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Key Points:

- Depth is the strongest predictor of hydraulic conductivity in shallow peat
- Peat decomposition is important to order of magnitude of hydraulic conductivity
- Our data indicate alterations that should be made to peatland development models

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Bridging the gap between models and measurements of peat hydraulic conductivity

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Abstract Peat saturated hydraulic conductivity, K_{sat}, declines strongly with increasing degree of decomposition, providing a potentially important negative ecohydrological feedback that may buffer peatlands from climate-induced drying. However, the quantitative nature of this relationship is poorly understood. We measured downcore changes in K_{sat} and carbon-to-nitrogen concentration quotients (C/N) in 14 shallow (~0.5 m deep, 0.1 m diameter) peat cores from a Swedish raised bog. We used the C/N measurements to approximate the fraction of original peat mass remaining. A linear mixed effects (LME) model predicts $\log_{10}(K_{sat})$ from (i) our C/N-derived estimate of fractional remaining mass; (ii) depth; (iii) microhabitat (hummock, hollow); and (iv) location (treeless bog center, treed bog margin). The LME model indicated no significant random effects or interactions between predictors, so we derived a nonlinear multiple regression (NLMR) model to predict K_{sat} on its original scale. Both LME and NLMR models predict that K_{sat} decreases exponentially with depth and that K_{sat} is lower beneath hollows than beneath hummocks for equivalent depths below the surface. Fractional remaining mass was an important predictor in the LME model, but not in the NLMR model. The distinction between central and marginal areas of the bog was not an important predictor. We demonstrate for the first time that the relationship between fractional remaining mass and K_{sat} is log-linear, and suggest revisions that should be made to peatland development models. In particular, depth—usually ignored in modeling studies—exerted a strong control over K_{sat} independently of decomposition and should be included explicitly in model algorithms.

1. Introduction

1.1. Background

Peatlands are archetypal examples of ecohydrological systems [*Belyea and Baird*, 2006]. Feedbacks between shallow groundwater dynamics, plant community composition, microbial decomposition of soil organic matter, and soil hydraulic structure determine the long-term development of peatlands and their short- to medium-term response to external forcings such as climate change [*Belyea*, 2009; *Waddington et al.*, 2015]. Peat hydraulic properties can exhibit variability in both space and time, in ways not seen in mineral soils. For instance, saturated hydraulic conductivity, K_{sat} (dimensions of L T^{-1}) decreases strongly with increasing degree of decomposition [*Boelter*, 1969; *Rycroft et al.*, 1975; *Quinton et al.*, 2008; *Grover and Baldock*, 2013]. As fresh peat decomposes, its structure alters so that large pore spaces are replaced by smaller ones; pores become less interconnected and sometimes also undergo vertical compression and structural collapse, evident as an increase in dry bulk density [*Johnson et al.*, 1990; *Thompson and Waddington*, 2014; although see *Chapman et al.*, 2009; *Wellock et al.*, 2011]. After the initial phase of rapid decomposition and structural change, further changes in peat hydraulic properties occur more gradually. Saturated hydraulic conductivity in near-surface peat can decline by orders of magnitude during a few decades of artificially aerated soil conditions and enhanced decomposition [*Moore et al.*, 2015]. The result can be a negative feedback to drying whereby rapid drainage leads to deep water tables, rapid oxic decomposition, and so a decrease in shallow K_{sat} which slows further drainage. This negative feedback may provide peat soils and their carbon stocks with an important buffer against degradation in the face of climate-induced drying.

The existence of a relationship between the state of peat decomposition and K_{sat} is broadly accepted, and is important to the behavior of numerical models of long-term peatland development [e.g., *Frolking et al.*, 2010; *Morris et al.*, 2011] and peatland response to climatic forcing [*Swindles et al.*, 2012]. It also forms an important link in conceptual models of peatland ecohydrology [*Waddington et al.*, 2015]. However, the functional form of this relationship is poorly understood. Previous studies have developed empirical models that may be used to predict peat hydrophysical properties including K_{sat} on the basis of easily measured physical or chemical indicators of state of decomposition such as fiber content [e.g., *Boelter*, 1969], von Post scores [e.g., *Boelter*, 1969; *Rycroft et al*., 1975; *Holden and Burt*, 2003], and light transmission [e.g., *Chason and Siegel*, 1986]; or on the basis of more sophisticated chemical indicators [*Grover and Baldock*, 2013]. However, none of these empirical models allows the satisfactory parameterization of peatland development models, which typically simulate peat decomposition using the concept of fractional remaining mass, *m* (where *m* is the proportion of a simulated peat cohort remaining at a specified time; values close to 1 represent fresh, undecomposed peat, while values close to zero represent highly decomposed peat). As such, a gap exists between the requirements of simulation models and the available empirical evidence.

Many peatlands exhibit strong vertical patterns in K_{sat} in the top 0.5–1.0 m of the peat profile, with the shallowest layers often being several orders of magnitude more permeable than those below [*Kneale*, 1987; *Waddington and Roulet*, 1997; *Fraser et al*., 2001; *Clymo*, 2004]. This issue is complicated by the fact that deeper, older peat is generally more decomposed than the younger peat above. As such, it is unclear whether depth exhibits a genuinely independent control over K_{sat}. In some peatlands, depth variation in K_{sat} is weak or nonexistent [*Chason and Siegel*, 1986]. Depth distributions of K_{sat} are important to determining rates of lateral drainage [*Ivanov*, 1981; *Beckwith et al*., 2003a], pore water residence times [*Morris and Waddington*, 2011], and to the development of a groundwater mound in raised bogs [*Ingram*, 1982; *Armstrong*, 1995].

Strong horizontal variations in peat K_{sat} exist at a range of scales. Many northern peatlands are covered in characteristic meter-scale (scale-level 1, or SL1) [*Baird et al*., 2009] patterns of alternating microhabitats such as hummocks and hollows. Although empirical evidence is sparse [*Ivanov*, 1981; *Belyea and Baird*, 2006; *Branham and Strack*, 2014], a number of modeling studies [e.g., *Swanson and Grigal*, 1988; *Morris et al*., 2013] assume that the peat produced by contrasting microhabitat types exhibits characteristic hydraulic properties, including K_{sat}. At larger scales of hundreds of meters to kilometers (SL3) [*Baird et al*., 2009], both theoretical [*Lapen et al*., 2005] and observational [*Baird et al*., 2008; *Lewis et al*., 2012; *Langlois et al*., 2015] studies have proposed that raised bogs may develop an aquitard of low-permeability peat around their margins, partly in response to enhanced decomposition in areas of water-table drawdown. Marginal areas of low permeability would likely help to maintain a high water-table mound in the bog center by impeding lateral drainage, and may therefore be important to bog development.

1.2. Aim and Objectives

Using an observational approach, we investigated the controls on K_{sat} in a raised bog. We wished to develop an empirical model that could be used to predict K_{sat} on the basis of: (i) a simple estimate of fractional remaining mass such as those used in peatland development models; (ii) depth; (iii) surface plant community type (e.g., hummock or hollow); and (iv) location relative to the bog margin. We focused on the uppermost 0.5 m of the peat profile, where changes in K_{sat} and state of decomposition are usually most pronounced.

2. Methods and Materials

2.1. Study Site

Ryggmossen (60.044°N, 17.327°E; 60 m above sea level) is an ombrotrophic raised bog and nature reserve occupying approximately 60 ha in Uppsala County, Sweden, 25 km north-west of the city of Uppsala. The site's protection status, as well as almost no history of peat cutting or logging, made it suitable for the recovery of pristine peat cores in which variations in peat hydrophysical and biogeochemical properties would be largely free from human disturbance. The bog dome is subcircular in plan with a diameter of between approximately 500 and 700 m, surrounded by upland pine forest to the north, west and south; and by a minerotrophic lagg fen to the east. Near the center of the bog dome, the peat deposit reaches a maximum thickness of 4.6 m and surface elevation is 3.5 m above the lagg fen. Mean annual temperature is 6.5°C and mean annual rainfall is 576 mm (CELCIUS, Uppsala University, unpublished data, 2015, http://celsius.met.uu.se/climate_tables/?id=13) (data for Uppsala, averaging period 1981–2011). The site possesses a pattern of distinct microhabitats and the associated vegetation and microtopographic relief that are characteristic of many northern peatlands: hummocks and ridges of *Sphagnum fuscum*, *Sphagnum rubellum*, *Calluna vulgaris*, and *Polytrichum strictum*; and lower lawns and hollows of *Sphagnum balticum*, *Sphagnum cuspidatum*, and *Eriophorum vaginatum*. The central area of the bog is treeless, has a surface topographic gradient close to zero and is dominated by *Sphagnum* mosses, often in broken, concentric patterns. The treeless central plateau is surrounded by a more steeply sloping annular marginal zone with dwarf trees including *Pinus sylvestris* and *Picea abies*. In this marginal zone, the abundance and average height of trees and the abundance of hummock-forming moss species generally increase with distance from the bog center, while wetter habitats become scarcer.

2.2. Sampling Design and Core Recovery

We selected eight locations from which to take shallow cores in the treeless, flatter, central area of the bog, four each from hummocks and hollows. We took a further six shallow cores from the sloping, annular, marginal area within 100 m of the edge of the bog, three each from hummocks and hollows. This resulted in an unbalanced 2×2 factorial sampling design. At each of the 14 locations we extracted a cylindrical core that extended from the surface to approximately 0.5 m depth, and which was 0.1 m in diameter. We used a scissor-cut protocol similar to that described by *Green and Baird* [2012] so as to limit physical damage to the samples, thereby minimizing biases in our subsequent laboratory estimates of K_{sat}. We discarded any core in which vertical compression was greater than 0.05 m. A sliding steel clamp allowed us to open the corer and transfer each peat core into a polyvinyl chloride cylinder of the same diameter. We then immediately wrapped the samples in thick plastic sheeting and sealed them with duct tape to prevent water loss and shrinkage, and stored them upright and refrigerated before laboratory analysis. The peat in our cores varied between fresh, live *Sphagnum* and other plant tissue at the surface; and mid to dark brown, moderately decomposed peat at 0.5 m depth.

2.3. Hydraulic Conductivity Measurements

We adapted the modified cube method described by *Surridge et al*. [2005] to measure horizontal K_{sat} at depth intervals in our cores. We first cut our cylindrical peat cores into $0.06 \times 0.06 \times 0.06$ m cubes using a sharp, nonserrated kitchen knife, and conserved and refrigerated the offcuts from each cube for subsequent chemical analysis. When subsampling each core into cubes, we discarded sections of peat that contained obvious cracks or weaknesses that may have indicated damage caused during core removal, transport, storage, and preparation. As such the 0.06 m depth intervals were not always contiguous within or between cores, and the number of subsamples per core varied between two and five. In six cores, the shallowest depth interval did not include the moss capitulum due to near-surface physical damage; in these cores we measured C/N (see below) in the surficial peat (nominal depth of zero) despite not measuring its K_{sat}. We encased the peat cubes in paraffin wax on all sides, built up to a thickness of 0.01 m using a cast made from medium density fiberboard. We performed steady state, constant head tests on each sample with hydraulic gradients close to unity, and calculated horizontal K_{sat} using Darcy's law [see *Beckwith et al*., 2003b; *Surridge et al*., 2005].

2.4. Estimating Fractional Remaining Mass

We used the method of *Kuhry and Vitt* [1996] to approximate fractional remaining mass from peat carbon-to-nitrogen concentration quotients (C/N) (see below, next paragraph). We chose to examine C/N from bulk peat samples rather than from the remains of particular species such as *Sphagnum fuscum* so as to allow comparison between hummocks and hollows with no species in common. For each depth interval we dried, ground and homogenized the peat offcuts left over from the preparation of samples for K_{sat} measurements, and determined C/N for each 0.06 m depth interval using an elemental analyzer (FlashEA 1112; Thermo Electron Corporation; Waltham, Massachusetts, USA). In order to gain a comprehensive picture of depth-variation in C and N cycling, we also took C/N measurements from some depth intervals in between those used for K_{sat} measurements, including sections of the peat that had been discarded due to physical damage (see above). In each core, we were able to identify a shallow subsurface peak in C/N, which indicates the depth at which the rate of N losses due mainly to plant uptake falls below the rate of C loss through respiration [*Malmer and Holm*, 1984]. Above this depth, *Kuhry and Vitt*'s [1996] method for approximating fractional remaining mass cannot be applied reliably. We determined the C/N peak for each core separately, rather than grouping cores according to factorial combinations of hummock/hollow and center/margin.

We define m (dimensionless) for each depth interval as the quotient of C/N at that depth divided by the near-surface peak C/N value in that core. Values close to unity indicate younger, fresher peat that has undergone little decomposition; values close to zero indicate heavily decomposed peat. The shallower the depth at which peak C/N occurs, the greater the proportion of the peat profile for which *m* can be estimated, and the closer *m* is to the true value of fractional remaining mass. Preliminary measurements of our own samples showed that, like *Malmer and Holm* [1984], the subsurface peak in C/N occurred at shallow depths, indicating that plant N uptake was only important at our site in the uppermost 0.05–0.10 m. Our *m* necessarily overestimates the true value of fractional remaining mass because it does not account for decomposition losses that occur above the depth of the C/N peak, and should therefore be interpreted cautiously. However, we took the apparently conservative behavior of peat N at our site below 0.10 m as an indication that the approximation is a reasonable one. The method also assumes net immobilization of N below the C/N peak. Some of the recycled inorganic N will be translocated to the live moss capitulum [*Malmer and Nihlgård*, 1980] and taken up by vascular plant roots [*Rosswall and Granhall*, 1980]; N losses due to gaseous emissions of nitrous oxide, leaching of ammonium N, and net movement by microorganisms are likely to be negligible [*Malmer and Holm*, 1984]. The method also assumes that C/N quotients in fresh peat have remained approximately constant through time at each core location.

2.5. Statistical Analysis

Our data are grouped according to the 14 cores, insofar as measurements from different depth intervals within the same core are not truly independent of one another, thereby potentially introducing a hierarchical structure to the data that would preclude the use of standard multiple regression. To overcome any within-core dependency, we developed a linear mixed effects (LME) model to describe our single response variable, K_{sat}, in terms of two continuous predictor variables—depth and our C/N-derived estimate of fractional remaining mass—and two categorical predictor variables: SL1 habitat type (hummock, hollow) and SL3 location (center, margin). The LME model treated each core as a random subject and allowed us to assess whether or not the grouping of our measurements within cores was a significant control on K_{sat}. Doing so revealed whether or not the assumption of independence required by multiple regression had indeed been met.

In developing the LME model, we followed the step-up protocol described by *West et al.* [2007]. We began with a model that contained fixed effects only and added random effects in a stepwise manner, starting with a random intercept that varied between cores and then including random slopes for individual cores for different combinations of the predictor variables. We also investigated fixed-effects interactions between SL1 habitat type (hummock, hollow) and SL3 location (center, margin); and between depth and fractional remaining mass. Each time we respecified the model we assessed both the incremental change in overall model performance using a likelihood ratio test; and the significance of individual random effects according to their associated Wald's *Z*. This step-up approach allowed us to strike an appropriate balance between model predictive power and generality, so as not to over-specify the model. We fitted all models using Type-III sum of squares and estimated random effects using an unstructured covariance matrix. Apart from stated exceptions, we conducted all statistical analyses using IBM's SPSS software package (version 20).

3. Results

3.1. Hydraulic Conductivity

Measured values of K_{sat} varied between 7.16×10^{-6} and 2.69×10^{-2} m s^{-1}. The harmonic mean of K_{sat}, which is appropriate for transfer rates, is 6.00×10^{-5} m s^{-1}; the high arithmetic mean of 2.65×10^{-3} m s^{-1} is dominated by a small number of highly permeable near-surface samples from hummocks. The eight highest values of measured K_{sat} were all from hummock samples, as was the single lowest value. The highest K_{sat} from a hollow sample was 2.73×10^{-3} m s^{-1}. K_{sat} declined strongly with depth (Figure 1; see also section 3.3, below). We log$_{10}$-transformed the K_{sat} data because preliminary LME models (not reported here in full) fitted to untransformed K_{sat} data displayed large departures from both homoscedasticity and linearity, both of which were remedied by our transformation. The transformation also ensured that model predictions would always be strictly positive (negative values of K_{sat} are physically meaningless).

3.2. Peat Decomposition From C/N

Measured C/N varied between 35 and 194, with a mean of 101 (Figure 2). Peak C/N values ranged between 99 and 194, with a mean of 130, and occurred at depths between 0.04 and 0.16 m below the surface. The

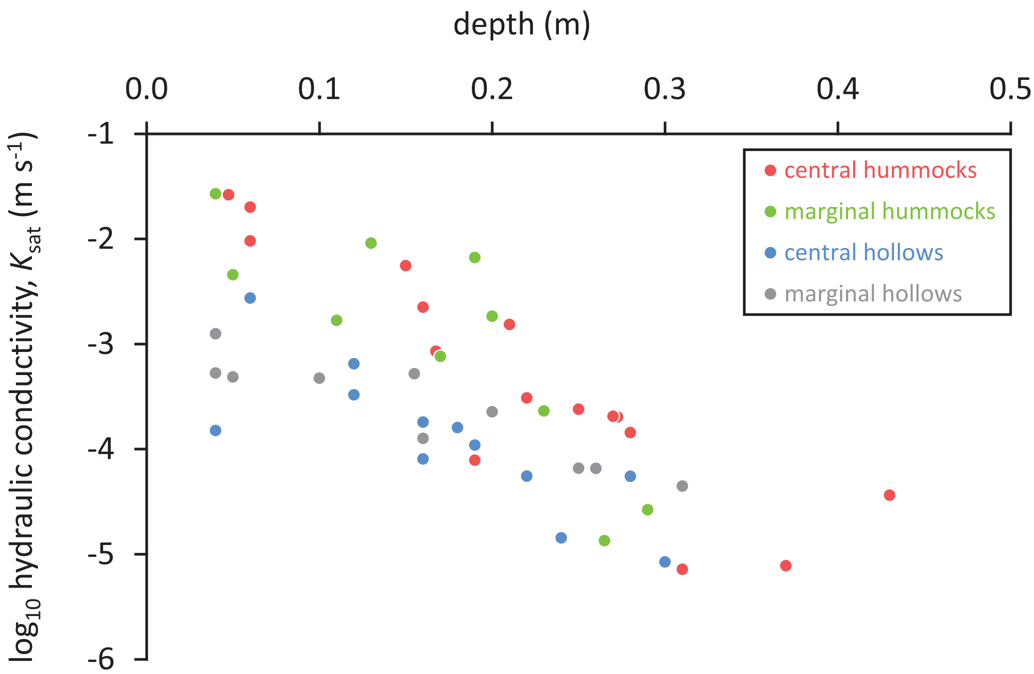

Figure 1. Depth variation in $\log_{10}$-transformed hydraulic conductivity.

six surface values of C/N occupied a comparatively narrow range, between 66 and 98. In all cores, C/N generally declined with increasing depth below the C/N peak. Fractional remaining mass, *m*, varied between 1.0 (for the C/N peak in each core) and 0.224 (hummock, central location, 0.31 m depth), although in the majority of cores *m* did not fall below 0.4. Fractional remaining mass declined strongly with increasing depth (Spearman's Rank, $r_s = -0.760$, $p < 0.001$) (Figure 3).

3.3. Statistical Modeling

Our step-up model-fitting procedure resulted in a LME model that contains fixed effects only. None of the random effects that we experimented with led to a significant stepwise improvement in overall model predictive power according to likelihood ratio tests (when the model was fitted using maximum likelihood;

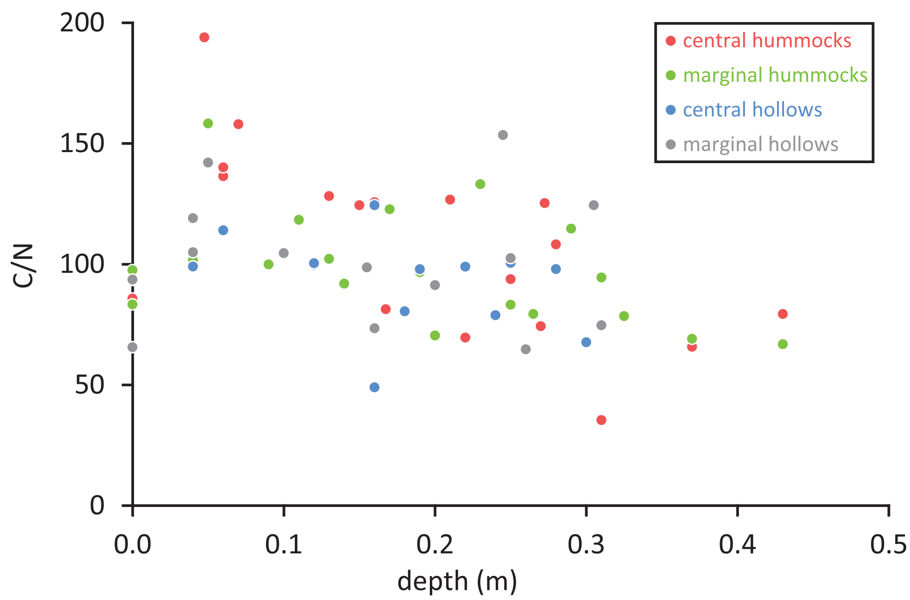

Figure 2. Depth variation in measured carbon/nitrogen concentration quotients, C/N.

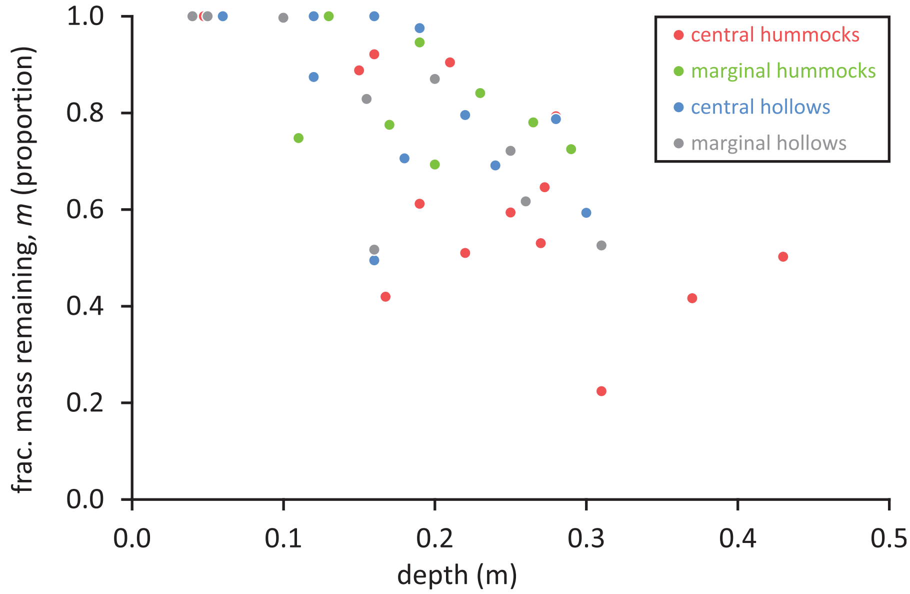

Figure 3. Depth variation in C/N-derived approximation of fractional peat mass remaining, *m*.

$p > 0.05$ in all cases), nor did any of the individual random effects explain a significant amount of variation in $\log_{10}$ (K_{sat}) according to Wald's *Z* statistic (when using restricted maximum likelihood; $p > 0.05$ in all cases). Similarly, neither of the fixed-effects interactions were significant predictors (*depth* $\times$ *m*, $F_{(1, 46)} = 0.658$, $p = 0.412$; *hollow* $\times$ *center*, $F_{(1, 46)} = 2.215$, $p = 0.143$), nor did they improve overall model performance significantly according to log likelihood ratio tests (*depth* $\times$ *m*, $p = 0.410$; *hollow* $\times$ *center*, $p = 0.141$) (definitions of variables given below equation (1)). We therefore omitted fixed-effects interactions and all random effects from the LME model because they would appear to lead to over-specification [*West et al.*, 2007]. The fixed-effects model predicts that log-transformed K_{sat} decreases with increasing depth and with decreasing fractional remaining mass, *m*. The model also predicts that K_{sat} is higher beneath hummocks than hollows. The model is summarized in Table 1 and equation (1), and its performance compared to measured, $\log_{10}$-transformed K_{sat} is illustrated in Figure 4.

$$\log_{10}(K_{sat}) = 1.200\ m - 6.147\ depth - 0.877\ hollow - 0.020\ centre - 2.87 \tag{1}$$

where *m* is fractional remaining mass derived from C/N quotients (dimensionless); *depth* is the midpoint depth of each subsample below the bog surface (m); *hollow* is a dummy variable with a value of 1 for peat beneath hollows, and 0 for peat beneath hummocks; and *center* is a dummy variable with a value of 1 for locations in the flat, treeless central plateau, and 0 for the sloping, forested bog margin.

In the LME model, the continuous fixed-effects *m* ($F_{48} = 6.833$, $p = 0.012$), *depth* ($F_{(1, 46)} = 38.965$, $p < 0.001$), and the intercept ($F_{(1, 46)} = 42.843$, $p < 0.001$) are all significant predictors of $\log_{10}(K_{sat})$ (Table 1). The dummy variable representing SL1 habitat type, *hollow*, is also highly significant ($F_{(1, 46)} = 46.101$, $p < 0.001$), and its effect size is large (Cohen's $d = 0.650$). The dummy variable that represents the categorical distinction between central and marginal location, *center*, is highly nonsignificant ($F_{(1, 46)} = 0.023$, $p = 0.880$) and its effect size is small (Cohen's $d = 0.284$). The lack of significant random effects indicates that the way in

Table 1. Summary of the Linear Mixed Effects Model Fitted to the $\log_{10}$-Transformed K_{sat} Data (See Also Equation (1))

Variable	Coefficient	Standard Error	*F*	Significance	Cohen's *d*
m	1.200	0.459	6.8	0.012	
depth	−6.147	0.985	39.0	<0.001	
hollow	−0.877	0.129	46.1	<0.001	0.650
center	−0.020	0.131	0.023	0.880	0.284
intercept	−2.871	0.518	42.8	<0.001	

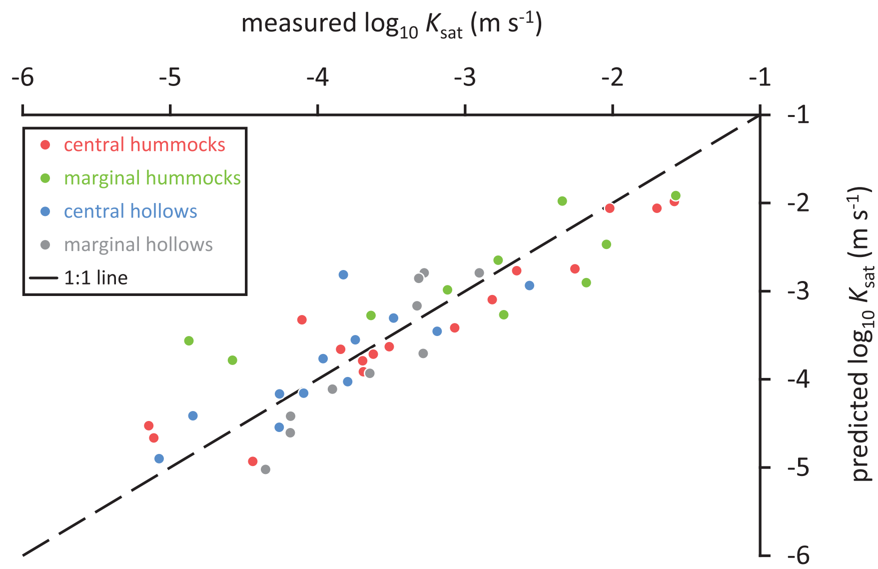

Figure 4. Performance of the linear mixed effects model (equation (1)), showing its predicted values of peat saturated hydraulic conductivity against the measured values used to generate the model.

which our samples are grouped by core has not introduced any bias to our K_{sat} data. The identity of the core that each sample came from is therefore unimportant beyond that core's SL1 habitat type (hummock, hollow), which is already modeled explicitly as a fixed effect (the dummy variable *hollow*).

In addition to the log-linear model shown in equation (1), we wished to derive a model from our data that could be used to predict K_{sat} on its original scale. Back-transforming any linear model fitted to transformed data without then applying a correction introduces skew to the distribution of residuals [*Miller*, 1984]. In the case of our exponential transformation, this skew would have been positive, causing the model to underestimate our measured K_{sat}. As such, simply exponentiating equation (1) would have led to a biased model. Rather than attempt to correct for this bias using one of a number of published techniques [e.g., *Duan*, 1983; *Miller*, 1984], we fitted a nonlinear multiple regression (NLMR) model to the untransformed K_{sat} data. This is justifiable based on the knowledge that: (i) the LME model contains no random effects and is therefore equivalent to standard linear multiple regression on the $\log_{10}$-transformed data; and (ii) an exponential relationship satisfies the assumptions of multiple regression. We used the minpack.lm package [*Elzhov et al.*, 2013] for R [*R Core Team*, 2014] to specify a model with a form and initial parameter estimates given by exponentiating equation (1). The fitted NLMR model is summarized in equation (2) and Table 2, and its performance in comparison to measured K_{sat} is illustrated in Figure 5.

$$K_{sat} = 10^{1.469\ m - 6.192\ depth - 1.278\ hollow + 0.113\ centre - 2.958} \tag{2}$$

Deviance explained by the model is 79.9% (relative to a null model with all coefficients apart from the constant set to zero). Unlike in the LME model, in the NLMR model the slope coefficient for fractional remaining mass, m, is highly nonsignificant ($t = 0.987$, $p = 0.329$); while the slope coefficient for *depth* ($t = -3.232$, $p = 0.002$) and the dummy variable representing SL1 habitat type, *hollow* ($t = -2.405$, $p = 0.021$) remain significant predictors of K_{sat}. The constant ($t = -1.914$, $p = 0.062$) and the dummy variable representing the

Table 2. Summary of the Nonlinear Multiple Regression Model Fitted to the Untransformed K_{sat} Data (See Also Equation (2))[a]

Variable	Coefficient	Standard Error	t	Significance	Cohen's d
m	1.469	1.489	0.987	0.329	
depth	−6.192	1.916	−3.232	0.002	
hollow	−1.278	0.531	−2.405	0.021	0.707
center	0.113	0.064	1.753	0.087	0.033
constant	−2.958	1.545	−1.914	0.062	

[a]Log likelihood is 215.4; residual standard error is 2.876×10^{-3} m s^{-1} (43 degrees of freedom).

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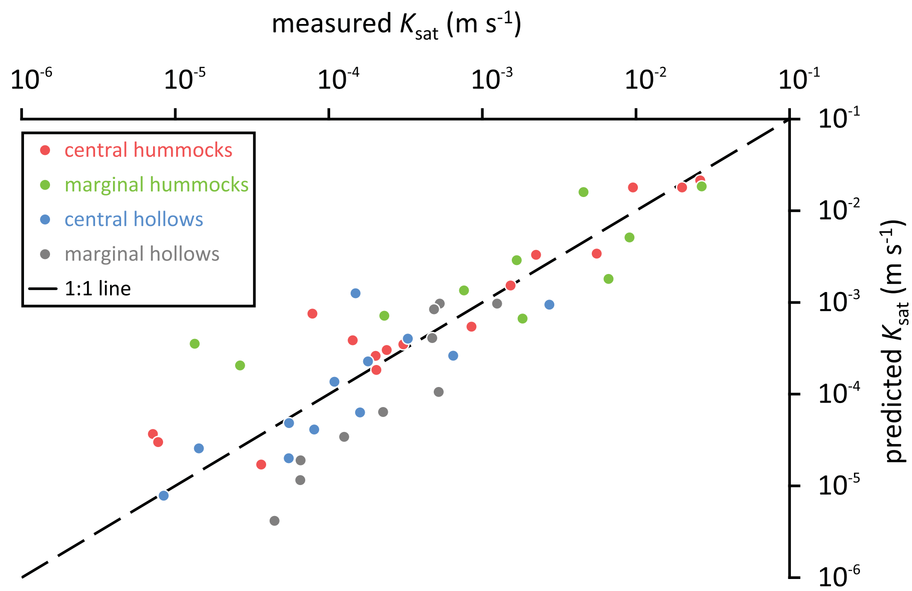

Figure 5. Performance of the nonlinear multiple regression model (equation (2)), showing its predicted values of peat saturated hydraulic conductivity against measured values. Model fitted to untransformed measurements, displayed here on log-log scale for convenience of presentation.

categorical distinction between central and marginal locations, *center* ($t = 1.753$, $p = 0.087$) are both marginally nonsignificant; the effect size of *center* is close to zero (Cohen's $d = 0.033$).

4. Discussion

Our findings of a negative relationship between K_{sat} and depth (in both the LME and NLMR models), and between K_{sat} and the state of peat decomposition (in the LME model), are broadly consistent with numerous existing reports [e.g., *Quinton et al.*, 2008; *Grover and Baldock*, 2013; *Branham and Strack*, 2014]. However, our findings illustrate for the first time the functional form of the relationship between peat fractional remaining mass and saturated hydraulic conductivity, and they are of direct relevance to those peatland development models that include that relationship. Both the Holocene Peat Model (HPM) [*Frolking et al.*, 2010; *Quillet et al.*, 2013] and DigiBog [*Morris et al.*, 2011, 2012] employ fractional remaining mass as the sole predictor of K_{sat} (strictly, HPM simulates K_{sat} as a function of peat bulk density, although bulk density is in turn simulated as a function solely of fractional remaining mass, so K_{sat} effectively reduces to a function of fractional remaining mass). We used the baseline parameterizations given in *Morris et al.* [2011, Table 1] and *Frolking et al.* [2010, Table 2] to compare the functions used in DigiBog and HPM, respectively, against our data. Figure 6 shows that DigiBog's exponential function overestimates our data, although it is close to hummocks for the majority of its domain in m. HPM underestimates the highest K_{sat} values for fresh peat with values of m close to unity; it is these high-K layers that are most important to determining drainage rates. Fit to our data could be improved for both models by adjusting their respective parameter sets, although only the exponential function employed in DigiBog is consistent with the functional form of our data set (equations (1) and (2)). HPM uses the error function, which gives a quite different shape to the relationship. Importantly, the gradient of the relationship between K_{sat} and m in HPM is close to zero for fresh peat, which would weaken the strength of the negative feedback between drainage, decomposition and K_{sat} that acts to moderate water table fluctuations [*Morris et al.*, 2011; *Swindles et al.*, 2012; *Waddington et al.*, 2015]. The peatland development model described by *Ise et al.* [2008] partitions the simulated peat profile into two layers according to state of decomposition, and assigns a canonical and invariant K_{sat} value to each, while MILLENNIA by *Heinemeyer et al.* [2010] contains a black-box representation of depth-changes in K_{sat} but effectively ignores the influence of decomposition. Of these models, DigiBog comes closest to representing equations (1) and (2) accurately. However, all of the models risk oversimplifying peatland hydrological behavior.

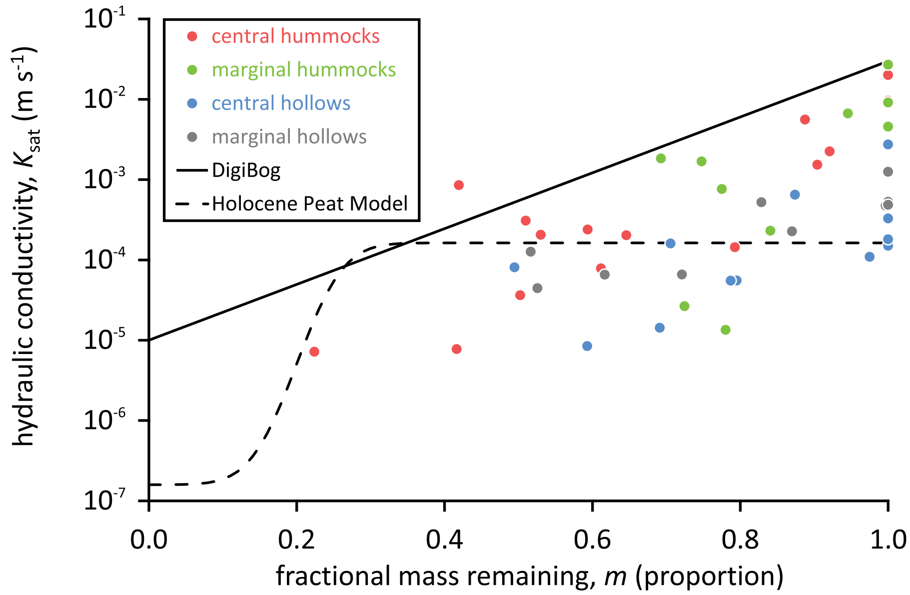

Figure 6. Relationship between C/N-derived approximation of fractional remaining mass, m, and measured saturated hydraulic conductivity. The solid and broken black lines illustrate the functions used by DigiBog (with the baseline parameterization used by *Morris et al.* [2011]) and the Holocene Peat Model (with the baseline parameterization given by *Frolking et al.* [2010]), respectively, to simulate hydraulic conductivity on the basis of fractional remaining mass.

The predictive power of depth independently of fractional remaining mass likely indicates an important near-surface compression effect at our site, possibly due to loading by pore water in near-saturated peat [*Clymo*, 1992]. A depth effect could be implemented easily in peatland development models that track the vertical development of a peat profile by using our equation (2), or through a more physically based representation of loading and compression. Not only is depth a more significant predictor than state of decomposition in our empirical models, but the estimated value of the *depth* coefficient is also large, indicating that K_{sat} declines by more than six orders of magnitude per meter of depth. This suggests that the inclusion of a process-based representation of peat compression [cf. *Zhang and O'Kelly*, 2014] is more important to the accurate simulation of K_{sat} in peatland development models than fractional remaining mass. Our measurements are from the top $\sim$0.5 m only of the peat profile, and extrapolation beyond this domain is inadvisable. Nonetheless, we find such a steep depth gradient in $\log_{10}$ (K_{sat}) unlikely to hold into much deeper layers because the total range of reported K_{sat} values is only approximately six orders of magnitude (see *Quinton et al.* [2008], the recent summary of published values by *Branham and Strack* [2014], and the measured values in the current study). On the other hand, the gradient of depth-changes in K_{sat} becomes less important as K_{sat} decreases, because the majority of groundwater flow will occur through near-surface, high-K_{sat} peat. The steep vertical gradient in our K_{sat} measurements is explained in part by the fact that they contain some high values from peat layers near the tops of hummocks (Figure 1). These peat layers rarely, if ever, experience saturated flow and so are often omitted from K_{sat} sampling strategies. However, measuring hummock-top K_{sat} is instructive partly because it defines the upper bound for unsaturated K (which tends to the value of K_{sat} as a soil approaches full saturation) and so is relevant to peatland-atmosphere exchanges of energy and water via evapotranspiration. We suggest that future studies should extend our approach into deeper peat. It would also be instructive to investigate whether similar relationships hold at raised bogs other than our study site. The fact that the only significant predictor variables in the NLMR model (equation (2)) are depth and SL1 microhabitat type means that the model could potentially be validated against numerous published depth profiles of K_{sat} measurements [e.g., *Fraser et al.*, 2001; *Clymo*, 2004; *Baird et al.*, 2008].

The group of cellular landscape models described by *Swanson and Grigal* [1988], *Couwenberg* [2005], and *Couwenberg and Joosten* [2005] seek to simulate the development of peatland patterning through a limited set of ecohydrological feedbacks. These models use SL1 designation (hummock or hollow) as the sole predictor of peat permeability, albeit in the form of transmissivity rather than hydraulic conductivity; our own recent exploration of these models [*Morris et al*., 2013] extended their routines to include a simple, two-layered depth variation in K_{sat}. Nonetheless, all of these models ignore the effects upon K_{sat} of changes in peat structure over time. Our current findings add weight to our previous argument [*Morris et al*., 2013] that the omission of peat decomposition and compression is a likely cause of the inability of these cellular models to produce genuine self-organization. Implementation of the empirical model shown in equation (2) within simulation models such as those described by *Eppinga et al*. [2009] or *Morris et al*. [2013] would allow this hypothesis to be tested. While the difference in K_{sat} between hummocks and hollows is highly significant at our site and the effect size is large, in the LME model the value of the *hollow* parameter is less than the order of magnitude often taken as a minimum in cellular models. Moreover, like *Branham and Strack* [2014], the direction of this difference was the opposite of that assumed in cellular patterning models, with peat beneath hummocks being more permeable than that below hollows. However, direct comparison of peat properties between hummocks and hollows for a given depth is complicated by differences in the surface datum caused by microtopographic differences. Hummocks at our study site typically protrude 0.3–0.4 m above nearby hollows; from the perspective of horizontal shallow groundwater flow it may therefore be reasonable to offset depths below hummocks by this amount when applying equations (1) and (2) so as to ensure depth-equivalence between SL1 habitat types [e.g., *Sherwood et al*., 2013; *Branham and Strack*, 2014]. Doing so would be sufficient to negate or even reverse the direction of the effect of SL1 unit type on K_{sat} (equations (1) and (2); Figure 1).

The lack of a significant difference in K_{sat} between central and marginal areas and the small effect size provide little evidence for the low-*K* marginal aquitard hypothesized by *Lapen et al*. [2005] and measured by *Baird et al*. [2008], *Lewis et al*. [2012], and *Langlois et al*. [2015]. Such an effect may be site-specific or may be most pronounced in deeper peat (the measurements by *Baird et al*. [2008] were taken at depths between 0.5 and 4.0 m).

The use of C/N to approximate the state of peat decomposition according to *Kuhry and Vitt*'s [1996] method is simple to apply, inexpensive, objective and reproducible; and in sites such as ours where the C/N peak occurs at shallow depths [also *Malmer and Holm*, 1984] its use as a proxy for true fractional remaining mass would appear reasonable. Our calculated *m* values necessarily overestimate true fractional remaining mass because they do not account for decomposition losses at depths shallower than the C/N peak. Particularly in hummocks where decomposition may be rapid due to oxic soil conditions, this error may be considerable, although it is difficult to quantify with any confidence. Any N losses below the C/N peak due to root uptake and translocation within mosses [*Malmer and Holm*, 1984] would have exaggerated this overestimation by inflating measured C/N. Although we did not quantify this error source it is likely to be secondary to that caused by shallow N losses [*Malmer and Holm*, 1984]. This consistent overestimation of *m* will cause equations (1) and (2) to underestimate K_{sat} in peatland development models, especially for fresh peat where the relationship is steep. Nonetheless, our C/N-derived *m* is a powerful predictor of the order of magnitude of K_{sat} in the LME model, leading us to hypothesise that it may also have some skill in predicting other hydrophysical properties such as dry bulk density, saturated water content, and unsaturated moisture-retention parameters, which could be investigated in future studies.

5. Summary and Conclusions

Our equations (1) and (2) provide a means of predicting the order of magnitude and absolute values, respectively, of saturated hydraulic conductivity in near-surface bog peat. Depth and microhabitat type both exhibited strong, independent controls on hydraulic conductivity, although the distinction between central and marginal areas of the bog had no effect. Our linear mixed effects model (equation (1)) illustrates for the first time the shape of the relationship between K_{sat} and an objective, reproducible and continuous estimate of fractional remaining mass, where the latter is used as a predictor of the former in two of the main groups of peatland development simulation models. We recommend that future studies extend our approach into deeper peat, and explore the utility of a C/N-derived approximation of fractional remaining mass as a predictor of other peat hydrophysical properties. Peatland development models should explore the possibility of simulating pore water loading and compression in near-surface peat and the effects upon hydraulic properties.

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References

Armstrong, A. C. (1995), Hydrological model of peat-mound form with vertically varying hydraulic conductivity, *Earth Surf. Processes Landforms*, *20*, 473–477, doi:10.1002/esp.3290200508.

Baird, A. J., P. A. Eades, and B. J. W. Surridge (2008), The hydraulic structure of a raised bog and its implications for ecohydrological modelling of bog development, *Ecohydrology*, *1*, 289–298, doi:10.1002/eco.33.

Baird, A. J., L. R. Belyea, and P. J. Morris (2009), Upscaling peatland-atmosphere fluxes of carbon gases: Small-scale heterogeneity in process rates and the pitfalls of 'bucket-and-slab' models, in Carbon Cycling in Northern Peatlands, Geophys. Monogr. Ser., vol. 184, edited by A. J. Baird et al., pp. 37–53, AGU, Washington, D. C., doi:10.1029/2008GM000826.

Beckwith, C. W., A. J. Baird, and A. L. Heathwaite (2003a), Anisotropy and depth-related heterogeneity of hydraulic conductivity in bog peat. II: Modelling the effects on groundwater flow, *Hydrol. Processes*, *17*, 103–113, doi:10.1002/hyp.1117.

Beckwith, C. W., A. J. Baird, and A. L. Heathwaite (2003b), Anisotropy and depth-related heterogeneity of hydraulic conductivity in bog peat. I: Laboratory measurements, *Hydrol. Processes*, *17*, 89–101, doi:10.1002/hyp.1116.

Belyea, L. R. (2009), Nonlinear dynamics of peatlands and potential feedbacks on the climate system, in Carbon Cycling in Northern Peatlands, Geophys. Monogr. Ser., vol. 184, edited by A. J. Baird et al., pp. 5–18, AGU, Washington, D. C., doi:10.1029/2008GM000829.

Belyea, L. R., and A. J. Baird (2006), Beyond "the limits to peat bog growth": Cross-scale feedback in peatland development, *Ecol. Monogr.*, *76*, 299–322, doi:10.1890/0012-9615(2006)076[0299:BTLTPB]2.0.CO;2.

Boelter, D. H. (1969), Physical properties of peats as related to degree of decomposition, *Soil Sci. Soc. Am. J.*, *33*, 606–609.

Branham, J. E., and M. Strack (2014), Saturated hydraulic conductivity in Sphagnum-dominated peatlands: Do microforms matter?, *Hydrol. Processes*, *28*, 4352–4362, doi:10.1002/hyp.10228.

Chapman, S. J., J. Bell, D. Donnelly, and A. Lilly (2009), Carbon stocks in Scottish peatlands, *Soil Use Manage.*, *25*, 105–112, doi:10.1111/j.1475-2743.2009.00219.x.

Chason, D. B., and D. I. Siegel (1986), Hydraulic conductivity and related physical properties of peat, Lost River Peatland, northern Minnesota, *Soil Sci.*, *142*, 91–99, doi:10.1097/00010694-198608000-00005.

Clymo, R. S. (1992), Models of peat growth, *Suo*, *43*, 127–136.

Clymo, R. S. (2004), Hydraulic conductivity of peat at Ellergower Moss, Scotland, *Hydrol. Processes*, *18*, 261–274, doi:10.1002/hyp.1374.

Couwenberg, J. (2005), A simulation model of mire patterning—Revisited, *Ecography*, *28*, 653–661, doi:10.1111/j.2005.0906-7590.04265.x.

Couwenberg, J., and H. Joosten (2005), Self-organization in raised bog patterning: The origin of microtope zonation and mesotope diversity, *J. Ecol.*, *93*, 1238–1248, doi:10.1111/j.1365-2745.2005.01035.x.

Duan, N. (1983), Smearing estimate: A nonparametric retransformation method, *J. Am. Stat. Assoc.*, *78*, 605–610, doi:10.1080/01621459.1983.10478017.

Elzhov, T. V., K. M. Mullen, A.-N. Spiess, and B. Bolker (2013), minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds, R package version 1.1–8. [Available at http://CRAN.R-project.org/package=minpack.lm.]

Eppinga, M. B., P. C. de Ruiter, M. J. Wassen, and M. Rietkerk (2009), Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning, *Am. Nat.*, *173*, 803–818, doi:10.1086/598487.

Fraser, C. J. D., N. T. Roulet, and M. Laffleur (2001), Groundwater flow patterns in a large peatland, *J. Hydrolol.*, *246*, 142–154, doi:10.1016/S0022-1694(01)00362-6.

Frolking, S., N. T. Roulet, E. Tuittila, J. L. Bubier, A. Quillet, J. Talbot, and P. J. H. Richard (2010), A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation, *Earth Syst. Dyn.*, *1*, 1–21, doi:10.5194/esd-1-1-2010.

Green, S. M., and A. J. Baird (2012), A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane—Including that due to episodic ebullition—From peatlands, *Plant Soil*, *351*, 207–218, doi:10.1007/s11104-011-0945-1.

Grover, S. P. P., and J. A. Baldock (2013), The link between peat hydrology and decomposition: Beyond von Post, *J. Hydrol.*, *479*, 130–138, doi:10.1016/j.jhydrol.2012.11.049.

Heinemeyer, A., S. Croft, M. H. Garnett, E. Gloor, J. Holden, M. R. Lomas, and P. Ineson (2010), The MILLENNIA peat cohort model: Predicting past, present and future soil carbon budgets and fluxes under changing climates in peatlands, *Clim. Res.*, *45*, 207–226, doi:10.3354/cr00928.

Holden, J., and T. P. Burt (2003), Hydraulic conductivity in upland blanket peat: Measurement and variability, *Hydrol. Processes*, *17*, 1227–1237, doi:10.1002/hyp.1182.

Ingram, H. A. P. (1982), Size and shape in raised mire ecosystems: A geophysical model, *Nature*, *297*, 300–303, doi:10.1038/297300a0.

Ise, T., A. L. Dunn, S. C. Wofsy, and P. R. Moorcroft (2008), High sensitivity of peat decomposition to climate change through water-table feedback, *Nat. Geosci.*, *1*, 763–766, doi:10.1038/ngeo331.

Ivanov, K. E. (1981), Water Movement in Mirelands, translated from Russian by A. Thompson and H. A. P. Ingram, Academic, London, U. K.

Johnson, L. C., A. W. H. Damman, and N. Malmer (1990), Sphagnum macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat-bog, *J. Ecol.*, *78*, 633–647.

Kneale, P. E. (1987), Sensitivity of groundwater mound model for predicting mire topography, *Nord. Hydrol.*, *18*, 193–202, doi:10.2166/nh.1987.014.

Kuhry, P., and D. Vitt (1996), Fossil carbon/nitrogen ratios as a measure of peat decomposition, *Ecology*, *77*, 271–275, doi:10.2307/2265676.

Langlois, M. N., J. S. Price, and L. Rochefort (2015), Landscape analysis of nutrient-enriched margins (lagg) in ombrotrophic peatlands, *Sci. Total Environ.*, *505*, 573–586, doi:10.1016/j.scitotenv.2014.10.007.

Lapen, D. R., J. S. Price, and R. Gilbert (2005), Modelling two-dimensional steady-state groundwater flow and flow sensitivity to boundary conditions in blanket peat complexes, *Hydrol. Processes*, *19*, 371–386, doi:10.1002/hyp.1507.

Lewis, C., J. Albertson, X. Xu, and G. Kiely (2012), Spatial variability of hydraulic conductivity and bulk density along a blanket peatland hillslope, *Hydrol. Processes*, *26*, 1527–1537, doi:10.1002/hyp.8252.

Malmer, N., and E. Holm (1984), Variation in the C/N-quotient of peat in relation to decomposition rate and age determination with ^{210}Pb, *Oikos*, *43*, 171–182.

Malmer, N., and B. Nihlgård (1980), Supply and transport of mineral nutrients in a sub-arctic mire, *Ecol. Bull.*, *30*, 63–95.

Miller, D. M. (1984), Transformation bias in curve fitting, *Am. Stat.*, *38*, 124–126, doi:10.1080/00031305.1984.10483180.

Moore, P. A., P. J. Morris, and J. M. Waddington (2015), Multi-decadal water-table manipulation alters peatland hydraulic structure and moisture retention, *Hydrol. Processes*, *29*, 2970–2982, doi:10.1002/hyp.10416.

Morris, P. J., and J. M. Waddington (2011), Groundwater residence time distributions in peatlands: Implications for peat decomposition and accumulation, *Water Resour. Res.*, *47*, W02511, doi:10.1029/2010WR009492.

Morris, P. J., L. R. Belyea, and A. J. Baird (2011), Ecohydrological feedbacks in peatland development: A theoretical modelling study, *J. Ecol.*, *99*, 1190–1201, doi:10.1111/j.1365-2745.2011.01842.x.

Morris, P. J., A. J. Baird, and L. R. Belyea (2012), The DigiBog peatland development model 2: Ecohydrological simulations in 2D, *Ecohydrology*, *5*, 256–268, doi:10.1002/eco.229.

Morris, P. J., A. J. Baird, and L. R. Belyea (2013), The role of hydrological transience in peatland pattern formation, *Earth Surf. Dyn.*, *1*, 29–43, doi:10.5194/esurf-1-29-2013.

Quillet, A., M. Garneau, and S. Frolking (2013), Sobol' sensitivity of the Holocene Peat Model: What drives carbon accumulation in peatlands?, *J. Geophys. Res. Biogeosci.*, *118*, 203–214, doi:10.1029/2012JG002092.

Quinton, W. L., M. Hayashi, and S. K. Carey (2008), Peat hydraulic conductivity in cold regions and its relation to pore size geometry, *Hydrol. Processes*, *22*, 2829–2837, doi:10.1002/hyp.7027.

R Core Team (2014), R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at http://www.R-project.org/.]

Rosswall, T., and U. Granhall (1980), Nitrogen cycling in a subarctic ombrotrophic mire, *Ecol. Bull.*, *30*, 209–234.

Rycroft, D. W., D. J. A. Williams, and H. A. P. Ingram (1975), The transmission of water through peat. I: Review, *J. Ecol.*, *63*, 535–556.

Sherwood, J. H., N. Kettridge, D. K. Thompson, P. J. Morris, U. Silins, and J. M. Waddington (2013), Effect of drainage and wildfire on peat hydrophysical properties, *Hydrol. Processes*, *27*, 13, 1866–1874, doi:10.1002/hyp.9820.

Surridge, B. W. J., A. J. Baird, and A. L. Heathwaite (2005), Evaluating the quality of hydraulic conductivity estimates from piezometer slug tests in peat, *Hydrol. Processes*, *19*, 1227–1244, doi:10.1002/hyp.5653.

Swanson, D. K., and D. F. Grigal (1988), A simulation model of mire patterning, *Oikos*, *53*, 309–314.

Swindles, G. T., P. J. Morris, A. J. Baird, M. Blaauw, and G. Plunkett (2012), Ecohydrological feedbacks confound peat-based climate reconstructions, *Geophys. Res. Lett.*, *39*, L11401, doi:10.1029/2012GL051500.

Thompson, D. K., and J. M. Waddington (2014), A Markov chain method for simulating bulk density profiles in boreal peatlands, *Geoderma*, *232–234*, 123–129, doi:10.1016/j.geoderma.2014.04.032.

Waddington, J. M., and N. T. Roulet (1997), Groundwater flow and dissolved carbon movement in a boreal peatland, *J. Hydrol.*, *191*, 122–138, doi:10.1016/S0022-1694(96)03075-2.

Waddington, J. M., P. J. Morris, N. Kettridge, G. Granath, D. K. Thompson, and P. A. Moore (2015), Hydrological feedbacks in northern peatlands, *Ecohydrology*, *8*(1), 113–127, doi:10.1002/eco.1493.

Wellock, M. L., B. Reidy, C. M. Laperle, T. Bolger, and G. Kiely (2011), Soil organic carbon stocks of afforested peatlands in Ireland, *Forestry*, *84*, 441–451, doi:10.1093/forestry/cpr046.

West, B. T., K. B. Welch, and A. T. Galecki (2007), *Linear Mixed Models: A Practical Guide Using Statistical Software*, Taylor and Francis, Boca Raton, Fla.

Zhang, L., and B. C. O'Kelly (2014), The principle of effective stress and triaxial compression testing of peat, *Proc. ICE*, *167*, 40–50, doi:10.1680/geng.12.00038.