

RESEARCH ARTICLE

Trait coordination in boreal mosses reveals a bryophyte economics spectrum

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Abstract

1. The study of plant trait spectra and their association with trade-offs in resource use strategy has greatly advanced our understanding of vascular plant function, yet trait spectra remain poorly studied in bryophytes, particularly outside of the *Sphagnum* genus. Here, we measured 25 traits related to carbon, nutrient and water conservation in 60 moss canopies (each dominated by one of 15 moss species) across diverse boreal forest habitats and used bi-variate correlations and multi-variate analyses to assess trait coordination and trait spectra.
2. We found substantial trait coordination along a main principal components axis driven by trade-offs in carbon, nutrient and water conservation strategies. Along this trait spectrum, traits varied from resource-acquisitive at one end (e.g. high maximum photosynthetic capacity, high tissue nitrogen content, low water-holding capacity) to resource-conservative at the other end, in line with resource economics theory.
3. Traits related to carbon turnover (photosynthesis and respiration rates, litter decomposability) were positively related to nitrogen content and to desiccation rates, in line with global trait spectra in vascular plants. However, architectural traits of the moss shoots and of the moss canopy were generally unrelated to the main axis of trait variation and formed a secondary axis of trait variation, contrary to what is observed for vascular plants.
4. Resource-conservative trait spectra dominated in moss canopies from open and wet habitats (i.e. mires), indicating that high irradiance and possibly high moisture fluctuation induce a resource-conservative trait strategy in mosses.
5. *Synthesis.* Our work suggests that trait relationships that are well established for vascular plants can be extended for bryophytes as well. Bryophyte trait spectra can be powerful tools to improve our understanding of ecosystem processes in moss-dominated ecosystems, such as boreal or arctic environments, where bryophyte communities exert strong control on nutrient and carbon cycling.

KEYWORDS

boreal forest, bryophyte, functional trait, leaf economics spectrum, moss, resource economics theory, trait spectra

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1 | INTRODUCTION

Plant traits are strong drivers of plant function and thus play a key role in ecosystem processes in terrestrial ecosystems (Díaz et al., 2016; Mazziotto et al., 2019; Reich, 2014). As such, plant trait co-variation is seen as a powerful tool to predict how environmental change alters plant traits and ultimately ecosystem functioning (Funk et al., 2017; Suding et al., 2008). Specifically, anthropogenic climate change can alter trait composition of plant communities through affecting species fitness and physiological adaptation (Henn et al., 2018; Springate & Kover, 2014), which can then impact on key ecosystem processes including carbon (C) and nutrient cycling (Cornwell et al., 2008; Madani et al., 2018). In vascular plants, there is ample evidence of trade-offs in their architectural, physiological and chemical trait spectra, which are driven by differences in the allocation of key resources (i.e. C, nutrients and water; Freschet et al., 2010; Reich, 2014). For example, low leaf mass per area tends to be associated with high leaf nutrient concentrations, high photosynthetic capacity and high litter decomposition rates (the 'leaf economics spectrum'; Wright et al., 2004). Compared to vascular plants, trait co-variation has been much less studied in bryophytes (Cornelissen et al., 2007; Mazziotto et al., 2019; Wang et al., 2017), despite the importance of bryophytes (especially mosses) in C and nutrient dynamics in many ecosystems (Hupperts et al., 2021; Lindo et al., 2013; Street et al., 2013; Turetsky et al., 2012). A better understanding of trait trade-offs in bryophytes is needed to more accurately predict how environmental change may alter bryophyte function (i.e. by altering their trait spectra; Cornelissen et al., 2007; Mazziotto et al., 2019) and impact ecosystem function in bryophyte-dominated ecosystems (Moor et al., 2017).

Research on trait trade-offs in bryophytes has so far provided mixed support for the existence of economics spectra similar to those observed in vascular plants. For example, a positive correlation between nutrient concentration and photosynthetic capacity in bryophyte shoots (in line with the leaf economics spectrum in vascular plants) has been found in some studies (Carricú et al., 2019; Wang et al., 2014, 2016) but not in others (Bengtsson et al., 2016; Laing et al., 2014; Rice et al., 2008; Waite & Sack, 2010, 2011). Similarly, while some studies support the expectation (based on trait correlations in vascular plants) that lower bryophyte shoot or canopy mass per area is associated with greater nutrient concentrations and photosynthetic rates (Carricú et al., 2019; Waite & Sack, 2010; Wang et al., 2016), others found limited or no support (Bengtsson et al., 2016; Laing et al., 2014; Waite & Sack, 2011). The discrepancy may be due in part to the fact that architectural traits can be measured at the shoot- or canopy-level. For example, for an analogue of the vascular plant trait 'leaf mass per area', some authors have used shoot-based measurements of mass per area (projected on the ground, Wang et al., 2016, or transversal to the shoot, Bond-Lamberty & Gower, 2007; Jonsson et al., 2015), while others have used measurements of canopy mass per ground area (Bansal et al., 2012; Waite & Sack, 2010). In this context, canopy-based measures may better reflect field conditions as they account

for effects of self-shading and moisture regulation, which operate at the canopy level (Cornelissen et al., 2007; Elumeeva et al., 2011; Rice & Cornelissen, 2014). Furthermore, much of the research on trait trade-offs in bryophytes has focused on wetlands and on *Sphagnum* mosses, which limits our understanding of whether and how economics spectra are established across wider bryophyte groups and habitat types.

Research on *Sphagnum* mosses has suggested that traits related to moisture dynamics may be crucial in shaping trait trade-offs, from species forming denser canopies with higher moisture retention capacity, low nutrient concentrations, low photosynthetic capacity and low litter decomposition rates (i.e. resource-conservative) to species forming low-density canopies with the opposite traits (i.e. resource-acquisitive; Bengtsson et al., 2016; Laing et al., 2014; Rice et al., 2008). Given that the functioning of bryophytes is often highly dependent on fast-changing moisture availability (Dilks & Proctor, 1979), traits related to moisture regulation are likely key in driving trait trade-offs also across a wider range of bryophyte functional groups. However, work on trait trade-offs including water traits in non-*Sphagnum* mosses is very limited and has so far only provided inconclusive evidence of a negative association between water retention capacity and maximum photosynthetic capacity (Wang & Bader, 2018). Moreover, no study has yet tested economics spectra jointly for traits related to C, nutrients and water regulation in a wide range of mosses.

Here, we investigate trait economics spectra in boreal forest mosses. Boreal forests are important drivers of global C dynamics and typically have high abundance of ground mosses (Hupperts et al., 2021; Nilsson & Wardle, 2005; Turetsky et al., 2012), yet research on moss trait co-variation is limited (Jonsson et al., 2015; Rice et al., 2011) and moss trait spectra remain untested in boreal forests. To investigate this, we measured architectural, physiological and chemical trait co-variation in a wide range of boreal forest mosses, including canopy traits, which are most relevant to ecosystem function (Rice & Cornelissen, 2014). We hypothesized that (H1) trait co-variation in bryophytes is structured around a single economics spectrum shaped by C, nutrient and water conservation. We expected to find a bryophyte spectrum similar to what has been shown for vascular plants, ranging from resource-conservative traits (e.g. high canopy mass per area, high moisture retention capacity, low photosynthesis and respiration rates, low shoot nutrient concentration, low litter decomposability) to resource-acquisitive traits. Specifically, we hypothesized that (H1a) C turnover (e.g. photosynthetic and respiratory rates, litter decomposability) would be positively correlated with tissue nitrogen concentration, as has been observed in vascular plants (Wright et al., 2004); (H1b) C turnover would be negatively associated with water-holding capacity of the moss canopy. This is because plant traits that maximize water retention are inherently conservative and cause a trade-off with C uptake and turnover (Mazziotto et al., 2019; Reich, 2014); (H1c) photosynthetic capacity would be negatively correlated with canopy-based architectural traits (e.g. canopy mass per area) but uncorrelated with shoot-based architectural traits (e.g. specific shoot area), because



FIGURE 1 Examples of the 15 types of moss canopies used as experimental units.

the latter do not account for important regulatory processes (e.g. self-shading) at the canopy level (Cornelissen et al., 2007; Waite & Sack, 2010). Finally, we hypothesized that (H2) resource-conservative strategies would dominate in mosses of open and wet habitats, while resource-acquisitive traits would dominate in dry and shaded habitats. We expected this based on work on *Sphagnum* mosses showing that reduced light and water availability are associated with resource-acquisitive traits (Mazziotta et al., 2019). By improving our understanding of bryophyte trait co-variation, our study can help predict how environmental changes may affect bryophyte function and thus ecosystem function in bryophyte-dominated ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study sites and moss sampling

Sampling was carried out in the forest research areas of Svartberget (areas: Svartberget, Nyängeskammen and Åheden) and Kulbäcksliden, in the municipality of Vindeln (64° 12' 11" N, 19° 43' 9" E), in northern Sweden, between 8 June and 2 September 2021. Permission to carry out fieldwork was granted by the land owner (Svartberget Research Station, Swedish University of Agricultural Sciences). Climate records from 1991–2019 from Svartberget show a mean air temperature of 15.3°C in July and –10.3°C in January,

mean annual precipitation of 620mm, and snow cover duration of 170 days/year (Svartberget Research Station, 2020). The sampling areas were selected to represent the wide range of boreal forest types that can be found in northern Fennoscandia and included naturally regenerated forests at least 140 years old dominated by *Pinus sylvestris*, mature managed forests 80–120 years old dominated by *P. sylvestris* or by *Picea abies*, c. 10-year-old *P. sylvestris* managed forests and transitional areas to mire. We selected 15 moss species (Figure 1) which are widespread in the area and which form monospecific layers (i.e. cover >90%) and collected one sample of each species at different locations on each of four sampling dates over the growing season (on 8 June, 8 July, 13 August and 2 September 2021), giving us a total of 60 samples. The four samples of each moss species were collected from different locations at different times, and therefore incorporate intra-specific trait variability due to effects of location (e.g. microclimate, nutrient availability) and time (e.g. seasonal changes, preceding weather). Sampling locations were selected to be as different and as far away from each other as possible to encompass the whole range of intra- and inter-specific trait variability in the sampling area. For each sample we cut a 7.8 × 7.8 cm area of the moss layer using scissors and trimmed the lower part to include only the live shoot. This included the upper photosynthetic section of the shoot and the middle section showing some senesced tissue, but excluded the lower part of the shoot showing no or little photosynthetic pigments and some highly decomposed material. Thickness of each sample was recorded at five points to

the nearest mm using a ruler (Table S1). The samples were put in 7.8×7.8×5 cm plastic pots with a permeable bottom, taking care to preserve the natural structure of the moss canopy. For samples comprised of thinner moss mats, the pot was cut to adjust the height to the sample.

To characterize habitat preferences of the moss species sampled, we estimated light and moisture availability, as these variables are important drivers of moss communities (Grau-Andrés et al., 2019; Laing et al., 2014). At each sampling location, moisture and light availability were estimated through measurements of soil moisture content and vascular plant cover, respectively. To do this, upon collecting each moss sample we also collected about 25 g of the top 5 cm of the underlying soil to measure soil moisture content. Soil moisture content was measured gravimetrically on a dry weight basis by oven-drying the samples at 70°C for 48 h. We used a wide-angle lens attached to a smartphone camera to take an image of all vascular plant cover above the moss surface (Smith & Ramsay, 2018) and calculated canopy openness from this image using the image analysis software *ImageJ* (Rasband, 1997).

The samples were transported to the laboratory immediately after sampling, where litter and bryophytes other than the target species were removed. To acclimate the bryophytes to constant conditions, as recommended for photosynthetic measurements (Bengtsson et al., 2016; Rice et al., 2011), the samples were kept moist in a climate chamber (16°C, 80% relative humidity, 35 μmol cm⁻² s⁻¹ photosynthetic photon flux density [PPFD]) for 4–6 days prior to photosynthetic measurements.

2.2 | Photosynthesis and respiration

Photosynthesis and respiration were measured both at full turgor (i.e. where mosses are fully hydrated but have minimal external excess water), which corresponds well with optimal photosynthetic capacity (Proctor et al., 2007), and after a 24 h drought period. To approximate full turgor, each sample was first watered to saturation with de-ionized water using a spray bottle and then placed on absorbent paper and left to air-dry in the lab environment for 20–40 min (Proctor, 2000). The sample was then weighed to be able to calculate moisture content at full turgor (MC_{tur}; see Table 1 for a summary of all measured variables).

Measurements of CO₂ using the closed static chamber method (Grau-Andrés et al., 2021) were immediately carried out to estimate photosynthetic and respiratory rates. We used a clear plastic chamber (light transmittance = 92%, dimensions = 12.35×12.35×16.05 cm) fitted with a CO₂ gas analyser (Vaisala GMP 343) to measure CO₂ exchange sequentially at PPFD values of 0, 23, 91, 180, 310, 480 and 0 μmol cm⁻² s⁻¹ at the moss surface (Busby & Whitfield, 1978; Waite & Sack, 2010; Wang et al., 2016). The PPFD range was based on pilot testing showing that photo-inhibition was common above 480 μmol cm⁻² s⁻¹. For samples that showed no strong levelling-off approaching PPFD = 480 μmol cm⁻² s⁻¹, we took a further measurement at PPFD = 780 μmol cm⁻² s⁻¹. The different PPFD values

were achieved using a 30×24 cm light panel for plant growth (430–700 nm; Sylstar GL1000 LED) fitted with a light intensity regulator. We let the samples acclimate to each PPFD level for 3 min, after which the chamber was closed and CO₂ was recorded at 5 s intervals for 4 min. To estimate dark respiration, we took for each sample two flux measurements at PPFD = 0 μmol cm⁻² s⁻¹, one at the beginning and one at the end of the measuring sequence. A small fan mixed the air in the chamber. The CO₂ flux measurements were repeated after letting the samples air-dry for 24 h in the lab (mean temperature ± SD = 21.2 ± 2.2°C, relative humidity = 48.9 ± 8.1%), using the exact same procedure as described above.

Photosynthetic parameters were calculated by fitting non-linear models to the CO₂ flux versus PPFD data (Marshall & Proctor, 2004; Marshall & Biscoe, 1980), following Peek et al. (2002):

$$y = a [1 - e^{-b(x-c)}], \quad (1)$$

where y (CO₂ flux) and x (PPFD) are the measured variables, a is the asymptote (i.e. the light-saturated CO₂ flux); b is the initial slope of the curve (i.e. the apparent quantum yield; A_{qe}) and c is the x -intercept (i.e. the light compensation point).

Model fitting was carried out in R software version 4.1.1 (R Core Team, 2021), using the functions *nls* (non-linear least squares) and *SSasyp* (self-starting asymptotic regression model). From the fitted curve we estimated respiration (R) of each sample as CO₂ flux at PPFD = 0 μmol cm⁻² s⁻¹. Photosynthesis (i.e. carboxylation minus photorespiration, sometimes referred to as apparent photosynthesis; Wohlfahrt & Gu, 2015) at light-saturation (A) was estimated as light-saturated CO₂ flux minus R . While this method probably overestimates A because R is often larger in the dark than in the light, it is adequate for comparing among experimental units (Wohlfahrt & Gu, 2015), as is our focus here. Additionally, we calculated the 95% saturation irradiance (PPFD_{95%}), that is, the PPFD needed to achieve 95% of A (Marshall & Proctor, 2004; Rice et al., 2008). For each sample, the photosynthetic variables A , A_{qe} and PPFD_{95%} were obtained for the wet samples (i.e. when mosses were at full turgor). To characterize photosynthetic responses to reduced moisture, we calculated the percent change in A and R after a 24 h drought, relative to the measurements on the wet samples. The photosynthetic measurements were expressed both on an area basis (i.e. relative to the 60.8 cm² ground area each sample occupied) and on a mass basis (i.e. relative to the dry mass of photosynthetic tissue in each sample, see below).

2.3 | Water-holding capacity

To estimate water-holding capacity we recorded the weight of each sample at saturation and at regular intervals as the samples air-dried in the lab (Elumeeva et al., 2011; Michel et al., 2012). After 4–7 days, when more than 50% of the initial water content had been lost, we oven-dried the samples at 40°C until constant weight to calculate moisture content on a dry weight basis. We

TABLE 1 Traits related to moss shoot and canopy architecture, carbon gain, water-holding capacity and litter decomposition

| Variables | Code | Description |
|---|--------------------------|--|
| <i>Architectural traits</i> | | |
| Canopy mass per area | CMA | Dry mass of the photosynthetic sections of the moss shoots per ground area, in g cm^{-2} |
| Specific shoot area | SSA | Area to dry mass ratio of the photosynthetic sections of the moss shoots, in $\text{cm}^2 \text{g}^{-1}$ |
| Shoot area index | SAI | Area of the photosynthetic shoot sections per ground area, in $\text{cm}^2 \text{cm}^{-2}$ |
| Dry bulk density | BD_{dry} | Bulk density of the whole sample after oven-drying, in g cm^{-3} |
| Wet bulk density | BD_{wet} | Bulk density of the sample at full turgor, in g cm^{-3} |
| <i>Carbon regulation traits</i> | | |
| Maximum photosynthesis (area) | A_{area} | Maximum photosynthetic rate at full turgor per ground area, in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ |
| Maximum photosynthesis (mass) | A_{mass} | Maximum photosynthetic rate at full turgor per photosynthetic moss mass, in $\text{mmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ |
| Respiration (area) | R_{area} | Respiration rate at full turgor per ground area, in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ |
| Respiration (mass) | R_{mass} | Respiration rate at full turgor per photosynthetic moss mass, in $\text{mmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ |
| Apparent quantum yield | A_{qe} | Initial rate of increase in $A_{\text{max-a}}$ with PPFD, in $\text{mol CO}_2 \text{mol}^{-1}$ |
| 95% saturation irradiance | $\text{PPFD}_{95\%}$ | Photosynthetic photon flux density required to achieve 95% of $A_{\text{max-a}}$, in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ |
| Change in A_{area} with moisture | ΔA_{area} | Change in area-based A_{max} due to a 24-h drought relative to A_{max} at full turgor, calculated as: $(A_{\text{max-dry}} - A_{\text{max-hydrated}}) / A_{\text{max-hydrated}}$, in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ |
| Change in R with moisture | ΔR_{area} | Change in area-based R due to a 24-h drought relative to R at full turgor, calculated as: $(R_{\text{dry}} - R_{\text{hydrated}}) / R_{\text{hydrated}}$, in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ |
| <i>Water-holding traits</i> | | |
| Moisture content at saturation | MC_{tur} | Moisture content of the sample at full turgor, on a % dry weight basis |
| Half-desiccation time | t_{50} | Time required for the sample to lose 50% of its moisture at full turgor, in hours |
| Drying rate | DR | Initial drying rate, in % dry h^{-1} |
| <i>Chemical traits</i> | | |
| Carbon | C | Mass fraction of carbon, in % |
| Nitrogen (mass basis) | N_{mass} | Mass fraction of nitrogen, in % |
| Nitrogen (area basis) | N_{area} | Area-based nitrogen content, in g cm^{-2} |
| C:N ratio | C:N | Carbon to Nitrogen ratio |
| Isotopic ratio of C | $\delta^{13}\text{C}$ | $^{13}\text{C}/^{12}\text{C}$ isotopic ratio expressed using the VPDB scale, in ‰ |
| Isotopic ratio of N | $\delta^{15}\text{N}$ | $^{15}\text{N}/^{14}\text{N}$ isotopic ratio expressed using the atmospheric nitrogen scale, in ‰ |
| pH | pH | pH of the photosynthetic sections of the moss shoots |
| Total phenols | Phen | Concentration of total phenols in the photosynthetic sections of the moss shoots, in $\text{mg catechin equivalent g}^{-1}$ dry weight |
| <i>Litter decomposability</i> | | |
| Litter decomposition rate | k | Lab-based litter decomposition rate constant, in days^{-1} |

fitted a non-linear asymptotic regression model to the moisture content versus time data for each sample (Wang & Bader, 2018) following the same procedure as for the CO_2 versus PPFD data described above (see Equation 1, where y is moisture content, x is time since watering and b is the initial drying rate, DR). Additionally, we calculated the time elapsed until half of the initial moisture content was lost (half-desiccation time; t_{50}). Both metrics of water-holding capacity were correlated with the thickness of the moss sample: thicker moss samples dried out faster than thinner moss samples (e.g. for log-transformed t_{50} , $F_{1,44} = 18.7$, $p = 0.001$). This is because smaller mosses generally form denser canopies (Table S1) with reduced light penetration, which results in thinner live sections.

2.4 | Canopy structure

To characterize architectural traits of the moss canopies, we first randomly selected 10 re-wetted shoots from each sample and separated the upper photosynthetic sections from the lower predominantly non-photosynthetic sections using a razor blade (Waite & Sack, 2011). We identified the point of separation between both shoot sections by visually estimating where shoots with mostly vivid pigmentation and sound structure gave way to shoots with mostly brown or faded colours and some signs of decay (Bond-Lamberty & Gower, 2007; Rice et al., 2011). The shoot sections were then scanned using a flatbed scanner (Epson Perfection V800). The software *ImageJ* was used to calculate the

projected areas of both the green and the brown set of shoot sections (Bond-Lamberty & Gower, 2007; Michel et al., 2012). The shoots were then oven-dried at 60°C for 24 h to calculate their dry weight. With these data we calculated, for each sample, the mass ratio of green moss to brown moss. We multiplied this ratio by the dry mass of the entire sample to estimate mass of photosynthetic moss and divided it by the ground area (60.8 cm²) to obtain canopy mass per area. The specific shoot area was calculated as the area to mass ratio of the photosynthetic moss sections. This was multiplied by the mass of photosynthetic moss and divided by ground area to estimate the shoot area index, that is, photosynthetic shoot area per ground area (Bond-Lamberty & Gower, 2007; Rice & Cornelissen, 2014). We also calculated canopy bulk density by dividing sample volume by dry weight.

2.5 | Moss tissue chemistry

We selected the upper photosynthetic part of the shoots for chemical analyses (Rice et al., 2011). Each sub-sample was milled into a powder using a ball mill, and mass fractions and isotope ratios of carbon (C) and nitrogen (N) were measured using an Elemental Analyser - Isotope Ratio Mass Spectrometer (EA-IRMS) (Flash EA 2000 and DeltaV, Thermo Fisher Scientific). Area-based N content was calculated by multiplying N mass fraction content by canopy mass per area. We also measured total phenolics and pH of moss tissue, which can be important drivers of moss decomposition (Cornelissen et al., 2007; Hájek et al., 2011; van Zuijlen et al., 2020). We measured total phenols using the Prussian Blue technique, following Stern et al. (1996). This method uses spectrophotometry to estimate total phenol concentrations in solutions extracted from 50 mg of dried moss powder in 50% methanol by comparing to catechin standards. Moss pH was measured following Cornelissen et al. (2006). For each sample, we added 12 ml of de-ionized water to 0.5 g of the dried moss tissue powder, shook for 1 h and centrifuged at 3000 rpm for 5 min. The pH was measured in the supernatant using a Mettler Toledo MP220.

2.6 | Litter decomposability

To infer litter decomposability, we set up a lab bioassay to measure litter decomposition rates by performing litterbag incubations (Bengtsson et al., 2016; van Zuijlen et al., 2020). Although incubations in standardized lab conditions do not account for important drivers of decomposition in the field (e.g. wide fluctuations in temperature and moisture, solar radiation), the method is adequate for estimating differences in litter decomposability between samples (i.e. those driven by the physical and chemical characteristics of the litter), which was our focus here. Moss samples were collected on 11 June 2021 from locations adjacent to where the above described samples were collected. To standardize the samples, we discarded the top photosynthetic part of

the shoots and retained the 3–4 cm brown senescent section below (Bengtsson et al., 2016). The samples ($N = 60$) were oven-dried at 60°C for 3 days and then placed in nylon litterbags (mesh size = 1.0 × 0.2 mm) with 1 g of dry fragments of moss shoots. The litterbags were put on one of three 50 × 29 × 6 cm plastic trays which had been filled with a 4-cm thick layer of organic soil (i.e. each tray contained 20 litterbags). This soil was a homogenized mixture of organic soils collected from all sample locations. The litterbags were laid flat on the soil surface on 14 June 2021 and left to incubate under stable conditions in the lab (monthly mean air temperature ± $SD = 20.7 \pm 1.2^\circ\text{C}$). The trays were covered in a permeable opaque cover to avoid potential moss regrowth and kept moist by weekly watering with de-ionized water. The litterbags were turned and their positions shuffled among the trays every 2 weeks. On 24 October 2021 (i.e. after 132 days), the litterbags were oven-dried at 60°C for 48 h, weighed and then placed back in the trays. On 4 March 2022 (i.e. after a total of 263 days of incubation), the litterbags were oven-dried and weighed a second time. We calculated the decomposition rate constant, k , by fitting the following first-order exponential decay model to each sample (Silver & Miya, 2001; Wider & Lang, 1982):

$$y = e^{-kt}, \quad (2)$$

where y is the proportion of dry weight remaining at time t (i.e. at 132 and 263 days) relative to the initial dry weight (time 0).

2.7 | Data analysis

We used R software version 4.1.1 for all statistical and graphical analyses and the package `VEGAN` version 2.5–7 (Oksanen et al., 2020) for multi-variate analyses. To assess the resource use strategy of the samples, we examined trait associations and identified the main axes of trait variation using principal component analysis (PCA). To improve clarity we excluded from the PCA the variable C content, which had low explanatory power (the length of the biplot arrow was c. 10% of that of the longest biplot arrow). The selected variables were log-transformed as appropriate to improve linearity and scaled to unit variance before analysis (Bengtsson et al., 2016; Elumeeva et al., 2011). To assess how trait spectra relate to light and moisture availability, we used the function `envfit` in the `VEGAN` package to fit vascular plant cover and soil moisture content onto the ordination and to test their fit through permutation tests. We further tested the association of vascular plant cover and of soil moisture content with each of the two main PCA axes by fitting linear mixed effects models using the function `lme` in the package `NLME` (Pinheiro et al., 2020). These models included the sample scores of the first PCA axis (and, separately, of the second PCA axis) as response variables, vascular plant cover and soil moisture as explanatory variables and moss species as a random factor.

We tested bi-variate correlations among all variables included in the PCA by computing Pearson's rank correlation coefficients using the package `Hmisc` version 4.5–0 (Harrell, 2021). Variables that were

log-transformed in the PCA were also log-transformed prior to the correlation analyses. We further explored relationships between key pairs of variables (area- and mass-based photosynthesis and respiration and mass loss versus tissue N concentration, half-desiccation time, canopy mass per area and specific shoot area) by fitting linear mixed effects models which included 'moss species' as a random factor. To assess trait variation within- versus between-species, we partitioned the variance extracted from a linear mixed effects model including PCA axis 1 sample scores (and, separately, PCA axis 2 sample scores) as the response variable and moss species as a random factor.

3 | RESULTS

The PCA showed that moss traits were structured along a first principal component axis (PCA 1) which was mainly associated with physiological and chemical traits, whereas the secondary axis (PCA 2) was most strongly associated with architectural traits (Figure 2a). Rates of maximum photosynthesis (A) and respiration (R) of the moss canopies (both on a mass and area basis) were positively correlated with PCA 1, concomitant to increased moss tissue pH, N concentration and litter decomposability (Table S2). Water-holding capacity of the moss canopies decreased with increasing PCA 1 scores, as indicated by lower half-desiccation times and by higher drying rates. Both these metrics were very highly correlated with wet bulk

density. The change in A and R due to drought were negatively correlated with PCA 1, meaning that moss canopies with high PCA 1 scores experienced a greater drop in A and R after a 24 h drought than moss canopies with low PCA 1 scores.

Fitting environmental variables onto the ordination yielded strong evidence that moss trait variation as described by the PCA was overall associated with vascular plant cover ($R^2 = 0.30$, $p = 0.001$) and with soil moisture content ($R^2 = 0.15$, $p = 0.006$). Furthermore, linear mixed effects models provided moderate to strong evidence that plant cover was associated with PCA 1 ($F_{1,43} = 5.9$, $p = 0.019$) and with PCA 2 ($F_{1,43} = 8.3$, $p = 0.006$) and that soil moisture was associated with PCA 1 ($F_{1,43} = 7.4$, $p = 0.010$). Conversely, we found no evidence that soil moisture was associated with PCA 2 ($F_{1,43} = 2.0$, $p = 0.165$). Species were distributed in the PCA along a soil moisture gradient, with species of wetter conditions (i.e. most *Sphagnum* species, *Dicranum affine*, *Aulacomnium palustre*) on one end, *Polytrichum* species on the opposite end, and most upland forest species in an intermediate position (Figure 2b). Species of shadier and/or drier habitats and with high PCA 1 scores, such as *Hylocomium splendens*, *Polytrichum juniperinum* and particularly *Polytrichum commune* (Figure 2b), had physiological and chemical traits in line with a resource-acquisitive strategy (e.g. high A and drying rates and low tissue C:N). In contrast, species of more open and of wetter habitats with low PCA 1 scores, such as *D. affine*, *Sphagnum fuscum* and *Sphagnum magellanicum*, had physiological and chemical traits in line with a resource-conservative strategy. Variance partitioning showed

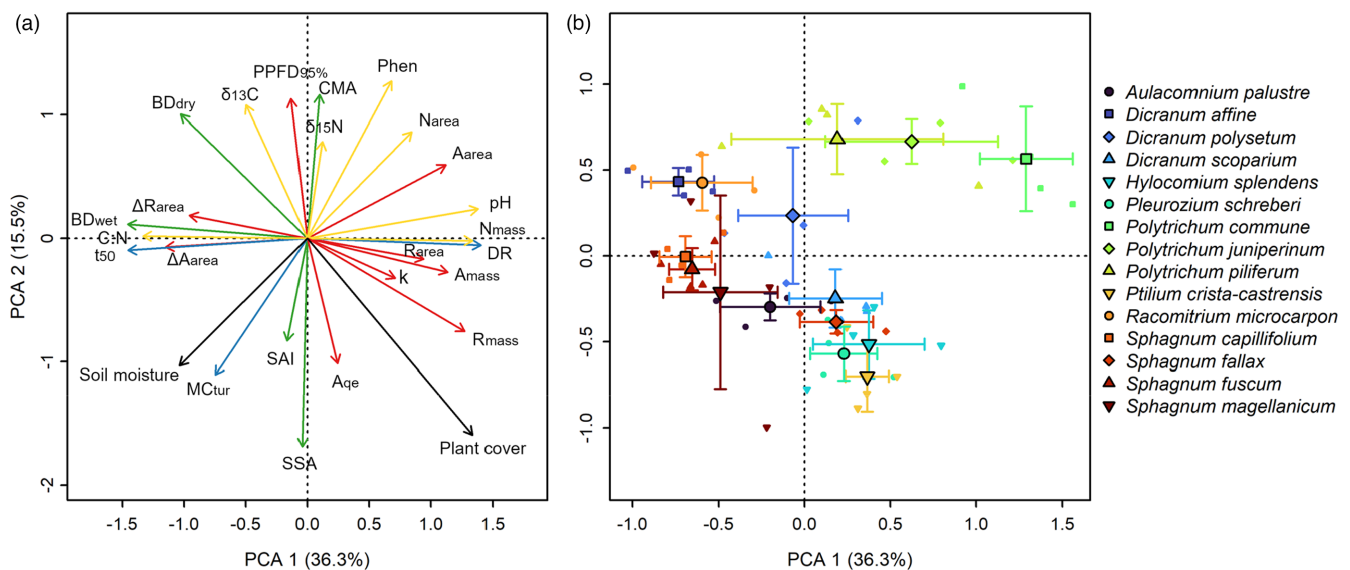


FIGURE 2 PCA showing (a) green arrows: Traits related to moss shoot and canopy architecture (canopy mass per area [CMA], specific shoot area [SSA], shoot area index [SAI], wet and dry bulk density [BD_{wet} and BD_{dry}]), red arrows: Carbon gain and litter decomposability (area- and mass-based photosynthetic capacity [A_{area} , A_{mass}] and respiration [R_{area} , R_{mass}], litter decomposition rate [k], apparent quantum yield [A_{qe}], change in A_{area} and R_{area} with moisture [ΔA_{area} , ΔR_{area}], 95% saturation irradiance [PPFD_{95%}], yellow arrows: Moss tissue chemistry (phenol concentration [Phen], area- and mass-based nitrogen content [N_{area} , N_{mass}], pH, carbon to nitrogen ratio [C:N], isotopic ratios of C and N [$\delta^{13}C$ and $\delta^{15}N$]), blue arrows: Water retention capacity (drying rate [DR], moisture content at saturation [MC_{tur}], half-desiccation time [t_{50}]) and black arrows: Environmental variables vascular plant cover and soil moisture content; (b) large symbols: Mean \pm 1 SE of PCA 1 and PCA 2 scores for each moss species, small symbols: Individual observations grouped by moss species ($N = 60$). The variance explained by each axis is given in parentheses. Pearson's rank correlation coefficients among moss traits and principal components sample scores are given in Table S2.

that within-species variation accounted for 24.3% of the variation in PCA 1, and for 21.2% of the variation in PCA 2 (Figure 3, Figure S1). We note that the relatively low number of observations for each species (i.e. four), which were each taken at different times over the growing season, prevented us from partitioning intra-specific trait variation into environmental (i.e. location) versus seasonality caused variation.

The second main axis of variation was most closely associated with shoot and canopy architectural traits (Figure 1a). High PCA 2 scores were associated with denser canopies (i.e. with higher canopy mass per ground area and dry bulk density), while low PCA 2 scores were associated with moss shoots with high surface area (i.e. with high specific shoot area) and high moisture content at full turgor. High PCA 2 scores were also associated with high values of 95% saturation irradiance and with low values of apparent quantum yield. Some chemical traits were also closely associated with PCA 2: C content, the isotopic signatures of C and N and total phenol concentration.

We found strong evidence that tissue N concentration was positively related to area-based photosynthetic capacity (A_{area} ; $F_{1,44} = 33.4$, $p < 0.001$), area-based respiration (R_{area} ; $F_{1,44} = 10.1$, $p = 0.003$) and litter decomposability ($F_{1,44} = 11.4$, $p = 0.002$; Figure 4a,e,i). Similarly, there was strong to moderate evidence that water retention capacity (measured as half-desiccation time) was negatively related to A_{area} ($F_{1,44} = 16.1$, $p < 0.001$), R_{area} ($F_{1,44} = 5.5$, $p = 0.024$) and litter decomposability ($F_{1,44} = 12.3$, $p < 0.001$; Figure 4b,f,j). While we found moderate support for a positive relationship between canopy mass per area and A_{area} ($F_{1,44} = 5.8$, $p = 0.021$) and R_{area} ($F_{1,44} = 7.3$, $p = 0.010$; Figure 4c,g), we found no evidence that specific shoot area was related to A_{area} ($F_{1,44} = 0.01$, $p = 0.923$) and R_{area} ($F_{1,44} = 0.4$, $p = 0.513$; Figure 4d,h). Compared to area-based photosynthetic capacity and respiration, A_{mass} and R_{mass} had similar relationships to mass-based tissue N concentration and to half-desiccation time, but A_{mass} was negatively correlated to canopy mass per area (Figure S2).

4 | DISCUSSION

Our findings generally support the idea that traits related to carbon (C), nutrient and water conservation in mosses are structured similarly to vascular plants along a single economics spectrum, in line with our first hypothesis (H1). As such, we found a main gradient of variation in moss traits which aligns with 'fast to slow' trade-offs, that is, with resource-acquisitive traits at one end (e.g. high rates of photosynthesis and respiration, high nutrient concentration, high litter decomposability, low water-holding capacity) and resource-conservative traits at the other end (e.g. low rates of photosynthesis and respiration, low nutrient concentration, low litter decomposability, high water-holding capacity). Previous studies on bryophyte trait spectra have also reported main axes of trait variation which included co-variation of photosynthetic capacity with nutrient content (Wang et al., 2016), litter decomposability (Bengtsson

et al., 2016) and water-holding capacity (Wang & Bader, 2018; Mazziotta et al., 2019). However, these studies assessed trait trade-offs in the allocation of just one or two resources (i.e. C, nutrients and/or water) or considered a much narrower range of taxa (i.e. only the *Sphagnum* genus). Furthermore, many studies investigating trait coordination in mosses are based on shoot-level measurements (Carriqui et al., 2019; Wang et al., 2016; Wang & Bader, 2018), which do not account for the important regulatory function of the moss canopy (Elumeeva et al., 2011; Rice & Cornelissen, 2014). As such, our study is the first to demonstrate for diverse moss canopies a resource economics spectrum jointly shaped by traits related to the allocation of the three key resources for plants: C, nutrients and water (Reich, 2014).

However, in contrast to our first hypothesis, we found little evidence that the primary axis of trait variation was associated with photosynthetic canopy mass per area or shoot area index, which are considered analogous to architectural traits of vascular plants driving the 'leaf economics spectrum' (Waite & Sack, 2010; Rice et al., 2011; Rice & Cornelissen, 2014). Instead, we found that architectural traits of the photosynthetic moss canopy were aligned on a second main axis of trait variation, along with traits related to moss chemistry (phenol concentration, isotopic ratios of C and N) and to photosynthetic response to irradiance (apparent quantum yield, 95% saturation irradiance). Interestingly, we found that the architectural trait wet bulk density was closely aligned with the primary axis of trait variation. Both our results and previous work indicate that wet bulk density is highly correlated with water-holding capacity in moss canopies, presumably because it relates to traits that drive conservation of external water at the shoot level (e.g. presence of concave leaves or tomentum) and at the canopy level (e.g. density and spatial distribution of shoots within the canopy; Elumeeva et al., 2011). External water greatly impairs photosynthesis in mosses through limiting air diffusion (Dilks & Proctor, 1979). Given this, our finding that the primary axis of trait variation was closely aligned with wet bulk density of the whole canopy but not with architectural traits of the upper (photosynthetic) canopy suggests that whole canopy-level water regulation is a more important driver of moss function than traits controlled by the architecture of the upper canopy, such as light penetration (Niinemets & Tobias, 2014). Our finding of two economics trait spectrum axes contrasts with the 'leaf economics spectrum', as well as previous bryophyte studies which have found single main axes of trait variation (Laing et al., 2014; Waite & Sack, 2010; Wang et al., 2014, 2016). Compared to vascular plants, the higher susceptibility of mosses to high irradiance levels (Hájek et al., 2011; Robinson & Waterman, 2014), could have led to stronger irradiance effects on traits and induced a second axis of trait variation. The greater taxonomic diversity of this study compared to previous bryophyte studies on canopy-level trait spectra including water-holding traits (Laing et al., 2014; Mazziotta et al., 2019; Rice et al., 2008) may have allowed us to separate architectural traits related to different functions (e.g. water regulation versus light penetration) onto different trait spectra.

We found strong support for our hypothesis H1a that C turnover, including photosynthetic and respiratory rates and litter

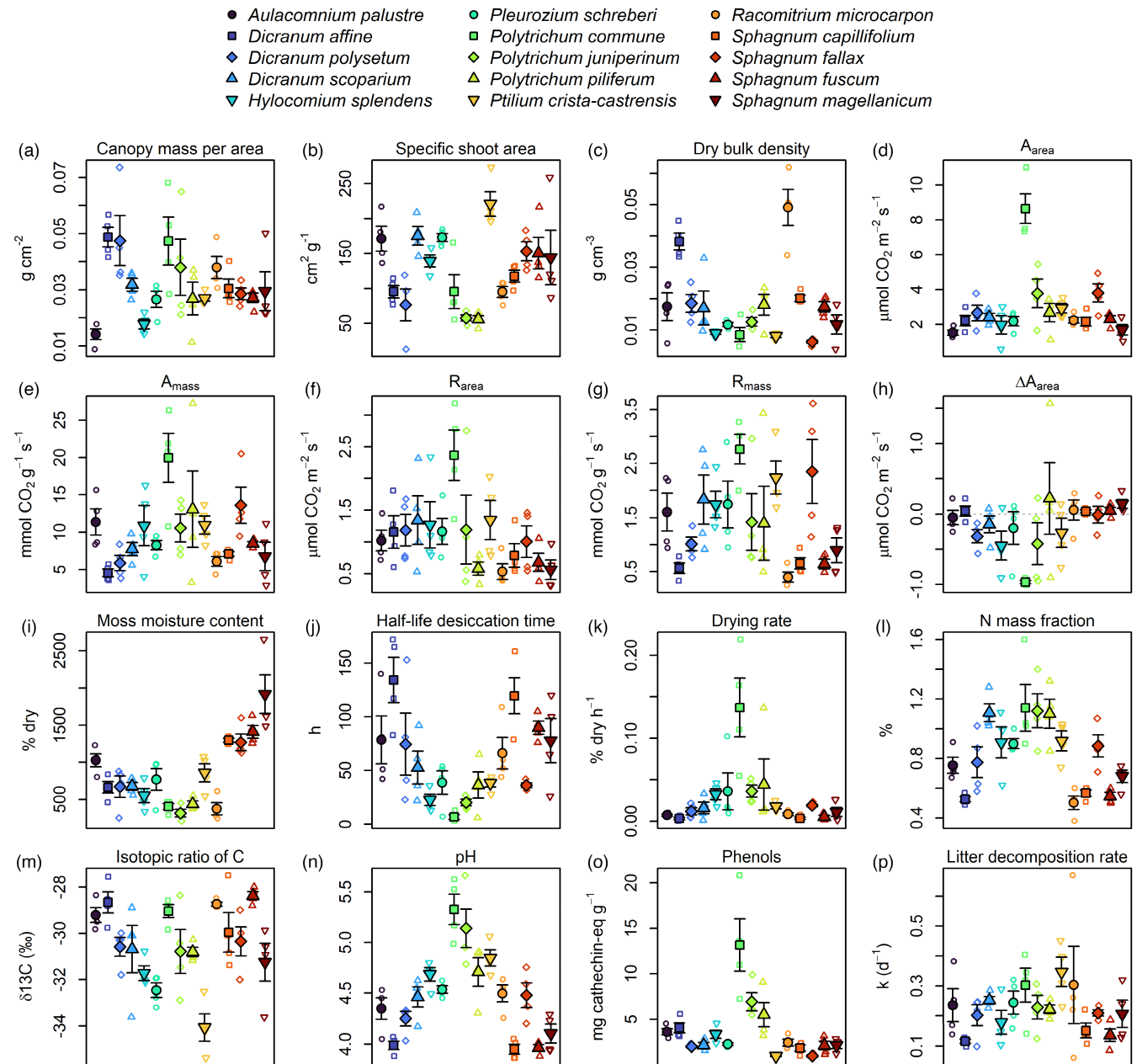


FIGURE 3 (a–p) Inter- and intra-specific trait variation for a wide selection of architectural, physiological and chemical moss traits. A_{area} and A_{mass} are area- and mass-based maximum photosynthesis, R_{area} and R_{mass} are area- and mass-based respiration, and ΔA_{area} is change in A_{area} with moisture. Open symbols are observations ($N = 4$ per species for each trait), filled symbols are means and bars are ± 1 SE. More traits are presented in Figure S1.

decomposability, would be positively correlated with tissue N concentration. Because photosynthesis requires substantial quantities of N, leaf N often correlates positively with photosynthetic capacity in vascular plants (Wright et al., 2004). However, for bryophytes a positive relationship between photosynthetic capacity and shoot nutrient concentration has been observed at the shoot level (Carriquí et al., 2019; Wang et al., 2014, 2016) but not at the canopy level (Bengtsson et al., 2016; Laing et al., 2014; Rice et al., 2008, 2011; Waite & Sack, 2010). Studies at the canopy level have proposed that the lack of photosynthesis–N correlations may be due to the similar trait spectra of the species included

in the studies, to the low range of environmental N concentrations considered, or to the relatively high allocation of N to non-photosynthetic shoot sections in *Sphagnum* (Laing et al., 2014; Oke & Turetsky, 2020; Rice et al., 2008). Our study considered a wider range of moss types, maximum photosynthetic capacity (0.58 – $11.01 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and tissue N concentration (0.38% – 1.6%) than previously considered in trait studies, which likely enabled us to detect this photosynthesis–N relationship clearly for the first time in moss canopies. Furthermore, moss litter decomposability was also positively related to tissue N concentration and to pH (van Zuijlen et al., 2020), but not to total phenols (Hájek

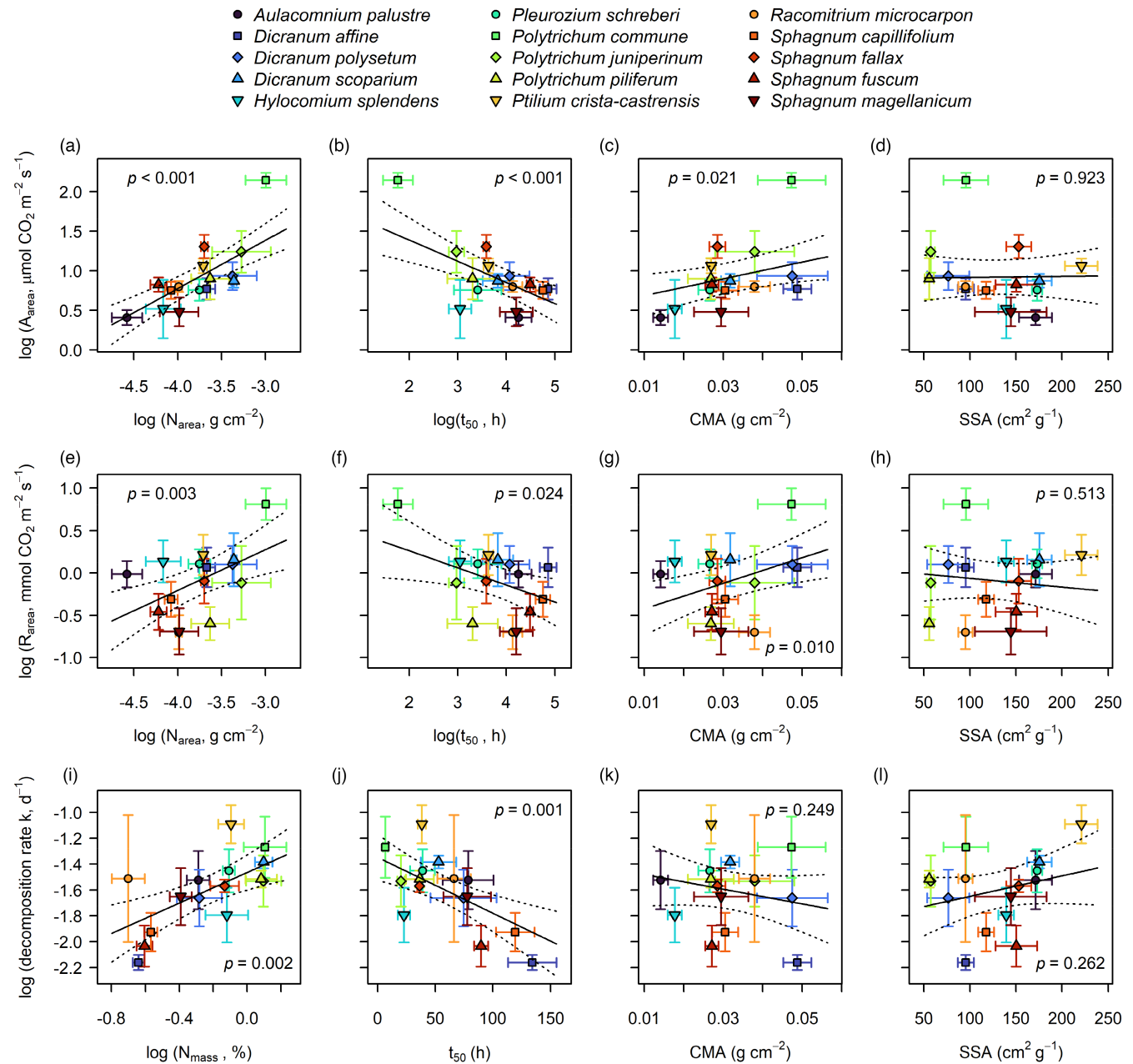


FIGURE 4 Relationships between moss traits related to carbon dynamics ([a–d] area-based measures of maximum photosynthetic capacity [A_{area}], [e–h] respiration [R_{area}] and [i–l] litter decomposition rate) and chemical (area- and mass-based N content), water retention (half-desiccation time [t_{50}]) and architectural traits (canopy mass per area [CMA] and specific shoot area [SSA]). Filled symbols are means of observations ($N = 4$) for each moss species, bars are ± 1 SE, black lines are regression-based linear fits and 95% confidence intervals. The same relationships with mass-based measures of A and R are given in Figure S2.

et al., 2011). Tissue pH was strongly associated with the main axis of trait variation, and with traits related to photosynthetic capacity, nutrients and water retention (e.g. mass-based photosynthetic rates, tissue N and half-desiccation time). Therefore, pH could be a useful soft trait to infer broad economic trade-offs of moss canopies (Cornelissen et al., 2006). Moreover, given that moss tissue $\delta^{15}\text{N}$ can be related to atmospheric N_2 fixation by epiphytic cyanobacteria (Deane-Coe & Sparks, 2016), the lack of correlation between $\delta^{15}\text{N}$ and tissue N concentration we observed suggests that other N sources dominated, or that $\delta^{15}\text{N}$ may not be a reliable

indicator of atmospheric N_2 fixation in mosses generally (Stuart et al., 2021). Overall, our results indicate that tissue chemistry, including N content, is an important control on C turnover in moss canopies of boreal forests, in line with the general N limitation that prevails in these habitats (Sponseller et al., 2016).

We also found strong support for our hypothesis H1b that C turnover is negatively associated with water retention capacity of the moss canopy (as measured by half-desiccation time and drying rates). While this is in agreement with leaf economic theory (Reich, 2014), empirical evidence in bryophytes has

previously only been found in *Sphagnum* (Mazziotta et al., 2019; Rice et al., 2008). Working on a greater variety of forest mosses, Wang and Bader (2018) found no consistent relationship between photosynthetic capacity and water retention at the shoot level, possibly because water retention is mainly controlled at the canopy level (Elumeeva et al., 2011). The trade-off between photosynthetic capacity and water retention occurs because traits that promote water retention (e.g. denser canopies and thicker cell walls, which improve retention of internal and external water) also impede light penetration and air diffusion, and decrease photosynthetic efficiency, thus impairing photosynthetic capacity (Dilks & Proctor, 1979; Rice et al., 2008; Waite & Sack, 2010). Our findings demonstrate that photosynthesis–water retention trade-offs occur not only in *Sphagnum* mosses but also across a much greater variety of moss types. Furthermore, litter decomposability was also negatively associated with water retention capacity, as has been suggested within the *Sphagnum* genus (Bengtsson et al., 2016). This could be because, to improve water retention, mosses may invest more in structural than in metabolic carbohydrates, thus producing less labile litter (Turetsky et al., 2008). Litter decomposability may also be driven by tissue N concentration (van Zuijlen et al., 2020), which correlates negatively with water retention. Together, the observed coordination of traits related to C turnover and to water retention along a main trait spectrum provides strong evidence of a trade-off between C turnover and water retention traits in mosses.

Photosynthetic and respiratory rates were positively associated with canopy mass per area but not with specific shoot area, in line with our hypothesis H1c. The negative correlation between mass-based photosynthetic capacity and canopy mass per area likely results from higher moss tissue density causing greater self-shading and impeding gas diffusion, thus decreasing photosynthetic capacity on a mass basis (Cornelissen et al., 2007; Waite & Sack, 2010). The effect of reduced air diffusion in impairing photosynthesis is supported by the negative correlation between $\delta^{13}\text{C}$ and mass-based photosynthetic capacity, and the positive correlation between $\delta^{13}\text{C}$ and canopy mass per area, as lower air diffusion due to denser canopies can cause a decrease in $^{13}\text{CO}_2$ fractionation through impeding C fixation (Rice et al., 2008). Conversely, the negative correlation between $\delta^{13}\text{C}$ and soil moisture content (Pearson $p = 0.051$) suggests that air diffusion was not impeded by high moisture availability (Stuart et al., 2021; Williams & Flanagan, 1996). While a negative correlation between mass-based photosynthetic capacity and shoot mass per area have been observed in moss shoot studies (Carriquí et al., 2019; Wang et al., 2016, 2017), our results suggest that, at the canopy level, shoot-level architectural traits are negligible controls of moss function and that canopy structure (i.e. shoot density and arrangement of shoots in space) exerts a much stronger influence on moss function (Cornelissen et al., 2007; Rice & Cornelissen, 2014; Waite & Sack, 2010).

Regarding Hypothesis H2, we found that low vascular plant cover and high soil moisture content (indicative of high availability

of light and water, respectively) were negatively correlated with the main axis of trait variation, which provides support that resource-conservative trait spectra dominate in wet and open habitats. This is in line with peatland research showing that water availability drives a trade-off in *Sphagnum* mosses between traits that promote water conservation and traits that promote C turnover (Laing et al., 2014; Mazziotta et al., 2019), as discussed above. The main trait axis was more weakly associated with soil moisture than with plant cover, possibly because soil moisture and moss moisture availability are sometimes disconnected (Grau-Andrés et al., 2021). Our results also agree with bryophyte research showing that higher irradiance is associated with resource-conservative traits, including lower mass-based photosynthetic capacity (Hájek et al., 2011; Laing et al., 2014; Waite & Sack, 2010). However, these results are opposite to patterns observed in vascular plants (Reich, 2014), which points to fundamentally different effects of environmental gradients in shaping trait trade-offs in mosses compared to vascular plants. These different effects likely result from the limited capacity of mosses to regulate internal moisture, because this involves physiological adaptations (e.g. lack of epidermal layers, presence of water retention structures) that limit their capacity to protect from and to utilize high irradiance (Hájek et al., 2011; Robinson & Waterman, 2014). Furthermore, high irradiance causes moisture stress in mosses (Heijmans et al., 2004). Therefore, our results support the idea that greater exposure to light promotes a resource-conservative economics strategy in mosses.

5 | CONCLUSIONS

Our study is the first to assess trait coordination jointly for traits related to carbon, nutrient and water regulation in moss canopies across multiple moss genera. Although our analyses benefitted from including many traits and a large and representative number of species, limitations of our study include a relatively low sample size for each moss species ($N = 4$) and the absence of important variables such as moss growth rates, litter metabolites or phosphorus concentrations (Mazziotta et al., 2019; Moor et al., 2017; Waite & Sack, 2011) among the traits we tested. Nevertheless, the substantial trait coordination we found provides compelling evidence that trait trade-offs in moss canopies shape trait spectra in line with resource economics theory. Specifically, we demonstrate that the positive relationship between photosynthetic capacity and nutrient content, which is central to global trait spectra in vascular plants (Reich, 2014; Wright et al., 2004), is also apparent at the canopy level in mosses. Given that bryophytes are largely ignored in global plant trait research (Díaz et al., 2016; Freschet et al., 2010; Wright et al., 2004), bryophyte trait studies such as ours are needed to extend our trait-based understanding of ecosystem processes to bryophyte-rich ecosystems, such as boreal forest and arctic tundra. As such, through reducing the complexity of diverse communities into functional spectra,

bryophyte trait spectra can be powerful tools to improve predictions of how global change may impact bryophyte-dominated ecosystems (Funk et al., 2017; Moor et al., 2017; Suding et al., 2008). Importantly, our finding that C turnover traits in mosses are aligned on a main axis of trait trade-offs can inform predictions of how changes in nutrient or moisture availability may affect C dynamics in moss-dominated ecosystems including peatlands, boreal forests and tundra, which store globally substantial amounts of C (Bradshaw & Warkentin, 2015). Furthermore, given that C turnover was better predicted by canopy-level than by shoot-level architectural traits, we recommend that future research on moss C dynamics is carried out at the canopy level. Overall, our results expand our understanding of the global economics trait spectra and provide an impetus for further studies on bryophyte trait coordination and for integrating bryophyte trait studies onto wider plant trait research.

AUTHORS' CONTRIBUTIONS

R.G.-A., M.J.G. and P.K. conceived and designed the study; R.G.-A. carried out the research and analysed the data; R.G.-A. wrote the manuscript with input from M.J.G. and P.K.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.9s4mw6mk4> (Grau-Andrés et al., 2022).

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