

Microform-scale variations in peatland permeability and their ecohydrological implications

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Running headline: Fine-scale lateral variation in peatland permeability

Supporting information: Appendices S1-S5

Summary

1. The acrotelm-catotelm model of peatland hydrological and biogeochemical processes posits that the permeability of raised bogs is largely homogenous laterally but varies strongly with depth through the soil profile; uppermost peat layers are highly permeable while deeper layers are, effectively, impermeable.

2. We measured down-core changes in peat permeability, plant macrofossil assemblages, dry bulk density and degree of humification beneath two types of characteristic peatland microform – ridges and hollows – at a raised bog in Wales. Six ^{14}C dates were also collected for one hollow and an adjacent ridge.

3. Contrary to the acrotelm-catotelm model, we found that deeper peat can be as highly permeable as near-surface peat and that its permeability can vary by more than an order of magnitude between microforms over horizontal distances of 1-5 metres.

4. Our palaeo-ecological data paint a complicated picture of microform persistence. Some microforms can remain in the same position on a bog for millennia, growing vertically upwards as the bog grows. However, adjacent areas on the bog (< 10 m distant) show switches between microform type over time, indicating a lack of persistence.

5. *Synthesis.* We suggest that the acrotelm-catotelm model should be used cautiously; spatial variations in peatland permeability do not fit the simple patterns suggested by the model. To understand how peatlands as a whole function both hydrologically and ecologically it is necessary to understand how patterns of peat physical properties and peatland vegetation develop and persist.

Key-words: acrotelm-catotelm model, ecological memory, microform, peatland, permeability, persistence, plant–soil (below-ground) interactions, raised bog.

Introduction

Problem statement and research questions

Raised bogs occur commonly in the tropics and at latitudes greater than 45°, especially in the Northern Hemisphere (Ingram 1983; Winston 1994). They are an important global carbon (C) store, and there is interest in how they function as ecosystems and in how they will be affected by climate change; as the climate warms, will they degrade and release their stored C back to the atmosphere, thereby re-enforcing current warming, or will they show some degree of resilience (Swindles *et al.* 2012)? To answer such questions it is necessary to understand how these peatlands behave as ecological and hydrological entities. Conceptually, raised bogs are often divided into two distinct functional layers: (i) an upper acrotelm (literally 'topmost marsh' – see Ingram (1978)) which is the zone in which most water moves and in which biogeochemical processes are most active; and (ii) a lower, poorly-permeable, and usually thicker catotelm in which water flow is slow or negligible and where biogeochemical processes occur at much lower rates (Ingram 1978). While raised bogs undoubtedly show strong vertical variations in peat properties and process rates (e.g. Morris, Baird & Belyea 2015), the usefulness of the simple acrotelm-catotelm dichotomy has been questioned. Morris *et al.* (2011), for example, noted that the model makes the inflexible assumption that a range of biogeochemical and hydrological processes vary in the same binary way with depth. In addition, despite some empirical support for the model, there are quite substantial gaps in our understanding of its applicability. In this paper, we address three questions relating to the model:

- (i) is so-called 'catotelm' peat poorly-permeable as assumed by the model?,
- (ii) does the permeability of this deeper peat vary laterally between microforms?, and
- (iii) how are spatial patterns in permeability related to microform persistence and explained by ecological memory?

Below, we provide a rationale for our focus on these questions.

Background and rationale

Ingram (1978) credited Ivanov (1953) with being the first to propose the concepts of acrotelm and catotelm, although Ivanov (1953, 1981) himself suggested the binary model was established by others before him. Despite emphasising the importance of vertical variations in peat properties, Ivanov (1981) also recognised that peatlands can exhibit distinct lateral variability. Horizontal patterning of peatland microforms (sometimes known as microhabitats or Scale Level 1 features – see Baird, Belyea & Morris (2009)) is seen on many raised bogs. For example, in mid- and high-latitude raised bogs, arrays of hummocks, lawns, and hollows (*sensu* Belyea & Clymo 2001) are common. Hummocks may be *c.* 0.05-0.6 m higher than adjacent hollows and lawns. They are typically 1-3 m in diameter, while the intervening lawns and hollows are often larger, although there is considerable variation in size. These microforms have characteristic plant assemblages. Hummocks tend to be dominated by ericaceous shrubs such as *Calluna vulgaris* (see Appendix S1 in Supporting Information for botanical authorities and common English names) and *Rhododendron groenlandicum*, sedges such as *Eriophorum vaginatum*, and small-leaved Sphagna such as *Sphagnum fuscum* and *Sphagnum capillifolium*. Lawns and hollows have a cover of larger-leaved Sphagna such as *Sphagnum papillosum*, *Sphagnum pulchrum*, and *Sphagnum cuspidatum*, with sedges such as *Rhynchospora alba* often co-dominant. (The species listed here may be found in peatlands in northwest Europe and parts of northeast USA and southeast Canada, and are examples only.) Because peat is the decomposing remains of plants, variations in the composition of the vegetation growing on a bog can be expected to produce variations in peat type; as a bog grows, different types of peat will build up under different types of vegetation.

Lateral variations in the peat under different vegetation types have been described using both direct observation and non-invasive geophysical methods. For example, in a palaeo-ecological study of a raised bog in northern England, Barber (1981) showed how hummocks and intervening lawns and hollows may persist over millenia as a peatland grows. He also suggested that lawns and hollows expand laterally during wet climatic phases and shrink during drier phases (when

hummocks expand), a suggestion made previously by Aaby (1976). Barber (1981) studied peat faces produced by peat cutters from which lateral variations in peat type could be directly recorded and sampled. More recently, Kettridge *et al.* (2008) used ground-penetrating radar (GPR) and complex electrical conductivity surveys complemented by hand coring to reveal horizontal zonation in peat geophysical properties to depths of *c.* 3 m along a 36-m transect in a raised bog in Maine in the USA. The observations made by Barber (1981) and Kettridge *et al.* (2008) may easily be verified by walking across a patterned bog: peat under hummocks is often firmer and safer to walk on than peat in lawns and hollows. However, such variations in structural strength may not necessarily translate into differences in hydrological properties such as water-storage capacity (e.g. specific yield or drainable porosity, s) and permeability or hydraulic conductivity (K).

Despite the recognition of lateral variability between microforms on bogs and an interest in how spatial patterns form (see below), there is little information on how hydrological properties vary between microforms. Some work has been done on poor fens (*sensu* Rydin & Jeglum 2006) which have similar types of vegetation to bogs. For example, in an undrained area of poor fen in Quebec, Canada, Whittington & Price (2006) found strong lateral variability in K of one-two orders of magnitude over distances of a few metres between a ridge (an elongated hummock or series of contiguous hummocks), a lawn and a 'mat', the latter a type of hollow. They also found that K declined by two to three orders of magnitude between depths of 0.25 and 1.25 m in these microforms, which is broadly what would be expected from the acrotelm-catotelm model. Therefore, lateral variability appears to be superimposed onto vertical variability. Whittington & Price's (2006) data are useful in showing that lateral variability can be substantial, but they only measured K at one location in one example of each microform, so their study lacked spatial replication. Ivanov (1981) reproduced empirical functions in which K at the same depth below the surface may vary by more than two orders of magnitude depending on microform type. However, it is not clear what data sets lie behind his functions (the number of measurements and sites from which the data behind the functions come are not listed) and they deal with shallow peat only

(upper ~ 0.4 m of peat profile). The latter issue – that of water flow in shallow *vs* deeper peat – is particularly pertinent, because, although he stressed the importance of lateral variation, Ivanov (1981) still considered shallow peat to be the main route for water flow, a key assumption of the acrotelm-catotelm model. There is abundant evidence that uppermost layers of bogs can be highly permeable (e.g. Boelter 1965; Hoag & Price 1995; Morris, Baird & Belyea 2015), but the situation with deeper peat is less clear. Some of the low K values reported for deeper peat may, in part, be measurement and sampling artefacts (see discussions in Koerselman (1989) and Baird, Surridge & Money (2004)). Where robust measurement protocols have been used there is evidence that deeper peat, on some sites at least, can be relatively permeable (e.g. Baird, Eades & Surridge 2008) and it is important that more work is done on estimating the K of deeper peat. Where permeable deeper peat is found, its effect on overall water flow through a bog will depend on whether it occurs in pockets isolated by poorly-permeable peat or whether it is connected to other higher-permeability zones (Belyea & Baird 2006). In other words, it is important to know both the absolute value of K and its spatial pattern – vertically and laterally – when considering the hydrological behaviour of bogs. The hydrological functioning of a peatland, often expressed in terms of the water-table regime, is closely linked with its ecological functioning (e.g. Belyea & Baird 2006; Roulet *et al.* 2007; Frohling *et al.* 2010; Morris, Baird & Belyea 2012), and anything that influences the behaviour of the water table will also affect key ecological processes such as litter production, vegetation composition, and depth-integrated rates of peat decay (e.g. Belyea & Clymo 2001).

A group of theoretical studies (Swanson & Grigal 1988; Couwenberg & Joosten 2006; Eppinga *et al.* 2009; Morris, Baird & Belyea 2013) used cellular landscape models to investigate the linkages between the hydrological and ecological functioning of peatlands, in particular how these linkages can lead to the development of hummock-hollow patterns. These models assume that the hydraulic properties of peat under different microforms are also different – they assume there is lateral variability – but also that most water flow occurs in the uppermost layers of a bog. Morris, Baird & Belyea (2013) showed that these models, despite considering horizontal variability, likely

lack some important ecohydrological feedbacks and may produce realistic patterns for the wrong reasons. Specifically, Morris, Baird & Belyea (2013) raised the question of whether microforms such as hummocks and hollows can be considered as features only of shallow peat, or whether their structural and hydrological importance at both the scale of the microform and the whole bog extends into deeper peat. They proposed a hypothetical mechanism for ecological memory (*sensu* Hendy & McGlade 1995) in peatlands whereby former surface vegetation patterns can leave a 3-dimensional imprint in the hydraulic structure of peat even after they are buried by litter from more recent plant assemblages. In a bog that possesses strong ecological memory of the type proposed by Morris, Baird & Belyea (2013), differences in peat properties (e.g. K) that characterise particular microform types would be evident not only near the surface in upper peat but also in deeper peat. Where a particular microform type had persisted for a long time, continued accretion would form a 3-dimensional pillar or curtain (*sensu* Belyea & Baird 2006) of peat that could be distinguished from adjacent peat produced by different microform types. In a bog with no ecological memory, deeper peat would be laterally homogenous in terms of the property of interest; i.e., even if microforms persisted in place for long periods, characteristic differences in the peat property of interest would only be identifiable in surficial layers and would not be preserved in deeper peat. A situation in which characteristic differences between microform types persist to a limited depth, or perhaps diminish gradually with depth, might be thought of as a weak ecological memory. It is clear that, to understand the patterning of peat hydrophysical properties in bogs, we must first understand how microforms develop and persist, and how peat properties change through time.

Materials and Methods

To address the first and second research questions on the magnitude and lateral variability of K in deeper peat, we measured K at two depths in two types of microform – ridges and hollows – in a Welsh raised bog. Measurements of the abundance of a range of plant macrofossils in cores of peat extracted from the bog were used to reconstruct the developmental history of the different

microforms used for the K measurements, thus providing data for answering the third research question. The plant macrofossil and K data were complemented with measurements of peat dry bulk density, degree of humification and age (from calibrated ^{14}C dates). Our combination of palaeoecological techniques and detailed measurements of hydrological properties is perhaps an unusual one, but serves as a powerful and novel tool for understanding ecohydrological memory in peatlands.

Field site and sampling rationale

The site chosen for study – Cors Fochno in west Wales – has been described in detail in Baird, Eades & Surridge (2008) and Kettridge *et al.* (2012). Its margins have been disturbed or damaged by drainage and peat cutting, but its central area is undamaged and contains maze-like and sometimes striped patterns of ridges, hummocks, lawns, and hollows that are typical of many raised bogs and northern peatlands more generally (see Eppinga *et al.* 2009). Four microforms in this central area were investigated: a ridge-hollow-ridge-hollow sequence at $52^{\circ} 30' 10.0''$ N and $4^{\circ} 00' 45.5''$ W. These features coincided with the first *c.* 10 m of the northern end of a 45-m transect used by Kettridge *et al.* (2012) for a GPR survey of the peat, and are, for convenience, named Ridge 1, Hollow 1, Ridge 2, and Hollow 2 (Fig. 1). Ridge vegetation comprised mostly *Calluna vulgaris*, *Eriophorum vaginatum*, and *Sphagnum capillifolium*, with some *Eriophorum angustifolium* and *Myrica gale*. Hollow vegetation was dominated by *Sphagnum pulchrum*, *Rhynchospora alba*, *Eriophorum angustifolium*, with occasional *Erica tetralix* and *Myrica gale* plants (see Appendix S1). The ground surface in the ridges was typically 0.05-0.10 m above that in the hollows (as measured using an optical level – data not reported). The location of the ridges and their position relative to the transect line used by Kettridge *et al.* (2012) is shown in Fig. 1.

We devised and conducted the study before the GPR data reported in Kettridge *et al.* (2012) were analysed. GPR reflections from their survey tend to dip, and appear to indicate that microforms at the site have migrated in one direction over time. However, the data obtained by

Kettridge *et al.* (2012) do not present a consistent picture. Dip angle decreases at depths of 1 m and less, suggesting that microform movement has slowed in the most recent period of bog development (last *c.* 1300 years according to data cited by Kettridge *et al.* (2012)). There are also sections along the 45-m transect (see Fig. 6c in Kettridge *et al.* (2012)) where the reflectors are flat, which suggests that some areas remain stable – their microforms do not move – while other areas, only a few metres away, are dynamic. Finally, for a 2.1-m section of the transect (27.4 m - 29.5 m) for which the GPR reflectors were dipping, detailed core analysis (eight cores at 0.30-m intervals) did not reveal any obvious dipping structures (Kettridge *et al.* 2012). As such it is unclear whether the microforms along our transect have been stationary or mobile through time. This issue relates directly to our third research question and we were able to determine if microforms had moved over time using our plant macrofossil and peat age data (see *Peat core collection and analysis* below).

Hydraulic conductivity (K)

To address the first and second research questions, K was measured in the four microforms using standpipe piezometers inserted into pre-augered holes. In each microform, five measurements were made at a nominal depth of 0.5 m and five at 0.9 m. These depths were chosen because they are below both the typical and the drought-year summer water table, and, therefore, represent what would usually be classified as the catotelm in the two-layer model (Ivanov 1981; Ingram 1983). Unpublished data from the site show that maximum water-table depths do not exceed 0.25-0.30 m in hollows and 0.40 m in ridges during summer drought. Separate locations were used for measuring K at the two depths. That is, we did not measure K at 0.5 m and then deepen the hole and measure K at 0.9 m; rather, we used separate holes, and these were at least 1 m distant from neighbouring holes. Therefore, we used a total of 40 locations for the K measurements. In this way we avoided a problem of repeated measures; each of our measurements could be regarded as independent at the scale of the microform.

Piezometer installation and K measurements followed the protocols presented by Baird, SurrIDGE & Money (2004), SurrIDGE, Baird & Heathwaite (2005), and Kelly *et al.* (2014). We used the same piezometer tubes as SurrIDGE, Baird & Heathwaite (2005). These have an outside diameter (OD) of 0.033 m, an inside diameter (ID) of 0.029 m and 0.21 m long intakes. The centre of the intake was placed at each nominal depth – 0.5 m and 0.9 m.

Following installation, the piezometers were 'developed' or cleaned (Butler 1998; Baird, SurrIDGE & Money 2004) to remove any smeared peat from around the intake. After development, a self-logging pressure transducer and a slug consisting of an acrylic rod were placed below the water level in each instrument. The water level was then allowed to stabilise before a head-recovery test was conducted by removing the slug. The removal of the slug caused the water level to fall by c . 0.04 m, and the subsequent rise in water level was recorded by the pressure transducer. Two types of pressure transducer were used – Mini-Diver and Micro-Diver units manufactured by Schlumberger Water Services (Delft, The Netherlands) – each with a resolution or precision of 0.002 m. A logging interval of 2 s was used for piezometers installed in the most permeable peat, while 4 s was used for slower-responding instruments. The shortest tests were completed within a few seconds; the longest took more than 12 hours (see below).

K was estimated from Hvorslev's (1951) equation:

$$K = -\frac{A}{Ft} \ln\left(\frac{h}{h_0}\right) \quad (1),$$

where A is the inside cross-sectional area of the piezometer standpipe (m^2), t is the time (s) at which the head difference, h (m) (see below), in the piezometer was recorded, h_0 is the initial head difference, and F is the shape factor (m) which is a function of the size and shape of the piezometer intake and the pattern of water flow around it (see Brand & Premchitt 1982). The head difference, h , is defined as the difference between the water level in the piezometer at any time during a head-recovery test and the water level prior to the withdrawal of the slug. h_0 is the difference at the moment the slug has been removed from the piezometer.

Strictly, equation (1) should only be applied to rigid media; peats are compressible and K tests in them may not yield the log-linear recovery of the equation. However, it has been shown (Baird & Gaffney 1994) that reliable estimates of K in peats may be obtained using the equation if the head ratio (h/h_0) is close to zero; here, a value of $h/h_0 = 0.05$ and its associated time (t_{95}) were used.

In some tests, the rate of water flow from the piezometer was so rapid that an initial head difference could not be satisfactorily established. For these tests, it was assumed that t_{95} was 2 s. In the 0.5-m tests carried out on Ridge 1, recovery was slow and coincided with a period of falling heads in the peat around the piezometer intakes, making it difficult to estimate t_{95} . An example is given in Fig. 2 which shows an apparent stalling of the head recovery. In these cases we assumed t_{95} occurred at the turning point as shown by the arrow in the figure. This assumption will always give a value of t_{95} that is too low, and therefore a value of K that is too high, compared to what would be the case if background heads around the intake remained stable. Ideally, a period of stable heads would have been used for the 0.5-m tests in Ridge 1. However, because recovery was so slow, it would have been very difficult to find a time when heads remained stable for 12-24 hours; in most bogs, heads often vary over such timescales due to gravitational water flow through the peat or evaporative losses of water. Our assumed t_{95} values were, in any case, conservative because all of the 0.5-m K estimates from Ridge 1 were lower than the lowest K recorded in any other feature at either depth.

Hydraulic conductivity reflects both the properties of the porous medium and the liquid flowing through it. As the viscosity of water changes with temperature so too does the hydraulic conductivity. Our pressure transducers also measured temperature and we were able to use the temperature data to convert our K values (as per Klute (1965)) to a standard temperature of 20°C.

Peat core collection and analysis

To reconstruct the developmental history of the microforms and to establish microform persistence (third research question), cores from each of the features were analysed for plant macrofossil remains, peat humification, and dry bulk density. In total, five cores were taken from each microform and each was 2 m in length. Three cores were taken from the centre of the microform (close to the intersection of the microform's long and short axes), each core being within 0.3 m of its two neighbours. One of these was analysed for peat decomposition or humification, one for dry bulk density (ρ_b), and one for plant macrofossils. Two additional 'humification cores', one from the western end and one from the eastern end of each feature (see Fig. 1) were also analysed. Plant fragments from the upper metre from two of the cores that were used for the macrofossil analysis – the cores from Ridge 2 and Hollow 2 – were ^{14}C dated (dates calibrated using IntCal09 – see below), and six dates from three depths in each core were obtained. All of the cores were taken with a Russian corer, with a semi-circular chamber with a diameter of 0.038 m.

Peat humification, an indicator of the degree of decomposition, was estimated visually from fresh peat in the field. The color and texture of the peat in the core were used to define peat layers, and each layer was classified using the von Post humification scale from H1 (completely undecomposed) to H10 (completely decomposed) (see Rydin & Jeglum 2006). The humification estimates were conducted by the same person (A.M.M.) for all cores, and the von Post descriptions given in Rydin & Jeglum (2006, p. 86) were used as a constant reference to ensure consistency in classification.

In the bulk density cores, samples were taken, where possible, from 0-0.02 m, 0.10-0.12 m, 0.20-0.22 m and so on below the surface. Poor recovery in parts of the cores meant that not all the required depths could be sampled. Seventeen samples were recovered from Hollow 1, six from Hollow 2, 18 from Ridge 1 and 19 from Ridge 2. The samples were placed in foil sachets in the field and then wrapped in clingfilm for later analysis. They were stored in a cold room below 4 °C upon return to the laboratory. After removal from storage, they were dried at 80 °C for 24 hours

before being cooled in a desiccator and weighed. The samples were not ashed, so the values of ρ_b that were calculated were not corrected for the presence of any non-organic material.

Each of the four macrofossil cores was divided into bulked samples for each 0.1-m depth interval. Thus, samples represented depths of 0-0.1 m, 0.1-0.2 m and so on, with each sample having a volume of *c.* $5.7 \times 10^{-5} \text{ m}^3$ depending on core recovery. It is unusual to use bulked cores like this for plant macrofossil analysis. More typically, samples that span a 0.01-m depth range are analysed. Sometimes these are contiguous, but, because they are time-consuming to analyse, they are often spaced at intervals of 0.02-0.08 m (Amesbury, Barber & Hughes 2010). The problem with the latter is that critical information may be lost. For example, there may have been a switch between vegetation types in the un-analysed zone between two 0.01-m samples; in effect, the record is incomplete, even though the information from a 0.01-m layer can be ascribed accurately to a particular depth and date. There is inevitably some loss of information and resolution with our method, but it guarantees that all plant types present within a 0.1-m length of core are recorded, including their abundance, making it possible to establish if there have been switches between vegetation types during the time period represented by the 0.1 m.

Each macrofossil sample (i.e., the entire $5.7 \times 10^{-5} \text{ m}^3$) was prepared for examination using standard techniques as detailed by Barber *et al.* (1994). Macrofossil examination followed the Quadrat and Leaf Count Method (Barber *et al.* 1994) but with some modifications as described below. Before examination, each prepared sample was mixed thoroughly and emptied into a large-diameter (0.15 m) Petri dish. A low-powered microscope fitted with a 10×10 square grid (quadrat) in the eyepiece allowed percentage coverage of different macrofossil components to be estimated. When possible, 100 *Sphagnum* leaves were picked from the sample, mounted on slides, examined at $\times 100$ -400 magnification and identified to species or at least section level. Differentiation between monocotyledon remains was also achieved when suitable epidermal tissue was found (Mauquoy, Hughes & van Geel 2010). Five quadrat estimations were completed for each sample. Seeds, ericaceous leaves and charcoal were counted separately.

We obtained six accelerator mass spectrometry (AMS) ^{14}C dates of the peat in the study area, three from Hollow 2 and three from Ridge 2 (Fig. 1). Plant fragments for dating were obtained from depths of 0.2-0.3 m, 0.5-0.6 m, and 0.9-1.0 m from the two cores used for the plant macrofossil analysis (see above). The mixed samples of peat from the 0.1-m intervals (see above) were washed with deionised water in a 125 μm sieve, and, in order to minimise potential contamination, *Sphagnum* leaves, branches, and stems were used for the dating, except for the 0.9-1.0 m interval in Ridge 2 where we used *Racomitrium lanuginosum* leaves and stems. Care was taken to remove ericaceous roots to prevent any possible reservoir effects as described by Kilian, van der Plicht & van Geel (1995). The plant fragments were dated at the ^{14}C CHRONO Centre at Queen's University, Belfast (an acid-alkali-acid pre-treatment was used). The ^{14}C dates were calibrated using IntCal09 (Reimer *et al.* 2009).

Data analysis

Except for those piezometers noted earlier where an initial head difference could not be established or where recovery stalled, we estimated t_{95} as the first reading where $h/h_0 \leq 0.05$. We conducted repeat K tests on some piezometers to help gauge within-instrument test variability and these showed similar consistency to previous studies (see Appendix S2 in Supporting Information). As well as differences in K between microform type (ridge, hollow) and depth, we were interested in all comparisons across the K data set to see whether differences between, say, ridges and hollows depends on which ridge and which hollow are being considered. We used a Bayesian multiple pairwise comparison developed by Kruschke (2011; chapter 18) that allows for non-homogenous variance between groups, a group being, for example, all the readings at 0.5 m in Hollow 1. We undertook the analysis on the \log_e transformed data. In the Bayesian analysis, the data as a whole (combined from all groups) are standardised to have a mean of zero and a standard deviation of 1. The model describing the standardised data is given by:

$$u_i = \beta_0 + \sum_j \beta_j x_{ji} \quad (2)$$

where u_i is the mean of the distribution of individual values (y_i), β_0 is a baseline value of u_i , while β_j is the deflection from β_0 for group j . x may take values of 0 or 1. β_0 is described by a normal distribution with a mean of zero and a precision of 0.001 (variance of 1000). β_j is also described by a normal distribution, which has a mean of zero and a precision specified by a folded t distribution with a mean of zero, a precision of 0.001 and a k or shape setting of 2. These priors for the models of both β_0 and β_j are highly non-committal and have a very small influence on the posterior (or outcome) of the Bayesian analysis. To account for unequal variance between groups, the precision of the distribution of y_i is estimated separately for each group from a gamma distribution (see Kruschke 2011).

The Bayesian method was applied using the data and multiple random sampling from the data models as specified with the non-committal priors. Sampling was performed using a Markov Chain Monte Carlo (MCMC) process (Kruschke 2011) with a sample size of 100 000 after a 'burn-in' of 5000 steps. The pair-wise analysis was carried out using R and JAGS (R Core Team 2012) and the code and its source are given in Appendix S3. The MCMC analysis yields distributions of differences in β_j for each pair of groups. In these distributions we may define a highest density interval or HDI in which 95% of the difference values lie. If the HDI does not include zero we may conclude that there is a credible difference in K between the groups.

To assess whether there is evidence of the persistence of each of the microforms over the period of time represented by the 2 m peat cores, we applied cluster analysis with multiple bootstrap resampling to the plant macrofossil biostratigraphic data. This analysis enables the calculation of p -values to identify statistically significant clusters (Suzuki & Shimodaira 2006) and was used to determine the similarity-dissimilarity of samples between the hollow and ridge cores. We also undertook nonmetric multidimensional scaling (NMDS; Minchin 1987) using the Bray-Curtis dissimilarity index to examine the main axes of variation in the plant macrofossil data. The Bray-Curtis dissimilarity index is a popular and effective index for ecological data and is defined as:

$$d^{BCD}(i, j) = \frac{\sum_{k=0}^{n-1} |y_{i,k} - y_{j,k}|}{\sum_{k=0}^{n-1} (y_{i,k} + y_{j,k})} \quad (3)$$

where d^{BCD} is the Bray-Curtis dissimilarity between the objects i and j , k is the index of a variable and n is the total number of variables y (e.g. Legendre & Legendre 1998). The stress was analysed in several runs to ensure a robust result was achieved. Ordination ‘spiders’ were used to demarcate the four microforms and assess similarity/dissimilarity. The analysis was carried out using the vegan package (v. 2.0-5) in R (v. 2.15.1) (Oksanen *et al.* 2012; R Core Team 2012).

It is common in plant macrofossil analysis to include Ericaceae as a class and we followed this convention when compiling our data (see **Results**; *Macrofossils, humification and bulk density*). However, Ericaceae was left out of the cluster and NMDS analysis because its main components – *Calluna vulgaris* and *Erica tetralix* – may, between them, occupy a range of wetness conditions from hollow to ridge. *Calluna vulgaris* is usually a reliable dry or ridge indicator. However, although *Erica tetralix* is often used by palaeoecologists as a dry indicator (e.g. Mauquoy *et al.* 2008), it is more flood-tolerant than *Calluna vulgaris* (e.g. Bannister 1964) and, unlike the latter, may be common in wet conditions such as the fringe of bog pools (Elkington *et al.* 2001). Rare taxa (with maximum values of 4% or less) were also excluded from the NMDS analysis.

Age-depth models for Ridge 2 and Hollow 2 were constructed using the ‘Bacon’ piece-wise linear accumulation model of Blaauw & Christen (2011) in R (R Core Team, 2012). In this model, the accumulation rate of sections depends to a degree on that of neighbouring sections, accumulation rates are constrained by a prior distribution (a gamma distribution with parameters acc.mean and acc.shape), as is the variability in accumulation rate between neighbouring depths (‘memory’, a beta distribution with parameters mem.mean and mem.strength). In our analysis, 0.05 m-thick sections were used along with acc.shape = 2 and acc.mean = 13 yr cm⁻¹. The prior information was combined with the radiocarbon dates and a 2011 date for the peat surface using millions of MCMC iterations (Blaauw & Christen 2011). The total chronological error (difference between maximum and minimum probability ages at 95 %) associated with each depth was

calculated from the model. Ages for the 0.1 m-thick dating samples were defined using the Bacon model and expressed in histograms (see Appendix S4).

Results

Hydraulic conductivity

The hydraulic conductivity (K) data are summarised in Fig. 3, with the data separated according to microform and depth. The data show that K varies by nearly four orders of magnitude across the site. The highest K values were more than $1 \times 10^{-3} \text{ m s}^{-1}$ while the lowest values were less than $1 \times 10^{-6} \text{ m s}^{-1}$, equivalent, respectively, to the K of a coarse sand and that of a silt (Domenico & Schwartz 1990). The data also suggest that there are differences in K between microforms. For depths of 0.5 m, hollow K appears to be significantly higher than ridge K , with nine of the 10 hollow values exceeding the highest value from the ridges. Four of the 10 hollow values exceed the highest ridge value by at least an order of magnitude and two of the 10 exceed the highest ridge value by a factor of *c.* 250. At a depth of 0.9 m, the differences between features are less clear. All of the values from Hollow 1 exceed all of the values from Ridges 1 and 2. However, there is an overlap between the values from Hollow 2 and both ridges. The data also suggest that there are differences in the K values between microforms of the same type and the same depth. For example, at 0.5 m depth, all of the K values from Ridge 2 are higher than those from Ridge 1. Similarly, all of the K values at a depth of 0.9 m in Hollow 1 are higher than the values at the same depth in Hollow 2.

The results from the Bayesian analysis are summarised in Table 1 and given in more detail in Appendix S3. Table 1 identifies those categories in which the highest density interval (HDI) of between-group differences in the deflections – β_j – does not include zero; as noted above (see **Materials and Methods; Data analysis**) this may be thought of as indicating a credible difference between a pair of groups based on the data that have been collected. In terms of between-group differences, the most interesting features from the Bayesian analysis are as follows.

Depths of 0.5 m. Ridge 1 is credibly different from all other groups at this depth (Ridge 2, and Hollows 1 and 2). Ridge 2 also differs from Hollows 1 and 2; therefore, despite the difference between Ridge 1 and Ridge 2, there is credible evidence that the ridges at 0.5 m are different from the hollows at the same depth.

Depths of 0.9 m. Hollow 1 is credibly different from both ridges at this depth. Hollow 2, however, is not credibly different from either ridge. These results contrast with those from 0.5 m where ridges and hollows show clear differences; at 0.9 m there is no such pattern in the data. Notably, Ridges 1 and 2 show no credible difference at this depth, unlike at 0.5 m.

The pairwise comparisons also suggest that there is a credible difference between depths in Ridge 1, but not in the other three microforms, although in Hollow 2 the HDI in the contrast between 0.5 m and 0.9 m only just straddles zero (Table 1), so there is some suggestion of a real difference in K values between depths. In Ridge 1 the 0.5-m or younger peat has a lower K than the deeper peat, while in Hollow 2 the opposite is the case.

Peat age-depth profiles

Radiocarbon dates of the extracted plant fragments from Hollow 2 and Ridge 2 are given in Table 2. The age-depth models that were derived from the data are given in Appendix S4. Age-depth curves for each feature are given in Fig. 4. These show different trajectories for each feature. For 1 m in Ridge 2 the modelled age is 1520-1330 cal. BP (mean = 1390 cal. BP) whereas for 1 m in Hollow 2 the modelled age is 1315-1080 cal. BP (mean = 1180 cal. BP).

The peat accumulation rates for Ridge 2 and Hollow 2 show variations. For Ridge 2 the accumulation rate was higher in the lower part of the core and decreased towards the top of the core (*c.* 0.11 cm yr⁻¹ from 0.57-1.00 m depth, compared with 0.05 cm yr⁻¹ from 0.00-0.57 m depth). For Hollow 2, the accumulation rates were more mixed, with lower and less variable rates in the lower part of the core (*c.* 0.07 cm yr⁻¹ from 0.57-1.00 m) and higher and more variable rates in the upper part. The maximum and minimum accumulation rates were similar, with maxima of 0.14 and 0.15

cm yr⁻¹ for Ridge 2 and Hollow 2, respectively, and a minimum of 0.05 cm yr⁻¹ for both features. These interpretations are somewhat tentative due to the relatively low number of radiocarbon dates.

Macrofossils, humification and bulk density

The macrofossil, humification and dry bulk density data for the three separate cores taken from the centre of each microform are shown in Figs 5a and 5b. The data from the additional humification cores (two per microform) are available in Appendix S5.

The four microforms differ in their peat profiles in terms of degree of decomposition, macrofossil composition and abundance, and dry bulk density. Taxa indicative of surface wetness (water tables close to the surface) are more abundant in the two hollow cores (Fig. 5a) than in the two ridge cores (Fig. 5b), and *vice versa*. For example, ridge cores are notably characterised by *Sphagnum austinii*, while hollow cores are dominated by *Sphagnum* section Cuspidata, *Rhynchospora alba* and *Sphagnum papillosum* with occasional abundance of monocotyledons and *Menyanthes trifoliata*. However, 'wetter' taxa are evident, and sometimes common, in the ridge cores and drier taxa in the hollow cores.

Our analysis revealed a number of statistically significant clusters ($p < 0.05$) (Fig. 6), and shows, generally, that the ridges and hollows are strongly differentiated from each other; Hollow 1 is most similar to Hollow 2, and Ridge 1 is most similar to Ridge 2. However, while Ridge 2 and Hollow 2 are mostly distinct features, there is considerable overlap between Ridge 1 and Hollow 1. The NMDS analysis of the macrofossil data shown in Fig. 7 gives a similar outcome to the cluster analysis. The major gradient in the dataset (NMDS axis 1; Fig. 7) follows a ridge-hollow/bog surface wetness gradient. It is apparent that Ridge 2 and Hollow 2 are separate from each other in the ordination space, whereas Hollow 1 and Ridge 1 overlap; the axis 1 scores illustrate this separation and overlap clearly. The analysis confirms what appears to be evident from the macrofossil diagrams: Ridge 2 and Hollow 2 have consistently been a ridge and hollow, respectively, throughout their developmental history as represented by their respective macrofossil

NMDS axis 1 scores. The cores from Hollow 1 and Ridge 1 have a more mixed signal in terms of macrofossils although Hollow 1 is more hollow-like than Ridge 1, and Ridge 1 is more ridge-like than Hollow 1.

Generally, the two ridge cores have more decomposed peat than the two hollow cores: the average humification from the Ridge 1 and 2 cores is H7 and H8, respectively (Ridge 1, $n = 44$; Ridge 2, $n = 53$), whereas the average humification for the Hollow 1 and 2 cores is H6 (Hollow 1, $n = 60$; Hollow 2, $n = 48$). However, there is considerable down-core variability in humification in all cores (see Appendix S5).

The dry bulk density (ρ_b) for all the microforms was below 100 kg m^{-3} and ranges from 21 to 86 kg m^{-3} (Figs 5a and 5b). The highest ρ_b values were recorded in Ridge 2, and the lowest in Hollow 1. The average ρ_b for Hollows 1 and 2 is, respectively, 35 kg m^{-3} ($n = 17$) and 33 kg m^{-3} ($n = 6$ due to poor core recovery); the averages for Ridge 1 and 2 are 45 kg m^{-3} ($n = 18$) and 60 kg m^{-3} ($n = 19$). The ρ_b values for Ridge 1 and 2 show little overlap with the values of Hollow 1 and 2: the ridges have consistently higher ρ_b than the hollows.

Discussion

High K in deeper peat

From an ecohydrological perspective the first two research questions on the magnitude and lateral variability of deeper-peat K only assume importance if the permeability of the deeper peat is sufficiently high to allow non-trivial rates of water flow. Even if there is an order of magnitude difference in the K of the deeper peat between hollows and ridges, the difference may be unimportant if those K values are low: for example, water flow through peat with a permeability in the range of $1\text{-}10 \times 10^{-9} \text{ m s}^{-1}$ will be negligible under natural hydraulic gradients, so it does not matter if different microform types lie at opposite ends of this range.

In the two-layer acrotelm-catotelm model, the acrotelm conducts the vast majority of water, with largely stagnant conditions prevailing in the catotelm because of its low K . While we found

that deeper-peat (catotelm) K can be low and consistent with the model, such as in Ridge 1 at a nominal depth of 0.5 m (Fig. 3), we also found that K in deeper peat could equal and exceed values for shallow, near-surface, peat at the site (Fig. 3) and for a range of other peatlands – see, for example, Boelter (1965), Hoag & Price (1995), Quinton, Hayashi & Carey (2008), Lewis *et al.* (2012), and Morris, Baird & Belyea (2015) (Fig. 3). In each of these studies, *Sphagnum* was often the main or an important peat-forming species, and the highest K values reported in each were generally associated with the least decomposed peat. Our results show that deeper bog peat has the potential to conduct non-trivial amounts of water; as such, our data are inconsistent with one of the principal features of the two-layer model. This finding adds weight to the growing argument (Holden & Burt 2003; Morris *et al.* 2011) that the two-layered model is too rigid a framework to be generally applicable, because the intricacies of peatland ecohydrological structures and functions do not necessarily partition neatly into two catch-all layers. However, whether the K values we observed in deeper peat layers actually lead to rapid flows will depend on the connectivity of zones of high K within the deeper peat, and more work is required on mapping subsurface structures at the site.

Microform persistence and K variations

Based on the age-depth model, Hollow 2 has persisted since at least *c.* 1200 cal BP and Ridge 2 since at least *c.* 1400 cal BP. Because they extend to twice the depth of the deepest dated samples, the macrofossil data show that both microforms have persisted for considerably longer than these ages. Both features are, therefore, ancient, persisting as the bog increased markedly in vertical extent. The other two microforms – Hollow 1 and Ridge 1 – show a mixed signal; they have undergone switches in their status over time. Nevertheless, Hollow 1 has been more hollow-like than ridge-like throughout its development, and Ridge 1 has been more ridge-like than hollow-like. Therefore, there is little evidence to support the suggestion of uni-directional microform movement at the site. This finding is not necessarily inconsistent with what is suggested in Kettridge *et al.*

(2012) who found that dipping reflectors indicative of microform movement were more steeply sloping in the peat at depths of 1-2.5 m than shallower depths; in other words that the evidence of microform movement in the uppermost metre of peat is less strong than the evidence from the deeper peat. Nevertheless, based on their GPR data, current microform spacing and an age-depth model constructed from data from Schulz (2004), Kettridge *et al.* (2012) suggested that a microform passing a fixed point would be expected to produce layers of peat with a mean thickness of *c.* 0.19 m. When superimposed on such layers, our contiguous 0.1-m samples should consist of some in which there is a hollow-only signal, some which are ridge-only, and some that contain a mixture of wet and dry indicators. Such a pattern of both pure and within-sample mixed signals is not evident in the data from Hollow 2 and Ridge 2, which contain, respectively, hollow-like and ridge-like properties throughout most of their profiles. In Hollow 1 and Ridge 1, there is evidence of switches in microform type but these don't conform to the pattern expected from 0.19-m layers, regardless of how a 0.1-m sampling interval is staggered. Therefore, the switches seen in Hollow 1 and Ridge 1 are more likely to be due to microform contraction/expansion as per the conceptual model of Aaby (1976) and Barber (1981). Whether such contraction/expansion resulted from climatic changes remains unclear (it may be autogenic or allogenic).

Multivariate statistical tools such as the cluster analysis and NMDS we apply here provide an objective statistical approach for classifying microforms and assessing how distinct they have been through their developmental history. NMDS enables the determination of whether plant assemblages in each microform have remained consistent, or whether switches in the microform characteristics have occurred. We contend that using robust statistical tools such as NMDS is less prone to bias than traditional approaches where stratigraphic data are zoned and classified by eye.

Peat formed in ridges (from ridge vegetation) is different, botanically, from that formed in hollows (from hollow vegetation), and the plant macrofossil data suggest that Hollow 2 has been more hollow-like than Hollow 1 throughout its history and Ridge 2 has been more ridge like than Ridge 1. With this in mind, we might expect the K at 0.5 m and the K at 0.9 m – $K_{0.5}$ and $K_{0.9}$ – to

show the greatest differences between Hollow 2 and Ridge 2, but this is not the case. The difference in $K_{0.5}$ between Hollow 1 and Ridge 1 is much greater than that between Hollow 2 and Ridge 2, while for $K_{0.9}$ the Bayesian analysis suggest that there is no credible difference between Hollow 2 and Ridge 2 although there is one between Hollow 1 and Ridge 1 (Fig. 3; Table 1; Appendix S3). These differences may be taken to suggest that ecological memory is relatively weak at the site; i.e., although Hollow 2 and Ridge 2 have persisted over time – considerably longer than *c.* 1200 and 1400 years – this persistence is not reflected in their K values. Such a conclusion might be premature because Hollow 2 and Ridge 2 are credibly different in terms of their $K_{0.5}$ values. Also, more generally, both ridges at 0.5 m separate clearly from hollows at the same depth, with higher K values in the hollows. It is notable that such a clear separation does not occur at 0.9 m, which may indicate a weakening of ecological memory with time. What is clear is that our data do not provide a simple answer to the third research question; patterns in K are not easily attributable to microform persistence and ecological memory.

The strong horizontal contrasts in $K_{0.5}$ are almost as striking as those that can occur vertically within the upper *c.* 0.2-0.5 m of the peat profile ('acrotelm'). For example, median $K_{0.5}$ varies by two orders of magnitude between Ridge 1 and the adjacent Hollow 1, and by an order of magnitude between Ridge 2 and its Hollow 2 neighbour (Fig. 3). Such strong horizontal gradients in K are further indication that our study site is not well described by the acrotelm-catotelm model, which is unable to account for horizontal variations.

Although there are patterns in the K data, it is important to recognise that deeper-peat K values may not fit neatly into simple categories or always correspond in a simple way to peat type (botanical composition and degree of decomposition). Care has to be taken to avoid over-interpreting the plant-macrofossil data from the central core of each of the studied microforms because the data from these cores may not apply to each piezometer location (the piezometers for the K tests were located across each feature). Nevertheless, if incursions of the 'other' peat type (hollow peat in a 'ridge' and ridge peat in a 'hollow') occur in the centre of a feature, they should

also occur across the rest of the feature where the piezometers were placed. Therefore, if an incursion recorded by the centrally-located macrofossil core corresponds to the depth at which K was measured, we can consider more closely how peat type affects K . If we look in detail at Ridge 1, for example, at the depth interval of *c.* 0.4-0.6 m (the range over which $K_{0.5}$ was measured) there is a hollow-like incursion: there are peaks in the abundance of *Sphagnum* section Cuspidata, *Sphagnum papillosum*, and *Menyanthes trifoliata* (Fig. 5b). The von Post score over this range shows a moderate degree of decomposition (H4), and ρ_b varies between *c.* 45 and *c.* 55 kg m⁻³. Despite such conditions, the $K_{0.5}$ values recorded for Ridge 1 were the lowest five from the 40-strong data set. In contrast, $K_{0.5}$ was very high in Hollow 1 for a very similar plant macrofossil signal and a higher von Post score (H4-H7), although ρ_b was lower (30-45 kg m⁻³) (Fig. 3 and Fig. 5a). Finally, and in a similar vein, the very high $K_{0.9}$ values recorded from Hollow 1 coincide with a peak in *Sphagnum austinii*, indicative of hummock or ridge-like conditions, relatively high von Post scores (H5-H7), but low ρ_b values (below 30 kg m⁻³).

Why do such apparent anomalies occur? The K of a porous medium is very sensitive to the pore size distribution, so one modest sized pore can conduct more water than multiple small pores with a combined cross-sectional area many times that of the single pore. This sensitivity to pore size or diameter is an outcome of the capillary bundle analogy and Poiseuille's law (Dingman 1984). A soil such as peat may be considered analogous to a bundle of capillary tubes. In each tube, flow is laminar and follows Poiseuille's law; it increases with the fourth power of pore diameter. Given the sensitivity of water flow, and therefore permeability, to one or two macropores, it is perhaps unsurprising that K does not always vary simply with peat or microform type.

Our data were collected from a small number of microforms and, arguably, stronger patterns might emerge were a larger study to be done, or many similar studies were done across a range of sites. We encourage other researchers to take up this challenge; if the work is extended, we will be in stronger position to understand the importance of peatland microforms to overall peatland functioning and to parameterise peatland models more accurately.

While our results indicate clear patterns in K between adjacent hummocks and hollows at 0.5 m depth, the picture is less clear at 0.9 m; the evidence for characteristic hydraulic structures associated with hummocks and hollows extending beyond the uppermost peat is mixed and it would be premature to assume that deeper-peat K differs in any consistent or predictable manner between microforms. As such, evidence for the mechanism for ecological memory in peatlands proposed by Morris, Baird & Belyea (2013) is similarly mixed. Our results indicate that while such an effect may exist, it is likely to diminish with depth and age as old peat layers become buried by younger peat.

We find that some peatland microforms may persist over millennial timescales (Hollow 2 and Ridge 2), while other, proximal, microforms are characterised by switches between wet and drier conditions (Hollow 1 and Ridge 1). We suggest that such switches are more likely to be contraction/expansion in line with the conceptual model of Aaby (1976) and Barber (1981) rather than the spatial migration of individual microforms. There is debate over whether such switches can be purely autogenic in nature, or if they correspond to climatic shifts. Our findings have important implications for understanding the functioning of peatlands – even over short distances there can be marked heterogeneity in terms of developmental history and ecohydrological dynamics.

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Data accessibility

The permeability and palaeo-ecological data (including dry bulk density and degree of humification) are available in the Dryad Digital Repository (Baird *et al.* 2015):

<http://dx.doi.org/10.5061/dryad.v5r86>.

The R script for the Bayesian pair-wise analysis is available as online supporting information.

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Table 1. Summary of the Bayesian pairwise comparisons of the *K* data

	R1 0.5	R2 0.5	H1 0.5	H2 0.5	R1 0.9	R2 0.9	H1 0.9	H2 0.9
R1 0.5		1.07, 3.79	2.72, 6.67	3.11, 6.87	0.69, 3.53	1.29, 4.09	3.06, 5.87	1.90, 4.58
R2 0.5			0.34, 4.19	0.73, 4.38	-1.77, 1.07	-1.16, 1.6	0.65, 3.36	-0.48, 2.14
H1 0.5				-1.92, 2.46	-4.60, -0.61	-3.99, -0.09	-2.16, 1.64	-3.32, 0.44
H2 0.5					-4.84, -1.07	-4.18, -0.48	-2.32, 1.28	-3.52, 0.05
R1 0.9						-0.84, 2.06	0.92, 3.8	-0.21, 2.56
R2 0.9							0.33, 3.13	-0.75, 1.94
H1 0.9								-2.55, 0.08

Note. R1 and R2: Ridges 1 and 2; H1 and H2: Hollows 1 and 2. 0.5: 0.5 m depth. 0.9: 0.9 m depth. The numbers indicate the limits of the 95% highest density interval (HDI). If these do not include zero, there is a credible difference between the groups (which is also indicated in bold). See text for further details. Positive values suggest that a row has a lower *K* value than a column.

Table 2. Details of the ^{14}C dates obtained from Hollow 2 and Ridge 2

Lab. no.	Code	Depth (m)	Material	^{14}C age	+/-	AMS $\delta^{13}\text{C}$	Cal. 2 σ range BP
UBA-20982	CFH2.30	0.2-0.3	<i>Sphagnum</i> leaves/branches/stems	82	21	-30.5	138- -4
UBA-20983	CFH2.60	0.5-0.6	<i>Sphagnum</i> leaves/branches/stems	477	24	-25.2	536-502
UBA-20984	CFH2.100	0.9-1.0	<i>Sphagnum</i> leaves/branches/stems	1206	21	-24.1	1179-1062
UBA-20985	CFR2.30	0.2-0.3	<i>Sphagnum</i> leaves/branches/stems	321	21	-25.9	460-307
UBA-20986	CFR2.60	0.5-0.6	<i>Sphagnum</i> leaves/branches/stems	1081	22	-26.1	1054-934
UBA-20987	CFR2.100	0.9-1.0	<i>Racomitrium</i> moss	1425	19	-23.1	1297-1315

Note. In the Code column CFH2 refers to Cors Fochno Hollow 2 and CFR2 refers to Cors Fochno Ridge 2.

Figure captions

Figure 1. Aerial photograph of the study area. The thick dashed line shows the location of the transect used by Kettridge *et al.* (2012), with the northernmost part of the line representing the start of the transect. The fine dashed lines delineate the areas from which the K readings were taken. The hollows were larger than the areas shown, but measurements were restricted to those parts of the hollows that contained the greatest cover of *Sphagnum pulchrum*.

Figure 2. Example of the apparently stalled response of some of the 0.5-m piezometers installed in Ridge 1. The piezometer water levels shown here are atmospherically-corrected. The arrow shows the assumed t_{95} . The grey dashed line indicates how background pore-water pressure may have fallen during the test (due to water flow through the bog and evaporative losses).

Figure 3. The values of hydraulic conductivity (K) for each microform and depth. $n = 5$ in each case, but over-plotting of similar values hides some symbols. All values are corrected to 20°C. Also shown are the ranges of K values found (i) in the uppermost 0.3 m from the central patterned area of the study site (unpublished data), and (ii) in the uppermost 0.5 m from a selection of raised and blanket bogs (see the named studies). The K range given for the near-surface peat at the study site is based on values corrected to 20°C; the minimum of this range is $4.8 \times 10^{-8} \text{ m s}^{-1}$. K was measured at a temperature of 18°C by Lewis *et al.* (2011), and their K values have been corrected to 20°C in the figure. The K values from the other studies are not temperature-corrected.

Figure 4. Age-depth curves for Hollow 2 and Ridge 2. The curves show the maximum probability ages from the Bayesian age-depth models.

Figures 5a and b. Macrofossil, humification, and dry bulk density data for three separate cores that were taken from the centre of each microform. In the macrofossil part of each figure the \ominus symbol indicates a null return (the macrofossil concerned was absent throughout the core). The pale grey bands indicate the depth intervals over which the *K* tests were done. Dry bulk densities are shown by filled circles joined by a dotted line, von Post scores by a continuous line with no symbols.

Figure 6. Cluster dendrogram of the plant macrofossil data. The initial letter and first digit of the sample codes refer to ridge (R) or hollow (H) and replicate (R1, R2, H1, H2). The remaining digit or digits refer(s) to sample depth in m multiplied by 10 (so a depth in the figure of 1 is 0.1 m).

Figure 7. NMDS ordination biplots of plant macrofossil data (sample codes are the same as in Fig. 6). Species codes are abbreviated (see Figs 5a and 5b for the full names). NMDS axis 1 follows a ridge-hollow/bog surface wetness gradient.

Figure 1.

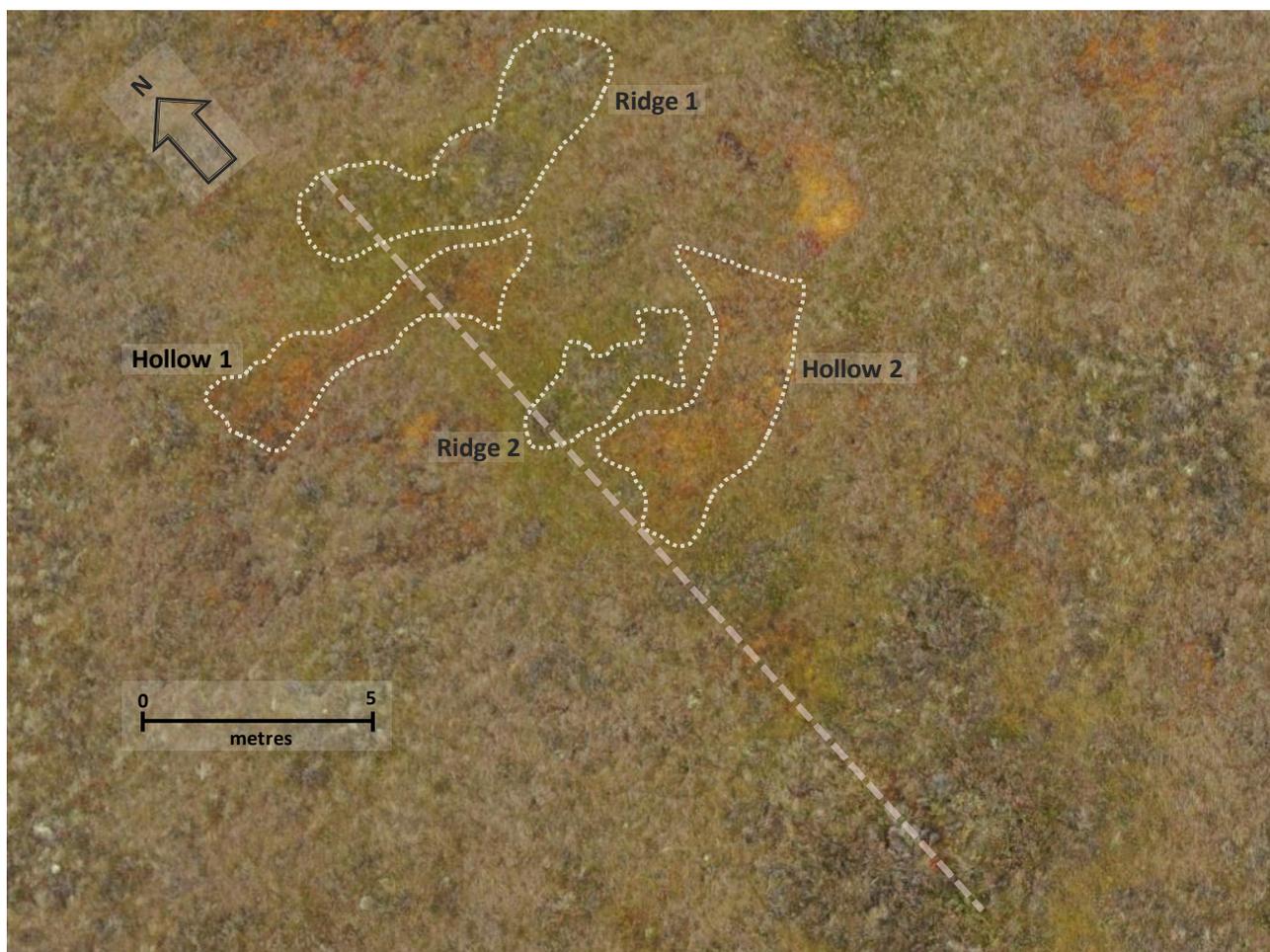


Figure 2.

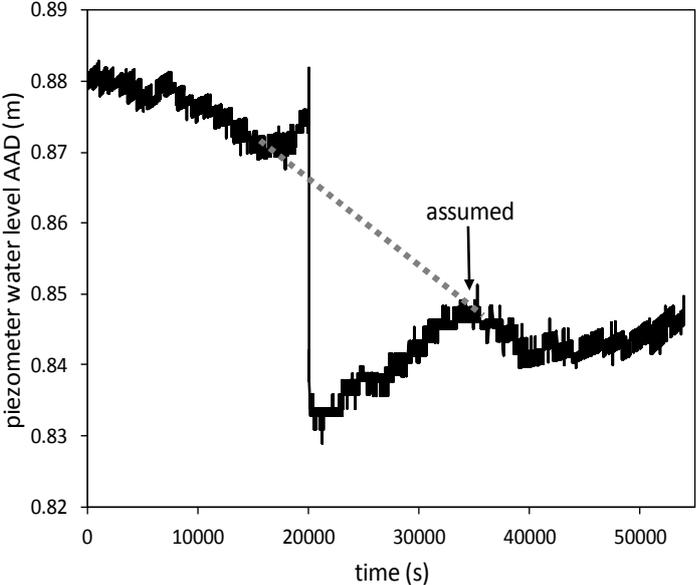


Figure 3.

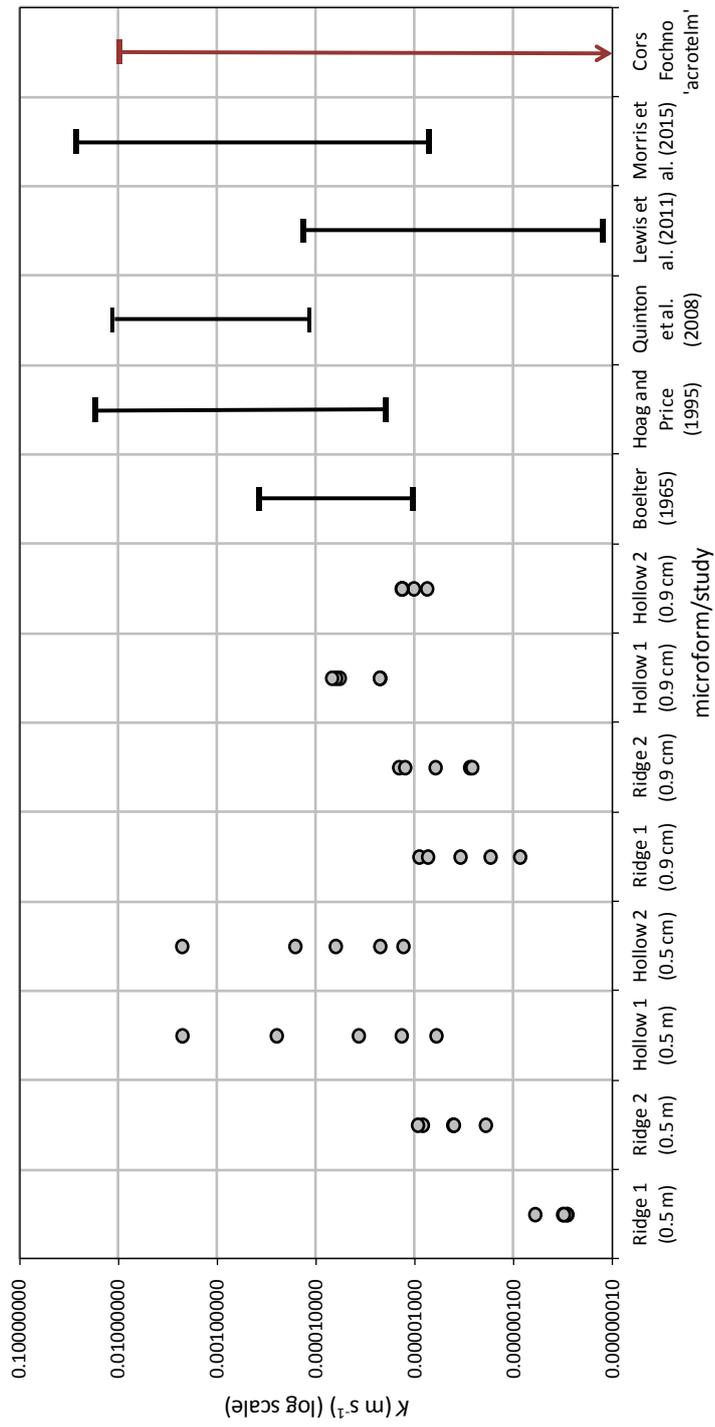


Figure 4.

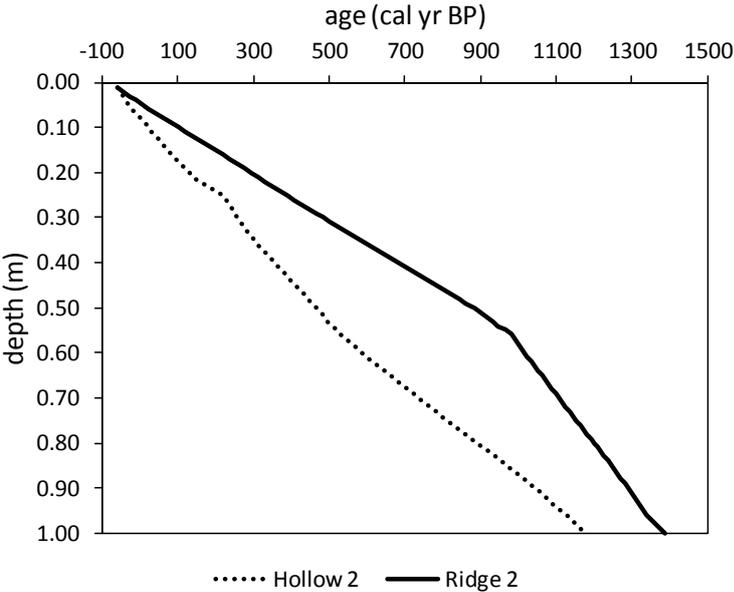


Figure 5a.

See separate pdf file.

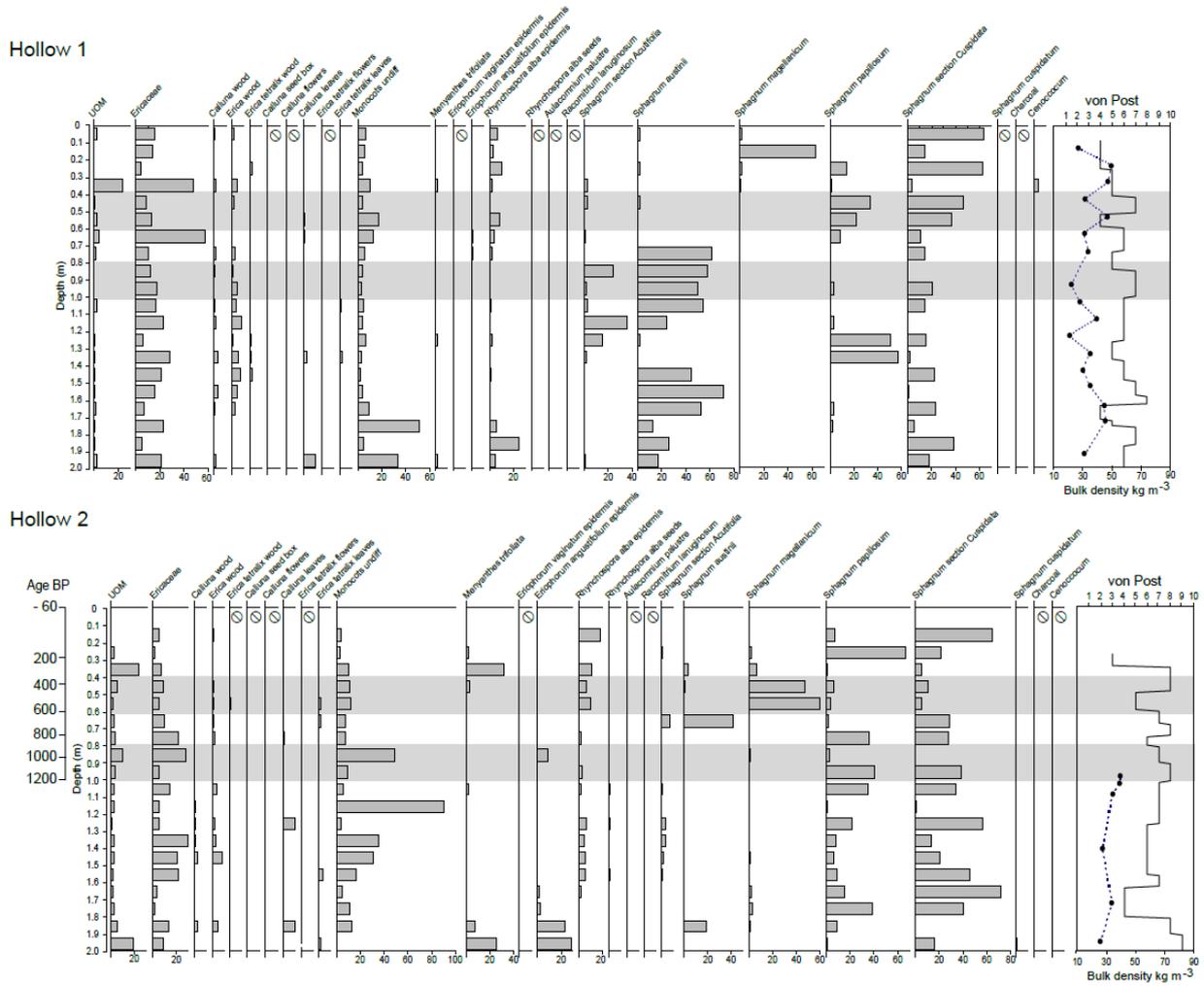


Figure 5b.

See separate pdf file.

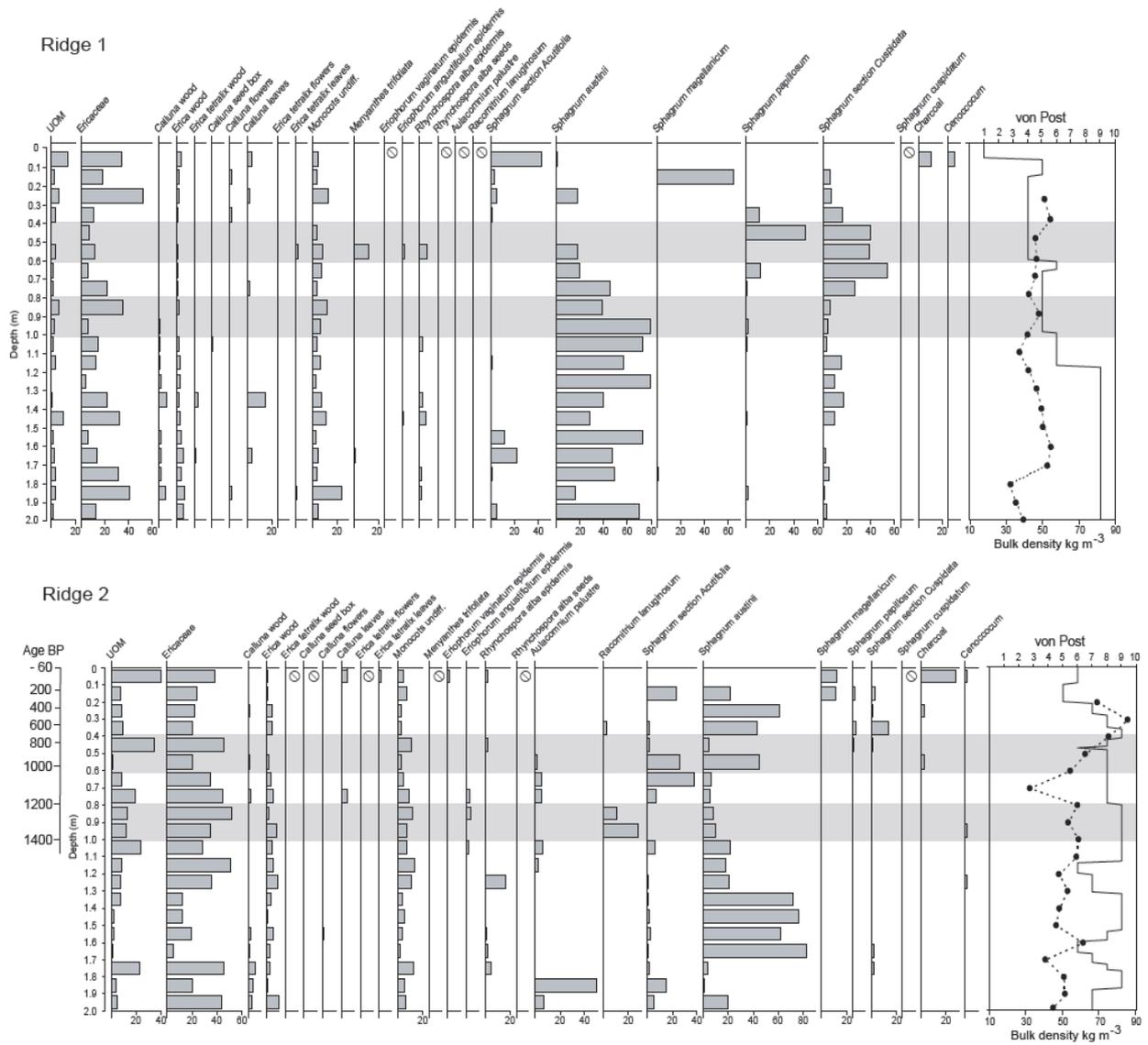


Figure 6.

Figure 7.

