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Connectivity among wetlands matters for vulnerable amphibian populations in wetlandscapes

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ABSTRACT

Wetlands have been degraded and destroyed, resulting in the decline of many wetland-dependent species populations. Many conservation efforts are based on protection of individual wetlands; however, fluxes of energy, materials and organisms between wetlands create important structural and functional connections upon which several species depend. We investigated the role of individual wetlands within a wetlandscape in sustaining an amphibian population. Wetlandscapes were represented as networks, where nodes were wetlands and links were flows of organisms described by an amphibian population model. Relationships between a wetland's connectivity to the other wetlands and the abundance of amphibians under different wetland management strategies were examined. The first finding was that wetlands within a network can be classified into *sinks* (where local mortality exceeds birth rate), *sources* (where local birth rate exceeds mortality), and *pseudo-sinks* (where excessive immigration maintains the population above the carrying capacity). These three wetland classes have low, medium, and high *Indegree* (a parameter reflecting a wetland's connectivity), respectively. The second finding was that management interventions in wetlands have different consequences according to the wetland's *Indegree*: wetland removal has the worst impact on amphibian populations if the wetland is a *source*, and wetland restoration has the best impact if the wetland is a *pseudo-sink*. These findings provide support for policies that managing wetlands not as independent objects but as integral parts of the wetlandscape.

1. Introduction

Wetlands are important ecosystems as they provide several functions and services (Calhoun et al., 2016; Yao et al., 2017; Creed et al., 2017) and constitute an important source of biodiversity (Costanza et al., 1997; Gibbs, 2000). In recent decades, many wetlands have been drained because of urban or agricultural expansion (Davidson, 2014; Dixon et al., 2016; Golden et al., 2017). Wetland loss impacts on biodiversity both directly, by removing habitat (Gibbs, 2000), and indirectly, by increasing the distance among remaining wetlands and resulting in functional isolation and increasing mortality of organisms migrating from one wetland to another (Baguette et al., 2013). Wetlands are not isolated features; on the contrary, they are dynamic, complex ecosystem with biotic and abiotic connections to other wetlands on the wetlandscape (Cohen et al., 2016; Thorslund et al., 2017). Understanding the ecological dynamics of wetlandscapes is important to sustaining biodiversity (Semlitsch and Bodie, 1998; Gibbs, 2000).

In particular, amphibians' survival is influenced by both wetland habitat and wetland connections to other wetlands (Dudgeon et al., 2006). In fact, these wetland qualities determine the success of amphibians' breeding (Mushet et al., 2012): wetland habitat is used by adults for mating and by offspring to complete their metamorphism from eggs. Factors such as availability of resources and dispersal capabilities influence the amphibian population in wetlands (Pechmann et al., 1989; Semlitsch, 1996). Availability of resources depends on wetland habitat properties (e.g., area, vegetation) and on the number of amphibians competing for available resources. Amphibian dispersal relies on wetland distribution within the surrounding terrestrial habitat. Every year, at the end of the summer, amphibians start their migration through the terrestrial habitat and the following spring they reach a

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new aquatic breeding habitat (Pittman et al., 2014). Alteration of wetland habitat and distribution within the landscape, such as wetland loss, negatively influences both breeding and dispersal success by decreasing wetland density and increasing travel distances for amphibians (Gibbs, 1993).

Management strategies have been implemented to protect biodiversity promoted by wetlands. Many of these management strategies focus on wetlands of special importance (Amezaga et al., 2002). Policy goals vary from “no net loss” to “net gain” (Accatino et al., 2018) to general statements about the need to address adverse impacts to these wetlands (e.g., Calhoun et al., 2016). Few of these management strategies focus on the physical, chemical, or biological connections among wetlands (e.g., Cohen et al., 2016). Although it is widely recognized that wetland connectivity is important for biodiversity (Semlitsch, 1996; Semlitsch and Bodie, 1998; Skelly et al., 1999; Marsh and Trenham, 2001; Cushman, 2006), concrete strategies in policies are still not well formulated. The lack in wetland policies of clear operational strategic schemes based on wetland connectivity is at least in part due to the lack or rarity of quantitative assessments of the role of wetland connectivity in sustaining wetland biodiversity. Important steps forward would be to determine if and how wetland connectivity plays a role in sustaining biodiversity in a wetlandscape (Fortuna et al., 2006; Albanese and Haukos, 2017), and to explore if management interventions on the wetland itself (i.e., wetland removal or restoration) are influenced by wetland connectivity.

The “*sink-source*” framework describes the distribution of species in the variety of interconnected habitat patches within a region (Pulliam, 1988; Watkinson and Sutherland, 1995). According to this framework, a productive patch serves as a *source* of individuals, which are dispersed to less productive patches called *sinks* (Pulliam, 1988; Dunning et al., 1992). Pulliam (1988) argued that in *sink* habitat patches reproduction is insufficient to balance local mortality, whereas in *source* habitat patches reproduction balances local mortality; the population in *sinks* is thus maintained by immigration from *sources*. Most studies classify *sinks* and *sources* only by demographic measures (i.e., birth and death rate) (Watkinson and Sutherland, 1995). The role of connectivity in the classification of *sinks* and *sources* has not been explored.

Models are useful to test the “*sink-source*” framework for exploring organism dispersal through wetlandscapes, especially when empirical data are lacking or extremely difficult and costly to collect (Pittman et al., 2014). Patch-based models (e.g., Skelly and Meir, 1997; Trenham, 1998) focus on population dynamics within patches, which are important to describe fundamental ecological processes such as breeding (Marsh and Trenham, 2001), interspecific competition, and predation (Wilbur, 1997; Beebee et al., 1996). Patch-based models were successfully applied to wetlandscapes (Marsh and Trenham, 2001; Wilbur, 1997). However, an exclusively patch-based approach does not consider the role of wetland isolation and the mobility of individuals to other wetlands (Cushman, 2006). In contrast, network-based models focus on connectivity within a network’s node and they can be applied to wetlandscapes too (e.g., Albanese and Haukos, 2017). They make it possible to quantify changes to the connectivity of wetlands and identify wetlands critical to the maintenance of the whole system connectivity. Network-based models are useful tools for combining both the within-wetland population dynamics and the dispersal of individuals among wetlands (Estrada and Bodin, 2008). Network-based models can be used to identify keystone patches that are integral to the persistence of populations (Urban and Keitt, 2001; Keitt, 2003) and to quantify the robustness of populations to wetland loss (Bunn et al., 2000; Hanski, 2001; Jordán et al., 2003).

In this paper, we addressed the role of wetland connectivity in determining the role of different wetlands to sustain amphibian populations. We focused on amphibian species characterized by a bi-phasic life-cycle, migrating into different wetlands during the course of their life. We built a model of amphibian population dynamics in a wetland network and we formulated scenarios to address two research questions: how does the connectivity of a wetland influence the abundance of the local population in the wetland itself? And, how does a management intervention on a single wetland (e.g., wetland removal or wetland restoration) influence the total landscape population by changing connectivity within the wetlandscape?

2. Methods

We focused on amphibian species with life history traits characterized by a terrestrial and an aquatic phase, but the approach could be adapted to amphibian species with other life history traits. In summer, amphibians congregate in wetlands for mating. At the end of the summer, amphibians leave wetlands and migrate through the terrestrial habitat searching food and refuges for overwintering until the next spring, when they disperse again, looking for aquatic breeding habitat (Pittman et al., 2014). Examples of species having such as life cycle are the northern leopard frog (*Rana pipiens*) having a dispersal distance ranging between 2 km and 10 km (Kendell, 2002), and the great plains toad (*Anaxyrus cognatus*) having a dispersal distance ranging between 300 m and 1300 m (COSEWIC, 2010).

2.1. Model description

We built a theoretical model for simulating the dynamics of a biphasic life-cycle amphibian population within a wetlandscape. The population dynamics of amphibians consist of a continuous repetition of reproduction phase and migration phase. In the reproduction phase, new offspring are produced in each wetland as a function of the abundance of the local population. In the migration phase, amphibians migrate from a wetland to another, according to how wetlands are connected and their mortality. Our model was conceived in the Medawar zone (Loehle, 1990; Grimm et al., 2005) (i.e., we included only the necessary elements for addressing our research questions and to avoid unnecessary details, such as predation phenomena or climate variables like air and surface water temperature of wetlands).

2.2. Wetlandscape

A network consists of a set of nodes that are defined as spatial elements, and links that represent linkages between nodes (Urban and Keitt, 2001). We represented a wetlandscape as a network, where the nodes are wetlands, whereas the links are flows of amphibians between wetlands. We connected two wetlands by a link if the distance between a given pair of wetlands was less than or equal to the maximum distance walkable by the amphibians (Fig. 1a). Links were assigned a weight equal to the potential connectivity $\tilde{c}_{ij}$, which is defined as the probability of an amphibian leaving wetland i to choose wetland j as breeding site the following year. To determine the connectivity between two wetlands either a boundary approach or a distance approach could be used. The boundary approach consists of methods that determine the weight based on the presence or the length of a shared boundary (Ermagun and Levinson, 2018). The distance approach consists of a set of methods that determine the weight using the geographic distance (Ermagun and Levinson, 2018). Both the boundary approach and the distance approach or a combination of them have been used to construct a theory-driven spatial weighting matrix (Dray et al., 2006), as well as biological considerations such as propagation process (Sokal and Oden, 1978), patch size (Hanski, 1994) and dispersion capability (Knapp et al., 2003). In our work, the potential connectivity represented only the spatial interactions among wetlands and combined the boundary approach and distance approach using a weighted average, with the parameter β as the weight to balance the relative importance of adjacency over the inverse distance. The underlying assumption is that amphibians will move from wetland i to wetland j if the two wetlands are adjacent (see below for definition) or if two