Metapopulation Dynamics of Wetland Species

20

Robert L. Schooley and Bradley J. Cosentino

Contents

Abstract

For species inhabiting naturally patchy or fragmented landscapes, conservation often is guided by metapopulation theory. A metapopulation is a set of spatially separated populations connected by movement of individuals among populations. The metapopulation can persist, despite extinctions of local populations, if populations are connected enough to allow for adequate recolonization of vacant habitat. Because wetlands occur as geographically isolated habitats, many wetland-associated species could display metapopulation dynamics. However, classical metapopulations may be rare, and metapopulations can have a diversity of spatial structures. Practical metapopulation approaches are grounded in the "area-isolation paradigm" in which the area of a habitat patch is the main predictor of local extinctions, and connectivity to other source populations is the main predictor of colonization. The generality of the area-isolation paradigm has been questioned, however, and its shortcomings relate to the need to consider habitat heterogeneity. Wetlands can differ in habitat quality and they are embedded in a heterogeneous terrestrial matrix. Functional connectivity of metapopulations depends on how movements of individuals interact with the terrestrial habitat

R. L. Schooley (✉) · B. J. Cosentino (✉)
Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, IL, USA
e-mail: schooley@illinois.edu; cosentino@hws.edu

matrix. Despite these complexities, recognition of metapopulation dynamics for wetland species has forced managers to think about biodiversity conservation at landscape scales and highlights the importance of wetland-upland linkages.

Introduction

For species inhabiting naturally patchy or fragmented landscapes, conservation often is guided by metapopulation theory (Hanski and Gaggiotti 2004). A metapopulation is a set of spatially separated populations connected by movement of individuals among populations. The whole metapopulation can persist, despite extinctions of local populations, if populations are connected enough to allow for adequate recolonization of suitable but vacant habitat. This on-and-off blinking of populations reflecting a balance between local extinctions and recolonizations is the hallmark of classical metapopulation dynamics (Fig. 1). The metapopulation concept was formalized by Levins (1969), but it has deeper roots including ideas on spatial dynamics of populations promoted by Andrewartha and Birch (1954). Maturation of the metapopulation approach and its application to biodiversity conservation, however, has mainly resulted from development of practical metapopulation models by Hanski and his colleagues (Hanski 1997; Hanski and Gaggiotti 2004).
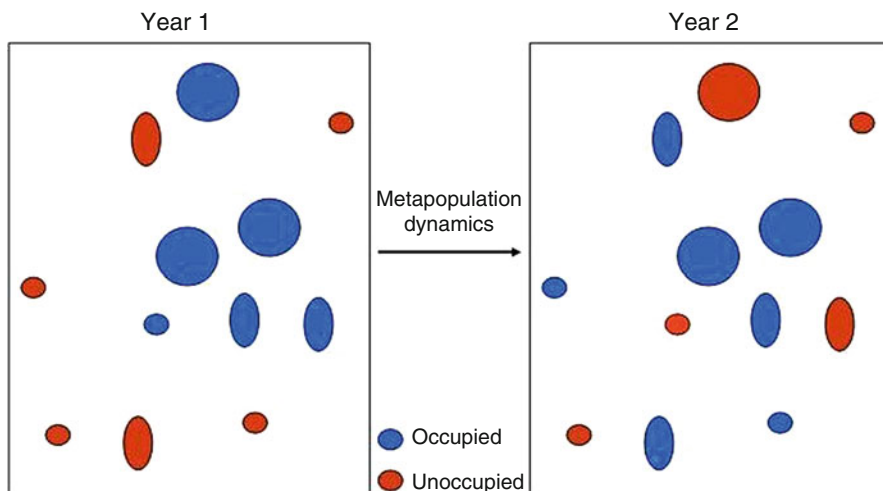

Fig. 1 Metapopulation dynamics for a hypothetical network of 12 wetlands. Wetlands in blue are occupied by a species; wetlands in red are unoccupied. Some wetlands experience local extinctions between years, and some vacant wetlands are recolonized
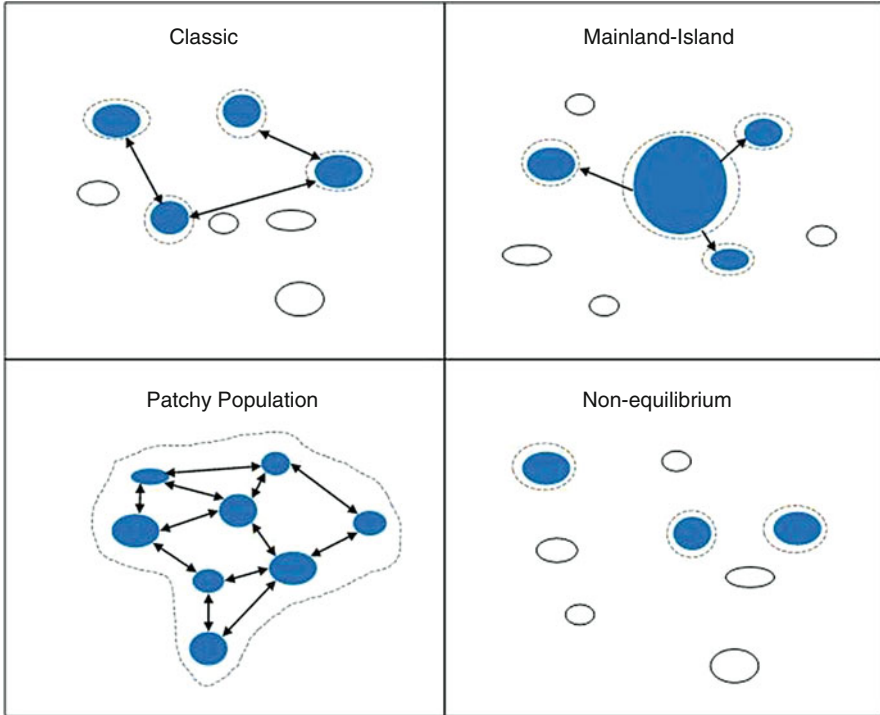
Fig. 2 Types of metapopulations (Harrison and Taylor (1997) with permission of Elsevier). Filled circles represent occupied wetlands; open circles represent unoccupied wetlands. *Arrows* indicate dispersal; *dotted lines* indicate boundaries of local populations. Metapopulation structure depends on degree and directionality of dispersal among wetlands

Hanski (1997) provided four conditions for a classical metapopulation: (1) suitable habitat occurs as discrete patches that can be occupied by local breeding populations, (2) the largest local population still has a nontrivial risk of extinction, (3) habitat patches are not too isolated so that recolonization is possible, and (4) local populations have asynchronous dynamics. Because wetlands often occur as geographically isolated habitats, many wetland-associated species could display metapopulation dynamics (e.g., Sjögren Gulve 1994; Schooley and Branch 2009). However, Marsh and Trenham (2001) warned against a naïve adoption of the "ponds-as-patches" view for wetland species such as amphibians that might not always function as metapopulations. More generally, Harrison and Taylor (1997) cautioned that classical metapopulations could be rare and that metapopulations in nature can have a diversity of structures including mainland-island, patchy population, nonequilibrium metapopulation (Fig. 2), and mixed structures at different spatial scales.

Area-Isolation Paradigm

Practical metapopulation approaches (Hanski and Gaggiotti 2004) are grounded in the "area-isolation paradigm" in which the area of a habitat patch is the main predictor of local extinctions, and connectivity to other source populations is the main predictor of colonization. For wetland species, large wetlands should contain relatively large populations and thus be less susceptible to extinction due to demographic stochasticity than are small populations occupying small wetlands. This area effect on local extinction probability holds true for some spatially structured wetland species such as round-tailed muskrats (*Neofiber alleni*; Schooley and Branch 2009) and painted turtles (*Chrysemys picta*; Cosentino et al. 2010). Size of wetlands also can affect colonization probabilities through the target effect in which larger wetlands are more likely to be colonized by individuals dispersing from other wetlands (Schooley and Branch 2009; Cosentino et al. 2010, 2011). Colonization of vacant wetlands should depend most on how isolated they are from other occupied wetlands. In fact, colonization probability has been positively correlated with connectivity for wetland-associated wildlife (Schooley and Branch 2009; Cosentino et al. 2010, 2011). Connectivity of wetlands can also reduce the likelihood of local extinctions through the rescue effect in which populations are bolstered by dispersers and maintained above levels highly vulnerable to effects of demographic stochasticity (Brown and Kodric-Brown 1977; Cosentino et al. 2011). For instance, isolated populations of the pool frog (*Rana lessonae*) in Sweden are more extinction prone than are more connected populations (Sjögren Gulve 1994).

   Despite this evidence that patch area and isolation can be important predictors of extinction-colonization dynamics, the generality of the area-isolation paradigm has been questioned. Pellet et al. (2007) tested the ability of area and isolation to predict metapopulation dynamics of 10 species from diverse taxa including amphibians and concluded there was not overall strong support for these two key variables arising from metapopulation theory. Patch size may not always be a good surrogate for population size, and patch isolation measured as simple, straight-line distances among patches may be inadequate (Pellet et al. 2007). Likewise, Prugh et al. (2008) conducted a meta-analysis of 785 animal species and concluded that patch area and isolation explained a surprisingly small amount of the variation in patch occupancy (i.e., the outcome of extinction and colonization processes).

Habitat Heterogeneity and Metapopulations

Many of the shortcomings of the area-isolation paradigm as applied to metapopulations relate to the need to consider habitat heterogeneity in multiple ways. Real landscapes are not binary; wetlands can differ in habitat quality and are embedded in a heterogeneous terrestrial matrix (Schooley and Branch 2007, Prugh et al. 2008). Habitat quality of wetlands can depend on many factors including hydroperiod, water chemistry, vegetation composition, resource abundance, and predation risk (e.g., Sjögren Gulve 1994; Cosentino et al. 2010, 2011). For instance,
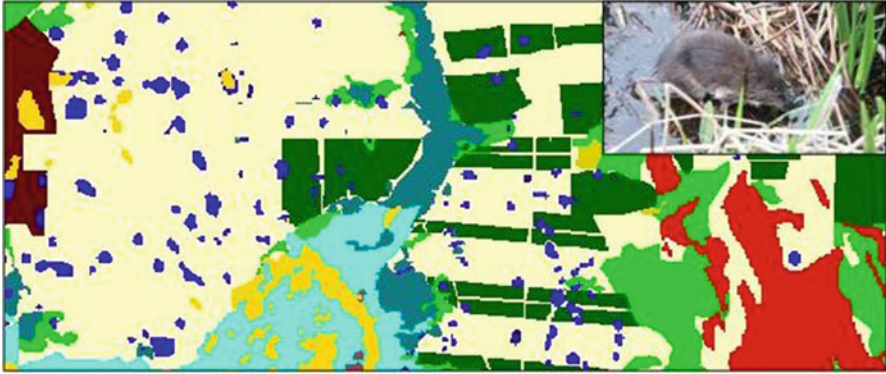
Fig. 3 The round-tailed muskrat (*Neofiber alleni*) is a species of conservation concern that exhibits metapopulation dynamics across depression marshes (*blue polygons*) in Florida, USA. Local extinctions and recolonizations depend not only on wetland area and geographic isolation, but also on habitat quality of wetlands and upland habitat between wetlands (Schooley and Branch 2009). Occupancy is less likely for wetlands surrounded by pine plantations (*dark green polygons*) and other forested upland habitat

site occupancy by round-tailed muskrats strongly depends on the cover of maidencane grass (*Panicum hemitomon*) in marshes because maidencane is the main diet item for muskrats, and they use it to build lodges (Fig. 3; Schooley and Branch 2007, 2009). Ignoring habitat quality is the likely reason that wetland size might not be a good substitute for local population size. In some situations, habitat quality can be the main driver of species distributions, extinctions are not stochastic but instead deterministic due to habitat becoming unsuitable, and species form a habitat-tracking metapopulation across fragmented landscapes (Thomas 1994). Habitat quality of wetlands could also affect colonization if dispersers actively select habitat before settling (Clobert et al. 2012), or the quality of nearby wetlands acting as sources of dispersers is variable in space (Schooley and Branch 2011).

Dispersal is a complex process influenced by many factors (Clobert et al. 2012). Functional connectivity of metapopulations depends on structural aspects of the landscape such as geographic isolation of wetlands, but also how movements of individuals interact with the terrestrial habitat matrix (▶ Chap. 13, "Dispersal and Wetland Fragmentation" by Cosentino and Schooley). Wetland pairs separated by the same straight-line distance could have different functional connectivity because the intervening habitat matrix varies in terms of movement costs (Fig. 3). For example, movement of Natterjack toadlets (*Bufo calamita*) is affected by land cover with forests providing greater resistance than more open habitats (Stevens et al. 2004). Hence, realized isolation of wetlands is species-specific and highly dependent on movement behavior.

For semiaquatic species, the role of habitat heterogeneity is even more complicated. For pond-breeding amphibians with complex life cycles that include a terrestrial stage, the distribution and quality of upland habitat may be especially important (Marsh and Trenham 2001). The joint habitat quality of wetlands and adjacent uplands may determine habitat suitability and the spatial distribution of species.

As such, delineating habitat patches for a wetland metapopulation could require going beyond just identifying wetlands from a map.

Conservation Implications and Future Challenges

Despite these complexities, many of which are related to how we should integrate habitat heterogeneity into the area-isolation paradigm, the metapopulation concept has been influential for land managers. The recognition of potential metapopulation dynamics for wetland species has forced managers to think about biodiversity conservation and restoration at landscape and regional scales instead of at the scale of single wetlands. Metapopulation dynamics also highlight the importance of landscape connectivity and wetland-upland linkages. Future challenges for conservation of wetland species forming metapopulations include maintenance of adequate habitat quality and connectivity despite ongoing habitat loss, fragmentation, and disturbance to the terrestrial matrix. Some species might already be functioning as nonequilibrium metapopulations (Fig. 2) just waiting for dynamics to play out. Finally, interactions between climate change and metapopulation dynamics (Opdam and Wascher 2004) will be crucial to persistence of many wetland species. Increased frequency of disturbances from large weather events will increase the temporal variability of wetland quality, and conservation of connectivity will be critical for facilitating shifts in geographic ranges.

References

Andrewartha HG, Birch LC. The distribution and abundance of animals. Chicago: University of Chicago Press; 1954.

Brown JH, Kodric-Brown A. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology. 1977;58:445–9.

Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal ecology and evolution. Oxford: Oxford University Press; 2012.

Cosentino BJ, Schooley RL, Phillips CA. Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle *Chrysemys picta*. Landscape Ecol. 2010;25:1589–600.

Cosentino BJ, Schooley RL, Phillips CA. Spatial connectivity moderates the effect of predatory fish on salamander metapopulation dynamics. Ecosphere. 2011;2(8):1–14. art 95.

Hanski I, Gaggiotti OE, editors. Ecology, genetics, and evolution of metapopulations. Amsterdam: Elsevier Academic Press; 2004.

Hanski I. Metapopulation dynamics: from concepts and observations to predictive models. In: Hanski IA, Gilpin ME, editors. Metapopulation biology: ecology, genetics, and evolution. San Diego: Academic Press; 1997. p. 69–91.

Harrison S, Taylor SH. Empirical evidence for metapopulation dynamics. In: Hanski I, Gilpin ME, editors. Metapopulation biology: ecology, genetics, and evolution. San Diego: Academic Press; 1997. p. 27–42.

Levins R. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am. 1969;15:237–40.

Marsh DM, Trenham PC. Metapopulation dynamics and amphibian conservation. Conserv Biol. 2001;15:40–9.

Opdam P, Wascher D. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Conserv. 2004;117:285–97.

Pellet J, Fleishman E, Dobkin DS, Gander A, Murphy DD. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. Biol Conserv. 2007;136:483–95.

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS. Effect of habitat area and isolation on fragmented animal populations. Proc Nat Acad Sciences USA. 2008;105:20770–5.

Schooley RL, Branch LC. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. Ecosystems. 2007;10:846–53.

Schooley RL, Branch LC. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecol App. 2009;19:1708–22.

Schooley RL, Branch LC. Habitat quality of source patches and connectivity in fragmented landscapes. Biodivers Conserv. 2011;20:1611–23.

Sjögren Gulve P. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology. 1994;75:1357–67.

Stevens VM, Polus E, Wesselingh RA, Schtickzelle N, Baguette M. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). Landscape Ecol. 2004;19:829–42.

Thomas CD. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conserv Biol. 1994;8:373–8.