Biological Connectivity of Seasonally Ponded Wetlands across Spatial and Temporal Scales

L.L. Smith, A.L. Subalusky, C.L. Atkinson, J.E. Earl, D.M. Mushet, D.E. Scott, S.L. Lance, and S.A. Johnson

Research Impact Statement: Seasonal wetlands are connected biologically to surrounding ecosystems through the movements of animals. This connectivity is critical to species conservation and ecosystem functioning.

ABSTRACT: Many species that inhabit seasonally ponded wetlands also rely on surrounding upland habitats and nearby aquatic ecosystems for resources to support life stages and to maintain viable populations. Understanding biological connectivity among these habitats is critical to ensure that landscapes are protected at appropriate scales to conserve species and ecosystem function. Biological connectivity occurs across a range of spatial and temporal scales. For example, at annual time scales many organisms move between seasonal wetlands and adjacent terrestrial habitats as they undergo life-stage transitions; at generational time scales, individuals may disperse among nearby wetlands; and at multigenerational scales, there can be gene flow across large portions of a species' range. The scale of biological connectivity may also vary among species. Larger bodied or more vagile species can connect a matrix of seasonally ponded wetlands, streams, lakes, and surrounding terrestrial habitats on a seasonal or annual basis. Measuring biological connectivity at different spatial and temporal scales remains a challenge. Here we review environmental and biological factors that drive biological connectivity, discuss implications of biological connectivity for animal populations and ecosystem processes, and provide examples illustrating the range of spatial and temporal scales across which biological connectivity occurs in seasonal wetlands.

(KEYWORDS: aquatic ecology; seasonal wetland; ephemeral wetland; rivers; streams; lakes; biota, fauna; habitat.)

INTRODUCTION

Seasonally ponded wetlands (hereafter seasonal wetlands) often occur in topographic depressions outside of floodplains, where they are embedded in upland matrices. Typical features of seasonal wetlands include short, seasonal periods of inundation (hereafter referred to as hydroperiod), a lack of perennial surface-water connections to other wetlands, and biota uniquely adapted to patterns of wetting and drying. However, seasonal wetlands may also have very long hydroperiods and may not always fill and dry annually. Seasonal wetlands, including northeastern vernal pools, Carolina bays, prairie potholes, Delmarva wetlands, depression marshes, and cypress domes, vary considerably in geomorphology, hydrology, landscape setting, natural disturbances,

and biotic communities. Because many seasonal wetlands are surrounded by uplands and often lack obvious surface-water connections to other wetlands or streams, they have been referred to as "geographically isolated" (Leibowitz 2003). However, this term has fallen out of favor, because it suggests a lack of connections to other aquatic systems and surrounding upland habitats (Mushet et al. 2015). In fact, seasonal wetlands can be connected to other wetlands and aquatic systems via groundwater, intermittent surface water (Cohen et al. 2016; Vanderhoof et al. 2017), geochemical processes (Marton et al. 2015), and as we detail here, seasonal wetlands are biologically connected to uplands and other aquatic ecosystems. Seasonal wetlands and their biota are critical elements in functioning landscapes (Cohen et al. 2016). Their contribution is through periodic or intermittent flows of water, materials, and organisms. While hydrologic and biogeochemical transfers are increasingly recognized (Cohen et al. 2016), biological connectivity is rarely considered.

Biological connectivity results from the movement of an organism across the landscape. This connectivity supports foraging, mating, migration, dispersal, and gene flow (Zeller et al. 2012). As with hydrological connectivity, biological connectivity can occur across a range of spatial and temporal scales. Understanding biological connectivity is critical to ensure that landscapes are protected at appropriate scales to conserve species and ecosystem function. However, our ability to measure biological connectivity is challenged by scales of spatial and temporal variability.

In many cases, the flux of organisms among systems is considerable, yet direct movement of animals between wetlands and other systems, including adjacent terrestrial and permanent water bodies, is difficult to measure. Moreover, there are tradeoffs among different methods in the scale at which biological connectivity can be studied. Choosing the best method to use for a given study will depend upon time and cost limitations of the investigator and the primary question asked. It may require multiple methods across a range of spatial scales to discern landscape and ecosystem patterns of connectivity.

Our understanding of the drivers of biological connectivity and their role in supporting populations is incomplete. Here we explore environmental and biological drivers of connectivity, consequences of biological connectivity, relevant spatial and temporal scales of connectivity, and provide examples demonstrating biological connectivity across these different scales. We provide a list of methods in Table 1 and detailed descriptions of methods for measuring biological connectivity as Supporting Information.

DRIVERS OF BIOLOGICAL CONNECTIVITY

Biological connectivity among wetlands and the surrounding habitat matrix is driven by both environmental and biological factors, as well as their interactions. Proximate weather conditions and climate are major

TABLE 1. Methods for measuring biological connectivity of seasonal wetlands with surrounding uplands, other wetlands, and permanent waters; the scale at which they are likely to be most informative; primary metrics resulting from each method; and key references.

Method	Wetland–upland	Wetland–wetland	Wetland–permanent water	Resulting metric	Selected references
Frog call	X			Presence/absence	Peterson and Dorcas (2010)
Egg mass surveys	X			Presence/absence; abundance	Grant et al. (2005); Paton and Harris (2010)
Insect emergence traps	X			Abundance; dispersal; resource transfer	Leeper and Taylor (1998); Stagliano et al. (1998)
Drift fences	X	X		Abundance; dispersal; resource transfer	Dodd and Scott (1994); Gibbons et al. (2006); Scott et al. (2013)
Visual surveys		X	X	Abundance; habitat use	Post et al. (1998); Subalusky, Smith, et al. (2009)
Mark-recapture		X	X	Abundance; habitat use; dispersal	Wood et al. (1998); Trenham et al. (2001)
Tracking animal movements	X	X	X	Habitat use; dispersal	Rittenhouse and Semlitsch (2006); Madison et al. (2010); Connette and Semlitsch (2011); Gourret et al. (2011)
Stable isotopes	X		X	Resource transfer; dispersal	Post (2002); Macneale et al. (2005); West et al. (2006); Scott et al. (2015)
Fatty acids	X	X		Resource transfer	Hebert et al. (2006); Whiles et al. (2010); Twining et al. (2016)
Genetics		X	X	Presence/absence (eDNA); population structure; dispersal	Storfer et al. (2007); Shoemaker and Gibbs (2013); Goldberg et al. (2016)

Note: For more detail on each method, see Supporting Information.

environmental drivers of connectivity since seasonal wetlands receive most of their water from precipitation or meltwater, which can facilitate movements of organisms through temporary surface flows (Todd and Winne 2006 and references therein). During drought, seasonal wetlands might not fill at all, and animals must have a mechanism to persist within the wetland basin or in the adjacent upland habitat, or must move to an alternate aquatic habitat type (Dietz-Brantley et al. 2002; Gibbons et al. 2006; Willson et al. 2006).

Wetland abundance and configuration on the landscape are also important environmental drivers of biological connectivity (see Mushet et al. 2018). Biological connectivity is generally greater in landscapes with high wetland density as animals have less distance to travel among wetlands. In addition, many animals use wetlands as stepping stones to move across a landscape (Amezaga et al. 2002; Spear et al. 2005). Thus, the intervening landscape also plays an important role in biological connectivity, with unfragmented natural habitat surrounding wetlands often playing a critical role enabling movements of biota.

Biological drivers of connectivity include habitat requirements, individual species traits, and population dynamics. Many species use only wetlands with a particular vegetation structure, e.g., wetlands with herbaceous vegetation vs. forested wetlands (Battle and Golladay 2001; Werner et al. 2007; Liner et al. 2008; but see Skidds et al. 2007). Species with complex life histories (some insects and amphibians) may require aquatic habitat for breeding and larval life stages, with individuals moving into surrounding uplands as juveniles or adults (Semlitsch and Bodie 2003), whereas others move to uplands for overwintering (Buhlmann 1995; Burke et al. 1995). For other species, individuals may undergo a dormant period within a dry wetland (Knepton 1954; Anderson and Smith 2004). Even when wetlands do not dry, individuals of some species leave wetlands seasonally to nest on dry land and return to wetlands following nesting and hatching (Buhlmann 1995).

CONSEQUENCES OF CONNECTIVITY

Biological connectivity between a seasonal wetland and its surrounding uplands, or among multiple nearby wetlands, is vital. First and foremost, an individual's ability to move among habitats of varying quality and resources has direct consequences for its survival and reproduction (=fitness), and thereby the maintenance of genetic variation within and among populations. When connectivity enhances an individual's survival probability, it also has consequences at the population level and above. Biological connectivity reduces odds of local extinction and increases likelihood of recovery if extinction does occur due to chance, drought, fire, disease, or other perturbations.

In landscapes where they occur, seasonal wetlands are recognized as hotspots of biogeochemical transformation and sequestration (Capps et al. 2014; Capps et al. 2015). Their ability to transform and redistribute materials at a landscape scale, often through animal movements, is an emergent property of their biological complexity and connectivity. This connectivity has consequences for community assembly and disassembly through species interactions including predation, competition, and transport of resources (Holt 2004; Vanni et al. 2004; O'Neill 2016; Leibold et al. 2017). Top predators in wetlands include both resident and transient species ranging in body size from large vertebrates (e.g., otter, wading birds, snakes, alligators, and fishes) to comparatively small, but abundant, predatory invertebrates (e.g., aquatic beetles, larval odonates, backswimmers, crayfish). These predators can influence the distribution, abundance, morphology, and behavior of prey (McCollum and Leimberger 1997), as well as the quantity, availability and distribution of nutrients provided by that prey (Schmitz et al. 2010).

Biological connectivity also has implications for ecosystem function. As animals move across ecosystem boundaries, they can transport energy and nutrients between ecosystems (Polis et al. 1997) and strengthen connections among heterogeneous habitat patches (Loreau et al. 2003; Leroux and Loreau 2008; Sitters et al. 2015). While energy and nutrients can be carried passively into wetlands, animal subsidies may move in both directions across wetland-terrestrial boundaries. Furthermore, due to the distinct shift in habitat use and in elemental composition during different life history stages in many taxa that depend on wetlands, energy and nutrients may be redistributed across the landscape (Regester et al. 2008; Capps et al. 2015; Tiegs et al. 2016). As a result, organisms with complex, biphasic life histories can significantly influence ecosystem nutrient-dynamics by altering the flux of energy and nutrients moving among ecosystems (Regester et al. 2006).

The net balance of these connections and the energy and nutrient subsidy loading by organisms depends on population size, survivorship rates, developmental stage, and net flux (Capps et al. 2015). Given the ontogenetic shifts that occur across many wetland-dependent organisms, the net flux of different nutrients can vary dramatically as a result of the life stage and the direction of movement. Maintenance of populations and flow of energy and nutrients depends on conserving both the terrestrial and aquatic systems. For example, intact uplands must be

maintained around the wetlands to support populations of adult amphibians, and wetland hydroperiod and vegetation must be sufficiently maintained to provide breeding, larval, and juvenile habitat (Semlitsch and Bodie 2003; Scott et al. 2013) and suitable access to this habitat for eggs, larvae, and metamorphs (Chandler et al. 2017). Recent evidence suggests that upland forest management also has direct effects on embedded wetland hydrology, which has implications for wetland biota including amphibians (Jones et al. 2018).

CONNECTIVITY ACROSS SPATIAL AND TEMPORAL SCALES

In the simplest case, biological connectivity occurs when organisms move to and from wetlands in search of resources (Figure 1). However, the spatial and temporal scales can vary widely. For example, during a single breeding cycle (or wetland hydroperiod), adult amphibians may move relatively short distances from the terrestrial landscape into nearby wetlands to breed and juveniles travel several hundred meters into the terrestrial system after metamorphosis (Semlitsch and Bodie 2003; Gibbons et al. 2006; see section below). During the same time period,
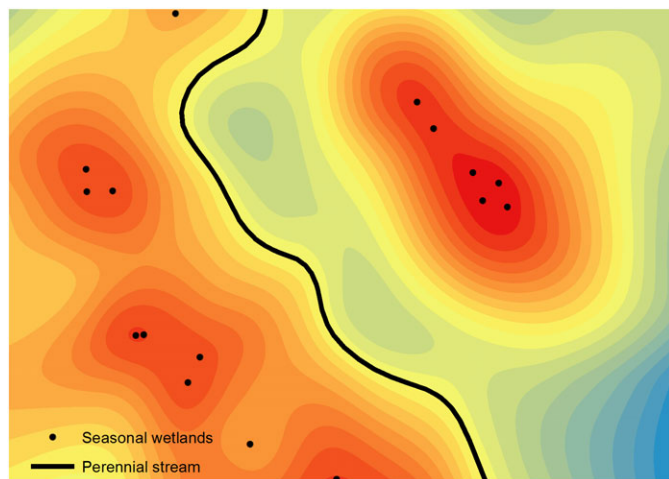

FIGURE 1. Conceptual diagram of the frequency and magnitude of biological connectivity among seasonal wetlands and a perennial stream. Warm colors (red and orange) indicate frequent and/or high magnitude of biological connectivity (e.g., aggregations of wetlands), intermediate colors (yellows) indicate less frequent connectivity, whereas, cool colors (blues) indicate infrequent biological connectivity, e.g., uplands distant from wetlands or adjacent to high resistance habitats. Seasonal wetlands and perennial streams (or lakes) experience moderate biological connectivity (yellow), particularly when the intervening habitat has low resistance and when wetlands can be used as stepping stones facilitating movement.

wading birds travel up to 30 km from colonies to forage in seasonal wetlands as water recedes and concentrates prey in smaller pools (Kushlan 1989; Strong et al. 1997; Gawlik 2002). These two examples of biological connectivity occur at similar temporal scales (seasonally), but very different spatial scales. Connectivity can also occur much less frequently, across much longer time scales (Figure 1). For example, organisms may move among wetlands and other aquatic systems through ontogenetic habitat shifts or dispersal related to metapopulation dynamics. In the section that follows we provide a description of the biological drivers, environmental drivers, and examples at three spatiotemporal scales at which biological connectivity can occur: small scale and short time frames, medium scale and moderate time frames, and large scale and long time frames. Among the three scales, biological connectivity at the small scale and shortest time frame is best understood, whereas medium-scale connectivity is less understood, and we know least about large-scale connectivity.

Small Scale and Short Time Frame: Wetland to Uplands

Seasonal wetlands and surrounding uplands are connected through a variety of processes, most of which occur on yearly or seasonal time scales. These connections can be passive or active. Passive connections include materials moved by gravity, wind, and water, while active connections are the result of animal movement. Passive connections are most likely to flow from uplands to wetlands; because of their location in topographic depressions, seasonal wetlands tend to accumulate materials (e.g., canopy invertebrates; Kraus et al. 2011). Active connections, the focus of this section, have net flows both into wetlands and into uplands. The direction of active flows and their effects on the recipient ecosystem depends on an organism's life history, trophic level, and stoichiometry, as well as on environmental conditions (Regester and Whiles 2006; Sitters et al. 2015; Luhring et al. 2017).

Biological Drivers of Connectivity: Small Scale. Animal movement between seasonal wetlands and uplands occurs frequently via two primary mechanisms. One is related to life history, when animals use both wetlands and uplands seasonally as part of their life cycle (i.e., breeding and reproduction), and the other occurs when animals move between ecosystems periodically to forage. Most organisms using both seasonal wetlands and uplands have either retained conservative traits such as aquatic developmental stages or have evolved to use both

ecosystems to increase their fitness (Werner and Gilliam 1984).

Aquatic insects and many species of amphibians use seasonal wetlands for breeding and reproduction, depositing eggs that develop into larvae and in some cases depositing larvae directly in the wetland (e.g., Reinhardt et al. 2013). The energy and nutrients for most insect eggs likely originate in the wetland itself, though dragonflies may be an exception (Anholt et al. 1991). Most amphibians that lay eggs in seasonal wetlands likely provision their eggs through terrestrial foraging (Jørgensen 1984). Some of these eggs develop into larvae, but many die at the egg stage. Amphibian eggs are more labile and nutrient rich than terrestrial plant material (Regester and Whiles 2006), which causes egg nutrients (including capsules, egg membranes, and unhatched embryos) to be rapidly incorporated into wetland food webs. A variety of factors can lead to catastrophic egg or larval mortality (Greenberg et al. 2017), which results in all of the nutrients and energy in amphibian eggs staying within the wetland. This has been shown to occur with very short hydroperiods, high levels of predation (Regester et al. 2006), extreme water temperatures, and low dissolved oxygen (Reinhardt et al. 2013).

Metamorphosis is another life-stage transition that connects wetlands and uplands. Amphibians and some aquatic insects go through metamorphosis and move from wetlands into upland ecosystems. Aquatic insects produce very large amounts of biomass emerging from lakes (e.g., Gratton et al. 2008), and this is seen in seasonal wetlands as well. Midges (Chironomidae) can make up very large proportions of biomass export from wetlands (Leeper and Taylor 1998; Stagliano et al. 1998). The biomass of metamorphosing amphibians emerging from a single wetland can also be very large, up to 1.49 tons (Gibbons et al. 2006), but there are very few estimates and they vary based on wetland size, drought history, and hydroperiod (Regester et al. 2006; Schriever et al. 2014). Exports of amphibians and aquatic insects can be of similar orders of magnitude, but no direct comparisons in the same wetlands have been made.

Freshwater turtles also connect seasonal wetlands to uplands through egg deposition. Many freshwater turtles spend large amounts of time foraging in wetlands and then bury eggs in friable upland soils. Reptile eggs are frequently depredated by mammals and birds, but unhatched eggs and eggshells may provide important nutrients for plants (see Vander Zanden et al. 2012).

Environmental Drivers of Connectivity: Small Scale. The main drivers of biomass export from wetlands are hydroperiod, predator abundance, and resource availability, though there are also anthro-pogenic factors (e.g., land conversion) that likely have large impacts (Willson and Winne 2016; Julia E. Earl, Louisiana Tech University, 2017, unpublished data). Both emergent insect and amphibian biomass and taxonomic diversity are highest in wetlands with intermediate hydroperiods (Pechmann et al. 1989; Whiles and Goldowitz 2001; Semlitsch et al. 2015). This is likely because wetlands with very short hydroperiods dry before many species are able to metamorphose, whereas wetlands with longer hydroperiods accumulate predators that limit the production of insects and amphibian larvae occupying lower trophic levels (Wellborn et al. 1996). The input of leaf material to wetlands can also influence the reciprocal export of organisms from wetlands back to uplands. Increasing plant litter inputs to ponds can increase the biomass of amphibian exports to uplands (Earl and Semlitsch 2012), though leaves with high concentrations of tannins may decrease that export (Earl et al. 2014).

The spatial distribution of insects and amphibians in uplands depends on the dispersal capabilities of these organisms following ontogenetic development (Pittman et al. 2014). Dispersal distances vary considerably among insect orders; Odonata, Coleoptera, and Hemiptera are likely capable of the greatest dispersal distances as they are strong fliers relative to other groups (Johnson 1969; Angelibert and Giani 2003). However, abundance likely declines rapidly with distance from the wetland and varies with vegetation type and structure, as seen with stream and lake insects (Jackson and Resh 1989; Gratton et al. 2008; Wesner 2010). The terrestrial distribution of amphibians has been characterized for some species; for example, some metamorph salamanders move beyond 175 m from the wetland (Johnson 2003; Scott et al. 2013) and juvenile frogs have been reported to disperse more than 2,500 m from a wetland (Berven and Grudzien 1990). It is not entirely clear what terrestrial habitat features structure the terrestrial distribution of juveniles, but some species have been found to orient toward forest during movement (Pittman and Semlitsch 2013; Cline and Hunter 2014). Some salamander juveniles may have clumped distributions, as they are attracted to burrows occupied by conspecifics (Greene et al. 2016).

Examples: Small Scale and Short Time Frame (Wetland to Upland Connectivity). The movements of certain amphibians provide excellent examples of small temporal- and spatial-scale connectivity between seasonal wetlands and uplands. Most ranid (true) frogs and ambystomatid (mole) salamanders breed once per year, depositing eggs into wetlands. Eggs are rich in energy and carbon, but lower in other nutrients, particularly calcium (Luhring et al. 2017). Egg and subsequent larval mortality in

wetlands is typically high. Amphibian eggs and larvae are often depredated by other wetland organisms (e.g., crayfish, leeches, caddisflies, salamander larvae, and snakes; Axelsson et al. 1997; Richter 2000; Chivers et al. 2001), infected by the fungus *Saprolegnia* (Robinson et al. 2003), or simply fail to hatch. Unhatched eggs and the gelatinous matrix around eggs decompose rapidly (Regester and Whiles 2006).

Most amphibians move from wetlands into the uplands shortly after metamorphosis. Orientation away from wetlands is nonrandom but does not always relate to habitat (e.g., Timm et al. 2007; Homan et al. 2010). Differences in movement ecology likely alter the distribution of metamorph amphibians in uplands (Pittman et al. 2014). Frogs tend to move farther from the wetland edge than ambystomatid salamanders, which likely makes their effects on upland ecosystems less concentrated than that of salamanders, though movements of both groups tend to occur on small spatial scales of 10s–100s of meters (Rittenhouse and Semlitsch 2007).

Juvenile amphibians tend to have high mortality during their first few months in uplands. This mortality may be high at the wetland edge if vertebrate predators are present (Roznik and Johnson 2009; Pittman et al. 2013). Studies estimate mortality as high as 75%–94% depending on density and terrestrial environment in the first few months of the juvenile stage (Todd and Rothermel 2006; Harper and Semlitsch 2007; Earl and Semlitsch 2013). Some mortality likely results in supplemental prey for terrestrial vertebrate scavengers, but a large proportion of carcasses is scavenged by invertebrates (Abernethy et al. 2017). In very dry conditions, many metamorphs likely desiccate, particularly if refuges are not available (Rittenhouse et al. 2008) and those carcasses may provide nutrients to upland ecosystems (Julia E. Earl, Luke Pauley, Raymond D. Semlitsch, University of Missouri, 2012, unpublished data).

Juvenile amphibians that survive their initial dispersal become predators primarily of small invertebrates in upland ecosystems and are thought to cause trophic cascades (McCoy et al. 2009). Metamorph depredation of invertebrates may also increase nutrient cycling as metamorphs digest and excrete nutrients that are otherwise unavailable in invertebrates (Hairston 1987). If they depredate decomposers, such as springtails (Collembola), juvenile amphibians may also impact upland decomposition rates as seen with terrestrial salamanders (Homyack et al. 2010).

The net flow of energy and nutrients between wetlands and uplands depends on many factors and varies by species (Luhring et al. 2017). For example, most amphibian species are characterized by boom-bust population cycles that are highly variable through time. Therefore, they generate temporally variable pulses of resources (e.g., carbon [C], nitrogen [N], and phosphorus [P]) across habitat boundaries. Previous work has demonstrated that both the nutrient content and the growth rates across organisms vary intra- and interspecifically, by developmental stage, and by biotic and abiotic conditions (Tiegs et al. 2016; Stephens et al. 2017). Potential variation in life histories across amphibian species makes it essential to understand how resource quality influences species-specific population structure and interspecific interactions in amphibian communities.

Medium Scale and Moderate Time Frame: Wetland to Wetland

Taxonomic groups differ in their habitat requirements as well as their abilities to move among suitable habitat patches. Body size, mode of locomotion, sensitivity to environmental variables, and numerous other factors affect an organism's ability to move among wetlands, i.e., biological connectivity. In this section, we attempt to follow the terminology of Semlitsch (2008), who described intrapopulation movements as "migration," and interpopulation movements as "dispersal." However, the difficulty in defining what constitutes a population in different taxa may cloud this distinction. Regardless, whether we deem an animal's movement as migration or dispersal, both represent the importance of biological connectivity. An individual may move among wetlands within its own lifetime, as a function of its resource needs, or a species may "move" across a landscape of wetlands over several generations, as a function of true one-way dispersal by individuals. Here we describe the conditions that prompt movements among wetlands, the individual traits, and landscape attributes that enhance the probability of successful dispersal or migration, and the role that interwetland biological connectivity plays in local extinctions, recolonization, and species persistence. We focus on amphibians and reptiles because these taxonomic groups differ in their habitat requirements as well as abilities to move between suitable habitat patches.

Biological Drivers of Connectivity: Medium Scale. For many (but not all) amphibian species that breed in seasonal wetlands, it is the egg and larval stages that require the aquatic habitat, and post-metamorphic animals that require upland habitats as described above. In the months or years prior to reproductive maturity, terrestrial subadult animals may move increasingly far from their natal wetland (Trenham and Shaffer 2005; Semlitsch 2008; Scott et al. 2013). Although most individuals that survive to reproductive maturity will migrate back to their

natal wetland as adults, some fraction will relocate to a new wetland. For these organisms, biological connectivity among wetlands equates to true dispersal (Semlitsch 2008), and the main impacts may be at the interpopulation level, e.g., the introduction of new genetic material and the rescue of locally depleted populations. Generally, adult salamanders are thought to be more philopatric than adult frogs (Vasconcelos and Calhoun 2004), but adults of some ambystomatid species can show high levels of dispersal to new wetlands (*Ambystoma californiense*, 26%, Trenham et al. 2001) and some anurans show relatively low interwetland movement (*Bufo quercicus*, 1.9%, Greenberg and Tanner 2005). Landscape genetics studies of amphibian species routinely find evidence of interwetland movements and admixture (Funk et al. 2005; Spear et al. 2005; Zamudio and Wieczorek 2007).

Exceptions to the "juvenile dispersal" hypothesis for wetland-breeding amphibians are the genera *Siren, Amphiuma*, and *Pseudobranchus*, which have fully aquatic adults that are generally restricted to permanent wetlands, and also have the ability to persist in seasonal wetlands by aestivating for prolonged periods when a wetland dries (Gelbach et al. 1973; Moler 2008). When siren and amphiuma occur in seasonal wetlands, they can function as keystone predators (Fauth 1999) with strong effects on the amphibian and invertebrate communities. Due to their diminutive limbs, all three genera are thought to be poor overland dispersers (Snodgrass et al. 1999). Distributional studies show that siren and amphiuma occur in longer hydroperiod seasonal wetlands and can apparently recolonize wetlands up to 0.7 km from other aquatic habitats (Fauth 1999; Snodgrass et al. 1999); thus, there is evidence of biological connectivity between seasonal wetlands and nearby more permanent waters even for these poor dispersers.

As with amphibians, the evidence for among-wetland connectivity in reptiles comes from a variety of studies. For turtles and some semiaquatic snakes, the egg and hatchling stages are terrestrial; subadults (juveniles) and adults use aquatic habitats. Females lay eggs or give birth adjacent to a wetland, and most surviving hatchlings are presumed to migrate back to the maternal wetland (e.g., *Trachemys scripta*, Frazer et al. 1990; *Kinosternon subrubrum*, Frazer et al. 1991). Species presence and abundance patterns (e.g., Ficetola et al. 2004; Willson et al. 2006) confirm the importance of unfragmented uplands to connect wetlands (Joyal et al. 2001; Guzy et al. 2013). When moving among wetlands, turtles tend to travel in straight-line movements (Bowne and White 2004) and to closer wetlands (Roe et al. 2009; but see Bowne et al. 2006). In general, habitat use and movement of turtles are related to the number, variety,

and isolation of wetlands in a complex (Joyal et al. 2001); habitat selection is based on the quality of the destination wetland (Bowne et al. 2006). Movement to new wetlands, when it occurs, is generally in response to resource needs, mate acquisition, and deteriorating environmental conditions (Gibbons 1990; Roe and Georges 2007). For aquatic snakes and turtles, true dispersal may occur (i.e., one-way movement to a new wetland), but much of the biological connectivity is due to back-and-forth migrations among wetlands, or even the use of multiple wetlands as part of an individual's home range (Roe and Georges 2007).

Environmental Drivers of Connectivity: Medium Scale. As with other spatial and temporal scales, wetland drying due to drought conditions is a primary driver of biological connectivity. However, not all organisms respond the same. As described above, fully aquatic salamanders can survive in seasonal wetlands during dry downs by aestivating below ground. Many other species respond to wetland dry downs by moving to more permanent water sources. For example, turtles and snakes respond to wetland drying (Gibbons et al. 1983; Buhlmann 1995; Bowne et al. 2006) by moving overland, and through time, longer hydroperiod wetlands exhibit more connectivity (Bowne et al. 2006; Roe et al. 2009).

There has been a long-standing interest in understanding what features of the landscape can affect connectivity via animal movement among seasonal wetlands (Taylor et al. 1993). A majority of early studies used species-assemblages across wetlands to infer impacts of habitat fragmentation and alteration of the upland matrix on animal movements and connectivity (e.g., Knutson et al. 1999; Skelly et al. 1999; Russell et al. 2002; Ficetola et al. 2004; Willson et al. 2006). These studies tend not to consider within-wetland conditions known to influence species composition (Caldwell et al. 1980; Morin and Johnson 1988; Tejedo 1993) but suggest that road density (Fahrig et al. 1995; Trombulak and Frissell 2000), land-use patterns (Attum et al. 2000; Ficetola et al. 2004), and wetland isolation (Bowne et al. 2006; Roe et al. 2009) all affect connectivity. Across these taxa, it is clear that roads can provide a strong barrier to movement due to road surface avoidance (Andrews and Gibbons 2005; Andrews et al. 2008) and high incidence of mortality (Vos and Chardon 1998; Steen and Gibbs 2004; Aresco 2005; Marsh et al. 2005). The presence of wetlands within intact forest, on the other hand, is consistently found to increase connectivity and potentially provide movement corridors (Gibbs 1988; Laan and Verboom 1990; Attum et al. 2000).

There are species- and life-stage-specific responses to types and quality of habitat surrounding wetlands

that lead to substantial variation in connectivity (Gibbs 1988; Marsh and Trenham 2001; Rothermel and Semlitsch 2002). Dispersal of both juveniles and experienced breeders has been linked to movement from small to large breeding populations, indicating that habitat selection is at the scale of the wetland and not the intervening uplands (Berven and Grudzien 1990; Richter et al. 2001; Gamble et al. 2007; Groff et al. 2017). Landscape genetic studies of amphibians not only consistently find an overall isolation by distance (Spear et al. 2005; Wang 2009; Richardson 2012) but also highlight the importance of landscape features such as roads, slope, elevation, and land cover (Funk et al. 2005; Spear et al. 2005; Greenwald et al. 2009; Wang et al. 2009; Goldberg and Waits 2010; Richardson 2012). Importantly, these studies reinforce the finding that barriers to movement are species-specific (Goldberg and Waits 2010; Richardson 2012) and that knowledge of adult usage of uplands does not necessarily translate to interwetland movements and connectivity (Wang et al. 2009).

There have been surprisingly few landscape genetics studies of aquatic reptiles. Genetic differentiation of reptiles among wetlands on a small scale may not be expected due to their relatively long life span and high vagility; however, frequent adult movements among wetlands may not correspond to genetic connectivity. In the bog turtle (*Glyptemys muhlenbergii*), a wetland-obligate species, Shoemaker and Gibbs (2013) did not find genetic structure among wetlands at fine scales (<2 km). In another wetland-obligate species, the copperbelly water snake (*Nerodia erythrogaster neglecta*), population structure occurred at the regional scale but was more closely tied to quality of habitat (disturbed vs. natural) than to geographic distance (Marshall et al. 2009). These patterns are likely lost in species that use streams and rivers in addition to seasonal wetlands and thus exchange genes across a greater area (Castellano et al. 2009).

Examples: Medium Scale and Moderate Time Frame (Wetland to Wetland Connectivity). Several studies on the Department of Energy's Savannah River Site (SRS) in South Carolina have documented wetland to wetland movements of amphibians and reptiles. The amphibian community at Rainbow Bay, a 1-ha, 1.4-m deep seasonal wetland, has been monitored daily since September 1978. Four other seasonal wetlands occur within 1 km of Rainbow Bay, and in wet years (>157 cm rain/yr), all sites are connected via human-made ditches to perennial stream headwaters. Intervening terrestrial habitat is mature mixed pine/hardwood. Scott (1994) estimated 5%–7% dispersal of 1-yr-old marbled salamanders (*Ambystoma opacum*) from their natal pond (Rainbow Bay) to the other four wetlands. Dispersal rates differed among wetlands and species. For example, the New Production Reactor (NPR) wetland generally has a longer hydroperiod than Rainbow Bay, is located ~500 m away, and in wet years connects hydrologically to Pen Branch Creek. Juvenile cohorts of marbled salamanders (21–6,064 individuals) emigrated from both wetlands each spring for five years (except for one year at Rainbow Bay). For the Rainbow Bay juveniles, 1%–3% of adult survivors bred at the NPR wetland; for the NPR juveniles, 20%–80% of known survivors returned not to NPR but to Rainbow Bay to breed (David E. Scott, Anne C. Chazal, Joseph H. K. Pechmann, Savannah River Ecology Laboratory, 1991-1995, unpublished data). Over the same period, mole salamanders (*A. talpoideum*) in Rainbow Bay had declined from thousands in the late 1970s to a few dozen breeding adults in the early 2000s (Daszak et al. 2005); the current population appears to consist almost entirely of dispersers from other wetlands (David E. Scott, Stacey L. Lance, Savannah River Ecology Laboratory, 2010-2017, unpublished data; Nunziata et al. 2017).

In 1983, the Department of Energy eliminated a 1-ha wetland (Sun Bay) after constructing four smaller (0.02 ha) wetlands 300–600 m from the original wetland (Pechmann et al. 2001). Despite the loss of this wetland and extensive clearing of the uplands within 300 m around Sun Bay, individuals of 10 amphibian species continued to return to the former Sun Bay wetland in the four years following elimination. Nearly half of mole salamander captures at the four created wetlands (46 of 99 individuals) were of salamanders initially marked at Sun Bay. Interestingly, in the first two years, when salamanders that originated at Sun Bay were captured at and placed in a created wetland, they exited within a few days and females remained gravid. It was not until 1986 that the original Sun Bay animals colonized and successfully produced juveniles in created wetlands, showing that observed connectivity may not result in demographic connectivity.

Reptile studies have been conducted at Ellenton Bay and surrounding wetlands on the SRS since 1967 (Gibbons 1990). Ellenton Bay is small herbaceous wetland encircled by a drift fence (see Supporting Information) that has been used to census amphibian and reptile movements. Approximately nine other seasonal wetlands, one perennial beaver pond, one perennial ox-bow lake, and two perennial streams occur within a radius of 3.5 km of Ellenton Bay. The Savannah River and its associated river swamp is 1 km west of Ellenton Bay. The uplands surrounding Ellenton Bay historically consisted of old fields in varying states of succession, mixed pine/hardwoods, and bottomland hardwoods adjacent to the streams (Davis and Janecek 1997). Although often referred to

as a "permanent" seasonal wetland, Ellenton Bay is known to have dried during at least four 1–3 year severe droughts from the mid-1950s through 1989. Here we focus on the biological connectivity among wetlands in the Ellenton Bay metapopulation of aquatic turtles and semiaquatic snakes, particularly in response to drought and wetland refilling events.

Burke et al. (1995) analyzed data for 26 years of capture–mark–recapture (Table 1; Supporting Information) of the yellow-bellied slider (*Trachemys scripta*) in the Ellenton Bay system. During the study (1967–1993), turtles were captured at 11 locations. Almost 4% of sliders marked at Ellenton Bay were recaptured at other wetlands. More than 7% of turtles first captured at the surrounding wetlands later emigrated to Ellenton Bay. Of particular note is that after 22 years previously marked turtles were still being found at new locations, suggesting that for long-lived reptiles such as turtles, numerous wetlands, both seasonal and perennial, may be occupied over the course of a lifetime.

Wetland drying due to drought conditions is a primary driver of biological connectivity of wetlands for aquatic turtles, but not all species respond similarly. A drought in 1980–1981 nearly caused Ellenton Bay to dry (Gibbons et al. 1983). Two species, yellow-bellied slider and Florida cooter (*Pseudemys concinna floridana*), emigrated from Ellenton Bay in large numbers compared to nondrought years; most of these emigrants oriented toward the nearest perennial water 400 m away, with subsequent trapping confirming the destination. Females of both species also reduced their reproductive output. Drought did not change emigration patterns for three other species (Gibbons et al. 1983).

Other factors also influence among-wetland connectivity for turtles, as evidenced by differences in movement patterns between sexes (Morreale et al. 1984). Male yellow-bellied sliders consistently showed greater among-wetland movements and longer travel distances than females. Using a technique (gamma/beta radiation counts) only possible on the SRS and a few other places, the authors documented that female sliders in contaminated wetlands had radiation counts nearly five times higher than males, indicative of a lower propensity to disperse. Aquatic snakes also exhibit routine among-wetland movements. They are attracted to seasonal wetlands when prey are abundant, and conversely may emigrate from wetlands when prey are scarce. During the 1985–1987 drought at Ellenton Bay, banded water snakes (*Nerodia fasciata*) emigrated during drying, with most orienting toward the Savannah River floodplain. A second species, black swamp snake (*Seminatrix pygaea*), also emigrated to other sites, but in response to a decline in prey (Seigel et al. 1995). Following a 2000–2003

drought, Willson et al. (2006) noted that cottonmouths (*Agkistrodon piscivorus*) emigrating from the Savannah River floodplain were the primary recolonizers of Ellenton Bay. Additional studies revealed that, at least for cottonmouths, overland movement between Ellenton Bay and adjacent wetlands was not solely a response to drought conditions but part of an annual migration among seasonal wetlands, which provide resource-rich summer forage and refugia-rich overwintering habitat (Glaudas et al. 2007).

Large Scale and Long Time Frame: Wetlands to Lakes/Rivers

Some species can fulfill all their resource needs within a complex of seasonal wetlands and upland habitat; however, other animals may rely upon perennial sources of water. Streams, rivers, and lakes provide complementary habitat resources to seasonal wetlands because of their larger size and perennial hydroperiod. Conversely, seasonal wetlands may provide critical foraging and nesting resources for animals that are primarily inhabitants of perennial water bodies. More frequent movements may be a critical component of the animal population's life history, and these movements may be important in moving resource subsidies between seasonal and permanent aquatic ecosystems. However, even very infrequent movements may be important for the maintenance of an animal population, e.g., by providing some genetic mixing in the population and allowing persistence during extreme drought conditions. This scale of connectivity is less well-studied than wetland–upland and wetland–wetland connectivity, partially because of the difficulty in studying animal movement patterns that may occur over tens of kilometers and range in frequency from seasonal to decadal. Documenting the occurrence of these potentially infrequent movements may require multiyear studies of the same population over an extended spatial area, which can be expensive and challenging to undertake. It also may be challenging to defend protection of travel corridors between seasonal wetlands and permanent waters if they are used infrequently. However, extended habitat matrices that include both seasonal wetlands and permanent waters are critical to the life histories of some species.

Biological Drivers of Connectivity: Large Scale. Movements among seasonal wetlands and perennial aquatic systems occur on a seasonal, annual, or semiannual basis for overwintering, reproduction, and foraging in certain species. Some amphibians and reptiles that are primarily wetland inhabitants move into perennial waters in search of

habitat during particularly dry or cold periods (Merrell 1977; Kennett and Georges 1990). These movements may happen yearly in response to seasonal changes, or only during more extreme climatic events. Other species may move between seasonal wetlands and perennial waters in response to ontogenetic shifts in habitat use or a resource base that necessitates deeper waters and larger prey. These movements may occur only once or twice in an individual's lifetime, although they may occur for a few individuals every year at the population level.

Our understanding of primary river and lake inhabitants moving into seasonal wetlands is somewhat limited, although there are several taxa other than amphibians and reptiles for which this has been documented. Bird species commonly found in lakes and rivers use seasonal wetlands for foraging and nesting, a behavior driven by high prey availability in seasonal wetlands coupled with their relative lack of larger predators (Mamo and Bolen 1999; Kennamer and Hepp 2000; Naugle et al. 2001; Bryan 2005; Kilgo and Bryan 2005). Foraging by birds may be particularly pronounced during wetland dry downs, when prey are concentrated (Kushlan 1989; Gawlik 2002). Bats also appear to use complementary resources provided by both habitat types, as southeastern myotis (*Myotis austroriparius*) presence was linked to proximity of both Carolina bays and bottomland hardwood communities (Ford et al. 2006). American alligators (*Alligator mississippiensis*) also move from perennial water bodies into seasonal wetlands to nest (Subalusky, Fitzgerald, et al. 2009).

Environmental Drivers of Connectivity: Large Scale. Primary environmental drivers of connectivity between seasonal wetlands and permanent water bodies include temperature, hydroperiod, and habitat availability. Temperature can be an important driver of habitat shifts, particularly in very hot or cold environments. Larger bodies of water have greater thermal inertia, which allows them to maintain a relatively more stable thermal profile than small bodies of water like seasonal wetlands. In cold climates, where shallow bodies of water freeze, large bodies of water may retain some unfrozen habitat, particularly in flowing waters.

Hydroperiod is also an important driver of connectivity. Animals may migrate into perennial waters during seasonal wetland drying. Perennial waters may be particularly important during droughts, when a greater proportion of seasonal wetlands become completely dry. Migrations into perennial waters allow wetland species to persist during dry seasons and droughts (Kennett and Georges 1990). Often, individuals migrate into seasonal wetlands rapidly following inundation, as wetlands provide more abundant food resources than perennial waters (Humphrey and Zinn 1982; Kennett and Georges 1990; Roe and Georges 2007; Steen et al. 2010). Flood events can also increase connectivity among wetlands and perennial waters, as intermitted surface-water flows between water bodies can allow increased movement of aquatic and semiaquatic organisms (Leibowitz and Vining 2003; Vanderhoof et al. 2017).

Perennial water bodies may be focal points of dispersal for animals from many seasonal wetlands, thus becoming important sites for genetic mixing of subpopulations. Animals that move between seasonal wetlands and perennial water sources are often large-bodied or more vagile. Their ability to disperse between habitats is dependent upon permeable habitat matrices and dispersal corridors that allow animals to move long distances through upland habitats, although very little is known about the particular habitat types needed by different species. The presence of "stepping stones" of habitat, such as seasonal wetlands that do not provide sufficient resources for long-term use but facilitate long-distance dispersal, may be particularly critical to such movements (Naugle et al. 2001).

Examples: Large Scale and Long Time Frame (Wetlands to Lakes and Rivers). The northern leopard frog (*Lithobates pipiens*) reproduces in the relatively shallow waters of seasonal wetlands throughout its range, where its eggs and larvae face fewer predators than in deeper and more permanent waters that typically contain a larger and more diverse predator community, often including fishes (Merrell 1977). Following breeding for adults and metamorphosis of the larvae, northern leopard frogs leave these reproductive wetlands and travel into the surrounding uplands, where they feed on insects until fall, when the need for overwintering habitat can drive long-distance dispersal (Pope et al. 2000). The northern leopard frog does not burrow into the substrates nor does it possess freeze-resistant physiological traits. It is one of the few amphibian species of northern latitudes that overwinters underwater and avoids freezing by seeking out a lake, wetland, or stream with water that is deep enough so as not to freeze completely (Merrell 1977). In addition, oxygen concentrations and salinity in the water under any ice-cover must remain within tolerable limits until ice-out. Suitable overwintering sites can often be widely distributed in portions of the northern leopard frog's range (Mushet 2010). This wide separation of essential habitats is often exacerbated in the upper Midwest, where periodic droughts reduce the depths of many potential wintering sites (Winter and Rosenberry 1998) below levels that would allow for the survival of overwintering leopard frogs. Thus, the northern leopard frog must be able to move,

often great distances, in its quest for a suitable overwintering site. In the spring, individuals that survive emerge from the overwintering wetland and travel back to a seasonal wetland to reproduce, often to the same site where they successfully bred in the past.

It is the complex pattern of using multiple, often widely dispersed, habitat types on the landscape (a process known as landscape complementation, Pope et al. 2000) that requires the northern leopard frog to be highly mobile and results in the intermixing of populations and flows of genetic material across great distances. In the upper midwest, homogeneous genetic structure of this species suggests that it exists as a single, highly mixed population rather than as multiple finer scale populations (Mushet et al. 2013; Fisher 2015).

Studies in other portions of the northern leopard frog's range showed similar patterns (e.g., Hoffman et al. 2004; Wilson et al. 2008). Thus, the complex life cycle of the northern leopard frog that necessitates long-distance movements is clearly reflected in the genetic datasets that have been assembled for this species. These data are in clear contrast to those of other amphibian species that lack the need to move to permanent waters and display fine-scale genetic separation on the scale of <1 km (e.g., Newman and Squire 2001).

The complex habitat needs of the northern leopard frog raise questions with important conservation implications. What happens if wintering habitats become even more widely separated as a result of more frequent and severe droughts as predicted under many climate change scenarios (Johnson et al. 2010)? What is the threshold beyond which the northern leopard frog can no longer reach and connect the several habitat types needed for its persistence? Paradoxically, land-use trends favoring agricultural production over grassland conservation may be favorable to northern leopard frogs (Mushet et al. 2014). Inczauskis (2017) found that the northern leopard frog is able to move quicker and therefore longer distances through crop rather than grassland cover types. McCauley et al. (2015) described how consolidation drainage, i.e., the practice of draining several small ponds into a single larger pond to allow for more areas to be planted to a crop, increased the number of deeper and more permanently ponded wetlands on the prairie landscape, which are more likely to be suitable as overwintering sites for the northern leopard frog. However, at the landscape scale, these practices reduce seasonal wetlands essential for breeding habitat. Thus, there is no clear answer as to the likelihood that this vagile species will continue to persist into an uncertain future. However, the loss from the prairie landscape of the currently abundant northern leopard frog would represent the loss of a significant piece from the region's biodiversity puzzle.

American alligators undergo distinct ontogenetic shifts in morphology, diet, and mobility as they grow, which can result in the use of different habitat types by juveniles and adults (Schreiber and Rudolf 2008; Subalusky, Fitzgerald, et al. 2009). Adult males are typically found in deep, open water, where perennial water and larger bodied prey are more likely to occur (Joanen and McNease 1972). Adult females use deep water for breeding and return to vegetated marsh to nest (Joanen and McNease 1970, 1980). Juveniles spend the first few years of their lives in vegetated marsh before dispersing to other habitats, which may be driven by higher densities of invertebrate prey and/or less exposure to predation and cannibalism (McNease and Joanen 1974; Deitz 1979; Rootes et al. 1991). In large lakes and coastal marshes, where the majority of alligator research has been conducted, these habitat shifts often take place within the same larger ecosystem. However, in inland portions of alligators' range, seasonal wetlands provide preferred nesting and juvenile habitat, and alligators must move overland to access deeper and more permanent bodies of water (Subalusky, Fitzgerald, et al. 2009; Subalusky, Smith, et al. 2009).

At the Joseph W. Jones Ecological Research Center (Jones Center) in southwest Georgia, alligators use both river systems and a matrix of seasonal wetlands embedded within longleaf pine uplands (Subalusky, Fitzgerald, et al. 2009). Trapping efforts in both river and seasonal wetland habitats showed that significantly larger individuals were found in the river than the wetlands. Although the ratio of females to males was close to one in the river, there were more females than males in wetlands. Movement patterns differed by sex and size class. The majority of subadults made multiple overland movements between multiple wetlands or between multiple wetlands and the river. The majority of adult females moved overland from the river to a complex of wetlands and then back to the river. None of the adult males tracked moved outside of the river system. Nest surveys documented nesting events only in seasonal wetlands and none in the river. Together, these data suggest adult males stayed in the deep water of the river ecosystem, adult females moved into rivers to breed and into seasonal wetlands to nest, and subadults moved between seasonal wetlands where they were born and rivers as they grew larger. This pattern of habitat use was also supported by stable isotope analysis of alligator tissue (Opsahl et al. 2010; Amanda L. Subalusky, Lora L. Smith, Carla L. Atkinson, Joseph W. Jones Ecological Research Center, 2010, unpublished data). Alligators preferred large, forested wetlands but may use smaller wetlands with shorter hydroperiods as "stepping stones" as they move between rivers and wetlands (Subalusky 2007).

Genetic analysis showed some fine-scale population structure on the landscape (Subalusky et al. 2012),

although this structure appeared to be due to mating patterns of adult males rather than any landscape features (Amanda L. Subalusky, Lora L. Smith, Stacey L. Lance, Travis C. Glenn, Yale University, 2017, unpublished data). Furthermore, in the wetland with the highest annual frequency of nesting, there was a low degree of relatedness among hatchlings from year to year, suggesting low nesting site fidelity by adult females (Amanda L. Subalusky, Lora L. Smith, Stacey L. Lance, Travis C. Glenn, Yale University, 2017, unpublished data). Together these data suggest a relatively high degree of mobility across this landscape by alligators. Other genetics studies have found some support for finer scale substructuring of populations within inland populations, suggesting that despite the vagility of alligators, there is some subdivision among alligator populations that may be influenced by life history differences and dispersal barriers (Ryberg et al. 2002).

Results from alligator research at the Jones Center suggest that, within the inland portion of alligators' range, seasonal wetlands may provide critical nesting and nursery sites for alligators. However, overland connections to other wetlands and more permanent bodies of water are critical for the maintenance of larger individuals. The average overland distance moved by alligators was 591 m, suggesting wetlands should be conserved within this proximity to one another or to more permanent bodies of water (Subalusky, Fitzgerald, et al. 2009). Alligators also play important roles in maintaining seasonal wetlands. Through transfers of nutrients and biomass during movements and nesting, alligators transport 1%–2% of the nitrogen and phosphorus contributed to seasonal wetlands by litterfall (Subalusky, Fitzgerald, et al. 2009). Although this is a relatively small amount, these nutrient subsidies from alligators contribute new and potentially more bioavailable nutrients to seasonal wetlands, as compared to litterfall, which is a form of internal nutrient cycling. Perhaps more importantly, alligators also act as ecosystem engineers in seasonal wetlands, digging burrows and building nest mounds that can substantially influence wetland hydroperiod and diversity (Mazzotti and Brandt 1994).

SUMMARY AND CONCLUSIONS

Biological connectivity, in the form of movements of organisms across the landscape, is driven by both environmental and biological factors and interactions between the two. Climate is a major environmental driver of biological connectivity, with fluctuations in animal movements associated with seasonal wetland hydroperiod and longer term cycles of water scarcity

and abundance. The landscape setting in which seasonal wetlands are embedded is also a major driver of connectivity. Biological drivers of connectivity include foraging, mating, migration, dispersal, and gene-flow processes (Zeller et al. 2012), all of which can interact with environmental drivers. Biological connectivity occurs across a range of spatial scales: from seasonal wetlands to surrounding uplands, among seasonal wetlands, and among seasonal wetlands and perennial aquatic ecosystems. The temporal scale at which connectivity occurs generally increases with increasing spatial scale. Collectively, such connectivity supports high regional biodiversity and has important implications for communities, ecosystems, and landscape functions (Polis et al. 1997; Leroux and Loreau 2008; Sitters et al. 2015). Wetlands are hotspots of biogeochemical transformation in landscapes and biological connectivity serves to redistribute biologically important materials (Capps et al. 2014; Capps et al. 2015).

Human activities greatly influence natural landscapes, either by increasing or decreasing biological connectivity (Hanski 1999; Ficetola et al. 2004). Construction of ditches alters wetland hydrology and can increase connectivity with potentially negative consequences, as they may serve as corridors for movement of predatory fish or invasive species into previously unoccupied wetlands (Hohausová et al. 2010). Ditches may also alter wetland hydrology and water quality, rendering habitat unsuitable for native species and thus indirectly affecting connectivity. Changes in land use and land cover around wetlands can also alter connectivity, often by increasing "landscape resistance" to animal movements, resulting in decreased biological connectivity (Forman 1995; Rothermel and Semlitsch 2002; Zeller et al. 2012).

Biological connectivity of seasonal wetlands with each other and other ecosystem types is likely to be affected by climate change, through changes in the frequency and severity of droughts, fires, and floods, changes in seasonality of precipitation, and timing and duration of wetland hydroperiods, and subsequent effects on salinity and other water chemistry parameters (Walls, Barichivich, Brown 2013; Walls, Barichivich, Brown, et al. 2013). Increased evapotranspiration can influence hydrology, including shortening hydroperiods and accelerating the rate of wetland draw-down (Chandler et al. 2017). Alternatively, increases in the frequency or magnitude of flood events may increase connectivity of previously isolated water bodies. Despite the scientific certainty and consensus on climate change (Oreskes 2004), ecological complexity precludes our ability to predict how climate change will affect biological connectivity due to myriad indirect pathways of how wetlands are connected. Even a seemingly straightforward direct impact of

climate change — e.g., geographic regions where future increased evapotranspiration leads to shortened hydroperiods — may have connectivity uncertainty when one factors in other aspects such as altered phenology of reproduction, mismatches in timing of breeding and metamorphosis, changes in disease transmission, and other unforeseen changes (Walls, Barichivich, Brown 2013; Walls, Barichivich, Brown, et al. 2013). Ecology is not rocket science — it is more complex and less predictable. There is no doubt climate change will affect the biological connectivity among wetlands, just as unforeseen land-use changes may fragment the landscape further in response to an ever-growing human population (Zeller et al. 2012).

Loss of biological connectivity among seasonal wetlands and uplands, other wetlands, and perennial waters will have negative consequences for species, communities, and ecosystems. At the species level, biological connectivity supports different life stages, and loss of these connections will lead to decreased population sizes and may eventually affect population viability (Semlitsch et al. 2017). Connectivity also helps buffer populations from decline and extinction, as immigration from other nearby habitats can play an important role in rescuing populations that have been negatively impacted by environmental perturbations, such as drought, fire, and disease. Lack of dispersal from other populations will also increase the degree of inbreeding within increasingly small, isolated populations, which also may eventually lead to their decline. The gradual decline and loss of various species from seasonal wetlands will alter community structure within seasonal wetlands, which may have additional impacts upon the native inhabitants.

Decline and loss of native species are likely to have effects at the ecosystem scale as well. Alterations in community composition could influence carbon and nutrient cycling within seasonal wetlands. Declines in connectivity will also decrease the input of resources that mobile animals bring with them, which may account for a substantial portion of the new carbon and nutrient inputs to the wetland each year. These biogeochemical changes could influence patterns of primary production and litter decomposition in the wetland, which would directly influence the basal food web resources of other wetland inhabitants. Thus, loss of biological connectivity could lead to declines in seasonal wetland productivity both directly and indirectly, and in ways that compound one another.

Given the patterns of land use and climate change that are threatening seasonal wetlands around the world, it is likely that individual wetlands and the linkages between them and other aquatic habitats will continue to decline or be lost entirely. Some degree of reduced connectivity will be surmountable, but it seems possible that a tipping point may be reached where insufficient connectivity will remain to support existing levels of biodiversity and ecological function in seasonal wetlands. Wetlands are hotspots of biogeochemical transformation in landscapes and biological connectivity serves to redistribute biologically important materials. Thus, it is of paramount importance that the drivers of biological connectivity identified above be protected and maintained within the context of intact matrices of seasonal wetlands, uplands, and permanent waters.

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: Description of methods for measuring biological connectivity among seasonal wetlands.

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