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Do geographically isolated wetlands influence landscape functions?

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Geographically isolated wetlands (GIWs), those surrounded by uplands, exchange materials, energy, and organisms with other elements in hydrological and habitat networks, contributing to landscape functions, such as flow generation, nutrient and sediment retention, and biodiversity support. GIWs constitute most of the wetlands in many North American landscapes, provide a disproportionately large fraction of wetland edges where many functions are enhanced, and form complexes with other water bodies to create spatial and temporal heterogeneity in the timing, flow paths, and magnitude of network connectivity. These attributes signal a critical role for GIWs in sustaining a portfolio of landscape functions, but legal protections remain weak despite preferential loss from many landscapes. GIWs lack persistent surface water connections, but this condition does not imply the absence of hydrological, biogeochemical, and biological exchanges with nearby and downstream waters. Although hydrological and biogeochemical connectivity is often episodic or slow (e.g., via groundwater), hydrologic continuity and limited evaporative solute enrichment suggest both flow generation and solute and sediment retention. Similarly, whereas biological connectivity usually requires overland dispersal, numerous organisms, including many rare or threatened species, use both GIWs and downstream waters at different times or life stages, suggesting that GIWs are critical elements of landscape habitat mosaics. Indeed, weaker hydrologic connectivity with downstream waters and constrained biological connectivity with other landscape elements are precisely what enhances some GIW functions and enables others. Based on analysis of wetland geography and synthesis of wetland functions, we argue that sustaining landscape functions requires conserving the entire continuum of wetland connectivity, including GIWs.

connectivity | navigable waters | significant nexus

Understanding connectivity—patterns of matter, energy, and organism exchanges among landscape elements and across scales—is a challenge that unites the fields

of ecology and hydrology (1). Connectivity enables dispersal of organisms and flows of water between landscape elements at multiple spatial and temporal scales

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(2), with implications for myriad processes, including gene transport (3, 4), solute and particle movement (5–7), biodiversity support (8, 9), and pollutant retention (10). Multiple flow paths (11) among landscape elements create a spatially and temporally dynamic (12–15) portfolio of connections that vary in mode, strength, timing, and direction (16). Landscape functions (e.g., water storage, base flow, sediment retention, nutrient cycling, biodiversity support) emerge from a portfolio of connections (17, 18), which can be enhanced (19, 20) and diminished (21, 22) by human activities. Quantifying these landscape functions (23, 24) and evaluating policies adopted to mitigate human impacts to them are imperative.

Wetlands are important landscape elements, providing hydrological (e.g., floodwater storage and release) (25), biogeochemical (e.g., material transformation, carbon sequestration) (26–28), and biological (e.g., habitat, refugia) (29–32) functions. Variation in wetland connectivity to other landscape elements impacts wetland functions, and thus which services are provided. Wetlands connected to other landscape elements via persistent surface flow paths provide a different blend of storage and water quality services than wetlands connected episodically or only via the sub-surface (33, 34). Likewise, varying hydrologic connectivity impacts organism dispersal and thus community composition (35), biodiversity (36, 37), and metapopulation viability (38, 39). Human activities that decrease (e.g., dams/levees, land cover change) or increase (e.g., canals/ditches, human-aided dispersal) wetland connectivity affect functions in individual wetlands and, by extension and combination, functions at the landscape scale.

Predicting connectivity of geographically isolated wetlands (GIWs) to other landscape elements is crucial to understanding their landscape function (40). GIWs are those wetlands surrounded by uplands. They span many wetland types and hydrogeomorphic settings (e.g., vernal pools, playas, Delmarva and Carolina bays, cypress domes, prairie potholes), grouped together by a shared absence of persistent surface-water connections. Geographic isolation is often interpreted as functional isolation, especially outside the scientific literature, but this interpretation is incorrect (41, 42). GIWs are not hydrologically, biogeochemically, or biologically isolated (43) from other landscape elements or downstream waters. Rather, they span the entire continuum of landscape connectivity, varying in mode, timing, duration, and magnitude (44), with antecedent moisture, geology, topography, land cover, and the specific material or organism. However, lack of persistent surface water connectivity to other elements means they occupy the lower end of the connectivity continuum, with functions controlled by episodic or slow transport of water and solutes, or constrained dispersal of organisms. Unambiguous generalizations about GIW connectivity with downstream waters are untenable, leading some (44) to argue the term is misleading. We retain it here as the default term since 2002 because proximity to drainage features informs our analyses and because it broadly represents wetlands imperiled by recent judicial interpretations of US Clean Water Act jurisdiction.

To address GIW impacts on landscape functions, we explore hydrological, biogeochemical, and biological connectivity to nearby and downstream waters. To support inferences about their functions, we present an analysis of GIW geometry, size, and arrangement. Using this analysis and literature synthesis, we evaluate the premise that GIWs contribute to multiple landscape functions, suggesting important consequences of altering their prevalence or connectivity.

Regulatory Background

Wetland protections in the United States derive from the Federal Water Pollution Control Act (FWPCA) (33 USC §1251 et. seq.), also known as the Clean Water Act (CWA), which establishes the structure for federal agencies to regulate pollutant discharges into “waters of the United States” and sets standards for surface water (though not groundwater) quality. Before 2001, virtually all wetlands (i.e., those that met the regulatory definition) were considered waters of the United States and federally regulated under the CWA. Challenges to federal authority over waters that did not meet legal standards of “navigability” (45) culminated in two Supreme Court decisions [*Solid Waste Agency of Northern Cook County v. United States Army Corps of Engineers*, 531 US 159 (2001); and *Rapanos v. United States*, 547 US 715 (2006)] that more narrowly interpreted the CWA scope (46, 47). In the former, the Court held that the US Army Corps of Engineers (USACE) exceeded its statutory authority in asserting jurisdiction over non-navigable, isolated, intrastate waters (later called “geographically isolated”) (40) based solely on use by migratory birds. In the latter, a concurrence opinion by Justice Anthony Kennedy limited federal jurisdiction to wetlands only with a “significant nexus” to navigable waters. The “significant nexus” term established a legal standard for scientific evidence to assert CWA jurisdiction, intending that protected wetlands possess a more than “speculative or insubstantial” connection. Under that standard, a wetland is jurisdictional where it, either alone or in combination with “similarly situated” waters in the region, significantly affects the physical, chemical, or biological integrity of downstream navigable waters.

In 2015, in light of these decisions, the USACE and US Environmental Protection Agency (EPA) issued regulations defining “waters of the United States” (the Clean Water Rule) (48). Based

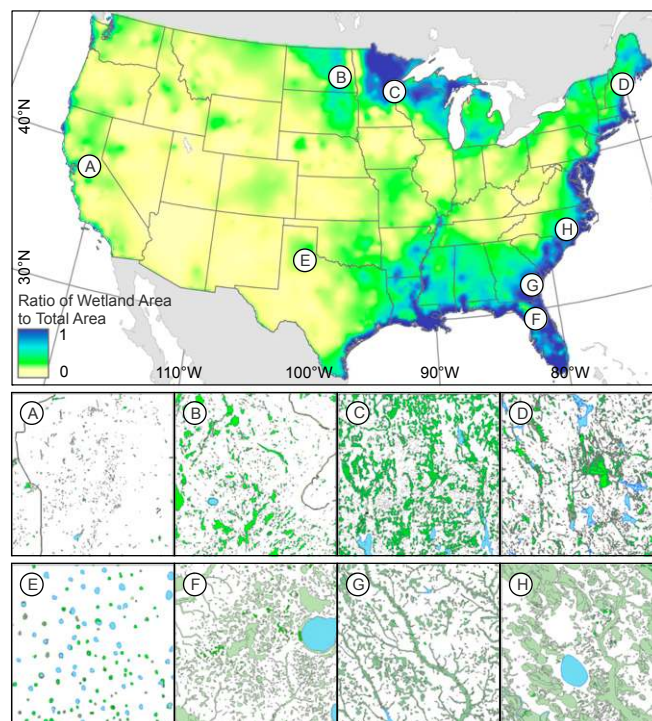


Fig. 1. Total wetland density (A–H, Upper) varies across the United States. We selected eight 1,000-km² blocks (Lower, showing spatial subsets in A–H) to evaluate wetland resources (green) and other aquatic habitats (blue) to analyze landscape patterns of geographically isolated wetlands using data from the National Wetlands Inventory.

on extensive scientific literature review (49), the Clean Water Rule established eight categories of waters for CWA jurisdiction, six of which are jurisdictional in all cases, without need for further analysis (traditional navigable waters, interstate waters, territorial seas, impoundments of waters of the United States, tributaries, adjacent waters), and two that can be jurisdictional if case-specific analysis demonstrates a “significant nexus” with “navigable waters.” Most GIWs fall in the latter.

A significant nexus criterion implies that some wetlands, alone or in combination with other similar wetlands, do not significantly influence the physical, chemical, or biological integrity of downstream waters. One challenge in evaluating this contention is that few studies empirically document GIW connectivity, and time variation thereof, across hydrological, biogeochemical, and biological pathways (49). Further, aggregate functions from complexes of similarly situated wetlands, a crucial facet in the significant nexus test, remain poorly understood. Finally, the role of weak connectivity (i.e., where material, energy, or organism exchange is slow or episodic) is insufficiently considered or quantified. Justice Kennedy expressly included functions derived from weak connectivity (e.g., slowing water and pollutant transport, limiting biological dispersal), stating that “it may be the absence of an interchange of waters . . . that makes protection of the wetlands critical to the statutory scheme.” This reasoning implies a significant nexus test based on consideration of functions, not connectivity strength. Under such a test, arbitrary connectivity thresholds for surface (i.e., based on frequency and duration) or subsurface pathways (i.e., based on travel times from distance and flow velocity) would be problematic. However, if the significant nexus test ultimately focuses on exceeding minimum thresholds in surface connectivity or falling below some subsurface travel time threshold, many GIWs will lose legal protections, and landscape functions where weak connectivity increases functional value, or is even a prerequisite, will be impacted.

Wetland Geography

Evaluating GIW landscape functions requires an inventory of their size, landscape position (vs. the drainage network and other wetlands), and geometry. Although GIWs exist in many settings (40) across multiple wetland types, useful generalizations emerge from geographic analysis of wetland resources across representative landscapes.

We obtained National Wetlands Inventory (NWI) (www.fws.gov/wetlands/) data for eight 1,000-km² landscape blocks across the conterminous United States where well-known GIW types remain prevalent (spatial subsets in Fig. 1 A–H, center coordinates in Table

1). These wetlands include California vernal pools (Fig. 1A), prairie potholes (Fig. 1B), basin wetlands (Fig. 1C), Maine vernal pools (Fig. 1D), playa lakes (Fig. 1E), cypress domes (Fig. 1F), coastal plain wetlands (Fig. 1G), and pocosins (Fig. 1H). Other iconic GIW landscapes (e.g., Nebraska Sandhills, Delmarva bays, Appalachian bogs) also merit attention. In each block, we analyzed only lacustrine and palustrine wetlands and merged contiguous wetlands. Although NWI limitations are well-documented (50, 51), with omission errors seriously underrepresenting small wetland prevalence and extent (51), it provides the seamless, semantically consistent, national-scale dataset required to assess geographic patterns. Geographic isolation was defined where wetland Euclidean distance exceeded 10 m from line or polygon elements in the National Hydrography Dataset (NHD) (1:24,000 scale; nhd.usgs.gov/). This distance is based on reported NHD positional accuracy (12 m) and is consistent with previous studies (52, 53). Although NHD neglects drainage network temporal variation (50), it is the only viable national database for assessing stream proximity.

We enumerated the total number of wetlands, total wetland area, and total wetland perimeter and computed GIW contributions for each (Table 1). In all blocks, most wetlands were GIWs, consistent with local analyses (50). Although GIWs were a smaller portion of total wetland area, they contributed a greater proportion of total wetland perimeter in all blocks. Functions enhanced at wetland–upland edges (54) are thus likely to be disproportionately delivered by GIWs.

To test the hypothesis that GIWs are small, we used logistic regression between wetland size (log-transformed to meet normality assumptions) and geographic isolation. Although fitted slopes differed across blocks (Table 1), the probability of geographic isolation always declined dramatically with increasing size (black lines in Fig. 2). The odds ratio inferred from fitted slopes (Table 1) suggests that a log-unit increase in wetland size lowers the odds of geographic isolation three- to eightfold. GIWs as a class are unambiguously small.

Wetland size controls edge density. Cumulative distributions of wetland area and perimeter consistently diverged (dashed and stippled gray lines in Fig. 2), with perimeter rising faster than area, as expected. This divergence increases with wetland area variance and decreases where shape complexity is size-dependent. The relationship between area and perimeter-to-area ratio (P:A) (green dots in Fig. 2) shows how ecotone length varies with size. Small wetlands are more circular (in Fig. 2, dashed black line shows P:A for a circle) than larger wetlands, likely because of mapping resolution, because larger wetlands coalesce multiple depressions, yielding complex shapes, and because human activities impact wetland shape (55). Despite nonlinear scaling of edges (Fig. 2),

Table 1. The number, area, and perimeter of wetlands, and associated proportions from geographically isolated wetlands (GIWs) in eight domains (letters under GIW type are from Fig. 1)

GIW type	Domain coordinates	Total count (% GIW)	Total area, ha (% GIW)	Total perimeter, km (% GIW)	Pr[GIW] ~ area	Odds ratio
California vernal pools (A)	38.5N, 121.2W	2,163 (82.0)	1,337 (58.5)	584 (67.5)	$5.25-1.15 \times \log(A)$	0.317
Prairie potholes (B)	47.1N, 98.2W	6,417 (97.7)	9,509 (64.1)	2,068 (86.5)	$7.58-1.09 \times \log(A)$	0.336
Basin wetlands (C)	34.6N, 78.4W	6,507 (94.8)	36,097 (13.3)	5,638 (29.8)	$10.9-1.99 \times \log(A)$	0.136
Maine vernal pools (D)	43.5N, 70.6W	5,734 (68.2)	14,093 (16.5)	3,553 (32.0)	$6.29-1.53 \times \log(A)$	0.216
Playa lakes (E)	34.1N, 101.7W	420 (82.1)	2,841 (62.8)	386 (72.8)	$38.8-7.59 \times \log(A)$	<0.001
Cypress domes (F)	29.9N, 82.2W	3,801 (77.6)	27,980 (16.9)	3,490 (40.0)	$7.72-1.58 \times \log(A)$	0.205
Coastal plain (G)	31.6N, 82.0W	1,966 (87.4)	63,360 (10.2)	6,606 (20.4)	$7.89-1.36 \times \log(A)$	0.258
Pocosins (H)	34.6N, 78.4W	1,387 (73.5)	46,424 (7.1)	4,194 (17.1)	$6.74-1.33 \times \log(A)$	0.265

Logistic regression results describe the probability of geographic isolation (Pr[GIW]) as a function of wetland area (A) (m²); the odds ratio quantifies how the odds of geographic isolation change given a unit increase in log(A). All regression results were statistically significant ($P < 0.0001$).

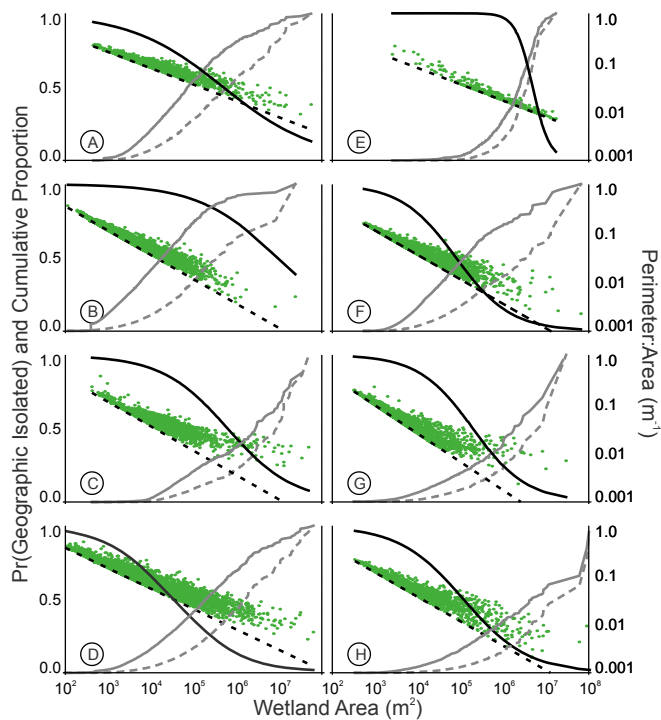


Fig. 2. Across blocks (A–H, maps in Fig. 1), the probability a wetland is geographically isolated declines with increasing wetland area (solid black lines). Small wetlands have higher perimeter-to-area ratios than larger wetlands (green dots) although large wetlands depart more from circular geometry (thick dashed black lines). The cumulative distribution of wetland perimeter (stippled gray lines) suggests that small wetlands provide a greater fraction of landscape total perimeter (ecotone) than total area (dashed gray lines), with implications for hydrologic, biogeochemical, and biological functions.

the inference that GIWs provide disproportionate edge density per area is clear.

Geographic separation (Euclidean distances) of wetlands vs. neighbors (nearest wetland) and vs. the drainage network (nearest stream) yields insights on the prevalence of wetland complexes. Although flow path distances may be more informative for hydrologic connectivity, measuring this distance requires high accuracy terrain and groundwater level data unavailable for all blocks. Nearest wetland (green dots in Fig. 3; all wetlands) and stream distances (yellow dots in Fig. 3; GIWs only because non-GIW distances are <10 m by definition) were similar across blocks. Fitted nearest wetland distances followed exponential scaling (except Playas), consistent with spatially random locations (gray lines in Fig. 3). Nearest wetland distances were also shorter than, and uncorrelated with, nearest stream distances, suggesting stronger interactions with nearby wetlands, forming complexes that impact landscape functions in aggregate. Nearest stream distances depended on wetland and drainage density (black lines in Fig. 3). In some landscapes (cypress domes, coastal plain, pocosins), stream distances were uniformly distributed up to ~350 m whereas a mode was evident in others (e.g., ~170 m in basin wetlands and ~810 m in prairie potholes) (Fig. 3). We infer that GIW distances from the streams are larger than expected at random, especially for playa lakes (Fig. 1), with implications for organism dispersal and habitat functions (56). Although links between connectivity strength and distance are uncertain, wetlands are clearly arrayed in a continuum of sizes and separation

distances. Although GIWs span the entire continuum, their size and spatial arrangement likely enable functions that wetlands that are larger or nearer streams do not support. Further, GIWs exist near other wetlands, likely forming complexes, and contributing to aggregate functionality (57) even when individual wetlands are far from streams.

Landscape Connectivity

Wetland are focal points for local catchments, and nodes within regional networks. Some functions impact the physical, chemical, and biological integrity of downstream waters, falling under CWA jurisdiction. Other functions, such as carbon storage, microclimate regulation, and endangered species habitat, fall outside that legal purview. Although protecting GIWs based on their full array of functions may be compelling, we consider here only hydrological, biogeochemical, and biological connectivity impacts on “traditional navigable” waters.

Hydrological Connectivity. A hydrologically isolated system would be both endorheic (i.e., no outflow) and ombrotrophic (i.e., entirely precipitation-fed), conditions that do not represent GIW hydrology. Although many natural GIWs (e.g., playa lakes, peat bogs) are ombrotrophic, to also be endorheic requires precipitation and evapotranspiration to balance over the long term. Persistent imbalances imply water flux across the system boundary, and thus hydrologic connectivity. Whether that connectivity extends to navigable waters is uncertain (e.g., outflows could evaporate before reaching such waters). However, a cautious assumption given the prevalence of wetland complexes (Fig. 3) is that flows eventually reach navigable waters despite indirect flow paths. A strictly endorheic system also creates hypersaline conditions from incremental evaporative solute enrichment. Although some GIWs, especially some prairie potholes, do have salinity indicative of prolonged hydrologic isolation (58), most exhibit only modest ion enrichment over rainwater (12, 58–63). It follows that GIWs connect to the hydrologic network over space and timescales sufficient to maintain low salinity, challenging assertions of hydrologic isolation.

Wetlands are storage nodes in flow path networks (64), with the mode and strength of hydrological connectivity varying with time and across wetland settings (Fig. 4A). For some settings, such as floodplain swamps, stream network connectivity is obvious and rapid, occurring bidirectionally as water flows into floodplains at high river stage, and reverses at lower stage (Fig. 4A) (65). For others, particularly GIWs that typically lack a persistent surface connection, hydrological connectivity may be less obvious. It occurs via unidirectional, episodic, and transient surface connections when depression storage is seasonally filled (e.g., vernal pools) (42, 65), or via slower moving subsurface flow paths (58, 66, 67). Despite uncertainty in quantifying timescales of hydrologic connectivity, GIWs have recently been shown to regulate (68, 69) and stabilize (70) potentiometric gradients that generate base flow in streams. These subsurface flow paths may be hard to see (71), but they are not speculative or insubstantial connections. Indeed, they are often large and quantifiable at both field and landscape scales (41, 66, 72–74). Crucially, the timescales of such connections are longer than for surface flow paths (75), manifest in base flow generation and water chemistry, implying potentially decadal delays in observing downstream effects of both wetland degradation and restoration activities.

Hydrological connectivity is temporally dynamic (Fig. 4A) (14, 15, 76, 77). Rainfall activates flow paths absent under drier conditions (16), and generally accelerates flow velocities. This effect is true across wetland types, with decreasing catchment travel times

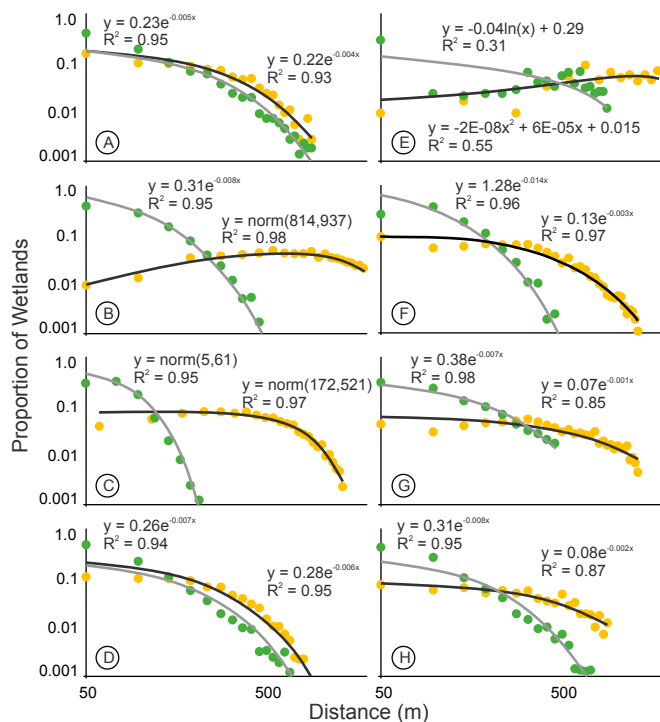


Fig. 3. Distributions of wetland distance to nearest wetland neighbor (green dots) and stream (yellow dots; GIWs only) for the eight landscape blocks (A–H, maps in Fig. 1). All fitted models (lines) were statistically significant ($P < 0.001$). Results suggest that GIWs exist in complexes with other wetlands, enabling cumulative landscape functions from interactions of numerous “similarly situated waters” even where stream distances are long.

as landscape wetness increases (Fig. 4A) (15), a process long referred to as variable source area runoff (72, 78). Such connectivity variation may be most pronounced in wetlands where fill-and-spill flow dynamics dominate because groundwater flow is limited by low permeability aquifers (41, 72). Vernal pools, for example, exhibit episodic surface connectivity, when rainfall fills depression storage, but slow groundwater connectivity during dry periods (79). Such bimodal connectivity highlights the role of depression storage in limiting peak flow frequency, magnitude, and duration and illustrates why snapshot assessments likely underestimate connectivity (20, 80).

Watershed responses are partly controlled by wetland number, area, and distribution, as well as connection paths (i.e., surface vs. subsurface) and velocities (Fig. 4B) (16, 81). Wetlands connected via perennial surface flow paths contribute dynamic storage during high flows (green in Fig. 4). In comparison, wetlands connected via intermittent fill-and-spill dynamics (yellow in Fig. 4) or via subsurface flow paths only (red in Fig. 4) constrain peak flow volumes, delay peak timing, impact recession rates, and control base flow (82). Indeed, recent modeling suggests that water storage in GIWs impacts downstream flow (69) and enables groundwater exchange, ultimately buffering stream flow variation (70). Watershed discharge integrates the entire continuum of hydrological connectivity, not just rapid or surface-connected flow paths.

Biogeochemical Connectivity. Wetlands are hotspots for sediment deposition (83), nutrient retention and transformation (84, 85), organic matter cycling and storage (27, 28), and metal and pesticide (86) immobilization. Predictably, downstream water quality

declines where wetlands are lost (87, 88). As with hydrologic functions, water quality functions likely vary with wetland connectivity and size (Fig. 4), but no systematic synthesis compares GIWs to other wetland types across biogeochemical functions.

Wetlands are important for sediment retention because low flow velocities (83) enhance settling and because plant sediment stabilization limits resuspension (87, 88). Because of their size (Table 1) and landscape position (surrounded by uplands, distant from streams) (Fig. 3), GIWs generally receive the first landscape flush of solutes and sediments, creating deposition and retention hot spots (41, 89). Low surface connectivity in GIWs also limits subsequent entrainment and export, providing long term storage (90).

Wetlands effectively retain nutrients, preventing downstream transport. However, nutrient retention efficiency for GIWs vs. other wetlands remains unknown, necessitating inference by analogy to streams and lakes. Stream nutrient retention decreases with increasing size because of variation in the following: (i) channel morphology that controls contact between solutes and sediments (91); (ii) chemical gradients (i.e., concentration, redox potential) (92) that controls reaction rates; and (iii) allochthonous inputs per unit storage (91, 93). Similar size-dependent functionality has been shown in lakes for plant biomass (94), organic and mineral burial (95), species richness (96), and fish yield (97), implying that small lakes contribute disproportionately to landscape functions (98). Four attributes of GIWs suggest similar size-dependent variation in biogeochemical reactivity. First, high primary production and anaerobic soils in GIWs enable retention of metals, nutrients, and pesticides in organic matter (99), and processes such as denitrification that remove nitrogen (100, 101). Second, like headwater streams and small lakes, GIWs dominate the total number of wetlands (Table 1) and generally occupy headwater positions (Fig. 3). Thus, GIWs interact first with solute and particle fluxes off the land, leading to dramatically enhanced reactivity (102). Further, GIWs likely exchange water and solutes with other wetlands before discharge to the drainage network; this wetlands-in-series configuration can enhance retention efficiency (41, 89). Third, GIWs are small (Fig. 2) (38, 64, 103), with high perimeter length per unit area (Fig. 2). Size-dependent reactivity in streams (91) and lakes (95, 98) is controlled by edge-to-area geometry. By analogy, because GIWs have high perimeter:area (Fig. 2), we expect commensurate increases in reactivity. An inverse correlation between wetland size and water quality (104) supports this inference. Finally, long residence times due to intermittent or slow connections (105, 106) facilitate completion of kinetically limited reactions (e.g., P sorption into minerals, complex organic molecule mineralization), enhancing sink functions. Although maximum retention efficiency occurs when reaction rates and residence times align (107), loss of high reactivity and long residence time landscape elements alters overall fluxes, particularly when GIWs are embedded in solute-generating areas (e.g., where fertilizer is applied) (101). Timescales for detecting changes may be long (75), indicating impacts principally to base flow chemistry. Inferences based on nutrients apply to other contaminants [metals (108) and pesticide (109)], where retention is enabled by low redox conditions and organic matter storage, common features of all wetland settings, including GIWs (28).

Wetlands spanning the entire connectivity continuum protect water quality, with GIWs likely playing important roles in sediment retention, base flow chemistry, and solute retention where residence time is a key determinant of retention efficiency. Moreover, it is precisely by performing functions along slow-velocity flow paths to the drainage network, an attribute interpreted as weak

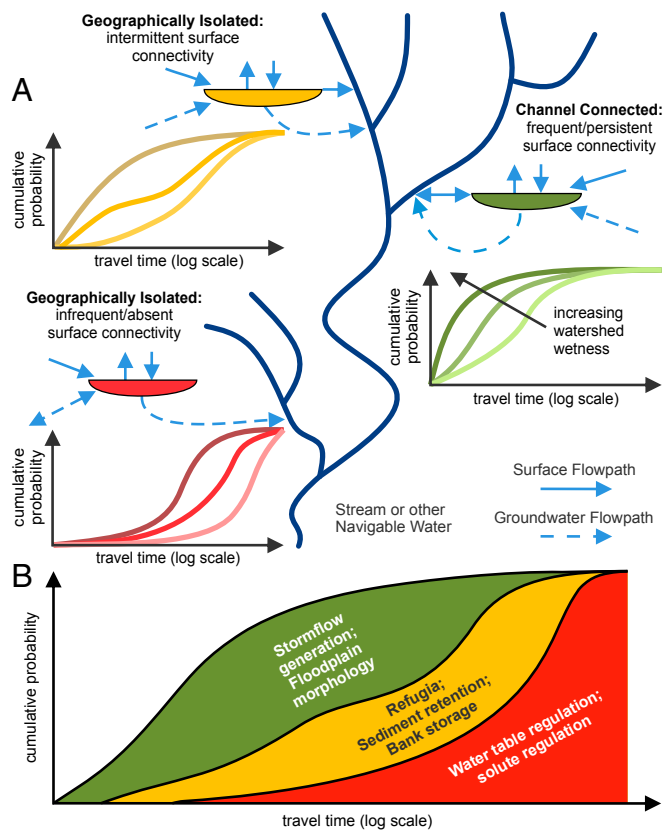


Fig. 4. (A) Hydrological connectivity between wetlands and downstream waters varies in space and time. Watershed travel time distributions are shortest for wetlands with persistent surface connectivity (green), intermediate (and bimodal) for wetlands with episodic surface connectivity (gold), and longest for wetlands without surface connections (red). Travel time distributions decline with increased watershed wetness. (B) Convolution of travel times means watershed exports are impacted by wetlands spanning the connectivity continuum. Differential protections across wetlands alter connectivity patterns and impact watershed functions and related ecosystem services.

connectivity, that high rates of solute and particulate matter retention are enabled.

Biological Connectivity. Variation in wetland connectivity affects biota and, thus, ecological condition (60, 61) within and across wetlands (110–113). However, biological connectivity, unlike water and solutes, is not always constrained by flow direction. For organisms that move over land or through air, connections among nodes are constrained by terrestrial landscape properties and species traits, rather than hydrologic flow paths (111). Organism movement among habitat patches occurs in response to ecological processes operating at multiple spatial scales. Travel distances also vary in time, responding strongly and nonlinearly to climate forcing (114), fire and other natural disturbances, and human impacts. Wetlands contiguous to surface dispersal pathways (e.g., streams, flyways) or near refugia (e.g., lacustrine habitats) differ in community structure from wetlands where dispersal is restricted, or desiccation more frequent, either due to shallow basin form or exclusively subsurface hydrologic connectivity (113).

Geographic isolation does not imply biological isolation (115) but can constrain aquatic plant and animal movement. Spatial and temporal heterogeneity in the frequency, timing, and duration of connectivity affects water-mediated movement and thus

community composition (116), with historical connectivity imprinted on contemporary diversity patterns (117). Geographic isolation selects plants with long-lived seeds (118) or long-distance dispersal strategies (e.g., via fauna or wind) (113), and animals such as amphibians that require competitor exclusion for all or part of their life cycles (119), or that rely on dynamic heterogeneity in aquatic resources (120, 121). For example, increased nearest wetland distance reduces local species richness of both native and nonnative fauna (36) and flora (113) but enhances both landscape biodiversity (122, 123), by creating taxonomically distinct communities, and meta-population stability (124), by creating spatial heterogeneity in the drivers of subpopulation dynamics. Frequent dry conditions and the absence of persistent surface connectivity can preclude fish population establishment or recruitment after extirpation (35, 125). Fish preclusion has implications for survival of juvenile amphibian, crustacean, and insect fauna (32, 126–128), many of which disperse as adults to upland habitats or downstream water bodies. Indeed, models predict that loss of GIW habitats would impact a wide array of fauna, not just permanent residents, and most prominently, turtles, amphibians, birds, and small mammals (36), many of which are imperiled (38). That many organisms use both GIWs and downstream waters [turtles (129), birds (130, 131), snakes (132), and alligators (30)], in different seasons (121) or life stages (30, 133), illustrates that the entire connectivity continuum, including GIWs, impacts habitat heterogeneity and redundancy, regional biodiversity, and, thus, the biological integrity of downstream waters.

Humans Alter Connectivity

Although losing wetland area poses the most obvious threat, changing wetland connectivity also impacts landscape functions, and humans have altered the continuum of connectivity (134). Modifications to reduce flood risks increase connectivity in headwater areas (e.g., via agricultural ditches, hardened urban streams, and drainage canals) and reduce connectivity downstream (e.g., via levees disconnecting river and floodplain). Coupled to systematic losses of some network elements (135), especially small wetlands (55), these changes impact the time and space variation of connectivity (66). Wetland losses are strongly biased toward removing wetlands far from drainage features, changing network topology (55), and impacting services derived from longer residence times, including sediment storage (87), nutrient and floodwater retention (25, 87), and controls on flood timing and magnitude (136). Network changes also impact aquatic ecosystem structure (137) and composition (24, 113) by affecting dispersal (17, 138, 139). Land use intensification (i.e., cropping, urbanization) also leads to more regular wetland shapes (55), lowering perimeter-to-area ratios and impacting functions associated with wetland edges (140). By short-circuiting or removing GIW storage, water, solute, and sediment retention functions are lost. By changing distances between wetlands (e.g., by removing GIWs), preferentially protecting large or perennially connected wetlands, and changing land cover between wetlands, crucial biological functions have also been lost (43).

Science and Policy Challenges

Conservationist and writer Aldo Leopold once remarked in reference to species protection that “to keep every cog and wheel is the first precaution of intelligent tinkering.” We apply this advice to protecting healthy landscapes. Wetlands connect to other water bodies, including downstream waters along a time-varying continuum of connectivity, from permanent to transient, from fast to slow, and from principally surface to exclusively subsurface flow paths. Landscape functions arise from the cumulative effects of the

full complement of connection types and strengths. As such, selectively eliminating some connection types and protecting others inadvertently prioritizes some functions over others, without adequate rationale. The significant nexus test explicitly requires regulators and the regulated community to evaluate the functions that GIWs provide. Our analysis and synthesis suggests that GIWs, which generally have less frequent or slower hydrologic connections than other wetlands, support a multitude of landscape functions, enhancing many, and provide some that other wetlands do not. As such, there is no obvious and nonarbitrary connectivity threshold (e.g., based on travel distance or time) to designate protections for downstream waters. Even before the Supreme Court decisions to limit federal protections, many GIWs were lost (52). Those that remain are imperiled by alterations to their geometry, connectivity (141, 142), surrounding land cover, and now legal protections. Although the consequences of these changes require further research, GIW losses alter the portfolio of landscape connectivity with negative effects on downstream waters. As the scientific community increasingly recognizes

and quantifies the frequency, timing, and duration of wetland connectivity across multiple flow paths, and the myriad ways in which weak or slow connectivity is important, a logical and precautionary inference is that all wetlands influence landscape functions.

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