

## Review

# Climate and Land Use Driven Ecosystem Homogenization in the Prairie Pothole Region

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**Abstract:** The homogenization of freshwater ecosystems and their biological communities has emerged as a prevalent and concerning phenomenon because of the loss of ecosystem multifunctionality. The millions of prairie-pothole wetlands scattered across the Prairie Pothole Region (hereafter PPR) provide critical ecosystem functions at local, regional, and continental scales. However, an estimated loss of 50% of historical wetlands and the widespread conversion of grasslands to cropland make the PPR a heavily modified landscape. Therefore, it is essential to understand the current and potential future stressors affecting prairie-pothole wetland ecosystems in order to conserve and restore their functions. Here, we describe a conceptual model that illustrates how (a) historical wetland losses, (b) anthropogenic landscape modifications, and (c) climate change interact and have altered the variability among remaining depressional wetland ecosystems (i.e., ecosystem homogenization) in the PPR. We reviewed the existing literature to provide examples of wetland ecosystem homogenization, provide implications for wetland management, and identify informational gaps that require further study. We found evidence for spatial, hydrological, chemical, and biological homogenization of prairie-pothole wetlands. Our findings indicate that the maintenance of wetland ecosystem multifunctionality is dependent on the preservation and restoration of heterogeneous wetland complexes, especially the restoration of small wetland basins.

**Keywords:** Prairie Pothole Region; wetlands; ecosystem function



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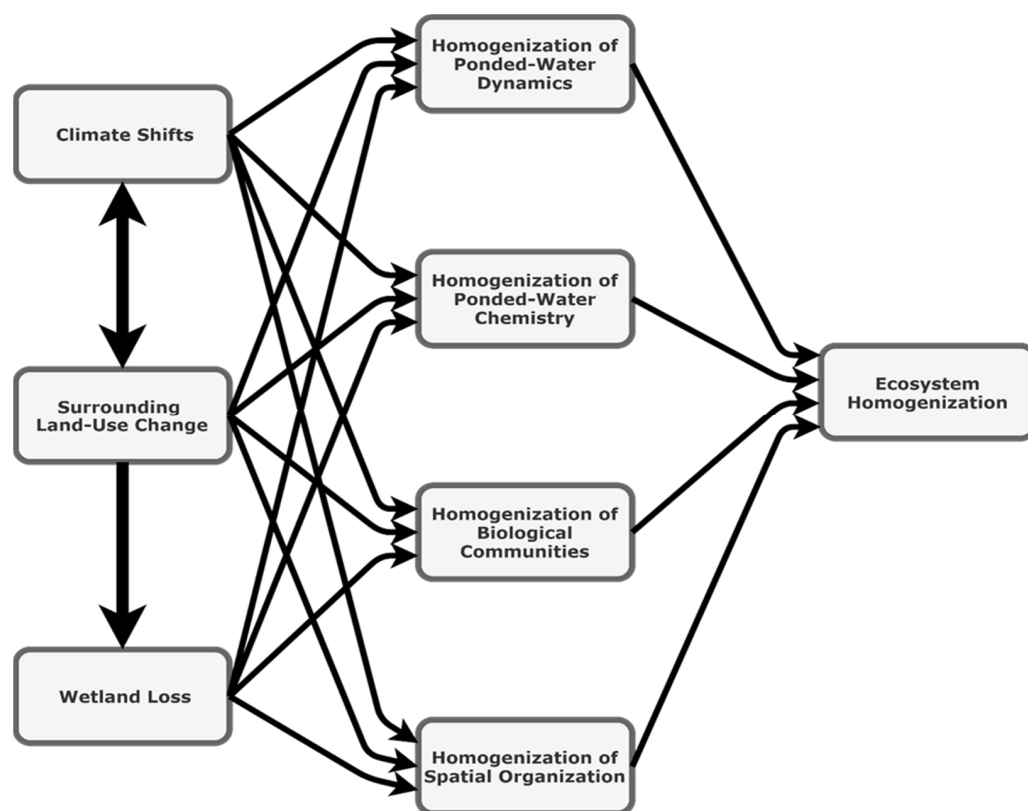
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## 1. Introduction

Globally, freshwater ecosystems are experiencing widespread habitat degradation and biodiversity loss [1,2]. An increasingly observed trend in freshwater ecosystems is the homogenization of both physical habitats and biological communities [3,4]. The decreasing variability in both physical habitats and biotic communities contribute to losses of ecosystem multifunctionality [5–8]. This loss of multifunctionality over time due to decreased variability in physical, chemical, and biological characteristics has been referred to as ecosystem homogenization [9]. For freshwater ecosystems, evidence for ecosystem homogenization has been demonstrated in lakes and rivers, many of which have been highly modified through damming and streambed channelization [4,10–12]. There has been considerably less attention focused on the homogenization of freshwater wetlands. However, freshwater wetland ecosystems are among the most vulnerable to habitat degradation and provide critical functions in maintaining local and downstream ecosystem functions [13].

Wetlands are perhaps one of the most important and often overlooked components of our freshwater systems and cover an area greater than 1.2 million hectares worldwide [14]. These temporally and spatially variable ecosystems provide numerous functions that are important for the health of the landscape [15,16]. Wetlands embedded entirely within

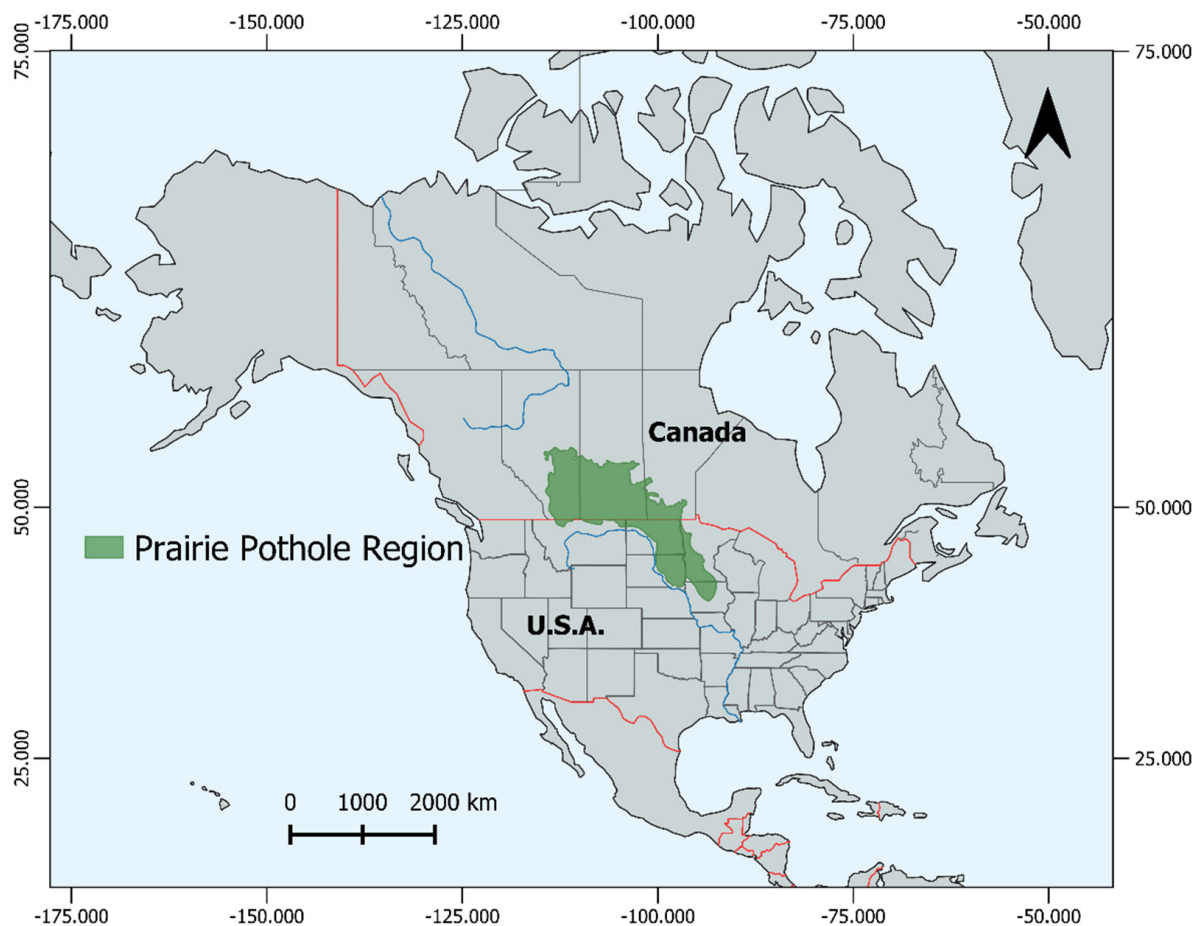
upland landscapes are particularly sensitive to anthropogenic modifications and climate change [17–19]. This sensitivity to climate and land-use change makes wetlands especially vulnerable to decreased hydrologic variability, increased biotic homogenization, and loss of ecosystem function, i.e., ecosystem homogenization [5,6,20,21]. Ecosystem functions provided by freshwater wetlands, e.g., nutrient cycling, groundwater recharge, and biodiversity reservoirs, often vary depending on a wetland’s geographic location (i.e., forested vs. non-forested), hydro-period, and hydrogeologic setting [22–24]. Bedford, 1999 [5] hypothesized that the non-random loss, degradation, and restoration of wetland ecosystems in the United States and Canada has likely resulted in a shift in the relative proportion of different types of wetlands on the landscape, which in turn has likely resulted in a net loss of wetland ecosystem multifunctionality. This prediction was based on how individual wetlands have physical and hydrological settings such as local climate, relationship to local groundwater, and contributing watershed size and characteristics [5,25,26]; many aspects of this were later encapsulated into the Wetland Continuum Concept [27]. Based on the hypothesis of Bedford, 1999 [5], we developed a conceptual model for wetland ecosystem homogenization (Figure 1). This framework incorporates how independent, interactive, and synergistic processes caused by directional shifts in climate, land-use change, and historical wetland loss can lead to ecosystem homogenization. In this manuscript, we use depressional wetlands located in the Prairie Pothole Region (PPR) of North America as a case study of wetland ecosystem homogenization.



**Figure 1.** Conceptual model indicating hypothesized connections between climate shifts, land-use change, wetland losses, and components of wetland ecosystem variability, leading ultimately to ecosystem-level homogenization.

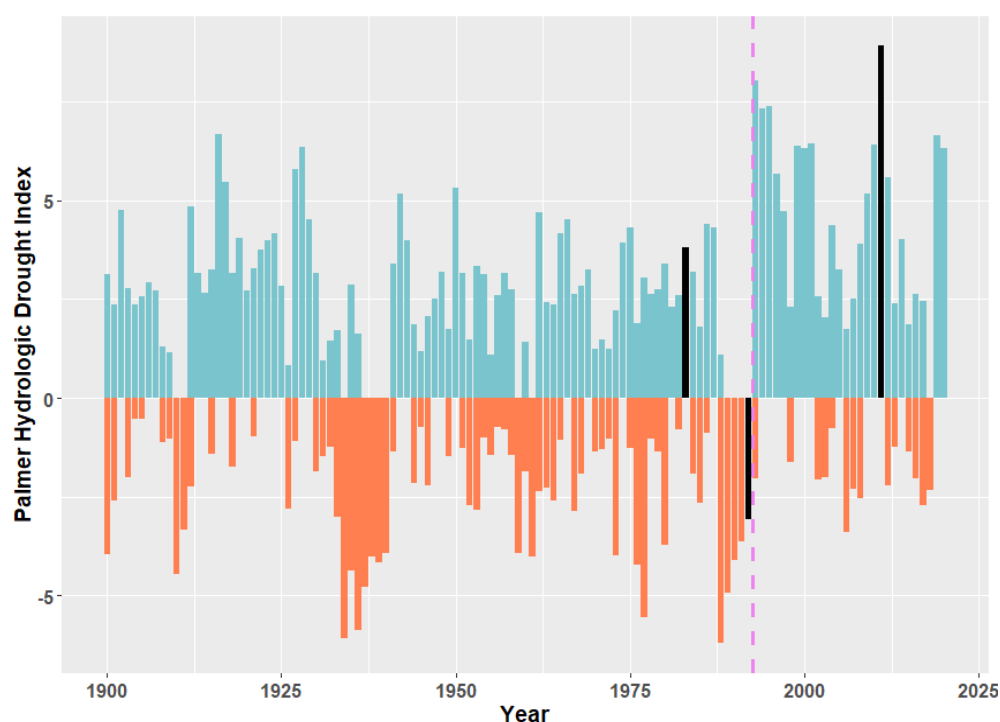
### *Prairie Pothole Wetland Ecosystem Variability and Function*

Pothole depressional wetlands are the predominant wetland type that occurs in the PPR. The PPR is one of the largest and most-modified, wetlands-dominated regions on earth. The PPR covers approximately 777,000 km<sup>2</sup>, spanning north and west from northwest Iowa through South and North Dakota in the United States into central Alberta in Canada (Figure 2 [28]). As such, it forms the largest wetland complex in North America [29]. Within the PPR, there are millions of individual wetland basins that can exhibit variable ponded-water permanence and chemistry [16]. The high spatial and temporal variability exhibited by prairie-pothole wetlands is a reflection of the high spatial and temporal variability in climate across the region [24,29]. The entire PPR's climate is highly variable within and among years.



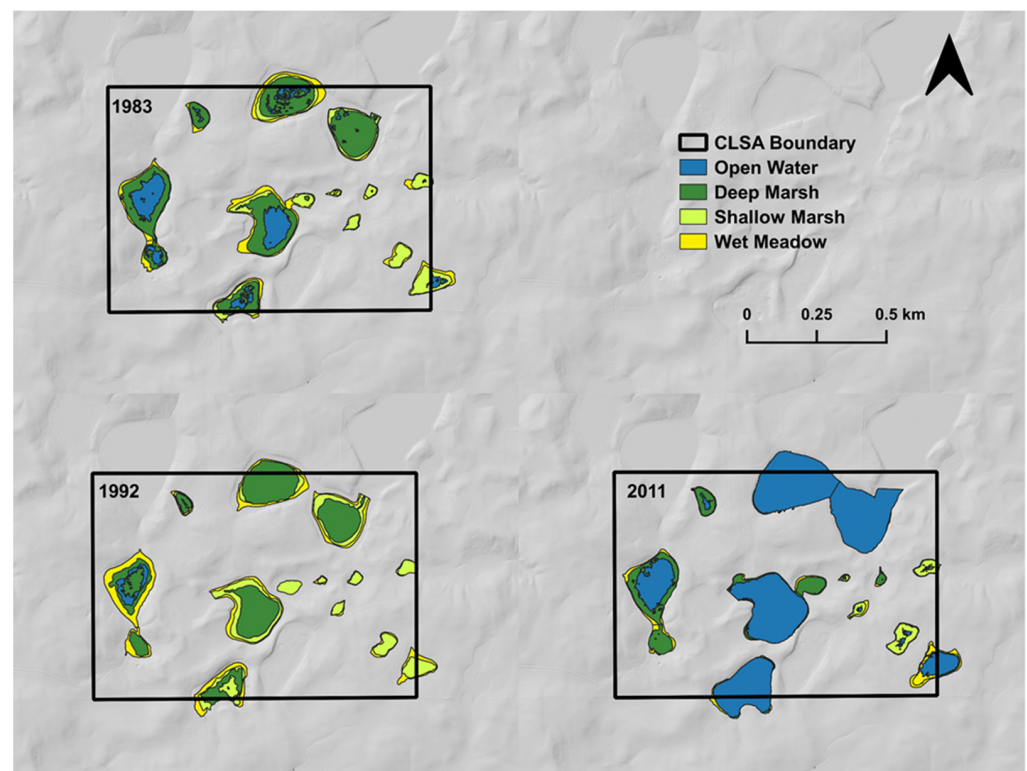
**Figure 2.** Map of the Prairie Pothole Region of North America. The Prairie Pothole Region boundary is indicated by the green polygon. The red lines indicate country boundaries and the blue lines indicate large rivers. The base map layers used in this figure were obtained from <https://www.naturalearthdata.com/> (accessed on 20 September 2022).

Annual maximum and minimum temperatures can range between 40 °C in the summer and −40 °C in the winter and mean annual precipitation can range from 30 cm/year to 90 cm/year. Typically, the northern portion of the PPR is cooler than the southern, and the eastern portion is wetter than the western. Precipitation can also exhibit both interannual variability and decadal oscillations in the form of wet-dry cycles ([30]; Figures 3 and 4). These wet-dry cycles can influence the distribution of ponded-water area among wetlands, especially during times of drought or extreme deluge (Figures 3–5). The typically closed-basin morphology and low-permeability substrates of prairie-pothole wetlands make them highly responsive to changes in surface-water inputs. However, they also accumulate or lose water to or from subsurface flows depending on a basin's relationship to the local groundwater table, such as the basin's proximity to the local water table and soil permeability [31]. Wetlands above the water table can recharge groundwater, are typically small, accumulate few salts, and have short hydroperiods, while wetlands below the water table receive groundwater discharge, are typically larger, accumulate salts (through groundwater), and have long hydroperiods [27,31]. Losses and accumulations of salts through the groundwater system, combined with climate-driven dilution and concentration effects, result in substantial variation in hydrogeochemistry [32] among prairie-pothole wetlands. For example, the temporal and spatial variability in their ponded-water salinity can range from extremely fresh (<0.8 mS/cm) to hypersaline (>60 mS/cm), i.e., saltier than sea water (~50 mS/cm [33,34]).



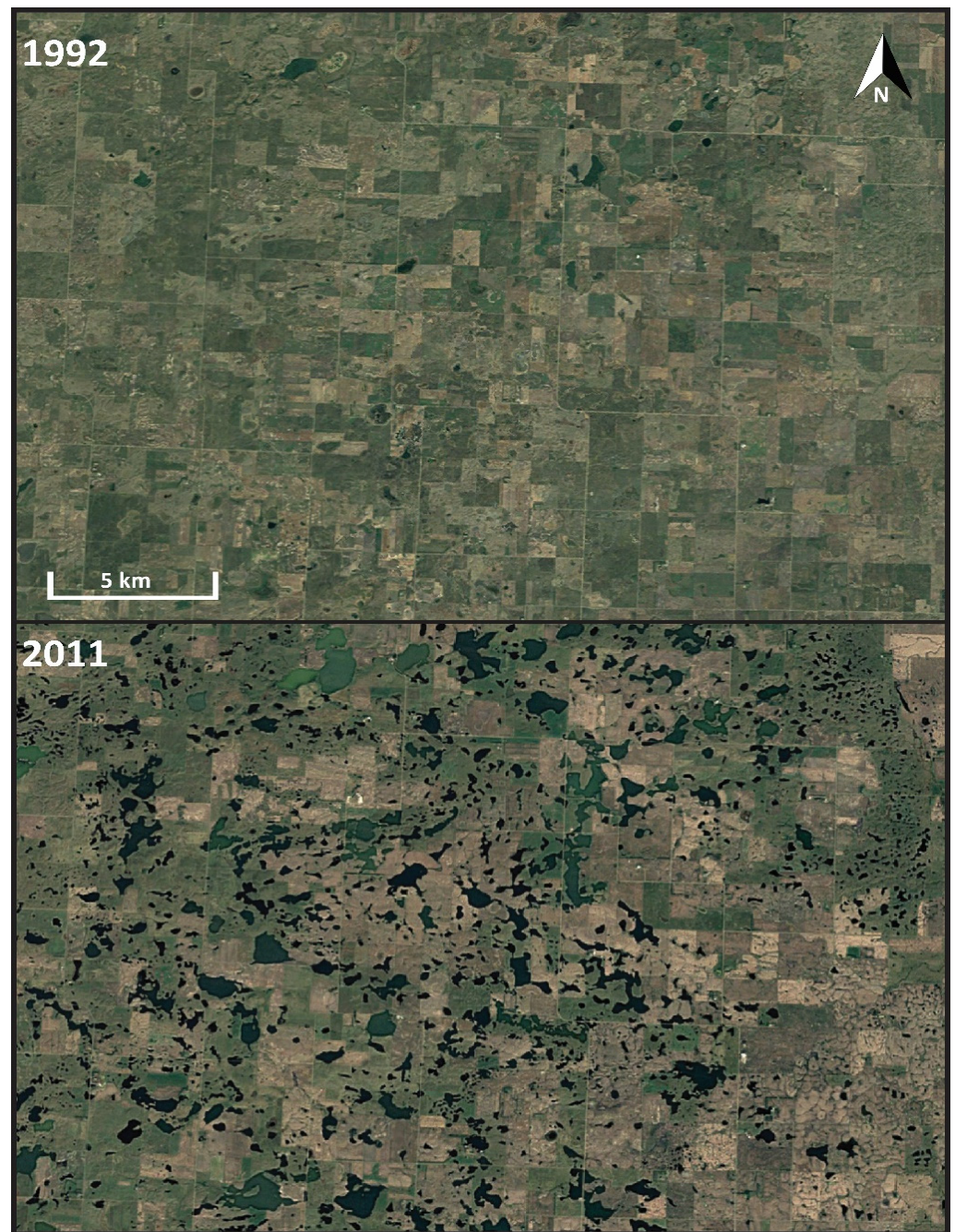
**Figure 3.** Graph of mean monthly Palmer Hydrologic Drought Index (PHDI) values for Central North Dakota (Climate Division 5) between 1900 and 2020. Blue values represent values that are wetter than average and red values are drier than average. The dashed line represents the start of an observed ecohydrological state shift (1993), and from left to right the black bars represent sample years that are 1) a wet year before the 1993 state shift, a drought year before the 1993 state shift, and a wet year after the 1993 state shift. PHDI data were accessed at <https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00005> (accessed on 20 September 2022).

The hydroecological variability of prairie-pothole wetlands contributes to the variety of ecosystem functions they perform [23,27,35,36]. Some of the more important functions include groundwater recharge, nutrient cycling, carbon sequestration, and stormwater retention [37–41]. Prairie-pothole wetlands also uniquely contribute to regional aquatic and intercontinental, aquatic, semiaquatic, and terrestrial biodiversity through the habitat and resources they provide [16,41,42]. For example, the PPR typically hosts around 50% of the continental breeding-duck population, making it a globally important area for wildlife management [43,44]. Many of these ecosystem functions are maintained through the aforementioned spatial and temporal variability exhibited by the wetlands. However, historical and contemporary changes in climate, landcover, and wetland drainage have altered this natural variability.



**Figure 4.** Three maps representing vegetation zone areas for cottonwood lake study are wetlands in 1983, a wet year before the 1993 state shift; 1992, a drought year before the 1993 state shift; and 2011, a wet year after the 1993 state shift. Cottonwood Lake study area vegetation zone spatial data are made publicly available by the U.S. Geological Survey and publicly available and can be downloaded at: <https://www.sciencebase.gov/catalog/folder/5853fea1e4b0e2663625f35d> (accessed on 20 September 2022).





**Figure 5.** Landsat satellite imagery obtained from Google Earth depicting wetland surface-water changes during a period of drought (1992) and deluge (2011) in Stutsman County, ND, USA. Spatial extent of satellite images is  $98^{\circ}58'29.75''$  W;  $99^{\circ}20'11.45''$  W;  $46^{\circ}55'7.28''$  N;  $47^{\circ}6'25.03''$  N.

## 2. Ecosystem Homogenization

Among-wetland ecohydrological variability of prairie-pothole ecosystems is driven by an individual wetland's hydrogeologic setting, local climate, and surrounding landscape characteristics. A wetland basin's setting is defined as a basin's topographic elevation, size, geomorphology, surrounding land use, and underlying substrate, which in turn influence its relationship with local surface-water and groundwater flows, and subsequently contribute to a wetland's capacity to pond and store water [31]. However, even wetlands with very similar hydrogeologic characteristics can exhibit high among-wetland variability due to spatial variation in climate and surrounding land use [45,46]. Wetlands and their functions are linked through landscape connections that determine how water,

nutrients, and biota move through the landscape [25,47–50]. Alterations of wetland-to-wetland landscape linkages, i.e., the uplands that connect wetlands, periodic surface connections between wetlands, and the geographic distance between wetlands can, in turn, influence the hydrologic and biotic variability of nearby wetlands [5,31,47,51,52]. Many wetland ecosystem functions, e.g., biodiversity maintenance, groundwater recharge, and stormwater retention, are maximized in complexes of wetlands with heterogeneous water regimes [24,53,54]. Therefore, the loss of variability in water regimes over time, altered spatial organization of wetland landscapes, and corresponding changes in functions can lead to ecosystem homogenization.

### 2.1. Conceptual Model for Ecosystem Homogenization

Spatial variability in topography or physical characteristics and temporal variability in climate are essential to maintaining local heterogeneous complexes of wetlands. However, large-scale landscape alterations and long-term or extreme changes in regional climate can have additive and often synergistic effects on wetland ecosystem functions [25,55–57]. Our conceptual model for wetland ecosystem homogenization (Figure 1) depicts how shifts in climate cause directional changes in wetland hydrology that, in turn, can cause a directional change in water and soil chemistry, and subsequently modified biotic communities. In addition to being a primary driver of wetland ponding, directional shifts in climate can influence wetland ecosystems by driving changes in surrounding land use, such as a change from pasture to crop production, which in turn affect wetlands through water-management decisions that can result in the movement of water off the uplands and small upland embedded wetlands into depressional waterbodies [56,58]. The wetland loss category refers to the deliberate draining, ditching, and filling of wetland basins. The loss of functioning wetlands not only simplifies the geographic configuration of remaining wetlands, but their displacement changes local surface-water flows, which in turn can alter the temporal and spatial dynamics of remaining wetlands on the landscape [5,13,59–61].

### 2.2. Mechanisms for Ecosystem Homogenization in the PPR

The landcover of the pre-European settlement PPR was primarily a mix of native grassland with embedded depressional wetlands. These relatively small, prairie-pothole wetlands covered an estimated 20% of the region's land area [39]. However, the interplay between European settlement, local topography, local climate, and agricultural production has led to spatial simplification of prairie-pothole wetland distributions [5,13,62,63]. This simplification was predominately driven by the conversion of wetlands and their surrounding native uplands (native prairie) to cropland. It has been estimated that 65% of the historical wetland basins in the PPR were lost due to anthropogenic influences [39]. This loss is spatially variable, ranging from 35% in South Dakota to >90% in the Des Moines lobe ecoregion of Iowa [63,64]. Since wetland losses in the PPR were primarily a result of the draining and filling of wetland basins for agriculture [65], losses were concentrated in the most heavily farmed areas [66]. In addition, a disproportionate number of wetlands that were drained or filled were the small, most temporarily ponded wetlands [5,62,63]. The preferential loss of these smaller wetlands not only decreased the hydrologic variability on the landscape but also led to the loss of spatial connectivity, i.e., the loss of small “stepping stone” wetlands that are important for biological dispersal, and facilitated ecosystem homogenization [51,61,67,68].

In addition to the loss of many historical wetlands, the conversion of uplands to farmland and consolidation of runoff from wetland drainage networks further altered the ecohydrological variability of remaining wetlands [57,59,69]. Most of the historical wetland drainage in the PPR in the form of surface ditching, which works by moving water from numerous small wetlands into a single, larger, terminal waterbody, i.e., wetland consolidation [69]. The increased water inputs results in increased ponded-water extent and duration in the terminal waterbody [57,59]. Along with consolidation, runoff rates have increased in the region due to the conversion of native uplands to cropland [31,61].



An estimated 90% of native grasslands in the PPR have been converted to other landcover types, typically cropland [70]. By contrast, widespread establishment of monotypic stands of invasive grasses in grassland-covered uplands surrounding wetlands can reduce runoff rates resulting in increased drying of wetland ponds [35]. Non-native grasses, primarily smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*), have invaded many remaining grasslands in the region [71–73]. Even in areas where wetlands and grasslands are restored, the revegetation of wetlands is limited to occurring seedbanks and the seeding of upland grass seed mixes [74]. In North Dakota, the absence of wetland-specific seed mixes during restoration has likely facilitated the replacement of native vegetation with non-native cool season grasses and other invasive species [74].

In the absence of prairie buffers (surrounding wetlands), agricultural runoff into wetlands is associated with greater rates of sedimentation, increased nutrient loads, and pesticide impacts [50,75–77], which in turn can alter the chemical and biotic composition of affected wetlands. The loss of surrounding grasslands also becomes a loss of habitat and inter-wetland connectivity for species that require grasslands in addition to ponded wetlands to complete their lifecycle, e.g., waterfowl, amphibians [78–81]. The cumulative effects of wetland loss and the conversion of prairie to cropland in the PPR have simplified the spatial distribution of wetland basins and the upland landscapes in which they are embedded, and reduced ponded-water variability in remaining wetlands. In the context of our ecosystem homogenization conceptual model, these changes also influence the sensitivity to climate of the remaining wetlands within this altered landscape (Figure 1).

Beginning in 1993, parts of the PPR experienced an extended multi-decadal wet period [56,82]. The combination of prolonged, uncharacteristically wet conditions (Figures 3–5), and landscape modifications have resulted in many prairie-potholes reaching high surface-water levels that have not likely been experienced within the last 500 years [30]. Even in the absence of anthropogenic land-use change, the magnitude of precipitation increases has resulted in cascading effects. The combination of rising groundwater tables and increased soil moisture in the region has resulted in increased surface-water runoff and reduced losses of water from wetlands to groundwater [56,83]. However, most of the PPR still experiences anthropogenic change, and the timing of this wet period coincided with continued loss of grasslands, an increase in row-crop agriculture, and an increase in tile drainage [56,66,84]. This observed directional shift in climate and land-use change, combined with the non-random losses of wetlands, has led to a shift towards reduced ecohydrological variability for much of the PPR [25,55,56,85,86].

### 3. Evidence for Ecosystem Homogenization

The response of prairie-pothole wetland ecosystems to increased precipitation has been highly variable and spatially dependent [87,88]. Based on our conceptual model, these patterns are intuitive considering that wetland loss, land-use change, and relative climates are regionally variable [62,63,85,89]. While some areas might experience greater change than others, most long-term studies in the PPR have indicated increases in hydroperiod, ponded-water surface area, depth, and connectivity over the last 15 to 30 years [56,62,68,83,85–88,90,91]. McLean et al. (2019 and 2022 [54,92]), also found that temporal variability (i.e., year to year variation) in wetland ponded-water area, vegetation structure, and certain biological communities might have also become less dynamic over time. While current wet conditions in the U.S. portion of the PPR have likely not been experienced in the last 500 years [30] there is also paleo-limnological evidence that historically semi-permanently ponded wetlands did not typically contain vegetative communities associated with permanent waterbodies for about 8000–10,000 years [93]. This change to more permanent hydrological conditions has also been indicated by changes in diatom assemblages and daphnia ephippia in sediment cores of prairie-pothole wetlands [94]. Linking the recently observed increases in depressional ponds and surface-water area to ecosystem homogenization is not necessarily intuitive. However, the ecosystem functions of these wetlands typically have less to do with the amount of water and are



more connected to the period of time they pond water and their location on the landscape (spatial organization and hydrogeologic setting), determining many of their physical and biological characteristics. These observed hydrological shifts often resulted in decreased variability of ponded-water regimes, homogenized water chemistries, and altered biotic communities [54,69,83,95–97].

Even though many, especially smaller, prairie-pothole wetlands have been drained or filled, in more contemporary time periods (i.e., the last 50 years) the mean number of wetland ponds and ponded-water surface area in the US PPR has increased over the last 15 to 30 years in response to wetter climate conditions [68,98–100]. Mushet et al., 2020 [91] described how wetlands can shift to different ecohydrological states. Using this framework it is also expected that small depressions that did not previously exhibit wetland characteristics could also shift to a wetland state if wet conditions persists for long periods of time. In fact, long-term monitoring efforts in central North Dakota have observed this phenomenon of terrestrial habitats developing wetland hydrology, soils, and plant communities [101]. However, without well-developed plant and invertebrate seed banks, it is still uncertain if these “new” wetlands produce the same functions as well-established systems. Many wetland inventory efforts that use satellite or aerial inventory often only detect the ponding of surface water, which does not necessarily indicate that they have other wetland characteristics (e.g., soils and wetland biota), which could lead to an overestimation of small wetland basins in wet years. The greater ponded-water area observed in recent years is predominately driven by an increased distribution of large-ponded basins [85]. This is in part due to the extreme saturation of wetlands on the landscape. As wetland basins become increasingly ponded, they fill until water spills into the next wetland basin. This dynamic is called “fill-and-spill” [102]. In the case where a larger lower-elevation basin increases in surface area and engulfs higher-elevation wetlands [62,85,99], it is called “fill-and-merge” [103]. Cressey et al., 2016 [88] compared ponded-water surface area, depth, and salinity for 80 prairie-pothole wetlands between two periods (1961–1966 and 2013–2014) and found that even at relatively small spatial scales (i.e., central ND) wetland complexes responded differently to changing hydroclimatic conditions. For example, wetland areas with low topographic relief and an absence of defined outlets typically had greater area for ponded water to expand and merge with nearby wetlands, and therefore exhibited the greatest hydrologic changes [88]. In contrast, wetlands with high topographic relief and defined outlets often exhibit less surface-water variability [54,88]. Vanderhoof and Alexander, 2016, [91] found through Landsat-derived surface-water maps from 1990 to 2011 that lake expansion in the PPR caused increased surface-water connectivity to nearby wetlands and sometime the inundation of wetlands tens of kms away by the expanding lake. At a smaller scale, long-term monitoring beginning in 1979 at the Cottonwood Lake Study Area in south central North Dakota indicated that after 1993 the 16 wetlands monitored had increased in surface-water depth, permanency, and connectivity compared to the previous two-decade averages [56,96,103]. Both climate driven fill-and-spill/fill-and-merge dynamics and consolidation of wetlands through drainage networks not only influence associated wetland ponded-water regimes but can also homogenize the composition and concentration of dissolved ions, nutrients levels, and biota found in the newly merged wetlands [53,88,103–106]. Similar increases in surface-water depth and permanency were observed in the Canadian portion of the PPR [31].

Increased atmospheric water inputs into wetlands and the merging of previously separate basins can have profound influences on the water chemistry of a wetland. Water chemistry, specifically dissolved-ion concentrations, in prairie-pothole wetlands is highly variable in space and time [83,96,107]. As dissolved-ion concentrations increase, biotic communities often shift to more salt tolerant taxa [27,41]. The increases in surface-water runoff and connectivity observed throughout much of the PPR have reduced the salinity gradient length and among wetland variability [83,107].

Dissolved-ion concentrations in wetlands are driven by salt inputs and losses, combined with dilution and concentration effects. Typically, wetlands situated above local

groundwater flows lose ponded water and dissolved salts to the soil, recharging the groundwater. By contrast, wetlands located at or below groundwater flows receive salts through groundwater discharge [23,27]. Atmospheric-water inputs (i.e., direct precipitation or precipitation driven runoff inputs) dilute the concentration of dissolved ions within a wetland, while evaporation and transpiration result in increased ion concentrations. When fill-and-spill or fill-and-merge dynamics are incorporated, dissolved ions mix, typically resulting in the saltier of the newly connected wetlands becoming fresher and the fresher wetland becoming more saline [83,88,103]. Two separate multi-county studies in central North Dakota found that since the 1960s and 1970s, saline wetlands have become significantly fresher and fresh wetlands have either remained static or slightly increased in salinity, resulting in less variability in salinity and a more homogenous salinity gradient [83,88]. Mushet et al., 2015, [83] found that for 167 large central North Dakota prairie-potholes sampled in the 1960s and 1970s, and resampled in 2012 and 2013, the specific conductance range between wetlands was 365  $\mu\text{S}/\text{cm}$  to 70,300  $\mu\text{S}/\text{cm}$  with a mean of 8376  $\mu\text{S}/\text{cm}$  in the earlier time period and decreased to a range of 449 to 40,350  $\mu\text{S}/\text{cm}$  with a mean of 2897  $\mu\text{S}/\text{cm}$  in the more recent sampling. Similarly Cressey et al., 2016 [88] found that for 80 central North Dakota wetlands with variable ponded-water regimes, wetlands that were saline in the 1961 to 1966 sampling period were much fresher during the 2013 to 2014 sampling period, and many of the smaller, historically fresher wetlands increased in salinity, which resulted in a much narrower and more homogenous salinity gradient in the later period. The cumulative changes in ponded water; volume, duration, extent, and chemistry have already started to alter species assemblages in the region [54,95,105,106,108].

The concept of biotic homogenization has a rich and still growing literature base in the aquatic sciences [109–111]. The dominant mechanisms that drive biotic homogenization are habitat simplification due to anthropogenic modification and the spread of invasive species [109,111]. These two mechanisms work hand in hand since habitat simplification can result in a loss of specialist taxa which provide an opportunity for non-endemic or other generalist taxa to replace them [110]. While habitat simplification of wetland ecosystems has occurred in the PPR, investigations of biotic responses in the context of biotic homogenization are limited [54]. The research that has indicated evidence for biotic homogenization in the PPR are mostly observations of decreased-beta diversity in wetland plant communities [95,112,113]. The potential homogenization of wetland animal communities, e.g., invertebrates and amphibians, is likely less understood due to the limited availability of long-term monitoring data [105].

Prairie-wetland vegetation dynamics and diversity are highly dependent on hydrologic dynamics [113]. Contemporary shifts towards larger, deeper, more connected wetland ponds in the PPR and the conversion of many uplands to cropland can simplify both the structure and taxonomical composition of wetland plant communities. Depending on a wetland's ponded-water regime, prairie-pothole wetlands can have open-water, deep-marsh, shallow-marsh, and wet-meadow vegetation zones [114]. Vegetation structure is different in each zone. For example, open-water zones in wetlands contain submergent vegetation, deep-marsh zones contain tall emergent species, shallow-marsh zones contain mid-height emergent vegetation, and wet-meadow zones contain shorter sedges [115]. When multiple vegetation zones are present, even minor changes in surface water can significantly change a wetlands vegetation structure [116]. The shift towards larger, deeper, more permanently ponded wetlands can lead to the loss of shallow marsh and wet meadow zones, which results with most of the wetland being in open-water or deep-marsh vegetation ([54]; Figure 4). Another widespread mechanism for loss in wetland vegetation structure has been the cultivation of wetland edges [85,117]. The simplification of vegetative structure through loss of vegetation zones, can in turn result in a loss of plant (and animal) species unique to the specific vegetation zones.

The stabilization of ponded-water regimes can result in a loss of plant communities that prefer dynamic surface-water fluctuations, which in turn can facilitate their replacement with exotic species [21,104,118]. Increased sedimentation and nutrient transport

into wetlands from surrounding croplands has also been attributed to the establishment of invasive wetland plants such as the non-native cattail *Typha angustifolia* and hybrid cattail (*Typha* × *glaucia*), reed canarygrass (*Phalarus arundinacea*), and common reed (*Phragmites australis*), which are known to spread rapidly and can choke out entire wetland basins [112,118]. For restored wetlands in the southeastern portion of the PPR, Aronson and Galatowitch, 2008, [113] found that beta diversity began to decrease after 12-years post reflooding when extinction rates began to exceed colonization rates. A major mechanism in these losses was the invasion of reed canary grass and hybrid cattails. The rise of invasive cattails and reed canary grass in shallow-marsh and wet-meadow zones has been observed in other studies within the region as well [94,104]. Jones, 2022, [74] found that for many wetlands restored in North Dakota where heavily invaded by non-native cool season grasses, this was likely attributed to weak, natural wetland seed banks and mechanically seeding the upland areas to cool season grasses that make up dense nesting cover. While the observed loss of vegetation structure and native species and increases in invasive species in prairie-pothole wetland plant communities appears to be a common pattern, the response of aquatic animal communities to habitat simplification has been less predictable [54], although shifts in aquatic plant communities would affect other organisms within these wetlands [119,120]. Hu et al., 2022 [94] used a paleolimnological approach to identify compositional changes in diatom communities in North Dakota Prairie pothole wetlands, and found increased abundances of more pelagic taxa that occurred around 1993 (i.e., start of current wet period), indicating a shift toward more lacustrine habitats that were novel to the 178-year period assessed.

McLean et al., 2019 [54] used long-term monitoring data from 16 wetlands in the PPR of North Dakota to investigate the simplification of ponded-water regimes observed through a shift towards more permanently ponded wetlands, and to determine if the shifts were correlated with decreases in aquatic-macroinvertebrate beta diversity. Overall, among-wetland beta diversity did not change over time (1992 to 2015). However, for the wetlands that shifted to more lake-like ponded-water regimes, they observed a clear shift towards a more novel and less dynamic invertebrate community composition [54]. Unfortunately, for the sites included in McLean et al., 2019 [54], aquatic-macroinvertebrate sampling did not begin until the start of an extended wet period, and consequently, their study was not able to quantify community composition that occurred in the more hydrologically dynamic periods that occurred before the start of the wet period (i.e., prior to 1993). The temporal limitations of this study can be expanded across the PPR, where there are very few, if any, aquatic-invertebrate studies that capture the taxonomic variability observed before and after 1993 [105]. Additionally, the wetlands sampled in McLean et al., 2019 [54], were also located on federal lands that have protected them from drainage, which limits its ability to generalize patterns that occur on the highly modified surrounding landscape.

Under contemporary ecohydrological conditions in the PPR, most wetland studies aimed at identifying environmental and surrounding land-use predictors of aquatic macroinvertebrates and or amphibians have been inconclusive in their findings [121]. However, using the information available, we can put together the pieces and generate hypotheses as to how climate and land-use driven simplification of wetland ecohydrological variability influences regional biodiversity. The preferential loss of small, temporarily ponded wetlands have likely resulted in localized or even regional loss of plant and animal communities that are specially adapted to these systems [5,59]. For example, many fairy shrimp (Anostraca) species require periodic drying of wetlands in order to complete their lifecycle. In regions outside the PPR, the loss of ephemeral wetland habitats has resulted in the regional loss or in some cases extinction of specific species [67,122]. However, for the PPR, there is very little literature that documents wetland macroinvertebrate communities present prior to the large-scale drainage of wetlands. While some invertebrates leave behind a record of their occur in wetland sediments, many leave behind no recalcitrant remains. Therefore, we will likely never know the actual extent of the pre-European-settlement species lost [123]. Another group of specialist wetland taxa that have likely become less

abundant on the landscape are the saline tolerant invertebrates (e.g., brine shrimp, brine flies) and plants [83,105]. The observed decreases in highly saline habitats and the loss of temporarily ponded wetlands have likely resulted in a loss of these specialist taxa. The current, fresher and larger wetland ponds have become suitable for a wider range of generalist taxa, and many can now support taxa that require permanent ponds to persist, e.g., fish that were not historically associated with prairie-pothole wetlands [106,124]. The increased presence of these fish communities has been identified as a major threat to aquatic-macroinvertebrate and amphibian communities [86,106,121,125–128]. While extreme precipitation events that have become common over the last 30 years likely provide new habitat for invertebrate communities, if the new ponds did not historically function as wetlands, it is possible that they do not have established invertebrate seed banks for some of the short hydroperiod specialist taxa, such as fairy shrimp.

For the most part, prairie-pothole wetlands have not been subjected to many exotic and invasive aquatic animals that have plagued other nearby aquatic ecosystems (e.g., zebra mussels, rusty crayfish, and faucet snails). The exception is the increased prevalence of fish communities. While most of the fish taxa associated with prairie-potholes are native to the region, they would historically be absent from most prairie-pothole wetlands [129]. Prior to 1993, most wetlands in the PPR were likely not consistently deep or fresh enough to support sustained populations of these fish [106]. It is likely that infrequent colonization of fish into prairie-pothole wetlands has naturally occurred. However, long-term persistence in these systems would be rare considering that even some of the largest potholes periodically dry or become too shallow to overwinter fishes [83,86,106,129]. In addition to historically being unsuitable for fish population persistence, the lack of surface-water connections would have limited fish dispersal from adjacent lakes and rivers. The cumulative effect of decreased ponded-water salinity, increased ponded-water volume and duration, and increased surface-water connectivity currently prevalent in the PPR have likely facilitated the colonization of fish into prairie-potholes [86,106]. The most prevalent fish species observed in prairie-pothole wetlands is the fathead minnow (*Pimephales promelas*). Gamefish, e.g., yellow perch (*Perca flavescens*), have also become increasingly prevalent in many wetlands in the U.S. portion of the PPR. In addition to dispersal through surface-water connections, the commercial and recreational value of baitfish such as minnows and gamefish such as perch has led to an increase in stocking previously fishless habitats. Since prairie-pothole wetland ecosystems did not evolve with fish, their presence in a wetland can lead to rapid changes to the native species that live and/or feed in wetlands [125,127,128]. For example, fathead minnow presence is correlated with decreased macroinvertebrate alpha diversity and biomass [105]. The presence of fish is also correlated with decreases in native amphibian abundance, particularly for barred tiger salamanders (*Ambystoma mavortium*) and northern leopard frogs (*Lithobates pipiens*), which both compete with and become prey to some fish species [106,108,127].

In addition to their negative effects on aquatic-macroinvertebrate and amphibian species distributions, the increased presence of fathead minnows also simplifies trophic networks and results in ecosystem degradation [125–130]. For example, fathead minnows can deplete small, herbivorous, zooplankton populations, which can often result in a trophic cascade if algal blooms arise. These algal blooms, in turn, reduce submergent vegetation by blocking sunlight [125,128,131]. As another example, when in competition with fathead minnows, brooding ducklings have reduced growth and survival rates [132].

#### 4. Consequences of Ecosystem Homogenization

While the distribution and variability of ecosystem functions provided by prairie-pothole wetlands has likely decreased due to historical wetland losses and shifting (wetter) ecohydrological conditions, remaining prairie-potholes still provide valuable habitat for regional biodiversity and perform critical ecosystem services [126]. In other regions where depressional wetlands occur in croplands dominated regions, such as the subtropical Pampa grasslands in Brazil, cropland-associated changes in abiotic conditions have been



attributed to the simplification of some invertebrate communities [133]. Further research could assess whether these patterns also occur in the PPR. The selective losses of small wetlands and saline wetlands in the PPR have likely resulted in a loss on the landscape of the unique taxa associated with these wetland types. However, the larger, more permanently ponded wetlands remaining on the landscape often have higher aquatic-macroinvertebrate taxon richness [134,135]. The increased presence of water on the landscape has also boosted local duck abundances and fish populations [106,124,136,137]. The increased duck populations and fishing opportunities in prairie-pothole wetlands have also benefited outdoor recreation in the region. However, the functional roles of prairie-pothole wetlands extend beyond wildlife and fisheries conservation. Homogenization of other prairie-pothole ecosystem attributes threaten their important landscape functions and the societal benefits they provide. The increased presence of more monotypic stands of non-native vegetative communities in the wetland marsh zones has been attributed to a decline in native wetland plant communities [74,95,112] and has been found to limit the abundance of certain secretive marsh bird densities [138,139]. However, the impacts of homogenized plant communities dominated by invasive plant species and other land-use related effects on wetland aquatic animal species (e.g., aquatic invertebrates and amphibians) are relatively unknown.

The smaller, temporarily ponded wetlands that were once much more common in the PPR landscape provide many important ecosystem services due to their unique properties [60]. For example, these smaller wetlands are the primary contributors to groundwater recharge to an aquifer [24,140] because they store and quickly lose water to groundwater. They can also capture a disproportionate amount of stormwater runoff compared to larger discharge wetlands, which helps alleviate overland and downstream flooding [40,87,141,142]. This is especially important under current climate conditions when many larger wetlands have remained at or near their spill point which limits their water-storage capacity. In addition to water storage, smaller wetlands are disproportionately important for their geochemical functions as well [60]. For example, smaller wetland basins have proportionally larger reactive zones, which make them more efficient in biogeochemical cycling [15].

During high precipitation years, such as 2011 (see Figure 5), there can actually be an increase in small-ponded wetlands, and potentially increased heterogeneity in the distribution of ponded-water areas among depressions. However, from a jurisdictional perspective, periodic ponding of water (or other hydrological indicators) is only one of the three defining characteristics of a wetland, and it is uncertain if many of the small ponds also have established hydric soils or wetland plant communities. While small depressional ponds that either have recently established wetland soils and vegetative communities or only contain hydrologic characteristics (ponds) likely contribute to wetland ecosystem heterogeneity, more research is needed to understand if they are functionally equivalent to the small wetlands that existed prior to the ecohydrological state shift that began in 1993.

## 5. Potential Impacts of Continued Climate Change

While ecohydrological conditions of wetlands in the PPR over the most recent 15 to 25 years have been wetter and resulted in larger wetland ponds than historical averages [56,83], these conditions are likely to change under future climate scenarios [142,143]. However, there is still much uncertainty as to the magnitude of seasonal and annual temperature and precipitation changes in the PPR, and how wetland ecosystems will respond to these changes [144–146]. One commonality in future climate predictions is that temperatures will continue to increase, and average ponded-wetland densities will decrease [145,147]. With increases in temperatures come increases in evaporation rates of wetland ponds. If evaporation and transpiration water losses exceed precipitation inputs into wetlands, then ponded wetland area will decrease, which could result in a loss of wetland network connectivity [142]. Considering that evaporation and transpiration rates decrease as the volume to surface-area ratio increases, and that smaller recharge wetlands lose more water to the soil during dry periods, short-term droughts could have a dispro-

portionate influence on the smaller wetland ponds [31,38,141]. LaBaugh et al., 2016 [148] found that even though salt concentrations in the more permanently ponded wetlands were decreasing due to dilution, the accumulation of salts has continued to increase over time in some wetland ponds. This could have serious consequences for local biota if these larger ponds begin to dry and concentrate these salt additions. Land-use change has also been a continuous process in the region that can either help or harm wetland ecosystems depending on our future management decisions. In addition to expected climate-driven decreases in the amount of time small wetlands pond water due to future changes in climate, in the absence of ponded water, wetlands will likely be more vulnerable to landscape modifications (e.g., draining and filling) that would prevent ponding in future years.

## 6. Conclusions

Depressional wetlands, such as prairie-pothole wetlands, are highly sensitive to adjacent landscape modifications and climate shifts [19]. Through our review of the prairie-pothole wetland literature, we found consistent patterns indicating climate- and land-use-driven shifts in wetland hydroecological variability. The synergistic effects of climate and land use are working to pull wetland ecosystems towards one of two stable states, a dry state or a permanently ponded state [91]. This is because prairie-pothole wetland systems are typically described as having dynamic or transitory states that would naturally fluctuate between the two stable states (i.e., terrestrial and permanently ponded). However, in the presence of climate change-associated patterns (extreme weather) and widespread anthropogenic modifications, there is enough energy to force these systems into more stable states [55,91]. Over the last few decades, many larger wetlands have shifted towards being more permanently ponded lakes. However, in the future, climate warming will likely shift wetlands towards a dry state, which will disproportionately influence smaller wetlands. Currently, the smaller temporarily ponded wetlands continue to be the most vulnerable to future losses and are perhaps the most valuable for maintaining wetland landscape multifunctionality [13,15,24,60]. While it is hard to predict all of the potential climate and land-use scenarios and how they might alter prairie-pothole wetland ecosystems in the future, understanding the vulnerabilities of these systems to potential changes is an important consideration for proactive conservation planning strategies.

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