Temporal and spatial patterns of wetland extent influence variability of surface water connectivity in the Prairie Pothole Region, United States

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Abstract

Context Quantifying variability in landscape-scale surface water connectivity can help improve our understanding of the multiple effects of wetlands on downstream waterways.

Objectives We examined how wetland merging and the coalescence of wetlands with streams varied both spatially (among ecoregions) and interannually (from drought to deluge) across parts of the Prairie Pothole Region.

Methods Wetland extent was derived over a time series (1990–2011) using Landsat imagery. Changes in landscape-scale connectivity, generated by the physical coalescence of wetlands with other surface water features, were quantified by fusing static wetland and stream datasets with Landsat-derived wetland extent maps, and related to multiple wetness indices. The usage of Landsat allows for decadal-scale analysis, but limits the types of surface water connections that can be detected.

Results Wetland extent correlated positively with the merging of wetlands and wetlands with streams. Wetness conditions, as defined by drought indices and runoff, were positively correlated with wetland extent, but less consistently correlated with measures of surface water connectivity. The degree of wetland–wetland merging was found to depend less on total wetland area or density, and more on climate conditions, as well as the threshold for how wetland/upland was defined. In contrast, the merging of wetlands with streams was positively correlated with stream density, and inversely related to wetland density.

Conclusions Characterizing the degree of surface water connectivity within the Prairie Pothole Region in North America requires consideration of (1) climate-driven variation in wetness conditions and (2) within-region variation in wetland and stream spatial arrangements.

Keywords Wetland inundation · Wetland-stream connectivity · Geographically isolated wetlands · Prairie Pothole Region · Landsat · Interannual variability

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Introduction

Wetland systems provide many critical ecological functions including groundwater recharge, floodwater retention, lotic base flow contributions, biogeochemical processing, water quality improvement, and

wildlife habitat (Mitsch and Gosselink 2000; Whigham and Jordan 2003; Millennium Ecosystem Assessment 2005; Brauman et al. 2007). Federal jurisdiction over wetlands, under the Clean Water Act, is informed by several court decisions including the U.S. Supreme Court Decisions in *SWANCC v. U.S. ACE* (531 U.S. 159 (2001)) and *Rapanos v. United States* (547 U.S. 715 (2006)). These decisions indicated that wetlands having a “significant nexus” with “navigable waters” may be jurisdictional under the Clean Water Act (Leibowitz et al. 2008). This has motivated research to determine the number and distribution of wetlands that could be jurisdictional (Tiner 2003; Frohn et al. 2012; Lane et al. 2012), their spatial relationships to streams (Lang et al. 2012), and the ecosystem functions that these wetlands provide (Whigham and Jordan 2003; Comer et al. 2005; Lane and D’Amico 2010).

The identification of potentially jurisdictional wetlands has focused on the subset of wetlands lacking obvious surface water connections (Tiner 2003; Lane et al. 2012). These wetlands are commonly referred to as potentially geographically isolated wetlands or pGIWs, although this phrase is controversial and can be misleading (Mushet et al. 2015). Although most efforts to identify these wetlands have relied on static wetland datasets (Tiner 2003; Lane et al. 2012), the actual degree of surface water connectivity varies among wetlands and for many can be expected to fluctuate over time (Leibowitz and Vining 2003; Winter and LaBough 2003; Shook et al. 2015).

Wetlands have the capacity to store precipitation and hydrologic inflows (Ludden et al. 1983; De Laney 1995), reducing peak stream flows and downstream flooding by temporarily reducing the contributing area for a watershed’s outlet (Philips et al. 2011; Shaw et al. 2013). However, under wet conditions many of these same wetlands intermittently exchange or contribute water to other wetlands and/or streams through temporary overland or shallow groundwater flows, ephemeral flows in channels, and/or the merging of wetland waters in low relief areas (Rains et al. 2006; Cook and Hauer 2007; Rains et al. 2008; Sass and Creed 2008; Kahara et al. 2009; Wilcox et al. 2011). Connectivity between wetlands within wetland complexes that eventually “fill and spill” (Tromp-van Meerveld and McDonnell 2006) into streams can result in highly non-linear relationships between basin water storage capacity and stream contributing area (Philips et al. 2011; Shaw et al. 2012, 2013).

The Prairie Pothole Region (PPR) in north-central North America contains a high density of depressional wetland features, a consequence of glacial retreat (Flint 1971), and provides habitat for large populations of waterfowl (Sorenson et al. 1998). Hydrological research efforts within the region have focused on quantifying the effect of inter- and intra-annual variations in water levels or wetland areas on waterfowl habitat availability (Johnson et al. 2004; Kahara et al. 2009; Niemuth et al. 2010; Liu and Schwartz 2011). However, few studies have explicitly examined how interannual variability in wetland area influences hydrological interactions between individual wetlands or between wetlands and streams within this region (Leibowitz and Vining 2003; Kahara et al. 2009).

In this study we quantified how surface water interactions between wetlands and streams varied both spatially and interannually at the landscape scale across the PPR. Our aim was to advance previous efforts using the static National Wetland Inventory (NWI) dataset to map wetlands lacking obvious surface water connections (Tiner 2003; Lane et al. 2012), and more recent efforts to map climatically variable biological connectivity among wetlands (McIntyre et al. 2014; Ruiz et al. 2014). Our objectives were to quantify (1) the interannual variation in wetland extent, (2) how spatial and interannual changes in wetland extent translate into variability in observed wetland–wetland and wetland–stream connectivity, and (3) how interannual variability in waterbody merging and connectivity is related to climate conditions and stream flow. Exploring surface water dynamics in regions with a high density of wetlands is critical to improving our understanding of how wetlands interact with downstream waters. Quantifying temporal and spatial variability in the degree of landscape-scale connectivity will inform our predictions of how climate change and human activities influence the distribution of surface water and magnitude of stream flow.

Methods

Study area and ecoregions

Ecoregions were used as the unit of analysis across two, non-adjacent, Landsat path/rows (Path 29, Row 29 and Path 31, Row 27) within the United States

portion of the PPR (Fig. 1). Spatial patterns in deposited glacial material following the retreat of the Laurentide icesheet continue to influence the topography and drainage systems across the PPR. The selected ecoregions correspond approximately to the extent of physiographic regions and captured the wide diversity of wetland and stream densities and configurations across the study area (Table 1). Ecoregion extent was based on the U.S. Environmental Protection Agency Level IV Ecoregion definitions (Omernik and Griffith 2014), and included (1) the Drift Plains, (2) the Missouri Coteau, (3) the Prairie Coteau, (4) Lowlands (included the Big Sioux Basin, James River

Lowland and Loess Prairie ecoregions), and (5) the Des Moines Lobe (included the Minnesota River Prairie and Tewaukon/Big Stone Stagnation Moraine ecoregion) (Fig. 1). Landcover across both path/rows was dominated by cultivated crops (51 and 62 % for p31r27 and p29r29, respectively), hay/pasture (16 and 10 % for p31r27 and p29r29, respectively), and herbaceous (14 and 13 % for p31r27 and p29r29, respectively) (Homer et al. 2015). Summer (June–August) (19.9 and 20.9 °C) and winter (December–February) (−9.2 and −8 °C) temperatures (1981–2010) were similar between p31r27 and p29r29, while precipitation was lower in p31r27

Fig. 1 Location of Landsat path/rows, ecoregion divisions, and stream gauge locations

Table 1 National Wetlands Inventory (NWI) wetland and National Hydrography Dataset (NHD) stream density by ecoregion

Ecoregion	Size (ha)	Annual Precip (1981–2010) Normal (mm)	NHD stream density (m ha ⁻¹)	NWI wetland area (m ² ha ⁻¹)	NWI wetland count (# per ha)	WSvc/nc count (%)	WSvc/nc area (%)
Lowlands	887,232	653	13.4	485.3	0.06	80.0	40.0
Des Moines Lobe	824,612	648	10.1	616.6	0.02	83.4	31.6
Prairie Coteau	1,215,080	646	9.7	1184.8	0.07	88.4	41.1
Drift Plains	2,337,680	507	4.4	1120.6	0.13	97.4	67.1
Missouri Coteau	524,552	484	3.0	1369.7	0.11	96.9	75.1

WSvc/nc (wetlands variably connected or not connected to a stream) were calculated as the NWI wetlands that did not intersect the NHD stream layer (including stream polygons and 14 m stream buffer). Precipitation data represent spatially averaged PRISM 30 year annual normals (1981–2010)

(496 mm year⁻¹), relative to p29r29 (649 mm year⁻¹) (1981–2010) (NOAA NCDC 2014).

Image processing

Seventeen Landsat images for p29r29 and sixteen Landsat images for p31r27 (<10 % cloud cover) were selected to coincide with snow-free conditions. Cloud cover was a significant obstacle for image selection, particularly during the spring months. The time series (1990–2011) captured a wide range of interannual hydrological conditions (Table 2; Fig. 2), but was not expected to capture peak annual conditions such as specific rain events that could have resulted in short-duration (hours or days) connection events between wetlands and streams. Indices used to characterize wetness conditions are described in “Additional datasets,” below. The images were atmospherically corrected and converted to surface reflectance values using the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) (Masek et al. 2006). The per pixel fraction water was derived using the Matched Filtering algorithm in the ENVI software package (Exelis Visual Information Solutions, Inc, Herndon, VA), then thresholded into inundated, saturated and non-saturated cover classes using a threshold analysis. The Matched Filtering algorithm is a partial unmixing method designed to detect the abundance of a known endmember (e.g. water) against a composite of unknown background endmembers (vegetation, soil, etc.) (Turin 1960), and has been used previously to identify depressional wetland features at a sub-pixel scale (Frohn et al. 2012). Additional steps taken to reduce error included applying a minimum noise fraction transformation (Green et al. 1988), linearly stretching the output values, and masking out impervious

surfaces, defined as low, medium and high density development (Homer et al. 2015), to reduce false positives.

The algorithm output maps representing the fraction water were then classified into inundated (inun), saturated (sat), and non-saturated cover using a threshold analysis. The mean fraction water was derived for five cover classes, with the aim to distinguish between water and vegetation: (1) inundation (i.e. open water) (258 total points), (2) saturation (i.e., visibly wet soil adjacent to open water features) (239 total points), (3) wet channel-swale features (261 total points), (4) non-photosynthetic vegetation (167 total points), and (5) photosynthetic vegetation (183 total points). These 1108 points were randomly selected and distributed across the two Landsat path/rows. Cover classes were identified from 1 m resolution National Agricultural Imagery Program (NAIP) imagery representing three dates per Landsat path/row (April 30, 2004, October 13, 2006 and October 8, 2010 for p29r29; July 1, 2004, October 5, 2004, and September 9, 2006 for p31r27). The inundation threshold represents a high confidence of surface water and was derived using the mean differences in the per pixel fraction water between the inundation and saturation cover classes. The saturated threshold was derived using the mean differences in the fraction water between the saturation and photosynthetic vegetation cover types. This second, more inclusive threshold, allowed for the inclusion of more mixed pixels (e.g. shallow water or shallow sub-surface flow, wetland edges, and vegetated water) (e.g. Sass and Creed 2008), a critical problem in using a moderate resolution source of imagery to detect inundation in a landscape with a

Table 2 Landsat TM images utilized in the analysis and corresponding monthly Palmer Hydrological Drought Index (PHDI) and Standardized Runoff Index (SRI) values

Path/row	Landsat TM image	PHDI	SRI	Path/row	Landsat TM image	PHDI	SRI
p29r29	10-May-1990	−3.55	−1.68	p31r27	9-Jun-1990	−4.12	−1.74
p29r29	13-May-1991	−0.69	−0.86	p31r27	12-Jun-1991	−2.45	−1.75
p29r29	15-May-1992	−1.15	−0.53	p31r27	27-Apr-1992	−1.93	−0.72
p29r29	23-Sep-1993	6.86	2.28	p31r27	26-Oct-1994	7.03	0.52
p29r29	15-Oct-1995	6.37	0.84	p31r27	27-Sep-1995	5.97	0.78
p29r29	14-Jun-1997	4.02	0.61	p31r27	14-Jul-1997	−0.085	0.82
p29r29	30-Apr-1998	2.77	−0.13	p31r27	1-May-1999	2.01	0.89
p29r29	8-May-2001	4.47	1.40	p31r27	9-Jul-2001	4.46	1.52
p29r29	19-Nov-2002	−1.69	−0.61	p31r27	5-Oct-2004	4.38	0.17
p29r29	28-Apr-2003	−2.01	−0.97	p31r27	18-Jun-2005	1.45	0.81
p29r29	1-Apr-2005	3.15	−0.90	p31r27	9-Sep-2006	−2.91	−0.80
p29r29	4-Apr-2006	4.2	−0.32	p31r27	12-Sep-2007	2.41	0.19
p29r29	13-Oct-2006	2.3	−0.13	p31r27	1-Sep-2009	3.28	0.47
p29r29	15-Apr-2010	5.43	0.40	p31r27	6-Oct-2010	6.43	0.52
p29r29	8-Oct-2010	9.63	2.37	p31r27	5-Jul-2011	6.61	0.95
p29r29	5-Jun-2011	8.37	1.32	p31r27	11-Sep-2011	8.92	1.49
p29r29	11-Oct-2011	5.88	0.59

Fig. 2 The Cumulative Distribution Function (CDF) for monthly PHDI values from 1895 to 2013 averaged across the NOAA NCDC Division 5 in North Dakota, Division 7 in South Dakota and Division 7 in Minnesota (March to November). The

distribution of PHDI values for the time series of Landsat images used for each ecoregion is also shown (via *triangles*, *circles*, and *squares*). Ecoregions were paired if they were both represented by a single PHDI data division

high density of small (<1 ha) depressional wetlands. Most small (i.e. ~3–10 m wide) channel-swale features represented a minor areal fraction of the Landsat pixel and on average were spectrally indistinguishable from non-saturated cover types.

Differences in the fraction water were larger between cover classes than between dates, justifying the application of thresholds across all dates and both path/rows. The outputs were inundation and saturation cover maps over the time series.

Validation analysis

The inundation and saturation cover maps were validated using (1) a random point analysis; and (2) a minimum wetland size detection analysis. Patterns of inundation were first validated using 1500 points (250 points per image and same NAIP dates as threshold analysis). Outcomes (wetland/upland) were compared between NAIP and the Landsat derived wetland (inun and sat) maps. Producer accuracy is the probability that a pixel is classified as a wetland (or water) given that a wetland (or water) is present on the ground; user accuracy is the probability that a wetland is present given a pixel classified as a wetland. Overall accuracy (percent of all points correctly classified) was 96.5 % (sat) and 95.3 % (inun). The producer accuracy for wetlands was 94.6 % (sat) and 77.9 % (inun), while the user accuracy for wetlands was 88.4 % (sat) and 98.3 % (inun) (Table 3). A lower producer accuracy for inundation wetland maps was largely a consequence of mixed pixels being misclassified as upland due to the usage of a conservative threshold. To determine the minimum wetland size that was reliably detected, we used NAIP imagery from the same dates to randomly select a total of 421 NWI wetlands from <0.1 to 1 ha in size. Wetlands were selected that 1) were individual wetland features (i.e., not part of a larger wetland complex), and 2) showed at least some open water. Using the more inclusive saturation

threshold, wetlands larger than 0.2 ha were reliably detected (79 %), while using the more conservative inundation threshold wetlands larger than 0.8 ha were reliably detected (70 % detected). The primary reason for this difference was that many smaller inundated features translated to mixed pixels in Landsat, resulting in a percentage of water high enough to be considered saturated but not inundated, and further supports our utilization of two thresholds. A comparison of wetland extent between NAIP imagery and Landsat in a wet and dry year are shown in Fig. 3. We note that areas classified as inundated and saturated are referred to as “wetlands” (including lakes and other open waters) in this analysis; however, the presence of standing water alone may not be sufficient to define a feature as a wetland as defined by Cowardin et al. (1979). Conversely, mapping only areas inundated with water may exclude areas that meet the Cowardin et al. (1979) definition of a wetland but do not contain open water at the time of the image, such as temporary or seasonal wetlands, or surrounding wet-meadow and shallow-marsh zones of more permanent wetlands.

Additional datasets

The National Wetland Inventory (NWI) dataset (USFWS 2010) was used as a static (non-changing) reference layer from which to compare interannual variation in wetland extent. This dataset is designed to

Table 3 Accuracy assessment for wetland maps, derived by comparing NAIP imagery against Landsat imagery, using both inundation and saturation thresholds

	NAIP—Wetland	NAIP—Upland	Total points
Saturation map accuracy			
Landsat—Wetland	283	37	320
Landsat—Upland	16	1164	1180
Total	299	1201	1500
Producer accuracy for wetland (%)	94.6		
User accuracy for wetland (%)	88.4		
Overall accuracy (%)	96.5		
Kappa statistic	0.9		
Inundation map accuracy			
Landsat—Wetland	232	4	236
Landsat—Upland	66	1198	1264
Total	298	1202	1500
Producer accuracy for wetland (%)	77.9		
User accuracy for wetland (%)	98.3		
Overall accuracy (%)	95.3		
Kappa statistic	0.8

Fig. 3 Comparison of wetland extent between **a** NAIP imagery in fall 2010, **b** Landsat derived wetland extent in fall 2010, **c** NAIP imagery in fall 2006, and **d** Landsat derived wetland extent in fall 2006

represent wetland extent under “average” hydrological conditions (USFWS 2010), which allows for changes between “average” and “wet” to be captured, but limits our ability to capture changes between “dry” and “average” conditions. Wetland boundaries, internal to a single, continuous NWI wetland, were dissolved. Stream occurrence was defined by the high resolution National Hydrography Dataset (NHD) (1:24,000) (USGS 2013a). A stream buffer was applied (± 14 m) to account for the nationally reported digital inaccuracy in the lateral location of stream features within this dataset (USGS 2000). To account for the channel width of large river features, stream and river polygons included within NHD Area layer were merged with the buffered stream layer. NHD has been shown to inconsistently map ephemeral and

intermittent streams and ditches (Lang et al. 2012; Fritz et al. 2013), therefore wetland-stream connectivity in headwater streams and agricultural areas should be assumed to be under-estimated by this analysis. Climate conditions were characterized using the monthly Palmer Hydrological Drought Index (PHDI), calculated from precipitation and temperature station data and interpolated at 5 km (NOAA NCDC 2014), and a monthly Standardized Runoff Index (SRI) (4 km $\times$ 5 km resolution) (Kingstse and Chen, written communication, 2014). The PHDI does not explicitly consider snow depth and snow melt, which results in a poor correlation between soil moisture and drought indices in spring months, when snowmelt is the dominant source of soil moisture (Dai et al. 2004). The SRI, in contrast, incorporates seasonal dynamics

by predicting runoff from the North America Land Data Assimilation Systems (NLDAS), a land-surface model (Shukla and Wood 2008). Runoff (mm month^{-1}) was also calculated from daily stream flow ($\text{m}^3 \text{s}^{-1}$). Stream flow was obtained from four USGS gauges that best represented the outflow points (downstream from the Landsat path/rows) for each ecoregion over the entire time series (1990–2011): (1) the Sheyenne River near Cooperstown, North Dakota (USGS Gauge #05057000) for the Drift Plains ecoregion, (2) Apple Creek near Menoken, North Dakota (USGS Gauge #06349500) for the Missouri Coteau ecoregion, (3) the Big Sioux River near Brookings, South Dakota (USGS Gauge #06480000) for the Prairie Coteau and Lowlands ecoregions, and 4) the Minnesota River at Montevideo, Minnesota (USGS Gauge #05311000) for the Des Moines Lobe ecoregion (Fig. 1). Limitations in stream gauge locations meant that the stream gauge data provided a tertiary source of wetness conditions and were not intended to predict outflow from the entire ecoregion.

Connectivity analysis

Wetland-wetland and wetland-stream connectivity were quantified from the detection of physical intersections of surface water boundaries. The term

“merging” in this analysis refers to the mechanism of physical connection occurring between features, while the terms wetland–wetland and wetland–stream connectivity refer to estimates of landscape-scale connectivity produced by merging of features. The resolution of Landsat can be expected to limit the detection of some types of connections, in particular narrow connections not documented by NHD, so that additional surface water connections likely occur that are not documented by this analysis. Wetland–wetland merging occurred when more than one NWI wetland was co-located within a single, continuous Landsat-derived wetland (Fig. 4). Wetland–wetland connectivity was then defined as the percent of NWI wetlands that merged with at least one other NWI wetland in a single image. Wetland–stream connectivity (WSc/vc, i.e. wetlands connected or variably connected to streams) was defined as the percentage of NWI wetlands that merged with a stream in a single image. NWI wetlands were considered to be connected to (i.e. merged with) a stream if they (1) intersected the NHD stream layer (including stream polygons and buffer) (WSc) or (2) intersected a stream-connected patch of surface water, as mapped by Landsat (WSvc) (Fig. 4). This second group of wetlands (WSvc) are NWI wetlands that do not intersect the NHD stream layer directly, but merge with a stream under wetter conditions as a river floods, or a stream-connected

Fig. 4 A schematic showing NWI wetland classification, where WSc indicates an NWI wetland that intersects a stream, a WScv indicates an NWI wetland that shows a variable connection to a stream, and a WScn indicates an NWI wetland for which no connection to a stream was documented. Wetland-

wetland connectivity occurs when more than one NWI wetland co-occurs within a single wetland, as defined by Landsat, while wetland–stream connectivity occurs when an NWI wetland intersects a stream or a stream-connected patch of surface water, as mapped by Landsat

lake or wetland expands, subsuming or connecting nearby wetlands (Kahara et al. 2009). The term WSvc/nc is used in this analysis instead of pGIW to refer to all NWI wetlands that do not intersect the stream polygons or stream buffer, and therefore includes all wetlands classified as WSvc. Wetland-wetland and wetland-stream connectivity were compared among ecoregions as well as over the time series using t-tests and linear regressions (R Core Team 2014).

This analysis aimed to measure surface water connections as defined above, and did not consider other mechanisms of surface (e.g. fill-and-spill, overland flow, channelized flows) or groundwater hydrologic connectivity. The moderate resolution of the Landsat imagery (30 m) was expected to influence (1) the number of small (<1 ha) wetlands that could be individually mapped, and (2) the types of surface water connections among wetlands and streams that could be detected. We quantified the percentage of NWI wetlands detected by Landsat in a wet-period image (spring 2011). In this image, 28 % (85 % of total NWI area) and 54 % (94 % of total NWI area) of the NWI wetlands intersected with the stream layer and the Landsat inundated or saturated wetlands, respectively, across the five ecoregions. The average sizes of undetected NWI wetlands in the spring 2011 image were 0.22 and 0.15 ha for the inundated and saturated classes, respectively. For reference, one Landsat pixel = 0.09 ha, meaning that undetected NWI wetlands were on average two to three pixels in size. Alternatively, many of these small wetlands could have been dry at the time of the Landsat image or converted to other land uses since the NWI dataset was derived ~30 years ago (Dahl 2014). To compensate for this source of error, estimates of wetland-wetland and wetland-stream connectivity were calculated from all NWI wetlands (detected and undetected); therefore, any NWI wetland that did not intersect the NHD stream layer (WSnc) or a Landsat-derived wetland (WSvc), remained a WSnc (or not connected) (acknowledging that wetlands are not “isolated;” Mushet et al. 2015).

Landsat imagery can also be expected to bias the analysis towards detection of surface water connections that occur through the expansion of relatively broad features such as river overflow into floodplains, increases in wetland water level that result in adjacent wetlands being subsumed or merging, or wetlands filling and spilling, merging with adjacent wetlands or

streams. Intermittent or temporary linear connections (e.g., ephemeral channels, swales, ditches) that connect some wetlands (e.g. Shaw et al. 2012) are often not well documented by NHD (Lang et al. 2012; Fritz et al. 2013) and are difficult to detect with Landsat. Although finer spatial resolution imagery (e.g. QuickBird, Worldview-2 and 3) may expand the types of connectivity captured, these data sources are often collected on-demand and therefore have limited ability to capture temporal changes as landscapes wet up and dry out over time. The advantage of Landsat imagery is that high temporal resolution, combined with large spatial extent, can provide unique insights into the hydrodynamics of stream and wetland landscapes across a range of climatic conditions. In summary, reported degrees of connectivity should be interpreted as a conservative estimate of water body merging (and an incomplete estimate of total surface water connectivity), as it is likely that a portion of wetlands for which no connection was observed have surface connections that are either intermittent or too small to be mapped by NHD (e.g. swales, ephemeral channels) or detected by Landsat.

Results

Ecoregions

Ecoregions showed substantial variation in NWI wetland total area and density as well as NHD stream density. The Lowlands and Des Moines Lobe contained fewer NWI wetlands and lower total wetland area, but greater stream density, relative to the other ecoregions (Table 1). The Drift Plains and Missouri Coteau, in contrast, contained a greater number of NWI wetlands and higher total wetland area, but a lower stream density (Table 1). A lower stream density in the Drift Plains and Missouri Coteau was associated with more wetlands classified as WSvc/nc (97 %, Table 1). In contrast, the higher stream density in the Lowlands and Des Moines Lobe was associated with fewer wetlands classified as WSvc/nc (80 and 83 %, respectively) (Table 1). In general, stream density between the ecoregions was negatively correlated with both the total area of NWI wetlands (Fig. 5) and the percentage of NWI wetlands classified as WSvc/nc.

Fig. 5 NWI wetland area (total) as a function of NHD stream density for each of the five ecoregions considered

Patterns of wetland extent

Actual wetland extent (1) changed from drought to deluge (i.e., the tails of the PHDI CDF curve, Fig. 2), (2) correlated positively with climate indices and runoff, and 3) varied among ecoregions. Wetland extent, as mapped using Landsat, changed substantially between the driest and wettest years. The time series of images represented a wide range of hydrological conditions, from approximately $Pr(0.06)$ to $Pr(0.99)$ of wet conditions derived from snow-free monthly conditions (1895–2013), as determined by the PHDI (Fig. 2). The change in area of inundation from the driest year to the wettest year ranged from a 117 % increase in wet area in the Prairie Coteau, to a 388 % increase in wet area in the Lowlands (Table 4). The increase in total wet area with increasingly wet climatic conditions was evident at very coarse scales (see Fig. 6), which shows the change in wetland extent from dry ($Pr(0.06)$ (PHDI)) to intermediate ($Pr(0.38)$ (PHDI)) to wet ($Pr(0.99)$ (PHDI)) conditions across the five ecoregions. The total amount of wetland area was greater using the saturation versus inundation threshold (Fig. 7a). The percentage wetland area (inun) also correlated positively with runoff (mm month^{-1}), SRI, and PHDI within all five ecoregions (Table 5).

Wetland–wetland connectivity

The merging of wetlands increased substantially as 1) the wetness threshold became more inclusive (i.e., at the saturation versus the inundation threshold) and 2) overall conditions became wetter (Table 4; Fig. 4). At

the inundation threshold, ecoregions showed minimal pair-wise differences in the degree of wetland–wetland connectivity, with the exception of the Lowlands, which showed a lower mean percent of wetland–wetland connectivity (Table 4). The increase in the percentage of merged wetlands between the inundated and saturated thresholds, however, was substantial in all ecoregions (Table 4). In the Drift Plains, for example, the mean percentage of merged wetlands increased from 3.5 ± 0.7 to 12.9 ± 2.6 %; in the Des Moines Lobe it increased from 4.2 ± 0.7 to 14.3 ± 1.7 % (Table 4). Wetland–wetland connectivity also increased significantly as conditions became wetter (i.e., total wetland area increased) (Table 6; Fig. 8). For instance, the percentage of wetlands that merged using the saturated threshold over the time series ranged from 1.5 to 30.7 % in the Drift Plains and 7.0–26.8 % in the Des Moines Lobe (Table 4). Increases in wetland merging were also correlated positively and significantly with monthly runoff and SRI in all five ecoregions under inundated conditions, and all except the Des Moines Lobe (SRI) under saturated conditions (Table 5). The relationship between PHDI and wetland–wetland merging was less consistent, however, with the relationship only significant in two of the five ecoregions, using the inundated threshold (Table 5).

Wetland–stream connectivity

Similar to wetland–wetland connectivity, the merging of NWI wetlands with streams correlated strongly with total wetland area and changes in wetness conditions. The percentage of WSc/vc was positively and significantly correlated with the percentage of wetland area, using both the inundation and saturation thresholds, in all ecoregions except the Drift Plains (Table 6). In contrast to wetland–wetland connectivity, ecoregions showed significant pair-wise (t test) differences in the mean percentage of WSc/vc, with the Lowlands, Des Moines Lobe and Prairie Coteau showing greater wetland–stream connectivity relative to the Missouri Coteau and the Drift Plains (Table 7). The percentage of wetlands merging with streams (WSc/vc) was positively and significantly correlated with monthly runoff in all ecoregions except the Drift Plains (inun) (Table 5). The climate indices performed relatively poor, however, with SRI and PHDI significantly correlated with wetland–stream connectivity (inun)

Table 4 Mean and range in the percentage of wetland area (using the inundated (inun) and saturated (sat) thresholds), the percentage increase in wetland area compared to the driest

year, and the percentage of NWI wetlands that merged with at least one other NWI wetland, by wetness threshold and ecoregion (1990–2011)

Ecoregion	Wetland area (inun) (%)	Wetland area (sat) (%)	Change in area from driest (inun) (%)	Change in area from driest (sat) (%)	NWI wetlands merged (inun) (%)	NWI wetlands merged (sat) (%)
Lowlands	1.9 ± 0.2 ⁴ (0.9–4.3)	5.1 ± 0.5 ³ (2.2–7.9)	387.7	260.4	1.7 ± 0.4 ² (0.3–7.0)	7.0 ± 1.3 ³ (2.0–21.9)
Des Moines Lobe	3.0 ± 0.2 ³ (2.1–4.6)	7.6 ± 0.6 ² (4.0–11.2)	120.0	236.0	4.2 ± 0.7 ¹ (1.1–10.7)	14.3 ± 1.7 ¹ (7.0–26.8)
Prairie Coteau	8.7 ± 0.5 ¹ (5.5–11.9)	12.4 ± 0.7 ¹ (7.5–16.2)	117.4	128.1	4.8 ± 0.8 ¹ (1.1–9.9)	11.3 ± 1.6 ^{1,2} (3.6–24.5)
Drift Plains	5.8 ± 1.1 ² (2.1–9.9)	10.3 ± 0.5 ¹ (3.3–16.8)	375.8	460.1	3.5 ± 0.7 ¹ (0.2–10.4)	12.9 ± 2.6 ^{1,2} (1.5–30.7)
Missouri Coteau	8.8 ± 0.7 ¹ (3.4–12.7)	12.1 ± 0.9 ¹ (5.4–17.8)	273.3	230.1	4.0 ± 0.6 ¹ (0.2–8.7)	9.3 ± 1.5 ^{2,3} (1.5–21.5)

Superscripts indicate significant ($p < 0.05$) pairwise differences between ecoregions. Plus and minus standard error

in three of the five ecoregions and one of the five ecoregions, respectively (Table 5). Across the five ecoregions, the size of individual wetlands appeared to influence the probability of merging. Although the percentage of NWI wetlands (count) merging with streams was generally less than 25 %, regardless of threshold or image wetness, the percentage of total NWI wetland area connected to streams was much greater (Fig. 7b). The mean percentage of NWI wetland area connected using the inundation threshold ranged from 68.9 ± 0.3 % in the Des Moines Lobe to 29.2 ± 0.4 % in the Missouri Coteau (Table 7).

Wetlands with variable stream connections

As wetland extent mapped by NWI wetland dataset is meant to represent extent under “average” hydrological conditions (USFWS 2010), its intersection with the stream layer, should capture all wetlands that intersect with streams under “average” hydrological conditions. Correspondingly, when the percentage of wetlands classified as WScv in a given image was averaged across the time series (i.e., mean hydrological conditions), the percentage tended to be low across all ecoregions (Table 7). However, under deluge conditions, more WScv/nc merge with streams (i.e. the number of WScv increases). Using the saturated threshold, for example, up to 8.1 % of the WScv/nc in a single image merged with a stream in the Des Moines Lobe, and up to 7.2, 7.1, 5.0 and 2.4 % in

the Lowlands, Prairie Coteau, Drift Plains and Missouri Coteau ecoregions, respectively (Table 7). By area, up to 20.9 % of NWI wetland classified as WScv/nc merged with a stream in a single image in the Prairie Coteau, for example (Table 7). The percentage of WScv (by count and area) also responded positively to changing wetness conditions, particularly to increasing runoff and lesser so to SRI (Fig. 9), showing correlation coefficients and significance identical to that shown by the wetland-stream connectivity analysis (Table 5).

When wetlands classified as WScv were aggregated across the entire time series, this category of wetlands became even more substantial. The percent NWI wetlands classified as a WScv in at least one image at the saturated threshold, exceeded the percent WSc wetlands in all ecoregions, except the Lowlands. For example, in the Des Moines Lobe, 16.6 % of its wetlands were WSc, or intersected the stream buffer layer, while 18.7 % were WScv. In the Drift Plains, only 2.6 % of its NWI wetlands were WSc, while 13.0 % were classified as WScv (Table 7).

Discussion

This study demonstrated that spatial and temporal variation in wetland extent resulted in variability in surface water connectivity across portions of the Prairie Pothole Region. Similar to the work of others (e.g.

Fig. 6 Patterns of Landsat-derived A) wetland cover (inundated) and B) wetland cover (saturated) for three wetness conditions (*left to right*), dry ($Pr(0.06)$ CDF PHDI) (spring 1990), intermediate ($Pr(0.38)$ CDF PHDI) (fall 2006) and wet ($Pr(0.99)$ CDF PHDI) (spring 2011) for p31r27 (*top row in a and b*) and p29r29 (*bottom row in a and b*). *Note* Not all wetlands are visible due to the scale of the images

Johnson et al. 2004; Kahara et al. 2009; Zhang et al. 2009; Niemuth et al. 2010; Huang et al. 2011), we found that total wetland area increased substantially from drought to deluge conditions (Table 4) and that total wetland area could be positively correlated to wetness indicators, in this case, PHDI, SRI, and runoff (Table 5). This study went further than previous work to

demonstrate that the merging of wetlands and wetlands with streams varied over time and correlated positively with total wetland area (Fig. 8). Despite the limitations regarding the types of connectivity Landsat is able to detect, this approach provided a largely unprecedented view of how wetland–wetland and wetland–stream connectivity changes over time across the PPR.

Fig. 7 Ecoregion comparison of **a** average percent wetland area over the time series, and **b** average percent NWI wetlands connected to streams (WSc/vc) over the time series, by count and area. Error bars show plus and minus one standard error

The degree of wetland merging in the PPR was previously explored by Kahara et al. (2009), who similarly found a positive correlation between wetland merging and total wetland surface area in the PPR. Here, we found wetland merging to also be sensitive to the definition of the wet-dry threshold. This is an important factor to consider, as any analysis of “wet” area typically translates a continuous variable, soil moisture, into a binary variable (wet or dry). Because a substantial portion of the saturated area occurred at wetland edges (e.g., mixed Landsat pixels of water and vegetation or vegetated water), wetland merging was greater using the saturation threshold relative to the inundated threshold. Although the saturated threshold improves the identification of small wetland features and vegetated wetland edges, it can also “merge” disconnected wetlands by classifying two adjacent, mixed pixels as water (Muster et al. 2013). The merging of wetlands with streams, in contrast, was

found to be less sensitive to the inundation/saturation threshold, at least for this scale and study area. Similarity in the degree of wetland–wetland merging among ecoregions indicates that merging may be independent of within-region variation in wetland density and total wetland area. It also indicates that substantial wetland–wetland interaction occurs even in areas where most NWI wetlands are initially classified as WSc/vc (e.g., >97 % of the Drift Plain’s NWI wetlands were considered WSc/vc, but >30 % of those NWI wetlands merged with at least one other NWI wetland during the wettest images).

Differences in the degree of wetland–stream connectivity between ecoregions is potentially attributable to differences in drainage density (Fig. 5). Variability in stream density among ecoregions, in turn, can be attributed to glacial history. Young moraine landscapes typically contain chaotic drainage networks where streams follow local

Table 5 Pearson correlation coefficients and significance for patterns of wetland area and wetland connectivity (using the inundation (inun) and saturated (sat) thresholds) in relation torunoff (mm month⁻¹), the Standardized Runoff Index (SRI), and the Palmer Hydrological Drought Index (PHDI) for each ecoregion

Ecoregion	Parameter	Wetland area (inun) (%)	Wetland area (sat) (%)	NWI wetlands merged (inun) (%)	NWI wetlands merged (sat) (%)	WSc/vc count (inun) (%) ^a	WSc/vc count (sat) (%) ^a	WSc/vc area (inun) (%) ^a	WSc/vc area (sat) (%) ^a
Lowlands	Runoff	0.82*	0.63*	0.85*	0.84*	0.82*	0.75*	0.88*	0.92*
	SRI	0.58*	0.45	0.50*	0.54*	0.43	0.50*	0.48	0.67*
	PHDI	0.64*	0.46	0.48	0.49*	0.42	0.50*	0.48	0.67*
Des Moines Lobe	Runoff	0.82*	0.19	0.85*	0.75*	0.80*	0.56*	0.82*	0.69*
	SRI	0.58*	0.5	0.50*	0.47	0.39	0.35	0.46	0.36
	PHDI	0.64*	0.45	0.41	0.44	0.28	0.31	0.35	0.34
Prairie Coteau	Runoff	0.74*	0.75*	0.79*	0.78*	0.78*	0.75*	0.63*	0.69*
	SRI	0.63*	0.71*	0.58*	0.59*	0.58*	0.57*	0.53*	0.64*
	PHDI	0.55*	0.64*	0.50*	0.52*	0.52*	0.52*	0.47	0.54*
Drift Plains	Runoff	0.52*	0.54*	0.56*	0.61*	0.39	0.51*	0.47	0.59*
	SRI	0.77*	0.69*	0.54*	0.55*	0.53*	0.57*	0.67*	0.73*
	PHDI	0.59*	0.62	0.48	0.49	0.49	0.67*	0.50*	0.69*
Missouri Coteau	Runoff	0.55*	0.60*	0.70*	0.63*	0.57*	0.64*	0.53*	0.71*
	SRI	0.80*	0.81*	0.73*	0.63*	0.65*	0.71*	0.72*	0.78*
	PHDI	0.61*	0.73*	0.58*	0.65*	0.44	0.70*	0.49	0.61*

^a Pearson correlation values and significance were identical for corresponding WScvc (%) category* $p < 0.05$

gradients without a dominating drainage direction. As a landscape ages, it develops a drainage direction and pattern through local and headward erosion, capture, and sedimentation (Ahnert 1996). Drainage density (stream density) in the PPR was greatest in the Lowlands ecoregion, in part because the Wisconsin glacier diverged around the Big Sioux Basin (in the Lowlands ecoregion), leaving the older (>20,000 BP) landscape with a well-developed drainage network (Clayton and Moran 1982). By 11,700 BP the glacier had retreated from the Lowlands, Des Moines Lobe and Prairie Coteau ecoregions—400 years prior to glacier retreat from the northern two ecoregions (Clayton and Moran 1982)—which may explain lower drainage densities in the northern two ecoregions. Additionally, the northern two ecoregions experience less precipitation (NOAA NCDC 2014), and the rate and density of stream development can also be expected to be influenced by climate (Ahnert 1996).

Wetland characteristics (size, density, shape) across the PPR, and potentially their spatial relationship to streams, are predominately the product of the

distribution and type of glacial debris (Flint 1971; Sloan 1972). The Drift Plains, which includes the Devil's Lake area, contains a high number and area of wetlands and lakes, a consequence of ground moraine and outwash, but the flat topography and young age of the landscape has limited drainage development, resulting in the lowest observed rate of wetlands merging with streams among the ecoregions. The Missouri and Prairie Coteau are dominated by dead-ice moraine, or stagnant glacial ice that melted under a sediment layer resulting in a high density of depressions of variable sizes (Kantrud et al. 1989). However, unlike the Missouri Coteau, the Prairie Coteau has a chain of large lakes, formed where there was minimal ice shear (USGS 2013b). These lakes, in addition to a greater stream density and a greater rate of precipitation relative to the Missouri Coteau, might explain why the mean percentage of NWI wetlands merging with streams was greater in the Prairie Coteau relative to the Missouri Coteau. The greater degree of wetland-stream connectivity observed in the Lowlands and Des Moines Lobe, in turn, can be attributed to a better

Table 6 Pearson correlation coefficients and significance for percentage wetland area (using the inundation (inun) and saturated (sat) thresholds) in relation to the degree of wetland–

wetland merging (NWI wetlands merged) and wetland-stream connectivity (WSc/vc) for each ecoregion

Threshold	Ecoregion	NWI wetlands merged (inun) (%)	WSc/vc count (inun) (%)	WSc/vc area (inun) (%)
Wetland area (Inundation) (%)	Lowlands	0.85*	0.80*	0.88*
	Des Moines Lobe	0.98*	0.91*	0.92*
	Prairie Coteau	0.97*	0.98*	0.96*
	Drift Plains	0.88*	0.28	0.53*
	Missouri Coteau	0.93*	0.72*	0.82*
Threshold	Ecoregion	NWI wetlands merged (sat) (%)	WSc/vc count (sat) (%)	WSc/vc area (sat) (%)
Wetland area (Saturation) (%)	Lowlands	0.79*	0.86*	0.76*
	Des Moines Lobe	0.65*	0.83*	0.67*
	Prairie Coteau	0.95*	0.96*	0.90*
	Drift Plains	0.96*	0.82*	0.82*
	Missouri Coteau	0.92*	0.95*	0.82*

* $p < 0.05$ **Fig. 8** Change in the degree of **a** wetland–wetland connectivity and **b** wetland-stream connectivity (WSc/vc) with change in wetland area (inundated), by ecoregion. Linear trend lines are shown with the correlation coefficient

developed drainage system, relative to the other ecoregions, as indicated by greater stream density, as well as fewer wetlands (in particular fewer wetlands

far from streams). The lower total wetland area and density in these two ecoregions is due not only to a greater abundance of well drained soils (USGS 2013b),

Table 7 The mean percentage NWI wetlands in each ecoregion that connected to a stream either directly (WSc), through expansion of Landsat-derived wetlands (WSvc), and the sum of these categories (WSc/vc) over the time series (1990–2011) (using the inundation (inun) and saturated (sat) thresholds)

Ecoregion	WSc (%)	WSc/vc (inun) (%)	WSvc ^a (inun) (%)	WSc/vc (sat) (%)	WSvc ^a (sat) (%)	WSvc (sat) aggregated ^b (%)
NWI wetland:	Count					
Lowlands	17.0	17.5 ± 0.1 ¹ (17.1–19.3)	0.7 ± 0.2 ² (0.1–2.8)	19.3 ± 0.4 ¹ (17.6–22.9)	2.8 ± 0.5 ^{2,3} (0.7–7.2)	13.8
Des Moines Lobe	16.6	17.3 ± 0.1 ² (16.7–18.4)	0.8 ± 0.1 ² (0.2–2.3)	20.0 ± 0.4 ¹ (17.6–23.3)	4.2 ± 0.5 ¹ (1.2–8.1)	18.7
Prairie Coteau	11.6	12.9 ± 0.2 ³ (11.8–14.5)	1.5 ± 0.2 ¹ (0.3–3.3)	14.6 ± 0.4 ² (12.5–17.8)	3.4 ± 0.5 ^{1,2} (1.0–7.1)	13.2
Drift Plains	2.6	3.1 ± 0.1 ⁵ (2.6–4.7)	0.5 ± 0.1 ² (0.02–2.2)	4.3 ± 0.4 ³ (2.7–6.8)	1.8 ± 0.4 ^{3,4} (2.6–5.0)	13.0
Missouri Coteau	3.1	3.6 ± 0.0.1 ⁴ (3.1–4.3)	0.6 ± 0.0.1 ² (0.02–1.3)	4.2 ± 0.2 ³ (3.2–5.4)	1.1 ± 0.2 ⁴ (0.2–2.4)	4.4
NWI wetland:	Area					
Lowlands	60.0	61.3 ± 0.2 ³ (60.2–63.2)	3.3 ± 0.5 ³ (0.6–7.9)	62.7 ± 0.3 ³ (61.2–65.7)	6.7 ± 0.8 ^{2,3} (2.9–14.2)	9.7
Des Moines Lobe	68.4	68.9 ± 0.1 ¹ (68.5–69.8)	1.8 ± 0.3 ⁴ (0.7–4.6)	70.2 ± 0.2 ¹ (69.0–71.9)	5.9 ± 0.6 ³ (2.0–11.2)	8.3
Prairie Coteau	58.9	62.3 ± 0.5 ² (59.5–65.5)	8.4 ± 1.1 ¹ (1.6–16.1)	64.1 ± 0.6 ² (60.4–67.5)	12.8 ± 1.3 ¹ (3.8–20.9)	13.0
Drift Plains	32.9	34.8 ± 0.3 ⁴ (33.1–37.7)	2.9 ± 0.4 ³ (0.4–7.2)	36.5 ± 0.6 ⁴ (33.5–41.4)	5.5 ± 0.8 ³ (0.9–12.8)	13.6
Missouri Coteau	24.9	29.2 ± 0.6 ⁵ (25.1–32.3)	5.6 ± 0.8 ² (0.3–9.7)	31.1 ± 0.6 ⁵ (27.4–36.0)	8.2 ± 0.8 ² (3.3–14.8)	13.0

Superscripts indicate significant ($p < 0.05$) pairwise differences between ecoregions. Plus and minus standard error

^a The percentage WSc is calculated from the percentage WSc/vc, not from all NWI wetlands

^b The percent of all NWI wetlands (count and area) that were classified as WSc in at least one image across the time series

but also to the extent of cultivated crops in these ecoregions (60 and 77 % cultivated crop cover in Lowlands and Des Moines Lobe, respectively) (Homer et al. 2015). Agricultural activity has greatly reduced the number of wetlands across the PPR (Dahl 2014), although its implications for landscape-scale surface water connectivity has not been quantified. In theory, agricultural activity can either increase or decrease aspects of wetland-stream connectivity. For example, ditches, pipes and field tiles can increase connectivity between wetlands and streams (e.g., 18 % of stream length in the Des Moines Lobe is classified as canal/ditch), whereas filling wetlands and lowering the water table can increase isolation of remaining wetlands (De Laney 1995; Blann et al. 2009).

The three wetness indicators (PHDI, SRI, runoff) showed generally strong associations with both

measures of connectivity, but correlation coefficients, indicating the strength and direction of the linear relationships, varied among ecoregions. PHDI tended to underperform relative to the other indicators. Differences in the strength of the linear relationships between these wetness indicators and connectivity could be related to stream density. Runoff was more correlated with connectivity in ecoregions with relatively greater stream density (i.e., Lowlands, Des Moines Lobe and Prairie Coteau), while the SRI was more correlated with ecoregions with relatively lower stream density (i.e., Drift Plains and Missouri Coteau). In the latter case, the Drift Plains and Missouri Coteau had lower mean rates of runoff relative to the other ecoregions, suggesting that, in addition to differences in precipitation and evapotranspiration, a smaller proportion of the drainage area is actively contributing to streamflow. This resulted

Fig. 9 Change in the **a** percent NWI wetlands that merged with streams (WSc/vc) and **b** percent WSc/vc that showed connections to stream (WScv), using Landsat-derived wetland

maps (inundated), against the Standardized Runoff Index, by ecoregion. Linear trend lines are shown with the correlation coefficient

in a less uniform distribution of runoff values over the time series in the Drift Plains and Missouri Coteau, relative to the other wetness indicators (SRI and PHDI), and could have weakened the power of runoff to predict landscape-scale patterns of connectivity within these two ecoregions (Table 5).

A complete analysis of wetland–wetland and wetland–stream connectivity would also need to consider narrow and temporary (e.g. in response to rain events) surface connections, groundwater connections, as well as chemical and biological connections (U.S. EPA 2015). Despite the limitations of our approach, our results support the idea that wetlands occur along a gradient from always connected to rarely connected (EPA 2015). In this analysis the subset of wetlands showing occasional stream connections have been grouped as WScv or variably connected wetlands. In a static analysis (*sensu* Tiner 2003) these and other

wetlands would likely be inappropriately classified. Our work also indicates that patterns of connectivity vary spatially in response to landscape-scale factors, including topography, glacial history, and climate. An improved understanding of the timing and spatial pattern of variable connections is necessary to quantify the distribution of wetlands along a gradient of hydrologic connectivity in diverse landscapes such as the Prairie Pothole Region.

Conclusion

In conclusion, this study considered both spatial and interannual variability in wetland–wetland and wetland–stream connectivity within five distinct ecoregions in the PPR. Increases in three measures of wetness condition (PHDI, SRI, runoff) correlated

positively with increases in wetland area, using both inundated and saturated thresholds, but showed variable correlations with wetland merging and the merging of wetlands with streams. Our analysis demonstrated that even regions with a high percentage of wetlands lacking channel connections, such as the Drift Plains and Missouri Coteau, can show substantial degrees of wetland merging under deluge conditions. Despite differences in the density and total area of NWI wetlands, the maximum degree of wetland–wetland connectivity was largely similar across the five ecoregions. The degree of wetland merging, however, responded strongly to changes in overall wetness and the selection of the wet-dry threshold (inundation versus saturation) used to classify Landsat pixels as wetland or upland. Although less-responsive to changes in overall wetness conditions and the selection of a wet-dry threshold, the merging of wetlands with streams varied significantly inter-annually and in particular, spatially. Ecoregions with a greater density of NHD streams showed a higher degree of wetland-stream connectivity. In addition, wetlands that variably merged with streams, when considered cumulatively, exceeded the number of NWI wetlands that intersected streams in most ecoregions. Several studies have called for the need to view wetlands and hydrologic connections over a continuum or varying over time and space (Leibowitz 2003; Leibowitz et al. 2008; Shook et al. 2015; U.S. EPA 2015). The utilization of Landsat imagery in our analysis improved our understanding of spatial and temporal variability in wetland–wetland and wetland-stream connectivity across the PPR, by allowing for a regional analysis over an extended time series. Limitations in the resolution of Landsat, however, call for further work to identify in particular, the frequency and distribution of narrow, temporary surface water connections. Additional work is also needed to improve our understanding of where variable merging of wetlands occurs, whether these types of connections can be predicted, and how they relate to overall surface water connectivity and hydrodynamics on a landscape.

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