

**Hydrological
transience in
peatland patterning**

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The role of hydrological transience in peatland pattern formation

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Abstract

The sloping flanks of peatlands are commonly patterned with non-random, contour-parallel stripes of distinct microhabitats such as hummocks, lawns and hollows. Patterning seems to be governed by feedbacks among peatland hydrological processes, plant micro-succession, plant litter production and peat decomposition. An improved understanding of peatland patterning may provide important insights into broader aspects of the long-term development of peatlands and their likely response to future climate change.

We recreated a cellular simulation model from the literature, as well as three subtle variants, to explore the controls over peatland patterning. Our models each consist of three submodels, which simulate: peatland water tables in a gridded landscape; a simple representation of microhabitat dynamics in response to water-table depths; and changes in peat hydraulic properties.

We found that the strength and nature of simulated patterning was highly dependent on the degree to which water tables had reached a steady state in response to hydrological inputs. Contrary to previous studies, we found that under a true steady state the models predict largely unpatterned landscapes that cycle rapidly between contrasting dry and wet states, dominated by hummocks and hollows, respectively. Realistic patterning only developed when simulated water tables were still transient.

Literal interpretation of the degree of hydrological transience required for patterning suggests that the model should be discarded; however, the transient water tables appear to have captured some aspect of real peatland behaviour that generates patterning. Recently-buried peat layers may remain hydrologically active despite no longer reflecting current vegetation patterns, providing a form of ecological memory. Furthermore, the models were highly sensitive to the assumed values of peat hydraulic properties, which we take to indicate that the models are missing an important negative feedback between peat decomposition and dynamic changes in peat hydraulic properties.

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Observational (e.g. Foster and Fritz, 1987; Belyea and Clymo, 2001; Comas et al., 2005) and modelling (e.g. Nungesser, 2003; Swanson, 2007) studies have identified a variety of aspatial or one-dimensional (vertical only) feedback mechanisms that may help to explain directionless clumping of SL1 units into larger features. However, understanding the highly directional nature of patterning seen in many peatlands clearly requires an explicit consideration of spatial interactions. This problem lends itself naturally to investigation using 2- or 3-dimensional simulation models, in which directional transfers of water, energy and nutrients, and their effects on pattern, can be explored directly. The idea of interplay between long- and short-range processes is a recurring theme in many apparently successful models of patterned landscapes, including peatlands (Rietkerk et al., 2004a, b; Eppinga et al., 2009) and other landscape types such as marsh tussocks (van de Koppel and Crain, 2006) and dryland tiger bush (Lefever and Lejeune, 1997).

One current hypothesis on peatland pattern formation, the ponding mechanism, has been explored using cellular landscape models, but forms the subject of a curious yet little-discussed disagreement between two groups of studies. The ponding mechanism consists of a feedback between water-table depth, peatland microhabitat succession, and peat hydraulic properties. Areas with deeper water tables are assumed to be more likely to support hummock vegetation, whereas areas with shallower water tables are assumed to be more likely to support hollow vegetation (cf. Rydin and Jeglum, 2005). Furthermore, hummock vegetation is assumed to produce near-surface peat that is less permeable than that produced in hollows (cf. Ivanov, 1981). Swanson and Grigal (1988), Couwenberg (2005) and Couwenberg and Joosten (2005) found that, when implemented in a numerical cellular landscape in which shallow groundwater flow is predominantly downslope, the ponding mechanism generated realistic-looking, contour-parallel stripes of hummocks and hollows at SL2 (we henceforth refer to these three papers, and the versions of the ponding model that they describe, collectively as SGCJ). However, Eppinga et al. (2009) came to different conclusions.

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Eppinga et al. (2009) used their own cellular model to explore the individual and combined effects of the ponding mechanism and two other feedbacks. They found that contour-parallel striped patterning such as that shown in Fig. 1 developed under several combinations of these feedbacks, but not when the ponding mechanism alone was used; i.e. when using the ponding model in isolation they were unable to find a combination of parameters that generated anything other than a homogeneous, un-patterned landscape, seemingly in disagreement with the earlier studies. Eppinga et al. (2009) employed in their models a scheme whereby every cell in the model landscape possesses continuous values of state variables such as hydraulic head, vascular plant biomass, and porewater nutrient concentration. This approach is distinct from the binary hummock/hollow designation, and the discrete developmental timesteps during which microhabitat transitions occur, used in the SGCJ models. These and other differences in implementation between the SGCJ models and the model of Eppinga et al. (2009) mean that direct comparisons cannot strictly be made. However, the fact that Eppinga et al. (2009) were unable to generate striped patterning in their version of the ponding model presents a curious disagreement between what would appear to be little more than alternative numerical implementations of the same essential conceptual model. Given that Eppinga et al. (2009) did not discuss this disagreement further, it is difficult to judge whether the ponding mechanism alone still represents a viable theory on peatland patterning.

1.2 Aim and objectives

We recreated a version of the ponding model to explore this disagreement. We investigated three characteristics of the SGCJ representation of the ponding mechanism that we suspected may have individually or collectively led to a Type-1 error in the SGCJ studies (i.e. causing a model to predict patterning despite the ponding mechanism being incapable of generating patterning in reality), and that might help to explain the disagreement:

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- 5 i. *Simplified hydrology*: the transmissivity, T [dimensions of $L^2 T^{-1}$] (see Table 1 for a glossary of algebraic terms), of any grid square in the original SGCJ models depends entirely on whether that square is currently a hummock or a hollow. Only two values of T are possible, one canonical value for hummocks, T_{hum} , and one for hollows, T_{hol} . A more realistic representation would have been to assign canonical values of a more intrinsic property of peat such as saturated hydraulic conductivity, K_{hum} and K_{hol} [$L T^{-1}$] to hummocks and hollows, respectively, and to calculate transmissivity as the product of K and the thickness of flow in that square, thereby allowing for continuous variation in T across the model landscape. We extended the hydrological submodel from the SGCJ models in this way in order to remove any unrealistic constraints that the simplified hydrology may have placed upon overall model behaviour. We also wished to explore the effects of the absolute values of T or K (as appropriate) upon model behaviour.
- 10
- 15 ii. *Impermeable deep peat*: the original SGCJ models considered only a shallow layer of near-surface peat, and assumed that deeper peat was impermeable to groundwater flow. The top few dm of peat are usually the most permeable (e.g. Fraser et al., 2001; Clymo, 2004) and are therefore prone to the most rapid sub-surface flow, although deeper peat is rarely truly impermeable. Indeed, a number of studies have indicated that drainage through deep peat layers may play an important role in peatland development and the ability of these ecosystems to self-organise (e.g. Ingram, 1982; Belyea and Baird, 2006; Morris et al., 2011). The assumption of impermeable peat below the uppermost few dm may have prevented the SGCJ models from representing a potentially important hydrological interaction between surficial hydraulic structures and deeper peat layers. In our version of the ponding model we experimented with the effects of incorporating a permeable lower layer.
- 20
- 25 iii. *Dependence on hydrological steadiness*: in the SGCJ implementation of the ponding mechanism, simulated water tables are, in theory, allowed to equilibrate

met. The output from the hydrological submodel is a map of water-table depths within the model landscape. The ecological submodel then simulates a new microhabitat map within the model landscape on the basis of the water-table map, such that every cell in the model landscape is assigned one of two binary microhabitat types: hummock or hollow. Finally, the soil properties submodel uses the new microhabitat map to reassign the spatial distribution of near-surface peat hydraulic properties. The new map of peat hydraulic properties is then used as an input to the hydrological model at the beginning of the next developmental step.

2.2 Hydrological submodel

The hydrological submodel uses a modification of the DigiBog model of peatland saturated hydrology (Baird et al., 2012). We took the original DigiBog Fortran 95 code and added routines to represent the ecological and hydrophysical submodels. In the current study we deactivated DigiBog's peat accumulation, decomposition and hydrophysical subroutines described by Morris et al. (2012). We refer the reader to Baird et al. (2012) for a comprehensive description of DigiBog's governing equations and numerical implementation, although a few points are pertinent here. DigiBog represents a peatland as a grid of vertical peat columns; in plan each column is equivalent to one square grid cell in the SGCJ models, although DigiBog also allows for vertical variation in peat hydraulic properties. Horizontal saturated groundwater flow occurs between adjacent columns (four-square neighbourhood) at a rate equal to the product of the harmonic mean of inter-cell transmissivity (the product of depth-averaged hydraulic conductivity and the thickness of flow) and inter-cell hydraulic gradient, according to the Boussinesq equation (see also McWhorter and Sunada, 1977). The hydrological model is run for a predetermined length of simulated time in order to allow the water-table map to change in response to the boundary conditions and the current distribution of hydraulic properties. In Models 1 to 3, the length of time that the hydrological model is allowed to run, Δt_e [T], before an ecological transition takes place (Sect. 2.3) determines how close to a genuine steady state the simulated water tables are. Short equilibration times lead

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water-table behaviour in an arguably more realistic manner than the short equilibration times used in Models 1 to 3.

2.4 Soil properties submodel

Hummocks are assumed to produce peat that is less permeable than that produced by hollows. DigiBog's implementation of the Boussinesq equation uses depth-averaged saturated hydraulic conductivity, K [$L T^{-1}$], and the thickness of flow to calculate saturated groundwater flux between adjacent columns. However, the original SGCJ models simply assigned a single value of transmissivity, T_{hum} [$L^2 T^{-1}$], to hummocks and another, higher value, T_{hol} , to hollows. Model 1 uses the simple treatment of canonical transmissivities as per the original SGCJ models. We assumed default transmissivity values of $T_{hol} = 2.0 \times 10^{-4} m^2 s^{-1}$ and $T_{hum} = 1.0 \times 10^{-5} m^2 s^{-1}$, thereby preserving the T_{hol} to T_{hum} ratio of 20 : 1 that led to strong patterning in the original SGCJ models. Models 2, 3 and 4 use a more sophisticated and realistic treatment allowed by DigiBog, whereby hummocks and hollows are assigned canonical values of hydraulic conductivity, K_{hum} and K_{hol} , respectively; T for each cell is recalculated during each iteration of the hydrological submodel as the product of K and the thickness of flow, H (height of water table above the model's impermeable lower boundary) (cf. Freeze and Cherry, 1979). In this way T is able to vary in a continuous manner based on water-table position, which is more realistic than the simple binary- T treatment of the original SGCJ models. For Models 2, 3 and 4 we assumed default values of $K_{hol} = 1.0 \times 10^{-3} m s^{-1}$ and $K_{hum} = 5.0 \times 10^{-5} m s^{-1}$, thereby giving a K_{hol} to K_{hum} ratio of 20 : 1. In models 1, 2 and 3 we also manipulated the default values of T or K by factors of between 0.05 and 20 in line with objective (i). In Model 1 we varied T_{hum} between 5.0×10^{-7} and $2.0 \times 10^{-4} m^2 s^{-1}$; and T_{hol} between 1.0×10^{-5} and $4.0 \times 10^{-3} m^2 s^{-1}$, whilst always maintaining a T_{hol} to T_{hum} ratio of 20 : 1. Similarly, in Models 2 and 3 we varied K_{hum} between 2.5×10^{-6} and $1.0 \times 10^{-3} m s^{-1}$; and K_{hol} between 5×10^{-5} and $2 \times 10^{-2} m s^{-1}$, whilst maintaining a K_{hol} to K_{hum} ratio of 20 : 1.

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2.5 Model spatial and temporal domains; boundary conditions

We implemented all simulations in a 70 (across-slope, x direction) \times 200 (along-slope, y direction) grid of 1×1 m grid squares. In Models 1 and 2, the simulated peat aquifer overlaid a sloping impermeable base (replicating the assumption of an impermeable lower peat layer in the SGCJ models). Both the peat surface and the impermeable base had a constant slope of 1 : 50; the permeable upper peat had a uniform thickness of 0.2 m. In Models 3 and 4 we assumed the thick, lower peat layer is also permeable with its own hydraulic conductivity, K_{deep} , meaning that K for each cell is depth-averaged to account for the vertical transition in K between the upper and lower layers. Baird et al. (2012) provide a full description of DigiBog's calculation of depth-averaged K and inter-cell T . We used the groundwater mound equation (Ingram, 1982) to calculate the dimensions of a deep peat layer that is hemi-elliptical in cross section, has a uniform K of $1.25 \times 10^{-5} \text{ m s}^{-1}$, is 200 m from central axis to the margin, is underlain by a flat impermeable base, and receives a net water input (from an implied upper peat layer) of 155 mm yr^{-1} . The resulting deep peat layer was 3.97 m thick along its central axis, curving elliptically down to the peatland's margin. Within DigiBog, this deep layer was overlain by a surficial, more permeable layer, which, like Models 1 and 2, was 0.2 m thick.

We allowed all simulations to run for 100 developmental steps; the initial condition consisted of randomly-generated water tables, between 0.0 and 0.05 m below the peat surface, in each cell. The initial microhabitat and soil-properties maps were based on this random initial water-table map in the usual manner described above.

We set the lateral (along-slope) boundaries to impermeable (von Neumann zero-flux condition) in order to simplify the representation of the simulated peatland within its local hydrogeological setting. In the simulations with an impermeable lower peat layer (Models 1 and 2) both the upslope and downslope boundaries were set to constant water-table (Dirichlet) conditions of 0.025 m below the surface such that the overall hydraulic gradient along the model was equal to the topographic gradient and the gradient

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calculated the relative variance, R [dimensionless], of hummocks per across-slope row of cells, following the method of Swanson and Grigal (1988), as an objective and reproducible metric of pattern strength. The value of R increases with pattern strength: values less than 2 indicate unordered landscapes without discernible patterning; values of R greater than 4 represent highly ordered landscapes with clear, strong patterning. We also calculated the proportion, S , of model cells occupied by hummocks during each developmental step. Finally, we calculated model turnover rate, Q , defined as the proportion of model cells that undergo a transition from hummock to hollow, or vice versa, in each developmental step.

3 Results

3.1 Hydrological transience

In Models 1, 2 and 3, the strength of across-slope, striped patterning at SL2 initially increased strongly with increasing hydrological steady-state criterion, from an apparently entirely unordered, random mixture of hummocks and hollows at SL1 when $\Delta t_e = 1$ h, to peak “strengths” at around $\Delta t_e = 100$ h (for Models 1 and 2) or 50 h (Model 3). This increase in patterning strength is evident from both a visual appraisal of the final microhabitat maps (Fig. 4), and an increase in the values of relative variance, R , with increasing Δt_e (Fig. 5a, b, c). For values of Δt_e greater than 50 h (Models 1 and 2) and 20 h (Model 3), an increase in the spatial scale of the simulated SL2 stripes is apparent with increasing Δt_e (i.e. the stripes became broader in the y (along-slope) direction). Increasing Δt_e also led to SL2 stripes whose upslope and downslope edges were increasingly straight and sharply defined (Fig. 4). For values of Δt_e greater than 100 h (Models 1 and 2) or 50 h (Model 3), the simulated SL2 stripes had broadened to the point of appearing to be “over-developed”, such that they no longer resembled realistic peatland striped patterning (cf. Fig. 1).

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As well as governing the spatial configuration of simulated patterning, the value of Δt_e also affected the temporal dynamics of Models 1, 2 and 3. For low values of Δt_e , turnover rates of model cells were high: when $\Delta t_e = 1$ h, approximately half of all cells would undergo a transition from designation as a hummock to a hollow (or vice-versa) during each developmental step, providing further indication of a random landscape. Increasing Δt_e led to a reduction in turnover rates in Models 1 and 2 as SL2 structures began to stabilise, to a minimum of approximately 30 % of cells per developmental step when $\Delta t_e = 100$ h (Fig. 5d, e). Increasing Δt_e had little effect on turnover rates in Model 3 until $\Delta t_e = 1000$ or 10 000 h (Fig. 5f). The temporal trends in SL1 turnover rate and proportional hummock coverage also indicate what appears to be a limit cycle in the behaviour of all models under highly stringent hydrological steady-state criteria. Particularly when $\Delta t_e = 17520$ or 10 000 h, and to a lesser extent when $\Delta t_e = 1000$ h, the models exhibited a cyclical behaviour in time whereby the simulated landscape would alternate on an approximately regular cycle of between four and ten developmental steps between two contrasting states: a dry landscape with deep water tables, dominated by hummocks; and a wet landscape with water tables near the bog surface, dominated by hollows (Fig. 5). The contrast between the wet and dry states was particularly pronounced in Model 2, which cycled between approximately 15 % and 95 % hummock coverage when $\Delta t_e = 10000$ h (Fig. 5h). The single simulation with Model 4 ($\Delta t_e = 17520$ h) behaved highly similarly to Models 1, 2 and 3 when $\Delta t_e = 10000$ h, predicting nearly homogeneous, unpatterned landscapes (Fig. 6) that cycled rapidly between being dominated by hummocks and hollows (Fig. 5f, i).

In all simulations that generated striped SL2 patterning, those SL2 units migrated consistently downslope (not shown) in the same manner as that previously reported in the published accounts of the SGCJ models.

3.2 Simplified calculation of transmissivity

Any artefacts introduced to model behaviour by the simple, binary treatment of peat permeability employed in the original SGCJ models (see objective i, above) would have

been evident as differences in behaviour between Model 1 (simple, binary transmissivity scheme, based solely on hummock/hollow designation) and Model 2 (continuous treatment of transmissivity as product of peat hydraulic conductivity and thickness of flow). Models 1 and 2 behaved highly similarly to one another, in terms of their response to both changing values of Δt_e and changing absolute values of peat permeability. Both models developed realistic looking, contour-parallel SL2 stripes over the entire model domain for intermediate value of Δt_e . In both models the striped patterning was weak and discontinuous for $\Delta t_e = 15$ and 20 h; the patterns were stronger and continuous when Δt_e was between 35 and 100 h; the SL2 stripes became unrealistically broad at $\Delta t_e = 1000$ h, and were mainly absent when $\Delta t_e = 10000$ h (Fig. 4). Temporal patterns of summary metrics (SL1 turnover rate, hummock proportion, relative variance of hummocks per row) were qualitatively and quantitatively similar between models 1 and 2, and again responded similarly to changes in Δt_e (Fig. 5) and the ratio of T_{hum} to T_{hol} or K_{hum} to K_{hol} (not shown).

3.3 Hydrogeological setting

Any artefacts introduced to model behaviour by the simplifying assumptions made in the original SGCJ models about the hydrogeological setting of the simulated peatland (see objective ii, above) would have been evident as differences in behaviour between Model 2 (impermeable deep peat layer; constant-head upslope boundary condition; zero rainfall addition; constant slope of peatland surface) and Model 3 (permeable deep peat layer; no-flow upslope boundary; constant net rainfall rate of 400 mm yr^{-1} ; hemi-elliptical aquifer shape). Model 2 simulations that generated patterning did so over the entire model domain, although the same was not true of Model 3. Striped patterning at SL2 developed in Model 3 only in the downslope portion of the model domain. Furthermore, the area of the model domain that exhibited patterning extended upslope with increasing value of Δt_e . For instance, when $\Delta t_e = 10$ h, Model 3 only produced striped patterning within 60 m or so of the downslope boundary, but when $\Delta t_e = 100$ h the patterned area covered the majority of the model domain and extended as far as

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approximately 140 m from the downslope boundary (Fig. 4). Clear, continuous striped patterning that extended all the way across the across-slope direction (x direction) of the model domain developed in Model 3 at much lower values of Δt_e than in Model 2. Continuous, closely-spaced SL2 stripes were evident in the downslope area of Model 3 when $\Delta t_e = 20$ h, although sharply defined, continuous SL2 stripes in Model 2 did not develop for values of Δt_e less than 35 h. Additionally, Model 3 behaved differently from Model 2 in terms of its responses to changes in the absolute values of peat hydraulic conductivity (see below).

3.4 Manipulation of peat properties

Modest changes in the absolute values of T or K brought about large changes in the nature and strength of simulated patterning in Models 1, 2 and 3, although the nature of these responses varied between models. In Models 1 and 2, the lowest values of T or K led to largely unpatterned landscapes, dominated by apparently random distributions of hummocks and hollows, with either a complete absence of patterning ($\times 0.05$ treatment) or very weak, discontinuous patterning ($\times 0.1$ treatment) (Fig. 7). In both Models 1 and 2, pattern strength increased with increasing values of T or K up to the default combination. For combinations of T and K greater than the default values, Models 1 and 2 both predicted an increase in the spatial scale of SL2 stripes in a manner similar to the effect of increasing Δt_e ; for the $\times 5$ and $\times 10$ treatments Model 1 became almost a uniform landscape of hummocks with only small SL2 groupings of hollows. The behaviour of Model 3 was quite different. Only the default and the $\times 0.2$ treatments generated any kind of contour-parallel stripes; all other treatments produced near uniform, unpatterned landscapes composed almost entirely of either hollows (for the $\times 0.05$ and $\times 0.1$ treatments) or hummocks (for the $\times 5$, $\times 10$ and $\times 20$ treatments).

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4 Discussion

4.1 Hydrological transience and ecological memory

The striking similarity between the patterns generated by our Models 1, 2 and 3 at intermediate values of Δt_e and the striped patterns reported by the previous SGJ authors, as well as the absence of patterning in our models under more stringent steady-state hydrological conditions, are highly suggestive that the previous SGJ authors had failed to attain a genuine steady state in their hydrological submodels. The dependence of realistic patterning in our models on intermediate equilibration times can be reconciled with the currently popular theory that landscape patterning generally arises from interplay between long- and short-range processes (e.g. Rietkerk and van de Koppel, 2008; see also Turing, 1952). When equilibration times are very short each grid square's water-table behaviour is influenced only by its immediate neighbours, and long-range influences are unable to propagate across the model domain. Conversely, the longest (and arguably most realistic) equilibration times cause the simulated water-table map to be dominated by its long-range boundary conditions, which, under steady state, eliminate much of the short-range effects of contrasting peat hydraulic properties in neighbouring SL1 and SL2 units. Without additional feedbacks such as those explored by Eppinga et al. (2009), it is only at intermediate values of Δt_e that the model strikes the balance of long- and short-range feedbacks seemingly required for patterning.

If the absolute values of Δt_e are taken literally then the model predicts that realistic patterning only occurs if micro-succession at SL1 operates on timescales of hours to days, rather than years. Such a prediction is clearly in error, meaning that it is perhaps initially tempting to discard the model in light of our work. However, we believe that this may be too rigid an interpretation of the hydrological steady-state criterion. It appears that simulations with transient water tables have inadvertently captured some genuine aspect of peatland ecohydrology that leads to SL2 patterning. Moreover, Model 4, in which we introduced water-table transience not through short equilibration times but

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through a daily rainfall series, did not generate patterning. This indicates clearly that it is the short equilibration times used in Models 1, 2 and 3, rather than simply non-steady water tables (which are also present in Model 4) that caused patterning in our simulations.

For lower values of Δt_e , the water tables across the model's domain are not in full equilibrium with the current distribution of hummocks and hollows. As such, those water-table maps reflect the distribution of hummocks and hollows during not only the current developmental step but also partly the previous developmental step. It may be that the formation of peatland patterning relies on some ecological memory effect (cf. Peterson, 2002), such as the influence of recently buried peat that no longer reflects current positions of hummocks and hollows but which remains hydrologically important due to its shallow depth. Despite DigiBog allowing for 3-dimensional variation in peat properties, the ponding model is in essence a 2-dimensional model insofar as the new microhabitat map during each developmental step supersedes the previous map entirely; the modelled system retains no memory of previous SL1 units or their associated soil properties. As such, our models neglect some of the structural complexity that peatlands exhibit in three spatial dimensions (e.g. Barber, 1981). Our simulations with non-conservative hydrological steady-state criteria (particularly $\Delta t_e = 50$ and 100 h) implicitly contain a type of ecological memory effect, because the influence of previous patterns of surface vegetation and shallow soil properties are expressed in the model's hydrological behaviour; this memory effect decreases in strength with increasingly stringent hydrological steady-state criteria. Our results indicate that this memory effect is important to the formation of patterning in the ponding model and should be investigated directly in future studies, perhaps via the use of cohort-based peat accumulation models (e.g. Frohling et al., 2010; Morris et al., 2011, 2012).

4.2 Peat hydraulic properties

Models 1, 2 and 3 were all highly sensitive to the absolute values of T or K , and patterning only occurred within a narrow area of parameter space. Even in the $\times 0.05$

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and $\times 20$ treatments, the values of T or K were well within reported ranges; the fact that these parameterisations failed to produce patterning suggests that a full suite of relevant processes and feedbacks has not been represented. Particularly in Model 3, in which model water-table levels are maintained by the simulated addition of rainfall, even modest changes in the absolute values of K_{hol} and K_{hum} caused simulations to “run away” to either wet or dry end-member states. In simulations with higher values of hydraulic conductivity Model 3 drained rapidly to the downslope boundary, causing water tables to fall below the transition zone and giving rise to uniformly dry simulated landscapes dominated by hummocks. Conversely, the simulations with lower values of hydraulic conductivity caused Model 3 to drain so slowly that water tables rose to the surface of all columns, leading to uniformly wet landscapes dominated by hollows. The same effect was not evident in Models 1 and 2 because the constant-head condition at the upslope boundary maintained water-table levels within the transition zone. Nonetheless, manipulating T and K in Models 1 and 2, respectively, still resulted in landscapes devoid of realistic patterning, demonstrating high sensitivity to the absolute values of those parameters.

The high sensitivity to the absolute values of T and K may be taken to suggest that our models are lacking at least one important negative feedback, namely that between peat decomposition and changes in peat hydraulic properties. For example, saturated hydraulic conductivity is known to decrease strongly with increasing time-integrated decomposition of peat (e.g. Boelter, 1969; 1972; Grover and Baldock, 2013). Areas with low water tables are prone to more rapid decomposition and more rapid collapse of pore spaces. The resultant reduction in hydraulic conductivity in turn causes peat to retain water more readily and leads to reduced decay rates, stabilising system behaviour (see Belyea, 2009; and Morris et al., 2012). This concept is partially represented in the ponding model by lower values of T or K in hummocks (where peat spends more time under oxic conditions, and hence peat at the water table is more degraded and less permeable) than in hollows (where peat has a shorter residence time under oxic conditions, producing better-preserved and more permeable peat at the

evidence of consistent downslope migration of any of these features over a 21 yr period. Kettridge et al. (2012) used data from a combination of ground-penetrating radar and soil cores to investigate the below-ground physical properties of peat soil in a raised bog in Wales. They found subsurface layers that dipped consistently towards the bog's margins, which they interpreted as evidence of down-slope migration of SL1 or SL2 units during the bog's development. More observational work is clearly required to ascertain whether or not the findings of Kettridge et al. (2012) hold in the general case, but it appears that the ponding model's prediction of the downslope migration of SL2 stripes cannot be used to falsify the model at this stage.

5 Summary and conclusions

Our numerical experiments suggest strongly that simulations reported in previous studies had not attained true hydrological steady-state conditions; under true steady-state conditions patterning does not occur. Realistic, striped patterns only form when microhabitat transitions occur in response to highly transient water-table patterns. The equilibration times required by the hydrological submodel to attain the level of transience necessary for patterning are of the order of hours to days: these timescales are largely meaningless in terms of vegetation dynamics. The models' reliance on the hydrological steady-state criterion indicates that ecological memory may play a role in pattern formation. Although ecological memory is not represented explicitly (or deliberately) in our models, the transient water tables appear to have inadvertently replicated such an effect.

We increased incrementally the sophistication and realism of the models' routines, chiefly by: representing a permeable deep peat layer; improving the models' calculation of transmissivity; and introducing a plausible temporal variation in rainfall. In doing so we removed a number of simplifying assumptions made in previous studies. However, these improvements had little effect on the models' behaviours, indicating that the

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sensitivity to hydrological steady state is a genuine facet of the models and is not an artefact of numerical implementation.

The models appear to be unrealistically sensitive to the absolute values of the parameters used to represent peat permeability. We interpret this sensitivity as indicating that the models are missing a negative feedback between peat decomposition and hydraulic conductivity, which previous studies have shown is important to the ability of peatlands to self-organise.

Peatland structures and processes exhibit complexity in three spatial dimensions. A logical next step for patterning research would be to combine 2-dimensional (horizontal only) cellular landscape models such as those presented here with (mostly 1-dimensional; vertical only) peatland development models that provide a more detailed and realistic representation of peat formation, decomposition and dynamic changes in soil hydraulic properties. This would allow a direct process-based exploration of both the mechanism involved in ecological memory, and a continuous relationship between peat decomposition and hydraulic properties.

Acknowledgements. This research was funded in part by a Queen Mary University of London Ph.D. studentship awarded to Paul Morris. We are grateful to Brian Branfireun (University of Western Ontario) for permission to use the photograph in Fig. 1; and to The Field Studies Council at Malham, in particular Robin Sutton, for providing us with the data from Malham Tarn Weather Station.

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Table 1. Glossary of algebraic terms, including default values where appropriate, for each of the four model versions.

Symbol	Description	Dimensions	Units	Model 1	Model 2	Model 3	Model 4
Δt_e	hydrological submodel run-time (steady-state criterion)	T	h	50	50	50	17 520 (2yr)
H	water-table height above impermeable base	L	m	auxiliary variable	auxiliary variable	auxiliary variable	auxiliary variable
K	hydraulic conductivity	$L T^{-1}$	$m s^{-1}$	–	–	–	–
K_{deep}	hydraulic conductivity of deep peat	$L T^{-1}$	$m s^{-1}$	–	0	1.25×10^{-5}	1.25×10^{-5}
K_{hol}	hydraulic conductivity of hollow peat	$L T^{-1}$	$m s^{-1}$	–	1.0×10^{-3}	1.0×10^{-3}	1.0×10^{-3}
K_{hum}	hydraulic conductivity of hummock peat	$L T^{-1}$	$m s^{-1}$	–	5.0×10^{-5}	5.0×10^{-5}	5.0×10^{-5}
p	probability of hummock formation	–	–	Figure 2	Figure 2	Figure 2	Figure 2
Q	hummock turnover rate	–	–	state variable	state variable	state variable	state variable
R	relative variance of hummocks per row	–	–	state variable	state variable	state variable	state variable
S	proportion of model landscape occupied by hummocks	–	–	state variable	state variable	state variable	state variable
T	peat transmissivity	$L^2 T^{-1}$	$m^2 s^{-1}$	–	–	–	–
T_{hol}	transmissivity of hollow cells	$L^2 T^{-1}$	$m^2 s^{-1}$	2.0×10^{-4}	–	–	–
T_{hum}	transmissivity of hummock cells	$L^2 T^{-1}$	$m^2 s^{-1}$	1.0×10^{-5}	–	–	–
U	net rainfall rate (precip. minus evapotran.)	$L T^{-1}$	$mm yr^{-1}$	0	0	400 (constant)	400 (time series)
x	spatial index (across-slope direction)	L	m	–	–	–	–
y	spatial index (along-slope direction)	L	m	–	–	–	–
Z_{final}	final water-table depth at end of developmental step	L	m	state variable	state variable	state variable	–
Z_{mean}	mean water-table depth during second half of dev. step	L	m	–	–	–	state variable

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Table 2. Summary of the four models and the objectives addressed by each.

Model	Transmissivity Scheme	Deep Peat Layer	Net Rainfall, U (precip. minus evapotran.)	Up-slope Boundary Condition	Aquifer Shape	Objectives Addressed
1	binary	impermeable	off	constant head, $Z = 0.025$ m	constant slope	iii
2	continuous	impermeable	off	constant head, $Z = 0.025$ m	constant slope	i, iii
3	continuous	$K_{\text{deep}} = 1.25 \times 10^{-5} \text{ m s}^{-1}$	400 mm yr^{-1} (constant)	impermeable (no-flow)	hemi-elliptical	i, ii, iii
4	continuous	$K_{\text{deep}} = 1.25 \times 10^{-5} \text{ m s}^{-1}$	400 mm yr^{-1} (time series)	impermeable (no-flow)	hemi-elliptical	iii

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Fig. 1. Aerial photograph showing contour-parallel, striped patterning on a peatland complex in the James Bay lowlands, Ontario, Canada. The directions of slope and regional water flow are from the top right to the bottom left of the picture. Horizontal distance between tops of successive ridges is approximately 5 to 10 m. Image belongs to Brian Branfireun, reproduced here with kind permission.

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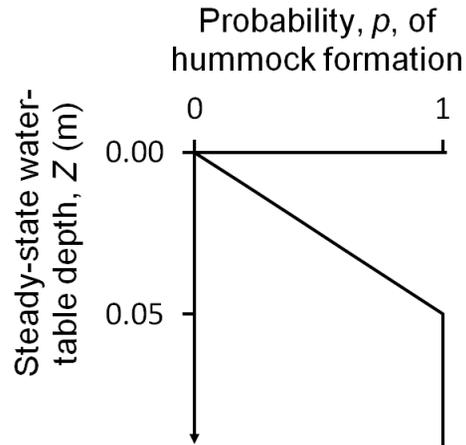


Fig. 2. Graphical representation of the linear probability function used by the ecological sub-model to assign hummock and hollow states to each model cell, based on water-table depth.

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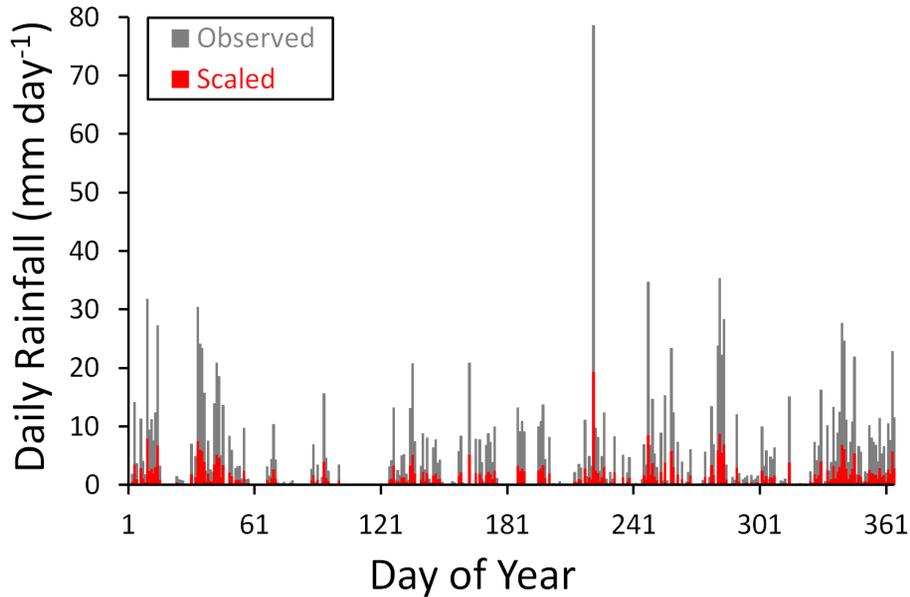


Fig. 3. 365-day time series of daily observed rainfall, and its conversion to net rainfall, U , after scaling by a factor of 0.245. See main text for full details.

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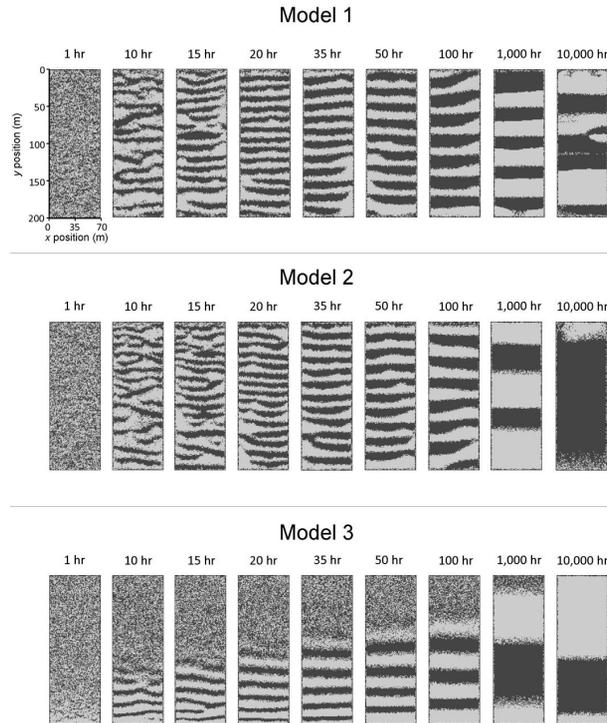


Fig. 4. Final microhabitat maps after 100 developmental steps, showing effects of increasing Δt_e on patterning in typical simulations with Model 1 (top panel), Model 2 (middle panel) and Model 3 (bottom panel). The value of Δt_e assumed for each simulation is indicated immediately above the map. Light pixels represent hummocks, dark pixels represent hollows. Low values of y represent upslope locations ($y = 0$ is the upslope boundary); high values of y represent downslope locations ($y = 200$ is the downslope boundary); as such, groundwater flow is generally down the page. All maps have the same horizontal (x, y) scale as that shown for the upper-leftmost map.

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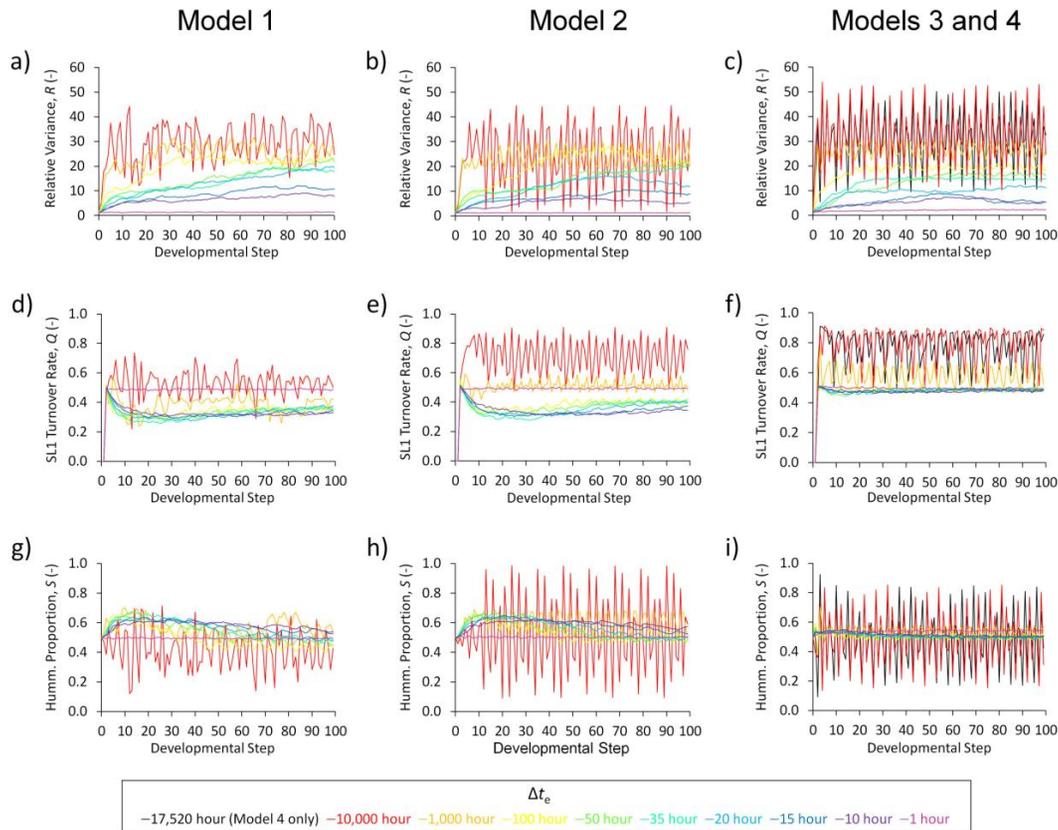


Fig. 5. Influence of hydrological equilibration time, Δt_e , over temporal development of relative variance of hummocks per model row, R (top row); SL1 turnover rate during, Q (middle row); and proportion of model landscape occupied by hummocks, S (bottom row); in Model 1 (left column), Model 2 (middle column), Model 3 and Model 4 (right column).

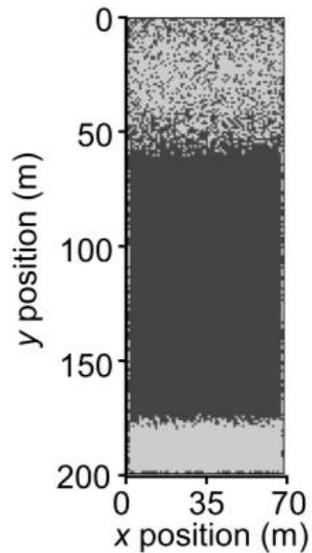


Fig. 6. Final microhabitat map after 100 developmental steps from Model 4, with $\Delta t_e = 17520$ h (2 yr). Light pixels represent hummocks, dark pixels represent hollows. Low values of y represent upslope locations ($y = 0$ is the upslope boundary); high values of y represent downslope locations ($y = 200$ is the downslope boundary); as such, groundwater flow is generally down the page.

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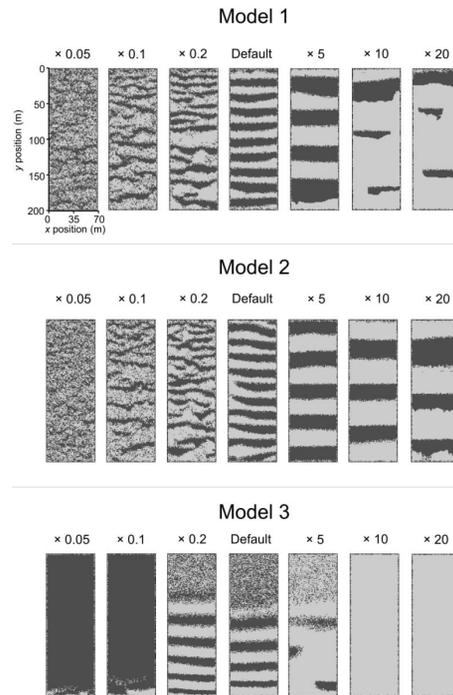


Fig. 7. Final microhabitat maps after 100 developmental steps, showing effects of different combinations of T_{hum} and T_{hol} (in the case of Model 1, top panel) or K_{hum} and K_{hol} (Model 2, middle panel; Model 3, bottom panel) on pattern geometries in typical model runs. The values of T or K used in each simulation are indicated immediately above the maps, and are expressed as a factor of the default values. See main text for full explanation. Light pixels represent hummocks, dark pixels represent hollows. Low values of y represent upslope locations ($y = 0$ is the upslope boundary); high values of y represent downslope locations ($y = 200$ is the downslope boundary); as such, groundwater flow is generally down the page. All maps have the same horizontal (x , y) scale as that shown for the upper-leftmost map.

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