Source-Sink Dynamics of Wetlands

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Contents

| Introduction | 2 |
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| Definition | 2 |
| Methods for Identifying Source-Sink Dynamics | 3 |
| Using Genetics to Infer Source-Sink Dynamics | 4 |
| Network Models | 4 |
| Future Directions and Challenges | 5 |
| Cross-References | 6 |
| References | 7 |
| | |

Abstract

Source-sink dynamics stem from metapopulation theory, where sources are populations with births exceeding deaths and emigration exceeding immigration, and sinks are populations with deaths exceeding births. Sink populations are sustained by immigration from nearby source populations, and thus functional connectivity among wetlands is key to maintaining source-sink dynamics among wetlands. The wood frog is an example pond-breeding amphibian where sourcesink dynamics among wetlands is critical to regional population persistence. We summarize how source-sink dynamics can be inferred from demographics, genetics, and network models. Challenges that remain include identifying source and sink wetlands within natural systems, as well as, incorporating source-sink dynamics into wetland mitigation.

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[©] Springer Science+Business Media Dordrecht 2016 C.M. Finlayson et al. (eds.), *The Wetland Book*, DOI 10.1007/978-94-007-6172-8 55-3

Keywords Connectivity • Genetics • Network models • Metapopulations • Mitigation wetlands

Introduction

Definition

Source populations are characterized as having birth rates that exceed death rates and thus an increasing population. This positive growth leads to emigration from the population, and the rate of emigration in source populations exceeds the rate of immigration. As such, sources are net exporters of individuals into the system. In contrast, sink populations are net importers or receivers of dispersing individuals. Sink populations are further characterized as having death rates that exceed birth rates, which leads to population decline. As such, the existence of such sink populations is entirely dependent upon the contributions of dispersers from source populations.

Source-sink dynamics stem from metapopulation theory, which has provided a useful framework to address conservation questions, especially in light of increasing loss or alteration of habitat and fragmentation due to land use that can jeopardize the persistence of species (Hanski and Ovaskainen 2000; Urban et al. 2009). Pulliam (1988) provided the formal description of the demographic source-sink model. Sources are populations in high quality habitat with births exceeding deaths and emigration exceeding immigration. In contrast, sink populations generally exist in low quality habitat, where deaths exceed births, and the populations are sustained by immigration from surrounding source populations. In order for source-sink dynamics to be realized, there must be functional connectivity among habitat patches on the landscape to allow successful dispersal and rescue of sink patches or for colonization of new habitat patches. Functional connectivity is a result of species vagility, distance between habitat patches, and quality of the matrix between patches.

Wetlands provide vital breeding and foraging habitat for many species, but are particularly important for reptiles and amphibians. Pond-breeding amphibians are distributed patchily across the landscape and are frequently assumed to exhibit metapopulation dynamics, especially in fragmented landscapes that limit connectivity (Semlitsch 2008a). Metapopulations of pond breeding amphibians can be viewed from a "ponds-as-patches" perspective (Marsh and Trenham 2001; Richter-Boix et al. 2007). There are several factors that should be considered when characterizing amphibian populations in this manner. First, the pond should be defined to include both the aquatic breeding habitat and the immediate surrounding terrestrial core habitat (95 % core area usually within 300 m) where the breeding adult population resides (Rittenhouse and Semlitsch 2007; Semlitsch 1998; Semlitsch and Bodie 2003). Second, several ponds that are in close proximity may function as a unit,

and thus several ponds compose the patch or population. This possibility occurs when the amount of amphibian breeding activity at one pond influences the amount at a neighboring pond or when adults shift breeding effort among several adjacent ponds across years (Petranka et al. 2004; Pope et al. 2000). Third, this characterization may not be true in all situations; despite the fact that many amphibians breed in distinct patches, not all amphibian populations exist as metapopulations. For example, if there is extensive movement among all ponds, then these ponds likely constitute a single population (Smith and Green 2005).

Methods for Identifying Source-Sink Dynamics

In the strictest sense, source-sink dynamics requires estimation of birth, death, immigration, and emigration rates. Estimation of these rates presents logistical challenges. Estimates of population growth rates often require detailed, long-term population monitoring (e.g., mark-recapture, nest survival). Such approaches can be both time and cost prohibitive, making robust estimates of these parameters unfeasible in many circumstances. There can also be significant difficulty in identifying movement among populations as this often involves direct monitoring of individuals in space and time. These observations have traditionally been made using mark-recapture or radio telemetry (Gamble et al. 2007; Gamble et al. 2006; Rittenhouse et al. 2009), which has generally limited the scope of inference to a few select populations. The increased accessibility of molecular methods is now allowing for direct quantification of movement among numerous populations. These genetic estimates represent a more complete picture of population connectedness as well as provide an estimate of realized dispersal resulting in successful reproduction (Wang et al. 2009).

Other approaches to assess population connectivity are based on resistance kernels (Compton et al. 2007; Wasserman et al. 2010), electric circuit theory (McRae et al. 2008), or graph theory (Urban et al. 2009). Each of these methods can assess the potential connectivity among populations as a function of distance and intervening habitat. When paired with demographic models of population size, reproduction rates, and dispersal kernels (Schick and Lindley 2007), graph-theoretic models can be used to identify source and sink populations on the landscape. Although potentially less informed and more reliant on model assumptions, these network models are less data intensive than empirical observations of movement, and less expensive than genetic approaches. Further, these models can provide a robust framework for assessing connectivity, directionality of movement among populations, as well as management effects on the network as a whole (e.g., effects of wetland loss or mitigation on connectivity and movement; Schick and Lindley 2007). Recently, Murphy et al. (2010) combined network-based gravity models with spatial population genetic data to infer functional connectivity.

Using Genetics to Infer Source-Sink Dynamics

Genetic estimates of connectivity may be simpler to obtain than direct observation of dispersing organisms, and they provide a means to assess population connectivity across generations. One potential limitation of these estimates is that they can reflect historical processes and may not be representative of current dispersal patterns (Pearse and Crandall 2004). Nonetheless, genetic data can allow for the estimation of parentage, effective population sizes, dispersal rates, and connectivity among populations, all of which can be used to infer source-sink dynamics (Manier and Arnold 2005; Martínez-Solano and González 2008; Peery et al. 2008). In a study of garter snakes (Thamnophis elegans and T. sirtalis) in California, Manier and Arnold (2005) found gene flow (i.e., dispersal) was asymmetric among the 23 populations studied, and that a few populations contributed a disproportionate number of dispersers to the metapopulation. Further, they found that genetic measures of effective population size and migration rates were often significantly different from those obtained through direct observation via mark-recapture. These findings underscore the potential power of genetic approaches and the difficulty in obtaining direct estimates of population vital rates. In another study, Martínez-Solano and González (2008) found that recently established populations of common toads (Bufo bufo) showed both genetic and demographic signatures of sink populations. Specifically, they had lower effective population sizes, had a greater of rate of immigration, and had greater frequency of heterozygotes than expected (heterozyote excess).

Network Models

Wood frogs (*Rana sylvatica*) are a widely distributed pond-breeding amphibian in North America. Extensive demographic and movement studies have been conducted on wood frogs (Berven 1990; Berven and Grudzien 1990; Rittenhouse et al. 2009), making them an ideal species for parameterizing demographic network models (Schick and Lindley 2007). Using 6 years of egg mass counts from 41 ponds in east-central Missouri, a demographic network model was parameterized to estimate: (1) number of metamorphic individuals produced at each pond, (2) the number of metamorph frogs that would reach maturity and return to their natal pond for reproduction, (3) the number of metamorph frogs that would reach maturity and successfully disperse to a new breeding pond, and (4) the ratio of immigrant to emigrant frogs at each pond (ratio >1 = source population, ratio <1 = sink population; Peterman et al. 2013). Parameters for survival, rates of dispersal, and dispersal distance were obtained from empirical estimates found in the literature (Berven 1990; Berven and Grudzien 1990). The average of the 6 years of observations is shown in Fig. 1. Being an average, this figure encompasses annual variation in reproductive success, which largely corresponded to variation in precipitation. This modeling approach, although simplistic and with many inherent assumptions, allows for spatial and temporal assessment of source-sink dynamics. Analyses similar to these could help inform future wetland mitigation to provide optimal



Fig. 1 A demographic network model of wood frog populations in east-central Missouri, USA. Each point represents the spatial location of a pond, and the numbers on each point represent the mean number of egg masses (equivalent to the number of breeding females) present at ponds from 2006 to 2010. Connectivity of ponds was determined as a function of distance and the number of potential dispersing juvenile frogs. Ponds with emigration rates greater than immigration rates were designated as sources

placement of wetlands in relation to existing populations. Alternatively, if wetlands were to be lost or altered, these models could be used to minimize the damages to the connectivity of the metapopulation.

Future Directions and Challenges

As a specific case of meta-population dynamics, source-sink dynamics may be particularly relevant in the study of wetlands, which are often viewed as habitat patches in the context of the species using them (Marsh and Trenham 2001). Future management of wetlands should take into consideration connectivity among populations, but also recognize that all populations are not equal. By identifying source and sink populations within the metapopulation, ranked conservation or management priority can be given to assure that the most robust populations are conserved. For example the number of individuals that complete metamorphosis and successfully emigrate from a pond is an important factor to consider when developing management plans (Semlitsch 2000). Alternatively, isolated populations or

perennial sink populations can be selectively targeted for conservation or restoration actions. Restoration of a wetland that is consistently a sink population (e.g., improper hydrology or presence of fish) has the potential to strengthen regional population persistence by increasing the number of source populations. If low connectivity due to low dispersal success is a concern, then restoration efforts may include the creation of new wetlands to serve as stepping stones (Petranka et al. 2007; Petranka and Holbrook 2006). An additional challenge to estimating connectivity using resistance kernels, circuit theory, or graph theory is determining the effects that land cover and landscape features have dispersing individuals. Current assessments often rely on expert opinion, but this approach should be used with caution as Charney (2012) demonstrated that expert models performed poorly.

Source-sink dynamics are important processes to consider within the context of wetland mitigation, and a future challenge for wetland managers will be to incorporate source-sink dynamics into wetland mitigation (Keagy et al. 2005). Filling one wetland and creating a new wetland in an alternative location may result in an equal number of wetland acres, but functions are not often realized in mitigated wetlands (Semlitsch 2008b). If source populations are continually destroyed and mitigated with sink populations, species persistence on the landscape will be greatly affected. A pond's role in the metapopulation can be dependent on within ponds features such as hydrology and vegetation that affect productivity (Shulse et al. 2012), as well as placement on the landscape, which affects connectivity with other ponds and can influence the species community that colonize mitigated ponds (Shulse et al. 2010). Wetland mitigation will be more effective when taking into consideration demographic and life history characteristics of species.

A major challenge in conducting source-sink analyses has been, and will continue to be, the estimation of the necessary population parameters. Although technology for directly tracking individuals continues to improve, these methods are likely to remain costly and labor intensive. In contrast, genetic studies for non-model species are continuing to become more affordable. Genetic methods have limitations, but their use in studies of source-sink dynamics has the potential to provide the most complete picture of cryptic movement among populations. At the very least, genetic analyses can provide a starting point for identifying which populations warrant more intensive empirical studies of vital rates.

Cross-References

- Connectivity of Wetlands
- Dispersal and Wetland Fragmentation
- ► Heterozygosity
- ► Landscape Ecology of Wetlands: Overview
- ► Landscape Genetics, Wetlands
- Metacommunity Dynamics of Riparian Ecosystems
- Metapopulation Dynamics of Wetland Species
- Population Genetics

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