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GEOGRAPHICALLY ISOLATED WETLANDS OF THE UNITED STATES

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Abstract: While many wetlands form along floodplains of rivers, streams, lakes, and estuaries, others have developed in depressions far removed from such waters. Depressional wetlands completely surrounded by upland have traditionally been called ''isolated wetlands.'' Isolated wetlands are not confined to basins, as some occur on broad flats and others form on slopes. The term ''geographically isolated wetlands'' better describes these wetlands, since many are hydrologically connected to other wetlands and waterbodies through ground-water flows or by intermittent overflows (spillovers). Numerous types of geographically isolated wetlands occur throughout the United States. They may be naturally formed or the result of human action. Naturally formed types include prairie pothole wetlands, playas, Nebraska's Rainwater Basin and Sandhills wetlands, West Coast vernal pools, sinkhole wetlands, Carolina bays, interdunal and intradunal wetlands, desert springs, terminal basins in the Great Basin, and kettle-hole bogs in glaciated regions. Human-caused isolated types may be intentionally built, such as ponds designed for various purposes and wetlands built on mined lands, or they may be accidentially created (e.g., natural wetlands that were once connected to rivers and streams but are now isolated by roads, railroads, and other development or isolated by altered river hydrology). Many of the functions and benefits attributed to non-isolated wetlands are present in isolated wetlands.

Key Words: alvar wetlands, Carolina bays, channeled scablands, coastal plain wetlands, cypress domes, desert springs, desert wetlands, floodplain wetlands, interdunal wetlands, intradunal wetlands, isolated wetlands, karst wetlands, kettle-hole bogs, playas, pocosins, prairie potholes, Rainwater Basin wetlands, salt flats, salt lakes, Sandhills wetlands, sinkhole wetlands, terminal wetlands, vernal pools

INTRODUCTION

Climate, hydrologic forces, geologic processes (e.g., aeolian, glacial, and tectonic), human activity, and other processes have shaped America's landscape and led to the formation of a diverse collection of wetlands. Many wetlands have developed in shallow water or on floodplains associated with estuaries, rivers, lakes, and streams. Others have become established in poorly drained depressions, many of which are completely surrounded by upland. The latter have been traditionally referred to as ''isolated'' wetlands or ''isolated basins'' (Damman and French 1987, Tiner 1996, Sharitz and Gresham 1998, Lentz and Dunson 1999, Winter 1999, Mitsch and Gosselink 2000). Isolated wetlands received increased attention after the January 2001 ruling of the U.S. Supreme Court (i.e., Solid Waste Authority of Northern Cook County vs. the Corps—the SWANCC decision; No. 99–1178, January 9, 2001). This paper provides an overview of isolated wetlands in the United States. It begins with some remarks on the definition question, then briefly characterizes numerous types of ''geographically isolated'' wetlands.

Geographically Isolated Wetlands Defined

With respect to wetlands, isolation is a matter of perspective or context (e.g., isolated from what or isolated from who's point of view?). The term ''isolated wetland'' is a relative one that can be defined from geographic, hydrologic, and ecologic perspectives, considering different scales in space and time. Geographic isolation is the easiest to determine since it describes the position of a wetland on the landscape, with the simplest definition of an isolated wetland being a wetland completely surrounded by upland. Other definitions of isolated wetland require more detailed examinations of hydrologic interactions (surface and subsurface) and ecological relationships (Tiner et al. 2002). While most, if not all, wetland scientists would agree that there is no such thing as an isolated wetland from an ecological standpoint (i.e., ''everything is connected to everything else''), there are wetlands that are

Figure 1. Geographically isolated wetlands surrounded by cropland in North Dakota. (R. Tiner photo) Note characteristic pothole zonation: open water-semipermanently flooded marsh-seasonally flooded marsh-temporarily flooded meadow.

completely surrounded by upland (e.g., hydrophytic plant communities surrounded by terrestrial plant communities or undrained hydric soils surrounded by non-hydric soils; Figure 1). These wetlands can be considered ''geographically isolated wetlands.''

These wetlands have been referred to as ''isolated wetlands'' because they did not appear to be linked to other wetlands or waters via a well-defined surface water connection. Yet, many of these ''isolated wetlands'' are hydrologically connected to other wetlands and waters through subsurface or ground-water connections (Figure 2) or by infrequent and/or short duration surface-water connections (i.e., spillovers to or from other wetlands and waterbodies). Although considerable effort is required to establish these interrelationships, a number of studies have substantiated these connections for many types of geographically isolated wetlands (e.g., Fretwell et al. 1996).

Scale is an important consideration when determining geographic isolation. At the local level, an individual wetland surrounded by upland is clearly geographically isolated, while wetlands along streams are not. However, when viewed at a regional or global level, some riparian wetlands are associated with certain watersheds or aquatic systems that are geographically isolated. Examples include riparian wetlands in closed basins (land-locked with no outlet to the sea) and in karst topography. At the local scale, riparian wetlands in these situations are not isolated because they are connected by streams. However, when viewed over a larger geographic area, such wetlands may be part of an aquatic system that is completely surrounded by upland. All wetlands and waters in closed watersheds (internal drainage only) may be considered geographically isolated systems since there is no outlet to the sea (e.g., the Great Basin). Similarly, riparian wetlands along a ''losing'' (disappearing) stream in a karst landscape may be considered geographically isolated because the wetland-stream system is completely encircled by upland once the stream goes underground. The above examples illustrate the importance of defining scale when determining geographic isolation (i.e., isolated from what?).

The term ''geographically isolated wetlands'' used in this paper generally refers to wetlands that are completely surrounded by upland at the local scale. Wetlands associated with terminal basins (including salt lakes) in the Great Basin have also been included in the discussion because they have been viewed as isolated waters of the United States. Since the definition used is not a regulatory one, wetlands identified as

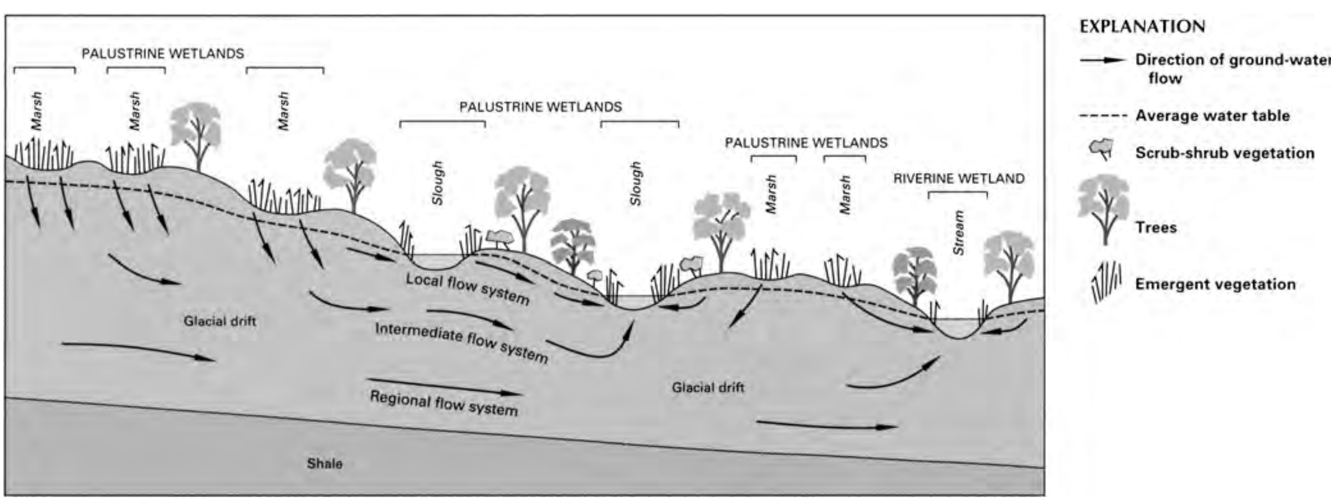


Figure 2. Generalized subsurface flows connecting geographically isolated pothole wetlands with riverine wetlands in South Dakota (Sando 1996).

''geographically isolated'' types in this paper may include jurisdictional wetlands regulated under the federal Clean Water Act or by state and local governments because criteria other than geographic isolation (e.g., ''navigability'' and ''adjacency'') are used to identify regulated areas.

GEOGRAPHICALLY ISOLATED WETLAND TYPES

Geographically isolated wetlands may be naturally formed or be the result of human activities. Naturally occurring isolated wetlands are mainly represented by the following types: prairie pothole wetlands, playas, Nebraska's Rainwater Basin and Sandhills wetlands, West Coast vernal pools, sinkhole wetlands, Carolina bays, interdunal and intradunal wetlands, desert springs, terminal basins in the Great Basin, and kettle-hole bogs in glaciated regions (Table 1). While most of these wetlands occur in depressions, some naturally isolated types form on broad flats and even on slopes. The predominant wetland types in many regions also include geographically isolated forms in closed basins.

Many geographically isolated wetlands are artifacts of civilization. Depressional wetlands built during mineland reclamation projects and artificial ponds are among those that were intentionally created. Others have resulted from fragmentation of the natural landscape by human development (e.g., levee construction, road construction, urban development, and cropland drainage) or by altered river hydrology (e.g., controlled flooding by upstream dams or river diversions).

Some types of geographically isolated wetlands are widely distributed across the United States, while other types are specific to a particular geographic region or geologic formation (Figure 3). Wide-ranging types include woodland vernal pools (i.e., where forests predominate), ponds, wetlands on inactive floodplains, and isolated wetlands created by human activities.

For discussion, geographically isolated wetlands are organized into ten types: 1) midcontinental prairie and steppe basin wetlands (prairie potholes, playas, Rainwater Basin wetlands, and Sandhills wetlands), 2) semi-desert and desert basin and flat wetlands (salt lakes, salt flats, channeled scablands, and desert springs), 3) kettle-hole wetlands, 4) Atlantic-Gulf Coastal Plain basin wetlands (Delmarva potholes, Carolina bays, and pocosins), 5) karst basin wetlands (cypress domes and limestone sinkholes), 6) vernal pool wetlands (West Coast vernal pools and woodland vernal pools), 7) coastal zone interdunal and intradunal wetlands, 8) Great Lakes alvar wetlands, 9) inactive floodplain wetlands, and 10) other potentially isolated wetlands. There is overlap among the types, and within several of them, two or more specific types are mentioned. The categories are intended to describe briefly the recognized types; other investigators may choose to arrange these wetlands differently. The discussion was largely extracted from Tiner et al. 2002; other papers in this special issue of *Wetlands* provide detailed information or citations for specific types.

Midcontinental Prairie and Steppe Basin Wetlands

The midcontinental region of the country (e.g., from North Dakota to Montana south into Texas) has a subhumid to semi-arid climate with precipitation ranging from 510–1020 mm in the prairies (grasslands) to 255–770 mm in the drier steppe (grass-shrublands) (Bailey 1995). Mean annual evaporation exceeds mean annual precipitation in most areas; in the drier steppe, evaporation is about twice the precipitation from May to October. The region experiences both short- and long-term droughts (U.S. Geological Survey 1970). Four types of geographically isolated wetlands are characteristic of this region: 1) prairie potholes, 2) playas, 3) Rainwater Basin wetlands, and 4) Sandhills wetlands (Figure 3). They are mostly closed basin wetlands (ponds, marshes, and wet meadows) dominated by herbaceous species.

Prairie Potholes. These basin wetlands formed during the last glacial advance in the north-central United States. When the Wisconsin glacier retreated northward more than 10,000 years ago, ice blocks were left on the newly shaped landscape. When the ice melted, water-filled depressions (''potholes'') formed. These basins now pockmark the northern prairie landscape (Figure 1), occurring in a variety of glacial deposits (e.g., end morraines, stagnation moraines, ground moraines, outwash plains, and lake plains) (Berkas 1996). Potholes represent the majority of North Dakota's one million ha of wetlands and South Dakota's 907,000 ha (Stewart and Kantrud 1973, Tiner 1999).

Most pothole wetlands lack a natural surface drainage network due to their origin and relative youth (i.e., erosional forces have not had sufficient time to develop a more integrated network of streams in this young post-glacial landscape). Over 80% of the James River Lowland in eastern South Dakota has surface drainage into closed basins (Johnson and Higgins 1997). During extremely wet periods, potholes may be filled with water and spillover may occur, thereby providing intermittent surface-water connections between otherwise ''isolated'' basins (Scientific Assessment and Strategy Team 1994, Vining 2002, Leibowitz and Vining 2003). Despite poor surface drainage, many potholes are hydrologically connected by groundwater; however, their subsurface connection to tributary streams may be very difficult to establish.

Table 1. Examples of geographically isolated wetlands in the United States. See Figure 3 for location of areas where these wetlands may be concentrated or most abundant. Note that some of these types are mostly geographically isolated wetlands, while others are mostly non-isolated. Wetlands are depressional or basin types, except where noted otherwise. An asterisk (*) denotes minor types.

Wetland Type	Brief Description	General Distribution
Prairie potholes	Marshes, aquatic beds, wet meadows, and ponds	Upper Midwest
Playas	Marshes, aquatic beds, wet meadows, and ponds	Southwest
Rainwater Basin wetlands	Marshes, aquatic beds, wet meadows, and ponds	South-central Nebraska
Sandhills wetlands	Marshes, aquatic beds, wet meadows, and ponds	North-central Nebraska
Salt flats and salt lake wetlands	Broad saline nonvegetated flats, inland salt marshes, and shallow-water zone of saline lakes	Great Basin
Channeled Scablands wetlands	Marshes, aquatic beds, wet meadows, vernal pools, and ponds	Eastern Washington
Desert spring wetlands	Marshes, aquatic beds, and ponds	Arid West and Southwest
Kettle-hole wetlands	Shrub and forested bogs, marshes, aquatic beds, and ponds	Glaciated Northeast and Midwest and Alaska
Delmarva pothole wetlands	Marshes, shrub swamps, forested wetlands, and ponds	Delmarva Peninsula
Coastal Plain ponds	Marshes, aquatic beds, and ponds	Atlantic-Gulf Coastal Plain
Gum ponds	Ponds with water gum or swamp black gum	Southeast
Carolina Bay wetlands	Marshes, aquatic beds, shrub swamps, forested wetlands, and ponds	South Atlantic Coastal Plain
Pocosin wetlands	Shrub swamps and forested wetlands	South Atlantic Coastal Plain
Cypress domes	Shrub swamps, forested wetlands, and ponds	Florida
Sinkhole wetlands	Marshes, aquatic beds, shrub swamps, forested wetlands, and ponds	Karst regions
West Coast vernal pools	Marshes, aquatic beds, wet meadows, and ponds	Pacific Coast; Washington to Mexico
Woodland vernal pools	Marshes, shrub swamps, and seasonal ponds surrounded by forest (either upland or wetland)	Forest regions
Interdunal and intradunal wetlands	Marshes, wet meadows, shrub swamps, and ponds within sand dune complex	Coastal zone (all coasts including the Great Lakes)
Alvar wetlands*	Flat or depressional wetlands forming on shallow limestone deposits	Great Lakes shoreline
Rock pool wetlands*	Seasonal pool in rock	Western U.S.
Geysers*	Wetlands associated with thermal springs	Western U.S.
Seepage slope wetlands	Forested wetlands, shrub swamps, and wet meadows on seepage slopes (including some bogs and fens)	Throughout U.S.
Precipitation-driven wetlands on permafrost	Wetlands formed on permafrost surrounded by upland	Alaska
Fens	Groundwater-fed, minerotrophic wetlands that may be typically non-isolated but isolated forms exist	Southeast Alaska and northern regions of U.S.
Inactive floodplain wetlands	Depressional and flat wetlands on alluvial soils now cut off from river flooding by natural processes (shift in river course) or by human actions (e.g., levee construction, river diversions, and dams)	Throughout U.S.
Natural ponds	Naturally-formed ponds lacking surface water outflow, typically dependent on precipitation or snow melt	Throughout U.S.
Tarn wetlands*	Montane wetlands associated with small lakes and ponds formed in glacial cirques	Mountains in recently glaciated regions
Volcanic-formed wetlands*	Wetlands formed in volcanic craters or in waterbodies created by volcanic activity	Hawaii, Pacific Northwest, Alaska, and Arizona
Excavated ponds	Ponds constructed by digging a depression that intersects water table	Throughout U.S.

Direct precipitation and runoff are major sources of water for pothole wetlands (Berkas 1996). Prairie potholes serve as both recharge and discharge areas, contributing to both local ground-water flow and regional flow (Lissey 1971). Water is recharged at topographic highs (wetlands at higher elevations) and discharged to regional lows (e.g., lakes and other wetlands) and eventually to local rivers and streams (Winter 1989;

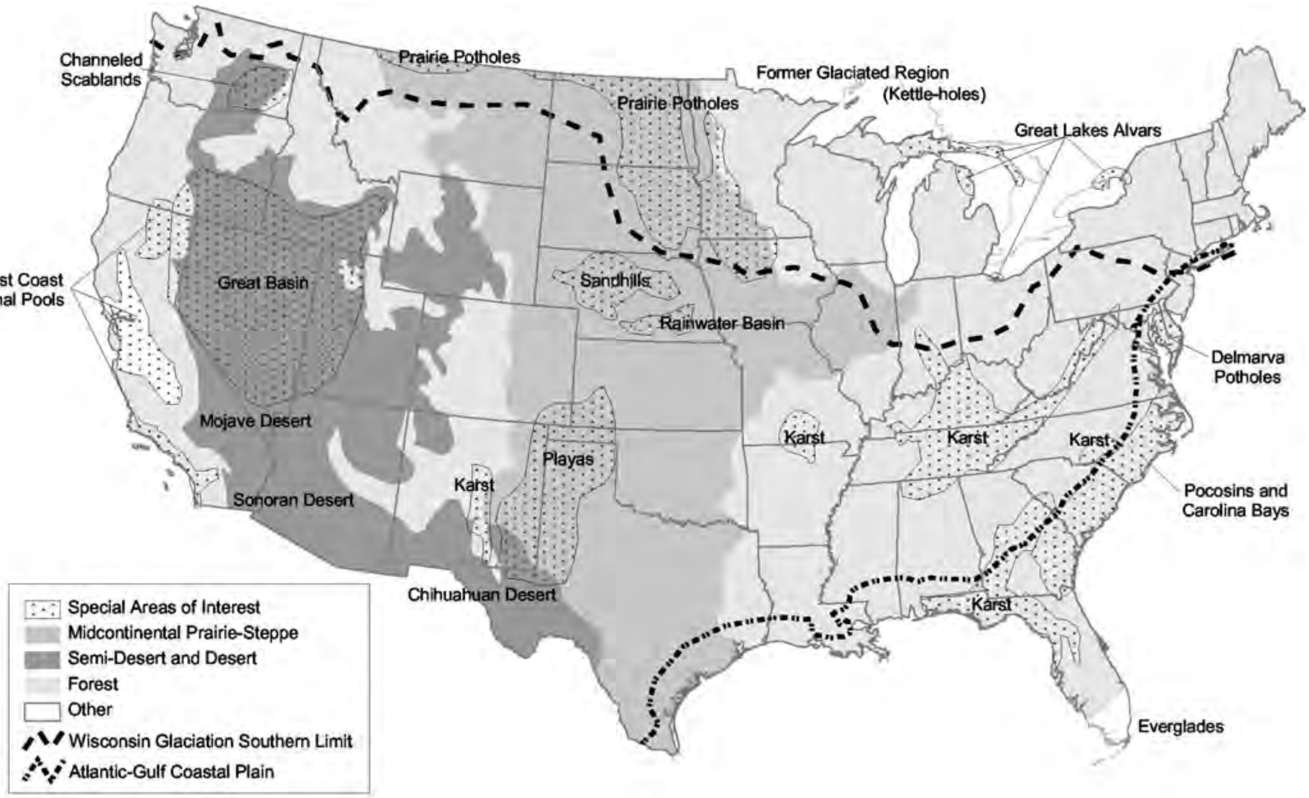


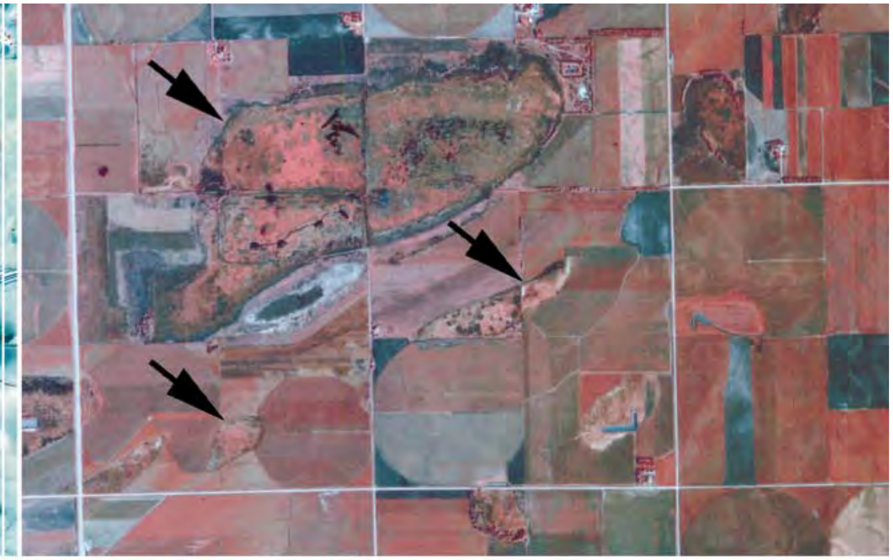
Figure 3. Map showing generalized regions where certain types of geographically isolated wetlands may be common.

Figure 2). Seasonal changes in functions may occur, with some wetlands contributing to ground water during high water periods (recharge in the spring) and receiving ground-water inputs during the dry season (late summer) due to high rates of evapotranspiration (Sando 1996).

The millions of ''isolated'' basins in this region provide considerable surface-water storage capacity and support wetland plant communities important to wildlife (Hubbard 1988). Pothole wetlands in North Dakota's Devils Lake Basin can store as much as 72% of the total runoff from a two-year frequency storm and about 41% from a 100-year storm (Ludden et al. 1983). Such storage controls seasonal flooding, thereby protecting cropland and rural communities from damaging floods (Kendy 1996). Although it represents only 10% of the continent's waterfowl breeding area, the Prairie Pothole Region of the U.S. and Canada produces half of North America's waterfowl in an average year (Smith et al. 1964). Successful breeding requires availability of a variety of wetlands because no single wetland/basin provides for all their reproductive needs through the breeding season (Swanson and Duebbert 1989). The existence of large numbers of small wetlands allows the birds to disperse across the landscape, thereby lowering their vulnerability to predation and diseases such as avian cholera, and increasing the likelihood for successful reproduction and brood-rearing (Kantrud et al. 1989).

About half of the original potholes in the Dakotas have been destroyed (60% in North Dakota and 40% in South Dakota; Tiner 1984), mostly by agriculture (Berkas 1996, Sando 1996). More than 99% of Iowa's original marshes have been lost, while 3.6 million hectares of potholes in western Minnesota have been drained. Destruction of pothole wetlands and alteration of natural vegetation buffers around remaining wetlands have significantly reduced valuable waterfowl nesting and rearing areas. Pothole drainage eliminates or severely reduces their surface-water storage function and makes potholes and their local watersheds contributing sources of potential floodwaters. Such water may also bring contaminants such as nutrients, herbicides, and pesticides into receiving watersheds.

Playas. Playas are nearly circular, shallow, nearly flat-bottomed, basin wetlands formed in deserts and semi-arid prairies (Plate 1). The original depressions were most likely created by aeolian processes. Over time, they have expanded through the dissolution of calcic soil and calcretes from water collecting in these depressions or by a combination of factors, including depositional, pedogenic, geomorphic (e.g., aeolian), and hydrologic processes (Kolm 1982, Haukos and



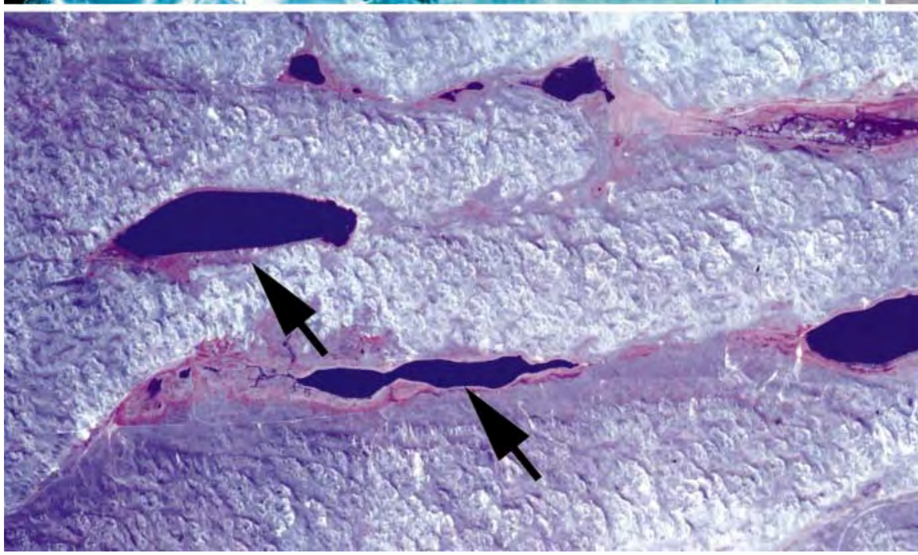


Plate 1. (Upper left) Aerial view of playas in west Texas.
Plate 2. (Upper right) Aerial view of Rainwater Basin wetlands. Note the circular pattern of central-pivot irrigation systems.
Plate 3. (Lower left) Aerial view of wetlands and lakes in the Nebraska Sandhills.
Plate 4. (Lower right) Salt flat wetland in the arid Southwest. (U.S. Fish & Wildlife Service photo)

Smith 1994, 1997). Playas represent the lowest points on the landscape in closed watersheds.

While present in the driest parts of most western states, the majority of playas occur in the Playa Lakes Region (Fretwell et al. 1996, Haukos and Smith 1997). The greatest density of playas is found in the Southern High Plains (SHP) (Haukos and Smith 1994), where nearly 22,000 basins occur (19,340 in Texas and 2,460 in New Mexico; Guthery and Bryant 1982).

Most playas derive water from rainfall and local runoff (including irrigation water), while very few receive ground-water inputs (Haukos and Smith 1994). Precipitation (350–630 mm, average annual) comes via localized thunderstorms from May through September (Bolen et al. 1989). Playas collect runoff from about 90% of the SHP and are particularly important as catchments for stormwater in developed areas (Haukos and Smith 1997). Playas are usually dry in late winter, early spring, and late summer. Multiple wet-dry cycles during a single growing season are common; these fluctuations promote nutrient cycling, biological productivity, and a dynamic plant community (Bolen et al. 1989, David Haukos, pers. comm. 2002). Playas vary from fresh to saline depending on hydrology and soils (Ogle 1996). The outer edges of playas are significant recharge sites that help maintain the Ogallala aquifer (Haukos and Smith 1997).

Playas are one of the few remaining native habitats in the SHP and may be the most important for maintaining its biodiversity (Haukos and Smith 1994). These wetlands produce an abundance of aquatic invertebrates—a prime food source for migrating shorebirds and waterfowl. Playas are vital wintering grounds for more than 90% of the region's waterfowl; over 90% of the midcontinent's population of sandhill cranes (*Grus canadensis* L.) frequent larger playas and salt lakes in the SHP (U.S Fish and Wildlife Service 1981, Nelson et al. 1983, Iverson et al. 1985). Playas are also essential habitats for several species of frogs and toads, the tiger salamander (*Ambystoma tigrinum* Green), and many other animals (Haukos and Smith 1994, Anderson and Haukos 1997, Anderson et al. 1999).

Many playas are cultivated or grazed by livestock, while others have been excavated to create pits for farm irrigation systems (Haukos and Smith 1994). Impacts to the remaining playas are mostly related to water pollution from runoff from cropland (pesticides and herbicides), oil fields (contaminated water), and cattle feedlots (Haukos and Smith 1994). The second source has led to widespread bird mortality, with the effects on invertebrates and other wildlife being unknown. Sedimentation of playas from adjacent farmland may be another major threat (Haukos and Smith 1994).

Rainwater Basin Wetlands. Aeolian forces created depressional wetlands in the Rainwater Basin, a nearly flat to gently rolling silty loess plain in south-central Nebraska (Plate 2). The climate ranges from semi-arid to subhumid, with average annual precipitation varying from less than 500 mm to over 800 mm (Frankforter 1996). These wetlands depend on precipitation and overland runoff for their water supply (Starks 1984, Gilbert 1989, Gersib 1991). Surface-water drainage is poorly developed, so closed basins with internal drainage predominate (Frankforter 1996). Water is primarily lost through evapotranspiration, and clay limits seepage to underlying water tables (Frankforter 1996).

Rainwater Basin wetlands have been designated as wetlands of international importance to migratory waterfowl and waterfowl habitat of major concern in North America (Gersib 1991, Gersib et al. 1992). Millions of waterfowl use these wetlands during spring migration, including 90% of the mid-continental population of white-fronted geese (*Anser albifrons* Scopoli), 50% of the continental breeding population of mallards (*Anas platyrhynchos* L.), and 30% of the continental breeding population of northern pintail (*A. acuta* L.) (Gersib et al. 1992). An abundance of fish and aquatic invertebrates produced in these wetlands provides critical food for migrating waterfowl in spring (Gersib et al. 1990). All or most Rainwater Basin wetlands have a high probability of providing wildlife habitat, food-web support, nutrient retention, flood storage, sediment trapping, and shoreline anchoring (Gersib et al. 1989).

Approximately 4,000 wetlands covering 38,000 ha originally existed in the Rainwater Basin (Gersib et al. 1992). By 1983, fewer than 10% of these wetlands and 22% of the area remained, for a 78% reduction in extent. Current estimates differ slightly, with about 13,800 ha of wetlands reported, which translates into a 66% loss of area (LaGrange 2001). Ninety percent of these wetlands are believed to be geographically isolated. Almost all of them have either been reduced in size or hydrologically altered. Agricultural activities such as drainage, clearing, and ground-water pumping have been the major causes of wetland loss and degradation. County road ditches have facilitated wetland drainage by providing outlets and are partly responsible for 50% of the area's wetland losses. Concentration pits, ditches to pits, wetland filling for pit construction, and land leveling account for the remaining losses (Gersib et al. 1992).

Losses of these wetlands have significantly reduced important wildlife habitat, especially waterfowl breeding and migration habitat. Waterfowl have been forced to concentrate in remaining wetlands, especially in dry years with late winter storms. Such overcrowding increases the likelihood for spread of diseases. In 1980,

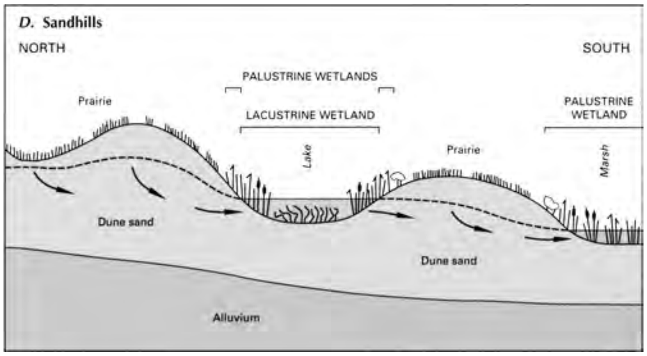


Figure 4. Generalized flow of water between Sandhills wetlands (Frankforter 1996). Note subsurface flow in north to south direction.

avian cholera killed about 80,000 waterfowl in the Basin; this was the second largest cholera die-off in the country. Cholera outbreaks have killed over 200,000 waterfowl since 1975 (Farrar 1982, Gersib et al. 1992).

Sandhills Wetlands. The Sandhills region of north-central and northwestern Nebraska is the largest sand dune ecosystem in the Western Hemisphere, covering about 52,000 km^2 (Bleed and Flowerday 1990). The climate is semi-arid, with less than 400 mm of annual average precipitation (Frankforter 1996). Aeolian forces have shaped and continue to shape this sandy landscape, while prairie grasses have stabilized the dunes. Marshes and wet meadows have formed in wind-swept depressions that include ponds and lakes (Plate 3; Frankforter 1996). The Ogallala aquifer supports most wetlands in the region through ground-water discharge, especially in the eastern Sandhills (Chuck Elliott, pers. comm. 2001).

Lakes and marshes in the central and eastern Sandhills are hydrologically connected by ground water and often have surface outlets (Ginsberg 1985, Novacek 1989). Most of the lakes are small, shallow waterbodies (4 ha or less in size and less than 2 m deep; Frankforter 1996). Wetlands in the western Sandhills have little or no surface outflow, yet most are interconnected with the regional ground-water network (Figure 4; LaBaugh 1986, Winter 1986, Frankforter 1996). About 60% of an estimated 529,000 ha of wetlands in the Sandhills may be geographically isolated (LaGrange 2001).

Sandhills wetlands have been identified as wetlands of international importance to wildlife. They provide spring staging areas, breeding areas, migration and wintering habitat for endangered species and for millions of migratory waterfowl in the Central Flyway (Elliott 1991, Gersib 1991). Wetlands are also an important water source for irrigation and livestock.

Threats to Sandhills wetlands are mostly due to agriculture, since the economy of this grassland region is primarily cattle grazing. Ditching of wet meadows has created large expanses of subirrigated meadows (with water tables near the surface) for cattle grazing and hay production. Wetland loss is mainly attributed to altered hydrology from center-pivot irrigation operations (i.e., mining ground water) and drainage. Land-leveling and filling are other significant causes of wetland loss. These combined activities are largely responsible for more than 30% of the loss of original Sandhills wetlands (Erickson and Leslie 1987).

Semi-Desert and Desert Wetlands

These wetlands occur in the driest areas of the country—in the Great Basin (e.g., Nevada and Utah), in the intermountain semi-desert (e.g., eastern Washington and Oregon, southern Idaho, and parts of Wyoming), and in the southwestern desert (e.g., Arizona, southern Nevada, and southern California) (Figure 3). Annual precipitation ranges from 130 mm to 490 mm or more at higher elevations, and long-term droughts impact this region (U.S. Geological Survey 1970, Bailey 1995). Geographically isolated wetlands vary from broad salt flats and extensive wetlands fringing salt lakes to small desert springs. Four types are briefly discussed: 1) salt lake wetlands, 2) salt flat wetlands, 3) channeled scablands, and 4) desert springs. Playas also occur in these desert landscapes.

Salt Lake and Salt Flat Wetlands. Terminal basins at the end of drainage systems in the Great Basin (a landlocked or closed system) are represented by salt lakes and salt flat wetlands that may be considered geographically isolated waters and wetlands. During the Pleistocene Epoch (1.8 million to 11,000 years before present), much of the Great Basin was inundated by two large lakes (Lake Bonneville and Lake Lahontan) and many smaller ones. About 10,000 to 20,000 years ago, the larger lakes were connected by rivers. Streams draining the Death Valley region (southeastern California) may have flowed into the Colorado River, as their fishes are related (Soltz and Naiman 1978). Today's salt flats, playas, and lakes are vestiges of these waterbodies.

Lying in the rain shadow of the Sierra Nevada Mountains, the Great Basin receives less than 100 mm mean annual precipitation in the lower elevations, with higher elevations receiving more than 760 mm (Minshall et al. 1989). Precipitation amounts and distribution vary greatly from year to year. In the northern part of the region, precipitation equals or exceeds evapotranspiration, while in the southeast, evapotranspiration significantly exceeds precipitation. Consequently, permanent lakes (e.g., the Great Salt Lake) form at the end of river systems in the north but not in the south where salt flats occupy the terminal basins. These salt flats contain water for short periods in winter and spring and become dry plains in summer (Plate 4).

In an arid landscape, waterbodies and associated wetlands are vital habitats for resident and migratory wildlife. Salt lakes, shoreline wetlands, and salt flats yield a vast food supply that sustains wildlife. This food is critical for birds migrating across arid lands as well as for nesting species. For example, the shallow-water wetlands of Mono Lake produce brine shrimp (*Artemia* spp.) and alkali or brine flies (*Ephydra riparia* Fallen). By feeding on Mono Lake's *Ephydra*, Wilson's phalaropes (*Phalaropus tricolor* Viellot) double their body weight before making their three-day, nonstop, 4,800-km flight to South America (www.monolake.org/naturalhistory/birds.htm). Likewise, 1.5 to 1.8 million eared grebe (*Podiceps nigricollis* Brehm) feed on *Artemia*, increasing their weight three-fold before migrating southward. From 44,000 to 65,000 California gulls (*Larus californicus* Lawrence) breed on an island in Mono Lake, while the nation's largest colony of American white pelicans (*Pelecanus erythrorhynchos* J.F. Gmelin) nests on an island in Pyramid Lake (Jehl 1994).

Most inland marshes are not threatened by development. Major impacts are from road and utility crossings. Salt flats in urbanizing areas are at greater risk due to encroachment from development and associated disruption of drainage patterns (Dennis Peters, pers. comm. 2001). Degradation of wet meadows may result from overgrazing. Ground-water withdrawal for irrigation has adversely affected the hydrology of some wetlands. River-water diversion for various purposes, including public water supply for Los Angeles, has negatively impacted riparian wetlands in the Great Basin (Minshall et al. 1989), although they may not be considered isolated wetlands by some definitions.

Channeled Scablands Wetlands. The rain shadow of the Cascade Mountains in eastern Washington produces a semi-desert environment that receives only 170 to 250 mm of rain annually (U.S. Fish and Wildlife Service 1998; Figure 3). Winters are cold and wet, while summers are hot and dry (Lane and Taylor 1996). About 12,000 to 15,000 years ago, the Spokane Floods, a post-glacial flood resulting from the collapse of glacial ice dams and the emptying of large glacial lakes in Montana, created channelized scablands and outwash lakes in this area. Today, only three creeks (Rock, Cow, and Crab Creeks) drain this region, which is pockmarked with isolated ponds, lakes, and cyclical wetlands (i.e., present during wet years and visually ''absent'' during drought years). Almost 85 percent of the wetlands in this area are isolated depressions (Lane and Taylor 1996). During high precipitation years, many geographically isolated wetlands and waterbodies are interconnected, creating large wetland-open water complexes (U.S. Fish and Wildlife Service 1998).

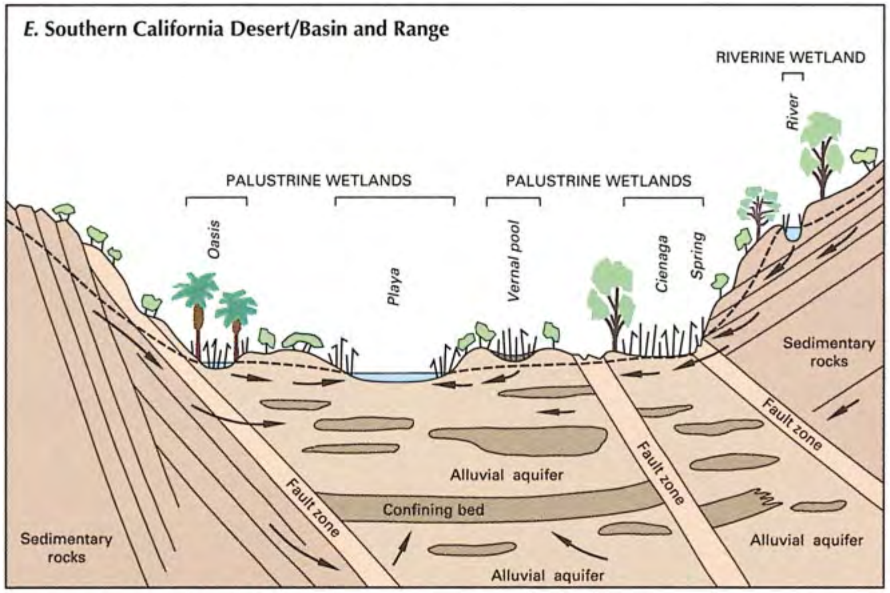
Marshes, wet meadows, playas, and ''West Coast'' vernal pools occur in this area. Crowe et al. (1994) described vegetation and soil characteristics of vernal pools in the Marcellus Shrub Steppe Natural Area Preserve. Some ponds contain the federally threatened water howellia (*Howellia aquatilis* Gray). Like other wetlands in arid to semi-arid regions, these wetlands are particularly valuable for waterfowl and other migratory birds, serving as staging areas during migration (early spring and fall) and breeding and brood-rearing habitat in summer. Nearly 100,000 individual waterfowl may breed in these wetlands (U.S. Fish and Wildlife Service 1998).

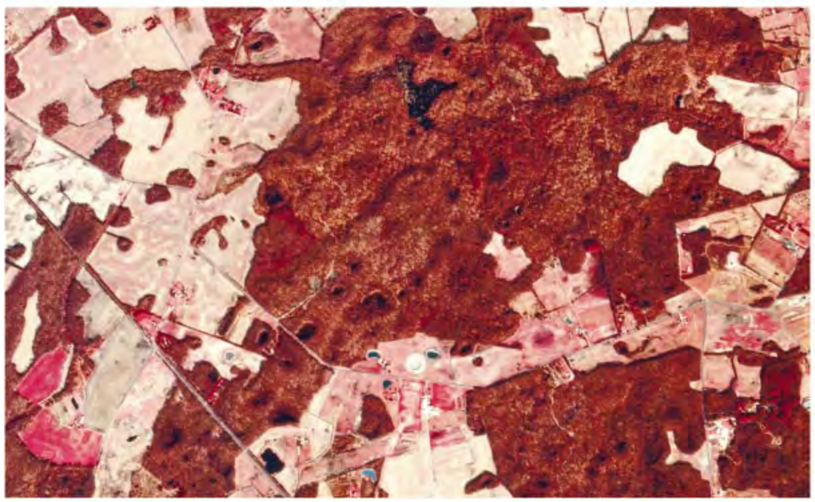
Since the major land use in this region is cattle ranching, the impacts from livestock may be significant. Cattle using ponds as wallows often interfere with waterfowl brood-rearing, while overgrazing of palustrine emergent wetlands also degrades wildlife habitat. Some large ponds have been drained and converted to hayfields and pasture. Introduction of carp (*Cyprinus carpio* L.), an invasive fish, has muddied many ponds and reduced their value to waterfowl. The growth of Spokane is expected to threaten these wetlands in the future (U.S. Fish and Wildlife Service 1998).

Desert Springs. Four deserts exist in North America: the Great Basin, the Mojave, the Sonoran, and the Chihuahuan (Figure 3). Annual precipitation averages less than 300 mm, with the Mojave having the least (<150 mm). The Great Basin desert receives most of its precipitation as winter snow and spring rain, while the Mojave and Sonoran deserts receive both winter and summer (monsoon) rainfall (National Park Service 2003). The Chihuahuan desert gets its precipitation mostly as summer rain.

Springs arise in the desert where ground water from large underground reserves discharges to the land surface through fractures in underlying rock strata (e.g., fault lines) or through porous materials (e.g., permeable carbonate rocks). These springs support small marshes (''cienagas''), oases (in California and Arizona), and extensive cattail and bulrush marshes (Plate 5; Bakker 1984, Minckley 1991, Bertoldi and Swain 1996). While some springs are isolated, others are headwaters of rivers like the Muddy River in Nevada. Some springs are hot (''thermal springs'') and support unusual microbial communities (Tracie Nadeau, pers. comm. 2002).

Isolation fosters endemism, and isolated waters in the desert provide unique habitats for the evolution of





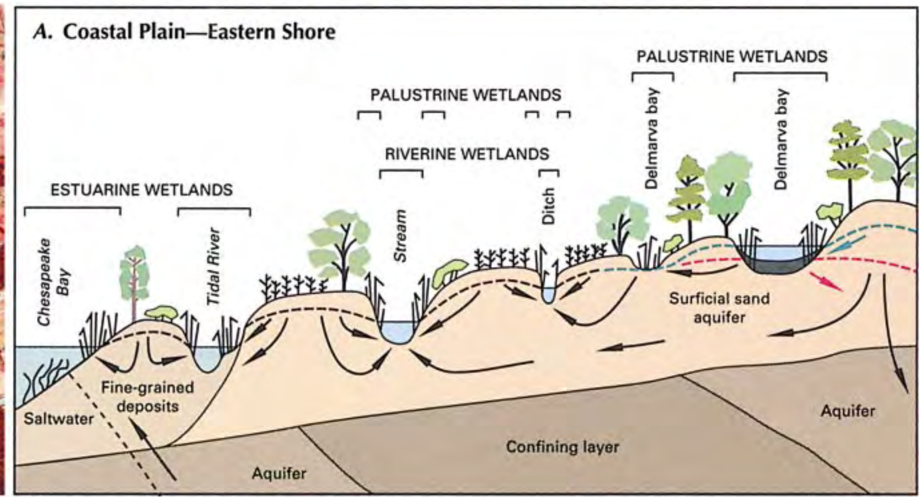


Plate 5. (Upper left) Generalized flow of water between different wetland types in southern California (Bertoldi and Swain 1996). The largest wetlands in this region are playas. Isolated marshes (cienagas) and oases are supported by springs and seeps.

Plate 6. (Upper right) Kettle-hole bog in New York. (R. Tiner photo)

Plate 7. (Lower left) Aerial view of Delmarva pothole wetlands in forested areas near the Maryland-Delaware border.

Plate 8. (Lower right) Generalized subsurface flow of water on Coastal Plain showing hydrologic connections between Delmarva bays (potholes), other wetlands, streams, and estuaries (Hayes 1996). Blue dashed lines and arrows represent wet season water tables and direction of groundwater flow, whereas red dashed lines and arrows indicate dry season conditions and similar black symbols average conditions, except diagonal dashed black line on lower left which represents saltwater-freshwater interface.

aquatic organisms. In the late 1970s, there were more than 20 isolated pupfish (*Cyprinodon* spp.) populations in the Death Valley region (Soltz and Naiman 1978). These populations were isolated for 12,000 to 20,000 years and represent excellent examples of biological adaptation and speciation. Since then, some of the species have become extinct, including the Ash Meadow killifish (*Empetrichthys merriami* Gilbert) and Tecopa pupfish (*Cyprinodon nevadensis calidae* Miller), while others are endangered, such as Owens pupfish (*C. radiosus* Miller), Devils Hole pupfish (*C. diabolis* Wales), and Warm Springs pupfish (*C. nevadensis pectoralis* Miller) (Soltz and Naiman 1978; Sada 1990). Some desert springs and their adjacent wetlands provide habitats for other threatened and endangered species or species of concern including spring-loving centuary (*Centaurium namophilum* Reveal, Broome, & Beatley), Ash Meadows gumplant (*Grindelia fraxinopratensis* Reveal & Beatley), Ash Meadows montane vole (*Microtus montanus nevadensis* V. Bailey), Devils Hole warm springs riffle beetle (*Stenelmis calida calida* Chandler), and endemic springtails (Collembola, Family Entomobryidae).

Pumping of ground water for agriculture in California and urban and energy development in Nevada pose the most serious threats to these species and the desert spring wetlands. Withdrawals may lower water levels and expose areas used for pupfish spawning (Sada 1990). The Pahrump Ranch poolfish (*Empetrichthys latos latos* Miller) was extirpated from Manse Spring, Nevada when the spring dried up due to ground-water withdrawal (U.S. Fish and Wildlife Service 1993). Livestock may have localized effects on desert spring wetlands, while introduction of exotic fishes threatens native biota.

Kettle-Hole Wetlands

In the coterminous U.S., most of the recently glaciated areas (Figure 3) have a humid or temperate climate. Annual precipitation ranges from 510 mm to 1150 mm, with lower amounts in the Dakotas (Bailey 1995). Snowfall is significant, with more than 2550 mm in the Adirondack and New England mountains. The abundance of water in this region and glacial processes shaping the landscape created conditions favoring the formation of extensive wetlands. When the Wisconsin continental glacier retreated 10,000–15,000 years ago, it left behind ice blocks of variable sizes, creating many depressions on the North American landscape. When these ice blocks melted, kettle-hole lakes and ponds (including prairie potholes) were formed. They may be abundant on pitted outwash plains but also occur on other glacial deposits (e.g., moraines). Many of these wetlands have outlets and are sources of streams, but others are geographically isolated. The latter derive their water mainly from precipitation (Damman and French 1987).

Kettle-hole wetlands are common in parts of the northeastern and north-central U.S. and less common in the Pacific Northwest (Plate 6). Some kettles are ponds formed in sandy coastal areas on glacial outwash deposits (e.g., Long Island and Cape Cod on the Atlantic Coast and along the Great Lakes). In Alaska, isolated bogs are common in the Southeast, South-central, and Interior Regions (Hall et al. 1994).

Bogs in several northeastern states are at the southern limits for many boreal plants including hare's tail (*Eriophorum spissum* Fern.), dragon's mouth (*Arethusa bulbosa* L.), bog rosemary (*Andromeda polifolia* L. var. *glaucophylla* (Link) DC.), and labrador tea (*Ledum groenlandicum* Oeder) (Damman and French 1987). Kettle-hole bogs and similar mountain bogs (to the south) harboring these species are important sites for conserving biodiversity.

Threats to bogs include peat mining, drainage, and conversion to open waterbodies (e.g., recreational lakes). The quality of remaining kettle-hole bogs may be further jeopardized by development of adjacent uplands, as the introduction of nutrients from runoff could alter plant composition.

Atlantic-Gulf Coastal Plain Basin Wetlands

The Atlantic and Gulf Coastal Plain generally extends from Long Island, New York to Florida and west into Texas (Figure 3). With abundant rainfall (1020–1530 mm; Bailey 1995) and a relatively flat topography, extensive areas of imperfectly drained soils have developed, providing favorable places for wetland formation. A wide variety of wetlands occurs in this region, with mostly non-isolated types (e.g., flatwood wetlands, floodplain wetlands, and estuarine wetlands) predominating. Four wetland types may include geographically isolated wetlands: 1) Delmarva potholes, 2) Coastal Plain ponds, 3) Carolina bays, and 4) pocosins. The former three types are basin wetlands; the latter type is mainly represented by wetlands occupying broad flats adjacent to streamside wetlands, but it also includes some small isolated depressional wetlands. Other naturally-formed, geographically isolated wetlands occurring in this coastal region include cypress domes, sinkhole wetlands, interdunal swales (on barrier islands), gum swamps, and grady ponds.

Delmarva Potholes. In the center of the Delmarva Peninsula, thousands of depressional, pothole-like wetlands (''Delmarva bays'' or ''potholes'') cover broad flat interfluves (Plate 7). Their origins are unknown, but theories of their origin include artesian springs, meteorites, coastal processes (segmented lagoon closure), shallow waterbodies in dune fields or interfluves, periglacial frost basins, and fish spawning areas (Tiner and Burke 1995). While they may occur throughout the Peninsula, Delmarva potholes are most abundant in a 32-km swath along the Maryland-Delaware border from the headwaters of the Sassafras River to the Nanticoke River.

Vegetation is variable from open glades (e.g., sedge marshes, *Carex walteriana* Bailey) to buttonbush swamps (*Cephalanthus occidentalis* L.) to forested wetlands. Potholes are biologically diverse communities supporting 68 percent of the amphibians of the Delmarva Peninsula and 61 rare vascular plants, including the federally endangered Canby's dropwort (*Oxypolis canbyi* (Coult.& Rose) Fern.) (Sipple and Klockner 1984, Sipple 1999).

Given their abundance, Delmarva potholes aid in temporary storage of surface water and thereby help reduce local flooding. They alternately serve as ground-water discharge (wet season) and recharge (dry season) areas (Phillips and Shedlock 1993), with some recharge water eventually discharging into coastal plain streams and contributing to base flows vital for sustaining aquatic biota (Plate 8; Hayes 1996).

Threats to these wetlands are from drainage usually associated with agricultural or silvicultural operations. Some wetlands may be planned for development (e.g., houses and commercial facilities).

Coastal Plain Ponds. Isolated ponds have formed in depressions where ground water flows to the land surface and rain water collects (Wolfe et al. 1988, U.S. Fish and Wildlife Service 1997). In southern glacial areas (e.g., Long Island, New York), these ponds developed in kettle-holes or in shallow depressions on outwash plains.

Some coastal plain ponds are hydrologically linked by ground water, while others are connected by small streams (Reschke 1990). Water levels fluctuate seasonally and among years, producing significant changes in vegetation (U.S. Fish and Wildlife Service 1997). Periodic high water levels eliminate woody seedlings that may colonize these ponds during drawdowns. Although the species differ, vegetation patterns are similar to those of prairie pothole wetlands, with concentric bands of vegetation reflecting different water regimes.

The fluctuating water levels and isolated nature of coastal ponds have resulted in ponds hosting some unique species, making these wetlands important for conserving biodiversity. For example, four globally rare species occur in coastal plain ponds in the New York Bight region: quill-leaf arrowhead (*Sagittaria teres* S. Wats.), pine barren bellwort (*Uvularia puberula* var. *nitida* (Britt.) Fern.), rose tickseed (*Coreopsis rosea* Nutt.), and creeping St. John's-wort (*Hypericum adpressum* Raf. ex W. Bart.) (Zaremba and Lamont 1993, U.S. Fish and Wildlife Service 1997). Rare dragonflies, damselflies, butterflies, and moths may also be found in these wetlands, along with animal species of concern such as the Pine Barrens treefrog (*Hyla andersonii* Baird), Cope's gray treefrog (*H. chrysoscelis* Cope), eastern spadefoot (*Scaphiopus holbrookii holbrookii* Harlan), spotted salamander (*Ambystoma maculatum* Shaw), *A. tigrinum*, and spotted turtle (*Clemmys guttata* Schneider).

Periodic drawdown has eliminated fish from many ponds, thereby making them excellent breeding areas for amphibians. The regionally rare *A. tigrinum* is one of several species (including many vernal pool-breeding amphibians) using coastal ponds for reproduction (U.S. Fish and Wildlife Service 1997). Coastal ponds in Florida may contain fish, but they still serve as breeding grounds for the southern toad (*Bufo terrestris* Bonnaterre), southern leopard frog (*Rana utricularia* Harlan), and pig frog (*R. grylio* Stejneger) (Wolfe et al. 1988). Coastal ponds on barrier islands often provide the only source of freshwater for local wildlife and migratory birds.

Coastal development poses significant threats to these ponds. Waste dumping, all-terrain vehicle driving on pond shores, water withdrawals, and water pollution from adjacent development (e.g., lawn, agricultural field, and road runoff) may adversely affect coastal plain ponds (U.S. Fish and Wildlife Service 1997).

Carolina Bay Wetlands. Somewhat egg-shaped (elliptical) basins called ''Carolina bays'' have formed on the Atlantic Coastal Plain from southeastern Virginia to Florida. They are most abundant in mid-coastal South Carolina and southeastern North Carolina (Figure 3). Carolina bays vary greatly in size, ranging from less than 50 m long to more than 8 km in length (Sharitz and Gibbons 1982) and commonly have a northwest to southeast orientation, often with a conspicuous sandy rim (Plate 9). According to Sharitz and Gresham (1998), most of the bays are hydrologically isolated, nutrient-poor (oligotrophic) ponds or ''naturally isolated habitats'' that derive water mainly from rainfall. They are depressional wetlands often surrounded by flatwood wetlands and upland forests in undisturbed areas or by farmland and urban land in developed areas. Some bays may merge with wet flatwoods that drain into coastal streams and rivers. Carolina bays include wet meadows, forested wetlands, shrub swamps, and seasonal ponds (e.g., vernal pools). Cypress savannas containing many rare species occur in some Carolina bays (Sharitz and Gresham 1998).

Carolina bays are valuable amphibian habitats.

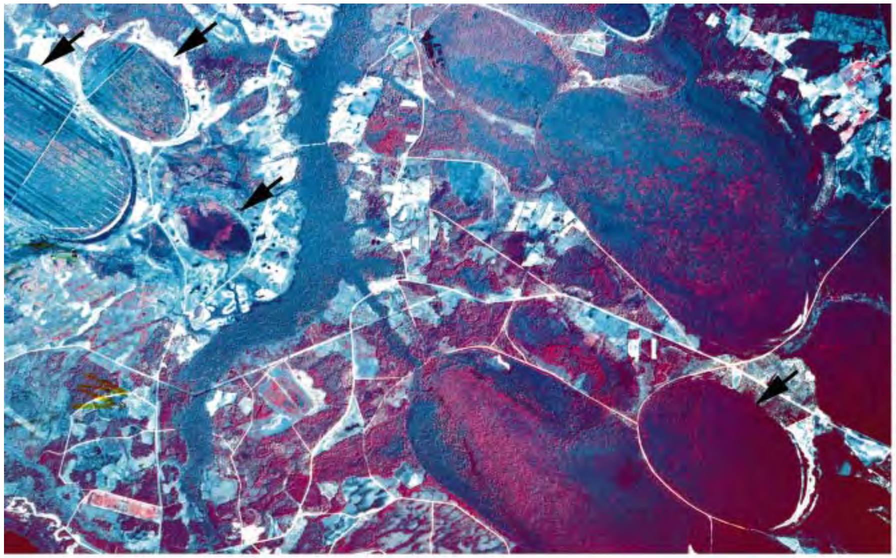
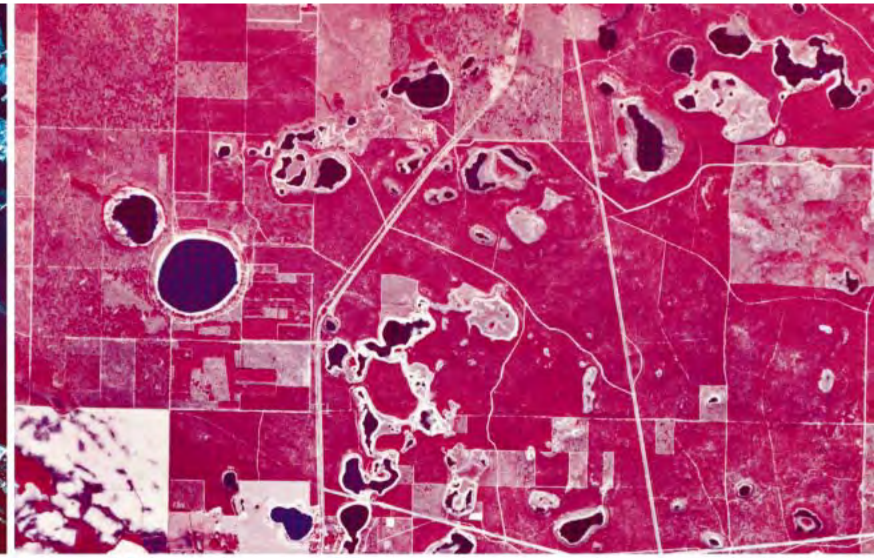



Plate 9. (Upper left) Aerial view of Carolina bay wetlands in Bladen County, North Carolina.
Plate 10. (Upper right) Aerial view of geographically isolated karst lakes and wetlands in northern Florida.
Plate 11. (Lower left) Vernal pool in the Jepson Prairie (near Sacramento, California) during the wet phase. (R. Tiner photo)
Plate 12. (Lower right) Seepage slope wetland in Alaska. (J. Hall photo)

Thousands of amphibians were counted in a 1-ha Carolina bay at the Savannah River Site (South Carolina) in 1979 (Sharitz and Gibbons 1982). Over a two-year period, researchers captured more than 72,000 amphibians, including nine species of salamanders and 16 species of frogs (Gibbons and Semlitsch 1981).

Many Carolina bay wetlands have been drained for crop production, mainly for corn and soybeans (Sharitz and Gresham 1998). In South Carolina, 71% of the Carolina bays greater than 0.8 ha have been altered by agriculture, while about one-third of the original wetlands have been disturbed by timber harvest (Bennett and Nelson 1991).

Pocosins. Pocosins are southern peatlands (with organic soils) generally located on interfluves along the Atlantic Coastal Plain from southern Virginia to Florida. They are most abundant in North Carolina, where about 70% of the nation's pocosin wetlands are located (Richardson et al. 1981). Many pocosins receive all or most of their water from precipitation (Sharitz and Gresham 1998). Their vegetation consists of a mixture of evergreen trees (e.g., pines and bays) and broad-leaved evergreen shrubs (Kologiski 1977, Richardson et al. 1981). Weakley and Schafale (1991) identified at least one isolated type (''small depression pocosin'') in their classification of pocosins. Other potentially isolated pocosins may occur in swales (e.g., in the Sandhills of the Carolinas) and in seasonally saturated interfluves. Most pocosins, however, have seasonal connections to drainageways leading to estuaries or are contiguous with other wetlands draining into perennial rivers and streams or estuaries.

Pocosins temporarily hold water and then slowly release it to adjacent wetlands. Given their proximity to estuaries, this function is especially important because it gives estuaries time to assimilate the freshwater runoff without rapid and drastic fluctuations in water quality (Daniel 1981). When pocosins are artificially drained into coastal streams, the value of this buffering capacity is lost, as ditched pocosins contribute more and possibly enriched water to streamflow. Landscape-level ditching of pocosins can produce significant detrimental effects on the quality of coastal waters. Pocosins also provide wildlife habitat for many animals, including rare species such as Hessel's hairstreak butterfly (*Callophrys hesseli* Rawson & Ziegler) and *Hyla andersonii* (Sharitz and Gresham 1998).

Forestry and agriculture have had major impacts on pocosins. About one million hectares of pocosins once existed in North Carolina; by the 1980s, roughly 405,000 ha remained in natural condition (Richardson et al. 1981). Since drainage increases timber productivity, some pocosins that were geographically isolated have been ditched and are now contributing sources for streamflow. Many former pocosins are cropped for soybeans and corn, but cultivation of remaining pocosins may have decreased recently due to removal of farm subsidies (Sharitz and Gresham 1998). Agricultural conversion of pocosins has 1) lowered salinity in adjacent estuaries, particularly during heavy rainfall periods due to introduction of more fresh water from cropland drainage, 2) increased peak flow rates (up to 3 or 4 times that of undrained areas) and decreased flow durations, 3) increased turbidity (ditches had 4 to 40 times greater turbidity than natural streams in pocosin areas), and 4) increased concentration of phosphate, nitrate, and ammonia in streams and adjacent estuaries (Sharitz and Gresham 1998). Drainage of pocosins and decreased salinity in estuaries may be having a negative impact on North Carolina's brown shrimp (Street and McClees 1981).

Karst Basin Wetlands

Karst landscapes are characterized by sinkholes, caves, losing streams (e.g., streams that disappear underground), springs, deep hollows, rolling hills, and valleys. Approximately 20% of the U.S. land surface is represented by karst terrain (www.virginiacaves.org; Figure 3).

Dissolution of underlying limestone (calcium carbonate) or dolomite (magnesium calcium carbonate) causes a slumping of the land surface, thereby creating distinct basins. Isolated sinkhole depressional wetlands are common features in karst landscapes. Two types of karst basin wetlands are highlighted: 1) cypress domes and 2) sinkhole wetlands.

Cypress Domes. Cypress swamps found in nearly circular isolated depressions are called ''cypress domes'' due to the dome-like appearance of the tree canopy (i.e., trees are much taller in the center of the pond than along its edges). These swamps are widespread in Florida's karst landscape and often form part of an ecological mosaic with extensive wet and dry pine flatwoods. Most cypress domes are less than 10 ha in size (Ewel 1998). Pond cypress (*Taxodium ascendens* Brongn.) and swamp black gum (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) predominate, with slash pine (*Pinus elliottii* Engelm.) co-dominant in partly drained cypress domes of north-central Florida (Mitsch and Ewel 1979, Mitsch and Gosselink 2000).

Cypress domes receive water from precipitation, ground-water flow, and sometimes runoff. Most of the water in South Florida arrives with summer rains, whereas winter and summer rains bring water to swamps in north Florida and southern Georgia (Ewel 1998).

These wetlands are important for maintaining re-

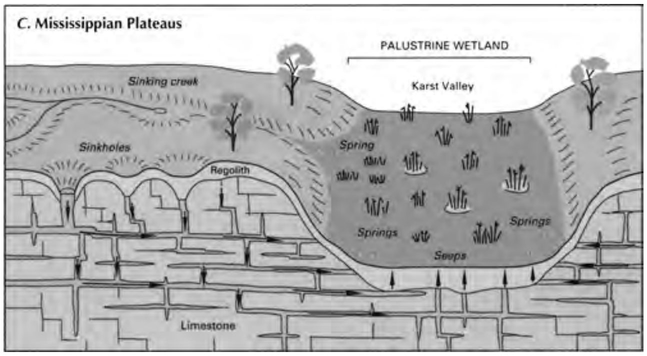


Figure 5. Generalized water flow patterns between wetlands in a karst region (Haag and Taylor 1996). Note: Stream entering a sinkhole (''sinking creek'') and flow of surface water to groundwater with later discharge as seeps in karst valley. Tadpole-like features represent springs.

gional biodiversity, since many domes are significant amphibian-breeding areas. Species such as the carpenter frog (*Rana virgatipes* Cope) reproduce in these isolated swamps (Ewel 1990). Also, since they hold water for long periods, cypress domes help prevent flooding of local areas and aid in ground-water recharge.

Virtually all cypress ponds in north Florida have been harvested, and in many, the trees have regenerated (Ewel 1990). While timber management has been performed in cypress dome-pine flatwood ecosystems for hundreds of years, the most detrimental human impact on these ecosystems is caused by development (e.g., conversion of natural habitat to residential subdivisions, commercial sites, and golf courses). Drainage of cypress domes causes oxidation of histosols, land subsidence, and an increase in fire susceptibility; such drainage could also lead to more local flooding (Ewel 1998).

Other Sinkhole Wetlands. Some of these wetlands receive ground-water discharge from underlying limestone deposits (e.g., in karst valleys), while others simply occur in basins formed by the dissolution of underlying limestone (Figure 5). Karst lakes and their marginal wetlands may be isolated features on this type of landscape. Many areas in Florida are pockmarked with isolated depressional wetlands and lakes due to the abundance of limestone on the peninsula (Plate 10). Some lakes drain into streams connecting to larger ones flowing to the sea, while others do not.

The vegetation of sinkhole wetlands varies geographically and in response to different hydrologies and other factors. Their plant communities may be diverse and contain regionally and nationally rare species. In western Maryland, Bartgis (1992) found 56 species in sinkhole ponds, including the federally endangered northeastern (barbed bristle) bulrush (*Scirpus ancistrochaetus* Schuyler). Lentz and Dunson (1999) reported this species in ''geographically isolated'' ponds in central Pennsylvania, while Terwilliger and Tate (1995) listed it and Virginia sneezeweed (*Helenium virginicum* Blake), a federally threatened species, as unique flora in sinkhole ponds of Virginia's Upper Shenandoah Valley. State rare, threatened, or endangered plants occurring in sinkhole ponds include smooth-barked St. John's-wort (*Hypericum lissophloeus* P. Adams, endangered Florida), karst pond xyris (*Xyris longisepala* Kral, endangered Florida), cypress-knee sedge (*Carex decomposita* Muhl., threatened Indiana), sharp-scaled manna-grass (*Glyceria acutiflora* Torr., endangered Indiana), roundleaf water hyssop (*Bacopa rotundifolia* (Michx.) Wettst., endangered Indiana), Hall's bulrush (*Schoenoplectus hallii* (Gray) S.G. Sm., species of concern Missouri), and dwarf burrhead (*Echinodorus tenellus* (Mart.) Buch., species of concern Missouri) (Wolfe et al. 1988, Indiana Department of Environmental Management 2000, Smith 2000).

Sinkhole ponds may be productive amphibian breeding grounds and feeding places for reptiles and other animals, and they may serve as keystone habitats in various locales (Mitchell and Buhlmann 1999 and other papers in *Banisteria* Vol. 13). More than 1500 adult amphibians were observed in a 0.2 ha Alabama pond: 527 mole salamanders (*Ambystoma talpoideum* Holbrook), 127 *A. tigrinum*, 269 gopher frogs (*Rana capito* LeConte), 241 *Rana utricularia*, and 191 ornate chorus frogs (*Pseudacris ornata* Holbrook) (Bailey 1999).

A rich cadre of organisms live in underground caves associated with karstlands. Specially adapted, aquatic cave animals (troglobites), such as Georgia blind salamanders (*Haideotriton wallacei* Carr), cave crayfishes (*Procambarus* spp.), cave shrimp (*Palaeomonetes cummingi* Chase), cave isopods (*Caecidotea* spp.), and cave amphipods (*Crangonyx* spp.), live in the subterranean pools and streams (Wisenbacker 2002). These aquatic communities are extremely sensitive to small changes in their environment (Loftus et al. 2001).

The intricate underground network of fissures and subterranean streams moves water rapidly through the system. Surface water entering the system can therefore quickly impact ground-water quality. Changes in landscape and ground-water supplies can induce sinkhole formation with negative impacts on the hydrology of wetlands and waterbodies (Tihansky and Knochenmus 2001). Threats to sinkhole wetlands and their biota include 1) water pollution from lawns, agricultural fields, and road runoff or from direct discharge of wastes (e.g., garbage), 2) ground-water withdrawals with effects such as lake drainage and drying up of springs, 3) timber harvest (terrestrial habitat for pond-breeding amphibians), 4) fish stocking of sinkhole ponds, and 5) filling from agricultural and residential development (Wolfe et al. 1988, Buhlmann et al. 1999).

Vernal Pool Wetlands

While most wetlands experience alternating wet and dry periods, vernal pools are particularly outstanding examples of extreme fluctuations in site wetness. Typically, they are seasonal or ephemeral natural ponds surrounded by grasslands, thickets, or forests. During the wet season, they are shallow ponds that later become exposed basins during dry periods. Depending on climate, geology, hydrology, and other factors, vernal pools may be dominated by woody species (trees and shrubs), by marsh and wet meadow species, by aquatic species, or they may be devoid of vegetation. Changes in vegetation patterns may occur and some vernal pools may even be colonized by nonhydrophytic species during prolonged droughts, especially in semi-arid regions.

The variety of vernal pool wetlands is considerable across the country, as they have formed in humid as well as arid climates. There is no single reference describing this variability. Two types of vernal pools have received considerable attention and are highlighted in this paper: 1) West Coast vernal pools and 2) woodland vernal pools. Note that some of the wetland types described earlier also include wetlands that may be classified as vernal pools (e.g., Carolina bays, Delmarva potholes, and Channeled Scablands wetlands).

West Coast Vernal Pools. West Coast vernal pools have formed in mound and swale topography and are found mostly in parts of the California steppe (Central Valley), coastal terraces and level terraces of California's coastal mountains (Zedler 1987), and semi-desert regions of eastern Oregon and Washington (Figure 3). They are cyclical wetlands with a marked seasonal shift in herbaceous cover from hydrophytic species to drier-site species (Jain 1976, Zedler 1987, Ikeda and Schlising 1990, Witham et al. 1998, Tiner 1999). Their vegetation may change drastically within and between years in response to changing environmental conditions (e.g., precipitation patterns).

Many vernal pools and associated seasonally flooded wetlands form a complex of depressional wetland and mound-swale features that are hydrologically linked during wet periods. The depressions and swales are typically filled by winter rains characteristic of the region's Mediterranean climate and may be flooded for weeks or months in some years (Baskin 1994; Plate 11). They reach their greatest size in extremely wet years when individual depressions coalesce to form enormous inundated complexes that may drain into intermittent streams, ditches, or perennial streams (Zedler 1987).

The isolated nature and unpredictable flooding of these wetlands promote endemism, thereby creating unique flora and fauna and making West Coast vernal pools vital sites for the conservation of biodiversity. In California alone, 17 distinct vernal pool regions are recognized (http://ceres.ca.gov/wetlands/geo_info/vernal_pools_map.html). Numerous federally listed threatened and endangered species, as well as state-endangered and rare species, are among the characteristic flora. Federally endangered species include San Diego mesa mint (*Pogogyne abramsii* J.T. Howell), Otay mesa mint (*P. nudiuscula* Gray), several species of Orcutt grasses (*Orcuttia* spp.), Solano grass (*Tuctoria mucronata* (Crampton) J. Reeder), San Diego button-celery (*Eryngium aristulatum* var. *parishii* (Coult. & Rose) Beauchamp), and Burke's goldfields (*Lasthenia burkei* (Greene) Greene). These plants are amphibious species that are found in both the aquatic phase and the drying phase of vernal pool ecosystem development (Zedler 1987). Vernal pools also support endangered and rare invertebrates such as the delta green ground beetle (*Elaphrus viridis* Horn) (Morris 1988).

In the past, vernal pool areas were used for grazing and agriculture. Grazing may have relatively little adverse effect on these ecosystems, in contrast to the destruction of vernal pools caused by tillage and plantings (Zedler 1987). More recently, population growth in California and corresponding urbanization have greatly reduced the extent of these ecosystems, while agriculture continues to play a major role in their demise (Keeler-Wolf et al. 1998). Many of these ecosystems have been destroyed, with the largest remaining complexes often found in the open lands associated with military airports and facilities (e.g., Miramar Naval Air Station and Camp Pendleton). Wilson (1992) listed southern California as one of 18 global hotspots for conservation concern due in part to the existence of and threat to vernal pools.

Woodland Vernal Pools. Virtually every forested region in the United States possesses examples of woodland vernal pools (Figure 3). Such pools may be associated with other wetland types discussed earlier (e.g., Carolina bays, sinkhole wetlands, and Delmarva potholes). The following discussion focuses on these wetlands in the northeastern United States, but the same principles apply to all woodland vernal pools (re: their significance to amphibians), although characteristic species will vary regionally.

Woodland vernal pools are often seasonal ponds that are inundated during the wet season, usually from late fall to mid- or late-summer in the Northeast (Figure 6).

Figure 6. Woodland vernal pool in eastern Massachusetts during wet season. (R. Tiner photo)

They may be surrounded by upland or part of a forested wetland. Pools range in size from a hundred square meters or less to a few hectares. Vernal pools may dry out every year or less often, thereby precluding the establishment of fish populations and making these pools extremely productive sites for amphibian reproduction. Species dependent on vernal pools for breeding in New England include marbled salamander (*Ambystoma opacum* Gravenhorst), spotted salamander (*A. maculatum* Shaw), Jefferson salamander (*A. jeffersonianum* Green), blue-spotted salamander (*A. laterale* Hallowell), wood frog (*Rana sylvatica* LeConte), and gray treefrog (*Hyla versicolor* LeConte). The abundance of vernal pools in an area serves as ''stepping stones'' to aid in amphibian dispersal and recolonization of suitable habitats (Gibbs 1993, Semlitsch and Bodie 1998, Semlitsch 2000). Turtles such as *Clemmys guttata* frequent vernal pools after winter hibernation to obtain an easy source of food (amphibian eggs and aquatic invertebrates) (Kenney and Burne 2000).

While the vernal pool breeders require such habitats for reproduction and growth of larvae, the juveniles and adults of salamanders spend the rest of their lives in the surrounding woodland as burrowing vertebrates, whereas frogs (e.g., *R. sylvatica* and *H. versicolor*) also live in the forests and burrow for hibernation. This makes vernal pools plus the surrounding forest critical habitats for amphibian survival and important for the conservation of biodiversity (Kenney and Burne 2000). Each pool is often used by multiple species for breeding (e.g., *A. opacum* in fall, *A. maculatum* and *R. sylvatica* in early spring, followed by spring peepers *Hyla crucifer* Wied-Neuwied and *H. versicolor*). Thousands of individuals may use a single pool (Tiner 1998).

Small vernal pools surrounded by upland are often destroyed by development (e.g., construction of houses, shopping malls, and commercial facilities), while pools located along roads may be used as stormwater detention basins. Others receive drainage from agricultural fields or residential areas that degrade their water quality. Mosquito-control spraying of pools, drainage, and development of contiguous upland habitat also threaten vernal pool wildlife. Ground-water withdrawals for private and public wells may draw-down vernal pool waters prematurely and prevent complete development of amphibian larvae (Kenney and Burne 2000).

Coastal Zone Interdunal and Intradunal Wetlands

Sandy beaches and dunes have formed along much of the U.S. coastline, including parts of the Great Lakes. A long history of water-level changes has created a rolling terrain of ridges and relatively narrow interdunal swales (Thompson 1992, Thompson and Baedke 1995). In some cases, aeolian processes have formed intradunal wetlands (pannes) closer to dune crests or on broader deflation plains. Wetlands form in these sands where swales and pannes intersect local ground-water tables (Figure 7).

Although most interdunal and intradunal wetlands are geographically isolated landforms surrounded by dunes, some are hydrologically connected to adjacent waters. The closer the wetland is to the nearby waterbody, the greater the likelihood for hydrologic linkage. For example, interdunal swale wetlands along the shores of the Great Lakes have water tables influenced by lake levels, while those further away are controlled by ground-water seepage (Doss 1993).

Vegetation in the dune wetlands is variable, depending on the hydrology and geography (Wiedemann 1984, Wilcox and Simonin 1987, Tiner and Burke 1995, Albert 2000). The wettest ones are ponds and marshes, whereas the drier ones are wet meadows, shrub swamps, and forested wetlands. Ericaceous shrub bogs and natural cranberry bogs are found in dune swales along Lake Superior (Albert 2000) and along the North Atlantic coast, respectively. Intradunal ponds often support a distinct flora (Hiebert et al. 1986) and may resemble vernal pools if evapotranspiration exceeds ground-water inflow and precipitation during hot summers.

Dune marshes and ponds are critical habitats for many species (Wiedemann 1984). Dune marshes along the Oregon coast are vital habitat for 61 bird species, 17 mammals, five amphibians, and two reptiles, including winter habitat for 49 species of waterfowl, shorebirds, and wading birds (Akins 1973). These habitats produce an abundance of aquatic insects in spring that are food for migratory birds. Some unique species are associated with intradunal pannes, including plants found nowhere else in some states (Hiebert et al. 1986). Houghton's goldenrod (*Solidago houghtonii* Torr. &

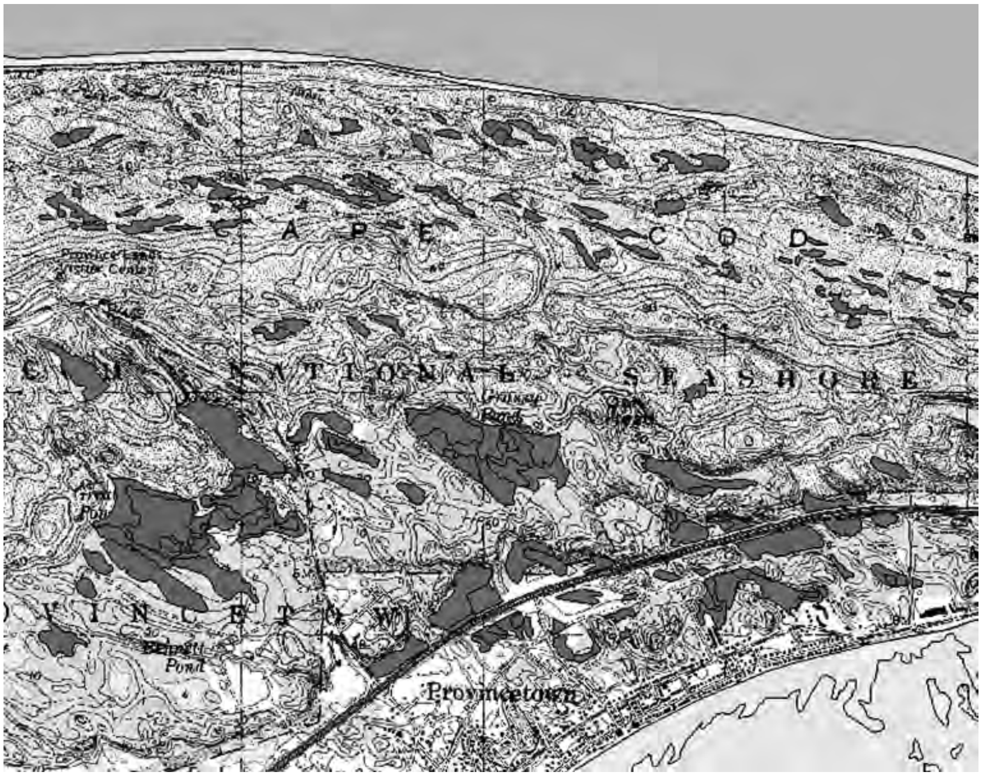


Figure 7. Geographically isolated wetlands are abundant among the sand dunes of Cape Cod National Seashore, Massachusetts (darker shaded areas represent isolated wetlands among the dunes). (Tiner et al. 2002)

Gray ex Gray), a federally threatened species, occurs in dune wetlands along Lakes Huron and Michigan. Other rare dune swale species include Lapland buttercup (*Ranunculus lapponicus* L.), round-leaved orchid (*Amerorchis rotundifolia* (Banks ex Pursh) Hulten), and butterwort (*Pinguicula vulgaris* L.) in Michigan and horned bladderwort (*Utricularia cornuta* Michx.) and seaside arrow-grass (*Triglochin maritimum* L.) in Indiana (Hiebert et al. 1986, Albert 2000, Doug Wilcox, pers. comm. 2001). Blanchard's cricket frog (*Acris crepitans blanchardi* Harper), rare in Michigan and endangered in Wisconsin, lives in shallow interdunal ponds.

The proximity to oceans and the Great Lakes have placed these wetlands at risk to development. Major threats include residential housing, golf courses, and resort development. Invasion by introduced species poses problems in Michigan (Wilcox 1995, Albert 2000).

Great Lakes Alvar Wetlands

Alvars are relatively flat, limestone/dolomite bedrock pavement landscapes in humid and subhumid climates (Reschke et al. 1999). In North America, they occur along the Great Lakes (Figure 3). They are open, rock garden-like environments with thin soils over horizontal bedrock outcrops, usually surrounded by forest. They are globally imperiled habitats that include both wetlands and terrestrial habitats (Reid 1996).

Most alvars are subjected to flooding in spring from snowmelt and precipitation and dry out by early summer (Reid 1996). Some alvars remain flooded for weeks; these wetter alvars may occur as isolated depressional wetlands within larger drier alvars (nonwetlands). Herbaceous hydrophytes characterizing these rocky wetlands include slender spikerush (*Eleocharis elliptica* Kunth), balsam ragwort (*Senecio pauperculus* Michx.), Crawe's sedge (*Carex crawei* Dewey), tufted hairgrass (*Deschampsia cespitosa* (L.) Beauv.), flat-stemmed spikerush (*E. compressa* Sullivant), and several mosses (e.g., *Bryum* spp. and *Drepanocladus* spp.) (Reschke 1990, Reschke et al. 1999). Rare species are typical of alvars (e.g., *E. compressa* and bulrush sedge *Carex scirpoidea* Michx.) (Dennis Albert, pers. comm. 2001). The combination of spring flooding and summer drought eliminates trees and a hot dry summer may cause a shift in vegetation to dry-site species (Reid 1996).

Threats to alvars, in general, include quarrying, rural development (e.g., cottages, vacation homes, and trailer parks along the shore), all-terrain vehicle traffic (disrupts hydrologic patterns, ruts alvar surfaces, and favors invasives), and the spread of invasive species (Reschke et al. 1999).

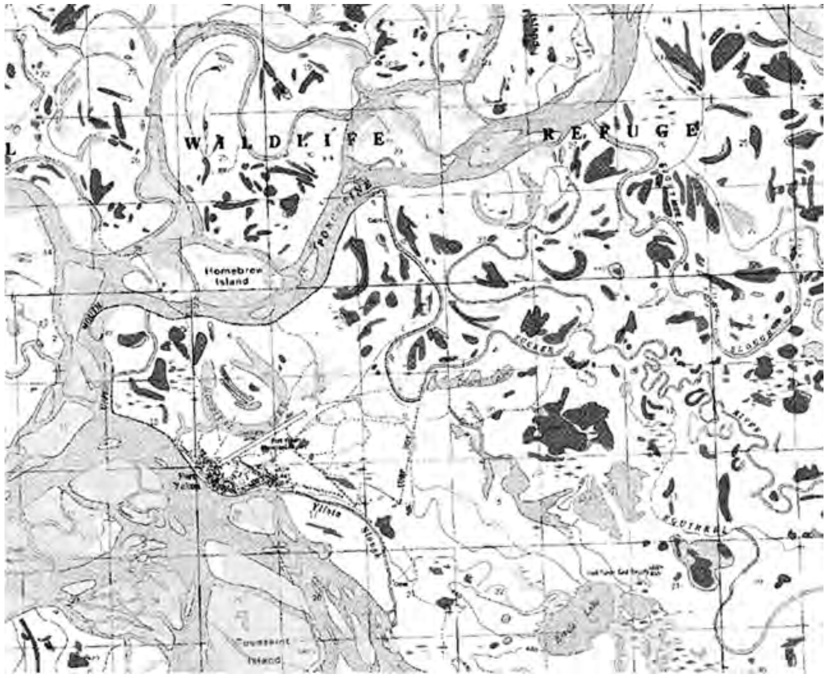


Figure 8. Isolated wetlands (darker shaded areas on map) represent former floodplain wetlands along Alaska's Porcupine River. The light shaded areas are waterbodies and non-isolated wetlands. (Tiner et al. 2002)

Inactive Floodplain Wetlands

Major shifts in river courses over time have left some wetlands isolated on former floodplains that are no longer actively flooded. These wetlands have been decoupled from the river by natural meandering processes and now occur on the inactive or historic floodplain. Although undoubtedly associated with most major U.S. river systems, these wetlands (''inactive floodplain wetlands'') may be most common in Alaska. Rivers such as the Yukon and Kuskokwim have migrated back and forth in broad valleys since glacial times. As a result of these shifts, many oxbow channels and meander scars are now isolated, sometimes many kilometers away from the active river channel. The historic floodplain of the Yukon River is over 24 km wide in places (Jon Hall, pers. comm. 2002). An outstanding example illustrating these types of isolated former floodplain wetlands can be seen along Alaska's Porcupine River (Figure 8). In the Yukon Flats, these types of isolated wetlands and lakes represent one of Alaska's most important waterfowl nesting areas, with an average breeding population of over one million ducks (Lensink and Derksen 1986).

Human actions have decoupled many floodplains from rivers. Levee and dike construction (to prevent flooding and to use ''protected'' lands for agriculture, development, or other purposes), river diversions, and damming rivers and controlling water releases (altered hydrology) have had major adverse effects on floodplain wetlands. The latter activities often deprive former floodplain wetlands of seasonal overflows. These wetlands, now separated from the river, may be considered geographically isolated.

Other Potentially Geographically Isolated Wetlands and Waters

Many other types of geographically isolated wetlands and waters exist (Table 1), but most are vegetatively similar to non-isolated wetlands in their respective regions (e.g., red maple swamps, peat bogs, cattail marshes, and alder seeps). They may be associated with isolated depressions, springs, seeps, or other features created by a variety of natural processes (e.g., geologic faulting, volcanic activity, glacial action, and aeolian forces) or by human actions (e.g., wetlands formed on mined lands and remnants of once larger wetlands fragmented by urban/suburban development). Alaska may have millions of hectares of geographically isolated wetlands, including seepage slope wetlands on North Slope of Alaska (Plate 12), fens on plateaus, permafrost wetlands on north-facing slopes, and precipitation-driven wetlands on discontinuous permafrost (Jon Hall, pers. comm. 2002). Other isolated wetlands are associated with geographically isolated waterbodies, including some glacial tarns, caldera lakes, other lakes of volcanic origin, and various types of ponds besides those mentioned previously (e.g., alpine and snowmelt ponds in northern regions, especially Alaska and mountainous areas in the coterminous U.S., gum ponds and grady ponds in the Southeast, and constructed ponds created by excavation in uplands).

SUMMARY AND CONCLUSIONS

Numerous types of wetlands are geographically isolated, and such wetlands are common features in many parts of the United States. Some wetlands (e.g., prairie potholes, playas, and Nebraska's Rainwater Basin wetlands) are typically isolated and are the predominant wetland type in a given region. Others are isolated forms of mostly non-isolated wetlands. While most geographically isolated wetlands probably form in closed basins (at least in the coterminous U.S.), many also develop on flats (e.g., terminal salt flats) and slopes (e.g., ground-water-discharge sites).

Many of the functions and benefits ascribed to non-isolated wetlands are present in isolated wetlands (e.g., surface-water storage/flood-water protection, nutrient transformation and cycling/water-quality maintenance, aquatic productivity, shoreline stabilization, and wildlife habitat) (Tiner et al. 2002). Most importantly from an ecological perspective, their geographic isolation and local and regional distribution have placed isolated wetlands in unique and strategic positions to support the nation's wildlife. This isolation has promoted endemism in plants and animals in some places (perhaps best illustrated by West Coast vernal pools and desert spring wetlands). North America's principal waterfowl breeding ground, the Prairie Pothole Region, is characterized by geographically isolated wetlands (i.e., prairie potholes). In arid and semi-arid regions, isolated wetlands (e.g., Rainwater Basin wetlands, Sandhills wetlands, playas, salt lake wetlands, and Channeled Scablands wetlands) are oases for resident and migratory wildlife (providing needed food and water) and vital stepping stones for wetland-dependent birds migrating across these dry landscapes. Many depressional isolated wetlands (e.g., woodland vernal pools, playas, Carolina bays, and sinkhole wetlands) are major breeding areas for various salamanders and frogs, while others provide needed overwintering habitat for waterfowl and other water birds (e.g., playas). Some geographically isolated wetlands include globally rare habitats (i.e., Great Lakes alvar wetlands) or globally rare species (e.g., coastal plain ponds).

Like other wetlands, geographically isolated wetlands continue to be threatened by many human activities. Habitat destruction (e.g., filling, land-leveling, drainage for agriculture, mining, and excavation), altered hydrology (e.g., ground-water withdrawals and drainage), and water pollution (e.g., runoff from developed areas and farmland and direct discharge of contaminated water) have already destroyed or degraded many isolated wetlands and put many of the remaining ones at risk. Ground-water withdrawal may pose the most insidious threat. Livestock grazing and invasive species (purposefully or accidentally introduced) negatively affect vegetation and biota in some areas.

Geographically isolated wetlands are among America's most valuable and threatened natural resources. All levels of government, environmental organizations, and concerned individuals should seek to increase public awareness of geographically isolated wetlands through education and various media. More research should be conducted to improve our understanding of the interrelationships between these wetlands and other aquatic and terrestrial habitats. Meanwhile, government agencies should consider strengthening regulatory measures and providing incentives for landowners to preserve the integrity of these wetlands voluntarily. Such efforts should include conservation of adjacent habitats, since wetland wildlife is often dependent on both wetland and upland habitats.

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