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RESEARCH ARTICLE

Fen ecohydrologic trajectories in response to groundwater drawdown with an edaphic feedback

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Abstract

Fens are high conservation value ecosystems that depend on consistent discharge of groundwater that saturates the near surface for most of the growing season. Reduced groundwater inputs can result in losses of native diversity, decreases in rare-species abundance and increased invasion by non-native species. As such, fen ecosystems are known to be particularly susceptible to changes in groundwater conditions including reduction in water levels due to nearby groundwater pumping. However, research is lacking on whether floristic degradation is influenced by feedbacks between hydrology and soil properties. We present a model of an archetype hillslope fen that couples a hydrological niche model with a variably saturated groundwater flow model to predict changes in vegetation composition in response to different groundwater drawdown scenarios. The model explores a potential edaphic feedback through the use of an observed relationship between fen floristic quality and soil/peat water retention characteristics that is attenuated with separate edaphic and floristic memory terms representing lags in biophysical responses to dewatering. Model parameters were determined based on data collected from six fens in Wisconsin under various states of degradation. We observed different water retention characteristics between sites that were minimally impacted versus degraded that are likely due to peat decomposition, oxidation and compaction at the degraded sites. These characteristics were also correlated with floristic quality. The results reveal a complex response to drawdown where changes in peat hydraulic properties following dewatering lead to even drier conditions and further shifts away from typical fen species.

KEYWORDS
drawdown, feedbacks, fens, groundwater, modelling, soil moisture, vadose zone, wetlands

Significance Statement

Fens are ecosystems dependent upon consistently wet soils from groundwater. Lowering of groundwater levels through activities such as well pumping can result in a substantial loss of habitat quality. We explore this dewatering process using a model based on observations of pristine and degraded fens in Wisconsin, USA. We find that a positive feedback with soil structural properties can accelerate and enhance the decline of the ecosystem as it becomes drier after a lowering of the groundwater level. This mechanism leads to fens being more susceptible to groundwater extraction and highlights a need for more monitoring and conservation.

1 | INTRODUCTION

Calcareous fens (hereinafter referred to as 'fens') are rare, often isolated, species-diverse, graminoid-dominated and groundwater-fed wetlands (Amon et al., 2002). Near constant root-zone saturation and low nutrient availability are common characteristics of the systems (Amon et al., 2002), and these stressors, which prohibit individual species from establishing dominance, are generally thought to account for high-species diversity (Carpenter, 1995) and a richness of rare species disproportionate to the area they occupy (Amon et al., 2002). Because of their rarity and their high diversity of rare and high-fidelity species, these systems are considered high conservation and restoration value targets in much of the United States (e.g., Epstein, 2017; Minnesota Office of the Revisor of Statutes, 2017) and Europe (Hajek et al., 2020).

In spite of their conservation value, fens are imperilled throughout much of their range (Amon et al., 2002; Hajek et al., 2020). Of particular concern are fens subjected to regional groundwater drawdown through pumping of high capacity wells (HCWs). As with most groundwater-dependent ecosystems, loss of groundwater influence from fens leads to declines in floristic quality, increases in cover of invasive and weedy species and loss of rare and specialist (having high fidelity to the system) species (Bart et al., 2020a; Orellana et al., 2012). Furthermore, dewatered peatlands are notoriously difficult to restore (Lamers et al., 2015). While in part these difficulties are due to the loss of propagules and resulting need for species re-introduction (e.g., Chimner et al., 2017; Hedberg et al., 2012), the fact remains that the soil water regime does not always return to pre-dewatering levels despite restoration efforts (Holden et al., 2004).

The response of ecosystems to human activities can be complex and non-linear, and it is these non-linear responses that may be part of the reason for the susceptibility of fens to groundwater extraction. In particular, dewatering alters peat hydraulic properties via enhanced oxidation and mineralization of organic matter (Hallema et al., 2015), higher rates of peat decomposition and compaction leading to higher bulk density, lower porosity (Gnatowski et al., 2010; Kechavarzi et al., 2010) and less soil water retention (Ankenbauer & Loheide, 2017). Once soils are dewatered, the altered hydraulic properties could then contribute to further peat drying (Holden et al., 2004). If this feedback is in place, then the decline in floristic quality after dewatering should be precipitous and greater than predicted if peat properties were assumed to stay constant. While these individual pieces in the degradation process have been analysed previously, a holistic and integrated assessment to explore this positive feedback process and its impact on floristic quality is still lacking.

For ethical and logistical reasons, conventional experimental approaches to understand the roles of these feedbacks are neither practical nor desirable. An alternative approach for investigating these feedbacks is to model an 'archetype' fen (a computer model with all the salient hydrologic, edaphic and floristic characteristics of a hydrologically intact fen) and simulate the decline in floristic quality after various levels of groundwater extraction both with and without these feedbacks.

Here, we develop an integrated ecohydrologic modelling framework to investigate whether edaphic feedbacks accelerate and enhance fen degradation following various scenarios of groundwater drawdown. While designing this integrated archetype model to explore feedbacks that are likely applicable to a wide range of environmental conditions, we estimate parameters based on observations collected across southern Wisconsin, a region where fens are impacted by groundwater drawdown with more pristine fens having a mean growing season water table depth between 0.00 to 0.04 m, while that of impacted fens are 0.02 to 0.65 m deeper (Bart et al., 2022, 2020a). We first develop a hydrological niche model linking floristic quality to surface soil moisture, a tactic similarly used to explore impacts of hydrologic change on floral communities (Araya et al., 2011; Booth & Loheide, 2012a; Deane et al., 2017; Lowry et al., 2011). While certainly not the only abiotic control on floristic quality, surface soil moisture is often the most important predictor of floristic quality in fen ecosystems (Bart et al., 2020a, 2020b). Next, we determine the relationship between floristic quality and peat hydraulic properties. We then develop a variably saturated groundwater flow model of a hillslope fen. The hydrological niche and groundwater flow models were coupled and used to simulate scenarios with different levels of drawdown, and with and without the associations between floristic quality and peat hydraulic qualities, to suggest whether an edaphic feedback further accelerates fen degradation.

2 | METHODS

2.1 | Soil and floristic quality analysis

We collected vegetation, hydrologic and soil data from 120 5 × 5-m plots at six fens (20 plots per fen) in southern Wisconsin (Figure 1) in May 2016. These fens represented pairs of sites with relatively high and low levels of predicted groundwater drawdown for their area of the state (see Bart et al., 2020a, for more details). For woody-plant presence and cover, we used point-intercept methods in a 0.5-m grid to give a 0–100% cover estimate. We determined herbaceous vegetation composition for each plot by establishing a 1 × 1-m subplot and recording percent cover for all species in June and August 2016, to aid in the identification of Cyperaceae and Asteraceae, respectively. Cover of each species was estimated along a log2 scale (Gauch, 1982),

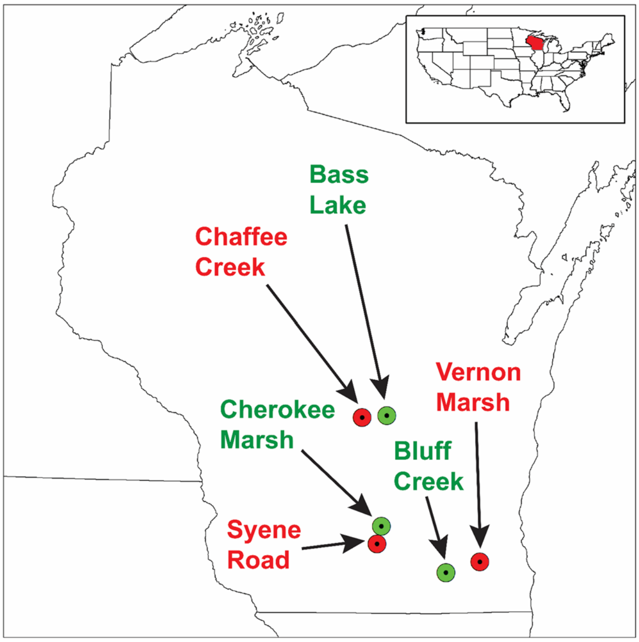

FIGURE 1 Map of study sites within the state of Wisconsin where green circles are relatively pristine fens and red circles are relatively degraded fens

mid-point covers for the class were recorded and used for analyses. Cover-weighted floristic quality index (wFQI) (Swink & Wilhelm, 1994) was then calculated for each plot as follows:

$$wFQI = \sqrt{N}\sum_{i}^{N} cvr_i * cc_i,$$

where N is the number of species per plot, cvr is the percent cover of each species and cc is the coefficient of conservatism. Values for cc range from 0 (non-native) to 10 (species highly intolerant to disturbance, restricted to narrow range of environmental conditions and high fidelity to native community, specifically fens in this case) and were estimated by panels of experts for the state of Wisconsin based on methods documented by Bernthal (2003). Values for wFQI have a similar interpretation as cc but at the community level and incorporate cover of each species. In the context of this study, wFQI is used as a plant-community-based indicator of fen health status, which is consistent with its intended purpose (Bernthal, 2003).

For hydrologic characterization of each plot, we measured biweekly surface soil moisture during the 2016 and 2017 growing seasons (1 May through 30 September) using a GS3 probe (Decagon Devices) calibrated using methods described in Cobos and Chambers (2010). Needle length of the probe is 5.5 cm, and output represents the mean value of the surrounding medium. Mean and maximum surface soil moisture across both growing seasons were then calculated for each plot.

For peat characterization and development of relationships to wFQI, soil samples were taken during the 2017 growing season from nine plots across three sites at a depth of 5 cm. Chaffee Creek and Bass Lake were eliminated from these analyses due to very thin peat and the presence of sand within 20 cm of the surface. A moisture release curve was produced for each sample using a HYPROP system (Decagon Devices). The moisture release curve was modelled using the van Genuchten water retention model (van Genuchten, 1980):

$$\theta(h) = \theta_r + \frac{\theta_s - \theta_r}{\left[1 + |\alpha h|^n\right]^m},$$

where θ is the volumetric water content ($m^3\ m^{-3}$); h is pressure head (m); θ_r and θ_s are residual and saturated water contents ($m^3\ m^{-3}$), respectively; α is related to the inverse of the air-entry pressure (m^{-1}); n is related to the pore-size distribution (–) and $m = 1\text{–}1/n$. Model parameters α and n were then estimated using SWRC-Fit (Seki, 2007), a non-linear, least-squares curve fitting program.

2.2 | Hydrologic niche model

We developed a non-parametric regression model using the software program HyperNiche 2 (McCune & Mefford, 2008) that predicts wFQI using mean growing season surface soil moisture. This method has been used extensively for habitat niche modelling across many types of ecosystems (e.g., Shinneman et al., 2016), including wetlands (Booth & Loheide, 2012b). We used vegetation and hydrologic data from all 120 plots to create the model. We chose mean surface soil moisture as our hydrologic predictor based on previous research that determined it was a better predictor of vegetation composition than other commonly measured variables such as depth-to-water table (Booth & Loheide, 2012b; Wheeler, 1999). Goodness of fit for the non-parametric regression model was determined using a cross-validated R^2 (χR^2) value. Additional discussion of methods and niche modelling results using observation datasets from the same fens can be found in Bart et al. (2020a).

2.3 | Variably-saturated groundwater flow model

We developed a numerical, two-dimensional (cross-sectional), transient, variably saturated groundwater flow model of a hillslope fen ecosystem. The conceptual model is based on van Loon et al. (2009) and assumes that intense groundwater discharge occurs at the upgradient margin of the fen and then moves laterally through the lower aquifer (silty sand) as well as the loose peat/soil as throughflow (Figure 2). We assumed several boundary conditions: (1) a specified head at the base of the hillslope (2-m wide) that represents the source of concentrated groundwater upwelling, (2) a specified head at the edge of the far field representing a stream and (3) a specified flux at the fen surface representing infiltration and soil evaporation. Root water uptake was also simulated as a sink term across the root zone (assumed to be 50 cm). For the surface flux and root water uptake terms, we followed identical methods to the 1-D model presented in Booth and Loheide (2010). Daily weather data from GridMET (Abatzoglou, 2013) for a point in south-central Wisconsin (43.2°N,

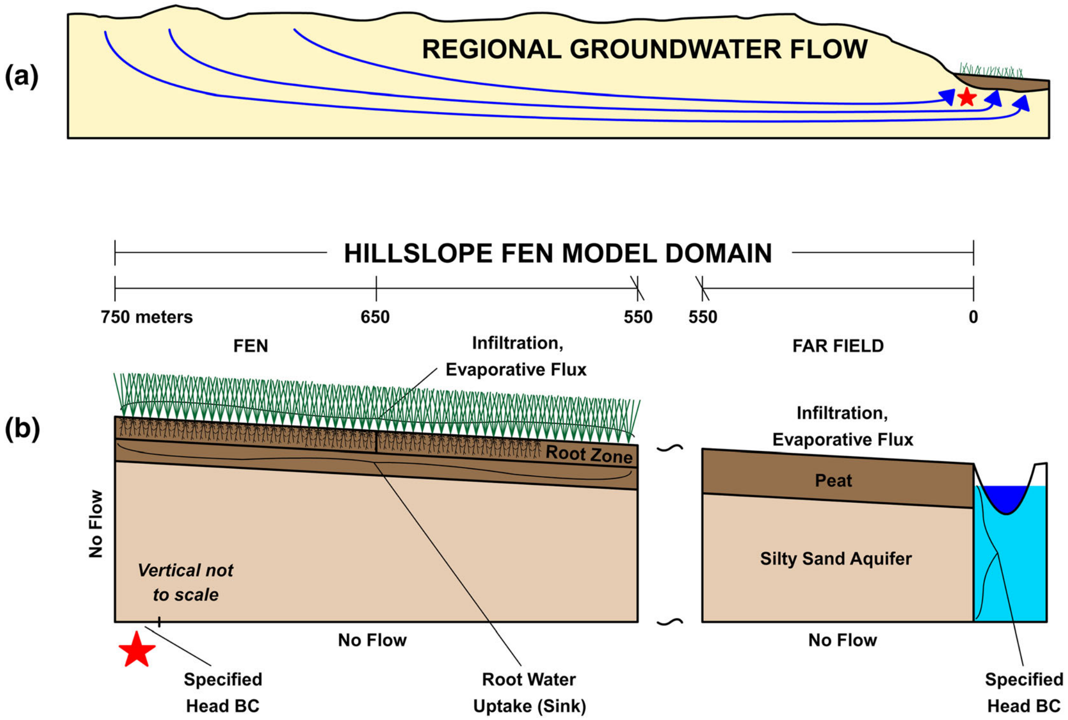

FIGURE 2 Conceptual diagram of a regional groundwater flow system (a) flowing to a hillslope fen, which is the domain of the variably-saturated groundwater flow model (b). Hillslope fen model diagram (b) is showing layers, boundary conditions and near-field and far-field domains. Red star on both diagrams indicates the location of the specified-head boundary condition at the base of the fen is modified based on groundwater drawdown scenarios.

89.3°W) was used to create representative forcings and to drive potential evapotranspiration—partitioned into soil surface evaporation and plant transpiration—following the FAO-56 Penman–Monteith method (Allen et al., 1998; Booth & Loheide, 2010). A 10-year weather time series—composed of randomly chosen years between 1979 to 2016—was repeated twice to create a 20-year stationary weather forcing dataset. We simulated the hillslope fen model using the general-purpose finite-element solver Comsol Multiphysics (version 5.4). Transient conditions were simulated at a 1-h time step.

The two-layer model is broken up into a near-field section representing the fen and near-hillslope area and a much wider far-field region (with no root water uptake) to minimize the effect of the stream boundary condition. The main area of interest representing the fen is a 100-m width section of the model that is offset 100 m from the edge of the model representing the base of the hillslope (between 550 and 650 m in Figure 2). Further, we focus our results on the midway point of that section ($x = 600$ in Figure 2) to best represent fen conditions under various scenarios. Values for additional model parameters are provided in Table 1 and represent common fen and peatland conditions.

TABLE 1 Parameters for variably-saturated groundwater flow model

Parameter	Value
K_{horiz} (peat)	86.4 cm/day
K_{vert} (peat)	69.1 cm/day
K_{horiz} (aquifer)	4,320 cm/day
K_{vert} (aquifer)	69.1 cm/day
vG n	1.34
LAI mid-season	2.0
REW	1.2 cm
Z_e	10 cm

Note: K_{horiz} and K_{vert} are horizontal and vertical saturated hydraulic conductivity, respectively. vG n is the n parameter in the van Genuchten water retention function, and LAI mid-season is the leaf-area index of the fen vegetation in the middle of the growing season. REW and Z_e are readily evaporable water and effective depth of evaporation, respectively, used in the FAO-56 method of evapotranspiration partitioning.

2.4 | Floristic-pedotransfer function

To connect changes in floristic quality to changes in peat hydraulic properties, we developed simple linear regression models to predict saturated volumetric water content and the van Genuchten α parameter using wFQI as a predictor. We used field data and modelled soil moisture release curves from nine plots to create each regression model. We estimated the saturated volumetric water content for each plot to be the maximum surface soil moisture across the two growing seasons. The growing seasons of 2016 and 2017 were above normal in terms of rainfall across southern Wisconsin, and all plots were very likely fully saturated at least once in the monitoring record. We hypothesize that as floristic quality declines (the fen becomes drier), α will increase and θ_s will decrease leading to an overall drier soil moisture characteristic curve primarily in the lower and mid-range suction head values where fewer available large pores due to peat composition and compaction will lead to lower water content.

2.5 | Fen ecohydrologic model

We developed an integrated model of an archetype hillslope fen that links a hydrological niche model with a variably saturated groundwater flow model to predict changes in vegetation composition in response to different groundwater drawdown scenarios. The model also accounts for a potential feedback between hydrology and soil/peat water retention properties through the use of a floristic-pedotransfer function that uses vegetation composition as a predictor of soil/peat hydraulic properties. These properties can then be attenuated using separate floristic and edaphic memory terms that represent the lags in the biophysical responses to dewatering. We connect vegetation composition and peat hydraulic properties for two reasons: (1) Peat hydraulic properties are strongly controlled by vegetative growth including input of organic matter to the soil, and (2) decreased floristic quality can be used as a proxy for hydrologic degradation that leads to soil carbon loss via oxidation and declining soil water retention. Thus, soil, and particularly peat, develops through time and reflects the composition and condition of vegetation growing at a location. Relationships between soil water retention and floristic quality were determined based on data collected from six fens in southern Wisconsin under various states of degradation due to nearby groundwater pumping.

Implementation of the model within the integrated ecohydrological model was done by taking the mean growing season surface soil moisture over the previous N years and using that value as the predictor in the hydrologic niche model. We refer to this N-year period as the floristic memory (FM) of the fen ecosystem and represents the concept that plant communities do not respond immediately to changing hydrologic conditions and instead will slowly respond to a press disturbance (Lake, 2000) that arrives sharply and is maintained at a constant level. This slow response is due to a combination of factors including long-lived perennial species that may remain in an ecosystem longer than annual species following a disturbance—which is akin to the concept of an extinction debt (Tilman et al., 1994)—and seed dispersal and germination processes, which will delay the appearance of successional species (Ellison & Bedford, 1995). At the end of each simulation year, wFQI for the following year is predicted based on the output of the hydrologic niche model, which uses the N-year mean surface soil moisture as a predictor. We chose to keep N constant at a value of 5 years for all simulations.

Similar to the hydrologic niche model, we implemented the floristic-pedotransfer function in the integrated model by introducing an edaphic memory (EM) term that tempers the predicted change in peat hydraulic properties (α and θ_s) to represent the concept that soil properties will not change rapidly in response to changes in vegetation composition (which is changing in response to hydrologic change). In reality, the process of dewatering of peat soils will lead to soil carbon loss through oxidation and respiration over the course of years to decades and ultimately impact peat structure and hydraulic properties (Holden et al., 2004; Waddington et al., 2015). At the end of each simulation year, the hydraulic properties for the following year are predicted based on the wFQI value predicted for the following year (after accounting for the floristic memory) and then tempered by the edaphic memory term as shown below:

$$\alpha_2 = \alpha_1 + EM(\alpha_{pred} - \alpha_1),$$

$$\theta_{s2} = \theta_{s1} + EM(\theta_{spred} - \theta_{s1}),$$

where α_2 and θ_{s2} are the following year's hydraulic properties, α_1 and θ_{s1} are the current year's hydraulic properties and α_{pred} and $\theta_{s,pred}$ are the predicted hydraulic properties based on the predicted wFQI value for the following year. Thus, a value of 1 for EM means that there is no edaphic memory in the system and the peat hydraulic properties can change instantaneously, and a very low value (e.g., 0.1) means that the edaphic memory is high and changes in properties are very limited from year-to-year as has been observed in some peatland restoration projects (Schimelpfenig et al., 2014).

2.6 | Model drawdown scenarios

We simulated four separate groundwater conditions: pristine with no drawdown (1) and gradual drawdown of 0.2, 0.4 and 0.6 m over a 5-year period (2–4) with no intra-annual variability. These varying conditions were manifested as a specified head boundary condition at the base of the hillslope (Figure 1) and are consistent with drawdowns of greater than 1 m observed and simulated near historical fens in south-central Wisconsin (Parsen et al., 2016). Following the potential drawdown period, we continued the simulation for another 15 years to look at the longer-term impacts of drawdown for a total of 20 simulation years. The first series of scenarios do not incorporate the edaphic feedback, and peat hydraulic properties are held constant through the simulation period. Then, we modified the series of scenarios by implementing the edaphic feedback using wFQI (which also serves as a proxy of the soil water regime due to the hydrologic niche model connection) to predict peat hydraulic properties. Finally, we further modified the scenarios with the edaphic feedback by incorporating the edaphic memory term, which tempers the annual change in hydraulic properties that are driven by a change in wFQI. We chose three different EM values to simulate—1 (no memory), 0.5 and 0.1—to encompass a full range of plausible values.

Each year is simulated separately within Comsol, and then, model inputs and parameters are adjusted within Matlab and incorporated into the following year of simulation in Comsol (Figure 3). The steps in the process are the following: (1) Model is initialized at steady-state, undisturbed hydrologic conditions across the fen; (2) wFQI is

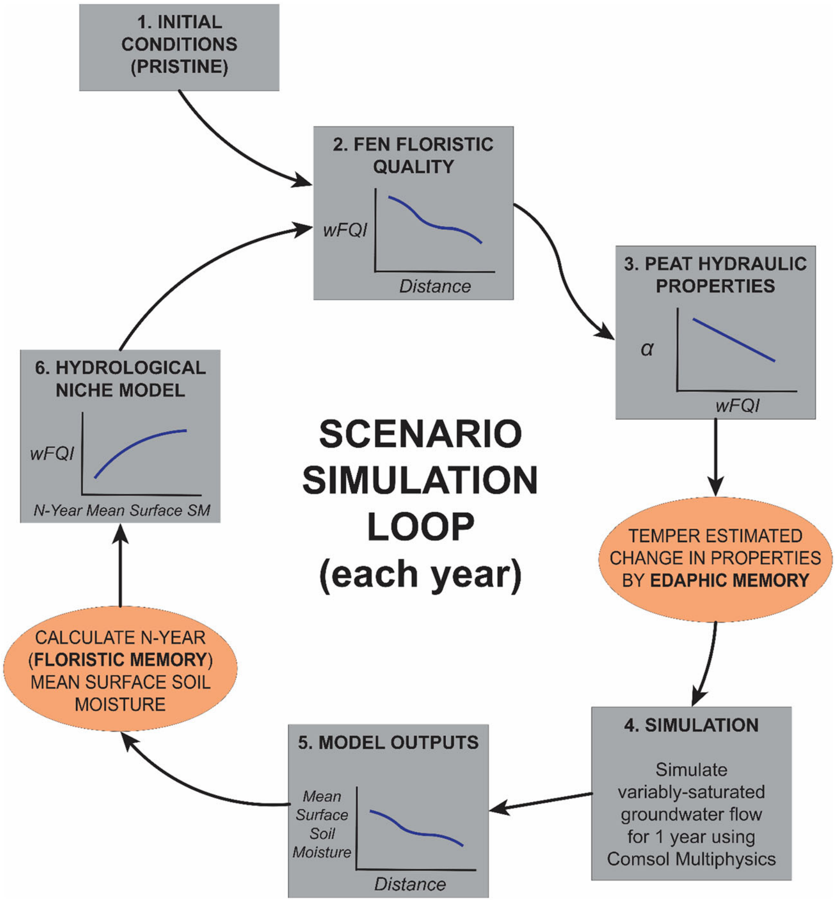

FIGURE 3 Diagram of model simulation process over one simulation year at each location across the 2-D archetype fen

initialized across the fen at a value of 27; (3) estimation of peat hydraulic properties across the fen (every 1-m) using wFQI as the predictor and then tempering of the estimated properties by the edaphic memory function; (4) 1-year simulation of fen hydrology using Comsol; (5) output of mean surface soil moisture over the simulated year and calculation of the previous N-year (floristic memory, set to 5 years) mean surface soil moisture across the fen; (6) estimation of wFQI using the N-year mean surface soil moisture as predictor (hydrologic niche model) and then returning to (2) initializing the model for the subsequent year using the new estimates of wFQI across the fen.

3 | RESULTS

3.1 | Hydrologic niche and floristic-pedotransfer models

The hydrologic niche model using nonparametric regression shows a fairly strong and expected positive non-linear relationship between wFQI and mean surface soil moisture (SSM) (Figure 4). Values of wFQI increase substantially between mean SSM values of 0.5 and 0.6 (saturation in less impacted fens typically occurs near 0.7) representing a shift from plant communities dominated by generalists to ones dominated by fen specialists.

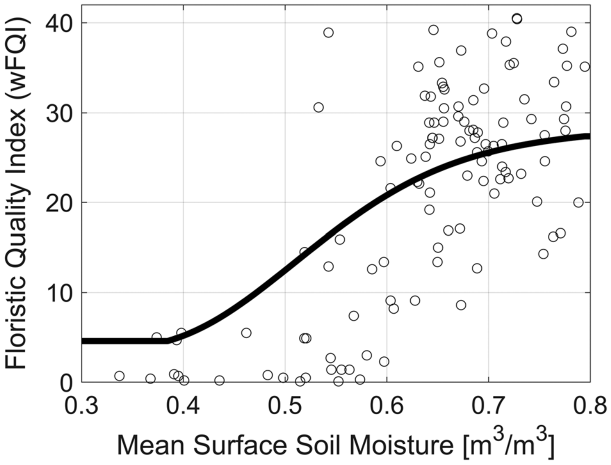

FIGURE 4 Hydrologic niche model (using nonparametric regression) predicting wFQI based on mean growing season surface soil moisture ($_{\chi}R^2 = 0.525$)

Field measurements also revealed that water retention characteristics vary across a degradation gradient in the study fens. Specifically, we found that van Genuchten α (related to the inverse of the largest pore size) has a negative relationship with wFQI and maximum surface soil moisture (proxy for saturated water content) has a positive relationship with wFQI (Figure 5). These two models combine to create a

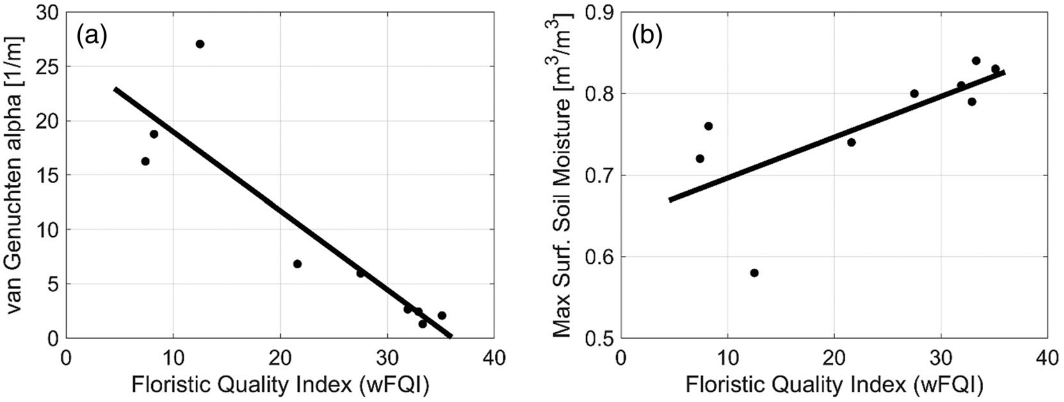

FIGURE 5 Floristic-pedotransfer function (using simple linear regression) predicting van Genuchten α parameter (a) and θ_s (b). R^2 values are 0.797 and 0.507, respectively.

gradient of soil water retention curves depending on the wFQI value (Figure 6). In particular, as wFQI values increase (fen is more dominated by fen-specialist species) moisture is retained at a higher level and does not begin to decline until higher suction pressure is reached compared to lower wFQI values.

3.2 | Fen ecohydrologic model scenarios

Hydrologic and floristic quality responses to a gradual groundwater drawdown of 0.6 m over 5 years are variable depending on whether the edaphic feedback is implemented and the values of the floristic and edaphic memory terms (Figure 7). At a point representing the middle of the hillslope-archetype fen ($x = 600$ m) under several scenarios, surface soil moisture (SSM) and wFQI decline over time, but lagging groundwater drawdown. We first start with a simulation where the edaphic feedback is not implemented and SSM declines from 80% for the pristine case to slightly less than 60% after 15 years following drawdown. This then leads to a decline in wFQI from approximately 28 to 18. However, once the edaphic feedback is implemented, SSM declines substantially more to approximately 35%, and wFQI declines to a value of 5. This strong positive edaphic feedback effect is making the fen more vulnerable to degradation via groundwater drawdown by initially dewatering the fen and lowering the SSM, then decreasing wFQI and associated moisture retention characteristics, which then leads to even lower SSM and wFQI values.

However, these initial simulations are assuming that the change in peat hydraulic parameters happens concurrently to the changes in wFQI (i.e., with no edaphic memory). In reality, soil properties can be slow to change, especially if they are dependent on relatively slow reactions such as oxidation of peat. Therefore, we implemented several different edaphic memory (EM) values (0.5 and 0.1) that act to temper the change in hydraulic properties for a given change in floristic quality. The simulation results show clearly the variable impact of these parameter changes where an EM value of 0.5 delays the decline in wFQI by only a few years and a value of 0.1 delays the decline by closer to 7 years. Ultimately, however, the floristic quality outcome after 20 years is nearly identical for each EM value.

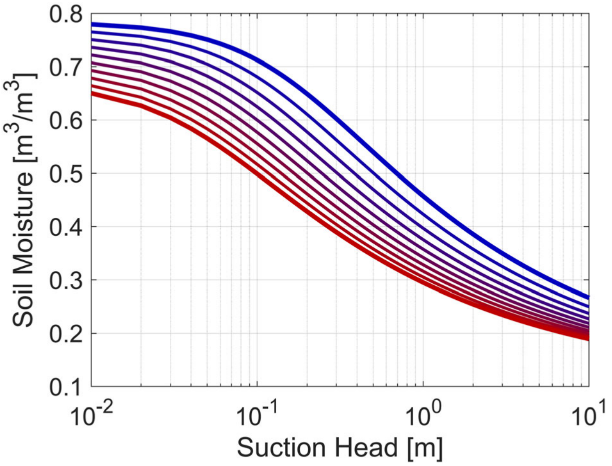

FIGURE 6 Soil moisture characteristic curve using floristic-pedotransfer function. Dark blue equals wFQI value of 27.4; dark red equals wFQI value of 4.5.

This differential response of SSM and wFQI depending on the magnitude of the edaphic feedback is also seen laterally across the fen (Figure 8). The mean SSM and wFQI of the last 5 years of the simulation are both lower as you move further away from the base of the hillslope (as x decreases) where the specified head boundary condition represents focused groundwater upwelling. This decline away from the base of the hillslope is much less for the pristine case as well as the scenario where the edaphic memory value is 1 or 0.5 (i.e., no or relatively short memory). The decline is larger for the scenario without an edaphic feedback and substantially larger for the scenario where the edaphic memory value is 0.1 (long memory). This is due to the soil water regime at the end of these scenarios being located where the soil moisture characteristic curve (Figure 6) is the steepest and where slight changes in pressure head would result in larger changes in SSM and wFQI.

To model the impacts of different levels of drawdown, we hold the edaphic memory at a value of 0.1 (limiting the potential rate of change of fen hydraulic properties) and simulated three levels of drawdown: 0.2, 0.4 and 0.6 m (Figure 9). The lowest drawdown

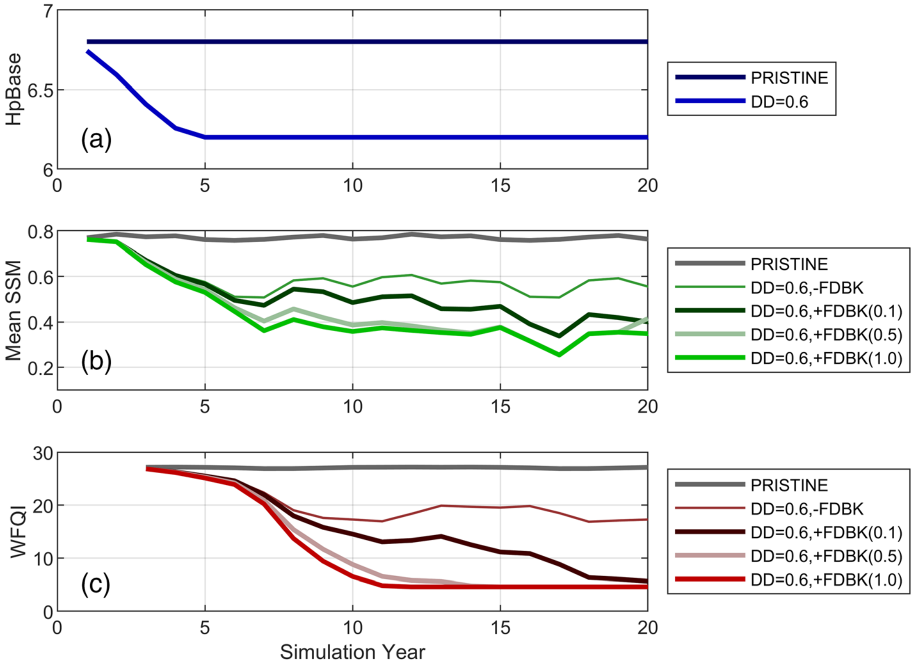

FIGURE 7 Specified pressure head at base of hillslope under pristine (PRISTINE) and 0.6-m groundwater drawdown ($DD = 0.6$) cases (a) and two sets of simulation results: mean surface soil moisture (b) and wFQI (c) at $x = 600$ m for pristine (PRISTINE), drawdown without edaphic feedback (-FDBK), and with edaphic feedback (+FDBK). The last parentheses denote the edaphic memory value that tempers the peat hydraulic properties response.

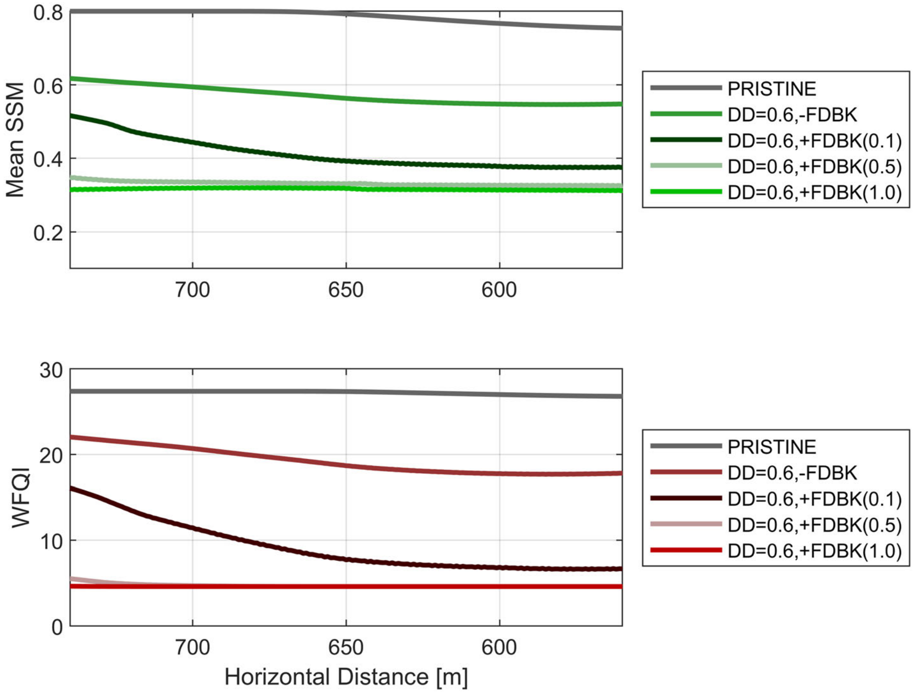

FIGURE 8 Mean simulation results—mean surface soil moisture (top) and wFQI (bottom)—for the last 5 years of the simulation (years 16–20) across the fen for pristine (PRISTINE), drawdown without edaphic feedback (-FDBK), and with edaphic feedback (+FDBK). The last parentheses denote the edaphic memory value that tempers the soil peat hydraulic properties response.

scenario (0.2 m) eventually leads to a rather modest decline in SSM of 5% and decreases wFQI by less than 5. However, with the next drawdown scenario (0.4 m), the simulations show that the response in SSM and wFQI becomes non-linear with declines of close to 20% and 8 for SSM and wFQI, respectively. The non-linear response is much more noticeable at the largest drawdown scenario (0.6 m), where the declines are approximately 40% and 20 for SSM and wFQI, respectively.

This non-linear relationship is also shown in Figure 10 where the values in year 20 only are plotted for the varying levels of drawdown. These results show a shallower non-linear response between 0 and 0.4 m of drawdown but a much steeper decline for wFQI between 0.4 and 0.6 m.

4 | DISCUSSION

Our field data analysis and integrated ecohydrologic model results suggest the following: (1) Peat hydraulic properties are impacted by groundwater drawdown; (2) there are positive relationships between

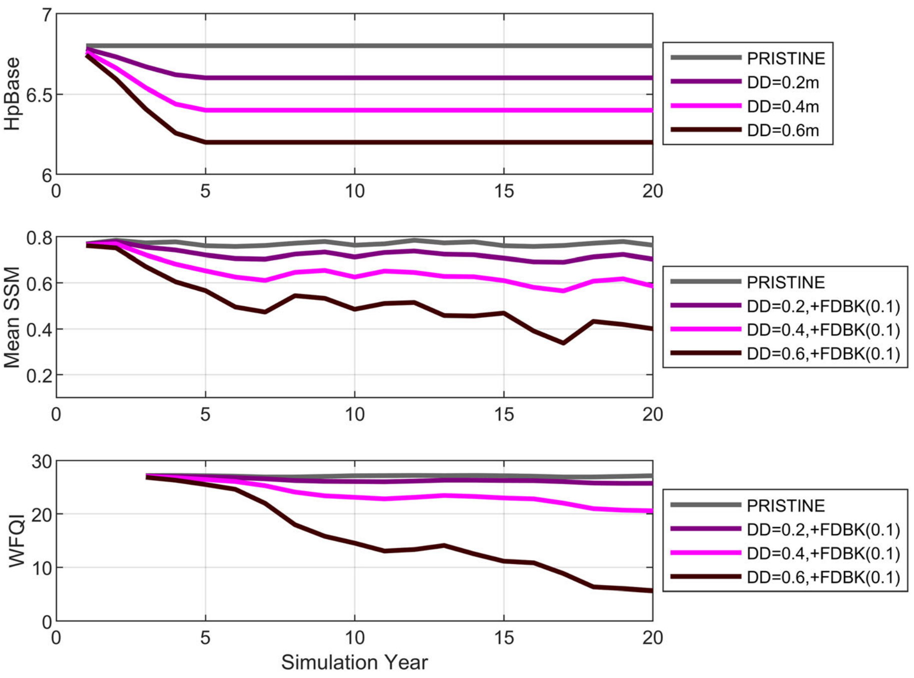

FIGURE 9 Specified head boundary condition representing groundwater level at base of fen for a pristine scenario and 0.2.-m, 0.4-m and 0.6-m drawdown scenarios (top), and mean surface soil moisture at $x = 600$ m (middle) and weighted floristic quality index at $x = 600$ m for several scenarios (bottom). PRIS, pristine conditions; $-$FDBK, no edaphic feedback; $+$FDBK, edaphic feedback implemented; (5y), 5-year floristic memory; (0.1), edaphic memory

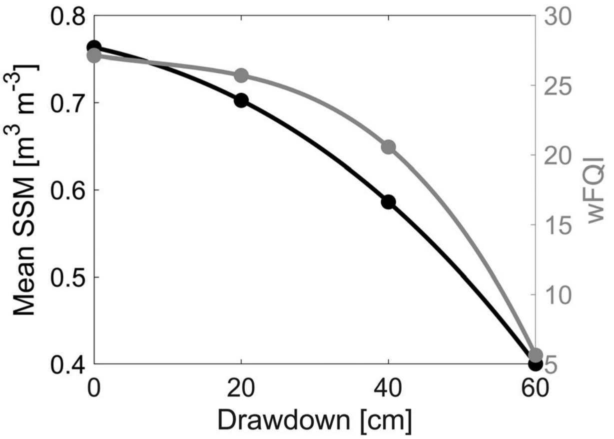

FIGURE 10 Relationship between drawdown and mean surface soil moisture (SSM) and floristic quality (wFQI) for year 20 of the scenario simulations at $x = 600$ m

indicators of maximum pore size, saturated water content and floristic quality; (3) declines of surface soil moisture (SSM) and floristic quality (wFQI) are nonlinear with increasing drawdown; and (4) a feedback among declining SSM, altered peat hydraulic properties and floristic quality cause a precipitous decline in floristic quality with modest groundwater drawdown. Our data and analyses suggest a cascading feedback as such: (1) Groundwater drawdown leads to a loss of SSM, which leads to (2) a decline in wFQI, and (3) a decline in van Genuchten α and saturated water content, which leads to (4) further declines in SSM, which results in further declines in wFQI. Heavily impacted fens show large declines in wFQI, high quality graminoids (e.g., *Carex lasiocarpa* and *Carex stricta*) and fen specialists (e.g., *Parnassia glauca* and *Carex sterilis*) (Bart et al., 2020a). Our integrated ecohydrologic models suggest that the magnitude of these declines might not have been nearly as large without these feedbacks.

The edaphic feedback uncovered by the integrated ecohydrologic model and represented by changes in peat hydraulic properties as a fen becomes more desiccated is consistent with field observations from Silins and Rothwell (1998) in degraded Alberta fens where upon drainage macropores collapse and water is drawn from deeper layers through increased capillary flow towards a drier surface. These changes thus result in a drying of large sections of the peat mat. By incorporating these alterations directly into our model and drawdown scenarios, we have provided evidence that drainage-altered peat hydraulic properties further decrease SSM beyond what would be predicted from drawdown alone.

Our models suggest that with the incorporation of altered peat hydraulic properties, hydrologic and floristic degradation increases non-linearly with increasing levels of drawdown. The shape of the degradation response to drawdown (Figure 9) will vary depending upon the values of model parameters including peat hydraulic properties and the shape of the hydrologic niche model. However, the non-linear aspect of this degradation response presents an important management consideration. Fen ecosystems appear to be highly susceptible to drawdown and may experience accelerated and non-linear degradation as peat hydraulic properties are altered causing further desiccation. Thus, more attention to monitoring and conservation of these unique ecosystems in regions experiencing stress from groundwater withdrawals may be warranted, as the process may not be reversable or may occur at different rates.

The model results for various parameter sets clearly show that without the edaphic feedback, neither SSM nor floristic quality would decline to levels measured in heavily impacted fens (Bart et al., 2020a). Furthermore, representations of edaphic and floristic memory built into the model only delayed the declines without changing the magnitude over the long term.

Fens can be difficult to restore in terms of hydrology and floristic quality (Lamers et al., 2015; Malson et al., 2008), and the success of some efforts has been much improved by soil scraping (Klimkowska et al., 2010; Patzelt et al., 2001). The feedback between SSM decline and changes in peat hydraulic properties could help explain why some fens do not rewet sufficiently after restoration, or why floristic quality may not return to restored drained fens without soil removal. Holden et al. (2004) describe the changes to peat hydraulic properties associated with drainage as 'permanent'. If this is similarly true for drawdown-impacted peat, then should groundwater extraction cease, a return of historic SSM may not occur. Indeed, Davenport et al. (2014) noted that near-surface soil moisture did not return in damaged fen peat, in some cases more than 70 years after agricultural activities were abandoned and decades after hydrologic restoration was attempted. Our modelling suggests that similar impacts may result from groundwater extraction, and therefore, fens may not recover without significant and expensive efforts such as peat stripping and reseeding.

Several limitations in the models will need to be addressed by future research. First, niche-modelling needs to account for multiple interactions among biotic and abiotic factors. The use of a single-factor model to predict floristic quality was chosen for simplicity as well as the relatively high predictive power of mean SSM. More complex models for individual fen species have demonstrated that multiplicative interactions between SSM and various measures of nutrient availability moderately improve predictive power for the occurrence of many fen species (Bart et al., 2020b), and it is likely that biotic interactions (e.g., competition and facilitation) will similarly interact with SSM. Second, reduction of the groundwater level below degrading fens will not typically occur as a step-change as these are often gradual processes; thus, it may be hard to study impacted fens and determine the 'time since disturbance' to help estimate the relationship with peat properties (that time of disturbance may not be a clear point in time). Third, the representations of floristic and edaphic memory are simplified to enable the exploration of their effect on degradation response. Our goal for including these tempering functions is to account for the delayed response that are inherent in biophysical systems. The values we chose to use are meant to be illustrative as a sensitivity analysis, but actual values for these parameters will likely vary across and within systems due to species-specific differences and soil heterogeneity. If memory is longer or shorter in a given system, the primary difference is the rate at which the system approaches a new state or dynamic equilibrium. Additional work will be required to estimate these poorly constrained memory parameters for actual fens using long-term monitoring data.

5 | CONCLUSION

Using an integrated ecohydrologic model of an archetype fen in the Upper Midwest, USA, that incorporated feedbacks between water regime and peat hydraulic properties, this study has shown a non-linear degradation response of floristic quality to groundwater drawdown. The feedback represents the cascading mechanism of a drying peat subsequently losing organic matter (through oxidation, respiration and decomposition), which leads to altered hydraulic properties that retain less moisture and, thus, further drying of the peat and loss of floristic quality. The response with this feedback implemented is more accelerated and stronger than if it was not implemented, suggesting that fen ecosystems are more susceptible to dewatering than expected using a hydrologic niche model and assuming constant peat properties. This finding highlights the importance of careful monitoring and renewed calls for protection of the fen ecosystems if their conservation and sustainability is prioritized by society.

The modelling has also shown that this non-linear degradation response can be modified based on ecosystem lag effects that we describe as memory both in the floristic and edaphic responses. The tempering effect of floristic memory represents the lagged response in plant community changes due to factors including long-lived perennial species and slow-moving dispersal and germination processes of successional species. Edaphic memory represents the concept that peat properties will not respond instantaneously to hydrologic and plant community changes because loss of soil organic matter can be a slow process acting over years to decades to ultimately impact peat hydraulic properties. Both of these memory terms represent important observed ecosystem phenomena that prevent an ecosystem from degrading quickly following a stressor, but they may also prevent the ecosystem from quickly rebounding if the stressor is removed.

While the relatively simple parameterization of this feedback within our archetype fen model has allowed for the exploration of this non-linear response, assessing the precise impact at actual fens will require new methods for parameter estimation and long-term monitoring data. Nevertheless, though the magnitude of this non-linear response will vary according to site-specific characteristics related to the plant community, peat and hydrogeologic conditions, the finding that this feedback leads to a more accelerated and more severe degradation response than expected (assuming no change in peat properties) is likely applicable to all groundwater-dependent peatlands and needs to be accounted for by water and ecosystem managers.

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DATA AVAILABILITY STATEMENT

Field observations and soil moisture release curve parameters from fen study plots are available through HydroShare: Booth, E. G. (2021). Fen Hydrology & Floristic Quality, HydroShare (http://www.hydroshare.org/resource/e7a4c9cc9f2a49f58ecc72e8e46bbd82).

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