrological gradient, with a N and P  
115 limitation for plant communities of the upland area, as opposed to no N and P limitation for the  
116 plant communities close to the lakeshore subjected to flooding.

117

## 118 **2. Materials and methods**

119

### 120 ***2.1 Study site***

121 The study was conducted in the wetlands along the southern shore of Lake Neuchâtel  
122 (46°54'28"N, 6°52'02"E) in Switzerland, which is the Ramsar site called "Grande Cariçaie".  
123 The climate is defined as pluvial sub-oceanic (Buttler, 1990) with a mean annual temperature  
124 of 9.4 °C and mean annual precipitation of 891 mm (MeteoSuisse,

125 <https://www.meteosuisse.admin.ch> - Payerne, period 1981-2010). Five main plant communities,  
126 respectively dominated by *Molinia caerulea* (L.) Moench, *Schoenus nigricans* L., *Carex*  
127 *panicea* L., *Carex elata* All. and *Phragmites australis* (Ca.) Steud. can be found moving from  
128 the upland wetland to the lake shoreline (Buttler et al., 1985; Buttler and Gallandat, 1989;  
129 Buttler and Muhlhauser, 1994). These plant communities experience an annual flooding regime  
130 depending on the lake water level, which is partly regulated and is on average low in winter,  
131 high in spring and intermediate in summer and autumn  
132 (<https://www.hydrodaten.admin.ch/fr/2149.html>). Thus, flooding by the intrusion of the lake  
133 into the wetland occurs mainly in spring and early summer time, and relates to the snowmelt in  
134 the Alps. Heavy rain can recharge the soil water rapidly in autumn, which translates into  
135 superficial flooding's event in the upland wetlands which are not influenced by the lake water  
136 (Buttler, 1987).

137

## 138 **2.2. Sampling design**

139 Distinct plant communities distributed along an elevation gradient (i.e. transects from  
140 lakeshore to upland) were selected, a method frequently used in wetland ecosystem studies (e.g.  
141 Li et al., 2017; Fu et al., 2018). The three plant communities dominated by *C. elata*, *C. panicea*  
142 and *S. nigricans* were selected for this study because they represent the interface between the  
143 vegetation influenced by the lake intrusion into the wetland, e.g. *Caricetum elatae* W. Koch 26,  
144 variant with *Phalaris arundinaceae*, the transitional vegetation, e.g. *Caricetum elatae* W. Koch  
145 26, variant with *Carex panicea* and the vegetation not reached by the lake, e.g. *Orchio-*  
146 *Schoenetum nigricantis* Oberd. 57, variant with *Galium palustre* (Buttler and Gallandat, 1989).  
147 Along this gradient, which is topographically characterized by a gentle slope with about 30-60  
148 cm increase of soil level towards the upland wetland, soils show a marked hydromorphic feature:

149 histic humaquept (*C. elatae* community), wet typic haplaquoll (*C. panicea* community) and dry  
150 typic haplaquoll (*S. nigricans* community) (Buttler and Gobat, 1991).

151 Four transects at least 1 km apart were established from the upland to the shoreline  
152 (Supplementary Fig. S1). In each of the three plant communities crossed by these transects, one  
153 10 m × 10 m plot was randomly selected, leading to a total of 12 plots (4 transects × 3 plant  
154 communities). The different botanical compositions in different plots are given in the  
155 Supplementary Table S1. One piezometer was installed in each plot to monitor the soil water  
156 level (Supplementary Fig. S2). *Carex elata* community was mostly flooded with decreasing  
157 water levels during the study period, *C. panicea* community experienced wet conditions with  
158 soil saturated in spring and a subsequent drop of water level below -35 cm in August, and *S.*  
159 *nigricans* community, typically never flooded with water level decreasing from -4 to -70 cm  
160 during the measurement period. Data loggers (Onset HOBO Water Temp Pro v2) were also  
161 installed in the soil at 5 cm depth to monitor the soil temperature (Supplementary Fig. S3).  
162 Overall, from March to August, the top-soil temperature increased regularly from 5 °C to more  
163 than 20 °C, with the soil in *C. elata* community being always slightly colder than that in *C.*  
164 *panicea* and *S. nigricans* communities, which had very similar temperatures.

165

### 166 **2.3. Plant and soil collection**

167 Plant and soil samples were collected in all plots at the beginning of the plant growing  
168 season (April 2018) and at the peak of plant biomass (July 2018) (Supplementary Fig. S4). In  
169 addition to the groundwater level measured with the piezometers, the soil volumetric water  
170 content was measured at 0-10 cm depth in each plot and at each sampling time using a portable  
171 TDR (FieldScout TDR100, UK).

172 Aboveground vascular plant biomass (AGB), moss biomass (MB) and plant litter (L)  
173 were collected in all plots using a 50 cm × 50 cm quadrat in *S. nigricans* and *C. panicea*

174 communities, and a 100 cm × 100 cm quadrat in *C. elata* community. Vascular plants were  
175 clipped at the ground level, while litter and mosses were picked up carefully to avoid soil  
176 particles. All the aboveground material was placed in separated bags, transported to the  
177 laboratory, and then oven-dried at 65 °C for 4 days. Once oven-dried, this plant material was  
178 weighted in order to estimate the dry mass (DM) per square meter for each plot and kept for  
179 further analysis.

180 Three soil cores (5.6 cm diameter × 30 cm depth) per plot were randomly collected (in-  
181 between the tussocks for *C. elata* and *S. nigricans* communities) for belowground biomass  
182 (BGB - roots and rhizomes) sampling. The same layers as for soil sampling (see below) were  
183 used and pooled so as to have a composite sample for each layer. Roots and rhizomes were  
184 carefully collected by gentle washing in water. As for the aboveground material, the  
185 belowground biomass was oven-dried at 65 °C during 4 days and weighted in order to estimate  
186 the dry mass (DM) per square meter for each plot and kept for further analysis.

187 Three other soil cores (5.6 cm diameter × 30 cm depth) per plot were collected in a similar  
188 way for the soil sampling as for the belowground biomass. Based on the soil color and texture,  
189 each soil core was divided into three parts: organic layer (OL), organo-mineral layer (OML),  
190 and mineral layer (ML) ([Supplementary Figs. S4 and S5](#)). The top 5 cm of the organic layers  
191 from the three soil cores were collected and pooled in one composite sample. For the organo-  
192 mineral layer, the 5 cm immediately below the entire organic layer were taken and pooled. For  
193 the mineral layer, the upper 2 cm of this layer was removed to avoid irregular transition and the  
194 following 5 cm below were collected, which again were pooled in one composite sample. These  
195 samples were placed in polyethylene bags, transported to the laboratory and stored at 4 °C until  
196 being further processed.

197 In order to determine the soil bulk density (BD), a last soil core was sampled and an intact  
198 piece (5.6 cm diameter × 5 cm depth) was taken for each soil layer and oven-dried at 105 °C

199 for 48 h and weighted. Bulk density was calculated by dividing the mass of the oven-dried soil  
200 sample by its volume and expressed as  $\text{g}\cdot\text{cm}^{-3}$ .

201

#### 202 ***2.4. Plant and moss C, N and P analyses***

203 A subsample of dry plant material was washed and dried again, then ground to a fine  
204 powder using a ball mill before chemical analysis. Total organic carbon (C) and total nitrogen  
205 (N) concentrations were determined by thermal combustion using an elemental analyzer (CE  
206 Instruments model NA2500 Nitrogen Carbon Analyzer) and expressed as percent of dry weight.  
207 Total phosphorus (P) concentration was determined by the molybdenum blue method after  
208  $\text{HClO}_4\text{-H}_2\text{SO}_4$  digestion using a continuous flow autoanalyser (FlowSys, Systea, Anagni, Italy)  
209 and expressed as percent of dry weight. Finally, C:N, C:P and N:P stoichiometric ratios were  
210 calculated for aboveground and belowground plant biomass, plant litter and moss biomass  
211 ([Supplementary Fig. S4](#)).

212

#### 213 ***2.5. Soil chemical analyses***

214 For chemical analyses, any visible coarse plant material in the soil samples was removed  
215 by hand-sorting. Soil samples were divided into two subsamples: i) a subsample was oven-dried  
216 at  $65\text{ }^\circ\text{C}$  for 4 days and ground to a fine powder using a ball mill in order to determine total  
217 organic C (TOC), N (TN) and P (TP) concentrations, and ii) a fresh subsample was stored at  $4$   
218  $^\circ\text{C}$  in order to determine soil pH, nitrate ( $\text{N-NO}_3^-$ ) and ammonium ( $\text{N-NH}_4^+$ ) concentrations,  
219 dissolved organic C (DOC), N (DN) and P (DP) concentrations, soil microbial biomass and soil  
220 enzymatic activities. For the determination of soil water content (SWC) and in order to quantify  
221 all the measured parameters per g of dry soil weight, 10 g of fresh soil samples for each replicate  
222 were oven-dried at  $105\text{ }^\circ\text{C}$  for 48 h. In addition, these oven-dried samples were burned at  $550\text{ }^\circ\text{C}$   
223 for 6 h in order to determine the soil organic matter content by loss of ignition (LOI).

224 TOC, TN and TP were determined for each replicate following the same methods as for  
225 plant and moss material and expressed as percent of dry soil weight. Soil pH was measured in  
226 1:5 (w/v) soil water suspension with a portable pH meter (WTW multi 3430, Weilheim,  
227 Germany) after stirring the mixture for 2 h. N-NH<sub>4</sub><sup>+</sup> and N-NO<sub>3</sub><sup>-</sup> concentrations were  
228 determined after extraction of 5 g of fresh soil with 30 ml of 1 M KCl extraction and filtration  
229 through 0.45 µm filter using a continuous flow autoanalyzer (SEAL Analytical, Germany) and  
230 the results were expressed as mg.kg<sup>-1</sup> oven dry soil.

231 Microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) were  
232 measured using the chloroform fumigation extraction method (Brookes et al., 1985). Three  
233 pairs of about 5 g of fresh soil (3 g for MBP) were weighed for each replicate. One sample from  
234 each pair was stored at 4 °C while the other sample was put in a vacuum desiccator and  
235 subjected to chloroform vapor. After 24 h of fumigation in the dark at ambient temperature, the  
236 fumigated soil samples and the corresponding ones kept unfumigated in the fridge were  
237 extracted with a 25 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub> for MBC and MBN and with 40 ml of 0.5 M NaHCO<sub>3</sub>  
238 for MBP. All solutions were filtered through a 0.45 µm filter before analysis. Organic C and N  
239 concentrations in the solutions from both fumigated and unfumigated samples were determined  
240 using a TOC/TN analyzer (Shimadzu TOC-V), while P concentration was determined by  
241 colorimetry using a spectrophotometer at 890 nm (Olsen et al., 1954). Soil DOC, DN and DP  
242 were determined as the concentrations obtained from the unfumigated samples. The soil MBC,  
243 MBN and MBP values were estimated as the differences between fumigated and unfumigated  
244 samples using an extractability factor of 0.45 for C (Vance et al., 1987), 0.54 for N (Brookes et  
245 al., 1985) and 0.40 for P (Brookes et al., 1982) and expressed as mg.kg<sup>-1</sup> oven dry soil.

246 In order to measure the soil enzymatic activities, 1 g of fresh soil was mixed with 10 ml  
247 of water, stirred for 1 h, and the supernatant was collected after centrifugation. The activities  
248 of extracellular hydrolase enzymes were measured by adding 50 µl of 4-methylumbelliferyl-β-

249 D-glucoside for the activity of  $\beta$ -glucosidase (BG), 4-MUF-N-acetyl- $\beta$ -D-glucosaminide for  
250 the activity of  $\beta$ -1, 4-N-acetylglucosaminidase (NAG), L-leucine-7-amido-4-methylcoumarin  
251 hydrochloride for the activity of leucine aminopeptidase (LAP) and 4-MUF-phosphate for the  
252 activity of phosphatase (PHO) to 250  $\mu$ l of the soil extract. After 2 h of incubation, the  
253 fluorescence was measured on a microplate reader (BioTek SynergyMX) at 450 nm emission  
254 and 330 nm excitation wavelength. To quantify product release and account for quenching  
255 effects, a set of standards was prepared using methylumbelliferone (MUF) and 7-amino-4-  
256 methylcoumarin (MUC) mixed with soil extract. Enzymatic activities were expressed as  $\mu$ mol  
257 of substrate (MUF and MUC) converted per min and per g (dry weight) of soil (Freeman et al.,  
258 2004).

259 The C:N, C:P and N:P stoichiometric ratios were calculated for bulk soil and its dissolved  
260 fraction and for microbial biomass.

261

## 262 **2.6. Data analysis**

263 Statistical analyses were performed with the R software 3.2.3 (R. Core Team, 2017).  
264 When necessary, data were log or square root transformed, and the normality and  
265 homoscedasticity of the distribution of residuals of models were visually verified.

266 We used a linear mixed effects model approach (“nlme” package, Pinheiro et al., 2020),  
267 followed by Tukey HSD tests for post hoc comparisons, to test the effects of vegetation type  
268 (*C. elata*, *C. panicea* or *S. nigricans* community), growing season (beginning or peak of the  
269 growing season), and their interactions on plant and moss parameters. To consider the fact that  
270 we had three plots per transect, the random part of the model indicated that the plots were nested  
271 within transects.

272 For what concerns the soil physico-chemical, microbial and enzymatic parameters, we  
273 used a linear mixed-effects model approach followed by Tukey HSD tests for post hoc

274 comparisons in order to test the effects of soil layers (organic, organo-mineral or mineral layer),  
275 vegetation type (*C. elata*, *C. panicea* or *S. nigricans* community), growing season (beginning  
276 or peak of the growing season), and their interactions, specifying soil layers nested into plots  
277 nested into transects as random factor.

278 A redundancy analysis (RDA) was used to link the plant chemical characteristics of the  
279 three vegetation types taken at two sampling times (C, N and P contents and their stoichiometry  
280 in above- and belowground plant biomass, moss biomass and plant litter) as a response to the  
281 soil characteristics (chemical and biological variables – see [Supplementary Tables S2 and S3](#)).

282 Finally, a principal component analysis (PCA) was used to determine the correlations  
283 between stoichiometry of C, N and P in the plant material, in the bulk soil and in its dissolved  
284 fraction, and in the microbial biomass.

285

### 286 **3. Results**

287

#### 288 ***3.1 Plant and moss parameters***

289 Litter mass and belowground biomass were between 2.4 and 3.5 times higher in *C. elata*  
290 community compared to *C. panicea* and *S. nigricans* communities ([Table 1 and 2](#);  
291 [Supplementary Table S2](#)), while differences in aboveground and moss biomass among the three  
292 plant communities were dependent on the sampling time during the growing season (significant  
293 vegetation type  $\times$  growing season interaction, [Table 1](#)). At the beginning of the growing season,  
294 aboveground biomass of *C. elata* community was lower than that of *C. panicea* and *S. nigricans*  
295 communities, while aboveground biomass of *C. elata* community was higher than that of *C.*  
296 *panicea* at the peak of growing season ([Fig. 1a](#)). Concerning moss biomass, there was no  
297 difference among plant communities at the beginning of growing season, while moss biomass  
298 of *C. elata* community was 5 times higher than that of the two other plant communities at the

299 peak of growing season (Fig. 1b). When summing all plant and moss materials, the organic  
300 matter stock was approximately 2.5-time higher in *C. elata* community (10'063 g.m<sup>-2</sup>) as  
301 compared to *C. panicea* (4'037 g.m<sup>-2</sup>) and *S. nigricans* (3'803 g.m<sup>-2</sup>) communities. The  
302 aboveground biomass increased more than 8 times during the growing season, while litter mass  
303 was 30% lower (Table 2; Supplementary Table S2). Belowground biomass decreased by 32%  
304 from the beginning to the peak of biomass period, while moss biomass increased 1.6-times,  
305 although these trends were not significant (Tables 1 and 2; Supplementary Table S2).

306 Carbon content in belowground biomass and litter were higher in *C. elata* community  
307 compared to *S. nigricans* community (Table 1; Supplementary Table S2). Nitrogen content in  
308 aboveground biomass of *C. panicea* community was similar to that of the *C. elata* community  
309 and higher than that of *S. nigricans* community at the beginning of the growing season, while  
310 it was similar to that of *S. nigricans* community and lower than that of *C. elata* community at  
311 the peak of the growing season (significant vegetation type × growing season interaction, Table  
312 1; Fig. 1c). Phosphorus content in aboveground biomass showed a trend of decrease according  
313 to the gradient *C. elata* > *C. panicea* > *S. nigricans*, i.e. from lakeshore to upland communities  
314 (Table 1; Supplementary Table S2). The decrease in P content in aboveground biomass during  
315 the growing season was dependent on the plant community (significant vegetation type ×  
316 growing season interaction, Table 1), since the P content decreased only in the *C. elata* and *C.*  
317 *panicea* communities (Fig. 1d).

318 Nitrogen and P content in moss biomass was also higher in *C. elata* compared to *S.*  
319 *nigricans* community (Table 1; Supplementary Table S2). In litter, C content increased, while  
320 N content decreased during the growing season, and in belowground biomass both N and P  
321 contents decreased during the growing season (Tables 1 and 2; Supplementary Table S2).

322

### 323 3.2 Soil physico-chemical parameters

324 Bulk density and pH increased according to the gradient organic > organo-mineral >  
325 mineral layers (i.e. soil depth) while, in the opposite, all other physico-chemical parameters  
326 decreased according to soil depth (Tables 3 and 4; Supplementary Table S3). Moreover, bulk  
327 density and pH increased from lakeshore to upland plant communities while, in the opposite,  
328 all other physico-chemical parameters decreased according to this vegetation gradient (Tables  
329 3 and 4; Supplementary Table S3). Overall, more physico-chemical parameters were  
330 significantly different between *C. elata* and *C. panicea* communities than between *C. panicea*  
331 and *S. nigricans* communities (Supplementary Table S3).

332 Except for soil pH and nitrate, the differences among the three plant communities were  
333 dependent on the soil layer (significant soil layer × vegetation type interaction, Table 3), with  
334 decreasing differences among plant communities according to increasing soil depth. For  
335 example, while we observed marked differences for soil total P (TP) and available P (DP) in  
336 organic layer among plant communities, the values of mineral layer were much less marked or  
337 similar between plant communities (Fig. 2a and b). The differences in soil available C (DOC)  
338 and nitrate contents among the 3 plant communities were also dependent on the growing season  
339 (significant vegetation type × growing season interaction, Table 3). Soil DOC values were  
340 similar between the 3 plant communities at the beginning of the growing season, while DOC  
341 was higher in *C. elata* compared to the two other communities at the peak of growing season  
342 (Fig. 3a). Soil nitrate was higher in *C. elata* and *C. panicea* communities compared to *S.*  
343 *nigricans* community at the beginning of the growing season, while similar values between the  
344 three plant communities were observed at the peak of growing season (Fig. 3b).

345 Only few soil physico-chemical parameters varied across the growing season (Table 3).  
346 Soil pH and DN increased while, on the opposite, nitrate decreased between the beginning and  
347 the peak of the growing season (Tables 3 and 4; Supplementary Table S3). The increase in soil  
348 available N (DN) across the growing season was higher in the organic and organo-mineral

349 layers compared to the mineral layer (significant soil layer  $\times$  growing season interaction, [Table](#)  
350 [3](#); [Fig. 4a](#)), while ammonium content increased only in the organic layer (significant soil layer  
351  $\times$  growing season interaction, [Table 3](#); [Fig. 4b](#)).

352

### 353 **3.3 Soil microbial biomass and enzyme activity**

354 Soil microbial biomass and enzymatic parameters decreased according to soil depth and  
355 according to the vegetation gradient from lakeshore to upland ([Tables 3 and 4](#); [Supplementary](#)  
356 [Table S3](#)). Contrary to microbial biomass, the four enzymatic activities varied across the  
357 growing season ([Table 3](#)), with higher values reported at the peak compared to the beginning  
358 of growing season ([Table 4](#); [Supplementary Table S3](#)).

359 Except for leucine aminopeptidase activity, the differences in microbial biomass and  
360 enzymatic parameters among the three plant communities were dependent on the soil layer  
361 considered (significant soil layer  $\times$  vegetation type interaction, [Table 3](#)), with decreasing  
362 differences according to increasing soil depth ([Fig. 2c and d](#)). Finally, the differences in  
363 enzymatic parameters among plant communities or among soil layers were stronger at the peak  
364 compared to the beginning of growing season (significant soil layers  $\times$  growing season and  
365 vegetation type  $\times$  growing season interactions, [Table 3](#)).

366

### 367 **3.4 Plant-soil interactions**

368 The redundancy analysis model (RDA) provides a synthetic view on the relationship  
369 between plant chemical characteristics as a response to soil characteristics in the upper organic  
370 layer at two sampling periods, April and July ([Supplementary Fig. S6](#)). *C. elata* community  
371 samples are strongly linked, along axis 1, to high values of N and P in aboveground biomass,  
372 moss biomass and plant litter, while belowground biomass samples vary mostly along axis 2,  
373 with higher P and N values in April.

374 The relationships among stoichiometry of C, N and P in all sampled compartments (plant,  
375 moss, soil and microbial biomass) in April and July are given in the principal component  
376 analysis (PCA) of the Fig. 5. *C. elata* community samples are mostly positively correlated to  
377 soil dissolved C:N ratio and strongly negatively correlated to C:P and N:P in microbial biomass.  
378 Samples of *C. panicea* community are mostly positively correlated to C:N ratios in  
379 belowground biomass, in bulk soil and also weakly in microbial biomass, and strongly  
380 negatively correlated to C:P and N:P ratios in bulk soil and in belowground biomass, as well as  
381 in soil dissolved C:P. Finally, samples of *S. nigricans* community are positively correlated to  
382 several ratios, in particular to C:P and N:P ratios in microbial biomass, to soil dissolved N:P,  
383 to bulk soil C:N ratio and to C:N, C:P and N:P ratios in aboveground biomass, moss and litter.  
384

#### 385 **4. Discussion**

386

##### 387 ***4.1 Plant biomass and its nutrients content reflect the hydrological gradient induced by the*** 388 ***lake flooding***

389 The seasonal pattern of aboveground biomass was different among the three vegetation  
390 types. In spring, before the vegetation started to grow, *C. elata* had the lowest aboveground  
391 biomass, but later in the season, at the peak of biomass period, the trend reversed and *C. elata*  
392 community developed more biomass compared to *C. panicea* and *S. nigricans* communities (in  
393 this later case the difference was only marginal). This reflects in the litter accumulation, which  
394 was higher in *C. elata* community. Mosses also developed more during the vegetation period  
395 in *C. elata* community due to the very favorable microclimatic conditions resulting from high  
396 soil moisture and shading conditions under the tussocks. The total plant biomass reflects well  
397 the hydrological gradient, with highest values in *C. elata* community and lowest in *S. nigricans*  
398 community. Li et al. (2017) found opposite results for biomass distribution along an elevation

399 gradient in Dongting Lake wetland (China), with increasing aboveground biomass with  
400 decreasing soil water content. This can be explained by the different hydrological conditions in  
401 these two wetlands. In Dongting Lake wetland, the upland plant community still experiences  
402 an annual flooding event, similarly to the community close to the lake shoreline and therefore  
403 its ecological functioning cannot be assimilated to a conservative nutrient poor biogeochemical  
404 cycle as in the *S. nigricans* community investigated in the present study.

405 As we hypothesized, plant nutrient content generally decreased along the hydrological  
406 gradient, with higher values in *C. elata* community, which is under the influence of the lake  
407 flooding. This was particularly true for N and P content in plant aboveground and moss  
408 biomasses. The concentrations of these two elements in aboveground biomass also showed the  
409 intermediate status of *C. panicea* community, as exemplified by its N content which was similar  
410 to *C. elata* in spring, when both vegetation types were flooded by the lake, and similar to *S.*  
411 *nigricans* later in the dryer season (Fig. 1c). Nutrients provided by the lake water are important  
412 sources for wetland plants, and indeed, in *C. elata* community, and to some extent also in *C.*  
413 *panicea* community, vascular plants and mosses could absorb more nutrients than in *S.*  
414 *nigricans* community, which contributed to the higher biomass accumulation. Furthermore, C  
415 and nutrients from the litter leachates (Demars and Edwards, 2007; Shrestha et al., 2014) and  
416 organic matter accumulation (Wilson et al., 2011; Swanson et al., 2017) under flooding  
417 conditions are also beneficial for the plant nutrient absorption and growth.

418 We assessed the nutrient content in aboveground and moss biomass by pooling the plant  
419 species, since each plant community was dominated by only a few species (Buttler, 1987, see  
420 also Supplementary Table S1). Nevertheless, plant nutrients can show a high interspecific  
421 variability and low phenotypic response to nutrient supply (Demars and Edwards, 2007; Li et  
422 al., 2017; Hu et al., 2018). Plants have lower nutrient resorption proficiency in nutrient-rich  
423 environment (Hopkinson, 1992; Mao et al., 2016), while under extremely low nutrient

424 availability, they can adapt by maintaining small nutrient concentrations in photosynthetically  
425 active tissues (Wang and Moore, 2014). In *S. nigricans* community, we can speculate that plants  
426 could transfer and store more nutrients into the living roots. It was also observed that shoots  
427 remain partly green over winter, which can contribute to the storage of nutrients, while all the  
428 aboveground biomass dies out in *C. elata* vegetation (*personal observations*). As a consequence,  
429 in *S. nigricans* community these nutrients could be mobilized during the growing season and  
430 allow for relatively high aboveground biomass production as compared to *C. elata* community  
431 (Fig. 1a, no statistical difference between CE and SN at the peak of biomass). Nutrient  
432 translocation was the reason why litter quality was increased with nutrient enrichment in N-  
433 limited wetlands (Mao et al., 2016). We did not detect any vegetation type  $\times$  growing season  
434 cross effect for accumulated litter and its quality (Table 1), so that we assume that the existing  
435 litter became similar in the different vegetation types during winter decomposition already.  
436 Litter decomposition was mostly related to leaf N content (de Neiff et al., 2006) and flooding  
437 can accelerate decomposition through increasing soil moisture (Shrestha et al., 2014; Heuck et  
438 al., 2015) and nutrient leaching (Baldwin and Mitchell, 2000; Shrestha et al., 2014). This could  
439 explain why, despite initial nutrient concentration differences in early senescent biomass and  
440 distinct nutrient translocation capacity in the three communities, there was no significant  
441 differences in litter N and P contents. However, C content in litter decreased along the  
442 hydrological gradient, with highest values in *C. elata* and lowest in *S. nigricans* communities.  
443 This difference of litter C content potentially provides more energy for microorganisms in the  
444 *C. elata* community.

445 From a stoichiometric perspective, in aboveground and moss biomass, C:N, C:P and N:P  
446 ratios were significantly lower in *C. elata* and higher in *S. nigricans* communities  
447 (Supplementary Table S4). Even if this trend is still visible in the litter, differences were non-  
448 significant, which could advocate for similar decomposition rates. In litter bags decomposition

449 experiments, [Buttler \(1987\)](#) found that  $k$  decomposition rates were 0.229, 0.224 and 0.253 for  
450 *C. elata*, *C. panicea* and *S. nigricans* communities, respectively, thus a higher decomposability  
451 for the litter in *S. nigricans* community was measured. This discrepancy can be explained by  
452 the quality of the litter used. Because of the plant morphology, fresh litter can easily be collected  
453 on *S. nigricans* tussocks at the end of the growing season as standing senescent leaves, while  
454 for *Carex* species, these senescent leaves tend to fall down and mix with older leaves on the  
455 ground, so that litter samples might be more heterogeneous and comprise leaves in a more  
456 advanced decomposition stage.

457

#### 458 **4.2 Soil organic matter quantity and quality reflects the flooding regimes**

459 Under intensive flooding, as happened in *C. elata* community near the lakeshore, there  
460 was more than double the amount of organic matter accumulated in the ecosystem, as compared  
461 to *C. panicea* and *S. nigricans* communities. With respect to the belowground biomass, which  
462 was also highest in *C. elata* community, it cannot be concluded on higher root growth as it was  
463 not possible to distinguish between living and dead roots, but lower soil bulk density can  
464 indicate higher organic matter content in relation to higher root productivity ([Rokosch et al.,](#)  
465 [2009](#)). As for litter, the strong decrease of belowground biomass during the growing season  
466 points to the degradation of dead organic matter. In the belowground biomass, there was no  
467 difference in plant N and P concentrations among the three communities, despite different soil  
468 nutrient conditions ([Table 4](#)). Like for the N:P ratio of above-ground biomass and mosses, the  
469 N:P ratio of belowground biomass was higher in the *S. nigricans* community where there is no  
470 flooding than in the other two communities. This result is contrary to the finding in [Wang et al.](#)  
471 [\(2018\)](#) where N:P ratio of belowground biomass was increased with flooding intensity. These  
472 opposed results might be explained by distinct nutrient limitation in the two study areas. Below-  
473 ground biomass C content decreased along the hydrological gradient, with highest values in *C.*

474 *elata* and lowest in *S. nigricans* communities, which mirrors in the trend for higher below-  
475 ground biomass C:N and C:P ratios in *C. elata* community. This reflected the humus types,  
476 which were marked differently by hydromorphic features: peaty anmoor, anmoor-hydromull  
477 and hydromull in *C. elata*, *C. panicea* and *S. nigricans* communities, respectively (Buttler and  
478 Gobat, 1991). This is consistent with the decrease of soil organic matter and C contents along  
479 the vegetation gradient, as well as in the increase of bulk density and pH (Table 4 and  
480 Supplementary Table S3).

481

#### 482 ***4.3 High organic matter in wetter soils triggers enzyme activity, which in turn accelerates*** 483 ***nutrient mineralization***

484 The soils in the three plant communities differed in their chemical and biological  
485 characteristics of their surface organic layer, which showed, as hypothesized, decreasing values  
486 for most of the parameters along the hydrological gradient, from *C. elata* to *S. nigricans*  
487 communities. Thus, higher soil fertility near the lakeshore also allowed higher microbial  
488 biomass. Along the growing season, DOC increased markedly in *C. elata* community, as a  
489 result of intense organic matter decomposition of the accumulated litter under high soil  
490 biological activity. Thus, higher organic matter contributed to the enzyme activity, which in  
491 turn could accelerate nutrient mineralization (Wilson et al., 2011; Heuck et al., 2015).  
492 Conversely, nitrate was higher at the beginning of the vegetation period, but decreased  
493 thereafter because it was used readily for the high biomass production, and consequently the  
494 soils could not be differentiated anymore by their nitrate content at the peak of biomass.  
495 Enzyme activity was affected not only by the availability of organic matter, but was also  
496 promoted by temperature increase during the growing season (Sinsabaugh et al., 2008; Manzoni  
497 et al., 2012).

498

#### 499 ***4.4 Plant-soil interaction and nutrient limitation in different hydrological conditions***

500 The three studied vegetation types are characterized by different nutrient requirements  
501 and, according to our hypothesis, this translates into different nutrient limitation and  
502 stoichiometric ratios in the plant material, soil and microbial pools. In *C. elata* community, N  
503 and P are not limiting because of the regular input of nutrients by lake water. With respect to  
504  $\text{NO}_3$ , values were on a yearly average  $1.7 \text{ mg.L}^{-1}$  in the lake water, as opposed to  $0.1 \text{ mg.L}^{-1}$  in  
505 the soil solution of the organic layer in the considered soils, while values for  $\text{PO}_4$  were  
506 indifferently  $0.1 \text{ mg.L}^{-1}$  in both the lake water and the upper horizon of these soils, but  
507 undetectable in the deeper horizons (Buttler, 1992). This shows that despite the inflow of  
508 nutrients from the lake in the wettest plant communities, the nutrient content in the soil does  
509 not discriminate the plant communities, despite obvious differences in biomass production and  
510 associated nutrient content (this study and Buttler, 1992). This is explained by the immediate  
511 uptake of nutrients for biomass production and its feedback effect onto the soil during the  
512 vegetation period in wetlands (Dykyjová and Úlehlová, 1978; Bayley et al., 1985). Indeed,  
513 hydrological differences among the various vegetation communities can affect soil organic  
514 matter accumulation and mineralization processes (Wilson et al., 2011; Swanson et al., 2017),  
515 as well as plant nutrient resorption (Wang et al., 2015a). Finally, losses of nutrients from soil  
516 organic matter and litter decomposition are important for the eutrophic vegetation influenced  
517 by the lake and contribute to a high C:N ratio in the soil dissolved fraction. It has been reported  
518 that dissolved organic carbon was higher under flooding than non-flooding condition in  
519 floodplain vegetation (Shrestha et al., 2014) and it was increased by flooding duration (Blodau  
520 and Moore, 2003; Kim et al., 2014). Therefore, for vegetation under the influence of lake  
521 inundation and high nutrient inputs, there is a rapid turnover of nutrients. Conversely, in the  
522 upland wetland vegetation characterized by *S. nigicans*, which is never affected by lake  
523 flooding, N and P are limiting, which translates in high N:P ratios in the soil dissolved fraction

524 as well as high C:N, C:P and N:P ratios in aboveground biomass, mosses and litter, as well as  
525 high C:P and N:P ratios in the microbial biomass. Under such low nutrient availability, nutrient  
526 translocation from senescing tissues is a strategy for plants to retard nutrient loss (Hopkinson,  
527 1992; Aldous, 2002). This translocation process of nutrients to roots by species such as *S.*  
528 *nigricans* (also *Molinia caerulea* and *M. arundinacea*, both present in *S. nigricans* community)  
529 is specific to a conservative biogeochemical cycle. In *C. panicea* community, which has an  
530 intermediate position along the vegetation gradient, only N is limiting, which translates into  
531 high C:N ratios in bulk soil, below-ground biomass and microbial biomass, and low C:P and  
532 N:P ratios in bulk soil and below-ground biomass, as well as low C:P ratio in the soil dissolved  
533 fraction.

534

## 535 **5. Conclusion**

536 High nutrient concentrations in plant leaves tend to be associated with the “live-fast/die  
537 young” end of the leaf economics spectrum (Wright et al., 2004; Kazakou et al., 2007), a  
538 characteristic which holds for the lakeshore vegetation under the influence of the lake flooding,  
539 as opposed to the upland wetland vegetation, which is never reached by lake flooding (Bueche  
540 et al., 1994). Our findings have strong implication for wetland management. The wetland  
541 hydrodynamic depends strongly on the lake level regulation at the outlet of the lake Neuchâtel,  
542 where a dam has been built (Buttler et al., 1995). It is a request to the hydraulic managers to  
543 consider the various stakeholders needs for setting the water level curve along the year.  
544 Constraints are given by the electricity power plants on the Aar river, navigation on the Rhin  
545 river, agriculture in the floodplains around the lake, fisheries and nature conservancy on the  
546 south shore of lake Neuchâtel which has become a Ramsar site. In this respect, the wetland  
547 vegetation and their soils are sensitive to lake flooding regime, as it was shown in this study. It  
548 is therefore important that the water level of the lake is set to optimize the flooding regime in

549 the wetland, more specifically that most of the vegetation of the type of *C. elata* along the  
550 lakeshore (but also the *Phragmites communis* belt near the lakeshore and ponds) can be flooded  
551 in spring, and the least possible vegetation of the type of *S. nigricans* (and neighboring *Molinia*  
552 *coarulea* vegetation) is reached by lake water (Buttler et al., 1995). These findings are  
553 important because they provide a threshold for flooding regime by the lake in the context of  
554 optimization of lake level regulation under various stakeholders needs. An inadequate water  
555 management would affect soil sustainability with a loss of C from the highly organic soils if  
556 they would be less flooded. In the opposite, dryer soils would also trigger shrub encroachments  
557 and lead to a loss of the most valuable habitats in connection with the lake, which are crucial  
558 for many organisms, as for example for fish and bird reproduction. Finally, a general flooding  
559 would suppress in the upland wetlands some plant and animal species of high naturalistic  
560 importance such as orchids or tree frog.

561

## 562 **Acknowledgements**

563 We thank Sylvain Lanz, Emmanuel Carino, Mitsuo Wada, Gil Fontannaz and Yannic  
564 Bernard for their contributions to the sampling in the field and some laboratory work. We are  
565 very grateful to Christian Clerc from the Association de la Grande Cariçaie, Champittet, for  
566 guidance and help for site selection. We also thank the China Scholarship Council for the PhD  
567 grant attributed to Wenjuan Feng, the National Key Research and Development Program of  
568 China (2018YFE0206400) and the EPFL for financial support.

569

570 **Conflict of interest:** The authors declare that they have no conflict of interest.

571

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773

774 **Tables**

775

776 **Table 1** Effects of vegetation type, growing season, and their interaction on plant and moss  
 777 parameters. *F*-values and associated *P*-values (\* for  $P < 0.05$ , \*\* for  $P < 0.01$  and \*\*\* for  $P <$   
 778 0.001) are indicated (see values of variables in [Supplementary Table S2](#)).

779

	Vegetation type	Growing season	VT × GS
Aboveground biomass (AGB)	3.5	189.0 ***	13.4 **
C content of AGB	3.5	2.4	0.0
N content of AGB	17.1 **	0.7	4.5 *
P content of AGB	111.7 ***	119.9 ***	27.4 ***
Litter (L)	14.6 **	7.4 *	1.9
C content of L	10.0 *	18.0 **	0.4
N content of L	1.2	9.5 *	0.2
P content of L	4.5	4.9	2.0
Moss biomass (MB)	3.2	2.9	7.8 *
C content of MB	3.0	0.6	0.6
N content of MB	6.5 *	0.8	1.1
P content of MB	13.2 **	4.7	2.1
Belowground biomass (BGB)	10.8 **	4.4	0.7
C content of BGB	7.9 *	4.9	0.1
N content of BGB	1.9	12.1 **	3.0
P content of BGB	0.4	32.9 ***	1.3

780

781

782 **Table 2** Synthesis of the effects of vegetation gradient and growing season on plant and moss  
783 parameters. Vegetation gradient is considered from lakeshore to upland (*i.e.* from *C. elata* to *S.*  
784 *nigricans* community) while growing season is considered from beginning to peak of growing  
785 season. ↘ indicates a significant decrease of the value (↘→ indicates a significant decrease only  
786 between two vegetation types), ↗ indicates a significant increase of the value and the absence  
787 of arrow indicates the absence of a significant effect (see [Table 1](#)).

788

	Vegetation gradient	Growing season
Aboveground biomass (AGB)		↗
C content of AGB		
N content of AGB	↘	
P content of AGB	↘	↘
Litter (L)	↘→	↘
C content of L	↘	↗
N content of L		↘
P content of L		
Moss biomass (MB)		
C content of MB		
N content of MB	↘	
P content of MB	↘	
Belowground biomass (BGB)	↘	
C content of BGB	↘	
N content of BGB		↘
P content of BGB		↘

789

790

791 **Table 3** Effects of soil layer, vegetation type, growing season, and their interaction on soil physico-chemical, microbial and enzymatic parameters.  
792 *F*-values and associated *P*-values (\* for *P* < 0.05, \*\* for *P* < 0.01 and \*\*\* for *P* < 0.001) are indicated (see values of variables in [Supplementary](#)  
793 [Table S3](#)).  
794

	Soil layer	Vegetation type	Growing season	SL × VT	SL × GS	VT × GS	SL × VT × GS
Bulk density (BD)	243.2 ***	21.5 **	1.9	6.2 ***	0.3	1.7	0.6 ***
Soil water content (SWC)	171.2 ***	15.4 **	3.7	2.6 *	0.9	3.1	0.1
Soil pH	139.8 ***	18.4 **	145.3 ***	1.0	0.5	2.8	1.3
Soil organic matter (LOI)	423.1 ***	23.4 **	0.6	16.1 ***	0.2	1.7	0.2
Soil organic C (TOC)	160.8 ***	15.7 **	0.9	7.0 ***	0.3	1.2	0.4
Soil N (TN)	422.8 ***	30.0 ***	0.3	11.2 ***	0.7	1.9	0.6
Soil P (TP)	240.3 ***	13.5 **	1.3	18.4 ***	0.2	0.3	0.6
Soil available C (DOC)	402.0 ***	10.7 **	0.0	10.6 ***	1.8	4.8 *	0.5
Soil available N (DN)	139.8 ***	2.7	138.3 ***	5.2 **	3.9 *	3.1	1.8
Soil available P (DP)	372.6 ***	19.2 **	2.0	6.5 ***	0.2	2.9	1.1
Ammonium (N-NH <sub>4</sub> )	193.5 ***	7.2 *	0.6	4.6 **	6.0 **	0.0	0.5
Nitrate (N-NO <sub>3</sub> )	41.4 ***	17.7 **	40.3 ***	2.6	2.1	3.2 *	0.5
Microbial biomass C (MBC)	467.0 ***	6.0 *	4.1	14.6 ***	0.9	2.9	1.9
Microbial biomass N (MBN)	804.2 ***	11.1 **	4.1	11.5 ***	0.5	1.0	0.6
Microbial biomass P (MBP)	525.9 ***	47.4 ***	0.3	22.2 ***	0.1	0.7	0.6
β-glucosidase (BG)	206.9 ***	67.5 ***	13.6 **	4.4 **	2.7	8.1 **	4.1 **
Leucine aminopeptidase (LAP)	642.1 ***	16.0 ***	20.5 ***	0.6	19.2 ***	18.2 ***	0.7
β-1, 4-N-acetylglucosaminidase (NAG)	156.0 ***	54.3 ***	29.4 ***	12.0 ***	2.0	0.7	10.0 ***
Phosphatase (PHO)	169.7 ***	29.9 ***	21.8 ***	7.2 ***	21.6 ***	6.9 **	4.5 **

795

796

797 **Table 4** Synthesis of the effects of soil depth increase, vegetation gradient and growing season,  
798 on soil physico-chemical, microbial and enzymatic parameters. Soil depth increase is  
799 considered from surface organic to lower mineral layer, vegetation gradient from lakeshore to  
800 upland (*i.e.* from *C. elata* to *S. nigricans* community), while growing season is considered from  
801 beginning to peak of growing season. ↘ indicates a significant decrease of the value (↘→  
802 indicates a significant decrease only between two vegetation types), ↗ indicates a significant  
803 increase of the value and the absence of arrow indicates the absence of a significant effect (see  
804 [Table 3](#)).

	Increasing soil depth	Vegetation gradient	Growing season
<i>Soil physico-chemical parameters</i>			
Bulk density (BD)	↗	↗	
Soil water content (SWC)	↘	↘	
Soil pH	↗	↗	↗
Soil organic matter (LOI)	↘	↘	
Soil organic C (TOC)	↘	↘	
Soil N (TN)	↘	↘	
Soil P (TP)	↘	↘	
Soil available C (DOC)	↘	↘→	
Soil available N (DN)	↘		↗
Soil available P (DP)	↘	↘	
Ammonium (N-NH <sub>4</sub> )	↘	↘→	
Nitrate (N-NO <sub>3</sub> )	↘	↘	↘
<i>Microbial parameters</i>			
Microbial biomass C (MBC)	↘	↘	
Microbial biomass N (MBN)	↘	↘	
Microbial biomass P (MBP)	↘	↘	
<i>Enzymatic parameters</i>			
β-glucosidase (BG)	↘	↘	↗
Leucine aminopeptidase (LAP)	↘	↘	↗
β-1, 4-N-acetylglucosaminidase (NAG)	↘	↘	↗
Phosphatase (PHO)	↘	↘	↗

806 **Figure legend**

807

808 **Fig. 1** Aboveground plant biomass (a), moss biomass (b), N content in aboveground plant  
809 biomass (c) and P content in aboveground plant biomass (d) according to the vegetation type  
810  $\times$  growing season interaction (Table 1). Each bar represents the mean value  $\pm$  SE; n= 4. For  
811 (a), (b) and (c), different letters denote significant differences among plant communities  
812 according to the selected growing season period with  $a > b > c$ . For (d), stars indicate significant  
813 differences between the beginning and the peak of growing season according to the selected  
814 plant community with \* for  $P < 0.05$ , \*\* for  $P < 0.01$  and *ns* for  $P > 0.05$ . CE = *C. elata*, CP =  
815 *C. panicea*, SN = *S. nigricans*, GS = growing season.

816

817 **Fig. 2** Soil total P content (a), available P content (b), microbial biomass C (c) and leucine  
818 aminopeptidase activity (d) according to the soil layer  $\times$  vegetation type interaction (Table 3).  
819 Each bar represents the mean value  $\pm$  SE; n= 8. Different letters denote significant differences  
820 among plant communities according to the selected soil layer with  $a > b > c$ . CE = *C. elata*, CP  
821 = *C. panicea*, SN = *S. nigricans*. LAP = leucine aminopeptidase.

822

823 **Fig. 3** Soil available C (a) and nitrate (b) contents according to the vegetation type  $\times$  growing  
824 season interaction (Table 3). Each bar represents the mean value  $\pm$  SE; n= 12. Different letters  
825 denote significant differences among vegetation types according to the selected growing season  
826 period with  $a > b$ . CE = *C. elata*, CP = *C. panicea*, SN = *S. nigricans*.

827

828 **Fig. 4** Soil available N (a) and ammonium (b) content according to the soil layer × growing  
829 season interaction (Table 3). Each bar represents the mean value ± SE; n= 12. Stars indicate  
830 significant differences between the beginning and the peak of growing season according to the  
831 selected soil layer with \* for  $P < 0.05$ , \*\* for  $P < 0.01$ , \*\*\* for  $P < 0.001$  and *ns* for  $P > 0.05$ .  
832 GS = growing season.

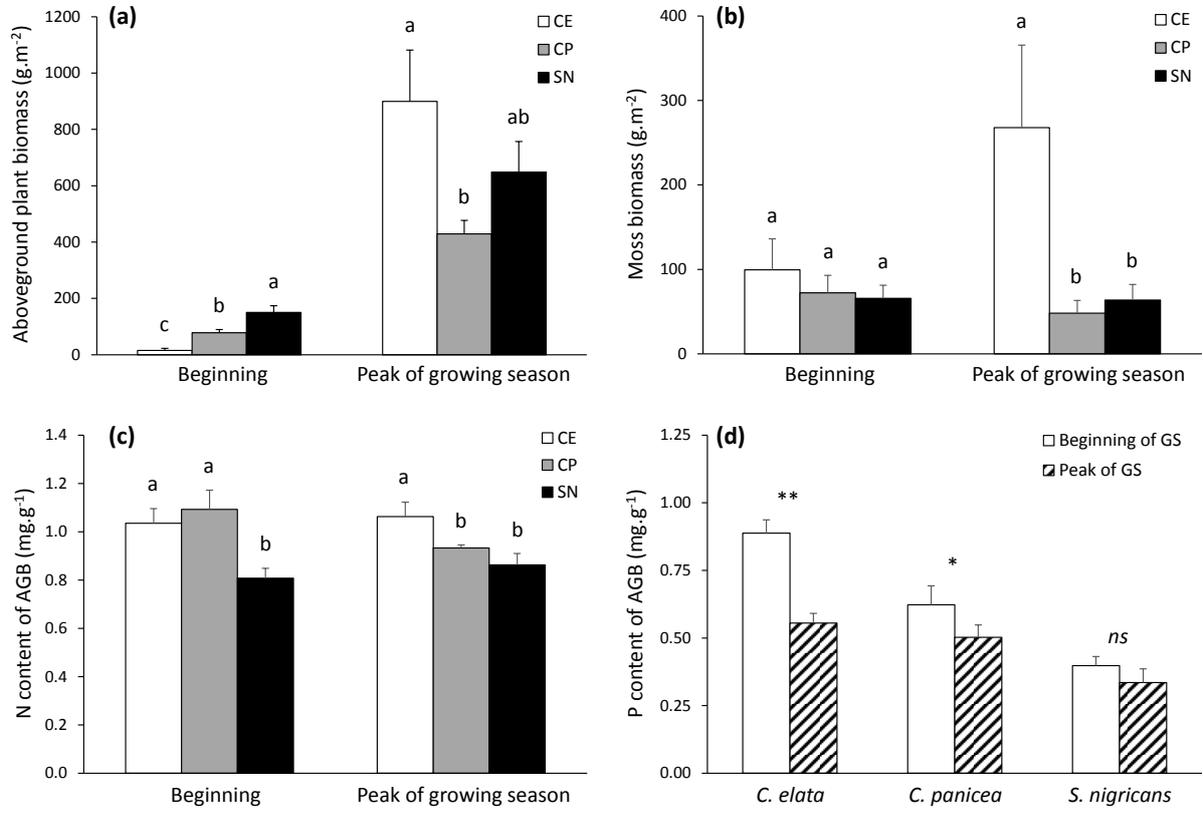
833

834 **Fig. 5** Principal component analysis (PCA) illustrating the relationship between stoichiometry  
835 of C, N and P in the plant material (above and belowground biomass, moss and litter), in the  
836 bulk soil and in its dissolved fraction, and in the microbial biomass in the organic layer at the  
837 two sampling periods, April and July. Samples are labelled with sampling period (A: April, J:  
838 July) and vegetation type (CE: *Carex elata*, CP: *Carex panicea*, SN: *Schoenus nigricans*).  
839 Variables are labelled as in Tables 1-4.

840

841 **Fig. 1**

842

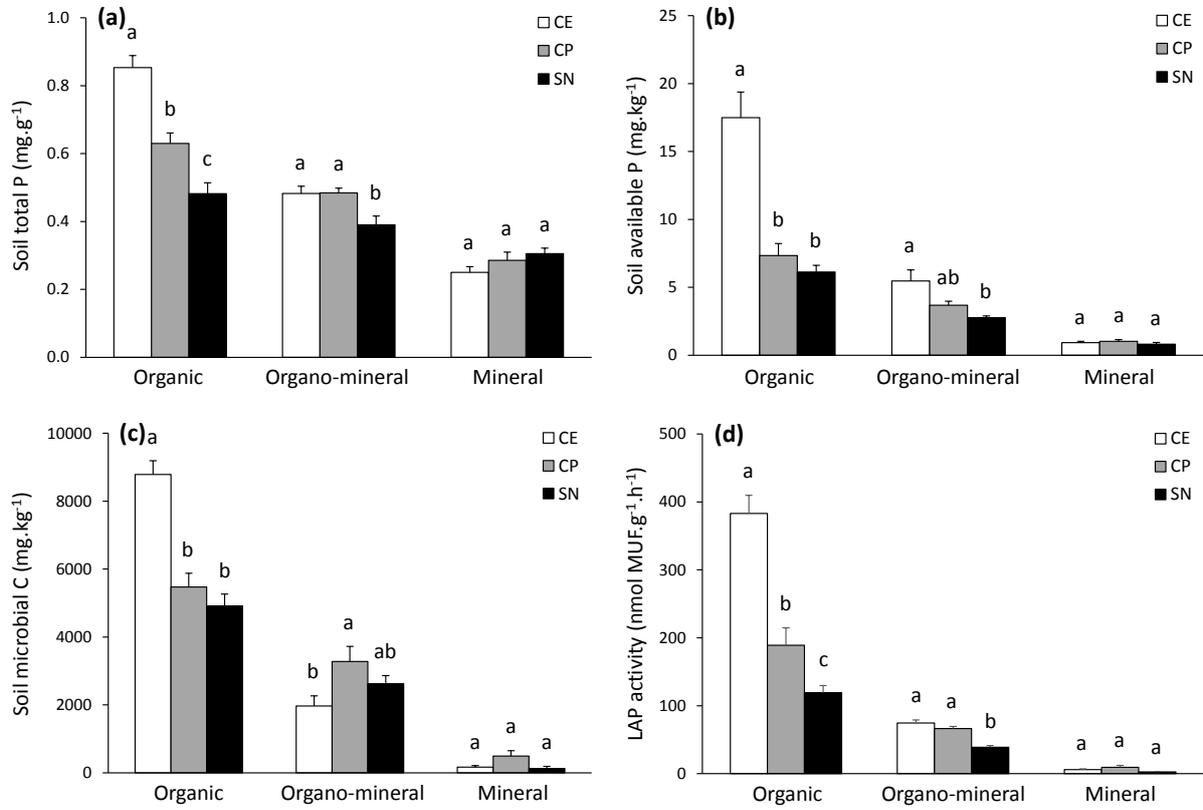


843

844

845 **Fig. 2**

846

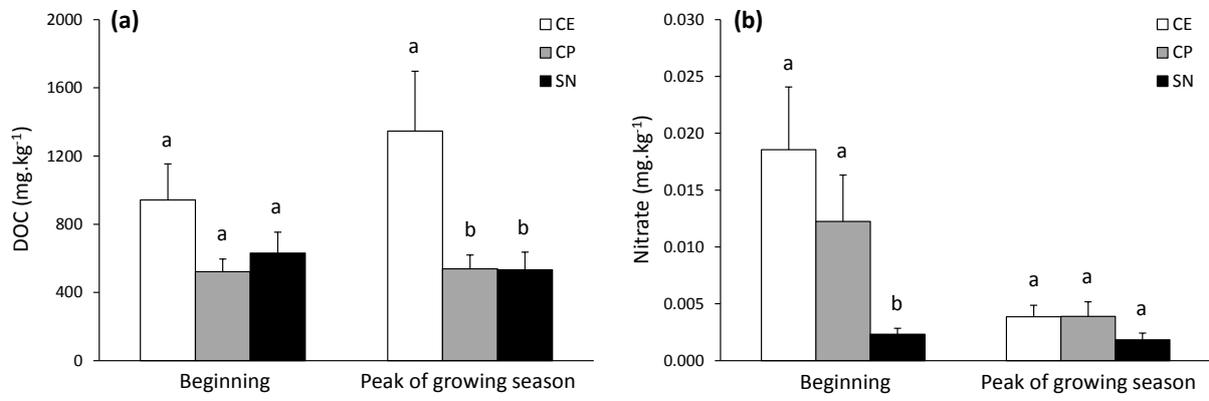


847

848

849 **Fig. 3**

850

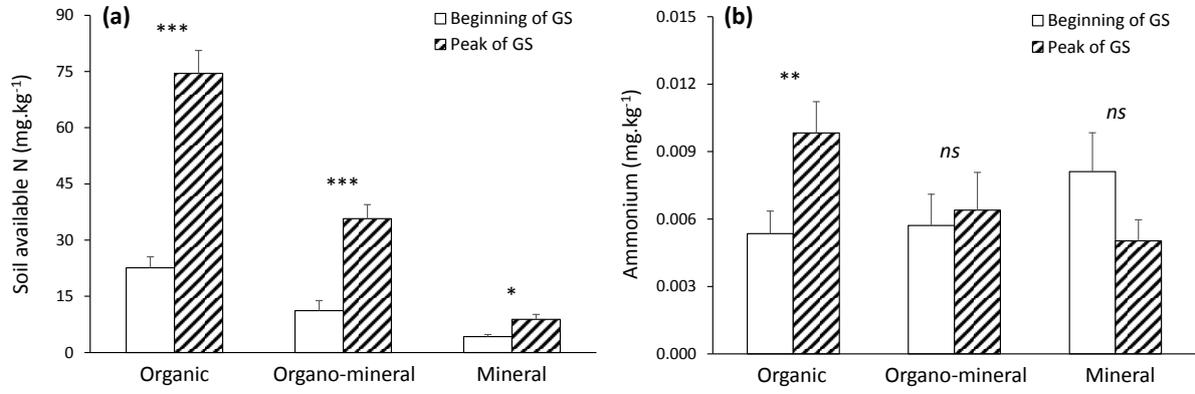


851

852

853 **Fig. 4**

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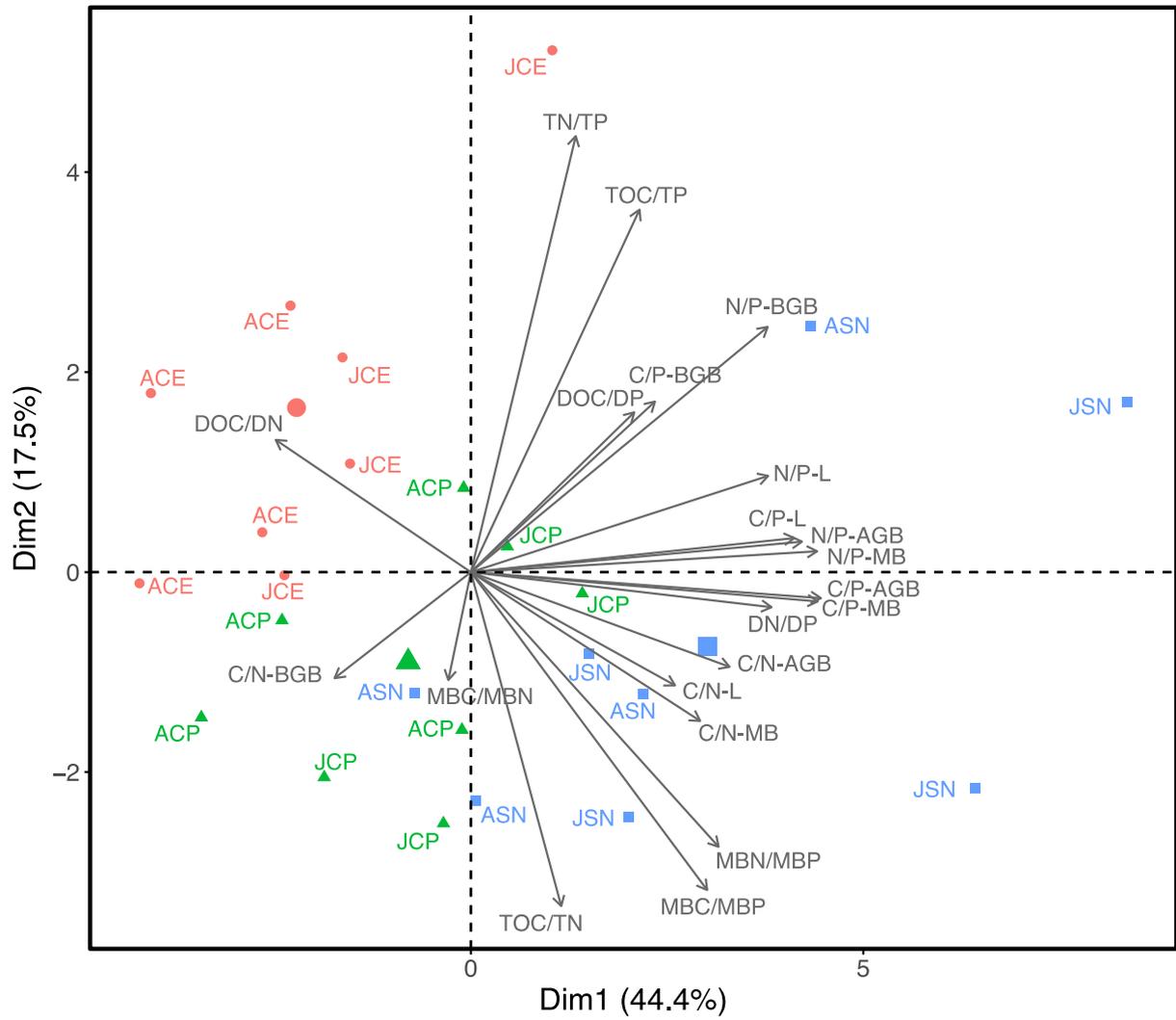


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856

857 Fig. 5

858



859

860