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Research papers

Ecohydrological feedbacks increase water storage, streamflow and resilience of natural peatlands

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A R T I C L E I N F O

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A B S T R A C T

Peatlands are hypothesized to enhance water storage, sustain baseflow, and mitigate drought impact at the landscape level. The importance of ecohydrological feedbacks for the peatland water cycle and the interaction with surrounding landscapes is, however, poorly understood. This thin scientific basis hinders effective land- and water management and understanding peatland restoration impacts on regional hydrology.

We developed the PECOSIM model (PEatland ECOhydrology and streamflow SIMulator) to quantify the impact of three ecohydrological feedbacks on streamflow and water storage: (1) the transmissivity feedback (2) elastic storage and (3) water table depth (WTD) – evapotranspiration feedback. Validation with seven years of hourly observations from Degerö Stormyr, an oligotrophic fen in northern Sweden, confirms strong model performance for growing season WTD and streamflow (Kling Gupta Model Efficiency: 0.88 and 0.87).

Using PECOSIM we show the synergy of all ecohydrological feedbacks quadruples growing season streamflow (66 mm vs 16 mm without feedbacks) and maintains a shallower, more stable WTD (0.13 m vs 0.55 m). Without feedbacks, ‘active’ streamflow generating storage during the growing season was absent (0 mm), whereas the feedbacks together provide 63 mm streamflow generating storage. The three feedbacks additionally sustain streamflow and storage regimes under water stress, boosting drought resilience of natural peatlands and their surrounding landscape.

This study provides scientific support for the crucial role of ecohydrological feedbacks in natural peatlands and highlights their function as nature-based solution by increasing water storage and baseflow. Degradation of natural peatlands will diminish feedback efficiency, and compromise peatland ecosystem services vital for sustainable water management.

1. Introduction

Hydrological processes are a key control on ecosystem functioning of peatlands (Waddington et al., 2015). Hydrology is tightly linked to biogeochemistry, accumulation and decomposition of organic matter, greenhouse gas exchange, energy balance partitioning, and vegetation composition (Kwon et al., 2022; Limpens et al., 2008; Moore et al., 2002). Natural peatlands, to which we refer as peatlands that have not been drained or otherwise altered significantly by anthropogenic intervention, provide numerous ecosystem services, including storing ~33 % of global terrestrial carbon, biodiversity, and water quality regulation (Martin-Ortega et al., 2014; Ratcliffe et al., 2021). Peatlands are generally recognized for their water storage and flow regulation services. More and more efforts are therefore put into restoring peatlands as “nature-based solutions” to increase water storage at the landscape scale in climate-resilient landscapes. Flow regulation is expressed by increased baseflow and reduced peakflow. Increased baseflow may prevent drought impact on the surrounding landscape during dry spells, while reduced peakflow can reduce flooding risk.

The body of empirical research on the hydrology of natural peatlands and their interaction with their surrounding landscape is growing (Bay, 1969; Branfireun & Roulet, 1998; Goodbrand et al., 2019; Karimi et al., 2023; Kværner & Kløve, 2008; Levison et al., 2014) and generally seems to support the view that natural peatlands may be an important

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freshwater resource during dry spells. However, critical examination of the empirical work shows inconsistent results (Acreman & Holden, 2013; Åhlén et al., 2022; Kharanzhevskaya & Sinyutkina, 2017). This is partly due to the large variability of peatland types. But more importantly, within the same peatland type, local geohydrology, climate, and landscape configuration are important controls on the hydrological behaviour of peatlands. Thus, observed differences between peatland catchments may originate either from catchment dissimilarities or differences in ecohydrological processes and peatland properties. As a consequence, it remains difficult to predict how ecohydrological processes in peatlands affect water storage, flow stabilization and other peatland ecosystem services related to their hydrology. Inconclusiveness about the hydrological role of peatlands means that the scientific basis is thin for generalized claims about the benefits of natural peatlands with respect to regulating water flows, and much less so, the restoration of peatlands. This thin scientific basis hinders setting priorities in land- and water management, and understanding how peatland restoration may impact regional hydrology and vice versa.

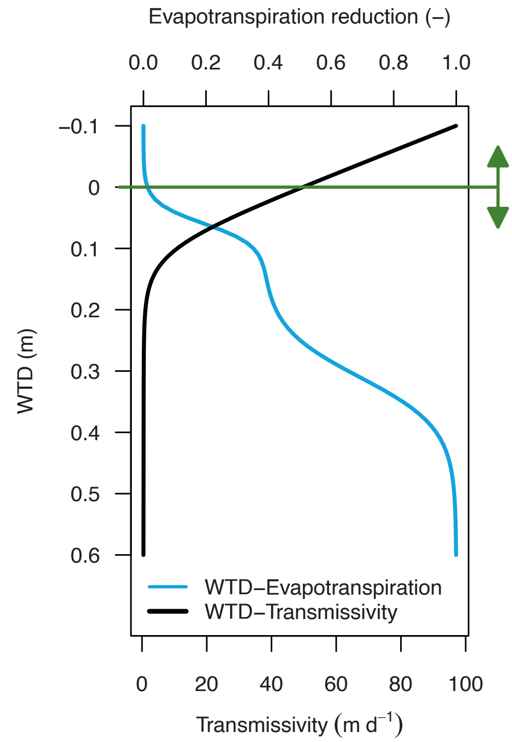
Part of the difficulty in conclusively predicting the hydrological role of natural peatlands is that they contain numerous ecohydrological feedbacks (Waddington et al., 2015). These feedbacks may stabilize and increase peatland water storage, which will then be slowly released to the surrounding landscape during drought as streamflow or infiltration to the subsoil (Box 1). In dynamic systems with feedbacks, resilience is an emergent characteristic: system structure and function is maintained when exposed to a stressor or perturbation (Holling, 1973; Newton & Spence, 2023). Due to ecohydrological feedbacks, peatlands exhibit resilience to e.g. changes in climate and land use (Page & Baird, 2016; van der Velde et al., 2021; Waddington et al., 2015), and may thus sustain their internal functioning and water storage and streamflow regulation services when put under hydroclimatic pressure. It is this relative impact of ecohydrological feedbacks on the water cycle of peatlands and their surroundings in the face of hydroclimatic pressures that remains to be more clearly defined.

Hydrological modelling is a powerful tool to overcome the aforementioned limitations of empirical studies to better understand the impact of peatland processes on the water cycle. With the use of models, climate, landscape configuration, and geohydrological setting can be controlled for, so that effects of individual feedbacks on the water cycle can be extracted in different hydroclimatic conditions.

Here, we aim to strengthen the scientific basis of peatland hydrology by quantitatively isolating the impact of ecohydrological feedbacks (Box 1) on peatland water storage and streamflow, and thus the contribution of natural peatlands to hydrological resilience in landscapes. Specifically, we developed the novel model PECOSIM (PEatland ECOhydrology and Streamflow SIMulator) to quantify the relative impact of three key ecohydrological feedbacks during the growing season: (1) reduced lateral groundwater flows as groundwater levels fall (2) elastic storage owing to the high compressibility of peat and (3) reduced evapotranspiration as groundwater levels fall (Box 1). While one or a combination of feedbacks has been incorporated in many peatland hydrology models (e.g. Baird et al., 2012; Bechtold et al., 2019; Eppinga et al., 2009; Frolking et al., 2010; Granberg et al., 1999; Kennedy & Price, 2004; Mahdiyasa et al., 2022; Nijp et al., 2017b; St-Hilaire et al., 2010; Yurova et al., 2007), to the authors' knowledge no model yet exists that includes all three feedbacks at operational timescales (hourly-weekly).

The model was validated using seven years of hourly data on streamflow, water table depth (WTD), and evapotranspiration from Degerö Stormyr, a natural mixed mire complex in northern Sweden. We hypothesise that both water storage and streamflow regulation services are improved with more ecohydrological feedbacks included, and that these feedbacks increase hydrological resilience to environmental change.

Box 1
Three ecohydrological feedbacks and the peatland water cycle.



Numerous ecohydrological feedbacks in natural peatlands can stabilize the internal water cycle of peatlands and their interaction with the environment (Waddington et al., 2015). In this research we focus on three feedbacks. The first feedback, the **WTD-transmissivity feedback**, includes three processes. With deeper water table (WTD) the hydraulic gradient and aquifer thickness are decreased, which reduce (1) the transmissivity and (2) groundwater discharge. These two negative feedbacks are, however, not unique to peatlands. Natural peatlands typically exhibit a strong increase of saturated hydraulic conductivity (K_s) from the peat base to the surface of 5–6 orders of magnitude, with K_s of 100–1000 m/d for the living *Sphagnum* layer in the topsoil to smaller than 0.001 m/d for decomposed, compacted peat (Ivanov, 1981; Nijp et al., 2017a; Päivänen, 1973). This decline originates from the increased degree of decomposition with depth. Due to this feedback, lateral drainage is expected to diminish with deeper WTD. This implies that water may be conserved during drought.

The second feedback is **elastic storage**. Peat has the capacity to swell upon wetting and compress during drying (Price, 2003). As a consequence the peat surface moves synchronously along with WTD fluctuations and buffers drought impact on vegetation (Nijp et al., 2017b). The elastic peat matrix also enhances water storage (Price & Schlotzhauer, 1999), which may be released as streamflow or infiltration to the surrounding landscape. This is particularly important for sustaining baseflow during dry spells.

The third feedback is the **WTD-evapotranspiration feedback**. Natural peatlands with shallow WTD typically are dominated by bryophytes (Bubier et al., 2006; Laine et al., 2012). Bryophytes lack vascular tissue and stomata, and are therefore unable to actively regulate water supply but rely on passive capillary water supply instead (Clymo, 1973; McCarter & Price, 2014; Nijp et al., 2014). As a consequence, evapotranspiration becomes limited by water availability at deep water tables (Kettridge & Waddington, 2014; Lafleur et al., 2005). This results in conservation of water and reduces water loss through evapotranspiration, and should leave more water for streamflow.

2. Material and methods

2.1. Overall approach and model philosophy

A new simulation model was developed to conceptualize ecohydrological processes in peatlands: PECOSIM (PEatland ECOhydrology and streamflow SIMulator). The aim was to simulate, at sub-daily timescales, internal water storage dynamics (water table depth, WTD) as well as interaction with the surrounding landscape through streamflow leaving the peatland catchment and an external water flux. Rather than aiming to fully capture the (spatial) complexity within peatlands we follow the concept of parsimony and keep the model as simple as possible to focus on the effect of feedbacks and minimize the number of required parameters to (a) allow for application under data-sparse conditions and (b) minimize equifinality issues (Beven, 2006). We therefore took a lumped yet physically based model approach, where parameters and feedback strength could be constrained with measurable quantities in the field. Model meteorological forcing, parameterization, calibration-, and validation data was based on 7 years of hourly observations of a northern peatland catchment (see Section 2.2). Required model forcings are air temperature, precipitation, and potential evapotranspiration. PECOSIM was developed in R software (version 4.2.2) and uses a modular structure in which processes can be switched on and off to isolate impacts of specific processes. The model is designed to allow for easy extension of additional feedback processes. Any time resolution can be used; here, we use hourly resolution.

The model is well-suited for application in various peatland types with mild slopes ($\lesssim$ 0.005 m/m), covering landscape settings from both bogs and fens. A snow- and soil-frost routine allows for application in both temperate and boreal climates, although the focus of process representation lies on the growing-season. In the following sections we first describe the site and data that were used for model validation. This is followed by a description of the model with all feedbacks activated (Table 1; hereafter referred to as 'full model') and how the impact of feedbacks is assessed. We focus on the main and novel aspects of the model structure. See Appendix A for a full model description.

2.2. Site description and data

Data for model calibration and validation were collected from the Degerö Stormyr catchment, a minerogenic and oligotrophic mixed mire complex in northern Sweden (64°N19°E), about 55 km inland from Umeå and 270 m.a.s.l. The catchment is 2.7 km^2 with 70 % peat cover and 30 % forest on predominantly mineral podzolic soils with higher topographic position. Water infiltrates in the upland forests in the SW-W and NE part of the catchment, and leaves the catchment at the Vargstugbäcken stream (Noumonvi et al., 2023). The peatland was formed in a local landscape depression shaped by (post-)glacial history through infilling and subsequent paludification of its surroundings (Peng et al., 2024). The mean peat thickness is 2.4 m, though locally may reach up to 8 m (Nijp, 2021; Nilsson et al., 2008; Peng et al., 2024). The peat deposits are underlain by impermeable gneissic bedrock belonging to the Svecokarelian orogeny (2.9–1.9 Ma), or highly resistant Quaternary glacial till. The climate is classified as boreal (Peel et al., 2007).

Hourly time series for the period 2014 – 2020 of streamflow, water table depth (WTD), meteorology, and soil temperature were provided through the ICOS (Andersson et al., 2021) and SITES (Svartberget Field Research Station (2020)) data portals. We refer to Andersson et al. (2021) for details on instrumentation. All data except streamflow were collected at the mire centre. The vegetation in the footprint is dominated by lawn and hollow microforms (76 % of the footprint area), with bryophytes of the genus *Sphagnum* (*S. majus*, *S. balticum*, *S. lindbergii*) that generally cover >50 % of the area. Vascular plant cover consists mainly of *Eriophorum vaginatum*, *Trichophorum cespitosum, Scheuchzeria palustris, Andromeda polifolia* and *Vaccinium oxycoccus* (Noumonvi et al., 2023).

Potential evapotranspiration was calculated following ASCE-EWRI (2005) guidelines at hourly timescale using measured net radiation, air temperature, relative humidity and wind speed. Actual evapotranspiration was calculated from the measured latent heat flux. Missing precipitation data were filled with data from a nearby station about 1 km away.

The median WTD of four groundwater wells within the footprint in different microforms was used to represent the spatially averaged WTD and water storage dynamics of the mire. During the growing season period free from soil frost (21 May – 30 September; day of year (DOY) 141 – 273), the spatially averaged WTD did not reach above the peat surface, indicating a minor role for overland flow in this period (5 %, 50 % and 95 % quantiles are 0.19 m, 0.11 m, and 0.02 m below the peat surface). See Appendix B1 for more information on WTD observations.

Streamflow provided by SITES (Svartberget Field Research Station, 2020) was measured at hourly frequency at the catchment outlet using a covered and heated trapezoidal flume. The flume stage-discharge rating curve was calibrated across a wide range of flow conditions. The flume was not overtopped at maximum flow records. On an annual basis, streamflow constitutes 55 % of total water output, with a range of 48 – 63 % representing the 5th and 95th percentiles across years. This reduces to just 28 % (10 – 40 %) during the frost-free growing season period. Evapotranspiration hence represents the major water loss during the growing season.

2.3. Model description

The flow domain is represented by a peatland catchment located upstream of open water (Fig. 1). For this catchment setting, we set up the water balance with the following components:

$$\frac{dS}{dt} = \mu_{tot}\frac{dH}{dt} = q_{rain} + q_{melt} - q_{gw} - q_{over} + q_{ext} - AET \tag{1}$$

where S = groundwater storage [mm], t is time [d], H is hydraulic head [m, relative to absolute datum, e.g. peat bottom], μ_{tot} is the total storativity [m^3/m^3], q_{rain} is effective precipitation [mm/d], q_{melt} is snowmelt, q_{ext} is an external in/efflux to represent e.g. upland forest or inflow of groundwater (seepage), AET = actual evapotranspiration (including sublimation), q_{gw} = groundwater discharge, and q_{over} = saturation excess overland flow. q_{rain} represents precipitation received by the ground surface after subtracting interception evaporation. Interception was included as a time-invariant fraction (f_i) of total precipitation.

Water leaves the catchment through groundwater discharge, saturation excess overland flow, evapotranspiration and sublimation. Satu-

Table 1
Overview of model implementation of three ecohydrological feedbacks and defining the reference model without feedbacks.

Feedback	Symbol	Description and approach
Transmissivity feedback	T	Reduced transmissivity with deeper groundwater table due to the strong decline of hydraulic conductivity with depth.
Peat volume change	P	Increased storage and stability of WTD due to elastic peat matrix.
Evapotranspiration – WTD feedback	E	Reduced actual evapotranspiration at deeper groundwater table.
None	Reference	This is the model variant without feedbacks. Hydraulic conductivity is homogeneous throughout the whole peat profile. No elastic storage: specific storage = 0 m^{-1}. No effect of WTD on actual evapotranspiration: f_{WTD} = 1.

rated groundwater flow was modelled using Darcy's law. The generally flat topography of peatlands (with the exception of e.g. strongly sloping blanket bogs, for which PECOSIM is less suitable) makes it possible to make use of the Dupuit-Forchheimer assumption that vertical water flow is negligible as compared to lateral flow. This concept was used in numerous previous peatland studies (Ballard et al., 2011; Guertin et al., 1987; Ivanov, 1981; Yurova et al., 2007) and for a flow domain with parallel streams can be described as:

$$q_{gw} = T(H)\ \frac{dH}{dx}\ \frac{dy}{A} \tag{2}$$

where q_{gw} is the specific groundwater discharge [m/d], A is the catchment area [m^2], dH/dx is the average gradient in hydraulic head between peat and stream [–], dy is the width of the peat aquifer [m] and $T(H)$ is the head-dependent transmissivity (m^2/d) (see Section 2.3.3 for more information). Eq. (2), however, is an idealisation of reality and assumes a rectangular catchment between two parallel streams. In reality, the catchment shape is complex and flow may converge into a stream at a single outlet. To represent such deviations we introduced a catchment geometry factor c_{geo}:

$$q_{gw} = \frac{c_{geo}}{A}\ T(H)\ dH \tag{3}$$

At the catchment boundary either a no-flow or prescribed time-invariant external flux (q_{ext}) can be provided. If the WTD exceeded a fixed ponding depth (D_P, m above peat surface), saturation excess overland flow was simulated. The ponding depth value was obtained through calibration (See Section 2.4). Given the high saturated hydraulic conductivity (>100 m/d) of the topsoil in natural peatlands (e.g. Nijp et al. (2017a)), we excluded infiltration excess overland flow.

Streamflow was calculated as the sum of overland flow (both over-ice and over-land) and groundwater discharge. This streamflow was delayed and redistributed in time to account for flow routing and storage components in both the groundwater and overland flow domain. Such delay could occur due to overland flow routing and resistance, and spatial variability of subsoil properties (hydraulic conductivity, porosity), which could store and delay groundwater supply to the stream (e.g. accumulation of water upstream of hummocks, which generally have lower hydraulic conductivity and delayed release). The delay was accommodated for by convolving streamflow with a symmetric triangular weight function (See Appendix A4 for details), similar to the broadly applied rainfall-runoff HBV model (Bergström, 1992). The delay does not depend on antecedent water storage, and we recognize there are more process-based alternatives to account for delay (e.g. Manning equation). However, with only one additional parameter δ [days] that describes the delay time, this is a parsimonious approach to account for a delayed response in both the groundwater- and overland flow domains.

2.3.1. *Feedback 1: Elastic storage*

In natural peatlands the peat matrix is elastic, so that the peat matrix can expand and contract upon wetting and drying, and provides extra storage (Box 1). Changes in peat volume are manifested through several processes, including primary compression, secondary consolidation, shrinkage, decomposition, and accumulation and release of entrapped gas (Price, 2003; Schothorst, 1977). We are aware detailed models exist to accommodate multiple of such processes (e.g. Kennedy & Price, 2004), but here too we choose parameter parsimony. Compression and expansion of the saturated peat matrix accounts for about 90 % of total peat volume change (Kennedy & Price, 2005), and is the dominant process in natural peatlands. We therefore focus on primary consolidation and adopt the approach by Nijp et al. (2017b), where the total storage coefficient of the unconfined peat aquifer is calculated as the sum of specific yield (S_y) and elastic storativity S_e:

$$\mu_{tot} = S_y + S_e = S_y + S_s\ b \tag{4}$$

where S_s [m^{-1}] is the specific storage and b [m] the aquifer thickness. S_s was set at 0.094 m^{-1} based on observations of Nijp et al. (2017b) for the same peatland and values reported by Schlotzhauer and Price (1999). Peat thickness is included as a state variable and WTD [m below peat surface, positive downward] was calculated as the difference between the hydraulic head and the position of the peat surface. S_y often varies with depth, especially in peatlands (Bourgault et al., 2017; Waddington et al., 2015). To ensure a parsimonious model structure and reduce the risk of equifinality, however, S_y was assumed constant with depth. Specific yield was calibrated based on realistic bounds from literature and peat thickness was based on measured site-averaged peat thickness (see Section 2.4 and Appendix B).

2.3.2. *Feedback 2: Transmissivity*

In the PECOSIM model, the transmissivity feedback (Box 1) is

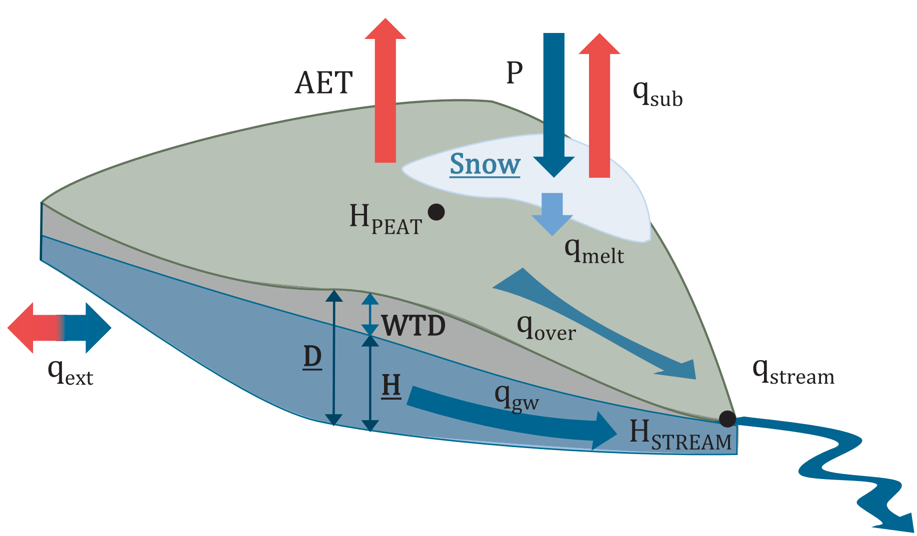


Fig. 1. Schematic overview of the model domain with water fluxes, and state variables (bold and underlined). State variables: H = hydraulic head, relative to peat-mineral soil interface, D = peat thickness, Snow = snow water equivalents, WTD = water table depth (D-H). H_{PEAT} and H_{STREAM} are hydraulic heads in peat and stream and control the gradient. P = precipitation, AET = actual evapotranspiration, q_{sub} = sublimation, q_{gw} = lateral groundwater, q_{melt} = snowmelt, q_{over} = saturation excess overland flow, q_{stream} = streamflow = q_{gw} + $q_{overland}$ + q_{melt}. q_{ext} is an external flux that can represent lateral and/or vertical in/outflow at the boundary of the model domain.

described by the integration of a vertical hydraulic conductivity (K_s; m d^{-1}) profile that can take different functional forms. Here, we used a generalized logistic function to describe hydraulic conductivity as a function of depth relative to the peat surface (z):

$$K(z) = K_{min} + \frac{K_{max} - K_{min}}{1 + e^{-T_b\ (z - WTD_{th})}} \tag{5}$$

where K_{min} and K_{max} represent respectively the minimum and maximum saturated hydraulic conductivity [m/d], WTD_{th} is the depth beneath the peat surface at which the change of conductivity is steepest [m], and T_b the rate of this change [m^{-1}]. The parameters K_{min} and K_{max} are based on local slug test measurements as described in Nijp et al. (2019) (See Supporting Information A3 for more information). Specifically, this function can capture an exponentially declining conductivity profile or follow the acrotelm-catotelm concept, with a maximum relatively homogeneous conductivity in the acrotelm (fibric peat), followed by a steep decline to the more impermeable catotelm. A time-varying water transport capacity as a function of WTD was obtained by integration of Eq. (5) over the saturated peat profile (See Supporting Information A3 for derivation).

2.3.3. Feedback 3: Evapotranspiration – WTD feedback

Actual evapotranspiration (AET) was estimated from potential evapotranspiration (PET) by accounting for vegetation phenology and water deficit using the two reduction functions $f_{gs}(DOY)$ and $f_{WTD}(WTD)$, respectively:

$$AET = f_{gs}(DOY) \cdot f_{WTD}(WTD) \cdot PET \tag{6}$$

Potential evapotranspiration from reference grass (PET; mm/d) was calculated at hourly resolution following ASCE-EWRI (2005). The factor f_{gs} (dimensionless) is a piecewise linear empirical relationship between the ratio of AET/PET and day of year (DOY) that accounts for vegetation physiology (greening-up and senescence). To remove confounding effects of limited moisture availability and too cold conditions to allow for plant activity, we filtered the selected time periods for the derivation of f_{gs} for well-watered conditions (WTD $>$ 0.15 m) and $T_{air} > 5$ °C. A comparison shows that the relation between f_{gs} and DOY was stronger than with growing degree days (See Appendix A1).

$$f_{gs} = \begin{cases} cf_{\min} & if \quad DOY < DOY_1 \\ cf_{\min} + c_1(DOY - DOY_1) & if \quad DOY_1 \leqslant DOY < DOY_2 \\ cf_{\min} + c_2(DOY - DOY_2) & if \quad DOY_2 \leqslant DOY < DOY_3 \\ cf_{\min} + c_3(DOY - DOY_3) & if \quad DOY_3 \leqslant DOY < DOY_4 \\ cf_{\min} & if \quad DOY \geqslant DOY_4 \end{cases} \tag{7}$$

The function f_{WTD} describes the evapotranspiration–WTD feedback and reduces potential evapotranspiration due to water deficit at deep water tables (dimensionless; values 0–1). We recognize that WTD is an indirect predictor for topsoil water content and that the relationship with water content breaks apart at deep WTD (Bartholomeus et al., 2008; Nijp et al., 2017b). This will reduce the correlation between WTD and AET, and may partly explain the limited experimental evidence for the WTD-ET feedback remains elusive (e.g. Moore et al. (2013) and Peichl et al. (2013), but see Lafleur et al. (2005)). From the perspective of parameterization in remote areas, we nevertheless regard WTD as a suitable estimator for degree of wetness. f_{WTD} was calculated during daytime and the mid-growing season only to exclude phenology effects on AET. Only days with negligible rain in the previous 48 h ($<$ 0.5 mm) were selected, as rain may replenish topsoil water content and potentially increase AET at deep WTD, but not necessarily becomes expressed as increased WTD (Nijp et al., 2014; Strack & Price, 2009). A double generalized logistic function appeared to describe the relation between observed hourly WTD and reduction of AET most parsimoniously (Eq. (8); Fig. 2, Appendix A1). The explained variance is moderate (R^2 = 0.39) and the mechanism behind the response is unknown and requires further research. Nevertheless, a plausible explanation is that AET losses originate from two sources: first the evaporation of *Sphagnum* lawn and hollow species becomes restricted at shallow WTD (>-0.10 m), after which vascular plant transpiration or hummock evaporation becomes reduced at deeper WTD ($>$-0.25 m). In Eq. (6), WTD_1 and WTD_2 [m] correspond to the water table depths of the two inflection points, k_1 and k_2 are the rates, and m_f would be the potential fraction of hollow *Sphagna*.

$$f_{WTD} = 1 - m_f \frac{1}{1 + e^{k_1\ (WTD - WTD_1)}} - (1 - m_f) \frac{1}{1 + e^{k_2\ (WTD - WTD_2)}} \tag{8}$$

The simulated AET using Eq. (7) and Eq. (8) corresponded well with observed hourly evapotranspiration (KGE = 0.88), confirming their adequacy.

2.3.4. Winter processes

PECOSIM primarily focusses on the growing season, but also includes simplified representations of winter processes to keep the model parsimonious. A degree-day based snow module was included to simulate snow accumulation and snow melt, including refreezing and liquid water retention in the snow pack. The occurrence of frozen soil can impact peatland hydrology in several ways. First, a continuous frozen soil layer could inhibit infiltration of melting water into the peat matrix. This induces overland flow during spring freshet and reduces groundwater recharge.

Second, frozen soil does not contribute to groundwater flow. This is especially important in (natural) peatlands, where the highly conductive topsoil may become frozen and groundwater supply to streamflow may reduce considerably. Frost- and thaw depth were simulated using a quasi-steady state approach (Romanov, 1968). Accounting for soil frost inhibiting infiltration did not improve model performance (Appendix A2.4). This may suggest that melting water could redistribute laterally and infiltrate to the groundwater via preferential flow paths. Melting water was therefore allowed to infiltrate to groundwater even if soil frost was present.

Water loss through sublimation can be considerable (e.g. Liston and Sturm (2004)), which was included to equal potential evapotranspiration corrected for the f_{gs} function (i.e. 0.4 × PET) if snow cover was present. Since sublimation is a relatively unknown process; with lack of data for calibration and validation, we assumed sublimation to be equal to potential evapotranspiration. At a given point in time, either evapotranspiration or sublimation can take place. See Appendix A2 for details on modelled winter processes.

2.4. Model calibration and validation

Model performance was assessed using a split-sample approach, where the calibration and validation sets were divided based on drought severity rather than consecutive years. This design enables both sets to encompass a broad range of hydrological conditions. Moreover, it avoids bias in validation performance caused by parameters being optimized under predominantly wet or dry conditions. See Appendix C for more details on calibration and validation. The calibration and validation were performed on the model variant with all feedbacks active; no recalibration was performed applied to the alternative model variants excluding feedbacks.

The free parameters (see Appendix B) were calibrated using a weighted multi-criteria objective function. This allowed for simultaneous optimization of streamflow and WTD, which were both considered equally important. Moreover, it better constrains the parameter space and reduces the risk of equifinality. As high- and low flows are of equal interest, we log-transformed streamflow. Although we focus on the growing season, also annual dynamics should be reasonably captured. We therefore assigned extra weight to the model performance during the growing season in the resultant weighted objective function φ:

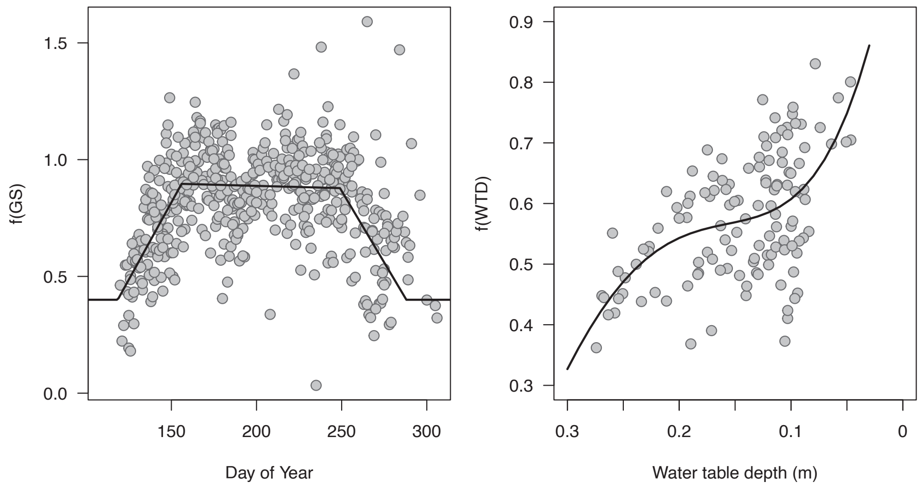


Fig. 2. Functions to account for phenology (left) and water table depth (right) effects to estimate actual evapotranspiration from potential evapotranspiration. The lines represent respectively Eq. (7) and Eq. (8).

$$\varphi = 0.35\ (NRMSE_{q,log,gs} + NRMSE_{WTD,gs})\ +\ 0.15\ (NRMSE_{q,log} + NRMSE_{WTD}) \tag{9}$$

Here, NRMSE represents the normalized root mean square error, where normalization was performed using the 5th and 95th percentiles of the observed values to account for outliers. The subscript gs denotes growing season. The objective function was evaluated on 60,000 parameter sets generated by Latin hypercube sampling. Parameter calibration ranges were based on field measurements and literature values (See Appendix B for details). To reduce the risk of equifinality we first calibrated the snow module and calibrated the remaining parameters afterwards.

In addition to φ, that summarizes model performance over multiple variables, we assessed performance of simulated WTD and streamflow individually using the Kling-Gupta Model Efficiency criterion (KGE; Gupta et al. (2009)). A KGE value of 1 indicates the simulations agree perfectly with observations, KGE = −0.41 corresponds to the mean WTD or streamflow as benchmark. To evaluate model performance focussing on either streamflow or WTD specifically, we also calibrated these individual components using KGE as objective function.

Model performance was additionally verified by checking the water balance error and comparing the total streamflow volume (V) between observed and simulated streamflow ($100\ \% \cdot (V_{obs} - V_{sim})/V_{obs}$). The total absolute water balance error was $< 10^{-10}$ mm, and volume error for simulated streamflow was 0.04 %.

For model application, we calibrated PECOSIM using the whole timeseries (2014–2020) to maximize use of information content in the limited observational data and establish more robust parameter estimates and model performance (Shen et al., 2022). Calibration over the complete time series ensures that parameters reflect a wide range of hydrological conditions. All results are based on the full-period parameter set with lowest φ unless stated otherwise.

2.5. Quantifying ecohydrological feedback impact on water storage and streamflow

To test the impact of ecohydrological feedbacks on streamflow and water storage, we set up models of all unique combinations of feedbacks activated or deactivated, resulting in eight model variants. This approach allowed for quantifying both individual and interactive effects of feedbacks. For example, the elastic storage feedbacks allows for continued evapotranspiration by reducing the depth to the water table. We refer to T as the transmissivity feedback, P for elastic storage due to peat volume change and E for the WTD-evapotranspiration feedback (See Table 1). The deactivation of feedbacks requires defining null model variants. Elastic storage was deactivated by setting specific storage S_s to 0 m^{-1}. In the transmissivity feedback, the transmissivity varies over time. In the null model, the transmissivity was fixed through time. We used the median growing season transmissivity of the model with all feedbacks activated to serve as time-invariant transmissivity in the null model. For the null WTD– evapotranspiration feedback, the function f(WTD) (Eq. (8) was set to the value 1. By doing so, transpiration and/or evaporation is not limited by WTD. We thus assumed that the peatmoss vegetation is replaced by vegetation that has unlimited water access (roots) and is not limited by oxygen availability either. Yet, vegetation phenology and canopy characteristics (‘crop’ factor function f_{gs}; Eq. (7) remain identical.

Feedback effects were quantified from the perspectives of both water storage and streamflow regulation services. All effects are calculated over the 2014–2020 simulation period, but only for the snow-free period after the snowmelt runoff peak has ceased (21 May – 30 September). We refer to this period as the growing season.

For functioning of peatland ecosystems, a shallow WTD is essential. The impact of feedbacks on WTD was quantified using quantiles, with the WTD_5, WTD_{50}, and WTD_{95} representing the shallowest, average, and deepest WTD, respectively. The seasonal amplitude of WTD was described with $WTD_{95} - WTD_5$. Feedback effects on streamflow were quantified for low flows (5th quantile; q_5), normal flow (50th quantile; q_{50}), and peak flows (95th quantile; q_{95}). Additionally, the buffering effect of elastic storativity on WTD is calculated as the difference between simulated WTD with elastic storage activated and WTD without peat deformation.

Also we investigated the effect of feedbacks on partitioning of water fluxes using the runoff coefficient (q/P), the evapotranspiration fraction of total water loss (EF; AET/(AET + q)), AET/PET, and growing season water balance components to understand feedback effects on the water cycle. Total water storage (S_{tot}; mm) was quantified as the median total extractable amount of water in the peat aquifer b during the growing season:

$$S_{tot}\ =\ b\ (S_y + S_s b) \tag{10}$$

Not all of this storage is active in the water cycle and of relevance for assessment of feedback impacts on water storage. We therefore quantified the amount of ‘active’ water storage that may contribute to streamflow, to which we refer as streamflow generating storage (S_{SG}; mm). S_{SG} was calculated as the water stored above the ‘active flow depth’ D_A (m) at which 99 % of the whole-profile transmissivity and hence streamflow generation occurs following Amvrosiadi et al. (2017), as the median growing season value:

$$S_{SG} = 1000(D_A - WTD_{med})(S_y + S_s\, b_{med}) \tag{11}$$

For all model variants, S_{SG} was based on the transmissivity profile with the transmissivity feedback activated. In this study active flow depth D_A corresponds to the upper 0.30 m. Larger S_{SG} values represent larger 'active' storage; negative values are set at 0 mm. Conceptually D_A is similar to the acrotelm, the principal site of matter and energy exchange sensu Ingram (1978).

2.6. Impact of ecohydrological feedbacks on hydrological resilience

Thus far, impact of ecohydrological feedbacks is quantified for a single catchment and climate. To broaden the implications for other landscape settings, we set up a model experiment to test the hypothesis that the ecohydrological feedbacks boost hydrological resilience under increasing water stress. Following Newton and Spence (2023), we define hydrological resilience as the maintenance of the current water storage and streamflow regime under increasing water stress as stressor (i.e. persistent pressure). The current streamflow and water storage regimes were characterized as the 10^{th} to 90^{th} quantile range during the growing season, which covers a broad range of current hydrological conditions including some more extreme events.

We conceptualize 'water stress' broadly as any long-term persistent impact, e.g. through drainage, groundwater abstraction for drinking water or industry, but also landscape position. In line with van der Velde et al. (2021), 'water stress' in the context of landscape position is represented as an additional time-invariant external flux (q_{ext} in Eq. (1) either in vertical or lateral direction. A positive external fluxes represents landscape settings with inflow of water, such as fens and riparian zones receiving upward groundwater seepage. Negative external fluxes represent landscapes with outflow of water, i.e. bogs with perched water tables and downward percolation losses to the subsurface. In a broader context, a negative external flux conceptualizes conditions with additional water loss and increased water stress.

We quantified median streamflow, water storage, and WTD during the growing season for a range of external fluxes ($-1.5 - 1$ mm/d) for the model variants with all feedbacks, one feedback, and no feedbacks included. All simulation settings remained identical as described in previous sections. Although the time-invariant external flux is a gross simplification of reality, this exploration provides insight in the impact of ecohydrological feedbacks on flow and storage regimes under different landscape settings.

3. Results

3.1. Model performance

Calibration of the newly developed model PECOSIM v1.0 and validation on an independent period demonstrate the model's ability to reproduce both observed streamflow and WTD. For the calibration set, the 'behavioural' model simulations (objective function $\varphi < 10$ %) have typical (median) φ values of 9.65 % but may be as low as 6.9 %, depending on the exact parameter set considered (See Appendix C1 for more information on model validation). For the validation set the typical and best performance are respectively 15 % and 11.6 %. Typical (median) KGE values of growing season streamflow and WTD in the validation set are 0.62 and 0.68, but may both reach up to 0.83 (Appendix C1). In our view, these results constitute an acceptable validation of the model. The results presented in the remainder of this section are based on the calibration using the full observational record.

The newly developed model PECOSIM v1.0 was well able to capture the dynamics of peatland water table depth and streamflow. General seasonal patterns and response to rain events are both also captured well. This is demonstrated by model performance statistics (Table 2) and visual confirmation of the simulated timeseries (Fig. 3). Growing season WTD could be estimated with an average error (RMSE) of 0.02 m and NRMSE of 9 %. The remaining discrepancy between measured and modelled WTD mainly originates from a too shallow modelled WTD during the 2018 drought. The RMSE of growing season streamflow is 0.53 mm/d (NRMSE = 8 %). The remaining mismatch primarily can be attributed to the underestimation of streamflow peaks arising of objective function φ focussing on log-transformed streamflow, as reflected by the lower KGE of q_{gs} (0.78) compared to $\log(q_{gs})$ (0.87) (Eq. (9); Fig. 3c).

When optimizing just for streamflow or groundwater table alone, model performance would be even better for the variable of interest (Table 2). A trade-off is present, where optimizing for water table depth results in reduced performance for simulating streamflow and vice versa, and objective function φ maximizes performance for both. Model performance for annual streamflow is worse (KGE $\log(q) = 0.75$) than for the growing season (KGE $\log(q_{gs}) = 0.87$).

3.2. Feedback impact on streamflow

With all feedbacks activated, the simulated median growing season streamflow was more than four times the streamflow of the variant without feedbacks (hereafter referred to as 'reference'; 16 mm compared to 66 mm; +313 %) (Fig. 4; Table 3). The model with all feedbacks activated leads to the largest baseflow and median flow of all feedback combinations. Including more feedbacks generally increased the proportion of rainfall converted into streamflow, as indicated by the larger runoff coefficient and lower contribution of evapotranspiration to total water loss (EF). Compared to the reference without feedbacks, elasticity and the WTD-ET feedback promote base flow and median flow, but peak flow remains similar. The elasticity feedback increases total growing season streamflow by 14 mm (88 %), while the WTD-ET feedback results in more than doubled streamflow (21 mm; +131 %). Nevertheless, the effects of these two feedbacks are not uniquely additive, as their combination results in a 24 mm (150 %) increase relative to the reference. When both these feedbacks are operational, the range between baseflow and peak flow is smaller, indicating streamflow is stabilized.

In contrast to our hypothesis, the transmissivity feedback reduces simulated baseflow, mean flow, and peak flows compared to the reference without feedbacks (Fig. 4). As indicated by baseflow (q_{10}) of 0 mm/d with only the transmissivity feedback activated, whether or not in combination with elasticity, it is even possible the stream dries up. This is caused by the high transmissivity that depletes the stored water at the onset of the growing season and leaves little storage buffer for the remainder. The median transmissivity during the growing season was 2.1 m^2d^{-1}, leading to a depth-averaged K_s of 0.92 m/d. The water transport capacity varied strongly over time, however, and decreased drastically during dry periods due to the transmissivity feedback (Fig. 5). Transmissivity and profile-averaged K_s varied throughout the growing season between 0.6 to 11.5 m^2d^{-1} and 0.26 and 4.79 m/d, representing the 5 % and 95 % quantile, respectively. Under dry conditions the transmissivity decreased by more than a factor of three relative to the mean growing season transmissivity.

3.3. Feedback impact on water storage and WTD

Relative to the reference model without feedbacks, the synergy of all three feedbacks drastically increased the total water storage and storage available for streamflow. Total water storage increased by more than a factor of three (from 262 to 819 mm; 217 %). The storage available for streamflow (S_{SG}) increased from 0 mm to 61 mm (Table 3). The S_{SG} of 0 mm is a result of the median growing season WTD that was 0.55 m in the reference model without feedbacks, which is deeper than the active flow depth of 0.30 m. Including all feedbacks prominently decreased the median growing season WTD by 77 % from 0.55 m to 0.13 m. The feedbacks stabilize the WTD within and between years, as demonstrated by the considerably narrower range between shallowest and deepest

Table 2
Overview of model performance under different objective functions (rows) considering only streamflow (q), log-transformed streamflow, and water table depth (WTD) for the whole year and the growing season (subscript gs), and performance for all other variables under each objective. For all objective functions the Kling-Gupta Model efficiency (KGE) values are presented, except for φ. φ is the weighted normalized root mean square error (NRMSE) objective function that considers both streamflow and WTD (Eq. (9). The bold values on the diagonal represent the objective function value for the objective, italic the model performance for the simulation used. The last two rows show best model performance among the 10 best parameter sets (i.e. lowest φ_{val}).

Objective	q	q_{gs}	log(q)	log(q_{gs})	WTD	WTD_{gs}	φ	RMSE q_{gs} (mm/d)	RMSE WTD_{gs} (m)
q	**0.76**	−0.4	0.46	0.40	−0.57	−0.35	37.2	1.25	0.16
q_{gs}	0.38	**0.78**	0.34	0.30	0.36	0.36	16.0	0.37	0.04
log(q)	0.59	0.63	**0.75**	0.78	0.55	0.55	15.2	0.49	0.05
log(q_{gs})	0.50	0.37	0.66	**0.87**	0.59	0.52	10.1	0.68	0.03
WTD	0.50	0.13	0.03	0.07	**0.87**	0.88	15.1	0.86	0.02
WTD_{gs}	0.50	0.13	0.03	0.07	0.87	**0.88**	15.1	0.86	0.02
φ	0.40	0.64	0.51	0.85	0.82	0.87	**10.3**	0.53	0.02

WTD. Moreover, the deepening of the WTD with the developing rainfall deficit during the growing season was averted (Fig. 4).

3.3.1. WTD – Evapotranspiration feedback

The WTD–evapotranspiration feedback reduced evaporative water loss in the growing season by 113 mm (24 %) as compared to the reference (Table 3). This reduction corresponds to nearly half of the growing season rainwater input and conserves more than 300,000 m^3 extra water within the studied peatland area (2,7 km^2). The extra water available is partly released as streamflow and also boosts water storage. The WTD–evapotranspiration feedback resulted in a shallower and more stable groundwater regime as compared to the reference (Fig. 4). All throughout the growing season it appears that limited capillary supply in the porous *Sphagnum* layer restricts water availability and evapotranspiration, as is shown by $f(WTD)$ having values in the range of 0.6–0.7 (Fig. 5). Especially during exceptionally dry periods, such as the droughts during 2018 and 2019, water availability constrains AET (Fig. 3; Fig. 5). As shown by the low standard deviation of total storage (Table 3), the WTD-ET feedback thereby also stabilizes water storage across years. Additionally, the WTD-ET feedback increased the storage available to generate streamflow (S_{SG} +24 mm).

3.3.2. Elasticity feedback

The extra storage provided by peat elasticity boosts mean growing season water storage by 560 mm (195 %) relative to the reference (Table 3). For the whole peatland catchment this translates to an additional water storage volume of more than 1,500,000 m^3. Elastic storage is important on an event basis, as it buffers WTD fluctuations and thereby prevents rapid overland flow. For example, for a 20 mm rain event, elastic storage reduces the rise in water table with 60 % (from 144 to 54 mm) as compared to a rigid matrix. All feedbacks together result in a simulated range of surface elevation fluctuations of 8 cm and thereby stabilize WTD (Fig. 5), which corresponds well with the observed range (Nijp et al., 2019).

Peat elasticity alone resulted in a 0.34 m shallower growing season WTD than the reference, but compared to when all feedbacks are active, the WTD is 0.05 m deeper and has a larger seasonal amplitude (Fig. 4). When combined with the WTD-evapotranspiration feedback, elastic storage results in the shallowest WTD of all feedback combinations (Fig. 4). The increased total water storage due to elastic storage strongly increased the streamflow generating storage (+61 mm).

3.3.3. Transmissivity feedback

Contrary to our hypothesis that the transmissivity feedback would reduce water losses and hence increase water storage in peatlands, it slightly reduced total water storage (–23 mm; −9%) as compared to the reference (Table 3). As described in Section 3.2, this is related to the high transmissivity and water loss at the onset of the growing season. In combination with other feedbacks, the transmissivity feedback increased water storage relative to the reference without feedbacks, but this effect originates from the other feedbacks (Table 3). Without other feedbacks, the transmissivity feedback resulted in a median WTD deeper than 0.5 m below the peat surface. Additionally, the seasonal WTD amplitude remains large and similar to the amplitude in the reference (Fig. 4).

3.4. Feedback impact on hydrological resilience

An imposed external water loss reduced streamflow and water storage, and increased WTD (Fig. 6). This effect, however, was mitigated across a wide range of 'water stress' when all feedbacks are operational. In landscape settings with an additional 'forced' water loss, i.e. more negative external flux, up to −0.5 mm/d (−180 mm/year), the current hydrological regime in terms of streamflow, water storage and WTD can be maintained with all feedbacks. Beyond this threshold especially the WTD and S_{SG}, but also streamflow, start to decline (Fig. 6c). The broader range of water stress under which the current regime can be sustained strongly suggests that the synergy of the three feedbacks increases hydrological resilience.

Without any of the feedbacks activated, the current regime cannot be sustained (Fig. 6). This finding underscores the importance of ecohydrological feedbacks in enhancing ecosystem resilience to long-term 'press' disturbance. With only the WTD-evapotranspiration feedback activated, the current WTD and streamflow regimes can be maintained in a broad range of water stress (external flux −0.5 – +0.25 mm/d), but S_{SG} is lower than the current regime (Fig. 6b). While the WTD-evapotranspiration maintains shallow WTD, it lacks the storage provided by the elasticity feedback. This suggests particularly the combination of the WTD-evapotranspiration and elasticity feedbacks seems important for hydrological resilience.

In landscape settings with additional inflow of water (positive external flux), such as fens or riparian zones, the current streamflow, WTD and storage regimes can be maintained if all ecohydrological feedbacks are active. With only the WTD-ET feedback active, the WTD continues to increase above the peat surface until the maximum ponding depth is reached (Fig. 6c) and thereby extends beyond the current regime. Importantly, the transmissivity feedback increases water loss at shallow WTD and thereby keeps the WTD within the current regime (Fig. 6c). Streamflow continues to increase linearly with increasing external flux (wetter landscape or climate setting) if all feedbacks are active, but does not surpass the current regime under increased water inputs (Fig. 6a).

4. Discussion

4.1. Ecohydrological feedbacks boost water storage and streamflow

In this study we aimed to fill the knowledge gap of how ecohydrological feedbacks in natural, undrained, (northern) peatlands impact water storage within these ecosystems and the streamflow regulation

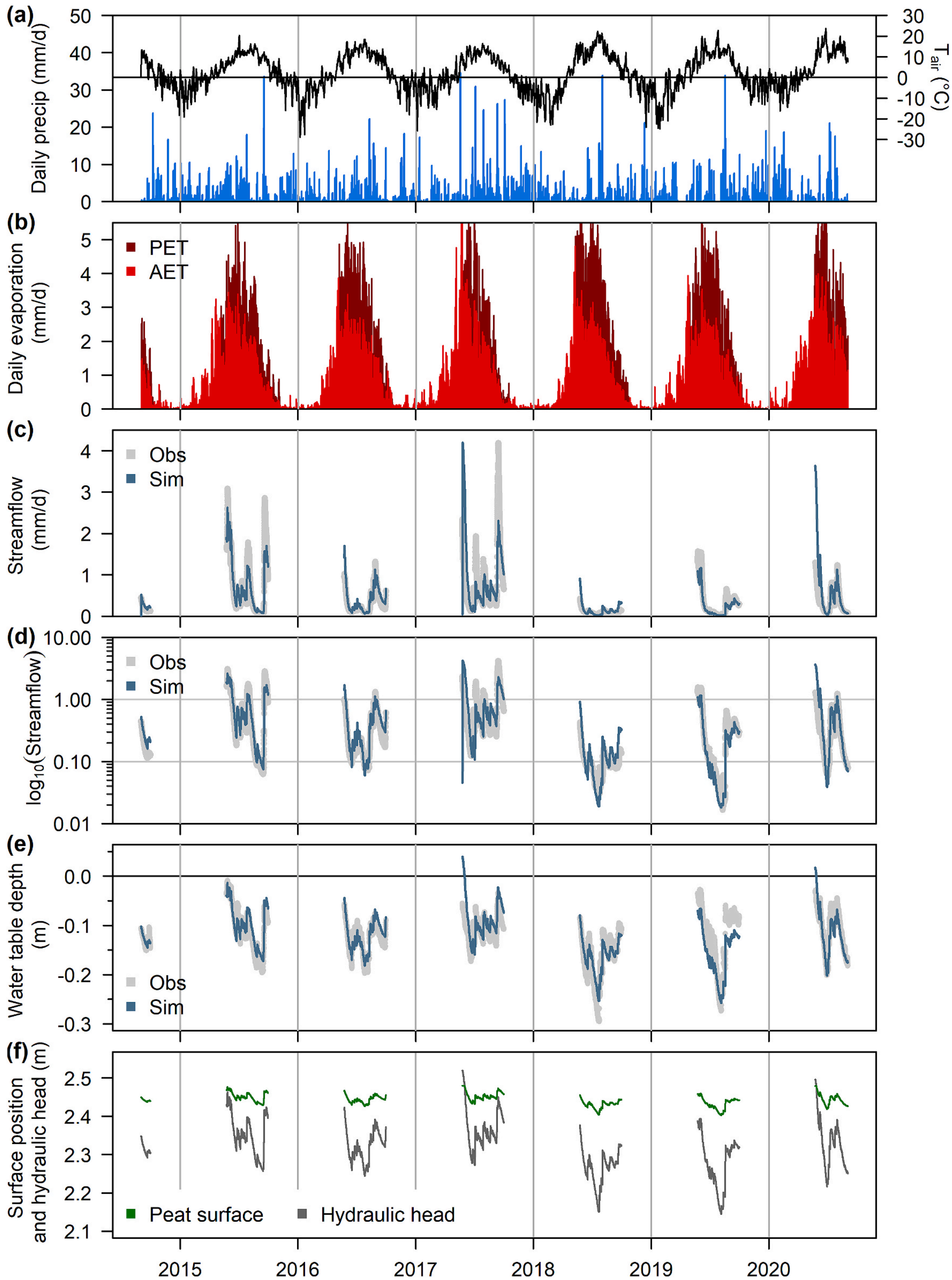


Fig. 3. Model forcing and simulations using the optimal parameter set for objective function φ. (a) observed daily precipitation sums (blue bars) and mean daily temperature (black line); (b) simulated daily potential and actual evapotranspiration; (c) observed and simulated hourly streamflow; (d) log-transformed streamflow (e), simulated water table depth and (f) simulated peat surface elevation and hydraulic head relative to bottom peat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

services they provide. These feedbacks include elastic storage, the transmissivity feedback, and reduced evapotranspiration at deep water tables (Box 1). Using the newly developed and validated PECOSIM model (**PE**atland **ECO**hydrology and **S**treamflow **SIM**ulator) we provide quantitative scientific support that these feedbacks increase growing season water storage and streamflow. As such, the feedbacks represent key mechanisms underlying the hydrological ecosystem services and resilience of natural peatlands. By enhancing process-based understanding our findings provide scientific support for natural peatlands as nature based solutions, addressing a critical knowledge gap for

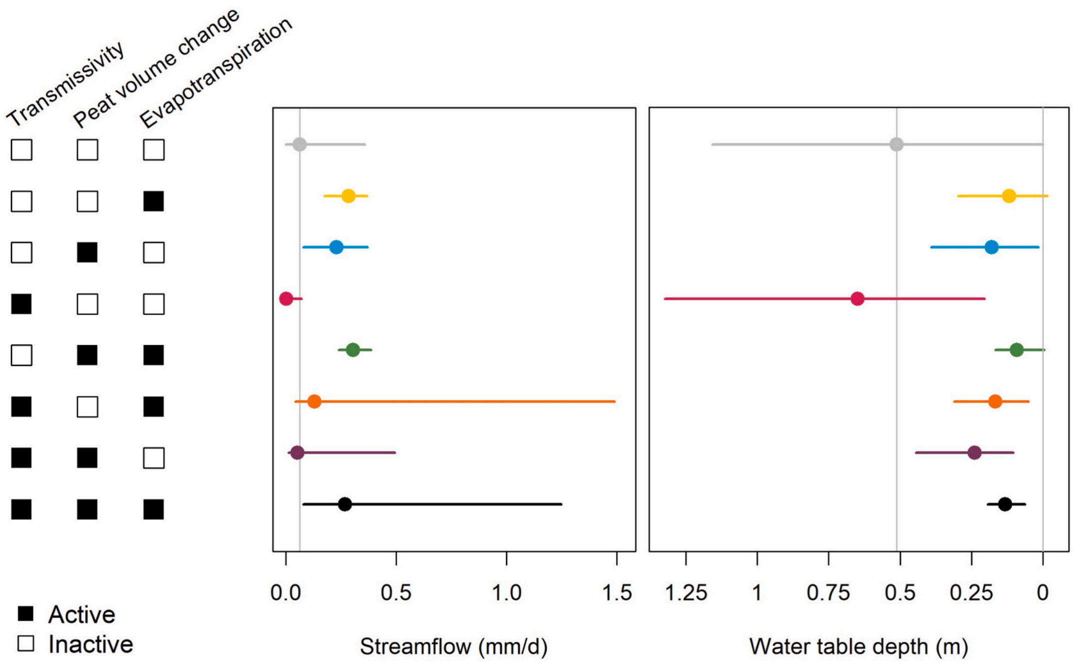


Fig. 4. Effect of feedbacks on specific discharge (left) and water table depth (right) during the frost-free growing season (21 May – 30 September; 2014–2020). The endpoints of the lines represent baseflow and peakflow (10% and 90% quantile; left) and the deepest and shallowest water table depth (10% and 90% quantile; right). Circles represent median streamflow (left) and median water table depth (right). The vertical grey line represents the median value of the reference without feedbacks.

Table 3
Effect of ecohydrological feedbacks on water balance components for the frost-free growing season (21 May – 30 September). Feedback T = transmissivity, P = peat volume change and E = WTD-evapotranspiration feedback. Water balance components (mean with standard deviation across years 2014–2020, in mm) comprise total precipitation (P), streamflow (q), potential reference evapotranspiration (PET), actual evapotranspiration (AET). q/P is the runoff coefficient, EF the fraction of AET in total water loss, AET/PET a measure of water availability constraints on evapotranspiration, with smaller values representing more drought stress. S_{tot} and S_{SG} are total water storage and streamflow generating storage (mm). Relative differences (Δ columns) are calculated as 100 % • (Feedback - 'None')/'None'. Mean growing season precipitation and potential evapotranspiration are 233 (51) and 361 (27) mm.

Feedback	q (mm)	Δq (%)	AET (mm)	ΔAET (%)	q/P	EF	AET/PET	S_{tot} (mm)	ΔS_{tot} (%)	S_{SG} (mm)
T-P-E	66 (36)	313	197 (9)	−36	0.28 (0.14)	0.75	0.54 (0.04)	819 (25)	213	61 (10)
T-P	30 (19)	88	309 (25)	0	0.13 (0.09)	0.91	0.86 (0.02)	728 (58)	178	14 (19)
T-E	65 (32)	306	165 (15)	−47	0.28 (0.10)	0.72	0.46 (0.06)	314 (5)	20	17 (5)
P-E	40 (8)	150	228 (16)	−26	0.18 (0.01)	0.85	0.63 (0.08)	851 (32)	225	77 (17)
P	30 (11)	88	309 (25)	0	0.13 (0.04)	0.91	0.86 (0.02)	776 (68)	196	39 (34)
E	37 (7)	131	196 (24)	−37	0.16 (0.01)	0.84	0.55 (0.09)	320 (7)	22	24 (8)
T	16 (15)	0	309 (25)	0	0.07 (0.07)	0.95	0.86 (0.02)	239 (37)	−9	0 (0)
None	16 (12)		309 (25)		0.06 (0.04)	0.95	0.86 (0.02)	262 (37)		0 (8)

understanding the role of peatlands in the regional water cycle.

The synergy of all three feedbacks together resulted in a more than fourfold increase of growing season streamflow (from 16 mm to 66 mm), a threefold increase of total water storage (from 262 mm to 819 mm) and reduced water loss by evapotranspiration by about 40 % (from 309 mm to 197 mm), relative to a reference without feedbacks. Similarly, the water table depth (WTD) is 80 % shallower and stabilized at optimal conditions for peatland plant communities (0.13 m compared to 0.55 m the below peat surface without the feedbacks) (Andrus et al., 1983; Rydin, 1986). The increased streamflow is reflected in larger baseflow, average flow, as well as peak flows. Compared to observed maximum flows during snow melt, which reach over 15 mm/d (99th percentile), the maximum observed growing season streamflow of 4.2 mm/d is not large. Hence, flood risk during the growing season is not a pressing issue in the boreal setting (Arheimer & Lindström, 2015), and any increase in growing season streamflow is of value for downstream ecosystems and water users.

It is generally accepted that the WTD – transmissivity feedback reduces lateral drainage at deep WTD and as such regulates WTD (Waddington et al., 2015). Indeed drainage reduced at deep WTD by more than threefold relative to mean growing season conditions. More importantly, however, our results signify the importance of the transmissivity feedback under wet conditions by releasing water surplus, especially at the onset of the growing season where transmissivity exceeds typical (median) growing season conditions by factor ten. As *Sphagnum* growth may be reduced at high water content due to limited CO_2 diffusion (Serk et al., 2021; Williams & Flanagan, 1996), the removal of excess water at shallow WTD may promote *Sphagnum* growth conditions.

The dominant water loss in Degerö Stormyr during the growing season was evapotranspiration (75 %; Table 3), which is typical for peatlands (Kellner & Halldin, 2002; Lafleur et al., 2005; Peichl et al., 2013). It is therefore no surprise that the WTD–evapotranspiration feedback is a dominant control on both WTD and streamflow, as it reduced AET by 112 mm (36 %) compared to the reference without feedbacks. Despite the uncertainty and extrapolation of the ET reduction

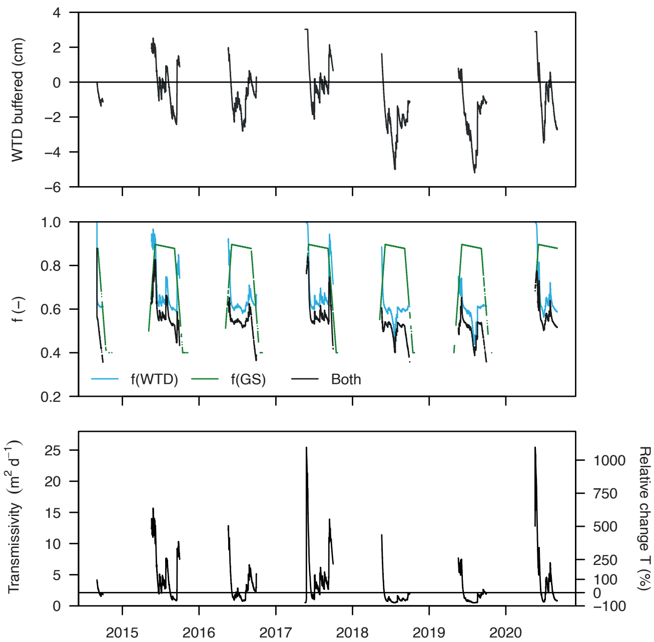


Fig. 5. Time series illustrating the effect of hydrological feedbacks. (a) Effect of the elasticity feedback by buffering WTD fluctuations, calculated as the difference between WTD in the model with all feedbacks and the model without elastic storage (T-E variant) (b) reduction factor f of evapotranspiration due to deep WTD(f(WTD)), phenology f(GS) and their combination during the growing season, and (c) variation of transmissivity over time (left axis) and relative change in transmissivity relative the median value (right axis). Simulations pertain to the model with all feedbacks activated (T-P-E).

function (Fig. 2b), the WTD at which evapotranspiration ceases (0.4–0.5 m) matches well with estimates for comparable *Sphagnum* dominated peatlands by e.g. Romanov (1968) and Kim and Verma (1996). Also a 'crop' coefficient of 0.73 under well-watered mid-growing season conditions is credible and representative for comparable peatlands under similar conditions (Isabelle et al., 2018; Kellner, 2001).

Future peatland evapotranspiration is projected to increase under optimal water supply due to higher vapor pressure deficit in the RCP4.5 and RCP8.5 scenarios (2091–2100) (Helbig et al., 2020b). Our results show that, under suboptimal water supply, evapotranspiration will be strongly reduced due to the WTD-ET feedback. Thereby the WTD-ET feedback will at least partly offset the projected increased peatland evapotranspiration. This feedback thus needs to be considered when assessing biophysical land–atmosphere feedbacks and climate mitigation potential (Helbig et al., 2020a).

The 'active flow depth', the upper portion of the peat profile contributing to water flow, defined following Amvrosiadi et al. (2017) as the depth above which 99 % of the total transmissivity occurs, was calculated at 0.30 m for the study site. This active flow depth of aligns well with (1) the deepest WTD of the ecological niche of lawn *Sphagna* (Andrus et al., 1983; Rydin, 1986) that dominates the vegetation in the studied peatland, (2) the deepest observed WTD (99 % percentile) at the study site, and (3) the WTD threshold for severe drought stress of a common lawn peatmoss species (*S. balticum*, Nijp et al., 2014). This alignment of active flow depth with the ecological niche underscores the strong coupling of water-vegetation feedbacks in northern peatlands.

In summary, the synergetic operation of the three feedbacks can be described as follows: Elastic storage increases water storage and reduces WTD fluctuations, while at deep WTD evapotranspiration is reduced due to the WTD-evapotranspiration feedback. Thereby also the ecosystem service of sustained baseflow during the growing season and water provisioning services to downstream ecosystems and other water users

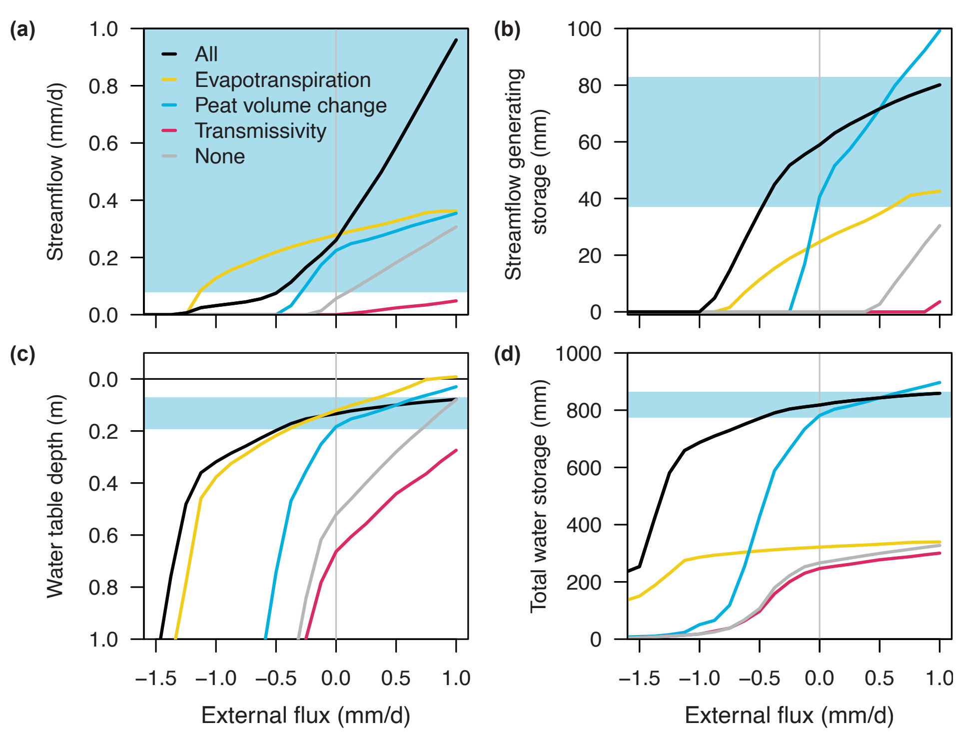


Fig. 6. Simulated effect of externally forced water stress on streamflow (a), streamflow generating storage S_{SG} (b) water table depth (c) and total water storage (d) during the growing season (medians of hydrological years 2014–2019), and how ecohydrological feedbacks control this relation. The time-invariant additional external water flux (x-axis) conceptualizes additional water stress in general and landscape position in particular. Negative values (to the left of the grey vertical line) represent additional water loss (e.g. drainage or bogs with perched water tables) Positive values indicate addition of water (e.g. fens or riparian zones with groundwater inflow). Blue areas show the current hydrological regimes as quantified by the 10–90 quantile range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

during drought is promoted. By contrast, at shallow WTD, the WTD-transmissivity feedback increases lateral drainage and prevents conditions too wet for *Sphagnum*.

The increases in streamflow and water storage created by the interactions of the ecohydrological feedbacks, characteristic of natural peatlands, are an important justification for seeing natural peatlands as nature-based solutions for landscape-level water management. However, generally not all of these fundamental ecohydrological feedbacks are not well-represented, if represented at all, in operational tools and hydrological models used to support decision making. Given the large impact of these interacting feedbacks on the water cycle in peatlands and their surrounding landscape, we stress the need to adequately represent peatland-specific processes and properties in hydrological models to improve their predictions. Given the strong coupling of hydrology and biogeochemical cycles in peatlands (Limpens et al., 2008; Waddington et al., 2015), it is essential that models simulating peatland carbon dynamics and greenhouse gas emissions also adequately incorporate these processes. Neglecting ecohydrological feedbacks poses a substantial risk of decision-making based on an inadequate, or even misleading, evidence base.

4.2. Ecohydrological feedbacks promote hydrological resilience

Our results demonstrate that the hydrological resilience of peatlands to 'water stress' strongly relies on the synergy of the three considered ecohydrological feedbacks. Here, we defined 'water stress' broadly as any long-term persistent impact, e.g. drainage, groundwater abstraction for drinking water or industry, but also landscape positions that can lead to inputs of water from different landscape elements such as forested hillslopes (such as fens), or outputs through infiltration (bogs) (Section 2.6). In line with van der Velde et al. (2021), the stress is conceptualized as a time-invariant additional external flux. This is of course a gross over-simplification and interpretation is speculative. Nevertheless this analysis provides useful insights as follows. When all feedbacks are active, the current streamflow, water storage, and WTD regimes are maintained under a broad range of 'water stress'. With only one feedback or none, peatlands can withstand much lower 'water stress' Without the processes characteristic of natural peatlands that promote water storage (i.e. the WTD-ET and elastic storativity feedbacks), small water stress moves the hydrological conditions outside the regime required for peatland functioning. The synergy of the three feedbacks thus boosts hydrological resilience and maintains peatlands in their current regime when water stress increases. This implies that, once established and with ecohydrological feedbacks at work, natural peatlands maintain their structure and function in landscapes or climatic settings that would otherwise be impossible without or with only one of the feedbacks, corroborating results of van der Velde et al. (2021). Future studies with actual scenarios may further detail the importance of feedbacks in a changing climate.

4.3. Implications for nature conservation and land & water management

By boosting both water storage and streamflow during the growing season, natural peatlands increase the value of hydrological ecosystem services in two ways (Seyam et al., 2003): (1) the increased water storage supports ecosystem functioning of the peatland, while (2) increased streamflow provides essential water resources for downstream ecosystems, agriculture, industry, and drinking water supply.

While ecohydrological feedbacks enhance peatlands resilience to hydroclimatic change, our results also signify that disrupting the efficacy of these feedbacks in natural peatlands will reduce the resilience of both peatlands and their downstream environment. Drainage of peatlands and/or their surroundings is one of the major disturbances that will reduce water storage and streamflow, as it will lead to the disappearance of ecohydrological feedbacks as follows. Deeper water tables promote the establishment of shrubs and trees with greater rooting depths and higher gross ecosystem productivity (Bubier et al., 2006; He et al., 2023; Korrensalo et al., 2018; Lieffers & Rothwell, 1987). As a consequence, transpiration continues during drought at deeper WTD. Drainage will also accelerate decomposition and lead to a denser peat matrix with smaller compressibility (Price et al., 2005). Thus drainage reduces both the specific yield and elastic storage capacity, weakening the elasticity feedback. The lower storage capacity results in a more variable WTD, water storage and streamflow. In addition, the increased decomposition of the topsoil will reduce its hydraulic conductivity (Boelter, 1969), diminishing the transmissivity feedback. Hence, to maintain the environmental benefits of ecohydrological feedbacks in natural peatlands and thereby promote climate-resilient landscapes, it is of vital importance to minimize disturbance of existing natural and restored peatlands. Besides drainage, the strength of hydrological feedbacks will depend on local site characteristics such as peat thickness (elastic storage and moisture content) (Moore et al., 2021), vegetation type (evaporative water loss) and subsurface hydraulic properties (transmissivity feedback; Waddington et al., 2015)).

Many ecohydrological feedbacks in natural peatlands are self-regulating processes. Once established after e.g. restoration, only minor management intervention is required. As such, preserving or re-establishing self-regulating processes in natural peatlands can be a cost-effective sustainable nature-based solution to establish robust climate-resilient landscapes.

4.4. Model limitations and future research directions

To our knowledge, the PECOSIM model is the first attempt to quantify the sensitivity of WTD and streamflow to (combinations of) different ecohydrological feedbacks. This is achieved with a parsimoniously parameterized modelling framework at timescales relevant for operational hydrological modelling and decision-making on land- and water management. PECOSIM combines, operationalizes and improves on existing hydrological modelling concepts tailored for peatlands (Bergström, 1992; Granberg et al., 1999; Nijp et al., 2017b; Waddington et al., 2015) in a modular approach where individual processes can be activated or disabled. The model effectively captures both the growing season dynamics of water storage, water table depth (WTD) and streamflow at hourly resolution, as demonstrated by the strong correspondence with seven years of hourly observations (Fig. 3). PECOSIM parameters were constrained by measurable parameters while remaining free parameters were calibrated using multiple objectives to reduce the risk of equifinality (Beven, 2006). Although equifinality cannot be completely ruled out, additional sensitivity tests and constraining parameters based on local measurements increased the confidence that the model is right for the right reason (Appendix E). Due to the multi-criteria objective function in model calibration, trade-offs needed to be made between WTD and streamflow simulations. When considering only streamflow or WTD, model performance for this specific objective is even better (Table 2), but increases the risk of equifinality.

PECOSIM captures the key ecohydrological feedbacks of northern peatlands. Model performance and process-based understanding could be further improved by including other feedbacks that affect streamflow regulation and water storage services (see Waddington et al. (2015) for an overview). These feedbacks operate at multiple timescales. Processes at shorter time scales (hours – seasonal) relevant for operational hydrological modelling include, for example, a decreasing specific yield with depth as a consequence of increased humification (Bourgault et al., 2017). At shallow WTD the relatively high specific yield reduces the impact of water loss on WTD, whereas at deep WTD it amplifies other WTD-regulated feedbacks (see e.g. Waddington et al. (2015)). Additionally, effects of peat volume change are currently only expressed in terms of water storage. Compression of the peat matrix can also reduce the hydraulic conductivity, although this effect seems more pronounced for disturbed peatlands or with large WTD fluctuations (Couwenberg et al., 2022; Price, 2003).

At longer timescales (interannual, decadal) dynamic interactions between water, vegetation, and peat physical properties will also come in play (Frolking et al., 2010). For example, a drier climate or drainage can promote establishment and growth of shrubs and trees, and increase water loss through transpiration (Bubier et al., 2006; Murphy et al., 2009). Drier soil conditions and oxygenation will further accelerate decomposition and reduce pore size. This will thereby reduce water storage capacity and hydraulic conductivity (Liu & Lennartz, 2019; Päivänen, 1973) and also impact streamflow. These feedbacks are less relevant for e.g. operational flood forecasting, but they are for climate change impact assessment and future-proof landscape management. The ecohydrological feedbacks mentioned above are examples of processes that are not yet included in the PECOSIM model. Depending on feedback direction, strength and landscape setting, these feedbacks may either promote or reduce peatland impact on water storage and streamflow.

The modular structure of PECOSIM allows for relatively easy extension with additional feedbacks to test their impact on the water cycle within peatlands and their surrounding landscape. Moreover, a sensitivity analysis can be performed to constrain the conditions and landscape settings where feedbacks enhance streamflow and/or water storage by altering key properties such as peat thickness, specific yield, hydraulic conductivity profiles, and evapotranspiration settings,.

Model application is currently limited to relatively flat, natural peatlands and assessment during the growing season. Potential extensions of PECOSIM include enabling application to disturbed and burned peatlands, coupling with the carbon cycle (St-Hilaire et al., 2010), more detailed inclusion of unsaturated zone processes (McCarter & Price, 2014; Nijp et al., 2017b), winter processes (Granberg et al., 1999), and dynamic interactions between water, vegetation and soil development (Frolking et al., 2010).

5. Conclusions

Ecohydrological feedbacks are often hypothesized to promote water storage in natural peatlands and increase baseflow leaving peatland headwater catchments. So far, however, such hypotheses have been difficult to quantify and test. Based on the field-validated simulations with the novel PECOSIM model, we demonstrate that three ecohydrological feedbacks characteristic of natural peatlands work together to increase growing season water availability in peatlands and their surrounding landscape. Total and streamflow generating storage increase more than threefold (from 262 mm to 819 mm and from 0 mm to 62 mm, respectively) when all three ecohydrological feedbacks are activated in the model, relative to a reference implementation of the model without these feedbacks. Similarly, streamflow increased by more than a factor four (from 16 to 66 mm). The feedbacks together resulted in a more stable and shallower water table depth (from 0.55 to 0.13 m beneath the peat surface). Our results stress that neglecting these ecohydrological processes in models and decision making will lead to erroneous conclusions.

In conclusion, this study provides scientific understanding of how ecohydrological feedbacks in natural peatlands regulate and stabilize both the internal and regional water cycle during the growing season. Thereby this work offers quantitative, process-based scientific support for recognizing and implementing peatlands as nature-based solution to enhance hydrological ecosystem services in environmental policy and management. Moreover, our results show that ecohydrological feedbacks promote hydrological resilience of natural peatlands and their surrounding landscape to environmental change. Disturbance or loss of natural peatlands from the landscape will weaken and ultimately remove these ecohydrological feedback mechanisms, thereby increasing drought risk at the landscape scale.

CRediT authorship contribution statement

Jelmer J. Nijp: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Reinert Huseby Karlsen:** Writing – review & editing, Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Mats B. Nilsson:** Writing – original draft, Validation, Supervision, Resources, Investigation, Funding acquisition. **Kevin Bishop:** Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Mats Nilsson reports equipmentwas provided by SITES. Kevin Bishop reports financial support was provided by Swedish Environmental Protection Agency. Mats Nilsson reports equipment was provided by ICOS-Sweden. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of generative AI in scientific writing

During the preparation of this work the authors used ChatGPT for inspiration to increase the readability of several sentences. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2025.134282.

Data availability

Data will be made available on request.

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