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Evolution of niche preference in *Sphagnum* peat mosses

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Peat mosses (*Sphagnum*) are ecosystem engineers—species in boreal peatlands simultaneously create and inhabit narrow habitat preferences along two microhabitat gradients: an ionic gradient and a hydrological hummock–hollow gradient. In this article, we demonstrate the connections between microhabitat preference and phylogeny in *Sphagnum*. Using a dataset of 39 species of *Sphagnum*, with an 18-locus DNA alignment and an ecological dataset encompassing three large published studies, we tested for phylogenetic signal and within-genus changes in evolutionary rate of eight niche descriptors and two multivariate niche gradients. We find little to no evidence for phylogenetic signal in most component descriptors of the ionic gradient, but interspecific variation along the hummock–hollow gradient shows considerable phylogenetic signal. We find support for a change in the rate of niche evolution within the genus—the hummock-forming subgenus *Acutifolia* has evolved along the multivariate hummock–hollow gradient faster than the hollow-inhabiting subgenus *Cuspidata*. Because peat mosses themselves create some of the ecological gradients constituting their own habitats, the classic microtopography of *Sphagnum*-dominated peatlands is maintained by evolutionary constraints and the biological properties of related *Sphagnum* species. The patterns of phylogenetic signal observed here will instruct future study on the role of functional traits in peatland growth and reconstruction.

KEY WORDS: **Bryophyte, comparative methods, peatland ecology, phylogenetic signal.**

Boreal peatlands are not just dominated by *Sphagnum* peat mosses—they are engineered by them (van Breemen 1995). Habitat variation within a peatland ecosystem can be substantial, and is generally characterized along two gradients (Rydin and Jeglum 2013)—an electrochemical gradient (defined by pH and other cations) and a hydrological gradient (variation in the availability of ground water due to microtopography). Some *Sphagnum* species both create and inhabit the raised microtopographic features (hummocks) because of their growth forms (Laing et al. 2014), water transport abilities (Granath et al. 2010), and low decay rates (Belyea 1996). The plants produce large amounts of organic acids, contributing to a lower pH, and yet maintain an effective uptake of solutes through cation exchange in extremely nutrient poor environments (Hemond 1980). By creating an environment that is wet, acidic, and anoxic (Clymo 1963), *Sphagnum* decomposes slowly and thereby triggers peat accumulation.

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Within these gradients, *Sphagnum* species are known to differentiate into narrow microhabitat preferences: in one survey in New York State, *Sphagnum contortum* was found only in areas with pH above 6.0, whereas *S. majus* was found only below pH 5.0 (Andrus 1986). Similar differentiation has been observed in other peatlands along the hummock–hollow and electrochemical gradients (Vitt and Slack 1984; Gignac 1992; Rochefort et al. 2012; Rydin and Jeglum 2013). Experimental transplants have revealed that while hummock-preferring species can survive more aquatic environments, a hollow-preferring species cannot survive the more stressful hummock environment (Rydin et al. 2006). Within hummock environments, some hummock species depend on the presence of other specific species for optimal establishment and growth (Chirino et al. 2006). The development and maintenance of boreal peatland ecosystems thus depends on the facilitation and competition of many species within the same genus.

What makes the microhabitat differentiation in *Sphagnum* more remarkable is the relatively young age of most *Sphagnum* species. The class Sphagnopsida is one of the earliest diverging groups of mosses, splitting from the rest of Bryophyta about 380 million years ago (mya; Newton et al. 2009). However, nearly all extant *Sphagnum* species originate from a radiation just about 14 mya (Shaw et al. 2010b), coinciding with the end of the mid-Miocene climatic optimum and the appearance of peatland ecosystems in the northern boreal zone. Of the 250–300 extant species of *Sphagnum* resulting from this radiation, approximately 40 of these species have circumboreal distributions and can be commonly found in peatlands throughout the high latitudes of the Northern Hemisphere. In a relatively small amount of geologic time, these 40 species have shaped peatland ecosystems through their extended phenotypes and microhabitat preferences.

Given the recent radiation of species, their narrow observed preferences and perhaps narrow physiological tolerances, it is reasonable to expect that microhabitat preferences in *Sphagnum* exhibit "phylogenetic signal"—closely related species are expected to be more similar than randomly selected species on a phylogeny (Blomberg and Garland 2002). However, despite many years of observing ecology of *Sphagnum* (reviewed in Clymo and Hayward 1982; Rydin and Jeglum 2013), the presence of phylogenetic signal has not been tested.

When considering the evolution of ecological niche descriptors, it is useful to distinguish between β-niche—climatic tolerances or macrohabitat affinity—and α-niche, within-community microhabitat affinity (Ackerly et al. 2006). Many studies model ecological niches using climatic BIOCLIM data from public databases, for example (Boucher et al. 2012), and focus on β-niches because data on α-niches are unavailable or impractical to collect. In cases where the α-niche is considered, phylogenetic signal can suggest whether habitat preferences underlie community assembly (Cavender Bares et al. 2004) and whether phylogenetic signal has been overwhelmed and erased for evolutionarily labile traits (Eterovick et al. 2010). Labile traits such as behavior (Blomberg et al. 2003) and ecological niche (Losos 2008) may not show phylogenetic signal. For ecological traits, phylogenetic signal must be demonstrated before inferences about, for example, community assembly or niche conservatism can be made.

Subgeneric classification in *Sphagnum* already gives some clue about phylogenetic signal of microhabitats in the genus. Two monophyletic subgenera, *Cuspidata* and *Subsecunda*, are generally characterized by species living at or near the water table (hollow), whereas members of subgenera *Acutifolia* and *Sphagnum* (also monophyletic) are more likely to form hummocks high above the water table. It was recently shown that although *Sphagnum* has a large cation exchange capacity, it does not exceed the capacity of other peatland mosses (such as brown mosses, Soudzilovskaia et al. 2010). This suggests that peatland acidification along the fen–bog gradient is due to peat accumulation, not to the actions of live *Sphagnum* plants. Therefore, phylogenetic signal may be more easily detected in hummock/hollow microhabitat descriptors, compared to the pH/ionic gradient.

The evolution of continuous traits on a phylogeny is commonly modeled using Brownian motion (BM), which predicts that trait variance increases along the phylogeny from root to tip (Felsenstein 1985). The BM pattern, however, may be masked by several factors, each of which is addressed by additional models. If the rate of trait evolution is not constant along the phylogeny, or the trait has accumulated more variance than is predicted by BM, the model may be a poor fit for the phylogeny and trait. Pagel (1999) developed models to detect phylogenetic signal under these conditions: a *lambda* model allowing for greater trait variance, and a *delta* model predicting that trait variance has accumulated faster at the root of the phylogeny compared to the tips.

The presence of one or more optimal trait values for *Sphagnum* species would constrain the trait evolution to values close to these optima. For instance, there may be an "ideal" pH preference for *Sphagnum* species, and therefore evolution of this niche descriptor would be constrained among *Sphagnum* species due to forces such as stabilizing selection (sensu Hansen 1997). Finally, if the rate of evolution in microhabitat preference is unconstrained or extremely fast, then phylogenetic signal for that trait may become undetectable.

Demonstration of phylogenetic signal for microhabitat preference in *Sphagnum* would further suggest that the underlying functional traits (such as growth rate, decomposition rate, water retention, or cation exchange ability, see, e.g., Rice et al. 2008 and Turetsky et al. 2008) would also show similar patterns. Presence of phylogenetic signal would provide information on how

contrasting peatland habitats (fens and bogs) and microhabitats (hummock and hollows) have developed over evolutionary time. This would guide the focus of future studies on functional traits and the Neogene development of peatland ecosystems.

In this study, we test whether *Sphagnum* microhabitat descriptors show phylogenetic signal using a variety of comparative models to test the tempo, direction, and heterogeneity of microhabitat niche evolution in the genus. To do this, we use ecological niche data for 39 *Sphagnum* species from three large published studies in northern Europe and North America, construct a phylogenetic tree using sequences from 18 genes, and analyze the comparative dataset containing eight univariate niche descriptors and two principal components representing the environmental gradients. Using methods designed to account for phylogenetic uncertainty and within-species measurement error, we test whether any of the niche descriptors (1) has phylogenetic signal; (2) whether this signal corresponds to or deviates from BM; and (3) if changes in evolutionary rates can be detected within *Sphagnum*.

Materials and Methods

NICHE DIFFERENTIATION

Peatland ecologists have noted the specificity of *Sphagnum* species along electrochemical and hydrological gradients for more than 40 years (Clymo 1973; Vitt and Slack 1984; Andrus 1986), and ideally, we would have used the microhabitat data from all available studies. However, we chose to focus on three recent major surveys of *Sphagnum* microhabitat specificity to ensure consistent measurements, the largest selection of species, and the most modern *Sphagnum* taxonomy. The three selected large surveys each recorded data from eight niche descriptors: Height above water table (HWT), percent vascular plant cover (as an indicator of shade), pH, electrical conductivity (EC), and several ionic concentrations (Ca, K, Mg, and Na). Each study represents a number of sites, and within each site, data were recorded for a number of plots along transects. Plot sizes varied among studies, with 25 × 25 cm square plots in Estonia, 50 × 50 cm square plots in Finland, and 70 cm diameter circular plots in Canada. In each plot, the eight niche descriptors were recorded, as well as the presence and relative abundance of each species in the plot. Each plot, therefore, may represent a datapoint for one or more species.

The first survey covered 498 sites in eastern (2647 datapoints) and western (944 datapoints) Canada (Gignac et al. 2004). The second study also included two areas of Canada: 23 sites in Quebec and New Brunswick (1369 datapoints) and one area in Estonia (Europe) where 11 sites were surveyed (389 datapoints, Pouliot 2011). The third study included 36 sites (714 datapoints across 29 mire complexes) in eastern Finland located in the mid-boreal zone (Tahvanainen 2004). Two of the mire complexes were sampled intensively in a separate substudy of 270 plots (258 datapoints; Tahvanainen et al. 2002). Taken together, these data represent 6533 observations of *Sphagnum* microhabitat associations, by far the most comprehensive dataset of its kind.

Fusion of the three major studies allows us to be confident that if a species was not observed in any plots, it is not a major contributor to boreal peatland diversity in Canada or northern Europe. A total of 40 species were recorded, but we excluded *S. auriculatum* because of low sample size ($N = 1$), yielding 39 species in the final dataset. Data were summarized across the three studies by weighting the means and SDs of each species by percent cover of the sampled plots, that is, giving more weight to plots where the species covered a larger area. Because most species occur in all regions covered by the three studies, we estimated the overall mean and variation in niche descriptors, across all sites and plots. This estimate will therefore not account for different ecotypes or large-scale (continental) differences in environmental conditions, but is instead a generalized estimate of the realized niche for each *Sphagnum* species.

The niche descriptor (ecological trait) for each species was transformed so that its mean was zero and its SD across the genus was 1. In addition to univariate descriptors, we also investigated the evolution of microhabitat niche in a multivariate sense, using a principal components transformation on all eight niche descriptors. The principal component analysis (PCA) scores from the first two ordinates (Fig. 1) were included in the analyses below. We also repeated the analyses using nonmetric multidimensional scaling (NMDS), but representing multivariate niche by this alternative ordination did not alter our major conclusions (results not shown).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

For each of the 39 *Sphagnum* species, we sampled representative DNA sequences from GenBank and from a database maintained by AJS; most sequences have been submitted previously, previously unpublished samples are identified as such in Table S1. We also selected one sample each of *Flatbergium serecium* and *Eosphagnum inretortum*, representing early diverging members of class Sphagnopsida, to serve as outgroups (Shaw et al. 2010a). Previous studies (Shaw et al. 2003b, 2010a) used 24 species to demonstrate that *Sphagnum* has four major monophyletic subgenera: *Sphagnum*, *Subsecunda*, *Cuspidata*, and *Acutifolia*. Our sampling of 39 species covers all four subgenera (Fig. 1) with more species in the latter two subgenera.

We followed protocols described in (Shaw et al. 2003b) to sample sequences from the following genes: photosystem II (PSII) reaction center protein D1 (*psbA*), PSII reaction center protein T (*psbT-H*), ribulose-bisphosphate carboxylase gene

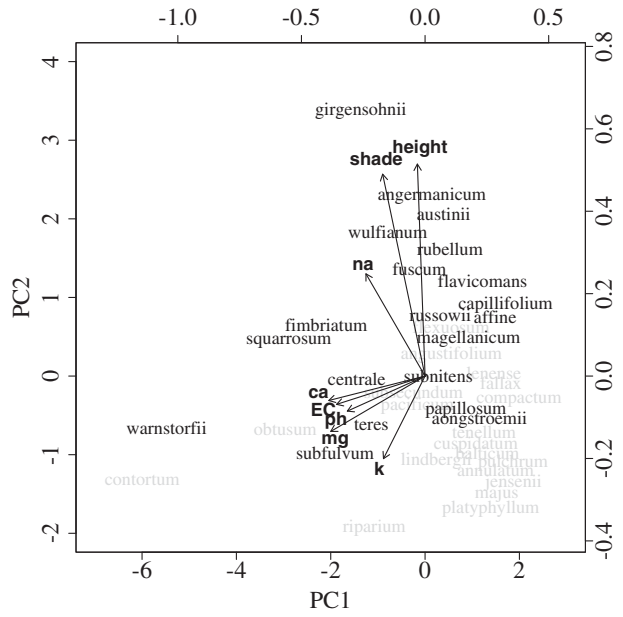

Figure 1. Biplot of principal components analysis (PCA) for eight microhabitat preferences in 39 species of *Sphagnum*. Each species is plotted in Euclidian space for the first two principal components, which cumulatively represent 61.4% of the total variance. Loadings upon each axis are indicated by arrows and lines—PC1 (43.9% of total variance) is a "pH–ionic gradient," whereas PC2 (17.5% of total variance) is predominantly a "hummock–hollow" gradient. Species in black are in subgenera characterized by hummock habitats (*Sphagnum* and *Acutifolia*), whereas species in gray are in subgenera characterized by hollow habitats (*Subsecunda* and *Cuspidata*). Left and bottom axes represent PC scores, right and top axes represent niche trait loadings upon the principal components.

(*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*) from the plastid genome; introns within NADH protein-coding subunits 5 and 7 (*nad5*, *nad7*, respectively) from the mitochondrial genome; the nuclear ribosomal internal transcribed spacer (ITS) region, two introns in the nuclear LEAFY/FLO gene (*LL* and *LS*), three anonymous nuclear regions (*rapdA*, *rapdB*, *rapdF*), and two sequenced nuclear microsatellite loci (*ATGc89* and *A15*) from the nuclear genome. Primer sequences for amplifying and sequencing for most loci were provided in Shaw et al. (2003b). For *rpoC1*, we used primers described in the Royal Botanic Gardens, Kew, web page: DNA Barcoding, phase 2 protocols (http://www.kew.org/barcoding/protocols.html). For the two microsatellite-containing loci, we used primer sequences: A15—F: 5′TGTGGAGACCCAAGTGAATG3′ R: 5′GGTGATGCTCAAAGGGCTTA3′; ATGc89—F: 5′CGTCGAACGGATTCAAAAAT3′ R: 5′AGGGGAAGAGACCATCAGGT3′. We used the Duke University Sequencing facility for Sanger sequencing of all samples. For GenBank accession numbers, see Table S1.

PHYLOGENETIC RECONSTRUCTION

Although phylogenetic relationships within the genus are not the primary focus of this study, it is worth noting that our taxon sampling (39 species) and genomic sampling (seven nuclear, eight chloroplast, and two mitochondrial genes) are the largest species-level phylogenetic analysis of *Sphagnum* to date.

Individual genes were aligned using MUSCLE (Edgar 2004) and adjusted manually using PhyDE (Muller et al. 2010). When concatenated, the dataset contained 14,918 characters, of which 636 were parsimony informative (Table S1). To obtain ultrametric trees required for phylogenetic comparative methods, we reconstructed the *Sphagnum* phylogeny via Bayesian inference on a concatenated 18-gene alignment, using BEAST (Drummond et al. 2012). For each gene, we chose a substitution model using the Bayesian information criterion from jModelTest (Guindon and Gascuel 2003; Posada 2008; Table S1). Branch lengths were inferred using uncorrelated relaxed clock model and a lognormal branch length prior, one model for each gene separately. We confirmed convergence to the same joint posterior distribution by replicating the BEAST analysis ($N = 2$), and visualizing the likelihood and parameter estimates from the two runs using Tracer version 1.75 (Rambaut and Drummond 2014). In each analysis, the chain ran for 200 million generations, sampling every 10,000 steps following a 20 million generation burnin. We summarized the 18,000 trees from the posterior distribution using a maximum credibility tree calculated by TreeAnnotator (Drummond et al. 2012), with node heights set to the median branch lengths. To marginalize phylogenetic uncertainty (topology and branch lengths) in the comparative methods, we randomly selected 1000 trees from the posterior density for most analyses.

EVOLUTION OF NICHES: MODEL CHOICE

Testing models of comparative evolution has recently become much easier because all of the models can be implemented and connected using the phylogenetic package ape (Paradis et al. 2004) in the statistical programming environment R (R Core Development Team, www.R-project.org). On each ecological niche descriptor, we evaluated the fit of three main models of evolution (Table 1). (1) White noise (*WN*)—the trait values are independent of phylogenetic distance; this represents our baseline model. Under this model, all internodes on the phylogeny are set to zero length, creating a star phylogeny—all trait evolution occurs at the tips, and phylogeny and trait variance are therefore completely unrelated. By using WN as a baseline, we assert that alternative models (below) must demonstrate better fit to the data than a model where the phylogeny does not contribute to trait evolution. Any model with a sample-size corrected Akaike information

Table 1. **Detailed information about the eight models of trait evolution tested.**

Model	Abbreviation	Description	Parameters	Equivalent to
White noise	WN	Trait values independent of phylogenetic distance	Covariance	
Brownian motion	BM	Trait variance increases with phylogenetic distance	β—Rate of evolution	WN if $\beta = \infty$
Brownie 2-rate	BM2	Separate rates of evolution in *Acutifolia* versus *Cuspidata*	β—Rate of evolution (one for each group)	
Ornstein–Uhlenbeck	OU	Random walk with central tendency (stabilizing selection)	β—Rate of evolution; α—strength of selection; θ—trait optimum	BM if $\alpha = 0$; WN If $\alpha = \infty$
Ornstein–Uhlenbeck	OU2	OU model with different optima for *Acutifolia* versus *Cuspidata*	β—rate of evolution; α—strength of selection; θ—trait optimum (one for each group)	
Lambda	lambda	Internal branch lengths multiplied; deviation from pure BM	β—rate of evolution, λ—multiplier	BM if $\lambda = 1$; WN if $\lambda = 0$
Delta	delta	Internal branch lengths raised to a power; if $\delta > 1$: evolution concentrated in tree tips	β—rate of evolution; δ—multiplier	BM if $\delta = 1$

For each model, the parameters estimated by maximum likelihood and the nesting of each model are also indicated.

criterion (AICc) score exceeding the score for WN is not a plausible alternative.

(2) BM—the trait increases in variance through evolutionary time at a constant rate (beta). Although this is the standard phylogenetic comparative model, signal may be masked by several other patterns of trait evolution, which are addressed with the remaining models. (3) Ornstein–Uhlenbeck (OU) model (Martins and Hansen 1997)—although the evolution of the trait contains phylogenetic signal, evolution is constrained by a strength parameter (alpha), causing the trait to trend toward an optimum value (theta). Two of the other models are nested within the OU model: BM (alpha = 0) and WN (alpha = infinite).

If either of the alternative models (OU or BM) is accepted, we further evaluate the fit of these models through two evolutionary parameters: The *Lambda* parameter (Pagel 1994)—the trait has phylogenetic signal, but deviates from a pure BM process. Specifically, the phylogenetic covariance is multiplied by a scalar, which is inferred via maximum likelihood. The WN model (lambda = 0) and BM model (lambda = 1) are nested within the lambda model, in which lambda is inferred as a free parameter. Values between 0 and 1 correspond to an "imperfect" BM model, where only some proportion (lambda) of the trait variance can be explained by phylogeny. The *Delta* parameter (Pagel 1997)—all node depths are raised to the power delta—values less than 1 provide evidence that much/most trait evolution occurred deep (early) in the phylogeny, whereas values greater than 1 indicate trait evolution concentrated in the tips. The BM (delta = 1) and WN (delta = infinite) models are nested within the WN model. For both the lambda and delta models, we can infer whether it is a better fit than the BM model (via a likelihood ratio test) and whether the maximum likelihood values inferred on 1000 trees significantly deviates from WN (lambda = 0) or BM (lambda and delta = 1) using one-tailed tests.

We fit the WN, BM, and lambda models using the R package phytools (Revell 2011), the delta model with geiger (Harmon et al. 2008), and the OU model was fitted using the pmc_fit method of the package pmc (Boettiger et al. 2012).

Many sources of error exist in the estimation of mean trait values for species, and phylogenetic comparative methods are improved when they account for measurement error (Ives et al. 2007). For each niche descriptor, we used methods in phytools for the BM, lambda, and delta models to incorporate measurement

error (SE, incorporating both SD and sample size); incorporation of measurement error is not implemented in pmc_fit, so it is absent from the OU models.

RATE CHANGES WITHIN *SPHAGNUM*

All of the methods above assume constant conditions on the entire *Sphagnum* phylogeny. To incorporate the possibility of different rates of niche evolution within the tree, which would mask the pattern when considering the entire genus, we used two different methods. In our first approach, we pruned the phylogeny to contain only members of subgenera *Acutifolia* and *Cuspidata*, which represented the two largest subgenera sampled. Every branch on the phylogeny was classified as an *Acutifolia* or a *Cuspidata* lineage. We tested whether a model allowing different rates of niche evolution in the two lineages (*BM2*) was supported over a single-rate model (*BM1*, the "Brownie" model; O'Meara et al. 2006), using the brownie.lite method in phytools. We also tested whether an OU model with different trait optima for the *Acutifolia* and *Cuspidata* lineages (*OU2*) was supported over a single-optimum *OU1* model, using pmc.

To visualize phylogenetic signal and rate change within the reduced dataset, we created traitgrams for the two principal components. A traitgram is constructed by reconstructing the ancestral traits for every node on the chronogram. The *x*-axis in a traitgram corresponds to time, whereas the *y*-axis corresponds to the reconstructed trait values. Our trait reconstructions and traitgrams were plotted using the "phenogram" function in the phytools package.

We also used a Bayesian MCMC approach on the full *Sphagnum* phylogeny to identify nodes where rate changes have occurred (Revell et al. 2012). This method samples evolutionary rates and locations of exceptional rate shifts in proportion to their posterior probability, which does not require any a priori hypothesis about the location of rate shifts. We ran the MCMC implemented in phytools under the default priors for evolutionary rate and proposal frequency, for 10,000 generations, sampling every 100 generations (the first 20 samples were discarded as burnin).

TAXON SAMPLING AND PHYLOGENETIC UNCERTAINTY

We conducted a sensitivity analysis to test whether individual species affected the fit of evolutionary models—for example, due to the wide variance in sampling frequency among *Sphagnum* species. Using the maximum credibility tree from BEAST, we analyzed each model for each descriptor 39 times, deleting one *Sphagnum* species each time. We compared the support for each model on the reduced trees to the WN model to assess the sensitivity for each descriptor.

Most phylogenetic comparative methods also unrealistically assume that the tree (topology and branch lengths) is known without error. To incorporate phylogenetic uncertainty into the model fitting procedure, we tested each model on 1000 trees randomly sampled from the BEAST posterior distribution. We recorded, for each descriptor and tree, the AICc scores for each model. The distribution of the AICc scores for each model and descriptor is an indication of model fit, averaged over phylogenetic uncertainty (Boucher et al. 2012). For the Bayesian MCMC approach, we used only the maximum credibility tree from BEAST.

For descriptors found to have significant phylogenetic signal, we used a phylogenetic generalized least squares (PGLS) model (Freckleton et al. 2002) to evaluate their correlated evolution, using the R package caper (Orme et al. 2011). For this analysis, the residuals were modeled using the best-supported model in the full analysis.

Results

NICHE DIFFERENTIATION

There is much variation in within-species sample sizes in the ecological dataset, from three (*S. wulfianum*) to 1055 (*S. fuscum*), reflecting the relative abundances of species in the study sites (Table S2). Among-species SD was lowest for pH and highest for shade. Microhabitats are grouped into two principal components (Fig. 1): PC1 representing an ionic gradient (excluding Na), and PC2 representing the "hummock–hollow gradient" (sodium along with HWT and percent shade). The first two PC axes accounted for 47.3% and 17.7% of the total variance, respectively. Variations along the sodium gradient may reflect the proximity to the sea, which was not tracked in the present study.

The covariation of shade and HWT mainly reflects the abundance of dwarf shrubs on hummocks and the relative scarcity of vascular plants in hollow habitats. The differentiation among subgenera confirms the picture that *Acutifolia* are largely hummock species (higher on PC2), and *Cuspidata* largely hollow inhabitants (lower on PC2), but there are some species deviating from this general pattern (Fig. 1). For example, *S. subfulvum* (subgenus *Acutifolia*) has a low PC2 score, whereas *S. flexuosum* (subgenus *Cuspidata*) is high on that scale. Notably, the subgenus *Sphagnum* is quite variable in HWT. On the ionic gradient, there is less agreement with subgeneric classification.

PHYLOGENETIC RECONSTRUCTION

Each gene in the DNA sequence matrix had varying amounts of missing data, ranging from two sequences missing (ITS) to 29 (nad5 and nad7), whereas sampling for each species ranged from two genes to the full 18 (Table S1). The maximum credibility tree from the Bayesian inference, using BEAST, is presented in Figure S1. The amount of missing data in the alignment does not appear to deflate support for the maximum credibility tree. All major subgenera are resolved at 99% posterior probability or

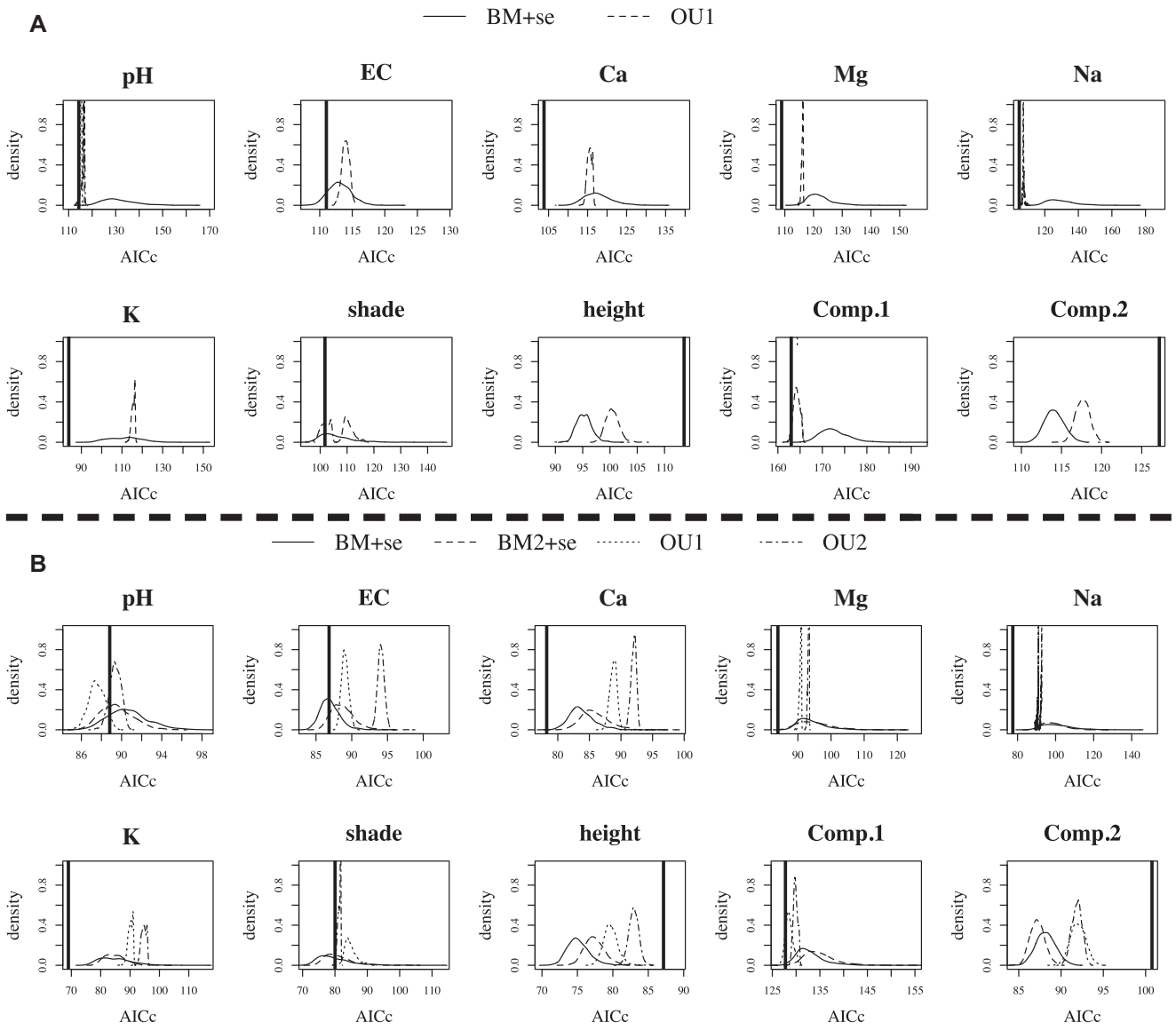

Figure 2. **Model choice using AICc distributions for alternative models of continuous trait evolution, on six niche descriptors—pH, electrical conductivity (EC), concentrations of potassium (K), sodium (Na), magnesium (Mg), and calcium (Ca), percent shade cover, and height above water table (HWT) and the first two principal components across 1000 trees. (A) The full dataset (all of *Sphagnum*). For each niche descriptor, the distribution of AICc scores is shown for Brownian motion (BM) and Ornstein–Uhlenbeck stabilizing selection model (OU). (B) The reduced dataset (subgenera *Acutifolia* and *Cuspidata* only), used to detect changes in niche preference evolution within the genus. For each niche descriptor, the AICc curves for BM1 (one rate) versus BM2 (separate rates) and OU1 (one optimum) versus OU2 (separate optima) are plotted. In each panel, the thick black line indicates the AICc score for white noise (no phylogenetic signal). Lower AICc scores are better; models with AICc distributions falling mostly or entirely to the left of the WN line are preferred.**

greater, while relationships among subgenera are less supported. This is consistent with previous reconstructions of *Sphagnum* phylogeny when both chloroplast and nuclear genomes are used (Shaw et al. 2010a). Notably, among-subgenera median branch lengths are very short; therefore, comparative methods that consider only phylogenetic distance (and not topology) should be relatively unaffected by topological uncertainty.

FULL DATASET: MODEL CHOICE

For five of the six ionic niche dimensions (pH, Ca, Mg, Na, and K), the model that best fits the data across all trees was *WN*, based on the AICc criterion, indicating a lack of phylogenetic signal for these niche descriptors (Table S3). These niche descriptors contribute primarily to the pH–ionic first principal component (except Na, Fig. 1), the evolution of which also is best fit by the white noise

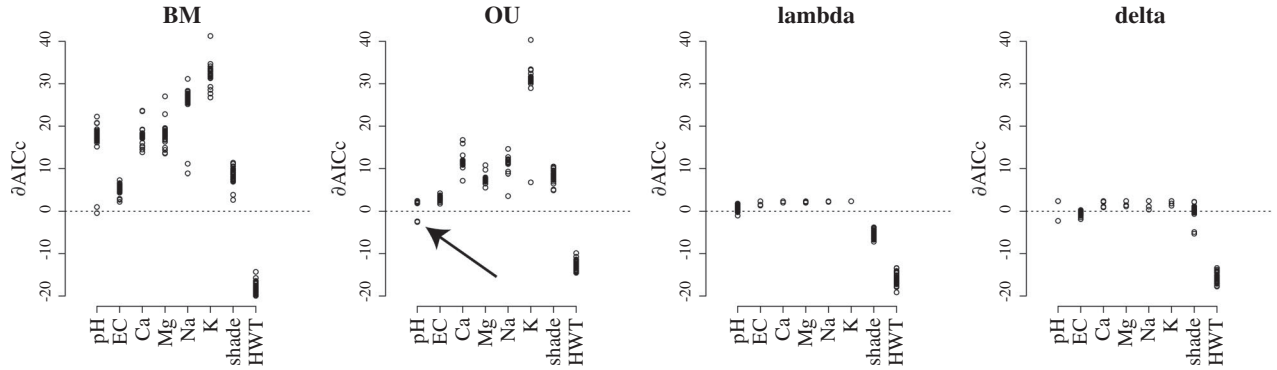

Figure 3. Sensitivity analysis for model selection in the full *Sphagnum* dataset. Each panel shows one of the four models of evolution at each of the eight niche descriptors (see Table 1 for a key to models). Each point represents the support for the model when individual species were removed from the maximum credibility tree. The *y*-axis is the ∂AICc score compared to WN (no phylogenetic signal). If the points for a model cross the line, it means that deletion of specific species from the analysis changes the interpretation of that model. For example, the arrow indicates two points, representing *S. magellanicum* and *S. centrale*. When either of these species is deleted, AICc supports the OU model (single optimum preference in *Sphagnum*) for pH. In all other combinations, the OU model is rejected for pH (points above the line).

model (Table S3 and Fig. 2A). There was little variability in the fit of the lambda model across all trees for a few niche descriptors, such as Ca and K (Fig. 2A). In these cases, the values of lambda inferred are very close to zero, providing additional evidence for lack of phylogenetic signal in these descriptors. On 79.7% of the trees, AICc supports *delta* model over *WN* for EC. Values of delta ranging from 2.33 to 18.51 suggest microhabitat evolution is extremely concentrated at the tips—as the value of delta increases to infinity, the delta model collapses to the *WN* model.

For pH, inferred lambdas range from 0.17 to 0.40, but *lambda* never exceeded *WN* in AICc on any of the 1000 trees. Additionally, a likelihood ratio test between *lambda* and *WN* on each tree fails to achieve significance at the $P < 0.05$ level on any tree (results not shown).

In contrast, models of phylogenetic signal are unambiguously a better fit than white noise for two traits—percent cover (shade) and HWT (Fig. 2A and Table S3). The *lambda* model best fits the data for shade, with values of lambda ranging from 0.50 to 0.71. Besides *lambda*, none of the other models were a better fit than *WN* for shade. Among the univariate traits, HWT shows the highest support for phylogenetic signal. The best model was *BM* with a single rate across *Sphagnum*, although all models tested have better AICc scores than *WN*. The distributions of AICc scores for shade, HWT, and PC2 (the hummock–hollow gradient) all indicate phylogenetic signal is strongly supported on all 1000 trees (Fig. 2A).

Sensitivity analyses indicate that the data are generally robust to influence from individual species. In nearly all cases, the AICc score difference between a model and *WN* changes very little, and we almost never observe a model losing support after deletion of individual species (Fig. 3). There are two exceptions: deletion of either *S. magellanicum* or *S. centrale* results in support for the *OU* model for pH, each of which showed a ∂AICc > 7, compared to *WN* (Fig. 2A).

Without phylogenetic correction, the species means for shade and HWT are significantly positively correlated ($t = 2.55$, $r = 0.36$, $P = 0.015$). Using the maximum credibility tree, a test for correlated evolution using lambda as a free parameter was not significant ($t = 1.92$, $r = 0.07$, $P = 0.062$). Because the correlation weakens when accounting for phylogeny, the small but significant correlation observed between shade and HWT may be derived from phylogenetic signal.

RATE CHANGE WITHIN *SPHAGNUM*

The reduced dataset used to investigate rate changes contains only species from subgenera *Acutifolia* (17 species) and *Cuspidata* (13 species). These subgenera contain the largest species sampling, represent one largely hummock (*Acutifolia*) and one largely hollow (*Cuspidata*) clade, and do not share a recent common ancestor within the genus (Fig. S1). For the eight niche descriptors and PC1, neither the *OU2* model nor the *BM2* models were supported (long-dashed line in Fig. 2B). On PC2, however, 91% of the trees supported the *BM2* model over the *BM1* model in the reduced dataset with an average ∂AICc of 1.01 (both models were always better than *WN*, Fig. 2B). The *BM2* model for PC2 inferred a mean evolutionary rate of 500 (range 220–1200) for subgenus *Acutifolia* and a mean evolutionary rate of 190 (range 81–500) for subgenus *Cuspidata*. A paired Student's *t*-test of AICc scores for BM1 versus BM2 on all 1000 trees indicates high support for separate rates of PC2 evolution between the subgenera (mean rate difference: 320, $P < 0.0001$). Traitgrams,

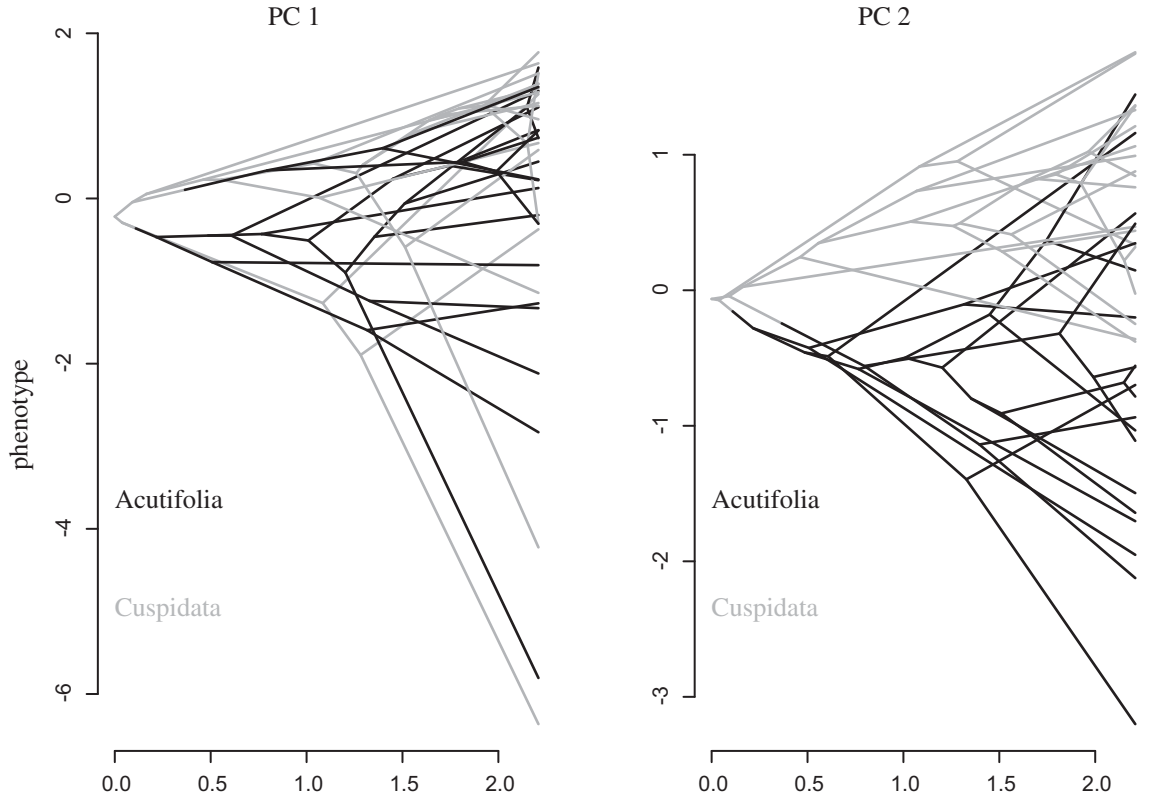

Figure 4. **Traitgrams illustrating the phylogenetic signal and rate change within the genus, for two principal components. Using the reduced dataset, ancestral states for the first two principal components were estimated using the maximum credibility chronogram from BEAST. For each tree, the position on the *x*-axis represents time, whereas the position on the *y*-axis represents reconstructed trait values. Dark branches correspond to subgenus *Acutifolia*, whereas lighter branches are subgenus *Cuspidata*. The left panel shows the fast evolution of microhabitat preference in the electrochemical gradient (PC1); the right panel illustrates phylogenetic signal in the hummock–hollow gradient (PC2) along with a difference in evolutionary rate between the two subgenera.**

reconstructed for the two principal components (Fig. 4), illustrate the evidence for phylogenetic signal and rate change in PC2 (right) but not PC1 (left).

Although there was no support for an *OU2* model for pH, the *OU1* model was supported in the reduced dataset—953 of the 1000 trees had better AICc scores for the *OU1* model than for *WN* (Table S3). The *OU* model was not supported in the full dataset; but as noted, the *OU* model was supported when either *S. magellanicum* or *S. centrale* were deleted in the sensitivity analysis (arrow in Fig. 3). Both species are in subgenus *Sphagnum*, and were therefore not included in analysis of the reduced dataset.

The Bayesian MCMC approach to identifying exceptional evolutionary rate changes within a phylogeny produces posterior probabilities for each node on the tree for each niche descriptor and microhabitat gradient. Only four descriptors had nodes with a mean posterior probability exceeding 10%. For pH, a rate change was supported within subgenus *Sphagnum*, either on the branch leading to *S. centrale* and *S. magellanicum* (29%) or on an immediately ancestral branch including *S. papillosum* (43%; Fig. 5A). Further evidence of an increase in evolutionary rate comes from the difference in pH preference between the closely related *S. centrale* (mean pH 5.75) and *S. magellanicum* (mean pH 4.14). This is a very large difference compared to other pairs of closely related species in the phylogeny (Fig. 5B).

Although the primary motivation for using the Revell method was to investigate the support for *OU* in pH preference in the sensitivity analysis, rate changes were moderately supported in a few other cases: on the terminal branches leading to *S. contortum*for EC (33%; Fig. S2) and the clade containing *S. fallax* and *S. pacificum* for Na (46%; Fig. S2). Finally, there is support for a rate change in K, either on a terminal branch leading to *S. riparium* (37%) or on the immediately ancestral branch that includes *S. lindbergii* (41%; Fig. S2). No rate change was found for PC2, either in the full dataset or in the reduced dataset (Fig. S2).

Discussion

Individual *Sphagnum* species inhabit narrowly defined microhabitat niches that are an extended phenotype of physical and chemical properties of the genus (Clymo and Hayward 1982).

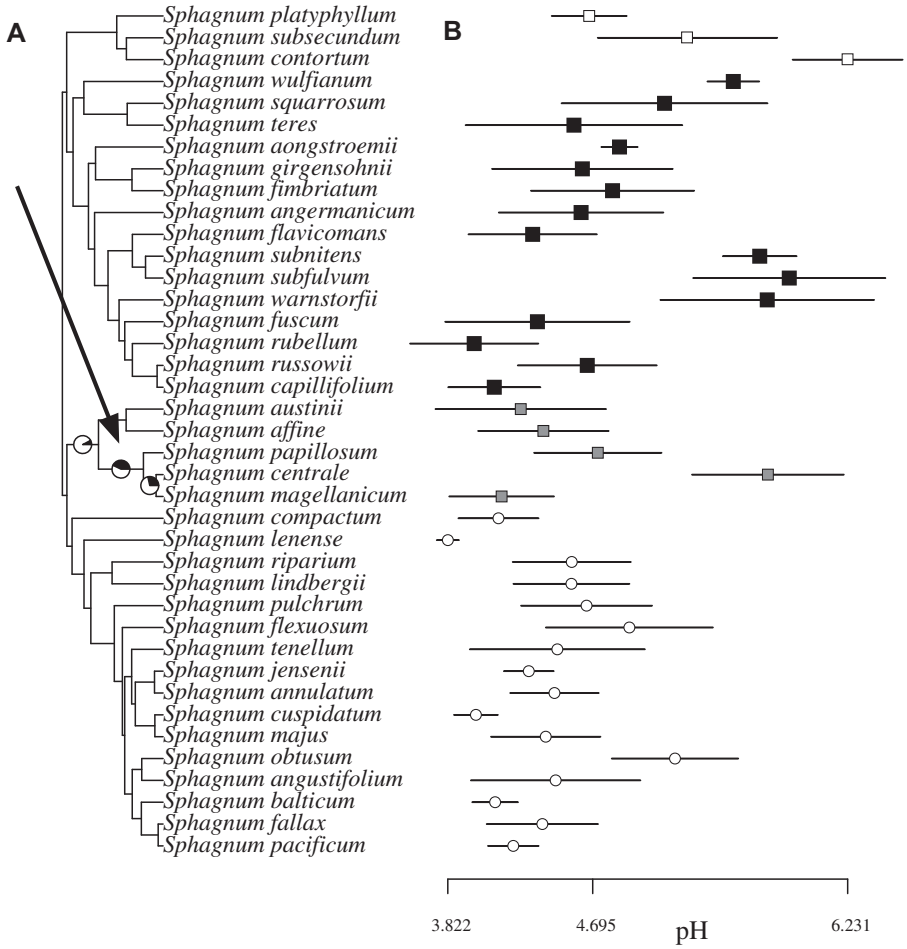

Figure 5. **Evidence for exceptional rate change in evolution of pH preference in *Sphagnum*. (A) Evidence of extreme pH preference shift via Bayesian MCMC (Revell et al. 2012)—pie charts indicate nodes receiving at least 10% posterior probability for a rate change. Black portions of each pie chart represent the support for a rate change at that node. The arrow indicates a 77% posterior probability for a rate change in subgenus *Sphagnum*. (B) Phylogenetic diversity of pH preference breadth in *Sphagnum*, by mean and SDs. The symbols represent species in subgenus *Subsecunda* (open squares), *Acutifolia* (black squares), *Sphagnum* (gray squares), or *Cuspidata* (open circles). Additional figures for the other niche descriptors can be found in the Supporting Information.**

Therefore, demonstration of phylogenetic signal in microhabitat preference (strongest for HWT) in *Sphagnum* suggests that constrained evolution of microhabitat preferences shapes peatlands with assemblages of related species within similar microhabitats. By contrast, the abiotic electrochemical gradient (pH and ions) may not be constrained, and thus preferences evolve too quickly for phylogenetic signal to be detected. Our tests for phylogenetic signal in *Sphagnum* also show the importance of incorporating several models of trait evolution, as signal may be masked by changes in the rate of trait evolution.

HWT, SHADE, AND MULTIVARIATE NICHE GRADIENTS

Our results clearly show the presence of phylogenetic signal in relation to the hummock/hollow gradient. Species in the major subgenera of *Sphagnum* are generally differentiated along this gradient. We find evidence for rate change in a multivariate niche gradient (encompassing shade and HWT) that suggests a higher rate of niche evolution in subgenus *Acutifolia*, which contains mostly hummock species, than in subgenus *Cuspidata*, which contains mostly hollow species. The strength of the phylogenetic signal indicates that across trees in the dataset, microhabitat preference for height is maintained within, as well as among subgenera. There is also phylogenetic signal in the shade cover of *Sphagnum* species (lambda model, Fig. 2A), and the shade and HWT values are correlated. However, when phylogenetic relatedness is removed with the PGLS model, the strength and significance of the correlation is highly reduced. The bulk of the relationship between HWT and shade is phylogenetically related, reflecting an ecological correlation between HWT and shading—ligneous vascular plants are dependent on oxygen for root

respiration and mycorrhiza, and grow almost exclusively in hummocks, where they provide shade.

We find additional support for a change in the rate of evolution of the multivariate niche gradient encompassing shade and HWT (PC2 axis, Fig. 1). Subgenus *Acutifolia* appears to be evolving faster along the shade–HWT gradient than is subgenus *Cuspidata*. This is apparent in the reconstructed traitgrams (Fig. 4), which show subgenus *Acutifolia* (black) spreading through the trait space much more rapidly than subgenus *Cuspidata* (gray). However, we did not find evidence for separate "optimum" values (*OU2*) in the two subgenera (Fig. 1). Instead, it appears that HWT preference may be more evolutionarily constrained in *Cuspidata*. The range of heights corresponding to "hollow" habitats (0–10 cm) is narrower than the range corresponding to "hummock" habitats (10–30 cm and above). Further, there is growing evidence for a physiological trade-off between hummock and hollow species in growth strategies. Hollow species tend to concentrate growth in the capitulum, maximizing photosynthesis while remaining sparsely packed at the water table (Rice et al. 2008). Conversely, plants with small capitula grow higher above the water table and yet maintain water availability by growing in densely packed hummocks, and thus avoid water stress. The driver behind this trade-off is related to the water flux (capillary rise, water retention) and the need to minimize surface roughness with increasing HWT to decrease water loss (Price and Whittington 2010).

Our results suggest that the classic microtopography of *Sphagnum*-dominated peatlands is caused by an extended phenotype of related species. Shoots of hollow species have high growth rate but decompose faster than hummock species (Turetsky et al. 2008). Because microhabitat preference on the hummock–hollow gradient contains phylogenetic signal, studies of *Sphagnum* functional traits related to this gradient (e.g., leaf and stem morphology, carbon allocation, decomposition rate) should also account for phylogenetic signal. It is likely that the trade-offs mentioned here largely contributed to the observed phylogenetic signal and possibly there is an evolutionary driver behind the microtopographic patterns in peatlands. Consequently, studies of community assembly in *Sphagnum*-dominated peatlands, and studies of functional traits may need to account for the phylogenetic relatedness of peat moss species, as similar habitats along the hummock–hollow will tend to be inhabited by related species.

IONIC GRADIENTS

In contrast, we find that evidence for phylogenetic signal in "ionic" preferences is mostly absent (all cations) or is concentrated in the tips of the phylogeny (EC). Despite the small niche breadth observed in many studies of *Sphagnum*, and that these microhabitat preferences make up much of the major axis of among-species niche variation, the lack of signal is consistent with the observation that the four species with highest PC1 scores ("ionic" niche descriptors excluding Na) represent different subgenera (Fig. 1).

A notable exception is pH, for which a complex pattern possibly including stabilizing selection and a rate change is suggested. Several pieces of evidence, when taken together, suggest that the evolution of the pH niche does in fact contain phylogenetic signal in *Sphagnum*. Although the full dataset failed to support any evolutionary model better than *WN*, the sensitivity analysis (Fig. 3) shows that deletion of either *S. magellanicum* or *S. centrale* provides support for an *OU* model in microhabitat pH evolution. When these species and other members of subgenus *Sphagnum* (and subgenus *Subsecunda*) are removed in the reduced dataset, there is strong support for an *OU* model with a single optimum for the whole genus (Fig. 2B). Moreover, the Bayesian analysis of exceptional rate changes (Revell method) showed strong support for a change in pH niche evolution within subgenus *Sphagnum* (Fig. 5A). These data therefore indicate that pH niche evolution in *Sphagnum* has two phases: (1) An *OU* model, where pH niche evolution deviates from a pure BM process by trending toward a genus-wide optimum of 5.5. Typically, support for an *OU* model is interpreted as evidence of stabilizing selection (Hansen 1997), but can also be interpreted as a bounded BM process. (2) An exceptional rate change occurred within subgenus *Sphagnum*, which masks the signal of the *OU* model when considering the entire genus.

Additional descriptors show evidence of exceptional rate change using the Bayesian MCMC method (Revell et al. 2012), and many of the branches identified are located near the tips of the tree (e.g., *S. contortum* for EC). If the purported rate changes were masking phylogenetic signal in these descriptors, as we suggest for pH, the sensitivity analysis should show model support when these tips are removed. However, none of the other sensitivity analyses indicate support for any model for any of the descriptors where rate changes are proposed by the Bayesian MCMC method. This suggests it is less likely for a rate change to obscure phylogenetic signal in these descriptors, compared to pH. The lack of support for an exceptional rate change in the evolution of the preference along the shade–HWT gradient seems to conflict with our other results, which show evidence for separate rates of PC2 evolution between subgenus *Acutifolia* and subgenus *Cuspidata*. However, the Bayesian MCMC approach was taken with the full dataset, where the rate change signal may be masked by the presence of the other two subgenera.

Several studies besides ours have found very limited intraspecific variation of ionic niche occupancy in *Sphagnum* (Vitt and Slack 1984; Andrus 1986; Gignac 1992). It therefore seems unlikely that the lack of phylogenetic signal is explained by new species preferring ionic microhabitats at random. Rather, microhabitat preference is more evolutionarily labile for these traits, and perhaps phenotypic plasticity or among-species interactions are

more important than phylogeny for the ionic microhabitat preferences (Eterovick et al. 2010). Several bog species have been shown to tolerate more minerotrophic waters from rich fens (Granath et al. 2010), suggesting that these species may have broader tolerances on the ionic gradient than suggested by their observed occurrences. Both of these factors could increase the rate of ionic habitat preference evolution beyond the ability of the comparative methods to detect phylogenetic signal. This would explain why models where trait evolution is concentrated on terminal branches (*delta* model with high value of delta) or completely eliminated in internal branches (*WN* model) are more highly supported for ionic preferences.

It is worth noting here that *Sphagnum*, as a bryophyte, has a haploid dominant life stage. Although allopolyploidy is common in *Sphagnum* (Karlin et al. 2010; Ricca and Shaw 2010), peatlands are primarily engineered by haploid plants. Any mutations that allow for broader physiological tolerances would be immediately exposed to natural selection. This may account for some of the increased rate of microhabitat preference evolution along the electrochemical gradient.

SPECIES INTERACTIONS AND UNCERTAINTIES

Because *Sphagnum* itself is largely responsible for its external microhabitat, and the fact that many *Sphagnum* species establish in patches of other *Sphagnum* species, additional studies are required to investigate the importance of interspecific interactions in definition of narrow microhabitat niches within peatlands. Observations and experiments involving damaged peatlands show that hummocks form several years after reestablishment of *Sphagnum* in a peatland (Pouliot et al. 2012), and that vigorous growth of some species (*S. magellanicum*) depends on the presence of other species (such as *S. fuscum*; Chirino et al. 2006). Therefore, it is clear that interspecies interactions play some role in the formation and maintenance of species diversity in peatlands. A more detailed study could test the role of species interactions serving as a filter in *Sphagnum* community assembly at the hummock/hollow, mineralogical, and peatland scales, by sampling the species diversity at hierarchal scales within one or more peatlands.

In general, our findings are robust to uncertainty introduced by within-species measurement error and phylogenetic uncertainty. Accounting for the former improved the model fits for a few niche descriptors, but did not alter any conclusions. This is not to suggest that within-species variability is unimportant. In their current forms, the methods employed here assume that error estimation of a species mean decreases with sample size, and does not explicitly model the niche breadth of each species. Topological phylogenetic uncertainty was low in our case, but the observations of overlapping AICc distributions, for example, in PC2 in the reduced dataset, indicates the necessity of including phylogenetic error in comparative methods to account for branch length uncertainty.

Conclusions

We have demonstrated the presence of phylogenetic signal in *Sphagnum* for microhabitat preference along the hummock–hollow gradient. Preference for narrow ranges on the ionic gradient appears to be uncorrelated with phylogeny, and further study may confirm whether phenotypic plasticity or infraspecific competition plays roles in eliminating phylogenetic signal. One exception is pH, for which we demonstrate a constraint on pH preference around a genus-wide optimum, although this signal is masked by an exceptional rate change in subgenus *Sphagnum.* The evolution of preferences on the hummock–hollow gradient, however, has a large component explained by phylogeny. The rate of evolution is heterogeneous; lineages classified as preferring hollow environments have lower rates of evolution and are constrained to prefer different multivariate microhabitat optima than hummock lineages.

Because our data represent the realized niches, we are in fact interpreting the combined evolution of physiological tolerances and biotic interactions. Niche preferences demonstrating phylogenetic signal may be more likely to have underlying functional traits related to *Sphagnum* peatland engineering, and may be more likely to be involved in peatland community assembly. The obvious next stage would be to gather data on the basic physiological and morphological traits behind the niches to trace their evolution. The importance of this study and its implications for functional trait evolution in *Sphagnum* are amplified by the recent acceptance of a proposal (A. J. Shaw and D. J. Weston, Principal Investigators) to the Joint Genome Institute (U.S. Department of Energy) to sequence a *Sphagnum* genome, with complementary analyses of gene expression using transcriptomics. This is in recognition of the global importance of *Sphagnum* for carbon sequestration, opening the possibility to link niche and functional trait evolution with global biogeochemistry and climate change.

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DATA ACCESSIBILITY

All DNA sequences have been deposited in GenBank; see Table S1 for accession information. Summarized ecological data, DNA alignments, and phylogenetic trees can be found on Dryad and R scripts used to analyze the data can be found at github.com/mehmattski.

DATA ARCHIVING

The doi for our data is: 10.5061/dryad.0p36h.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. GenBank accession numbers for each species at each gene.
Table S2. Species mean and SD for eight niche descriptors, summarized over five ecological sampling studies.
Table S3. Model selection for trait evolution using AICc in eight niche descriptors and two microhabitat gradients.
Figure S1. Maximum credibility tree from BEAST analysis, created using TreeAnnotator.
Figure S2. Bayesian inference of rate change in niche preference for eight niche descriptors and two multivariate niche gradients.
Figures S3. Distributions of niche preferences in eight niche characters, aligned with the maximum credibility tree.