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Biogeosciences

Environmental and taxonomic controls of carbon and oxygen stable isotope composition in *Sphagnum* across broad climatic and geographic ranges

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Abstract. Rain-fed peatlands are dominated by peat mosses (*Sphagnum* sp.), which for their growth depend on nutrients, water and CO_2 uptake from the atmosphere. As the isotopic composition of carbon (^{12,13}C) and oxygen (^{16,18}O) of these *Sphagnum* mosses are affected by environmental conditions, *Sphagnum* tissue accumulated in peat constitutes a potential long-term archive that can be used for climate reconstruction. However, there is inadequate understanding of how isotope values are influenced by environmental conditions, which restricts their current use as environmental and palaeoenvironmental indicators. Here we tested (i) to what extent C and O isotopic variation in living tissue of *Sphagnum* is species-specific and associated with local hydrological gradients, climatic gradients (evapotranspiration, temperature, precipitation) and elevation; (ii) whether the C isotopic signature can be a proxy for net primary productivity (NPP) of *Sphagnum*; and (iii) to what extent *Sphagnum* tissue δ^{18}O tracks the δ^{18}O isotope signature of precipitation. In total, we analysed 337 samples from 93 sites across North America and Eurasia us-ing two important peat-forming *Sphagnum* species (*S. magellanicum*, *S. fuscum*) common to the Holarctic realm. There were differences in δ^{13}C values between species. For *S. magellanicum* δ^{13}C decreased with increasing height above the water table (HWT, $R^2 = 17\%$) and was positively correlated to productivity ($R^2 = 7\%$). Together these two variables explained 46 % of the between-site variation in δ^{13}C values. For *S. fuscum*, productivity was the only significant predictor of δ^{13}C but had low explanatory power (total $R^2 = 6\%$). For δ^{18}O values, approximately 90 % of the variation was found between sites. Globally modelled annual δ^{18}O values in precipitation explained 69 % of the between-site variation in tissue δ^{18}O. *S. magellanicum* showed lower δ^{18}O enrichment than *S. fuscum* (-0.83 ‰ lower). Elevation and climatic variables were weak predictors of tissue δ^{18}O values after controlling for δ^{18}O values of the precipitation. To summarize, our study provides evidence for (a) good predictability of tissue δ^{18}O values from modelled annual δ^{18}O values in precipitation, and (b) the possibility of relating tissue δ^{13}C values

to HWT and NPP, but this appears to be species-dependent. These results suggest that isotope composition can be used on a large scale for climatic reconstructions but that such models should be species-specific.

1 Introduction

Peatlands in temperate, boreal and arctic regions form large reservoirs of carbon, which are vulnerable to release under expected changes in global climate and land management (Rydin and Jeglum, 2013; Loisel et al., 2014). Because peat decomposes slowly and gradually accumulates, it preserves information on past peatland ecosystem dynamics and responses to allogenic and autogenic forcings. Palaeoenvironmental studies of peat may, therefore, help to anticipate the future responses of these globally important ecosystems to climate change (Loader et al., 2016). Past climate and local hydrology can be estimated using a variety of biotic and biogeochemical proxies, including the δ^{13}C and δ^{18}O values of organic material (e.g. van der Knaap, 2011; Royles et al., 2016; Lamentowicz et al., 2015). However, the environmental (e.g. climate) and biotic (e.g. species identity) controls of isotope differentiation in peatland-dwelling plants are still poorly understood and current assumptions regarding these controlling factors are yet to be tested on larger spatial scales.

Sphagnum mosses are the most dominant peat-forming plant group in acidic peatlands. The composition of stable isotopes of carbon and oxygen in their tissues is affected by different environmental conditions, operating through their impact on fractionation processes. When not submerged, carbon isotope signals in bulk tissues or components such as cellulose depend mainly on the concentration and isotopic composition of CO_2 in the chloroplast, which alters isotope discrimination during biochemical fixation of CO_2 (Farquhar et al., 1989; O'Leary, 1988). In mosses, the CO_2 concentration in the chloroplast, $[CO_2]_c$, is determined by temperature, light availability, CO_2 partial pressure and, most importantly, plant water status (Finsinger et al., 2013; van der Knaap et al., 2011; Ménot and Burns, 2001; Ménot-Combes et al., 2004; Royles et al., 2014; Skrzypek et al., 2007a; Kaislahti Tillman et al., 2013). When wet, external water films on leaf surfaces impede diffusion and $[CO_2]_c$ is lowered (Rice and Giles, 1996; Rice, 2000; Williams and Flanagan, 1996); consequently, the proportion of fixed ^{13}C increases due to internal drawdown of the preferred isotope ^{12}C. When submerged, assimilation of respired or methane-derived CO_2 can alter $[CO_2]$ and also the isotopic composition of C in *Sphagnum* (Raghoebarsing et al., 2005). Even when not submerged, respiratory carbon can be refixed by *Sphagnum* (Turetsky and Wieder, 1999; Limpens et al., 2008). Given that respired CO_2 is isotopically lighter than that in the atmosphere, it may also contribute to variation in tissue isotope values. Despite many detailed studies, there remains uncertainty about how the multiple controls on ^{13}C isotope values combine to determine isotopic composition, and how universal the proposed mechanisms are on a global scale. This uncertainty currently restricts the utility of C isotope signals as palaeoclimatic or palaeoenvironmental indicators in peatlands (Loader et al., 2016).

Oxygen isotope values in moss tissues depend on the isotopic composition of the water sources, enrichment associated with evaporation from the moss surface and biochemical fractionation (Dawson et al., 2002). Once on the plant, ^{18}O present in water equilibrates with that in atmospheric CO_2 prior to fixation as well as being incorporated directly during hydrolysis reactions, especially during the initial stages of carbon fixation (Gessler et al., 2014; Sternberg et al., 2006). Hence, variation in tissue oxygen isotopes reflect environmental conditions that control source water (rainfall, snowfall, groundwater) as well as fractionation caused by evaporation prior to fixation, which is controlled by micrometeorological conditions (mainly temperature, relative humidity and incident energy) (Daley et al., 2010; Moschen et al., 2009; Royles et al., 2013; Kaislahti Tillman et al., 2010). Oxygen isotope composition has, therefore, been used to reconstruct climatic conditions and to infer the dominant water source in peatlands (Aravena and Warner, 1992; Ellis and Rochefort, 2006; van der Knaap et al., 2011). Ongoing measurements of oxygen isotopes in precipitation across the globe (Bowen, 2010; IAEA/WMO, 2015) have generated models that predict spatial patterns in oxygen isotope composition of precipitation based on temperature, elevation, atmospheric residence time and circulation patterns (e.g. Bowen, 2010). Once isotopic composition of the source water is accounted for, variation in moss tissue isotopic values should be largely determined by fractionation that accompanies evaporation from the surface of plants. How well oxygen isotopes in *Sphagnum* tissues reflect atmospheric water or plant surface water depends on local weather conditions such as precipitation, air temperature and humidity. For example, Bilali et al. (2013) suggest that oxygen isotopes in *Sphagnum* mosses from maritime bogs will track variation in precipitation patterns whereas isotopic values in continental habitats will be more dependent on summer temperature, as temperature and humidity are more variable in those regions. On local scales, oxygen isotope values also vary as a function of temperature and humidity. Aravena and Warner (1992) found differences that correspond with changes in microtopography. Elevated microsites (hummocks) were enriched in ^{18}O, which they ascribed to higher evaporation compared to that of neighbouring wet depressions (hollows). However, as with ^{13}C, there remains uncertainty in how ^{18}O signatures relate to environmental factors and species identity and to what extent global ^{18}O patterns in precipitation dominate over local processes.

Stable isotopes can also serve as indicators of net primary productivity (NPP) (Rice and Giles, 1996; Williams and Flanagan, 1996; Rice, 2000). However, few studies have explored these relationships in the field. In a multispecies

comparison of peat mosses, Rice (2000) found that plants with higher relative growth rates had lower discrimination against ^{13}C and therefore were more enriched in ^{13}C. This was attributed to the local environment, with fast-growing plants of wetter microhabitats having thicker water films that inhibit CO_2 diffusion into the plant and to species-specific differences in maximum rates of photosynthesis. Both factors would reduce internal $[CO_2]$ and thereby lower discrimination. In line with this, a warming experiment by Deane-Coe et al. (2015) reported a positive relationship between moss net NPP and $\delta^{13}C$ values for tundra mosses (*Dicranum*, *Pleurozium*, *Sphagnum*). Clearly, carbon isotope values show promise as indicators of peat moss contemporary growth and potentially as an NPP proxy in palaeoecological studies. This could be particularly valuable to differentiate productivity and decomposition controls in long-term carbon accumulation studies. To date, we are not aware of attempts to explore the robustness of these relationships across large spatial scales.

Together, tissue carbon and oxygen isotope compositions are controlled both by environmental factors at micro- and macro-scales, and by species-specific differences that relate to water balance and carbon dynamics in peat mosses. Palaeoecological studies rely on such environment–isotope relationships for environmental reconstructions (Ellis and Rochefort, 2006; van der Knaap et al., 2011). The underlying mechanisms are, however, rarely fully explored using known environmental gradients (but see Ménot and Burns, 2001 for an example) or only tested across narrow bands of environmental variation, often with sets of correlated environmental factors (Loader et al., 2016). Moreover, interactions with biotic factors such as species identity have received little attention despite the large variations in *Sphagnum* species dominance commonly observed down peat cores (e.g. Ménot and Burns, 2001). Here we aim to provide a robust, cross-scale evaluation of how environmental factors and species identity influence the C and O isotope compositions of *Sphagnum* using two common and widely distributed peat-forming species (*S. magellanicum* and *S. fuscum*) that are primarily rain-fed. To achieve this, we performed an unprecedented large sampling campaign across the Holarctic realm.

Specifically, we (i) investigated relationships between C and O isotope values and factors known to influence plant water availability (height above the water table – HWT, temperature, evaporation and precipitation) and CO_2 partial pressure (elevation), and tested whether their effects were modified by species identity; (ii) tested the prediction that *Sphagnum* tissue $\delta^{13}C$ values are associated with NPP; and (iii) tested whether tissue $\delta^{18}O$ in rain-fed *Sphagna* is predicted by the $\delta^{18}O$ isotope signature in precipitation but modified by negative relationships with precipitation and positive ones with temperature/evaporation. Across these objectives we examined how C and O isotope values varied with scale (within-peatland versus between-peatlands) and to what extent HWT and NPP could explain variation within and between peatlands.

2 Materials and methods

2.1 Study species and collection sites

Our study focused on two common peat-forming *Sphagnum* species, *S. fuscum* (Schimp.) H. Klinggr. (circumpolar distribution) and *S. magellanicum* Brid. (cosmopolitan distribution). In general, these species are confined to primarily rain-fed peatlands (bogs) and described as hummock (*S. fuscum*) and lawn (*S. magellanicum*) species. However, *S. magellanicum* is a species with a very broad niche and found in a range of habitats with varying degrees of groundwater influence (Flatberg, 2013). These species are easy to identify, but recent research has shown that the dark European morph of *S. fuscum* is conspecific to the North American *S. beothuk* (Kyrkjeeide et al., 2015), and *S. magellanicum* has been shown to consist of two genetically diverged morphotypes (Kyrkjeeide et al., 2016) that recently were separated at the species level (Hassel et al., 2018). Unpublished genetic data suggest that samples collected in our study consist of both *S. magellanicum* morphs (approximately 50/50) and possibly one or two samples of *S. beothuk* (Narjes Yousefi, personal communication, 2018). Hence, we here treat our species as aggregates (i.e. species collectiva), *S. fuscum* coll. and *S. magellanicum* coll.

The two species were sampled across the Holarctic region at a total of 93 sites (Fig. 1; Table S1 in the Supplement) at the end of the growing season. To make comparisons between species and between sites possible, we focused on habitats where both species can be found and have low influence of surrounding groundwater. Thus, we only sampled bogs (including a few poor fens with ombrotrophic character) and open (no tree canopy) habitats. Sampling was conducted mainly during 2013, but a few sites were sampled at a similar time of year in 2014. At each site two patches (minimum 10 m apart) for each species were sampled (except for 11 sites that contained only one patch for one species). At each sampling patch we recorded moss growth, HWT and GPS coordinates, and collected a moss sample (78 cm^2 and 5 cm deep) at the end of the growing season (September to November depending on location and generally coincided with when there was a risk of the first snowfall to occur). Moss samples were dried (24 h at 60–65 °C) within 72 h or immediately frozen and later thawed and dried. The apical part (the capitula, top 1 cm) of the dried plant shoots was used for isotope analysis, while the stem section was used for bulk density estimation to calculate moss NPP.

2.2 Isotope determination

Ten capitula from each patch were selected and finely chopped with a single-edge razor by hand and mixed. Ca-
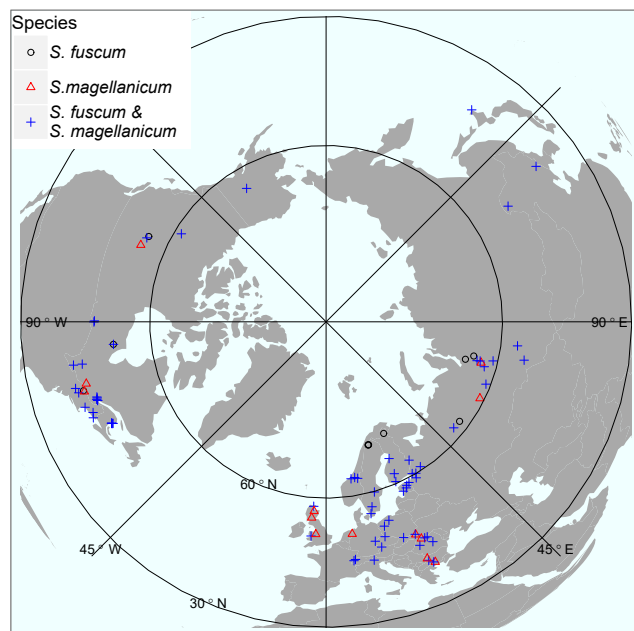
Figure 1. Map illustrating sample sites for the investigated species. At some sites only one of the two *Sphagnum* species was sampled, indicated by red triangles or black circles. Otherwise sites contained both species (blue crosses). The map is centred on the North Pole and has an orthographic projection. Geographical ranges: latitude 41.6–69.1 N, elevation 2 – 1829 m a.s.l. See Table S1 for details.

pitula were chosen as they reflect the most recently fixed organic matter and should relate better to recent growing season conditions. In *Sphagnum*, $\delta^{13}C$ from the capitulum is similar to that of branches within the top 15 cm of plants but is approximately 1–2 ‰ less negative than stems (Loader et al., 2007). For $\delta^{18}O$, the offset between branches and stems is around 1 ‰ (Moschen et al., 2009). Standard deviations of repeated samples were 0.6 ‰ and 0.7 ‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. Approximately 0.5 mg of dry sample was packed in tin cups for $\delta^{13}C$ analyses, and ~ 0.2 mg in silver cups for $\delta^{18}O$ analyses. Samples were analysed at Union College (Schenectady, NY, USA) using a Thermo Delta Advantage mass spectrometer in continuous flow mode connected (via a ConFlo IV) to a Costech Elemental Analyzer for $\delta^{13}C$ analysis or a Thermo TC/EA for $\delta^{18}O$ analyses. Isotope values are presented as $1000 \times (R_{sample} / R_{standard} - 1)$, where R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes (e.g. $^{13}C / ^{12}C$) and are referenced to VPDB and VSMOW for C and O, respectively. Carbon isotope data were corrected using sucrose (IAEA-CH-6, -10.449 ‰), acetanilide (in house, -37.07 ‰) and caffeine (IAEA-600, -27.771 ‰). Oxygen isotope data were corrected using sucrose (IAEA-CH-6, 36.4 ‰), cellulose (IAEA-C3, 31.9 ‰) and caffeine (IAEA-600, -3.5 ‰) with values from Hunsinger et al. (2010). Oxygen isotope standardization was further checked with the whole wood standards USGS54 and

USGS56. The combined instrument uncertainty for $\delta^{13}C$ (VPDB) is < 0.1 ‰ based on the in-house acetanilide standard and < 0.5 ‰ for $\delta^{18}O$ (VSMOW) based on the cellulose standard (IAEA-C3).

We performed isotope analyses on whole-plant tissue rather than on cellulose extracts. In living *Sphagnum* samples, there is a strong linear relationship between the isotopic composition of these two components for both $\delta^{13}C$ (R^2 values 0.89–0.96; Kaislahti Tillman et al., 2010; Ménot and Burns, 2001; Skrzypek et al., 2007b) and for $\delta^{18}O$ (R^2 values 0.53–0.69; Kaislahti Tillman et al., 2010; Jones et al., 2014). Focussing on whole-plant tissue allowed us to analyse a higher number of samples for this study, allowing larger numbers of sites and more replication.

2.3 Environmental variables

The modelled $\delta^{18}O$ signal in meteoric water (precipitation) (Bowen and Wilkinson, 2002) was obtained from http://www.waterisotopes.org (last access: 2 October 2017) as annual and monthly isotope ratio estimates at 10 arcmin resolution. These global estimates have shown to be highly accurate ($R^2 = 0.76$ for mean annual $\delta^{18}O$ in precipitation) and are based on absolute latitude and elevation and account for regional effects on atmospheric circulation patterns (for details see Bowen, 2010, 2017; IAEA/WMO, 2015). To test which temporal period of $\delta^{18}O$ values in precipitation showed the highest correlation with tissue $\delta^{18}O$ values, we calculated annual (January–December), growing season (May–October) and winter–spring (January–April) mean isotope ratio. We calculated both unweighted and weighted means against precipitation for each month. Monthly precipitation (PRECTOTCORR), land evapotranspiration (EVLAND) and surface air temperature (TLML) for each site and year of sampling (2013 or 2014) were retrieved from the NASA GESDISC data archive, land surface and flux diagnostics products (M2T1NXLND, M2TMNXFLX; resolution longitude 0.667°, latitude 0.5°; Global Modeling and Assimilation Office, 2015a, b). Total precipitation and evapotranspiration (ET), and mean temperature, from April to October were used as predictors in the statistical models. As ET can be compensated for by precipitation, we used the ET/P quotient as a predictor for the effect of water loss. A high value (> 1) indicates a net loss of water to the atmosphere. Site altitude was retrieved from a global database using the R package *elevatr* (ver 0.1-2, Hollister and Shah, 2017).

The distance from the moss surface to the water table (HWT) was measured using water wells (commonly a PVC pipe, 2–5 cm in diameter and slotted or perforated along the sides) with a "plumper" (a cylinder on a string that makes a "plump" sound when it hits the water surface) or a "bubbler" (a narrow tube that makes bubbles when it hits the water surface while the user blows into it). HWT was measured in the spring and in the autumn and there was a strong correlation between the two time points ($r = 0.74$). As growth mainly

Table 1. Sample sizes, standard variation and overall partitioning of measured variation for each species and response (δ^{13}C and δ^{18}O). N_{site} is the number of sites and N_{obs} the total sample size. Standard deviation of the responses is given for within and between sites, together with the proportion of total variance measured between sites and within sites.

	Species	N_{site}	N_{obs}	Within site		Between sites	
				SD	Proportion of variance (%)	SD	Proportion of variance (%)
δ^{13}C	*S. fuscum*	80	169	0.9	56	0.8	44
	S. magellanicum	83	168	1	51	0.98	49
δ^{18}O	*S. fuscum*	80	168	0.7	13	1.83	87
	S. magellanicum	83	167	0.67	10	2	90

occurs in late summer to autumn in temperate and boreal regions, we used HWT at the end of the season as the proxy of relative HWT between sites.

2.4 Moss growth

Moss growth (or productivity, NPP) was measured with a modified version of the cranked wire method (see Clymo, 1970; Rydin and Jeglum, 2013 for details), with bristles from a paint brush spirally attached to a wire. These "brush wires" were inserted in the moss layer with the end of the wire protruding above the surface. Height increment (i.e. vertical growth) was measured over the growing season as the change in distance (to nearest millimetres) between the moss layer and the top of the wire. A minimum of three wires were inserted within a 1×1 m uniform area (same microhabitat, vegetation and general structure). To determine moss bulk density (kg m^{-3}), we dried (24 h at 60–65 °C) the top 30 mm of the stems (area 78 cm^2) in our collected core (see Sect. 2.1). Biomass growth on an area basis (g m^{-2} yr^{-1}) was calculated as height increment × bulk density.

2.5 Statistical analyses

To test and quantify the influence of environmental variables and species identity on isotope composition, we used linear mixed models in R (R core team, 2016), employing the R package *lme4* ver 1.1-12 (Bates et al., 2015). Site dependence (i.e. multiple samples from the same site) was accounted for by adding site as a random factor. For tissue δ^{13}C, we first fitted two separate models to test the independent effects of HWT, NPP and species identity (*S. fuscum* and *S. magellanicum*), and whether the HWT or NPP effect varied between species by fitting a species interaction term. To test the explanatory power of environmental variables (ET/P, precipitation, temperature, elevation) we first constructed a base model with HWT and NPP, as they were identified as the main predictors in literature. For simplicity we removed negligible interactions from this model. Each environmental variable and its interaction with species was then tested against the base model. For tissue δ^{18}O, we first explored

which temporal period of modelled δ^{18}O$_{precip}$ (annual, growing season, winter–spring) had the highest explanatory power and whether the relationship varied between species. The identified best model was then used as the base model to separately test each environmental variable (HWT, ET/P, precipitation, temperature) and its interaction with the species.

The proportion of variance explained by the predictors was calculated at the site level (Gelman and Hill, 2007) or as marginal R^2 (Nakagawa and Schielzeth, 2013; R package *piecewiseSEM* ver 1.1-4; Lefcheck, 2016). Although our study focused on explained variance by predictors, we also performed statistical tests of predictors and their interactions using type-2 (main effects tested after all the others in the model but without the interaction term) F tests, applying Kenward–Roger adjustments to the degrees of freedom, as implemented in the *car* package (ver. 2.1-3, Fox and Weisberg, 2011). Standard model checking was performed (e.g. residual analyses and distribution of random effects) to ensure compliance with model assumptions. Covariances between predictors were small ($r < 0.15$) or moderate ($r = 0.40$–0.50 between ET/P, precipitation and temperature) and this multicollinearity had minor impact on model estimates.

3 Results

Data collection from a geographically broad area resulted in large variation of isotope values and explanatory variables (Table S2). Due to uncertainty in height increment measurement we recorded a few negative values resulting in negative NPP. These values were kept in the analyses. The means and standard deviations (in parenthesis) of height increment (HI, millimetres) were 14.3 (10.1) for *S. fuscum* and 19.5 (14.1) for *S. magellanicum*, and the means and standard deviations of bulk density (BD, kg m^{-3}) were 17.8 (9.9) for *S. fuscum* and 10.2 (7.6) for *S. magellanicum*.

Table 2. Results from linear mixed models for δ^{13}C values. Statistical tests are based on type-2 F test using Kenward–Roger-adjusted degrees of freedom. The second model only included *S. magellanicum*. Elevation (m a.s.l.) and the three climatic variables (growing season sums and means: ET/P, P in millimetres, temperature in degrees Celcius) were tested one by one in the model including HWT (height above the water table in centimetres), species and NPP (g m^{-2} yr^{-1}). For simplicity, the negligible HWT × NPP term was dropped from this model ($P = 0.36$). Estimated effects ($\pm$ SEs) are only given for the main effects if interactions were considered negligible. These effects are slopes for continuous variables (all variables except species) and for species (categorical) the difference between *S. magellanicum* and *S. fuscum* (i.e. *S. fuscum* being the reference level). In the presence of an interaction between HWT and species, the species effect was estimated at mean HWT. R^2_{site} is explained between-site variance; R^2_{marginal} is explained total variance.

Variable	Effect	F	DF	P	N	R^2_{site}	R^2_{marginal}
HWT		26.8	1, 67	< 0.001	311		
Species	-0.88 ± 0.13*	43.0	1, 274	< 0.001			
HWT × species	S. fus: -0.021 ± 0.008	6.0	1, 235	0.01		0.32	0.18
	S. mag: -0.045 ± 0.008						
HWT (*S. magellanicum*)	-0.04 ± 0.008	26.0	1, 134	< 0.001	158	0.33	0.17
NPP	0.0023 ± 0.0005	23.1	1, 309	< 0.001	318	0.12	0.07
Species	-0.38 ± 0.12	9.4	1, 266	< 0.01		0.01	0.01
NPP × species	NS	0.7	1, 290	0.41			
HWT		25.5	1, 246	< 0.001	295		
Species	-0.62 ± 0.13 (HWT $= 28$ cm)	22.1	1, 269	< 0.001			
NPP	0.0022 ± 0.0005	22.4	1, 281	< 0.001		0.11	0.07
HWT × species	S. fus: -0.012 ± 0.007	10.6	1, 267	< 0.01		0.20	0.12
	S. mag: -0.042 ± 0.007						
Elevation	0.00035 ± 0.0002	2.7	1, 81	0.11	295	0.03	0.01
Elevation × species	NS	0.5	1, 233	0.47			
ET/P		0.2	1, 90	0.66	295		
(ET/P) × species	S. fus: -0.33 ± 0.40	5.0	1, 266	0.03		-0.02	0.01
	S. mag: 0.78 ± 0.44						
P	-0.00013 ± 0.0006	0.0	1, 80	0.83	295	-0.01	0.00
P × species	NS	1.2	1, 248	0.27			
T		0.0	1, 91	0.97	295		
T × species	S. fus: -0.051 ± 0.034	9.7	1, 273	< 0.01		-0.05	0.02
	S. mag: 0.087 ± 0.041						

* The effect of *S. magellanicum* compared to *S. fuscum* at HWT 28 cm.

3.1 δ^{13}C signal

Variation in *Sphagnum* tissue δ^{13}C values was marginally greater within sites than between sites (Table 1). HWT predicted the δ^{13}C values, but the relationship differed between the two species (Table 2, Fig. 2). Although δ^{13}C values decreased with increasing HWT for both species, the slope was less steep for *S. fuscum* and this species had slightly higher δ^{13}C values overall. In separate models for the two species, HWT for *S. fuscum* had near-zero explanatory power, while for *S. magellanicum* HWT explained 33 % of the between-site variation and 17 % of the total variance (i.e. marginal R^2).

Measured δ^{13}C values were related to moss NPP and δ^{13}C values increased by 0.0023 ‰ (SE: 0.00048) for each milligram of biomass produced per square metres. NPP ex-

plained 11 % of the between-site variation in δ^{13}C and 7 % of the total variation. HWT and NPP explained 48 % of the between-site variation of δ^{13}C in *S. magellanicum* and 24 % of the total variation. Corresponding values for *S. fuscum* were 6 % and 7 %. Of the additional environmental variables tested, we found weak evidence that ET/P and temperature were positively correlated with δ^{13}C but only for *S. magellanicum* (Table 2).

3.2 δ^{18}O signal

Sphagnum tissue δ^{18}O values varied more between sites than within sites, and at similar magnitudes and proportions for both species (Table 1). Tissue δ^{18}O values were predicted by the spatially explicit estimates of δ^{18}O value isotope signature in precipitation (Fig. 3, Table 3). Annual mean δ^{18}O$_{\text{precip}}$

Table 3. Results from linear mixed models for $\delta^{18}O$ values. Statistical tests are based on type-2 F test using Kenward–Roger-adjusted degrees of freedom. Three time periods for modelled $\delta^{18}O$ values (‰) in precipitation were tested individually: annual mean, growing season (April–September) and spring (January–April). The three climatic variables (growing season sums and mean: ET/P, P (mm), temp [°C]) were tested one by one in a model including HWT (cm) and mean annual $\delta^{18}O$ values). Estimated effects ($\pm$ SEs) are only given for the main effects if interactions were considered negligible. These effects are slopes for continuous variables (all variables except species) and for species (categorical) the difference between *S. magellanicum* and *S. fuscum* (i.e. *S. fuscum* being the reference level). R^2_{site} is explained between-site variance; R^2_{marginal} is explained total variance.

Variable	Effect	F	DF	P	N	R^2_{site}	R^2_{marginal}
Annual precipitation $\delta^{18}O$	0.43 ± 0.035	148.4	1, 95	< 0.001	335	0.69	0.50
species	-0.83 ± 0.083	101.3	1, 250	< 0.001			0.05
Annual precipitation $\delta^{18}O \times$ species		1.9	1, 261	0.16			
Apr–Sep precipitation $\delta^{18}O$	0.49 ± 0.049	100.5	1, 94	< 0.001	335	0.58	0.42
species	-0.83 ± 0.083	99.4	1, 249	< 0.001			0.05
Apr–Sep precipitation $\delta^{18}O \times$ species		1.4	1, 256	0.24			
Jan–Apr precipitation $\delta^{18}O$	0.37 ± 0.027	187.2	1, 96	< 0.001	335	0.75	0.55
Species	-0.84 ± 0.083	102.3	1, 252	< 0.001			0.05
Jan–Apr precipitation $\delta^{18}O \times$ species		2.3	1, 265	0.13			
Annual precipitation $\delta^{18}O$	0.41 ± 0.038	111.9	1, 88	< 0.001	310	0.64	0.46
HWT	0.015 ± 0.005	10.4	1, 288	< 0.01		0.00	0.01
ET/P		0.1	1, 99	0.81	335		
(ET/P) $\times$ species	S. fus: -0.39 ± 0.48	3.5	1, 266	0.06		0.00	0.00
	S. mag: 0.28 ± 0.50						
P	-0.0005 ± 0.0008	0.4	1, 99	0.54	335	0.00	0.00
$P \times$ species		0.8	1, 257	0.37			
Temp	-0.14 ± 0.051	7.4	1, 96	0.01	335	0.02	0.02
Temp $\times$ species		1.6	1, 274	0.21			

explained 69 % of the variation in $\delta^{18}O_{\text{tissue}}$ between sites. This was similar to mean winter–spring (January–April) $\delta^{18}O_{\text{precip}}$ values (75 % explained) but higher than the growing season (April–September) $\delta^{18}O_{\text{precip}}$ (58 %). Using precipitation-weighted $\delta^{18}O_{\text{precip}}$ values resulted in lower percentages of explained variance for all three time periods (R^2_{site}: annual 52 %, January–April 65 %, April–September 52 %). *S. magellanicum* had consistently lower $\delta^{18}O$ values than *S. fuscum* (-0.83‰), but both species had a similar relationship between tissue $\delta^{18}O$ and $\delta^{18}O_{\text{precip}}$ (Fig. 3, Table 3).

HWT at the end of the growing season was, on average, 11 cm lower in *S. magellanicum* patches (wetter habitat) compared to *S. fuscum* (HWT = 33 cm) patches ($F_{1,224} = 131.9$, $P < 0.0001$). However, we found only very weak support for the hypothesis that HWT predicts tissue $\delta^{18}O$ values, as HWT explained < 1 % of the $\delta^{18}O$ variation (Table 2). There was negligible influence of the additional environmental variables on $\delta^{18}O$ values (Table 2). ET/P was associated with higher $\delta^{18}O$ values in *S. magellanicum* and lower in *S. fuscum* (but not different from the zero effect), while increasing temperature was weakly associated with overall lower $\delta^{18}O$ values.

4 Discussion

4.1 Stable carbon isotope discrimination in *Sphagnum*

Our data were consistent with the hypothesis that moss growing closer to the water table (low HWT) has reduced carbon isotope fractionation, leading to greater fixation of $^{13}CO_2$ and more ^{13}C-enriched tissue (Rice and Giles, 1996; Williams and Flanagan, 1996). Given that the water table position was measured in different places at different times and all are one-time measurements, this result is remarkably robust. For example refixation of ^{12}C-enriched substrate-derived CO_2 in living *Sphagna* (Turetsky and Wieder, 1999; Raghoebarsing et al., 2005) can potentially contribute to within-site variation in $\delta^{13}C$ as it potentially affects both the ambient concentration of CO_2 as well as its isotopic composition. Interestingly, the strength of the $\delta^{13}C$ – HWT relationship differed in the two species, with *S. magellanicum* exhibiting a greater reduction in $\delta^{13}C$ in response to drier conditions (high HWT) than *S. fuscum*. The weaker effect of HWT on $\delta^{13}C$ values in *S. fuscum* is likely a consequence of limited fluctuation in tissue water content, as this species is well known to store abundant water within capillary spaces
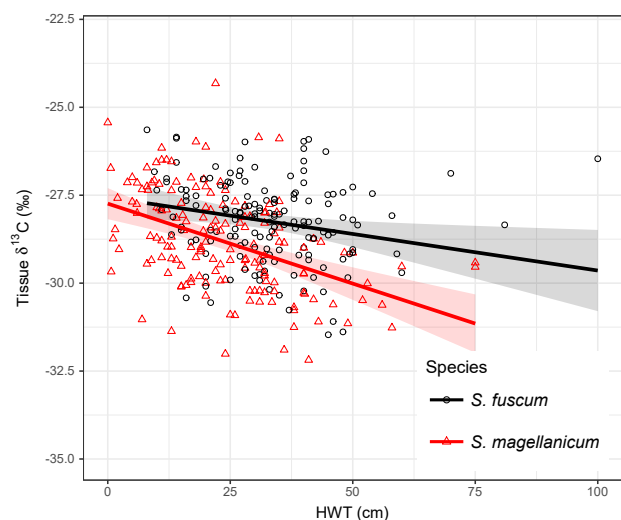
Figure 2. Relationship between height above the water table (HWT, measured at the end of the growing season) and δ^{13}C values in two *Sphagnum* species sampled across the Holarctic realm. Lines show the pooled regression line in a mixed-effect model. Shaded areas indicate approximate 95 % confidence intervals (2 × SE) of the regression coefficients that do not include the uncertainty of the random effects. Equations: *S. fuscum*, δ^{13}C = $-27.56 - 0.021 \times$ HWT; *S. magellanicum*, δ^{13}C = $-27.74 - 0.045 \times$ HWT. N_{site} = 83, N_{total} = 311. See also Table 1.

Figure 3. Association between modelled annual mean δ^{18}O$_{precip}$ values and δ^{18}O values in two *Sphagnum* species. Data show site means for each species and error bars represent the standard deviation (at some sites only one sample of a species was taken). Regression lines with different intercepts ($P < 0.001$, Table 2) illustrate the relationship between modelled δ^{18}O$_{precip}$ and *Sphagnum* δ^{18}O. Equations: *S. fuscum*, $26.36 + 0.43 \times \delta^{18}O_{precip}$ ($n = 1–2$, N_{site} = 80); *S. magellanicum*, $25.53 + 0.43 \times \delta^{18}O_{precip}$ ($n = 1–2$, N_{site} = 83). Shaded areas indicate approximate 95 % confidence intervals (2 × SE) of the regression coefficients that do not include the uncertainty of the random effects.

and resist drying (Rydin, 1985), thus maintaining the water-film that results in reduced fractionation. Loader et al. (2016) reported a similar slope estimate for *S. magellanicum* in a single peatland, and several studies have confirmed the effects of contrasting microtopography (i.e. hummock – hollow differences) using multi-species comparisons (Price et al., 1997; Loisel et al., 2009; Markel et al., 2010). As such, our results suggest that species-specific differences in carbon isotope discrimination in *Sphagnum* are related to water retention capacity and, consequently, become more apparent under drier conditions. This supports the results of previous, smaller-scale studies (Rice, 2000).

The influence of species identity on the relationship between δ^{13}C values and water table position has important implications for palaeoenvironmental reconstructions based on δ^{13}C values. The relationship between δ^{13}C and HWT has been used in palaeoecological reconstructions of surface wetness (e.g. Loisel et al., 2009). In our data set the strength of the relationship was weaker than previously reported. For instance, Loader et al. (2016) reported $R^2 = 54\%$ for *S. magellanicum* in a single site. Given the characteristics of our data (large-scale, circumpolar), the explanatory power ($R^2_{marginal} = 17\%$) can be considered acceptable and comparable to other proxies such as testate amoebae (16 % in Loader et al., 2016; Sullivan and Booth, 2011). Our results imply that isotopic signals of peatland wetness in hummock-dwelling species (such as *S. fuscum*) may be weaker or ab-
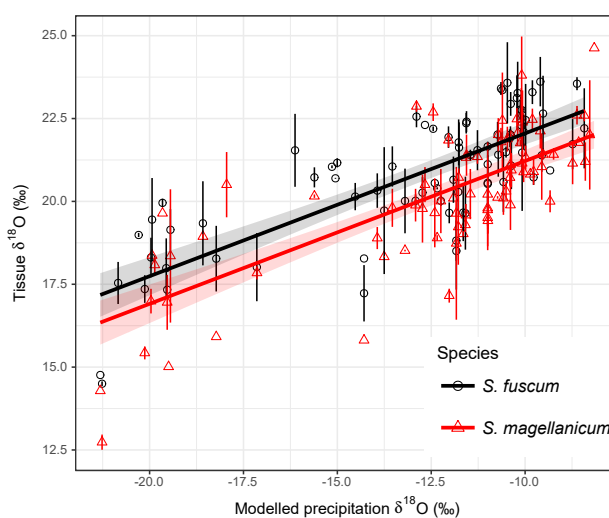
sent compared to lawn species. It is therefore important that the same species or species type (e.g. lawn species as they likely have a broad HWT niche) is used if δ^{13}C values are employed as a proxy to infer changes in HWT.

We also identified evidence that evapotranspiration (ET) and NPP modify δ^{13}C values, although the effect of ET was weak and restricted to *S. magellanicum*. We expected a stronger relationship, as ET and temperature control δ^{13}C by increasing water loss at the moss surface and reducing the diffusive resistance (i.e. reducing CO_2 limitation), enabling increased discrimination against ^{13}C (Williams and Flanagan, 1996). NPP only explained a small proportion of the variation in δ^{13}C values, but the relationship was apparent across species. Several studies have proposed the use of δ^{13}C values to infer *Sphagnum* productivity (e.g. Rice and Giles, 1996; Rice, 2000; Munir et al., 2017) and our study is the first to test this at the pan-Holarctic scale. Deane-Coe et al. (2015) investigated δ^{13}C values across moss species (including *Sphagnum*) and years at one site and found a weak relationship between productivity and δ^{13}C values ($R^2 = 0.10$ and 0.31). Similarly, Rice (2000) reported that the relative growth rate explained about 25 % of the variation in ^{13}C discrimination. We did not find as strong a relationship ($R^2 < 0.12$), but our study was geographically broader and less controlled; consequently, our results were likely influ-

enced by more complex interactions among environmental factors that affect *Sphagnum* growth across our sites. Nevertheless, our results indicate independent effects of evaporation and productivity on $\delta^{13}C$ values. The lack of a strong NPP pattern somewhat limits the ability to infer productivity of *Sphagnum* in palaeoecological studies.

4.2 Global patterns of $\delta^{18}O$ values in *Sphagnum*

Modelled $\delta^{18}O$ values in precipitation (Bowen, 2010) explained much of the variation in $\delta^{18}O_{tissue}$ values between sites ($R^2 = 68\%$ for annual mean $\delta^{18}O_{precip}$). The percent variance explained was even higher if the spring period for modelled $^{18}O_{precip}$ was used but was lower for the growing season average. This result does not necessarily mean that spring season water was utilized by the plants during the growing season. Between-site variation in $^{18}O_{precip}$ values are much larger in the winter (Fig. S1), more effectively discriminating maritime and continental regions (Bowen, 2010). The better fit may simply be an effect of a more distinct separation of $^{18}O_{precip}$ in the winter data. Although the $\delta^{18}O_{tissue} - ^{18}O_{precip}$ relationship presented here is robust, a few $\delta^{18}O$ values are less well predicted by the regression model and they originate from Northwest Territories (Canada) and West Siberia (Russia). Likely, this suggests that the $^{18}O_{precip}$ model is less accurate in these interior regions with fewer precipitation collection stations.

In contrast, the data did not support a negative correlation between precipitation amount and $\delta^{18}O_{tissue}$ values and $\delta^{18}O_{tissue}$ values were only weakly affected by predictors associated with water loss (ET/P and/or temperature) and species identity. The indication of ^{18}O enrichment in *S. magellanicum* due to ET/P was expected as the lighter isotope ^{16}O needs less energy to vaporize. However, the opposite trend was suggested for *S. fuscum*, and surprisingly, higher surface temperatures decreased ^{18}O enrichment. Hence we conclude that climatic variables associated with water loss were weak predictors after controlling for $\delta^{18}O_{precip}$ values. This result may not be too unexpected as laboratory experiments have so far failed to relate ^{18}O enrichment in *Sphagnum* to differences in evaporation rates (Brader et al., 2010).

There have been few regional studies on moss $\delta^{18}O_{tissue}$ values that span gradients of $\delta^{18}O_{precip}$ values (Royles et al., 2016; Skrzypek et al., 2010) and most interpretations of moss $\delta^{18}O_{tissue}$ – climate relationships come from peat core studies (e.g. van der Knaap et al., 2011). In Antarctic non-*Sphagnum* peat banks variation in $\delta^{18}O_{cellulose}$ values tracked $\delta^{18}O$ values in moss water across a latitudinal gradient (61–65° S) despite a lack of difference in $\delta^{18}O_{precip}$. This result led Royles et al. (2016) to suggest that moss water and tissue $\delta^{18}O$ values are better temporal integrators of source water than point rainfall measurements. The authors interpreted site-to-site differences as relating to differential evaporative enrichment and other physio-chemical factors that affect ^{18}O exchange, fixation and biochemical synthesis. Skrzypek et

al. (2010) explored variation in *Sphagnum* $\delta^{18}O_{tissue}$ values across a regional altitudinal gradient and found no consistent trend or significant relationship linking $\delta^{18}O_{tissue}$ values to altitude, where $\delta^{18}O$ in source water is expected to differ. Although fractionation in source water caused by adiabatic cooling with altitude should lead to altitudinal effects, differences in precipitation amount can confound this pattern (Gat et al., 2000). Unfortunately, there are limited regional studies that have tested the effects of variation in source water on $\delta^{18}O_{tissue}$ values. The present study provides a much greater range of geographical and environmental variation and shows strong support for *Sphagnum* strongly tracking source water.

Interestingly, the relationship between $\delta^{18}O_{tissue}$ and $\delta^{18}O_{precip}$ values detected here is very similar to that proposed some time ago by Epstein et al. (1977); $\delta^{18}O_{cellulose} = 27.33 + 0.33 \times \delta^{18}O_{precip}$ (note that Jones et al., 2014, show high correspondence between $\delta^{18}O_{cellulose}$ and $\delta^{18}O_{tissue}$ values). However, our data suggest a slightly steeper slope and lower intercept, particularly for *S. magellanicum*. The species effect on $\delta^{18}O$ suggests a difference in the degree of evaporation from the plant surface prior to the uptake of water. The lower $\delta^{18}O$ values for *S. magellanicum* compared to *S. fuscum* ($-0.83‰$) is comparable to the results from bogs in Canada for the same species ($-2.2‰$, Aravena and Warner, 1992) and between a hollow and a hummock species in the Netherlands ($-2‰$, Brenninkmeijer et al., 1982). This suggests that the absorbed water in *S. magellanicum* was subject to less evaporation. In *Sphagnum* plants, surface water is largely affected by capillarity, water storage and reducing conductance with compact morphology. Plant traits that enhance these functions are more pronounced in species and individuals found at high HWT as these characteristics maintain high tissue water content (Hayward and Clymo, 1982; Laing et al., 2014; Waddington et al., 2015). Consequently, during droughts, *Sphagnum* species growing close to the water table will dry out quickly as the evaporative demand cannot be balanced, and simultaneously photosynthesis is shut down. *Sphagnum* species higher above the water table wick water from below and store water effectively, thereby remaining photosynthetically active while water is lost due to evaporation. This mechanism would result in ^{18}O enrichment being higher above the water table (Brenninkmeijer et al., 1982; Aravena and Warner, 1992) and explains the positive relationship between HWT and $\delta^{18}O$ in *S. magellanicum* reported by Loader et al. (2016) along a 10 m transect. We found a weak positive relationship of $\delta^{18}O$ with HWT, which suggests that HWT cannot entirely explain species-specific differences in ^{18}O enrichment. Instead, this can be attributed to lower water retention (i.e. higher evaporation at the same water deficit) in *S. magellanicum* compared to *S. fuscum* (Clymo, 1973; McCarter and Price, 2014). Although species differences in ^{18}O have been reported (Aravena and Warner, 1992; Zanazzi and Mora, 2005; Bilali et al., 2013), our study suggests that the species-specific $\delta^{18}O$ signals may not simply be a consequence of growing at different HWT

but can rather reflect distinct water retention capacity in these species.

The strong influence of $\delta^{18}O_{precip}$ values and, to a much lesser extent, environmental variables related to water loss, combined with a relatively small within-site variation in $\delta^{18}O_{tissue}$ values, suggest that macroclimatic drivers, such as precipitation inputs, largely determine the $\delta^{18}O$ value of peatland moss tissue. These results are promising for the use of oxygen isotopes in large-scale palaeoecological reconstructions from peat cores (Ellis and Rochefort, 2006; Chambers et al., 2012; Daley et al., 2010), although a better understanding of O isotope fractionation within tissue components and their decay relationships would improve their utility. Moreover, the simple relationships presented here can potentially be utilized to trace changes in $\delta^{18}O_{precip}$ values that mirror climate variability.

5   Conclusions

Our study provides new insights into large-scale variation in *Sphagnum* tissue isotopic signature and suggests that isotopic composition can be used for climatic reconstructions. We show a close link between precipitation and tissue $\delta^{18}O$ values and conclude that variation in $\delta^{18}O$ values are mainly driven by the macroclimate, but species differences exist. In contrast, $\delta^{13}C$ values were strongly related to local microtopography, while the influence of macroclimate was negligible. As suggested in earlier studies, $\delta^{13}C$ values were also weakly associated with NPP. These conclusions were most strongly supported for the cosmopolitan *S. magellanicum* complex and species identity should be accounted for in future carbon isotope studies to avoid spurious conclusions.

Code and data availability. Data and R-script used to reproduce results are available on Figshare, https://doi.org/10.6084/m9.figshare.6969497 (Granath et al., 2018).

The Supplement related to this article is available online at https://doi.org/10.5194/bg-15-5189-2018-supplement.

Author contributions. SKR, GG and HR initiated the study and formulated the research objectives. All authors were involved in data collection and SKR, NB, KP, AV and DPG performed the isotope analyses. GG performed the statistical analyses and wrote the first draft with input from SKR and HR. All authors read and commented on the manuscript and approved the final version.

Competing interests. The authors declare that they have no conflict of interest.

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