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Functional trait evolution in *Sphagnum* peat mosses and its relationship to niche construction

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Summary

- Species in the genus *Sphagnum* create, maintain, and dominate boreal peatlands through 'extended phenotypes' that allow these organisms to engineer peatland ecosystems and thereby impact global biogeochemical cycles. One such phenotype is the production of peat, or incompletely decomposed biomass, that accumulates when rates of growth exceed decomposition. Interspecific variation in peat production is thought to be responsible for the establishment and maintenance of ecological gradients such as the microtopographic hummock-hollow gradient, along which sympatric species sort within communities.
- This study investigated the mode and tempo of functional trait evolution across 15 species of *Sphagnum* using data from the most extensive studies of *Sphagnum* functional traits to date and phylogenetic comparative methods.
- We found evidence for phylogenetic conservatism of the niche descriptor height-above-water-table and of traits related to growth, decay and litter quality. However, we failed to detect the influence of phylogeny on interspecific variation in other traits such as shoot density and suggest that environmental context can obscure phylogenetic signal. Trait correlations indicate possible adaptive syndromes that may relate to niche and its construction.
- This study is the first to formally test the extent to which functional trait variation among *Sphagnum* species is a result of shared evolutionary history.

Introduction

Boreal peatlands, dominated by *Sphagnum* peat mosses, occupy less than one-tenth of the Earth's landmass yet store over one-quarter of the terrestrial carbon stock (Gorham, 1991; Yu, 2012). *Sphagnum* species both create and modify these environments through 'extended phenotypes' that enable them to outcompete other plant life (Dawkins, 1982; Jones *et al.*, 1994; van Breeman, 1995). One such phenotype is the production of peat, or incompletely decomposed biomass, that results when rates of growth exceed those of decomposition. It has been speculated that *Sphagnum* has more influence on global carbon cycling than any other genus of plants because of the accumulation of carbon stored in peat (Clymo & Hayward, 1982).

In addition to affecting biogeochemical cycles, *Sphagnum* has been a model for community structure and niche differentiation (Horton *et al.*, 1979; Vitt & Slack, 1984; Belyea, 2004). Interspecific variation in the propensity of *Sphagnum* to produce peat contributes to the establishment and maintenance of ecological gradients along which sympatric species sort within communities (Rochefort *et al.*, 1990; Rydin & Jeglum, 2013). Such niche differentiation permits as many as 20 or more species of *Sphagnum* to co-occur within some peatlands.

Certain species of *Sphagnum* form elevated hummocks while other species live in hollows at or near the water table. The hummock-hollow gradient is thought to be related to rates of growth and decomposition with hummock-forming species both growing and decaying more slowly than hollow-dwelling species (Reader & Stewart, 1972; Johnson & Damman, 1991; Hogg, 1993; Hájek, 2009). Position along the hummock-hollow gradient is phylogenetically conserved, meaning that closely related species tend to be more similar than species selected at random from the peat moss phylogeny (Johnson *et al.*, 2015). Indeed, phylogenomic analyses of *Sphagnum* suggest that predominantly hummock-forming and hollow-inhabiting clades within the genus diverged relatively early in the evolution of peat mosses (Shaw *et al.*, 2016). As niche preference with regard to the hummock-hollow gradient is phylogenetically conserved and this gradient is thought to result from interspecific variation in *Sphagnum* functional traits, it may be that the traits themselves are phylogenetically conserved.

Some comparative studies on *Sphagnum* have addressed interspecific functional trait variation, but most such studies have compared just a few species (for example Johnson & Damman, 1991; Belyea, 1996; Limpens & Berendse, 2003). Nevertheless, many authors have made the generalisation that hummock-forming species share a suite of functional traits that correlates with their typical positions relative to the hummock-hollow gradient. The most extensive studies on *Sphagnum* functional traits to date sampled 15 species, quantified intraspecific trait variation

and included both laboratory and field measurements (Bengtsson *et al.*, 2016, 2018). In their first paper, Bengtsson *et al.* (2016) found support for trade-offs between traits, such as growth and decay, using traditional statistical methods and suggested that one plausible inference of phylogenetic relationships (Johnson *et al.*, 2015) accounts for 6−26% of trait principal component variation in phylogenetic multiple regression models. However, their consideration of phylogeny was limited to a single tree and did not therefore incorporate phylogenetic uncertainty. In a second paper, Bengtsson *et al.* (2018) showed that for the same samples used in their 2016 study, the trade-off between growth and decay is largely determined by the quality of the litter and that litter quality may differ between subgenera, as evidenced by traditional ANOVA and PCA analyses. Both studies from Bengtsson *et al.* attempted to incorporate phylogenetic relationships into their comparative analyses, as has become increasingly common in ecological studies of organismal traits or habitat preference (Anacker *et al.*, 2014; Valverde-Barrantes *et al.*, 2014; Cadotte *et al.*, 2017), but did not specifically test for phylogenetic signal in their ecological data, nor did they test trait correlations using phylogenetic comparative methods. Bengtsson *et al.* (2018) used taxonomy as a proxy for phylogenetic relationships.

Evidence for phylogenetic signal can come from multiple sources and the degree of concordance among these sources can help to establish confidence in a hypothesis that such signals exist in the data. One approach is to use different methods for assessing the presence of phylogenetic signal; the likelihoods of various evolutionary models can be compared, or the signal can be quantified with metrics and explicitly tested against predictions under phylogenetic independence. Model selection based on minimising an information criterion score does not necessarily imply that the null model is false given a particular significance level because information criteria provide relative model support and do not constitute formal hypothesis tests. However, if models are nested then likelihood ratio tests can be implemented. Furthermore, failing to account for uncertainty in the true phylogeny and intraspecific variation (Ives *et al.*, 2007) could contribute to improperly rejecting a null hypothesis of phylogenetic independence.

Through the utilisation of phylogenetic comparative methods and previously published trait data (Bengtsson *et al.*, 2016, 2018), this study seeks to rigorously evaluate the influence of phylogeny on interspecific functional trait and niche descriptor variation while accounting for intraspecific variation and phylogenetic uncertainty. Specifically, we aim to test, first, whether *Sphagnum* functional traits are phylogenetically conserved; second, how these traits co-vary with one another when phylogeny is taken into consideration; and, third, which traits are correlated with the microtopographic hummock-hollow niche gradient.

Materials and Methods

Trait and niche descriptor data

Trait and niche descriptor data were obtained from Bengtsson *et al.* (2016, 2018). These datasets were chosen as they include the greatest number of species ($N = 15$) in any available study of *Sphagnum* traits. The species included represent a small fraction of the 350–500 species in the genus *Sphagnum* (Shaw *et al.*, 2010; The Plant List, 2013), yet are a substantial component of the dominant taxa found at northern latitudes and therefore have nontrivial ecological impacts. The same species and samples were used to generate both datasets. The species investigated include *S. angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid., *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll. The niche descriptor height-above-water-table and 22 functional traits related to litter quality, stand structure, decomposition rate, growth rate and photosynthetic capacity were selected from the Bengtsson studies for further analyses (Table 1). Data for plant length increase, shoot density, bulk density, biomass increase per shoot and biomass increase per area were restricted to field season 2012 as this was when the niche descriptor data were collected. Each trait and niche variable had at least four sampling points for each species. *Sphagnum magellanicum* Brid. was treated a single taxon in accordance with other recent ecological studies (Bengtsson *et al.*, 2016, 2018; Mazziotta *et al.*, 2018) despite the current taxonomic status of *S. magellanicum sensu lato* as a species complex (Hassel *et al.*, 2018).

Sequence data and phylogenetic reconstruction

Gene sequences for 16 loci were used for phylogenetic reconstruction. These sequences were obtained from the GenBank database and an in-house database containing unpublished data. Each of the 15 species was represented by at least two loci, with an average of 10 loci per species. Plastid loci included photosystem II reaction centre protein T (*psbT*), ribulose-bisphosphate carboxylase large subunit (*rbcL*), plastid ribosomal gene (*rpl16*), RNA polymerase subunit beta (*rpoC1*), ribosomal small protein 4 (*rps4*), tRNA(Gly) (UCC) (*trnG*) and the trnL (UAA) 59 exon-trnF (GAA) region (*trnL*). Nuclear loci included a ribosomal internal transcribed spacer (*ITS*), two introns in the *LEAFY/FLO* gene (*LL* and *LS*) and five anonymous regions (*A15*, *ATGc89*, *rapdA*, *rapdB* and *rapdF*). One mitochondrial locus, an intron within the nicotinamide adenine dinucleotide (NADH) protein-coding subunit 5 (*nad5*), was included. Associated accession numbers are given in Supporting Information Methods S1. In total, 37 of the 156 included sequences were previously unpublished (*c.* 24%).

Each locus was aligned using MAFFT (Katoh & Standley, 2013) and alignments were manually refined using ALIVIEW (Larsson, 2014). These refined alignments were concatenated to produce a final dataset of 12 788 molecular characters. Each locus was assigned to a separate dataset partition with plastid loci treated as a single partition. Phylogenetic inference was performed using the program BEAST 2 (Bouckaert *et al.*, 2014). A

Table 1 Trait and niche variables used in comparative analyses.

Variable	Description	Category	Study
Mass loss in field	Mass loss under field conditions (%)	Decomposition	Bengtsson *et al.* (2016)
Mass loss in laboratory	Mass loss under laboratory conditions (%)	Decomposition	Bengtsson *et al.* (2016)
Height-above-water-table	Distance between water table and top of plant shoots (mm)	Niche descriptor	Bengtsson *et al.* (2016)
Litter nitrogen concentration	Concentration of nitrogen as % of dry litter mass (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Litter carbon concentration	Concentration of carbon as % of dry litter mass (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Litter C : N ratio	Ratio of carbon concentration to nitrogen concentration in dry litter	Litter quality	Bengtsson *et al.* (2018)
Litter phosphorous concentration	Concentration of phosphorous in perchloric acid-treated litter (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Holocellulose concentration	Concentration of polysaccharides in chlorite-treated litter (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Sphagnan concentration	Concentration of hot-water hydrolyzable pectic polysaccharides (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Cation exchange capacity	NH_4^+ exchange capacity at pH 7.0; proxy for unesterified pectic polysaccharides (meq g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Soluble phenolic concentration	Concentration of acetone-soluble simple phenolics with 4-hydroxybenzoic acid standard (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Insoluble Klason lignin concentration	Concentration of acid-insoluble lignin-like polyphenolics (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Soluble Klason lignin concentration	Concentration of acid-soluble lignin-like polyphenolics (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Total Klason lignin concentration	Concentration of total lignin-like polyphenolics (mg g^{-1})	Litter quality	Bengtsson *et al.* (2018)
Absorbance ratio	Ratio of light absorbance at 205 nm to absorbance at 280 nm in acid-digested litter; proxy for carbohydrate chemical degradability	Litter quality	Bengtsson *et al.* (2018)
Shoot density	Number of shoots per unit area for field season 2012 (cm^{-2})	Stand structure	Bengtsson *et al.* (2016)
Bulk density	Shoot mass per unit volume for field season 2012 (g cm^{-3})	Stand structure	Bengtsson *et al.* (2016)
Length increase	Shoot length increase for field season 2012 (mm)	Growth	Bengtsson *et al.* (2016)
Biomass increase per shoot	Biomass increase per shoot for field season 2012 (g)	Growth	Bengtsson *et al.* (2016)
Biomass increase per area	Biomass increase per unit area for field season 2012 (g cm^{-2})	Growth	Bengtsson *et al.* (2016)
Photosynthetic capacity per shoot	CO_2 net exchange rate per shoot (mg h^{-1})	Photosynthesis	Bengtsson *et al.* (2016)
Photosynthetic capacity per dry weight	CO_2 net exchange rate per unit dry mass (mg g^{-1} h^{-1})	Photosynthesis	Bengtsson *et al.* (2016)
Photosynthetic capacity per area	CO_2 net exchange rate per unit area (mg cm^{-2} h^{-1})	Photosynthesis	Bengtsson *et al.* (2016)

Data are from Bengtsson *et al.* (2016, 2018). A short description and category are provided for each trait or niche descriptor. The species investigated include *Sphagnum angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid., *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll.

log-normal uncorrelated relaxed clock branch length prior was assigned to each dataset partition (Drummond *et al.*, 2006). Site and substitution models were inferred during the phylogenetic analyses with bModelTest (Bouckaert & Drummond, 2017).

Resolution of deep nodes in the *Sphagnum* phylogeny were weakly supported in analyses like the one described here based on limited numbers of loci, so we enforced reciprocal monophylly of the clade containing species in subgenera *Sphagnum* and *Acutifolia* relative to that containing species in subgenera *Cuspidata* and *Subsecunda* because this topology was strongly supported in previous analyses based on organellar (plastid, mitochondrial) genome data (Shaw *et al.*, 2016). Three replicate Beast 2 analyses were conducted with each chain allowed to run for 100 million generations. For each analysis, a 10% burn-in was applied and logs were stored every 100 000 generations. Convergence and acceptable mixing were evaluated using Tracer (Rambaut *et al.*, 2018) and the R package 'rwty' (Warren *et al.*, 2017). Tree files for the three analyses were concatenated and the resulting posterior distribution of 2703 trees was summarised into a maximum clade credibility tree with median node heights using TreeAnnotator within the Beast 2 toolkit.

Modelling continuous trait and niche descriptor evolution

Phylogenetic comparative methods were used to determine which model of evolution best fit each continuous functional trait and niche descriptor. Model fitting was performed using the 'geiger' package (Pennell *et al.*, 2014) in the R statistical programming environment (R Core Team, 2018). For each variable, five commonly used models of evolution were evaluated: White Noise (WN), Brownian Motion (BM), Ornstein–Uhlenbeck (OU), delta (δ) and lambda (λ). White Noise served as the null model in which the species values are independent of phylogenetic relatedness. The BM model (Felsenstein, 1985) predicts that variance in trait or niche descriptor values increases at a constant rate proportionate to evolutionary distance, with more closely related species having more similar values, indicating that the variable has phylogenetic signal. The OU model (Martins & Hansen, 1997), described by some authors as a model of stabilising selection (Butler & King, 2004), also predicts phylogenetic signal but values are allowed to trend towards some optimal value. Two additional models, λ and δ, allow for deviations in the BM model (Pagel, 1999). In the λ model, a trait or niche variable can have phylogenetic signal that is weaker than predicted under the BM model; a λ

value of zero is equivalent to the WN model and a λ value of one is equivalent to the BM model. Finally, the δ model predicts phylogenetic signal with value changes concentrated towards either the base ($\delta < 1$) or tips ($\delta > 1$) of the tree; a δ value of one is equivalent to the BM model. The BM model is nested within the OU, λ and δ models while the WN model is nested within all four other models.

Data for each trait and niche descriptor were assessed for normality using a Shapiro–Wilk test (Shapiro & Wilk, 1965). Raw data for mass loss in the field, plant length increase, cation exchange capacity and shoot density were natural log-transformed to meet assumptions of normality present in the evolutionary models. A negative reciprocal transformation was applied to litter phosphorous concentration data. Model fitting utilised both the maximum clade credibility (MCC) tree and a randomly selected set of 1000 trees from the Bayesian posterior distribution to account for topological uncertainty. As intraspecific variation and/or measurement error can affect phylogenetic comparative methods (Ives *et al.*, 2007), trait and niche variable means and associated standard error estimations for each species were included as input data for models incorporating phylogenetic signal. Models were evaluated under maximum likelihood with a small-sample-size corrected version of the Akaike information criterion (AICc) and the model with the lowest AICc score was preferred (Burnham & Anderson, 2002). Preferred models that incorporate phylogenetic signal were also required to be significantly different from the null WN model in likelihood ratio tests for acceptance. Additionally, the maximum likelihood value for Pagel's λ was estimated and its significance was evaluated with a likelihood ratio test against a null model in which λ was constrained at zero. Blomberg's *K* (Blomberg *et al.*, 2003) was estimated as another test of phylogenetic signal and the significance of the observed *K* value was evaluated with 1000 permutations of the data using the R package 'PICANTE' (Kembel *et al.*, 2010). A value of one for Blomberg's *K* corresponds to the BM model and values larger than one indicate that the trait or niche descriptor has more phylogenetic signal than predicted under the BM model. Significance testing for likelihood ratios, Pagel's λ values and Blomberg's *K* values across the set of trees from the posterior distribution were adjusted using the Benjamini–Yekutieli procedure to control the false discovery rate at 0.05 for multiple comparisons under dependence (Benjamini & Yekutieli, 2001).

Trait and niche variable correlations

Pairwise trait and niche variable correlations ($N = 253$) were assessed with linear regressions under ordinary least squares (OLS). Data for mass loss in the field, mass loss in the laboratory, height-above-water-table, sphagnan concentration, cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration, total Klason lignin concentration, shoot density, length increase, biomass increase per shoot, photosynthetic capacity per area and photosynthetic capacity per dry weight were natural log-transformed for regression analyses to meet assumptions of residual error normality. A negative reciprocal transformation was applied to litter phosphorous concentration data. Residual errors were tested for heteroskedasticity with Breusch–Pagan tests (Breusch & Pagan, 1979) and for autocorrelation with Durbin–Watson tests (Durbin & Watson, 1950, 1951). Regression models with autocorrelated or heteroskedastic residuals were evaluated using generalised least squares (GLS) with the R package 'NLME' (Pinheiro *et al.*, 2018).

Several papers have suggested that the application of phylogenetic regression is inappropriate unless the residuals, not the variables themselves, possess phylogenetic signal (Revell, 2010; Uyeda *et al.*, 2018). As such, each set of residual errors was also evaluated for phylogenetic signal by fitting evolutionary models on the MCC tree. Phylogenetic signal was determined by the selection of a model incorporating phylogenetic signal based on AICc score and rejection of the null WN model following a likelihood ratio test. If a given set of residuals had phylogenetic signal when either of the trait or niche variables was the response, then the regression was evaluated using phylogenetic generalised least squares (PGLS; Grafen, 1989; Martins & Hansen, 1997), with the R package 'CAPER' (Orme *et al.*, 2018). The MCC tree was used to estimate the evolutionary variance–covariance matrix for PGLS models. The *P*-values from all regression models were then adjusted with the Benjamini–Yekutieli procedure to control the false discovery rate. The R^2 coefficient was obtained using the R package 'CAPER' (Orme *et al.*, 2018) for PGLS models and the R package 'PIECEWISESEM' (Lefcheck, 2016) for GLS models, although the disputed definition of R^2 in such models with correlated data is noted (Nakagawa & Schielzeth, 2013; Ives, 2019).

For trait and niche variables possessing phylogenetic signal consistent with the BM model, multivariate evolutionary models were fitted using the R package 'MVMORPH' (Clavel *et al.*, 2015) as additional tests of correlation. The niche descriptor height-above-water-table and six functional traits were selected for these analyses; these traits included mass loss in the laboratory, biomass increase per area, cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration and total Klason lignin concentration. For each pair of variables, a bivariate BM model was fitted and the evolutionary covariance between the variables was estimated. The likelihood of this model incorporating variable covariance was compared with a constrained model without covariance using a likelihood ratio test and the resulting *P*-values were adjusted using the Benjamini–Yekutieli procedure to control the false discovery rate.

Data availability

Trait and niche descriptor data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.62054 Bengtsson *et al.* (2016); https://doi.org/10.5061/dryad.4f8d2.2 Bengtsson *et al.* (2018). The molecular dataset and phylogenetic trees available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1fp853q.

Results

Phylogenetic analysis

The dataset of 12 788 molecular characters contains 12 127 constant characters (94.8%), 454 variable parsimony-uninformative characters (3.6%) and 207 parsimony-informative characters (1.6-%). Within subgenus *Cuspidata*, the sister relationship of *S. balticum* (Russow) C.E.O. Jensen to *S. fallax* (H. Klinggr.) H. Klinggr. was resolved at 0.999 posterior probability, while the sister relationship of *S. tenellum* (Brid.) Brid to the clade containing *S. cuspidatum* Ehrh. ex Hoffm. and *S. majus* (Russow) C.E.O. Jensen was resolved at 0.996 posterior probability. Within subgenus *Acutifolia*, the sister relationship of *S. fuscum* (Schimp.) H. Klinggr. to *S. warnstorfii* Röll was resolved at 0.612 posterior probability. All other nodes in the phylogeny, with the exception of the single constrained node, were resolved at 1.00 posterior probability (Fig. 1). Substitution models for each dataset partition inferred during phylogenetic inference are given in Table S1.

Evaluation of univariate evolutionary models

The evolutionary model that best describes the majority of traits (16 of 22) is WN, suggesting a lack of phylogenetic signal (Table 2). Discordance among the various methods for detecting phylogenetic signal was absent for mass loss in the field, litter C : N ratio, litter phosphorous concentration, holocellulose concentration, soluble Klason lignin concentration, shoot density, bulk density, length increase, photosynthetic capacity per shoot and photosynthetic capacity per dry weight providing strong support for the independence of phylogeny and interspecific variation in these traits. Model preference based on AICc scores indicated that litter nitrogen concentration, litter carbon concentration, sphagnan concentration, absorbance ratio, biomass increase per shoot and photosynthetic capacity per area are phylogenetically conserved. However, likelihood ratio tests using both the MCC tree and the posterior tree distribution did not reject the null WN model (Tables 2, S2). Sphagnan concentration had significant values of Blomberg's K for the MCC tree and of Pagel's λ for both the MCC tree and 99.6% of the posterior tree distribution, despite the inability to reject the null WN model (Tables 2, S3). Absorbance ratio and biomass increase per shoot also had significant values of Blomberg's K for the MCC tree contributing to discordance among methods (Table 2).

The BM model of evolution, incorporating phylogenetic signal, was preferred for the niche descriptor height-above-water table and the other six traits (Table 2). Discordance among methods was absent for cation exchange capacity, insoluble Klason lignin concentration and total Klason lignin concentration. Interspecific variation in mass loss in the laboratory, the niche descriptor height-above-water-table, soluble phenolic concentration and biomass increase per area is consistent with the BM model. However, likelihood ratio tests across the majority of the posterior tree distribution failed to reject the null WN model after controlling the false discovery rate (Tables 2, S2). Furthermore, values of Blomberg's K for soluble phenolic concentration and height-above-water-table were significant for the MCC tree, but not different from randomised data for the posterior tree distribution after controlling the false discovery rate (Tables 2, S3).

Trait and niche variable correlations

Fourteen of the 253 pairwise linear regressions between trait and niche variables were significant at $P < 0.05$ after controlling the false discovery rate (Table 3). More than one-third of regression models (37.5%) required the application of PGLS (Table S4). Mass loss in the laboratory is negatively correlated with litter quality measurements of soluble phenolic concentration, insoluble Klason lignin concentration and total Klason lignin concentration. These litter quality measurements are positively correlated with one another. Litter C : N ratio is negatively correlated with litter nitrogen concentration. Biomass increase per shoot is negatively correlated with shoot density and is positively correlated with both length increase and

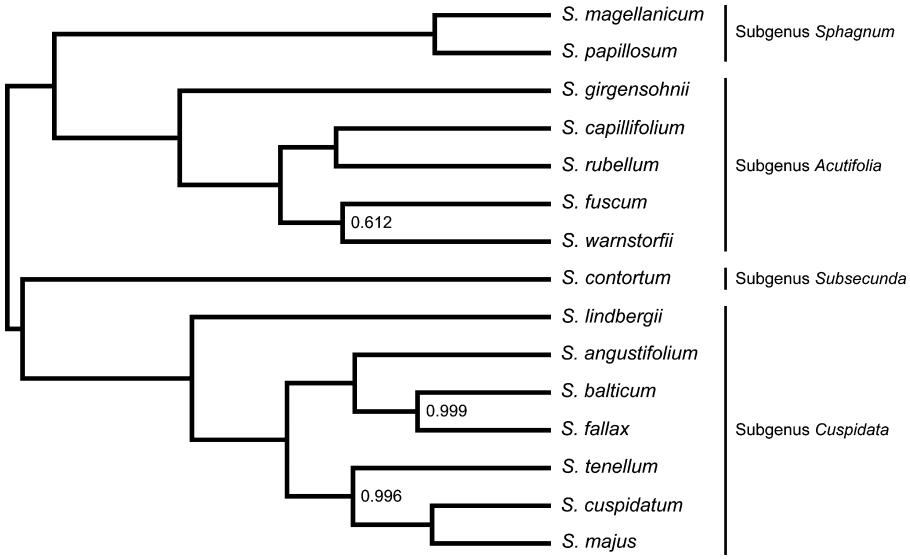

Fig. 1 Maximum clade credibility tree. Species in the subgenera *Sphagnum* and *Acutifolia* tend to form elevated hummocks, while those in subgenera *Subsecunda* and *Cuspidata* tend to occur in hollows at or near the water table. Nodes not supported at 1.0 posterior probability are labelled. The species investigated include *Sphagnum angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid., *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll.

Table 2 Summary of tests for phylogenetic signal in trait and niche variables.

Variable	Phylogenetic signal	Accepted model	LRT significance	λ (significance)	*K* (significance)	Discordance (source)
Mass loss in field	Absent	WN	na	<0.001 (ns)	0.507 (ns)	Absent
Mass loss in laboratory	Present†	BM†	**	1.000 (**)	1.370 (***)	Present (LRT – posterior)
Height-above-water-table	Present†	BM†	*	0.761 (*)	0.981 (*)	Present (LRT – posterior) (Blomberg's *K* – posterior)
Litter nitrogen concentration	Absent†	WN†	ns	< 0.001 (ns)	0.790 (ns)	Present (AICc – Both)
Litter carbon concentration	Absent†	WN†	ns	0.852 (ns)	0.792 (ns)	Present (AICc – both)
Litter C : N ratio	Absent	WN	na	< 0.001 (ns)	0.724 (ns)	Absent
Litter phosphorous concentration	Absent	WN	na	< 0.001 (ns)	0.560 (ns)	Absent
Holocellulose concentration	Absent	WN	na	< 0.001 (ns)	0.559 (ns)	Absent
Sphagnan concentration	Absent†	WN†	ns	0.720 (*)	0.960 (*)	Present (AICc – both) (Pagel's λ – both) (Blomberg's *K* – MCC)
Cation exchange capacity	Present	BM	***	1.000 (***)	1.943 (***)	Absent
Soluble phenolic concentration	Present†	BM†	**	1.000 (**)	1.175 (**)	Present (LRT – posterior) (Blomberg's *K* – posterior)
Insoluble Klason lignin concentration	Present	BM	**	1.000 (**)	1.774 (**)	Absent
Soluble Klason lignin concentration	Absent	WN	na	<0.001 (ns)	0.687 (ns)	Absent
Total Klason lignin concentration	Present	BM	**	1.000 (**)	1.861 (**)	Absent
Absorbance ratio	Absent†	WN†	ns	0.662 (ns)	0.943 (*)	Present (AICc – both) (Blomberg's *K* – MCC)
Shoot density	Absent	WN	na	<0.001 (ns)	0.707 (ns)	Absent
Bulk density	Absent	WN	na	<0.001 (ns)	0.563 (ns)	Absent
Length increase	Absent	WN	na	0.110 (ns)	0.547 (ns)	Absent
Biomass increase per shoot	Absent†	WN†	ns	0.658 (ns)	0.814 (*)	Present (AICc – both) (Blomberg's *K* – MCC)
Biomass increase per area	Present†	BM†	**	1.000 (**)	1.240 (**)	Present (LRT – posterior)
Photosynthetic capacity per shoot	Absent	WN	na	0.036 (ns)	0.623 (ns)	Absent
Photosynthetic capacity per dry weight	Absent	WN	na	0.093 (ns)	0.714 (ns)	Absent
Photosynthetic capacity per area	Absent†	WN†	ns	0.583 (ns)	0.708 (ns)	Present (AICc – both)

Variables were scored for the presence of phylogenetic signal based on the accepted evolutionary model using the maximum clade credibility tree (MCC) and for the presence of discordance (†) among methods relative to the accepted model. Accepted models had the lowest corrected Akaike information criterion (AICc) score and those incorporating phylogenetic signal were distinguishable from the null White Noise model at $P < 0.05$ in a likelihood ratio test (LRT); significance of LRTs on the MCC is reported. If a model incorporating phylogenetic signal had the lowest AICc score but was not different from the null model in LRT(s), the null model was accepted and AICc score was listed as a source of discordance. Pagel's λ and Blomberg's *K* were calculated as additional metrics of phylogenetic signal and significance of these metrics was assessed with LRT(s) against a null model where λ was constrained at zero and a permutation test with 1000 permutations of the data, respectively. Values for Pagel's λ and Blomberg's *K* on the MCC and their corresponding significance was reported. The Benjamini–Yekutieli procedure was used to control the false discovery rate for all tests performed across the Bayesian posterior tree distribution. Sources of discordance are described for results from the MCC, across the majority of the Bayesian posterior tree distribution (Posterior) or both the MCC and Posterior (Both) that conflict with the accepted evolutionary model. The species investigated include *Sphagnum angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid. *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll. BM, Brownian motion; WN, White noise; ns, not significant; na, not applicable.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

photosynthetic capacity per shoot. The litter quality trait cation exchange capacity is positively correlated with both sphagnan concentration and the niche descriptor height-above-water-table, while sphagnan concentration is negatively correlated with biomass increase per area. Plant bulk density is negatively correlated with the growth trait of length increase. A detailed summary of all linear regression models is given in Table S4.

Table 3 Trait and niche variable correlation indicated by significant linear regression models.

Variable 1	Variable 2	Model	Slope	R	R^2	Significance
Mass loss in laboratory	Soluble phenolic concentration	OLS	−1.730	−0.872	0.761	**
Mass loss in laboratory	Insoluble Klason lignin concentration	OLS	−1.375	−0.815	0.663	*
Mass loss in laboratory	Total Klason lignin concentration	OLS	−1.886	−0.838	0.702	*
Height-above-water-table	Cation exchange capacity	OLS	4.899	0.883	0.780	**
Litter nitrogen concentration	Litter C : N ratio	OLS	−0.013	−0.992	0.984	***
Sphagnan concentration	Cation exchange capacity	OLS	0.901	0.804	0.646	*
Sphagnan concentration	Biomass increase per area	OLS	−18.387	−0.830	0.689	*
Soluble phenolic concentration	Insoluble Klason lignin concentration	OLS	0.746	0.877	0.768	**
Soluble phenolic concentration	Total Klason lignin concentration	OLS	1.003	0.884	0.781	**
Insoluble Klason lignin concentration	Total Klason lignin concentration	GLS	1.329	0.997	0.994	***
Shoot density	Biomass increase per shoot	PGLS	−0.709	−0.889	0.790	**
Bulk density	Length increase	PGLS	−0.007	−0.840	0.705	*
Length increase	Biomass increase per shoot	OLS	0.631	0.822	0.676	*
Biomass increase per shoot	Photosynthetic capacity per shoot	OLS	39.323	0.838	0.702	*

Regression models were fitted under ordinary least squares (OLS) for each of the 253 variable pairs. Regression model residuals were evaluated for the presence of phylogenetic signal using evolutionary models on the maximum clade credibility tree; acceptance of an evolutionary model incorporating the presence of phylogenetic signal required such a model to have the lowest corrected Akaike information criterion score and be distinguishable from the null White Noise model at $P < 0.05$ in a likelihood ratio test. Models were evaluated under phylogenetic generalised least squares (PGLS) if the residuals had phylogenetic signal and under generalised least squares (GLS) if either heteroskedasticity or autocorrelation was detected. The maximum clade credibility tree was used to estimate the variance–covariance matrix for PGLS models. All tests of significance for regression models had 13 degrees of freedom. The trend line slope when variable 1 is the response, R, R^2, and significance were reported for those regression models that are significant at $P < 0.05$ following control of the false discovery rate using the Benjamini–Yekutieli procedure. The species investigated include *Sphagnum angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid., *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Multivariate BM models for trait and niche variables that possess phylogenetic signal indicated that most of these variables have significant evolutionary covariance (Fig. 2). These variables included the traits mass loss in the laboratory, cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration, total Klason lignin concentration and the niche descriptor height-above-water-table. In total, 20 of the 21 bivariate models were significant at $P < 0.05$ after controlling the false discovery rate. The model including the traits soluble phenolic concentration and cation exchange capacity was the only model not significantly different from a constrained model with covariance absent. Mass loss in the laboratory has positive covariance with biomass increase per area and negative evolutionary covariance with cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration, total Klason lignin concentration and the niche descriptor height-above-water-table. Biomass increase per area has negative evolutionary covariance with the litter quality traits and the niche descriptor height-above-water-table. All other bivariate models indicated positive covariance between variables. A detailed summary of all multivariate evolutionary models is given in Table S5. Seven of the 21 significant evolutionary models were also significant in linear regression, while all significant regression models for these variables were also significant in evolutionary models (Table S6).

Discussion

Detectable phylogenetic signal is present for the niche descriptor height-above-water-table and only a handful of traits ($N = 6$) investigated. Interspecific variation in height-above-water-table and the traits mass loss in the laboratory, biomass increase per area, cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration and total Klason lignin concentration is phylogenetically conserved and best explained by the BM model of evolution. Variation among species for the majority of *Sphagnum* traits ($N = 16$) is independent of phylogeny, suggesting that the traits are evolutionarily labile and fast rates of evolution had erased any phylogenetic signal. Results obtained from various methods of measuring phylogenetic signal were not entirely consistent, as discordance between methods was present for 10 of the 23 trait and niche variables and such discordance may reflect the relatively small number of species included in the dataset ($N = 15$). When phylogenetic signal was detected, the BM model was always accepted and the inability to prefer models with additional parameters (Ornstein-Uhlenbeck, λ, or δ models) might be due to the low statistical power associated with small sample sizes (Blomberg *et al.*, 2003; Cressler *et al.*, 2015).

An important finding of this work is that some of the traits hypothesised to drive interspecific variation along the hummock-hollow ecological gradient are phylogenetically conserved. The detection of phylogenetic signal in height-above-water-table in this study is in accordance with a previous study of *Sphagnum* niche preference (Johnson *et al.*, 2015) and the results presented here suggest that mass loss in the laboratory, biomass increase per area and various traits related to litter quality are also phylogenetically conserved. Multivariate evolutionary models indicated significant evolutionary covariance between the niche descriptor height-above-water-table and the traits biomass increase per area,

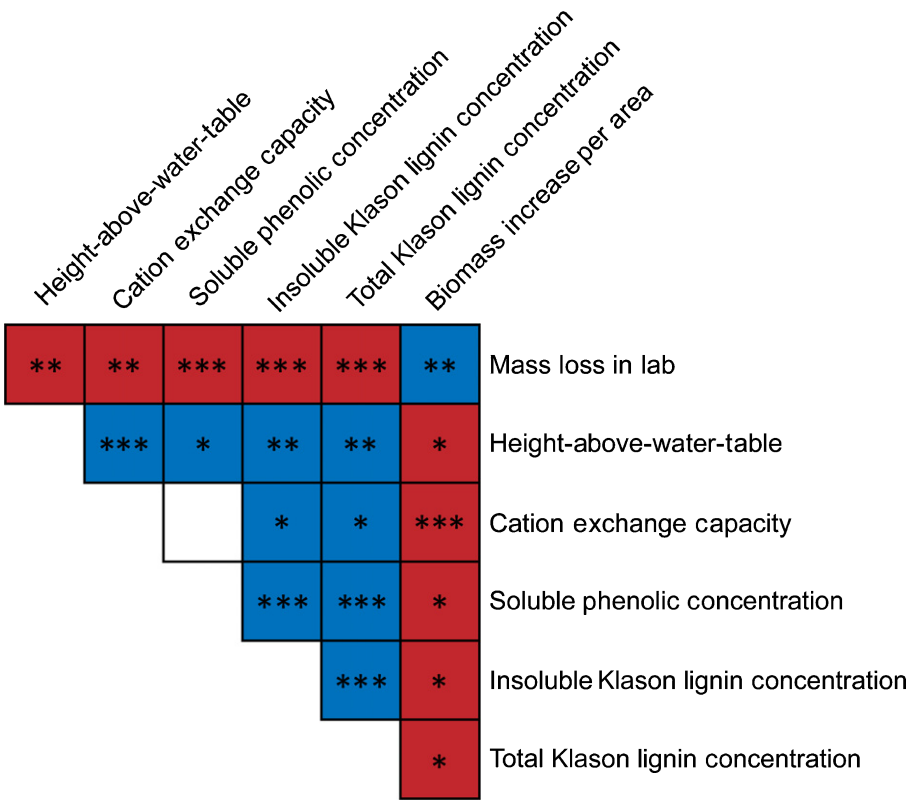

Fig. 2 Multivariate models indicated evolutionary covariance between trait and niche variables that have phylogenetic signal. Bivariate Brownian motion evolutionary models were fitted for variables that have phylogenetic signal on the maximum clade credibility tree. Significance was assessed using likelihood ratio tests against models constrained by the absence of evolutionary covariance between variables. Evolutionary covariance was scored as positive (blue), negative (red), or absent (white). The Benjamini–Yekutieli procedure was used to control the false discovery rate. The species investigated include *Sphagnum angustifolium* (Russow) C.E.O. Jensen, *S. balticum* (Russow) C.E.O. Jensen, *S. capillifolium* (Ehrh.) Hedw., *S. contortum* Schultz, *S. cuspidatum* Ehrh. ex. Hoffm., *S. fallax* (H. Klinggr) H. Klinggr., *S. fuscum* (Schimp.) H. Klinggr., *S. girgensohnii* Russow, *S. lindbergii* Schimp., *S. magellanicum* Brid., *S. majus* (Russow) C.E.O. Jensen, *S. papillosum* Lindb., *S. rubellum* Wilson, *S. tenellum* (Brid.) Brid. and *S. warnstorfii* Röll. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

mass loss in the laboratory, cation exchange capacity, soluble phenolic concentration, insoluble Klason lignin concentration and total Klason lignin concentration. However, the only trait related to height-above-water-table in linear regression models is the litter quality trait of cation exchange capacity that may indicate that the other relationships are nonlinear or which the number of taxa sampled ($N = 15$) was insufficient to statistically support linear relationships. Overall, there was support for the often quoted tenet that *Sphagnum* species growing higher above the water table tend to have lower decomposability, lower productivity and higher litter concentrations of phenolics and pectic polysaccharides (Turetsky *et al.*, 2008; Hájek *et al.*, 2011; Limpens *et al.*, 2017).

However, many traits hypothesised to be correlated with height-above-water-table or decomposability had no detectable phylogenetic signal and such widespread covariance was not evident from our analyses. Contrary to some previous observations (Coulson & Butterfield, 1978; Bragazza *et al.*, 2006) and in agreement with others (Thormann *et al.*, 2001; Moore *et al.*, 2007; Turetsky *et al.*, 2008), litter C : N ratio is not significantly correlated with measurements of decomposability or height-above-water-table. No support was found for a relationship between shoot density or bulk density and either height-above-water-table or decomposability in disagreement with previous studies that did not account for phylogeny (Hájek, 2009; Elumeeva *et al.*, 2011; Mazziotta *et al.*, 2018). Indeed, even the trade-off between rates of growth and decomposition *per se* (Turetsky *et al.*, 2008; Laing *et al.*, 2014) is only supported for biomass increase per area and mass loss in the laboratory in multivariate evolutionary models consistent with recent analyses that acknowledged that support for such a trade-off is weak (Mazziotta *et al.*, 2018). It should be noted, however, that the increased probability of type II error associated with small sample size in this study likely contributes in part to the observation of relatively few significant regression models.

This meta-analysis highlights the importance of using phylogenetic comparative methods when addressing questions related to the evolutionary history of organismal traits and correlations between traits. Bengtsson *et al.* (2018) argued that clustering of species in a traditional principal component analysis of litter quality traits was an indication of 'strong phylogenetic signal'. Such an analysis does not address whether phylogenetic signal is present in the data, nor does it account for nonindependence between species. Bengtsson *et al.* (2018) also argued that phylogenetic signal could be inferred from the observation of significant differences among subgenera in mean trait values following post

hoc ANOVA tests. However, the problem of sample nonindependence between and within subgenera remains and phylogenetic signal was not explicitly tested. Furthermore, variation partitioning using redundancy analyses that treat taxonomic classifications as explanatory variables do not test for phylogenetic signal. For example, Limpens *et al.* (2017) employed such a strategy and suggested that interspecific variation in *Sphagnum* holocellulose concentration is driven by shared phylogenetic history, a finding not recapitulated in this study. In summary, stating that traits have phylogenetic signal is inappropriate and sometimes positively misleading unless the methods employed are explicitly testing for such signal. While Bengtsson *et al.* (2016) utilised phylogenetic multiple regression to quantify the extent to which functional trait principal component variation is explained by phylogeny, they first did not test the residuals for phylogenetic signal to justify the inclusion of an evolutionary variance-covariance matrix in the model and, second, did not show that such a model was statistically distinguishable from a null model with no phylogenetic covariance. Moreover, 37 of the 42 significant pairwise linear correlations among litter quality traits and decay reported in Bengtsson *et al.* (2018) were not significant when species were used as the units of comparison (rather than replicates as in Bengtsson *et al.*, 2018) and regression residuals were corrected for the presence of phylogenetic signal when appropriate (Table S7). For example, Bengtsson *et al.* (2018) reported a significant positive linear relationship between mass loss in the laboratory and litter nitrogen concentration, yet this study found no such support.

These results also indicate that additional nuance may sometimes be needed in the description of interspecific variation in *Sphagnum* traits. For example, phylogenetic signal is present for mass loss in the laboratory but not for mass loss in the field. Bengtsson *et al.* (2016) suggested that the two measurements are positively correlated ($P = 0.0006$) but used all replicates ($N = 155$) as independent data points rather than the number of species ($N = 15$). In fact, all their assessments of trait correlations inflated degrees of freedom by considering each replicate to be an independent data point. When species, rather than replicates, are treated as the units of comparison, this correlation between mass loss in the laboratory and that in the field is not evident (Table S8). Significant correlations between mass loss in the laboratory and various other traits were not observed for mass loss in the field. Laboratory-based measurements of *Sphagnum* decay are perhaps more accurate measurements of intrinsic biomass decomposability as field-based measurements are more heavily influenced by environmental input. If there is an interaction between field decomposition rate estimates and the microenvironment in which the experiment was conducted, as expected, results of such analyses would likely vary from study to study depending on the environmental impacts. Furthermore, annual variation in environmental factors may impact the inference of phylogenetic signal. Biomass increase per area has phylogenetic signal in a wet season (year 2012) but not in a dry season (year 2013) or when the data are averaged over both seasons (Tables S9, S10). The limited growth of many *Sphagnum* species in drier seasons (Bengtsson *et al.*, 2016) may influence patterns of interspecific variation. However, such discrepancies were absent in the other four traits for which data from multiple field seasons were gathered.

Since Darwin's seminal publication of *On the Origin of Species* (Darwin, 1859), biologists have recognised that phylogenetic history plays an essential role in shaping interspecific variation in organismal traits. Phylogenetic conservatism, in which closely related species tend to be more similar than species selected at random from a phylogeny, has been previously invoked without sufficient evidence to explain patterns of interspecific variation in various functional traits of *Sphagnum* peat mosses. Indeed, generalities on how hummock species differ in functional traits relative to hollow species (that is those that differ relative to height-above-water-table) have been based on just one or a few hummock species compared with a similar number of hollow species (for example Johnson & Damman, 1991; Belyea, 1996) before the studies of Bengtsson *et al.* (2016, 2018). The results presented in this study suggest that many *Sphagnum* traits investigated are in fact not phylogenetically conserved, perhaps because the traits are evolutionarily labile and that a high rate of evolution has erased any phylogenetic signal. Although future studies that include a greater number of species are likely to be required to fully describe the suite of functional traits that underlie niche construction in peat mosses, these results demonstrate phylogenetic conservatism in traits related to *Sphagnum* growth, decomposability and some aspects of litter quality, while providing evidence for their correlated evolution with specificity along the ecological hummock-hollow gradient.

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Author contributions

BTP and AJS planned and designed the research. BTP performed data analyses. BTP and AJS wrote the manuscript.

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References

Anacker BL, Klironomos JN, Maherali H, Reinhardt KO, Strauss SY. 2014. Phylogenetic conservatism in plant-soil feedback and its implications for plant abundance. *Ecology Letters* **17**: 1613–1621.

Belyea LR. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* **77**: 529–539.

Belyea LR. 2004. Beyond ecological filters: feedback networks in the assembly and restoration of community structure. In: Tempterton VM, Hobbs RJ, Nuttle T, Halle S, eds. *Assembly rules and restoration ecology: bridging the gap between theory and practice*. Washington, DC, USA: Island Press, 115–131.

Bengtsson F, Granath G, Rydin H. 2016. Photosynthesis, growth, and decay traits in *Sphagnum* - a multispecies comparison. *Ecology and Evolution* **6**: 3325–3341.

Bengtsson F, Rydin H, Hájek T. 2018. Biochemical determinants of litter quality in 15 species of *Sphagnum*. *Plant and Soil* **425**: 161–176.

Benjamini Y, Yekutieli D. 2001. The control of the false discovery rate in multiple testing under dependency. *The Annals of Statistics* **29**: 1165–1188.

Blomberg SP, Garland T Jr, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.

Bouckaert RR, Drummond AJ. 2017. bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology* **17**: 42.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10**: e1003537.

Bragazza L, Freeman C, Jones T, Rydin H, Limpens J, Fenner N, Ellis T, Gerdol R, Hájek T, Iacumin P *et al.* 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proceedings of the National Academy of Sciences, USA* **103**: 19386–19389.

van Breeman N. 1995. How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution* **10**: 270–275.

Breusch TS, Pagan AR. 1979. A simple test for heteroskedasticity and random coefficient variation. *Econometrica* **47**: 1287–1294.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn*. New York, NY, USA: Springer-Verlag, 323–328.

Butler MA, King AA. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist* **164**: 683–695.

Cadotte MW, Livingstone SW, Yasui SLE, Dinnage R, Li JT, Marushia R, Santangelo J, Shu W. 2017. Explaining ecosystem multifunction with evolutionary models. *Ecology* **98**: 3175–3187.

Clavel J, Escarguel G, Merceron G. 2015. mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution* **6**: 1311–1319.

Clymo RS, Hayward PM. 1982. The ecology of *Sphagnum*. In: Smith AJE, ed. *Bryophyte ecology*. London, UK: Chapman & Hall, 229–289.

Coulson JC, Butterfield J. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *Journal of Ecology* **66**: 631–650.

Cressler CE, Butler MA, King AA. 2015. Detecting adaptive evolution in phylogenetic comparative analysis using the Ornstein-Uhlenbeck model. *Systematic Biology* **64**: 953–968.

Darwin C. 1859. *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*. London, UK: John Murray, 80–170.

Dawkins R. 1982. *The extended phenotype: the long reach of the gene*. Oxford, UK & New York, NY, USA: Oxford University Press, 195–208.

Drummond AJ, Ho SY, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: e88.

Durbin J, Watson GS. 1950. Testing for serial correlation in least squares regression, I. *Biometrika* **37**: 409–428.

Durbin J, Watson GS. 1951. Testing for serial correlation in least squares regression, II. *Biometrika* **38**: 159–179.

Elumeeva TG, Soudzilovskaia NA, During HJ, Cornelissen JHC. 2011. The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. *Journal of Vegetation Science* **22**: 152–164.

Felsenstein J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125**: 1–15.

Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1**: 182–195.

Grafen A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B: Biological Sciences* **326**: 119–157.

Hájek T. 2009. Habitat and species controls on *Sphagnum* production and decomposition in a mountain raised bog. *Boreal Environment Research* **14**: 947–958.

Hájek T, Balance S, Limpens J, Zijlstra M, Verhoeven JTA. 2011. Cell-wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition *in vitro*. *Biogeochemistry* **103**: 45–57.

Hassel K, Kyrkjeeide MO, Yousefi N, Prestø T, Stenøien HK, Shaw AJ, Flatberg KI. 2018. *Sphagnum divinum* (*sp. nov.*) and *S. medium* Limpr. and their relationship to *S. magellanicum* Brid. *Journal of Bryology* **3**: 197–222.

Hogg EH. 1993. Decay potential of hummock and hollow peats at different depths in a Swedish raised bog. *Oikos* **66**: 269–278.

Horton DG, Vitt DH, Slack NG. 1979. Habitats of circumboreal-subarctic sphagna: I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. *Canadian Journal of Botany* **57**: 2283–2317.

Ives AR. 2019. R^2s for correlated data: phylogenetic models, LMMs, and GLMMs. *Systematic Biology* **68**: 234–251.

Ives AR, Midford PE, Garland T Jr. 2007. Within-species variation and measurement error in phylogenetic comparative methods. *Systematic Biology* **56**: 252–270.

Johnson LC, Damman AWH. 1991. Species-control *Sphagnum* decay on a south Swedish raised bog. *Oikos* **61**: 234–242.

Johnson MG, Granath G, Tahvanainen T, Pouliot R, Stenøien HK, Rochefort L, Rydin R, Shaw AJ. 2015. Evolution of niche preference in *Sphagnum* peat mosses. *Evolution* **69**: 90–103.

Jones CH, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.

Laing CH, Granath G, Belyea LR, Allton KE, Rydin H. 2014. Tradeoffs and scaling of functional traits in *Sphagnum* as drivers of carbon cycling in peatlands. *Oikos* **123**: 817–828.

Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* **30**: 3276–3278.

Lefcheck JS. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* **7**: 573–579.

Limpens J, Berendse F. 2003. How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* **103**: 537–547.

Limpens J, Bohlin E, Nilsson MB. 2017. Phylogenetic or environmental control on the elemental and organo-chemical composition of *Sphagnum* mosses? *Plant and Soil* **417**: 69–85.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist* **149**: 646–667.

Mazziotta A, Granath G, Rydin H, Bengtsson F, Norberg J. 2018. Scaling functional traits to ecosystem processes: towards a mechanistic understanding in peat mosses. *Journal of Ecology* **107**: 843–859.

Moore TR, Bubier JL, Bledzki L. 2007. Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. *Ecosystems* **10**: 949–963.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**: 133–142.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018. *caper: comparative analyses of phylogenetics and evolution in R. CRAN: R*

package v.1.0.1. [WWW document] URL https://CRAN.R-project.org/package=caper/.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, FitzJohn RG, Alfaro ME, Harmon LJ. 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30**: 2216–2218.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2018. *nlme: linear and nonlinear mixed effects models. CRAN: R package version 3.1-137*. [WWW document] URL https://CRAN.R-project.org/package=nlme/.

R Core Team. 2018. *R: a language and environment for statistical computing. Version 3.5.0*. R Foundation for Statistical Computing, Vienna, Austria. [WWW document] URL https://www.R-project.org/

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**: 901–904.

Reader RJ, Stewart JM. 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. *Ecology* **53**: 1024–1037.

Revell LF. 2010. Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* **1**: 319–329.

Rochefort L, Vitt DH, Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimental acidified conditions. *Ecology* **71**: 1986–2000.

Rydin H, Jeglum JK. 2013. *The biology of peatlands*, 2nd edn. Oxford, UK & New York, NY, USA: Oxford University Press, 199–229.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika* **53**: 591–611.

Shaw AJ, Cox CJ, Buck WR, Devos N, Buchanan AM, Cave L, Seppelt R, Shaw B, Larraín J, Andrus R *et al.* 2010. Newly resolved relationships in an early land plant lineage: Bryophyta class Sphagnopsida (peat mosses). *American Journal of Botany* **97**: 1511–1531.

Shaw AJ, Devos N, Liu Y, Cox CJ, Goffinet B, Flatberg KI, Shaw B. 2016. Organellar phylogenomics of an emerging model system: *Sphagnum* (peatmoss). *Annals of Botany* **118**: 185–196.

The Plant List. 2013. *The Plant List: a working list of all plant species. Version 1.1*. [WWW document] URL http://www.theplantlist.org/. [accessed 14 March 2019].

Thormann MN, Bayley SE, Currah RS. 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. *Canadian Journal of Botany* **79**: 9–22.

Turetsky MR, Crow SE, Evans RJ, Vitt DH, Wieder RK. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology* **96**: 1297–1305.

Uyeda JC, Zenil-Ferguson R, Pennell MW. 2018. Rethinking phylogenetic comparative methods. *Systematic Biology* **67**: 1091–1109.

Valverde-Barrantes OJ, Smemo KA, Blackwood CB. 2014. Fine root morphology is phylogenetically structured, but nitrogen is related to the plant economics spectrum in temperate trees. *Functional Ecology* **29**: 796–807.

Vitt DH, Slack NG. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. *Canadian Journal of Botany* **62**: 1409–1430.

Warren DL, Geneva AJ, Lanfear R. 2017. RWTY (R We There Yet): an R package for examining convergence of Bayesian phylogenetic analyses. *Molecular Biology and Evolution* **34**: 1016–1020.

Yu ZC. 2012. Northern peatland carbon stocks and dynamics: a review. *Biogeosciences* **9**: 4071–4085.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Sequences used for phylogenetic reconstruction.

Table S1 bModelTest substitution model posterior support for each dataset partition.

Table S2 Evolutionary model selection for trait and niche variables.

Table S3 Quantification of phylogenetic signal using Pagel's λ and Blomberg's *K* for trait and niche variables.

Table S4 Summary of linear regression models.

Table S5 Summary of multivariate evolutionary models.

Table S6 Comparison of results from analyses of trait and niche variable correlation.

Table S7 Comparison of linear regressions conducted by this study and Bengtsson *et al.* (2018).

Table S8 Comparison of linear regressions conducted by this study and Bengtsson *et al.* (2016).

Table S9 Evolutionary model selection for traits by individual field season.

Table S10 Quantification of phylogenetic signal using Pagel's λ and Blomberg's *K* for traits by individual field season.

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