RESEARCH ARTICLE

Demographic network and multi-season occupancy modeling of *Rana sylvatica* reveal spatial and temporal patterns of population connectivity and persistence

William E. Peterman · Tracy A. G. Rittenhouse · Julia E. Earl · Raymond D. Semlitsch

Abstract Many populations are spatially structured with frequent extinction–colonization events. A clear understanding of these processes is necessary for making informed and effective management decisions. Due to the spatially and temporally dynamic nature of many systems, population connectivity and local extinction–colonization processes can be difficult to assess, but graph theoretic and occupancy modeling approaches are increasingly being utilized to answer such vital ecological questions. In our study, we used 6 years of egg mass counts from 34 ponds for *Rana sylvatica* to parameterize spatially explicit demographic network models. Our models revealed that the studied populations have spatial structure with strong source–sink dynamics. We also assessed the colonization and persistence probability of each pond using multi-season occupancy modeling. We observed extreme fluctuation in reproductive effort among years, resulting in variable levels of connectivity across the landscape. Pond colonization and persistence were most influenced by local population dynamics, but colonization was also affected by precipitation. Our demographic network model had moderate ability to predict reproductive effort, but accuracy was hindered by variation in annual precipitation. Source populations had higher colonization and persistence rates as well as a greater proportion of ravine habitat within 1,000 m than sink populations. By linking a spatially explicit connectivity model with a temporal occupancy/persistence model, we provide a framework for interpreting patterns of occupancy and dispersal that can serve as an initial guide for future habitat management and restoration.

Keywords Functional connectivity · Graph theory · Missouri · Ozark · Source–sink dynamics · Spatially structured populations · Wood frog

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Introduction

The complex interplay between local population dynamics (per capita birth and death rates) and species'

dispersal rate and ability (emigration and immigration) poses significant challenges to describing population dynamics in space and time, but understanding these processes is critical for making informed and effective management decisions for regional persistence of species (Wennergren et al. 1995; Bowne and Bowers 2004). Description of spatially structured populations has typically focused on patterns of extinctions and colonizations to define metapopulations, rather than the processes underlying the pattern (Hanski and Gilpin 1997). Studies of metapopulations are often utilized in a conservation or management context (Kuussaari et al. 2009), but simulation studies have demonstrated the extremely narrow parameter space and limited real-world application that classic meta-population dynamics have (Fronhofer et al. 2012). Spatially structured populations have varying rates of immigration, emigration, births, and deaths. Because of these processes, spatially structured populations exhibit a range of patterns. If we consider birth–death and emigration–immigration processes as components of two axes, then spatial population dynamics can be assessed from a scale-dependent, process-based approach (Thomas and Kunin 1999). Population dynamics can differ regionally; large populations in well-connected habitat may rarely experience turn-over, but population and dispersal dynamics can be markedly different in peripheral populations or in fragmented landscapes (Brown 1984; Hecnar and M'Closkey 1996). As such, assessment of populations must be made on a case-by-case basis to account for local population dynamics, habitat heterogeneity, and dispersal characteristics. A process-based approach (Thomas and Kunin 1999) allows for more critical assessment of population processes as a function of scale, and presents a more ecologically relevant framework from which to assess spatial population dynamics and develop conservation solutions.

Critical to spatial population dynamics is an understanding of movement and connectivity among populations. Assessing connectivity among spatially subdivided populations can be challenging given uncertainty about species movement behavior and ability (Baguette and Van Dyck 2007). A major challenge in assessing population connectivity is discerning between structural connectivity and functional connectivity. Structural connectivity often refers to connectedness or arrangement of the physical habitat, while functional connectivity refers to the behavior and ability of a dispersing organism to navigate between two habitat patches (Baguette and Van Dyck 2007). As such, two habitat patches can be structurally connected, but organisms inhabiting each patch may remain isolated if they are unable to move between patches. Functional connectivity has a foundational influence upon ecological and evolutionary phenomena such as gene flow, population genetic structure, extinction, source–sink dynamics, and ultimately to population persistence (Calabrese and Fagan 2004; Taylor et al. 2006; Nathan et al. 2008). Recently, Kool et al. (2013) reviewed the rapidly developing field of connectivity science, specifically highlighting advances in connectivity modeling for conservation purposes.

Among the numerous methods and approaches for modeling and assessing functional connectivity is graph theory. Graph theory is a body of mathematics that is increasingly being used to answer ecological, conservation, and management questions concerning connectivity and movement in a spatially explicit context (Urban et al. 2009), and has been exceptionally useful in addressing questions concerning spatial structured populations (Urban and Keitt 2001; Minor and Urban 2007; Schick and Lindley 2007). In its simplest form, a graph model consists of nodes that are connected by edges, with nodes representing habitat patches or populations and edges representing functional connections between populations (Harary 1969; Urban and Keitt 2001; Urban et al. 2009). Although caricatures of real systems, the simplicity and visual representation provided by graph models makes them powerful tools for assessing metapopulation dynamics (Brooks 2006; Schick and Lindley 2007; Rozenfeld et al. 2008). Ecological graph models can generally be classified into three categories: (1) unweighted or regular graphs, (2) directed unweighted graphs (digraph), or (3) weighted digraph (see Fig. 1 of Schick and Lindley 2007). Briefly, if we consider two nodes, a and b, connected by an edge, in an unweighted or regular graph the connection is bidirectional ($a \leftrightarrow b$) and both nodes are equal. Such graphs demonstrate binary functional connectivity, but do not provide information concerning the strength or directionality of the connection. In contrast, a directed unweighted graph (digraph) provides directionality concerning the connection ($a \rightarrow b$), but still does not provide information concerning the strength of the connection or include node properties. Finally, weighted digraphs convey the most information,

including node characteristics as well as strength and direction of edge connections (Schick and Lindley 2007; Bang-Jensen and Gutin 2010). Because directionality can significantly affect dynamics within a system (Gustafson and Gardner 1996), digraphs and weighted digraphs provide a framework for assessing asymmetric and directed connectivity.

We conducted egg mass counts of peripheral populations of *Rana sylvatica* (wood frog) for 6 years at all available breeding ponds within a conservation area located in east-central Missouri, USA. We constructed spatially explicit weighted digraphs to estimate directional connectivity among the breeding ponds (Schick and Lindley 2007). Further, we used multi-season occupancy models to estimate pond-level probabilities of colonization and persistence as they relate to population, landscape, and climate factors (MacKenzie et al. 2003). The specific objectives of our study were to (1) assess the annual and average level of connectivity among ponds, (2) determine the role of climate and landscape configuration as factors affecting population dynamics, (3) determine each pond's status as either a net contributor (i.e. source; Pulliam 1988) or a net receiver (i.e. sink), and (4) calculate pond-specific colonization and persistence probabilities, relating these estimates to source–sink population designations, climate, and landscape configuration. Due to the highly philopatric nature of *R. sylvatica* (Berven and Grudzien 1990), we hypothesized that local population structure would be evident and that dispersal and connectivity would be greatest among adjacent ponds. Based upon previous research (Rittenhouse and Semlitsch 2007; Rittenhouse et al. 2008; Rittenhouse and Semlitsch 2009; Rittenhouse et al. 2009), we also hypothesized that rainfall and ravine habitats would be important covariates for describing pond turnover (i.e. colonization and persistence probabilities). Lastly, we hypothesized that source and sink ponds would differ significantly in their respective colonization and persistence probabilities due to local demographic differences.

Materials and methods

Study area

Our study took place at Daniel Boone Conservation Area (DBCA) in east-central Missouri. This area is situated on the upper Ozark Plateau physiographic region (38.78°N, −91.39°W) in mature (80–100 years old) second-growth forest with an overstory dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), with varying amounts of sugar maple (*Acer saccharum*) and red cedar (*Juniperus virginiana*) in the understory (Semlitsch et al. 2008). DBCA encompasses 1,424.5 ha, and has >40 manmade ponds. These ponds are 27–47 years old, are generally <0.05 ha, and were originally constructed for other wildlife such as deer (*Odocoileus virginianus*) and turkey (*Meleagris gallopavo*). These ponds are known to support up to 16 species of pond breeding amphibians (Hocking et al. 2008), and on average, are separated by 2,000 m (246–3,900 m).

Study species

Rana sylvatica (wood frog) are one of the most widely distributed species of North American frogs, ranging from Alaska to Maine, throughout the eastern and midwestern USA, and extending south through the Appalachian and Central Highlands (Lannoo 2005). Breeding usually occurs in small, ephemeral, fishless wetlands in late winter and early spring. Breeding populations tend to have male-biased sex ratios, which has been attributed to differential rates of maturity, with females maturing later (2–3 years) than males (1–2 years), and subsequently suffering greater mortality prior to reproduction (Berven and Grudzien 1990). *R. sylvatica* is an explosive breeder, whereby nearly all reproduction occurs over a few nights (Wright and Wright 1949). Additionally, they breed "communally", which makes the floating egg masses conspicuous (Lannoo 2005). In east-central Missouri, *R. sylvatica* are at their range limit; populations tend to be scattered, but often locally abundant.

Data collection and surveys

Each spring in 2006–2011, we conducted visual encounter surveys for egg masses in ponds at DBCA. Surveys were conducted by two researchers independently walking the perimeter of the pond. When eggs were present, the number of masses was estimated by each researcher, and a consensus value was determined. To determine detection probabilities, surveys in 2010 were conducted as in previous seasons, but surveyors did not disclose whether egg masses had

been seen or counted. After both surveyors had completed their search of the pond, a consensus number of egg masses in the pond was determined. A second round of surveys was conducted in May of 2006–2010, prior to *R. sylvatica* metamorphosis to determine if ponds still contained water and *R. sylvatica* larvae. In this study, we utilize a variety of statistical models with outputs from some analyses being used as inputs for others. To aid in interpretation of our workflow, a conceptual diagram describing the analyses conducted in this study is presented in Fig. 1.

Covariates

To determine if environmental factors influenced wood frog breeding, we collected weather data for the months of June–September, for 2003–2011. Historical weather data from the closest known weather station (8 km) was downloaded from www.wunderground.com. *R. sylvatica* metamorphoses in June (Hocking et al. 2008) and thus June–September is the summer active period for juveniles and adults. Because *R. sylvatica* take 1–3 years to reach maturity (Berven and Grudzien 1990), we hypothesized that weather conditions in years preceding our sample years could be important (Church 2008). We determined daily precipitation (mm), maximum temperature (°C), average number of days between 10 mm rainfall events, and maximum number of days between 10 mm rainfall events. These last two variables are known to be critical to desiccation of *R. sylvatica* in Missouri (O'Connor et al. 2006). Ten millimeters of rain is the amount of rain needed to reach the forest floor and to recharge the leaf litter with water

(O'Connor et al. 2006). Seasonal covariates used in subsequent modeling corresponded to either the average in the preceding year, or the average of the 3 years preceding. The 3-year time frame was explored because female *R. sylvatica* require 2–3 years to reach maturity.

Site-level covariates for multi-season persistence/colonization modeling were measured in ArcGIS 9.3 (ESRI, Redlands, CA), and included the number of source ponds (determined from the average graph model described below) within 1,200 m (the average dispersal distance measured by Berven and Grudzien 1990) as well as the distance to nearest ravine. The latter metric was included because *R. sylvatica* migrate to ravine habitats following breeding (Rittenhouse and Semlitsch 2007) and microclimates in ravines are conducive to water conservation and survival (Rittenhouse et al. 2008). Location and extent of ravine habitat was estimated using the topographic position index (TPI; Jenness 2006) as implemented in the Topography Toolbox for ArcGIS (Dilts 2010). We used a 3-m resolution digital elevation model (http://seamless.usgs.gov/), and assessed each pixel relative to the surrounding 90 m area; all areas with TPI < -4 were designated as ravine. The final site covariate used for modeling was the percent of the estimated population size at each pond that was self-recruited (i.e. diagonal elements of matrix N; see "Materials and methods" section below).

Graph construction

Our graph analyses mirrored that of Schick and Lindley (2007). Briefly, to construct our weighted

Fig. 1 Conceptual model of data analyses used in this study. *Gray boxes* represent models used in the analysis, and *white boxes* are preliminary or intermediate data used as inputs for the models
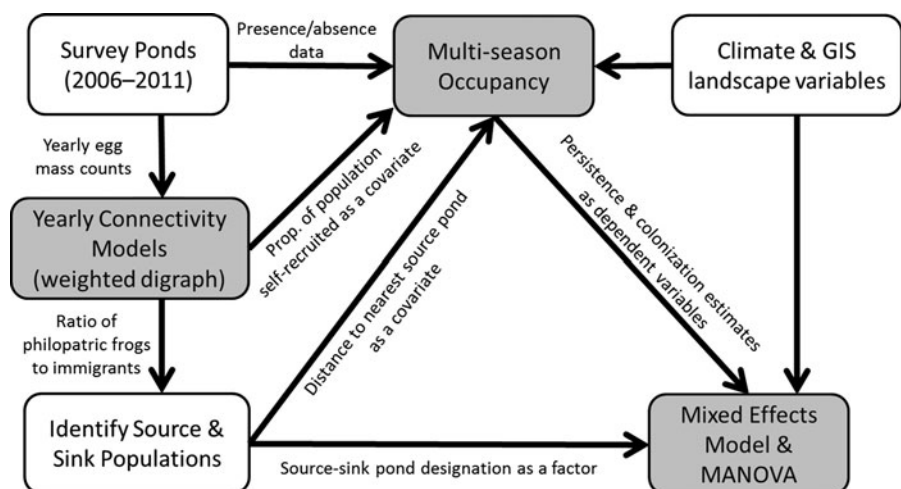
digraph, four data structures were needed: (1) a vector X of population size, (2) a full distance matrix D of all interpopulation (between-pond) Euclidean distances, which represent structural connectivity, (3) a dispersal equation, and (4) a dispersal matrix M of the probability of successful dispersal from a source to a target pond. With these data structures, a migration matrix N representing functional connectivity can be calculated to determine the direction and strength (weight) of edges connecting ponds (nodes), as detailed below.

For our model, we assume that each *R. sylvatica* female lays a single clutch, therefore an egg mass represents one female. The number of eggs per clutch was set to 850 based upon estimates of clutch size reported in Trauth et al. (2004) for Ozark region *R. sylvatica*. By averaging values from Berven (1990), we determined that the probability of a single egg surviving to metamorphosis was 0.009825. We then multiplied the number of eggs in each pond by the individual egg survival probability to calculate the juvenile population vector X, which we assume is half male, half female. The probability that a juvenile *R. sylvatica* survives to return to a pond to breed differs among sexes (Berven and Grudzien 1990), so we modified matrix X to account for female (X^x) survival differences as measured by Berven (1990); matrix $X^x = 0.5X \times 0.06484$.

To estimate interpond movements, it is necessary to have a portion of the metamorph frogs from a pond disperse to other ponds. Berven and Grudzien (1990) described a mean dispersal probability (m) (i.e. straying probability, sensu Schick and Lindley 2007) of approximately 20 % among surviving juvenile frogs. The probability p_{ij} of successfully dispersing from pond i to pond j is a function of the dispersal ability and interpond distance (d_{ij}). Distances between ponds were contained in matrix D, and were determined using ArcGIS 9.3 (ESRI, Redlands, CA). We used the modified negative exponential equation of Berven and Grudzien (1990) to calculate p_{ij}:

$$p_{ij} = 0.4392 \times 10^{-0.000560 \times d_{ij}}. \qquad (1)$$

The dispersal matrix M is a combination of dispersal probability, m, and the probability of successful interpond dispersal, p_{ij}. The off-diagonal elements of M were set to mp_{ij} and the diagonal elements were set to $1 - m$ to represent the 80 % site philopatry. We then multiplied the sex-specific juvenile population vector, X^x, by the dispersal matrix M to calculate the

female migration matrix $N = X^x M$. The diagonal elements of N represent pond self-recruitment, the sums of each row are the number of frogs emigrating from the pond, and the sums of each column are the number of frogs immigrating to the pond (sensu Schick and Lindley 2007). Matrix N contains the necessary components to construct and visualize a graph model.

Ponds were considered connected if the number of simulated frogs emigrating from pond i to pond j was ≥ 1, as determined from the row sums in migration matrix N. To examine source–sink characteristics of each pond (Pulliam 1988), we measured the ratio of frogs that originated from a pond (philopatric individuals, P) relative to the number of immigrants (I; P:I ratio). Populations were designated as sources (P:I >1) or sinks (P:I <1). Although we note that this definition deviates from traditional births > deaths, emigrants > immigrants definitions of source populations (reverse relationship for sinks), we feel our definition is most descriptive of our system where 80 % of individuals are philopatric to their natal pond (Berven and Grudzien 1990).

As part of our 6-year sampling, each pond was visited after eggs had hatched, but prior to metamorphosis in years 2006–2010. Three of the ponds used by *R. sylvatica* always dried before metamorphosis could occur; therefore we set all row values to zero for these ponds as they never contributed recruits to the system. Because females mature at 2–3 years of age, our models follow a 2-year time lag (i.e. 2006 egg mass counts were used to model 2008 reproductive effort). As such, we constructed four graphs (2008–2011) from our 6 years of data. Female *R. sylvatica* can reproduce in multiple consecutive years (up to 14 %; Berven 1990), but from 2004 to 2007, only 1 of 126 (0.78 %) individually marked females from DBCA was observed breeding a second year (Semlitsch unpublished data), so we did not include multiple cohorts in our model.

Model assumptions

Our demographic network model examines connectivity among discrete populations as a function of survival probability and the probability of successful dispersal between ponds. These factors remain constant through time, and as such, our model does not incorporate potential density-dependent effects during

larval development, individual variation in movement behavior, habitat heterogeneity (slope, canopy cover, etc.) or stochastic climatological processes.

Graph model validation

To validate our yearly model predictions from the graph models we calculated the Spearman's rank correlation coefficient between all pond-specific estimates of female population size with the number of egg masses counted each year. We then calculated the correlation coefficient for each year independently, as well as conducted Bonferroni-corrected-independent samples t test comparing the yearly egg mass observation from each pond to the estimated number of females from our female population matrix X^x. Lastly we used linear mixed-effects models to assess how climate variation affected the accuracy of our model across years. We used the difference between empirical observations and model predictions at each pond as the dependent variable (field egg counts − model predicted counts). The independent variable was the precipitation deviation from the 10-year average. This was calculated by subtracting 10-year average precipitation for June–September from the average June–September precipitation from the 2-year period preceding the model/observation year. As such, negative differences correspond to below average precipitation while positive differences correspond to above average precipitation. Ponds were modeled as random effects to account for repeated observations over years.

Multi-season colonization/persistence modeling

We used logistic modeling approaches described by Mackenzie et al. (2003) to model occupancy (ψ), colonization (γ), and persistence ($1 - \varepsilon$; complement of extinction) as a function of covariates at DBCA. To investigate the relationships between these parameters and environmental variables, we used an information-theoretic approach to model selection (Burnham and Anderson 2002). We ranked a priori models based on AIC$_c$, calculated Akaike weights (ω_i) and selected a best model from among the models tested (Burnham and Anderson 2002). All analyses were conducted with program PRESENCE 3.1 (Proteus Research and Consulting, Dunedin, New Zealand) to fit models to the annual sampling data. We selected a set of

biologically and ecologically relevant variables to test their relationship to ψ, γ, and $1 - \varepsilon$. Prior to use, covariates were standardized by subtracting the mean and dividing by the standard deviation (SD).

Generally, model selection follows a multi-step process whereby covariates significant to species detection are first determined by holding site occupancy constant. We did not conduct repeated sampling within a season due to the high detectability of *R. sylvatica* egg masses. We verified this using our 2010 two-observer data set, which estimated *R. sylvatica* detection to be 0.983 with no correlation to covariates. We proceeded with our multi-season analysis, holding detection probability constant across seasons at 0.983. Models were constructed with different combinations of site and environmental covariates (see "Covariates" section above), and were parameterized to determine if *R. sylvatica* persistence and colonization across years was dependent upon (1) recent weather, (2) historical weather, (3) local site characteristics, (4) a combination of weather and site characteristics. We also modeled the effect of time (i.e. year) in combination with covariates.

To determine the relationship between colonization and persistence probabilities to our designation of DBCA ponds as sources or sinks (i.e. metapopulation status; see "Graph construction" section above), we used linear mixed-effects models. We used the model averaged parameter values for colonization and persistence of all models with ΔAIC$_c$ of <7 in the analysis of mixed-effects models. Two separate analyses were conducted: one with pond-specific colonization as the dependent variable, and one with pond-specific persistence as the dependent variable. We used year as a repeated measure in the analysis, with source–sink status as a factor. Multiple covariance structures were fit to the data using SPSS 17 (SPSS Inc., Chicago, IL), and the best covariance structure was determined as the model with the lowest AIC$_c$ score.

To further assess the differences between source and sink designated ponds, we conducted a multivariate analysis of variance. For this analysis we calculated the proportion of area that was ravine habitat within 100, 500, and 1000 m of each pond. We also included pond volume, as this measure could correlate with hydroperiod and/or density-dependent effects that could influence growth, survival, or turnover (Wilbur 1987; Taylor and Scott 1997; Werner et al. 2007).

Results

Survey results

Over the 6-year survey period, a total of 34 different ponds were used for reproduction by *R. sylvatica*. In any given year 6–30 ponds contained eggs (mean, ±SD; 18, ±9.27) with 36–752 (371 ± 236) clutches of eggs being observed each year. This resulted in an average of 10 (±5.12) clutches per pond, per year. Variation in annual egg counts was significantly and positively associated with average amount of precipitation in the preceding 2-year period ($p < 0.001$). The mean distance between ponds used for breeding was 1,972 m (28–4,997 m).

Graph modeling results

On average, *R. sylvatica* breeding ponds at DBCA were well connected (Fig. 2), but the highly variable reproductive effort across years led to similarly variable interpond connectivity. When reproductive effort was low, and localized at a few ponds (2008; 36 egg masses), the resultant connectivity network is extremely sparse with only 19 linkages between ponds (Fig. 2). In contrast, in years with high recruitment (2010; 752 egg masses) the network is highly connected (294 pond linkages) with no isolated ponds (Fig. 2). We found that the average edge length (i.e. distance between connected ponds) differed among years. When recruitment was low, as in 2008, the average distance between connected ponds was 412 m (80–786 m). In contrast, when recruitment was highest in 2010, the average distance was 1,204 m (49–3,022 m). The average network had a mean distance between connected ponds of 1,153 m (49–3,828 m). In assessing the average network, we found 11 ponds acting as sources and 23 ponds acting as sinks with 208 linkages between ponds. Seven of the 11 sources and 12 of 23 sinks had constant source–sink designations across modeled years. The average minimum distance between these seven constant source ponds is 1,053 m (501–1,711 m) and the average mean distance was 2,182 m (1,575–3,086 m). Repeated measures analysis of variance revealed that constant source ponds contributed a significantly greater proportion of eggs across years (mean = 7.86 %, ±5.45 SD), than either the constant sink ponds (1.08 %, ±0.86) or ponds that changed source–sink status (2.13 %, ±1.58;

$p < 0.001$). The greater reproduction at these source ponds contributed 61.2 % of all dispersing emigrants in the system. We also found a significant year by designation (i.e. constant source, constant sink, variable source–sink) interaction in the model predicting the number of egg masses (designation × year: $p < 0.001$). Specifically, the number of clutches in each pond changes from year to year, but these changes were less in constant source ponds compared to sink or variable source–sink ponds.

Graph model validation

Over all years combined, our graph models had a highly significant correlation with field egg mass counts (Spearman's $\rho = 0.562$, $p = 0.001$). Year-specific correlations ranged from 0.508 to 0.632. Despite these correlations, there were still discrepancies between model predictions and empirical counts at the pond level across years, as indicated by Bonferroni-corrected t tests. These tests showed that 2008 and 2010 observations were significantly different from field counts ($p \leq 0.006$), but 2009 and 2011 did not differ ($p \geq 0.10$). Linear mixed-effects models revealed that differences in precipitation significantly affected the accuracy of the demographic model. The differences between field egg counts and model estimation of egg counts were significantly predicted by the difference in precipitation from the 10-year average ($p < 0.001$) with above average precipitation leading to model under prediction, and below average precipitation leading to model over prediction.

Multi-season colonization/persistence modeling results

We found good support for the top model, which is 4.8 times more likely than the next competing model. The top model differed from the next competing model by including time between soaking rain events as a parameter for the estimation of colonization (Table 1). We found pond-specific self-recruitment rates to be an important covariate to all estimated parameters (occupancy, colonization, persistence; Table 1). Additionally, the interval between soaking rain events was an important predictor for colonization, and persistence estimates were year-specific (Table 1). Self-recruitment had a positive relationship with all parameters,

Fig. 2 Connectivity of *R. sylvatica* breeding ponds at Daniel Boone Conservation Area, Missouri, USA, in relation to low (2008), high (2010) and 4-year average recruitment. Connections between ponds were determined through demographic network modeling
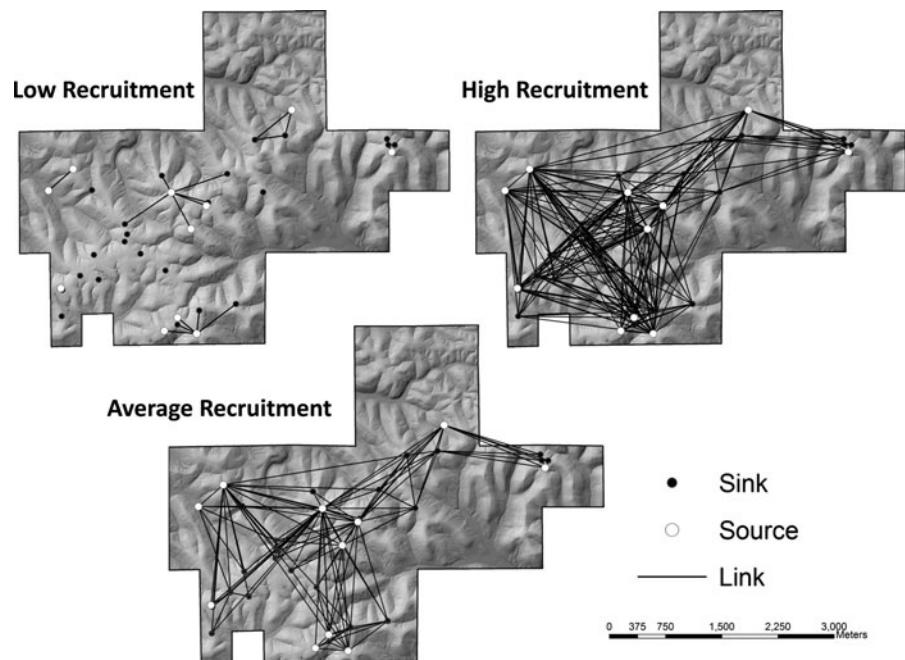
while time between soaking rain events negatively affected colonization rates (Table 2).

To further assess how or if colonization and persistence estimates from multi-season occupancy modeling related to our average source–sink pond designations (from the network model above), we again used linear mixed-effects models. The best-fit error covariance structure to account for repeated observations in time, as determined through AIC model assessment, was a heterogeneous Toeplitz structure. Because our survey intervals were uniformly spaced this is an appropriate error structure (Verbeke and Molenberghs 2000). Using this structure, we fit separate models using persistence and colonization estimates from the occupancy modeling as dependent variables, and pond source–sink status as a fixed factor. We found that source ponds had significantly higher colonization and persistence probabilities than sink ponds across all years (Fig. 3a, b). Persistence probability was relatively constant among years for source ponds (0.88–0.91), but exhibited greater variability in sink ponds (0.76–0.84; Fig. 3a). Colonization showed greater variation among years because of the significance and role of rainfall interval in estimating colonization (Fig. 3b; Table 1).

Given the significant differences in persistence and colonization estimates for source and sink ponds, we

wanted to know if there were inherent differences between these ponds with regard to structural pond characteristics or location of ponds within the landscape. Our multivariate analysis of variance model was significant ($F_{4,29} = 3.56$; Wilk's $\lambda = 0.670$; $p = 0.017$), but only the proportion of ravine habitat at 1,000 m was significant within the model ($F_{1,32} = 4.66$; $p = 0.039$). At this scale, source ponds had an average of 72.00 ha (± 3.95) of ravine habitat surrounding them, while sink ponds were surrounded by 68.18 ha (± 4.84) of ravine.

Discussion

Graph theoretic approaches to modeling and describing connectivity are often lauded for their simplicity and limited data requirements (Minor and Urban 2007), but graph models can also incorporate biological complexity (Schick and Lindley 2007). For our model, we were able take easily and reliably collected egg mass counts and then utilize a wealth of empirical data concerning *R. sylvatica* natural history and demography to estimate connectivity as the number of metamorphic frogs successfully dispersing to new ponds. By incorporating population characteristics along with a probability function for successful

Table 1 Summary table of multi-season model results from PRESENCE

Models	AIC_c	ΔAIC_c	ω_i[a]	K[b]	$-2 \times$ Loglikelihood
ψ(SELF), γ(SELF + SOAK.INT), $1 - \varepsilon$(YEAR + SELF), p(0.983)	195.27	0	0.7307	11	170.27
ψ(SELF), γ(SELF), $1 - \varepsilon$(YEAR + SELF), p(0.983)	199.04	3.77	0.1109	10	176.57
ψ(SELF), γ(YEAR + SELF), $1 - \varepsilon$(YEAR + SELF), p(0.983)	200.47	5.20	0.0543	13	170.24
ψ(SELF), γ(SELF + D.SOURCE), $1 - \varepsilon$(YEAR + SELF), p(0.983)	201.21	5.94	0.0375	11	176.21
ψ(SELF), γ(SELF + SOAK.INT), $1 - \varepsilon$(YEAR + D.SOURCE), p(0.983)	201.34	6.07	0.0351	11	176.34
ψ(SELF), γ(SELF + PRE.3), $1 - \varepsilon$(YEAR + SELF), p(0.983)	201.56	6.29	0.0315	11	176.56

Only models with ΔAIC_c of <7 are reported. Covariates in the top models included pond self-recruitment (SELF), days between rainfall events of $\geq$10 mm (SOAK.INT), precipitation in the preceding 3 years (PRE.3), year (YEAR), and distance to nearest source pond (D.SOURCE)

ψ Occupancy, γ colonization, $1 - \varepsilon$ persistence, p probability of detection

[a] Probability that the current model (i) is the best approximating model among those tested

[b] Number of parameters included in the model

Table 2 β estimates and 95 % confidence intervals for parameters in the most supported multi-season model

Parameters	Covariates	β	Lower 95 % CI	Upper 95 % CI
Occupancy (ψ)	SELF	3.814	0.176	7.452
Colonization (γ)	SELF	6.585	2.450	10.721
	SOAK.INT	−0.982	−1.654	−0.310
Persistence ($1 - \varepsilon$)	SELF	6.398	3.031	9.765

dispersal, we were able to more realistically model functional, directed linkages between populations, and in this way, we avoided the need to set arbitrary distance or probability cutoffs to determine when two populations are functionally connected. Our modeling approach is also novel in that we combined multi-season colonization/persistence modeling with our graph models. In doing so, we achieved corroborative support that colonization/persistence processes are highly dependent upon the level of self-recruitment, and that source and sink ponds significantly differ in their persistence and colonization probabilities.

One of the objectives of our study was to identify populations as sources or sinks, and to make comparisons between them. Source and sink have specific meaning within the metapopulation literature. Specifically, source populations can be generalized as net producers to the system, and sink populations as net receivers (Pulliam 1988; Thomas and Kunin 1999). In our study, *R. sylvatica* were found to be dynamic in space and time as a result of variable recruitment. We observed high turnover in our populations (79 %). Of the 34 ponds used for reproduction, only 11 were ever

designated as sources that contributed dispersers to the system, and only 7 of these ponds were identified as sources in all years. Although accounting for 21 % of the breeding ponds, constant source ponds contributed a disproportionate 61.2 % of the emigrants to the pond network. We also found that source ponds had greater stability in time and were predicted to have a greater probability of colonization following local extinction. Given the turnover rate and the disproportionate contribution of a small number of ponds to the network, we interpret the patterns observed in our system as clearly describing a source–sink population (Harrison and Taylor 1997), with little support that they exist as a patchy population. These insights would not be possible without explicitly modeling the spatial demographic processes.

A recent population genetic study from Missouri corroborates our model results of limited dispersal. Peterman et al. (2013) found that *R. sylvatica* at this conservation area and two adjacent conservation areas showed significant genetic differentiation among populations that were 1–3 km apart (mean $F_{ST} = 0.016$; 7 of 9 comparisons significant). The
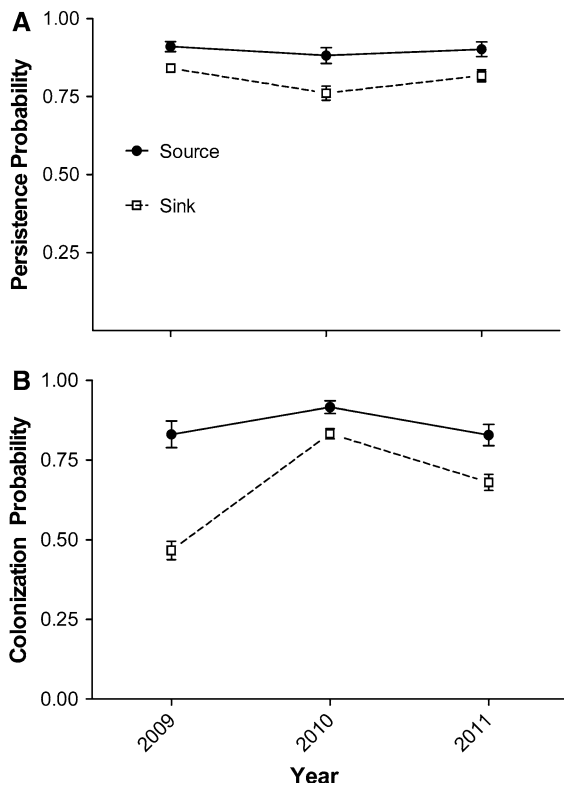
Fig. 3 Estimated marginal means for persistence probability (**a**) and colonization probability (**b**) of source and sink ponds, as determined by linear mixed-effects models. Sources and sinks differ significantly across years ($p \leq 0.004$) for both persistence and colonization. *Error bars* represent standard errors of the estimate

amount of genetic diversity and scale of genetic structure observed in this study are both much smaller than those described in larger, central populations of *R. sylvatica* (Crosby et al. 2008; Zellmer and Knowles 2009; Richardson 2012), and is expected in peripheral populations. These findings underscore the need to carefully assess each population. The spatial scale of populations, life history of species, and regional differences in ecology and movement can affect spatial population dynamics, and these differences may lead to different conservation and management recommendations (Fronhofer et al. 2012).

Rana sylvatica populations have been described as being self-perpetuating (Berven and Grudzien 1990). In accordance with this, we found that pond self-recruitment was an important covariate in our study for estimating colonization and persistence probabilities at a pond, both of which increased as pond self-

recruitment increased. Over the years we modeled, the mean number of dispersing emigrants produced by a pond was 3.56 (0–29), which also affected the overall extent of the network. When reproduction is low few metamorphs are produced, and as a result, successful long distance dispersal is curtailed. We observed a nearly 60 % decrease in mean distance between connected ponds when comparing the wettest year (2010, mean distance = 1,204 m) and the driest year (2008, mean distance = 412 m). This result may be counterintuitive, that functional connectivity can change from year to year when the structural connectivity (i.e. distance between ponds) remains static. In part due to the simplicity of our model, dispersal probability between ponds decreases as a function of interpond distance. As such, more dispersers (i.e. metamorphs) are necessary to achieve long distance connections. Interestingly, the mean distance between connected ponds in 2010 as well as for the average network (1,204 and 1,153 m, respectively) is very similar to the empirical mean estimate for interpond dispersal for *R. sylvatica* reported by Berven and Grudzien (1,126 m; 1990).

Given these empirical observations of movement behavior and implied importance of ravines as refugia from water loss (Rittenhouse and Semlitsch 2007; Rittenhouse et al. 2008), we hypothesized that rainfall and ravine habitats would play an important role in colonization–persistence processes, especially in drier regions, like Missouri. In support of this, we did find that the interval between soaking rain events had a significant, negative effect on colonization, suggesting that as the time between soaking rain events increased, the probability that previously unoccupied pond being colonized decreased. In contrast, distance to the nearest ravine was not included in any of the top models. We did find, however, that ponds designated as sources through the demographic network model had significantly more ravine habitat within 1,000 m than sink ponds. Although the differences in amount of ravine between source and sink ponds are relatively small (72 and 68 ha, respectively), the scale of this process (1,000 m) corresponds with reported juvenile dispersal distances (Berven and Grudzien 1990) as well as the model-optimized spatial scale at which *R. sylvatica* respond to the landscape (Charney 2012).

In addition to influencing colonization, differences in annual rainfall affected our ability to accurately predict female reproductive effort. Specifically, our

model significantly under predicted reproduction in years with above average precipitation, while in years with below average rainfall our model over predicted. These results may indicate that survival is higher in wet years and lower in dry years, or alternatively, that dispersal costs are lower in wet years, resulting in a more continuous distribution. There is clearly more stochasticity and complexity in this system than what is being accounted for in our model. The mismatches in our demographic model with observed female reproduction could result from several factors. First, our demographic model assumes stationarity in all parameters, and does not incorporate parameters that are known to be important for movement and survival of amphibians, such as rainfall (Rittenhouse and Semlitsch 2007; Rittenhouse et al. 2009). Second, our results might suggest behavioral plasticity in that females, which mature in 2 years (Berven 1990), may be able to forego reproduction in dry years to attempt to breed in a subsequent year when conditions may be more suitable. This strategy would likely result in increased mortality within the cohort, which Berven (1990) estimated to be 78.4 % annually, but such a reproductive strategy could be viable and necessary under more stochastic climate conditions. Time to maturity in our peripheral populations existing in a hotter, drier climate may also be more variable and dependent upon climatic conditions than reported in central populations, meaning that in any given year the females breeding in a pond are comprised of 1, 2, and 3-year old individuals. Such a dynamic, especially if tied to climate, would be poorly accounted for in our demographic model.

Important to interpreting our results, is recognizing the assumptions and limitations of our modeling approach. We emphasize that our analysis of this system contains many simplifying assumptions and describes pattern, but not necessarily process. First, our models represent structural connectivity simply as distance, and we do not account for habitat heterogeneity such as ravine habitat or topography between breeding ponds. Second, as described above, we have not incorporated climatological variation directly into our models. Third, functional connectivity is inferred from our model, but we have no direct observations of interpond movements. The importance of rainfall and habitat have been previously demonstrated and further supported by our study. Future, more parsimonious, modeling efforts should seek to directly incorporate rainfall and habitat heterogeneity to better understand the relative role of each in survival, successful dispersal, and spatial population dynamics. Additionally, we do not have empirical data as to what makes a population a source or what makes a population a sink. A more detailed inspection of local within pond factors such as hydroperiod, predator community, water chemistry, etc., as well as regional landscape factors relating to source–sink designations is also warranted, as our study makes no attempts to elucidate processes underlying the observed patterns.

Using basic field data on reproductive effort, we built a set of graph models to infer spatial population dynamics. The identification of ponds as sources or sinks now provides a solid starting point to direct future empirical studies. We do note, however, that graph models can provide many other insights into ecological networks, such as network stability, patch importance, or link importance (Urban and Keitt 2001; Saura and Rubio 2010). Recently, significant advances have been made in developing ecologically relevant graph metrics to assess network characteristics, including tools to calculate graph metrics and assess network properties (Saura and Torne 2009; Saura and Rubio 2010). Given the versatility, and potentially minimal data requirements, graph-based methods hold great promise for providing novel insight into ecological systems. Our approach should be generalizable to many other systems with long-term demographic data, and can serve as a powerful tool to assess connectivity and identify ecological processes to better manage and conserve species' populations.

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