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ARTICLE

Spatial and Temporal Variation in Wet Area of Wetlands in the Prairie Pothole Region of North Dakota and South Dakota

Neal D. Niemuth · Brian Wangler · Ronald E. Reynolds

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Abstract Because of their sensitivity to temperature and precipitation, wetlands in the Prairie Pothole Region (PPR) are predicted to undergo changes in number, wet area, and hydroperiod as a result of climate change. However, existing PPR wetland monitoring programs are insufficient to accurately describe broad-scale variation in hydrology that might obscure signals of climate change. We assessed spatial and temporal patterns in wet area of ~40,000 wetland basins sampled each May from 1988–2007 in the U.S. PPR. The percentage of basins containing water, the wet area of basins relative to a baseline, the coefficient of variation of wet area of basins, and correlations of wet area values with values from previous years all varied temporally, spatially, and among water regimes that characterized annual duration of surface inundation. High variability in wetness suggests that monitoring programs designed to detect changes in PPR wetlands due to climate change must be implemented over broad spatiotemporal scales and consider natural and anthropogenic factors that influence water levels to be able to distinguish directional change from natural variation. Ancillary information such as annual indices of water conditions can greatly enhance the value of wetland classification schemes such as that used in the National Wetlands Inventory.

Keywords Climate change · Surface water variability · Waterfowl · Wildlife

N. D. Niemuth (✉) · B. Wangler · R. E. Reynolds
U.S. Fish and Wildlife Service Habitat and
Population Evaluation Team,
3425 Miriam Avenue,
Bismarck, ND 58501, USA
e-mail: Neal_Niemuth@fws.gov

Introduction

The Prairie Pothole Region (PPR) is located in north-central North America where areas of high wetland density intersect with grasslands of the northern Great Plains. Because of the large amounts of wetland and grassland habitat in the region, the PPR is renowned for harboring large proportions of continental waterfowl, waterbird, and grassland bird populations (Batt et al. 1989; Peterjohn and Sauer 1999; Beyersbergen et al. 2004). The PPR is characterized by high inter-annual and regional variation in precipitation (Bragg 1995; Woodhouse and Overpeck 1998), which greatly influences the number of wetland basins in the PPR that contain water each year, water levels within those basins, and abundance of wetland-associated wildlife (Kantrud et al. 1989).

Wetlands in the PPR are highly sensitive to changes in temperature and precipitation, as most wetland surface water comes from precipitation (Sorenson et al. 1998; Winter 2000; Johnson et al. 2005). Precipitation is greatest in the east and potential evaporation typically exceeds precipitation, with the precipitation-evaporation deficit increasing to the west (Kantrud et al. 1989; Winter 1989). Because of the potential vulnerability of PPR wetlands to drying associated with climate change and the ecological and economic importance of waterfowl in the region, several investigators have appraised the potential effects of global climate change on wetlands in the PPR (e.g., Larson 1995; Poiani et al. 1996; Sorenson et al. 1998; Conly and van der Kamp 2001; Johnson et al. 2005; Johnson et al. 2010). However, the diversity of wetland types, geologic settings, and land uses, along with strong variation in annual water conditions in the PPR complicate predictions about changes in wetland condition associated with climate change. Given the importance of the region to wildlife, the magnitude of conservation programs in the PPR (Niemuth et al. 2008a), and the response of wildlife to variation in wetland numbers in the region, it is essential that assessments of the effects of climate change on PPR wetlands and subsequent management recommendations be based on data and relationships that are sufficiently comprehensive to accurately describe the dynamics of PPR wetlands. We address this issue by evaluating spatiotemporal patterns in the area of wetland basins that is inundated each May for wetlands of varying permanency class.

Variation in water levels of wetlands in the PPR has been previously studied (Winter 1989; Larson 1995; Johnson et al. 2004; van der Valk 2005), with most wetland monitoring falling into one of two general types (Conly and van der Kamp 2001). The first is measurement of water levels in wetlands and their surrounding catchments (e.g., Meyboom 1963; Winter and Rosenberry 1998; Johnson et al. 2004). This approach has been central to understanding the hydrology and dynamics of individual wetlands. However, the intensive nature of this approach limits the number of wetlands that can be assessed, reducing the ability to characterize wetland dynamics over broad spatial extents and under a variety of conditions. For example, data used to calibrate and test the wetland dynamics model used in Poiani et al. (1996) and Johnson et al. (2005), came from a single semipermanent wetland in north-central North Dakota. Similarly, data used to parameterize and test the wetland dynamics model used in Johnson et al. (2010) came from 10 wetlands and 40 groundwater wells at one site in eastern South Dakota.

The second general survey type consists of annual estimates of May pond numbers derived from waterfowl breeding population and habitat surveys conducted by the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) (e.g., Smith 1995), which take place over broad geographic areas. However, no wetland data other than the number of wetlands containing water are collected during these surveys, precluding inferences about how individual wetlands vary in time and space or as a function of water regime or local conditions. For example, Larson (1995) used data collected on annual aerial surveys from portions of two states and three provinces to determine how much of the variation in May pond numbers was accounted for by temperature and precipitation. Even though the May pond data set contained observations of many thousands of wetlands, inferences that could be made were necessarily limited because wetlands that contain surface water for less than three weeks are not included in the sample and the data do not provide information about the specific location of wetlands, their water regime, or the area of water in each basin (USFWS and CWS [1987] Standard operating procedures for aerial waterfowl breeding ground population and habitat surveys in North America. Unpublished report, USFWS Office of Migratory Bird Management, Laurel, Maryland).

Given the limitations of the above types of wetland monitoring, additional long-term monitoring is necessary to better understand and accurately describe the hydrology of wetlands in the PPR, as well as detect possible effects of climate change and land use on wetlands in the region (Sorenson et al. 1998; Conly and van der Kamp 2001). We assessed the area of surface water in wetland basins of four water regimes using data collected annually from 1988–2007 at ~40,000 wetland basins across portions of three states in the U.S. PPR. Wetland water regimes of basins (Table 1) characterized the duration of surface flooding each year and were based on the Cowardin et al. (1979) wetland classification system. Our first goal was to describe

Table 1 Definitions of water regime modifiers from Cowardin et al. (1979) and associated basin wetland water regimes used in integration of palustrine wetland zones into basins classified by the most permanent water regime identified by the National Wetlands Inventory. All lacustrine wetlands were assigned to the "lake" water regime, regardless of water regime modifier

Modifier	Definition and assignment
Saturated	The substrate is saturated to the surface for extended periods during the growing season, but surface water is seldom present. Assigned to the "temporary" basin water regime.
Temporarily flooded	Surface water is present for brief periods during the growing season, but the water table usually lies well below the soil surface for most of the season. Plants that grow both in uplands and wetland are present. Assigned to the "temporary" basin water regime.
Seasonally flooded	Surface water is present for extended periods especially early in the growing season, but is absent by the end of the season in most years. When surface water is absent, the water table is often near the land surface. Assigned to the "seasonal" basin water regime.
Semipermanently flooded	Surface water persists throughout the growing season in most years. When surface water is absent, the water table is usually at or very near the land surface. Assigned to the "semipermanent" basin water regime.
Intermittently exposed	Surface water is present throughout the year except in years of extreme drought. Assigned to the "lake" basin water regime.
Permanently flooded	Water covers the land surface throughout the year in all years. Vegetation is composed of obligate hydrophytes. Assigned to the "lake" water regime.

spatial and temporal patterns of wetness and variation in wetness. We anticipated that these patterns would be useful in understanding the range of variation within which climatologists will need to detect what may be comparatively small signals of climate change relative to natural variation. In addition, we anticipated that the patterns would provide broad-scale insights into wetland dynamics in the region, providing direction for development of wetland- and region-specific models of water conditions under differing climate scenarios over broad geographic extents and time frames.

The second goal was to determine how inter-annual dynamics of wetlands were related to the water regimes assigned to those wetlands by the National Wetlands Inventory (NWI; Wilen and Bates 1995). The NWI program delineated wetland boundaries and assigned water regimes based on stereoscopic photo-interpretation of aerial photographs taken when wetland basins contained sufficient water to identify, delineate, and classify wetlands (Wilen and Bates 1995). Understanding broad-scale dynamics of wetland water regimes identified by the NWI would allow users to better relate digital NWI data to wetlands and wildlife habitat over large areas. This is particularly important as digital wetlands data such as the NWI are increasingly being used to develop spatial habitat models and to guide monitoring activities (e.g., Munger et al. 1998; Reynolds et al. 2006; Niemuth et al. 2008a; Johnson et al. 2009). To our knowledge, no previous studies have explicitly assessed spatial variation in water conditions over time at this scale in the PPR.

Methods

Study Area

The study area was that portion of North Dakota and South Dakota east and north of the Missouri River, approximating the PPR of these states, as well as three counties in northeastern Montana (Fig. 1). The landscape surface was formed by glacial action and is characterized by numerous depression wetlands and prairie flora (Bluemle 1991). The climate is cool and dry, and soils are typically heavy-textured (Winter 1989). Agriculture is the primary land use, with cropland dominating in the eastern portion of the study area and the amount of grassland generally increasing further west. "Pothole" basins in the PPR contain a variety of wetland types ranging from wet meadows and shallow-water ponds to saline lakes, marshes, and fens (Cowardin et al. 1979; Kantrud et al. 1989). Most wetlands in the PPR are <0.5 ha in area and wetland density often exceeds 40/km^2 (Kantrud et al. 1989).

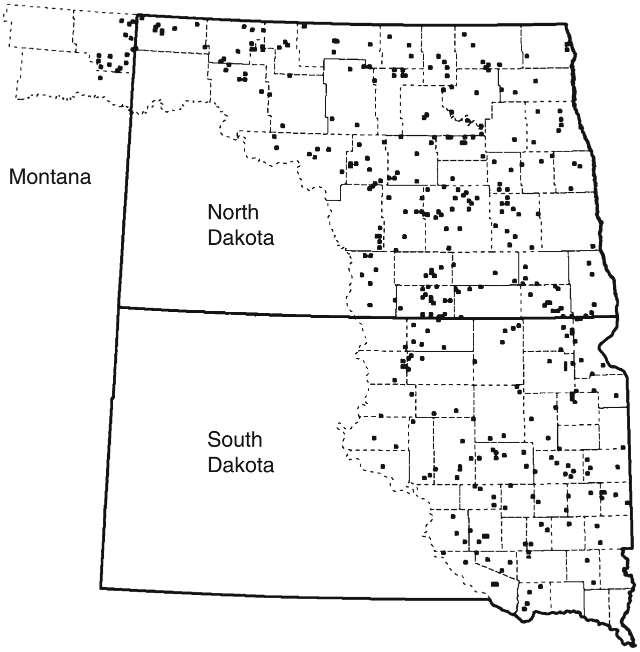

Fig. 1 Location of 380 (most recent number) 10.4-km^2 primary sampling blocks (black squares) in the Prairie Pothole Region of North Dakota, South Dakota, and northeastern Montana

Determining the Wet Area of Wetland Basins

We assessed wetland basins on 263–380 10.4-km^2 primary sampling blocks (Fig. 1) that were drawn from 93.2-km^2 civil townships that were stratified by the area of land that the USFWS owned or had limited easement interest (Cowardin et al. 1995). We assessed all wetland basins that were partially or completely within each 10.4-km^2 primary sampling block; however, the number of blocks changed over time as survey effort increased (Table 2). We determined wet area of wetland basins each year using modified digital NWI data as a baseline. Data for baseline polygons in the PPR were collected during periods of "optimum" water conditions (Wilen and Bates 1995) when basins were full but not overflowing. Because point and linear wetlands identified by the NWI have no area when represented in a geographic information system (GIS), we added buffers of 7.6 m and 7.3 m around point and linear wetlands, respectively, to create polygons (Cowardin et al. 1995; Johnson and Higgins 1997). These distances represent the mean dimensions of point and linear wetlands in the study area as determined from aerial photographs (Cowardin et al. 1995). Some digital polygons represented complex wetlands with more than one wetland zone identified by the NWI. We combined these into individual depressional wetland basins classified by the most permanent water regime associated with each basin (Cowardin et al. 1995; Johnson and Higgins 1997). Because of similar characteristics and small sample size (<0.5% of total

Table 2 Number of 10.4-km^2 primary sampling blocks, number of wetland basins by wetland water regime, and total number of wetland basins assessed on annual surveys in the Prairie Pothole Region of North Dakota, South Dakota, and northeastern Montana, 1988–2007

Year	Sample blocks	Wetland water regime				Total
		Temporary	Seasonal	Semipermanent	Lake	
1988	263	14,541	15,326	2,852	147	32,866
1989	315	16,976	17,681	3,435	168	38,260
1990	335	19,218	19,140	3,742	187	42,287
1991	335	16,750	17,114	3,279	169	37,312
1992	335	19,222	19,565	3,776	190	42,753
1993	335	19,290	19,493	3,778	190	42,751
1994	335	18,956	19,301	3,721	185	42,163
1995	335	18,749	19,290	3,731	188	41,958
1996	335	19,167	19,554	3,776	191	42,688
1997	335	18,826	19,422	3,751	190	42,189
1998	335	19,122	19,552	3,758	191	42,623
1999	335	18,940	19,473	3,750	191	42,354
2000	335	19,252	19,564	3,761	190	42,767
2001	335	19,121	19,520	3,763	190	42,594
2002	335	19,318	19,593	3,775	190	42,876
2003	335	19,315	19,603	3,779	191	42,888
2004	346	20,238	20,179	3,913	193	44,523
2005	380	22,329	21,567	4,265	196	48,357
2006	380	22,309	21,566	4,264	195	48,334
2007	380	22,256	21,542	4,261	196	48,255
mean	338	19,195	19,402	3,757	186	42,540

basins), we combined palustrine permanent wetlands and lacustrine wetlands into a "lake" wetland class. Similarly, basins with saturated soils were combined with the temporary water regime (Table 1).

We collected aerial imagery for each sampling block annually from small, fixed-winged aircraft in May when prairie wetland water levels are typically highest (Kantrud et al. 1989; van der Kamp et al. 1999). During 1987–2006, we videographed wetlands using analog video cameras at a flight altitude of 3,500 m above ground level. Images were then digitized using video capture hardware and software; resulting imagery had a spatial resolution of 8 × 8 m. During 2007, we used digital cameras at a flight altitude of 2,280 m above ground level; resulting imagery had a spatial resolution of 1.3 × 1.3 m. During all years, we assessed imagery immediately after flights for proper lighting, equipment function, and completeness of coverage for each sampling block. When necessary, surveys were re-flown the next day, weather permitting, for blocks where initial image quality was poor.

We determined wet area of wetlands on each sampling block each year using TNTmips software (MicroImages, Inc., Lincoln, Nebraska) and a combination of supervised classification and photo interpretation. During processing the digital wetlands polygon layer for each block was displayed over the image and each wetland site was assessed to ensure that all wetlands with the potential to contain surface water were classified. We created a raster layer of classified surface water for each sample block, and then calculated the wet area expressed as a percentage relative to the baseline NWI polygon area, for each wetland. Values for wet area (%) could range from 0, which indicated no water in a basin, to >100, which indicated that the area of water exceeded the area of the baseline NWI polygon. One person processed ~85% of the images; to ensure consistency, this person error-checked and re-processed earlier images processed by two other individuals. No formal validation of the process for determining wet area was conducted.

Creation of Interpolated Surfaces

To provide a graphical representation of patterns of wetness across space, we used the POINTINTERP command within the ArcGIS software package (Environmental Systems Research Institute, Redlands, California) to create interpolated raster data layers, or grids, of wetness from annual estimates of basin wet area. POINTINTERP uses a smoothed exponential weighting function to create a grid surface from point features, in this case wet area (%) values from annual videographs assigned to the center of each wetland polygon. This process gives more weight to points close to a cell being interpolated than points farther away, i.e., it assumes that water conditions of basins show positive spatial autocorrelation, as would be expected given patterns of precipitation, land use, and local soil types. Before proceeding with analysis, we visually assessed output from different interpolation settings to identify factors that influenced results, carry interpolations to the boundaries of the study area, and ensure that the process adequately characterized wetness conditions over time. Based on these assessments, we assigned equal weight to all wetlands within 5 km of a grid, with the weight of points dropping off exponentially in a circular neighborhood to 0 at 150 km. We selected a grid size of 600 m, which provided a compromise between fine resolution and the ability to include multiple wetlands. Grids were created for each of the four basin water regimes each year. We excluded wet area (%) values >1,000 for all analyses. Values >1,000 represented <0.4% of all observations and were typically anomalies associated with point wetlands or small portions of large wetlands sampled at the edge of a 10.4-km^2 primary sampling block where the measured portion of the wetland increased greatly in size during

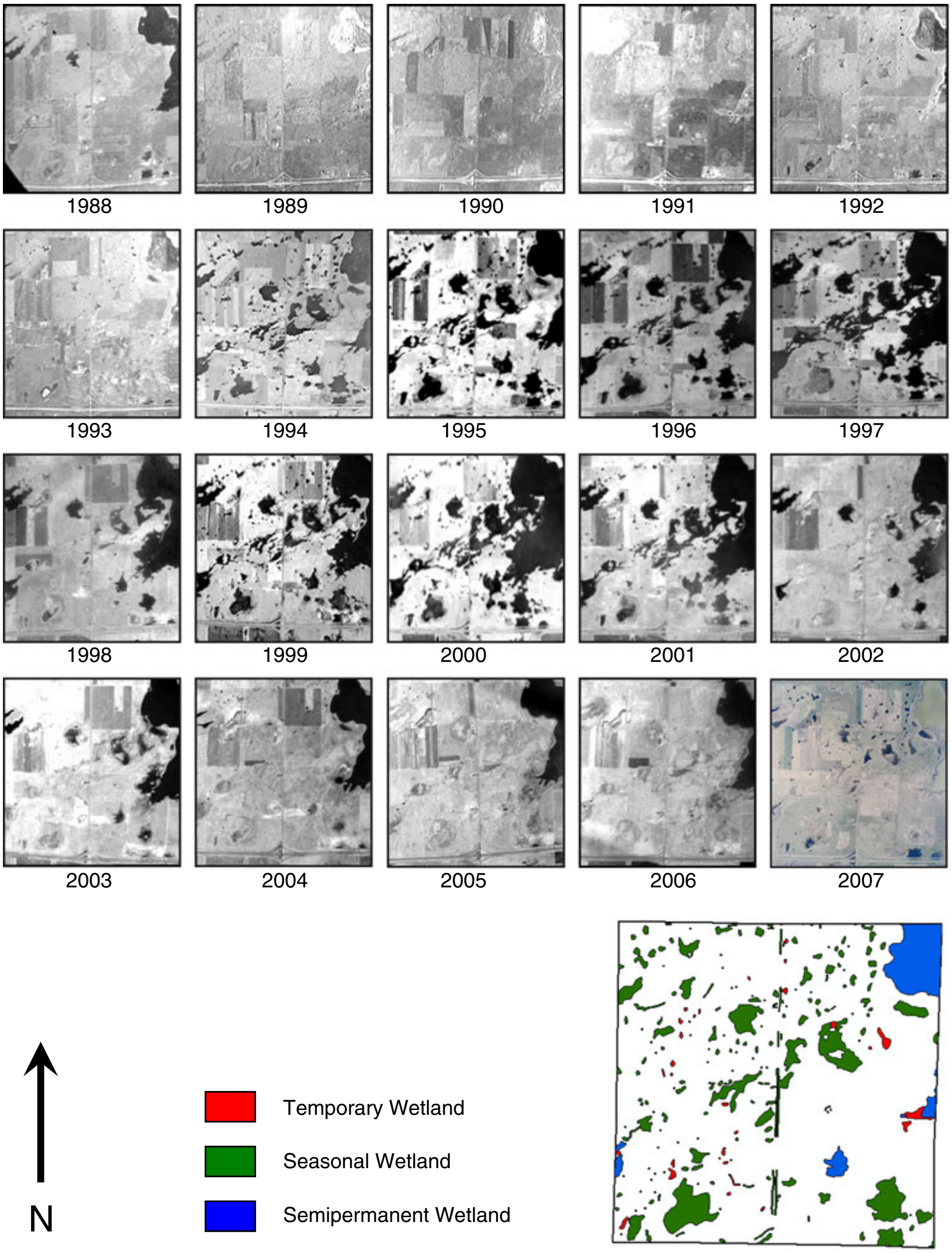

Fig. 2 Aerial photographs for an example of a 10.4-km^2 primary sampling block, 1988–2007. Panel in lower right shows same 10.4-km^2 primary sampling block with wetland basins and associated water regimes as identified by the National Wetlands Inventory (wetlands with permanent water regimes did not occur in this sampling block). Note the interconnections of some wetland basins that occurred during periods of deluge (e.g., late 1990s, early 2000s)

periods of deluge. The formula used by POINTINTERP for calculating output cell values values was

$$\widehat{z}_i = \frac{\sum z_i e^{-pd_i}\left(r^2 - {d_i}^2\right)}{\sum e^{-pd_i}\left(r^2 - {d_i}^2\right)}$$

where $\widehat{z}_i$is the predicted wet area (%) value for cells in the output grid; z_i is the wet area (%) value for a wetland basin within the circular neighborhood; d_i is the distance from the grid cell center to the center of the wetland basin *i*; r is the 150-km radius of the circular neighborhood; and p is a decay function, estimated using distance from output cell center, controlling how quickly the weighting of points diminishes with distance from the output cell center. In our application, there was no decay within 5 km of the output cell center.

We chose exponentially weighted interpolation over kriging for two reasons. First, interpolated values would not be greater or less than observed values as can be the case with kriging (Legendre and Legendre 1998). Second, exponentially weighted interpolation was conducive to using the same parameters for creating all grids rather than basing parameters on assessments of statistical dependence among observations for each water regime and year. Thus, any spatial patterns among years and water regimes or limitations introduced by our choice of analysis would be consistent among water regimes and years. We used data from Montana when reporting basin observations and for creating interpolated grids, but only used the North Dakota and South Dakota portions of the study area when reporting results of grid analyses because sample points were absent throughout much of the Montana portion of the study area (Fig. 1).

Statistical Analyses of Basin Wet Area

We first analyzed data in a non-spatial context by calculating the percentage of all basins, by water regime, that contained at least some water (wet area [%] >0) each year. This provided a simple index to the number of wetland basins containing water each year similar to results of the May waterfowl surveys, except that we analyzed data by water regime. We then calculated mean wet area (%) and the accompanying standard deviation for all wetlands each year, again by water regime. Because wetland size and hydroperiod vary among water regimes, we reported the coefficient of variation (CV) as a measure of dispersion rather than the standard deviation to better demonstrate relative differences in variation among water regimes.

We assessed grids of interpolated wet area values for each year to gain insight into spatial patterns in the data. First, we calculated a correlation matrix for all 20 grids of annual interpolated wetness values for each water regime over the 20-year period using ArcGIS's STACKSTATS command. This procedure related the value of each cell in a grid to values of the corresponding cell in all grids under consideration. A correlation coefficient (*r*) was then output for every grid combination; possible values for *r* ranged from +1, indicating a perfect direct relationship between grids, to −1, indicating a perfect inverse relationship. High positive correlations between grids would indicate that spatial patterns in wetness across the study region were similar, whereas high negative correlations would indicate that spatial patterns were dissimilar. We then plotted mean values of *r* among grids at lags of 1–10 years; sample size for these means (the number of *r* values) ranged from 19 for a lag of one year to nine for a lag of 10 years. This analysis illustrated potential similarity in spatial patterns of wetness (i.e., autocorrelation) and how these patterns varied over time and among water regimes.

We also calculated the mean wet area (%) and CV for interpolated grid layers of each wetland water regime over the 20-year period using ArcGIS's GRID module. This procedure also works on a cell-by-cell basis, calculating the desired statistic for a given cell and the corresponding cells

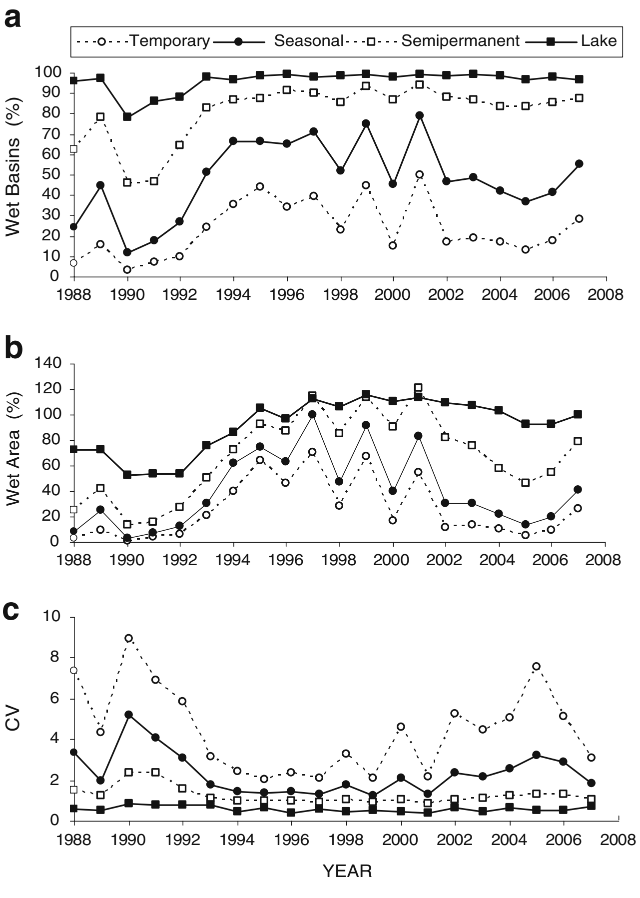

Fig. 3 (**a**) The percentage of wetland basins containing water and (**b**) the mean wet area (%) of wetland basins varied among years, 1988–2007, and increased with permanency of water regime as classified by the National Wetlands Inventory. (**c**) The coefficient of variation (CV) for mean wet area (%) of the same wetland basins decreased with permanency of water regimes

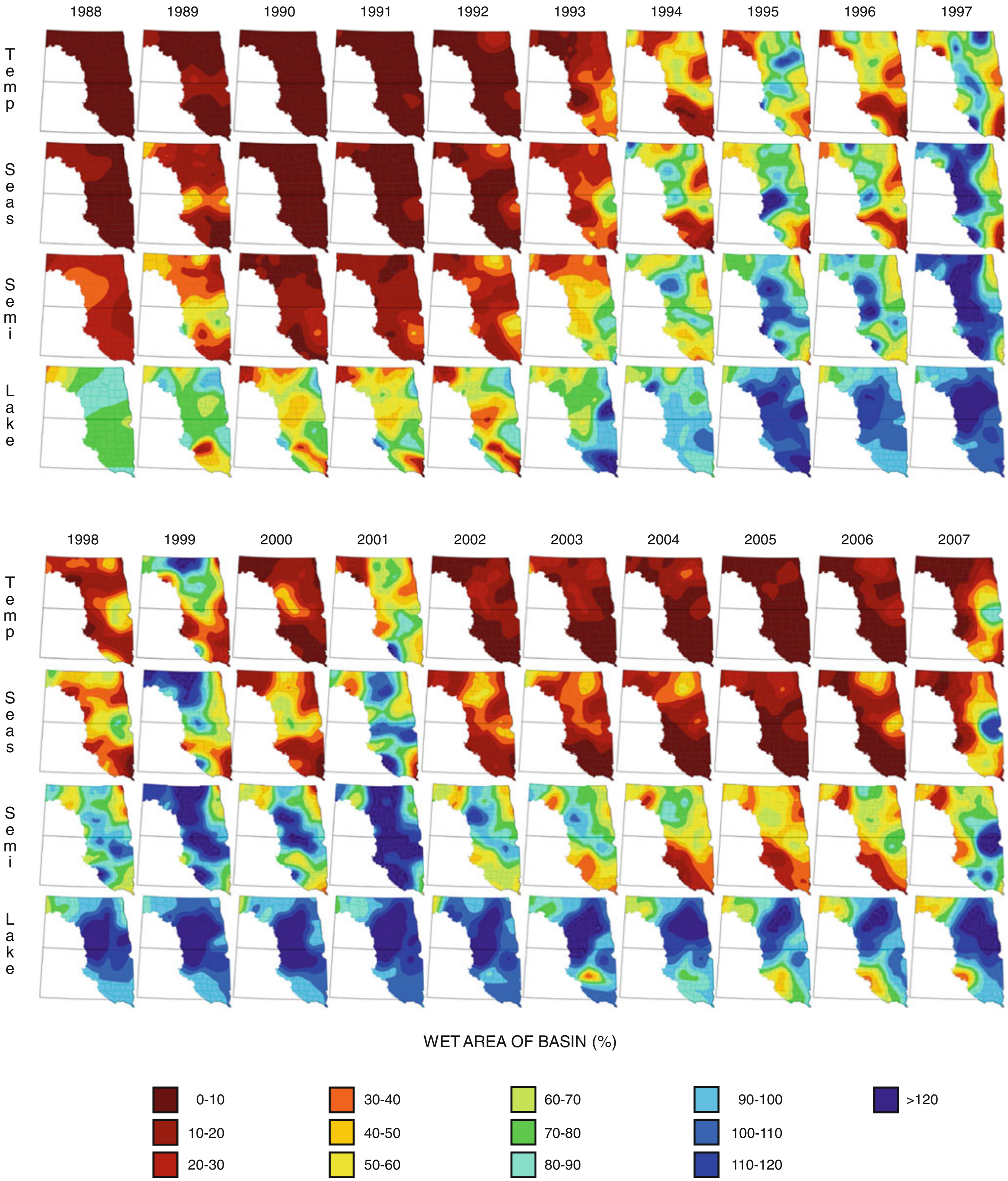

Fig. 4 Interpolated wet area (%) of temporary (Temp), seasonal (Seas), semipermanent (Semi), and lake wetland basins varied spatially and temporally within and among wetland water regimes in the U.S. Prairie Pothole Region, 1988–2007

in all 20 grids. We used this analysis to illustrate spatial patterns over the 20-year period. Finally, we calculated correlations among the four grids showing 20-year means of interpolated wet area (%) for each wetland water regime, again using the STACKSTATS command; we also calculated correlations among the four grids showing the CV for 20-year means of interpolated wet area (%) for each wetland water regime. If mean patterns of wetness and variation in wetness were spatially similar for each water regime, correlations among grids would be high, whereas low correlations would indicate that wetness and variation in wetness differed across the study region for the four wetland water regimes.

Results

The mean number of basins sampled annually over the 20-year period was 42,540, with temporary and seasonal basins comprising ~90% of the total (Table 2). The sample period included times of drought (1988–1992 and 2002–2005) and deluge (1993–2001; Figs. 2 and 3). The percentage of basins containing water varied among years, but was consistently lowest for temporary wetlands and increased with permanency of the NWI-identified water regime (Fig. 3a); mean wet area (%) followed a similar pattern (Fig. 3b). Variation in mean wet area (%) of basins differed among wetland water regimes, with the CV consistently highest for temporary wetlands and decreasing with permanency of the water regime (Fig. 3c).

Patterns of wet area (%) varied temporally and spatially within and among water regimes (Fig. 4). Correlations with values from previous years were consistently highest for lakes and lowest for temporary wetlands (Fig. 5). Correlations generally were strongest at a lag of one year and decreased as the lag period increased, particularly for lake and semipermanent wetlands (Fig. 5). During the time period we sampled, wet area (%) values did not average out across space or suggest an east-west gradient in wetness, as grids of mean wet area (%) and CV over the 20 years demonstrated substantial spatial variation within water regimes (Fig. 6). Consistent with non-spatial results, mean wetness values for interpolated grids were lowest and CV was highest for temporary wetlands (Fig. 6). Correlations (*r*) between grid layers indicate that spatial patterns of wetness and variation in wetness over the 20-year survey period were most similar among temporary, seasonal, and semipermanent wetlands; spatial patterns for lake wetlands were least similar to those of other wetland water regimes (Table 3).

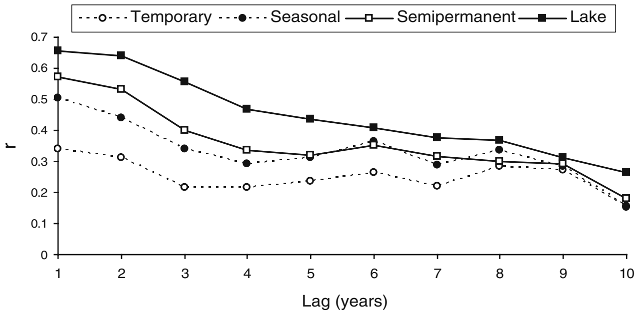

Fig. 5 Mean correlation (r) of interpolated grids of wet area (%) at lag intervals from 1 to 10 years was highest for lake wetland basins, lowest for temporary wetland basins, and decreased with time in the Prairie Pothole Region of North Dakota, South Dakota, and northeastern Montana from 1988–2007

Discussion

Our data were collected annually in May, and therefore cannot provide insight into intra-seasonal variation of wet area of wetlands. However, prairie wetlands typically experience highest water levels in spring (van der Kamp et al. 1999), and consistent differences in water dynamics among water regimes suggest that factors influencing patterns of intra-annual variation used to classify wetlands also may influence patterns of inter-annual variation. Other characteristics such as surrounding land use also influence water levels and dynamics (Euliss and Mushet 1996; van der Kamp et al. 1999), but exceed the scope of this analysis, which was intended to address broad patterns among water regimes across space and time. Also, observed dynamics depend in part on baselines established by the NWI. Large CVs for temporary and seasonal wetlands in non-spatial analyses may be caused in part by differences in surrounding land use and wetland-specific characteristics, but are also inflated by regional differences in wetness. Our wetness interpolations explicitly show spatial patterns that are lost in simple, non-spatial summary statistics, but do not reveal variance that is present at the scale of individual wetlands or wetland complexes. Climatic variability is the primary driver of water conditions in the PPR, but dynamics of wetlands in our analysis varied spatially and among water regimes, suggesting that precipitation and temperature alone would be insufficient to explain annual wetland water conditions in the PPR. Consequently, the predictive ability of models that do not consider water regimes or spatial patterns will be limited, whether they are predicting water conditions or numbers and distribution of wildlife.

Wetlands have a continuum of characteristics and dynamics and do not fit into neat categories (Meyboom 1963; Lissey 1971; Stewart and Kantrud 1971; Cowardin et al. 1979; Euliss et al. 2004). The wetland dynamics we documented generally followed a permanency gradient where temporary wetlands had the least water, were the

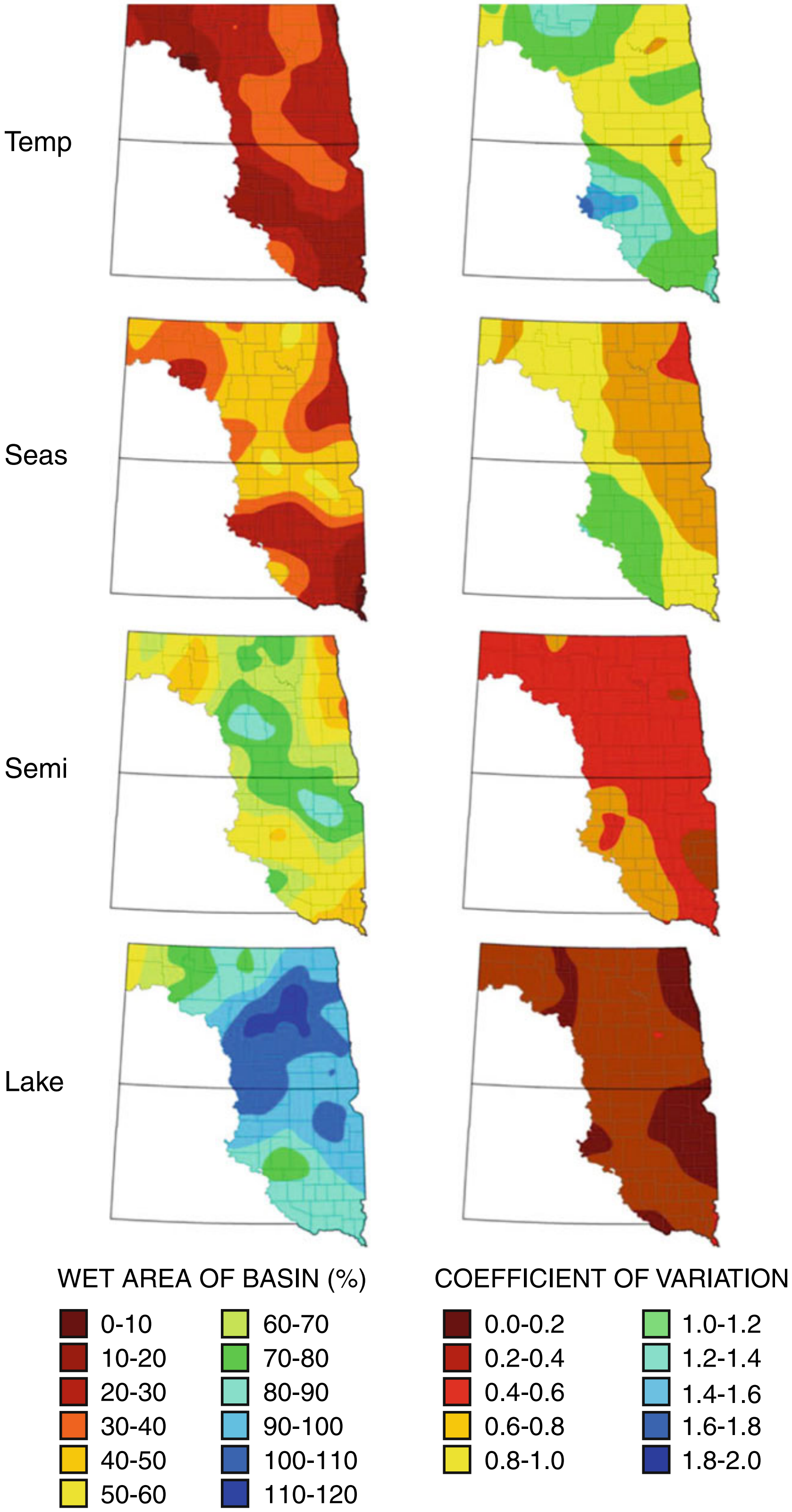

Fig. 6 Mean wet area (%) of wetland basins (left) and coefficient of variation for mean wet area (%) of wetland basins (right) from 1988 to 2007 varied spatially and with permanency of water regime for temporary (Temp), seasonal (Seas), semipermanent (Semi), and lake wetlands

Table 3 Correlations among grid layers representing 20-year mean wetness values for temporary, seasonal, semipermanent, and lake wetland basins in the Prairie Pothole Region of North Dakota and South Dakota. Correlations among grid layers for the coefficient of variation in wetness values are shown in parentheses

	Temporary	Seasonal	Semipermanent
Seasonal	0.80 (0.84)		
Semipermanent	0.70 (0.70)	0.75 (0.82)	
Lake	0.53 (0.21)	0.34 (0.33)	0.43 (0.34)

most variable, and had wet area (%) values that were least similar to values from previous years, while lake wetlands had the greatest wet area (%), were least variable, and were most similar to conditions from previous years. Wet area (%) of wetlands in our analysis varied greatly over the years, including considerable overlap in the range of values among water regimes, but with consistent relative differences among water regimes. Although we did not measure the length of time that water persisted in wetland basins each year, high inter-annual variation in numbers of basins containing water and amount of water in basins may indicate shifts in water regime. Van der Valk (2005) also noted that, over time, a wetland could experience water-level fluctuations with different means, ranges, and periods such that wetlands classified as having a semi-permanent water regime could function as seasonal wetlands during a dry period, and wetlands classified as having a seasonal water regime could function as semi-permanent wetlands during wet periods. Our results suggest that some of the shortcomings of traditional, static, wetland classifications used for inventory can be overcome and the value of digital data based on these classification systems (e.g., NWI) can be greatly enhanced when linked to ancillary information such as annual wet area. For example, spatial models predicting distribution and density of wetland-dependent wildlife are greatly improved when estimates of wetness are linked to NWI data (Niemuth et al. 2008a).

Temporary and seasonal wetlands are generally small, shallow, and—by definition—contain water for only a portion of the growing season each year. Because they typically contain water in spring when farmers plant crops but are dry much of the rest of the year, wetlands with these water regimes often are viewed as being impediments to agriculture and having little ecological value (Leitch 1989). However, small, shallow wetlands have high ecological value because they warm earlier than larger, deeper wetlands, vegetation that grows during the dry period is often flooded during wet periods, and frequent drying mobilizes nutrients and eliminates fish that reduce availability of invertebrate prey for immature waterfowl (see Swanson and Duebbert 1989; van der Valk 2005). In short, high variability of temporary and seasonal wetlands make them preferred habitat for many species of wetland-dependent wildlife (Kantrud and Stewart 1984; Niemuth et al. 2006). However, because they are shallow and often dry, the margins and basins of these wetlands are more vulnerable to degradation by agricultural activities than wetlands with more permanent water regimes (Bartzen et al. 2010).

Semipermanent wetlands were less variable than temporary and seasonal wetlands. Although important ecologically, semipermanent wetlands were the only water regime considered in several models assessing the effects of climate change on PPR wetlands (Poiani and Johnson 1991; Poiani et al. 1996; Johnson et al. 2005) and speculation about climate change impacts on waterfowl. Temporary, seasonal, and lake wetlands have different dynamics, and should also be considered more thoroughly in assessments of potential effects of climate change (see Johnson et al. 2005; Johnson et al. 2010).

The spatial and temporal variation in wetness that we documented may be unusually high because the 20-year period for which we analyzed data included the second driest drought of the 20th century (1988–1992) and the wettest period in the past 130, possibly 500, years (Winter and Rosenberry 1998). These close periods of extreme conditions may simply reflect normal fluctuations in precipitation, or may be a symptom of climate change, which is sometimes predicted to be characterized by high variation in temperature and precipitation.

It is necessary to distinguish natural variability from directional change when evaluating potential changes in climate and consequences to wetlands (Winter and Rosenberry 1998). The tremendous spatial and temporal variation in wet area that we documented emphasizes the value of long-term data collected over broad geographic extents for monitoring wetlands, as well as the need to consider additional factors that influence water levels in wetlands. Wetland size, basin morphometry, soil type, land use, catchment size, topographic position, and wetland drainage patterns, as well as precipitation, influence water levels in PPR wetlands (Kantrud et al. 1989; Euliss and Mushet 1996; van der Kamp et al. 1999). Spatial models incorporating these factors might provide additional insight into patterns of wetness in PPR wetlands. But even with an increased understanding of processes affecting water dynamics in PPR wetlands, predicting future conditions will still be difficult as the magnitude and speed of changes in warming and precipitation are uncertain (Johnson et al. 2005). Climate change would likely mean changes in potential evapotranspiration as well as the frequency and intensity of precipitation. The dynamic nature of prairie wetlands and the often-shifting interplay between precipitation, evapotranspiration, and groundwater flow (Winter and Rosenberry 1998; van der Kamp and Hayashi 2009) will further complicate predictions of future conditions.

Monitoring programs and subsequent analyses and projections of wetland conditions in the PPR should consider wetland water regimes and their dynamics, the relative abundance and spatial distribution of wetlands of each water regime, and spatial and temporal variation in water conditions of wetlands with different water regimes. For example, Larson (1995) found that no time lags greater than one year entered into any models when assessing variables associated with numbers of May ponds. However, that finding may have been influenced by characteristics of the May pond survey data, which does not distinguish among water regimes (USFWS and CWS [1987] Standard operating procedures for aerial waterfowl breeding ground population and habitat surveys in North America. Unpublished report, USFWS Office of Migratory Bird Management, Laurel, Maryland). The dynamics of seasonal wetlands, which showed less of a correlation with values of wet area (%) from previous years than semipermanent or lake wetlands, could drive results derived from May pond surveys. Seasonal wetlands are very abundant, and account for 85% of the seasonal, semipermanent, and lake wetland basins mapped by the NWI in our study area (USFWS, unpublished data). In addition, seasonal wetlands exhibited greater annual variation in wetness than semipermanent or lake wetlands, and likely accounted for substantial variation in May pond numbers. Similarly, the Palmer Drought Severity Index (Palmer 1965), which calculates a hydrological water budget based on monthly precipitation and temperatures, is strongly correlated with May pond numbers and breeding duck populations and has been used as an index to climatic factors influencing duck populations (Sorenson et al. 1998).

Perhaps most importantly, the conservation community must recognize that climate change is but one stressor on wetlands in the PPR, with considerable uncertainty at this time as to what its effects will be and what can be done to reduce those effects on wetland-dependent wildlife. Many species of wildlife are adapted to the PPR's variable environment and respond to water conditions by changes in distribution and numbers (Smith 1970; Stewart and Kantrud 1973; Peterjohn and Sauer 1997; Niemuth and Solberg 2003; Niemuth et al. 2008b) and reproductive effort (Krapu et al. 1983; Pietz et al. 2000). However, loss of wetlands and grasslands from habitat conversion is a well-defined, ongoing problem with a demonstrated negative effect on populations of wetland-dependent wildlife (Bethke and Nudds 1995; Reynolds et al. 2006) that can be readily addressed with existing knowledge and programs. Our results highlight tremendous spatial and temporal variation in wetland dynamics that can influence our ability to discern climate change effects in the region. Physical and biological mechanisms that influence wetland dynamics as well as social and economic factors that influence the cost of conservation must be considered across broad spatial and temporal scales to develop effective conservation strategies, regardless of the stressors being addressed by conservation efforts.

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