

Spatial connectivity moderates the effect of predatory fish on salamander metapopulation dynamics

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Abstract. In predator-prey metapopulations, persistence of prey in patches with predators may depend on the rescue effect in which immigration from nearby sources prevents local extinction. Thus, constraints on spatial connectivity may have important implications for predator-prey coexistence. We tested the hypothesis that metapopulation dynamics of Ambystoma tigrinum (tiger salamander) depend on combined effects of predatory fish and spatial connectivity. Because matrix heterogeneity can influence dispersal, we also considered how a proximate constraint on amphibian dispersal-desiccation risk-scales up to influence metapopulation dynamics for A. tigrinum. Occupancy and subsequent turnover patterns were quantified in a network of 90 wetlands for three years in an agricultural landscape in Illinois. Our previous field experiments demonstrated that desiccation risk varies among matrix habitats, and that individuals orient movements towards habitat with low desiccation risk. We used cost-distance modeling to generate a connectivity metric that accounted for desiccation risk. Occupancy and colonization probabilities were related negatively to fish occupancy and positively to connectivity. Matrix structure had a strong influence on colonization, and the connectivity metric based on desiccation risk was a better predictor of colonization than alternative metrics. The positive effect of desiccation-informed connectivity on colonization was strongest in wetlands with fish, indicating matrix composition can moderate the effects of predation on amphibians. We detected a rescue effect in which extinction probability was related negatively to connectivity, and this effect was strongest in sites with fish. The matrix did not have a strong effect on occupancy or extinction probabilities, and we discuss why matrix effects may vary for different aspects of population turnover. Our results suggest effects of fish predators on metapopulation dynamics of amphibians depend on spatial connectivity, and that immigration may be essential for maintaining persistence of amphibians in systems with fish. This study also demonstrates that the mechanisms underlying dispersal limitation for A. tigrinum may include desiccation risk.

Key words: *Ambystoma tigrinum;* amphibian; connectivity; dispersal; fish; Illinois; landscape structure; least-cost; metapopulation; predation; rescue effect; salamander.

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INTRODUCTION

Metapopulation theory predicts a balance between stochastic extinction and subsequent recolonization, underscoring the importance of dispersal for regional persistence (Hanski and Gaggiotti 2004). In systems in which patch area and isolation are poor predictors of extinction and colonization (Baguette 2004, Pellet et al. 2007, Prugh et al. 2008), habitat heterogeneity may be a primary factor driving observed turnover dynamics (With 2004, Schooley and Branch 2009, Cosentino et al. 2010). For example, extinction can be deterministic in patches with poor habitat quality (Thomas 1994), and recolonization and immigration can depend on effects of matrix heterogeneity on dispersal (Ricketts 2001). For prey species with patchily distributed predators, local habitat suitability, including predator presence, and landscape connectivity are likely important for predicting occupancy and turnover dynamics.

In predator-prey metapopulations, the patchy occurrence of predators can create strong spatial variation in survival and reproductive success for prey. Persistence of prey in patches with predators can depend on the rescue effect (Brown and Kodric-Brown 1977, Stacey et al. 1997) or sourcesink dynamics (Pulliam 1988) in which immigration from predator-free sources prevents local extinction (Amezcua and Holyoak 2000, Caudill 2003, 2005, Woodford and McIntosh 2010; we follow Stacey et al. 1997 and use the term "rescue effect" as a general form of source-sink dynamics). Thus, the degree to which patches are connected through dispersal is likely to affect predator-prey coexistence. Prey populations in isolated sites should be more susceptible to deterministic extinction by predators than populations in connected sites. Furthermore, the rescue effect may be reinforced or inhibited in complex landscapes depending on how matrix structure facilitates or impedes dispersal (Cronin and Haynes 2004).

Fish predation is an important source of mortality for pond-breeding amphibians in permanent or semi-permanent wetlands (Wellborn et al. 1996), and introduction of nonnative fish is a significant cause of amphibian declines (Kats and Ferrer 2003). Predatory fish consume the eggs and larvae of many pond-breeding amphibians, and fish negatively influence amphibian reproductive behavior, survival, abundance, and species richness (Sexton et al. 1994, Hecnar and M'Closkey 1997, Werner et al. 2007, Pope 2008). Although predatory fish can strongly limit the spatial distribution of amphibians (Pilliod et al. 2010), the rescue hypothesis may explain the persistence of amphibians in wetlands with fish (Sjögren Gulve 1994, Pilliod and Peterson 2001). If dispersal moderates the risk of local extinction at sites with fish, conservation efforts may benefit from a spatial perspective on fish-amphibian interactions.

We collected three years of data on wetland occupancy and spatial turnover for Ambystoma tigrinum tigrinum (eastern tiger salamander, Ambystomatidae) to address the hypothesis that metapopulation dynamics depend on the combined effects of predatory fish occupancy and connectivity. Like many pond-breeding amphibians, A. tigrinum is susceptible to predatory fish and can be excluded from sites occupied by fish (Sexton and Phillips 1986). We investigated how connectivity among breeding populations of A. *tigrinum* interacts with the spatial distribution of predators to influence occupancy, colonization, and extinction probabilities of A. tigrinum. We predicted fish occupancy would have negative effects on occupancy and colonization, and a positive effect on extinction. If immigration counteracts the deterministic effects of predators, then wetland connectivity should have positive effects on occupancy and colonization, and a negative effect on extinction for sites with fish.

Because the distribution and movement patterns of amphibians can depend on matrix heterogeneity (Joly et al. 2001, Stevens et al. 2004, Mazerolle and Desrochers 2005, Rittenhouse and Semlitsch 2006), we also evaluated support for different models of connectivity. Desiccation risk has been identified as an important cost of movement for juvenile dispersers due to their small bodies, permeable skin, and high surface-area-to-volume ratio compared to adults (Spight 1968, Rothermel and Semlitsch 2002). In a field experiment on A. tigrinum conducted in our study area, desiccation rates varied significantly among dominant matrix habitats. Desiccation was greatest in corn and grassland and lowest in forest and soybean (Cosentino et al. 2011). A second field experiment demonstrated salamanders consistently moved into habitats that minimize desiccation risk when given a choice at habitat boundaries (Cosentino et al. 2011). These results indicate desiccation for A. tigrinum varies among matrix habitats, and movement decisions of individuals are influenced by desiccation risk. To evaluate consequences of this physiological constraint at the population-level, we used cost-distance modeling to examine how well a connectivity metric based on habitat-specific desiccation risk explained site occupancy and turnover compared to connectivity metrics representing Euclidean distance and expert opinion.

Methods

Study species and site

Ambystoma tigrinum is mainly subterranean, using mammal burrows and self-excavated burrows in upland forests and grasslands for refuge during most of the year. Breeding migrations occur between late fall and early spring, and adults breed in ponds from February to April. Juveniles emigrate from ponds between July and September and can become sexually mature within two years (Petranka 1998). Consistent with other pond-breeding amphibians (Semlitsch 2008), interpond dispersal for this species is rare for adults but more common for juveniles (Church et al. 2007).

Our study was conducted at a 9300-ha area in northern Illinois centered at the Richardson Wildlife Foundation property (West Brooklyn, IL; 41°42′26.6″ N, 89°11′25.0″ W). The landscape is dominated by row-crop agriculture (corn, soybean) and patches of grassland and forest (Fig. 1). Yearly crop rotation between corn and soybean is common, but corn cover increased while soybean cover declined between 1999 and 2008 (B. J. Cosentino, *unpublished data*). In 2008, cover by corn was 50% and cover by soybean was 21%. Suitable breeding habitat for *A. tigrinum* in this landscape consisted of freshwater wetlands with variable hydroperiods, which represented only 0.8% of the landscape.

We documented the occupancy status of *A. tigrinum* in 90 wetlands (median area = 0.56 ha; range = 0.01–5.29 ha) in 2007, 2008, and 2009. The median nearest-neighbor distance between wetlands sampled in this study was 245 m (range = 36–2830 m). Wetlands were identified using 1:24000 National Wetland Inventory quadrangles and aerial photographs, and all temporary pools (i.e., those that held water only after heavy rains) were excluded from sampling. Wetland emergent vegetation was dominated by *Alisma subcordatum, Eleocharis* spp., *Phalaris arundinacea, Polygonum* spp., *Pontederia cordata, Sagittaria* spp., *Scirpus* spp., and *Typha* spp. Other amphibians encountered during surveys included *Acris crepitans, Anaxyrus americanus, Hyla chrysoscelis, Pseudacris crucifer, Lithobates catesbiana, L. clamitans,* and *L. pipiens.*

Wetland surveys: salamanders and predatory fish

We surveyed each wetland a single time in sampling sessions of 1-4 consecutive days between late May and early August in each year. Sites were surveyed for ≥ 3 consecutive days in 97% of sampling sessions across seasons. Sites were not sampled randomly due to logistical constraints. Instead, wetlands were grouped by spatial proximity, and we randomized the sequence in which we surveyed groups in each year. Collapsible minnow traps $(45.7 \times 30.5 \text{ cm})$ with two 6.4-cm entrances; Promar, Gardena, California, USA) were used to detect the presence or absence of *A. tigrinum* larvae at each wetland. We set 1-13 traps within 10 m of the shoreline, and sampling effort was standardized by wetland area. Traps were checked within 24 hr of deployment.

We documented adult and juvenile fish at each wetland using minnow traps and collapsible hoop traps. The most common fish encountered were yellow bullhead (Ameiurus natalis), green sunfish (Lepomis cyanellus), and bluegill (L. macrochirus). Ameiurus spp. and Lepomis spp. are both documented predators of pond-breeding amphibians (e.g., Sexton and Phillips 1986, Hecnar and M'Closkey 1997, Babbitt et al. 2003). We used occupancy models that account for imperfect detection (MacKenzie et al. 2006) to estimate the probability of fish predators occupying a wetland. The program PRESENCE 3.1 was used to build single-season occupancy models (MacKenzie et al. 2006) to estimate wetland occupancy probability given a site's detection history for fish in each year (Appendix). The conditional occupancy probability (ψ_{fish}) for wetlands in which fish were detected was 1. When fish were not detected, conditional occupancy probabilities were less than one ($0 \le \psi_{\text{fish}} < 1$). Predatory fish occurred in \geq 31% of wetlands each year, and fish occupancy was temporally dynamic (27 observed turnover events).

Wetland area and connectivity

Patch area and connectivity metrics were



Fig. 1. Naïve occupancy pattern of *Ambystoma tigrinum* among 90 wetlands surveyed for three years (2007–2009) in northern Illinois. Wetlands were unoccupied by salamanders in all years (open circles), occupied in one year (closed triangles), occupied in two years (closed squares), or occupied in all three years (closed circles).

measured with ArcMap 9.3 (ESRI, Redlands, California, USA) after digitizing wetlands using aerial photographs from 2007. To measure connectivity of each wetland, we used a metric that includes a negative exponential dispersal kernel and accounts for distances to potential wetlands that function as sources of dispersers (Hanski 1994, Moilanen and Nieminen 2002). The connectivity (C_i) of wetland *i* was defined as

$$C_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij}) \tag{1}$$

where p_j is the probability of occupancy by *A*. *tigrinum* larvae at source wetland *j*, α is a parameter scaling the effect of distance on dispersal (1/ α is the mean dispersal distance), and d_{ij} is the distance between target wetland *i* and source wetland *j*.

Observed colonizations were used to estimate the mean dispersal distance $(1/\alpha)$ for *A. tigrinum* (Prugh 2009). The ability of three connectivity metrics to explain occupancy dynamics was assessed when α was set to represent the mean distance ± 1 SE (550 ± 99 m) between colonized wetlands and the nearest occupied source (451, 550, and 649 m). A metric with $\alpha = 0.0022$ (mean dispersal distance = 451 m) was a better predictor of occupancy patterns than alternative metrics (Cosentino 2011), so we specified α as 0.0022 in subsequent analyses.

We calculated C_i by setting p_j equal to 0 for source wetlands in which *A. tigrinum* was undetected in all three years, 0.33 for source wetlands occupied in one year, 0.67 for source wetlands occupied in two years, and 1 for source wetlands occupied in all three years.

Cost-distance modeling

We used cost-distance modeling to incorporate matrix heterogeneity into our connectivity metric (Adriaensen et al. 2003). To account for variation in dispersal cost among matrix habitats, cost surfaces were created in ArcMap 9.3 by assigning movement resistances to each habitat in the landscape. Then, distances along paths between source and target wetlands that minimize cost were estimated (i.e., effective distances) using PATHMATRIX in ArcView 3.2 (Ray 2005). Finally, effective distances were substituted for Euclidean distances (d_{ij}) in the formula for C_i to generate a connectivity measure that accounted for matrix heterogeneity.

We used USDA Cropland Data Layer Maps to generate cost surfaces ((http://www.nass.usda. gov/research/Cropland/SARS1a.htm)). We collapsed land-cover types into seven categories: corn, soybean, other crop (mainly alfalfa and winter wheat; <1% of landscape), forest, grassland, developed or road, and water. We developed three resistance sets that represented different hypotheses about how the landscape influences movement. In all resistance sets, we assigned the value of 1.0 to water, assuming that wetlands function as stepping stones for dispersal. For set R_{EUC} (Euclidean), resistances were set as 1.0 for each habitat to represent a homogeneous matrix. For set R_{EXP} (Expert Opinion), we assigned resistances to reflect expert opinion for agricultural landscapes in which the common assumption is that all crops impose a uniformly high cost on dispersal (e.g., Compton et al. 2007, Greenwald et al. 2009). Thus, we assigned an equally high resistance value of 500 to all agricultural crops, and forested habitats were assigned a lower resistance value than grassland habitats (Fig. 2; forest = 100, grassland = 200; e.g., Rothermel and Semlitsch 2002). For set R_{DES} (Desiccation), the relative rankings of movement resistances were directly informed by experimental data on A. tigrinum desiccation risk and movement behavior (Cosentino et al. 2011). Soybean and forested areas received equally low resistances of 100, and corn and grassland areas received equally high resistances of 500 (Fig. 2). We assigned a resistance value of 500 to crops other than corn and soybean and a value of 1000 to roads and developed areas in all sets. The three resistance sets were used to generate three measures of connectivity: C_{EUC} , C_{EXP} and C_{DES} . Resistance values for each set are relative values (Adriaensen et al. 2003), and our results were not sensitive to changes in absolute cost values when the relative rankings remained the same (B. J. Cosentino, unpublished data).

Due to temporal variation in crop cover

associated with crop rotations, we created yearspecific cost surfaces for sets R_{EXP} and R_{DES} (Fig. 2). When evaluating the effect of connectivity on demographic parameters, we used connectivity metrics generated from cost surfaces in the year previous to the parameter-year combination being modeled. For example, the 2007 cost surfaces were used to generate connectivity metrics to explain colonization patterns in 2008. That is, we assumed most dispersal contributing to spring colonization occurs during the previous growing season when agricultural crops are on the landscape. However, we note that cost surfaces based on R_{EXP} exhibited minimal yearly variation because corn and soybean were assigned equally high resistance values (Fig. 2). If most dispersal contributing to colonization occurs in spring when agricultural landscapes are barren, R_{EXP} may be a good representation of dispersal cost because amphibians avoid moving in barren areas associated with high desiccation (e.g., Mazerolle and Desrochers 2005).

Data analysis

Data from repeated occupancy surveys within each year were used in a multiple-season occupancy model that accounts for imperfect detection probability (ρ) to assess how metapopulation factors (i.e., area and connectivity) and fish occupancy influenced initial occupancy probability (ψ_{2007}), colonization probability (γ), and extinction probability (ɛ) for A. tigrinum larvae. A repeated survey was defined as a group of minnow traps within a wetland open for one night. We considered using a two-species parameterization to model the co-occurrence of fish and A. tigrinum, but that parameterization was not available in a multiple-season framework (Mac-Kenzie et al. 2006). We conducted all analyses in the program PRESENCE 3.1 using a logit link function to model effects of covariates on amongwetland variation for each rate parameter. Covariates did not exhibit strong multicollinearity (all r < 0.31). Initial analyses were conducted to select a model accounting for variation in p while holding ψ_{2007} , γ , and ε constant. Potential detection covariates included survey day within sampling session (1–4), Julian date (calendar date of the first survey day), and year. We then modeled ψ_{2007} , γ , and ε sequentially, starting with ψ_{2007} and ending with ε . The most supported



Fig. 2. Dispersal cost surfaces for *Ambystoma tigrinum* in a northern Illinois landscape for 2006, 2007, and 2008. Movement resistances were either representative of expert opinion in agricultural landscapes (A–C) or based on empirical data on desiccation risk and movement behavior (D–F).

model for each rate parameter was maintained when modeling the remaining parameters. While we could have considered all combinations of model structures on each parameter in a single candidate set, modeling each parameter separately allowed us to greatly reduce the overall number of models, which minimizes the chance of spurious results (Burnham and Anderson 2002).

The Akaike Information Criterion corrected for small sample size (AIC_C) was used to rank the support of 31 candidate models representing the effect of different combinations of metapopulation factors and fish occupancy on ψ_{2007} , γ , and ε . The candidate set was the same for each rate parameter. The first model constrained the parameter of interest to be equal among sites

(constant). The next three models included the effects of fish occupancy (F) and metapopulation factors (A = area, C = connectivity) individually (F, A, C). The next four models included additive effects of metapopulation factors and fish occupancy (A + C, F + A, F + C, F + A + C). Because the importance of connectivity may vary between sites with and without fish, we then added a fish \times connectivity interaction effect (F \times C) to models that contained fish occupancy and connectivity $(F + C + F \times C, F + A + C + F \times C)$. Finally, we added an area \times connectivity interaction effect (A×C) to models that contained wetland area and connectivity $(A + C + A \times C, F + A + C + A \times C)$ C, $F + A + C + F \times C + A \times C$). Importantly, models including connectivity were constructed separately using each metric: C_{EUC}, C_{EXP}, or C_{DES}.

Akaike weights (w_i) were estimated for each model, and model-averaged point estimates of ψ_{2007} , γ , and ε were calculated for each wetland using all models from candidate sets specific to each rate parameter (Burnham and Anderson 2002). To evaluate the hypothesis that desiccation risk scales up to influence *A. tigrinum* occupancy dynamics, we compared the relative support of C_{EUC}, C_{EXB} and C_{DES} in explaining ψ_{2007} , γ , and ε . Each connectivity metric was in nine models for each candidate set, and Akaike weights were summed across models within each set to evaluate the relative importance of each connectivity metric (Burnham and Anderson 2002).

Results

Ambystoma tigrinum was detected at 29 wetlands (naïve occupancy = 0.32) in 2007, 43 wetlands (0.48) in 2008, and 45 wetlands (0.50) in 2009. Using a constant model of ψ in singleseason occupancy models, yearly occupancy probabilities after accounting for imperfect detection were 0.42 (SE = 0.06) in 2007, 0.55 (SE = 0.06) in 2008, and 0.51 (SE = 0.05) in 2009. Of the 90 sites, 35 sites (38.9%) were never occupied, 12 sites (13.3%) were occupied once, 23 sites (25.6%)were occupied twice, and 20 sites (22.2%) were occupied during all three years (Fig. 1). Turnover was common in both transition periods. Observed local colonizations outnumbered local extinctions between 2007 and 2008 ($N_C = 20$, N_E = 6) and between 2008 and 2009 ($N_C = 9$, $N_E = 7$).

Multiseason occupancy and turnover models

A constant model of ρ indicated the daily detection probability for *A. tigrinum* was generally high ($\rho = 0.82$, SE = 0.02). The most supported model of detection probability in our multiseason models included effects of Julian date in 2007 and 2008, and survey day in 2009 (accounting for three parameters). Specifically, Julian date had a negative effect on detection probability in 2007 and 2008. In 2009, detection was greatest on the second day of each sampling session.

The top model of initial occupancy probability for salamanders included additive effects of fish occupancy, wetland area, and Euclidean connectivity (Table 1). Initial occupancy was related negatively to fish occupancy and positively to wetland area and connectivity (beta estimate ± 1 SE for the top model, F=-1.63 ± 0.43 , A=0.78 ± 0.36 , C_{EUC} = 0.67 ± 0.40). A competing model (Δ AIC_C ≤ 2) included only effects of fish and wetland area (Table 1).

The top model of colonization probability included effects of fish occupancy and connectivity accounting for desiccation risk (C_{DES}; Table 1). In general, colonization probability was greatest in fishless sites and lowest in sites with fish, and colonization increased with connectivity (Fig. 3A–B; beta estimate \pm 1 SE for the top model without interaction effects, $F = -1.30 \pm$ 0.37, $C_{\text{DES}} = 0.76 \pm 0.43$). However, connectivity interacted with both fish occupancy and wetland area (Table 1). Connectivity interacted positively with fish occupancy (beta estimate \pm 1 SE, F \times $C_{\text{DES}} = 3.90 \pm 1.95$) indicating the positive effect of connectivity on colonization was strongest in wetlands with fish. Connectivity interacted negatively with wetland area (beta estimate ± 1 SE, $A \times C_{DES} = -4.14 \pm 1.80$) indicating the positive effect of connectivity on colonization was strongest in small wetlands. Colonization probability also increased with wetland area in fishless sites with low to moderate connectivity (Fig. 3A).

The most supported model of extinction probability included additive effects of fish and connectivity based on Euclidean distance (Table 1). Local extinctions were most common in wetlands with fish and low connectivity (Fig. 4; beta estimate ± 1 SE for the top model, F = 0.80 \pm 0.35, C_{EUC} = -0.84 \pm 0.44). There was marginal support for a positive interaction between fish occupancy and connectivity (Δ AIC_C = 1.04 for model F + C_{EUC} + F × C_{EUC}), suggesting the effect of connectivity on extinction probability was strongest in wetlands with fish.

Cost-distance connectivity metrics: summed Akaike weights

Given model selection uncertainty (Table 1), the summed Akaike weights were the most effective way to assess relative support for the three connectivity metrics. Cost-distance models accounting for matrix heterogeneity (C_{EXP} C_{DES}) did not have more support than Euclidean connectivity (C_{EUC}) for predicting initial occupancy and extinction probabilities (Fig. 5). In contrast, a connectivity metric accounting for

Rate Parameter	Model	ΔAIC_C	ω _i	-2l	Κ
Occupancy ₂₀₀₇	$F + A + C_{FUIC}$	0.00	0.19	634.51	9
1 , 2007	$F + A + C_{DFS}$	0.95	0.12	635.46	9
	$F + A + C_{EXP}$	0.96	0.12	635.47	9
	F + A	1.31	0.10	637.96	8
Colonization _{2008,2009}	$F + C_{DFS} + F \times C_{DFS} + A + A \times C_{DFS}$	0.00	0.45	602.61	14
	$F + C_{FXP} + F \times C_{FXP} + A + A \times C_{FXP}$	0.79	0.30	603.40	14
Extinction _{2008,2009}	$F + C_{FUC}$	0.00	0.10	590.95	16
	$F + C_{FUC} + F \times C_{FUC} + A$	0.18	0.09	586.55	18
	$F + C_{FXP}$	0.21	0.09	591.16	16
	$F + C_{FLIC} + A$	0.64	0.07	589.31	17
	$F + C_{DFS}$	0.77	0.07	591.72	16
	$F + C_{EXP} + A$	0.92	0.06	589.59	17

Table 1. Model selection statistics for initial occupancy, colonization, and extinction probabilities of *Ambystoma tigrinum* from 90 wetlands in northern Illinois.

Notes: Years are indicated as subscripts for each rate parameter. Main effects include fish occupancy probability (F), wetland area (A), Euclidean connectivity (C_{EUC}), expert opinion connectivity (C_{EXP}), and desiccation risk connectivity (C_{DES}). Summary includes relative difference between model AIC_C and AIC_C for the best model (Δ AIC_C), Akaike weights (ω_i), twice the negative log-likelihood (-2l), and number of parameters (K). Effects of Julian date and survey day on detection probability were included in all models (3 parameters). Only models with Δ AIC_C \leq 2 are presented for occupancy and colonization and Δ AIC_C \leq 1 for extinction.

upland desiccation risk was more supported than Euclidean and expert opinion models for predicting colonization probability (Fig. 5).

DISCUSSION

Predatory fish strongly limited the spatial distribution of *A. tigrinum*, which is consistent with previous studies on fish-amphibian interactions (Hecnar and M'Closkey 1997, Pilliod and

Peterson 2001, Pilliod et al. 2010). By explicitly focusing on metapopulation processes, our work illustrates how distributional constraints result from high extinction risk and low colonization success at sites with fish predators. However, these deterministic effects of fish on amphibians were moderated by spatial connectivity in two ways: (1) extinction probability was related negatively to connectivity, suggesting a rescue effect in which immigration prevents local



Fig. 3. Relationships of predicted colonization probability of *Ambystoma tigrinum* to desiccation-informed connectivity and wetland area in sites (A) without and (B) with fish predators.



Fig. 4. Relationship of predicted extinction probability to Euclidean connectivity in sites without (open circles) and with (closed circles) fish predators. For purposes of presentation, sites with fish occupancy probabilities >0.85 were defined as present, and sites with <0.15 were defined as absent.

extinction, and (2) colonization probability was related positively to connectivity at sites with fish, indicating a substantial number of immigrants can overcome fish predation during colonization. Furthermore, we found that desiccation risk for *A. tigrinum* dispersers scales up to influence colonization probability, thereby linking population-level isolation effects to a physiological constraint on dispersal. Overall, these results support the view that predator-prey interactions and resulting patterns of community structure can be mediated by dispersal and landscape context in spatially structured systems (Urban 2004, Richter-Boix et al. 2007).

Fish predators and spatial connectivity

If fish typically have strong deterministic effects on pond-breeding amphibians, what explains the pattern of co-occurrence between *A. tigrinum* and fish predators in highly connected wetlands? One hypothesis is that source-sink dynamics could generate this pattern (Pulliam 1988). In connected networks, persistence of *A. tigrinum* at sites with fish may depend on continual dispersal from nearby sources without fish (e.g., Caudill 2003, 2005). If resources are limited in fishless sites because of large population sizes, intense competition for resources may



Fig. 5. Relative support of cost-distance connectivity metrics based on summed Akaike weights for models of initial occupancy probability, colonization probability, and extinction probability of *Ambystoma tigrinum*. Cost-distance models represented Euclidean distance (white bars), expert opinion (gray bars), and desiccation risk in matrix habitats (black bars).

force some individuals to colonize low-quality sites with fish.

Although source-sink dynamics may be generated by active dispersal and habitat selection (Pulliam 1988), optimal habitat selection is unlikely for A. tigrinum. Adults are generally philopatric to breeding ponds (Church et al. 2007), and ambystomatid juveniles have limited perceptual range (e.g., <50 m; Rothermel 2004) and are not known to exhibit sophisticated searching strategies. In addition, some ambystomatids are unable to detect fish predators using olfaction (Sexton et al. 1994). If A. tigrinum individuals disperse and select habitat randomly (Semlitsch 2008), an expected strategy when the direction of suitable habitat is unpredictable (Hawkes 2009), then colonization probability at sites with fish may be a simple function of the total number of dispersers moving through an area. Connected networks may also generate the rescue effect in which a large number of immigrants reduces the overall chance of local extinction probability (Fig. 4; Brown and Kodric-Brown 1977). If isolated sites receive fewer immigrants than connected sites, isolated sites may be more susceptible to extinction due to the combined effects of fish predation and demographic stochasticity. In contrast, colonization of connected wetlands without fish may be less dependent on high propagule size, which would explain why the effect of connectivity on colonization probability was strongest for sites with fish. Although oviposition by a single female may result in successful colonization in fishless sites (Trenham et al. 2001), a greater breeding effort is likely required in sites with fish predators.

Interestingly, colonization probability was related positively to wetland area when connectivity was low. For ground-dispersing animals, the probability of intercepting a patch increases with the linear size of the patch, and linear size scales positively with patch area (Bowman et al. 2002). Thus, our results suggest a target effect for isolated sites in which larger wetlands function as larger targets for dispersers (Lomolino 1990). However, the effect of area on colonization was substantial only among fishless wetlands (Fig. 3A-B). In isolated sites, the deterministic effects of fish on A. tigrinum may overwhelm the structural effect of large area on colonization, particularly if population size or diversity of fish increases with wetland area. In our study area, some permanent, large wetlands were stocked with large numbers of fish, whereas small wetlands were often colonized naturally by relatively few individuals (B. J. Cosentino, personal observation). In connected networks with a high density of dispersers, a target effect on successful colonization may not occur because the probability of at least one propagule intercepting a patch is not strongly related to patch area. Patch area may be more important for colonization in isolated locations where the density of dispersers is low.

Although persistence of *A. tigrinum* in sites with fish may depend on immigration, sources of emigrants underlying the rescue effect are not likely to be stable over time. During our study, the spatial distribution of fish varied temporally due to local extinctions and colonizations, suggesting that *A. tigrinum* should exhibit strong spatiotemporal variation in recruitment resulting from fish metapopulation dynamics. Spatiotemporal variation in recruitment may also be driven by climate and local hydrology (Church 2008). Precipitation was above average during the last two years of our study, and hydroperiod was not a strong driver of *A. tigrinum* turnover (Cosenti-

no 2011). However, survival and reproductive success of *A. tigrinum* can be low in dry years and in wetlands with short hydroperiods (Church et al. 2007). Thus, breeding populations may shift between functioning as sources and sinks over time (Stacey et al. 1997, Johnson 2004) due to stochastic climatic conditions and fish turnover. Effective conservation in such systems likely requires maintaining an assemblage of wetlands connected via dispersal that vary in hydrology and suitability for predatory fish.

In our system, fish occupancy was related positively to wetland hydroperiod and negatively to both emergent vegetation cover and canopy cover (Appendix). Thus, one possible interpretation is that *A. tigrinum* turnover dynamics can be explained by habitat variables as opposed to fish presence. However, occupancy modeling of fish and habitat variables indicated that hydroperiod, emergent vegetation, and canopy cover were not strong predictors of *A. tigrinum* turnover compared to fish presence (Cosentino 2011). Thus, we are confident that fish predation is a major factor driving *A. tigrinum* colonization and extinction dynamics.

Dispersal costs and landscape connectivity

Our results indicate that the mechanistic basis of dispersal limitation for A. tigrinum likely involves the physiological risk of desiccation. Wetlands separated by matrix habitats with a low risk of desiccation (forest and soybean) were more likely to be colonized than wetlands separated by high-risk habitat (corn and grassland). Although a connectivity model based on expert opinion had competitive support (Table 1), summed Akaike weights across all models indicated that desiccation-informed connectivity had more overall weight for predicting colonization (Fig. 5). Given the limited timeframe of our study and the similarity in most cost values between models C_{DES} and C_{EXP} (Fig. 2), the power to detect strong differences in support between C_{DES} and C_{EXP} was likely low. However, there was little support for a Euclidean model of connectivity (Fig. 5), which indicated that matrix heterogeneity in general had a strong effect on wetland colonization.

Previous cost-distance studies have used model-fitting techniques (e.g., Sutcliffe et al. 2003) and expert opinion to estimate habitat-specific movement resistances. Less frequently, experimental data have been used to inform resistances by assessing movement rates in matrix habitats and movement decisions at habitat boundaries (Schooley and Wiens 2004, Stevens et al. 2004, 2006, Castellón and Sieving 2006, Desrochers et al. 2011). Our study extends this approach by mechanistically linking a physiological constraint on small-scale movement decisions to landscape-scale population dynamics (Lima and Zollner 1996).

In spatially structured systems, population dynamics can be strongly dependent on the ability of animals to disperse among habitat patches (Bowler and Benton 2005). For pondbreeding amphibians, water economy plays an essential role in determining mortality risk and overall resistance to dispersal in matrix habitats. Desiccation can decrease locomotor performance (Preest and Pough 1989), habitat permeability (Rothermel and Semlitsch 2002, Mazerolle and Desrochers 2005), and survival (Rittenhouse et al. 2009) in amphibians. Additionally, habitat choices at forest-clearcut edges are commonly biased towards forest, where desiccation risk is presumed to be low (Chan-McLeod 2003, Rittenhouse and Semlitsch 2006, Cosentino et al. 2011). Taken together, these studies indicate physiology can be a major constraint on dispersal, and our results reveal the consequences of that constraint for wetland colonization and predatory-prey interactions.

Matrix effects on occupancy dynamics

Few empirical studies have assessed how matrix effects vary among occupancy, colonization, and extinction (e.g., Schooley and Branch 2009). The absence of matrix effects on initial occupancy and extinction for A. tigrinum may be related to the dynamic nature of landscape structure in agricultural systems dominated by annual row crops. Matrix habitats in agroecosystems are temporally dynamic due to yearly crop rotations and long-term trends in crop plantings. However, habitat maps in ecological studies generally represent a snapshot of landscape structure. When dispersal costs vary among agricultural crops, snapshot maps may have important limitations. Occupancy and extinction patterns in a given year may reflect long-term stochastic processes, delayed responses to deterministic factors, or immigration patterns over multiple years. Therefore, historical effects of matrix structure on immigration may go undetected by using a snapshot of landscape structure. In contrast, matrix effects on colonization should be easier to detect with snapshot maps if the timing of colonization aligns with the period for which land cover is represented. For pondbreeding amphibians like A. tigrinum, wetland colonizations are likely punctuated events resulting from recent dispersal across matrix habitats (Semlitsch 2008). To account for historical effects in cost-distance modeling, cost surfaces for different years may be merged using GIS methods. However, such an approach is difficult due to uncertainties about the timeframe for ecological processes and the appropriate scheme for weighting resistance values over time.

Conclusion

The introduction of non-native fish predators is a well-documented cause of amphibian declines and local extinction (e.g., Kats and Ferrer 2003, Pilliod et al. 2010). We show that extinction risk may be greatest for amphibians when fish are introduced to isolated sites where the potential for the rescue effect is low. This study also demonstrates how matrix structure may constrain the potential for recolonization after extinction when wetlands are surrounded by habitats with high desiccation risk. Overall, our results underscore the importance of population connectivity and landscape structure for maintaining pond-breeding amphibians in wetland networks with predatory fish. We suggest that a more complete understanding of effects of fish predators on the distribution of amphibians requires a spatial perspective on demography and turnover dynamics.

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APPENDIX

Table A1. Occupancy models for fish predators from 90 wetlands in northern Illinois in 2007, 2008, and 2009.

Year	Model	ΔAIC_C	ω_{i}	-2l	Κ
2007	$L1 + L2 \\ L1 + A$	0.00 7.96	0.97	80.63 88 59	5
2008	L1 + L2 L1 + L2 L1 + A	0.00	0.90	231.80	4
2009	L1 + L2 L1 + S	0.00 4.48	0.78 0.08	266.22 270.70	5 5

Notes: Main effects include wetland area (A), the number of stream inlets/outlets at a wetland (S), and PCA scores for two axes that explained 91.8% of the variation in local habitat characteristics (canopy cover, emergent vegetation cover, and hydroperiod). The first PCA axis (L1) was positively correlated with emergent vegetation and negatively correlated with hydroperiod (factor loadings: canopy = 0.03, emergent vegetation = 0.95, hydroperiod = -0.79). The second axis (L2) was positively correlated with canopy cover and negatively correlated with hydroperiod (factor loadings: canopy = 0.98, emergent vegetation = -0.11, hydroperiod = -0.50). Models are presented with the relative difference between model AIC_C and AIC_C for the best model (Δ AIC_C), Akaike weights (ω_i), twice the negative log-likelihood (-21), and the number of parameters (K). Effects of Julian date on detection probability were included in all models for 2007 and 2009 (accounting for 2 parameters). The average detection probability \pm 1 SE was 0.94 \pm .01 in 2007, 0.82 \pm 0.03 in 2008, and 0.73 ± 0.01 in 2009. The top two models are included for each year. Fish occupancy was related negatively to emergent vegetation and canopy cover and positively to hydroperiod in each year (beta estimates for top models \pm 1 SE: L1₂₀₀₇ = -2.51 \pm 0.59, L2₂₀₀₇ = -3.98 \pm 1.59; L1₂₀₀₈ = -1.11 \pm 0.28, L2₂₀₀₈ = -0.94 \pm 0.38; L1₂₀₀₉ = -1.12 \pm 0.29, L2₂₀₀₉ = -0.84 \pm 0.35).