Indirect connectivity estimates of amphibian breeding wetlands from spatially explicit occupancy models

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Abstract
1. In conservation science, metapopulation models are frequently used to explore the spatial dynamics of organisms, and ultimately guide management decisions for threatened and endangered species. Pond-breeding amphibians are often touted as a classic example of metapopulation structure. However, empirical assessment of this assumption is lacking for many species owing to the prohibitively high costs of movement studies. Our aim was to use spatially explicit occupancy models to evaluate metapopulation dynamics in an endangered amphibian.

2. First, dynamic, spatially explicit occupancy-based metapopulation models were fitted to 8 years of presence–absence data for the endangered reticulated flatwoods salamander, Ambystoma bishopi. Models were constructed to evaluate the spatial distribution of salamanders across the landscape, rate of patch turnover, and connectivity between patches. Second, the same data were analysed adopting an eigenvector mapping approach and spatial correlograms to investigate habitat characteristics associated with occupancy state. The second approach also yields an independent measure of patch connectivity to corroborate findings from the dynamic model.

3. Both models predicted a steep drop-off in connectivity with increasing isolation, and no evidence was found of interactions between wetlands separated by distances greater than 1.5 km. The best predictor of salamander occupancy status was the amount of understorey vegetation in wetland basins.

4. Taken together, the two modelling approaches provide complementary information regarding the key determinants of occupancy in the focal species. Furthermore, several results directly translate to management recommendations. Connectivity between distant sites is low, and thus management units should be demarcated accordingly. Understorey vegetation represents egg-laying habitat and refugia for larvae, and hence should be targeted in future restoration efforts. The methodologies employed in this paper have broad applicability to studies of pond-breeding amphibians, particularly in situations where direct measures of dispersal are unobtainable.
1 | INTRODUCTION

Increasingly, conservation plans are adopting the language of ‘evolutionarily significant units’ and ‘management units’ to replace the traditional ‘species’ and ‘population’ levels of monitoring. This shift in focus has arisen in response to genetic considerations to improve the ability of conservation actions to preserve adaptive potential, evolutionary processes, and natural rates of gene flow among populations (Allendorf & Luikart, 2009). Management units are often demarcated with metapopulation structure in mind (Cronin, 2006; Frankham, Ballou, & Briscoe, 2010), and hence typically consist of discrete habitat patches connected by dispersing individuals, subject to stochastic local extinction and colonization events (Hanski, 1998, 1999). Management units tend to operate on this scale because multiple interconnected populations experiencing source–sink dynamics can greatly enhance the long-term viability of a species as a whole (Hanski, 1998, 1999).

Ephemeral wetlands provide important breeding habitat for many south-eastern US amphibians (Bailey, Holmes, Buhlmann, & Mitchell, 2006; Means, 2006). These breeding wetlands exist in patchworks across the landscape and are often referred to as a classic example of metapopulation structure (Smith & Green, 2005). Metapopulations have been documented for a range of amphibian taxa, characterized by strong site fidelity to natal wetlands with limited movement between patches (Wells, 2007). In addition, ephemeral wetlands within described amphibian metapopulations exhibit highly variable environmental and hydrological conditions across years, making apparent patch-level extinction and inter-patch-level colonization events likely. Many amphibian metapopulation models to date, however, are constructed using detection–non-detection data from larval sampling methodologies (Herrmann, Babbitt, Baber, & Congalton, 2005; Miller et al., 2018; Richter-Boix, Llorente, & Montori, 2007). Inferences concerning rates of patch turnover within metapopulations (colonization–extinction) must be made with caution from occupancy studies that only sample the larval life stage; if the only data available come from dipnet or funnel traps targeting larvae, there is additional uncertainty in the timing and frequency of local extirpations of breeding populations. Even in amphibian studies that use data from breeding individuals (e.g. call surveys, drift fences), it is important to distinguish between reproductive failure in a given year and extinction of the entire breeding population. In studies of amphibian metapopulations, it is unclear how often failed breeding years are conflated with extinction events followed by immediate recolonization. In fact, if the entire metapopulation is considered as the unit of study, failed breeding attempts should be interpreted as a non-detection rather than true extinction. Although management units for pond-breeding amphibians are increasingly couched in metapopulation theory, challenges such as the aforementioned remain, and empirical support of metapopulation dynamics is lacking for most species (Smith & Green, 2005). Amphibians are thought to be especially susceptible to the impacts of fragmentation and climate change (Alford, 2010). Management of these imperilled species would benefit from evaluating connectivity between breeding wetlands, clarifying the role of detection in explaining apparent high rates of turnover, and elucidating the habitat characteristics that determine occupancy.

Ideally, connectivity between wetlands would be measured directly by quantifying movement using radio-telemetry (Ferreras, 2001; Sweeney, Logan, & Hornocker, 2000), mark–recapture techniques (Schtickzelle, Choult, Goffart, Fichefet, & Baguette, 2005; Wahlberg, Klemetti, Selonen, & Hanski, 2002), or through assessments of landscape genetics (gene flow) that provide insight into metapopulation dynamics (Huey, Schmidt, Balcombe, Marshall, & Hughes, 2011; Murphy, Dezzani, Pilliod, & Storfer, 2010; Tero, Aspi, Siikamäki, Jäkäläniemi, & Tuomi, 2003). However, these methods are often expensive, both in terms of equipment cost and time, and may be impractical for many small-bodied species. Spatially explicit occupancy models provide an alternative method to evaluate metapopulation dynamics and define management units at an appropriate scale (Chandler et al., 2015; Howell, Muths, Hossack, Sigafus, & Chandler, 2018; Moilanen, 1999; Sjörgren & Hanski, 2000; Sutherland, Elston, & Lambin, 2014). Rather than providing insight into changes in population size and demographics as permitted by direct assessments of metapopulation dynamics, they use detection–non-detection data collected across time to model patch extinction and colonization rates across time and space as functions of environmental variables of interest (e.g. patch area, shape, isolation; Prugh, Hodges, Sinclair, & Brashares, 2008, Prugh, 2009). They can be used for predicting effects of landscape changes, such as habitat loss or fragmentation, on patch occupancy and metapopulation persistence, and thus are important for the management of data-poor species at risk from human impacts (Howell et al., 2018; McIntire & Fajardo, 2009; Royle & Kery, 2007; Sutherland et al., 2014). However, the small datasets associated with imperilled species often preclude overly complicated models and quickly become overparameterized with the inclusion of multiple environmental covariates. Thus, it may be necessary to conduct several simpler analyses to garner a complete picture of the underlying ecological processes.

The reticulated flatwoods salamander (Ambystoma bishopi, hereafter ‘flatwoods salamanders’; Figure 1) is Federally Endangered (US Fish and Wildlife Service, 2009) and considered vulnerable by the International Union for Conservation of Nature (Pals & Hammerson, 2008) as a result of population decline and range contraction in response to habitat loss and degradation. Flatwoods salamanders inhabit longleaf pine (Pinus palustris) flatwoods and savannas in the south-eastern Coastal Plain in the USA. Adults are fossorial and occupy mesic upland

**KEYWORDS**

Ambystoma bishopi, boosted regression trees, conservation, dispersal, eigenvector mapping, habitat restoration, metapopulation
habitats, but migrate to ephemeral wetlands with well-developed herbaceous ground cover and relatively open forest canopy to breed (Gorman, Bishop, & Haas, 2009; Gorman, Powell, Jones, & Haas, 2014). A dense, standing graminaceous component to the herbaceous vegetation is associated with use by multiple life-stages. Females lay eggs in areas with abundant herbaceous ground cover that includes a structurally complex mix of low-lying forbs and more vertically structured graminoids (Gorman et al., 2014). Larvae are associated with inundated stands of graminoids (Gorman et al., 2009; Sekerak, Tanner, & Palis, 1996), and both metamorphs and adults have been documented climbing on wiregrass (Jones, Hill, Gorman, & Haas, 2012). Because adults deposit eggs in wetland basins in autumn before inundation, and larvae need the ponds to remain inundated until spring so they can develop and metamorphose, the duration of hydroperiod is critical to reproductive success (Chandler et al., 2017). In addition, the depth of the pond has been shown to influence abundance of some invertebrate prey (Chandler, Haas, & Gorman, 2015). The loss and alteration of preferred habitat are often implicated in the decline of populations (Means, Palis, & Baggett, 1996; US Fish and Wildlife Service, 1999). Climate change may also have ramifications for the persistence of flatwoods salamander populations if it leads to shifts in the timing of breeding movements, or if it influences the dispersal capabilities of individuals. Researchers are currently in the process of defining management units and recovery goals for the species, and thus elucidation of the metacommunity structure and dynamics and key drivers of occupancy is of pressing concern.

First, a dynamic, spatially explicit occupancy-based metapopulation model for flatwoods salamanders is described. The ubiquity of metapopulation structure in pond-breeding amphibians has been questioned (Marsh & Trenham, 2001; Smith & Green, 2005); comparatively few studies directly test the assumptions of metapopulation theory (but see Chandler, Muths, et al., 2015; Heard et al., 2015; Tournier, Besnard, Tournier, & Cayuela, 2017), and the literature contains a strong bias towards anurans. Thus, there is a need for more case-specific studies, particularly for underrepresented taxa. The dynamic model presented allows detection probabilities to vary across years and sampling methods, permitting an unbiased assessment of extinction–colonization rates. The dynamic model also produces a threshold connectivity distance beyond which dispersal is unlikely.

Second, to investigate the habitat characteristics that predict flatwoods salamander occupancy, independent analysis of the same data amalgamated across years was conducted using Moran’s eigen-vector mapping techniques (Borcard & Legendre, 2002; Dray, Legendre, & Peres-Neto, 2006). This static approach allows site-specific habitat characteristics to be investigated that could not be included in the dynamic model yet still accounted for residual spatial patterns. Furthermore, the static analysis produces a measure of connectivity between neighbouring patches that can be compared with that from the dynamic model. The legitimacy of inferring dynamic biological processes from static spatial models has been established in recent years through various studies in which biological processes are known a priori (Chapman, Oxford, & Dytham, 2009; Ficetola, Manenti, Bernardi, & Padova-Schioppa, 2012; McIntire & Fajardo, 2009). Together, the dynamic and static models assess the determinants of occupancy in the focal species.

2 | METHODS

2.1 | Study area

The study was conducted on Eglin Air Force Base (Eglin), Okaloosa and Santa Rosa counties, Florida, USA (Figure 2) from 2009 to 2017. Eglin is a large military installation (188,459 ha) primarily consisting of actively managed longleaf-pine-dominated sandhills (approximately 145,000 ha) interspersed with treeless open test ranges, pine plantations, and mesic flatwoods. The landscape is punctuated by ephemeral wetlands consisting of shallow depressions of low topography, which fill in the autumn and typically remain inundated throughout the spring (Chandler, Rypel, Jiao, Haas, & Gorman, 2016).

The study focused on 29 ephemeral wetlands that have been monitored intensively for flatwoods salamander larvae since 2009. The wetlands range in size from 0.1 to 20.9 ha and are characterized by open overstories dominated by longleaf pine, slash pine (Pinus elliottii), and pond cypress (Taxodium ascendens), and midstories dominated by myrtle dahooon (Ilex cassine var. myrtifolia), Chapman’s St. John’s-wort (Hypericum chapmanii), and swamp titi (Cyrilla racemiflora). Ground cover of the study wetlands is dominated by pineland threeawn (Aristida stricta Michx.), flattened pipewort (Eriocaulon compressum Lam.), and blue-stems (Andropogon spp.). Distances between wetlands and their nearest neighbour average 550 m, and range from 100 to 3,900 m.

2.2 | Field surveys

Wetlands were surveyed for salamander larvae using standard dipnet sampling techniques (Bishop, Palis, Enge, Printiss, & Stevenson, 2006; Heyer, Donnelly, McDarmid, Hayek, & Foster, 1994; Wilkinson, 2006; Heyer, Donnelly, McDarmid, Hayek, & Foster, 1994; Wilkinson,
between 2009 and 2017. To account for imperfect detection, at least three surveys were conducted annually, spaced one per calendar month. Surveys were conducted during the months of January until May, and survey effort was standardized to 30 min for each occasion. In addition, night-time spotlighting surveys for larvae were conducted sporadically between 2012 and 2017 when low water levels or sensitive vegetation precluded dipnetting. Spotlight data were included from 13 of the 29 sites for which repeated surveys within a year were conducted. Spotlighting was the only sampling technique used at two sites that had fragile habitat structure.

Site variables historically considered important determinants of occupancy (wetland area, maximum water depth, hydroperiod, and the availability of mixed herbaceous habitat) were recorded or calculated based on field visits (Table 1). Wetland area and availability of mixed herbaceous habitat were recorded or calculated using ArcMAP (v10.5; ESRI, Redlands, CA, USA). Wetland depth and hydroperiod were calculated following Chandler et al. (2017, 2016). Portions of wetlands that were designated as ‘mixed herbaceous habitat’ were areas larger than 1 m² dominated by herbaceous ground cover that included a structurally complex mix of low-lying forbs and more vertically structured graminoids. Portions of wetlands not included as mixed herbaceous habitat were excluded because they did not match characteristics of habitat where egg laying is known to occur (Gorman et al., 2014), including areas with little or no herbaceous ground cover and areas with high canopy cover that would not support graminoids but which still contained a substantial presence of shade-tolerant forbs. Both the total extent of mixed herbaceous habitat and the proportion of the wetland consisting of mixed herbaceous habitat were included in the analyses. For habitat variables, the estimates were either one-time estimates or averaged across years (mean hydroperiod), so annual values could not be included in a dynamic model.

2.3 | Statistical analyses

2.3.1 | Dynamic approach

Although it is possible to model spatiotemporal dynamics across a landscape solely with detection–non-detection records, occurrence data are prone to imperfect detection that can bias parameter estimates (MacKenzie, 2005; MacKenzie & Royle, 2005; Moilanen, 2002; Royle, Kery, Gautier, & Schmid, 2007). To overcome these limitations, models were constructed in a hierarchical Bayesian framework that accounts for imperfect detection (Royle & Kery, 2007; Sutherland et al., 2014).

Dynamic occupancy models were used to investigate spatial and temporal trends in flatwoods salamander populations. The inclusion of colonization and extinction parameters in occupancy models allows occupancy states that are permitted to change over time via colonization and extinction processes, such that occupancy state $z_{it}$ of site $i$ in year $t$ is modelled as

$$z_{it} = (1 - z_{i, t-1})y_{it} + z_{i, t-1}f$$

where $y$ is the site- and year-specific colonization probability, $e$ is the extinction rate, and $z_{i, t-1}$ is the occupancy state of site $i$ in the previous year. Colonization rates are dependent on the occupancy states of neighbouring sites in the previous year. The contribution of each occupied neighbouring site to the

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wetland area (ha)</td>
<td>2.9</td>
<td>4.2</td>
<td>0.1-20.9</td>
</tr>
<tr>
<td>Maximum wetland depth (cm)</td>
<td>35.3</td>
<td>14.8</td>
<td>11.9-72.0</td>
</tr>
<tr>
<td>Area of egg-laying habitat (ha)</td>
<td>0.7</td>
<td>0.9</td>
<td>0.0-4.7</td>
</tr>
<tr>
<td>Proportional area of breeding habitat</td>
<td>0.3</td>
<td>0.4</td>
<td>0.0-1.0</td>
</tr>
<tr>
<td>Average hydroperiod (months)</td>
<td>3.8</td>
<td>1.4</td>
<td>2.0-7.2</td>
</tr>
</tbody>
</table>

FIGURE 2 Map of study location in the Florida Panhandle in the south-eastern USA. Data were collected in Okaloosa and Santa Rosa counties (highlighted in blue) from 29 wetlands situated across Eglin Air Force Base.
overall colonization pressure experienced at site $i$ is calculated based on their respective proximity to site $i$ using a negative exponential weighting function:

$$y_{it} = 1 - \exp\left(-\sum_{j \neq i} z_{ij} e^{-\alpha d_{ij}}\right)$$

where $d_{ij}$ is the distance between sites and $\alpha$ is a scaling parameter relating to average dispersal distance. For a detailed description of model parameterization, see Supporting Information Appendix S1 and Sutherland, Elston, and Lambin (2012) and Sutherland et al. (2014). Occupancy states are assumed to be constant within years but can change via colonization and extinction across years. Detection probabilities were allowed to vary across years and between survey methods. Event-specific covariates were either unavailable (e.g. habitat variables were not remeasured at every sampling event) or resulted in problems with identifiability, and thus were not included in the dynamic occupancy model.

Non-informative priors were placed on occupancy probability in the first year $\Psi_t$ and extinction rates. Detection probabilities were allowed to vary across years $t$ and sampling methods $m$. The connectivity scalar $\alpha$ was assigned a vague uniform prior:

$$\text{logit} \frac{\Psi_t}{1-\Psi_t} \sim \text{Uniform}(0, 10)$$
$$\log(\epsilon_t) \sim \text{Uniform}(0, 10)$$
$$\log(\epsilon_{t,m}) \sim \text{Uniform}(0, 10)$$
$$\alpha \sim \text{Uniform}(0, 1)$$

Model fitting was implemented in WinBUGS using the R package R2WinBUGS (R Core Team, 2015; Spiegelhalter, Thomas, Best, & Lunn, 2004). Three chains of Markov chain Monte Carlo samples were generated from the posterior distributions of the model parameters, each of length 50,000 with the first 1,000 values being discarded as burn-in. To minimize autocorrelation, only every 100th sample was drawn for posterior summaries. Convergence of chains was assessed via inspection of trace plots and calculation of Gelman–Rubin statistics (all potential scale-reduction factors <1.1). All reported parameter estimates are posterior means with 95% Bayesian credible intervals (CIs).

### 2.3.2 Static approach

An additional spatial analysis was performed to investigate the influence of landscape variables on site occupancy of flatwoods salamanders. As in the dynamic model, the static model also considered proximity to neighbouring occupied wetlands in determining a given site’s occupancy status. A Moran’s eigenvector mapping approach (Dray et al., 2006) was used to generate eigenvectors that act as explanatory variables to account for spatial autocorrelation. Eigenvectors were computed with principal coordinates of neighbour matrices using the ‘codep’ package in R (Guénard, Legendre, Boisclair, & Bilodeau, 2010; R Core Team, 2015). The weighting function was defined as

$$a_{ij} = 1 - \left(\frac{d_{ij}}{d_{\max}}\right)$$

where $d_{ij}$ is the Euclidian distance between sites $i$ and $j$, and $d_{\max}$ is the furthest distance between any two sites.

In this analysis, only eigenvectors associated with positive and significant eigenvalues were considered, as they always represent significant spatial patterns and are readily interpretable (Borcard, Gillet, & Legendre, 2011; Franklin & Miller, 2009). Owing to the lack of normality, positive eigenvalues were tested for significance through a randomized permutation approach. Eigenvalues associated with eigenvectors are equivalent to Moran’s $I$ coefficients, and can be used as a measure of spatial autocorrelation (Borcard & Legendre, 2002; Dray et al., 2006).

Taking both landscape variables and spatial eigenvectors, boosted regression trees (BRTs) were used to investigate the relationships between explanatory variables and occupancy states. BRTs are a machine-learning tool that combines regression trees with boosting to discern patterns between regressors and the response (Elith, Leathwick, & Hastie, 2008). Multiple combinations of tree complexity and learning rate were fitted to check the sensitivity of results to model conditions. Inspection of cross-validated correlation coefficients was made to optimize model parameters.

Analyses were conducted using the gbm.step function from the dismo package (Hijmans, Phillips, Leathwick, & Elith, 2017). Variance partitioning and partial dependence plots were generated to elucidate the relative contributions of environmental and purely spatial components (Ficetola et al., 2012).

Lastly, correlograms were constructed, iterated over multiple distance classes, to produce a second estimate of connectivity among sites that can be compared with the one obtained from the dynamic model (Dale & Fortin, 2002). Thus, the dynamic and static approaches produce independent estimates of the maximum distance threshold for connectivity, while providing complementary information regarding the exogenous and endogenous factors in determining site occupancy.

### 3 RESULTS

#### 3.1 Dynamic approach

Detection probabilities of flatwoods salamanders using dipnet methods differed drastically across years, ranging from 0.88 (CI 0.72–0.98) in the fifth year of the study to 0.01 (CI 0.00–0.08) in year 4 (Figure 3). Estimates from the dynamic model indicate that in the year with the highest detection probabilities over the duration of the study, only two or three sampling occasions within a season were required to determine a site’s occupancy status at the 95% confidence level (Figure 3). Conversely, in years with low detection, determining occupancy status with any degree of confidence was practically impossible. Detection probabilities of spotting surveys also differed across years, ranging from 0.96 (CI 0.80–0.99) in the seventh year of the study to 0.62 (CI 0.26–0.93) in year 4. Detection probabilities via spotlighting were higher than those from dipnetting in all years available for pairwise comparisons (years 4–8), and two or three sampling occasions was always sufficient to determine a site’s occupancy status at the 95% confidence level with this method.
Of the 29 wetlands surveyed, the model estimated 10 to be occupied by flatwoods salamanders on at least one sampling occasion between 2009 and 2017. The number of sites estimated to be occupied remained fairly constant across years (range: 6–10 sites). Estimated occupancy states exceeded naive occupancy in six of eight years, with the maximum discrepancy occurring in 2012 when only one detection was made despite eight sites being occupied. In the remaining two years, naive occupancy and estimated states were equivalent.

Overall levels of colonization were low across the study system, but colonization probabilities differed greatly between sites (mean 0.15, CI 0.01–0.78). Colonization was influenced by distance from the nearest occupied wetland; colonization probability decreased sharply with increasing isolation, becoming negligible at distances >1.5 km (Figure 4). Colonization pressure, often taken as a proxy for average dispersal distance (Sutherland et al., 2012), was \( \log(2)/\alpha = 232 \text{ m} \) (CI: 183–288 m). Extinction rates were low across all sites (mean 0.08, CI 0.01–0.37). Despite this, extinction rate exceeded colonization rate (i.e. negative turnover) at 19 of the 29 sites for the entire duration of the study.

### 3.2 Static approach

Correlograms constructed with distance classes greater than 1.3 km showed no signs of spatial autocorrelation, suggesting a maximum dispersal kernel of 1.3 km. Correlograms exhibited positive spatial autocorrelation over short distances, indicative of connectivity between closely neighbouring sites. In addition, Moran’s eigenvector mapping analysis suggested a high degree of spatial autocorrelation
in site occupancy. Two positive eigenvectors were identified, both of which provided evidence for purely spatial determinants of salamander occupancy (first eigenvector: Moran’s I = 0.98, P < 0.001; second eigenvector, Moran’s I = 0.37, P < 0.001).

Model performance from the BRT analysis tended to increase with decreasing tree complexity and decreasing learning rate. The results were qualitatively similar across parameterizations. Those reported here are for a learning rate of 0.001, and tree complexity of 2. The model that included all landscape variables and both positive spatial eigenvectors explained 58% of the variation in occupancy states across the study system. The total area of understorey vegetation suitable for egg deposition was the only significant environmental predictor of site occupancy, accounting for 52% of the total variable importance. Partial dependence plots showed that sites with less than 0.2 ha (n = 9) of available breeding habitat in the wetland basin were never occupied by flatwoods salamanders. Somewhat surprisingly, hydroperiod, wetland area, and depth, all previously identified as important for flatwoods salamander breeding wetlands, were not good predictors of species’ occupancy (<3% combined). The first positive spatial eigenvector accounted for 44% of the variable importance.

4 DISCUSSION

Our results demonstrate that metapopulation dynamics of pond-breeding amphibians can be elucidated with indirect methods in a spatially explicit occupancy framework. Both site-specific covariates and spatial configuration helped to explain flatwoods salamander occupancy probabilities. The dynamic model showed that apparent colonization and extinction events occurred across the patchwork of breeding wetlands, with colonization probabilities decreasing with increasing isolation. The static approach yielded estimates of connectivity that were very similar to the dynamic model and provided additional insight into the non-spatial determinants of occupancy. Taken together, the two approaches lend mutual support to the maximum distance between connected sites and provide complementary information regarding the exogenous and endogenous drivers of the distribution of flatwoods salamanders across Eglin.

The interannual variability of detection probabilities in the study system indicate that some suggested monitoring programmes for flatwoods salamanders (e.g. sampling on two occasions per year as recommended by Bishop et al., 2006) are inadequate to discern the occupancy status of breeding wetlands in some years. These were years when ponds did not hold water, so presumably the inability to detect breeding would be obvious to observers. Imperfect detection is a salient problem in ecology, and accounting for false absences has become a ubiquitous feature in methodological papers (Ficetola, 2015; MacKenzie et al., 2002; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Despite this, the majority of ecological studies still fail to account for non-detection error (Kellner & Swihart, 2014), and in pond-breeding amphibians this is likely to result in overestimated rates of turnover.

Extinction probabilities are often the most difficult parameters to estimate (MacKenzie et al., 2006). For species that breed in ephemeral wetlands, it is common for complete recruitment failure to occur in dry years. Because dipnetting and spotlighting techniques only sample larvae, dry years generate zeros in datasets that can be misinterpreted as an extinction followed by immediate recolonization. It is more accurate, however, to treat such circumstances as problems with detection (Almeida-Gomes, Rocha, & Vieira, 2016; Goméz-Rodríguez, Bustamante, Díaz-Paniagua, & Guisan, 2012); it is not until after the entire adult population dies off, typically after several years of successive recruitment failure, that a ‘true’ extinction event occurs. Without data on breeding individuals or additional information concerning the environmental correlates of successful breeding, it is impossible to discern between real and pseudo-extinction events. This is a prominent concern for researchers of pond-breeding amphibians that needs addressing. Similar to previous work (Jenkins, McGarigal, & Gamble, 2002), spotlighting surveys achieved higher detection than dipnetting. Spotlighting also showed less interannual variability in detection probabilities, and thus would reduce the likelihood of mischaracterizing wetland dynamics. To improve detection probabilities and inference of population turnover for flatwoods salamanders, we recommend either to use spotlighting rather than dipnetting or to conduct at least three or four dipnetting samples per season rather than only the two recommended by Bishop et al. (2006).

This study provides valuable information to inform current management practices and future conservation of flatwoods salamanders. The connectivity estimates derived here define the boundary conditions for a single metapopulation, and they can be used by managers to define appropriate management units and biologically meaningful recovery goals. By explicitly modelling colonization, the need to rely on anecdotal reports or published values that often suffer from small sample sizes is eliminated (Risk, de Valpine, & Beissinger, 2011; Sutherland et al., 2012). The maximum dispersal distance previously cited for the species appears high (1,700 m; Ashton, 1992). The results yielded a threshold isolation distance ~1.5 km, with the approximate average dispersal distance being considerably lower at ~230 m. In concordance, concurrent genetic and drift fence studies suggest that inter-pond movements beyond 1 km are extremely rare (Wendt, 2017). Furthermore, these results are more consistent with observed dispersal distances for other species in the genus Ambystoma (40–380 m; Scott, Komoroski, Croshaw, & Dixon, 2013). When defining management units and identifying clusters of wetlands that operate as metapopulations, managers should err on the side of caution. The dispersal model in pond-breeding amphibians is probably of the stepping-stone kind, with many individuals over multiple generations involved in the transfer of genes over estimated maximum dispersal distances (Semlitsch, 2000). Thus, for an expeditious recovery of flatwoods salamanders, wetlands with multiple neighbouring sites well within the maximum dispersal threshold of 1.5 km should be favoured (Semlitsch, 2000).

This study reveals a promising avenue for habitat restoration efforts. Priority should be given to recovery of the understorey plant communities that represent larval habitat and egg-laying sites.
Although the artificial extension of hydroperiod is likely to prevent the stochastic loss of populations through recruitment failure, if extirpated sites are to be successfully recolonized, either naturally or through reintroduction efforts, restoration efforts should focus on the herba-
ceous and graminaceous vegetation that the species depends on for key life stages (Bishop & Haas, 2005; Gorman et al., 2009, 2014; Gorman, Haas, & Himes, 2013; Sekerak et al., 1996).

The failure of hydroperiod to predict flatwoods salamander occu-
pancy is somewhat surprising. Previous research of amphibians breeding
in ephemeral pools has identified hydroperiod as a key determinant of site occupancy status (e.g. Johnson, 2015; Walls, Barichivich, & Brown, 2013). This may have resulted from the compar-
tively narrow range of hydroperiods contained within the data (Table 1). All sites in this analysis had been selected as candidate wet-
lands based on previous knowledge of flatwoods salamander ecology, and thus extremes of hydroperiod were excluded.

The methods used in this research have broad applicability to stud-
ies of pond-breeding organisms that lack the data to quantify meta-
population dynamics directly. They may be used to help plan creation of artificial ponds for species of conservation concern or to
assess the success of wetland restoration activities (Frisch, Cottenie, Badosa, & Green, 2012; Hamer et al., 2016; Stevens & Baguette, 2008; Thiere et al., 2009). Detection–non-detection datasets typically
cover a longer time span than either radio-telemetry studies or genetic
analyses. Estimating connectivity from long-term data has the benefit
of capturing temporal as well as spatial dynamics—an important con-
ideration if connectivity is thought to have changed over time in
response to habitat loss or fragmentation. Even for species that lack
long-term data, the eigenvector mapping approach may provide suffi-
cient information on spatial patterns to inform management decisions.
Benefits would be gained from future work that evaluated the sensi-
tivity of parameter estimates from both approaches to sample size
and study duration.

Metapopulation theory posits that increasing isolation results in an
increase in the probability of local extinction through reduced coloni-
ization rates (i.e. rescue effects), particularly for small populations
(Hanski, 1999). In addition, the extinction risk posed to isolated popu-
lations is dependent on the species’ life history. Species that are greg-
arious, or depend on unpredictable resources, or display strong site
fidelity are all predicted to exhibit a heightened sensitivity to habitat
fragmentation (Lawes, Mealin, & Piper, 2000). Worryingly, many pond-breeding amphibians, flatwoods salamanders included, possess
all of these traits, and thus are predisposed to the detrimental impacts
of an increasingly fragmented landscape (Wells, 2007). By combining
multiple analytical approaches, a better understanding of the dynamics
of amphibian populations across wetland mosaics and the abiotic
factors that shape their distributions is garnered. This, in turn, will combat
the often untested assumptions made regarding metapopulation structure in amphibian studies, shed light on the differences between
taxonomic groups, and ultimately lead to informed conservation
action.

For amphibian conservation to be effective, its focus must shift
from the single pond to that of the metapopulation (Pittman, Osbourn,
& Semlitsch, 2014; Semlitsch, 2000). This changing perspective from
the site to the landscape scale is important in the face of continuing
land-use conversion and future climate change predictions. Not only
will this refocusing increase population persistence into the future,
but it will also reduce the amount of effort expended on sites that lack
either long-term viability or biological significance. By using this land-
scape approach, managers can more effectively prioritize habitat res-
toration in areas that will also increase metapopulations, facilitate
improved movement among local sites, and potentially aid in identifying
areas on which to focus population management (Bulman et al.,
2007; O’Donnell et al., 2017). Moreover, this approach is timely,
because recovery planning is underway, and having a rigorous recov-
ery plan in place is necessary to move towards species recovery (Walls
et al., 2017).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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