

Nutrients and Hydrology Indicate the Driving Mechanisms of Peatland Surface Patterning

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ABSTRACT: Peatland surface patterning motivates studies that identify underlying structuring mechanisms. Theoretical studies so far suggest that different mechanisms may drive similar types of patterning. The long time span associated with peatland surface pattern formation, however, limits possibilities for empirically testing model predictions by field manipulations. Here, we present a model that describes spatial interactions between vegetation, nutrients, hydrology, and peat. We used this model to study pattern formation as driven by three different mechanisms: peat accumulation, water ponding, and nutrient accumulation. By on-and-off switching of each mechanism, we created a full-factorial design to see how these mechanisms affected surface patterning (pattern of vegetation and peat height) and underlying patterns in nutrients and hydrology. Results revealed that different combinations of structuring mechanisms lead to similar types of peatland surface patterning but contrasting underlying patterns in nutrients and hydrology. These contrasting underlying patterns suggest that the presence or absence of the structuring mechanisms can be identified by relatively simple short-term field measurements of nutrients and hydrology, meaning that longer-term field manipulations can be circumvented. Therefore, this study provides promising avenues for future empirical studies on peatland patterning.

Keywords: spatial patterns, hummock-hollow, positive feedback, scale-dependent feedback, evapotranspiration, hydraulic conductivity.

Introduction

A key challenge in ecosystem ecology is to explain landscape-scale patterns that emerge from smaller-scale structuring mechanisms (Levin 1992; Solé and Bascompte 2006). Spatial vegetation patterns are among the most striking landscape-scale patterns and have been observed in a variety of ecosystems. Examples include arid ecosystems (Klausmeier 1999), savannas (Lejeune et al. 2002),

ribbon forests (Hiemstra et al. 2006), and marsh tussocks (Van de Koppel and Crain 2006). Identification of the smaller-scale structuring mechanisms that explain these kinds of spatial vegetation patterning is important, because it also provides insight in other aspects of ecosystem functioning, such as responses to increased anthropogenic pressure or global climate change (Rietkerk et al. 2004b; Kéfi et al. 2007; Scanlon et al. 2007). Spatial surface (and hence vegetation) patterning is also observed in boreal peatland ecosystems. A considerable amount of attention has been paid to this phenomenon in the peatland literature of the past century (Foster et al. 1983; Charman 2002). Several modeling studies (Swanson and Grigal 1988; Hilbert et al. 2000; Belyea and Clymo 2001; Rietkerk et al. 2004a; Couwenberg and Joosten 2005) suggest that these large-scale surface patterns emerge from smaller-scale structuring mechanisms (Belyea and Baird 2006). These models, however, focused on different kinds of peatland surface patterns and also suggested different kinds of structuring mechanisms. We will explain these differences in more detail.

One of the most commonly observed patterns in peatlands is the spatial structure consisting of distinct microforms, namely, hummocks and hollows with a characteristic spatial scale of 1–10 m (Belyea and Clymo 2001). Hummocks are elevated above hollows because of a thicker acrotelm, which is a layer of aerobic peat. Hollows have a much thinner acrotelm or no acrotelm at all. Below the acrotelm, the water-saturated peat layer, or catotelm, is situated. This means that the acrotelm-catotelm boundary is determined by the seasonal minimum water table (e.g., Holden and Burt 2003). Plant growth in peatlands is limited by water stress, which can occur both at high water tables because of waterlogging and at low water tables because of desiccation (Ridolfi et al. 2006). Because plant production determines the organic matter input into the peat layer, peat growth is optimal at intermediate acrotelm thickness (Hilbert et al. 2000; Belyea and Clymo 2001). This implies that below the optimum acrotelm thickness

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for plant growth, there is a positive feedback between net rate of peat formation and acrotelm thickness, mainly because of increased production of vascular plants (Wallén et al. 1988; Belyea and Clymo 2001). This positive feedback is a structuring mechanism that explains how peatland microforms may develop either into a wet, sparsely vegetated, low-productive state or a dry, densely vegetated, high-productive state. Thus, slight differences between wetter and drier sites may further amplify and lead to spatial patterning of sharply bounded microforms. From here on we refer to this structuring mechanism as the peat accumulation mechanism.

Another type of pattern comprises merged hummocks forming linear ridges alternating with lower and wetter hollows, oriented along the contours of mire slopes, with a characteristic spatial scale of 10^2 – 10^3 m (Sjörs 1983). A possible mechanism that can explain this type of patterning is a lower hydraulic conductivity of ridges as compared to hollows (Swanson and Grigal 1988). As a result of lower hydraulic conductivity, water may accumulate upslope of ridges, which stimulates the formation of hollows. Models show that such a water ponding mechanism (cf. Rietkerk et al. 2004a), which originates from differences in hydraulic conductivity, can indeed explain the formation of ridge-hollow patterns on peatland slopes (Swanson and Grigal 1988; Couwenberg 2005; Couwenberg and Joosten 2005).

Furthermore, peatland maze patterns on flat ground consist of merged hummocks forming ridges that are star- or netlike, enclosed by lower and wetter hollows (Wallén et al. 1988; Rietkerk et al. 2004a). The term “maze pattern” is used, because the densely vegetated ridges are connected in an almost continuous network without a clear orientation, but occasionally the bands form dead ends, somewhat resembling the corridors within a maze (Rietkerk et al. 2004a). In arid ecosystems, similar patterns are called labyrinths (Rietkerk et al. 2002). Peatland maze patterning can be induced by nutrient accumulation under ridges, which is driven by increased evapotranspiration rates by vascular plants (especially shrubs and trees) that grow on these ridges (Rietkerk et al. 2004a; Wetzel et al. 2005; Ross et al. 2006). This structuring mechanism would imply that because of higher evapotranspiration rates, there is a net flow of water and dissolved nutrients toward ridges. Subsequently, the nutrients become trapped on ridges through uptake by vascular plants. Thus, during their life span, vascular plants that grow on ridges accumulate nutrients originating from outside the ridge. Nutrients become available again through mineralization of vascular plant litter, but this only increases nutrient availability on the local scale at which the litter is deposited (within the ridge). Models predict that this local recycling effect outweighs the effect of nutrient uptake, meaning that nutrient con-

centrations in the mire water under ridges also increase (Rietkerk et al. 2004a; Eppinga et al. 2008, 2009). Because higher nutrient availability will lead to an increase in vascular plant biomass, this is a self-reinforcing process, which will be referred to as the nutrient accumulation mechanism (cf. Rietkerk et al. 2004a). Models show that the nutrient accumulation mechanism could indeed explain the formation of maze patterns on flat ground (Rietkerk et al. 2004a; Eppinga et al. 2009). Moreover, model simulations show that the nutrient accumulation mechanism may also drive the formation of individual hummocks on flat ground and linear ridge-hollow patterning on peatland slopes (Rietkerk et al. 2004a; Eppinga et al. 2009). This means that the nutrient accumulation mechanism provides an alternative explanation for the types of patterning previously associated with the peat accumulation and water ponding mechanisms.

Thus, until now, three different structuring mechanisms for peatland patterning have been proposed and modeled, namely, peat accumulation through differences in net rate of peat formation, water ponding through differences in hydraulic conductivity, and nutrient accumulation through differences in evapotranspiration. These three mechanisms, however, are inextricably linked in nature: acrotelm thickness not only controls net rate of peat formation but also affects evapotranspiration rates (Lafleur et al. 2005) and hydraulic conductivity of the peat (Romanov 1968; Ivanov 1981). In turn, evapotranspiration and hydraulic conductivity influence the water balance and, hence, regulate acrotelm thickness (Hilbert et al. 2000; Belyea and Malmer 2004; Belyea and Baird 2006). The possibility of a combination of mechanisms together driving peatland surface patterning has also been suggested in previous theoretical (Larsen et al. 2007; Eppinga et al. 2009) and empirical (Eppinga et al. 2008) studies. Therefore, there is a need to investigate the interaction between these mechanisms with respect to peatland pattern formation, rather than studying the mechanisms in isolation using separate models.

Furthermore, it is important to identify key variables in patterned peatlands that can be measured in order to accept one (combination of) structuring mechanism(s) and thereby reject other hypotheses. Until now, the theoretical models were too different from each other to be able to identify such key variables. In other words, the current lack of an integrated theoretical framework limits the inferential power of empirical research that is aimed at identifying and rejecting structuring mechanisms that drive peatland surface patterning.

The aim of this study was to integrate the three aforementioned mechanisms into one mechanistic model in order to study the interaction between these mechanisms and to identify key variables that discriminate between

likely and unlikely structuring mechanisms of a peatland surface pattern. More specifically, we aimed to derive hypotheses on the manner in which the occurrence of different structuring mechanisms would be reflected in peatland surface patterning and also in underlying patterns in nutrients and hydrology. We developed a model framework that integrates the three mechanisms into one model. The model contained four state variables: vascular plant biomass, acrotelm thickness, groundwater table, and available nutrient pool. Therefore, the model enabled predictions of how surface patterns (i.e., patterns in vegetation and peat height) are associated with underlying patterns in nutrients and hydrology. Each mechanism could be switched on or off, which allowed the performance of a full-factorial analysis. Model simulations were run both on flat ground and on peatland slopes.

The Model

Model System and Study Approach

The study was designed to study the effects of three mechanisms on peatland pattern formation: peat accumulation, water ponding, and nutrient accumulation. It should be noted that many other mechanisms have been proposed as explanations for pattern formation (see Eppinga et al. 2008, 2009 for reviews), but in this study we focused on the three mechanisms that have been most prominently examined in recent model studies. We combined elements of the models of Hilbert et al. (2000), Belyea and Clymo (2001), Pastor et al. (2002), Rietkerk et al. (2004a), and Couwenberg (2005). In order to focus our study on the mechanisms of pattern formation, we made a number of simplifying assumptions of the peatland model system. First, we considered the water table in the modeled peatland area as being independent from the surroundings, meaning that larger-scale regional groundwater flows were not explicitly taken into account. Also, we assumed that the extent of the peatland area is fixed, meaning that we do consider vertical growth of the peatland but not lateral expansion of the peatland. It is well known that lateral peatland expansion and the regional geographical context of peatlands strongly interact with peatland hydrology and development (Ingram 1982; Clymo 1984; Belyea and Baird 2006), but taking into account these aspects would require site-specific model parameterization (Borren and Bleuten 2006). The aim of this study, however, was to answer general questions and not to focus on site-specific properties. Second, we followed Pastor et al. (2002), who formulated a model applicable to both fens and bogs. Pastor et al. (2002) could simulate the succession from fens to bogs by including a negative relationship between the thickness of the peat layer and the supply of nutrients by groundwater.

In this study, however, we assumed a constant nutrient input rate that is independent of the peat layer thickness. This means that our model could be parameterized to resemble either a fen or a bog but not the succession from one peatland type to the other during a model simulation. It should also be noted that such a transition also strongly depends on larger-scale regional water flow (Glaser 1992a, 1992b), which was not considered in this study (see above). Third, we distinguished the acrotelm and catotelm as distinct peat layers with different decomposition rates (Hilbert et al. 2000), but we did not consider heterogeneity within these layers. Small-scale heterogeneity in the peat layers could create preferential flow channels that greatly affect peatland transport processes (Holden 2005), but here we focused on the transport processes as generated by the three pattern-forming mechanisms of interest. Fourth, following Hilbert et al. (2000) and Rietkerk et al. (2004a), we considered only one functional plant group. Competition between functional plant groups can be important (Van Breemen 1995; Ohlson et al. 2001), and the species composition affects peat decomposability (Moore et al. 2007) and carbon sequestration rates (Belyea and Malmer 2004), but interactions between functional plant groups are beyond the scope of this study. How competition between different functional plant groups may affect pattern formation is treated in detail elsewhere (Eppinga et al. 2009).

Figure 1 shows a schematic diagram of the state variables and the nonspatial processes that were considered in this study. All spatial processes followed the model of Rietkerk et al. (2004a), except for the modeling of gravity-induced water flow on peatland slopes. For this process, we explicitly included a gradient in one direction in the impermeable mineral subsoil (see app. A in the online edition of the *American Naturalist*, which also includes apps. B–G, for analytical details; Brolsma and Bierkens 2007).

The null model contained none of the three mechanisms. The peat accumulation mechanism was introduced in the model by making plant growth most favorable at intermediate acrotelm thickness (Hilbert et al. 2000; Belyea and Clymo 2001). The water ponding mechanism was introduced in the model by letting hydraulic conductivity of the peat decrease with increasing acrotelm thickness (Romanov 1968; Couwenberg 2005). The nutrient accumulation mechanism was introduced in the model by letting transpiration rate increase with increasing vascular plant biomass (Rietkerk et al. 2004a). Thus, each mechanism could be switched on or off, which allowed the performance of a full-factorial analysis. In the next section, we explain how the dynamics of the four state variables were modeled. Subsequently, we explain how each of the three mechanisms was included in the model. The mathematical formulation of the null model is presented in

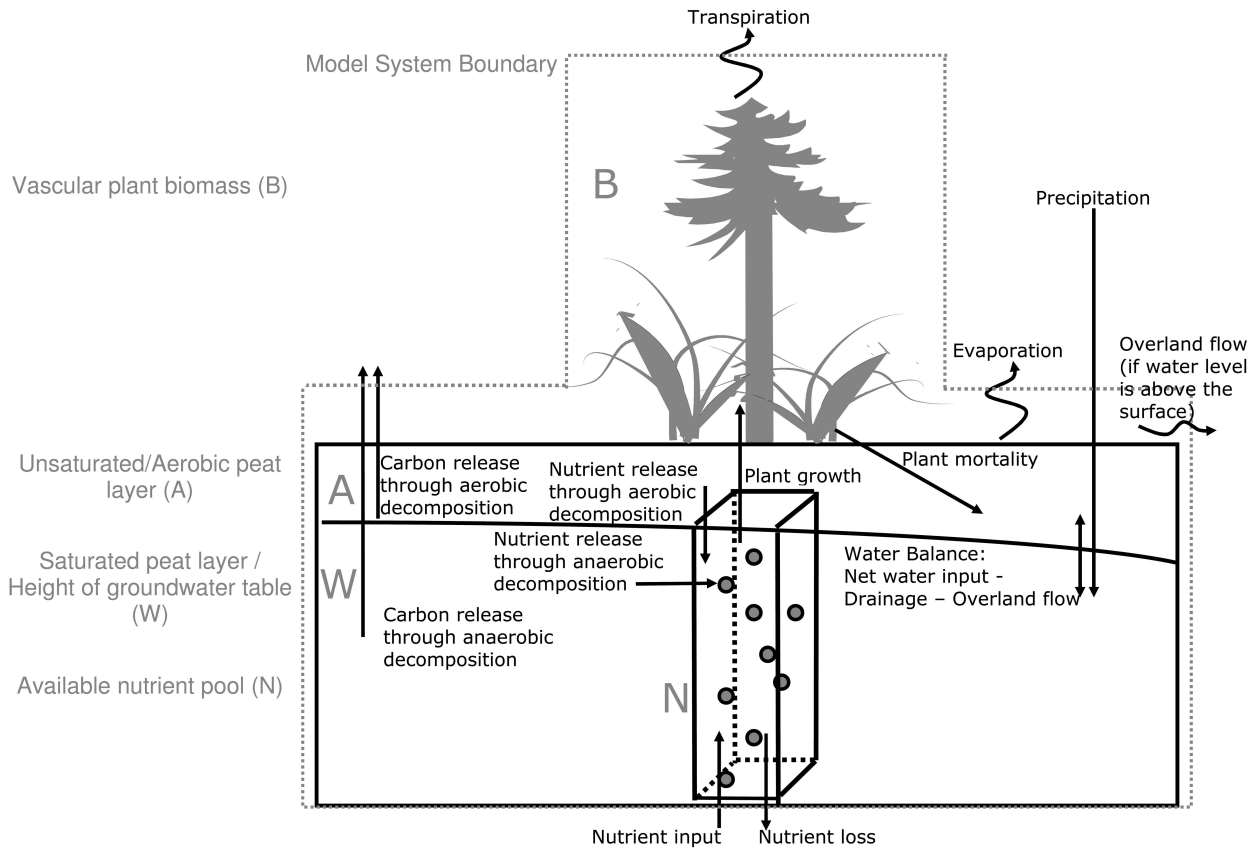


Figure 1: Schematic diagram of the state variables and the nonspatial processes in the model (all spatial processes follow Rietkerk et al. 2004a and Broilmsa and Bierkens 2007). The model consists of four state variables, represented by compartments in the diagram: vascular plant biomass, height/thickness of the aerobic peat layer (acrotelm), height/thickness of the saturated peat layer (or height of the water table), and available nutrient pool. Nutrient concentration in the groundwater is the quotient of the available nutrient pool and the height of the water table. Arrows indicate flows of biomass, water and nutrients from one compartment to the other, or flows crossing the model system boundaries. Decomposition processes involve two arrows: a release of nutrients and a loss from the system of organic matter. Curled arrows indicate losses of water through evaporation, transpiration, and overland flow.

figure 2. The explanation of the model parameters is presented in table 1. The estimation of parameter values was based on literature and is explained in detail in online appendix B. The full-factorial analysis of the effects of the three mechanisms on peatland pattern formation is specified in table 2.

The Null Model

State Variable 1: Vascular Plant Biomass

Vascular plant dynamics comprise growth (model term “I” in fig. 2), respiration (II), mortality (III), and dispersion (IV). Growth is limited by nutrient availability. We assumed that vascular plants grow faster when nutrient availability increases, asymptotically reaching a maximum growth rate at high levels of nutrient availability (e.g.,

DeAngelis 1991). Also, we assumed that plant growth is inhibited when the water conditions are not optimal; herein we refer to this process as water stress. In this study, model parameters were set to mimic a vascular plant community, but the plant growth and water stress functions can also be adjusted to mimic functions in *Sphagnum* species (Nungesser 2003). In the null model, we assumed that water stress occurs as soon as the groundwater table drops below a certain depth. As the water table drops further, water stress increases linearly with depth until the rooting depth of the plant is reached; at that point, plants can no longer grow (Feddes et al. 1978; Rodriguez-Iturbe and Porporato 2004). So, in the null model, water stress occurs only as a result of desiccation. Further, we assumed that mortality and mass loss through respiration increase linearly with increasing vascular plant biomass (Rietkerk et al. 2004a). Finally, the dispersion of vascular plants, either

State variable	Equation	
Plant biomass (B)	$\frac{\partial B}{\partial t} = \underbrace{\frac{g[N]}{s+[N]} Bf^*}_{\text{I growth}} - \underbrace{bB}_{\text{II respiration}} - \underbrace{dB}_{\text{III mortality}} + \underbrace{D_B \left(\frac{\partial^2 B}{\partial x^2} + \frac{\partial^2 B}{\partial y^2} \right)}_{\text{IV dispersion}}$	
Acrotelm thickness (A)	$\frac{\partial A}{\partial t} = \underbrace{\frac{dB}{\rho_D}}_{\text{V litter input}} - \underbrace{r_a A - r_w W}_{\text{VI decomposition}} - \underbrace{\frac{\Delta W_C^* - d_w W}{\theta}}_{\text{VII water input}} - \underbrace{\frac{k^*}{\theta} \left(\frac{\partial}{\partial x} W \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} W \left(\frac{\partial W}{\partial y} \right) \right)}_{\text{VIII drainage Darcy flow}}$	If $A \geq 0$
	$\frac{\partial A}{\partial t} = \frac{dB}{\rho_D} - r_w(A+W) - \frac{\Delta W_C^* - d_w W}{\theta} + \underbrace{oA}_{\text{IX overland flow}} - \frac{k^*}{\theta} \left(\frac{\partial}{\partial x} W \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} W \left(\frac{\partial W}{\partial y} \right) \right)$	If $A \leq 0$
Groundwater table (W)	$\frac{\partial W}{\partial t} = \frac{\Delta W_C^* - d_w W}{\theta} + \frac{k^*}{\theta} \left(\frac{\partial}{\partial x} W \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} W \left(\frac{\partial W}{\partial y} \right) \right)$	If $A \geq 0$
	$\frac{\partial W}{\partial t} = \frac{\Delta W_C^* - d_w W + oA}{\theta} + \frac{k^*}{\theta} \left(\frac{\partial}{\partial x} W \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} W \left(\frac{\partial W}{\partial y} \right) \right)$	If $A \leq 0$
Nutrient availability (N)	$\frac{\partial N}{\partial t} = \underbrace{I_N}_{\text{XV nutrient input}} - \underbrace{r_N N}_{\text{XVI nutrient loss}} + \underbrace{\rho_D u (r_a A + r_w W)}_{\text{XVII decomposition}} - \underbrace{u \frac{g[N]}{s+[N]} Bf^*}_{\text{XVIII plant uptake}} + \underbrace{W \theta \left(D_N \left(\frac{\partial^2 [N]}{\partial x^2} + \frac{\partial^2 [N]}{\partial y^2} \right) + \frac{k^*}{\theta} \left(\frac{\partial}{\partial x} [N] \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} [N] \left(\frac{\partial W}{\partial y} \right) \right) \right)}_{\text{XIX nutrient diffusion}} + \underbrace{\frac{k^*}{\theta} \left(\frac{\partial}{\partial x} [N] \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} [N] \left(\frac{\partial W}{\partial y} \right) \right)}_{\text{XX nutrient advection (Darcy flow)}}$	If $A \geq 0$
	$\frac{\partial N}{\partial t} = I_N - r_N N + \rho_D u (r_w (W+A)) - u \frac{g[N]}{s+[N]} Bf^* + \underbrace{oA[N]}_{\text{XXI overland flow}} + W \theta \left(D_N \left(\frac{\partial^2 [N]}{\partial x^2} + \frac{\partial^2 [N]}{\partial y^2} \right) + \frac{k^*}{\theta} \left(\frac{\partial}{\partial x} [N] \left(\frac{\partial W}{\partial x} \right) + \frac{\partial}{\partial y} [N] \left(\frac{\partial W}{\partial y} \right) \right) \right)$	If $A \leq 0$

Figure 2: Null model equations. Symbols indicated with an asterisk vary for the different model versions and are specified for each model version in table 2.

by seed dispersal or clonally, is approximated as a diffusion process (e.g., Okubo 1989). This means that the amount of dispersed biomass is linearly proportional to the gradient in biomass density.

State Variable 2: Acrotelm Thickness

Acrotelm thickness dynamics include input of plant litter (V, fig. 2), decomposition losses (VI), and changes in the

Table 1: Model parameters, state variables, and functions and their interpretation

Parameter	Interpretation	Units
g	Plant growth rate	year ⁻¹
b	Plant respiration rate	year ⁻¹
d	Plant mortality rate	year ⁻¹
s	Nutrient saturation constant	g m ⁻³
D_B	Diffusion coefficient of biomass	m ² year ⁻¹
ρ_D	Peat dry bulk density	g m ⁻³
r_A	Acrotelm decomposition rate	year ⁻¹
r_W	Catotelm decomposition rate	year ⁻¹
d_W	Drainage parameter	year ⁻¹
o	Overland flow parameter	year ⁻¹
θ	Peat porosity	
I_N	Nutrient input rate	g m ⁻² year ⁻¹
r_N	Nutrient loss rate	year ⁻¹
u	Nutrient content of organic matter	g g ⁻¹
D_N	Diffusion coefficient of nutrients	m ² year ⁻¹
P_{Excess}	Net water input (for null model)	m year ⁻¹
A_{Opt}	Optimum distance to water table for vegetation growth (for peat accumulation mechanism)	m
c	Controlling decline of evapotranspiration away from optimum (for peat accumulation mechanism)	
γ	Controlling width of evapotranspiration plateau close to optimum (for peat accumulation mechanism)	m ^{-γ}
t_V	Maximum transpiration rate (for nutrient accumulation mechanism)	m ³ g ⁻¹ year ⁻¹
E_T	Maximum evaporation rate (for nutrient accumulation mechanism)	m year ⁻¹
h_1	Distance to water table below which stress occurs (for nutrient accumulation mechanism)	m
h_2	Rooting depth (for nutrient accumulation mechanism)	m
z	Reference height (for nutrient accumulation mechanism)	m
P	Net water input rate (for nutrient accumulation mechanism)	m year ⁻¹
k^*	Range of hydraulic conductivity (for water ponding mechanism)	m year ⁻¹
k_0	Hydraulic conductivity (in null model)	m year ⁻¹
k_{Opt}	Hydraulic conductivity when distance to the water table equals A_{Opt} (for water ponding mechanism)	m year ⁻¹
β	Controlling decline in hydraulic conductivity with increasing acrotelm thickness (for water ponding mechanism)	m ^{-2β}
α	Angle of peatland slope (see app. A)	degrees
B	Vascular plant biomass	g m ⁻²
A	Acrotelm thickness	m
W	Water table height	m
N	Available nutrient pool	g m ⁻²
$[N]$	Nutrient concentration in the groundwater	g m ⁻³
k^*	Hydraulic conductivity function	m year ⁻¹
ΔW_C^*	Net water input rate	m year ⁻¹
f^*	Function(s) for plant water stress and evaporation	
f_{Plant}	Plant water stress function	
f_{Evap}	Evaporation function	

Note: Appendix A is in the online edition of the *American Naturalist*.

groundwater table (VII–X). Plant litter mass is converted into a height increase of the acrotelm by dividing this mass by the dry bulk density of the peat (Belyea and Clymo 2001). Dry bulk density generally increases with distance below the peatland surface, whereas effective porosity and hydraulic conductivity of peat generally decrease (e.g., Ry-

croft et al. 1975; Belyea and Clymo 2001; Frohling et al. 2001). In this study, however, we did not take into account vertical variation in the peat layers. Hence, we made the simplifying modeling assumption that the peat characteristics bulk density, effective porosity, and hydraulic conductivity do not vary vertically. Decomposition leads to

Table 2: Mathematical formulation of the full-factorial analysis of the effects of peat accumulation (PA), water ponding (WP), and nutrient accumulation (NA) on peatland pattern formation

Model version	f^* (between 0 and 1)	ΔW_C^*	k^*
Null model	$\frac{W-z-h_2}{h_1-h_2}$	P_{Excess}	k_0
PA	$\frac{1}{1+c(A-A_{\text{Opt}})^y}$	P_{Excess}	k_0
NA	$\frac{W-z-h_2}{h_1-h_2}$	$P - t_V B f^* - E_{\text{T}} f^*$	k_0
PA + NA	$f_{\text{Plant}} = \frac{1}{1+c(A-A_{\text{Opt}})^y}$ $f_{\text{Evap}} = \frac{1}{1+c \max(0, A)^y}$	$P - t_V B f_{\text{Plant}} - E_{\text{T}} f_{\text{Evap}}$	k_0
WP	$\frac{W-z-h_2}{h_1-h_2}$	P_{Excess}	$\frac{k_{\text{Aopt}}}{\{1 + [(\max(0, A))^2 - A_{\text{Opt}}^2]\}^\beta}$
PA + WP	$\frac{1}{1+c(A-A_{\text{Opt}})^y}$	P_{Excess}	$\frac{k_{\text{Aopt}}}{\{1 + [(\max(0, A))^2 - A_{\text{Opt}}^2]\}^\beta}$
WP + NA	$\frac{W-z-h_2}{h_1-h_2}$	$P - t_V B f^* - E_{\text{T}} f^*$	$\frac{k_{\text{Aopt}}}{\{1 + [(\max(0, A))^2 - A_{\text{Opt}}^2]\}^\beta}$
PA + WP + NA	$f_{\text{Plant}} = \frac{1}{1+c(A-A_{\text{Opt}})^y}$ $f_{\text{Evap}} = \frac{1}{1+c \max(0, A)^y}$	$P - t_V B f_{\text{Plant}} - E_{\text{T}} f_{\text{Evap}}$	$\frac{k_{\text{Aopt}}}{\{1 + [(\max(0, A))^2 - A_{\text{Opt}}^2]\}^\beta}$

Note: See table 1 for interpretations of parameters and their assigned values.

mass loss from the peat layer, which implies a decrease in acrotelm thickness (fig. 1). We assume that the amount of mass loss through decomposition increases linearly with layer thickness (Hilbert et al. 2000; Pastor et al. 2002). Decay rate, however, is different for the two layers: acrotelm decay is faster than catotelm decay (Hilbert et al. 2000). Finally, we assumed that the groundwater table defines the acrotelm-catotelm boundary (Belyea and Malmer 2004), meaning that a change in the groundwater table affects acrotelm thickness. More specifically, acrotelm thickness decreases if the groundwater table rises, whereas acrotelm thickness increases when the groundwater table lowers (Hilbert et al. 2000).

State Variable 3: Groundwater Table

Groundwater table dynamics consist of water input (XI, fig. 2), losses of water from the peatland toward the surroundings (drainage; XII), loss through overland flow (XIII), and lateral transport of water that is driven by differences in hydraulic head (XIV). We assumed that the long-term net water input rate is constant (Belyea and Clymo 2001) and that loss through drainage increases linearly with catotelm thickness (Hilbert et al. 2000). Also, when the water table is above the peatland surface (hollow state), it is indicated by a negative acrotelm thickness. In this case, the porosity of this upper water layer is set to 1 (Hilbert et al. 2000), and limited infiltration capacity of hollows is mimicked by including a loss term through

overland flow (Foster et al. 1983; Foster and King 1984; Glaser 1992a; Belyea 2007). Overland flow and drainage, however, are not modeled explicitly in this study, because these depend on the regional setting of the peatland (Ingram 1982; Clymo 1984; Belyea and Baird 2006). Hence, we modeled overland flow and drainage as water losses from the model. Lateral transport of water through the peat was described by Darcy's law (Rycroft et al. 1975; Rietkerk et al. 2004a; Borren and Bleuten 2006), meaning that lateral transport of water is driven by differences in hydraulic head.

State Variable 4: Available Nutrient Pool

Available nutrient pool dynamics comprise external input (XV, fig. 2), nutrient losses (e.g., through leaching; XVI), release through decomposition (XVII), plant uptake (XVIII), diffusion due to nutrient concentration gradients (XIX), advection due to groundwater movement (XX), and loss of nutrients through overland flow (XXI). We model nutrients in the soluble reactive phase, which can be taken up by plants. Nutrient concentration is defined as the quotient of available nutrient pool and the amount of water (i.e., height of the water table multiplied by the effective porosity). We assumed that external input of nutrients into the system (e.g., by atmospheric deposition) is constant (Rietkerk et al. 2004a). We also assumed that decomposition leads to mineralization, meaning that nutrients become available for plants and that, for example, microbes

do not immobilize them. In our model, nutrient content of the plant biomass does not change when it dies and turns into litter. Subsequently, the nutrient content of plant litter does not change during storage in acrotelm and catotelm (Rietkerk et al. 2004a; Eppinga et al. 2008). Removal of nutrients through plant uptake was assumed proportional to plant growth. Further, we assumed that nutrient losses (e.g., by leaching) increase linearly with available nutrient pool (Pastor et al. 2002; Rietkerk et al. 2004a). We assumed that Fick's law could describe the nutrient diffusion process, meaning that the flux of nutrients increases linearly with increasing nutrient concentration gradient (Rietkerk et al. 2004a). Finally, nutrients are dissolved in the groundwater, meaning that groundwater flow also implies advective transport of dissolved nutrients.

Mechanisms Associated with Peatland Pattern Formation

Mechanism 1: Peat Accumulation

The peat accumulation mechanism was switched on by making plant growth most favorable at intermediate acrotelm thickness. Therefore, plant water stress needed to become a function of acrotelm thickness. For this we assumed that water stress occurs both at high water tables because of waterlogging and at low water tables because of desiccation. Therefore, the water stress function was modeled as an optimum curve, with highest values (least stress) occurring at intermediate acrotelm thickness (fig. 3A; Hilbert et al. 2000; Belyea and Clymo 2001). It can be shown intuitively why this water stress function describes the peat accumulation mechanism. In the case that vascular plant biomass, available nutrient pool, and groundwater table are in equilibrium, acrotelm thickness will reach equilibrium when input of plant litter equals losses through decomposition. Because plant litter production is linearly related to plant biomass (see "State Variable 1: Vascular Plant Biomass"), litter production will follow the same shape as the water stress function (fig. 3A). Because decomposition is linearly related to acrotelm thickness (see "State Variable 2: Acrotelm Thickness"), mass loss through decomposition will be a linear function of acrotelm thickness (fig. 3A). Figure 3A shows that this yields three possible situations in which the acrotelm thickness is in equilibrium: a stable, low-productivity wet state and a stable, higher-productivity dry state, with a tipping point in between at which the acrotelm thickness is in equilibrium but such that a slight perturbation will move the system toward one of the stable states. If acrotelm thickness increases at this tipping point, production exceeds decomposition and the acrotelm will grow toward

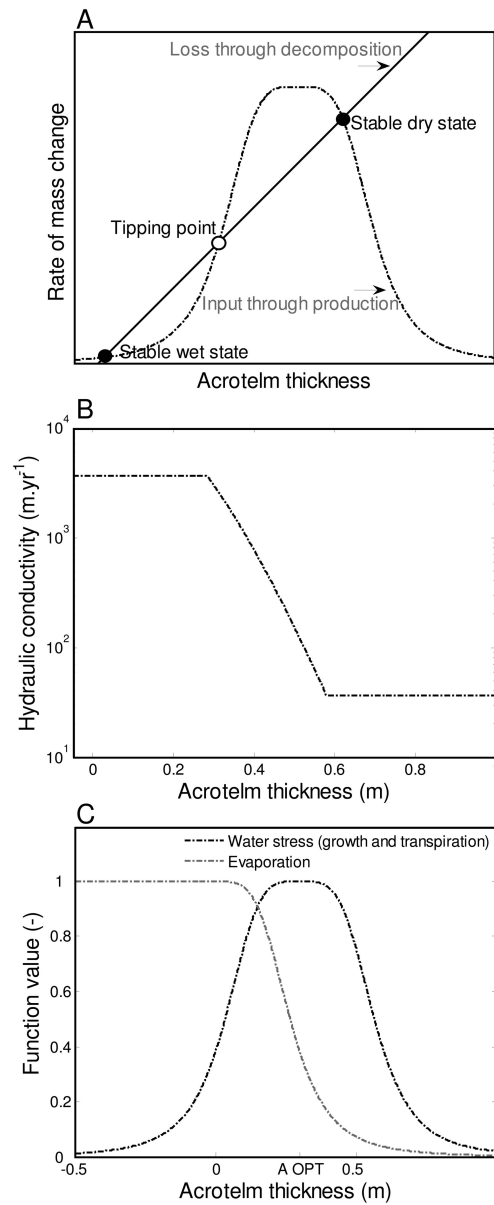


Figure 3: A, Conceptual graph illustrating the peat accumulation mechanism. Just above the tipping point, production exceeds decomposition, meaning development toward a stable dry state. Just below the tipping point, decomposition exceeds production, meaning development toward a stable wet state. B, If the water ponding mechanism is switched on, a negative relation between acrotelm thickness and hydraulic conductivity is assumed. The graph shows the specific numerical form of this relation, using the parameter values as specified in appendix B in the online edition of the *American Naturalist*. Note that the Y-axis is logarithmic. C, If the nutrient accumulation mechanism and the peat accumulation mechanism are both switched on, evaporation rate and vegetation water stress are controlled by acrotelm thickness. It is assumed that evaporation decreases with increasing acrotelm thickness. Water stress occurs when the water table is higher (inhibition because of waterlogging) or lower (inhibition because of desiccation) than the optimum acrotelm thickness A_{OPT} .

the dry state. If acrotelm thickness decreases at this tipping point, decomposition exceeds production and the acrotelm will shrink toward the wet state. Further, the peat accumulation mechanism is also expressed by a negative relationship between evaporation rate and acrotelm thickness (table 1; Hilbert et al. 2000)

Mechanism 2: Water Ponding

The water ponding mechanism can be switched on by letting hydraulic conductivity of the peat decrease with increasing acrotelm thickness. This decrease may be due to the increased degree of decomposition with depth (Ivanov 1981; Swanson and Grigal 1988) and to increased pressure of the overlying peat mass (Belyea and Clymo 2001). Empirical studies indeed show that the hydraulic conductivity of the peat decreases with acrotelm thickness (Romanov 1968; Ivanov 1981), suggesting that the depth-integrated conductivity (transmissivity) of the peat layer is lower for ridges and hummocks than for hollows (Ivanov 1981; Swanson and Grigal 1988; Couwenberg and Joosten 2005). We assumed that hydraulic conductivity exponentially increases with decreasing acrotelm thickness (fig. 3B; Romanov 1968). To limit the number of parameters in the model, we scaled the hydraulic conductivity function relative to the acrotelm thickness for optimal plant growth (table 2). Further, we assumed a maximum difference in hydraulic conductivity between hollows and hummocks of 2 orders of magnitude (fig. 3B; Waddington and Roulet 1997; Givnish et al. 2008). It is important to note that we did not take into account vertical variations in hydraulic conductivity. We used the acrotelm thickness to calculate the hydraulic conductivity (fig. 3B) and assumed that this calculated value was constant for the entire peat column. This approach is similar to the approach used in previous studies that modeled the water ponding mechanism (Swanson and Grigal 1988; Couwenberg 2005; Couwenberg and Joosten 2005). Instead of considering two vegetation states and two values of hydraulic conductivities, however, our model uses a functional relationship between conductivity and acrotelm thickness (fig. 3B). Although this is a simplification of reality, this approach does introduce lower conductivity of hummocks/ridges as compared to hollows in the model, which subsequently affects lateral transport. So, this approach is suitable for our current purpose.

Mechanism 3: Nutrient Accumulation

The nutrient accumulation mechanism was switched on by letting transpiration rate increase with increasing vascular plant biomass. This creates the possibility of nutrient accumulation, because patches with higher vascular plant

biomass will transpire more water than their surroundings, and therefore, water and nutrients will flow toward these high-density vegetated patches (Eppinga et al. 2008). If the nutrient accumulation mechanism is switched on, transpiration and evaporation are both explicitly addressed in the model (table 2). The growth of vascular plants may promote an increase in transpiration rates (Frankl and Schmeidl 2000; Andersen et al. 2005). We assumed that transpiration could be reduced due to water stress (Rietkerk et al. 2004a; Ridolfi et al. 2006; Broolsma and Bierkens 2007). Therefore, we applied the same water stress function for transpiration as used for plant growth (table 2). The same water stress function was also used for evaporation. This was done to separate the effects of acrotelm thickness (and the peat accumulation mechanism) and the nutrient accumulation mechanism (table 2). Hence, evaporation became a function of acrotelm thickness if the peat accumulation and the nutrient accumulation were switched on simultaneously (table 2). Then, we assumed that the rate of evaporation decreases toward zero as acrotelm thickness increases (Hilbert et al. 2000) and that the maximum evaporation rate is reached when acrotelm thickness is close to zero (Hilbert et al. 2000; Nungesser 2003). To minimize the number of parameters in the model, we assumed similar shapes for the functions for evaporation and water stress, the latter controlling plant growth and transpiration (fig. 3C).

Model Analyses

We studied the effect of three mechanisms on peatland pattern formation, using a full-factorial design. Hence, we analyzed eight model versions (table 2), both on flat ground and on peatland slopes. We performed a linear stability analysis for the model versions on flat ground. This analysis is used to identify for each model version the environmental conditions (in terms of nutrients and precipitation regime) under which pattern formation can occur. The linear stability analysis is presented in online appendix C. We also performed numerical simulations on a two-dimensional domain to study the emerging patterns (see app. B for details). Subsequently, we tested the sensitivity and robustness of the model results by performing an elasticity analysis (e.g., Hartemink et al. 2008) and by identifying the sensitivity range (Eppinga et al. 2006) of the model parameters. These analyses are presented in online appendix D. Finally, we compared the spatial scale of the modeled patterns with field observations of patterned peatlands from previous studies (presented in online app. E), using a geostatistical method originally developed for the analysis of self-organized spatial fracture patterns on frozen ground (Plug and Werner 2001).

Peat accumulation

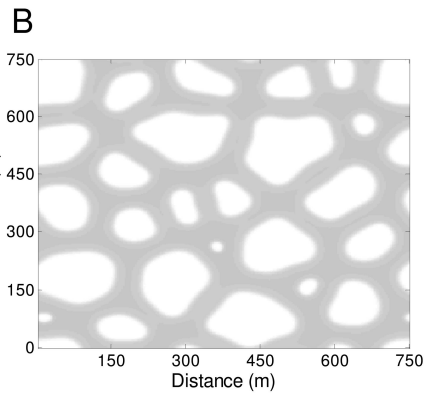
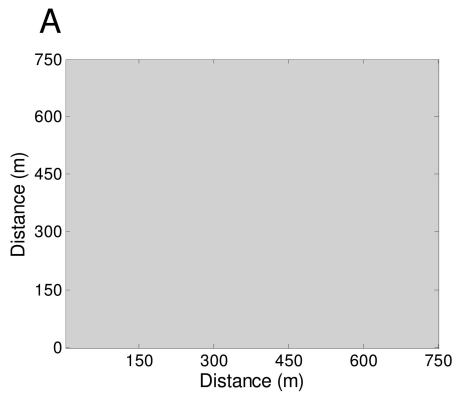
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Peat accumulation

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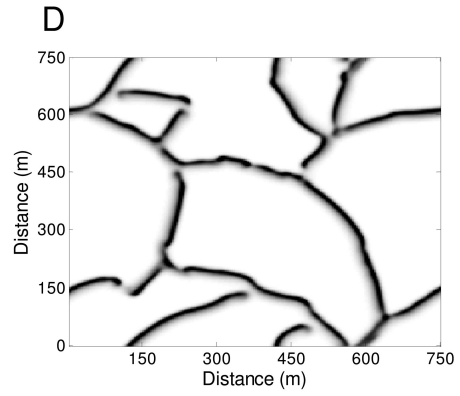
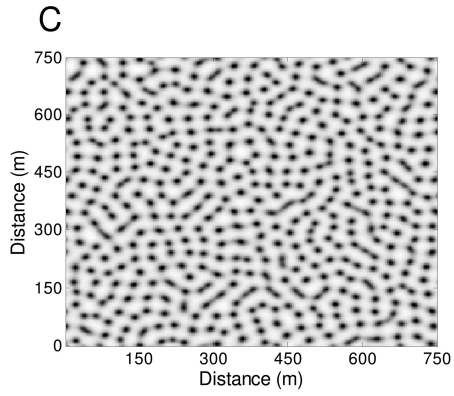
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Nutrient accumulation



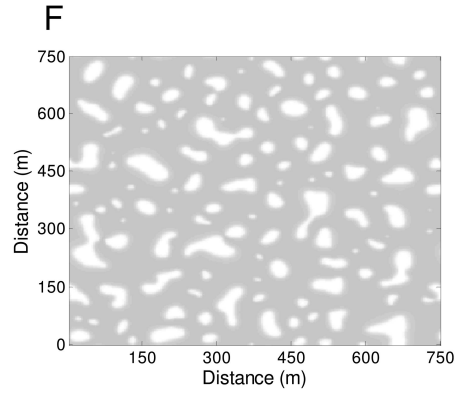
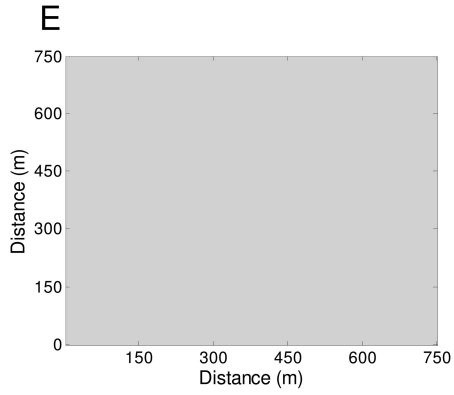
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Nutrient accumulation



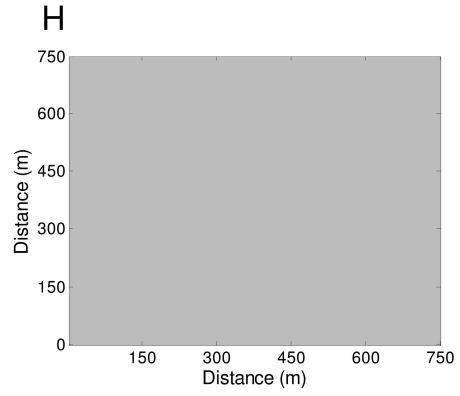
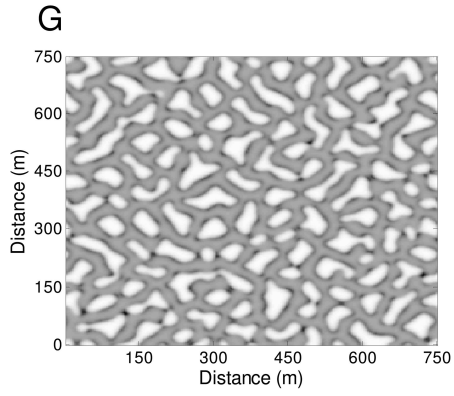
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Nutrient accumulation



ON

Nutrient accumulation



Water ponding

OFF

Water ponding

ON

Results

Peatland Pattern Formation on Flat Ground

We selected for each model (if possible) a parameterization leading to pattern formation on flat ground (fig. 4). The null model showed that in the absence of the three mechanisms, the peatland developed into an area that was homogeneously covered with vascular plants (fig. 4A).

Due to the peat accumulation mechanism, sparsely vegetated hollows emerged within a matrix of densely vegetated hummocks (fig. 4B). The underlying pattern in hydrology revealed that the water level in hollows was lower than in hummocks (see online app. F for a detailed overview). Further, the underlying pattern in nutrients revealed higher nutrient concentrations in hollows as compared to hummocks (app. F).

If the nutrient accumulation was switched on, a pattern emerged because of a scale-dependent feedback; areas with higher biomass transpire more water and hence attract water and nutrients from the surroundings, which further amplifies spatial differences in biomass. This resulted in a pattern of densely vegetated hummocks surrounded by more sparsely vegetated hollows (fig. 4C). If the peat accumulation mechanism and the nutrient accumulation mechanism were both switched on, expansion of the hollows forced hummocks into the narrow spaces between separate hollows. As a result, the hummocks merged into narrow ridges, forming a netlike or maze structure (fig. 4D). The underlying pattern in hydrology revealed that the water level under ridges was lower than in hollows (app. F). The underlying pattern in nutrients revealed higher nutrient concentrations in ridges as compared to hollows (app. F).

If only the water ponding mechanism was switched on, no peatland patterning emerged (fig. 4E). If the water ponding was added to the model with the peat accumulation mechanism, the size of the hollows somewhat decreased, but there was no qualitative change in the patterning (fig. 4F vs. 4B). If the water ponding was added to the model with the nutrient accumulation mechanism, the individual hummocks merged to a maze pattern of connected hummocks merging into ridges (fig. 4G vs. 4C).

If all three mechanisms were switched on simultaneously, formation of a stable pattern was not possible (fig. 4H). If the parameterization was set within the parameter region of pattern formation (the Turing instability region; see app. C), a pattern formed initially, but this pattern was not stable and died out, meaning that the system developed to a uniform wet state with no biomass (data not shown).

A more detailed explanation of the relation between the modeled mechanisms and the morphology of the emerging patterns on flat ground is described in online appendix G.

Peatland Pattern Formation on Slopes

We also examined pattern formation on slopes (fig. 5). Similar to the model simulation on flat ground, the null model showed that in the absence of the three mechanisms, the peatland developed into a slope that was homogeneously covered with vascular plants (fig. 5A).

Due to the peat accumulation mechanism, a linear ridge-hollow pattern emerged, in which the ridges and hollows were oriented perpendicular to the slope (fig. 5B). The nutrient accumulation mechanism also drove the formation of a linear ridge-hollow pattern, but in this case the orientation of the stripes was parallel to the slope (fig. 5C). If the peat accumulation and the nutrient accumulation mechanism were both switched on, an elongated netlike or maze pattern developed, meaning that the large hollows in between the ridges were wider in the direction of the slope (fig. 5D). Therefore, the dominant orientation of the ridges was also parallel to the slope (fig. 5D).

If only the water ponding mechanism was switched on, no pattern formation occurred (fig. 5E). If the water ponding mechanism was added to the model with the peat accumulation mechanism, the dominant orientation of stripes was still perpendicular to the slope, but connecting ridges parallel to the slope also emerged (fig. 5F). If the water ponding mechanism was added to the model with the nutrient accumulation mechanism, stable pattern formation was not possible (fig. 5G).

Interestingly, if the water ponding mechanism was

Figure 4: Two-dimensional numerical model simulations mimicking peatlands on flat ground. Each panel representing a plan view of the vascular plant biomass distribution on a square peatland area of 750 m × 750 m. Darker colors indicate areas with higher vascular plant biomass (B), the color map ranging from white (0 g B m⁻²) to black (2,500 g B m⁻²). For the simulations the following parameters values were used: $P_{\text{excess}} = 0.35$ m, $P = 2$ m, $I_N = 1.7$ g N m⁻² year⁻¹ (Brooks 1992; Bobbink et al. 1998; Hilbert et al. 2000; Eppinga et al. 2008). Other parameter values are reported in appendix A in the online edition of the *American Naturalist*. The different panels together show a full-factorial analysis of the effects of peat accumulation, nutrient accumulation, and water ponding mechanisms. A, Null model; B, model with only the peat accumulation mechanism; C, model with only the nutrient accumulation mechanism; D, model with both the peat accumulation and the nutrient accumulation mechanisms; E, model with only the water ponding mechanism; F, model with both the peat accumulation and the water ponding mechanisms; G, model with both the water ponding and the nutrient accumulation mechanisms; H, model with the peat accumulation, water ponding, and nutrient accumulation mechanisms.

Peat accumulation

OFF

Peat accumulation

ON

OFF

Nutrient accumulation

ON

Nutrient accumulation

OFF

Nutrient accumulation

ON

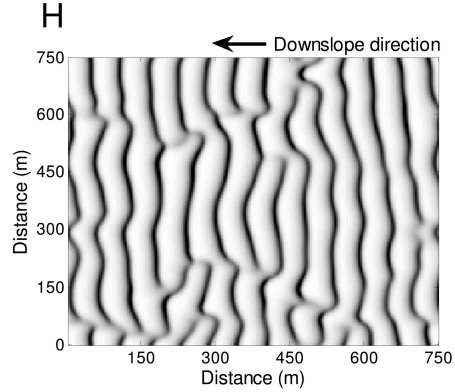
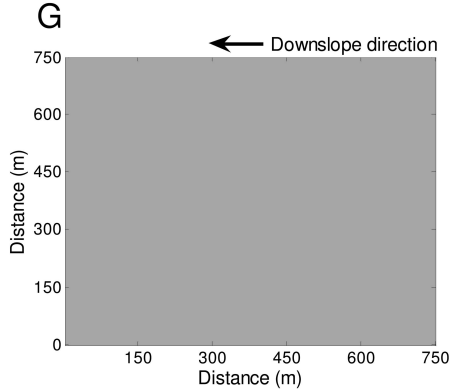
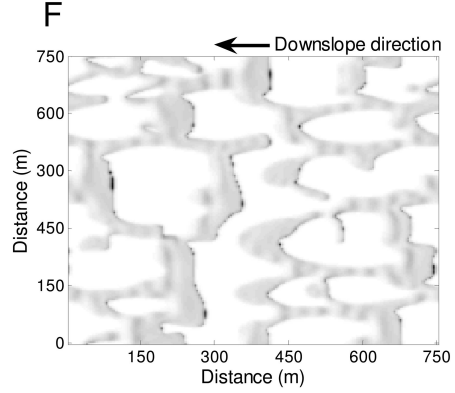
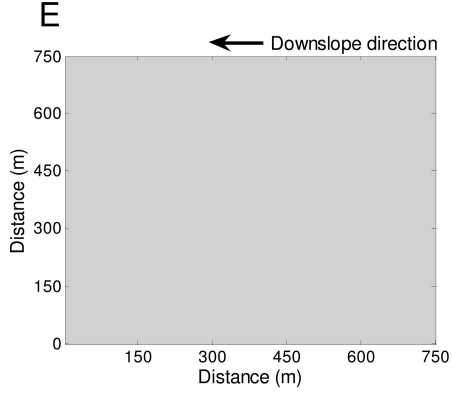
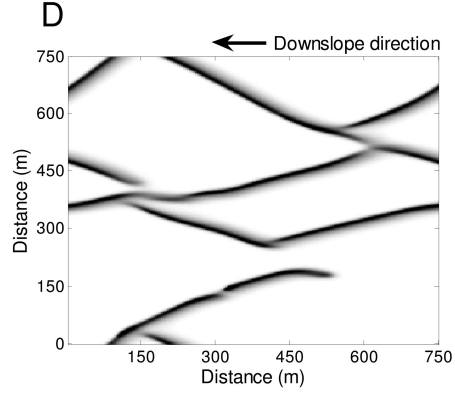
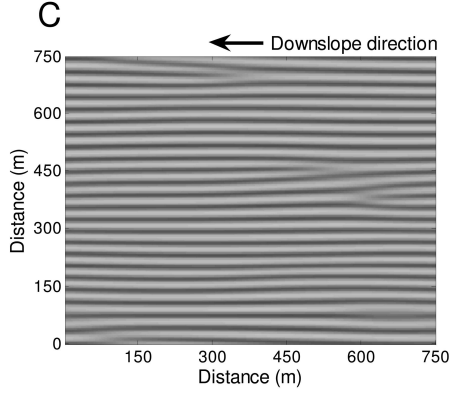
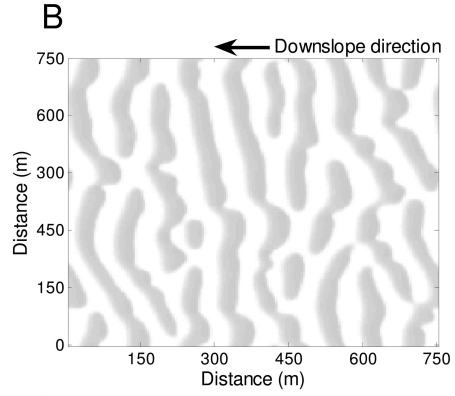
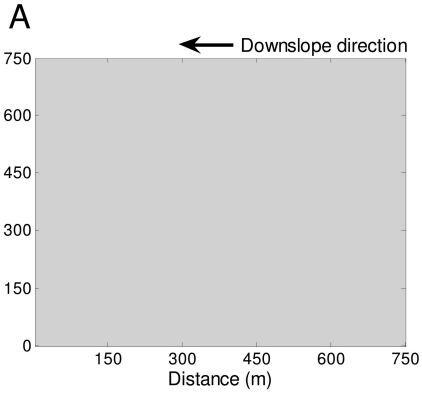
Nutrient accumulation

Water ponding

OFF

Water ponding

ON



added to the model with the nutrient accumulation mechanism and the peat accumulation mechanism (meaning that all three mechanisms were switched on), the orientation of the stripes reversed (fig. 5H vs. 5D). A more detailed explanation of the relation between the modeled mechanisms and the morphology of the emerging patterns on peatland slopes is described in appendix G.

Sensitivity and Robustness of the Model Results

Pattern formation could occur over a large range of nutrient input and precipitation rates. However, the parameter space for model versions without the nutrient accumulation mechanism was quite narrow (app. C), meaning that for a fixed value of net water input rate, for example, pattern formation occurred only in a small range of nutrient input rates. Other parameters that imposed strong constraints on pattern formation were the plant respiration and mortality rates and the vascular plant transpiration parameter (app. D). The state variables in the model were most sensitive to changes in hydrological conditions as regulated by water input in the system (app. D). Further, the model was also sensitive to parameters related to the vascular plant physiology (app. D). The spatial scales of the modeled patterns were within the observed range in field studies, mostly at the upper end of this range (app. E).

Discussion

Our model results suggest that the structuring mechanism(s) driving peatland surface patterning can be identified by analysis of the underlying patterns in nutrients and hydrology (see app. F for a detailed overview). Until now, such specific predictions were not possible, because this is the first study that explicitly linked spatial surface patterning to underlying patterns in nutrients and hydrology for different (combinations of) structuring mechanisms. It is necessary to take into account underlying patterns in nutrients and hydrology, because the presence or absence of a structuring mechanism cannot be inferred from the surface pattern alone (Rietkerk et al. 2004a; Ep-

pinga et al. 2009; figs. 4, 5). The presented modeling framework could simulate the variety of peatland patterns that occurs in nature, namely, hummock-hollow patterning and maze patterns on flat ground (fig. 4) but also linear patterns on peatland slopes (fig. 5). These patterns were generated by a combination of structuring mechanisms that have been proposed and modeled before but were not yet integrated into a single model. Importantly, the fact that we generated contrasting hypotheses with this approach (app. F) will increase the inferential power of empirical studies on peatland surface patterning, which we now explain in further detail.

Our study suggests that measuring the nutrient concentration in the mire water under hummocks and in hollows indicates whether the peatland surface pattern is driven by the nutrient accumulation mechanism (app. F). In the field, water samples can be taken at both hummocks and hollows to quantify the difference in nutrient status. An alternative way to quantify the nutrient status in hummocks and hollows is to harvest a plant species that grows both on hummocks and in hollows and measure the nutrient content and stoichiometry in these samples (De Wit et al. 1963; Vermeer and Berendse 1983; Wassen et al. 1995). The presence of the nutrient accumulation mechanism would induce higher nutrient concentrations on hummocks as compared with hollows. In the absence of the nutrient accumulation mechanism, this pattern in nutrients would be reversed. Another way to test the model predictions (app. F) is to measure the height of the water table under hummocks and in hollows. The presence of the nutrient accumulation mechanism would induce lower water tables in hummocks as compared with hollows. In the absence of the nutrient accumulation mechanism, this hydrological pattern would be reversed (app. F). These hydrological measurements are more demanding than nutrient measurements, but even a few measurement points of water table height in hummocks and hollows can provide enough information to accept or reject hypotheses (Eppinga et al. 2008). Note that both types of measurements are relatively simple and short-term measurements in the field, meaning that longer-term field manipulations can be circumvented. These measurements of nutrients

Figure 5: Two-dimensional numerical model simulations mimicking peatlands on slopes (arrows indicate the downslope direction). Each panel representing a plan view of the vascular plant biomass distribution on a square and sloping peatland area of 750 m × 750 m. Darker colors indicate areas with higher vascular plant biomass, the color map ranging from white (0 g B m⁻²) to black (2,500 g B m⁻²). For each panel, the downslope direction is from right to left. Parameter values are the same as in figure 3, except for *B* and *F*. In these two simulations, stable patterns formed only at lower nutrient input rates, so lower values were used for these two simulations (1.25 g N m⁻² year⁻¹ instead of 1.7 g N m⁻² year⁻¹). The different panels together show a full-factorial analysis of the effects of peat accumulation, nutrient accumulation, and water ponding mechanisms. *A*, Null model; *B*, model with only the peat accumulation mechanism; *C*, model with only the nutrient accumulation mechanism; *D*, model with both the peat accumulation and the nutrient accumulation mechanisms; *E*, model with only the water ponding mechanism; *F*, model with both the peat accumulation and the water ponding mechanisms; *G*, model with both the water ponding and the nutrient accumulation mechanisms; *H*, model with the peat accumulation, water ponding, and nutrient accumulation mechanisms.

and hydrology have been carried out for a maze-patterned peatland in western Siberia (Eppinga et al. 2008). Our new model results have two new implications. First, measurements of nutrients and hydrology can also be used to identify the structuring mechanisms in other types of patterned peatlands, namely, hummock-hollow and linearly patterned sloping peatlands (app. F). Second, measurements of nutrients and hydrology can also be used to discriminate between alternative hypotheses (app. F). Therefore, the model study presented here increases the inferential power of future empirical studies on peatland patterning.

Our modeling framework also enabled the investigation of the effect of combinations of mechanisms on peatland patterning. For example, the water ponding mechanism in isolation could not drive pattern formation, but the synergy with the other mechanisms was important on slopes (fig. 5) because it yielded a different orientation of stripes (perpendicular to the slope; app. G) as compared to stripes that formed due to the nutrient accumulation mechanism only (parallel to the slope; app. G). Thus, perpendicular-oriented linear patterning on slopes requires occurrence either of the peat accumulation mechanism or a synergetic combination of peat accumulation, nutrient accumulation, and water ponding (fig. 5; app. G).

The structuring mechanisms driving peatland patterning have been the field of much speculation, but the long time span of these mechanisms hampers actual experiment (Moore and Bellamy 1974). A common approach to circumvent this problem is inferring past process from current spatial patterns. Interpretations of current patterns benefit from a priori construction of multiple hypotheses (Platt 1964; Loehle 1987), a method of hypothesis testing that differs fundamentally from hypothesis generation based on a posteriori interpretation of data (Belyea and Lancaster 2002). Our model results generated contrasting hypotheses about different structuring mechanisms driving peatland patterning and how the occurrence of each structuring mechanism would be reflected in surface pattern and underlying patterns in nutrients and hydrology (app. F), which will benefit interpretations of empirical studies on peatland patterning.

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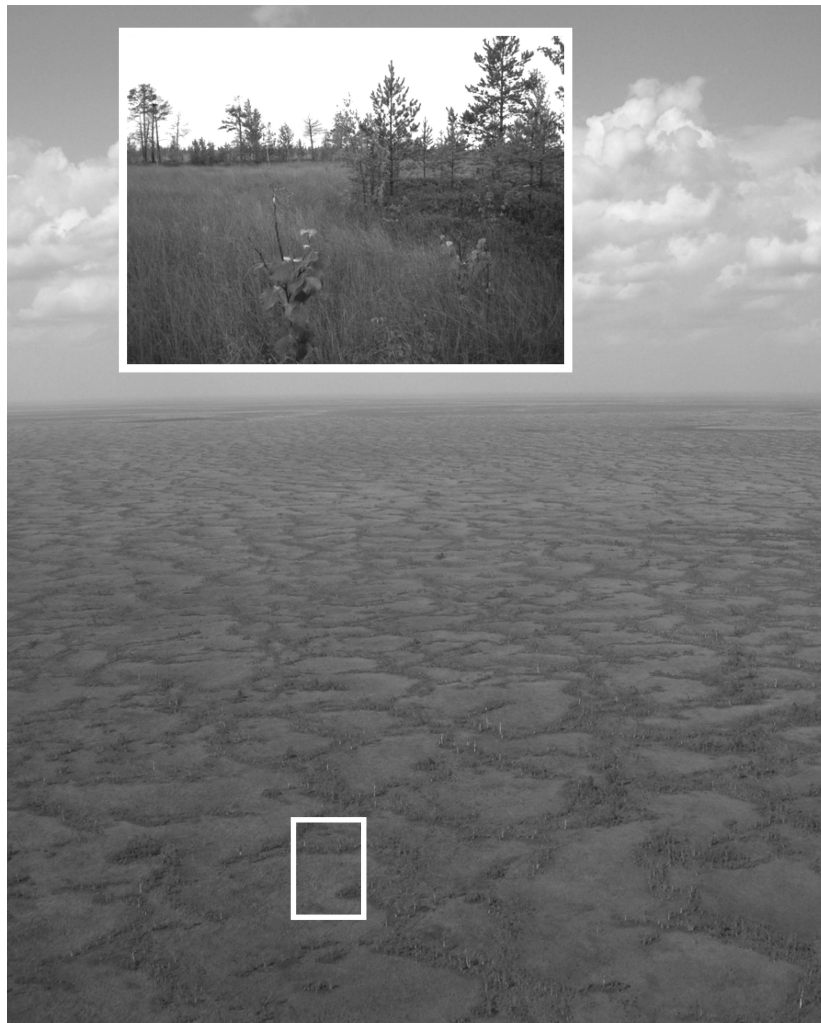
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Photograph (taken from a helicopter) of a maze pattern from a relatively flat area in the Great Vasyugan Bog of western Siberia. The inset photograph shows the pattern from the ground, formed by densely vegetated patches of shrubs and trees within a more sparsely vegetated matrix (photographs by M. Eppinga).