Published in final edited form as:

*J Am Water Resour Assoc*. 2018 March 01; 54: 346–371. doi:10.1111/1752-1688.12633.

# HYDROLOGICAL, PHYSICAL, AND CHEMICAL FUNCTIONS AND CONNECTIVITY OF NON-FLOODPLAIN WETLANDS TO DOWNSTREAM WATERS: A REVIEW[1]

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## Abstract

We reviewed the scientific literature on non-floodplain wetlands (NFWs), freshwater wetlands typically located distal to riparian and floodplain systems, to determine hydrological, physical, and chemical functioning and stream and river network connectivity. We assayed the literature for source, sink, lag, and transformation functions, as well as factors affecting connectivity. We determined NFWs are important landscape components, hydrologically, physically, and chemically affecting downstream aquatic systems. NFWs are hydrologic and chemical sources for other waters, hydrologically connecting across long distances and contributing compounds such as methylated mercury and dissolved organic matter. NFWs reduced flood peaks and maintained baseflows in stream and river networks through hydrologic lag and sink functions, and

[1]Paper No. JAWRA-17-0073-P of the *Journal of the American Water Resources Association* (JAWRA).

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Former JAWRA Editor Kenneth J. Lanfear served as acting editor in chief for all articles in this featured collection. Parker J. Wigington, Jr., an author on some of the collection papers and who was JAWRA editor in chief at the time the collection was submitted, had no role in the review or editorial decisions for any part of the collection.

sequestered or assimilated substantial nutrient inputs through chemical sink and transformative functions. Landscape-scale connectivity of NFWs affects water and material fluxes to downstream river networks, substantially modifying the characteristics and function of downstream waters. Many factors determine the effects of NFW hydrological, physical, and chemical functions on downstream systems, and additional research quantifying these factors and impacts is warranted. We conclude NFWs are hydrologically, chemically, and physically interconnected with stream and river networks though this connectivity varies in frequency, duration, magnitude, and timing.

### Keywords

connectivity; function; non-floodplain; river networks; wetlands

## INTRODUCTION

Wetlands are landscape elements existing along a continuum of connectivity, climatically and hydrologically interacting with other landscape elements through space and time (Ward 1989; Cohen et al. 2016). Instream, riparian, and floodplain wetlands experience fast and/or near-continuous hydrologically mediated connections and interactions. Wetlands are also connected through extremely slow or diffuse pathways (e.g., deep groundwater or atmospherically connected; Rains et al. 2015; Cohen et al. 2016). Researchers are using increasingly advanced and novel methods to quantify wetland locations along this conceptual connectivity continuum (e.g., Jones 2015; Klaus et al. 2015; Vanderhoof et al. 2016; Brooks et al. 2018; Thorslund et al., unpublished data).

Wetlands are functionally part of the landscape, performing hydrological, chemical, and biological functions affecting downstream systems (e.g., Marton, Creed, et al. 2015; Rains et al. 2015; Cohen et al. 2016; Biggs et al. 2017; Schofield et al. 2018). Paradoxically, some functional contributions of wetlands might be inversely related to their rate of connectivity or position along the connectivity continuum (i.e., slower connections could result in larger effects). For instance, wetlands that intercept storm runoff store water and process entr materials (e.g., nutrients). While the subsequent connection with downstream waters may be slow or diffuse (e.g., via groundwater or atmospheric), the functional effect of retaining nutrients and stormwater may be great.

However, functional connections for wetlands are challenging to quantify, requiring elucidation of both the connection pathway and the variable of interest. Descriptors of connectivity include the frequency, duration, magnitude, timing, and rate of change of fluxes to, and exchanges with, downstream waters (Poff et al. 1997; Poff et al. 2007). Current estimates are that ~45 million wetland hectares exist in the conterminous United States (U.S.) (Dahl 2011), and each hectare exists along a continuum of connectivity. There is thus a need to analyze and synthesize the available peer-reviewed scientific literature on the connectivity and quantifiable functional effects of wetlands on other waters to establish a baseline understanding of the interchange of materials, organisms, and energy among and between landscape elements (e.g., Hynes 1975; Forman 1995). This information, the connectivity and effects of wetlands on other waters, provides management agencies and stakeholders with information germane to the sustainable use and management of aquatic resources. Armed with sufficiently robust scientific information, federal, state, and local agencies can endeavor to establish and promulgate guidelines and regulations designed to safeguard aquatic resource integrity while concurrently providing guidance on wise management and growth.

To address this data need, the USEPA (2015) analyzed and synthesized over 1,300 peer-reviewed publications in a 408-page report, summarizing the state of science on the connectivity between streams, wetlands, and downgradient systems, which is the topic of this featured collection (Alexander et al. 2018). Connectivity as used by USEPA (2015, A-2; Leibowitz et al. 2018) and maintained here in this updated review refers to "[t]he degree to which components of a river system are joined by various transport mechanisms; … determined by the characteristics of both the physical landscape and the biota of the specific system." The primary transport mechanisms considered in this expanded and updated review are surface water and shallow groundwater flows and the transport and transformation of physical and chemical materials, all of which connect watersheds in four dimensions (i.e., longitudinal, lateral, vertical, and temporal, Ward 1989; see also Covino 2017).

This contribution, as well as others (e.g., Alexander et al. 2018; Fritz et al. 2018; Goodrich et al. 2018; Leibowitz et al. 2018; Schofield et al. 2018), builds on the findings of USEPA (2015) with updated literature and scientific advances in quantifying aquatic system connectivity. While USEPA (2015) addresses wetlands in riparian and floodplain areas as well as wetlands not so situated, this review is specifically focused on hydrological, physical, and chemical connectivity of non-floodplain wetlands (NFWs), freshwater wetlands not spatially located within riparian areas or floodplains of river networks, further described below. In the U.S., NFWs may cover more than 6.6 million hectares and comprise >16% of the total freshwater wetland acreage (Lane and D'Amico 2016; Figure 1). Biological connectivity and functions of NFWs are covered in a separate review (Schofield et al. 2018). The review is organized into the following sections: (1) Definitions and Conceptual Approach; (2) Hydrological, Physical, and Chemical Functions of NFWs; and (3) Synthesis and Implications.

## EFINITIONS AND CONCEPTUAL APPROACH

### Floodplain and Non-Floodplain Wetlands: Definitions

All rivers and streams have riparian areas, defined as transitional zones between terrestrial and aquatic ecosystems distinguished by gradients in biophysical conditions, ecological processes, and organisms. However, not all portions of river and stream networks — the hierarchical, interconnected populations of perennial, intermittent, and ephemerally flowing channels that drain water to a river — have floodplains. Floodplains are level areas bordering stream or river channels that are formed by sediment deposition from those channels under present climatic conditions. Floodplain and associated river channel forms (e.g., meandering, braided, anastomosing) are determined by interacting fluvial factors, including sediment size and supply, channel gradient, and streamflow (Church 2002, 2006). As stream channels increase in size and decrease in slope, a mixture of erosion and deposition processes usually is at work. At some point in the lower portions of river networks, sediment deposition becomes the dominant process and floodplains form. Floodplains are inundated during moderate to high water events (Leopold 1994; Osterkamp 2008).

Like riparian areas, wetlands are transitional areas between terrestrial and aquatic ecosystems. Wetlands include areas such as swamps, bogs, fens, marshes, ponds, and pools (Mitsch et al. 2009). According to Cowardin et al. (1979), an area is classified as a wetland if it has one or more of the following three attributes: (1) the area supports predominantly hydrophytes (i.e., water-loving plants) at least periodically; (2) the land has substrate that is predominantly undrained hydric soil; or (3) the land has nonsoil substrate that is saturated with water or covered by shallow water at some time during the growing season of each year. Note that the Cowardin et al. (1979) definition requires only one of these characteristics, in contrast to the U.S. federal regulatory definition, which requires all three (33 Code of Federal Regulations 328.3(b); see also USACE 1987). Thus, as used in this review, a wetland need not meet the U.S. federal regulatory definition.

Floodplain wetlands are portions of floodplains that meet the aforementioned Cowardin et al. (1979) definition of a wetland. Floodplain wetlands have hydrologic connections to streams and rivers that are predominantly bidirectional (i.e., from wetlands to streams and rivers and vice versa) through lateral movement of surface water and groundwater between the channel and floodplain areas, either through overbank flooding (i.e., lateral expansion of the network) or hyporheic flow (USEPA 2015).

NFWs are found in landscape settings where the potential exists for predominantly unidirectional, lateral hydrologic flows from wetlands (sensu Cowardin et al. 1979) to the river network through surface water or groundwater. Such a setting would typically include upgradient areas such as hillslopes or upland areas outside of the floodplain (e.g., Lane et al. 2017). Any wetland setting where water could normally only flow from the wetland toward a river network (i.e., unidirectionally) would be considered a non-floodplain setting, regardless of the magnitude and duration of flows and of travel times (sensu Ward 1989).

Thus, the terms “floodplain” and “non-floodplain” are meant to describe the landscape setting in which wetlands occur and do not refer to a particular Cowardin et al. (1979) wetland type or class. Many wetland types occur in both settings. For example, a palustrine emergent wetland (Cowardin et al. 1979) could be located outside a floodplain, or it could be located within a floodplain and subject to bidirectional hydrologic flows. A wetland that is classified as depressional in the hydrogeomorphic approach could have any combination of inlets and outlets or none at all (Smith et al. 1995). Such a wetland would be grouped with floodplain wetlands if it had both an input and output channel, since it would have bidirectional flow. A depressional wetland with a surface outlet channel and no inlet or with no outlets and inlets, however, would be considered non-floodplain because water could flow downgradient only from the wetland to the river network, and not from a stream to the wetland. For instance, wetlands that serve as origins for streams are grouped with NFWs because they have unidirectional flow through their outlet channel.

Hence, the hydrologic connections with river networks fundamentally differ for floodplain wetlands and NFWs. Hydrologic connections between NFWs and river networks originate via surface water spillage or merging, or near-surface groundwater flow when water inputs exceed outputs (e.g., evapotranspiration, deep groundwater loss) and available storage. A major consequence of the two different landscape settings is that while waterborne materials can be transported only from the NFW to the river network, waterborne materials can be transported both from the floodplain wetland to the river network and from the river network to the floodplain wetland (see Fritz et al. 2018). In the latter case, there is a mutual, interacting effect on the structure and function of both the floodplain wetland and river network. In contrast, a NFW can materially affect a river through the transport of waterborne materials, but the opposite is generally not true. Note that we limit our use of floodplain and non-floodplain landscape settings to the direction of hydrologic flow; the terms cannot be used to describe directionality of geochemical or biological flows. For example, mobile organisms can move between a stream and NFW and vice versa (e.g., Subalusky et al. 2009a, b; Mushet et al. 2013). In Alaska, transport of live salmon or their carcasses from streams to riparian areas by brown bears (*Ursus arctos*) accounts for more than 20% of riparian nitrogen budgets (Helfield and Naiman 2006). Although this example is in a floodplain setting, it shows how geochemical fluxes can be decoupled from hydrologic flows. Furthermore, we recognize that there may be exceptions to our unidirectional flow paradigm. For instance, flooding events may create conditions that belie the typical unidirectional flow regime. We consider the “normal” or typical flow patterning in determining the flow regime, though that, too, is replete with qualifiers.

## Wetland Functions in This Review

Leibowitz et al. (2008) identified three functions by which wetlands (and streams) influence material fluxes into downstream waters: source, sink, and refuge. USEPA (2015) expanded on this framework to include two additional functions: lag and transformation (Leibowitz et al. 2018). These five functions (summarized and defined in Table 1) provide the conceptual framework for understanding how physical and chemical connections between NFWs and downstream waters influence river systems. This rubric similarly provides a framework to link other landscape elements (Forman 1995) within watersheds (i.e., providing a means to compare functions between streams, floodplain wetlands, and NFWs; USEPA 2015). This review focused on four of the five functions: source, sink, transformation, and lag in NFWs. Schofield et al. (2018) analyze biological connectivity and the refuge function of streams, floodplain wetlands, and NFWs.

## Literature Review Approach

We focused entirely on peer-reviewed, publicly accessible sources of information about surface water and shallow (or near-surface) groundwater connections and interactions of NFWs that influence the function and condition of downstream surface waters. We conducted keyword searches using terms including the types of waters, connections, and downstream effects of interest (e.g., [wetland* AND [river* OR stream*] AND [connect* OR isolat*]]). We used science citation databases and search engines available through Web of Science and Google Scholar to search primary (original research) and secondary (review) literature. These searches included references citing or cited in relevant publications obtained through initial searches. We additionally reviewed and included citations provided by peer-review panels and in public comments on drafts of the USEPA (2015) report, which we co-authored. In addition, we expanded and updated the findings from USEPA (2015) by incorporating recently published material in this review. Finally, as most authors do not use the aforementioned term "non-floodplain wetland" in describing their study objects, we ascribed wetland typology and setting based on information in the paper and/or our knowledge of the study areas available in the peer-reviewed literature.

# HYDROLOGICAL, PHYSICAL, AND CHEMICAL FUNCTIONS OF NFWS

We examined the NFW literature and herein report findings demonstrating source, sink, transformation, and lag functions with potential links to downstream systems. We then review the hydrologic and physical pathways by which NFWs may affect downstream waters. Finally, we couple the two, providing updated analyses and syntheses of our findings from the literature on the individual and cumulative effects of NFWs on downstream waters.

## NFW Source Function

**Hydrologic Source.—**An NFW functions as a hydrologic source to downgradient ecosystems when total water inputs minus outputs (e.g., evapotranspiration, groundwater recharge) exceed the storage capacity of the wetland basin and subsequent outflow connects it via surface water to another aquatic system. This occurs when water inputs to the wetland — contributing area precipitation (including snowmelt) and saturation excess flow or near-surface groundwater discharge — fill the available soil pore space and topographic volume of NFWs. Subsequent inputs minus outputs exceed total wetland storage capacity and flow through a surface or near-surface water pour-point downgradient in what has been termed "fill-and-spill" hydrology (Spence and Woo 2003; Tromp-van Meerveld and McDonnell 2006).

NFWs can serve as the hydrologic sources or origins of headwater streams (Fergus et al. 2017; Fritz et al. 2018) when the unidirectional excess flow continues directly into an adjacent, downgradient stream system (USEPA 2015; Figure 2a). These surface connections can be perennial, intermittent, ephemeral, or episodic. White and Crisman (2016) reported that 90% of headwater streams analyzed across Florida originated from wetlands and seeps (a type of NFW). Perennial streams emanated from wetlands more frequently than impermanent streams, while the opposite was found for seeps (White and Crisman 2016). Seeps, springs, and some wetlands are expressions of groundwater at the surface (e.g., Winter and Rosenberry 1995; Euliss et al. 2004; Hayashi et al. 2016). Morley et al. (2011) reported that NFWs primarily supplied by groundwater discharge (i.e., seeps) provided 40%–80% of the water volume for the streams to which they were connected via perennial surface flow. Tufford (2011) monitored four headwater seepage wetlands in the South Carolina Coastal Plain and found that the water table dynamics varied seasonally and annually, intermittently creating hydrologic sources that connected NFW seeps to a downgradient floodplain through swales (i.e., landscape features lacking defined beds and banks or channels that convey flow especially during storm events or snowmelt; USEPA 2015; e.g., Figure 2b).

In addition to a wetland filling and spilling and reaching the stream network, wetlands can also fill-and-merge within a basin (Huang et al. 2011; Barton et al. 2013; Leibowitz et al. 2016; Wu and Lane 2016), creating NFW complexes that frequently exchange materials within and among the surface water–connected wetland systems (Figure 3; Wu and Lane 2016; Calhoun et al. 2017). Like fill-and-spill wetlands, fill-and-merge wetlands are hydrologic sources when the maximum capacity of the bounding basin is exceeded and the wetland complex connects via continuous surface water to another aquatic system (Shaw et al. 2012; Wu and Lane 2017). That is, fill-and-merge wetlands become fill-and-spill systems when the internal storage is exceeded and no additional merging can occur within a given basin (see also the discussion on NFW Hydrologic Lag Functions, below).

While part of the hydrologic cycle (see Cohen et al. 2016), water in these wetland complexes may or may not eventually connect as surface water or near-surface groundwater into a stream network. For instance, Wilcox et al. (2011) found that nearly 20% of precipitation that fell on a Texas Gulf Coast complex of depressional wetlands spilled into a nearby water body, the Armand Bayou, over a four-year study period. By contrast, Vanderhoof and Alexander (2016) examined two nonadjacent Landsat imagery path/row combinations in the Prairie Pothole Region (PPR) across both drought and deluge conditions over a 21-year period and reported that under wet conditions, 21% of the wetlands merged with at least one other wetland and 7% of wetlands connected with lakes and streams, most via connecting to other “stepping-stone” wetlands (Vanderhoof and Alexander 2016). Vanderhoof et al. (2016) and Vanderhoof et al. (2017) showed that filling and merging of wetlands, and of wetlands and streams, was a function of landscape position relative to other aquatic systems as well as antecedent and prevailing hydrologic conditions. Brooks et al. (2018) conducted a water isotope analysis of surface water origins in a watershed within the PPR, determining that NFWs cumulatively contributed water to streamflow in 11 of 12 sampling events (based on the surface water evaporative enrichment signal in the stream). They furthermore determined that the surface (or near-surface) water connections between the NFWs and the stream networks occurred year-round and that landscape storage and subsequent downgradient flow sustained flow in the stream network.

The scientific literature we found focused primarily on wetland-to-wetland connectivity, not wetland-to-stream. Nevertheless, the literature on wetland-to-wetland connectivity demonstrates NFWs exhibiting surface water connections with other water bodies, while illustrating the variable nature of these hydrologic connections. For instance, Leibowitz and Vining (2003) reported that fill-and-spill dynamics affected 28% of NFWs within a 40-$km^2$ area in the PPR of North America, including 22 wetland complexes (i.e., two or more connected wetlands) during a wetter-than-average year. Conversely, none of the connections observed by Leibowitz and Vining (2003) existed in a drier year. Bowling et al. (2003) analyzed a 471 $km^2$ Alaskan watershed using synthetic aperture radar and reported inundation and connectivity of wetlands and tundra varied between 15% and 67% over two years, depending on available antecedent surface water storage. Leibowitz et al. (2016) explored longer term connectivity in the PPR, determining that some wetlands were filling and spilling to other wetlands over days to weeks, whereas others connected via fill-and-merge hydrology were surficially connected over decades. Kahara et al. (2009) analyzed typological changes in the abundance of different NFW basins, reporting that wetland merging increased with increasing annual precipitation and this changed the abundance of different NFW types (e.g., temporary, seasonal, and semipermanently inundated or saturated wetlands). For instance, one area of the PPR showed decreases in the areal extent of temporary (−47%) and seasonal (−25%) NFWs with increased precipitation, but these losses were offset by concomitant increases in semipermanent wetland area (+185%).

Hydrologically connected wetlands have different physical and hydrologic source properties than relatively unconnected systems. Cook and Hauer (2007) found wetlands that merged due to snowmelt in a Montana prairie setting had longer hydroperiods and volume, as well as higher specific conductance and primary productivity, than nonmerged wetlands. Similarly, Leibowitz et al. (2016) reported differences in dissolved ions, water levels, and macroinvertebrates between merged wetlands and those that did not merge but connected over shorter durations via fill-and-spill hydrology. These field-based measures may inform future connectivity assessments. For instance, Ali et al. (2017) recently developed an electrical conductivity (EC) indicator of potential groundwater-driven wetland-to-stream connectivity. Similarly, Thorslund et al. (unpublished data) analyzed stream and NFW chloride concentrations across several North American study sites; a mass-balance analysis demonstrated NFWs were active sites of catchment-scale flow-generation, though with abundant local to regional heterogeneity.

NFWs can recharge near-surface and deeper groundwater (see Figure 2c), or function simply as an aquatic system embedded within an upland or terrestrial area and not as a vertical or lateral hydrologic "source" for any other waters (e.g., see Figure 2d, Hayashi et al. 2016; but see Cohen et al. 2016). For instance, Hayashi et al. (1998a, b) demonstrated that a NFW received 30%–60% of snowmelt runoff from its basin, but that summer evapotranspiration at the wetland margin effectively removed an abundance of the runoff into the wetland, leaving little water for deep-groundwater recharge (see NFW Sink Function, below).

Much of the literature on NFWs as hydrologic sources has focused on stream baseflow. Groundwater discharge wetlands connected via overland/near-surface flow to streams, such as fens or seeps (e.g., Tufford 2011), are important sources of stream baseflow (Morley et al. 2011). Moreover, as noted, wetlands can be focal points for groundwater recharge, which may contribute to baseflow. Rains (2011), for example, found that perched and flow-through wetland ponds in southwestern Alaska were sites of net groundwater recharge. Given the high prevalence of ponds on the landscape (Rains 2011), these wetlands could substantially affect stream baseflow via groundwater inputs (see Groundwater Connectivity below).

In summary, NFWs are hydrologically dynamic, and are frequently sources of surface waters to other wetlands and other aquatic bodies. NFWs serve as the hydrologic origins or sources of headwater streams (White and Crisman 2016; Fritz et al. 2018). An abundance of research in the North American PPR has demonstrated fill-and-spill and fill-and-merge behaviors, as well as surface water connections to stream and lake systems (e.g., Vanderhoof and Alexander 2016; Vanderhoof et al. 2016; Vanderhoof et al. 2017; Brooks et al. 2018). NFW fill-and-spill behavior occurs in other physiographic regions (e.g., California vernal pools, Rains et al. 2006; Delmarva Ponds, Jones et al. 2018) suggesting similar controlling landscape and climatological factors. Wetlands that merge or connect with other systems

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were found to substantially affect the physical and chemical characteristics of the receiving water (e.g., Cook and Hauer 2007; Leibowitz et al. 2016; Ali et al. 2017; Brooks et al. 2018).

**Chemical Source.—**NFWs can be major chemical sources to other waters, contributing dissolved organic compounds (e.g., Mulholland and Kuenzler 1979; Urban et al. 1989; Eckhardt and Moore 1990; Koprivnjak and Moore 1992; Kortelainen 1993; Clair et al. 1994; Hope et al. 1994; Dillon and Molot 1997; Gergel et al. 1999), methylated mercury (MeHg) (St. Louis et al. 1994; Ullrich et al. 2001), nutrients (e.g., phosphorus, Flaig and Reddy 1995; Lane and Autrey 2016), and salts (e.g., Hayashi et al. 1998a, b; Euliss et al. 2004; Heagle et al. 2013; Nachshon et al. 2014; Ali et al. 2017). For instance, boreal forest basins composed of NFWs in central Ontario, Canada, exported between 11.4 and 31.5 kg C/ha/yr as dissolved organic carbon to downstream waters (Creed et al. 2003). While dissolved organic materials such as carbon are important sources of energy for aquatic communities (Hobbie 1992; Reddy and DeLaune 2008), they can have negative effects on downstream waters because contaminants, such as MeHg (see below) can adsorb to dissolved organic matter (Thurman 1985; Driscoll et al. 1995) and under some conditions dissolved organic compound exports can increase the acidity of downstream waters. For instance, Gorham et al. (1986) addressed watershed factors associated with lake and forest acidification in Nova Scotia, Canada. In addition to atmospheric deposition of acid precipitates, they found that the ratio of non-floodplain muskeg peatlands to lakes was significantly correlated with lake acidification, as muskeg wetland–dominated watersheds exported high-molecular-weight organic acids via either overland or shallow groundwater flow. Further linking NFWs to lakes, Gorham et al. (1986) reported that even small amounts of dissolved organic carbon can greatly affect lake water pH; the pH of waters with a dissolved organic carbon value of 4.5 mg/L (the log-normal mean) was 100 times more acidic than waters with a dissolved organic carbon value of <1 mg/L (the minimum concentration).

Wetland soils are important sources of methylmercury, a particularly toxic and mobile form of the element frequently entrained and transferred downgradient with dissolved organic compounds (Grigal 2002). Mercury enters the global atmosphere primarily through waste incineration and coal combustion; it can directly enter wetland systems or can be deposited on terrestrial areas and then transported into riparian areas and wetlands via rainfall and runoff (St. Louis et al. 1994). Ullrich et al. (2001) noted that methylmercury production was linked to low pH, low salinity, and presence of decomposable organic matter in reducing environments, factors that are present in wetlands. The redox conditions found in the presence of a fluctuating water table are thought to be a strong driver of mercury methylation (Heyes et al. 2000; Branfireun and Roulet 2002; Branfireun 2004). Once formed through microbial or other processes in wetlands, mercury and methylmercury export is controlled by the export of organic matter, such as dissolved organic compounds and humic and fulvic acids (Linqvist et al. 1991; Mierle and Ingram 1991; Driscoll et al. 1995). For example, Branfireun et al. (1996) reported 58% of MeHg-laden peat porewater leaving a headwater catchment study area occurred during stormflow, 41% during baseflow, and 1% transported via groundwater. St. Louis et al. (1994) found that boreal forest catchments in Minnesota with NFWs had lower total mercury concentrations than catchments lacking

NFWs, but had yields of MeHg from wetlands that were 26–79 times higher than upland areas. This yielded 1.84–5.55 mg MeHg/ha/yr to streams in the Great Lakes basin, where mercury could be incorporated into lake-wide food webs. Porvari and Verta (2003) found that bioaccumulating methylmercury export from non-floodplain peatlands to downstream waters ranged from 0.03 to 3.8 ng MeHg/L, and that catchments with greater wetland abundances had greater methylmercury export.

Nutrients that are mobilized into wetlands via near-surface runoff may create high concentrations in the wetland soils (Flaig and Reddy 1995; Reddy and DeLaune 2008; Hoffmann et al. 2009). The nutrients may stay absorbed to (or bonded with) the soils until a rainfall or precipitation event creates a concentration gradient in the wetland such that the nutrients, such as phosphorus, are released from the soil into the water column (see Chemical Sink function, below). For example, a suggested agricultural nutrient runoff management practice to decrease nutrient loading to Lake Okeechobee, Florida, suggested by Flaig and Reddy (1995) is to use NFWs for phosphorus assimilation. However, they note that the capacity is finite and, furthermore, that the NFWs could become nutrient sources if loading rates are high enough and the wetlands are subsequently connected (e.g., via ditches or major precipitation events). Lane and Autrey (2016, 45) analyzed phosphorus (P) concentrations in NFWs across Florida and concluded that NFWs "… have high potential to retain P, but that the entrained P may be remobilized … depending on storm and groundwater input P concentrations." Hoos et al. (2013) found nitrate-nitrogen concentrations in streams to be positively associated with the abundance of a likely NFW type (East Gulf Coastal Plain Near-Coast Pine Flatwoods) in their application of the SPARROW (Spatially Referenced Regression on Watershed Attributes) model. They hypothesized that the short-term hydroperiod of the NFWs created aerobic conditions for nitrate formation in wetland soils, and (similar to phosphorus example above) the nutrients were mobilized during precipitation events that connected the wetland to the stream (including shallow groundwater flows).

NFWs can also be sources of elevated salts which, like mercury, can originate in wetland catchments and be entrained or dissolved and hydrologically transported to NFWs. Hayashi et al. (1998a, b) noted that snowmelt in a PPR non-floodplain basin transported 4–5 kg/yr of chloride from the surrounding area to the wetland, suggesting a sink function. However, with growing-season evapotranspiration, the solute also moved from the wetland into the surrounding upland; mass balance equations suggested that 0.1–0.6 kg/yr of chloride was lost to deep groundwater. Nachshon et al. (2014) analyzed 20 years of surface and near-surface salinity data in an upland/NFW setting in Canada's PPR. They found that NFWs existed across a continuum of salinities (e.g., Euliss et al. 2004), ranging from diluted freshwater systems with EC of <500 μS/cm to brackish systems (EC between 500 and 5,000 μS/cm) to brackish-saline wetlands (EC > 5,000 μS/cm). Summer rainfall flushed accumulated salts from the landscape to NFWs along surface and near-surface flowpaths. Some NFWs became salinity sources to other wetlands when fill-and-spill dynamics (noted above) or near-surface potentiometric heads forced high-density waters downgradient; terminal or receiving wetlands could be considered a chemical sink for high-salinity waters (see Chemical Sink functions, below). These findings suggest that NFWs can be salinity sinks at the landscape scale, but at the local or wetland scale, they may be sources of

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elevated chloride to the proximal upland areas (Hayashi et al. 1998a, b; Nachshon et al. 2014) or to other systems if they merge (as noted above; see Cook and Hauer 2007; Vanderhoof et al. 2016; Vanderhoof et al. 2017). Interestingly, Nachshon et al. (2014, 1261) noted that if a series of extremely wet years in the PPR was followed by extreme drought, "… salt concentrations in the upper soil horizons of the wetlands [could be found] at concentrations that were never measured before …" with potential impacts on other waters if or when connectivity subsequently occurred through merging or filling.

In summary, biogeochemical characteristics (e.g., high microbial activity in anoxic soils with available carbon) and physical characteristics (e.g., evapotranspiration) in NFWs create conditions conducive to chemical source functions. Examples from the literature on MeHg and salinity, hydrologically exported through dissolved organic matter entrainment or dissolution, demonstrate some of the mechanisms by which processes and functions internal to NFWs may affect other systems (see Factors Affecting Hydrologic Connectivity of NFWs, below). Conditions such as drainage ditches or subsurface tiling that expedite the delivery of NFW-sourced compounds can have negative consequences on receiving systems (e.g., Nair et al. 2015).

## NFW Sink Function

**Hydrologic Sink.—**In addition to serving as a hydrologic source, NFWs can serve as hydrologic sinks when the storage capacity is not exceeded by net inflows (e.g., surface water and groundwater) minus outflows from evaporation or transpiration (e.g., Haan and Johnson 1968; Boelter and Verry 1977; Bullock and Acreman 2003). Storage volumes in NFWs can vary greatly. Field-measured storage volume in 10 NFWs in southern Florida ranged from 900 to 20,488 $m^3$ and averaged 6,836 ± 7,163 $m^3$ (Haag et al. 2005). Lane and D'Amico (2010) used light detection and ranging (LIDAR) data and calculated that over 8,500 NFWs in central Florida had a median storage value of 876 $m^3$ (1,619 $m^3$ average), and that this varied by Cowardin et al. (1979) wetland type. However, Evenson et al. (2016) calculated that ~50% of the >24,000 NFWs in the ~1,800 $km^2$ Pipestem Creek, North Dakota watershed had small storage capacities (<100 $m^3$). Wu and Lane (2016) used LIDAR collected during drought conditions to identify over 12,000 NFW depressions in a North Dakota watershed. They found that surface area in NFWs with standing water averaged over 2 ha and these wetlands currently stored, on average, ~32,000 $m^3$ of water despite a drought during the data collection period. Dry wetlands (74% of the total) averaged two orders of magnitude less storage per wetland, ~366 $m^3$ (Wu and Lane 2016).

Rainfall and snowmelt runoff can flow into NFWs where high evaporation and low discharge rates, coupled with high surface storage capacity, can result in large hydrologic sink functioning at the watershed scale (Shaw et al. 2012). The proportion of NFW area to wetland catchment area ($A_w/A_c$) is a proxy measure to account for NFW hydrologic sink functions: higher $A_w/A_c$ values suggest greater potential hydrologic sink functioning as more precipitation would be routed to NFWs. Wu and Lane (2017) reported $A_w/A_c$ of ~14% in a study of over 30,000 depressions in the PPR using LIDAR. A large-scale analysis by Watmough and Schmoll (2007) reported $A_w/A_c$ of 8% in the Canadian PPR, similar to the 9% reported by Hayashi et al. (2016). NFWs stored from 11% to 20% of the precipitation in their respective watersheds in a PPR region study by Gleason et al. (2007). Hayashi et al. (2004, 95) analyzed isotopic signatures in a 152 km$^2$ basin in the PPR and found that, "… the majority of [over-winter precipitation storage] is probably stored in wetlands (i.e. fens and bogs) covering 30% of the basin …" Bowling et al. (2003) reported that 24%–42% of snowpack in an Alaskan watershed could be maintained in surface storage (i.e., stored in NFWs).

Evaporation and transpiration losses in particular can be substantial in NFWs. For instance, Lide (1997) estimated that evaporation accounted for 78% of water losses from a wetland system; Duever et al. (1994) noted that evapotranspiration can account for 70%–90% of input precipitation. Van der Kamp et al. (1999) reported that ~75% of input precipitation to a studied Canadian NFW was lost to evapotranspiration at the wetland margins. Bowling et al. (2003) estimated ~50% of snowmelt in an Alaskan basin was evaporated from open water areas (i.e., NFWs).

It is the aboveground volume in NFW wetlands that makes them so effective at landscape water storage. Wetlands effectively store water because their aboveground portions frequently contain a largely empty volume for water storage, in contrast to belowground water storage which is only partly available for water storage due to the presence of soil particles (Johnson 1967; McLaughlin et al. 2014). As noted, stored surface water is acted upon by evaporation, transpiration, and deep groundwater recharge sink functions that result in the water being, in essence, removed from the local — and landscape — hydrologic processes. Among the benefits of water storage in NFWs is that this reduces streamflow (Vining 2002) and the downstream flooding associated with peak streamflow (e.g., Hubbard and Linder 1986; Evenson et al. 2015, 2016; Fossey and Rousseau 2016; Evenson et al., in press). Hubbard and Linder (1986), for example, calculated the water retention capacity of more than 200 non-floodplain prairie pothole wetlands in northeastern South Dakota. They observed that a large amount of snowmelt and precipitation could be cumulatively held by many small wetlands, reducing the potential for flooding at downstream locations. Jones et al. (2018) analyzed NFWs in the Delmarva region (Delaware, Maryland, and Virginia) and identified that 48% of 102,000 depressional NFWs were affected by some sort of ditch; plugging or filling those ditches could increase landscape-scale water storage capacity by 80%. Vanderhoof et al. (in press) analyzed Landsat imagery between 1985 and 2015 covering over 300,000 km$^2$ of the PPR (North and Northwest Drift Plains) and the Northwestern Great Plains (NGP). The NFWs of the PPR had 2.6 times the surface water extent of the NGP (under median climatic conditions), demonstrating that the PPR wetlands were serving, "… a surface water storage function during wet periods, reducing the amount of water contributing to downstream flooding." Evenson et al. (in press) modeled the hydrologic effects of 13,000 NFWs in the PPR and found that NFWs attenuated peak flows; increased flooding likelihood came from wetland area (and concomitant volume) losses.

Hayashi et al. (1998a, b) determined that NFWs received 30%–60% of snowmelt runoff in their Canadian study area. Similarly, a U.S. Geological Survey study in the PPR found that wetlands, including both depressional (including NFWs) and nondepressional types, stored about 11%–20% of the precipitation that fell in a given watershed, and that storage could be increased by wetland restoration (Gleason et al. 2007). Evenson et al. (2015) simulated the effects of 280 NFWs on watershed hydrology in a North Carolina watershed, finding that NFWs decreased peak flows through the lag function (see below). Vining (2002) concluded that wetland storage in the Starkweather Coulee Subbasin of North Dakota likely resulted in decreased streamflow. Fossey and Rousseau (2016) modeled both riparian and NFW effects, finding NFWs decreased peak flows by 7%–16% depending on the severity of flow (2-, 20-, or 100-year return interval stormflows); NFWs were found to maintain baseflows under drought conditions. Rovansek et al. (1996) found snowmelt to be the most important source of water for wetlands and ponds in the Alaskan Arctic Coastal Plain, and that these wetlands and ponds functioned as surface storage, thereby removing water from snowmelt floods. In contrast, both Roulet and Woo (1986) and Ford and Bedford (1987) found surface storage in cold-weather regions to be limited by frozen soils and ice, limiting the lag (and sink) function in wetlands.

Regression equations developed to predict peak flows during flooding events frequently use lake and wetland storage areas as variables. Using this approach for Wisconsin watersheds, Novitzki (1979) estimated that peak flood flows were only 20% as large in watersheds with 40% lake and wetland area relative to watersheds without lakes or wetlands. Johnston et al. (1990) found that small losses of wetlands in watersheds with <10% wetlands could have major effects on flood flow in basins around Minneapolis, Minnesota. Wang et al. (2010) modeled the influence of wetlands on hydrologic processes in Manitoba and Minnesota and found that the loss of 10%–20% of the wetlands in the study basins would increase peak discharge by 40%. Similarly, Yang et al. (2010) calculated restoration of 600 ha of wetlands in a ~25,000-ha watershed would decrease peak stream discharge by 23%. Peak streamflows were shown to be negatively correlated with lake and wetland storage in Minnesota (Jacques and Lorenz 1988), although a later study found peak flows to be correlated with lake storage only and not wetland storage (Lorenz et al. 2010).

Though NFWs affect floodwaters through hydrologic sink functions, there is a finite capacity to this function. Shaw et al. (2012, 3148) observed, "[h]ighfrequency, low runoff volume [precipitation or snowmelt] events … can be completely or partially attenuated through impoundment by landscape depressions …." However, Shaw et al. (2012) continued and noted that once a NFW and soil macropore storage volume capacity threshold is exceeded by precipitation and downgradient connections are created by runoff, the contributing area of the basin is substantially increased and storage in wetland depressions has little effect on downstream flood severity. Shaw et al. (2012) found that only 39% of NFWs in a PPR study area contributed to the basin pour-point flow during snowmelt; the remaining 61% of NFWs acted as hydrologic sinks. In a modeling analysis, Evenson et al. (in press) found larger NFWs served as gate-keepers (i.e., wetlands with a high water storage capacity threshold), storing surface runoff and attenuating peak flows in a downstream network. Modeled loss of the larger systems by Evenson et al. (in press) led to larger contributing areas affecting streamflow. Smaller wetlands (<3.0 ha) in Evenson et al. (in press) comprised 95% of the study wetlands but only 35% of the cumulative storage capacity. The modeled effects of losses in small wetland landscape storage resulted in a 90% decrease in landscape residence time, as surface flow following precipitation or snowmelt events drained across the landscape essentially unimpeded by depression water storage.

In summary, the literature regarding hydrologic sink functioning of NFWs is abundant (e.g., Shaw et al. 2012; Shook et al. 2015; Vanderhoof et al., in press). With seasonally dependent high evapotranspiration rates and basin storage, NFWs perform hydrologic sink functions that affect downstream systems, particularly by reducing peak flows. The effects of this function are similar to the lag function (below), which also affects water flow to downgradient pour points. Structural limitations, such as the maximum storage capacity of a NFW or NFW complex, create thresholds affecting hydrologic sink functioning (e.g., Roulet and Woo 1986; Ford and Bedford 1987; Shaw et al. 2012; Evenson et al., in press).

**Chemical Sink.—**NFWs retain compounds through chemical (and physical) processes such as denitrification, ammonia volatilization, microbial and plant biomass assimilation, sedimentation, sorption and precipitation reactions, biological uptake, and long-term storage in plant detritus (Reddy et al. 1999; Reddy and DeLaune 2008). Marton, Creed, et al. (2015) reviewed the literature on sediment, carbon, phosphorus, and nitrogen storage and transformation in geographically isolated (i.e., non-floodplain) wetlands, concluding (and titling their review) that, “Geographically isolated wetlands are important biogeochemical reactors on the landscape.” Storage or sink rates for NFWs reported from the literature by Marton, Creed, et al. (2015) were: sediment (230–3,600 g/m$^2$/yr), carbon (21–317 g/m$^2$/yr), and phosphorus (0.01–5.0 g/m$^2$/yr) (see NFW Chemical Transformation Function, below for nitrogen findings). The substantial rate variation reported by Marton, Creed, et al. (2015; see also Marton, Chowdhury, et al. 2015) was ascribed to spatial (i.e., size, shape, landscape position) and temporal (i.e., temperature, soil moisture, redox, etc.) variables.

Many studies have addressed chemical sink functions of wetlands, with an abundance of papers focusing on nutrients, namely nitrogen and phosphorus. NFWs inundated with human sewage were shown to remove more than 95% of the phosphorus, nitrate, ammonium, and total nitrogen (Dierberg and Brezonik 1984; Ewel and Odum 1984 and chapters therein). Craft and Chiang (2002) determined that wetland soils stored a disproportionately large share of nitrogen compared with upland soils in spite of uniform soil organic matter across the landscape. A bog NFW in Massachusetts was reported to sequester nearly 80% of the system’s various nitrogen inputs, including precipitation that had a range of 1.2–1.9 mg N/L (Hemond 1983). Hoos et al. (2013) modeled nitrogen and phosphorus dynamics in the southeast U.S. using the SPARROW model and reported the abundance of two typical NFW types (Atlantic Coastal Plain Peatland Pocosin and Southern Coastal Plain Nonriverine Cypress Dome) were factors significantly associated with decreased transport of those nutrients. According to Heagle et al. (2013), the repeated wet–dry cycling of closed-basin NFWs in their PPR study area resulted in substantial subsurface accumulation of sulfate; up to $10^7$ kg was estimated in the soils of a 5-ha PPR NFW. Craft and Chiang (2002) quantified sediment accumulation rates between floodplain and non-floodplain wetlands in southwestern Georgia (951 and 1,289 g/m$^2$, respectively); no difference was found between accumulation rates for organic carbon, total nitrogen, or total phosphorus. Craft et al. (2017) summarized published mean nutrient and sediment storage functions from nine NFW studies and 17 floodplain wetlands; NFW storage of organic carbon was 152% that of floodplain wetlands, but 12%–14% of nitrogen and phosphorous and ~25% that of sediment, though no meta-analysis statistics were conducted. Lane and Autrey (2017) reported that nitrogen and carbon soil accumulation rates in NFWs, measured using cesium-137 radioisotope concentrations in three ecoregions in the U.S., averaged 3.1 ± 3.1 g N/m$^2$/yr and 43.4 ± 39.0 g organic C/m$^2$/yr, respectively. Sediment accretion averaged 0.6 ± 0.4 mm/yr and did not differ by ecoregion, whereas phosphorus accumulation in NFWs was significantly greater in the Erie Drift Plain (0.10 ± 0.10 g P/m$^2$/yr) vs. the Middle Atlantic Coastal Plain (0.01 ± 0.01 g P/m$^2$/yr) or Southern Coastal Plain wetlands (0.04 ± 0.04 g P/m$^2$/yr) (Lane and Autrey 2017). Lane and Autrey (2016) found that phosphorus-sorption capacity varied by Cowardin et al. (1979) wetland type, with forested NFWs having three times the sorption capacity of emergent marsh NFWs (1,275 mg P/kg soil and 418 mg P/kg soil, respectively). In another example, phosphorus retention in NFW marshes of the lower Lake Okeechobee, Florida Basin ranged from 0.3 to 8.0 mg soluble reactive P/m$^2$/day (Dunne et al. 2006). This retention represents a sizeable amount of phosphorus removal, because only about 7% of the watershed was comprised of NFWs. Similarly, NFWs in the Lake Okeechobee Basin were found to have greater storage of total phosphorus than the uplands in which they were embedded (236 kg/ha and 114 kg/ha, respectively; Cheesman et al. 2010). Marton et al. (2014) found that NFWs in Ohio had greater phosphorus-sorption capacities than uplands (297 mg P/kg soil and 86 mg P/kg soil, respectively). These findings were echoed by Dunne et al. (2007), who reported that more phosphorus was stored in NFW plant biomass and soil than in corresponding upland compartments, with wetland surface soils (0–10 cm) representing the largest phosphorus reservoir (>87%) and soil organic matter accounting for >69% of the soil total phosphorus variability. They further suggested that restoring 5%–20% of the NFW area in priority basins draining to Lake Okeechobee, Florida could increase phosphorus storage in NFWs by up to 13 kg P/ha (Dunne et al. 2007). However, Bhadha et al. (2011) found that NFW phosphorus losses from infiltration to groundwater accounted for 14% of phosphorus flux, which suggests that near-surface flow dynamics are also important to managing phosphorus at the landscape level (and reiterating that NFWs may be chemical and hydrologic sources to other systems; Nair et al. 2015). Marton et al. (2014) reported that natural NFWs outperformed both restored and riparian systems in phosphorus retention. However, other studies have also shown that floodplain wetlands have a higher sink capacity than NFWs for phosphorus retention (Craft and Casey 2000; Cohen et al. 2007). Wolf et al. (2013) found greater sedimentation and nitrogen sedimentation in floodplain wetlands vs. NFWs, but reported phosphorus mineralization did not differ between types in floodplain and non-floodplain settings.

Cheng and Basu (2017) conducted a meta-analysis using over 600 published reports on wetland, lake, and reservoir nutrient retention rates. Smaller wetlands were more reactive (i.e., greater retention rates) than larger wetlands and the ratio of sediment contact area to volume was critical to these findings. Cohen et al. (2016, 1980) reported that NFWs are “unambiguously small” and that each order of magnitude increase in wetland size decreases the likelihood that a wetland is a NFW by a factor of three to eight times depending on the ecoregional setting. McCauley et al. (2015) noted that consolidation drainage in the PPR results in landscape changes from many, smaller wetlands to fewer, larger wetlands. Van Meter and Basu (2015), Serran and Creed (2016), and Serran et al. (2017) found that smaller wetlands have been disproportionately lost across the Prairie Pothole landscape. Evenson et al. (in press) found that small NFW removal resulted in decreased inundation time at the landscape scale. Integrating the findings from Marton, Creed, et al. (2015), McCauley et al. (2015), Cohen et al. (2016), Cheng and Basu (2017), and Evenson et al. (in press) suggests biogeochemical functions are affected by the loss of NFWs.

Other pollutants and compounds can be mitigated by NFW sink processes (and/or transformation; see below). For example, microbial methanogenesis completely removed the pesticide atrazine from a mountainous bog in North Carolina (Kao et al. 2002). The environmental contaminants cobalt (Co) and nickel (Ni) were remediated by wetland plants common in forested NFWs; plant concentrations were found to range from 1 to 530 mg Co/kg and up to 250 mg Ni/kg (Brooks et al. 1977). An extensively studied NFW bog in Massachusetts annually stored 54 mg/$m^2$ magnesium, 36 mg/$m^2$ potassium, and 46 mg/$m^2$ lead; the bog also provided acid rain buffering for downstream waters (Hemond 1980).

In summary, the literature is replete with examples of substantive chemical sink functions performed by NFWs. The studies reviewed focused on nutrient compounds (i.e., nitrogen and phosphorus) describing the rates and associated mechanisms across a wide range of NFW types and ecoregions. Factors affecting processing rates include source concentrations and biogeochemical conditions (frequently determined by temporal and spatial conditions and characteristics; e.g., Cheng and Basu 2017; Evenson et al., in press). The collective implication of these studies is that the sink function of NFWs is significant. For instance, in a meta-analysis of NFW biogeochemical functions, Marton, Creed, et al. (2015, 415) estimated that NFW losses in the PPR have negatively affected downstream systems due to lost sink functionality, resulting in "… an increase of between 5 and 140 Tg per year (1 Tg = $10^{12}$ g) of sediment entering surface waters and decreases of 0.84–13 Tg per year C sequestration, 0.00040–0.20 Tg per year P storage, and 0.032–0.21 Tg per year [in lost] denitrification potential." However, intact NFWs, such as the >1.2 million ha identified by Lane et al. (2012) in the southeastern U.S., "… have the potential to sequester 0.25–3.8 Tg of organic C each year … 1.4–42.7 Tg of sediment, [and] 0.00012–0.059 Tg of P …" (Marton, Creed, et al. 2015, 415).

## NFW Chemical Transformation Function

Freshwater wetlands and peatlands are active areas for microbially mediated transformations (Boon 2000, 2006) such as the aforementioned mercury methylation and reactive nitrogen (Nr) transformation to $N_2$ through denitrification. Galloway and Cowling (2002, 71) define Nr as, "… biologically active, photochemically reactive, and radiatively active N compounds in the atmosphere and biosphere … [including] inorganic reduced forms of N (e.g., $NH_3$, $NH_4^+$), inorganic oxidized forms (e.g., $NO_x$, $HNO_3$, $N_2O$, $NO_3^-$), and organic compounds (e.g., urea, amines, proteins)." Transformations of Nr to $N_2$ are prevalent in wetlands that are exposed to Nr and have anoxic conditions, labile carbon, and facultative microbial communities (Reddy and DeLaune 2008). Jordan et al. (2011) reported ~20% of the Nr load reaching wetlands in the contiguous U.S. was removed through plant uptake, denitrification, absorption, burial, and anaerobic ammonium oxidation. As noted, Cohen et al. (2016) determined that wetlands typifying non-floodplain systems (e.g., vernal pools, prairie potholes, etc.) were typically small. With this small size, they found, came a high perimeter length per unit area; since wetland edges are areas of most active biogeochemical processing, these wetland systems are of particular importance in landscapelevel functioning (such as transformative processes; see Cohen et al. 2016; Holgerson and Raymond 2016). Indeed, Ghermandi et al. (2010) found that water quality exported from wetlands was inversely related to size. Cheng and Basu (2017) constructed a nutrient-removal model in wetland systems based on over 600 published studies and found that 50% of the total nitrogen load was removed by wetlands smaller than ~0.03 ha (~300 $m^2$) in size. Losing smaller wetlands, they conclude, "… will lead to a greater fraction of the landscape removal potential lost because of the higher reactivity of smaller wetlands" (5051).

Marton, Creed, et al. (2015) reviewed the literature on biogeochemical processes in NFWs, reporting that denitrification rates ranged from 0.8 to 2.0 g/$m^2$/yr and varied with spatial and temporal variables; input $NO_3^-$ concentrations were found to also control transformation rates. Racchetti et al. (2011) reported that 60%–100% of $NO_3^-$ inputs to geographically isolated (i.e., non-floodplain) wetlands were transformed. NFWs in Michigan were found by Whitmire and Hamilton (2008) to remove nitrate-nitrogen ($NO_3$-N) and sulfate ($SO_4^{2-}$) at rates of 0.04–0.55 mg $NO_3$-N/L/ha and 0.06–0.30 mg $SO_4^{2-}$/L/ha. These rates are significant, considering that nitrate concentration in Michigan groundwater was reported to average 0.5 mg $NO_3$-N/L (Whitmire and Hamilton 2008), though groundwater concentrations >3 mg $NO_3$-N/L are considered contaminated (Madison and Brunett 1985). Prairie pothole NFWs in the upper Midwest removed >80% of the nitrate load via denitrification (Moraghan 1993). A large marsh NFW removed 86% of nitrate, 78% of ammonium, and 20% of phosphate through assimilation and sedimentation, sorption, and other mechanisms, including transformation (Davis et al. 1981). In a study of NFWs of North Carolina and Florida, Lane et al. (2015) reported average denitrification rates of 6.89 ± 5.02 μg N/kg soil dry weight (DW)/h; differences were found based on vegetation structure, with emergent marsh NFWs denitrifying at almost triple the rate of forested NFWs. This was hypothesized to result from the greater abundance of labile carbon in the marsh wetlands (Lane et al. 2015). Marton, Chowdhury, et al. (2015) analyzed NFWs in Indiana and found denitrification rates of 88.8 μg N/kg DW/h. NFWs studied in Maryland and Delaware had microbially mediated denitrification rates of 0.06–0.76 mg N/kg soil/day (Jordan et al. 2007). Because these NFWs comprised >70% of the wetland area in the study basin, this value indicates a significant watershed denitrification capacity. Marton, Chowdhury, et al. (2015) found that NFWs denitrified at twice the rate of upland systems, 12.3 ± 4.5 ng N/g soil/h vs. 5.3 ± 1.7 ng N/g soil/h. NFW samples amended with carbon, nitrogen, or both have been found to dramatically increase the denitrification rate (e.g., Lane et al. 2015; Marton, Chowdhury, et al. 2015) suggesting that NFWs have substantial chemical transformation functioning that may be limited by inputs (see also Ullah and Faulkner 2006; Dodla et al. 2008). Using spatial data from Lane et al. (2012), Marton, Creed, et al. (2015) estimated that the intact NFWs of the southeastern U.S. collectively transform, or denitrify, 0.0095–0.063 Tg N/yr.

In summary, NFWs perform substantial chemical transformation functions, the rates of which frequently depend on factors such as temperature, available energy sources, soil characteristics (e.g., anaerobic or aerobic conditions), and chemical compound concentration (e.g., Marton, Creed, et al. 2015; Marton, Chowdhury, et al. 2015). Much of the literature we found focuses on transformation of nitrogen species to $N_2$, though other compounds were also discussed (e.g., $SO_4^{2-}$; MeHg in the chemical source functions, above).

## NFW Hydrologic Lag Function

While hydrologic sinks discussed above affect the volume of water on the landscape due to processes such as evapotranspiration, hydrologic lags delay water delivery without substantially affecting quantity through temporary storage or by routing water through flowpaths with long travel times. The lag, sink, and source functions work in conjunction with one another. In essence, the lag function can be viewed as the time-integrated sink and source functions. That is, water initially stored by wetlands can be released over time, reducing peak flows and increasing low or baseflows. Fossey and Rousseau (2016) modeled both riparian and NFW effects, finding NFWs decreased peak flows by 7%–16% depending on the severity of flow (2-, 20-, or 100-year return interval stormflows), while maintaining baseflows under drought conditions. Fossey and Rousseau (2016) concluded that, "… at any event scale any type of wetlands [e.g., floodplain and non-floodplain wetlands] plays a role in reducing peak flows … and sustaining low flows." As noted above, Evenson et al. (2015) simulated the effects of 280 NFWs on the hydrology in a North Carolina watershed, finding that NFWs decreased peak flows through the lag function.

The lag function is a result of two mechanisms affecting flow. First, a lag occurs when surface and near-surface groundwater inputs to a NFW fill available space below a spill elevation. With lag functions (vs. sink functions), the wetland storage capacity is ultimately exceeded resulting in surface runoff or near-surface flow. When storage capacity is exceeded by storm events during otherwise dry periods, watersheds containing extensive wetlands can require more time for water discharge to rise and fall in response to storm events due to the lag function (Lindsay et al. 2004). Second, a lag occurs through the routing of water to near-surface groundwater and then to stream systems. Water routed through near-surface groundwater-to-stream systems, as opposed to movement via surface water, would be expected to take longer (i.e., to lag) due to the tortuous pathways required by soil particles (and rocks, roots, etc.) — see Groundwater Connectivity, below.

The ability of wetlands to reduce flooding via storage and the lag function varies, with topography exerting an influence (e.g., slope). Using stable hydrogen and oxygen isotopes of water, McEachern et al. (2006) found that snowmelt in boreal forests was discharged rapidly in a sloped watershed. In contrast, in a lowland watershed, much of the snowmelt was stored by wetlands, particularly by bog NFWs with headwater stream channel outlets. In northern Canada, stream runoff was positively correlated with slope and the presence of channel fens, but negatively correlated with lowland depressional NFWs (Quinton et al. 2003). A literature review of wetlands having no direct inlets or outlets to a river system concluded that those wetlands reduced or delayed flooding (Bullock and Acreman 2003). Findings by Bullock and Acreman (2003) were more varied for slope wetlands with direct connectivity to a river: 26 of 62 studies found reduced flooding, while 27 of the 62 studies concluded that those wetlands increased flooding.

Antecedent moisture conditions and currently available wetland storage also affect the lag function. Boelter and Verry (1977) noted that two storms of nearly equal volume and intensity produced different runoff responses from the same peatland. One storm occurring in the spring at a time of already high water tables led to runoff. The other, in midsummer at a time of low water tables, increased the water depth in the NFW but did not exceed the wetland's water storage capacity, precluding runoff. This mechanism has been observed in simulations of prairie pothole wetland hydrology, in which wetlands reduced streamflow until storage capacity was exceeded (Haan and Johnson 1968; Shaw et al. 2012). Thus, NFWs can function as a sink in dry periods if storage capacity is not exceeded and evaporation rates surpass groundwater recharge (see Hydrologic Sink function, above). These same wetlands can function as sources in wet periods if NFW storage capacity has been exceeded. Finally, the same wetlands can create a lag during the filling process in advance of the spilling event by initially storing inputs but producing surface runoff if their storage capacity is exceeded. This phenomenon explains in part how wetlands can both increase and decrease streamflows (Bullock and Acreman 2003) — see also Factors Affecting Hydrologic Connectivity of NFWs, below.

Thus, NFWs provide hydrologic lag functions when depressions fill with precipitation, snowmelt, or other surface and near-surface inputs. The lag functional is dependent on a NFW basin spill threshold; after such a point is passed, the contributing area transitions from terminating at the NFW to affecting flow in downstream systems (e.g., Boelter and Verry 1977; Shaw et al. 2012; Jones et al. 2018; Brooks et al. 2018; Evenson et al., in press). Hydrologic models have demonstrated that when contributing area flow terminates at a NFW, near-surface and groundwater recharge functions maintain baseflow in downgradient streams (e.g., Evenson et al. 2015; Fossey and Rousseau 2016). Similarly, basin filling from overland or near-surface inputs creates a temporal lag that can decouple stormflow events, even in systems where pervasive overland flow connects landscape elements within watersheds to a downgradient pour-point (Bullock and Acreman 2003; Brooks et al. 2018). However, when NFW storage volume is at capacity, the lag function is effectively bypassed (Shaw et al. 2012).

## Factors Affecting Hydrologic Connectivity of NFWs

**Surface Water Connectivity.—**Multiple factors affect whether a potential surface connection exists between a NFW and another water body and, if and when actualized, the duration, frequency, and magnitude of that connection. These factors can be organized into three major categories: (1) those characteristic of the intervening area between the NFW and the receiving water body; (2) those intrinsic to the NFW or NFW complex itself; and (3) exogenous forcing factors, such as climate. In the first category, intervening distance is a first-order factor (Cohen et al. 2016). Le and Kumar (2014) analyzed NFWs in five study areas across the U.S. and found that potential hydrologic connectivity, as determined by nearest-neighbor distances, followed a universal power law distribution, with most wetlands connecting over short distances. The short intervening distances between wetlands can cause rapid increases in hydrologic connectivity during precipitation/snowmelt events as different parts of the watershed connect (or fill, merge, and spill) and the watershed contributing area increases quickly (Le and Kumar 2014). Neff and Rosenberry (2017) found that the quantity of modeled NFW groundwater provided to the stream network decreased with increasing distance from the network. Vanderhoof et al. (2016) and Vanderhoof and Alexander (2016) found that hydrologic connections between NFWs and streams were positively correlated with stream density, suggesting that connections increase with decreasing distances between wetlands and streams. However, with wet conditions, wetlands were observed connecting to streams over long distances (up to 37 km; Vanderhoof and Alexander 2016). Ameli and Creed (2017) found that both surface water and groundwater inputs from NFWs contributed to river flows, with surface inputs affecting flows up to 8 km from the river system (and groundwater flows affecting the river system up to 30 km away). Human activity can alter this relationship. Historical loss of NFWs in Iowa has increased distances between wetlands that remain (e.g., McCauley et al. 2015; Van Meter and Basu 2015). For example, human activities have also increased the mean distance of Iowa and Nebraska NFWs to streams due to relatively higher rates of drainage and loss of upland-embedded NFWs farther away from the stream network (Uden et al. 2014; Van Meter and Basu 2015).

Other characteristics of the intervening area between NFWs and the stream network include topography, vegetation, soil, and human alterations, all of which can affect flow characteristics. For instance, slope has been positively correlated with streamflow (McEachern et al. 2006), as areas of lower slope typically have a lower potentiometric head. Quinton et al. (2003) reported that stream runoff was negatively correlated with the abundance of lowland bog NFWs. Precipitation events on soils with low infiltration capacity are more likely to result in overland flow whereas soils with higher infiltration capacity are more likely to result in groundwater flowpaths. In their literature review, Bullock and Acreman (2003) found that studies of NFWs with no direct surface water connectivity reduced or delayed flooding downstream. However, 42% (i.e., 26 of 62) of the slope (NFW) wetland studies that were reviewed resulted in reduced flooding and 44% (i.e., 27 of 62) of those increased downstream flooding, which suggest antecedent moisture conditions, wetland storage, and characteristics of the connection between the NFWs and another system (e.g., vegetation, roughness, pore space, hydraulic conductance, etc.) affect connectivity dynamics.

Storage is a function intrinsic to NFWs, affecting connectivity via the fill-and-spill or fill-and-merge of surface waters. As described above, spilling or runoff from a wetland occurs when wetland storage minus losses (via evaporation or groundwater recharge) are exceeded by inputs (via precipitation, groundwater discharge, or overland flow). The inputs and losses are driven in part by climate. Everything being equal, under wetter conditions, wetland storage capacity is more likely to be exceeded. In the PPR, temporary overland connectivity between NFWs has been observed in wet years (e.g., Leibowitz and Vining 2003; Cook and Hauer 2007; Leibowitz et al. 2016). Brooks et al. (2018) found that on average, 33% of the Missouri Coteau (part of the PPR) was connected using Landsat imagery analyses, and determined that this was mostly via the fill-and-merge process between NFWs as the stream network was poorly developed in their study area. Although these studies focused on NFW-to-NFW connections, their findings illustrate that connectivity is a dynamic process, and that NFWs can exhibit temporary surface water connections with other water bodies during wet periods (e.g., Wilcox et al. 2011; Vanderhoof and Alexander 2016; Vanderhoof et al. 2016; Brooks et al. 2018).

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Research into the frequency, duration, magnitude, and timing of surface connections of NFWs to river networks has received less attention than those of riparian and floodplain wetlands (see Fritz et al. 2018), though this has changed markedly in recent years through advances in hydrologic modeling, statistical approaches, and remote sensing and geostatistical analyses, especially in the North American PPR and portions of the Atlantic Coastal Plain (e.g., Wilcox et al. 2011; Lang et al. 2012; Golden et al. 2014; Golden et al. 2015; Huang et al. 2014; Evenson et al. 2015; Shook et al. 2015; Fossey and Rousseau 2016; Vanderhoof et al. 2016; Vanderhoof et al. 2017; Ameli and Creed 2017; Jin et al. 2017; Thorslund et al., unpublished data). Where connections have been reported, the duration of a connection is more often described (i.e., whether the connection is perennial, intermittent, or ephemeral). The frequency of a connection, in the case of intermittent or ephemeral flows, or the magnitude of that connection (i.e., the amount of flow between a wetland and a river network) has been less empirically studied or reported due in part to the difficulties in attributing source waters (but see McDonough et al. 2015; Vanderhoof et al. 2016; Brooks et al. 2018; Thorslund et al., unpublished data). A combination of small-scale field-based studies coupled with larger scale remote sensing applications and modeling will effectively quantify surface water connectivity of non-floodplain systems (Golden et al. 2017; see Brooks et al. 2018).

**Groundwater Connectivity.—**In addition to surface water connections, groundwater flow can connect NFWs with other water bodies, potentially over great distances (e.g., 30 km; Ameli and Creed 2017). Studies have shown NFWs can receive groundwater discharge, contribute to groundwater recharge, or connect via both pathways (Lide et al. 1995; Devito et al. 1996; Matheney and Gerla 1996; Rosenberry and Winter 1997; Pyzoha et al. 2008). For example, a study of four North Dakota prairie NFWs by Arndt and Richardson (1989) demonstrated groundwater connections as one wetland recharged groundwater, one was a flow-through wetland, and one was a groundwater discharge system (Euliss et al. 2004). Using stable isotopes, Matheney and Gerla (1996) concluded that although most of the water in a depressional NFW came from precipitation, groundwater connections accounted for the high salinity of the wetland soil. High salinity can be indicative of net groundwater discharge to a wetland (Brinson 1993; Ali et al. 2017). Min et al. (2010) reported that 38% of rainfall that entered four NFWs in Florida was recharged to groundwater. Bullock and Acreman (2003) found 69 studies making reference to groundwater recharge from wetlands; of these, 32 observed groundwater recharge from a wetland whereas 18 did not. Rosenberry and Winter (1997) determined that groundwater mounding may prevent connections that would otherwise follow topography. Neff and Rosenberry (2017) conducted a model analysis suggesting that groundwater mounding could be short-circuited by the presence of sand layers promoting lateral conductivity or drought conditions decreasing the presence of the water table mounds.

Groundwater flow-through wetlands are sites of both groundwater discharge and recharge, in essence a surface expression of the groundwater system (Richardson et al. 1992; Kehew et al. 1998; Ferone and Devito 2004). This dynamic has been shown in many locations, including prairie pothole NFWs (Richardson et al. 1992), NFWs in glacially formed landscapes in southwest Michigan (Kehew et al. 1998), Alaskan pond NFWs (Rains 2011),

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Florida cypress dome NFW systems (Sun et al. 1995), and small Wisconsin lakes (Born et al. 1979). The lakes and NFWs of the Nebraska Sand Hills are also predominantly flow-through and an expression of a large regional groundwater system (Winter 1999).

Like surface water, groundwater connections can vary in duration, frequency, and magnitude, and these connections can be affected by a number of factors. Whether a wetland recharges groundwater, is a site of groundwater discharge, or both, is determined by topography, geology, soil features, and seasonal position of the water table relative to the wetland (Neff and Rosenberry 2017). Shedlock et al. (1993), for example, concluded that groundwater discharged into a NFW bog along Lake Michigan through a breach in the sediments underlying the wetland. In dry periods when water tables are low, water tends to move from wetlands into the groundwater, while in wetter periods with higher water tables, water can flow in the opposite direction from shallow groundwater into the wetlands (Phillips and Shedlock 1993; Pyzoha et al. 2008; McLaughlin et al. 2014). Lide et al. (1995) observed both groundwater flow into and from a Carolina bay NFW, with discharge to the wetland when the water table was high and recharge to the groundwater when the water table was low. Sun et al. (1995) observed similar phenomena in a Florida cypress dome NFW. This exchange and temporary storage of water represents a lag function (see NFW Hydrologic Lag Function, above; see also McLaughlin et al. 2014) that can make NFWs particularly important for groundwater recharge during dry periods. Rosenberry and Winter (1997) indicated that groundwater discharge to a wetland often alternates with flow from the wetland to groundwater, and the direction of flow is controlled by the balance of recent precipitation with current evapotranspiration demands.

The magnitude and transit time of groundwater flow from a wetland to other surface waters depends on the intervening distance and the properties of the rock or unconsolidated sediments between the water bodies (i.e., the hydraulic conductivity of the material). In some carbonate or volcanic rocks, for example, groundwater can flow relatively freely through large openings; while in unconsolidated material, such as gravel, sand, silt, or clay, the spaces between particles determine the time required for water to flow a given distance (Winter et al. 2003). In porous material, such as gravel, water can travel a kilometer in a few days; in fine-textured materials, such as silt or clay, hundreds to thousands of years might be required for water to travel the same distance (Winter and LaBaugh 2003).

In agricultural regions, the transit time of subsurface flows is increased substantially by artificial subsurface drainage pipes, known as tile drains (Schiller et al. 2012). Wetlands in these areas are sometimes fitted with inlets that connect directly to tile drains, quickly moving temporarily ponded water through the subsurface and to outlets that discharge directly to ditches or streams (Tomer et al. 2010). Ditching wetlands can not only make them into sources of water but also sources of nutrients and ions from their legacy performing sink functions on the landscape (e.g., Brunet and Westbrook 2012; Nair et al. 2015).

In summary, NFWs can recharge groundwater, receive discharging groundwater, or be flow-through wetlands, and sometimes all three in a given water-year (Sun et al. 1995). Impermeable layers underlying some NFWs may create perched systems with low groundwater connectivity to other systems; these layers may also be breached or be discontinuous underneath larger wetlands, permitting connections to near-surface or deeper groundwater. NFW connections to groundwater encompass sink, source, and lag functions affecting downgradient base and stormflows; groundwater connections can be relatively quick, or ponderously slow. Further examinations into the NFW groundwater connections and factors affecting these interactions and subsequent connections to downstream systems require additional analyses and research, especially in areas outside of the North American PPR.

## SYNTHESIS AND IMPLICATIONS: HYDROLOGICAL, PHYSICAL, AND CHEMICAL EFFECTS OF NFWS ON DOWNSTREAM WATERS

NFWs lack well-defined surface water inlets and/or outlets to other water bodies and may include depressions, slopes, flats, and other similar wetland types, as well as regionally described systems such as some Prairie Potholes, playa lakes, vernal pools, and Carolina bays (e.g., Tiner 2003). NFWs are abundant aquatic systems throughout the U.S.; Lane and D' (2016) conducted a coterminous U.S. spatial analysis using a geospatial floodplain proxy to identify more than 8.4 million potential NFWs covering more than 6.6 million hectares (see Figure 1). Hydrologic flows through NFWs are predominantly unidirectional, in contrast to bidirectional flows that occur in riparian and floodplain wetlands. Much of the updated literature we examined on NFWs indicates that these systems have important hydrologic and water quality functions that affect downstream waters and rivers (Creed et al. 2017). In USEPA (2015), the literature did not sufficiently support a definitive conclusion regarding non-floodplain connectivity of particular groups or classes of wetlands, though USEPA (2015) acknowledged that NFWs which intersect surficial and near-surface runoff can perform substantive chemical sink and transformative functions. Recent scientific contributions to the literature, additional sources now included in this updated review, and advances in hydrologic modeling (e.g., Evenson et al. 2015, 2016; Fossey and Rousseau 2016; Ameli and Creed 2017; Cheng and Basu 2017; Evenson et al., in press; Thorslund et al., unpublished data), remote sensing analyses (e.g., Vanderhoof et al. 2016; Vanderhoof et al. 2017; Jones et al. 2018), field-based observations (e.g., Shaw et al. 2012; Ali et al. 2017), and emerging coupled field and remote sensing studies (e.g., Brooks et al. 2018) have further informed our analyses and synthesis of the literature such that we now conclude all NFWs are interconnected with stream and river networks (Cohen et al. 2016), though this connectivity varies in frequency, duration, magnitude, and timing (Ward 1989; Covino 2017). This complex landscape-scale connectivity, in turn, affects water and material fluxes — the resultants of substantial hydrological, physical, and chemical functioning in NFWs — that modify the characteristics and function of downstream waters (e.g., Marton, Creed, et al. 2015; Rains et al. 2015; Cohen et al. 2016; Calhoun et al. 2017).

It is evident that NFWs that are connected to the river network through surface water are hydrologic sources and will have an influence on downstream waters, regardless of whether the outflow is permanent, intermittent, ephemeral, or episodic (e.g., Wilcox et al. 2011; Rains et al. 2015; Calhoun et al. 2017; Brooks et al. 2018). Such NFWs include wetlands that are the origins of streams or are connected downstream to the river network through ditches, as well as those connected through swales. It is the quality (i.e., concentrations of entrained or dissolved compounds) and quantity of surface water exports from NFWs that informs this conclusion. The finding may have important research and management implications. For instance, White and Crisman (2016) concluded that NFWs are headwaters to ~90% of mapped streams they studied in Florida, and Nadeau and Rains (2007) estimated that up to 60% of stream km in the conterminous U.S. may be first- or second-order systems (i.e., headwaters). However, the most highly refined spatial stream data available for the U.S., the National Hydrography Dataset (NHD; 1:24,000), does not typically identify stream systems of <1.6 km, and there are significant omission errors. For instance, Lang et al. (2012) reported that the NHD identified 66% of stream length compared with a product developed using higher resolution LIDAR data. Thus, it is evident that NFWs serve as abundant stream origins in certain parts of the country, though the origins of the vast majority of streams in the U.S. are unmapped and hence unreported.

NFWs that do not connect to the river network through surface water can still be a source of water (or be connected) through local, intermediate, or regional groundwater flows, often covering great distances (e.g., over 30 km, Ameli and Creed 2017) and providing meaningful hydrologic inputs that maintain baseflows (e.g., 313 $m^3$/day modeled to provide to river flow from groundwater recharging NFWs; Ameli and Creed 2017). Connectivity between these NFWs and downstream waters will vary within a watershed as a function of local factors (e.g., position, topography, and soil characteristics) as well as time, as the river network and water table expand and contract in response to local climate (e.g., Vanderhoof et al. 2016; Vanderhoof et al. 2017).

NFWs that lack a surface or near-surface/groundwater hydrologic connection to other water bodies also influence downstream systems by acting as sinks, creating lags, and/or transforming material. These wetlands can effectively reduce peak flow and flooding, while potentially increasing low flows. The physical storage of water in NFWs, dependent on available volume (e.g., not affected by volume storage reductions due to frozen soils or ice), is incontrovertibly and empirically occurring across the landscape (e.g., Boelter and Verry 1977; Shaw et al. 2012; Brooks et al. 2018). However, once a NFW (or complex) has reached capacity, the storage capacity and impact on downgradient flow mitigation is effectively negligible.

Chemical sink and transformation functions of NFWs have effects on the water quality of downstream waters when these wetlands intersect the flowpath between pollutant source and downstream waters. Wetland chemical sink functions are likely to be greatest when the wetland is located downgradient from pollutant sources and upgradient from a stream or river. The ability of NFWs to perform sink functions is such that maintaining, restoring, and protecting these wetlands have been promulgated as part of watershed nutrient management plans (e.g., Zhang et al. 2009). The literature demonstrates that transformation and sink functions in NFWs provide significant removal of certain pollutants (e.g., transformation of nitrogen species; sink of phosphorus species; but see MeHg studies noted above). The rates depend on pollutant source-area contributions, modes of transportation (i.e., entrained or dissolved), as well as hydrology, temperature, available carbon, and other factors (Marton, Creed, et al. 2015; Marton, Chowdhury, et al. 2015; Cohen et al. 2016; Cheng and Basu 2017).

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The updated literature we reviewed provides ample evidence that NFWs can and do provide hydrologic and chemical functions that affect material fluxes to other waters, including other wetlands within a basin, streams and lakes, and groundwater. These results suggest the cumulative influence of many individual NFWs within watersheds can strongly affect the spatial scale, magnitude, frequency, and duration of hydrologic and chemical fluxes or transfers of water and materials to downstream waters.

Caveats associated with this review include the fact that the term “non-floodplain wetland” was infrequently used in the literature, and our designation as such was frequently based on the context, study location, or other information available in the published research that may have resulted in errors of commission. Errors of omission occurred in this review, as the welcome increase in scientific literature on NFW functions portends a better understanding of their downstream effects. Increasing the spatial distribution of NFW studies to encompass the full breadth of ecoregions and wetland typologies will result in increased certainty of the conclusions. Contributions were dominated by studies from researchers of the North American PPR; our understanding will be further improved by additional studies in other areas and ecoregions.

The updated literature supports the following conclusions in this review on the hydrological, physical, and chemical functions of NFWs and their effects on downstream systems:

1. NFWs exist across a gradient of connectivity from poorly connected systems to well-connected wetlands and wetland complexes.

2. All NFWs are therefore interconnected with stream and river networks, though this connectivity varies in frequency, duration, magnitude, and timing. This complex landscape-scale connectivity affects water and material fluxes — the resultants of substantial hydrological, physical, and chemical functioning in NFWs — that modify the characteristics and function of downstream waters.

3. NFWs can be hydrologically connected directly to river networks through natural or constructed channels, nonchannelized surface flows, or subsurface flows, the latter of which can travel long distances to affect downstream waters. Through this connection, NFWs act as a source of water and other materials to downstream waters.

4. Water storage by NFWs well outside of riparian or floodplain areas affects streamflow through the sink and lag functions.

5. NFWs act as sinks, sources, and transformers for various pollutants, especially nutrients.

6. The connectivity of NFWs with other systems, as well as the relative size of their contributing area, may vary in space and time along with their functions that affect watershed-scale hydrodynamics and chemical fluxes.

7. There are a number of factors that influence the magnitude, frequency, and duration of connections between wetlands and streams. These include spatial proximity, wetland storage capacity, climate, and characteristics of intervening area between wetlands and the stream (e.g., soil permeability).

NFWs are abundant landscape elements important for multiple functions taking place across temporal and spatial scales that contribute to watershed integrity (e.g., Creed et al. 2017). The connectivity of NFWs with other systems, as well as the relative size of their contributing area, may vary in space and time along with their functions that affect watershed-scale hydrodynamics and chemical fluxes. We agree with Shook et al. (2015), as well as Cohen et al. (2016) who in particular note that, "[w]atershed discharge integrates the entire continuum of hydrologic connectivity, not just rapid or surface-connected flow paths." A corollary to this conclusion is that as hydrology mediates and facilitates much of the physical and chemical functions of NFWs, the material concentration of watershed discharge reflects the time and space-varying contributions and effects of all landscape elements, including NFWs (cf. Hynes 1975).

## ACKNOWLEDGMENTS

This review benefited from discussions held at the "North American Analysis and Synthesis on the Connectivity of 'Geographically Isolated Wetlands' to Downstream Waters" Working Group supported by the John Wesley Powell Center for Analysis and Synthesis, funded by the U.S. Geological Survey and the U.S. Environmental Protection Agency (USEPA) Office of Research and Development, National Exposure Research Laboratory. We greatly appreciate the technical reviews conducted by Rose Kwok of the USEPA Office of Water. The views expressed in this manuscript are solely those of the authors and do not necessarily reflect the views or policies of the USEPA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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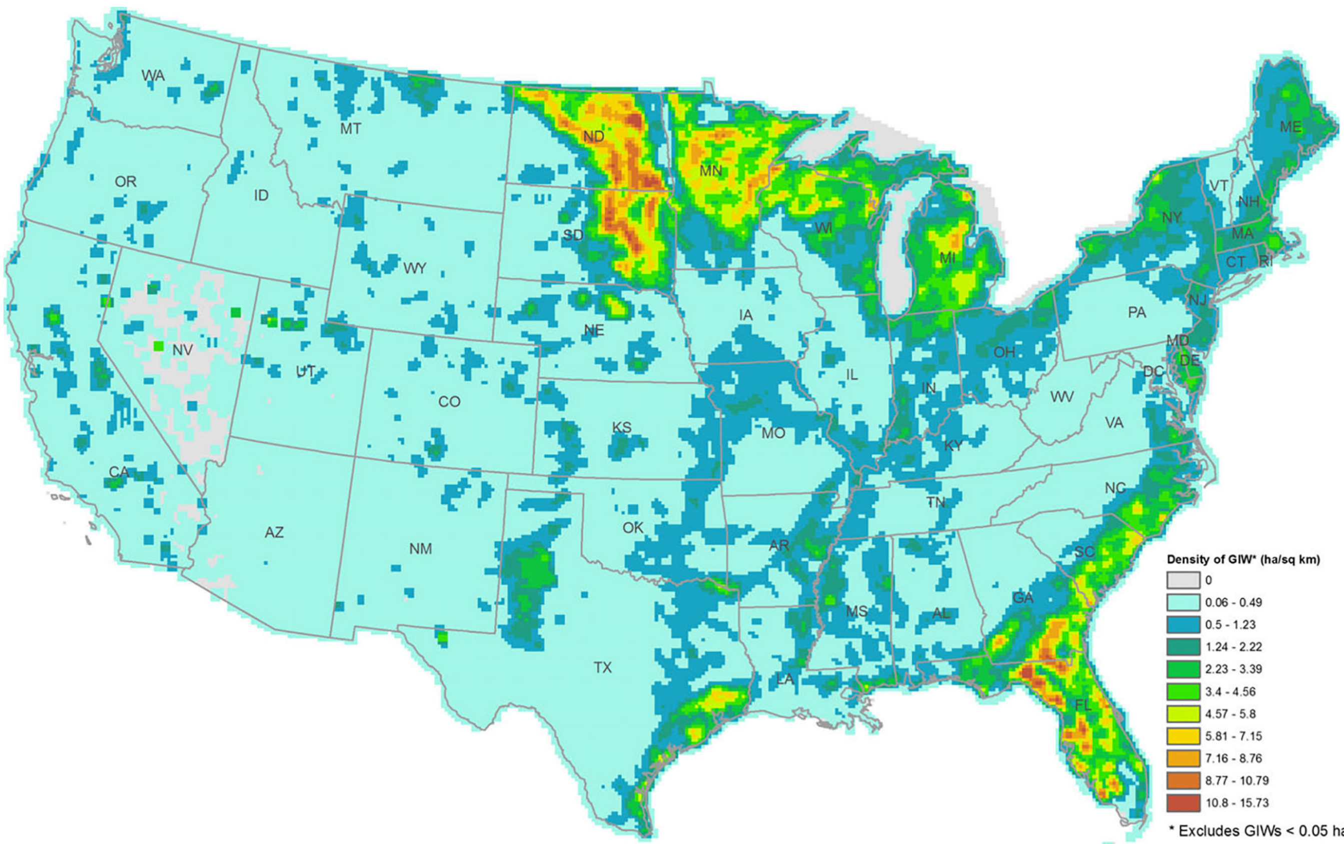



**FIGURE 1.**

Spatial distribution (heat map of ha/km$^2$) of NFWs (or "geographically isolated wetlands," GIWs in Lane and D'Amico 2016) derived from geographic information system analyses of a floodplain proxy (Lane and D'Amico 2016). Approximately 8.4 million NFWs covering more than 6.6 million ha were reported by Lane and D'Amico (2016). Source: Figure reproduced from Lane and D'Amico (2016). State abbreviations are given in the figure.

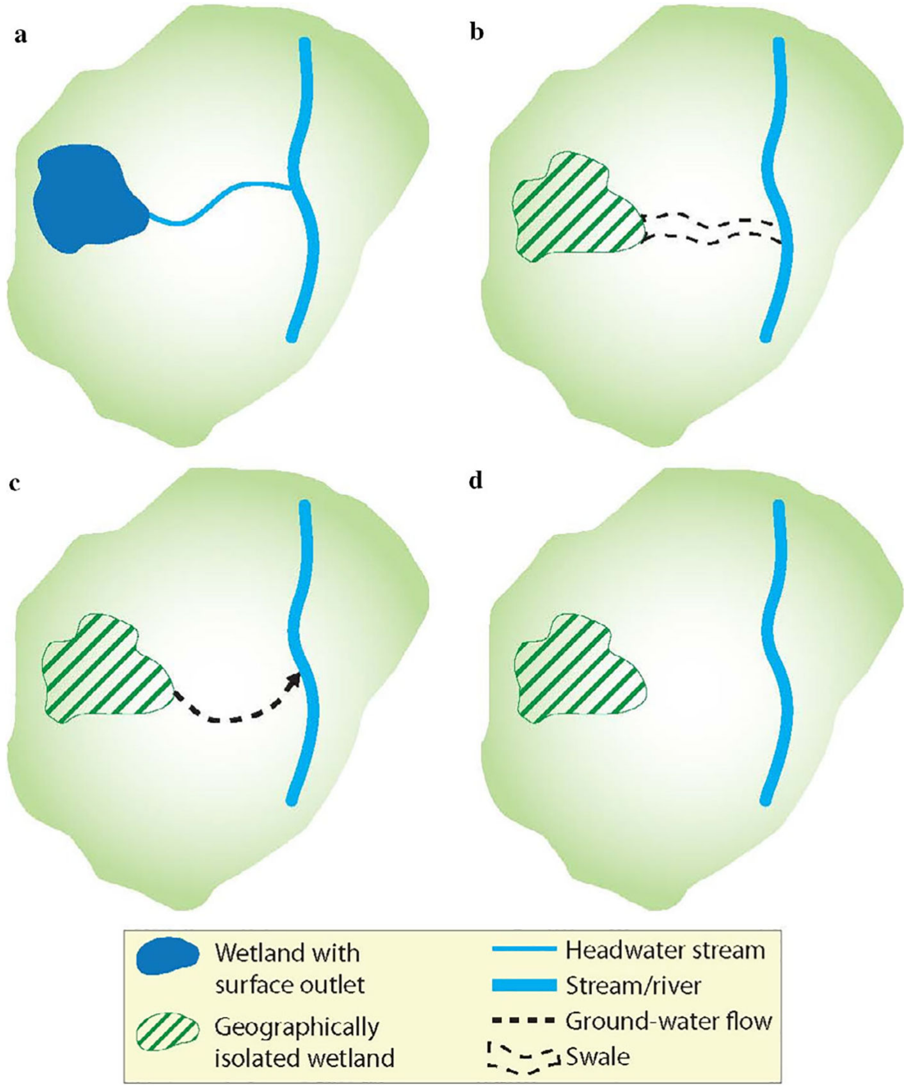



**FIGURE 2.**

Types of hydrologic connections between NFWs and streams or rivers. (a) A wetland connected to a river by surface flow through a headwater stream channel. (b) A wetland connected to a river by surface flow through a nonchannelized swale. (c) A NFW connected to a river by groundwater flow (flowpath can be local, intermediate, or regional). (d) A NFW that is hydrologically isolated from a river. Note that in a–c, flows connecting the wetland and river may be perennial, intermittent, or ephemeral. Source: Figure reproduced from USEPA (2015).

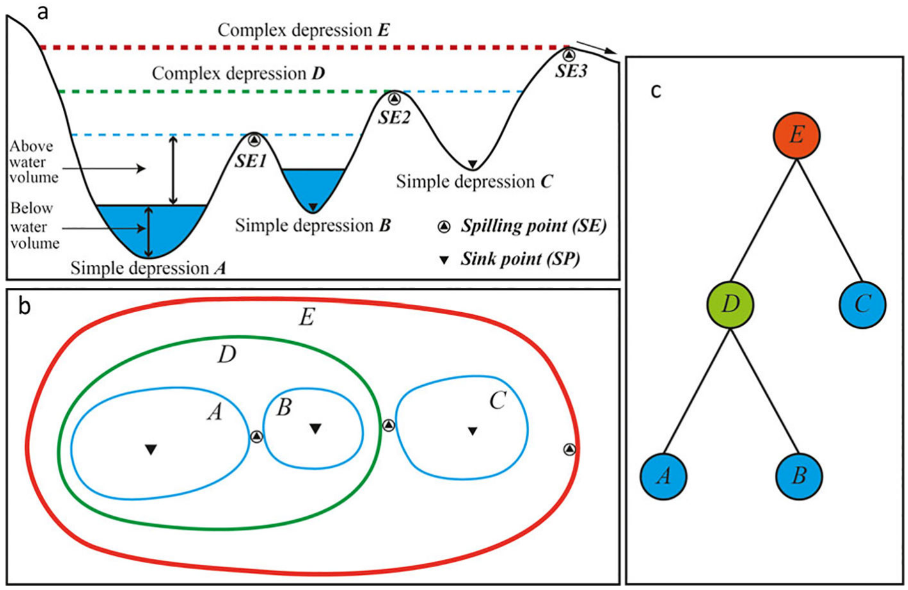
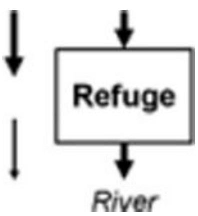



**FIGURE 3.**

Conceptual model of simple and complex depressions that merge and spill: (a) profile view, (b) plan view, (c) hierarchical view. A schematic example of fill-and-merge behavior where simple depressions (e.g., Simple depression A, Simple depression B) merge with increasing inundation to form Complex depression D. Additional inundation merges Simple depression C with Complex depression D to create Complex depression E, which “spills” at spill elevation #3 (SE3) to another water body. Source: Wu and Lane (2016); reproduced with permission of Springer.

**TABLE 1.**

Functions by which NFWs affect material and energy fluxes to downstream waters.

| Function | Definition | Wetland examples |
|---|---|---|
|   | Net increase in a material or energy flux (exports > imports) | Phytoplankton production from floodplain (Schemel et al. 2004; Lehman et al. 2008) |
|   | Net decrease in a material or energy flux (exports < imports) | Sediment deposition, denitrification (Johnson 1991) |
|   | Avoidance of a nearby sink function, thereby preventing a net decrease in material or energy flux (exports = imports) | Riparian wetlands as aquatic refuges in dryland rivers (Leigh et al. 2010) |
|   | Temporary storage and subsequent release of materials or energy without affecting cumulative flux (exports = imports); delivery is delayed and can be prolonged | Flood attenuation (Bullock and Acreman 2003) |
|   | Conversion of a material or energy into a different form; the amount of the base material or energy is unchanged (base exports = base imports), but its composition (e.g., mass of the different forms) can vary | Mercury methylation (Galloway and Branfireun 2004; Selvendiran et al. 2008) |

Source: Table reproduced from USEPA (2015).

Note: This review focused on source, sink, lag, and transformation functions; see Schofield et al. (2018) for refuge functions.