Connectivity of Wetlands

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Abstract

Connectivity implies connection or movement of resources across the landscape. Wetlands are dynamic ecosystems imbedded within or at the edges of larger systems and thus wetlands are natural "connectors" between upland and aquatic systems. Although many ecological processes have been used to describe wetland connectivity, here the focus is the movement of water and animals within and among wetlands as these are known agents of connectivity. Prior to these examples, a brief discussion of how connectivity has been used in the legal protection of wetlands demonstrates why connectivity is important to the conservation of wetlands.

Keywords

Animal movements • Amphibians • Buffer zone • Hydrology • Metapopulations • Isolated wetlands • Water • Wildlife

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Introduction

Connectivity implies connection or movement of resources across the landscape (Taylor et al. 1993). It is widely accepted that connectivity is an important ecological process that greatly influences resource patterns on the landscape. Research addressing this topic has identified several forms or definitions of connectivity. One common distinction is between structural connectivity and functional connectivity (Baguette and Van Dyck 2007). In other words, how connected is the vegetation or land cover on the landscape as opposed to how connected are populations, species, or ecosystem processes as a result of landscape features. Alternatively, connectivity has been defined based on three classifications: landscape connectivity, habitat connectivity, and ecological connectivity (Fischer and Lindenmayer 2007).

Wetland connectivity results from the connections provided by both biotic and abiotic resources, including water, nutrients, carbon, pollutants, and wildlife species, which move across the landscape. Wetlands are dynamic ecosystems at the edges of larger systems making them natural "connectors" between upland and aquatic systems (Brinson 1993). Furthermore, wetland connectivity extends to the movement of resources among wetlands that are spatially separated yet exchanges resources. Notably, the connectivity among these dynamic systems is not always readily evident, as resources may flow above, over, and below ground.

This entry focuses on the movement of water and wildlife among wetlands as these resources are widely known as common agents of connectivity among wetlands. Prior to these examples, this entry includes a brief discussion of how legal protections of wetlands have been justified based on this ecological process of connectivity.

Connectivity Used to Define Legal Protection of Wetlands

In the United States, some wetlands receive legal protection through the Clean Water Act. Regulated wetlands are defined based on their connection to navigable waters or inclusion in the definition of navigable waters (Downing et al. 2003). Therefore connectivity via the movement of water is central to the definition of regulated wetlands. The US Supreme Court case Solid Waste Agency of Northern Cook County (SWANCC) versus US Army Corps of Engineers (Corps) (351 U.S. 159, 2001) put into question federal jurisdiction over isolated wetlands. The Court found that the Corps' use of the Migratory Bird Rule, which was based on connectivity via movement of wildlife among critical wetland habitats, exceeded regulatory authority (Kusler 2001).

Legal documents use the term "isolated wetlands." This term implies that wetlands can be classified as connected or isolated. Classification is a way to simplify and improve understanding of systems, but classification does not represent the full complexity of dynamic systems. Wetland systems exist along gradients that constantly change over both space and time. Distinctions between hydrologically isolated or ecologically isolated wetlands have been made, yet the movements of water or wildlife among wetlands are both examples of functional connectivity. Guidance documents produced by the Corps are now under review and many groups have provided comments on wetland connectivity. Comments from Ducks Unlimited summarize various forms of connectivity documented in peer-reviewed literature (Schmidt 2011).

Other countries use a less regulatory approach to protection of water resources and wetlands. For example, the Water Framework Directive serves as the guiding document for maintaining and enhancing the quantitative status of all water bodies in the European Union. A review of the directive highlights the importance of connectivity and uses a definition that recognizes connectivity as process along a continuum (Peacock 2003). Connectivity is defined as "the ease with which organisms, matter or energy transverse ecotones between adjacent ecological units" (Ward et al. 1999). The review documents situations where connectivity is being lost in natural systems in the European Union, such as the loss of hydrological connections between main stem channels of rivers and other water bodies within the floodplain (Peacock 2003).

Wetland Connectivity via Flow of Water

Connectivity occurs via flow of water between wetlands and surrounding uplands, lakes, rivers, coastal waters, or other wetlands. Furthermore, it is the hydrologic conditions of wetlands that support the structure and function of these systems and provide distinctions among wetland types. The entry briefly highlights three wetland types with different hydrologic pathways. These example wetland types span the connectedness gradient and demonstrate how wetland connectivity varies across that landscape.

Ombrotrophic bogs provide a clear example of a wetland ecosystem with limited hydrologic connectivity with adjacent ecosystems. These are perched wetlands only receiving water and nutrients from precipitation and largely losing water via evaporation. Evaporation occurs as evapotranspiration through plants or through moss, and thus the level of the water table affects rate of water loss from the wetland to atmosphere (Lafleur et al. 2005).

Hydrologic connections are often hidden. For example, the prairie pothole region is a landscape that when viewed from aerial images contains a large number of spatially separated wetlands that appear to have limited connectedness via flow of water. Surface flow may differ among years with drought or abundant rainfall. The lack of surface water flow is not an indication of limited hydrologic connectivity. Pothole wetlands are fundamentally connected through groundwater (Tiner 2003). The placement in the landscape and ground water levels may influence whether a wetland is a recharge wetland, a flow through wetland, or a discharge wetland. Furthermore, the biological communities within the wetlands align along the continuum of the hydrologic connectivity to ground water (Euliss et al. 2004).

Tidal marshes and mangrove swamps provide examples of wetland ecosystems with readily apparent hydrologic connectivity. Water flows between the ocean and upland ecosystems such that the wetlands undergo daily and seasonal fluctuations of water level. Water levels that fluctuate affect salinity concentrations, transport nutrients, and aerate the soil within these wetlands (Furukawa et al. 1997; Kaplan et al. 2010; Menon et al. 2000).

Wetland Connectivity via Movement of Wildlife

Wetlands provide habitats for foraging, cover, overwintering, and reproduction to many wildlife species. Each species' unique use of wetland habitat creates connectivity with the surrounding upland habitat matrix, other wetlands, or both (Semlitsch and Bodie 2003). Disruption of movements among habitats can have profound implications for the persistence of local wildlife populations (Marsh and Trenham 2001). Migratory movements of birds among wetlands occurring at various densities and spatial patterns on the landscape affects the functional connectivity of wetlands at local, regional, and continental scales (Amezaga et al. 2002; Haig et al. 1998). A variety of other organisms also provide connectivity among wetlands including turtles, plants, and invertebrates (e.g., Roe et al. 2009).

Amphibian movements among wetlands are one apparent example of connectivity via movement of wildlife. The more common movements made by pond breeding amphibians are annual, round-trip migrations between terrestrial uplands surrounding wetlands that serve as nonbreeding habitat and wetlands that serve as breeding sites. Migratory movements have been documented by radio-tracking adult amphibians (Fig. 1) and these movements define the core habitat or life zone used by amphibians (Semlitsch and Bodie 2003). Core habitat is composed of both breeding and nonbreeding habitat (Fig. 2a). Wetland buffers must include and extend beyond core habitat to provide protection for amphibians (Semlitsch and Jensen 2001). Although the use of core habitat is highest near wetlands, local populations use habitat up to 664 m from wetlands (Rittenhouse and Semlitsch 2007; Fig. 3). Annual migratory movements of amphibians connect wetlands to uplands, but can also provide connections among wetlands. For example, wood frogs breeding in vernal

Fig. 1 Wood frog belted with a radio-transmitter

pools, migrate to forested wetlands for the summer, and then overwinter in upland hardwood stands (Baldwin et al. 2006). Migratory movements are distinct from the less common but ecologically very important dispersal movements (Semlitsch 2008; Fig. 2b, c).

Dispersal is the permanent movement of an individual from its birth site to the place where it reproduces (Johnson and Gaines 1990). Amphibian dispersal is a process that connects wetlands and is defined as the one-way movement from the natal wetland to a different wetland to breed (Semlitsch 2008; Fig. 2c). The majorities of individuals breed in their natal wetland and thus never disperse. Dispersal movements primarily occur during the juvenile life stage but occasionally adults may disperse. Dispersal is difficult to detect, but a 7-year mark-recapture study of marbled salamanders at 14 wetlands showed that 9 % of successful breeding juveniles moved among ponds and <2 % of breeding adults moved among ponds (Gamble et al. 2007; Fig. 4). Amphibian dispersal is an example of how wildlife provides connectivity among wetlands: a critical ecosystem function. Amphibian dispersal among wetlands also decreases the risk of extinction of local populations especially in short-lived species such as wood frogs, and thus successful dispersal among wetlands is crucial to the long-term persistence of amphibian populations (Harper et al. 2008).

The density of wetlands is one factor that affects connectivity among wetlands. The likelihood that amphibians will successfully disperse among wetlands is greatest when wetlands are in close proximity to one another. Connectivity among wetlands that results from amphibian movements has been used to identify areas of conservation priority for wetlands within the state of Massachusetts, USA (Compton et al. 2007). Land use in the uplands between wetlands also influences connectivity among wetlands provided by amphibians. Urban development (Hamer and McDonnell 2008; Safner et al. 2011), road or railways (Eigenbroda et al. 2008; Gibbs and Shriver 2005), and agriculture (Gagne and Fahrig 2007; Rittenhouse and Semlitsch 2006) are often highly resistant land cover types that prevent amphibian dispersal among wetlands. However, land use effects on dispersal can be nuanced upon detailed examination. For example, salamanders oriented toward and experienced lower desiccation risks in soybeans compared to corn (Cosentino et al. 2011).

Since dispersal movements involve a small proportion of an animal population, detecting connectivity among wetlands by observing the movement of individuals requires monitoring a large number of marked animals. Such endeavors are often time and cost prohibitive. Further, there is no guarantee that an observed dispersal event results in functional population connectivity via the transfer of genes. Landscape genetic methods provide an alternative approach to estimate connectivity, rate of movement, and/or differentiation of populations across the landscape (Storfer et al. 2007). Such methods are particularly suited for studies of wetlands because a wetland provides a discrete boundary from which to sample individuals. Landscape genetic approaches not only allow for the assessment of connectivity but provide a direct framework for determining the effect of the intervening habitat matrix on animal movement (Zeller et al. 2012). The effective distance between any two wetlands can be measured as a function of the intervening habitat matrix. By

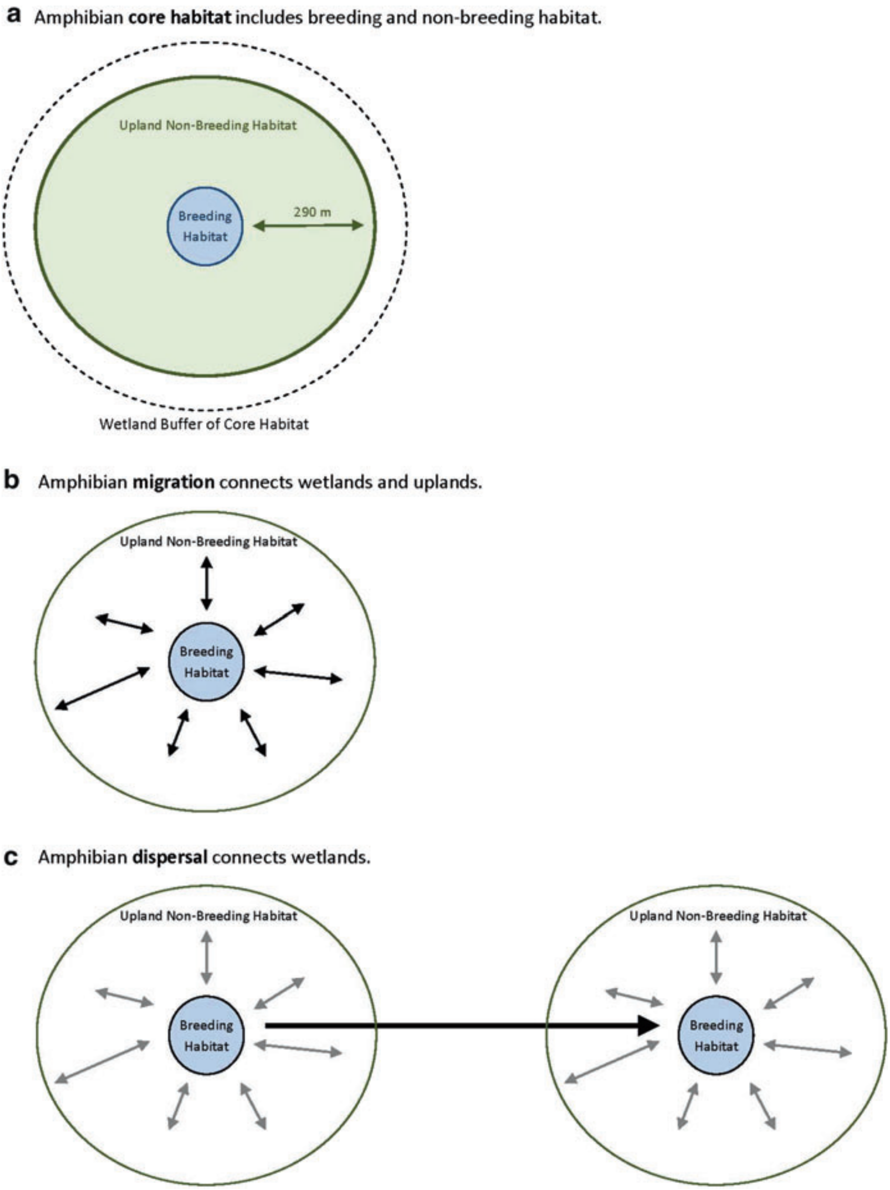

Fig. 2 Core habitat (**a**) is comprised of breeding and nonbreeding habitat (Modified from Semlitsch and Bodie 2003). Migration (**b**) is round-trip, annual movements connecting wetlands to uplands. Dispersal (**c**) is one-way movement that provides connectivity among wetlands (Modified from Semlitsch 2008)

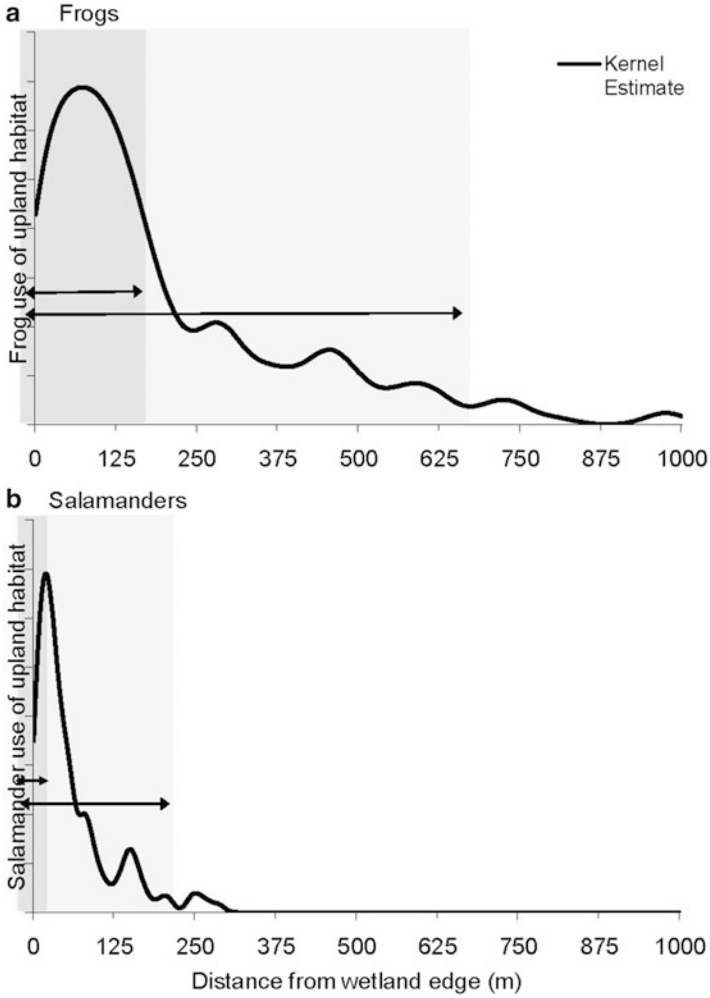

Fig. 3 Amphibian use of upland habitat surrounding wetlands. The wetland edge is at 0 m and the x-axis is the distance from the wetland edge. For frogs (**a**), 50 % of a local population lives within 183 m and 95 % of the population lives within 703 m. For salamanders (**b**), 50 % of the local population lives within 41 m and 95 % of the population lives within m. For all pond-breeding amphibians (frogs and salamanders together), 50 % of the population lives within 93 m and 95 % of population lives within 664 m (Modified from Rittenhouse and Semlitsch 2007)

evaluating genetic distance or gene flow estimates with these effective distance estimates, one can test a variety of hypotheses concerning the relative influence of different landscape features (e.g., roads, agriculture, etc.) as they relate to the successful dispersal of genes between wetlands.

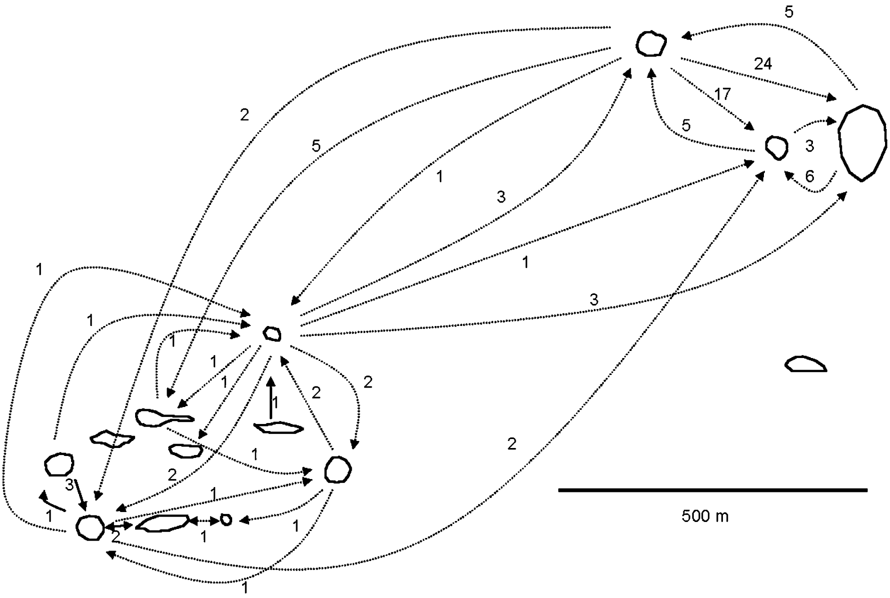

Fig. 4 This figure was published in Gamble et al. (2007). This research included an incredible mark-recapture effort that documented the number of marbled salamanders dispersing among wetlands from 1999 to 2005.

Conclusion and Future Challenges

Wetland connectivity is really about the movement of resources within and among wetlands. Future challenges will include how climate change is and will continue to alter connectivity in wetlands (Roelke et al. 2012). Hydrological flows among wetlands as well as the abundance of wildlife moving among wetlands are dynamic processes providing functional connectivity. These processes vary spatially and temporally, changing with climate and land use (Johnson et al. 2010; Wright 2010). Wetlands may become more or less functionally connected if the frequency between droughts and floods change, which may severely impact connectivity and metapopulation capacity of wetland networks in the future (Wright 2010). Alternatively, the magnitude of these events may change while the frequency remains relatively constant. Is wetland connectivity the same in a system with high magnitude/low frequency of movement as opposed to a system with low magnitude/high frequency? Furthermore, altered flow regimes within riverine systems are known to greatly affect biodiversity within wetlands. As climate change results in altered precipitation patterns, one should expect that effects on biodiversity in other wetland types could be as evident as that described in riverine wetlands (Bunn and Arthington 2002).

A difficult aspect of understanding connectivity via animal movement is the behavior and motivation of each individual in the population. Experiments that seek to describe these characteristics, such as movement rate, distance, path sinuosity, etc., often reveal tremendous intrapopulation variation. A promising future research path is the incorporation of these fine-scale, experimental data on movement behavior to parameterize individual-based models (IBMs) (DeAngelis and Mooij 2005). Such models incorporate individual variation in behavior, while assessing the broader-scale properties that emerge from simulation experiments. Once parameterized, IBMs can be utilized to conduct virtual experiments to determine the effects of land use, fragmentation, and habitat loss on movement and connectivity.

Although genetic data provide direct estimates of realized movement (i.e., gene flow), there is still great difficulty and uncertainty in determining the effects of the intervening habitat matrix on movement (Zeller et al. 2012). Resistance values for landscape features are often determined based upon expert opinion, but such approaches should be used with caution as expert-parameterized models may perform suboptimally (Charney 2012). Analytical methods and frameworks for determining optimal landscape resistance values as they relate to movement and/or genetic data remain an area of active research. Methods for determining least-cost paths (Sawyer et al. 2011) or landscape resistance (McRae 2006) are continually being evaluated and developed, and their integration with tools for assessing connectivity (Carroll et al. 2012) should make future regional assessments of wetland connectivity much more objective.

One caveat to promoting wetland connectivity is the potential for invasive species to propagate throughout the wetland network (Aquiloni et al. 2005; Peterson et al. 2013). Invasive species such as red crayfish (*Procambarus clarkia*) and the North American bullfrog (*Rana catesbeiana*) can have dramatic effects on local wetland processes and biodiversity. Further, wetlands are particularly susceptible to invasion by nonnative plants (Zedler and Kercher 2004). While functional connectivity of wetlands is critical for the maintenance of native biodiversity, serious consideration must be given to the potential for invasive species colonization.

Cross-References

- ▶ Corridors
- ▶ Landscape Genetics
- ▶ Metapopulation Dynamics of Wetland Species
- ▶ Riparian Buffer Zone for Wetlands
- ▶ Source-Sink Dynamics of Wetlands
- ▶ Wetland Hydrology

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