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Abstract

Located in the interior of North America straddling the US/Canada border, the Prairie Pothole Region (PPR) encompasses more than 770,000 km² and is one of the richest, most diverse, and unique wetland-grassland ecosystems in the world. The PPR is named for the millions of depressional wetlands called “prairie potholes” dispersed throughout the landscape. The potholes formed as subterranean masses of ice melted following the retreat of glaciers at the end of the last ice age. A majority of wetlands within the PPR are depressional and receive water by snowmelt or rain. Differences in topography, soil type, longitude, and latitude all determine the depth and ecological function of prairie potholes. Wetlands and

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grasslands in the PPR provide vital habitat for a diverse array of plant and animal species; large populations of migratory birds including waterfowl, waterbirds, and grassland birds depend on this habitat base during the breeding season and migration. Prairie pothole wetlands confer a variety of ecological good and services to society, but wetland drainage has substantially reduced wetland abundance relative to pre-European settlement levels. Although programs have reduced the rate of loss, more work is required to slow wetland and grassland conversion.

Keywords

Adaptive management · Conservation · Energy development · Grasslands · Joint venture · Landscape conservation · Planning · Prairie Pothole Region · Wetland ecosystems

Introduction

Located in the interior of North America, the Prairie Pothole Region (PPR) is one of the richest, most diverse, and unique wetland-grassland ecosystems in the world (Baldassarre and Bolden 2006). The PPR straddles the US/Canada border and encompasses more than 770,000 km² including parts of five US states, the northern tier of Montana, northern and eastern North Dakota, eastern South Dakota, western Minnesota, and north-central Iowa; and three Canadian provinces, southwestern Manitoba, southern Saskatchewan, and southern Alberta (Fig. 1). The PPR is named for the millions of depressional wetlands called “prairie potholes” dispersed

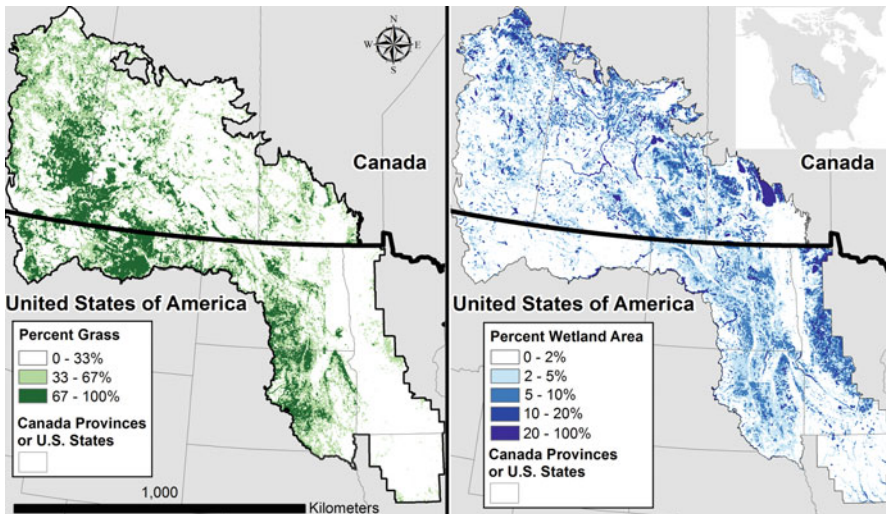


Fig. 1 Distribution of 29.2 million grassland ha and 8.3 million wetland ha (percent within 10.4 km² [4 mile²] area) within the Prairie Pothole Region of North America, circa 2000 (original figure by US Fish and Wildlife Service, held in the public domain)

throughout the landscape. The vast area of the PPR ecosystem and high density of wetlands (exceeding 40/km² in some areas; Kantrud et al. 1989) make the PPR region unique.

Formed as subterranean masses of ice melted following the retreat of glaciers at the end of the last ice age, the PPR historically ranged from areas of vast grasslands in the south to grasslands interspersed with deciduous trees (parklands) in the north. The eastern portion of the PPR historically supported tall-grass prairie vegetation. Short-grass prairie dominated the western portion, with mixed-grass prairie located centrally. Parklands represent the transition from grassland to boreal forest and are interspersed with stands of aspen *Populus tremuloides* and other woody species. These gradients in vegetation reflect variation in precipitation and evapotranspiration rates across the region (Millett et al. 2009). Areas to the south and west tend to be drier than more northerly or easterly regions. The historic disturbance regime in this area was driven by wildfire, grazing by native ungulates, and drought and deluge precipitation patterns. Since settlement, wildfire has been suppressed and in many places native grasslands have been largely replaced by annual cropland. Regions of the PPR with higher annual precipitation have experienced higher rates of conversion to cropland. Accordingly, tall-grass prairies, which occur at the higher end of the moisture gradient of global grasslands, are almost extirpated (Samson and Knopf 1994).

Grasslands and wetlands within the PPR, especially the eastern PPR, are some of the most altered landscapes in the world because much of the land is privately owned, is productive as cropland, and is relatively easy to cultivate (see Fig. 4 in Hoekstra et al. 2005). Prior to European settlement, prairie pothole wetlands may have encompassed > 20% of total land area in the PPR (Euliss et al. 2006). Since settlement, up to 89% of wetlands have been lost to agricultural drainage in some parts of the PPR (Dahl 1990). Native prairie losses have exceeded rates of all other biome losses within North America (Samson and Knopf 1994). Grasslands in the PPR complement wetland resources, as many species of wetland-dependent birds nest in surrounding grasslands and grass cover is essential for successful nesting for a wide variety of ground nesting birds from passerines to waterfowl (Klett et al. 1988; Stephens et al. 2005; Winter et al. 2005). Loss of grassland, especially native grassland, has resulted in large declines in grassland bird populations, making them one of the most imperiled guilds of birds in North America (Brennan and Kuvlesky 2005).

Hydrology

A majority of wetlands within the PPR are depressional and receive water by snowmelt or rain. Differences in topography, soil type, longitude, and latitude all determine the depth and ecological function of prairie potholes (Labaugh et al. 1998). Wetlands within the PPR are classified by how long they retain water during the growing season. Temporary wetlands retain water for 1–3 weeks during the growing season, seasonal wetlands retain water for 3 weeks to 90 days, and semipermanent wetlands retain water through the growing season for many consecutive years (Stewart and Kantrud 1971). Detailed mapping of wetland types in the

US PPR indicates 3.44 million wetland basins covering 3.68 million ha in temporary (13.0% of total area), seasonal (23.7%), semipermanent (24.1%), riverine (7.7%), and permanent wetlands or lakes (31.4%) within the boundaries of the US PPR region (Fig. 1). In the Canadian PPR, detailed mapping of all individual wetlands has not been completed; however, current estimates place wetland area near 4.6 (± 1.1) million ha (Watmough and Schmoll 2007). Temporary and seasonal basins comprise an estimated 24% of this area, whereas semipermanent and permanent basins comprise 61.7 and 11.8% of wetland area, respectively (Ducks Unlimited Canada, unpublished data). Most wetlands in the PPR hold water temporarily or seasonally. In the USA, semipermanent and permanent wetlands comprise 8.6 and 1.2% of wetland basins, respectively, yet these deeper basins account for 55.5% of total wetland area. In Canada, semipermanent and permanent basins comprise 23.9 and 1.2% of wetland basins but account for 73.5% of wetland area (Ducks Unlimited Canada, unpublished data). Wetland types have different ecological values for different species. For example, northern pintail *Anas acuta*, a species that has experienced population declines since the 1970s is associated with temporary and seasonal wetlands.

The climate of the PPR is extremely variable, characterized by high interannual and regional variation in precipitation (Niemuth et al. 2010), which greatly influences the number of wetland basins in the PPR that contain water each year, water levels within those basins, and abundance of wetland-associated wildlife. Even in the absence of anthropogenic wetland drainage, wetland basin area and basin numbers are not static in the prairies. This is because large variation in precipitation causes wetland area to increase and decrease through time (Niemuth et al. 2010). Further, wetland numbers and function may change during wet/dry precipitation cycles. For example, during high precipitation years as water tables rise, many temporary wetlands are subsumed within the boundaries of seasonal or semipermanent wetlands and may function ecologically as a deeper water regime wetland (Niemuth et al. 2010). Conversely, during drought years, semipermanent wetlands may function as a temporary or seasonal wetland and temporary wetlands may remain dry for several years. Periodic drying is essential to maintain the productivity of prairie wetlands by accelerating nutrient cycling and allowing seeds of annual plants to germinate (Murkin 2000).

Biodiversity

Remaining wetlands and grasslands in the PPR provide vital habitat for a diverse array of plant and animal species, including threatened and endangered mammals (Clark 2000), fishes (Peterka 1989), amphibians (Lehtinen et al. 1999), and a variety of invertebrates (Wrubleski and Ross 2011). Most notably, large populations of migratory birds including waterfowl (Johnson and Grier 1988), waterbirds (Peterjohn and Sauer 1997), and grassland birds (Niemuth et al. 2008) depend on this habitat base for food and cover primarily during the breeding season but additionally during migration. In 2011, approximately two third of all ducks

estimated in the entire Waterfowl Breeding Population and Habitat Survey area occurred within the US and Canadian PPR (Zimpher et al. 2011).

The myriad of wetlands also makes the PPR valuable to other migratory birds. For example, estimates suggest that PPR harbors 70% of the continental population of Franklin's gull *Larus pipixcan*; > 50% of the continental population of pied-billed grebe *Podilymbus podiceps*, American bittern *Botaurus lentiginosus*, sora *Porzana carolina*, American coot *Fulica americana*, and black tern *Chlidonia niger*; and 30% of the continental population of American white pelican *Pelecanus erythrorhynchos* and California gull *Larus californicus* (Beyersbergen et al. 2004) as well as ~80% of the North American population of marbled godwit *Limosa fedoa*. Remaining grasslands also support large populations of grassland birds including 91% of Baird's sparrow *Ammodramus bairdii*, 87% of Sprague's pipit *Anthus spragueii*, and 71% of chestnut-collared longspur *Calcarius ornatus* (Rich et al. 2004).

Ecosystem Services

In addition to providing habitat for a broad suite of wetland-dependent wildlife species, prairie pothole wetlands confer a variety of ecological good and services to society.

Surface water storage and flows – Prairie wetlands store water during the spring runoff and following prolonged precipitation events. Slowing runoff rates reduce annual economic losses from flood damage to infrastructure such as roads, drainage systems, and urban housing (Murkin 1998). Miller and Nudds (1996) attributed increasing magnitude of flood events in the Mississippi River, in part, to wetland losses in the upper reaches of the watershed in the PPR.

Groundwater recharge – Surface waters contained within prairie potholes interact with ground water in a variety of ways. Subsurface connectivity of water flows affects both water chemistry and a variety of biological processes. Depressional wetlands can be both areas of local recharge to groundwater at topographic highs and areas where groundwater discharges to the surface at topographic lows (Labaugh et al. 1998). Prairie wetlands can be important for recharging regional aquifers at rates ranging from 2 to 45 mm/year (van der Kamp and Hayashi 1998). In the PPR of northwest Minnesota, Cowdery et al. (2008) demonstrated that surface aquifers were recharged in significant part from seasonal and ephemeral wetlands.

Controls for contaminants, excess nutrients, and sediments – Prairie wetlands play an important role in mediating transport of a variety of contaminants and serve as sinks for excess nutrients (Murkin 1998). Agricultural applications of fertilizers and pesticides have increased substantially in the PPR since the 1960s (Crumpton and Goldsborough 1998). Accordingly, prairie potholes often receive substantial inputs of chemicals, excess nutrients, and sediments from surrounding agricultural or other industrial operations. In some cases wetlands are able to incorporate undesirable chemicals and breakdown these compounds into less toxic by-products and sediments (Goldsborough and Crumpton 1998; Murkin 1998). Excess nutrient

inputs to wetlands are incorporated into wetland flora and fauna (Murkin 1998), thereby removing nitrates and phosphorous with important consequences for downstream water quality and subsequent eutrophication of receiving waterbodies (Crumpton and Goldsborough 1998). Further, wetlands reduce peak river flows allowing sediments to settle out of the water column which reduces stream turbidity. Unfortunately, increased siltation within wetlands may subject them to premature filling and impair other ecological functions (Gleason and Euliss 1998).

Greenhouse gas flux – Prairie wetlands have been documented to be important carbon stores (Gleason et al. 2009), but the same conditions that lead to the accumulation of organic carbon can also lead to the production of methane, a greenhouse gas that is more effective at trapping heat than carbon (Badiou et al. 2011). Until recently it was unknown whether prairie potholes were net sources or sinks of greenhouse gases. Badiou et al. (2011) measured the changes in soil organic carbon, and methane and nitrous oxide emissions in newly restored, long-term restored, and reference wetlands across the Canadian prairies to determine the net greenhouse gas mitigation potential associated with wetland restoration. Their research estimated that restored prairie potholes have the potential to sequester a net of approximately 3.25 Mg CO₂ equivalents ha⁻¹ year⁻¹, after accounting for increased CH₄ emissions. Thus, restoration of wetlands within the PPR could help mitigate greenhouse gas emissions (Badiou et al. 2011).

Restoring ecological goods and services through wetland restoration – It is possible to restore many of the ecological functions associated with prairie potholes (Galatowitsch and van der Valk 1994; Begley et al. 2012). Yang et al. (2010) modeled the consequences of restoring 619 ha of wetlands lost through drainage between 1968 and 2005 within Broughton's Creek watershed in southwestern Manitoba. They estimated that peak discharge at the outlet of this 25,139 ha watershed would be reduced by 23.4%. Similarly, sediment loading would be reduced by 16.9%, while total phosphorous and nitrogen loadings would be reduced by 785 and 4,219 kg year⁻¹, respectively, equivalent to 23.4% of current loads. However, recent meta-analyses of 621 wetland sites through the world indicate that biological structure and biogeochemical function in restored wetlands were 26 and 23% lower, respectively, than wetlands that have not been drained (Moreno-Mateos et al. 2012). Moreno-Mateos et al. (2012) also found depressional wetlands and wetlands in colder climates, such as the PPR, are the slowest to recover full ecological functions.

Conservation Status and Threats

Wetlands – Since European settlement, wetland drainage has substantially reduced wetland abundance relative to pre-European settlement levels (Dahl 1990), yet millions still exist (Doherty et al. 2013). Historic wetland losses (state-scale estimate) across individual states ranged from 27% in Montana to 89% in Iowa (Dahl 1990). Minnesota, North Dakota, and South Dakota lost 42, 49, and 35% of their wetlands, respectively, compared to presettlement conditions (Dahl 1990). The percent of wetlands lost in the PPR portion of Minnesota is actually much higher, because state-scale estimates include

many non drained wetlands in the northern deciduous and coniferous forest biomes of Minnesota (Oslund et al. 2010). In the Canadian PPR, it is estimated that between 40% and 70% of historical wetlands have been drained for agriculture development since settlement (Environment-Canada 1986; Watmough and Schmoll 2007).

Drainage peaked across the USA during the period from the 1950s to early 1970s, when 185,346 ha of wetlands were drained annually (Dahl 2011). When compared to the 44.6 million ha of wetland area remaining across the lower 48 states in 2009, this would equate to a yearly drainage rate of 0.42% (Dahl 2011). Peaks in wetland drainage were a result, in part, of larger, more powerful farm equipment and efficiencies derived in larger crop fields (Higgins et al. 2002). Within the US PPR approximately 34.4% of wetlands are protected from conversion by legal mandate, such as federal ownership or conservation easements with private landowners. Currently, wetland protection under the US Farm Bill (conservation subtitle Swampbuster provision; Public Law 99–198) is the primary protective legislation for wetlands in agriculture landscapes (van der Valk and Pederson 2003). This leaves 65.6% of remaining wetlands having protection by farmers' voluntary participation in US farm programs (Doherty et al. 2013).

Active draining is currently occurring across the PPR, especially for shallow temporary and seasonal wetlands embedded in an agricultural matrix. In the eastern portion of the US PPR, wetland loss and drainage rates are high (Oslund et al. 2010). The documented 15% loss from 1980 to 2007 (0.57% per year) in the Prairie Coteau ecoregion in Minnesota is comparable to the nationwide peak of wetland drainage during the 1950s to early 1970s (Dahl 2011). Losses in the Prairie Coteau ecoregion in Minnesota provide further evidence for higher wetland loss rates in agriculture-dominated landscapes. Between 1985 and 2001 in the Canadian PPR, wetland area losses were 5–6% among provinces and wetland basin losses were 5–8% (Watmough and Schmoll 2007).

Grasslands – Large extents of grassland still exist, with approximately 10.7 and 18.5 million ha remaining in the PPR of the USA and Canada, respectively (Fig. 1). Conversion of grasslands for crop production continues today (Stephens et al. 2008; Rashford et al. 2011). In the Missouri Coteau region of North and South Dakota, 0.4% of grasslands (–36,540 ha) were lost per year during 1989–2003 (Stephens et al. 2008). A recent study documented 1.33% of grasslands were lost per year during 1979–1997 across the entire United States Prairie Pothole Region (Rashford et al. 2011). Major drivers of grassland conversion are soil quality and agricultural commodity prices (Rashford et al. 2011). Federal farm program subsidies also drive grassland conversion in the US PPR region (G.A.O. 2007). US Federal farm programs reduce financial risks associated with cropping marginal soils and make farming more profitable, which creates economic incentives to convert privately owned grasslands from ranching operations to agricultural cropland (G.A.O. 2007). Within the US PPR approximately 81.6% of remaining grasslands have no legal protection and are vulnerable to conversion (Doherty et al. 2013). While grassland loss has been a historical trend within the Canadian portion of the PPR, the recent trend has been toward increasing grasslands at the expense of cropland. Contributing factors include removal of grain transportation subsidies in 1995, federal and

provincial programs encouraging conversion of marginal cropland, and expansion of the cattle industry increasing demand for pasture and hayland forage (Prairie Habitat Joint Venture 2008). Differences in grassland trends between the US and Canadian PPR highlight the importance of agricultural policies at the national level on individuals' land use decisions. Despite increases in overall grassland cover in Canada, native grasslands have continued to decline. Native grasslands declined by about 10% within the PPR from 1985 to 2001 (Watmough and Schmoll 2007).

Conservation Future – Many species of wildlife are adapted to the PPR's variable environment and respond to water conditions by changes in distribution and numbers, including waterfowl (Johnson and Grier 1988), waterbirds (Peterjohn and Sauer 1997), and grassland birds (Niemuth et al. 2008). In addition, reproductive effort can also be influenced by water conditions (Krapu et al. 1983). High variability complicates conservation planning and management but also provides insight into what happens when conditions are dry and what the future may hold if wetlands continue to be drained, resulting in a "permanent drought."

Protecting wetlands and grasslands from conversion is a primary step necessary for future opportunities to influence habitat quality, especially when habitat is being lost (see Figs. 3 and 4 in Doherty et al. 2013; Watmough and Schmoll 2007). Continued private landowner acceptance of conservation programs is imperative in the PPR given the amount of land privately held (Doherty et al. 2013). Focusing research on the economic and social aspects of agriculture, while specifically incorporating species-specific responses in abundance, survival, and reproduction in the PPR, may identify which agricultural practices are most favorable to wildlife yet still acceptable to private landowners (Barnes 2011). Lastly, as evidenced by the large differences in amounts of wetlands and grasslands under conservation planning scenarios in the US PPR (Doherty et al. 2013) and increases in grass cover in the Canadian PPR (Watmough and Schmoll 2007), agricultural policies that do not incentivize conversion of marginal soils, or even slow wetland and grassland conversion rates by tenths of a percent, can drastically change the future of wetlands and grasslands in the PPR.

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