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Depressional wetlands affect watershed hydrological, biogeochemical, and ecological functions

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Abstract

Depressional wetlands of the extensive U.S. and Canadian Prairie Pothole Region afford numerous ecosystem processes that maintain healthy watershed functioning. However, these wetlands have been lost at a prodigious rate over past decades due to drainage for development, climate effects, and other causes. Options for management entities to protect the existing wetlands, and their functions, may focus on conserving wetlands based on spatial location vis-à-vis a floodplain or on size limitations (e.g., permitting smaller wetlands to be destroyed but not larger wetlands). Yet the effects of such management practices and the concomitant loss of depressional wetlands on watershed-scale hydrological, biogeochemical, and ecological functions are largely unknown. Using a hydrological model, we analyzed how different loss scenarios by wetland size and proximal location to the stream network affected watershed storage (i.e., inundation patterns and residence times), connectivity (i.e., streamflow contributing areas), and export (i.e., streamflow) in a large watershed in the Prairie Pothole Region of North Dakota, USA. Depressional wetlands store consequential amounts of precipitation and snowmelt. The loss of smaller depressional wetlands (<3.0 ha) substantially decreased landscape-scale inundation heterogeneity, total inundated area, and hydrological residence times. Larger wetlands act as hydrologic "gatekeepers," preventing surface runoff from reaching the stream network, and their modeled loss had a greater effect on streamflow due to changes in watershed connectivity and storage characteristics of larger wetlands. The wetland management scenario based on stream proximity (i.e., protecting wetlands 30 m and ~450 m from the stream) alone resulted in considerable landscape heterogeneity loss and decreased inundated area and residence times. With more snowmelt and precipitation available for runoff with wetland losses, contributing area increased across all loss scenarios. We additionally found that depressional wetlands attenuated peak flows; the probability of increased downstream flooding from wetland loss was also consistent across all loss scenarios. It is evident from this study that optimizing wetland management for one end goal (e.g., protection of large depressional wetlands for flood attenuation) over another (e.g., protecting of small depressional wetlands for biodiversity) may come at a cost for overall watershed hydrological, biogeochemical, and ecological resilience, functioning, and integrity.

Supporting Information

Keywords

Prairie pothole region; biogeochemistry; ecology; geographically isolated wetlands; hydrologic connectivity; hydrologic model; non-floodplain wetlands; soil and water assessment tool; wetlands

Introduction

In belated acknowledgement of the myriad benefits provided by wetlands (Zedler and Kercher 2005), the United States established a "no net loss" wetland policy in 1989 (Salzman and Ruhl 2005). This came far too late for much of the United States, as an overwhelming abundance (>50%) of the nation's wetlands had been previously lost (e.g., ditched, drained, filled; Dahl 1990). This is particularly true for a large subset of wetlands outside of the floodplain and completely surrounded by uplands, often termed geographically isolated wetlands (GIWs; Tiner 2003, Leibowitz 2015), non-floodplain wetlands (Lane et al. 2018, U.S. EPA 2015), or upland-embedded wetlands (Mushet et al. 2015). Under recent federal U.S. policies, many of these wetland systems require a clear demonstration of their individual or cumulative effects on downstream waters to be specifically considered for management (Alexander 2015). Here, we focus on the effects of such wetlands on both watershed and downstream functions in the North American Prairie Pothole Region (PPR), where spatially distributed, small depressional wetlands (i.e., prairie potholes) punctuate the landscape (e.g., Shook and Pomeroy 2011, Shaw et al. 2012, Van Meter and Basu 2015).

Although wetland losses have slowed in some areas as a result of management activities, losses continue unabated in some regions and these systems continue to be vulnerable (Creed et al. 2017). Such continued and substantive losses are particularly acute for depressional wetlands in the PPR, which covers approximately 800,000 km^2 of Canada and the United States. In the PPR of North and South Dakota, ~5,000 to 6,000 ha/yr of wetlands have been lost since the ~1980s largely due to land use transitions to agriculture (Johnston 2013). These losses are projected to continue due to land use change and variations in future climate conditions (Sofaer et al. 2016).

The cumulative watershed-scale effect of depressional wetland losses and alterations is substantive (Lane et al. 2018, Cohen et al. 2016, Golden et al. 2016). Wetlands are frequently intimately intertwined with local surface and groundwater hydrology (McLaughlin et al. 2014, Rains et al. 2016). They temporarily store and subsequently release surface runoff, direct precipitation, and snowmelt (i.e., via a lag function; Rains et al. 2016), regulating landscape inundation patterns and attenuating potential downstream flood conditions. Depressional wetlands are also important biogeochemical reactors distributed across watersheds (Marton et al. 2015). Because of their surface areas, volumes, and extended residence times, they intercept, transform, and remove pollutants (via sink and transformation functions; Marton et al. 2015, Cohen et al. 2016) that would otherwise be transported to the stream (Lane et al. 2018, Leibowitz et al. 2008). They thereby improve or mediate potential threats to local and downstream water quality.

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Further, depressional wetlands influence biological diversity both within the watershed and downstream aquatic habitats (Schofield et al. 2008). They regulate extent and distribution of inundation across the watershed, affecting habitat mosaics for migratory waterfowl (Niemuth and Solberg 2003, Skagen and Thompson 2007), invertebrates (Anderson and Vondracek 1999, Jenkins and Boulton 2003, Euliss et al. 2004), and amphibians (Mushet et al. 2012, 2013). Through water storage and biogeochemical functions, wetlands also affect downstream habitat integrity via influences to flow regimes, benthic substrates, and water quality (Marton et al. 2015, Cohen et al. 2016).

Both localized and downstream functions are largely regulated via hydrologic connections (and disconnections) among depressional wetlands and the drainage network. Hydrologic connectivity of depressional wetlands can be defined by the degree to which they are linked to one another and other water bodies (e.g., streams, rivers) by surface, shallow subsurface, and/or deep groundwater flowpaths (Golden et al. 2017). In the PPR, the dominant mode of hydrologic connectivity between depressional wetlands is via overland flows (van der Kamp and Hayashi 2009). For this surface-water connectivity to occur, depressional wetlands must fill until a critical water depth or volume threshold is reached. Once reached, the wetlands then “spill” and generate surface flows (i.e., “fill-and-spill”; Spence and Woo 2003), whereby wetlands can become hydrologically connected to another water body, including other wetlands or stream systems (e.g., Shook and Pomeroy 2011, Evenson et al. 2016, Leibowitz et al. 2016, Vanderhoof et al. 2016, 2017). During the period of “filling,” a wetland remains hydrologically disconnected from other waters, thereby providing critical lag, sink, and transformation functions (Lane et al. 2018). At the watershed scale, the spatial distribution and cumulative storage capacity of depressional wetlands can thus regulate overall watershed connectivity and associated downstream flows, where disconnected wetlands reduce the total area contributing surface runoff to the drainage network (Shaw et al. 2012, Cohen et al. 2016).

Quantifying the extent to which depressional wetlands impact watershed hydrology is challenging and requires abundant watershed-scale data and robust modeling methods (Golden et al. 2017). Recent work has begun to examine questions about watershed-scale effects of depressional wetlands via in situ measurements of surface water connections across the landscape (McDonough et al. 2015) and remote sensing approaches to understand wetland inundation dynamics (Vanderhoof et al. 2016, 2017, DeVries et al. 2017). Increasingly, models are being developed and applied to quantify cumulative effects of depressional wetlands on groundwater (McLaughlin et al. 2014) and surface water systems via hybrid (Golden et al. 2016) or process-based watershed modeling approaches (Shook et al. 2013, Pomeroy et al. 2014, Evenson et al. 2015, 2016, Fossey et al. 2016). These models provide an approach to expand beyond the spatial and temporal boundaries of measured data to better predict how loss of depressional wetlands affects overall watershed integrity (Golden et al. 2014).

In the PPR, as in other wetland-rich landscapes, smaller wetlands have frequently been preferentially destroyed via filling or ditching. For example, in parts of North Dakota, many depressional wetlands with smaller surface areas have been combined to form fewer yet larger depressional wetlands as a consequence of drainage activities (McCauley et al. 2015).

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In the Des Moines Lobe (Iowa, USA), preferential loss of smaller wetlands has led to general homogenization of wetland size distributions (Le and Kumar 2014, Van Meter and Basu 2015, Serran and Creed 2016). In response to these and other wetland alterations, regulatory protections have been proposed for wetlands most likely to have surface water connections with downgradient waterways (e.g., wetlands that are proximate to streams; see Alexander 2015). As such, there is critical need to better understand how wetland losses that vary by wetland size and/or watershed position affect watershed hydrologic, biogeochemical, and biological functions.

Here, we evaluated how depressional wetlands that are potentially vulnerable to destruction (e.g., small wetlands, those farther from streams) influence watershed functions in the PPR. We did this by quantifying the extent to which depressional wetlands regulate watershed-scale storage (inundation patterns and residence times), connectivity (streamflow contributing areas), and export (streamflow) under different loss scenarios. We applied a watershed-scale hydrologic model of the ~1,700 km^2 Pipestem River watershed in the PPR of North Dakota, USA, and explored three categories of loss scenarios:

1. Complete (i.e., 100%) loss of depressional wetlands.
2. Loss of depressional wetlands based on surface area extent (i.e., preferential loss by different size classes).
3. Loss of depressional wetlands based on stream proximity (i.e., complete losses outside specified distances from stream networks).

Across these scenarios, we discuss the implication of the changes in storage and export for watershed hydrological, biogeochemical, and ecological functions.

Methods

Study area

The Pipestem River watershed is located in the southeastern portion of the North American PPR (Fig. 1). The watershed includes two physiographic regions, with the Missouri Coteau to the west and the Drift Plain to the east. The watershed is dominated by agriculture (~43%), herbaceous grasslands (~26%), and pastures and hay production (~15%; Homer et al. 2015). The annual hydrograph at the watershed's outlet (USGS gage #06469400) is characterized by consistently high flows during spring months (via snowmelt) and occasional rain-event-driven flows of lesser magnitude during the rest of the year. The Pipestem River drains to the Pipestem Lake, a human-made reservoir ~10 km downstream of the USGS gage. Below the Pipestem Lake, the Pipestem River drains to the James River and then to the Missouri River.

The Pipestem River watershed contains a large number of prairie pothole depressional wetlands (see Fig. 1). These wetlands range in storage capacities, degree of surface connectivity, and inundation dynamics (e.g., from perennial to ephemeral; LaBaugh et al. 1998). Pothole water levels typically increase during spring snowmelt and then gradually decrease via evapotranspiration (ET) and groundwater losses during the summer and autumn months, with intermediate rain-induced increases. During periods of increased water levels, snowmelt and rainfall can induce temporally variable inter-wetland hydrologic connections where some upgradient wetlands fill and then spill (i.e., “fill-spill”) to downgradient wetlands and drainage networks (Tromp-van Meerveld and McDonnell 2006).

Preliminary data processing

We conducted preliminary data preparation and analyses to characterize the watershed’s depressional wetlands for our model. First, we identified depressional wetlands using the National Wetland Inventory (NWI; U.S. FWS 2015) and the National Hydrology Dataset (NHD; Simley and Carswell 2009, accessed 2016) following Lane et al. (2012) and Lane and D’Amico (2016). In short, depressional wetlands were delineated based on distance to stream as a floodplain proxy; any NWI wetland that was >10 m from an NHD feature was considered a depressional wetland (see Lane and D’Amico 2016 for additional information). Second, we estimated each depressional wetland’s maximum storage capacity (volume, m^3) using a digital elevation model (DEM) and a storage estimation tool in ArcGIS (v. 10.2; ESRI 2012) following Lane and D’Amico (2010). These estimates were used to specify water storage and spillage depth thresholds for individual depressional wetlands. Depressional wetlands with storage capacities <100 m^3 were excluded from our analysis to decrease the computational complexity of our model. Lastly, we delineated the watershed’s depressional wetland fill-spill network, which we define as the upgradient to downgradient network of depressional wetlands through which surface water may flow before reaching a stream. To do so, we used the DEM and a topographic flow analyses as described by Evenson et al. (2016). The resultant network delineation was used to direct surface water (i.e., fill and spill) flows within our hydrologic model. The preliminary analysis identified ~13,000 depressional wetlands with storage capacities >100 m^3 (our minimum) to be included in our hydrologic model (Table 1).

Modeling approach

In previous work, we constructed and calibrated a hydrologic model for the Pipestem River watershed by modifying the Soil and Water Assessment Tool (SWAT; Evenson et al. 2016). Here, we briefly discuss model improvements, data inputs, and calibration; see Evenson et al. (2016) for complete model information, which also includes a detailed section on model assumptions and limitations. SWAT is a watershed hydrologic model operating at a daily time step that is commonly applied to evaluate land management strategies in agriculturally dominated landscapes (Arnold et al. 2012) but is limited in its representation of individual wetland hydrologic processes (Evenson et al. 2016). As such, we constructed a modified SWAT model, as described in Evenson et al. (2016), to represent watershed’s depressional wetlands as individual simulation units (i.e., hydrologic response units, HRUs) that conformed to the spatial boundaries of identified depressional wetlands. Our model also identified upland (i.e., non-wetland) simulation units that drained to each depressional wetland. If water volume within a depressional wetland exceeded its maximum storage capacity, the excess (i.e., spillage) was routed to the next immediately downgradient wetland or the stream if no such depressional wetland simulation unit existed. In this way, our model simulated daily water storage and fill-spill connections of depressional wetlands, and their impact on watershed water storage (inundation areas and residence time) and streamflow generation.

We constructed the Pipestem River watershed model using spatially continuous data for elevation (Gesch et al. 2002), soils (Schwarz and Alexander 1995), and land use (Homer et al. 2015), as well as daily precipitation and temperature observations (Thornton et al. 2014). We calibrated the model to daily streamflow observations at USGS gage #06469400 at Pingree, North Dakota, USA as described by Evenson et al. (2016). We utilized a calibration period of three years (1 January 2009 to 31 December 2011); a verification period of two years (from 1 January 2012 to 31 December 2013); and a three-year model spin-up period (a period of time to stabilize the model to the initial conditions and the forcing functions, such a precipitation and temperature inputs; 1 January 2006 to 31 December 2008). Based on precipitation records from 1990 to 2013, the calibration period included "average" (2009, 2011) and "wet" (2010) years; the verification period included average (2013) and "dry" (2012) years ("dry" was less than one standard deviation from the mean [<428.9 mm]; "average" was within one standard deviation of the mean; and "wet" was greater than one standard deviation of the mean [>611.7 mm]).

The model's calibration was executed using an uncertainty fitting algorithm (Sequential Uncertainty Fitting v.2; Abbaspour et al. 2007). The objective of the calibration procedure was the discovery of a suite of model parameter combinations that produced acceptable performance with respect to the replication of observed streamflow values at the watershed outlet. We used this approach to capture the uncertainty surrounding simulated model outputs, which differed from traditional calibration procedures that identify a single "optimal" set of parameters for the model. Specifically, our procedure resulted in 250 parameter combinations that produced Nash-Sutcliffe Efficiency (NSE) values >0.5 (NSE is a commonly used performance metric and NSE values >0.5 imply acceptable model performance; Moriasi et al. 2007). The model was then executed once for each of the 250 parameter combinations; the range of simulation outputs across the combinations represented uncertainty with respect to model outputs. While these 250 parameter combinations met or exceeded performance threshold criteria, the model verification indicated that the model could not replicate variability in streamflow at streamflow magnitudes less than ~4 m^3/s (see Evenson et al. 2016 for additional information).

Scenarios of depressional wetland loss and management

Our modified model (including ~13,000 depressional wetlands) and its 250 different parameter combinations constituted the baseline model. We then developed three categories of scenarios that removed depressional wetlands from the baseline model to assess how wetlands vulnerable to loss and subject to potential management efforts affect watershed functions. The first scenario (ALLWETX; Table 1) sought to evaluate the cumulative effects of depressional wetlands via 100% removal of the watershed's depressional wetlands. The second set of scenarios aimed to assess effects of the preferential loss of wetlands by surface area extent. Here, we evaluated two cases: loss of depressional wetlands with surface areas above and below a 3.0-ha threshold (WET > 3 haX and WET < 3 haX; Table 1), which corresponded to a natural break in the distribution of depressional wetland surface areas. Our third set of scenarios were intended to evaluate management strategies that protect depressional wetlands according to their proximity to streams. These scenarios removed depressional wetlands via measures of Euclidean distance to National Hydrology Dataset

(NHD) flow lines (approximate mid-point of the stream system) and included two cases: loss of wetlands that are 30 m (WET > 30 mX) and 457 m (WET > 457 mX) from the stream. The distances selected (i.e., 100 feet and 1,500 feet, respectively [1 foot = 0.30 m) approximate those for which managers may establish thresholds for wetland protection, as discussed by Alexander (2015).

Scenario analysis

For each scenario, depressional wetlands were removed from the baseline model, and the model was executed once for each of the 250 parameter combinations to assess uncertainty in model outputs. We evaluated three daily outputs for each scenario: (1) wetland inundated area and residence times across the watershed, (2) watershed area contributing surface runoff to the stream, and (3) streamflow. Wetland inundated area was determined using each wetland's simulated daily storage volume (m^3), assuming an inverted conic reservoir with DEM-delineated slopes as described by Evenson et al. (2016). Wetland residence times were calculated as the quotient of each wetland's simulated daily storage volume (m^3) to total simulated daily outflows (m^3/d). Areas contributing surface runoff to the stream (hereafter referred to as contributing area) on any given day were identified as (1) upland areas that drained directly to the stream (i.e., not to a wetland) and had either snowmelt or received precipitation on that day, (2) upland areas that drained to a wetland that was hydrologically connected to the stream on that day, or (3) wetland areas that were hydrologically connected to the stream on that day. We considered a wetland to be hydrologically connected to the stream on any given day if the depressional wetland either spilled directly to the stream or to a network-path of spilling depressional wetlands that were terminally connected to the stream. Simulated daily streamflow at the watershed outlet (USGS gage #06469400, see Fig. 1) was also tracked across scenarios to assess how changes in watershed storage and connectivity influenced cumulative water export.

Results

Watershed storage: wetland inundation and residence times

As we removed depressional wetlands from the model, cumulative wetland inundated area and residence time decreased (Table 2). The larger depressional wetlands had a greater impact on cumulative simulated inundated area relative to the smaller depressional wetlands. Removal of the larger wetlands (>3.0 ha) resulted in a mean daily cumulative inundated area of ~1,745 ha (~48% decrease relative to the baseline). Notably, the larger wetlands (>3.0 ha) accounted for just ~5% of wetlands within the baseline simulation. Conversely, we observed that the smaller depressional wetlands had a greater effect on cumulative simulated residence times. The model predicted a cumulative residence time of ~238 × 10^4 d (~2.9% decrease relative to baseline) following removal of the larger wetlands (>3.0 ha) compared to ~25 × 10^4 d (~90% decrease relative to baseline) following removal of the smaller wetlands (<3.0 ha).

The largest decreases in watershed-scale inundated area and residence times resulted from scenarios that removed wetlands according to their proximity to a stream (WET > 30 mX and WET > 457 mX; Table 2). These scenarios unsurprisingly created the largest decrease in wetlands as few depressional wetlands were found in the areas proximate to stream. Less than 1% and ~20% of the wetlands were preserved after removing wetlands >30 m and >457 m from the stream, respectively. Concordantly, the model predicted large decreases in cumulative inundated area (~98% and ~85% declines relative to the baseline for WET > 30 mX and WET > 457 mX, respectively) and residence time (~99% and ~75% declines relative to the baseline for WET > 30 mX and WET > 457 mX, respectively; Table 2).

Model simulations also highlight effects of loss scenarios on the watershed distribution of wetland inundation and residence times. The numerous small depressional wetlands (<3.0 ha) played an important role in maintaining landscape heterogeneity for inundation patterns and residence times. Discontinuous concentrations of inundated area and residence time developed as we removed the smaller depressional wetlands (Figs. 2A, B, 3A, B; WET < 3 haX), whereas removal of larger wetlands resulted in a more continuous spatial distribution (Figs. 2C, 3C; WET > 3 haX). Removing wetlands by their proximity to the stream resulted in inundated area and residence time concentrations adjacent to the stream with the majority of the watershed devoid of wetlands (Figs. 2D,E, 3D,E, WET > 30 mX, WET > 457 mX).

Watershed connectivity and export: contributing areas and streamflow

Depressional wetlands acted as “gatekeepers” that decreased overall watershed connectivity by preventing surface runoff from reaching the stream network. As wetlands were removed from the model, overland runoff otherwise intercepted and stored within the wetlands instead entered the stream network. Hence, runoff contributing area increased across all scenarios (Table 2). However, we observed that larger depressional wetlands played a greater role in regulating watershed connectivity relative to smaller wetlands. When removing large wetlands, mean daily cumulative contributing area increased to ~17.1% of the watershed, which represented a ~54% increase in connected area relative to the baseline (Table 2). Removal of small wetlands resulted in a mean contributing area of ~14.0% of the watershed (~26% increase relative to the baseline; Table 2). Evaluation of the spatial distribution of contributing areas across the scenarios further highlighted the role of larger depressional wetlands in decreasing watershed connectivity (Fig. 4). The probability of streamflow contribution was markedly higher in portions of the watershed following removal the larger wetlands (Fig. 4C) relative to removal of the smaller wetlands (Fig. 4B) in a significant portion of the watershed.

Loss of wetlands distant from stream (WET > 30 mX and WET > 457 mX) induced a striking increase in overall watershed connectivity. These scenarios resulted in ~175% (WET > 30 mX) and ~133% (WET > 457 mX) increases (relative to the baseline simulation) in runoff contributing area (Table 2). Further, these scenarios predicted distinct spatial patterns of runoff contribution relative to the baseline, with probabilities of contribution exceeding ~40% in significant portions of the watershed (Fig. 4D, E).

Wetland loss that resulted in increased watershed connectivity was reflected downstream by increases in peak flows. These results were particularly pronounced during the spring snowmelt period as indicated by comparing baseline and ALLWETX spring hydrographs for the 2009–2011 simulation period (Fig. 5). For example, the median simulated streamflow for 14 April 2009 (arbitrarily chosen as a representative day during the spring snowmelt period) was 144 m^3/s for the baseline simulation but 169 m^3/s for the ALLWETX scenario, a 17% increase. Wetland effects on peak streamflow were also evident across the simulation period as indicated by divergent baseline and ALLWETX probabilities of exceedance (PE) for all magnitudes of streamflow (Fig. 6A). These plots showed that PE at high flows was consistently higher following depressional wetland removal. Importantly, our observation that depressional wetlands attenuate peak streamflow was robust: 241 of the 250 (~96%) parameter combinations showed this effect (see Fig. 5). In contrast, we found that depressional wetlands did not have a sizable impact on baseflow (i.e., PE for low flow events; Fig. 5).

Larger depressional wetlands had a greater impact on peak streamflow relative to smaller depressional wetlands. The resultant increase in PE from removing the larger depressional wetlands (WET > 3 haX) was approximately twice the increase that resulted from removing only the smaller depressional wetlands (WET < 3 haX; Fig. 6B). The smaller depressional wetlands (<3.0 ha) constituted ~95% of the watershed's depressional wetlands population but just ~35% of the watershed's cumulative storage capacity (i.e., the sum of maximum storage capacity across all depressional wetlands). Thus, through greater storage capacity, larger depressional wetlands (>3.0 ha) had a more substantive impact on PE, though the larger wetlands represented a smaller portion of the wetland population.

Scenarios of loss by distance from stream resulted in near-identical and significant increases in peak streamflow (Fig. 6C). These scenarios (WET > 30 mX and WET > 457 mX) resulted in ~99% and ~80% depressional wetland losses, respectively, and resulted in peak streamflow increases approaching the increase projected by ALLWETX (for which all depressional wetlands were removed). Thus, protecting depressional wetlands based on proximity to stream (delimited via 30-m or 457-m stream buffers) in our study area was not associated with maintaining or reducing peak streamflow compared to the baseline model.

Discussion

Depressional wetlands demonstrate a clear capacity to modify landscape hydrological functions (McLaughlin et al. 2014, Evenson et al. 2015, Rains et al. 2016). Anthropogenic influences, such as drainage ditches, human-mediated climate change, and land management activities have and will lead to potential variations or losses in depressional wetlands, particularly in specific regions (Johnston 2013, Sofaer et al. 2016), and of different wetland size classes (Le and Kumar 2014, Van Meter and Basu 2015, Serran and Creed 2016). Here, we project the consequent implications on watershed functions resulting from preferential depressional wetland losses and potential management efforts in the Prairie Pothole Region (PPR) of North Dakota. We also assess the potential applications of this work and highlight future research needs.

Depressional wetlands affect watershed storage: hydrological, biogeochemical, and ecological implications

Our simulation results confirmed that depressional wetlands affect watershed water storage, with associated influences on inundation area and residence times. Specifically, we found that loss of small wetlands resulted in changes to the spatial distribution of wetlands across the watershed and greater reductions in cumulative inundated area and residence times (Table 2, Figs. 2, 3). Notably, preservation of only those wetlands proximate to stream resulted in a substantive loss of inundated area and residence times across the entire watershed (Figs. 2, 3).

The spatial distribution of depressional wetlands plays a significant role in maintaining landscape heterogeneity and thus biological connectivity and provisioning of vital habitat for numerous species (Gibbs 1993, Schofield et al. 2008). This role is particularly strong for small wetlands. As small depressional wetlands (<3 ha) were removed in our scenario analyses, a discontinuous, low density patchwork of large wetlands with large surface areas remained (Fig. 2B). If large depressional wetlands (>3 ha) were removed, a more spatially contiguous network of small wetlands remained, providing increased potential for inundated habitat and biological connectivity for wetland-dependent species (Fig. 2C). Niemuth and Solberg (2003), for example, describe a strong positive correlation between the number of prairie pothole wetlands and the density and distribution of regional waterfowl populations. Uden et al. (2014) suggest that managers should promote shorter migratory pathways (via maintenance of numerous small wetlands) to promote native anurans (types of frogs and toads) and increase overall system resilience. Similarly, Mushet et al. (2012, 2013) indicate that shorter migratory pathways promote genetic diversity and thereby system resilience in amphibian populations such as the northern leopard frog (*Lithobates pipiens*). Collectively, studies suggest that if the wetland management target is biological connectivity, a dense network of small depressional wetlands with short pathways between them is preferable (Schofield et al. 2008). This highlights the importance of protection and restoration of small wetlands for ecological targets.

Water quality maintenance or improvement across the watershed may also be mediated by depressional wetlands (Marton et al. 2015, Cohen et al. 2016). Water residence times in depressional wetlands exert considerable control over a watershed’s potential for nutrient, metal, and other pollutant transformation, retention, and removal (Powers et al. 2012, Marton et al. 2015, Cohen et al. 2016). Long water residence times, which can be cumulatively extensive across a network of depressional wetlands, allow kinetically limited reactions to complete (Holland et al. 2004). Our scenarios highlight that depressional wetland loss decreases the cumulative watershed residence times and, by extension, the watershed’s biogeochemical processing potential. Our scenarios also highlight that smaller depressional wetlands account for a significant portion of the watershed’s cumulative residence time. Removal of the smaller wetlands (<3 ha) resulted in a ~90% reduction in cumulative residence time relative to the baseline (Table 2). Small depressional wetlands can be bioreactor hotspots due to their high perimeter-to-area ratios (Marton et al. 2015, Cohen et al. 2016), which provide variation (over space and time) in soil moisture, redox conditions, and associated biogeochemical processes (Hefting et al. 2013). Finally, our scenarios also highlight that loss of depressional wetland distant from the stream resulted in complete loss of depressional wetlands in headwater areas (Fig. 2D,E). Headwater wetlands are often the most efficient biogeochemical processors (e.g., for sediment and phosphorus removal; Cohen and Brown 2007), highlighting potential consequences of prioritizing protection of near-stream wetlands.

Depressional wetlands affect watershed connectivity and export: hydrological, biogeochemical, and ecological implications

Depressional wetlands regulate watershed hydrologic connectivity, where disconnected wetlands reduce areas that contribute surface runoff to the stream. Loss of depressional wetlands across all scenarios resulted in increased watershed connectivity and attendant increases in peak streamflow magnitudes (Table 2; Figs. 4–6). These effects were greatest when larger wetlands or ones distant from stream were removed (Figs. 4D,E, 5B,C). This was particularly evident during the spring snowmelt season, and is consistent with large depressional wetlands serving as “gatekeepers” for watershed-scale water storage and flood prevention in the PPR (Pomeroy et al. 2014). Our findings concur with previous studies that demonstrate the role of depressional wetlands in attenuating peak streamflow in the PPR (Vining 2002, Shook and Pomeroy 2011, Pomeroy et al. 2014) and more broadly (Evenson et al. 2015, Fossey et al. 2016, Golden et al. 2016). Therefore, limited protection of depressional wetlands in this system may contribute to flood events in the larger James and Missouri Rivers, which exist downstream of the study watershed.

Increased peak flow magnitudes with depressional wetland loss can have consequential impacts on in-stream ecological structure and functions. It is well recognized that alterations in aquatic flow regimes can affect physical habitat structure, which modifies the biotic composition of the stream, alters species viability, and enhances the introduction and invasion of new species (Bunn and Arthington 2002, Poff and Zimmerman 2010, Poff et al. 2010). High stream flows can maintain some critical ecological functions in streams (e.g., sediment mobilization and habitat enhancements on floodplains; Doyle et al. 2005). However, increased peak flow magnitudes as a result of depressional wetlands losses (Records et al. 2014) can negatively impact the biological integrity of the stream by shifting it to a new hydrologic regime (Arkle et al. 2010, Poff and Zimmerman 2010). For example, peak flows that increase in magnitude and frequency can lead to stream bank scour, which modifies the material transported to downstream habitats and thereby the structure and function of the aquatic ecosystem (Doyle et al. 2005). Increases in magnitude and frequency can also lead to stream down-cutting, which decreases stream–floodplain interactions to further increase peak flows (stream–floodplain disconnection indicates decreased residence time) and negatively affect baseflow (decreased residence times in floodplains indicates decreased contributions to the hyporheic zone). Our predictions of increased peak flows with depressional wetland loss is akin to the shift in hydrology and associated aquatic ecological impacts of an urbanizing watershed. For example, streams in urbanizing systems that transition to more frequent and higher magnitude peak flow conditions often convert to having low biodiversity, simple trophic structures, and dominance by a few taxa (Konrad and Booth 2005).

Increased watershed connectivity and associated peak flow magnitudes from depressional wetland removal can also impact stream water quality by elevating solute and particulate transport and downstream loads. This is particularly true if sources are readily available at surface and/or in upper soil layers (e.g., as with forms of nitrogen; Bechtold et al. 2003, Secchi et al. 2011). Elevated transport of dissolved nutrients and sediment during peak flow periods may lead to eutrophication, decreased water clarity, and shifts in the trophic structure of receiving streams (Biggs and Close 1989). Consequences of depressional wetland loss would also extend to loading of other contaminants (e.g., pesticides, road salts) present in the watershed, highlighting the broad role of these systems to reduce runoff, store water, and improve water quality.

Broader applications and future research

Our work provides both scientific insights and a general modeling framework to advance adaptive approaches for the wise management of depressional wetland resources (e.g., Creed et al. 2017). Our results suggest that substantial watershed hydrological, ecological, and biogeochemical functions may be compromised by continued depressional wetland losses in the PPR. As such, we conclude that PPR depressional wetlands in the study watershed have both quantifiable hydrologic connections to and aggregate hydrological, ecological, and biogeochemical effects on downgradient waters. Therefore, local, tribal, state, or regional resource management entities may consider targeting remaining PPR depressional wetlands to limit the functional losses and deleterious effects on downstream systems associated with limited wetland protections (e.g., Lane et al. 2018, U.S. EPA 2015). More broadly, our modeling approach explicitly represents individual depressional wetlands and explores specific scenarios of their loss, providing a general framework that can be applied in other depression-rich landscapes to inform specific management actions. Such applications, however, would require requisite data inputs, calibration, and verification of our refined model or use of an alternative model that explicitly represents depressional wetlands.

Both empirical and modeling research should continue to evaluate the extent to which wetland losses affect attendant watershed functions under diverse scenarios across different physiographic regions to better understand the potential range of impacts. Such efforts are particularly important as loss of these vulnerable waters continues across the globe (Creed et al. 2017). Wetlands and wetland networks in other physiographic regions may function differently and have distinct impacts on watershed functioning, requiring region-specific data inputs and approaches.

Advances in research are also needed to assess the sensitivity of our model and other modeling approaches to variations in input data, such as those used to identify depressional wetlands and potential wetland fill-spill relationships. For example, we used the National Wetland Inventory (NWI) to identify depressional wetlands. NWI wetlands may exist within larger, merged depressions that have high storage capacities, which may result in potential overestimates in the simulated rates of wetland spillage. Similarly, DEM resolution may have an effect on how wetland fill-spill drainage networks are derived in the model, an area of study that should be further pursued.

Conclusions

Effective landscape-scale management requires consideration and optimization of trade-offs in specific ecosystem functions. Collectively, our results point to large depressional wetlands regulating runoff generation and thereby streamflow. However, the historical loss of small wetlands in the PPR deserves critical examination because this creates problematic shifts in landscape inundation patterns and associated biodiversity in the region (Van Meter and Basu

2015) and alters processes related to the retention of nutrients and pollutants (Marton et al. 2015, Cohen et al. 2016). Therefore, optimizing one management goal (e.g., protection of large depressional wetlands for flood attenuation) over another (e.g., protecting of small depressional wetlands for biodiversity) may come at a cost for overall watershed resilience and integrity. Moreover, focusing protection on wetlands proximate to stream may have large consequences for a full suite of wetland functions distributed across the watershed.

We conclude that depressional wetlands have a substantial impact on PPR watershed functions. Our work provides supportive evidence and a general modeling approach for informed management of depressional wetlands aimed at limiting the depletion of watershed-scale functions. Our results suggest that management strategies based solely on the size of depressional wetlands or their distance to the stream will not preserve the suite of beneficial functions these systems confer on a watershed (i.e., peak flow attenuation, aquatic habitat mosaics that contribute to biodiversity, and ample biogeochemical processing potential). Therefore, as wetland losses and modifications across a range of size classes and stream proximities continue from encroaching threats (e.g., hydrologic alterations from variations in precipitation and temperature patterns, ditching or drainage for development), a concomitant decline in PPR watershed functions may be expected.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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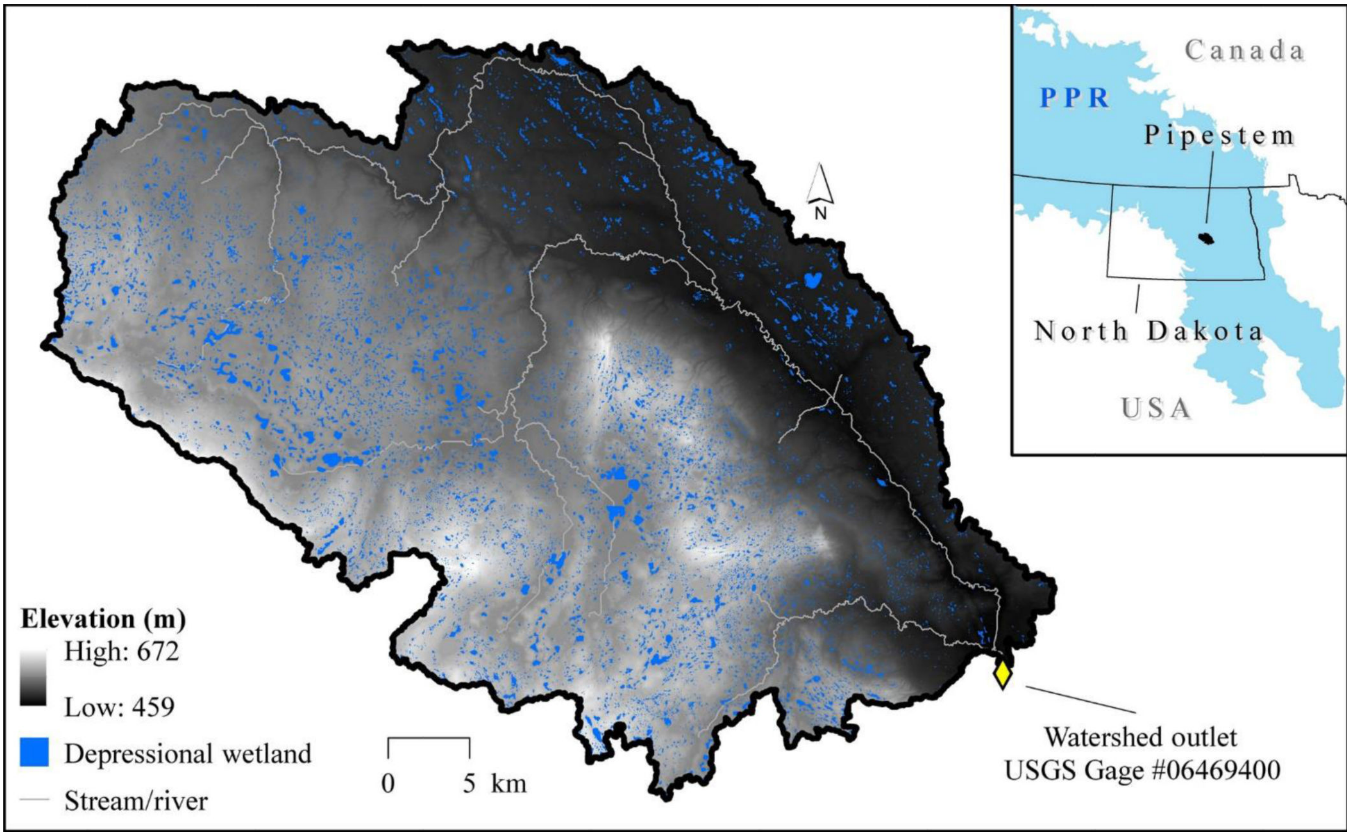

Figure 1.

Project study site. The Pipestem River watershed, located in the Prairie Pothole Region (PPR) in North Dakota, USA, is ~1,700 km^2. Depressional wetlands were identified using National Wetland Inventory and are shown on a 30-m digital elevation model (DEM) along with the DEM-delineated stream network.

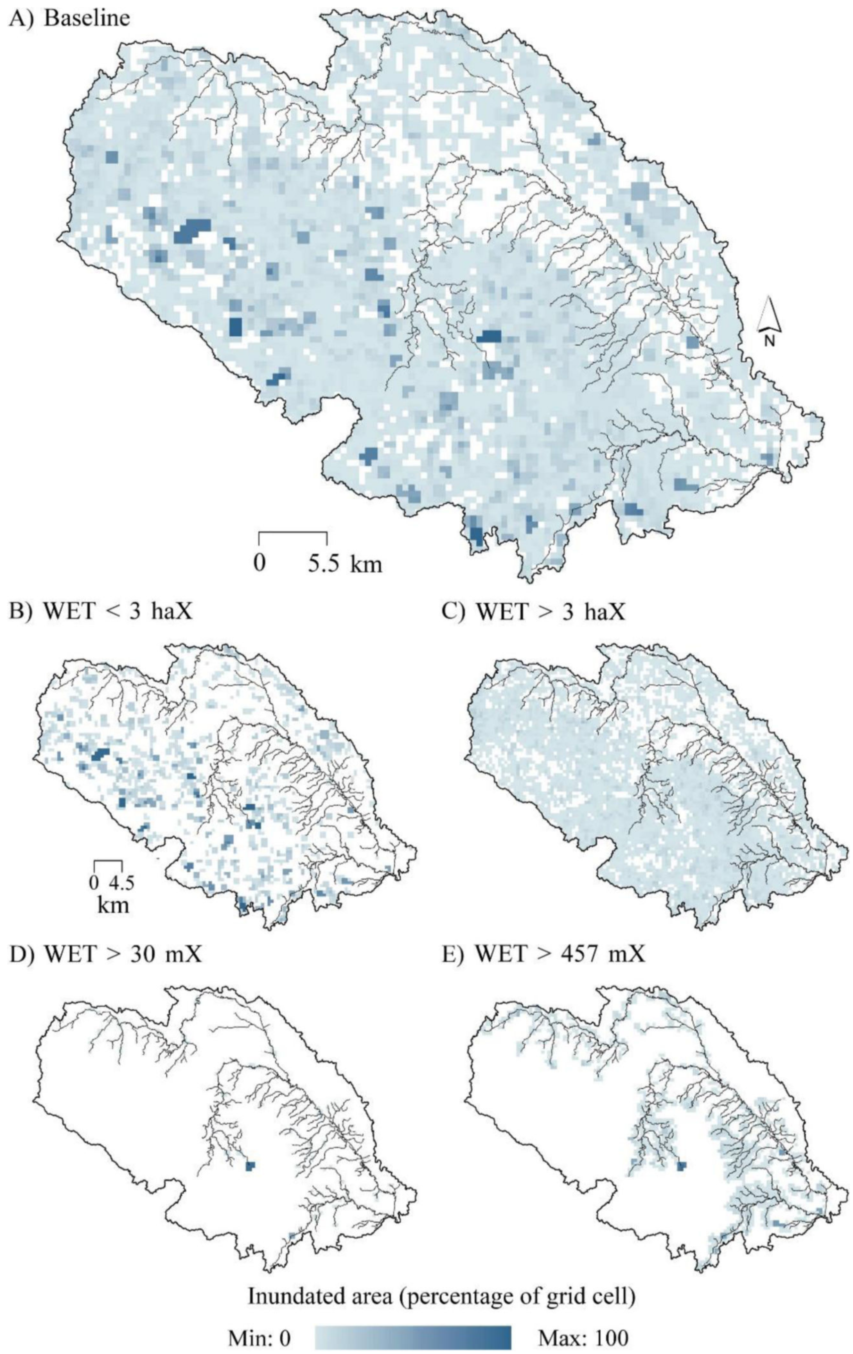

Figure 2.

Simulated median daily inundated area (ha) under the baseline model and scenario conditions. Median daily inundated areas for each depressional wetland were calculated for the full simulation period and the 250 different model parameter combinations. Estimates were then aggregated to a 0.5-km grid-resolution to improve map readability.

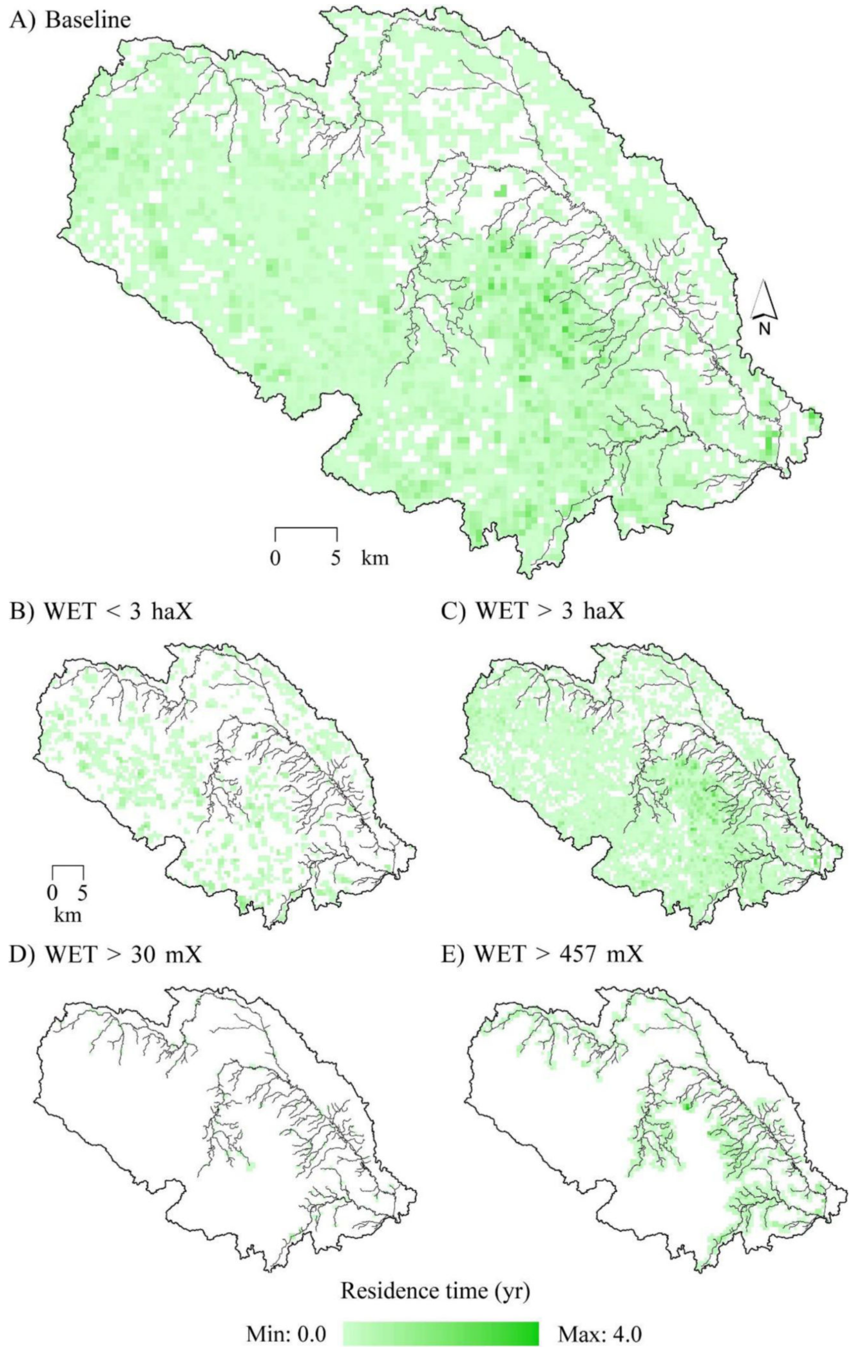

Figure 3.

Simulated median daily wetland residence times under baseline model and scenario conditions. Median daily surface areas for each depressional wetland were calculated for the full simulation period and the 250 different model parameter combinations. Estimates were then aggregated to a 0.5-km grid-resolution to improve map readability.

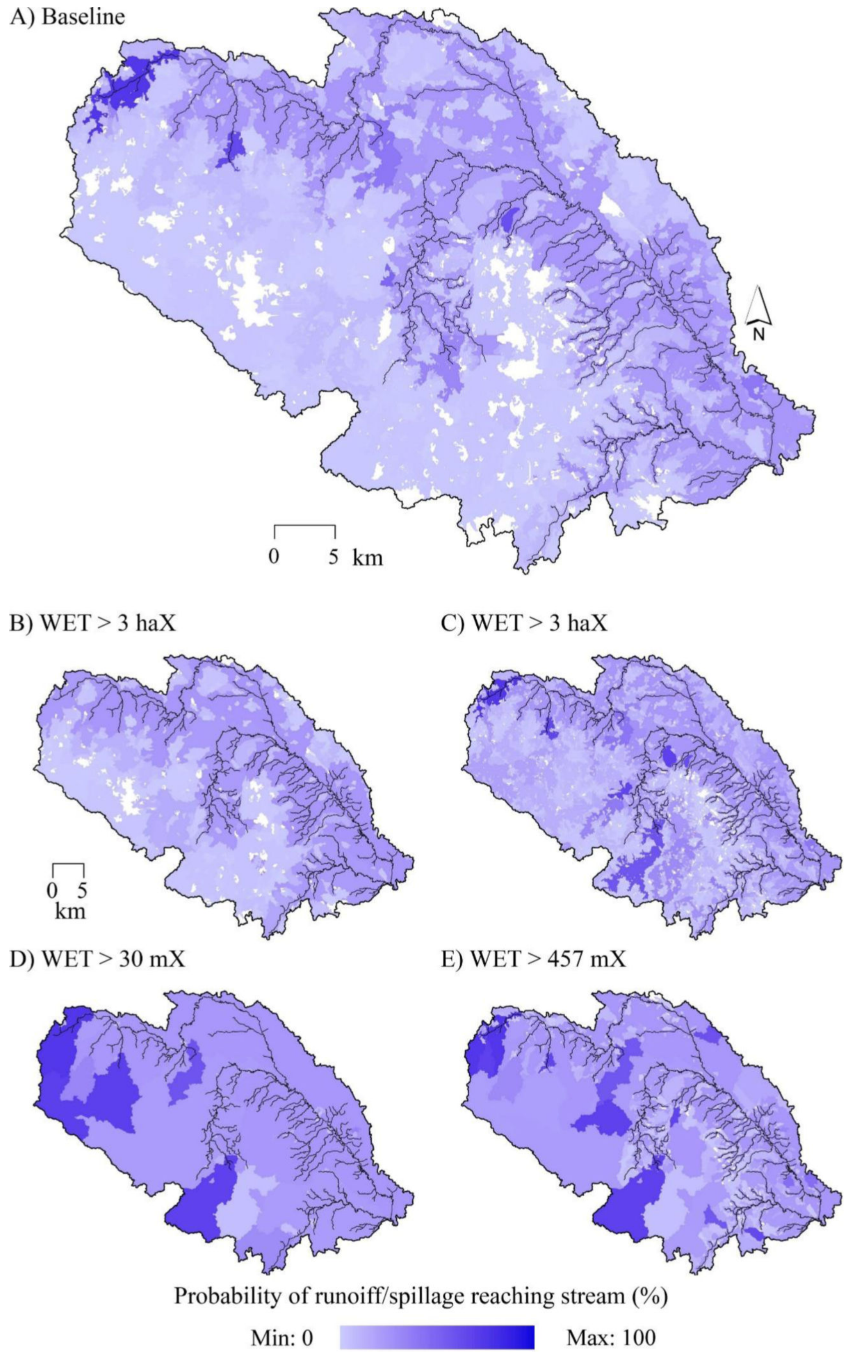

Figure 4.

Simulation results demonstrating the temporal probability of watershed runoff or wetland spillage reaching the stream network (via direct upland overland flow or surface flow among hydrologically connected wetlands) under baseline and scenario conditions. Each probability calculation on the map represents the median value for the full simulation period (2009–2011) across the 250 different model parameter combinations.

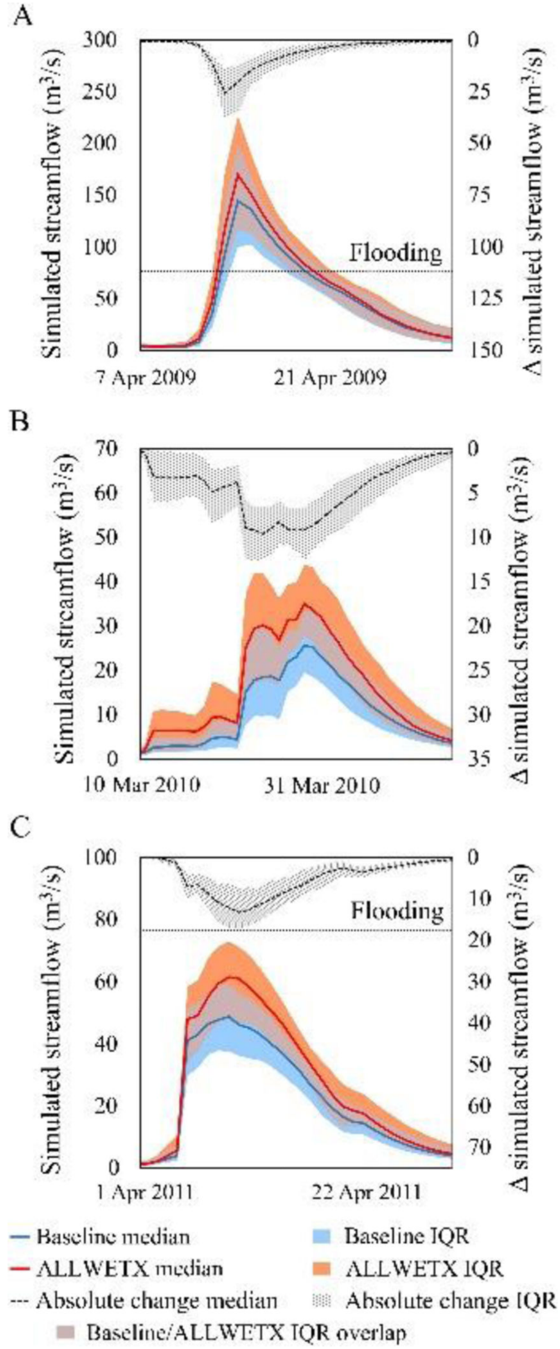

Figure 5.

Hydrograph of the baseline and ALLWETX simulations during the spring snowmelt periods of 2009, 2010, and 2011. The left *y*-axis shows the median and interquartile range (IQR) of daily simulated streamflow (m^3/s; for the baseline and ALLWETX) across the 250 different model parameter combinations. The right *y*-axis shows the median and IQR of the change in daily simulated streamflow (ALLWETX minus baseline; m^3/s) for the 250 different model parameter combinations. The lateral dashed line for "flooding" threshold denotes the

National Weather Service flooding threshold (76.5 m^3/s; estimated using USGS observed streamflow values). Note the change in left and right *y*-axis values among figure panels.

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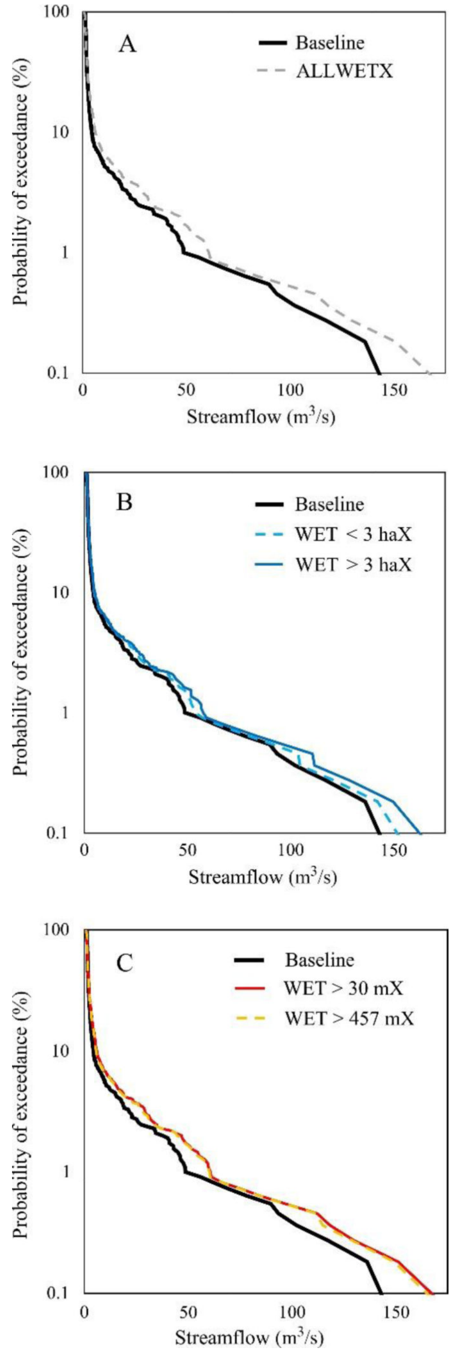

Figure 6.

Probability of streamflow exceedance for each set of scenarios. The plots show the simulated median daily streamflow across the 250 different model parameter combinations. Note log scale of *y*-axes.

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Table 1.

Descriptive statistics for the input depressional wetland data used for the baseline model and each scenario

	Count	Maximum volume (10^4 m^3)	Surface area (ha)	Distance to stream (m)
Baseline	12,921	0.04 (2.4)	0.3 (2.6)	1,633 (2760)
ALLWETX	0	NA	NA	NA
WET < 3 haX	616	2.5 (9.5)	5.0 (9.1)	2,430 (2973)
WET > 3 haX	12,305	0.04 (0.3)	0.3 (0.5)	1,599 (2742)
WET > 30 mX	120	0.03 (3.0)	0.2 (6.6)	18.4 (10.0)
WET > 457 mX	2,668	0.04 (1.2)	0.2 (1.8)	219.3 (124)

Notes - Values are medians with SD in parentheses. NA, not applicable.

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Table 2.

Descriptive statistics for the simulation outputs

	Inundated area (ha)			Residence time (10^4d)			Runoff contributing area (percentage of watershed area)
	Mean[a]	**SD**[a]	**Sum**[b]	**Mean**[a]	**SD**[a]	**Sum**[b]	**Sum**[b]
Baseline	0.26	0.09	3351	0.73	2.59	245	11.1
WET < 3 haX	2.98	0.73	1835	1.20	4.56	25	14.0
WET > 3 haX	0.14	0.06	1745	0.69	2.51	238	17.1
WET > 30 mX	0.43	0.15	52	0.37	1.64	3	30.5
WET > 457 mX	0.19	0.06	508	0.74	2.95	62	25.9

[a]Calculated as the per wetland mean or standard deviation across all days and all parameter sets.

[b]Calculated as the mean daily sum across all wetlands and all parameter sets.