



Effects of cropland encroachment on prairie pothole wetlands: numbers, density, size, shape, and structural connectivity

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Abstract

Context Agricultural expansion is the greatest source of wetland loss in the Prairie Pothole Region (PPR) of North and South Dakota, a critical waterfowl production area in North America. It is unknown how wetland losses from grassland conversion may alter structural connectivity in the prairie pothole network, however.

Objectives We examined how agricultural expansion over the period 2001–2011 altered the number, size, shape, and structural connectivity of PPR wetlands. We hypothesized that the loss of wetlands or wetland area would decrease structural connectivity on the landscape.

Methods We analyzed a published raster database that quantified 2001–2011 agricultural conversion of wetlands in the Dakotas. A suite of structural connectivity metrics was computed using the *igraph* R package.

Results Wetland area decreased by 25% within the study area, density decreased by 16%, and average size decreased from 2.41 to 2.16 ha with no increase in perimeter:area ratios, thus indicating changes more

from the splitting of larger wetlands (accounting for 23% of area lost) and “nibbling” at patch area (38%) than from complete wetland elimination (39%). Despite loss of wetlands and wetland area to cropland, however, the network did not display constrained structural connectivity.

Conclusions Structural connectivity has not been significantly affected by wetland losses because of the large number of remaining wetlands, but wetlands will continue to be lost with ongoing grassland conversion and climate shifts. It is unknown where the tipping point of wetland losses lies in the PPR that will incur ecological costs.

Keywords Prairie Pothole Region · Connectivity · Wetland losses · Grassland conversion

Introduction

The Prairie Pothole Region (PPR) of North America is one of the most important areas in the world for waterfowl and other wetland-associated birds, owing to the presence of millions of glacially formed wetlands (Naugle et al. 2001). Agricultural expansion in the PPR, particularly within North and South Dakota (hereafter, DPPR), reduced wetland area during the early part of the twenty-first century. Prairie conversion rates were particularly high during

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2006–2014, when the convergence of high commodity prices and advances in technology created an economic environment that incentivized corn acreage expansion (Claassen et al. 2011; Fausti 2015; Wang et al. 2017). The recent conversion of wetlands to croplands has been confirmed by multiple authors, with computed loss rates as high as 0.35% per year (Oslund et al. 2010; Faber et al. 2012; Johnston 2013; Wright and Wimberly 2013; Dahl 2014). Losses of some types of wetlands have been mitigated by Section 404 of the Clean Water Act, which prohibits discharges without a permit into the “waters of the US” (NRC 2001). However, most prairie pothole wetlands do not fall within the definition of the “waters of the US” due to their isolation from navigable waters. In some states, the definition of waters of the US has been expanded by the US Environmental Protection Agency’s 2015 Clean Water Rule, but this definition does not yet apply in North and South Dakota due to ongoing litigation (<https://www.epa.gov/wotus-rule/definition-waters-united-states-rule-status-and-litigation-update>). Wetland drainage has also been discouraged by the 1985 Food Security Act and subsequent Farm Bills that reduce subsidy payments to farmers who drain wetlands (NRC 1995). Although these measures have reduced the pace of wetland loss, prairie wetlands continue to be lost, and agriculture is the primary cause of that loss (Dahl 2014).

All PPR wetlands are not equally susceptible to agricultural conversion, depending on their density, size, hydroperiod, and context. Several forms are especially vulnerable: wetlands within an agricultural context, small wetlands, isolated wetlands, wetlands with a short hydroperiod (which is itself often a function of wetland area), and farmed wetlands (Dahl 2014; Van Meter and Basu 2015). Farmed wetlands, which are wetlands that have been used to produce an agricultural commodity but retain some wetland characteristics such as seasonally ponded water, are vulnerable to drainage for agricultural crop production because they are usually small, are embedded within existing farm fields, and can be easily drained (in some cases without penalty under existing regulations). Indeed, Dahl (2014) found that wetlands were often lost to agriculture even during periods of abnormally high water conditions.

Although biodiversity is often positively associated with wetland area, even small or temporary wetlands

are important because they provide disproportionately greater ecosystem services than do larger and more permanently flooded wetlands, owing partly to their sheer abundance (Semlitsch and Bodie 2001; Zedler 2003). For example, small wetlands are important for the conservation of turtles and small mammals (Gibbs 1993), and temporary and seasonal wetlands are particularly important habitat for ducks and shorebirds (Kantrud and Stewart 1977; Krapu et al. 1997). Thus, the area of wetlands in the surrounding landscape is important to biodiversity, so the collective loss of even small wetlands in the landscape may have a detrimental effect on biodiversity.

Power law relationships (Korcak 1940) that plot number of wetlands versus wetland size on a logarithmic scale have been used to demonstrate such changes in the relative proportion of wetlands by size with changes in climate and human alteration (Downing et al. 2006; Van Meter and Basu 2015). For example, a power law analysis of eastern South Dakota potholes showed that the numbers of wetlands exhibited a consistent pattern of size abundances across multiple years, such that the power law exponents were consistently about -1.7 despite a range of dry (1992) to wet (1997) conditions (Zhang et al. 2009). The power law exponents changed seasonally, however, between April (-1.8) and August (-1.59), which the authors attributed to preferential reduction in the areas of smaller wetlands between early spring and late summer via seasonal weather-related precipitation dynamics. Such an approach can therefore be used to determine whether rates of change in wetland losses exist by size category and whether these rates differ at different points in time.

As a related consequence of changing wetland habitat patch area, changes in wetland shape can also affect their habitat value. A study that modeled the habitat characteristics of wetland bird species in the PPR of Iowa found that perimeter-to-area ratio was the variable most often included in the best models (8 of 15 models) (Fairbairn and Dinsmore 2001). This variable was positively associated with edge species such as Swamp Sparrow and Red-winged Blackbirds, such that more convoluted shapes increased nesting density for these species. Interior-nesting species (Pied-billed Grebe, Least Bittern, American Coot, Marsh Wren, and Yellow-headed Blackbird) had a negative association with the perimeter-to-area ratio variable (Fairbairn and Dinsmore 2001).

Furthermore, the loss of wetlands can also decrease wetland density, resulting in an increase in between-wetland distances, thereby preventing access by organisms with limited vagility such as amphibians, waterfowl with flightless chicks, or waterfowl in wing molt (Ringelman 1990; Lehtinen et al. 1999). Structural characteristics of the landscape elicit functional responses from organisms; consequently, a distinction must be made between structural and functional connectivity (Taylor et al. 2006). A decrease in structural landscape connectivity can thus have population consequences beyond what would be predicted by area loss alone, indicating the importance of taking a landscape ecology approach to examining effects of wetland losses on wildlife. Thus, cropland expansion in the DPPR may potentially affect the amount, quality, and accessibility of habitat for a variety of wildlife species, but there have been few assessments of these effects. This lack of information will hinder management and conservation of wetlands and wetland-associated wildlife in agricultural landscapes. In addition, these effects illustrate the importance of considering wetland structure at multiple scales (Fairbairn and Dinsmore 2001). Habitat patches, as objects of management themselves, also exist within a larger habitat network. Therefore, an approach is needed that examines not only the effects of land conversion on patch size but also on their shape and positioning in the landscape (see also Naugle et al. 2001; McIntyre et al. 2018).

We took such an approach in quantifying multiple consequences of documented losses of prairie pothole wetlands. Previously, Johnston (2013) demonstrated rapid losses of wetland area in the DPPR due to conversion to cropland from 2001 to 2011. In that study, wetland area loss rates were computed for each of 1755 $7.5' \times 7.5'$ quadrangles in the DPPR, but individual wetlands were not identified. Here, we extend that study by quantifying losses of individual wetlands to assess consequent impacts on structural connectivity, and to examine how agricultural expansion altered the spatial pattern of DPPR wetlands between 2001 and 2011. Because the number, spacing, and shape of wetlands can affect their habitat value for wildlife, alterations to these properties as a result of land conversion may result in cascading effects on wildlife populations. Some wetlands may be lost entirely whereas others may be reduced in size by dividing them (e.g. via roads or berms) or by altering

their edges (shrinking the wetland from the outside inwards). We therefore hypothesized that loss of wetland area due to agricultural expansion over time would:

1. cause a decrease in wetland density (i.e., a decrease in the number of wetland patches per unit area of landscape as wetlands are eliminated);
2. cause a decrease in average area of wetland patches as wetlands are drained or tilled;
3. cause a decrease in average perimeter of wetlands as they are drained or tilled (with large farm machinery potentially smoothing out irregular wetland borders, making wetland polygons become more compact in shape);
4. disproportionately affect small wetlands, causing power law lines to have flatter slopes (since smaller wetlands would be easier to drain or till than would larger ones); and
5. decrease the structural connectivity of the landscape (as indicated by various independent landscape metrics) as wetland patches become sparser and more distant from each other.

These changes to wetland properties may have different effects depending on taxon. For example, volant taxa such as birds may be less affected by changes to habitat availability than overland dispersers such as amphibians would be (Bélisle 2005). However, the sheer scale of agricultural expansion occurring in the DPPR provides strong justification that its effects on wetlands should be quantified in terms of their numbers, density, size, shape, and structural connectivity so that appropriate conservation actions can be advised.

Consistent with the usage in our source data (Johnston 2013), we use the term “wetland loss” to mean a pixel that was mapped as wetland or water on the 2001 National Land Cover Database (NLCD) (Homer et al. 2007; Wickham et al. 2010) but mapped as corn or soybeans by the 2011 cropland data layer (CDL) (USDA NASS 2011). These wetland losses may or may not be permanent, and we did not consider wetland losses other than those caused by cropland displacement of 2001 wetlands. Although climatic drying can also cause wetland losses, the DPPR had experienced three successive springs of abnormally wet weather as of 2011, so the landscape was much wetter than it had been in 2001 and climatic drying should not have been a factor in the wetland losses

analyzed (Johnston 2014; Vanderhoof and Alexander 2016).

Methods

The DPPR consists of lands in North and South Dakota east of the Missouri River, the approximate limit of Wisconsinan glaciation. Wetlands and open water cover about 8.5% of the region, in the form of millions of prairie potholes (Dahl 2014; Skagen et al. 2016). Average annual precipitation ranges from about 700 mm/yr in the southeastern corner of the region to only 300 mm/yr in northwestern North Dakota (Millett et al. 2009). The Palmer Hydrological Drought Index for South Dakota was 2.51 (moderately moist) in 2001 and exceeded 7.0 (extremely moist) in 2011, indicating overall wet conditions over our focal time periods (NCEI 2018). Row crop and small grain agriculture is the main land use, constituting 56% of the landscape in 2012, with grassland covering an additional 30%, forests and shrublands 1%, developed and barren areas 4%, and the remaining (8%, plus rounding) as water and wetlands (Johnston 2014). The region contains few urban areas, and human development covers only 4.4% of the region. Land planted in corn or soybeans increased by 27% between 2010 and 2012, at the expense of wheat, grasslands, and wetlands (Wright and Wimberly 2013; Johnston 2014). This is thus a wetland-studded region that has recently experienced extensive land conversion.

This study utilized maps of wetland losses previously published by co-author Johnston, who used row crops (corn and soybeans) mapped in the 2011 USDA cropland data layer (CDL) (USDA NASS 2011) to mask out wetlands depicted by the 2001 NLCD National Land Cover Database (NLCD) (Homer et al. 2007), with the rationale that the row crop presence was an indicator of wetland loss (Johnston 2013). The two datasets (2001, 2011) have the same spatial resolution (30 × 30 m pixels) and alignment. Although these two original data sources are accurate, both have inherent errors. Within the PPR, NLCD producer accuracies for emergent herbaceous wetlands and water were 80.2% and 86.8%, respectively (Table 3 in Wickham et al. 2010). Producer accuracies for 2011 CDL corn and soybeans ranged from 90.9 to 95.7% (Table 1 in Johnston 2013). Johnston also evaluated the accuracy of wetland losses identified by

this masking method, and found that only 6.8% of the area evaluated was misclassified due to errors in the 2011 CDL layer (e.g., cattails mapped as corn) (Table 3 in Johnston 2013). Our study did not attempt further accuracy evaluation but rather utilized the maps as previously published.

Study sites with high wetland loss rates were selected from the 2001–2011 wetland loss maps, for which wetland areal loss statistics had been computed for each of the 1755 7.5' × 7.5' quadrangles in the DPPR (see Fig. 6b in Johnston 2013). We selected five 7.5' × 7.5' quadrangles (total area = 672 km²) with high rates (13–39%) of wetland loss between 2001 and 2011 (Table 1), averaging 24.9% loss. These quadrangles were not intended to be random or representative of the region as a whole, because the intent of this study was to determine how high wetland loss rates would affect connectivity. These quadrangles were selected from within the Drift Prairie physiographic region to minimize potential differences due to geomorphology, and we avoided quadrangles that contained extensive floodplain wetlands, large lakes, or urban wetlands (all hydrologically different from prairie potholes). In addition, quadrangles were selected to span the north–south gradient of this physiographic region (Fig. 1). The Red River floodplain forms the DPPR's eastern border. West of it lies the Drift Prairie, a region of gently rolling hills, in contrast to the more sharply uplifted region immediately to its west, the Missouri Coteau, which forms the westernmost border of the DPPR. Physiographic differences in terrain among these regions can lead to differences in land use, so we made sure to sample within the same physiographic region. All of our focal quadrangles were intensively farmed, with corn or soybean crops constituting 38–74% of the landscape (Table 1).

Within the study quadrangles, we used procedures in ArcGIS 10.5 (ESRI 2017) to convert the raster representations of the 2001 and 2011 wetlands into polygon wetland patches (Raster to Polygon with simplify polygons option, 4-neighbor rule as standard in ArcGIS). Area was computed for each polygon, and small polygons (< 4 pixels, 0.36 ha) were eliminated, consistent with the limitations in the original image resolution (Homer et al. 2007; Zhang et al. 2009). The centroid coordinates and the perimeter were computed for each remaining polygon. The shoreline irregularity index (SI), a shape metric commonly used in

Table 1 Study site quadrangles

Quadrangle name	Quadrangle code	Primary county and state abbreviation	Wetland area, 2001 (ha)	Wetland area, 2011 (ha)	Wetland area loss (ha), 2001–2011 (% loss)	Area in corn or soybeans, 2011 (% of quadrangle) (%)
Cresbard	o45098b8	Faulk, SD	896.15	543.91	352.24 (39.3%)	61.5
Bridgewater East	o43097e4	McCook, SD	1060.19	856.99	203.20 (19.2%)	74.2
Eldridge SE	o46098g8	Stutsman, ND	934.72	810.70	124.02 (13.3%)	51.8
Fingal SW	o46097g8	Barnes, ND	737.95	529.26	208.69 (28.3%)	50.9
Logan Center	o47097g7	Grand Forks, ND	1016.36	748.16	268.20 (26.4%)	37.8

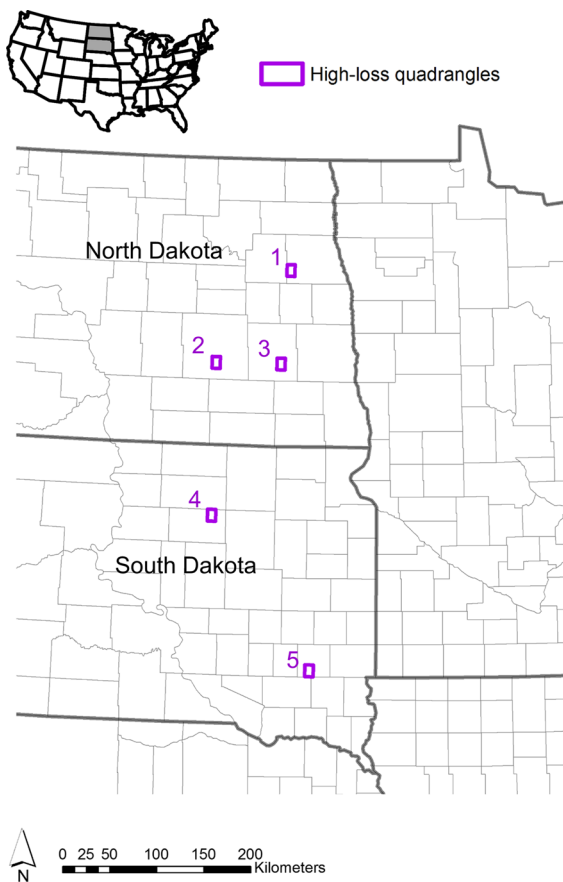


Fig. 1 Map of our five focal quadrangles (purple polygons) in North and South Dakota (shaded states). The northernmost quadrangle (number 1) is the Logan Center, North Dakota, quadrangle referenced in Figs. 3 and 4. (Color figure online)

limnology to assess perimeter:area (Hutchinson 1957; Van Meter and Basu 2015), was then calculated as:

$$SI = \frac{L}{2\sqrt{\pi A}} \tag{1}$$

where L is the perimeter length and A is the polygon area. A polygon with $SI = 1.0$ is a perfect circle, and more convoluted shapes have larger values.

Individual wetlands were counted by size class bins in 0.09 ha (size of a raster cell) increments. The logarithm of bin wetland area was then plotted against the logarithm of the wetland count for that bin, and a linear regression was fitted to the data to generate a power law function. According to this relationship, the number of wetlands (N) in any size class varies as a function of wetland size:

$$N = c(A)^b \tag{2}$$

where A is the wetland surface area in m^2 , and b and c are the exponent and coefficient of the relationship, respectively. The power law analysis was applied to wetlands up to 57,600 m^2 in area; beyond that size there were too few wetlands representing the largest size classes. Ninety-five percent confidence intervals (95% CI) around these lines allowed us to compare slopes by wetland size and year.

The fate of each 2001 polygon as of 2011 was determined by intersecting the 2001 wetland polygon file with the 2011 wetland centroid file to which the 2011 polygon area attributes had been assigned. This analysis included an initial step of shifting the location of wetland centroids that fell outside of polygon boundaries, as in the case of horseshoe-shaped wetlands. This ensured that every 2011 polygon was assigned to a corresponding 2001 polygon. Polygons from 2001 that lacked a matching 2011 centroid were

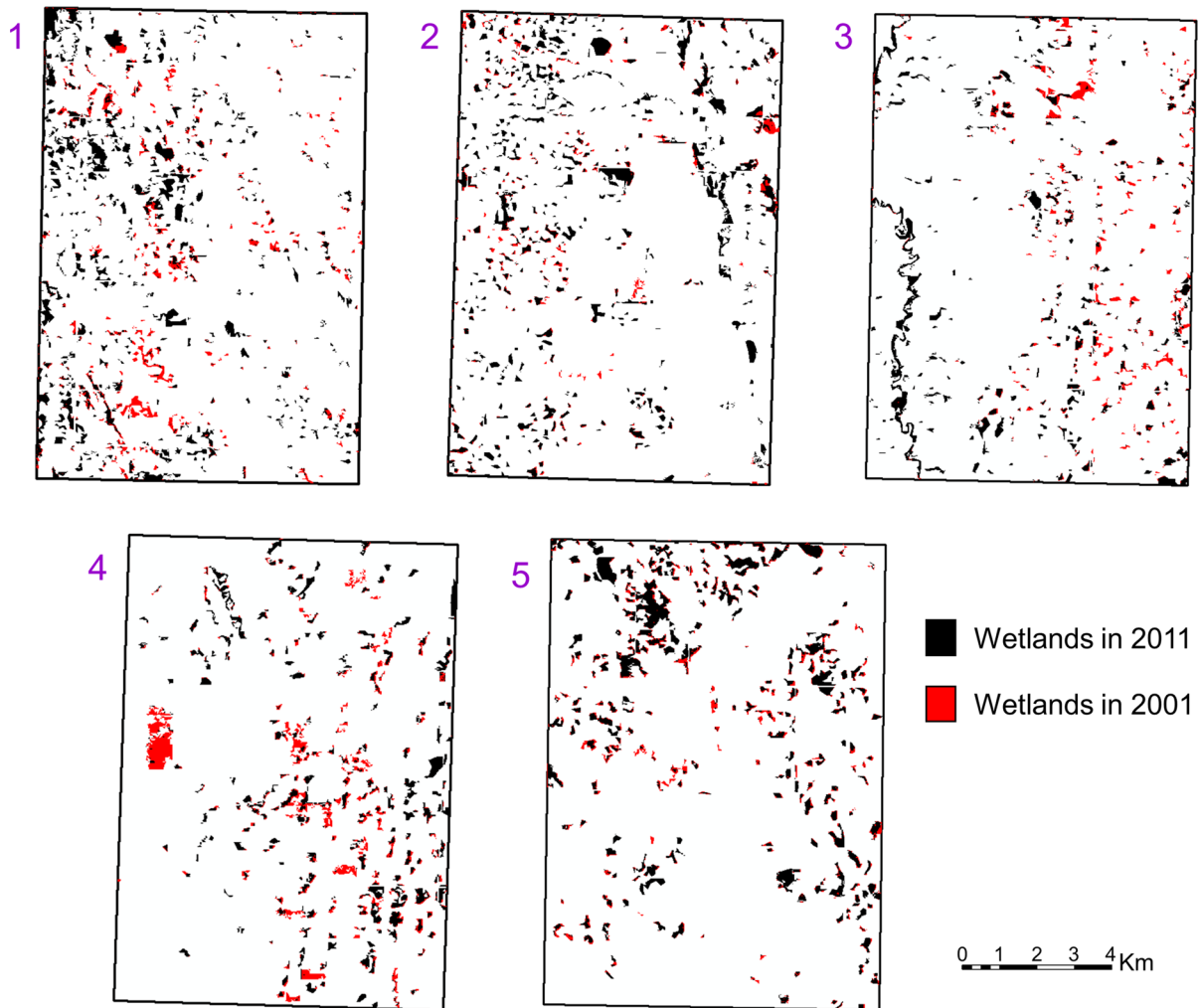


Fig. 2 Distribution of wetland areas for each of our five focal quadrangles (numbers as in Fig. 1) in 2001 and 2011. Red = wetlands lost between 2001 and 2011 (i.e., mapped by the 2001 NLCD database that were corn or soybeans as of 2011),

black = wetlands still remaining (i.e., mapped by the 2001 NLCD database that were not corn or soybeans in 2011). (Color figure online)

considered to be wetlands that had been eliminated from the landscape, a relationship that was verified for random polygons by viewing 2012 National Agriculture Imagery Program (NAIP) aerial photographs (USGS 2018). The parent–child relationships between 2001 and 2011 polygons were then summarized for each quadrangle to tally 2001 polygons that remained present, were eliminated entirely, or were split into two or more polygons. Any wetland polygon with a decrease in area $< 800 \text{ m}^2$ (i.e., less than the size of one 900 m^2 pixel from the original imagery) was considered to be an intact wetland, with any such small differences in wetland area between 2001 and 2011

attributed to measurement or mapping errors differing between the two products and so were not included in area loss calculations (Fig. 2).

Graph theory, a well-established mathematical approach to structural connectivity that is now being applied to conservation planning (Fall et al. 2007; Minor and Urban 2007), has been increasingly used to assess the topology of changing wetland landscapes, with wetlands forming the nodes of a graph and linkages representing potential movement pathways between wetlands. Previous examinations of connectivity of wetland networks have mostly investigated semi-arid and arid regions where entire waterbodies

appear or disappear in response to precipitation shifts (Wright 2010); these studies have shown decreasing structural landscape connectivity as numbers of wetlands decrease (McIntyre et al. 2014; Tulbure et al. 2014; Bishop-Taylor et al. 2015; Drake et al. 2017). Taking a graph theory approach, structural connectivity among the wetlands within each quadrangle was assessed using the package *igraph* (Csardi and Nepusz 2006) in R 3.1.1 (R Core Team 2014), following procedures similar to those used to quantify connectivity in networks of wetlands in Texas and Arizona (McIntyre et al. 2014, 2016; Drake et al. 2017).

There are numerous graph theory-based metrics with which to quantify structural landscape connectivity of the entire network of wetlands as well as at the scale of the importance of individual wetlands in supporting the potential for flow through the network (Laita et al. 2011). We selected a suite of relatively independent and informative metrics from both these scales to examine structure connectivity (see McIntyre et al. 2018) within each of our focal quadrangles at the two time points. The *coalescence distance* is the Euclidean distance between the centroids of the two neighboring nodes that are farthest from each other at coalescence (i.e., farthest nearest-neighbor distance). Coalescence of the entire network present within each quadrangle thus occurred when all wetlands were connected to at least one other wetland, forming a single, connected cluster of wetlands (Fig. 3 illustrates an example of this). At coalescence, we counted for each study quadrangle the number of *nodes* (i.e., wetlands), the number of *links* connecting the nodes (i.e., Euclidian distances \leq the coalescence distance among wetlands), and the number of *cutpoints*, which represent wetlands that if removed increase the coalescence distance of the system (Keitt et al. 1997). We also calculated for each study quadrangle the average values for path length, graph density, betweenness centrality, Kleinberg's hub score, and graph diameter. *Path length* is the number of links connecting each node, with lower values indicating greater potential dispersal efficiency as a consequence of less path redundancy through the network (i.e., fewer path options). *Graph density* is the ratio of wetland linkages present to all possible wetland linkages within the network at coalescence; relatively low values (i.e., near 0) indicate the presence of few paths through the network. The *betweenness centrality* of a node is the number of shortest paths between pairs

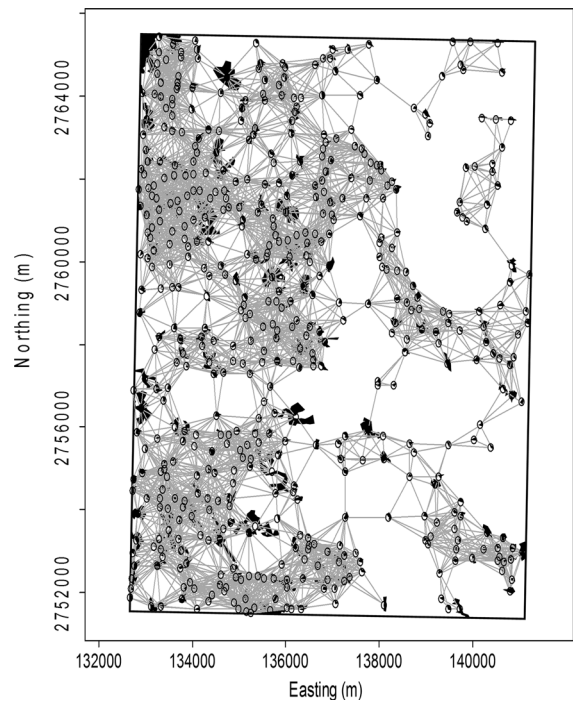


Fig. 3 Graph depiction of coalescence for the Logan Center quadrangle from 2001. Wetland polygons ($N = 533$) are in black; centroids are depicted as circles, and links between wetlands that are \leq the coalescence distance (in this case, 1119 m) are depicted as gray lines ($N = 4663$)

of other nodes that run through that node (Girvan and Newman 2002); higher values indicate greater importance of a node as a potential stepping-stone through the network. *Hubs* are nodes that are connected to many other wetlands, and *graph diameter* is the longest path (in units of number of links) between the farthest two connected points within a cluster (Csardi and Nepusz 2006). Changes over time in these metrics were compared with paired *t* tests (wetlands within a given quadrangle in 2001 compared to those in the same quadrangle in 2011) in R. Euclidian distances between wetland centroids were calculated rather than edge-to-edge distances. Since most of the wetlands were small relative to the distances between them (see e.g. Fig. 2), calculating distances between centroids rather than edges is more computationally efficient while still accurately representing graph topology (Fig. 3; see also Galpern et al. 2011). Although some metrics may change value when examining connectivity between patch edges rather than centroids (e.g. coalescence distance), we chose a suite of metrics that were relatively insensitive to this choice (number of

nodes, number of links, path length, graph density, betweenness, Kleinberg's hub score, number of cut-points, and graph diameter). These metrics are not repetitive; rather, they are complementary in collectively quantifying wetland network structure.

Results

Initial wetland area in 2001 of our focal quadrangles averaged 6.9% of the landscape. Wetland area decreased overall by 24.9% within the study area between 2001 and 2011 (Table 1). All five of our focal quadrangles showed wetland losses over that time, with loss rates ranging from 13.3 to 39.3% (Table 1). There were no clear patterns in terms of which quadrangles showed the highest or lowest wetland loss rates with respect to the starting amount of wetland area or the prevalence of agriculture in each quadrangle. In addition to a loss in overall wetland area, wetland density decreased by 16% over that same span, from 2.89 to 2.42 wetlands per km² (Table 2). The size and shape of wetlands likewise changed: average wetland size decreased from 2.41 to 2.16 ha. Patch perimeter did not change significantly over time, but there was an increase in the shoreline irregularity index, which indicates that contrary to expectations, wetlands became slightly less circular by 2011 (Table 2).

Overall, the number of wetland polygons decreased by 17.5% from 2001 to 2011, with losses occurring across all five focal quadrangles (Table 3). Across the focal quadrangles, there were 828 wetlands that

remained unchanged, constituting 42.9% of the 2001 wetlands and 40.5% of the 2001 wetland area. Only 423 wetlands (456 ha) were eliminated entirely by 2011, representing only 39% of total wetland area loss. The eliminated wetlands were mostly small, with an average area of 1.08 ha/wetland, but eight others were larger, with areas of 5–18 ha. There were 608 wetland polygons that remained in place but were reduced in size (i.e., were “nibbled”) with a cumulative area of 446 ha, representing 38% of total wetland loss, at an average loss of 0.73 ha/wetland. The remaining 70 wetland polygons were split into 2–4 “children.” In all cases, the splitting of 2001 polygons was also associated with wetland area losses: the sum of child polygon areas was always less than the area of the parent wetland polygon. The average area lost from this source was 3.79 ha/wetland, much larger than that from elimination or nibbling, but because it affected fewer wetlands, the cumulative loss from this source was only 265 ha. Large wetlands were most susceptible to splitting: of the 63 wetlands larger than 11 ha in 2001, 36.5% were split into two or more wetlands by 2011. The splitting of 2001 polygons increased the 2011 count of polygons by 84, so the net loss of polygons was only 339 between 2001 and 2011 (Table 3).

Power law analysis showed that there was a linear decrease in number of wetlands when plotted logarithmically against increasing wetland area ($R^2 = 0.91$) (Fig. 4). The two power law lines for 2001 and 2011 converged at the smallest wetland size class (overlap in 95% CI), but the exponent of the 2011 power law relationship (i.e., slope of the 2011

Table 2 Comparison of average (mean \pm SD) wetland area, number, and shape indices, 2001 versus 2011

Variable	2001	2011	Comparison
<i>Quadrangle</i>			
Wetland area % of total quad	6.91 \pm 0.89	5.19 \pm 1.11	$t = -6.143$, $df = 4$, $p = 0.0035$
Wetlands/km ²	2.89 \pm 0.97	2.42 \pm 0.75	$t = -3.158$, $df = 4$, $p = 0.0342$
<i>Patch</i>			
Area per wetland patch, ha	2.41 \pm 4.21	2.16 \pm 3.73	$W = 1,644,294$, $p = 0.00536$
Perimeter of wetland patch, m	733 \pm 704	701 \pm 658	$W = 1,604,521$, $p = 0.1404$
Shoreline irregularity index per patch	1.444 \pm 0.310	1.461 \pm 0.298	$W = 1,465,723$, $p = 0.00196$

Quadrangle-scale comparisons are paired *t* tests; patch-scale comparisons are Wilcoxon Mann–Whitney tests. Comparisons in bold font are statistically significant ($p < 0.05$)

Table 3 Fate of wetland polygons, 2001 to 2011, summarized by quadrangle

Variable	Quadrangle					
	1	2	3	4	5	All
Net loss of polygon area (ha)	272	126	211	356	205	1170
Polygons eliminated	138	70	111	75	29	423
Polygons present in both years, not split	380	410	241	199	205	1435
Polygons split into two polygons	12	6	6	17	18	59
Polygons split into three polygons	3	1	2	0	2	8
Polygons split into four polygons	0	0	0	2	1	3

Quadrangle numbers are shown on Fig. 1

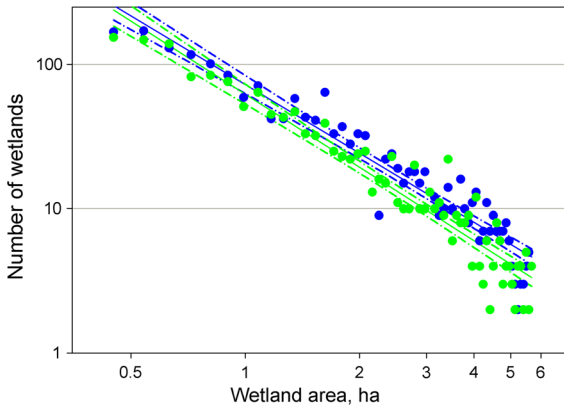


Fig. 4 Power law analysis of wetlands between 0.36 and 6 ha within the study area, 2001 (blue symbols) and 2011 (green). Solid lines are linear regression lines (log–log axes); dashed lines are 95% confidence intervals. The bin size is 0.09 ha. (Color figure online)

regression line: -1.68) was slightly steeper than that of the 2001 power law relationship (-1.58), significantly diverging at the largest wetland size classes (Fig. 4). In other words, when examining the relationship between the number of wetlands present and their sizes at two points in time, there were more smaller than larger wetlands in both years, the number of wetlands present was lower in 2011 than in 2001, and the loss of wetlands was primarily driven by loss of large wetlands via splitting and nibbling (Fig. 4).

Despite the fact that there were fewer wetlands (nodes) on average across our focal quadrangles in 2011 than in 2001 (and thus fewer links between them), there was no significant difference in any of the other seven graph metrics we calculated (Table 4). This indicates that the remaining wetlands in 2011 were still sufficiently numerous and closely spaced to form an ecological network that was structured similar to that in 2011. Thus, network coalescence occurred at the relatively short distance of ~ 1.35 – 1.4 km in both

years, meaning that the maximum distance a disperser would need to travel between neighboring wetlands would have been roughly the same in 2011 as in 2001. Average path length in both years was about 6.5 links, and graph density at coalescence in 2011 was about 5% of all possible linkages within each quadrangle (a non-significant decrease from 12.8% in 2001). There were roughly the same number of wetlands that played key roles as stepping-stones, hubs, or cutpoints between 2001 and 2011. Finally, the similarly large values of graph diameter between 2001 and 2011 indicate that the wetland network still had a dense and complex structure. Thus, the loss of wetland area that we observed did not significantly decrease the computed structural connectivity of the wetland network.

The Logan Center quadrangle, a high-loss quadrangle located ~ 50 km west of Grand Forks, North Dakota (denoted as quadrangle 1 in Fig. 1), provides a case study for illustrating patterns of wetland loss (Fig. 5). Few wetlands in this area were lost in their entirety between 2001 and 2011. Instead, wetland displacement by corn and soybeans tended to occur along upland edges, shrinking but not eliminating the wetlands. Wetland remnants that were perhaps too wet to farm often persisted even where wetlands were otherwise mostly displaced by agriculture. The largest wetland complex lost within that quadrangle was a series of interconnected potholes in a farm field, draining to an intermittent stream at the southeastern corner of the field. Plow lines skirted the wetland complex on 2003 USDA NAIP imagery, consistent with the 2001 NLCD depiction, but ran straight through it in 2010 (Fig. 6). Rectangular areas of bare soil in the 2010 image are residual wet spots that were presumably planted with a GPS-controlled variable-rate seeding system that allowed the farmer to drive the planter through the wet spots without seeding them, so as not to waste seed that would germinate

Table 4 Average connectivity metrics from graph analysis of wetlands within sample quadrangles

Metric	2001	2011	Comparison
Number of nodes	385.6	323.6	t = 3.192, p = 0.033
Number of links	3387	2786	t = 3.259, p = 0.031
Coalescence (m)	1350	1433	t = - 1.54, p = 0.197
Path length	6.585	6.510	t = 0.263, p = 0.805
Graph density	0.1283	0.0564	t = 0.924, p = 0.408
Betweenness	1222	1002	t = 1.793, p = 0.147
Kleinberg's hub score	0.1479	0.1562	t = - 0.766, p = 0.486
Number of cutpoints	3.6	4.2	t = - 0.739, p = 0.501
Graph diameter	19,448	20,925	t = - 2.190, p = 0.094

Comparisons in bold font are statistically significant ($p < 0.05$)

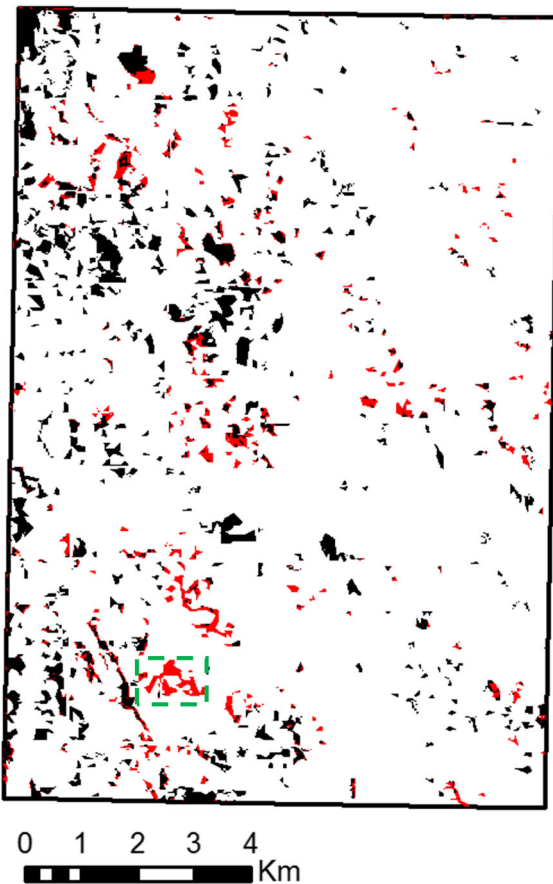


Fig. 5 Raster wetland loss map for a portion of the Logan Center, North Dakota, quadrangle. Red = wetlands lost between 2001 and 2011 (i.e., mapped by the 2001 NLCD database that were corn or soybeans as of 2011), black = wetlands still remaining (i.e., mapped by the 2001 NLCD database that were not corn or soybeans in 2011). Dashed green box surrounds field enlarged in Fig. 6. (Color figure online)

poorly. Linear connections between the wet spots may also indicate land sculpting and/or installation of tile

lines to promote drainage. The wet spots were entirely gone by the 2012 USDA NAIP imagery; only the drainageway remained.

Discussion

Unlike studies that simply documented change in numbers of open-water wetlands in the Prairie Pothole Region (Wright 2010; Liu and Schwartz 2012), our analysis also included vegetated wetlands that might be more persistent but less readily detectable than would pools of water. These wetlands were embedded in agricultural terrain that was flatter than the knob and kettle topography typically associated with DPPR wetlands, and some were located along or draining to stream channels. These conditions (i.e., range of wetland types in rolling agricultural terrain drained by streams) are typical of the Drift Prairie but may not represent the PPR as a whole. However, the Drift Prairie is where the majority of recent wetland losses have occurred within the PPR (Johnston 2013). Within this area, although the wetland area losses that occurred also induced a decrease in wetland density (Hypothesis 1) and average area per wetland patch (Hypothesis 2), the decrease was insufficient to change the structural connectivity of the landscape (Hypothesis 5). Average wetland perimeter did not change significantly, with wetlands effectively shrinking as they were being nibbled away (Hypothesis 3). Indeed, our average shoreline irregularity index values of ~ 1.45 were more circular than those reported for PPR wetlands in Iowa (1.56; Van Meter and Basu 2015).

We documented a difference in power-law relationships between 2001 and 2011; we think that this is due to the impact of splitting and nibbling on large

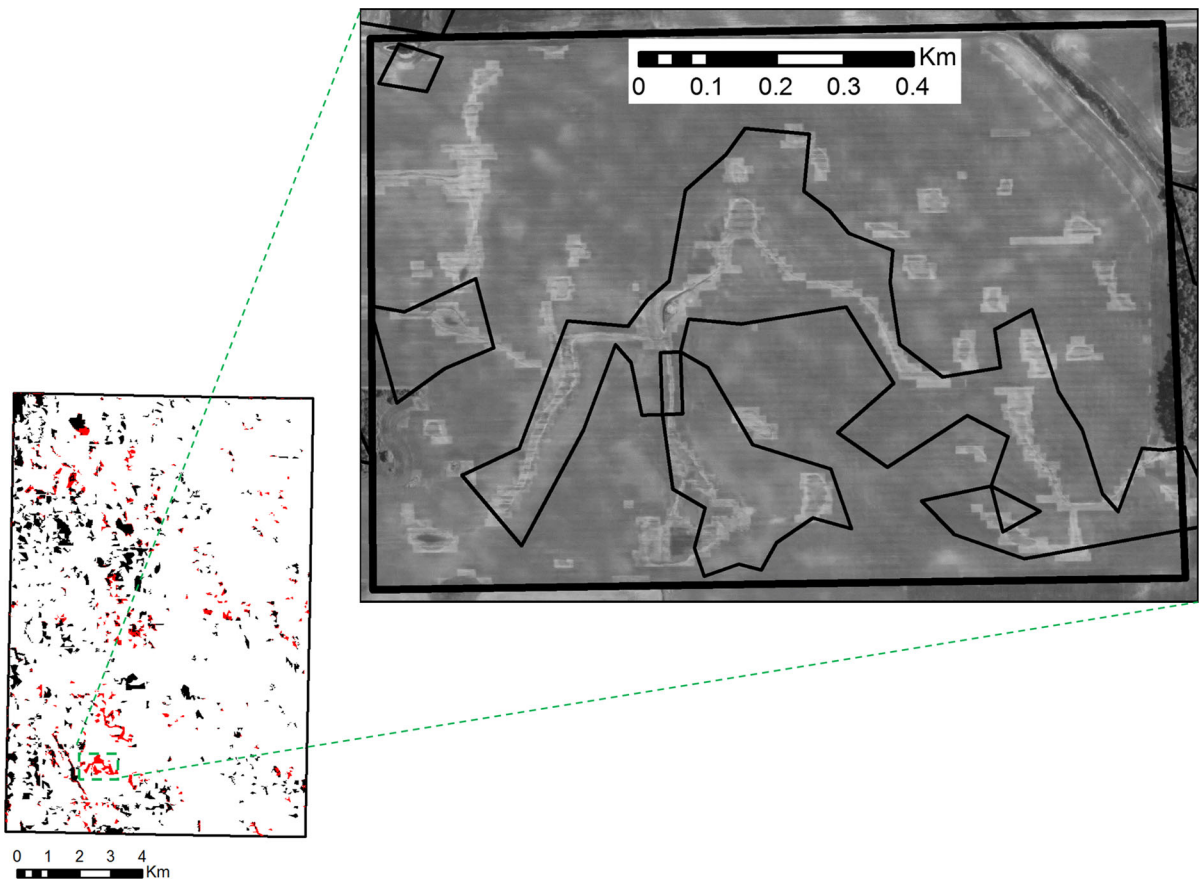


Fig. 6 Inset of Fig. 5 with enlarged view of 2010 USDA aerial photograph showing wetland polygons eliminated within a field in the Logan Center quadrangle. Rectangular areas of bare soil in the image show the location of former wetlands

wetlands over that time. Although eliminated wetlands tended to be small, the nibbling and splitting of larger into smaller ones resulted in some replacement of those small size classes, so the power law line became steeper rather than flatter (Hypothesis 4). These findings illustrate that the pattern of wetland loss due to anthropogenic alteration may be different from the pattern of loss due to precipitation differences. Additionally, the average wetland loss per patch was small, usually 1 ha or less. This type of ramp disturbance, gradually increasing in time and space (Lake 2000), can have the same cumulative impact as a more rapid, radical wetland alteration (Johnston 1994), but is less alarming to observers because the degradation is gradual and distributed.

The archetypal pattern of wetland loss due to drying is shrinkage and disappearance: the area of individual wetlands decreases as water levels decline, and the smallest wetlands disappear as they dry up completely

(Larson 1995; Johnson et al. 2004). In our system, however, the pattern of wetland loss that we observed due to agricultural expansion was splitting, nibbling, and elimination. Nibbling and elimination are analogs of drought-induced shrinkage and disappearance caused by agricultural machinery rather than drying. The splitting of wetlands can occur when farming divides elongated wetlands in drainageways into two or more parts.

Wetland patch elimination may or may not be permanent. The wetland conservation provisions of the US Farm Bill allow cropping of “prior converted croplands” and “farmed wetlands,” areas designated by the USDA Natural Resource Conservation Service as having been manipulated and used to produce an agricultural commodity prior to 23 December 1985 (USDA NRCS 2018). If such an area was wetland in 2001 and cropped in 2011, then we would have counted it as a wetland loss, even though it might

revert back to wetland during a subsequent year. However, wetlands removed by the installation of tile drainage systems between 2001 and 2011 would be a much more permanent loss because their hydrology would have been altered. Unfortunately, no spatial data are available that show the location of tile drain installation, so the potential reversibility of wetland losses could not be evaluated.

In this study, we accepted as correct the wetland loss database created by Johnston (2013) from the NLCD (Homer et al. 2007) and CDL (USDA NASS 2011). As with any spatial data, there are biases associated with those datasets, which are analyzed and discussed elsewhere in the literature (Wickham et al. 2010; Boryan et al. 2011; Johnston 2013). One potential bias associated with the CDL is due to the USDA's focus on agriculture: a plowed wet spot in a crop field that might retain some wetland functions would probably be classified as cropland (and hence represent a lost wetland) by the CDL. Thus, our analyses may have over-estimated wetland losses between 2001 and 2011, but this potential bias should not have affected the patterns of wetland shape or structural connectivity that we saw, lending credence to those conclusions. Wetland gains were not considered, nor were wetland losses from causes other than agricultural expansion. Moreover, biological degradation can also accompany areal loss but was not quantified here. Finally, the US Environmental Protection Agency's National Wetland Condition Assessment found that 41% of herbaceous wetlands in the US Interior Plains region were subject to ditching, 55% were subject to vegetation removal, 56% were subject to hardening (e.g., soil compaction), and 63% were subject to high or very high stress by nonnative plant species (USEPA 2016). As a result of these factors, by the time many wetlands finally disappear, they may be hardly recognizable as wetlands due to incremental degradation in prior years.

Our analysis showed that the decrease in number of wetland patches (by 17.5%) in our study area was much less than the decrease in wetland area (24.9%). Given the demonstrated loss of wetland area, the lack of change in structural connectivity was surprising. Each of the nine metrics we examined quantifies a different aspect of structural connectivity, including the importance of individual nodes in various roles, overall network complexity, and network redundancy. The fact that only the number of nodes (wetlands) and

links (connections between wetlands) showed any statistically significant differences between 2001 and 2011 is indicative that the wetlands remaining in 2011 still form an ecological network. Wetland elimination constituted only 39% of the wetland area loss, the rest being attributed to nibbling (loss of wetland area without loss of patch numbers) and splitting (loss of wetland area with an increase in patch numbers) that would have smaller effects on connectivity as calculated between wetland centroids (with the distance between wetland centers being statistically equivalent in 2001 and 2011). Certainly splitting wetlands creates more centroids, thereby increasing wetland density while decreasing inter-wetland separation. Our study did not examine changes in the edge-to-edge distance between wetlands, which possibly would have shown more of an effect given that wetlands were getting smaller (meaning that their edges were shrinking from each other). Our approach was more conservative than examining changes in structural connectivity from wetland patch edge to edge, but we did not anticipate that we would see nearly as many wetlands shrink as entirely lost, nor did we anticipate that we would see as many wetlands that were split into multiple, smaller wetlands. Although calculating the distance between nearest patch edges may be of high importance to overland dispersers with limited vagility in an otherwise hostile matrix, the structural connectivity metrics we used were relatively insensitive to choice of examining interpatch distances with respect to edges or centroids, thereby representing structural connectivity for a variety of organisms along a spectrum of vagility.

We did not evaluate the effect of shrinking wetland size nor surrounding land-cover type on habitat suitability, although the surrounding landscape has well-documented effects on water quality and hydroperiod in prairie wetlands (Voldseth et al. 2007; Collins et al. 2014). Indeed, anthropogenic landscape changes are known to influence the dispersal of organisms between habitat patches, often resulting in non-optimal movement (Fahrig 2007). However, having a relatively constant (i.e., predictable and high) wetland density could be beneficial to organisms that must travel overland between wetlands. The lack of change in structural connectivity that we saw may also be due to the fact that despite their reduced area, prairie pothole wetlands remained well-distributed throughout the study area, still

constituting at least 4% of each quadrangle in 2011. Given that our focal quadrangles were selected to represent heavily impacted areas, the sheer number of wetlands still present means that there are multiple connectivity options that are contributing to resiliency against wetland losses in the DPPR, at least up to a critical threshold of loss (Albanese and Haukos 2017).

Weather (specifically, precipitation variability) was not a factor in the wetland losses we observed because of the extremely wet conditions in 2011 (indeed, our wetland loss estimates are likely underestimates because of the wet year in 2011), but climate change-driven alterations to weather patterns may be expected to contribute to future wetland losses both directly and indirectly, and the interaction between anthropogenic and climate-driven wetland losses will also likely affect habitat availability and connectivity in the future. Specifically, climate change models forecast increasing temperatures across the region and increased likelihood of drought (Karl et al. 2009), although portions of the PPR have experienced increasing precipitation (and a resulting increase in the number of wetlands) since the 1990s (Millett et al. 2009; Liu and Schwartz 2012). Temperature increases are predicted to outpace changes in precipitation, however, ultimately leading to drier conditions predicted for much of the Prairie Pothole Region (Johnson et al. 2005, 2010), with potentially devastating effects on wetland-associated wildlife (Sorenson et al. 1998). Such changes to climatic regimes are also likely to alter the distribution and type of agriculture in this region (Rashford et al. 2016). Land use/land cover change has also been implicated in losses of wetlands in the DPPR (Voldseth et al. 2009; Johnston 2013; Wright and Wimberly 2013), so although a shifting climatic regime of the PPR may offset some wetland losses from grassland conversion, the twin forces of land-use change and climate change will collectively lead to future losses of wetlands in the PPR (Voldseth et al. 2009).

Although many wetland losses in the Prairie Pothole Region may be due to activities that cause wholesale wetland loss (such as tile drainage or infill), we documented a more subtle form of wetland loss whereby farming activities nibble at wetland edges, making them gradually smaller and smaller. From 2001 to 2011, such changes were not associated with concomitant reductions in structural connectivity of the system. It remains to be seen whether, as the

wetlands become increasingly smaller over time, that habitat and food resources will become more constrained, with cascading functional effects on populations of waterfowl, shorebirds, amphibians, and other wetland-associated wildlife. A clear distinction should thus be made between assessments of structural and functional connectivity, because confusion between structural and functional landscape connectivity may result in ill-informed management actions and policies, with disastrous conservation outcomes for species occupying the landscape (Taylor et al. 2006). Certainly more study of species-landscape interactions is needed to understand functional landscape connectivity. Our analysis of graph theoretic metrics for sampled landscapes in our study area suggests that structural wetland connectivity has not been significantly affected by demonstrated wetland losses because of the large number of remaining wetlands. It is unknown just where is the tipping point of wetland loss in the PPR that will induce deleterious ecological effects, but wetland and grassland conversion continues the movement toward that ecological phase transition. Our results may be useful in shaping current thinking about natural resource conservation in the region by indicating that wetland numbers and density may not be the best indicators of landscape change (because we documented how land conversion can cause an increase in these metrics via wetland splitting, which may maintain structural connectivity). A focus on quantifying functional connectivity may provide a very different picture of the regional landscape ecology.

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