Is Moss Stoichiometry Influenced by Microtopography in a Boreal Peatland of Northeast China?

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Abstract: To examine the effects of microtopography on the stoichiometry of carbon (C), nitrogen (N) and phosphorus (P) in mosses along the hummock-hollow gradient in boreal peatlands, we investigated species-level C:N, C:P and N:P ratios of five mosses (*Sphagnum magellanicum, S. perichaetiale, S. palustre, S. girgensohnii* and *Aulacomnium palustre*) in the hummocks, hollows and their intermediate zones, and then assessed community-level spatial patterns in a boreal ombrotrophic peatland of north of the Great Xing'an Mountain, Northeast China. The results show that at the species level, C:N, C:P and N:P ratios of the selected *Sphagnum* mosses remained stable in the hummock-hollow complexes due to unchanged C, N and P concentrations, whereas the non-*Sphagnum* moss (*A. palustre*) in the hummocks and intermediate zones had lower P concentrations and thus greater C:P ratios than that in the hollows. At the community level, moss N concentration and C:N ratio remained constant along the hummock-hollow gradient, whereas hummocks and intermediate zones had higher community-level moss C:P and N:P ratios than hollows because of greater C and lower P concentrations. These findings imply that the effects of microtopography on moss C:N:P stoichiometry are scale-dependent and reveal spatial heterogeneity in C and nutrient dynamics. These results provide a more comprehensive understanding of biogeochemical cycles in boreal peatlands.

Keywords: hummock-hollow complex; microtopography; scale-dependent; *Sphagnum*; stoichiometric homeostasis

1 Introduction

Boreal peatlands store a large fraction of terrestrial organic matter in soils and play a critical role in global carbon (C) and nutrient budgets (Gorham, 1991). Mosses, especially the genus *Sphagnum*, form a major component of boreal peatlands and substantially contribute to ecosystem function (Lindo and Gonzalez, 2010). In these peatlands, mosses have key influences on ecological processes, such as litter decomposition, soil organic matter accumulation, nutrient availability, species composition and ecosystem productivity (Aerts et al., 1999; Gunnarson, 2005; Gornall et al., 2011).

In most boreal peatlands, small-scale hummock-hollow microtopographic features occur along a gradient of water-table depth (Belyea and Baird, 2006; Rydin and Jeglum, 2013). Compared with hollows, hummocks are generally drier, warmer and have lower nutrient availability (Laine et al., 2011; Rydin and Jeglum, 2013). Because of the substantial differences in moisture and nutrient status between hummocks and hollows, there is a high spatial variability in moss growth and related

ecophysiological properties (Malmer, 1988; Weltzin et al., 2001; Laine et al., 2011). Turetsky et al. (2008) found that mosses in hummocks and hollows differed in carbohydrate partitioning strategies and suggested that key moss traits related to growth rate, physiology and litter chemistry should be assessed based on microtopography.

Nitrogen (N) and phosphorus (P) are essential nutrients for plant growth in terrestrial ecosystems (Elser et al., 2007). Ecological stoichiometry refers to the balance of energy and such essential elements in ecological interactions (Elser et al., 2010) and subsequent biogeochemical cycles, including C sequestration/emission and nutrient absorption/translation. Thus, the stoichiometry, or relative abundance, of C, N and P in vegetation regulates many important ecological processes related to biogeochemical cycles, such as plant growth (Minden and Kleyer, 2014), organic matter decomposition (Manzoni et al., 2010), food web (Elser et al., 2010), species composition (Güsewell et al., 2005) and ecosystem structure and stability (Yu et al., 2010). In boreal peatlands, previous studies have found that hollow *Sphagnum* mosses had higher N concentration and lower C:N ratio than hummock *Sphagnum* mosses (e.g. Malmer, 1988; Rice, 2000; Larmola et al., 2014). However, these studies did not examine the effect of microtopography on C:N:P stoichiometry for the same moss species; therefore, they could not determine whether this stoichiometric variation is caused by microtopography or intrinsic growth strategies. Recently, Wang and Moore (2014) observed relatively constant proportions of tissue nutrient concentrations, i.e. ecological homeostasis, in *Sphagnum* mosses in an ombrotrophic peatland, despite seasonal variations in nutrient availability. Therefore, moss C:N:P stoichiometry changes with microtopography in the hummock-hollow complexes in boreal peatlands remains an open question, and addressing it would provide a more comprehensive understanding of ecosystem C and nutrient cycles.

Within boreal peatlands, moss species composition generally varies along hummock-hollow gradients (Weltzin et al., 2001; Strack et al., 2006). However, the effect of microtopography on moss C:N:P stoichiometry has only been assessed at the species level (Malmer, 1988; Rice, 2000), which may not yield sufficient accurate information about the spatial patterns of moss

C:N:P stoichiometry. At the community level, C:N:P stoichiometry not only depends on C, N and P concentrations of moss species, but also on the richness and dominance of moss species within the community. Therefore, knowledge about the spatial variations of moss C:N:P stoichiometry at the community level is needed to better understand biogeochemical cycles in hummock-hollow complexes in boreal peatlands.

In the present study, we investigated moss C, N, and P concentrations and C:N:P stoichiometry in three microtopographic positions (hummocks, intermediate zones and hollows) in hummock-hollow complexes of an ombrotrophic peatland at north of the Great Xing'an Mountain, Northeast China. The specific objectives of this study were to 1) examine the influence of microtopography on C:N:P stoichiometry for the same moss at the species level by measuring C, N and P concentrations of five moss species (*Sphagnum magellanicum*, *S. perichaetiale*, *S. palustre*, *S. girgensohnii* and *Aulacomnium palustre*); and 2) understand whether altered moss species composition induced by microtopography can cause a spatial variation in community-level C:N:P stoichiometry in hummock-hollow complexes.

2 Materials and Methods

2.1 Study site

This study was conducted in a boreal ombrotrophic peatland (52.94°N, 122.86°E, 467 m above sea level, Fig. 1) in Mohe County, north of the Great Xing'an Mountain, Northeast China. The area of this peatland is approximately 240 ha. The study site is located in the continuous permafrost zone with a cold-temperate continental monsoon climate. During the 1980–2009 period, annual mean precipitation was about 450 mm, 45% fell in July and August. Mean annual temperature was –3.9℃, ranging from –29.7℃ in January to 18.4℃ in July. The active layer of soil was about 70 cm in depth, and peat depths ranged from 40 to 100 cm. At the study site, surface microtopography is a mosaic of hummocks, hollows and lawns. According to the relative areal proportion of each microtopographic zone within each plot (Weltzin et al., 2001), hummocks comprise about 49% of the surface area, while hollows occupy about 20% of the surface. *Betula fruticosa* (tall deciduous shrub), *Rhododendron lapponicum* (tall

evergreen shrub), *Vaccinium uliginosum* (dwarf deciduous shrub) and *Ledum palustre* (dwarf evergreen shrub) are the dominant vascular plants across the hummock-hollow gradients. Other vascular plants include *Salix rosmarinifolia*, *S. myrtilloides*, *Chamaedaphne calyculata*, *Eriophorum vaginatum*, *Carex globularis* and *Calamagrostis angustifolia*. The dominant mosses in the hummock-hollow complexes are *Sphagnum* species (Appendix Table S1). *S. magellanicum*, *S. perichaetiale*, *S. palustre*, *S. girgensohnii* and *A. palustre* are the most common moss species along the hummock-hollow gradients.

2.2 Sample collection

Given that mosses effectively resorb nutrients from older senescing organs to newly formed growing organs (Rydin and Clymo, 1989; Aldous, 2002), we sampled moss biomass during the peak growing season (early August) to avoid the possible effects of seasonal fluctuations. In early August 2011, we established a 400 m linear transect in the study site and configured eight plots along this transect. To minimize pseudoreplication within plots, the distance between each plot and the adjacent plot was at least 20 m. We assumed that a distance of more than 20 m was sufficient to ensure adequate independence among plots, due to the high spatial heterogeneity in the study site. In each plot, we randomly chose six well-developed hummock-hollow complexes, and sampled moss biomass from hummocks, intermediate zones and hollows using quadrats (20 cm × 20 cm) along each hummock-hollow gradient. In total, every microtopography consists of six quadrats in each plot. Furthermore, to attain a representative sample for

each plot, we thoroughly mixed the moss biomass collected from the same microtopography. 12 moss species were collected; five of the species (*S. magellanicum*, *S. perichaetiale*, *S. palustre*, *S. girgensohnii* and *A. palustre*) were observed in more than or equal to three plots in each microtopography, and the other seven species appeared only in some plots of the three microtopographies (Appendix Table S1). Therefore, only five moss species found at all sites (*S. magellanicum*, *S. perichaetiale*, *S. palustre*, *S. girgensohnii* and *A. palustre*) were used to assess the effect of microtopography on species-level C:N:P stoichiometry, and all 12 moss species were included in the community-level estimates of C:N:P stoichiometric ratios.

2.3 Sample preparation and measurement

Mosses were placed in plastic bags, transported to the laboratory, and then stored in a refrigerator. Thereafter, we separated the upper, green (or red) segments (including capitula, branches and stems) from the brown (or yellow) senesced tissues using scissors (Waite and Sack, 2011). For each moss species, the green (or red) segments were transferred to paper bags, oven-dried at 60℃ for at least 48 h, weighed and then ground for analysis of C, N and P concentrations. Species dominance was expressed as the percentage of each species' biomass in the total community biomass (Yu et al., 2010). Carbon concentration was measured using the dry combustion method (Multi N/C 2100 Analyzer, Analytik Jena, Germany). Nitrogen concentration was determined using the sodium salicylate-sodium hypochlorite colorimetric method with a continuous-flow autoanalyzer (AutoAnalyzer III, Bran+Luebbe GmbH, Germany). Phosphorus concentration was assayed using the molybdenum blue colorimetric method with a Shimazu UV-1750 spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Moss C:N, C:P and N:P ratios were expressed on a mass basis. Detailed information about moss species dominance, and C, N and P concentrations in the hummock-hollow complexes are shown in Appendix Table S1.

At the community level, moss C, N and P concentrations were calculated from the following formula:

Moss C (or N and P) concentration =

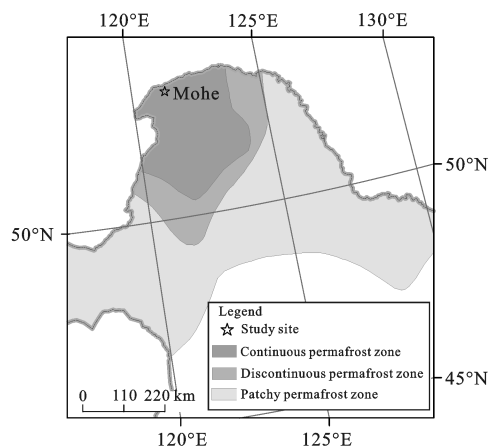$$\left(\sum_{i=1}^{n} B_i \times C_i \right) \Big/ \left(\sum_{i=1}^{n} B_i \right) \tag{1}$$

Fig. 1 Location of study area

where B_i is the biomass (g/m^2) for moss species i within each community and C_i is C (or N and P) concentration of moss species i in the community.

2.4   Statistical analyses

Statistical analyses were conducted with SPSS (Version 19.0) for Windows, and P-values smaller than 0.05 were considered statistically significant. Levene's test was used to test data normality, and C concentration, C:N ratio and N:P ratio were $\log_{10}(x)$ transformed. At the species level, a two-way analysis of variance (ANOVA) was used to examine the effects of moss species, microtopography and their interaction on C, N and P concentrations, and their stoichiometric ratios. The Bonferroni test, following one-way ANOVA, was used to compare differences in means among microtopographies for the same moss species or among moss species for the same microtopography. Tukey's HSD method was used to examine the effects of microtopography on C, N and P concentrations, and their stoichiometric ratios at the community level.

3   Results

3.1   Moss C:N:P stoichiometry at the species level

Moss C and P concentrations, C:P and N:P ratios varied significantly with microtopography (Table 1). *A. palustre* in the hollows had significantly greater P concentrations than that in the intermediate zones (Table 2). Consequently, C:P ratios for *A. palustre* growing in the hummocks and intermediate zones were higher than those in hollows (Table 2). However, for the four *Sphagnum* mosses (*S. magellanicum*, *S. perichaetiale*, *S. palustre* and *S. girgensohnii*), microtopography had no

significant effects on C and P concentrations and C:P ratio (Table 2). In addition, N concentration, C:N and N:P ratios for all selected five moss species did not vary with microtopographic positions (Table 2).

Moss C, N and P concentrations and C:N, C:P and N:P ratios differed among species (Table 3). In the hummocks and intermediate zones, compared with *S. magellanicum*, *S. perichaetiale*, *S. palustre* and *S. girgensohnii*, *A. palustre* generally had greater C concentration and lower N concentrations, and thus higher C:N ratios (Table 2). Meanwhile, *A. palustre* generally had higher P concentrations and lower C:P ratios than the other four mosses both in the intermediate zones and hollows (Table 2). In addition, N:P ratios for the selected four *Sphagnum* mosses was generally greater than that of *A. palustre* in each microtopographic position (Table 2). Among the selected four *Sphagnum* mosses, *S. magellanicum*, *S. perichaetiale* and *S. palustre* in the hollows had higher C:P ratios than *S. girgensohnii* (Table 2). Moreover, in the hummocks and intermediate zones, N:P ratios of *S. girgensohnii* were generally low in *Sphagnum* mosses (Table 2).

3.2   Moss biomass and C:N:P stoichiometry at the community Level

At the community level, *Sphagnum* moss biomass, non-*Sphagnum* moss biomass and total moss biomass did not significantly change with microtopography (Table 4). Moreover, moss C:N:P stoichiometric ratios varied with species and microtopography (Table 1). Among the three microtopographic positions, there were no significant differences in moss N concentrations and C:N ratios (Table 5). However, mosses had lower C concentrations and greater P concentrations in the hollows than in the hummocks and intermediate zones

Table 1   Coefficients of variations (%) for moss carbon (C), nitrogen (N) and phosphorus (P) and C:N, C:P and N:P ratios

		C	N	P	C:N	C:P	N:P
	hummock	1.4	12.9	15.4	13.8	15.6	19.8
Among species	Intermediate zone	1.2	15.0	10.7	15.5	10.2	23.8
	hollow	1.8	4.9	7.7	5.6	7.4	12.3
Among microhabitats	*Sphagnum* moss	1.6	2.7	11.6	2.0	13.2	13.4
	Non-*Sphagnum* moss	1.8	6.7	12.7	8.5	14.5	6.3

Notes: Coefficient of variation (CV) was derived from $\log_{10}$-transformed data (Güsewell and Koerselman, 2002). $CV = \dfrac{1/2(10^{(\overline{X}+SD)} - 10^{(\overline{X}-SD)})}{10^{\overline{X}}} = \overline{X} = \dfrac{10^{SD} - 10^{-SD}}{2}$,

where $\overline{X}$ and SD are the $\log_{10}$-transformed data of the mean and standard deviation, respectively

Table 2 Spatial variations in moss C, N and P concentrations and C:N:P stoichiometry in the hummock-hollow complexes at the species level

Species	Microtopography	C (mg/g)	N (mg/g)	P (mg/g)	C:N	C:P	N:P
S. magellanicum	Hummock	501 (4)	11.07 (0.02)a	1.08 (0.11)	45.3 (0.3)b	474 (45)	10.47 (1.06)ab
	Intermediate zone	504 (2)abc	11.97 (0.69)a	0.96 (0.01)b	42.4 (2.3)b	522 (6)a	12.39 (0.55)a
	Hollow	492 (3)	11.33 (0.60)	1.19 (0.06)b	43.8 (2.3)	418 (20)a	9.64 (0.77)a
S. perichaetiale	Hummock	501 (3)	11.39 (0.48)a	1.13 (0.10)	44.4 (2.0)b	457 (40)	10.27 (0.67)ab
	Intermediate zone	504 (3)bc	10.94 (0.32)a	1.06 (0.06)b	46.2 (1.6)b	480 (25)a	10.47 (0.86)ab
	Hollow	497 (7)	11.74 (0.55)	1.18 (0.05)b	42.6 (2.6)	423 (21)a	9.99 (0.66)a
S. palustre	Hummock	507 (1)	12.05 (0.42)a	1.07 (0.04)	42.2 (1.5)b	474 (19)	11.22 (0.13)a
	Intermediate zone	505 (2)b	11.52 (0.41)a	1.18 (0.05)ab	44.2 (1.4)b	433 (18)ab	9.82 (0.36)b
	Hollow	500 (2)	11.78 (0.38)	1.23 (0.03)b	42.7 (1.4)	409 (8)a	9.64 (0.42)a
S. girgensohnii	Hummock	496 (6)	11.82 (0.24)a	1.51 (0.16)	42.0 (0.5)b	336 (36)	8.00 (0.76)bc
	Intermediate zone	491 (2)c	10.61 (0.34)ab	1.12 (0.01)ab	46.4 (1.4)b	440 (6)ab	9.49 (0.24)b
	Hollow	490 (4)	12.20 (0.70)	1.45 (0.07)ab	40.5 (2.1)	342 (19)b	8.51 (0.73)ab
A. palustre	Hummock	509 (2)AB	8.99 (0.29)b	1.38 (0.07)B	57.0 (1.9)a	376 (17)A	6.58 (0.19)c
	Intermediate zone	514 (2)Aa	9.06 (0.23)b	1.35 (0.05)Ba	57.0 (1.6)a	385 (16)Ab	6.77 (0.23)c
	Hollow	504 (4)B	10.07 (0.48)	1.61 (0.06)Aa	50.8 (2.6)	316 (11)Bb	6.30 (0.34)b

Notes: Data are presented as means with standard errors (in parentheses, $n = 3–8$). Different upper- and lowercase letters are significantly different among microtopographic positions for the same moss species and among moss species for the same microtopographic position, respectively, at $P < 0.05$

Table 3 Two-way ANOVA of microtopography and moss species on C:N:P stoichiometry in the hummock-hollow complexes

	C		N		P		C:N		C:P		N:P	
	df	*F*	*df*	*F*	*df*	*F*	*df*	*F*	*df*	*F*	*df*	*F*
Microtopography	2	7.1[**]	2	2.1	2	8.7[***]	2	2.8	2	11.9[***]	2	4.2[*]
Moss species	4	11.7[***]	4	19.3[***]	4	16.5[***]	4	25.0[***]	4	15.7[***]	4	43.3[***]
Microtopography × Moss species	8	0.6	8	1.0	8	1.7	8	0.9	8	1.4	8	1.7

Notes: [*], $P<0.05$; [**], $P<0.01$; [***], $P<0.001$

Table 4 Spatial variations in moss species biomass in hummock-hollow complexes in a boreal peatland, Northeast China

Microtopography	*Sphagnum* moss (g/m^2)	Non-*Sphagnum* moss (g/m^2)	Total (g/m^2)
Hummock	424.7 (30.1)	28.2 (6.0)	452.9 (28.3)
Intermediate zone	466.5 (29.4)	26.6 (6.0)	493.1(31.1)
Hollow	525.5 (33.3)	31.1 (12.4)	556.6 (34.3)

Notes: Data are presented as means with standard errors (in parentheses, $n = 8$)

Table 5 Spatial variations in moss C, N and P concentrations and C:N:P stoichiometry in hummock-hollow complexes at the community level

Microtopography	C (mg/g)	N (mg/g)	P (mg/g)	C:N	C:P	N:P
Hummock	502 (1)a	10.98 (0.30)	1.13 (0.07)b	45.97 (1.21)	456 (27)a	9.90 (0.48)a
Intermediate zone	503 (1)a	11.12 (0.27)	1.10 (0.03)b	45.44 (1.16)	460 (12)a	10.19 (0.43)a
Hollow	492 (2)b	10.98 (0.39)	1.31 (0.04)a	45.16 (1.51)	377 (10)b	8.42 (0.40)b

Notes: Data are presented as means with standard errors (in parentheses, $n = 8$). Means with different letters are significantly different among microtopographic positions at $P < 0.05$

(Table 5). Thus, C:P and N:P ratios of mosses in the hummocks and intermediate zones were higher than those in the hollows (Table 5).

4 Discussion

Annual bulk dissolved inorganic N deposition in the Great Xing'an Mountain ranges from 0.41 g/m^2 to 0.48 g/m^2 (Zhan et al., 2014). Consequently, the average N concentration of *Sphagnum* mosses (about 11.1 mg/g) in the present study is comparable to values in ombrotrophic peatlands under moderate N deposition (0.8 $g/(m^2 \cdot yr)$; Wang and Moore, 2014), but lower than the threshold value (12.0 mg/g) for N-saturated *Sphagnum* mosses (Lamers et al., 2000) and values in ombrotrophic peatlands under high N deposition (more than 1.0 $g/(m^2 \cdot yr)$; Bragazza et al., 2004; Jiroušek et al., 2011). In addition, *Sphagnum* moss N concentrations were higher than fen–bog transitions under low N deposition (0.3 $g/(m^2 \cdot yr)$; Larmola et al., 2014). In contrast, mean *Sphagnum* moss P concentrations (1.09–1.30 mg/g) were much higher than ombrotrophic peatlands in North America (Bombonato et al., 2010; Wang and Moore, 2014) and Central-West and North European (Bragazza et al., 2004; Larmola et al., 2014), and were close to ombrotrophic peatlands in Central-East Europe (Jiroušek et al., 2011). Moreover, the N:P ratio in vegetation can be indicative of nutrient limitation, with a value < 14 or > 16 indicating N or P limitation, respectively (Koerselman and Meuleman, 1996), and such approach has been applied to mosses (e.g. Jiroušek et al., 2011; Wang and Moore, 2014). In this study, N:P ratios of *Sphagnum* mosses in the hummock-hollow complexes were much lower than 14, indicating that N probably limits moss growth in this ombrotrophic peatland.

We did not find spatial variations in C:N, C:P and N:P ratios for the four *Sphagnum* species, due to unchanged C, N and P concentrations along the hummock-hollow complexes in the boreal peatland. However, the C:P ratio of *A. palustre* (the non-*Sphagnum* species) differed with microtopography. Specifically, *A. palustre* had lower P concentration and thus greater C:P ratio in the hummocks and intermediate zones than in the hollows. In the hummock-hollow complexes, hollows generally have greater N and P availability than hummocks due to the transfer of nutrients from hummocks to hollows via runoff (e.g. Laine et al., 2011; Rydin and Jeglum, 2013).

Therefore, the inconsistent spatial patterns of *Sphagnum* and non-*Sphagnum* moss C:N:P stoichiometry at the species level may be explained by differences in their ability to maintain stoichiometric homeostasis (Elser et al., 2010; Wang and Moore, 2014). In our study, *Sphagnum* mosses exhibited strong stoichiometric homeostasis and could maintain constant proportions of C, N and P concentrations along the hummock-hollow gradient. In contrast, compared with hummocks and the intermediate zones, the relatively higher P availability in hollows resulted in greater P concentration and lower C:P ratio for non-*Sphagnum* species (*A. palustre*).

In this study, C:N:P stoichiometry of *Sphagnum* mosses did not vary with microtopography at the species level in the hummock-hollow complexes in this boreal peatland. However, previous studies found that hummock and hollow *Sphagnum* mosses differed in nutrient concentration and C:nutrient ratios due to differences in site conditions and growth patterns (Malmer, 1988; Rice, 2000). These previous studies did not examine spatial variations in C:N:P stoichiometry for the same moss species in the hummock-hollow complexes, which may have masked the effect of microtopography or the intrinsic growth strategies. In a greenhouse study, Rice (2000) found that, in the case that all *Sphagnum* species received similar N inputs, hummock and hollow *Sphagnum* mosses still showed substantial differences in C:N ratios and suggested that variations in *Sphagnum* moss C:N ratios reflected differences in growth strategies. In our study, C, N and P concentrations also differed substantially among moss species occupying different microtopography. These results imply that, to distinguish intrinsic moss characteristics, the effect of microtopography on C:N:P stoichiometry should be assessed for the same moss species in boreal peatlands.

Notably, community-level moss N concentration did not change along hummock-hollow gradients, whereas mosses in drier habitats (hummocks and intermediate zones) had higher C and lower P concentrations, and thus greater C:P and N:P ratios than those in the wetter habitats (hollows). Because *Sphagnum* moss C:N:P stoichiometric ratios at the species level remained constant along the hummock-hollow gradient, substantial changes in moss species frequency and dominance would account for the spatial variation in community-level moss C:N:P stoichiometry. Given that recent studies have focused mostly on species-level moss C:N:P

stoichiometry, and moss species compositions generally vary with microtopography, our results suggest that community-level C:N:P stoichiometry can provide a more complete understanding of spatial patterns of moss-related biogeochemical cycles in hummock-hollow complexes in boreal peatlands.

In boreal ombrotrophic peatlands, the main sources of nutrients to mosses are precipitation, dry deposition and aboveground vascular plant litters (Malmer, 1988). Generally, hummocks receive greater inputs of N and P via dry deposition than hollows (Malmer, 1988; Wiedermann et al., 2009). However, moss-associated cyanobacteria in hollows have much higher N_2 fixation rates than those in the hummocks and can increase N availability for moss growth (Larmola et al., 2014). Thus, community-level moss N concentrations remain stable along the hummock-hollow gradient. Compared with hummocks and intermediate zones, higher moss P concentrations in the hollows may be explained by greater P availability induced by the transfer of P from hummocks to hollows via runoff (Macrae et al., 2013), highly soluble P under anoxic conditions (Moser et al., 2009), the ability of *Sphagnum* species growing in the wetter habitats to maintain high P-uptake (Jiroušek et al., 2011) and intrinsic growth strategies (Malmer, 1988). According to the growth rate hypothesis (Elser et al., 2010), lower C:P and N:P ratios can explain faster growth rates, and thus greater biomass, of hollow moss species.

In boreal peatlands, global warming will likely lower the soil water-table and lead to warmer, drier climatic conditions in these ecosystems, which may cause a replacement of hollow moss species with hummock moss species (Rydin, 1993; Robroek et al., 2007). Considering that mosses are crucial in boreal peatland habitats (Rydin and Jeglum, 2013; Graham and Vitt, 2016), our results provide insights into ecological processes in these ecosystems in the context of global warming. First, unchanged species-level *Sphagnum* moss C, N and P concentrations along the hummock-hollow gradients suggests that, until the shift in moss species composition, the mosses have the ability to tolerate environmental changes and maintain relatively constant C:N:P stoichiometry. Second, increased moss C:P and N:P ratios induced by changed species composition will slow down moss growth rates (Elser et al., 2010). This may decrease ecosystem net primary productivity, given

that mosses contribute significantly in boreal peatlands (Gunnarsson, 2005; Elbert et al., 2012). Third, mosses generally have slow decomposition rates because of low substrate quality, leading to soil organic matter accumulation and C sequestration in boreal peatlands (Lindo and Gonzalez, 2010). Because litter C:N:P stoichiometry is a primary driver of decomposition and nutrient dynamics (Manzoni et al., 2010), increased moss C concentration and lowered P concentration would increase litter recalcitrance and hamper decomposition, which may strongly influence the detrital food web and thus C and nutrient cycles (Hobbie et al., 2002; Jassey et al., 2013).

5 Conclusions

In this study, we examined the effect of microtopography on moss C:N:P stoichiometry at both species and community levels along the hummock-hollow gradient in a boreal peatland. At the species level, *Sphagnum* moss species maintained constant C:N:P stoichiometry along the hummock-hollow gradient, whereas the C:P ratio of *A. palustre* (a non-*Sphagnum* moss species) varied with microtopography. At the community level, the spatial variations in moss C:N:P stoichiometric ratios were largely driven by changes in P concentration in the hummock-hollow complexes. Specifically, mosses had higher C:P and N:P ratios in drier habitats (hummocks and intermediate zones) than in the wetter habitats (hollows), but maintained stable C:N ratios in hummock-hollow complexes. These findings imply that the effects of microtopography on moss C:N:P stoichiometry in the hummock-hollow complexes are highly scale-dependent and help comprehensively understand C and nutrient cycles in boreal peatlands. Notably, because hummock-hollow complexes represent distinct environmental gradients (e.g., soil moisture, nutrient availability and microclimate), and moss species composition generally varies along this microtopographic gradient, our findings provide critical insights into possible future changes in C:N:P stoichiometry and hence C and nutrient dynamics in boreal peatlands in the context of climate change.

Acknowledgements

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Appendix:

Table S1 Species dominance, and carbon (C), nitrogen (N) and phosphorus (P) concentrations of mosses in the hummock-hollow complexes (sample numbers in parentheses)

Species	Hummocks				Intermediate zones				Hollows			
	Species dominance (%)	C (mg/g)	N (mg/g)	P (mg/g)	Species dominance (%)	C (mg/g)	N (mg/g)	P (mg/g)	Species dominance (%)	C (mg/g)	N (mg/g)	P (mg/g)
S. girgensohnii	4.37 (3)	495.8	11.8	1.5	15.62 (3)	491.5	10.6	1.1	13.62 (4)	490.3	12.2	1.4
S. falcatulum	–				1.14 (1)	504.6	9.1	1.1	–			
S. squarrosum	–				–				13.52 (1)	482.2	9.9	1.1
S. rubellum	9.29 (1)	497.7	10.1	1.0	3.74 (1)	502.40	13.2	1.1	5.40 (1)	485.7	12.7	1.3
S. jensenii	–				1.04 (1)	504.4	8.8	1.3	8.66 (1)	482.1	9.5	1.4
S. palustre	4.65 (3)	507.2	12.1	1.1	23.85 (8)	505.2	11.5	1.2	27.97 (6)	500.1	11.8	1.2
S. subsecundum	–				–				9.99 (2)	474.2	10.0	1.6
S. perichaetiale	45.32 (5)	501.4	11.4	1.1	37.30 (4)	503.6	10.9	1.1	5.86 (3)	497.1	11.7	1.2
S. magellanicum	30.15 (3)	501.6	11.1	1.1	11.92 (3)	504.0	12.0	1.0	9.39 (4)	492.2	11.3	1.2
Aulacomnium palustre	5.01 (8)	508.9	9.0	1.4	5.39 (8)	514.1	9.1	1.3	4.50 (7)	503.7	10.1	1.6
Polytrichum commune	1.21 (2)	516.5	8.8	1.1	–				–			
Ptilium crista-castrensis	–				–				1.08 (1)	490.9	10.2	1.4

Note: '–' means no data