## **RESEARCH ARTICLE**

# Mosses and vascular plants show diverging diversity patterns along a latitudinal gradient in boreal bogs and fens

Stéphanie Pellerin<sup>1,2,3</sup>

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Élise Deschênes<sup>1,2,3</sup> | Monique Poulin<sup>3,4</sup> | Marie-Hélène Brice<sup>1,2,3</sup> | Pierre Legendre<sup>1,3</sup> |

<sup>1</sup>Département de Sciences Biologiques, Université de Montréal, Montréal,

**Ouebec**, Canada

<sup>2</sup>Jardin botanique de Montréal, Montréal, Quebec, Canada

<sup>3</sup>Ouebec Centre for Biodiversity Science. Department of Biology, McGill University, Montréal, Quebec, Canada

<sup>4</sup>Department of Phytology, Université Laval, Québec, Quebec, Canada

#### Correspondence

Stéphanie Pellerin, Département de Sciences Biologiques, Université de Montréal, Montréal, Quebec, Canada. Email: stephanie.pellerin.1@umontreal.ca

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Abstract

Questions: The latitudinal biodiversity gradient; i.e., the increase in biodiversity towards the equator, is one of the most prominent biodiversity patterns. Nevertheless, many questions remain to be answered about the influence of multiple environmental factors on the latitudinal biodiversity gradient, especially for mosses, and the functional diversity of mosses and vascular plants. This study aims at evaluating the influence of latitude, climate, environmental variables, and habitat types (bog vs fen) on taxonomic and functional diversity ( $\alpha$ -diversity and  $\beta$ -diversity) and the composition of vascular plant and moss species.

Location: 49°N to 55°N in Northwestern Quebec, Canada.

Taxon: Mosses, vascular plants.

Methods: We used a database containing 376 phytosociological plots (400 m<sup>2</sup>) sampled in boreal peatlands located along a 600-km latitudinal gradient. We evaluated changes in  $\alpha$ -diversity and  $\beta$ -diversity in response to latitude, longitude, climate, and local abiotic variables for both taxonomic groups using linear mixed effect models. We evaluated the effects of these variables on taxonomic and functional composition using variance partitioning by redundancy analysis.

Results: Moss diversity increased with latitude, although the effects were masked by environmental variables, whereas vascular plant diversity decreased with latitude in fens and did not vary with latitude in bogs. We observed a decrease in taxonomic and functional uniqueness with latitude. Moss and vascular plant taxonomic and functional composition were primarily structured by contrasting local conditions in bogs and fens, whereas climatic variations along the latitudinal gradient played a secondary role.

Conclusions: Our results highlight the contrasting biodiversity patterns in both peatland types and the importance of local habitat conditions in structuring vascular plant and moss diversity. These patterns varied depending on the diversity indicator used, as  $\alpha$ - and  $\beta$ -diversity and functional and taxonomic diversity were often decoupled. Future studies should therefore include more than one diversity indicator and consider the differences between ecosystems and taxon groups.

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#### KEYWORDS

bog, composition, fen, functional traits, latitudinal gradient, mosses, peatlands, vascular plants,  $\alpha$ -diversity,  $\beta$ -diversity

## 1 | INTRODUCTION

The reduction in biodiversity from the tropics towards the poles is often regarded as the most prominent broad-scale gradient of biodiversity (Willig et al., 2003; Kinlock et al., 2018; Zhang et al., 2022). Several hypotheses have been proposed in recent decades to explain this latitudinal biodiversity gradient (LBG), mainly related to: (a) historical and evolutionary mechanisms, (b) climatic and energy mechanisms, (c) spatial and null mechanisms and (d) biotic mechanisms (Willig et al., 2003; Schemske & Mittelbach, 2017; Kinlock et al., 2018; Pontarp et al., 2019), but no consensus has yet been reached. Historical and evolutionary mechanisms are often pinpointed as the main underlying causes (Schemske & Mittelbach, 2017; Mannion, 2020), operating through speciation and diversification rates and time for species accumulation (Pontarp et al., 2019; Zhang et al., 2022). Furthermore, there is an extensive literature showing that spatio-temporal climate dynamics produce major biodiversity patterns, even though many ecological factors vary concurrently along the climatic gradient and are difficult to untangle (Saupe et al., 2019; Zhang et al., 2022). For example, polar regions are highly seasonal, spatially homogeneous and physiologically restrictive because of low temperatures, winter extremes and short growing seasons, favoring a small pool of species with large climatic tolerance and extensive spatial ranges (Qian & Ricklefs, 2007; Pinto-Ledezma et al., 2018; Šímová et al., 2018; Saupe et al., 2019). Conversely, the climate of equatorial regions is seasonally homogeneous but varies over shorter distances, which could favor species with highly restricted environmental tolerances and limited dispersal ability across environmental barriers, leading to greater speciation (Qian & Ricklefs, 2007; Soininen et al., 2007; Kraft et al., 2011). These general climatic differences may not only induce latitudinal patterns in species richness ( $\alpha$ -diversity), but also in species assemblages across space and associated  $\beta$ -diversity, with ecosystems closer to the poles having more regionally homogeneous species assemblages than equatorial ones (Anderson et al., 2011; Pinto-Ledezma et al., 2018).

The nature of biodiversity changes along latitude and associated environmental gradients as well as the strength of the relationship between biodiversity and explanatory variables are, however, highly dependent on the spatial extent (entire studied geographical area) and grain size (area of the sampling unit) investigated. For instance, whereas the reduction in vascular plant richness from the tropics toward the poles stands at global or continental scales using a coarse grain size (Qian, 1998; Kier et al., 2005; Sabatini et al., 2022), hotspots of richness appear outside the tropics (e.g., the Appalachian Mountains) when finer grain sizes are used (Večeřa et al., 2019; Biurrun et al., 2021; Sabatini et al., 2022). Furthermore, meta-analyses have shown that the effect of climate variables relative to that of other variables on plant diversity increases with spatial scale, both in terms of extent and grain size (Field et al., 2009; Siefert et al., 2012). For example, Siefert et al. (2012) showed that the primacy of edaphic variables over climatic variables was maximal when the extent of the study was smaller than 1,995 km<sup>2</sup> and sampling units were smaller than 295 m<sup>2</sup>.

Although the LBG has been widely studied for vascular plants, bryophytes (mosses, liverworts, hornworts) have received much less attention and results tend to diverge from the classical paradigm (but see Wang et al., 2017 for liverworts and hornworts). For instance, at the global scale (broad grain), no particular gradient in moss diversity has been found (Shaw et al., 2005; Geffert et al., 2013; Möls et al., 2013). Moss richness hotspots are rather scattered in tropical, temperate, boreal and tundra regions, and hotspot locations depend on the taxonomic group (Geffert et al., 2013). Despite the absence of richness patterns at these spatial grains and extents, species turnover among pleurocarpous moss was found to increase toward tropical zones (Hedenäs, 2007). At the European scale, Mateo et al. (2016) showed, using a broad grain size, that overall moss richness increases northward, whereas  $\beta$ -diversity does not show a specific pattern along the latitude gradient. A similar inversed latitudinal pattern of moss and liverwort diversity was also found in southwestern South America (Rozzi et al., 2008) and in China for liverworts, but not for mosses (Chen et al., 2015). Patterns of bryophyte richness over large geographical extents using fine grain sizes still need to be explored. However, at the European extent, Biurrun et al. (2021) showed that patterns of bryophyte diversity in grasslands and other open habitats vary greatly depending on the grain size used, even at the scale of ecological communities (grain varying from 0.0001 to 1,000 m<sup>2</sup>). Nevertheless, they also observed that the highest richness values for bryophytes tended to be found at high latitudes and elevations, thus following the inverse latitudinal pattern also found in regional or continental studies (Rozzi et al., 2008; Mateo et al., 2016). Increased bryophyte richness toward the poles may be associated with their failure to radiate, their adaptation to cold conditions, their poikilohydric nature (tolerance to desiccation), and their high dispersal capacity, which result in larger geographic ranges as well as lower species turnover rates (Glime, 2007; Patiño et al., 2014; Mateo et al., 2016; Sanbonmatsu & Spalink, 2022).

In some ecosystems, such as peatlands, vascular plants and bryophytes interact closely to maintain ecosystem processes and functions. Peatlands are wetlands formed by the accumulation of partially decayed organic materials and are characterized by harsh environmental conditions, such as prolonged anoxic periods (Moor et al., 2017). Peatlands range from purely precipitation-fed ombrotrophic peatlands (bogs) to surface- and groundwater-connected minerotrophic peatlands (fens), with intermediate successional stages of moderate-rich and poor fens (Locky & Bayley, 2006). Bogs FIGURE 1 Location map of the 376 plots sampled in peatlands (156 bogs, 220 fens) of northwestern Quebec (Canada).



and poor fens are acidic and poor in mineral elements, whereas moderate and rich fens have a higher (more basic) pH and are richer in mineral elements, owing to surface and underground water inputs (Wheeler & Proctor, 2000). Fens are typically more environmentally heterogeneous than bogs, and, consequently, their species assemblages are richer and more variable from site to site (Vitt et al., 1995; Anderson & Davis, 1997; Locky & Bayley, 2006). Because environmental conditions differ between bogs and fens, analyzing how biodiversity varies along the latitudinal gradient in both habitats concurrently may improve our understanding of how environmental conditions interact with latitude and produce variable species assemblages in space.

Because species respond to environmental filters through their functional traits (Pinto-Ledezma et al., 2018; Šímová et al., 2018), studying taxonomic and functional diversity simultaneously may lead to a better understanding of the links between community assemblages and ecosystem functions (Díaz et al., 2007; Mayfield et al., 2010). More restrictive environments should contain nonrandom assemblages of functionally similar species adapted to their conditions, limiting the diversity of possible functional traits, and increasing the evenness of functional groups (Swenson & Enquist, 2009; Schumm et al., 2019). For instance, a cold climate favors small, fast-growing and stress-adapted vascular species, whereas warmer environments favor tall and large seeded species (Swenson et al., 2012; Pinto-Ledezma et al., 2018; Šímová et al., 2018). Overall,  $\alpha$ - and  $\beta$ -functional diversity have been shown to decrease toward higher latitudes for vascular species (Swenson et al., 2012; Pinto-Ledezma et al., 2018), and increase in certain cryptogams such as lichens (Chagnon et al., 2021). For bryophytes, some local studies have shown that  $\alpha$ -functional diversity increases with altitude (Araújo et al., 2022; Asplund et al., 2022), but patterns along latitude remain to be explored.

This study aims at evaluating the influence of latitude, climate, local environmental variables, and habitat type (bog vs fen) on

taxonomic and functional diversity as well as the composition of vascular plant and moss species. We used a narrow latitudinal gradient extent, <20° (sensu Willig et al., 2003), and a fine grain size (400 m<sup>2</sup>). We studied both  $\alpha$ - and  $\beta$ -diversity, measured as species richness for the former and local contributions to  $\beta$ -diversity for the later (uniqueness of a site compared with all other sites; Legendre & De Cáceres, 2013). We expected that latitude and associated climatic variables should be the predominant drivers of biodiversity, with different patterns for vascular plants and mosses, and between bogs and fens. Vascular plant taxonomic and functional  $\alpha$ -diversity should decrease northwards and inversely for mosses. Compared with bogs, fens are naturally species-rich and spatially heterogeneous habitats, they should become less unique toward the north, whereas no latitudinal pattern should be found among bogs. Finally, latitude and associated climatic variations should structure species and trait composition by favoring small, fast-growing, stress-tolerant species with high dispersal abilities with increasing latitude.

## 2 | METHODS

#### 2.1 | Study area

The study area is in northwestern Quebec (Canada) and extends from 49° to 55°N in latitude and from 68° to 80°W in longitude, covering a total area of ca. 360,000 km<sup>2</sup> and a 600-km gradient from south to north (Figure 1). The area is dominated by spruce-moss forests in the south, transitioning towards open spruce-lichen stands and forested tundra in the north. Precambrian rocks underlie most of the study area. Along James Bay, marine and glacifluvial deposits are locally present, whereas glacial deposits cover most of the eastern part of the study area. In the southwestern portion, peatlands mostly lay on deposits inherited from the proglacial Ojibway Lake or on tills (of compressed clay) formed by a readvancing of the

## Journal of Vegetation Science 📚

ice sheet (Vincent & Hardy, 1977). Peatlands are abundant in the region (covering between 20% and 50% of the landscape; Pellerin & Poulin, 2013), partly because thick clay deposits impede water drainage (mostly in the southwestern portion), partly because high precipitation and cold climatic conditions slow the decomposition of organic matter (Warner & Asada, 2006). The annual mean temperature ranges from  $-5^{\circ}$ C in the northeast to  $+1.5^{\circ}$ C in the southwest. Average annual precipitation ranges between 670mm in the northwest and 1,200mm in the southeast, of which 30%-50% falls as snow (Environment Canada, 2021). The region is sparsely populated and minimally developed, with scattered mines, infrastructures for hydroelectricity production, as well as forestry activities.

#### 2.2 | Database and site selection

We used data from the Capital-Nature Inventory data set built for ecological classification of the territory in 1980 (Gérardin, 1980). This data set contains phytosociological inventories and environmental information such as peat deposit thickness, extent of free surface water, substratum (mineral soil type and texture under the peat deposit), and soil drainage classes. Soil nutrient status and conductivity were not evaluated, whereas the pH measurement data were incomplete. At each sampling location, the cover of every vascular plant and bryophyte species was assessed by the same observers using six classes: <1%, 1%-5%, 5%-25%, 26%-50%, 51%-75%, and 76%-100%. Liverworts and lichens were not included in this study because they were often not identified to the species level or were overlooked.

A total of 442 phytosociological plots, each 400 m<sup>2</sup>, were sampled in 221 peatlands (between one and five plots per peatland) in the study area in 1979 and 1980. Because the geographic coordinates at that time were not accurate by today's standards, we reassigned each plot to the coordinates of the center of the sampled peatland to which it belonged. Plots with nearby disturbances (<50 m from the plot) and plots with less than 90% of species identified to the species level were left out. A total of 376 plots met these criteria.

#### 2.3 | Environmental variables

Along with latitude and longitude, we studied the effects of several other abiotic variables on plant biodiversity patterns (Table 1). To test the influence of climate, we extracted 19 bioclimatic variables for each plot from the WorldClim database, based on 30-year monthly average climate data covering the years 1971 to 2000 (Fick & Hijmans, 2017). This period overlaps with the period in which vegetation data were collected. To avoid multicollinearity among the numerous climatic variables, we visually inspected the two first axes of variation of a principal component analysis (PCA), identified two groups of correlated variables, and selected annual mean temperature and annual total precipitation for further analysis (Appendix S1). Habitat type (bog vs fen), peat deposit thickness and percentage of TABLE 1 Abiotic variables that characterize the 376 plots sampled in peatlands (156 bogs, 220 fens) in northwestern Quebec (Canada). Groups correspond to variable subsets (spatial, climatic, local) used in the variation partitioning analysis.

Groups and variables	Description and unit
Spatial	
Latitude	Latitude of the peatland center (Decimal degrees)
Longitude	Longitude of the peatland center (Decimal degrees)
Climatic	
Annual mean temperature	Annual mean temperature (°C)
Annual total precipitation	Sum of all total monthly precipitation values (mm)
Local	
Peat thickness	Thickness of the peat deposit in the plot (cm)
Substratum	Texture classes: 1, fine (mostly composed of clays, loams and fine sands); 2, medium (mostly composed of silts and medium sands); 3, coarse (mostly composed of gravels, pebbles or blocks); 4, rock (bedrock). Texture classes are available in Saucier et al. (1994) and Rayfield et al. (2021)
Surface water	Percentage of free surface water in the plot

free surface water were available for each plot from the Capital-Nature data set (Gérardin, 1980). Substratum information (texture of soil deposit) was available for about one-third of the plots in the Capital-Nature data set. We completed these data using surface deposit open access maps (available at: donneesquebec.ca/recherche/ dataset/depots-de-surface and donneesquebec.ca/recherche/dataset/carte-des-depots-de-surface-du-nord-quebecois). We grouped substratum data into four ordinal classes depending on the size of the particles that made up the soil (Table 1; Appendix S2).

The distinction between bogs and fens was mainly based on species assemblages; i.e., *Sphagnum*-heath-dominated plant assemblages were considered bogs and graminoid-brown moss-dominated assemblages were considered fens; some pH measures were available punctually for confirmation. To confirm that we had two distinguishable habitats in terms of plant assemblages, we performed a distance-based test of homogeneity for multivariate dispersion (Anderson, 2001; Anderson et al., 2006; Appendix S3) and a PCA of species composition (Appendix S4). Correlations between environmental variables in both habitats (bogs and fens) are also presented in Appendix S5 and difference in environmental variables between bogs and fens in Appendix S6. All explanatory variables were standardized before analysis.

A generally clear distinction was observed between bogs and fens in terms of plant assemblages, especially for vascular species;

Section Science Science

however, not without some overlap. This likely results because some poor fens were classified as bogs because of the dominance of *Sphagnum* and ericaceous shrubs, and because some bogs and poor fens plots likely included richer minerotrophic microhabitats caused by the sampling area size (400 m<sup>2</sup>), as indicated by the presence of minerotrophic indicators species in bog plots such as *Caltha palustris* or *Sphagnum warnstorfii* (Appendices S7 and S8).

#### 2.4 | Functional traits

To explore possible drivers of community distribution, we gathered information on plant traits from various published sources (Appendices S9 and S10). Because environmental conditions (temperature, solar radiation, seasonality) vary with latitude, traits were selected to reflect the adaptations needed to survive in high-latitude environments; i.e., dispersal, establishment, and persistence capacity (Soininen et al., 2007; Kraft et al., 2011). We selected four functional traits for vascular plant species (growth form, seed mass, maximum height, and specific leaf area [SLA]), all linked to the leafheight-seed scheme of Westoby (1998) and known to be closely related to fundamental ecological strategies of vascular plants. For mosses, we selected eight functional traits (life form, bryophyte group, shoot length, seta length, spore diameter, sexual condition, peristome type, and presence of tomentum). We used more traits for mosses because their functional variation along gradients is less well known and therefore more exploratory.

Quantitative traits were converted to qualitative traits to facilitate comparison among traits with different units. We created a [site × trait class] abundance matrix that can be used similarly to a species abundance matrix (for calculating community-weighted means). The raw [species  $\times$  trait] matrix was used to decompose all qualitative traits into binary trait states (yielding 12 states for vascular plant species, 24 states for mosses; Appendices S9 and S10), and producing a [species  $\times$  trait classes] matrix containing absence/presence data (0/1) for each trait class. The [site  $\times$  species] abundance matrix was then multiplied by the [species x trait classes] matrix to produce the [site × trait classes] matrix containing species abundances per trait class. Because it contains species abundances for each trait class, the matrix can be treated as a [site  $\times$  species] matrix. Data in the form of abundances are suitable for calculation of ordination and calculations of local contributions to  $\beta$ -diversity (LCBD) indices (Legendre & Legendre, 2012). All hypothesized drivers of plant community changes and expected shifts in functional traits are presented in Appendix S11.

#### 2.5 | Data analysis

#### 2.5.1 | Alpha-diversity

Taxonomic  $\alpha$ -diversity was calculated as species richness; i.e., the number of different species recorded per plot. Functional dispersion

(FDis) was used as an estimator of functional α-diversity (Laliberté & Legendre, 2010). FDis corresponds to the mean distance of species from the centroid of the resulting multivariate trait space, each distance weighted by the relative abundance of species. The FDis indices were computed from the raw [species × trait] matrix and the untransformed [site × species abundances] matrix (see dbFD function). We fitted linear mixed effect models to determine the effects of all environmental variables and the interaction between habitat and latitude (Table 1) on four response variables: vascular plant and moss richness, and vascular plant and moss FDis. We also conducted a supplementary univariate model of bryophyte richness as a function of latitude, because models indicated no effect but visual interpretation suggested an increase with latitude. Because each plot was nested within a peatland, a random effect for the peatland was added. Residuals met the assumptions of normality and homoscedasticity; taxonomic vascular plant richness was log-transformed to ensure that these conditions were met. Variance inflation factors were verified and were always less than 20, which we used as a cutoff value (Ter Braak & Smilauer, 2002).

#### 2.5.2 | Local contribution to beta-diversity

We estimated LCBD indices, a measure of ecological uniqueness representing the relative contribution of a given site to the total  $\beta$ diversity of a group of sites (Legendre & De Cáceres, 2013). Large LCBD values indicate unique sites in terms of composition, meaning that they make a greater than average contribution to  $\beta$ -diversity. We ran LCBD analysis on the Hellinger-transformed [site × species] matrix for taxonomic LCBD indices and the Hellinger-transformed [site x trait classes] matrix for functional LCBD indices. The Hellinger transformation is appropriate for constrained ordination analyses on community composition data because it has all necessary properties, notably it is double-zero asymmetrical (Legendre & De Cáceres, 2013). We first computed the total sum of squares of the community dissimilarity matrices; i.e., the sum of the squared deviations of sites from the species/trait means, representing the variation in species/traits composition (or  $\beta$ -diversity) among the sites. LCBD values were calculated by dividing the sum of squares of a given site by the total sum of squares for the study area. The same linear mixed effect modeling approach as for  $\alpha$ -diversity was used on taxonomic vascular plant LCBD, taxonomic moss LCBD, functional vascular plant LCBD, and functional moss LCBD. All LCBD indices were log-transformed to ensure that model assumptions were met.

## 2.5.3 | Species and trait composition

Environmental variables were divided into three groups (spatial, climatic, and local variables) to assess their relative effects on species and trait composition (Table 1). Variation partitioning based on redundancy analysis (RDA) was used to assess the relative and unique fraction of variation associated with each group of

## Journal of Vegetation Science 📚

variables (Borcard et al., 1992). The significance of each testable (unique) fraction was obtained by a permutation test with 9,999 permutations. We conducted the variation partitioning on the Hellinger-transformed [site  $\times$  species] and [site  $\times$  trait classes] matrices. Appendix S12 presents a PCA on the Hellinger-transformed [site  $\times$  trait classes] matrix for visualization of correlations between trait classes.

We performed all statistical analyses using R (version 4.1.0, R Core Team, R Foundation for Statistical Computing, Vienna, AT). We performed multiple linear mixed effects models using nlme (version 3.1-160, R Core Team, R Foundation for Statistical Computing, Vienna, AT). Marginal effects of interaction terms were estimated using emmeans (version 1.8.2, R Core Team, R Foundation for Statistical Computing, Vienna, AT). Hellinger transformations, canonical analysis, variation partitioning, and tests of significance of the fractions were done using the vegan package (version 2.6-4, R Core Team, R Foundation for Statistical Computing, Vienna, AT). LCBD values were obtained from the adespatial package (version 0.3-20, R Core Team, R Foundation for Statistical Computing, Vienna, AT). We computed the [site × trait class] abundances matrix from the FD package, as well as the functional dispersion indices (version 1.0-12.1, R Core Team, R Foundation for Statistical Computing, Vienna, AT).

### 3 | RESULTS

#### 3.1 | Alpha-diversity

A total of 176 species occurred in the 376 plots sampled, 128 vascular plants and 48 mosses (Appendices S7 and S8). The 156 plots in bogs contained 151 species (109 vascular plant species, 42 mosses), whereas the 220 plots in fens comprised 176 species (128 vascular plant species, 48 mosses). All species in bogs were present in fens. However, species as *Chamaedaphne calyculata*, *Picea mariana*, *Rhododendron groenlandicum*, and *Rubus chamaemorus* clearly preferred bogs, whereas *Carex exilis*, *Carex limosa*, *Menyanthes trifoliata*, and *Trichophorum cespitosum* were mostly associated with fens (Appendix S4). An average of 20 species per plot was observed in bogs (10–53) and 25 species per plot in fens (5–49).

Vascular plant species richness increased with peat thickness and longitude (toward the west) and decreased with annual total precipitation (Table 2). Habitat had a significant interactive effect with latitude. Vascular plant richness decreased with latitude in fens but did not vary significantly with latitude in bogs (Figure 2a). Vascular plant richness was higher in fens but seemed to converge with that of bogs at higher latitudes (Figure 2a).

Moss richness was influenced only by the substratum (Table 2) decreasing from peatlands overlying fine texture substratum to those overlying bedrock. Although the multiple regression model indicated no significant effect of latitude on moss richness, Figure 2b suggests an increase in bryophyte richness with latitude. A univariate regression model of bryophyte richness as a function of latitude indicated

that moss richness increased with latitude (t=4.99, p<0.0001), but the effect was confounded with that of other variables within the multivariate regression.

Vascular plant FDis decreased with surface water and was lower in fens than in bogs (Table 2; Figure 2c). Moss FDis decreased with latitude, annual mean temperature, annual total precipitation, and peat thickness (Table 2). Moss FDis was lower in bogs than in fens but tended slightly to converge in both habitats at higher latitudes (Figure 2d).

#### 3.2 | Local contributions to beta-diversity

Vascular plant taxonomic LCBD indices increased with surface water, whereas they decreased with latitude, annual mean temperature, annual total precipitation, and peat thickness (Table 3; Figure 3a). Moss taxonomic LCBD indices increased with longitude and surface water and decreased with latitude and annual total precipitation (Table 3; Figure 3b). Vascular plant and moss taxonomic LCBD indices were always higher in fens than in bogs (Figure 3a,b).

Vascular plant functional LCBD indices decreased with peat thickness (Table 3). Moss functional LCBD indices decreased with latitude and annual total precipitations, and increased with substratum (from fine texture to bedrock) and longitude; i.e., toward the west (Table 3). Habitat and latitude had an interactive effect on moss functional LCBDs (Table 3), where the decrease in LCBD indices with latitude was stronger in fens than in bogs, and LCBD indices converged in both habitats at higher latitudes (Figure 3d). Bogs had usually lower LCBD indices than fens, and the difference between bogs and fens decreased strongly with latitude for moss functional LCBD (Figure 3).

#### 3.3 | Composition

All abiotic variables explained 17.8% and 19.1% of the vascular plant taxonomic and functional composition (adjusted  $R^2$ ), respectively, and 11.6% and 14.8% of the moss taxonomic and functional composition, respectively (Figure 4). Vascular plant species composition (taxonomic and functional) was better explained by the whole set of environmental variables than for mosses. Within the explained variation, both taxonomic and functional composition of vascular plant and moss species were primarily structured by local conditions, which were more important than spatial and climatic variables combined.

Vascular plant trait composition primarily followed a gradient of surface water from wet fens to drier bogs along the first axis (87.9% of the variance explained, Figure 5a). Along this gradient, plant height (Height 3), the presence of low SLA (SLA 1) and woodiness (shrub, tree) increased towards dry bog communities. Towards the other end of the gradient (i.e., wetter fens), herbaceous, smaller (Height 1, Height 2) and mid-range SLA (SLA 2) species were more frequent. Secondary gradients (including longitude, temperature,

7 of 16

TABLE 2 Effect of abiotic variables and their interaction on taxonomic richness and functional dispersion of vascular plant and moss species in peatland of northwestern Quebec (Canada), tested with linear mixed effect models.

	Vascular plant			Moss				
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
Richness								
Habitat (bog or fen)	0.19	0.04	4.34	<0.001	0.13	0.29	0.44	0.660
Latitude	-0.15	0.09	-1.52	0.130	0.68	0.65	1.04	0.300
Longitude	0.24	0.08	3.00	0.003	0.32	0.52	0.61	0.540
Annual mean temperature	<0.01	0.09	0.10	0.920	-0.02	0.62	-0.03	0.980
Annual total precipitation	-0.17	0.07	-2.28	0.020	0.22	0.48	0.47	0.640
Peat thickness	0.06	0.03	2.34	0.020	-0.24	0.16	-1.47	0.140
Surface water	0.02	0.02	0.77	0.440	-0.14	0.14	-1.04	0.290
Substratum	-0.01	0.02	-0.57	0.570	-0.32	0.16	-2.01	0.040
Habitat $ imes$ Latitude	-0.09	0.04	-2.01	0.040	0.04	0.28	0.15	0.880
	Intercept		Residual		Intercept		Residual	
1  Site (SD)	0.16		0.37		1.08		2.43	
FDis								
Habitat (bog or fen)	-0.02	<0.01	-02.81	0.006	0.03	0.01	4.47	<0.001
Latitude	< 0.01	0.01	-0.006	0.990	-0.06	0.02	-3.78	<0.001
Longitude	<-0.01	0.01	-0.38	0.780	0.01	0.01	0.65	0.520
Annual mean temperature	<0.01	0.01	0.29	0.770	-0.04	0.02	-2.37	0.020
Annual total precipitation	<-0.01	0.01	-0.40	0.690	-0.05	0.01	-3.84	<0.001
Peat thickness	<-0.01	<0.01	-1.01	0.310	-0.02	<0.01	-4.07	<0.001
Surface water	<-0.01	<0.01	-2.30	0.020	<-0.01	<0.01	-0.10	0.920
Substratum	<0.01	<0.01	0.43	0.670	< 0.01	< 0.01	0.28	0.780
Habitat  imes Latitude	<-0.01	<0.01	-0.48	0.630	-0.01	0.01	-1.44	0.150
	Intercept		Residual		Intercept		Residual	
1  Site (SD)	<0.01		0.06		0.03		0.06	

*Note*: Values in bold indicate significant differences (*p* < 0.05). All variables were tested with 149 degrees of freedom; random effects (sites) have 218 groups. Estimate = standardized coefficient.

Abbreviations: FDis, Functional dispersion; SE, standard error.

peat thickness, and latitude) along the second axis seemed to occur in both bogs and fens, without specific patterns in traits (see Appendix S13 for regression between each trait states and latitude).

Moss trait composition was constrained by a gradient of peat thickness along the first axis (Figure 5b, 56.9% of the variance explained). *Sphagnum* species (which are species with no seta, no peristome, large spores, and turf growth form) were associated with thick peat deposit, mainly found in bogs. At the other end of the gradient, toward fens with thinner peat deposits, there was an increase in pleurocarpous and acrocarpous mosses, with long seta, small spores, tomentum, and perfect peristome. Therefore, the first axis represents the distinction between *Sphagnum* species, which inhabit bogs with thick peat deposits, and brown mosses, which are more abundant in fens. Along the second axis (Figure 5b, 30.3% of the variance explained), moss trait composition was structured along a gradient of temperature, free surface water, longitude, and latitude. There was an increase in dioicous species presenting a specialized peristome toward warmer, southwestern regions, and drier bogs. Toward the other end of the gradient, i.e., wetter northeastern regions and fens, there was an increase in small and large mosses (Shoot 1 and 3), with monoicous reproduction and mid-range spore sizes (Spore 2; see Appendix S14 for regression between each trait states and latitude).

## 4 | DISCUSSION

Our results show contrasting  $\alpha$ -diversity (species richness) patterns between vascular plant and moss species in bogs and fens along the latitudinal gradient. Furthermore, we find that higher latitudes are associated with lower community uniqueness for both species groups and functional decrease in uniqueness for mosses in both habitats. Moss and vascular plant taxonomic and functional composition are primarily structured by contrasting local conditions



FIGURE 2 Predicted values (marginal effects) of (a) vascular plant richness, (b) moss richness, (c) vascular plant functional dispersion (FDis) and (d) moss FDis as a function of latitude in bogs (red) and fens (blue) of northwestern Quebec, Canada. All other variables in the model were fixed at their means. Est, non-standardized estimated marginal means; *p* value, significant if <0.05. Significant simple effects of habitat are presented as fen > bog or vice versa.

between bogs and fens, whereas spatial and climatic variations along the latitudinal gradient seem to play a secondary role.

## 4.1 | Alpha-diversity differs between bogs and fens along the latitudinal gradient

Our results indicate that vascular plant richness in bogs and fens converge toward the north, as fens become poorer, whereas bog richness is unaffected by latitude. The pattern in fens concurs with our expectation of decreased vascular plant richness towards the north, likely because of increased abiotic filtering that constrains biodiversity (Swenson et al., 2012). However, vascular plant richness in bogs does not vary significantly toward the north, also supporting our hypothesis. We suggest that the convergence of vascular plant richness between bogs and fens northward is caused by a decrease in the spatial heterogeneity of the surrounding landscape when moving north, which reduces the species pool and thus the diversity in both bogs and fens. Bogs generally have a limited species pool of vascular plants, which explains their initial lower richness, whereas reduced habitat filtering in fens favors greater richness and functional dispersion (Dyderski et al., 2016). Bogs are often seen as more resilient than fens to environmental change because of their increased stability in trait and species composition as well as the dominance of Sphagnum species that tolerate and potentially temper changes in environmental conditions (Laine et al., 2021).

We expected moss richness to increase northward in both habitats but found confounding effects between latitude and other variables, notably precipitation. Nevertheless, moss richness seems to increase toward the north in both habitats. Similar results were found in several other studies at regional or subcontinental scales using both coarse or fine grains (Rozzi et al., 2008; Mateo et al., 2016), suggesting that this pattern is not specific to peatlands and seems to be frequent at these scales (Patiño & Vanderpoorten, 2018). Moreover, moss FDis and LCBD indices decrease northward, similarly to vascular plants. The contrasting patterns between moss richness and FDis along the latitudinal gradient indicate that although southern moss communities are not species-rich, they are much more functionally diverse, whereas northern moss communities are much less functionally diverse, regardless of their higher richness. This would imply strong trait-based community assembly for mosses, because the colonizing species had increasingly similar traits, which may be caused by extreme environmental conditions northward that select for optimal trait values (Robroek et al., 2017).

# 4.2 | Decrease in uniqueness toward the north and climatic effects

LCBD indices typically decrease with latitude, indicating that single local plant communities tend to be less unique toward the north (Qian, 2009; Pinto-Ledezma et al., 2018). We observe this pattern

Section Science Journal of Vegetation Science

TABLE 3 Effect of abiotic variables and their interaction on taxonomic and functional local contributions to  $\beta$ -diversity (LCBD) indices of vascular plant and moss species in peatland of northwestern Quebec (Canada), tested with linear mixed effect models.

	Vascular plant			Moss				
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
Taxonomic								
Habitat (bog or fen)	0.23	0.03	8.48	<0.001	0.19	0.03	6.91	<0.001
Latitude	-0.24	0.06	-3.97	<0.001	-0.18	0.06	-3.08	0.002
Longitude	0.03	0.05	0.64	0.520	0.15	0.05	3.08	0.003
Annual mean temperature	-0.13	0.06	-2.25	0.030	<0.01	0.06	0.006	0.990
Annual total precipitation	-0.12	0.05	-2.74	0.007	-0.14	0.04	-3.20	0.001
Peat thickness	-0.04	0.02	-2.25	0.030	0.02	0.02	0.98	0.330
Surface water	0.04	0.01	3.09	0.002	0.04	0.01	3.00	0.003
Substratum	0.01	0.02	0.62	0.540	0.01	0.01	0.65	0.510
Habitat  imes Latitude	-0.03	0.03	-1.08	0.280	<-0.01	0.03	-0.05	0.960
	Intercept		Residual		Intercept		Residual	
1  Site (SD)	0.1		0.23		0.04		0.25	
Functional								
Habitat (bog or fen)	0.18	0.08	2.25	0.030	0.27	0.09	3.19	0.002
Latitude	-0.15	0.16	-0.94	0.350	-0.69	0.19	-3.57	<0.001
Longitude	-0.16	0.13	-1.26	0.210	0.49	0.16	3.16	0.002
Annual mean temperature	-0.16	0.15	-1.03	0.300	0.01	0.18	0.04	0.970
Annual total precipitation	-0.05	0.12	-0.46	0.650	-0.74	0.14	-5.19	<0.001
Peat thickness	-0.15	0.04	-3.48	<0.001	0.02	0.05	0.47	0.640
Surface water	0.03	0.04	0.82	0.410	0.08	0.04	1.84	0.070
Substratum	-0.01	0.04	-0.23	0.820	0.13	0.05	2.70	0.008
Habitat  imes Latitude	0.10	0.08	1.30	0.190	-0.18	0.08	-2.15	0.030
	Intercept		Residual		Intercept		Residual	
1  Site (SD)	0.0002		0.71		0.32		0.73	

*Note*: Values in bold indicate significant differences (*p* < 0.05). All variables were tested with 149 degrees of freedom; random effects (sites) have 218 groups. Estimate = standardized coefficient.

Abbreviation: SE, standard error.

in both habitats and for both taxonomic groups, as well as for moss functional LCBD indices. Such a decrease in uniqueness with latitude may be associated with stronger seasonality at high latitudes, resulting in smaller species pools and less turnover between areas (Tang et al., 2012; Pinto-Ledezma et al., 2018). Furthermore, the effects of latitude and longitude are deeply shared with the effects of climate in the variation partitioning analysis, because their combined effects are stronger than their independent effects, at least for vascular plants. This implies that latitudinal effects in our study are, at least in part, driven by climatic variations within our study. This is further underscored by the non-significant marginal effects of latitude on moss richness when other environmental variables are included. Other environmental variables recognized as important in explaining peatland biodiversity patterns, such as watertable depth, productivity, pH, nutrient concentrations, and shade (Vitt et al., 1995; Wheeler & Proctor, 2000; Økland et al., 2001; Laine et al., 2021), were not evaluated in this study and could explain some of the patterns observed (Pontarp et al., 2019). The only LCBD indices that do not vary with latitude are functional vascular plant LCBD, potentially because of the high functional redundancy of vascular plant species in peatlands. According to Robroek et al. (2017), species turnover might be associated with deterministic replacement of functionally similar species, especially for harsh ecosystems such as peatlands, which may select for optimal traits. However, this could also simply reflect the specific functional traits used in our study. We also observe higher LCBD indices in fens than in bogs along the latitudinal gradient, although this difference is no longer present at higher latitudes for moss functional LCBDs, likely because fens have a higher community heterogeneity, lower peat thickness, higher water, and high nutrient availability (Vitt et al., 1995; Anderson & Davis, 1997; Locky & Bayley, 2006; Dyderski et al., 2016).



FIGURE 3 Predicted values (marginal effects) of (a) vascular plant taxonomic local contributions to  $\beta$ -diversity (LCBD), (b) moss taxonomic LCBD, (c) vascular plant functional LCBD and (d) moss functional LCBD as a function of latitude in bogs (red) and fens (blue) of northwestern Quebec, Canada. All other variables in the model were fixed at their means. Est, non-standardized estimated marginal means; *p* value, significant if <0.05. Significant simple effects of habitat are presented as fen > bog.

# 4.3 | Taxonomic and functional diversity depends on local habitat variations

Although climatic and spatial variables (latitude and longitude) have significant effects on species and trait composition, local variables (peat thickness, surface water, substratum, and habitat type) are the most influential. Similar results were observed for lake macrophytes by Alahuhta et al. (2017) and were related to the fact that aquatic environments can buffer extreme climatic conditions and decrease temperature variations. In the absence of disturbances, peatlands are considered highly stable environments with their own suite of limiting conditions (Robroek et al., 2017), likely explaining the importance of local environmental conditions. More specifically, we found that surface water increases taxonomic LCBD indices, whereas peat thickness increases vascular plant richness but decreases moss FDis and vascular plant LCBD indices. The presence of surface water has previously been shown to significantly increase plant diversity in peatlands because of increased habitat heterogeneity, a condition enhancing diversity in fens (Poulin et al., 2002; Fontaine et al., 2007). However, the peat deposit is thicker in bogs than in fens (Appendix S6), and the establishment of ombrotrophic conditions with peat accretion is associated with a decrease in vascular plant richness and an increase in spatial similarity (Anderson & Davis, 1997; Locky & Bayley, 2006; Laine et al., 2021). For mosses, we also find that richness decreases with increasing texture of the substratum. Fine-textured substrata (e.g., clay) are usually more

nutrient-rich than coarser ones or bedrock in the study area (Légaré et al., 2001). Fens and bog margins may, therefore, receive mineral elements from surface and underground waters, and such enrichment may favor diversity (Wheeler & Proctor, 2000). Overall, our results suggest that the effects of environmental variables reflect the local variations between bogs and fens. Finally, variation partitioning also shows that the unique effect of local variables is proportionately greater for vascular plant species than for mosses. These species are more impacted by dispersal limitation and habitat heterogeneity than mosses (Chen et al., 2015; Bertuzzi et al., 2019), for which spatial and climatic variables are relatively more important in our study, enhancing these differences between taxonomic groups.

Functional composition is mainly structured along a successional gradient from humid fens to drier bogs, whereas latitude and climate play secondary roles. Drier bogs are rich in tall, woody and slow-growing (low SLA) species, whereas humid fens display smaller, faster-growing (higher SLA) and herbaceous species. Bogs generally have lower water availability, but a greater number of ericaceous and woody species (Anderson & Davis, 1997; Wheeler & Proctor, 2000), as also found in our study. These results could imply that species in peatlands modify their resource acquisition strategies to better adapt to changing conditions (Laine et al., 2021). In fens, fast-growing herbaceous species such as forbs and graminoids take up resources efficiently and rapidly. In bogs, thick peat produces a restrained growth environment, favoring species with more conservative resource acquisition strategies (slow growth rates, resistance FIGURE 4 Variation partitioning by redundancy analyses (RDA) of (a) vascular plant taxonomic, (b) moss taxonomic, (c) vascular plant functional and (d) moss functional composition explained by local, climatic and spatial variables (Table 1) in peatlands of northwestern Quebec, Canada. Percentages in the partitioning are adjusted  $R^2$  of each variable subset estimated by RDA, and circle sizes are their approximation, which are proportional within a quadrant but not between quadrants. All *p*-values for testable fractions were significant (*p* < 0.05).



to herbivory, high litter accumulation) to enhance survival, such as evergreens, trees, shrubs, and *Sphagnum* (Laine et al., 2021).

Similarly, the functional traits of mosses seem mainly influenced by local-scale variations between bogs and fens. For example, a long seta is associated with wet fens. Long seta may allow the moss capsule to reach the moving air in habitats where herbaceous vascular plant species thrive (Hedenäs, 2001), like in the studied fens. A longer seta may indeed be adapted to release spores at low wind speeds, because it facilitates the vibration of the sporophyte (Johansson et al., 2014). Longer seta may also be favored by increased water abundance (Hedenäs, 2001), conditions favored in fens compared with bogs in the study area (higher free surface water; Appendix S6). Most other traits reflect the distinction between Sphagnum and brown mosses (spore size, peristome type, presence of tomentum), and highlight the environmental differences between bogs and fens; bogs have a greater abundance of Sphagnum species, whereas fens are rich in brown mosses. Therefore, moss compositional analyses further underscore the importance of habitat filtering along the bog-fen gradient in structuring biodiversity within the study area. This concurs with the fact that ecological factors usually prevail in determining moss diversity compared with other factors such as

historical and disturbance factors (Fenton & Bergeron, 2008; Patiño & Vanderpoorten, 2018). The only trait that shows a clear gradient along latitude is the sexual condition. Dioicous species are mainly associated with bogs of the southern and warmer regions, whereas monoicous species thrive in fens of the northern and cooler regions. This pattern seems to go along with the hypothesis that monoicous moss species usually have a larger distribution range size than dioicous moss species because of the greater probability of self-fertilization than cross-fertilization (Longton & Schuster, 1983). We do not find that monoicous species are favored in drier habitats as suggested by Wyatt (1982), likely because bogs and fens are both relatively wet habitats.

#### 4.4 | Issues relevant to the study

Patterns of biodiversity may be influenced by a number of methodological constraints, such as the choice of explicative variables, the scale (extent and grain) of the study as well as the number and choice of traits used in functional analyses. Here, we use only a subset of local environmental variables (surface water, peat

FIGURE 5 Constrained ordination diagrams of the redundancy analyses on the Hellinger-transformed functional trait data for (a) vascular and (b) moss species, constrained by all environmental variables. Fitted site scores for bogs and fens are visible. Scaling=2. Variables and traits with small effects were removed from plots to facilitate visual interpretation. See Appendices S9 and S10 for trait descriptions.



thickness, substratum) known to influence peatland plant diversity and composition (Vitt et al., 1995; Wheeler & Proctor, 2000; Økland et al., 2001; Locky & Bayley, 2006; Laine et al., 2021). Other important variables, namely water-table level, pH and mineral nutrient concentrations (Wheeler & Proctor, 2000; Økland et al., 2001), were unfortunately not available. Considering them within our models might have increased the primacy of local variables over spatial and climatic ones (Siefert et al., 2012), although we acknowledge that an unknown portion of the unexplained variance in our models might also be due to nonlinear relations between species distribution and explanatory variables (Økland, 1999).Nevertheless, the primacy of local variables would have likely been even higher with smaller sampling units because peatland flora patterns are often influenced by nutrient concentrations in peat and water (mostly in fens), and by watertable level that can vary at very fine scales (Økland et al., 2001; Hájková et al., 2004). Smaller sampling units would have also insured more uniform plant communities within each unit and greater relation with local environmental variables, especially in bog sites. Indeed, the high richness of our bog sites, especially at the southern portion of the study area (see Figure 2a), suggests a relative high habitat heterogeneity on these sites likely associated with the presence of microtopography (hummocks and hollows), minerotrophic microhabitats, or ponds. By contrast, smaller grain size might have increased species interactions that are not taken into account in environmental variables, as well as the spatial mismatch between local and climatic variables, which might, in turn, have reduced the predictability of the models (Bergauer et al., 2022). Besides, a greater spatial extent of the studied latitudinal gradient, for instance extending from the temperate to the tundra region, could have increased the influence of climatic variables (Siefert et al., 2012). Finally, the number and the choice of traits are known to affect functional diversity measurement (Lefcheck et al., 2015; Legras et al., 2020). Although we carefully chose traits in relation to the specific hypotheses tested (Appendix S11), we were limited by data availability, especially for mosses, which also showed variations in trait values between databases, likely because of their high phenotypic plasticity (Oke et al., 2020). Consequently, we chose to limit the selected traits to more generalist and available traits, which, for most of them, did not vary between Sphagnum species. Integrating a larger suite of traits would have allowed us to better understand the ecological preferences and functions between congeneric species. Finally, we studied only a subset of non-vascular species, because liverworts and lichens were not included. We thus likely underestimated the diversity of the studied peatlands.

## 5 | CONCLUSION

Our results underscore that vascular plant and moss composition in northern peatlands is primarily structured by environmental filtering between bogs and fens, whereas climatic variations along spatial gradients play a secondary role. Therefore, future studies should consider the differences between peatland types, as biodiversity does not manifest the same patterns in both habitats. Furthermore, both taxonomic groups showed different patterns, which also depend on the diversity indicator used ( $\alpha$ -diversity and LCBD, taxonomic and functional). To set priorities in conservation, decisions must be based on multiple diversity indicators and consider differences between habitats and taxonomic groups (Möls et al., 2013). Understanding the drivers of biodiversity is critical in predicting the impact of future climate change in these ecosystems and can directly contribute to biodiversity conservation policies.

#### AUTHOR CONTRIBUTIONS

ÉD, SP and MP conceived the ideas and planned the study. SP collected the data. ÉD analyzed and interpreted the data. ÉD, SP, MP and M-HB drafted or revised the manuscript. PL provided advice on the methods of multivariate data analysis, performed some analysis and revised the manuscript.

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Section Science Section Science

#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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#### DATA AVAILABILITY STATEMENT

All the data used in the study as well as R scripts to reproduce the analyses and the figures are available at https://github.com/edesc henes/peatland\_latitude.

#### ORCID

Stéphanie Pellerin <sup>D</sup> https://orcid.org/0000-0002-5148-1065

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## – Journal of Vegetation Science 🛸

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Climatic variables.

Appendix S2. Substratum map.

Appendix S3. Homogeneity of plant communities.

Appendix S4. Species composition.

- Appendix S5. Correlations between variables.
- Appendix S6. Differences between habitats.
- Appendix S7. Vascular species.
- Appendix S8. Moss species.
- Appendix S9. Vascular plant trait details.
- Appendix S10. Moss trait details.
- Appendix S11. Hypothesized drivers.
- Appendix S12. PCA of functional traits.
- Appendix S13. Vascular plant traits along latitude.
- Appendix S14. Moss traits along latitude.

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