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Fire Ecology

ORIGINAL RESEARCH

Prescribed fire promotes colonization by the Florida bog frog

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Abstract

Background Understanding the link between prescribed fire and occupancy dynamics can aid in managing at-risk species. Knowledge of how fire return interval influences rates of colonization and persistence is essential to effectively mitigate extinction risk, particularly for species endemic to fire-maintained habitats with restricted geographic ranges. The current geographic range of the Florida bog frog (*Rana okaloosae*, hereafter bog frog) is largely restricted to one military installation in the Florida panhandle. The bog frog is currently listed as a state species of special concern owing to its inherent rarity and habitat loss across its limited range. We conducted call surveys for bog frogs at 151 stream-associated sites on Eglin Air Force Base from 2006 to 2022 to map their distribution and evaluate the effectiveness of habitat management. We constructed a spatially explicit, dynamic occupancy model to identify habitat characteristics associated with bog frog presence and quantify the effect of prescribed fire on turnover dynamics.

Results Historical fire return interval was the only predictor of initial site occupancy; sites that burnt every 2 years on average from 1985 to 2005 were twice as likely to be occupied in 2006 as sites that burnt once every 10 years in that time period. Additionally, we found that colonization rates were a function of proximity to neighboring sites and burn frequency. Most dispersal events occurred between sites less than 0.33 km apart and unoccupied sites more than 2 km from their nearest neighbors were never colonized. Colonization rates were higher at sites that had seen an increase in burn frequency during the study period compared to the preceding two decades.

Conclusions The bog frog benefits from frequent fire in its native stream habitat. Conservation activities should focus on protecting high-quality sites and targeted burns to restore fire-suppressed sites near occupied sites. More broadly, our study highlights the value of long-term monitoring to ensure management activities for at-risk species match the scale of dynamic biological processes.

Keywords Burn frequency, Detection, Habitat management, *Rana okaloosae*, Metapopulation dynamics, Occupancy analysis, Prescribed fire

Resumen

Antecedentes Conocer la(s) interacción(es) entre las quemas prescriptas y la dinámica de la ocupación del terreno puede ayudar a manejar especies en riesgo. El conocimiento sobre cómo el intervalo de retorno del fuego influencia las tasas de colonización y persistencia, es esencial para mitigar el riesgo de extinción, especialmente para aquellas especies endémicas de hábitats mantenidos por el fuego, y con rangos de dispersión geográfica restringidos. El rango de ocupación geográfica actual de la rana de *okaloose* (*Rana okaloosae*), está casi totalmente restringido a una

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instalación militar en el Panhandle de Florida. Esta rana está listada como una especie de especial consideración en el estado de Florida debido a su inherente rareza y la pérdida de hábitat en su limitado rango de ocupación territorial. Condujimos relevamientos para determinar las ranas de *okaloose* ubicadas en sitios asociados a arroyos en la base aérea de Eglin desde 2006 y hasta 2022, mapear su distribución y evaluar la efectividad del manejo de su hábitat. Construimos un modelo espacial explícito y dinámico de ocupación para identificar características de hábitats asociados con la presencia de ranas de *okaloose* y cuantificar los efectos de las quemas prescriptas en la dinámica de su recambio.

Resultados El intervalo de retorno histórico del fuego fue el único predictor de la ocupación inicial del sitio; sitios que fueron objeto de quemas prescriptas cada año en promedio desde 1985 hasta 2005 fueron dos veces más probable que fuesen ocupados en 2006, que sitios que fueron quemados una vez cada diez años en ese período de tiempo. Adicionalmente, encontramos que las tasas de colonización fue en función de de la proximidad de sitios vecinos y la frecuencia de quema. Los eventos más dispersos ocurrieron entre sitios a menos de 0,33 km entre ellos, y los sitios no ocupados a más de 2 km de los vecinos más cercanos nunca fueron colonizados. Las tasas de colonización fueron mayores en los sitios en los que hubo incrementos en la frecuencia de las quemas durante el período de estudio comparado con las dos décadas precedentes.

Conclusiones Las ranas de *okaloose* se benefician con fuegos frecuentes en su hábitat nativo cercano a arroyos. Las actividades de conservación deberían enfocarse en proteger sitios de alta calidad, con quemas orientadas a restaurar los sitios en los que el fuego fue suprimido en cercanía de sitios ocupados por esa rana. De manera más amplia, nuestro estudio subraya el valor del monitoreo a largo plazo para asegurar que actividades de manejo para especies en riesgo alcancen la escala de procesos biológicos dinámicos.

Background

Understanding the interplay between occupancy dynamics and landscape attributes is crucial for effective conservation and management strategies aimed at maintaining population viability in the face of environmental change (Kéry et al. 2013; Chandler et al. 2015). Knowledge of patch dynamics is necessary for species that depend on habitat maintained by drivers such as fire or grazing (Askins et al. 2007). In the longleaf pine ecosystem, changes to historical fire regimes have altered these dynamics resulting in changes to plant populations and declines in endemic wildlife species (e.g., Palik et al. 2002; Brockway et al. 2005; Winiarski et al. 2017; Mugnani et al. 2019). Although there is recognition of the importance of fire regime and patch dynamics to bird and butterfly populations (Fuhlendorf et al. 2006; Cayton et al. 2023), the role of fire-maintained habitat patches for amphibian populations using riparian areas needs further exploration (Pilliod et al. 2003, dos Anjos et al. 2021).

Patch persistence and dispersal capabilities determine metapopulation dynamics (Amarasekare and Possingham 2001). Dispersal plays a fundamental role in determining the colonization potential of species across habitat patches, influencing both local population size and overall range size (Lester et al. 2007; Alzate and Onstein 2022). Species with greater dispersal abilities are more likely to colonize new patches, facilitating population expansion and connectivity among fragmented habitats (Hanski 1994; Amarasekare and Possingham 2001; Alzate and Onstein 2022). However, the success of dispersal in sustaining populations also hinges on the availability of suitable, unoccupied patches (Amarasekare and Possingham 2001). If the number of suitable patches is reduced, it could jeopardize metapopulation dynamics and overall species persistence (Hanski 1994).

Dynamic occupancy modeling provides a robust framework for assessing a species' presence and distribution across changing landscapes (Kéry et al. 2013; Miller and Grant 2015). By integrating field data with statistical models, researchers can estimate the colonization and extinction dynamics that generate spatial patterns of occupancy (MacKenzie et al. 2003; Kéry et al. 2013). The number of occupied sites can be considered a measure of current status for a species in relation to the overall distribution of populations (Johnson 1998; MacKenzie et al. 2006; Miller and Grant 2015). Discerning changes in occupancy over time is particularly important for microendemic species with restricted ranges, because a reduction in the number of occupied sites will have a strong bearing on the risk of range-wide extinction (Johnson 1998; Harris and Pimm 2008; Newsome et al. 2020). Moreover, occupancy models help to identify key habitat features and management actions influencing species dynamics, facilitating informed decision-making in conservation planning and resource management efforts (Kéry et al. 2013; Chandler et al. 2015).

Prescribed fire is a common management tool used to maintain habitat quality and biodiversity in various ecosystems (Fernandes et al. 2013; Ryan et al. 2013; Hiers et al. 2020). Through controlled applications, the goal of prescribed fire is to mimic natural fire regimes, promoting ecosystem processes such as nutrient cycling, seed germination, and vegetation rejuvenation. By reducing fuel loads and controlling nuisance species, prescribed fire helps create and maintain diverse habitat structures, benefiting a wide array of plant and animal species (Darracq et al. 2016; Saab et al. 2022; Brooks et al. 2023). Moreover, prescribed fire plays a crucial role in ecosystem restoration efforts, particularly in fire-adapted ecosystems where fire suppression has led to vegetation encroachment and habitat degradation (Brooks et al. 2023).

Prescribed fire carries both potential benefits and risks for amphibians and their habitats. When applied judiciously, prescribed fire can create and maintain suitable habitat conditions for amphibians by promoting vegetation diversity, enhancing breeding sites, and reducing habitat encroachment by woody vegetation (Pilliod et al. 2003; Schurbon and Fauth 2003; Gorman et al. 2013; Brooks et al. 2023). In fire-prone ecosystems, periodic burning can mimic natural disturbance regimes, fostering ecological processes that support amphibian populations, such as nutrient cycling and habitat heterogeneity (Schurbon and Fauth 2003; Hossack and Corn 2007). However, the effects of prescribed fire on amphibians can vary depending on factors such as fire intensity, burn frequency, and habitat characteristics (Darracq et al. 2016; Lindsay et al. 2023). High-intensity fires may pose direct threats to some amphibians, including habitat destruction, mortality, and increased predation risk (Schurbon and Fauth 2004, Rochester et al. 2010, Flores et al. 2011, Hossack and Pilliod 2011; but see Means et al. 2004). In the context of amphibian metapopulations, fire may restore patch connectivity and promote the natural recolonization of extirpated sites or render certain sites unsuitable and increase patch extinction rates. Developing a better understanding of how fire impacts amphibian occupancy dynamics is important for effectively managing at-risk species.

The Florida bog frog (*Rana okaloosae*, hereafter bog frog) is in the species group *Rana catesbeiana* (Anura: Ranidae; Austin et al. 2003) and endemic to northwestern Florida with most of the species' range occurring within the boundaries of Eglin Air Force Base. The species was discovered and described in 1982 (Moler 1985), and many aspects of its natural history and ecology remain unknown (Jackson 2004; Florida Fish and Wildlife Conservation Commission 2013). Oviposition sites typically comprise slow-moving, shallow water patches with relatively open canopy and dense herbaceous vegetation (Gorman and Haas 2011; Florida Fish and Wildlife Conservation Commission 2013), like those of another stream-breeding anuran, mountain yellow-legged frog (*Rana boylii*; Kupferberg 1996, Lind et al. 2016). Stream characteristics related to sediment deposition are integral to the formation of egg-laying habitat, and regular burns are necessary to maintain the appropriate vegetation composition at breeding sites. The bog frog is listed as threatened within the state (Florida Fish and Wildlife Conservation Commission 2022) owing to its inherent rarity and habitat loss due to inadequate fire maintenance. Prescribed fire is a management practice currently being used by land management agencies in the southeastern United States as part of a long-running effort to restore the longleaf pine ecosystem (Lewis and Harshbarger 1976; Schurbon and Fauth 2003; Brockway et al. 2005; Darracq et al. 2016). The predominant management activity on Eglin Air Force Base is prescribed fire but has, until recently, been concentrated in upland areas to support forest health and red-cockaded woodpecker (*Picoides borealis*) populations. The impact of this burn regime on non-target species in lowland habitats has yet to be evaluated.

Despite being relatively coarse scale, this study is an example of using available data sets to address important questions about amphibian response to fire. Records of fire history are available on Eglin within burn blocks of approximately 500 ha in size. We paired this data with data we collected from roadside call surveys. Specifically, we used 17 years of call surveys for the bog frog to document long-term population trends and the impact of prescribed fire on occupancy dynamics across space and time on Eglin Air Force Base. We constructed dynamic occupancy models to (1) describe the distribution of the bog frog across Eglin Air Force Base, (2) identify habitat characteristics associated with the probability of a site being occupied, (3) estimate rates of population turnover for the 17-year study period, and (4) test for a link between habitat management and turnover dynamics. Specifically, we were interested in whether prescribed fire had facilitated the colonization of historically fire-suppressed sites. We discuss our findings in the context of viable bog frog metapopulations and more broadly as they relate to longleaf pine restoration.

Methods

Study area

The study area was located at Eglin Air Force Base (Eglin) in the counties of Okaloosa, Santa Rosa, and Walton in northwestern Florida. Eglin is a large military installation (187,375 ha) that plays an integral role in the nation's defense because it is a base that develops and tests weapons (Hardesty and Kindell 1997). However, Eglin is also one of the most biologically diverse Air Force bases in the nation (Hardesty and Kindell 1997). Eglin is situated in the Coastal Plain physiographic province and, overall, the topography of the study area has little relief. However, there are numerous steep ravines associated with headwater streams (i.e., steepheads) where slopes can be > 30% (Means 1975). Riparian areas were dominated by black titi (*Cliftonia monophylla*), sweetbay magnolia (*Magnolia virginiana*), white cedar (*Chamaecyparis thyoides*), swamp titi (*Cyrilla raceformia*), and blackgum (*Nyssa sylvatica*). Beyond the riparian areas, the study area was dominated by a longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) sandhill community.

Data collection

We conducted call surveys to document presence/absence of bog frogs at 151 sites on Eglin Air Force Base from 2006 to 2022 (Fig. 1; Scott and Woodward 1994). These surveys were part of a more extensive survey effort across the base that was scaled back in 2009. Survey points for the long-term monitoring program were established using the following criteria: Points were readily accessible by car or required no more than a 5-min walk from the car. Points were located on all stream drainages with known occurrences and originally on drainages in intervening areas. We established survey points at locations where roads crossed streams or came close to likely habitat patches. Because bog frog calls can be detected confidently at distances up to 50–100 m (Gorman 2009), the point locations do not themselves reflect bog frog habitat. But, if bog frogs are detected, we know that they are occupying habitat within a 125 m buffer width (see *Environmental covariates*). This approach did not exhaustively survey all potential breeding locations. From walking transects (Gorman 2009), we know that there are sometimes occupied sections of drainages that are too far from the road to be heard. Based on recommendations by Bishop (2004), surveys were conducted primarily from May to July on nights without rain. Each site was surveyed three times a year, typically once in May, once in June, and once in July, but always separated by at least 2–3 weeks. Surveys started 0.5 h after sunset and ended before 2 am. Surveys were standardized to 5 min and observers recorded air temperature, relative humidity, sky condition (i.e., cloudiness), and wind speed. Because not all sites were sampled every year, we filtered the road surveys to include only those that had been continuously surveyed and for which environmental covariates could be extracted, resulting in the 151 focal sites (Fig. 1).

Environmental covariates

To assess the influence of vegetation structure and landscape metrics on the probability of occupancy, we extracted land cover types from the Florida Natural Areas Inventory (FNAI 2010). Using GIS, we created a 125 m buffer surrounding each survey location and quantified the proportion of various habitat types within each buffer. Specifically, we calculated the proportion of

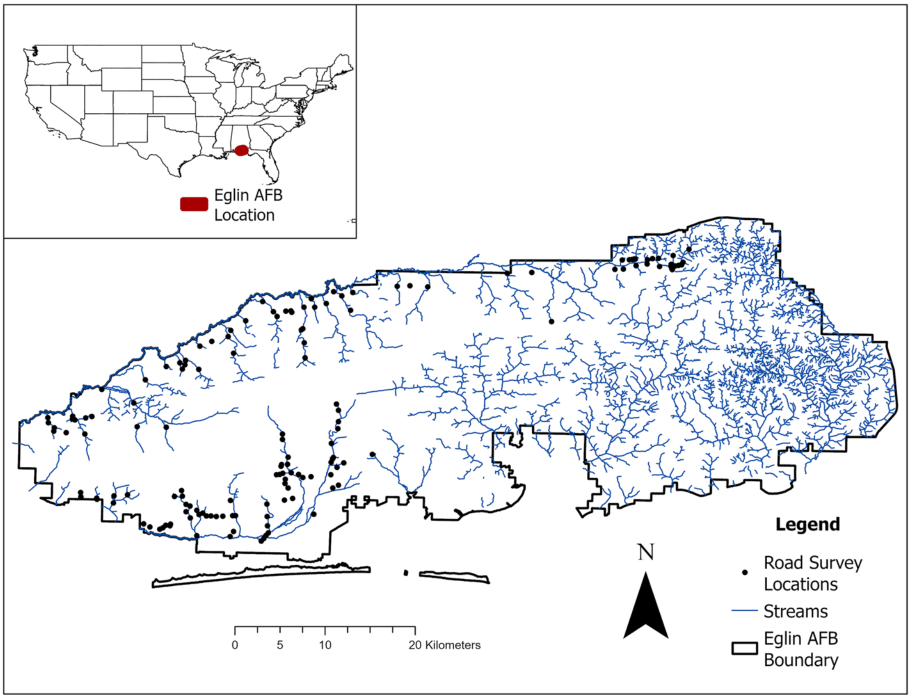

Fig. 1 Map depicting the study area in northwest Florida and the 151 survey locations (black points) monitored from 2006 to 2022

upland habitat (which includes sandhill, hardwood forest, and pine production), wetland habitat (which includes mixed forest wetlands, floodplain swamps, dome swamps, wet prairies, and seepage slopes), and flatwoods habitat (including mesic, wet, and scrubby flatwoods) occurring within each 125 m buffer. We chose 125 m because this was approximately the maximum known distance moved by an individual bog frog (Gorman et al. 2009). Because these three metrics are proportions of a defined habitat area, they will inherently covary. However, all pairwise correlations had $r < 0.7$, and we felt comfortable including all three predictors in the same model (Dormann et al. 2013).

Additionally, we included stream sinuosity as a predictor of bog frog occupancy. Stream sinuosity is a measure of variability in fluvial geomorphology (Braun et al. 2012; Allan et al. 2021). As stream sinuosity increases, the sediment erosion and deposition process results in greater habitat heterogeneity, creating multiple patches of varying flow/depth regimes suitable for egg deposition (Braun et al. 2012; Allan et al. 2021). Greater stream habitat heterogeneity is associated with a higher biodiversity of macroinvertebrates (Baattrup-Pedersen et al. 2018; Karna et al. 2018), potentially increasing an available food source as aquatic invertebrate larvae metamorphose into adult stages. While a higher biodiversity score may not necessarily equate to higher abundances, increased species richness will raise the probability of adult insect emergence occurring across several months, potentially serving as a consistent food source for the extended breeding season of bog frogs (Moler 1992). We calculated sinuosity of the streams within each buffer by dividing the total length of the stream by the straight-line distance between the farthest points within the buffer (which never exceeded 250 m, the diameter of the buffer).

Lastly, we calculated the fire return interval for the burn block that contained each survey location using data (on prescribed burns and wildfires) provided by the Eglin Natural Resources Branch. Although available data are not at a scale to show whether a given burn penetrated the riparian zone near a given survey point, the frequency of fire within the burn block can be taken as the maximum number of times that fire could have occurred in or near the riparian zone during the study period. Fires within the block may also have some effect on water chemistry. This data set contains continuous records dating back to 1985; thus, we could look at fire return intervals before and during the study. We calculated the average fire return interval for each site from 1985 to 2005 and used this quantity as a predictor of initial occupancy status in 2006. We then calculated the average fire return interval for each site from 2006 to 2022 and used this quantity as a predictor of colonization rates during the monitoring period.

Occupancy model

We constructed a multiple-season occupancy model that comprises both ecological process and observation process sub-models (Mackenzie et al. 2003; Bailey et al. 2004; Mazerolle et al. 2007). We employed a spatially explicit formulation that treats colonization as a function of distance between sites (Sutherland et al. 2014; Chandler et al. 2015). The multiple-season framework produces estimates of site- and year-specific occupancy (ψ), colonization (γ), extinction (ε), and detection probability (p). Following Zylstra et al. (2019), we modeled the true occupancy state (z) of site i in the first year as a Bernoulli random variable with probability ψ_1:

$$z_{i,1} \sim Bern(\psi_{i,1})$$

For all subsequent sampling occasions, occupancy probability is conditional on the state of the previous sampling occasion, with transitions between states controlled by colonization (γ) and extinction (ε) parameters:

$$\psi_{i,t} = \left(1 - z_{i,t}\right)\gamma_{i,t} + z_{i,t}(1 - (\varepsilon_t \times (1 - \gamma_{i,t}))$$

$$z_{i,t+1} | z_{i,t} \sim Bern(\psi_{i,t})$$

In this formulation, we included a pseudo-rescue effect in the parameterization $(1 - \gamma_{i,t})$ to account for sites that go extinct and are instantly recolonized by close neighbors (Chandler et al. 2015). We allowed colonization (γ) to vary as a function of distance from neighboring occupied sites, such that:

$$\gamma_{i,t} = 1 - e^{-S_{i,t}}$$

$$S_{i,t} = \sum_{i \neq j} \delta_i \cdot z_{j,t-1} e^{-\theta d_{i,j}}$$

$S_{i,t}$ is a measure of connectivity that describes the cumulative influence of neighboring patches that were occupied in the previous year, $d_{i,j}$ represents the euclidean distance between sites i and j, θ describes how connectivity between sites declines as a function of distance (Sutherland et al. 2014), and δ_i is the baseline colonization rate (Zylstra et al. 2019). Our choice to use Euclidian distance stems from a previous genetics study that failed to find support for more nuanced patterns of population structure and connectivity (Austin et al. 2011). We measured the spatial autocorrelation of survey sites to infer long-term patterns of dispersal and connectivity (i.e., metapopulation dynamics; González-Megias et al. 2005).

Model implementation

We modeled the dynamics of bog frogs on Eglin Air Force Base from 2006 to 2022 using 17 years of call surveys. Input data consisted of $y_{i,k,t} = 1$ if bog frogs were detected at site i during survey k in year t, and $y_{i,k,t} = 0$ if not. We assume closure within years such that differences in input data at a site within the same year can be attributed to imperfect detection. We modeled detection-nondetection data using a Binomial distribution with the number of trials equal to the total number of surveys (K) conducted at site i in year t. True occupancy states are linked to observations through the probability of detection, p, such that:

$$y_{i,,t} \sim Binomial(p_t z_{i,t}, K)$$

We modeled initial occupancy, colonization, extinction, and detection probabilities as logit-linear functions. For each component, probability on the logit scale is modeled with an intercept (α) and a set of fixed or random effects. Extinction and detection were assigned a random effect of year, such that each year's (t) values were drawn from normal distributions with hyperparameters describing the mean (α) and standard deviation (σ) of those distributions.

$$logit(\varepsilon_t) = \alpha_\varepsilon + \beta_{\varepsilon.t}$$

$$\beta_{\varepsilon.t} \sim N(0, \sigma_\varepsilon^2)$$

$$logit(p_t) = \alpha_p + \beta_{p.t}$$

$$\beta_{p.t} \sim N(0, \sigma_p^2)$$

Although several site characteristics likely influence demographic rates and hence the probability of extinction (e.g., area of egg-laying habitat, average hydroperiod), we did not believe that our coarse measures of habitat sufficiently capture these nuances and thus chose not to include them as predictors of extinction. Similarly, multiple environmental factors influence surveyors' ability to detect bog frogs. However, given that our primary interest was in occupancy trends over time, we treated detection as a random effect for simplicity. We modeled initial site occupancy (ψ_1) as a function of stream sinuosity, and historical fire return interval, and the proportion of the buffer area classified as wetlands, uplands, or flatwoods. We employed the inverse-logit transformation to obtain a probability of occupancy and model the occupancy of each site ($z_{i,1}$) as a Bernoulli trial with mean ψ_1. The five parameters controlling the effect of covariates, along with the intercept term (β_0), were assigned weakly informative logistic priors, such that:

$$logit(\psi_1) = \alpha_\psi + \beta_{\psi.wetland}(wetland) + \beta_{\psi.upland}(upland) + \beta_{\psi.flatwoods}(flatwoods) + \beta_{\psi.sinuosity}(sinuosity) + \beta_{\psi.fire}(historic\_fire)$$

To test the hypothesis that dispersing animals are more likely to colonize recently burned sites, we allowed colonization rates to vary by site as a function of current fire return interval:

$$logit(\delta_i) = \alpha_\delta + \beta_{\delta.fire}(fire)$$

We acknowledge that by using fire return interval across the contemporary period we lose the ability to attribute direct causation of fire to changes in occupancy states. However, given that our prescribed fire records only include their general location, and a crude measure of acres burnt, there are potentially fires in our dataset that did not impact bog frog breeding habitat. Further, there is likely considerable variability in how quickly bog frogs respond to fire; species specific dispersal dynamics, distance from source populations, or delays in vegetation response will all influence the lag-time between fire and colonization (Hossack et al. 2013; Barrile et al. 2022). Given these uncertainties, we opted to use a simple metric of burn frequency. In addition, although there are potentially myriad factors that impact bog frog movement, we lacked the detailed demographic data needed to explicitly test additional hypotheses related to dispersal and thus chose to only include fire return interval and distance as predictors of colonization.

We used weakly informative priors for all parameters. Following Northrop and Gerber (2018), we assigned the intercepts in each logistic model a logistic prior, L(0,1), which equates to a Uniform(0,1) prior when all covariates equal zero. We assigned all regression coefficients describing the effects of covariates N(0,10) priors. Random effects were assumed to follow a normal distribution with mean 0 and standard deviation, σ. We assigned σ a vague gamma prior, Gamma(1,1). Finally, we assigned a Gamma(1,1) prior for θ, the scaling parameter of the dispersal kernel. All analyses were performed in JAGS and R using the *jagsUI* package (Plummer 2003; Kellner 2021, R Core Team 2022). Three chains of MCMC (Markovian Chain Monte Carlo) samples were generated, each of length 20,000 with the first 4000 values being discarded as burn-in. To minimize autocorrelation, only every 80th sample was drawn for posterior summaries. Calculated $\widehat{R}$ values for all parameters were < 1.1, indicating adequate mixing (Gelman and Rubin 1992). Visual inspection of the trace plots also confirmed convergence within and between chains. All reported parameter estimates are posterior medians with 95% credible intervals. We determined to what extent covariates explained variation in initial occupancy and colonization probabilities by whether 95% credible intervals excluded zero.

Results

From 2006 to 2022, we conducted 6994 surveys at 151 sites. All sites were surveyed a minimum of 10 times over the study period. Bog frogs were detected at least once at 86 sites. The average probability of detecting bog frogs during a single call survey, conditional on a site being occupied, was 0.56 (95% CI: 0.52, 0.61; Fig. 2). Thus, given that the current monitoring protocol for bog frogs on Eglin Air Force Base involves three surveys per year, the annual detection probability for an occupied site is 0.92 (95% CI: 0.86, 0.94). However, we observed some variability in detection across years, with the probability of detection being lowest in 2007 at 0.44 (95% CI: 0.35, 0.52) and highest in 2010 at 0.71 (95% CI: 0.63, 0.79). As such, the probability of detecting frogs calling in 2007 during the three standard surveys was 0.83 (95% CI: 0.73, 0.86) and in 2010 was 0.98 (95% CI: 0.95, 0.99).

Table 1 Posterior medians, standard deviations, and credible intervals for a spatially explicit occupancy model for Florida bog frogs on Eglin Air Force Base, USA. Intercept terms are represented by for logistic regression models of initial occupancy (ψ), extinction (ε), colonization (δ), and detection (p). Regression coefficients are denoted by β's and random effects are denoted by σ's. θ represents the scaling parameter of the dispersal function. Parameters for which the 95% CIs did not include zero are highlighted in bold

Parameter	Mean	SD	95% CI
Initial occupancy			
α_{ψ}	**−0.79**	**0.21**	**−1.21, −0.37**
$\beta_{\psi.upland}$	−0.20	0.42	−1.13, 0.62
$\beta_{\psi.wetland}$	0.07	0.44	−0.83, 0.94
$\beta_{\psi.flatwoods}$	0.04	0.28	−0.44, 0.59
$\beta_{\psi.sinuosity}$	−0.20	0.26	−0.75, 0.25
$\beta_{\psi.fire}$	**−0.48**	**0.24**	**−1.03, −0.03**
Extinction			
α_{ε}	**−2.34**	**0.19**	**−2.76, −1.99**
$\sigma_{\varepsilon.year}$	**0.36**	**0.25**	**0.02, 0.94**
Colonization			
θ	**3.90**	**0.23**	**3.45, 4.37**
$\beta_{\delta.fire}$	**−0.59**	**0.17**	**−0.89, −0.24**
Detection			
α_{p}	**0.26**	**0.10**	**0.08, 0.45**
$\sigma_{p.year}$	**0.34**	**0.09**	**0.19, 0.55**

Across all sites, initial site occupancy probability was 0.31 (95% CI: 0.23, 0.41) and was higher for sites with a shorter historical fire return interval (Table 1, Fig. 3). Specifically, sites that had burned 10 times between 1985 and 2005 were twice as likely to be occupied

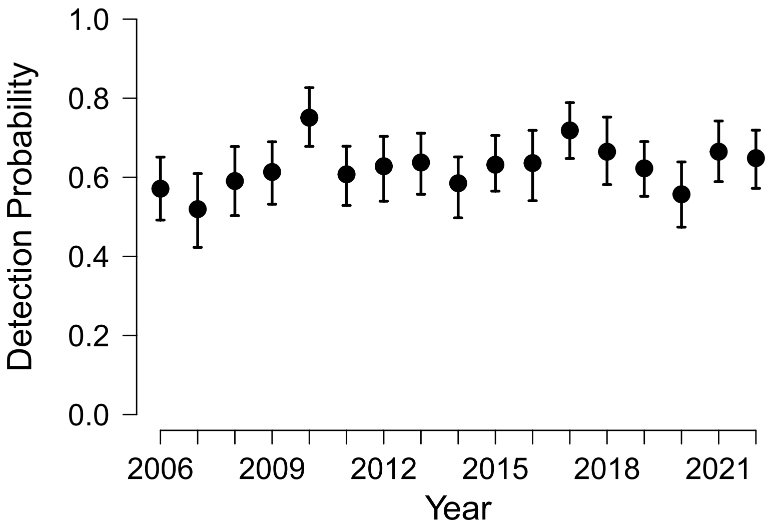

Fig. 2 Detection probability for a single survey across years. Points are mean estimates and bars indicate the 95% credible intervals

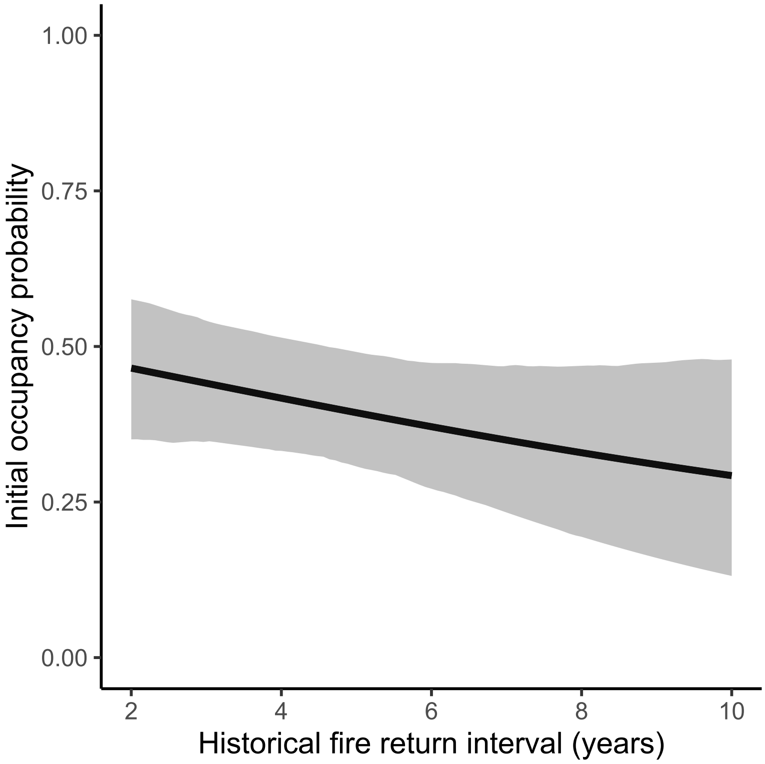

Fig. 3 Initial occupancy probability as a function of historical fire return interval. Sites that had been burned every 2 years on average during 1985–2005 were twice as likely to be occupied in 2006 compared with sites that had only been burned once every 10 years

in 2006 compared to sites that had only burned two times in those preceding years ($\beta_{\psi.fire}$ = − 0.48, 95% CI: − 1.03, − 0.03). In contrast, we found no evidence that stream sinuosity ($\beta_{\psi.sinuosity}$ = − 0.20, 95% CI: − 0.75, 0.25) or the proportion of wetland ($\beta_{\psi.wetland}$ = − 0.07, 95% CI: − 0.83, 0.94), upland ($\beta_{\psi.upland}$ = − 0.20, 95% CI: − 1.13, 0.62), or flatwoods ($\beta_{\psi.flatwoods}$ = − 0.04, 95% CI: − 0.44, 0.59) within a 125 m buffer of the site were related to initial site occupancy (Table 1, Fig. S1).

The number of sites occupied remained relatively stable for the first 8 years of the study before dropping slightly

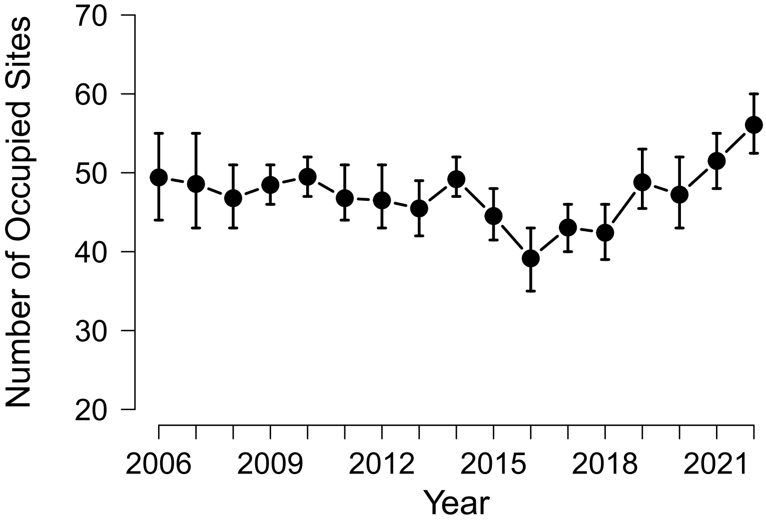

Fig. 4 Predicted number of sites (out of a total of 151 surveyed) on Eglin Air Force Base occupied by bog frogs from 2006 to 2022. Points are mean estimates and bars indicate the 95% confidence intervals

from 2014 to 2016, and then consistently increasing from 2016 to 2022. The maximum number of sites occupied in any given year was 56 (95% CI: 52–60) in 2022, and the minimum was 39 (95% CI: 35–43) in 2016 (Fig. 4). Over the 17 years of monitoring, the median extinction rate was estimated to be 0.09 (95% CI: 0.06–0.12; Table 1, Fig. S2). The probability of extinction was highest in 2007 at 0.13 (95% CI: 0.04, 0.23) and lowest in 2021 at 0.07 (95% CI: 0.03, 0.12). Colonization rates varied as a function of distance from neighboring sites and burn frequency (Table 1). Specifically, colonization of an unoccupied site was more likely when the distance to the nearest occupied site was low (< 1 km). Unoccupied sites further than 2 km from the nearest occupied sites were never colonized (Fig. 5), and the average dispersal distance estimated was 0.30 km (95% CI: 0.23–0.37 km). However, we did find evidence for spatial autocorrelation between sites up to 20 km apart when considering occupancy patterns across the entire study region (Fig. S3).

Accounting for distance between neighboring sites, unoccupied sites were more likely to be colonized if they had been frequently burned during the study period ($\beta_{\delta.fire} = -0.59$, 95% CI: $-0.89, -0.24$; Table 1, Fig. 6). Sites burned five times between 2006 and 2022 were twice as likely to be colonized as those never burned during this period (Fig. 6). For example, the probability of being colonized by an occupied neighboring site 500 m away was 0.08 (95% CI: 0.08–0.09) at sites with zero burns during the study period and 0.17 (95% CI: 0.12, 0.23) at sites burned five times during the study period. Sites burned eight times between 2006 and 2022 were three times as likely to be colonized as sites that had not burned (Fig. 6). The probability of being colonized by an occupied neighboring site 500 m away was 0.24 (95% CI: 0.14–0.39) at sites with eight burns.

Discussion

Here we describe the occupancy dynamics of bog frogs on Eglin Air Force Base over 17 years of monitoring and habitat management. Despite significant site turnover during the study, the overall occupancy rate was relatively stable over time. Habitat characteristics did not explain bog frog occurrence, but sites with shorter historical fire return intervals were more likely to be occupied at the start of the study. Dispersal was limited to neighboring sites less than 2 km apart, and colonization rates of unoccupied sites were highest at sites regularly burned during the study period. Understanding the habitat associations of bog frogs and how populations respond to prescribed fire is crucial to assess the status of the species and plan future management activities.

Our failure to find a relationship between habitat characteristics and bog frog occupancy is surprising, particularly given that prior studies have found an association

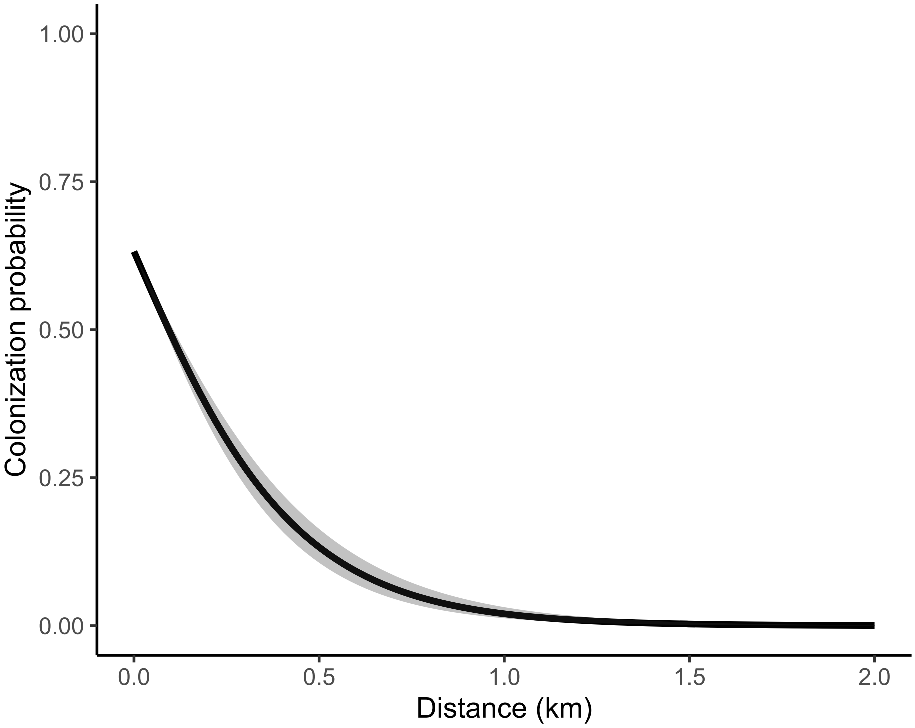

Fig. 5 Colonization probability as a function of distance. The dispersal kernel is modeled as a decreasing exponential function, with parameter θ controlling the rate of decay. See methods for details

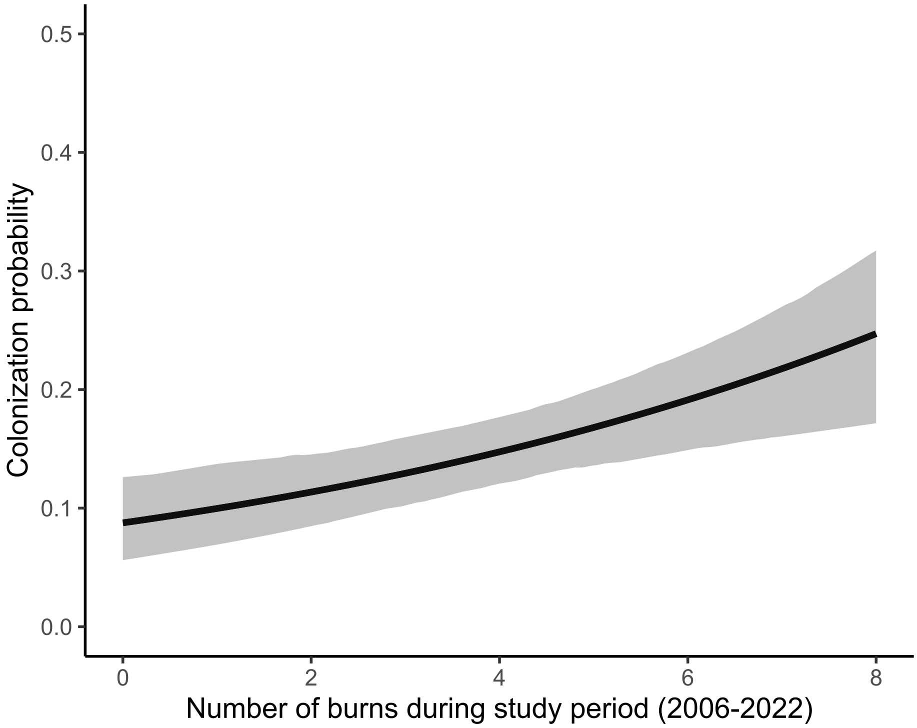

Fig. 6 Predicted relationship between contemporaneous burn frequency and colonization probability. Note that probabilities are scaled to represent colonization pressure from an occupied site 500 m away from the focal site

with the same variables (Gorman 2009). This discrepancy may be due to the difference in the number of years surveyed and/or the buffer being centered on the road point rather than the actual location of a calling frog. Distances between the surveyor and calling individuals varied across survey points, and thus, how accurately habitat conditions could be classified at actual breeding locations was not consistent. Alternatively, bog frogs may be responding to different scales and types of habitat characteristics than we could assess remotely. The strong relationship between historical fire return interval and initial occupancy may be a result of the response of herbaceous vegetation cover to fire both in the uplands and in wetlands (Brockway and Lewis 1997; Glitzenstein et al. 2003; Martin and Kirkman 2009), and the species' response to this microhabitat feature. Specifically, unoccupied sites may have adequate wetland habitat or suitable stream characteristics for bog frog reproduction but are heavily degraded due to the absence of fire. Bog frogs select areas along streams with abundant emergent vegetation (Gorman and Haas 2011; Florida Fish and Wildlife Conservation Commission 2013). The eggs or larvae of several other species of amphibians, including dusky gopher frogs (*Rana sevosa*), ornate chorus frogs (*Pseudacris ornata*), and reticulated flatwoods salamanders (*Ambystoma bishopi*), are also associated with the presence of fire-maintained emergent herbaceous vegetation, likely because it can provide structure for attachment and cover from predators, can increase oxygenation of water, and can provide a food source (Bishop and Haas 2005; Kopp et al. 2006; Gorman et al. 2013, 2014; Lance and Pechmann 2024). Fire can stimulate herbaceous seed production and germination and reduce competition for light (Martin and Kirkman 2009; Stonecypher et al. 2024). Fire can improve amphibian hatching success through its influence on water chemistry and dissolved oxygen levels by reducing decaying organic matter or influencing the type of litter deposited (Sacerdote and King 2009; Burrow and Maerz 2022).

Based on patterns of spatial autocorrelation in site occupancy, the bog frog occurs in what appear to be three distinct metapopulations on Eglin Air Force Base. Although two metapopulations appear well connected and resilient, the third has apparently gone extinct with no detections in the Titi Creek area since 2011. The risk of localized extinction increases with increasing isolation. Therefore, dispersal between sites is essential for long-term persistence (Moilanen and Hanski 1998; Lawes et al. 2000). Additionally, if the number of occupied patches falls below a threshold or the distance between patches exceeds a threshold, the metapopulation is likely to collapse (Moilanen and Hanski 1998; Lawes et al. 2000).

Studies investigating the demographics at individual sites, to elucidate source-sink dynamics, will help quantify the vulnerability of metapopulations to future environmental change (Nelson and Graves 2004; Stevens and Paszkowski 2004). Estimates of population size are available for only four populations, and these have all been small, ranging from no more than 8 to 28 adult males (da Silva Neto et al. 2014), suggesting there must be connectivity between sites for such small populations to persist. Management activities directed at increasing the number of occupied sites may be warranted to safeguard the species' future.

Within metapopulations, colonization of unoccupied sites was relatively common, despite documented daily movements of bog frogs typically less than 10 m (Gorman et al. 2009). Only one movement over 100 m was observed for a marked individual at a study area monitored for two seasons (Gorman et al. 2009). As with other ranid frogs (e.g., Martof 1956; Schroeder 1976), juveniles likely account for most of the between-site movement, but because the bog frog occurs predominantly along streams, tadpoles may also contribute to colonization (Kraaijeveld-Smit et al. 2005). Although we do not know what factors might favor dispersal or settling of dispersing tadpoles, there is evidence that survival and growth of larval amphibians tends to be higher in areas with emergent herbaceous vegetation, so we could expect that tadpoles would be attracted to more frequently burned areas with more emergent vegetation (Burrow and Maerz 2022). However, we have a limited understanding of how bog frogs interact with terrestrial upland habitat surrounding breeding sites. In other species of amphibian, upland habitat does influence dispersal (Todd et al. 2009; Hossack and Corn 2007; Murphy et al. 2010; Youngquist & Boone 2014; Barrile et al. 2022). Because patch connectivity is critical for maintaining local populations within a metapopulation, future research should be directed toward identifying the dispersal phase (either through genetics or tracking studies) to further understand movement between sites.

Recurrent disturbance, such as fire, is important for patch connectivity and colonization in metapopulation dynamics (Zeigler and Fagan 2014). Here we show that for the bog frog, historical burn regimes predict initial occupancy states and sites with shorter fire return intervals during the study period were more likely to be colonized. Aside from maintained powerline right of ways, fire is the primary driver creating the conditions necessary for successful breeding of bog frogs through controlling woody vegetation and promoting the growth of herbaceous vegetation. Therefore, it is unsurprising that fire drives turnover dynamics in this system (Hossack and Corn 2007; Hossack and Pilliod 2011). For example, Barrile et al. (2022) found that dispersal of a boreal toad increased post-wildfire. While the authors suggest that dispersal away from occupied sites immediately post-fire could be attributed to reduced quality of breeding habitat, they suspect that fire-induced habitat changes, such as increased bare ground, facilitated movement to previously unoccupied sites in the 2 years immediately following the fire. While we cannot rule out ease of movement as a mechanism driving the relationship between fire and colonization rates in our study, Barrile et al. (2022) caution that experimental manipulations are needed to correlate an increase in landscape permeability post-fire to increased dispersal.

Prescribed fire on Eglin Air Force Base did not historically target bog frog habitat, which may account for the wide credible intervals in the association between fire and colonization. The fire data we have is not at a scale to show whether a given burn penetrated the riparian zone and impacted bog frog habitat. As such, there is likely not a one-to-one translation between recorded fire and changes to bog frog habitat. If the benefits to habitat are more sporadic than the fire history suggests, this may help explain why bog frog populations appear relatively stable over the study period rather than increasing. Only in recent years has the burning of riparian habitats been a specific management priority, despite Eglin Air Force Base's well-established prescribed fire program. Indeed, the instigation of burns explicitly targeting bog frog habitat corresponds with a steady upward trend of occupancy rates starting in 2016 (Fig. 2). It seems likely, therefore, that bog frog populations could benefit from continuing these practices and, conversely, that without such direct management populations may decline.

Conclusions

Spatially explicit occupancy models can be used to assess long-term trends in range-wide occurrence and identify the scale and dynamics of metapopulations. Once such information is known, managers can delineate metapopulations and scale management activities accordingly, which can elucidate when assisted translocations or strategies to improve connectivity between sites are necessary (Semlitsch 2002; Seigel and Dodd 2002). For conservation to be successful, practitioners must be able to assess changes in populations of rare or endangered species in response to management strategies once they have been implemented (Chandler et al. 2015). In many management plans for at-risk amphibians, the response of populations to fire is simply assumed (Darracq et al. 2016). Explicitly quantifying population dynamics in response to fire, as demonstrated here, presents a far more powerful assessment of management activities (Hossack and Corn 2007; Hiers et al. 2020). For the bog frog, fire appears to be an effective tool to improve and maintain habitat quality. We recognize that other factors besides frequency, such as seasonality or burn intensity, are likely to have important effects (Hossack and Pilliod 2011; dos Anjos et al. 2021; Chergui et al. 2022), but were beyond the scope of this study. More detailed studies to assess the influence of fire on vegetation and structural components of habitat and how those components influence reproduction and survival would be valuable next steps. To maximize the effectiveness of targeted management, prescribed burns should be planned to correspond with predicted dispersal patterns and directed at clusters of sites with high connectivity. More broadly, our work demonstrates how knowledge of the links between occupancy dynamics and landscape attributes can aid in decision-making related to the management of rare and endangered species.

Supplementary Information

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Supplementary Material 1: Figure S1. Posterior predictions for the relationship between habitat characteristics and initial occupancy state. Figure S2. Posterior distributions for extinction probabilities across years. Figure S3. Spatial autocorrelation of bog frog sites across Eglin Air Force Base. Points represent autocorrelation observed at different distance classes. The blue shaded region indicates the 95% confidence interval, such that points outside of the shaded region are significantly different from zero ($p < 0.05$).

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Authors' contributions

TAG and CAH conceived of the presented idea. BKR and TAG designed and carried out the field methods. GCB, TAG, and CP performed the statistical analysis. GCB led the writing of the manuscript. All authors read and approved of the final manuscript.

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Data availability

All data and code needed to replicate our analyses have been permanently archived on Zenodo and can be accessed at https://doi.org/https://doi.org/10.5281/zenodo.14846463.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors have no competing interests to declare.

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References

Allan, J. D., M. M. Castillo, and K. A. Capps. 2021. *Stream ecology: Structure and function in running waters*, 3rd ed. Cham, Switzerland: Springer.

Alzate, A., and R. E. Onstein. 2022. Understanding the relationship between dispersal and range size. *Ecology Letters* 25: 2303–2323.

Amarasekare, P., and H. Possingham. 2001. Patch dynamics and metapopulation theory: The case of successional species. *Journal of Theoretical Biology* 209: 333–344.

Askins, R. A., F. Chavez-Ramirez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, et al. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. *Ornithological Monographs* 64: 1–46.

Austin, J. D., S. C. Lougheed, P. E. Moler, and P. T. Boag. 2003. Phylogenetics, zoogeography, and the role of dispersal and vicariance in the evolution of the *Rana catesbeiana* (Anura: Ranidae) species group. *Biological Journal of the Linnean Society* 80: 601–624.

Austin, J. D., T. A. Gorman, and D. Bishop. 2011. Assessing fine-scale genetic structure and relatedness in the micro-endemic Florida bog frog. *Conservation Genetics* 12: 833–838.

Baattrup-Pedersen, A., S. E. Larsen, D. K. Andersen, N. Jepsen, J. Nielsen, and J. J. Rasmussen. 2018. Headwater streams in the EU water framework directive: Evidence-based decision support to select streams for river basin management plans. *Science of the Total Environment* 614: 1048–1054.

Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004. Estimating detection probability parameters for *Plethedon* salamanders using the robust capture-recapture design. *Journal of Wildlife Management* 68: 1–13.

Barrile, G. M., A. D. Chalfoun, W. A. Estes-Zumpf, and A. W. Walters. 2022. Wildfire influences individual growth and breeding dispersal, but not survival and recruitment in a montane amphibian. *Ecosphere* 13:e4212.

Bishop, D. C. 2004. *Summary of surveys for Florida bog frogs and flatwoods salamanders on Eglin Air Force Base through 2004. Dissertation*. Blacksburg, Virginia: Virginia Polytechnic Institute and State University.

Bishop, D. C., and C. A. Haas. 2005. Burning trends and potential negative effects of suppressing wetland fires on flatwoods salamanders. *Natural Areas Journal* 25: 290–294.

Braun, A., K. Auerswald, and J. Geist. 2012. Drivers and spatio-temporal extent of hyporheic patch variation: Implications for sampling. *PLoS One* 7:e42046.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167–183.

Brockway, D. G., K. W. Outcalt, D. J. Tomczak, and E. E. Johnson. 2005. *Restoration of longleaf pine ecosystems. Gen. Tech. Rep. SRS-83*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Brooks, G. C., T. A. Gorman, K. C. Jones, H. C. Chandler, B. K. Rincon, M. A. Sisson, J. Himes, and C. A. Haas. 2023. Removing duff layers in fire-suppressed wetlands can aid habitat restoration efforts. *Wetlands* 43: 95.

Burrow, A., and J. Maerz. 2022. How plants affect amphibian populations. *Biological Reviews* 97: 1749–1767.

Cayton, H. L., N. M. Haddad, E. H. Henry, G. K. Himes Boor, E. M. Kiekebusch, W. F. Morris, and E. T. Aschehoug. 2023. Restoration success varies based on time since restoration in a disturbance-dependent ephemeral wetland ecosystem. *Restoration Ecology* 31:e13883.

Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack. 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *Journal of Applied Ecology* 52: 1325–1333.

Chergui, B., C. Ayres, and X. Santos. 2022. Assessing the response of amphibians to wildfire according to forest type and bioregion affinity of species. *Basic and Applied Herpetology* 36: 5–17.

Da Silva Neto, J. G., T. A. Gorman, D. C. Bishop, and C. A. Haas. 2014. Population demographics of the Florida bog frog (*Lithobates okaloosae*). *Southeastern Naturalist* 13: 128–137.

Darracq, A. K., W. W. Boone IV., and R. A. McCleery. 2016. Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. *Forest Ecology and Management* 378: 214–221.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, et al. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.

dos Anjos, A. G., M. Solé, and M. Benchimol. 2021. Fire effects on anurans: What we know so far? *Forest Ecology and Management* 495: 119338.

Fernandes, P. M., G. M. Davies, D. Ascoli, C. Fernández, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega, and D. Molina. 2013. Prescribed burning in southern Europe: Developing fire management in a dynamic landscape. *Frontiers in Ecology and the Environment* 11: 4–14.

Flores, C., D. L. Bounds, and D. E. Ruby. 2011. Does prescribed fire benefit wetland vegetation? *Wetlands* 31: 35–44.

Florida Fish and Wildlife Conservation Commission. 2013. A species action plan for the Florida bog frog. Tallahassee, Florida. https://myfwc.com/media/2116/florida-bog-frog-species-action-plan-final-draft.pdf.

Florida Fish and Wildlife Conservation Commission. 2022. Florida's endangered and threatened species. Updated 2022. https://myfwc.com/media/1945/threatened-endangered-species.pdf.

Florida Natural Areas Inventory (FNAI). 2010. *Guide to the natural communities of Florida: 2010 edition*, 2010th ed. Tallahassee, FL: Florida Natural Areas Inventory.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16: 1706–1716.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7: 457–472.

Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (Pinus palustris P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23: 22–37.

González-Megias, A., J. M. Gómez, and F. Sánchez-Pinero. 2005. Consequences of spatial autocorrelation for the analysis of metapopulation dynamics. *Ecology* 86: 3264–3271.

Gorman, T. A. 2009. *Ecology of two rare amphibians of the Gulf Coastal Plain. Dissertation*. Blacksburg, VA: Virginia Tech.

Gorman, T. A., and C. A. Haas. 2011. Seasonal microhabitat selection and use of syntopic populations of *Lithobates okaloosae* and *Lithobates clamitans clamitans*. *Journal of Herpetology* 45: 313–318.

Gorman, T. A., D. C. Bishop, and C. A. Haas. 2009. Spatial interactions between two species of frogs: *Rana okaloosae* and *R. clamitans clamitans*. *Copeia* 2009: 138–141.

Gorman, T. A., C. A. Haas, and J. G. Himes. 2013. Evaluating methods to restore amphibian habitat in fire-suppressed pine flatwoods wetlands. *Fire Ecology* 9: 96–109.

Gorman, T. A., S. D. Powell, K. C. Jones, and C. A. Haas. 2014. Microhabitat characteristics of egg deposition sites used by reticulated flatwoods salamanders. *Herpetological Conservation and Biology* 9: 543–550.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology & Evolution* 9: 131–135.

Hardesty, J. L., and C. Kindell. 1997. Conserving ecosystems at Eglin AFB. *Endangered Species Bulletin* 22: 8–9.

Harris, G., and S. L. Pimm. 2008. Range size and extinction risk in forest birds. *Conservation Biology* 22: 163–171.

Hiers, J. K., J. J. O'Brien, J. M. Varner, B. W. Butler, M. Dickinson, J. Furman, M. Gallagher, D. Godwin, S. L. Goodrick, S. M. Hood, and A. Hudak. 2020. Prescribed fire science: The case for a refined research agenda. *Fire Ecology* 16: 1–15.

Hossack, B. R., and P. S. Corn. 2007. Responses of pond-breeding amphibians to wildfire: short-term patterns in occupancy and colonization. *Ecological Applications* 17: 1403–1410.

Hossack, B. R., and D. S. Pilliod. 2011. Amphibian responses to wildfire in the western United States: Emerging patterns from short-term studies. *Fire Ecology* 7: 129–144.

Hossack, B. R., W. H. Lowe, and P. S. Corn. 2013. Rapid increases and time-lagged declines in amphibian occupancy after wildfire. *Conservation Biology* 27: 219–228.

Jackson, D. R. 2004. *Management guidance document for species at risk on Eglin Air Force Base, Niceville, Florida: Florida bog frog* (*Rana okaloosae*). *Final report to the U.S. Fish and Wildlife Service*. Florida Natural Areas Inventory: Tallahassee, FL.

Johnson, C. N. 1998. Species extinction and the relationship between abundance and distribution. *Nature* 294: 272–274.

Karna, O., J. Heino, M. Gronroos, and J. Hjort. 2018. The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity. *Ecological Indicators* 94: 420–429.

Kellner, K. 2021. jagsUI: a wrapper around "rjags" to streamline "JAGS" analyses. *R package version* 1 (1).

Kéry, M., G. Guillera-Arroita, and J. J. Lahoz-Monfort. 2013. Analysing and mapping species range dynamics using occupancy models. *Journal of Biogeography* 40: 1463–1474.

Kopp, K., M. Wachlevski, and P. C. Eterovick. 2006. Environmental complexity reduces tadpole predation by water bugs. *Canadian Journal of Zoology* 84: 136–140.

Kraaijeveld-Smit, F. J. L., T. J. C. Beebee, R. A. Griffiths, R. D. Moore, and L. Schley. 2005. Low gene flow but high genetic diversity in the threatened Mallorcan midwife toad *Alytes muletensis*. *Molecular Ecology* 14: 3307–3315.

Kupferberg, S. J. 1996. Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). *Ecological Applications* 6: 1332–1344.

Lance, C. M., and J. H. Pechmann. 2024. Assessing factors that increase dusky gopher frog larval performance in open-canopy wetlands. *The Journal of Wildlife Management* 88:e22559.

Lawes, M. J., P. E. Mealin, and S. E. Piper. 2000. Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. *Conservation Biology* 14: 1088–1098.

Lester, S. E., B. I. Ruttenberg, S. D. Gaines, and B. P. Kinlan. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* 10: 745–758.

Lewis, C. E., and T. J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina coastal plain. *Rangeland Ecology & Management* 29: 13–18.

Lind, A. J., H. H. Welsh Jr., and C. A. Wheeler. 2016. Foothill yellow-legged frog (*Rana boylii*) oviposition site choice at multiple spatial scales. *Journal of Herpetology* 50: 263–270.

Lindsay, M. N., D. B. Lewis, N. Halstead, and A. M. Gainsbury. 2023. Fire severity effects on the herpetofaunal diversity of the Florida scrub, a biodiversity hotspot. *Biodiversity and Conservation* 32: 1857–1878.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84: 2200–2207.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling: Inferring patterns of species occurrence*. Boston, MA: Academic Press.

Martin, K. L., and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the southeastern USA. *Journal of Applied Ecology* 46: 906–914.

Martof, B. S. 1956. Growth and development of the green frog, *Rana clamitans*, under natural conditions. *American Midland Naturalist* 55: 101–117.

Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: Accounting for detectability in herpetological field studies. *Journal of Herpetology* 41: 672–689.

Means, D. B. 1975. Competitive exclusion along a habitat gradient between two species of salamanders (*Desmognathus*) in western Florida. *Journal of Biogeography* 2: 253–263.

Means, D. B., C. K. Dodd, S. A. Johnson, and J. G. Palis. 2004. Amphibians and fire in longleaf pine ecosystems: Response to Schurbon and Fauth. *Conservation Biology* 18: 1149–1153.

Miller, D. A., and E. H. C. Grant. 2015. Estimating occupancy dynamics for large-scale monitoring networks: Amphibian breeding occupancy across protected areas in the northeast United States. *Ecology and Evolution* 5: 4735–4746.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79: 2503–2515.

Moler, P. E. 1985. A new species of frog (Ranidae: *Rana*) from northwestern Florida. *Copeia* 1985: 379–383.

Moler, P. E. 1992. Florida bog frog, *Rana okaloosae*. In *Rare and endangered biota of Florida, vol. III: amphibians and reptiles,* ed. P. E. Moler, 30–33. Gainesville, Florida: University Press of Florida.

Mugnani, M. P., K. M. Robertson, D. L. Miller, and W. J. Platt. 2019. Longleaf pine patch dynamics influence ground-layer vegetation in old-growth pine savanna. *Forests* 10: 389.

Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying Bufo boreas connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91: 252–261.

Nelson, G. L., and B. M. Graves. 2004. Anuran population monitoring: Comparison of the North American Amphibian Monitoring Program's calling index with mark-recapture estimates for *Rana clamitans*. *Journal of Herpetology* 38: 355–359.

Newsome, T. M., C. Wolf, D. G. Nimmo, R. K. Kopf, E. G. Ritchie, F. A. Smith, and W. J. Ripple. 2020. Constraints on vertebrate range size predict extinction risk. *Global Ecology and Biogeography* 29: 76–86.

Northrup, J. M., and B. D. Gerber. 2018. A comment on priors for Bayesian occupancy models. *PLoS One* 13: e0192819.

Palik, B. J., R. J. Mitchell, and J. K. Hiers. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: Balancing complexity and implementation. *Forest Ecology and Management* 155: 347–356.

Pilliod, D. S., R. B. Bury, E. J. Hyde, C. A. Pearl, and P. S. Corn. 2003. Fire and amphibians in North America. *Forest Ecology and Management* 178: 163–181.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing* 124: 1–10.

Rochester, C. J., C. S. Brehme, D. R. Clark, D. C. Stokes, S. A. Hathaway, and R. N. Fisher. 2010. Reptile and amphibian responses to large-scale wildfires in southern California. *Journal of Herpetology* 44: 333–351.

Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment* 11: 15–24.

R Core Team. 2022. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Saab, V. A., Q. R. Latif, W. M. Block, and J. G. Dudley. 2022. Short-term benefits of prescribed fire to bird communities of dry forests. *Fire Ecology* 18: 1–19.

Sacerdote, A. B., and R. B. King. 2009. Dissolved oxygen requirements for hatching success of two ambystomatid salamanders in restored ephemeral ponds. *Wetlands* 29: 1202–1213.

Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. *American Midland Naturalist* 1976: 471–474.

Schurbon, J. M., and J. E. Fauth. 2003. Effects of prescribed burning on amphibian diversity in a southeastern US national forest. *Conservation Biology* 17: 1338–1349.

Schurbon, J. M., and J. E. Fauth. 2004. Fire as friend and foe of amphibians: A reply. *Conservation Biology* 18: 1156–1159.

Scott, N. J., and B. D. Woodward. 1994. Surveys at breeding sites. In *Measuring and monitoring biological diversity: Standard methods for amphibians*, ed. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, 118–125. Washington, D.C: Smithsonian Institution Press.

Seigel, R. A., and C. K. Dodd Jr. 2002. Translocations of amphibians: Proven management method or experimental technique? *Conservation Biology* 16: 552–554.

Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic breeding amphibians. *Conservation Biology* 16: 619–629.

Stevens, C. E., and C. A. Paszkowski. 2004. Using chorus-size ranks from call surveys to estimate reproductive activity of the wood frog (*Rana sylvatica*). *Journal of Herpetology* 38: 404–410.

Stonecypher, E. T., L. S. Lee, S. M. Weir, E. G. King, C. E. Davis, and S. L. Lance. 2024. Efficacy and costs of restoring wetland breeding habitat for imperiled amphibians in the southeastern US. *Wetlands* 44: 65.

Sutherland, C. S., D. A. Elston, and X. Lambin. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. *Ecology* 95: 3149–3160.

Todd, B. D., T. M. Luhring, B. B. Rothermel, and J. W. Gibbons. 2009. Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *Journal of Applied Ecology* 46: 554–561.

Winiarski, J. M., C. E. Moorman, J. P. Carpenter, and G. R. Hess. 2017. Reproductive consequences of habitat fragmentation for a declining resident bird of the longleaf pine ecosystem. *Ecosphere* 8:e01898.

Youngquist, M. B., and M. D. Boone. 2014. Movement of amphibians through agricultural landscapes: The role of habitat on edge permeability. *Biological Conservation* 175: 148–155.

Zeigler, S. L., and W. F. Fagan. 2014. Transient windows for connectivity in a changing world. *Movement Ecology* 2: 1.

Zylstra, E.R., Swann, D.E., Hossack, B.R., Muths, E. and Steidl, R.J., 2019. Drought-mediated extinction of an arid-land amphibian: insights from a spatially explicit dynamic occupancy model. *Ecological Applications* 29(3): e01859.

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