



Dispersal and Wetland Fragmentation

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Abstract

Wetlands provide habitat for a diverse array of aquatic and semiaquatic species, many of which provide direct economic and recreational value. Despite the ecosystem services provided by wetland fauna and flora, historical wetland loss has been dramatic. Wetland loss was >50% in the USA and 60–70% in Europe by the 1980s, with most losses resulting from agriculture and urban development. Although habitat loss can result from natural, stochastic events, anthropogenic habitat loss and subsequent fragmentation are among the most important drivers of biodiversity loss. One mechanism underlying the loss of biodiversity after habitat loss and fragmentation is the breakdown of wetland connectivity previously maintained by dispersal.

Keywords

Biodiversity · Connectivity · Dispersal · Fragmentation · Landscape

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Introduction

Wetlands provide habitat for a diverse array of aquatic and semiaquatic species, many of which provide direct economic and recreational value (Woodward and Wui 2001). Despite the ecosystem services provided by wetland fauna and flora, historical wetland loss has been dramatic. Wetland loss was >50% in the USA and 60–70% in Europe by the 1980s, with most losses resulting from agriculture and urban development (Groom et al. 2006). Although habitat loss can result from natural, stochastic events, anthropogenic habitat loss and subsequent fragmentation are among the most important drivers of biodiversity loss (Millennium Ecosystem Assessment 2005). One mechanism underlying the loss of biodiversity after habitat loss and fragmentation is the breakdown of wetland connectivity previously maintained by dispersal.

Importance of Dispersal

For wetland species, dispersal is the one-way movement of an organism between its natal wetland and the wetland in which it reproduces (Clobert et al. 2012). Dispersal is a fundamental biological process that influences individual fitness, population dynamics, and community structure (Clobert et al. 2012). Dispersal can be essential for the maintenance of biodiversity because it increases species persistence by counteracting demographic stochasticity (i.e., rescue effect; Groom et al. 2006). Additionally, dispersal can lead to gene flow between populations, which can be important for introducing beneficial alleles into populations and minimizing the loss of genetic variation due to genetic drift and inbreeding (Groom et al. 2006).

For many insects and vertebrates, dispersal occurs through direct, active movement of individuals overland or along water corridors. For fully aquatic species such as fish, physical connections among wetlands can be essential for dispersal. Alternatively, plants and some invertebrates rely on passive dispersal of gametes or zygotes. Waterfowl play an important role in maintaining wetland connectivity over large scales by transporting the pollen, seeds, and eggs of other species, including fish (Amezaga et al. 2002).

One-way dispersal from natal to breeding wetlands can be contrasted with movements of individuals to and from breeding wetlands (i.e., migration; Clobert et al. 2012). Many semiaquatic organisms have complex life cycles with both terrestrial and aquatic stages. For example, many amphibians use uplands for foraging and overwintering and wetlands for breeding, whereas many turtles use uplands for nesting and wetlands for breeding and foraging (Semlitsch and Bodie 2003). Movement between terrestrial and aquatic habitats is critical for semiaquatic organisms to complete their life cycles. Compared to among-wetland dispersal, breeding migrations are generally completed by direct, active movements of individuals.

Landscape Connectivity in Wetland Networks

For wetland species, landscape connectivity can be defined as the degree to which the landscape facilitates movement of organisms among wetlands or between wetland and upland habitats (Taylor et al. 2006). From a physical perspective, structural connectivity depends strictly on the spatial configuration of habitat in the landscape (Taylor et al. 2006). Wetland species should have high rates of dispersal between wetlands separated by short distances, whereas dispersal should be uncommon to wetlands that are spatially isolated. Similarly, breeding migrations of semiaquatic species are facilitated when required terrestrial habitat is adjacent to a wetland. The simplest index of structural connectivity is nearest-neighbor distance, which may be calculated as the distance from a wetland to the nearest wetland or upland habitat (Calabrese and Fagan 2004). More complex measures of connectivity include graph-theoretic and incidence function metrics that incorporate spatially explicit occupancy data and information on the focal species' dispersal ability (Calabrese and Fagan 2004).

Structural connectivity can be distinguished from functional connectivity, which considers how landscape features affect the movement behavior of organisms during dispersal (Taylor et al. 2006). Landscape features vary in their effects on movement due to differential resource availability, habitat complexity, predation risk, and physiological costs. For example, movement of the tiger salamander (*Ambystoma tigrinum*), a pond-breeding amphibian, was constrained by desiccation risk in upland habitats, and desiccation risk varied dramatically among habitats (Fig. 1; Cosentino et al. 2011a). Furthermore, the effects of desiccation risk on individual movement scaled up to affect the probability that tiger salamanders colonized uninhabited wetlands across a metapopulation (Cosentino et al. 2011b; ► Chap. 20, "Metapopulation Dynamics of Wetland Species" by Schooley and Cosentino). Wetlands surrounded by habitats with low desiccation risk were more likely to be



Fig. 1 Interpond movements of amphibians are influenced by desiccation risk experienced in upland habitats. For example, desiccation risk for tiger salamanders (*Ambystoma tigrinum*) in Illinois, USA is greater in prairie and corn than in forest and soybean habitats, and individuals orient their movements towards low-risk habitats (Cosentino et al. 2011a)

colonized than wetlands surrounded by habitats with high desiccation risk. Thus, movements among wetlands or between wetland and upland habitats can be limited by the composition and spatial configuration of habitats with variable dispersal costs. Least-cost modeling can be used to quantify the distances along paths between habitats that minimize dispersal costs (i.e., effective distances, Adriaensen et al. 2003), although parameterization of least-cost models requires detailed information about how habitats in the landscape affect movement behavior.

Compared to species that move over land, connectivity for species confined to aquatic habitat (e.g., fish) depends more strongly on aquatic connections such as stream linkages and overland sheet flow. Structural connectivity for fully aquatic species is predominantly determined by distances between wetlands along stream corridors or across areas inundated by water. However, stream flow and sheet flow can both depend on precipitation, introducing temporal variation in connectivity among wetlands (Leibowitz and Vining 2003). Functional connectivity for fully aquatic species may be limited by factors such as topography (e.g., stream cascades) and predation risk experienced within streams during movement between wetlands.

Wetland Fragmentation

Habitat fragmentation occurs when habitat is reduced in size and the distance between remaining habitat patches increases. Although wetlands are naturally patchy and separated by a terrestrial matrix, structural and functional connectivity can be disrupted by habitat loss and fragmentation in two main ways. First, when wetland habitat is lost or entire wetlands are destroyed, the density of wetlands decreases and the physical isolation of remaining wetlands increases (Fig. 2, Gibbs 2000). For species that move among wetlands over land or via passive dispersal,

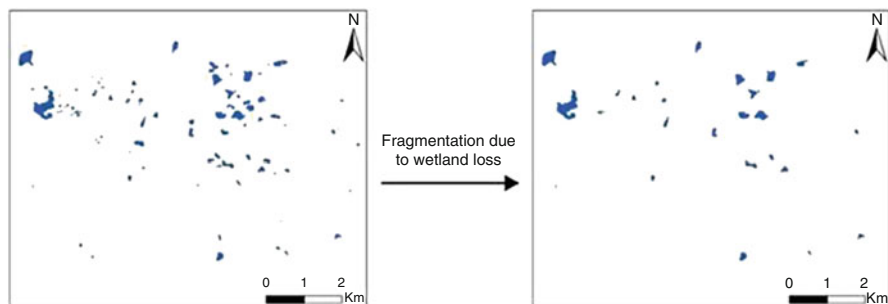


Fig. 2 Fragmentation increases spatial isolation of wetlands remaining after wetland loss

even small or isolated wetlands can be important by functioning as stepping-stones for dispersal to other wetlands (Semlitsch 2000). Thus, reducing the density of wetlands in the landscape, even small wetlands, decreases the likelihood of direct or indirect dispersal between wetlands. This reduction in structural connectivity can leave populations susceptible to extinction due to inbreeding and low population size (Clobert et al. 2012). Increased isolation also reduces the probability of colonization of uninhabited wetlands, which can be particularly important for regional persistence of species that exhibit metapopulation dynamics (Hanski and Gilpin 1997; ► Chap. 20, “Metapopulation Dynamics of Wetland Species” by Schooley and Cosentino). For species confined to aquatic habitats, the loss of stream linkages may also decrease wetland connectivity. Headwater streams are frequently lost from developed landscapes due to drainage, channelization, filling, piping, and groundwater withdrawal (Meyer and Wallace 2001).

Second, fragmentation occurs at a smaller spatial scale when terrestrial habitat surrounding wetlands is lost. Wetlands are linked to upland habitats through migratory movements of semiaquatic species (Semlitsch and Bodie 2003), and migration of semiaquatic species can be an important mechanism of energy and nutrient transfer between wetland and upland systems (e.g., Regester et al. 2008). In fragmented landscapes, maintaining wetland-upland linkages and connectivity among wetlands are primary goals for conserving biodiversity. Small, terrestrial buffer zones are often designated around wetlands to protect water resources and ecosystem services, but larger buffer zones are recommended to protect core terrestrial habitat used by semiaquatic species (Fig. 3; Semlitsch and Bodie 2003; Rittenhouse and Semlitsch 2007).

Maintaining Connectivity in Wetland Networks

In general, structural connectivity can be maintained by (1) minimizing the loss of wetlands and other aquatic habitats that function as corridors between wetlands (e.g., streams), and (2) maintaining core terrestrial habitats immediately surrounding wetlands. However, because some species move extensively among wetlands, maintenance of wetland connectivity likely requires management at the landscape scale (Amezaga et al. 2002). Within seasons, many species make temporary movements among wetlands that can vary dramatically in quality (e.g., vegetation structure, food, hydroperiod). For example, turtles tend to use permanent lakes during drought, but they move to ephemeral wetlands during periods of high precipitation (Roe and Georges 2007). Because wetlands vary in the resources they provide, conservation of wetland biodiversity likely requires a heterogeneous assemblage of wetlands each with terrestrial buffers, as well as the presence of upland habitats that allow seasonal movements and dispersal (see Fig. 3, Roe and Georges 2007).

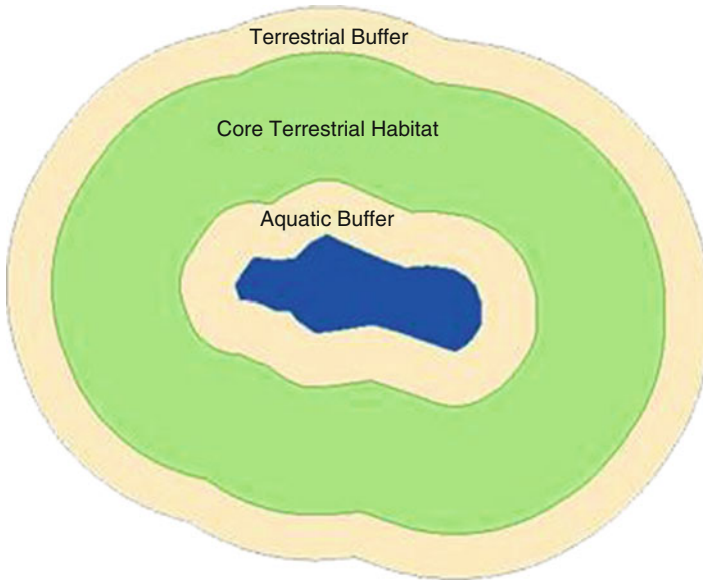


Fig. 3 Habitat buffers around wetlands are recommended to maintain wetland-upland connectivity for semiaquatic species. Semlitsch and Bodie (2003) recommend an aquatic buffer (30–60 m wide) to protect water resources, a zone to preserve core habitat for amphibians and reptiles (142–289 m, encompassing the aquatic buffer), and an additional 50-m buffer to protect core terrestrial habitat. Rittenhouse and Semlitsch (2007) indicate that some species require much greater areas of core habitat (upwards of 700 m) (The illustration is based on the original concept from Semlitsch and Bodie (2003))

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