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Scaling functional traits to ecosystem processes: Towards a mechanistic understanding in peat mosses

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Abstract

1. The role of trait trade-offs and environmental filtering in explaining the variability in functional traits and ecosystem processes has received considerable attention for vascular plants but less so for bryophytes. Thus, we do not know whether the same forces also shape the phenotypic variability of bryophytes. Here, we assess how environmental gradients and trade-offs shape functional traits and subsequently ecosystem processes for peat mosses (*Sphagnum*), a globally important plant genus for carbon accumulation. We used piecewise Structural Equation Modeling (SEM) to understand how environmental gradients influence vital processes across levels of biological organization.

2. We gathered data on functional traits for 15 globally important *Sphagnum* species covering a wide range of ecological preferences. Phenotypes lie along well-established axes of the plant economic spectrum characterizing trade-offs between vital physiological functions. Using SEM, we clarified the mechanisms of trait co-variation and scaling to ecosystem processes. We tested whether peat mosses, like vascular plants, constrain trait variability between a fast turnover strategy based on resource acquisition via fast traits and processes, and a strategy of resource conservation, via slow traits and processes.

3. We parameterized a process-based model estimating ecosystem processes linking environmental drivers with architectural and functional traits. In our SEM approach the amount of variance explained varied substantially ($0.29 \leq R^2 \leq 0.82$) among traits and processes in *Sphagnum*, and the model could predict some of them with high to intermediate accuracy for an independent dataset. R^2 variability was mainly explained by traits and species identity, and poorly by environmental filtering.

4. Some *Sphagnum* species avoid the stress caused by periodic desiccation in hollows via resource acquisition based on fast photosynthesis and growth, while other species are adapted to grow high above the water-table on hummocks by slow physiological traits and processes to conserve resources.

5. *Synthesis.* We contribute to a unified theory generating individual fitness, canopy dynamics and ecosystem processes from trait variation. As for vascular plants, the

functional traits in the *Sphagnum* economic spectrum are linked into an integrated phenotypic network partly filtered by the environment and shaped by trade-offs in resource acquisition and conservation.

KEYWORDS

bryophytes, ecosystem processes, peatlands, piecewise SEM, plant development and life-history traits, plant economic spectrum, Sphagnum, Structural Equation Modeling

1 | INTRODUCTION

A major challenge in plant ecology is to understand how changing environmental conditions influence vital processes across levels of biological organization and how these processes can eventually buffer or intensify these changes. The response of species to environmental gradients is likely to be mechanistically captured by a combination of plant response traits, while effect traits are likely to mediate the effect of ecosystem processes on the environment (Moor et al., 2017; Suding et al., 2008) (Figure 1a). For vascular plants, the role of trade-offs and environmental filtering in explaining the variability of functional traits and ecosystem processes is well studied (Díaz, Cabido, & Casanoves, 1999; Violle et al., 2007; Wright et al., 2004).

However, little is known to what extent the same rules and forces also shape the phenotypic variability of mosses (Cornelissen, Lang, Soudzilovskaia, & During, 2007).

Recent studies in peat mosses (genus *Sphagnum*) have indicated both similarities and dissimilarities with vascular plants (Bengtsson, Granath, & Rydin, 2016a; Laing, Granath, Belyea, Allton, & Rydin, 2014a; Rice, Aclander, & Hanson, 2008), which warrants further investigations on both a theoretical and empirical basis. Understanding how changing environmental conditions influence *Sphagnum* is crucial given their role as ecological engineers, since they form nontropical peatlands by peat accumulation and maintain these important carbon sinks through many hydrological and ecological feedbacks (Page & Baird, 2016; Rydin & Jeglum, 2013; Waddington
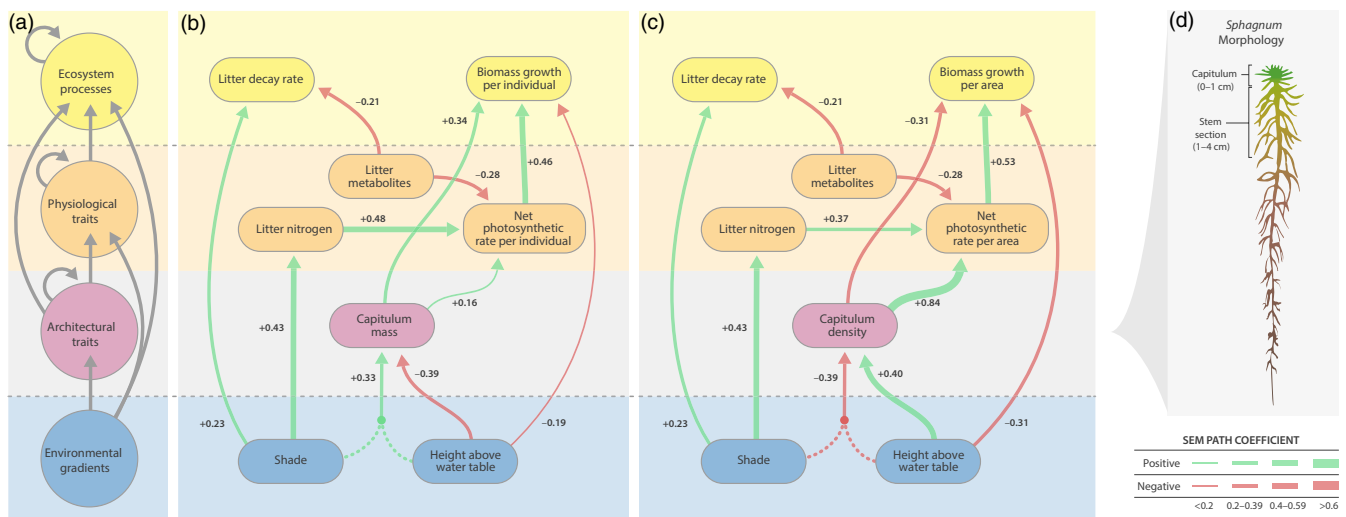

FIGURE 1 Upscaling traits to processes in *Sphagnum* peat mosses. Image credit: J Lokrantz/Azote. (a) Conceptual representation of the mechanistic pathway upscaling the effects (arrows) of environmental gradients on plant resource allocation to functional traits and emergent ecosystem processes. Straight arrows represent direct upscaling effects and curved arrows indirect effects. Circular arrows represent the effects that architectural traits, physiological traits, and ecosystem processes have on other traits of the same category. (b, c) Graphical representation of the mechanistic pathway estimated via piecewise SEM. (b) The individual-based model predicts emergent ecosystem processes at shoot level for a general *Sphagnum* species from individual-based architectural and physiological traits differentially affected by two main environmental gradients. In the model, arrows connect indicators (ovals) for environmental gradients, architectural traits, physiological traits, and ecosystem processes. Green arrows correspond to positive effects (linear standardized path coefficients in the piecewise SEM) and red arrows to negative effects. The head of the arrow corresponds to the direction of the mechanistic pathway. Thicker arrows correspond to stronger mechanistic relationships and are associated with a higher absolute value of the linear path coefficient (legend at the bottom right of Figure 1). The SEM path coefficients and predictive power are also summarized in Tables 3 and 4 (intercepts omitted here). Indirect effects are summarized by partial regression coefficients in the Section 3. Equation parameters are estimated from values for 15 species of *Sphagnum* peat mosses. (c) The area-based model predicts emergent ecosystem properties at canopy level from area-based architectural and physiological traits differentially affected by two main environmental gradients. (d) Definition of the capitulum and stem sections of the *Sphagnum* plant [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2015). It is debated whether an increased temperature and lowering of the water-table in northern peatlands could cause a carbon release through enhanced aerobic microbial decomposition (Bragazza et al., 2016; Dorrepaal et al., 2009; Fenner & Freeman, 2011) or a carbon accumulation by increasing *Sphagnum* productivity via a higher photosynthetically active radiation and growing season length (Charman, Blundell, Chiverrell, Hendon, & Langdon, 2006; Klein, Yu, & Booth, 2013). Thus, to further advance our knowledge on how global change affects *Sphagnum*—and consequently the function of many peatlands—we need to understand how moss traits scale to ecosystem processes.

To assess how functional traits in *Sphagnum* peat mosses scale up to ecosystem processes and determine trade-offs in their ecological strategies, we must investigate how the environment within their communities controls trait variability. For this, it is important to determine the role that different mechanisms have in predicting trait variability (Clark, 2016), specifically evaluating the impact of (a) environmental gradients, (b) trait trade-offs (trait covariation among species), and (c) species diversity (interspecific trait variability). Environmental variability (a) determines resource allocation between architectural (e.g., structural support) and physiological functional traits (e.g., photosynthesis) (Figure 1a). Architectural and physiological traits represent physical and energetic constraints on the use and allocation of resources in plants (Brown, Gillooly, Allen, Savage, & West, 2004; Demetrius, 2006; Messier, Lechowicz, McGill, Violle, & Enquist, 2017). Trait trade-offs in the plant trait spectrum (b) derive from covariation between architectural traits related to plant maintenance (high allocation to large structures) and physiological traits related to their metabolism (high resource capture rate) (Grime, 2001; Messier et al., 2017). In plants, the economic spectrum of functional response traits determines emergent ecosystem processes, like growth and decomposition, which regulate carbon cycling. In mosses, the dependence between the trait economic spectrum (Wang, Liu, Bader, Feng, & Bao, 2017) and processes (Wang & Bader, 2018) takes place at two levels, the shoot level and the canopy level. The interplay between architectural and physiological traits mediates the effects of environmental gradients on ecosystem processes (Falster, Brännström, Dieckmann, & Westoby, 2011; Moor et al., 2017) (Figure 1a). Finally, trait variability (c) is the result of an increasing number of species in the community, as new species potentially broaden the trait distribution for a community (Clark, 2016; Michel, Lee, During, & Cornelissen, 2012). Integrating these three mechanisms makes it possible to build realistic ecological models that are constrained in multivariate space by allometric relationships, covariation (trade-offs, selection) and species co-occurrences (environmental filtering and biotic interactions) (for an example of model constrained in this way, Clark, 2016).

Environmental variability, trait trade-offs, and interspecies trait variability in *Sphagnum* are intermingled in generating the observed large diversity in the economic spectrum at different scales (e.g., Bengtsson et al., 2016a; Rice et al., 2008). Environmental gradients may affect resource allocation between

architectural and physiological traits, which scale to stand properties (Laing et al., 2014a). The high species-specificity in traits and processes for some *Sphagnum* species may account for a large fraction of the trait variability (Bengtsson et al., 2016a; Limpens, Bohlin, & Nilsson, 2017). Specifically, the environmental gradients affecting the *Sphagnum* trait trade-offs are water availability (distance to the water-table in peatlands) and light availability (Laing et al., 2014a). The further away from the water-table, the more *Sphagna* are likely to invest in a dense architecture to maintain water content through increased capillarity, while less is invested in photosynthetic capacity. Light availability drives a trade-off between investments in physiological traits related to photosynthesis in shaded habitats and structural and protective tissue in open habitats (Laing et al., 2014a; Wright et al., 2004). These two axes of variation in the *Sphagnum* economic spectrum evidently affect ecosystem processes such as biomass growth and litter mass loss related to carbon cycling in peatlands (Laing et al., 2014a). The *Sphagnum* economic spectrum reveals interspecific variability in traits and processes with respect to nutrient cycling (cf., Reich, 2014), which reflects alternative ecological strategies responsible for trait trade-offs (Grime, 2001): *Sphagnum* species with fast nutrient cycling are characterized by a large apical growing part (capitulum), scattered canopy (low capitulum density), high maximum photosynthetic rate and fast ecosystem processes in terms of better growth and high litter mass loss, while slow nutrient cycling species tend to have a small capitulum, dense canopy, and canopy dominated by these species tend to have slow ecosystem processes (Laing et al., 2014a; Moor et al., 2017; Rice et al., 2008) (Figure 2). Within these two extremes lies the huge interspecific variability of *Sphagnum* ecological strategies emerging from its complex economic trait spectrum.

Despite the recent advances in trait ecology, for bryophytes we still lack attempts to construct coherent process-based models, describing how environmental gradients affect functional traits and ecosystem processes, while accounting for trait covariation and trade-offs. This paper aims to (a) build a coherent trait-based *Sphagnum* model and (b) test the Reich's (2014) hypothesis that environmental gradients constrain trait variability between strategies of stress avoidance via resource acquisition (covariation between fast traits and processes) and stress tolerance via resource conservation (slow traits and processes). We will achieve aim (a) by constructing a mechanistic pathway predicting ecosystem processes for *Sphagnum* species from functional traits. We will achieve aim (b) by disentangling the different sources of trait variability and improving predictions of *Sphagnum* processes at a community level, which can account for differences in ecological strategies with different resource availabilities. Specifically, our modelling approach (a) identifies the main sources of trait and process variability in *Sphagnum*, (b) analyses trait trade-offs between resource acquisition and conservation (Messier et al., 2017) to evaluate Reich's (2014) hypothesis. Additionally, our work can also be useful for quantifying the possible effects of climate change on the capacity of *Sphagnum* peat mosses
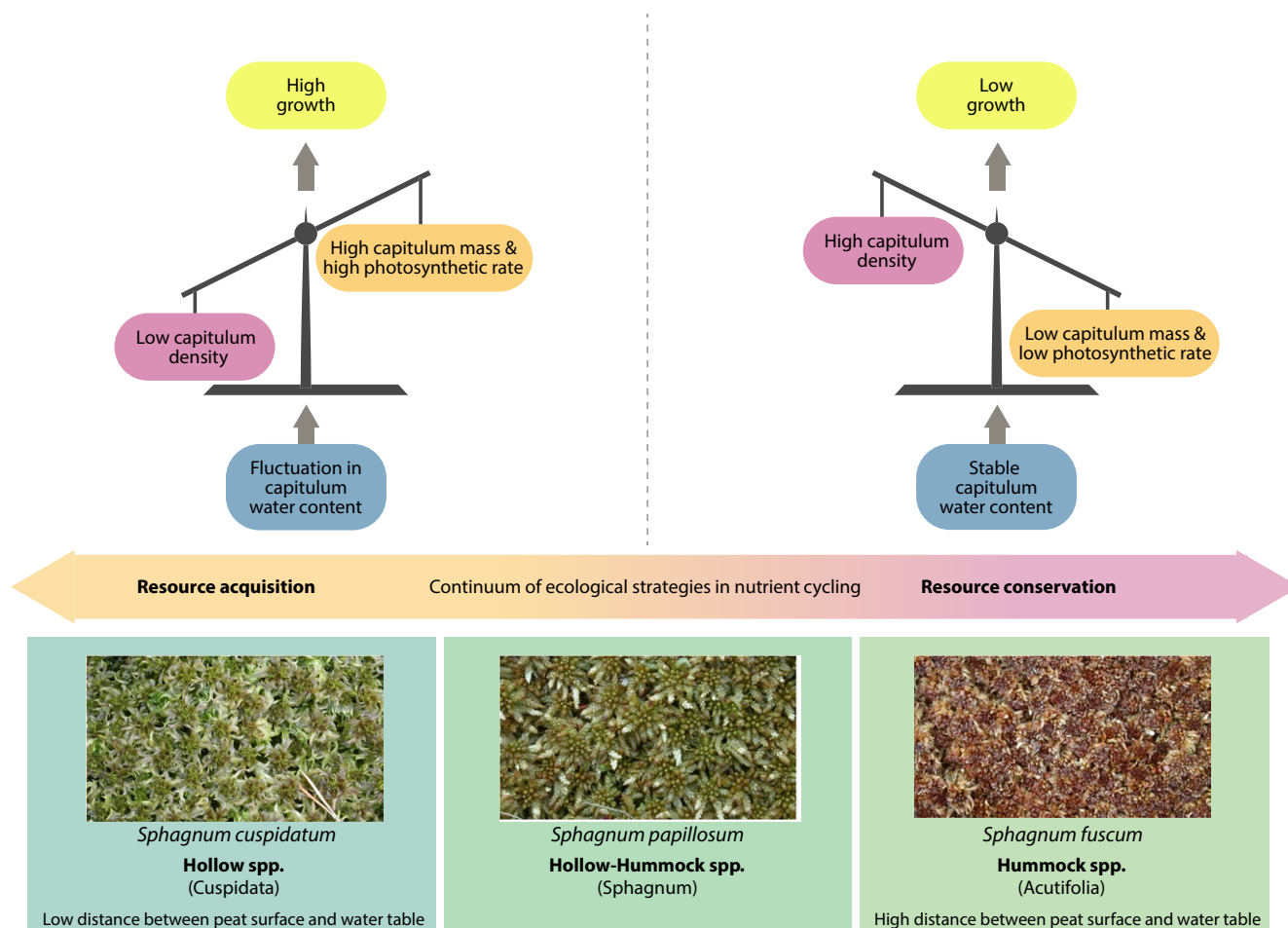
FIGURE 2 The continuum of ecological strategies driving trait trade-offs in the *Sphagnum* economic spectrum. Image credit: J Lokrantz/ Azote. Hollow species with fast nutrient cycling have short distance from the groundwater, fluctuating water content in the capitulum, large capitulum, low capitulum density, high maximum photosynthetic rate and fast growth; slow nutrient cycling hummock species have high distance from the groundwater, a stable water content in the capitulum, small capitulum, dense canopy, low photosynthetic activity, and slow growth. In-between rates for species with large microtopographical variability [Colour figure can be viewed at wileyonlinelibrary.com]

to sequester and accumulate organic carbon in peatlands (Bacon et al., 2017; Hedwall, Brunet, & Rydin, 2017).

2 | MATERIALS AND METHODS

2.1 | Study sites

Data on environmental gradients (water level and shade), functional traits (architectural and physiological), and ecosystem processes (production and decomposition) for 15 *Sphagnum* species have been collected from the three study sites in the boreonemoral zone by Bengtsson, Granath, and Rydin (2016a, 2016b), Bengtsson, Rydin, and Hájek (2018), Laing et al. (2014a) and Laing, Granath, Belyea, Allton, and Rydin (2014b) (Supporting Information Appendix S1; refer to Table 2 for explanations of abbreviations and units). We refer to this literature for further information about the procedures for measuring environmental variables and trait estimation.

The sites in the Bengtsson et al. (2016a) study were Kulflyten, a mire complex in central southern Sweden (59°54′N, 15°50′E), and

Glon, a small rich fen (60°31′N, 17°55′E). In Laing et al. (2014a), the study site was the Ryggmossen bog complex in eastern central Sweden (60°3′N, 17°20′E).

2.2 | Measurement of environmental gradients

Water level: Height above water-table (HWT in mm) is the distance between the moss surface and the water-table and varies along the microtopography of peatlands (Table 2).

Habitat openness: Habitats were categorized along a gradient of openness, corresponding to a decreasing level of light availability for the peat mosses and to an increasing level of shading from trees (Table 2).

2.3 | Sampling functional traits and ecosystem processes

Selected functional traits and emergent ecosystem processes were measured on individual and area basis for the dominant *Sphagnum*

species growing at different positions along the hollow to hummock gradient (different levels of HWT) and in different habitats (bog plateau, bog margin, lagg fen, and swamp forest).

Traits and processes used in individual-based and area-based Structural Equation Modeling (SEMs) were defined as follows:

Capitulum numerical density (n, capitula cm^{-2}): Was measured in the laboratory by counting the number of capitula (i.e., the cluster of branches at the top of the shoot) in the collected cores, and in pictures for wet species, within a circle of 38 cm^2 (Figure 1d).

Capitulum and stem section mass: Dry masses of the capitulum and of the upper stem (respectively, Mcap, expressed in mg, and Mstem, mg mm^{-1}) (Figure 1d).

Dry bulk density (bulkd, mg cm^{-3}): The weight of all stems (below capitula) in a core divided by the volume of the cylinder.

Net photosynthetic rate: The net CO_2 fixation rate under saturated light conditions (i.e., the maximum photosynthetic rate, per individual Npi, mg CO_2 h^{-1}, and per area, Npa, mg CO_2 h^{-1} cm^{-2}) was estimated for the capitulum at optimal water content. For the details concerning the measurement of Npi and Npa, see Granath, Strengbom, and Rydin (2012).

Litter metabolites: litter quality parameters affecting intrinsic decay resistance (litter mass loss) were summarized via a scaled sum of three variables (LM, % in litter)—sphagnan, soluble phenolics, and lignin-like phenolics. For the details concerning the measurement of the three metabolites, see Bengtsson et al. (2018).

Litter N: Nitrogen proportion in the litter (Nlit, percentage by mass, %).

Length increment (LI), growth in biomass per individual (Gi), growth in biomass per area (Ga), and litter mass loss (L) were standardized by measuring period length (number of days) in each year to allow for comparison (respectively, for LI, Gi, and Ga: 153 days in 2009, 117 days in 2012, and 143 days in 2013; for L: 117 days in 2012).

Length increment: Stem elongation per day (LI, mm day^{-1}).

Biomass growth per individual: Growth in biomass per individual per day (Gi, g day^{-1}) was calculated as the product between Mstem (mg mm^{-1}) and LI (mm).

Biomass growth per area: Growth in biomass per area per day (Ga, g m^{-2} day^{-1}) was calculated as the product between bulkd (mg cm^{-3}) and LI (mm).

Decay rate: Litter mass loss per day (L, % per day) was expressed as the proportion of original mass lost from the *Sphagnum* litter.

2.4 | Modelling the mechanistic pathway for Sphagnum

It has been shown that generalized linear models fitted for each trait independently miss probabilistic relationships between traits (Clark, 2016) and a SEM of semimechanistic relationships can be built with multivariate data and general knowledge about correlations in traits and processes. We constructed the mechanistic pathway via a SEM approach that permits the specification of a network of relationships characteristic of complex systems (Grace, 2006). In

SEM, the standardized path coefficients that describe the statistical relationships among variables are similar to partial regression coefficients, and the absolute values of these coefficients can be ranked to compare their impact on an ecosystem process (Funk et al., 2017). We parameterized the model from the data exposed in the previous paragraph collected for 15 globally important *Sphagnum* species from different parts of the *Sphagnum* phylogenetic tree, and with different ecological preferences in terms of degree of shading and microtopography (Table 1). We defined the mechanistic model for a generic *Sphagnum* peat moss borrowing strength across species (Evans, Merow, Record, McMahon, & Enquist, 2016), that is, treating the species identity (categorical variable) as a random effect, given the high species-specificity in traits and processes which for some of them accounted for a large fraction of the total variation in the model (Bengtsson et al., 2016a). This approach is justified by the equal representation of all 15 species in the model. Including several species in the model also allowed for evaluation of how species identity affects trait variation. Different sources of trait data were harmonized in a single SEM, with the assumption of ignorable sampling design (Clark, 2016). This was possible as we analysed the response of many species, which reflected unmeasured axes of trait variation (Li, Ives, & Waller, 2017), obtaining a trait sampling response as it would have been obtained from different locations along the whole of environmental gradients (Clark, 2016; Evans et al., 2016).

Mosses form monolayers of individual shoots and traits can be viewed at the individual shoot scale or at the aggregated scale (Laing et al., 2014a; Rice et al., 2008). The latter can be referred to as canopy scale or area based and can have different properties compared to the sum of the individual shoots. Thus, to capture the complexities of mosses, we constructed separate models for both scales (individual shoot and area based). We modelled via Piecewise SEM (Lefcheck, 2016) the pathway of mechanistic relationships for *Sphagnum* describing how traits (a) respond to environmental gradients, (b) covary, and (c) scale to ecosystem processes. The ensemble of mechanistic pathways was generated on the ground of relationships tested experimentally either in the field or in the laboratory defining the following: (a) the direct response functions of *Sphagnum* ecosystem processes to environmental gradients (height of water-table, which identifies the species microtopographical position in the peatland, that is, hummock-hollow gradient; light availability, expressed by the degree of tree shading) (Hayward & Clymo, 1983; Laing et al., 2014a); (b) the response functions of architectural and physiological traits to environmental gradients (Laing et al., 2014a; Rydin & Jeglum, 2013); (c) the relationships between architectural and physiological traits via scaling equations (Bengtsson et al., 2018; Laing et al., 2014a; Rice et al., 2008); (d) the relationships between *Sphagnum* processes such as growth and decay (Bengtsson et al., 2016a). We acknowledge that many models are possible to fit but here we present interpretable models given our current knowledge of *Sphagnum* and functional trait scaling that fulfil the statistical requirement of independence between predictor and response. A few exploratory analyses were performed to test additional direct links between environmental variables and traits but they were removed as they had little statistical support.

TABLE 1 The 15 *Sphagnum* species object of modelling, with indication of their phylogeny (belonging to the four different subgenera), and their main affinity to microtopographical position (i.e., height above the water table) and habitat openness in the study regions explored in Laing et al. (2014a), Bengtsson et al. (2016a) and Bengtsson et al. (2018). The number of records (*N*) for each species (Tot) and for each combination of microtopography and openness are also reported. Nomenclature follows Flatberg (2013) but it should be noted that *S. magellanicum* found in Europe was recently split into two species (Hassel et al., 2018) and our data likely contain samples from both species

Sphagnum species	Subgenus	Author citation	Microtopography	Openness	N (tot = 671)
S. angustifolium	Cuspidata	(Russow) C.E.O. Jensen			Tot = 46
			Low Hummock	Open	40
			Hollow	Semi	3
			Hollow	Shaded	3
S. balticum	Cuspidata	(Russow) C.E.O. Jensen	Hollow (lawn)	Open	Tot = 39
S. capillifolium	Acutifolia	(Ehrh.) Hedw.	Hummock	Semi	Tot = 40
S. contortum	Subsecunda	Schultz	Hollow (lawn)	Open	Tot = 24
S. cuspidatum	Cuspidata	Hoffm.	Hollow (carpet-pool)	Open	Tot = 40
S. fallax	Cuspidata	(H.Klinggr.) H. Klinggr.	Hollow (lawn)	Open	Tot = 43
S. fuscum	Acutifolia	(Schimp.) H. Klinggr.			Tot = 73
			Hummock	Open	70
			Hummock	Semi	3
S. girgensohnii	Acutifolia	Russow	Hummock	Shaded	Tot = 36
S. lindbergii	Cuspidata	Lindb.	Hollow (carpet)	Open	Tot = 40
S. magellanicum	Sphagnum	Brid.			Tot = 111
			Hollow (lawn-carpet)	Open	40
			Hummock	Semi	43
			Hummock	Shaded	28
S. majus	Cuspidata	(Russow) C.E.O. Jensen	Hollow (carpet)	Open	Tot = 36
S. papillosum	Sphagnum	Lindb.	Hollow (carpet)	Open	Tot = 43
S. rubellum	Acutifolia	Wilson	Low hummock	Open	Tot = 40
S. tenellum	Cuspidata	(Brid.) Brid.	Hollow (lawn)	Open	Tot = 36
S. warnstorfii	Acutifolia	Russow	Low hummock	Open	Tot = 24

2.5 | Harmonizing the datasets

The model was built by making use of the field and laboratory measurements of environmental variables, traits, and emerging ecosystem processes from the two datasets presented above and analysed in Bengtsson et al. (2016a, 2016b), Bengtsson et al. (2018), Laing et al. (2014a) and Laing et al. (2014b) (Tables 1 and 2). Similar methodologies of measurement were applied in both datasets (see the specific paragraph). The full raw dataset is reported in the Supporting Information Appendix S1 (explanations and units in Table 2) while the standardized dataset in Supporting Information Appendix S2 (in Mazziotta, Granath, Rydin, Bengtsson, & Norberg, 2018) was used in the R code in Supporting Information Appendix S3 (data in Mazziotta et al., 2018) to build the Piecewise SEM.

Systematic differences occurred in the measurement of the same environmental gradients, traits, and ecosystem processes between the two datasets, reflecting measurements from different years (2009, 2012, and 2013) and differences in the locality. To remove the effect that these small differences could have in our model, species identity was treated as a normally distributed random variable for each SEM claim (see below). The effect of the trait variability among species was calculated as the difference between the variance explained by the conditional R^2 (cR^2, dependent both on the explanatory power of gradients and traits and on species identity) and the marginal R^2 (mR^2, dependent only on gradients and traits) ($\Delta R^2 = cR^2 - mR^2$). Finally, all the variables in the piecewise SEM were scaled between 0 and 1 to allow for comparison between magnitude and sign of the path coefficients.

2.6 | Statistical specifications of the Piecewise SEM

The mechanistic path analyses for *Sphagnum* peat mosses was identified by solving systems of linear equations via a Piecewise SEM technique (Lefcheck, 2016), where each equation *i* is a claim with the general structure:

$$y_i = \sum_{j=1}^{n} (\beta_j \times x_j) + \alpha_i + \zeta_i$$

TABLE 2 Definitions, abbreviations, and units for each environmental driver (blue in Figure 1), architectural (pink in Figure 1), and physiological (orange in Figure 1) traits, and ecosystem processes (in yellow in Figure 1) as reported in the text, appendices and in the individual-based and area-based *Sphagnum* SEMs. Specifications for each variable are reported in the text

Definition	Abbreviation	Units
Environmental drivers		
Degree of shading. Open (1), Semi-open (2), Shaded (3)	shade	-
Height above the water-table	HWT	mm
Interaction term between HWT and shade	shade_HWT	mm
Architectural traits		
Numerical density of capitula per unit area	n	cm^{-2}
Mass of capitulum (field sample, dry weight)	Mcap	mg
Mass of upper stem, length-specific (field sample, dry weight)	Mstem	$mg\ mm^{-1}$
Dry bulk density	Bulkd	$mg\ cm^{-3}$
Physiological traits		
Maximal net photosynthetic rate, individual basis	Npi	$mg\ CO_2 h^{-1}$
Maximal net photosynthetic rate, area basis	Npa	$mg\ CO_2\ h^{-1}\ cm^{-2}$
Litter N proportion	Nlit	% by mass
Litter metabolites	LM	% by mass
Ecosystem processes		
Length Increment (2009, 2012, 2013)	LI	$mm\ day^{-1}$
Growth in biomass per individual (2009, 2012, 2013)	Gi	$g\ day^{-1}$
Growth in biomass per area (2009, 2012, 2013)	Ga	$g\ m^{-2}\ day^{-1}$
Litter mass loss (14 months decay in the lab, data collected in 2012)	L	% by mass day^{-1}

In each equation (Tables 3 and 4), y_i corresponds to one of the architectural and physiological traits and emerging ecosystem processes that we want to characterize via a linear combination of *n* independent explanatory environmental drivers and/or traits (*x*). The error of prediction ζ_i for the response variable y_i is the marginal part of the model. ζ_i represents the unexplained (residual) variance in the claim and it is related with the square of the Pearson correlation coefficient for y_i ($R^2_{y_i}$) as follows:

$$\zeta_i = (1 - R^2_{y_i})^{1/2}$$

ζ_i represents the normally distributed random effect of species identity. The importance and the direction of the *j*th effect of *x* (x_j) on y_i are given respectively by the magnitude and size of the standardized path coefficients (β_j), which represent the conditional part of the model, while α_i is the intercept at *x* = 0 (reported in Tables 3 and 4).

The goodness-of-fit of the full piecewise SEM was evaluated in terms of the Shipley's test of direct separation. This procedure tests the assumption that all variables are conditionally independent, that is, there are no missing relationships among unconnected variables. The significance of any single independence claim, that is its *p*-value, can be estimated and extracted. The test of direct separation is

conducted by combining all *p*-values across the basis set in a test statistic, the Fisher's *C*.

$$C = -2 \sum_{i=1}^{k} \ln (p_i)$$

where p_i is the *i*th independence claim in a basis set consisting of *k* claims. *C* can then be compared to a chi-squared distribution with 2 *k* degrees of freedom. The hypothesized relationships are considered to be consistent with the data when there is weak support for the sum of the conditional independence claims, that is where the collection of such relationships represented by *C* could have easily occurred by chance, in which case *p* for the chi-squared test is greater than the chosen significance threshold (typically α = 0.05).

The full piecewise SEM path analysis (system of linear equations) includes the main categories of mechanistic relationship detailed in the paragraph *Modeling the Mechanistic Pathway for* Sphagnum. Each relationship derives from former field and laboratory experiments (Bengtsson et al., 2016a, 2018; Granath et al., 2012; Hayward & Clymo, 1983; Laing et al., 2014a; Rice et al., 2008). The categories of mechanistic relationships are represented in Figure 1a. Mechanistic relationships are analysed in the results and represented at individual and area basis in Figure 1b,c, with path coefficients and explained variances (R^2) for each linear equation reported in Tables 3 and 4.

TABLE 3 Individual-based mechanistic pathway predicting ecosystem properties for a general *Sphagnum* species from relevant architectural and physiological traits differentially affected by two main environmental gradients. Each of the five equations corresponds to one of the *n* trait and ecosystem properties (y) that we want to characterize via a linear combination of independent predictors (x). The importance and the direction of the significant effects of x on y are given respectively by the magnitude and sign of the standardized path coefficients, while the intercept (α) is estimated at $x = 0$. The proportion of variance in y explained by the linear combination of predictors is defined by R^2. Marginal R^2 refers to the pure effect of the predictors, while conditional R^2 accounts also for the variability among species, a random effect in the model. ΔR^2 ($cR^2 - mR^2$) is the increase in variance explained by interspecific variability. Equation parameters are estimated from values for 15 species of *Sphagnum* peat mosses. Refer to Table 2 for exact definitions of predictors and responses in the model. The significance levels of each path coefficient are reported in the superscript (NS = non-significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$)

Casual claim $y_i = \sum_j(\beta_j^* x_j) + \alpha_i + \zeta_i$	y_i	Predictor (x_j)							α_i	Marginal R^2	Conditional R^2	ΔR^2
		HWT	shade	shade_HWT	Mcap	Npi	Nlit	LM				
1	Mcap	−0.39**		0.33***					−0.07 (NS)	0.034	0.74	0.71
2	Npi				0.16 (p = 0.16)		0.48***	−0.28**	<0.01 (NS)	0.31	0.77	0.46
3	Gi	−0.19*	0.23**		0.34**	0.46***			0.44***	0.44	0.50	0.06
4	L		0.23**					−0.21**	−0.16 (NS)	0.16	0.74	0.58
5	Nlit		0.43***						−0.04 (NS)	0.19	0.29	0.10

TABLE 4 Area-based mechanistic pathway predicting ecosystem properties for a general *Sphagnum* species from relevant architectural and physiological traits differentially affected by two main environmental gradients. Legend like in Table 3

Casual claim $y_i = \sum_j(\beta_j^* x_j) + \alpha_i + \zeta_i$	y_i	Predictor (x_j)							α_i	Marginal R^2	Conditional R^2	ΔR^2
		HWT	shade	shade_HWT	n	Npa	Nlit	LM				
1	n	0.40**		−0.39***					0.03 (NS)	0.028	0.82	0.79
2	Npa				0.84***		0.37**	−0.28*	0.13 (NS)	0.38	0.7	0.32
3	Ga	−0.31**			−0.31*	0.53***			0.33**	0.38	0.43	0.05
4	L		0.23**					−0.21**	−0.16 (NS)	0.16	0.74	0.58
5	Nlit		0.43***						−0.04 (NS)	0.19	0.29	0.10

The portion of variance in traits and ecosystem processes explained, either directly or indirectly (via other traits) by the environmental gradients and trait covariation (arrows in Figure 1a), was estimated via partial regression coefficients calculated from the path coefficients in our SEM and contributing to the mR^2. The effect of species variability on traits, that is, how much more trait variability is accounted for when considering more species, was estimated in our model by the difference between cR^2 and mR^2 (ΔR^2 in Tables 3 and 4).

The R code (R Core Team, 2017) to define the system of linear equations and solve them via Piecewise SEM is described in Lefcheck (2016).

2.7 | Analysis of model sensitivity

In order to evaluate the effect that each of the 15 *Sphagnum* species had on the general *Sphagnum* model, we performed a sensitivity analysis via a leave-one-out procedure by sequentially removing each species from the full SEM and refitting it, estimating both the path coefficients and the explanatory power (R^2) of the 15 models with 14 species each. Then we compared the variability in path coefficients and R^2 of the 15 models with 14 species with the values for the full model (see Supporting Information Appendix S4).

2.8 | Model validation

We evaluated the predictive capacity of the *Sphagnum* SEMs by predicting architectural traits (capitulum density, mass of the capitulum)

and ecosystem processes (biomass growth) for an independent testing dataset for two species (*Sphagnum fuscum* and *S. magellanicum*). These came from two sampling sites in southern Sweden (i.e., Store Mosse and Traneröds Mosse) surveyed in 2013 and 2014 by two of us (F.B. and G.G.) (data in Supporting Information Appendix S5 in Mazziotta et al., 2018). We used a Generalized Linear Model (with gamma distribution for the response variables and log-link functions) to compare measured means and ranges of variation for traits and processes for the testing dataset with the SEM predictions. Predicted values and uncertainty were obtained by the SEM estimates from the test dataset overall and drawn separately for the two species from the average response (measures and predictions are reported in Figure 3).

3 | RESULTS

3.1 | The Sphagnum mechanistic pathway

We examined the role of species identity (trait variability among species), environmental gradients, and trait covariation (trait trade-offs) in explaining the variability of architectural and physiological traits, as well as the main ecosystem processes in which they emerge for a general *Sphagnum* species (Figure 1a). The full models for the *Sphagnum* mechanistic pathways (Tables 3 and 4, Figure 1b,c) reproduced the data well based on a comparison of the Fisher's C statistic to a chi-squared distribution (for the individual-based model: $C = 45.29$, $df = 38$, $p = 0.19$; for the area-based model for biomass growth: $C = 21.13$, $df = 38$, $p = 0.99$). We found a large variability
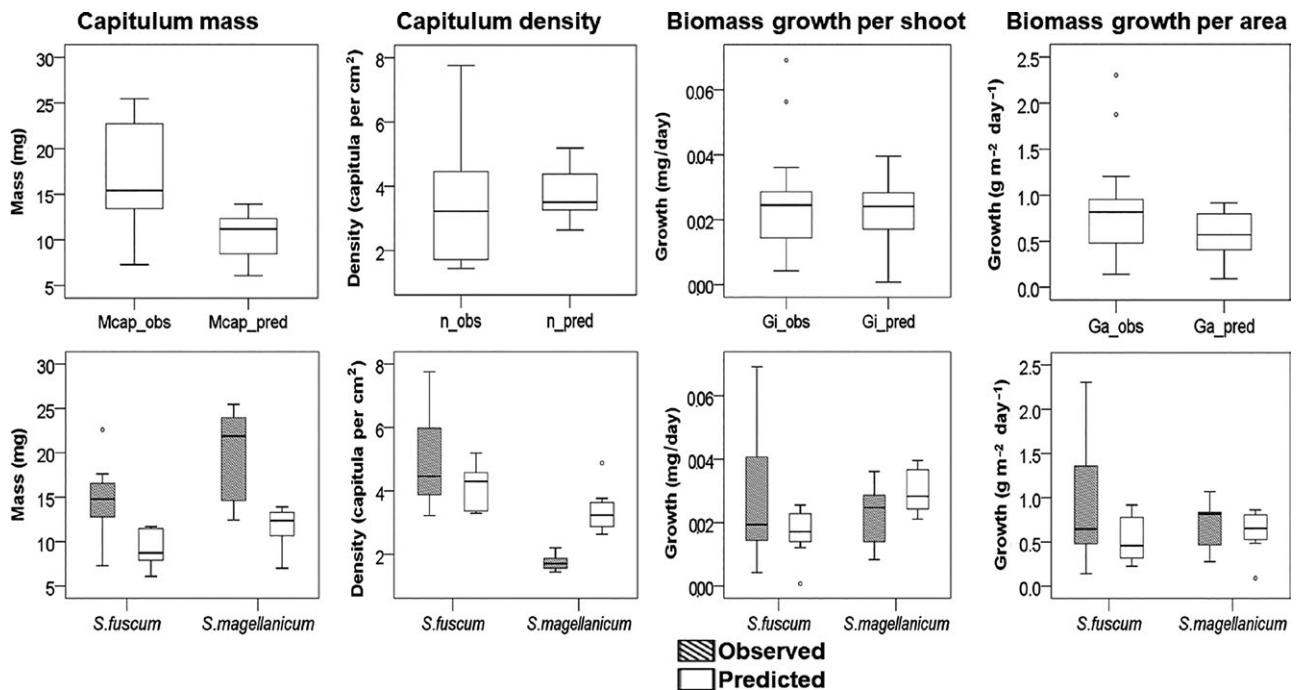

FIGURE 3 Model validation. Evaluation of the Sphagnum SEM model by comparing the medians (dark lines in the middle of the boxes) and ranges of variation (box: interquartile ranges, whiskers: 95% conf. intervals, points: outliers) measured for traits and processes for the Bengtsson–Granath test dataset (X_obs) with the medians and ranges predicted by the SEM model (X_pred). Results are shown for the total dataset and separately for the two species in the testing dataset (i.e., *Sphagnum fuscum* and *S. magellanicum*)

in how well architectural and physiological traits were explained, and characterized by a combination of environmental gradients and other functional traits. In Tables 3 and 4, marginal R^2 (mR^2) refers to the pure effect of the predictors, while conditional R^2 (cR^2) accounts also for the variability among species, a random effect in the model. The explanatory power (mR^2) of the environmental gradients and traits was the lowest for capitulum mass in the individual-based model (Mcap in Table 3) and for capitulum density in the area-based model (n in Table 4). Litter mass loss (L) and litter nitrogen (Nlit) were also comparatively poorly predicted, with low mR^2 (Tables 3 and 4). Net photosynthetic rate (Npi and Npa) and growth in biomass (Gi and Ga) were well predicted by a combination of environmental gradients and individual- and area-based traits with relatively high mR^2 values (Tables 3 and 4).

3.2 | Species effects on trait and process variability

The predictive power (in terms of variance explained, R^2) of our SEM mechanistic pathways for individual- and area-based traits and ecosystem processes dramatically increased by accounting for the identity of species as a random factor, especially for those traits and processes that showed a large interspecific variability. Increase in variance ($\Delta R^2 = cR^2 - mR^2$) explained by interspecific variability ranged between 0.05 and 0.79 (Tables 3 and 4). Interspecies variability had a large role in explaining much of the variability in capitulum density (n), mass of the capitulum (Mcap), net photosynthetic rate (Npi and Npa), and decay rate (L) (see ΔR^2 in Tables 3 and 4). Other traits and processes were more constant among species, with little improvement in the variance explained when accounting for species variability in nitrogen in the litter (Nlit) and biomass growth (Gi and Ga) (see ΔR^2 in Tables 3 and 4).

3.3 | Effects of environmental gradients on trait and process variability

In our *Sphagnum* model, environmental gradients showed a direct but opposite effect on the mass of the capitulum (Mcap) in the individual-based model compared to capitulum density (n) in the area-based model (Figure 1b,c; Tables 3 and 4). Specifically, while an increase in the height above the water-table (HWT) reduced Mcap and increased n, it had an opposite effect in shaded habitat (HWT × Shade interaction). An increase in HWT also had a weak effect in reducing the growth in biomass per individual (Gi) and per area (Ga) (Tables 3 and 4; Figure 1b,c). Shading positively affected mass loss (L) and nitrogen levels in the litter (Nlit) (Tables 3 and 4; Figure 1b,c).

However, HWT and shading showed also indirect effects on other traits and processes via their effects on Mcap, n, and Nlit (Figure 1b,c). Given the direct positive effect of these three *Sphagnum* traits on the net photosynthetic rate, the indirect effects of the environmental gradients on the net photosynthetic rate were similar, but of lower magnitude, to the effects that environmental gradients had on these three traits from which photosynthesis depends

on (Figure 1b,c). Specifically, a higher HWT positively affected the photosynthetic rate per area (mediating by n: r (HWT-Npa) = 0.34) but not per individual (mediating by Mcap: r (HWT-Npi) = −0.062). A higher level of shading weakly positively affected the photosynthetic rate per individual (mediating by Nlit: r (shade-Npi) = 0.21) and per area (mediating by Nlit: r (shade-Npa) = 0.16). An increase in HWT in shaded habitats weakly positively affected Gi and Ga via its effect on the corresponding architectural traits (mediating by Mcap: r (shade_HWT-Gi) = 0.11; mediating by n: r (shade_HWT-Ga) = 0.12).

3.4 | Effects of trait covariation on trait and process variability

Mcap and n were the architectural traits that directly mediated the effects of environmental drivers on the photosynthetic activity, which resulted in biomass growth. At individual level, the indirect effect of Mcap on Gi was weaker considering its photosynthetic activity (mediating by Npi: r (Mcap-Gi) = 0.074) than just its direct mass effect (r (Mcap-Gi) = 0.34). On the other hand, at area level while the direct effect of n on Ga was negative (r (n-Ga) = −0.31) the effect was positive when considering its effect on photosynthetic activity (mediating by Npa: r (n-Ga) = 0.45).

An evaluation of the net effect of Mcap and n on biomass growth was conducted by summing from the path coefficient directly linking them the product of the path coefficients indirectly connecting them via net photosynthetic rate. Mcap had a net positive effect on biomass growth (net effect: 0.34 + (0.16 × 0.46) = 0.41) (Tables 3 and 4; Figure 1b,c). On the other hand, the effect of n on biomass growth was positive but weak (net effect: −0.31 + (0.84 × 0.53) = 0.14) (Tables 3 and 4; Figure 1b,c).

An increase in litter metabolites (LM) weakly negatively affected both biomass growth and decay rate (L). Gi and Ga were indirectly negatively affected by LM via the weak negative effect of LM on net photosynthetic rate (mediating by Npi: r (LM-Gi) = −0.13; mediating by Npa: r (LM-Ga) = −0.15). In both the individual- and area-based models, L was directly weakly negatively regulated by LM (Tables 3 and 4; Figure 1b,c).

3.5 | Model sensitivity analysis

We found that the sequential removal of the majority of the species from the model did not significantly alter the structure of the model itself in terms of path coefficients. The interquartile range of the differences between the path coefficients estimated for the full model and the coefficients of the n-1 species models (excluding the intercepts) ranged between −12.6% and +10.8% for the individual-based model and between −9.4% and +9.5% for the area-based model (Supporting Information Appendix S4). This agreement means that the all-species model well captured the norm of the responses of architectural and physiological traits to environmental gradients and the scaling effect of traits to ecosystem processes.

With respect to the model with all the species, the removal of species dramatically reduced the predictive power for some traits

and processes (Supporting Information Appendix S4). In particular, for architectural and physiological functional traits, the difference between the cR^2 of the full model and the cR^2 of the n-1 species models was moderate both at individual and area levels: for the individual-based model, ΔMcap = (−8.0%, 4.2%), ΔNpi = (−13.1%, 2.3%); for the area-based model, Δn = (−12.8%, 5.6%), ΔNpa = (−25.9%, −1.7%). In both models the difference was also low for litter mass loss (ΔL = (−15.9%, 7.6%)). On the other hand, the difference was dramatically high for litter nitrogen (ΔNlit = (−19.4%, 33.5%)) and biomass growth (the % ranges of differences with the full model were ΔGi = (−20.5%, 27.5%), ΔGa = (−52.4%, 45.8%) respectively). In other words, the removal of each species did not significantly alter the predictive power for architectural traits and photosynthesis and litter decay, while it varied the predictive power for litter nitrogen and biomass growth.

3.6 | Model validation

The individual- and area-based models accounting for species variability were successful in predicting the variability in traits and processes for an independent dataset of two *Sphagnum* species (*S. fuscum* and *S. magellanicum*). We found no significant difference for the capitulum density between the mean values observed in the dataset and the mean values predicted by our model (GLM results: Likelihood Ratio chi-squared (n) = 0.37, df = 1, p = 0.54, $n_{obs.}$ = 3.46 capitula cm^{-2}, $n_{pred.}$ = 3.78 capitula cm^{-2}) (Figure 3). There were also no differences between observed and predicted mean values of biomass growth per individual (χ^2 (Gi) = 0.19, df = 1, p = 0.66, $Gi_{obs.}$ = 2.55×10^{-5} g day^{-1}, $Gi_{pred.}$ = 2.33×10^{-5} g day^{-1}) and per area (χ^2 (Ga) = 3.63, df = 1, p = 0.057, $Ga_{obs.}$ = 0.85 g m^{-2} day^{-1}, $Ga_{pred.}$ = 0.57 g m^{-2} day^{-1}) (Figure 3). Instead we found that our model predicted significantly lower mean values of capitulum mass compared with the test dataset (GLM results: Likelihood Ratio χ^2 (Mcap) = 19.38, df = 1, p < 0.001, $Mcap_{obs.}$ = 17.31 mg, $Mcap_{pred.}$ = 10.47 mg) (Figure 3).

Capitulum density (n) and biomass growth per area (Ga) were well predicted only for one of the two species. Capitulum density was well predicted for *S. fuscum* (for n: mean predicted values nondifferent from observed at p = 0.068, $n_{obs.}$ = 4.95 capitula cm^{-2}, $n_{pred.}$ = 4.12 capitula cm^{-2}), but not for *S. magellanicum* (for n: at p < 0.001, $n_{obs.}$ = 1.75 capitula cm^{-2}, $n_{pred.}$ = 3.40 capitula cm^{-2}) (Figure 3). Mean biomass growth per area was well predicted for *S. magellanicum* (for Ga: at p = 0.49, $Ga_{obs.}$ = 0.75 g m^{-2} day^{-1}, $Ga_{pred.}$ = 0.61 g m^{-2} day^{-1}), but not for *S. fuscum* (for Ga: at p = 0.036, $Ga_{obs.}$ = 0.97 g m^{-2} day^{-1}, $Ga_{pred.}$ = 0.53 g m^{-2} day^{-1}) (Figure 3).

On the other hand, the GLM returned good predictions for individual-based biomass growth for both species (Figure 3): for *S. fuscum* (for Gi: mean predicted values nondifferent from those observed at p = 0.061, $Gi_{obs.}$ = 2.89×10^{-5} g day^{-1}, $Gi_{pred.}$ = 1.68×10^{-5} g day^{-1}) and for *S. magellanicum* (for Gi: at p = 0.24, $Gi_{obs.}$ = 2.24×10^{-5} g day^{-1}, $Gi_{pred.}$ = 2.98×10^{-5} g day^{-1}). Finally, the predicted mean mass values of the capitulum were not congruent with the measured values at p < 0.001 for both the species: respectively, for *S. fuscum*

mean $Mcap_{obs.}$ = 14.77 mg, $Mcap_{pred.}$ = 9.24 mg, and for *S. magellanicum* $Mcap_{obs.}$ = 19.85 mg, $Mcap_{pred.}$ = 11.69 mg).

4 | DISCUSSION

4.1 | Sources of variation in traits and processes

We parameterized a process-based model estimating growth and decay in *Sphagnum* peat mosses by linking data on environmental drivers and architectural and functional traits (Evans et al., 2016). Our SEM approach explained with large variability ($0.29 \leq cR^2 \leq 0.82$) the variation in traits and processes in *Sphagnum* peat mosses. Our process-based analysis successfully quantified the variation in traits and processes that comes from: (a) trait syndromes (the inherent tendency for certain traits to be associated with others), (b) interspecific diversity, and (c) environmental variation that affects both species and trait diversity (Clark, 2016). In *Sphagnum*, trait and process variability were mainly explained by trait syndromes (mR^2 explained by trait covariation considering also indirect significant effects ranging between 0.22 and 0.45), while microenvironmental variation had a limited role in explaining traits and processes ($mR^2 \leq 0.19$) (Supporting Information Appendix S6). Interspecific variability (ΔR^2) in traits and processes explained by microenvironmental variation was always higher (0.1–0.79) than the corresponding variation explained by trait syndromes (0–0.46) (Supporting Information Appendix S6). We found that trait syndromes explained variability in physiological traits and processes better than microenvironment, while microenvironment explained variability in traits and processes better than interspecific variability. In other words, while there was a large interspecific variation in the response of architectural traits to microenvironmental gradients, the response of physiological traits and processes was more univocally determined by a fixed mechanistic pathway with a limited variation among species. This is in agreement with Clark's (2016) finding that although trait syndromes dominate variation in some traits, others are strongly controlled by variation in species diversity (Evans et al., 2016). In the genus *Sphagnum*, the strong weight of interspecific variability is explained by a complementarity effect in the capacity of each species to increase or reduce the explained variance in the model.

There was congruence between some trait trade-offs found by Wright et al. (2004) for vascular plants at mass level and the trade-offs we found for *Sphagnum*. Wright *et al.* found for vascular plants that leaf N concentration (N_{mass}) was positively correlated on a log-scale with photosynthetic assimilation rate (A_{mass}) (r^2($N_{mass} - A_{mass}$) = 0.53, at p << 0.0001). In the corresponding individual-level model for *Sphagnum* we also found that litter N (Nlit) had a direct positive effect (0.43) on individual net photosynthetic rate (Npi).

On area basis, Wright *et al.* found for vascular plants that N_{area} was weakly positively correlated with A_{area} (r^2($N_{area} - A_{area}$) = 0.13). In the corresponding area-based model for *Sphagnum* we found a positive effect of Nlit on Npa (0.37). To summarize, both in vascular plants and in *Sphagnum*, higher nitrogen concentration increases photosynthesis.

Like for vascular plants, the functional traits in the *Sphagnum* economic spectrum are linked into an integrated phenotypic network ruled by physiological and mechanical constraints. They extend beyond the branches of the capitulum to include litter metabolites, a trait phylogenetically preserved at the subgenus level (Bengtsson et al., 2018), reflecting trade-offs in resource acquisition and conservation (Messier et al., 2017). Thus, the effects we observed of environmental gradients and trait trade-offs on trait variability support the hypothesis by Reich (2014) for vascular plants, namely that the degree of environmental stability determines the species ecological strategies by regulating the speed of functional traits and ecosystem processes.

4.2 | Variability in scaling traits to ecosystem processes

We observed a high species-specificity in the predictive power of our mechanistic pathways for architectural and physiological traits and decomposition, but less so for biomass growth (Robroek et al., 2017). Such high interspecific variability in traits is not unique to *Sphagnum* (cf., Michel et al., 2012; Clark, 2016) and may indicate that species of *Sphagnum* are distributed along several environmental gradients. However, in our study, the main environmental drivers (height above the water-table and shade) did not explain a large proportion of this interspecific variation, suggesting that both the environment and intrinsic species effects drive variation in *Sphagnum*'s resource allocation to photosynthesis, metabolites, morphological, and canopy structure in ways that influence their physiological functions (Rice et al., 2008; Rydin & Jeglum, 2013). Specifically, traits were highly variable and species-specific, including decomposition for which variability depended on the phylogenetically distinct litter metabolites, while biomass growth and nitrogen content were well predicted by environmental gradients and functional traits. For example, *Sphagnum* species showed interspecific variation in the distribution of mass in the capitulum and in its density, which also reflected the observed interspecific differences in the photosynthetic rate (Laing et al., 2014a).

In our model, *Sphagnum* species growing on hummocks, that is, at a higher distance from the water table, were characterized by a high density of capitula. This represents the typical situation for many (but not all) species of the subgenus Acutifolia that, in contrast to hollow-dwelling Cuspidata species, form densely packed small capitula. This together with their close-set leaves forming small-interconnected capillary spaces enables them to maintain a high and stable capitulum water content even when the water-table falls far below the surface. In contrast, the normally short distance between the moss surface and the water-table for hollow species gives large capitulum with high water content at lower density (dense and tiny *S. tenellum* being an exception), even though these species may not have an efficient capillarity (Rydin & Jeglum, 2013). However, Acutifolia species living under high tree cover (i.e., *S. girgensohnii*) experience reduced surface evaporation (Waddington et al., 2015) and can conversely maintain large

capitula with high water content at a lower density compared to other Acutifolia species in open bogs. The normally low capitulum density in Cuspidata species was also further reduced in the case of *S. angustifolium*, the sole Cuspidata species living in shaded conditions on low hummocks (Table 1; Figure 1b).

Investment in capillarity for maintaining capitulum water content explains the lower capitulum mass for hummock compared to the hollow species and, subsequently, the lower biomass growth on hummocks due to a limited metabolic rate. As a result and supported by previous research (Laine, Juurola, Hájek, & Tuittila, 2011), net photosynthesis per area was the lowest for characteristic hummock species such as *Sphagnum fuscum*, *S. rubellum*, and *S. warnstorfii*. This suggests a trade-off in *Sphagnum* similar to the one observed in vascular plants (Messier et al., 2017) between slow turnover species, characterized by high resource conservation, and fast turnover species, characterized by high resource acquisition. High canopy cover (i.e., shading and less surface evaporation: Waddington et al., 2015), in the habitats of the bog margins and swamp forest, reduces the need for high capitulum density, increasing the size of the capitula and consequently the photosynthetic rate for certain species on hummocks (i.e., *S. girgensohnii*; Bengtsson et al., 2016a; Hájek, Tuittila, Ilomets, & Laiho, 2009; Rydin & Jeglum, 2013). This likely explains why the negative effect of a high height above the water-table on biomass growth and mass loss was mainly present in open habitats. In addition, photoinhibition has been proven to occur in *Sphagnum* under high light conditions (Hájek et al., 2009; Marschall & Proctor, 2004; Murray, Tenhunen, & Nowak, 1993), which may limit biomass growth during the season but not affect maximum net photosynthesis.

4.3 | Effects of trait covariation in ecosystem processes

Capitulum size is driving *Sphagnum* metabolism and is a function of shoot density due to intraspecific competition for finite resources. Thus, the capitulum plays an important role in determining the pace of *Sphagnum* metabolic processes, regulating them through architectural and physiological traits and their trade-offs. The negative relationship between capitulum density and biomass points out that the number of capitula that can be supported in a given area is related to the rate of supply of limiting resources (water and carbon), and the rate at which each individual capitulum uses those resources (Laing et al., 2014a) and allocates them to the stem. In other words, larger capitula allocate fewer resources to the stem section than smaller capitula.

The positive relationship between the density of the capitula and photosynthesis is stronger compared to the relationship between capitulum mass and photosynthesis. In fact, Sphagna with high capitulum density tend to have resource acquisition via high photosynthesis (Figure 2). On the other hand, Sphagna with low capitulum density allocate resources to larger capitula that can assimilate more carbon (Bengtsson et al., 2016a). A high photosynthetic rate ultimately promotes biomass growth (Bengtsson et al., 2016a)

while decomposition is explained by the identity of *Sphagnum* metabolites which is phylogenetically conserved within each subgenus (Bengtsson et al., 2018). The positive scaling of mass from the capitulum to shoot growth via photosynthetic activity is in agreement with the general notion that plant productivity depends on the amount of solar radiation absorbed by the leaves (Reich, 2012).

The *Sphagnum* production of recalcitrant metabolites in the litter (i.e., sphagnan, soluble phenolics, and lignin-like phenolics, Bengtsson et al., 2018; Johnson & Damman, 1991, 1993) limits *Sphagnum* growth by decreasing photosynthesis (i.e., less nutrients allocated to photosynthesis) and decomposition (slow decay rate means less nutrients released) (Coulson & Butterfield, 1978). Slow decomposition will result in long-term peat accumulation, creating an unfavourable habitat for other plants and contribute to the role of *Sphagnum* as ecosystem engineer (Van Breemen, 1995). Our results suggest a cost of producing metabolites that negatively affects growth and gives further insight on the mechanisms behind the trade-off between growth and decay in peatlands (Bengtsson et al., 2016a; Turetsky, Crow, Evans, Vitt, & Wieder, 2008). However, this trade-off appears weak and complex (Bengtsson et al., 2016a) and other factors, such as tissue structure that determines water retention and conductivity, can play an important role but remain to be investigated.

In synthesis, our findings provide insights into how to generalize the models already available for vascular plants to bryophytes defining ecosystem processes as an outcome of architectural and physiological traits (Suding et al., 2008), contributing to build a unified theoretical approach generating individual fitness, canopy dynamics, and ecosystem processes from trait variation (Falster et al., 2011).

4.4 | The fast-slow economic spectrum in Sphagnum

The pathway exposed in this study offers compelling evidence that the investigated species of peat mosses exhibit a trade-off similar to the one observed in vascular plants (Messier et al., 2017), between a slow turnover strategy, characterized by high resource conservation, and a fast turnover strategy, characterized by high resource acquisition (Reich, 2014). Independently of scale, individual shoot, or canopy, we identified in *Sphagnum* species a continuum of ecological strategies between two extremes in resource (nutrient) turnover (Grime, 2001). We can refer to the bog hollows as "unstable" as they are characterized by fluctuating water content in the capitula (i.e., the photosynthetically active tissue) over the season. Hollow species (like *S. cuspidatum* living in carpets and pools) avoid this stress via resource acquisition, showing trade-offs between low values for architectural traits (low capitulum density) and "fast" (high values, sensu Reich, 2014) physiological traits (high photosynthetic rate) and processes (biomass growth) (Figure 2). A low capitulum density leads to deeper light penetration, which favours photosynthesis while at the same time leads to lower capillarity. The water-table in the hollows may vary from flooding to >20 cm below the surface. As the water-table drops the capitula will dry out, hence the large fluctuation in water content. In the hummock, the water-table may be

20–50 cm below the surface. The hummock species (like *S. fuscum*) can maintain a more stable water content by adapting their morphology and capitulum density (Rydin, 1985), leading to resource conservation via fast architectural traits (high capitulum density), but slower photosynthesis and growth (Figure 2) (Bengtsson et al., 2016a; Gunnarsson, 2005; Luken, 1985; Turetsky et al., 2008). For species at intermediate microtopography, like *S. papillosum* (subgenus *Sphagnum*), the rate of processes is intermediate (Figure 2). Other environmental gradients, like shading, could be more important than microtopography in determining the rate of mass loss. For example, *S. girgensohnii* can grow high above the water-table as can other Acutifolia species, but in contrast to the other species, it is a species with a high metabolic rate (Bengtsson et al., 2016a). This different strategy can be explained by the low light conditions in forests where this species is thriving.

4.5 | Implications for global change scenarios

Our area-based SEM can be a valid tool to model the response of ecosystem processes to climate change in *Sphagnum* communities at a local scale. This is possible by identifying the correlations between macroclimatic gradients and microenvironmental drivers and the mechanistic links between microenvironmental drivers, traits, and processes. On a large geographic scale, *Sphagnum* growth and decay depend on macroclimatic gradients, where mean annual temperature in combination with precipitation can increase growth and peat accumulation (Gerdol, 1995; Gunnarsson, 2005; Wang, Zhuang, Yu, Bridgham, & Keller, 2016). The microenvironmental drivers examined in the present study (i.e., water level and shading) mediate the effect of macroclimate on *Sphagnum* processes on a local scale. There are experiments that indicate that warming may indirectly promote *Sphagnum* growth by increasing the growth of dwarf shrubs in the bog-fen complex, which promote *Sphagnum* growth via a shading effect cooling the peat surface (Walker, Ward, Ostle, & Bardgett, 2015). Indeed, we found that growth and mass loss would be higher in shaded conditions. Higher precipitation increases *Sphagnum* growth by reducing the distance between the peat moss surface and the water-table (Gerdol, 1995). This supports the experimental evidence (Belyea, 1996; Clymo, 1965; Hayward & Clymo, 1983) that high distance of the moss surface from the water-table reduces growth and decomposition by maintaining anoxic conditions in the peat profile, ultimately supporting peat accumulation. On the other hand, an increase in temperatures associated with drought promotes aerobic decay reducing the *Sphagnum* growth, in this way limiting carbon accumulation (Bragazza et al., 2016).

To summarize, a climate scenario based only on increasing mean annual temperatures is expected to generally increase *Sphagnum* growth and mass loss. However, this pattern may vary because of regional changes in the precipitation regime directly affecting the depth of the water-table in the peatland through differences in annual water deficit (Granath, Moore, Lukenbach, & Waddington, 2016). Water deficit induced by climate change may be more important than temperature for defining *Sphagnum* response at the two

ends of its economic spectrum (Granath et al., 2016). For example, models predict greater (maximum) annual water deficits (i.e., less water available) for northern Europe by 2050, which could lower the water-table by roughly 10 cm compared to 1981–2000. Such a lowering of the water-table has minor direct changes in our model, indicating the high resistance of boreal peatlands to climate change (Robroek et al., 2017; Waddington et al., 2015). By the end of the century (2071–2100) the downscaled IPCC scenarios for Sweden confirm a consistent increase in temperatures (average T increase respect to the period 1961–1990, interval depending on the climate scenario: winter +2 ...+7°C; summer +1 ...+4°C) and precipitation (average P increase: winter +30 ... +50 mm per month; summer −30 ... +40 mm per month) across Sweden (Utredningar, 2007). This joint increase is expected to enhance *Sphagnum* growth directly or indirectly because of the decrease in the depth to the water-table. However, in the southern part of the country the climatic scenarios show a reduction in the precipitations over summer (Utredningar, 2007), which could have a negative effect on *Sphagnum* growth and positive effect on decomposition by increasing the depth to the water-table.

Additionally, eutrophication by increasing the deposition of nitrogen in the peat layer is expected to alter the response of the *Sphagnum* processes to climate change (Granath, Limpens, Posch, Mücher, & Vries, 2014; Limpens et al., 2011). While we found that high nitrogen in the litter per se is expected to increase photosynthetic rate and hence *Sphagnum* growth, N deposition in combination with high temperatures seems to affect *Sphagnum* performance negatively, both directly (physiological effects) and indirectly, by stimulating shrub and tree growth and thereby out-competing *Sphagnum*. These effects joint with higher decomposition under higher temperatures and drought may ultimately cause peat carbon loss (Bragazza et al., 2016, 2006). Effectively, in southern Sweden, chronosequence data (from 1996 to 2012) (Hedwall et al., 2017) suggested that the accumulation of nitrogen deposition across decades has overruled climate change by increasing woody vegetation at the expense of the cover in *Sphagnum* mosses, hence limiting the peatland potential of peat accumulation. While nitrogen deposition may have been a major driver of vegetation change in southern Sweden, increasing temperatures have likely been the cause of an increase in *Sphagnum* cover in the north (Hedwall et al., 2017).

4.6 | Future model improvements

The agreement between the modelled mechanistic pathway and the data at hand justified the use of Structural Equation Models to describe how functional traits in *Sphagnum* emerge into ecosystem processes in peat bogs, confirming the importance that Funk et al. (2017) give to this technique when analysing the impact of traits across scales.

Intraspecific trait variability is the capacity of a species to respond to variations in environmental factors via two complementary mechanisms (Albert et al., 2010): (a) genetic variability and (b) phenotypic plasticity. This dimension of trait variability was somewhat

accounted for in our model by multiple measurements of the same trait and process for each species (Albert et al., 2010; Schliep, Gelfand, Mitchell, Aiello-Lammens, & Silander, 2018). However, it must be considered that the species-rich *Sphagnum* assemblage under study is likely to limit the contribution of intraspecific over interspecific trait variability in explaining ecosystem processes (Siefert et al., 2015).

Given its limited spatial resolution (site level), our model misses feedback regarding ecosystem processes on species occurrence and abundance (Evans et al., 2016). However, at this stage, the aim of our model was more to describe the mechanistic pathway scaling functional traits to ecosystem processes rather than predict species distribution ranges. Given its limited time resolution, our model misses feedback of ecosystem processes on the peat environment via response traits (Waddington et al., 2015). In fact, the model describes the relationships between environmental gradients, *Sphagnum* functional traits and ecosystem processes on a short time-scale. However, ecosystem processes may affect environmental gradients within a larger time frame and their effect involves other groups of species besides the community of *Sphagnum* species. For example, peat accumulation, and the consequent stability of bog microforms, is the result of the interactions between the decomposition process in the *Sphagnum* community and in other communities of vascular plants with the bog environment. Furthermore, across long periods (years, decades) peat accumulation has a stabilizing effect on the depth of water level in the peatland (Eppinga, Rietkerk, Wassen, & Ruiter, 2009; Waddington et al., 2015).

Our model does not capture changes in trait values due to evolutionary changes. Although many ecosystem and regional models have adopted the concept of plant functional types (PFTs: groupings of plant species sharing similar characteristics and roles in ecosystem function), recent work suggests that parameterization of PFTs with current trait values may not be valid under future environmental conditions because trait values and trait–trait relationships may change (Van Bodegom et al., 2012). In this regard, our model has limitations if employed in other environmental scenarios. To overcome these limitations, we will benefit from population genomics programs—like the Sphagnome Project—where population genetics, genomics, and phenotype analysis can be used to statistically model genome features to trait value predictions that can be entered as parameters in our SEM (Weston et al., 2018).

AUTHORS' CONTRIBUTIONS

A.M., G.G., H.R., and J.N. conceived the study and developed the model framework; F.B. and G.G. collected the data and A.M. performed the

analyses; F.B., G.G., H.R., and J.N. contributed to the editing of the manuscript; A.M. led the writing and editing of the manuscript.

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REFERENCES

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: Extent, structure and sources of variation. *Journal of Ecology*, *98*, 604–613. https://doi.org/10.1111/j.1365-2745.2010.01651.x

Bacon, K. L., Baird, A. J., Blundell, A., Bourgault, M.-A., Chapman, P. J., Dargie, G., … Young, D. M. (2017). Questioning ten common assumptions about peatlands. *Mires and Peat*, *19*, 1–23.

Belyea, L. R. (1996). Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, *77*, 529–539. https://doi.org/10.2307/3545942

Bengtsson, F., Granath, G., & Rydin, H. (2016a). Photosynthesis, growth, and decay traits in Sphagnum – A multispecies comparison. *Ecology and Evolution*, *6*, 3325–3341. https://doi.org/10.5061/dryad.62054

Bengtsson, F., Granath, G., & Rydin, H. (2016b). Data from: Photosynthesis, growth, and decay traits in Sphagnum - a multispecies comparison. *Ecology and Evolution*. https://doi.org/10.5061/dryad.62054

Bengtsson, F., Rydin, H., & Hájek, T. (2018). Biochemical determinants of litter quality in 15 species of *Sphagnum*. *Plant and Soil*, *425*, 161–176. https://doi.org/10.1007/s11104-018-3579-8

Bragazza, L., Buttler, A., Robroek, B. J., Albrecht, R., Zaccone, C., Jassey, V. E., & Signarbieux, C. (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, *22*, 4114–4123. https://doi.org/10.1111/gcb.13319

Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., … Toberman, H. (2006). Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 19386–19389. https://doi.org/10.1073/pnas.0606629104

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Charman, D. J., Blundell, A., Chiverrell, R. C., Hendon, D., & Langdon, P. G. (2006). Compilation of non-annually resolved Holocene proxy climate records: Stacked Holocene peatland palaeo-water table reconstructions from northern Britain. *Quaternary Science Reviews*, *25*, 336–350. https://doi.org/10.1016/j.quascirev.2005.05.005

Clark, J. S. (2016). Why species tell more about traits than traits about species: Predictive analysis. *Ecology*, *97*, 1979–1993. https://doi.org/10.1002/ecy.1453

Clymo, R. S. (1965). Experiments on breakdown of *Sphagnum* in two bogs. *Journal of Ecology*, *53*, 747–758. https://doi.org/10.2307/2257633

Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N. A., & During, H. J. (2007). Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, *99*, 987–1001. https://doi.org/10.1093/aob/mcm030

Coulson, J. C., & Butterfield, J. (1978). An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *Journal of Ecology*, *66*, 631–650. https://doi.org/10.2307/2259155

Demetrius, L. (2006). The origin of allometric scaling laws in biology. *Journal of Theoretical Biology*, *243*, 455–467. https://doi.org/10.1016/j.jtbi.2006.05.031

Díaz, S., Cabido, M., & Casanoves, F. (1999). Functional implications of trait–environment linkages in plant communities. In E. Weiher, & P. Keddy (Eds.), *Ecological assembly rules – Perspectives, advances, retreats* (pp. 338–362). Cambridge, UK: Cambridge University Press.

Dorrepaal, E., Toet, S., van Logtestijn, R. S., Swart, E., van de Weg, M. J., Callaghan, T. V., & Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, *460*, 616–619. https://doi.org/10.1038/nature08216

Eppinga, M. B., Rietkerk, M., Wassen, M. J., & De Ruiter, P. C. (2009). Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecology*, *200*, 53–68. https://doi.org/10.1007/s11258-007-9309-6

Evans, M. E., Merow, C., Record, S., McMahon, S. M., & Enquist, B. J. (2016). Towards process-based range modeling of many species. *Trends in Ecology & Evolution*, *31*, 860–871. https://doi.org/10.1016/j.tree.2016.08.005

Falster, D. S., Brännström, Å., Dieckmann, U., & Westoby, M. (2011). Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: A theoretical investigation. *Journal of Ecology*, *99*, 148–164. https://doi.org/10.1111/j.1365-2745.2010.01735.x

Fenner, N., & Freeman, C. (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, *4*, 895–900. https://doi.org/10.1038/ngeo1323

Flatberg, K. I. (2013). *Norges torvmoser*. Oslo: Akademika.

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., … Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, *92*, 1156–1173. https://doi.org/10.1111/brv.12275

Gerdol, R. (1995). The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures. *Journal of Ecology*, *83*, 431–437. https://doi.org/10.2307/2261596

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge, UK: Cambridge University Press.

Granath, G., Limpens, J., Posch, M., Mücher, S., & De Vries, W. (2014). Spatio-temporal trends of nitrogen deposition and climate effects on *Sphagnum* productivity in European peatlands. *Environmental Pollution*, *187*, 73–80. https://doi.org/10.1016/j.envpol.2013.12.023

Granath, G., Moore, P. A., Lukenbach, M. C., & Waddington, J. M. (2016). Mitigating wildfire carbon loss in managed northern peatlands through restoration. *Scientific Reports*, *6*, 28498. https://doi.org/10.1038/srep28498

Granath, G., Strengbom, J., & Rydin, H. (2012). Direct physiological effects of nitrogen on Sphagnum: A greenhouse experiment. *Functional Ecology*, *26*, 353–364. https://doi.org/10.1111/j.1365-2435.2011.01948.x

Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed., pp. 1–41). Chichester: Wiley.

Gunnarsson, U. (2005). Global patterns of *Sphagnum* productivity. *Journal of Bryology*, *27*, 269–279.

Hájek, T., Tuittila, E.-S., Ilomets, M., & Laiho, R. (2009). Light responses of mire mosses – A key to survival after water-level drawdown? *Oikos*, *118*, 240–250. https://doi.org/10.1111/j.1600-0706.2008.16528.x

Hassel, K., Kyrkjeeide, M. O., Yousefi, Y., Prestø, T., Stenøien, H. K., Shaw, A. J., & Flatberg, K. I. (2018). *Sphagnum divinum* (sp. nov.) and *S. medium* Limpr. and their relationship to *S. magellanicum* Brid. *Journal of Bryology*, *40*, 197–222. https://doi.org/10.1080/03736687.2018.1474424

Hayward, P. M., & Clymo, R. S. (1983). The growth of *Sphagnum*: Experiments on, and simulation of, some effects of light flux and water-table depth. *Journal of Ecology*, *71*, 845–863. https://doi.org/10.2307/2259597

Hedwall, P.-O., Brunet, J., & Rydin, H. (2017). Peatland plant communities under global change: Negative feedback loops counteract shifts in species composition. *Ecology*, *98*, 150–161. https://doi.org/10.1002/ecy.1627

Johnson, L. C., & Damman, A. W. H. (1991). Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos*, *61*, 234–242. https://doi.org/10.2307/3545341

Johnson, L. C., & Damman, A. W. H. (1993). Decay and its regulation in *Sphagnum* peatlands. *Advances in Bryology*, *5*, 249–296.

Klein, E. S., Yu, Z., & Booth, R. K. (2013). Recent increase in peatland carbon accumulation in a thermokarst lake basin in southwestern Alaska. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *392*, 186–195. https://doi.org/10.1016/j.palaeo.2013.09.009

Laine, A. M., Juurola, E., Hájek, T., & Tuittila, E.-S. (2011). *Sphagnum* growth and ecophysiology during mire succession. *Oecologia*, *167*, 1115–1125. https://doi.org/10.1007/s00442-011-2039-4

Laing, C. G., Granath, G., Belyea, L. R., Allton, K. E., & Rydin, H. (2014a). Tradeoffs and scaling of functional traits in *Sphagnum* as drivers of carbon cycling in peatlands. *Oikos*, *123*, 817–828.

Laing, C. G., Granath, G., Belyea, L. R., Allton, K. E., & Rydin, H. (2014b). Data for 'Tradeoffs and scaling of functional traits in *Sphagnum* as drivers of carbon cycling in peatlands'. https://qmro.qmul.ac.uk/jspui/handle/123456789/6179

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Li, D., Ives, A. R., & Waller, D. M. (2017). Can functional traits account for phylogenetic signal in community composition? *New Phytologist*, *214*, 607–618. https://doi.org/10.1111/nph.14397

Limpens, J., Bohlin, E., & Nilsson, M. B. (2017). Phylogenetic or environmental control on the elemental and organo-chemical composition of Sphagnum mosses? *Plant and Soil*, *417*, 69–85. https://doi.org/10.1007/s11104-017-3239-4

Limpens, J., Granath, G., Gunnarsson, U., Aerts, R., Bayley, S., Bragazza, L., ... Xu, B. (2011). Climatic modifiers of the response to nitrogen deposition in peat-forming Sphagnum mosses: A meta-analysis. *New Phytologist*, *191*, 496–507.

Luken, J. O. (1985). Zonation of *Sphagnum* mosses: Interactions among shoot growth, growth form, and water balance. *The Bryologist*, *88*, 374–379. https://doi.org/10.2307/3242680

Marschall, M., & Proctor, M. C. F. (2004). Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll b and total carotenoids. *Annals of Botany*, *94*, 593–603. https://doi.org/10.1093/aob/mch178

Mazziotta, A., Granath, G., Rydin, H., Bengtsson, F., & Norberg, J. (2018). Data from: Scaling functional traits to ecosystem processes: Towards a mechanistic understanding in peat mosses. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.1720vg5

Messier, J., Lechowicz, M. J., McGill, B. J., Violle, C., & Enquist, B. J. (2017). Interspecific integration of trait dimensions at local scales: The plant phenotype as an integrated network. *Journal of Ecology*, *105*, 1775–1790. https://doi.org/10.1111/1365-2745.12755

Michel, P., Lee, W. G., During, H. J., & Cornelissen, J. H. C. (2012). Species traits and their non-additive interactions control the water economy of bryophyte cushions. *Journal of Ecology*, *100*, 222–231. https://doi.org/10.1111/j.1365-2745.2011.01898.x

Moor, H., Rydin, H., Hylander, K., Nilsson, M. B., Lindborg, R., & Norberg, J. (2017). Towards a trait-based ecology of wetland vegetation. *Journal of Ecology*, *105*, 1623–1635. https://doi.org/10.1111/1365-2745.12734

Murray, K. J., Tenhunen, J. D., & Nowak, R. S. (1993). Photoinhibition as a control on photosynthesis and production of Sphagnum mosses. *Oecologia*, *96*, 200–207. https://doi.org/10.1007/BF00317733

Page, S. E., & Baird, A. J. (2016). Peatlands and global change: Response and resilience. *Annual Review of Environment and Resources*, *41*, 35–57. https://doi.org/10.1146/annurev-environ-110615-085520

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from www.R-project.org.

Reich, P. B. (2012). Key canopy traits drive forest productivity. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1736), 2128–2134. https://doi.org/10.1098/rspb.2011.2270

Reich, P. B. (2014). The world-wide "fast–slow" plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Rice, S. K., Aclander, L., & Hanson, D. T. (2008). Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in *Sphagnum* mosses (Sphagnaceae). *American Journal of Botany*, *95*, 1366–1374. https://doi.org/10.3732/ajb.0800019

Robroek, B. J. M., Jassey, V. E. J., Payne, R. J., Martí, M., Bragazza, L., Bleeker, A., ... Verhoeven, J. T. A. (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications*, *8*, 1161. https://doi.org/10.1038/s41467-017-01350-5

Rydin, H. (1985). Effect of water level on desiccation of Sphagnum in relation to surrounding Sphagna. *Oikos*, *45*, 374–379. https://doi.org/10.2307/3565573

Rydin, H., & Jeglum, J. K. (2013). *The biology of peatlands* (2ed.). Oxford: Oxford University Press.

Schliep, E. M., Gelfand, A. E., Mitchell, R. M., Aiello-Lammens, M. E., & Silander, J. A. (2018). Assessing the joint behaviour of species traits as filtered by environment. *Methods in Ecology and Evolution*, *9*, 716–727. https://doi.org/10.1111/2041-210X.12901

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M. L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Turetsky, M. R., Crow, S. E., Evans, R. J., Vitt, D. H., & Wieder, R. K. (2008). Tradeoffs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, *96*, 1297–1305. https://doi.org/10.1111/j.1365-2745.2008.01438.x

Utredningar, S. O. (2007). *Sweden facing climate change–Threats and opportunities*. Stockholm, Sweden: Swedish Commission on Climate and Vulnerability (SCCV).

Van Bodegom, P. M., Douma, J. C., Witte, J. P. M., Ordoñez, J. C., Bartholomeus, R. P., & Aerts, R. (2012). Going beyond limitations of plant functional types when predicting global ecosystem–atmosphere fluxes: Exploring the merits of traits-based approaches. *Global Ecology and Biogeography*, *21*, 625–636. https://doi.org/10.1111/j.1466-8238.2011.00717.x

Van Breemen, N. (1995). How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution*, *10*, 270–275. https://doi.org/10.1016/0169-5347(95)90007-1

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, *8*, 113–127. https://doi.org/10.1002/eco.1493

Walker, T. N., Ward, S. E., Ostle, N. J., & Bardgett, R. D. (2015). Contrasting growth responses of dominant peatland plants to warming and vegetation composition. *Oecologia*, *178*, 141–151. https://doi.org/10.1007/s00442-015-3254-1

Wang, S., Zhuang, Q., Yu, Z., Bridgham, S., & Keller, J. K. (2016). Quantifying peat carbon accumulation in Alaska using a process-based biogeochemistry model. *Journal of Geophysical Research: Biogeosciences*, *121*, 2172–2185. https://doi.org/10.1002/2016JG003452

Wang, Z., & Bader, M. Y. (2018). Associations between shoot-level water relations and photosynthetic responses to water and light in 12 moss species. *AoB Plants*, *10*, ply034-ply034. https://doi.org/10.1093/aobpla/ply034

Wang, Z., Liu, X., Bader, M. Y., Feng, D., & Bao, W. (2017). The 'plant economic spectrum' in bryophytes, a comparative study in subalpine forest. *American Journal of Botany*, *104*, 261–270. https://doi.org/10.3732/ajb.1600335

Weston, D. J., Turetsky, M. R., Johnson, M. G., Granath, G., Belyea, L. R., Rice, S. K., … Piatkowski, B. T. (2018). The Sphagnome Project: Enabling ecological and evolutionary insights through a genus-level sequencing project. *New Phytologist*, *217*, 16–25.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Flexas, J. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

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