

## ISOLATED WETLANDS AND THEIR FUNCTIONS: AN ECOLOGICAL PERSPECTIVE

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**Abstract:** The recent U.S. Supreme Court case of *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers* (SWANCC) has had profound implications on the legal status of isolated wetlands. As a result, policymakers need ecological information on the definition and functions of isolated wetlands to respond to this decision. The term “isolated wetlands” is of fairly recent usage and has been poorly defined. In response, I recommend Tiner’s (2003b) definition as wetlands “that are completely surrounded by upland.” Isolation needs to be considered with respect to specific processes and functions. I suggest that isolation not be viewed discretely but be considered within an isolation-connectivity continuum. Isolation has a fundamental influence on the way water enters and leaves a wetland. This consequently affects any wetland function that depends on water as a vector (e.g., pollutant transport and certain types of dispersal). These wetlands can also have a high level of endemism, extensive plant zonation, and high biodiversity. Isolated wetlands, however, do not represent ecologically isolated habitat for many organisms. I conclude that the effect of isolation may not be as significant as the term “isolated wetlands” suggests: many of the biological features of isolated wetlands may result from environmental conditions that also occur in non-isolated wetlands. As a result of SWANCC, assessment methods are needed that can help regulators distinguish between jurisdictional and non-jurisdictional isolated wetlands. I propose that the merger of simple, source-sink-transport vector concepts with landscape-level assessment methods could be useful in this regard. I point to the need for documented examples of organisms that spend most of their lives in waters of the U.S. but also require isolated wetlands. I conclude that wetland science would benefit from the development of a comprehensive view of isolation as a formative process across different regional wetland types.

**Key Words:** dispersal, isolation, connectivity, isolation-connectivity continuum, depressional wetlands, SWANCC, Clean Water Act, waters of the United States

### INTRODUCTION

On January 9, 2001, the U.S. Supreme Court issued a ruling in the case of *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers*, 531 U.S. 159 (2001) (SWANCC). In a 5–4 decision, the Court found that the Migratory Bird Rule, which deemed waters of the United States to include isolated intrastate waters that provide habitat for migratory birds, exceeded the U.S. Army Corps of Engineers’ (Corps) authority under the Clean Water Act (531 U.S. 159 (2001)). The SWANCC decision limited the kind of wetlands that are within Federal jurisdiction and, thus, subject to regulation under the Clean Water Act (Downing et al. 2003).

Given the controversy over isolated wetlands and the regulatory turmoil caused by the SWANCC decision, now is an opportune time to review our scientific understanding of isolated wetlands. One motivation for this is that such information could be useful for future

policymaking, both at federal and state levels. Information in three areas could be particularly helpful: what isolated does and does not mean; the functions of isolated wetlands; and ways in which isolated wetlands and their functions contribute to the physical, chemical, and biological integrity of other waters of the U.S.

Beyond its potential usefulness for policymakers, there is a more fundamental reason for a review of isolated wetlands: to assess our state of understanding and to identify holes in our knowledge of this common wetland type. In particular, one issue that has received little attention is how wetlands respond to isolation. Isolation is considered an important factor in much of ecology. Darwin’s studies of the finches of the Galápagos Islands demonstrated that isolation plays a critical role in evolutionary biology. Isolation is also recognized as being a fundamental influence on the biogeographic distribution of species, population genetics,

and community structure. While isolation clearly characterizes many wetlands, the functioning of isolated wetlands need not result from isolation *per se*, but could be due to other factors. Thus, a basic question is whether isolation is an important property in the functioning of isolated wetlands. Articulating the role of isolation in these wetlands could provide a better understanding of isolation as a general ecological process.

In this paper, I use the literature to provide an overview of isolated wetlands and their functions. First, I discuss scientific definitions of isolated wetlands. I then consider whether isolated wetlands are isolated from an ecological perspective. Next, I examine the ecological functions of isolated wetlands and consider the role isolation plays in these functions. This is followed by a discussion of the ecological effects of isolated wetland modification. Finally, I provide a brief review of the SWANCC case and consider how scientific information could be useful in light of that decision.

#### ECOLOGICAL DEFINITIONS OF “ISOLATED WETLANDS”

The term “isolated wetlands” is a fairly recent usage. Although the term appears in the literature, it has not been consistently applied, as summarized by Likens et al. (2000:6–7): “The term ‘isolated’ wetland or pond is not a precise, scientific (or even regulatory) term. In general, the term is used loosely to define wetlands or ponds that lack a surface outlet to downstream rivers and bays. Such wetlands and ponds typically form in depressions in the landscape and are ‘isolated’ because the higher elevation of the land around them keeps water from flowing further downhill and downstream through even small rivulets. . . ‘isolated’ is generally a matter of degree and for this reason there is no accepted scientific definition of ‘isolated’ ponds or wetland.” In their report on wetland characteristics and boundaries, the National Research Council defines an isolated wetland simply as a “wetland not adjacent to another body of water” (NRC 1995:287). Other researchers describe isolated wetlands as “rare and highly dispersed habitats” (Pearson 1994), “highly disjunct” (Godt et al. 1995), and as “islands in a terrestrial landscape” (Edwards and Sharitz 2000). Tiner (2003b) points out that the term “isolated wetland” can be defined with respect to various processes (e.g., geographical, hydrological, or ecological). He, therefore, proposes the term “geographically isolated wetlands” to refer to “wetlands that are completely surrounded by upland (e.g., hydrophytic plant communities surrounded by terrestrial plant communities or undrained hydric soils surround-

ed by nonhydric soils. . .)” (Tiner 2003b). These descriptions collectively suggest a landscape of smaller wetland patches contained within a larger upland matrix. I revisit the definition of isolated wetlands at the conclusion of the next section.

The term “isolated wetlands” has also been used to refer to specific regional wetland types such as prairie potholes, pocosins, playa lakes, Delmarva bays, vernal pools, alpine wet meadows, Carolina bays, limesink ponds, and cypress ponds (NRC 1995, Kirkman et al. 1999, Likens et al. 2000; see Tiner 2003b for a more comprehensive list). Most of the major types of isolated wetlands (Table 1) are considered depressions under the hydrogeomorphic (HGM) classification (Brinson 1993, Smith et al. 1995). While isolated wetlands are relatively common in the U.S. (Tiner 2003a,b) and are the main wetland type in some regions, there is no firm information on the number or area of these wetlands. However, Likens et al. (2000) estimated that isolated wetlands comprise no more than 20% of the wetland area in the contiguous U.S.

#### ARE “ISOLATED” WETLANDS ISOLATED?

##### Hydrologic Connections

The word “isolated” suggests an object that is completely separate from and lacks interactions with other objects. While there may be no accepted scientific definition of an isolated wetland, it is clear from the ecological literature that interactions between such wetlands and other waters can occur. One way in which isolated wetlands can interact is through ground-water connections (Winter and LaBaugh 2003). For example, subsurface connectivity is well-documented in the prairie pothole region (PPR; e.g., Winter 1989, Winter and Rosenberry 1995), providing a mechanism for both water and certain chemicals to be transported between wetlands. The presence of ground-water connections, however, depends upon the hydrogeologic setting of the specific landscape. In the PPR, connections are often through the shallow ground water. In contrast, karst ponds in Florida are supplied by deeper underground sources, having variations in water level on the scale of decades (Sutter and Kral 1994). For playa lakes, ground-water inflows are minimal, since they are lined by relatively impermeable Randall clays (Bolen et al. 1989, Laubhan and Fredrickson 1997).

Although it has not been well-investigated, there is mention in the literature of intermittent surface-water connections among isolated wetlands during flooding (e.g., Halyk and Balon 1983, Zedler 1987, Snodgrass et al. 1996, Dunson et al. 1997, Russell and Hanlin 1999, Babbitt and Tanner 2000, Cook 2001, Leibowitz and Vining 2003, Winter and LaBaugh 2003). For ex-

Table 1. Hydrologic landscape setting (Winter 2001), dominant water source, and introductory references for major regional isolated wetland types. All these wetland types are considered depressions under the hydrogeomorphic classification (Brinson 1993, Smith et al. 1995).

Wetland Type	Hydrologic Landscape	Dominant Water Source	References
Carolina Bays	Flat Coastal	Precipitation and discharge from local groundwater systems	Richardson and Gibbons 1993, Sharitz and Gresham 1998, Sharitz 2003
Playa Lakes	High Plains	Surface runoff and precipitation	Bolen et al. 1989, Haukos and Smith 1994, 2003
Vernal Pools	Arid Plains and Plateaus	Precipitation	Zedler 1987, 2003, Witham et al. 1998
Prairie Potholes	Hummocky Glacial	Variable dependent upon landscape position	Kantrud et al. 1989, van der Valk 1989, van der Valk and Pederson 2003

ample, Leibowitz and Vining (2003) found that 28% of the wetlands within an area in central North Dakota had temporary surface-water connections during high water in 1996. They suggested that these intermittent connections would be expected to occur during the wetter portions of the region's wet-dry cycle. Isolated wetlands can also have surface-water connections with other waters, such as streams, at such times. This has been reported for prairie potholes (Stichling and Blackwell 1957) and vernal pools (Zedler 2003). Acknowledging the potential for such surface-water connections, Snodgrass et al. (1996:444) defined isolated wetlands as "depression wetlands that *under average surface-water levels* are not connected to other aquatic habitats by surface waters" (emphasis added).

#### Biotic Connections

Isolated wetlands can be connected to each other and to other aquatic systems through the movements of plants and animals. This movement could be in response to complex habitat requirements. For example, birds may rely upon a variety of wetland types for their food, shelter, nesting, and rearing needs (Batt et al. 1989, Yerkes 2000). Dispersal can occur as a normal part of the reproductive cycle (e.g., seed dispersal by wind) (Johnson et al. 1981). Movement may also be a response to poor habitat conditions, for example, emigration of individuals due to predation pressure or overcrowding.

Most of the studies that have considered biotic connections between isolated wetlands have focused on organisms or reproductive propagules that disperse through the air or over land (Gibbs 1993, Semlitsch and Bodie 1998, Lehtinen et al. 1999). Intermittent surface-water connections between wetlands can also serve as corridors for movement. Dispersal of seeds by water, or hydrochory, plays a role in riparian community structure (Schneider and Sharitz 1988). Hydro-

chory may also occur between isolated wetlands. Galatowitsch and van der Valk (1996) suggested that overflow through connecting swale zones used to serve as a mechanism for dispersion of floating plant propagules in Iowa prairie potholes. Such spillage is now rare because of drainage and farm conversion (Galatowitsch and van der Valk 1994, 1996).

Animal dispersal also occurs through intermittent surface-water connections. In Florida, connections between wetlands and drainage ditches during localized flooding allowed fish to enter these normally isolated wetlands (Babbitt and Tanner 2000). Snodgrass et al. (1996) suggested that fish species richness in Carolina bays will be highest in wetlands that have frequent and longer duration surface-water connections, since immigration will allow for recolonization. Duration of connections can also affect fish production and community structure in floodplain pools (Halyk and Balon 1983).

Biotic connections can occur between isolated wetlands and other aquatic and terrestrial ecosystems. For example, many animals, including amphibians (Gibbons 2003), require both aquatic and terrestrial habitat at different life history stages.

#### The Isolation-Connectivity Continuum

The foregoing discussion illustrates the point that "isolated" is generally a matter of degree (Likens et al. 2000). Within the landscape, wetlands occur within a continuum between completely isolated and connected. [Similarly, Puth and Wilson (2001) proposed that boundaries and corridors be viewed as a continuum of ecological flow control.] This isolation-connectivity continuum has both hydrologic and biotic expressions. Regarding the former, Leibowitz and Vining (2003) have suggested that intermittent connections help define a gradient between wetlands that are completely isolated with respect to surface water and those

that are completely integrated (i.e., connected by a stream network). As an example, the western PPR was formed from dead-ice glacial moraine, producing hummocky terrain with high local relief. Consequently, this area tends to have deep wetlands and little or no integrated drainage. In contrast, the Red River Valley in the eastern PPR consists of an ancient lake bed with deep deposits of silt and clay; the area, therefore, has shallow wetlands and stream networks are present. The eastern portion of the PPR also receives more precipitation than the west. It is hypothesized that both the temporal frequency and magnitude of connections between individual wetlands should increase in the PPR from west to east, resulting in a gradient of increasing connectivity (Leibowitz and Vining 2003). However, this natural pattern is distorted in the Red River Valley through extensive drainage by humans, which can connect and hydrologically integrate isolated wetlands. Although wetland function can vary between these regions (e.g., Austin 2001), evaluating whether this is influenced by the distribution of connectivity is difficult due to confounding factors (e.g., precipitation, geomorphology, wetland number and type, cropping patterns, and drainage impacts).

The degree of hydrologic connectivity can also vary within the same area. Cook (2001) examined 34 intermontane depressional wetlands in a 130-ha study area in western Montana, all of which lacked connections with deep ground water. Half of these geographically isolated wetlands had connections to up-gradient wetlands, either through temporary surface-water connections (spillage) and/or through longer duration soil-water pathways. The other half of the study sites were hydrologically isolated, only receiving inputs of water from direct precipitation and within-catchment runoff. Significant differences in hydrology, water chemistry, and vegetation were observed between these two groups of wetlands (Cook 2001).

Isolation can be expressed biotically through a number of mechanisms. MacArthur and Wilson's (1967) theory of island biogeography links species richness to isolation through dispersal. In their model, the immigration curve for a new species is controlled by distance: islands nearer to a source region have steeper immigration curves than distant islands (i.e., higher initial rates of migration) and, therefore, a greater number of species at equilibrium. Island biogeography also shows how stepping stones—located between more distant islands—can influence community composition by decreasing isolation (MacArthur and Wilson 1967). Although Brown and Lomolino (2000) have questioned whether species diversity is at equilibrium and suggested that other factors can also influence migration, isolation is still considered to play an important role in the species composition of islands.

Isolation is also an important factor in evolutionary biology, population genetics (Godt et al. 1995, Edwards and Sharitz 2000), source/sink dynamics (Pulliam 1988), and metapopulation dynamics (discussed in the next section).

At its simplest, spatial isolation is the result of the distances between wetlands. For a particular landscape setting, the frequency distribution of these distances will be a function of both wetland density and the pattern of their distribution (i.e., dispersed or clumped). Organisms whose dispersal would be controlled by distance would include plants with wind-borne seeds (Johnson et al. 1981) and birds. For other organisms, movement through the landscape is controlled by the presence of corridors or barriers. For example, a study by Wilcox (1989) found that highways could function as dispersal corridors for the invasion of wetlands by the exotic, purple loosestrife (*Lythrum salicaria* L.). This discussion illustrates two different kinds of spatial controls (Hansson 1991): limitation by dispersal distance and limitation by corridors. Dispersal can also be limited temporally (e.g., in the case where corridors or barriers between patches occur intermittently).

The probability that an organism or reproductive propagule can disperse to a particular location depends on the interaction between the spatial and temporal characteristics of the physical environment, as just described, and the organism's maximum dispersal distance. This can range widely. For example, the maximum dispersal distance for wetland-associated salamanders, frogs, and small mammals is on the order of one km (Gibbs 1993), while wetland seeds ingested by mallards might typically be transported 20–30 km and perhaps as far as 1400 km (Mueller and van der Valk 2002). Dispersal need not be limited if the maximum dispersal distance for an organism is large relative to the average distance between wetlands. Thus, van der Valk and Pederson (2003) have concluded that prairie potholes are not ecologically isolated habitats for most groups of organisms. Besides maximum dispersal distance, other life history attributes such as the organism's mode of transport and its ability to survive in the intervening uplands would also affect dispersal. For example, fish are excluded from most prairie potholes because these wetlands occasionally dry out and typically lack surface-water connections (van der Valk and Pederson 2003). Given the diversity of dispersal mechanisms and the range and variability in dispersibility and distances between wetlands, isolation should be defined with respect to a specific process or organism and not be considered a generic property of the wetland.

From an analytical perspective, considering isolation as a continuum allows it to be measured quanti-

tatively using spatial databases. Perhaps the most common measure for the degree of isolation is the nearest neighbor distance between wetlands. In cases where movement of the organism is facilitated by corridors or constrained by barriers, distance along the corridor or around the barrier would more accurately reflect dispersibility. Measures of temporal isolation would have to account not only for the presence and location of the connection, but also its frequency and duration. Temporary connections could be characterized by a frequency distribution, much in the same way that floodplain inundations are characterized (Leibowitz and Vining 2003).

Given that isolation exists as a continuum, it is necessary to revisit the definition of isolated wetlands. An isolation-connectivity continuum exists because hydrologic and biotic connectivity are not discrete characteristics, but vary in their magnitude and spatial-temporal occurrence. Therefore, using hydrologic or biotic criteria to categorize wetlands as isolated or non-isolated can be problematic since the degree of isolation can be difficult to assess. However, wetlands can be discretely classified as isolated or non-isolated based on geographic criteria. In particular, defining isolated wetlands as wetlands that are completely surrounded by upland (Tiner 2003b) has three main advantages over other definitions. First, it does not rely on hydrologic or ecologic processes that can be difficult to assess in the field and that can have considerable variability. Secondly, this definition avoids the need for arbitrary decisions in ambiguous situations where some level of connectivity exists (e.g., a depressional wetland within a five-year floodplain). Thirdly, most wetland scientists and regulators are comfortable with drawing boundaries between wetlands and uplands based on the three parameter approach of wetland vegetation, soils, and hydrology (<http://www.epa.gov/owow/wetlands/facts/fact11.html>). This definition should be easier to implement in the field than other definitions. I recommend that ecologists adopt Tiner's definition of isolated wetlands, and I use it in the remainder of this paper unless otherwise stated. However, it must be stressed that geographically isolated wetlands can vary in their degree of hydrologic and biotic connectivity (e.g., surface-water connections with other wetlands may or may not occur).

## FUNCTIONS OF ISOLATED WETLANDS

### Hydrologic and Water Quality Functions

A number of studies have examined the hydrologic and water-quality function of isolated wetlands (e.g., Stichling and Blackwell 1957, Moore and Larson 1979, Zedler 1987, Neely and Baker 1989, Winter

1989, and Dunson et al. 1997). Most of this information describes how individual or local groups of wetlands function. Studies are needed that examine how isolated wetlands contribute to regional hydrology or water quality and the extent to which these functions are influenced by isolation.

To the extent that a wetland is hydrologically isolated with respect to surface water, precipitation or local runoff entering the wetland must either return to the atmosphere by evapotranspiration or enter the ground-water system. Which of these pathways dominate depends upon the specific setting. Some isolated wetlands are underlain by impervious layers that restrict water loss to the deeper ground-water system. Examples of this are playa lakes (Bolen et al. 1989, Laubhan and Fredrickson 1997), vernal pools (Holland and Griggs 1976), and "clay-based" Carolina bays (Sharitz and Gresham 1998). However, water removal can occur through shallow soil-water flows, even when movement to the deeper ground-water system is restricted (Cook 2001). In the absence of surface-water outlets and ground-water connections, water loss is dominated by evapotranspiration. Ground water plays a stronger role with other isolated wetlands (e.g., prairie potholes (Winter 1989, Winter and Rosenberry 1995), "peat-based" Carolina bays (Sharitz and Gresham 1998), and karst ponds in Florida (Sutter and Kral 1994)). Both of these mechanisms of water removal tend to reduce flood peaks in comparison with surface runoff: evapotranspiration reduces total runoff volume, while belowground movement slows delivery and desynchronizes runoff.

While the hydrologic pathways just discussed dominate under ordinary conditions, other pathways may play important roles during episodic or more extreme storm events. For example, the impermeable Randall clay liner that underlies playa lakes thins out and is replaced by an annular area of highly permeable soil on surrounding upslopes (Bolen et al. 1989). Thunderstorms that produce heavy localized rainfall raise water levels to the elevation of these more permeable soils (David Haukos, U.S. Fish and Wildlife Service, pers. comm.), resulting in infiltration. Infiltration of water through this annular area is the principal recharge source for the underlying Ogallala aquifer (Osterkamp and Wood 1987). Intermittent surface-water connections between depressional wetlands can also occur during extreme events (Leibowitz and Vining 2003); this can define a gradient between complete isolation (all water stored locally) and integration (all water delivered to the stream network).

The effect of isolation on wetland water-quality function has received relatively little attention (e.g., Whigham and Jordan 2003). In perhaps the only study of its kind, Cook (2001) found that geographically iso-

lated wetlands that were connected to other wetlands through temporary surface-water connections and/or through soil-water pathways had significantly higher specific conductance and pH than hydrologically isolated wetlands (ground-water connections were absent for both groups of wetlands). These results were unexpected. The hydrologically isolated wetlands lost a larger percentage of their stored water, which should have concentrated dissolved ions. Also, these wetlands had significantly smaller wetland:catchment ratios, which should have led to higher dissolved ion loadings. However, hydrologically connected wetlands had more positive hydrologic fluxes during precipitation periods and more potential for carry-over of stored water between years. Cook (2001) concluded that these factors, repeated over time, would lead to higher concentrations of dissolved ions in the hydrologically connected wetlands.

Wetlands that are distributed across the landscape as geographically isolated basins should function differently from other wetland types, based on landscape configuration. For example, streams and rivers concentrate water collected over a large surface into a relatively small area comprised of a limited number of channels. Riverine wetlands should, therefore, receive relatively high loadings of pollutants or nutrients per wetland area. Extensive wetlands, such as bottomland hardwood forests, may represent the opposite extreme: water is distributed over a large surface area, potentially minimizing pollutant or nutrient loadings per wetland area. Yet, large, extensive areas share a minimal amount of border with upland sources of nonpoint pollutants, and actual loadings into these systems may be relatively low.

In contrast, landscapes containing geographically isolated wetlands focus water from a large area into numerous local depressions rather than funneling it into a regional drainage system. Each wetland is surrounded by a small drainage area compared to streams and rivers. Thus, pollutant and nutrient loadings per wetland area should be intermediate in comparison with riverine or extensive wetlands, with perhaps maximal potential for input of nonpoint source pollutants (since average distances between upland and wetland areas are minimized). Given that pollutants and excess nutrients can have deleterious effects on wetland condition, the intermediate levels of loadings delivered to isolated wetlands may allow for water-quality improvement in a manner that does not exceed capacity. However, it should be cautioned that the geochemistry and water-quality function of isolated wetlands can be highly variable due to wetland occurrence over a wide range of climatic and geologic settings. Whigham and Jordan (2003) review the water-quality function of isolated wetlands.

## Habitat Function

Hydrology is a primary factor determining the habitat characteristics of many isolated wetlands. Depressional wetlands—the HGM class that comprises the major types of isolated wetlands (Table 1)—often encompass a wide range of hydrologic conditions within a region (e.g., from shallow temporary ponds to deeper permanent waters). This leads to a diversity of habitat types and quality, both within and among wetlands (Laubhan and Fredrickson 1997, Sharitz 2003). Habitat diversity contributes to biological function in several ways. The habitat diversity of depressional wetlands can support a wide range of habitat specialists. This can result in high species richness both within and between depressional wetlands. One of the ways in which plant diversity expresses itself is through zonation—concentric rings of vegetation containing different species which occur across the moisture gradient. Zonation is a feature of many depressional wetlands, including prairie potholes (Kantrud et al. 1989), Carolina bays (Richardson and Gibbons 1993), and vernal pools (Schlising and Saunders 1982). While moisture gradients can result from variations in surface-water hydrology, zonation can also occur in wetlands dominated by ground water, such as Florida karst ponds (Sutter and Kral 1994).

Zonation results from spatial variation in moisture conditions. Depressional wetlands also experience temporal variation in hydrology. Moisture conditions in depressional wetlands can vary over the year and affect the timing of habitat availability. For example, shallow wetlands in the PPR may thaw earlier than deeper wetlands (NRC 1995, Robinson 1995). Many depressional wetlands dry out annually (e.g., Carolina bays (Sharitz 2003), vernal pools (Zedler 2003), playa lakes (Bolen et al. 1989), and seasonal and temporary prairie potholes (Kantrud et al. 1989)). Annual drying precludes organisms that require permanent water and favors species adapted to fluctuating water levels. These fluctuations cause within-year variations in community structure, as populations are replaced by species better adapted to prevailing moisture conditions. Moisture conditions can also vary over longer time periods. In the PPR, a 20-year wet-dry cycle produces a vegetation cycle consisting of dry, regenerating, degenerating, and lake marsh phases (Kantrud et al. 1989). The diversity of depressional wetlands is not limited to plant communities; a number of studies have also shown high amphibian richness in depressional wetlands (Semlitsch and Bodie 1998, Babbitt and Tanner 2000, Snodgrass et al. 2000).

The habitat specialists found on depressional wetlands can include endemic species. California's vernal pools are noted for supporting a fauna that is both

highly diverse and endemic (King 1998, Simovich 1998). This is partly due to patchy and restricted dispersal between pools, which can restrict gene flow, as well as the variety of physical and chemical conditions found in various pool types. Carolina bays (Sharitz 2003) and Florida's karst ponds (Sutter and Kral 1994) are other examples of depressional wetlands that support endemic species. However, other ephemeral systems with high diversity lack this level of endemism (e.g., playa lakes (Haukos and Smith 2003) and prairie potholes (van der Valk and Pederson 2003)).

Not all depressional wetland species are specialists. Most species using playa lakes are generalists (David Haukos, U.S. Fish and Wildlife Service, pers. comm.). A playa wetland does not have high within-basin habitat diversity at any one time (i.e., there is no zonation (David Haukos, U.S. Fish and Wildlife Service, pers. comm.)), nor is there the kind of variation in basin types that is found within prairie potholes (e.g., temporary vs. permanent). Instead, the habitat diversity of playa lakes results from spatial and temporal variation in environmental conditions, especially rainfall, across the region (David Haukos, U.S. Fish and Wildlife Service, pers. comm.).

Finally, high habitat diversity between depressional wetlands can in some instances support populations having broad life history requirements. The PPR supports a large abundance of breeding ducks and other waterfowl because complexes of depressional wetlands and surrounding uplands provide these birds with the diverse habitat they need for feeding, breeding, nesting, brood-rearing, etc. (Batt et al. 1989, Kantrud et al. 1989, Yerkes 2000). Small temporary and seasonal wetlands provide feeding habitat earlier in the season, before deeper wetlands thaw; this allows survival and breeding under a range of weather conditions (Robinson 1995). This high habitat diversity is similarly important for migratory waterfowl that use these wetlands as stopover or staging areas. Playa lakes also support species with broad habitat needs, including waterfowl and mammals (David Haukos, U.S. Fish and Wildlife Service, pers. comm.). Research is needed to assess whether support of such species occurs in other types of depressional wetlands.

The preceding discussion has focused on depressional wetlands. Other isolated wetland types having comparable hydrologic and habitat variability should function similarly. However, isolated wetlands can also occur among HGM types that have more stable hydrology (e.g., certain slope wetlands fed by ground water). Thus, not all isolated wetlands would be expected to share these characteristics. Studies are needed to compare habitat function across different isolated wetland types and to determine the environmental characteristics that influence habitat function for these

classes. Also, many authors use the term "high" to describe the biodiversity of isolated wetlands, but quantitative comparisons with other wetlands and non-wetland ecosystems are lacking. Research is, therefore, needed to verify that the diversity of these systems really is high relative to other systems. Even if the diversity of isolated wetlands is not greater than other systems, these wetlands can still contribute to regional biodiversity if they serve as the sole habitat for particular species.

The habitat functions discussed to this point can occur in geographically isolated wetlands but may not be determined by isolation *per se*. However, hydrologic isolation can produce biotic effects. Cook (2001) found that plant species composition, evenness, and net primary productivity of hydrologically isolated intermontane wetlands were significantly different than wetlands connected with temporary surface-water connections and/or soil-water pathways. A likely explanation for these vegetation patterns was differences in salinity and inundation observed between the groups of wetlands (Cook 2001).

There are a number of ways that biotic isolation can influence habitat function. Isolated wetlands can lack certain predators that otherwise dominate food webs and depress diversity (Babbitt and Tanner 2000, Sharitz 2003, van der Valk and Pederson 2003). For example, fish can enter normally isolated Florida wetlands that are near drainage ditches through connections during localized flooding. The result of this temporary connection on amphibians was a relative reduction in species adapted to temporary wetlands and a relative increase in those adapted to permanent wetlands and the presence of fish predators (Babbitt and Tanner 2000). In contrast, species composition was unaffected in wetlands that were outside of the area of flooding. However, the absence of fish is not solely a function of isolation but is also dependent on water permanence (Snodgrass et al. 1996).

Isolation may also contribute to wetland function by supporting metapopulations. Levins (1970) introduced the term "metapopulation" to refer to a population of populations. Metapopulation dynamics consist of local extinctions of individual populations within distinct habitat patches, due to environmental or demographic stochasticity, and recolonization of this habitat from neighboring patches through dispersal (McCullough 1996). The degree of isolation between habitat patches has a fundamental effect on a metapopulation, since this influences dispersal. Metapopulation dynamics are increasingly being recognized as playing an important role in the long-term sustainability of isolated wetland communities (Gibbs 1993, Semlitsch and Bodie 1998, Lehtinen et al. 1999). Isolated wetlands can also play a role in supporting metapopulations of upland species.

For example, metapopulations of the worm snake *Carpophis amoenus* Say may move from mesic ecotones surrounding wetlands into xeric uplands during wet periods when the wetlands expand (Russell and Hanlin 1999).

Many of the wetland metapopulation studies have been conceptual or analytical, and they lack observational data. An important research area is to determine the extent to which metapopulations function in isolated wetlands. More generally, research is needed to evaluate whether isolation is really an important factor influencing the habitat function of isolated wetlands or whether they mostly respond to factors that can also operate in other wetland types (e.g., hydrologic variability). It is especially important to recognize that isolated wetlands need not be ecologically isolated. For example, van der Valk and Pederson (2003) suggest that prairie potholes lack ecological isolation and, therefore, do not differ from other regional wetland types in function or composition.

## LOSS OF ISOLATED WETLANDS

### Historical Loss

The National Wetlands Inventory (NWI) quantifies wetlands by type, but there is no class for isolated wetlands (Cowardin et al. 1979, Tiner 2003a). Thus, there is no simple way to assess changes in isolated wetland area. Estimating changes in the area and location of isolated wetlands must be based on local studies, general wetland trends, or the best professional judgment of regional experts. Bennett and Nelson (1991) estimated that 97% of the Carolina bays in South Carolina have been disturbed, either by agriculture (71%), logging (34%), or both. Agricultural drainage of these wetlands occurred from the 1800s through the mid-1900s (Sharitz 2003).

Playa lakes have experienced relatively little physical loss from conversion; perhaps only 5–7% of these basins have been converted to other land covers (David Haukos, U.S. Fish and Wildlife Service, pers. comm.). The reason for this is that playas are low points on the landscape that cannot be drained. The major threat to playa integrity is sedimentation (Haukos and Smith 1994, 2003), although playas impacted in this manner still support wetland vegetation when wet (David Haukos, U.S. Fish and Wildlife Service, pers. comm.). In the past, playas were modified to hold runoff of irrigation water taken from the Ogallala Aquifer (Haukos and Smith 2003). However, this practice diminished as farmers moved towards center pivot irrigation. Playa lakes can also receive effluent from confined feedlot operations through runoff.

The main threat to California's vernal pools has

been agriculture, although urban conversion and suburbanization have also contributed to loss. For the Central Valley, it is estimated that 60–85% of wetland area was lost by 1973 (U.S. FWS 1994). More recently, Holland (1998) estimated county loss rates of 0.0–6.2% per year. In southern California, as much as 97% of vernal pool habitat may have been lost (Bauder and Wier 1990, as cited in King 1998).

In the five PPR states of Iowa, Minnesota, Montana, North Dakota, and South Dakota, about 49% of the historical 113,000 km<sup>2</sup> of wetlands were lost between the 1780s and 1980s (Dahl 1990). Loss rates may be as high as 75–99% in sections of Iowa (Arnold van der Valk, Iowa State University, pers. comm.). Most of the loss in the PPR has been attributed to agricultural drainage (Tiner 1984, Galatowitsch and van der Valk 1994).

### Ecological Effects of Loss

*Direct Habitat Loss.* Impacts that degrade a wetland cause some of its ecological functions to be lost. The effect of degradation on wetland function need not be linear: damage to critical processes could exceed natural thresholds and cause non-linear responses. Conversion represents the extreme case, in which the functions that were provided by the wetland may be completely lost. The degree to which different functions are lost is specific to the combination of the particular wetland and the impacts affecting it (e.g., the severity and kind of impacts, the functions that were originally present, and the sensitivity of those functions to the specific impacts). However, wetlands within the same regional type and the same HGM class share many functions (Brinson 1993, Smith et al. 1995); therefore, there should be general similarities in their response to comparable impacts.

Because isolated wetlands are often small, their loss might be expected to have minimal significance. However, a number of recent studies emphasize that the magnitude of functional loss is *not* proportional to size (Gibbs 1993, Robinson 1995, Semlitsch and Bodie 1998, Naugle et al. 2000). Much of the importance attributed to smaller, isolated wetlands is related to biodiversity: these wetlands often have high species richness due to moisture gradients caused by gentle slopes and seasonally varying moisture conditions. They can also contain endemic species because of their physical isolation. As a result, loss of these wetlands may have a disproportionate effect on regional biodiversity, relative to other wetlands.

*Cumulative Loss.* Loss of an individual wetland can be regionally significant if, for example, it is the only site supporting an endangered species. Usually, how-



ever, it is the cumulative loss of many wetlands that causes regional consequences. A study by King (1998) illustrates how cumulative wetland loss can affect biodiversity. She conducted a simulation to examine species extinction curves as a function of habitat destruction. King compared results using a hypothetical species distribution profile, containing a large number of common species, with the actual distribution of crustaceans in northern California vernal pools—which included a large number of endemics (17 out of 67 species occurred in only one of the surveyed pools). She found that the extinction curve for the hypothetical profile was less steep than that for the actual crustacean distribution. For the hypothetical distribution, conversion of 85% of the habitat resulted in an 8% loss in species; only 28% of the habitat had to be converted to produce a similar loss in species using the actual crustacean distribution (King 1998). This study illustrates that the probability that a local loss of a species will result in the regional loss of that species is partially a function of the species' endemism (Schweiger et al. 2002). To the extent that isolated wetlands harbor rare and/or endemic species, even moderate cumulative loss could cause species extirpations.

Wetland loss can alter the spatial configuration of the landscape by reducing landscape connectivity and increasing isolation. Lower connectivity could decrease recolonization because the pool of individuals available for dispersal would be reduced and the average distance between wetlands would increase (Gibbs 1993, Semlitsch and Bodie 1998). Thus, the minimum amount of habitat area required to maintain a viable population is larger for isolated areas and for less mobile species (Brown and Lomolino 1998). Increasing isolation, therefore, increases the likelihood that a given loss in area will push the resource below the minimum habitat requirement and cause local extinctions.

Complete loss of wetland area is not necessary for landscape connectivity to be reduced; certain types of degradation may also decrease connectivity. For example, lowering the water table may decrease the frequency of overflow between Iowa wetlands through connecting swale zones. This may reduce dispersal rates and recolonization of restored wetlands by wet-adapted plant species (Galatowitsch and van der Valk 1996).

*Off-site Effects of Cumulative Loss.* Increased flooding due to loss of hydrologic function is often mentioned as an off-site effect of cumulative wetland loss. Drainage of a significant portion of the PPR's wetlands has increased watershed integration and has been suggested as a cause of greater flooding (Campbell and

Johnson 1975, Vining et al. 1983). However, it should be noted that drainage from wetlands does not have to enter the stream network; the water can be drained locally into other wetlands (McAllister et al. 2000). In this case, drainage would not contribute to increased downstream flooding.

The influence of wetlands in reducing flood peaks is greatest for small storm events occurring when wetlands have a large capacity for storage. It is least for large floods when soil and wetland storage are saturated before the flood peak (SAST 1994). In a hydrologic model of Iowa prairie potholes, Haan and Johnson (1968) found greater peak flows with increased drainage for long duration, low intensity rain events, but not for large volume, high intensity events. Similarly, results from simulation modeling found that pothole wetlands reduced flooding of an annual event by 9–23%, compared with 5–10% for a 100-year event (SAST 1994). Off-site changes in hydrology can affect water quality. For example, streambank erosion can increase because of the greater kinetic energy of larger flood peaks. In agricultural regions of the upper Midwest, streambank erosion contributes significantly to stream sediment load (Likens et al. 2000).

Cumulative loss of isolated wetlands can impact off-site biological communities. As an example, impacts to migratory waterfowl from prairie pothole loss could affect community composition at continental scales. Off-site effects would perhaps be greatest for species that have stage-specific requirements for both aquatic and terrestrial habitat. For instance, many amphibian species require aquatic habitat, including ponds, for breeding and larval development but are largely terrestrial during juvenile and adult life stages (e.g., the long-toed salamander (*Ambystoma macrodactylum* Baird), Pacific treefrog (*Hyla regilla* Baird and Girard), and western toad (*Bufo boreas* Baird and Girard) (Nussbaum et al. 1983)). Loss of isolated wetlands could reduce or eliminate these species from their upland habitat. This could then have a ripple effect on other species, for example, through altered habitat use and modified interactions with predators or competitors. In contrast, facultative species that can exploit other habitat if isolated wetlands are not available should be less affected.

## ISOLATED WETLANDS AND SWANCC

### Overview

The SWANCC case presented the Supreme Court with two issues (531 U.S. 159 (2001), Waxman et al. 2000, Downing et al. 2003): (1) whether an isolated water could be considered part of the "waters of the United States," as defined in the Clean Water Act

(CWA), and thus subject to the Corps of Engineers' regulatory authority under Section 404 of the CWA, solely based on its use by migratory birds; and, if so, (2) whether Congress had the constitutional authority under the Commerce Clause to include these as waters of the United States. In particular, the Court considered the Migratory Bird Rule, which regarded isolated waters that provide habitat for migratory birds as waters of the United States. The January 9, 2001 decision found that the Migratory Bird Rule exceeded the Corps' authority under the CWA (531 U.S. 159 (2001)). The majority opinion, authored by Chief Justice William Rehnquist, found that there is "nothing approaching a clear statement from Congress that it intended. . . to reach an abandoned sand and gravel pit such as we have here" (531 U.S. 159 (2001)). Finding that the CWA did not confer the Corps with the statutory authority to regulate such waters, the Court did not address the broader constitutional issue of whether the Commerce Clause would allow Congress to include such isolated waters as waters of the U.S. A detailed analysis of the SWANCC case is given in Downing et al. (2003).

Although the particular isolated waters in the SWANCC case were not wetlands, since they did not support hydrophytic vegetation, the Court's ruling applies to isolated wetlands, since these are a subset of isolated waters. However, it should be noted that in a jurisdictional context, "isolated" could be defined as lacking surface hydrologic connections to navigable waters, their tributaries, and/or other interstate waters, and where the water is not neighboring, bordering, or contiguous to such waters. This could include wetlands that do not meet the Tiner (2003b) definition. For example, two intrastate wetlands that were connected to each other by surface water, but which lacked connections to interstate or navigable waters and their tributaries, would be jurisdictionally isolated. Also, certain fens and pocosins could be jurisdictionally isolated if they do not connect to waters of the U.S. (Richardson 2003, Sharitz 2003).

The SWANCC decision has had profound implications on the legal status of isolated wetlands. Following this ruling, the Corps and the U.S. Environmental Protection Agency took the position that use of waters or wetlands by migratory birds is no longer sufficient as the sole basis for the assertion of regulatory jurisdiction under the CWA (Downing et al. 2003). Since then, the courts have, for the most part, held that SWANCC does not affect jurisdiction over interstate waters, traditional navigable waters and their tributaries, or wetlands adjacent to any of these waters (Downing et al. 2003). The courts have not yet defined the extent that jurisdiction after SWANCC may be as-

serted over non-navigable, isolated waters on grounds other than migratory bird use.

While the Court struck down the Migratory Bird Rule, it did not nullify the regulations upon which it was based (Downing et al. 2003). The Supreme Court indicated in SWANCC that an isolated water (including isolated wetlands) might be considered a water of the U.S. if it had a "significant nexus" with a water that is navigable-in-fact, either directly or via other waters of the U.S. (see Downing et al. 2003). The specific meaning of significant nexus is a policy and legal matter that is still evolving (Downing et al. 2003). However it is defined, the regulatory community will need better scientific information to define the line between jurisdictional and non-jurisdictional isolated wetlands and to implement this policy in the field.

Scientifically determining whether an isolated wetland has significant nexus with a water of the U.S., whatever final definition is adopted, requires knowledge of the wetland's specific functions and how these interact with off-site waters located at some distance. This could require process-level information that is costly and time-consuming to obtain. Perhaps more importantly, the effects of an individual wetland on another water may be hard to detect. However, it may not be necessary for the effects to result from an individual wetland. According to aggregation theory (Harrington 2001), a single activity that itself has no discernible effect on interstate commerce could still be regulated if the aggregate effect of all similar activities has such an effect. If aggregation theory applies, then significant nexus could result if impacts to a class of wetlands in aggregate have an effect on waters of the U.S.

#### Science Needs

Demonstrating significant nexus for a class of wetlands can be facilitated by recent approaches that attribute functions to regional wetland types. Examples of this include the HGM classification (Brinson 1993, Smith et al. 1995), which assigns wetland functions and ecological significance based on geomorphic setting, water source, and hydrodynamics; Winter's (2001) concept of hydrologic landscapes, which defines a fundamental hydrologic landscape unit consisting of land-surface form, geology, and climate; and wetland templates, which are the landscape settings where hydrogeologic and climatic factors interact to promote the formation and maintenance of wetlands (Bedford 1996, 1999).

Implementation of HGM for regional subclasses involves two steps that could help demonstrate significant nexus (Smith et al. 1995): development of func-

tional profiles that describe the physical, chemical, and biological characteristics of regional subclasses; and development of assessment models that define the relationship between wetland and landscape attributes and the wetland's functional capacity. Future development of functional profiles and assessment models could explicitly include functional linkages between the wetland subclass and waters of the U.S. As a first step, this could rely on the literature and the best professional judgment of regional experts. As field data from reference wetlands become available, these linkages can be confirmed and described more fully.

Concepts such as HGM, hydrologic landscapes, and wetland templates can be useful for classifying wetlands. This can make it easier to collect and analyze field data, and therefore demonstrate significant nexus, in two ways. First, classification into groups of wetlands allows statistical comparisons of the characteristics of the wetland classes (independent variables) with those of the waters of the U.S. (response variables). For example, the relationship between suspended sediment levels in streams and the density of isolated wetlands within the surrounding watershed can be tested statistically. Secondly, a sample of wetland sites can be selected from the regional wetland class and then field-evaluated for significant nexus. If the sample is representative, results from the field evaluation can be related to the entire class.

A landscape perspective is required to link performance of wetland functions with off-site effects on waters of the U.S. For example, water-quality function generally depends on three elements (Leibowitz et al. 2000, McAllister et al. 2000): (1) sources of the pollutant, for example, agricultural nonpoint runoff or industrial outfalls; (2) wetland sinks that have the capacity to chemically, biologically, and/or physically remove or transform the material; and, because they are normally separated in space, (3) transport vectors that carry the pollutant from sources to sinks (e.g., hydrologic connectivity). There is a fourth requirement if water-quality function is to be useful in preventing degradation of waters of the U.S.: interception needs to occur before the pollutant impacts the off-site water. In other words, the transport vectors need to deliver the pollutants to the isolated wetlands before these substances reach the waters of the U.S. Information derived from HGM, hydrologic landscape, and/or wetland template analyses could be used as a first order assessment of whether the above four elements are present for a particular wetland type. This would be useful in evaluating whether a significant nexus exists. Examples are needed to demonstrate the applicability of such landscape approaches to the determination of significant nexus.

Given the importance of hydrologic connectivity as

a transport vector, the variable source area concept could be useful. This states that only a portion of the watershed is usually involved in actively generating runoff, and the contributing area dynamically shrinks and swells in response to moisture conditions (Satterlund and Adams 1992). This shrinking and swelling occurs over various time periods (e.g., episodically (individual storm events) and seasonally). These connections provide a pathway whereby isolated wetlands could affect waters of the U.S. The level of hydrologic connectivity necessary to establish significant nexus is a policy issue. However, the ability to define the extent of hydrologic connection with respect to different flood recurrence intervals (Leibowitz and Vining 2003) would be useful in implementing such a policy. Determining these recurrence intervals could involve analysis of imagery representing various moisture conditions, as well as hydrologic modeling.

Ecologists need to define more clearly the role of isolated wetlands in supporting organisms that spend most of their life history in navigable waters, their tributaries, or adjacent wetlands. Any impacts to such organisms due to isolated wetland loss would affect the biological integrity of waters of the U.S., possibly representing significant nexus. Two species of snakes in the genus *Farancia* (Amphiuma and American eel) may provide examples of this. As adults, these two species are extreme dietary specialists and live in river swamps and streams, which would be considered waters of the U.S. Anecdotal observations suggest that the juveniles are primarily found in Carolina bays, where they feed on larval salamanders (J. Whitfield Gibbons, University of Georgia, pers. comm.). If these life history requirements are verified, then loss or degradation of Carolina bays could impact the biotic integrity of waters of the U.S. Research on the role of isolated wetlands in supporting the biota of U.S. waters could be critical for helping regulators respond to SWANCC.

More fundamentally, basic information quantifying the number and total area of isolated wetlands and the amount of historic loss is required. Wetland scientists can also provide a better understanding of the ecological effects of isolated wetland loss, in general, and possible losses that may result from SWANCC. A study by Petrie et al. (2001) begins to address this topic. They concluded that SWANCC will have little affect on wintering waterfowl. However, there could be significant impacts for breeding and migratory waterfowl, especially if Swampbuster is eliminated or weakened. While this is critical information, the analysis by Petrie et al. (2001) was limited to the potential impacts of SWANCC on waterfowl. Thus, more comprehensive analyses are required. The approach used by Tiner (2003a) to quantify at-risk isolated wetlands

could be useful if repeated for multiple time periods. Understanding the effects of cumulative loss of isolated wetlands will require a fundamental knowledge of landscape relationships, including an examination of the regional hydrogeologic and climatic factors that control and influence wetland function (Bedford 1999).

#### SUMMARY AND CONCLUSIONS

The SWANCC decision created the need for scientific information to help inform future policymaking at both the federal and state levels. Also needed are new approaches that can help regulators distinguish between jurisdictional and non-jurisdictional isolated wetlands. In particular, assessment methods are required that can help establish whether or not significant nexus is present. In this paper, I suggested several conceptual approaches that could potentially be useful in such evaluations. For example, waters of the U.S. could be included as a potential endpoint in the development of functional profiles and assessment models for HGM regional subclasses. Another approach that is particularly promising is the merger of landscape-level classification and assessment methods, such as HGM, with simple source-sink-transport vector concepts. This could be useful in evaluating whether isolated wetlands intercept pollutants before they impact waters of the U.S. Methods that can be used to determine recurrence intervals for different levels of hydrologic connectivity should be helpful. However, these conceptual approaches need to be refined further and their utility demonstrated before they will be of use to the regulatory community. Basic research on the role of isolated wetlands in supporting the biota of U.S. waters is also critical for helping regulators respond to SWANCC. In particular, there is a need for documented examples of organisms that spend most of their lives in waters of the U.S. but also require isolated wetlands.

SWANCC provides researchers with the opportunity to assess the state of our ecological understanding of isolated wetlands. The term "isolated wetlands" is of fairly recent usage and, as such, has been poorly defined. In this paper I adopt and recommend Tiner's (2003b) definition as wetlands "that are completely surrounded by upland." This simple definition has three main operational advantages: it does not rely on hydrologic or ecologic processes that can be difficult to assess in the field and that can have considerable variability; it avoids the need for arbitrary decisions in ambiguous situations where some level of connectivity exists; and it allows boundaries to be drawn using an approach that wetland scientists and regulators are familiar with (e.g., the three parameter approach of wet-

land vegetation, soils, and hydrology). However, wetlands classified as geographically isolated, based on Tiner's (2003b) definition, can still vary in their degree of hydrologic and biotic connectivity. Basic information is needed quantifying the number and total area of wetlands meeting this definition and the amount of historic loss they have experienced.

It is clear from the ecological literature that isolated wetlands are not completely isolated. Interactions between such wetlands and other waters do occur hydrologically, through ground-water and intermittent surface-water flows, and biologically through dispersal of plants and animals. Isolation is not a generic, across-the-board property, but needs to be considered with respect to specific processes and functions. Isolated wetlands are islands in a terrestrial landscape (Edwards and Sharitz 2000) and, thus, are an example of insular systems. However, they vary from classic islands in that they occur at much greater densities. Consequently, they have much greater connectivity than settings where islands are sparser. Therefore, these wetlands may not be ecologically isolated for many species. As Zedler (2003) observes for vernal pools, these wetlands have evolved in a balance between isolation and connectedness. Thus, isolated wetlands may occupy an intermediate position within the isolation-connectivity continuum. Scientists can obtain a more comprehensive understanding of how ecosystem function and population dynamics respond to isolation by considering the ecology of isolated wetlands.

Isolation has a fundamental effect on the way water enters and leaves a wetland. This consequently affects any wetland function that depends on water as a vector (e.g., pollutant transport and certain types of dispersal). However, studies are needed that examine how isolated wetlands contribute to regional hydrology or water quality and the extent to which these functions are influenced by isolation. Hydrology also plays a critical role in the biology of these wetlands. Isolated wetlands are small, moisture-rich environments within a larger matrix of drier land. The presence of moisture gradients that vary rapidly over space and time produces a variety of physical habitats. This can have a number of consequences, including plant zonation, endemism, and high biodiversity, although research is needed to verify that the diversity of these systems is really high relative to other systems. Studies are also needed to assess further the ecological consequences of isolated wetland loss in general and possible losses that may result from SWANCC.

Ecological isolation may be an important influence in determining certain community characteristics of isolated wetlands (e.g., in reducing competition and supporting metapopulations). However, the effect of isolation may not be as significant as the term "iso-

lated wetlands'' seems to suggest: many of the biological features of isolated wetlands may result not from isolation *per se* but from environmental conditions that can also occur in non-isolated wetlands. Thus, studies are needed to determine the influence of ecological isolation on wetland structure and function, relative to other environmental factors. Developing a comprehensive view of isolation as a formative process across different regional wetland types will contribute to our understanding of wetland ecology.

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