Population-level effects of prescribed fires on terrestrial salamanders

Alison E. Ochs [*], Robert K. Swihart, Mike R. Saunders

Purdue University, Department of Forestry and Natural Resources, 715 West State Street, West Lafayette, IN 47907, USA

A B S T R A C T

Prescribed fires are widely used for oak (*Quercus*) regeneration in hardwood forests, but the reported effects on terrestrial salamanders are variable, with some authors describing little to no effect of prescribed fire on salamanders and others reporting negative results. Factors such as variable fire intensity, sampling methodology, and imperfect salamander detection, which vary by study, may influence the effects of prescribed fires on salamanders. We examined the response of red-backed (*Plethodon cinereus*) and zig-zag (*Plethodon dorsalis*) salamanders to prescribed fire in forests of the Midwest U.S., accounting for changes in salamander behavior and detection by accounting for capture probability, and considering the influence of local fire intensity. We also explored the effects of fire on environmental variables (leaf litter depth, soil moisture, soil temperature, and soil pH) to identify possible mechanisms driving fire's influence on salamanders. From spring 2019 through fall 2022, a total of 4922 salamander captures were recorded, representing 1939 individually marked salamanders at six coverboard grids in southern Indiana. Occurrence of fire affected survival and temporary emigration of salamanders, likely indicating that salamanders retreated underground, on two of the four grids. Fire occurrence and intensity did not significantly affect environmental variables except for leaf litter depth, which was negatively affected. However, soil moisture had a stronger influence on salamander capture probability than leaf litter. Overall, effects of prescribed fires on salamander populations in this study were inconsistent. In contrast, environmental factors had strong impacts on salamanders, but themselves exhibited either no relationship or a short-term relationship to prescribed fire variables. Notably, large salamander populations may be better able to tolerate prescribed fires. Such populations will be important to support during prescribed fire management to protect the species, especially as the effects of repeated prescribed fires and compounding effects are unknown. Understanding the interplay between forest management practices and wildlife habitat features such as soil moisture and leaf litter will be critical to identifying best practices for supporting wildlife populations reliant on such features during prescribed fires.

1. Introduction

After a century of fire exclusion in the United States, forest managers seeking to restore fire-adapted ecosystems and decrease wildfire risk are increasingly turning to controlled surface fires, also called prescribed burns or fires, for forest management (Hanberry et al., 2014; Nowacki and Abrams, 2008; Pausas and Keeley, 2014; Pilliod et al., 2003; Pyne and willey, 1996). Prescribed fires are particularly useful tools to promote oak (*Quercus* spp.) regeneration in eastern North America, as fires reduce competition by mesophytic hardwoods and remove thick litter and duff layers that impede oak seedling growth (Brose et al., 2014). However, prescribed fires can also have strong effects, both directly and indirectly, on wildlife depending on wildlife species, geographic location, method of burning, timing of burning, and fire intensity (Campbell

et al., 2018; Fontaine and Kennedy, 2012; Hanson, 1978; Landers and Crawford, 1995; Main and Richardson, 2002; Rieman and Clayton, 1997; Russell et al., 2009; Tiedemann et al., 2000). As prescribed fire grows in use by both forest managers and indigenous caretakers (Panek and Kipfmueller, 2021; White et al., 2021), understanding how the practice affects vulnerable species will be critical to forest conservation efforts and maintaining ecosystem services.

Research on the effects of prescribed fires on herpetofauna has lagged relative to other wildlife (Bury, 2004; Russell et al., 1999). Terrestrial salamanders are critical components of most forest ecosystems, consuming and controlling invertebrates that decompose leaf litter and providing food for birds and other species (Mathewson, 2007; Wyman, 1998). They spend much of their time underground, emerging on the surface during warm, rainy nights to forage and retreating to moist

refuges under coarse woody debris or lower in the soil column during hot, dry conditions (Bailey, 2002; Taub, 1961). Salamanders may also serve as indicators of forest health (Welsh and Droege, 2001; Welsh and Hodgson, 2013; Welsh Jr. and Ollivier, 1998). Prescribed fires may adversely affect terrestrial salamanders, as they are highly responsive to changes in soil moisture and temperature (Feder, 1983; Spotila, 1972), variables that can be strongly affected by prescribed fire (Bury et al., 2002; Pilliod et al., 2003). Prescribed fires may also remove leaf litter and duff layers and combust coarse woody debris (CWD) on the forest floor, leaving salamanders without refuges during daytime foraging, which may further limit their survival and movement, especially during hot, dry conditions in mid-summer (Bury et al., 2002; Pilliod et al., 2003).

Studies on the effects of prescribed fire on terrestrial salamanders have so far produced conflicting results. Several studies have found few to no effects of prescribed fire on terrestrial salamanders in the years immediately following burning (Ford et al., 2010, 1999; Greenberg et al., 2018; Jacobsen et al., 2020; Keyser et al., 2004; Moseley et al., 2006; Sutton et al., 2013), whereas others have described effects on movement, availability, or abundance (Hromada et al., 2018; Jacobsen et al., 2020; Mitchell, 2000; O'Donnell et al., 2016, 2015). Methodology of a study may influence results, as studies reporting little to no effects of prescribed fire on salamanders used drift fencing and pitfall traps for counts (Ford et al., 1999; Greenberg et al., 2018; Hromada et al., 2018; Keyser et al., 2004; Moseley et al., 2006; Sutton et al., 2013) – which may be less successful at measuring more sedentary species such as terrestrial salamanders (McDade and Maguire, 2005; Mendes et al., 2015) – failed to account for changes in salamander detection (Ford et al., 1999; Greenberg et al., 2018; Hromada et al., 2018; Keyser et al., 2004; Moseley et al., 2006; Sutton et al., 2013), studied responses to low-intensity fires (Ford et al., 2010; Moseley et al., 2006), or did not numerically report fire intensity (Jacobsen et al., 2020; Sutton et al., 2013). Intensity of prescribed fire can also vary spatially, with areas of higher intensity seeing a higher degree of impact on the local environmental conditions, with stronger impacts on the microclimate potentially affecting salamander occupancy (Major, 2005). Beyond direct impacts measurable by reductions in short-term salamander counts, prescribed fires could also indirectly affect salamanders by reducing prey availability, cover, and surface soil moisture, which could force salamanders to remain underground and lead to longer-term effects on survival and reproduction (O'Donnell et al., 2015).

Despite the increased use of prescribed fire for oak regeneration in eastern North America, research on the effects of prescribed fire on salamanders in oak-dominated Midwestern forests is limited (Fontaine and Kennedy, 2012; Hocking et al., 2012), with only a few studies on the more xeric forests of Missouri (O'Donnell et al., 2016, 2015). As the practice becomes more common in these forests, research on how prescribed fire across a range of intensities and severities affects terrestrial salamanders will be critical to avoid unnecessarily impacting salamander communities, to determine baselines for salamander monitoring, and to eventually develop best management practices for salamander conservation.

We examined the responses of terrestrial salamander populations to prescribed fire in the oak-dominated forests of southern Indiana. While accounting for changes in salamander detection probability at each site, we examined the influence of fire occurrence and fire intensity on salamander survival, temporary emigration, and abundance. We expected that the occurrence of fire would lead to lower apparent survival, higher temporary emigration, and thus lower abundance following fire, and that effects would be stronger with higher fire intensity. We also accounted for potential effects of soil moisture and leaf litter on detection and considered possible effects of prescribed fire on environmental variables that could lead to changes in salamander habitat quality, such as soil moisture, leaf litter, soil temperatures, or changes to soil pH.

2. Methods

2.1. Study area

Our study took place at the Hardwood Ecosystem Experiment (HEE) in south-central Indiana, in Morgan-Monroe (39.2°N, 86.3°W) and Yellowwood (39.1°N, 86.3°W) State Forests. These forests experienced intense clearing, burning, farming, and grazing by European settlers in the 1800 s and early 1900 s. The State of Indiana acquired these lands from the late 1920 s through the 1950 s, shifting the management focus to restoring forests to the landscape. The state forests share a similar composition of oak-hickory and beech-maple cover types, dominated by sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Q. alba*), black oak (*Q. velutina*), shagbark hickory (*Carya ovata*), tulip poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*) (Swihart et al., 2013). Oaks and hickories dominate ridgetops and south-facing slopes, while mesic north-facing slopes are dominated by tulip poplar, beeches, maples, and hickories. The bedrock consists of siltstone, shale, and sandstone, covered by silt-loam soils common to the Wellston-Berks-Gillpin complex, and the topography is characterized by dry ridges and steep ravines. While there are occasional ephemeral streams draining into medium and low gradient creeks, there are otherwise very few natural water features; some man-made ponds can be found in unusual topographic positions (Swihart et al., 2013). Anderson (1982) fuel models are generally Model 9 (consisting of uncompacted hardwood litter) for most stands for any fall prescribed fires and within stands with higher oak dominance for any spring burns; Model 8 (consisting of compacted hardwood litter) is appropriate for spring burns in most other conditions, particularly under heavy maple cover.

Nine HEE study units were established across Morgan-Monroe and Yellowwood State Forests to study the long-term impacts of forest management on Indiana hardwood forests. Units consist of a core research area bounded by a buffer zone (ranging in size from 303 to 483 ha) to prevent neighboring management activities from affecting research areas. In 2006, units were assigned to either even-aged management, uneven-aged management, or unharvested control sites, with three replicates of each treatment type (e.g. Fig. 1; Swihart et al. 2013).

2.2. Prescribed fire

Within each of the three even-aged units, four 4.05 ha unharvested areas were designated as sites for prescribed fires, which began in 2015 (Fig. 1). The goal of these fires was to spur oak regeneration by creating better seedbeds and reducing density of midstory competitors. Initial burns reduced leaf litter and duff depth and top-killed small woody and herbaceous competitors, while subsequent burns, higher in intensity, created mineral soil exposure and top-killed larger woody competitors. Four burn (B) sites in total across all three even-aged units were selected for this study, two on mesic, northeast-facing slopes (m) and two on xeric, southwest-facing slopes (x). Site Bm1 was burned in early spring of 2015 and fall of 2020; site Bx1 was burned in the fall of 2016 and early spring of 2021; site Bm2 was burned in the early spring of 2017 and 2021; and site Bx2 was burned in fall of 2019. Two locations previously used for salamander monitoring (MacNeil and Williams, 2014) were also selected for this study, both within a control (C) unit for comparison with burned sites: sites Cx and Cm.

Prescribed fires were carried out by staff of the Indiana Department of Natural Resources – Division of Forestry's Fire Headquarters. Burns were conducted during the dormant season, either fall (November) or early spring (February – mid-April) and within narrow weather prescriptions (air temperature 1.7–21.1°C, surface winds 8–24.1 km/h, relative humidity 25–45%); the management schedule targeted a 3–5-year burn interval. Fire ignition patterns always began with a backing fire at the ridgetop, followed by flanking fires and then ringing the fire from the bottom of the slope. Target flame heights were 0.3–0.9 m, and
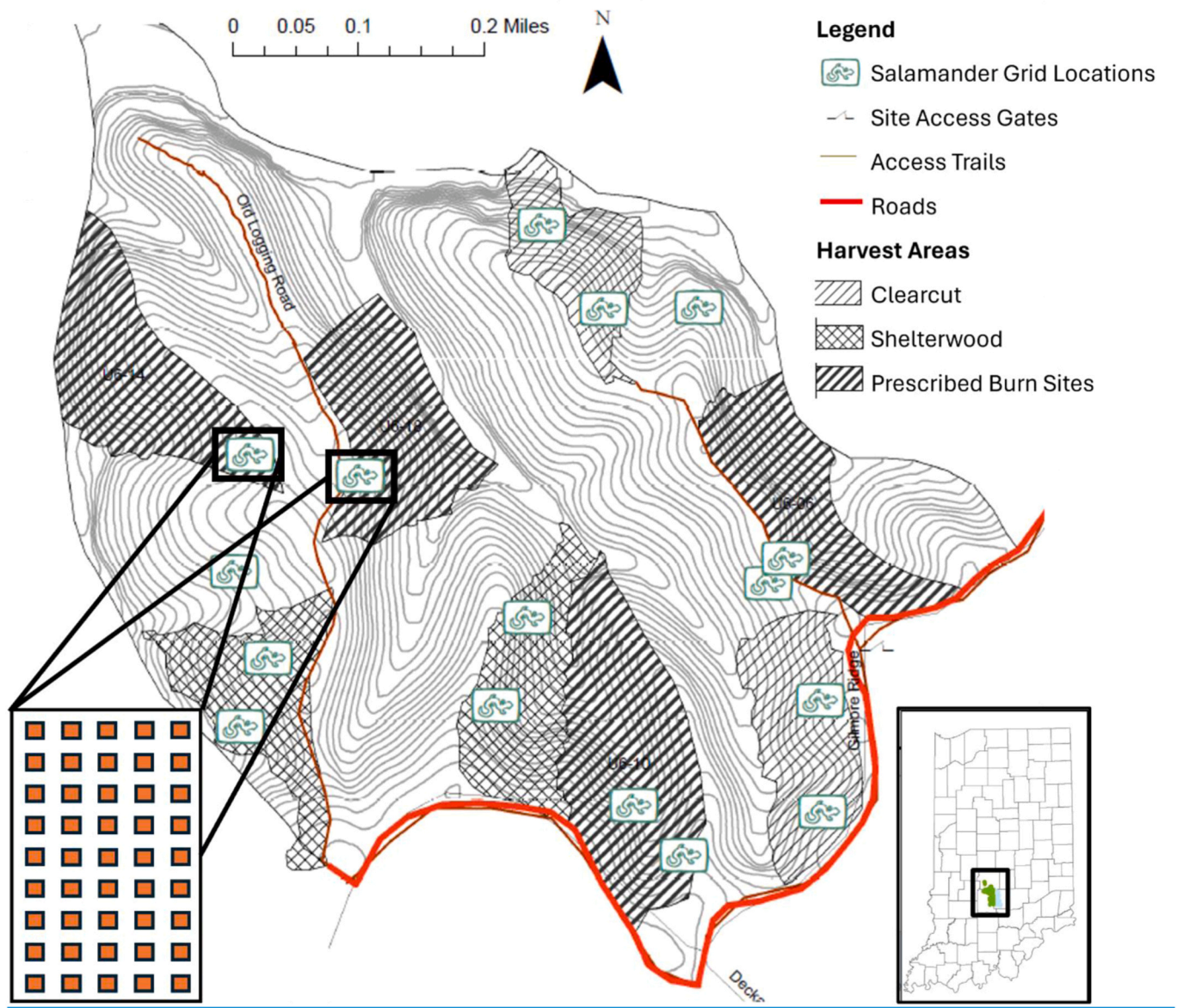
Fig. 1. Hardwood Ecosystem Experiment (HEE) Unit 6, which received even-aged management (clearcuts and shelterwood harvests) and prescribed burns. Salamander grid locations were identified within each management area. At two salamander grid locations within prescribed burn areas in this unit (Bm2 and Bx1), artificial cover object (ACO) grids were established, consisting of 45 ACOs set 1 m apart in a 9×5 pattern as shown in the left insert. Elevation lines indicate a 10 ft change in elevation.

if observed flame heights exceeded 1.2–1.5 m, strip head fires were used on the interior of the burn area to reduce the fetch of the slope and slow fire build up.

2.3. Field work

In the spring of 2019, six artificial cover object (ACO) grids were established, one within each of the six selected sites. ACO grids consisted of 45 untreated 30×30×5cm tulip poplar boards placed 1 m apart in a 9×5 pattern (Fig. 1). ACO grids were allowed to weather for at least 2 weeks before the start of field work (Hesed, 2012).

Beginning in March of 2019, we checked grids every 4–8 days until the end of April, 8 weeks in total (Marsh and Goicochea, 2006). All grids were checked on the same day to control for precipitation, with the order of grids alternating to control for time-of-day bias. Field work then resumed in mid-September through mid-November, and repeated the following year, through 2022. In spring of 2019, one additional field

week was included, and in fall of 2019 and 2022 field work was cut short by a week due to inclement weather. Observers checked under each ACO, carefully collected any salamanders found and placed them in plastic bags labelled with the ACO position. Salamanders were thus collected and brought back to the processing area, where mass, snout-vent length, and total length were measured. They were then candled for the presence of eggs or sexual characteristics and checked for visual implant elastomer (VIE) marks. If unmarked, salamanders were marked for individual identification following the protocol described by the VIE website (Northwest Marine Technology Inc., 2019), with marks recorded clockwise from the salamander's upper right leg. Once marked and measured, salamanders were released next to the ACO under which they were found. Handling and marking were conducted with approval of the Purdue Animal Care and Use Committee (Protocol #1902001849).

At each grid, three ACOs were randomly selected for environmental data collection. During salamander surveys, observers measured the soil

pH and temperature using a FieldScout SoilStik™ pH Meter, leaf litter depth using a ruler placed flush to the surface of the soil, and volumetric water content of the soil using a HydroSense™ II meter next to each selected board. After measuring environmental data at all three ACOs, air temperature and relative humidity were measured using a handheld Kestrel 5500 Fire Weather Meter Pro unit held at arm's length from the body while standing in shade near the grid.

Prior to prescribed fires, pyrometers (i.e., paint tags) were placed in a 25 m x 25 m grid pattern across the whole of the burn site to record flame temperatures. Pyrometers consisted of a numbered 2.5 cm×7.0 cm aluminum tag with six dots of Tempilaq® temperature-indicating paint. Tags could, therefore, measure 7 potential temperature thresholds: 79°, 121°, 163°, 204°, 316°, 427°, and 661°C (tag melts). Leaf litter and fuel amounts (by size class) were measured at each paint tag location. After the burn, measurements of percent mineral soil exposed, percent char, and scorch heights were taken. Measurements taken ≤50 m from the coverboard grid were averaged for the analysis, with paint tag data aggregated by quartile. ACOs were left in place during burns, as fire temperatures were too low to damage the wooden boards.

2.4. Statistical analyses

We used R for Statistical Computing version 4.2.2 (R Core Team, 2022) and MARK (White and Burnham, 1999) interfaced through R using package RMark (Laake, 2013) for analyses. We constructed encounter histories for each marked salamander captured at each grid, which were used to estimate salamander abundance, apparent survival (S), random temporary emigration (γ) – which in this study was unable to separate salamanders leaving the site from salamanders unavailable for sampling due to moving underground, although the latter is by far more likely for these species (Bailey, 2002) – and capture probability (p) using a Robust Design model in Rmark (Kendall et al., 1995; Pollock, 1982). The Robust Design method involves temporally clustering capture-mark-recapture surveys into 'primary' sessions, when the population is assumed to be open to demographic processes, and 'secondary' sessions, which are separated by short enough time intervals that demographic closure can be assumed. This approach allowed us to assume an overall open population and obtain abundance estimates for each sampling season while accounting for both availability of salamanders for capture and their detection probability. As mortality and permanent emigration cannot be distinguished in these models, true survival rates are typically underestimated, and we instead report the apparent survival, which represents the probability that an individual both survives and stays within the study area (Lebreton et al., 1992). Notably, adult red-backed salamanders maintain and defend home ranges and preferred cover objects (Mathis, 1990), which may reduce occurrences of permanent emigration. Temporary emigration is likewise expected to be primarily due to salamanders moving up and down the soil column,

rather than leaving the site (Bailey, 2002).

Grids were distant enough from each other to treat each as an independent population; hence, we modeled captures from each grid separately. We examined total salamander captures (*P. cinereus* and *P. dorsalis*) because model sets examining species individually failed to produce reliable results in four of six grids, likely due to lower captures of single species in those grids. We sorted data both into primary sessions by field season (spring and fall for each year of the study), and further split data from field seasons containing fires into two primary sessions, one before and one after the fire occurred. We were thus able to examine changes in apparent survival and temporary emigration before and after fires at burn sites and potential fire effects on population abundance. We modeled initial capture and recapture probabilities as equal ($p=c$), and examined models with monthly apparent survival (S) and random temporary emigration (γ) varying before and after fire or held constant (null models); models with capture probability varying with soil moisture, with leaf litter, with season (spring or fall), or held constant (null models); and models with survival and emigration varying with fire and capture probability varying with soil moisture or leaf litter (Table 1). All models used the logit link function. Soil moisture and leaf litter were chosen as the variables most likely to affect salamander capture probability, as salamanders are known to seek deeper refuges when soils are dry and use leaf litter for refuges on the surface (Grover, 1998). Since only one primary sampling session occurred in grid Bx2 before its first prescribed fire, we were not able to estimate survival or emigration before fire in that grid, and therefore could not compare survival and emigration before and after fire in grid Bx2. Additionally, as we caught no salamanders in grid Bx2 during the fall of 2019, that period was removed from the model and time intervals adjusted to reflect the longer interval. A model set comparing all grids together was also attempted, but models containing both grid and fire effects failed to produce reliable results, possibly due to too few captures in some grids.

We extracted coefficient estimates with 95% confidence intervals from the model outputs for the following covariates: presence of fire, soil moisture, and leaf litter. A coefficient estimate with a confidence interval that did not overlap zero was considered to indicate a significant effect of the variable on the parameter of interest (S, γ, or p). We then visually examined changes in estimates of abundance from the best-fitting model, using model selection with AIC (Akaike, 1998) with corrections for small sampling size (AICc, Sugiura, 1978; Hurvich and Tsai, 1991) over time and between grids (Figure 3.3).

Following the capture-mark-recapture analysis, we examined the effect of fire on environmental variables (leaf litter, soil moisture, soil temperature, and pH) using linear mixed-effects models to account for the random effect of grid. We tested seven models on each environmental variable. The first examined the effect of a binary (Before=0, After=1) fire factor variable alone (Model 1, Table 2). The second examined the effect of a binary Before/After fire factor variable, an effect of season (Spring=0, Fall=1), and their interaction (Model 2, Table 2). The third examined the effect of a binary Before/After fire factor variable, an effect of aspect (NE=0, SW=1), and their interaction (Model 3, Table 2). The fourth, fifth, and sixth models examined the continuous variable Percent Char rather than a binary fire variable in models examining fire alone, fire and season, and fire and aspect (Models 4–6, Table 2). The final model examined the effects of season, aspect, and their interaction, without the effect of fire or fire intensity (Model 7, Table 2). We examined the conditional Akaike Information Criterion (cAIC; Saefken et al. 2014) of each model and reported results from the model containing the explanatory variables of interest (fire, percent char, season, or aspect) with the lowest cAIC. Data and R code used for the study are available from the authors.

Table 1

Variables affecting parameters (S=apparent survival, γ=temporary emigration, p=capture probability) in each of the eight mark-recapture models. BA indicates a before/after fire variable. Each grid was modeled separately; control grids Cm and Cx and grid Bx2 only examined Null, Soil Moisture, Leaf Litter, and Season models.

	Parameters		
Models	S	γ	p ($=c$)
Null	~1	~1	~1
Before/After Fire	~BA	~BA	~1
Before/After Fire, Soil Moisture	~BA	~BA	~Soil Moisture
Before/After Fire, Leaf Litter	~BA	~BA	~Leaf Litter
Before/After Fire, Season	~BA	~BA	~Season
Soil Moisture	~1	~1	~Soil Moisture
Leaf Litter	~1	~1	~Leaf Litter
Season	~1	~1	~Season

Table 2

Parameterization of linear mixed-effects models of environmental variables (leaf litter, soil moisture, soil temperature, and pH) by a binary before/after fire variable (Fire), percent char, season (spring or fall), aspect (NE or SW), and interactions between, with the random effect of grid. An X indicates that the variable is included in the model; Interaction indicates that an interaction between the two variables was also included.

| Model | Variables | | | | | Random Effects |
	Fire	Percent Char	Season	Aspect	Interaction	(1|Grid)
1	X					X
2	X		X		X	X
3	X			X	X	X
4		X				X
5		X	X		X	X
6		X		X	X	X
7			X	X	X	X

3. Results

3.1. Fire effects on environmental variables

Fire temperatures averaged 157.7°C across grids, with the highest temperatures in grid Bm1 with a maximum temperature of at least 426.7°C and lowest temperatures in grid Bx1 with a maximum temperature of 121.1°C (Table 3). Leaf litter depth was significantly lower after fires of higher intensity than before fires (p=0.001, R^2 = 0.49, Table 4). Leaf litter depth was also significantly higher in fall (p=0.021, R^2 = 0.49, Appendix). For leaf litter depth, models of fire intensity did not perform substantially better than models of fire presence (ΔAIC<10, Appendix). Fire did not affect soil moisture, soil pH, or soil temperature (p>0.1, Table 4, Appendix). Soil pH was slightly lower on southwest slopes compared to northeast slopes after fire (p=0.061, R^2 = 0.36, Appendix) and with slightly greater fire intensity (p=0.053, R^2 = 0.37, Appendix). There was a significant effect of season on soil moisture (p<0.001, R^2=0.75, Table 4), with greater soil moisture in the spring.

Soil temperature exhibited some seasonal trends, often appearing higher in fall than in spring, but with large variation, particularly in the spring of 2021 and 2022, and did not noticeably vary between grids (Fig. 2a). Soil pH remained fairly stable and consistent among grids (Fig. 2b). Soil moisture differed between seasons, with all grids behaving similarly (Fig. 2c). Leaf litter depth declined sharply after the first field season but otherwise was reasonably stable (Fig. 2d).

3.2. Fire effects on salamander populations

We conducted 63 checks of the salamander grids over eight field seasons between 2019 and 2022 and recorded a total of 4922 salamander captures: 2923 *P. cinereus*, 1947 *P. dorsalis*, and 52 unidentified salamanders that could have been either species. These captures represented 1939 marked individuals: 1003 *P. cinereus* and 936 *P. dorsalis*. While some grids had noticeably more salamanders than others, the range of total captures in control (216–613 salamanders) and burn grids (149–523 salamanders) was similar (Table 5).

Effects of fire were observed in two of three analyzed fire grids (Bm1 and Bx1), with lower temporary emigration (γ) in grid Bm1 after burns and lower apparent survival (*S*) in grid Bx1 following burns (Table 6). Notably, while grid Bm1 experienced the highest maximum fire temperatures, on average fires were hottest in grid Bm2 (Table 3), which had no effect of fire on salamanders (Table 6). Leaf litter depth had a

Table 3

Fire intensity measurements used in analysis from each grid: paint tag temperatures (median and maximum) and percent char.

Grid	Median Temp °C	Max Temp °C	Mean % Char
Bm1	162.8	≥426.7	90
Bx1	121.1	121.1	86.7
Bm2	183.6	315.6	84.3
Bx2	162.8	315.6	90

Table 4

Results of linear mixed-effects models predicting soil temperature, soil pH, soil moisture, and leaf litter depth. Predictors included effects of fire occurrence (B/A), percent char (PC), season (fall), aspect (southwest-facing slopes), and two-way interactions. The fixed R^2 (Zhang, 2020) is reported for each model. Only models with the lowest cAIC are shown.

Response (R^2)	Predictor	Coefficient	SE	p-value
Soil Temperature (0.192)	B/A	1.281	1.351	0.351
	Season	-1.602	1.280	0.221
	B/A x Season	-0.854	1.752	0.630
Soil pH (0.374)	PC	0.005	0.002	0.054
	Aspect	-0.237	0.406	0.602
	PC x Aspect	-0.008	0.004	0.053
Soil Moisture (0.751)	PC	0.049	0.031	0.120
	Season	**19.136**	2.822	**<0.001**
	PC x Season	-0.029	0.042	0.492
Leaf Litter (0.401)	PC	-0.011	0.003	**0.001**
	Aspect	0.062	0.339	0.862
	PC x Aspect	0.001	0.004	0.877

positive effect on capture probability (*p*) in two of three analyzed fire grids (Bm2 and Bx1) and a negative effect on capture probability in the third fire grid (Bm1, Table 7). Including control grids, soil moisture had a positive effect on capture probability in all grids except grid Cm. Season also affected capture probability in most analyzed grids, with lower capture probability in the fall in four of five grids (Bm1, Bx1, Bx2, Cx, but not Cm, Table 7). Due to low captures, the effect of season could not be analyzed in grid Bm2 (Table 5).

Models of salamander survival and temporary emigration with soil moisture effects on capture probability included were superior to other models, as determined by AICc, in all grids except for Bx2 and Cm: for grid Cm, all models were very similar, with no effect of predictor variables. Models with the before/after fire variable also had low AICc, and models with soil moisture and fire had the lowest AICc in all burn grids except for Bx2 (Table 8). Grid Cm had the lowest overall *S*, while Bx1 had the highest (Table 9). γ varied between grids from 0.191 after fire in grid Bm1 to 0.492 after fire in grid Bx2 (Table 9).

Examining abundance estimates from the best models by AICc for each grid showed that grids Cx, Bx1, Bm2, and Bx2 all appeared to behave similarly regardless of fire, with generally low abundance increasing in fall of 2021 through spring 2023. Grids Bm1 and Cm likewise appeared to show similar trends, although abundance in Bm1 decreased slightly while others increased in spring of 2023; the increase in Cm in 2023, meanwhile, was larger than the increase in other grids (Fig. 3).

4. Discussion

We observed few effects of prescribed fire on salamander apparent survival and temporary emigration, with differing but negative effects seen in only two of three grids; effects further declined to only one grid
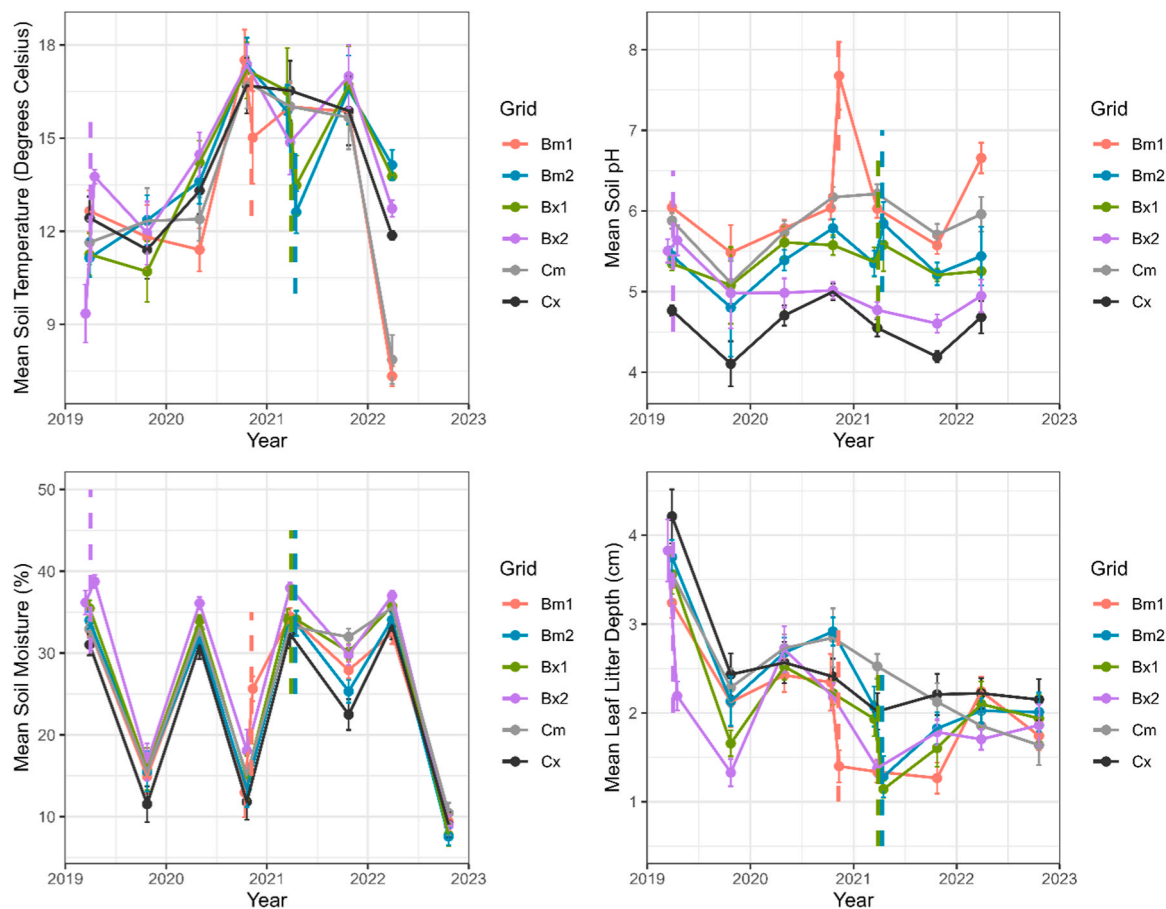
Fig. 2. Variation in environmental variables: soil temperature, soil pH, soil moisture, and leaf litter depth in response to prescribed burns. Error bars indicate standard errors around the mean for each field season. Vertical lines indicate burns corresponding to grid color.

Table 5
Number of marked salamanders at each grid in total and by species, morphology and sex.

Grid	Total	*P. cinereus*	*P. dorsalis*	Males	Females	Unknown sex
Bm1	**523**	163	360	115	117	291
Bx1	**185**	97	88	52	57	76
Bm2	**253**	144	109	39	54	160
Bx2	**149**	124	25	39	49	61
Cm	**613**	311	302	68	90	455
Cx	**216**	164	52	50	41	125

when the effect of soil moisture on capture probability was considered. Prescribed fire in one grid (Bm2) had no effect on salamander populations, and effects in other grids were on either temporary emigration (Bm1) or survival (Bx1), with no effect on survival after the effect of soil moisture on capture probability was included. This suggests that effects of prescribed fire were sporadic and may be moderated by other factors.

Indeed, salamander abundance over time appeared to fluctuate somewhat similarly across all grids including control grids, suggesting that annual variation or the characteristics of individual grids may be more influential than prescribed fire in driving variation in salamander populations.

The intensity of prescribed fires in our study was deliberately constrained to meet management goals, but our fires were higher intensity than fires reported in previous studies in the Appalachians (Ford et al., 2010; Greenberg et al., 2018, 2016; Keyser et al., 2004), for winter burns (O'Donnell et al., 2015), and for spring burns in southern hardwood ecosystems in Missouri (O'Donnell et al., 2016). According to Major (2005), fire intensity may affect the strength of fire effects on salamanders. However, the range of intensities presented in previous studies, the variability in their effects independent of fire intensities, and our results suggest that average fire intensity within the range considered may be less important to determining fire effects than other unexplored factors. Prescribed fires in this study were directly comparable

Table 6
Coefficients, standard errors, and 95% confidence intervals (upper and lower) from capture-mark-recapture models examining effects of before/after fire and percent char on apparent survival (*S*) and temporary emigration (γ) in burn grids, with model specifications listed. Estimates and confidence intervals are bolded where estimates do not overlap zero. Before/After Fire models were parameterized as: *S*(~Before/After), γ''= γ'(~Before/After), *p*(~1) to examine the effects of fire alone. γ' is defined as the probability remaining outside the study area between primary sessions, while γ'' is defined as the probability of an individual leaving the study area between primary sessions.

Before/After Fire								
Grid	*Coefficient (S)*	SE	Lower	Upper	*Coefficient* (γ)	SE	Lower	Upper
Bm1	-0.261	0.166	-0.586	0.065	**-1.562**	0.393	**-2.333**	**-0.791**
Bx1	**-1.103**	0.506	**-2.094**	**-0.112**	0.006	0.459	-0.894	0.906
Bm2	0.173	0.415	-0.639	0.986	0.581	0.416	-0.235	1.396

Table 7
Coefficient estimates, standard errors, and 95% confidence intervals (upper and lower) from capture-mark-recapture models examining effects of soil moisture, leaf litter, and season on capture probability (p, with $p=c$) in salamander sampling grids, with model specifications listed. Estimates and confidence intervals are bolded where estimates do not overlap zero. Models were parameterized as: $p(\sim$Soil Moisture$)$; $p(\sim$Leaf Litter$)$; or $p(\sim$Season$)$.

Soil Moisture				
Grid	Coefficient (p)	SE	Lower	Upper
Bm1	**0.027**	0.004	**0.02**	**0.034**
Bx1	**0.066**	0.007	**0.052**	**0.081**
Bm2	**0.025**	0.005	**0.015**	**0.034**
Bx2	**0.056**	0.009	**0.039**	**0.073**
Cm	-0.001	0.003	-0.008	0.005
Cx	**0.04**	0.005	**0.031**	**0.050**
Leaf Litter				
Bm1	**-0.152**	0.037	**-0.225**	**-0.080**
Bx1	**0.467**	0.066	**0.337**	**0.597**
Bm2	**0.117**	0.052	**0.015**	**0.219**
Bx2	0.088	0.073	-0.056	0.232
Cm	-0.02	0.036	-0.091	0.050
Cx	0.011	0.047	-0.081	0.104
Fall Season (as compared to Spring)				
Bm1	**-0.737**	0.078	**-0.890**	**-0.584**
Bx1	**-0.911**	0.136	**-1.178**	**-0.644**
Bx2	**-1.301**	0.185	**-1.663**	**-0.938**
Cm	-0.057	0.089	-0.231	0.117
Cx	**-0.825**	0.107	**-1.035**	**-0.616**

Table 8
Model rankings of top models (ΔAICc<5 and Akaike weight>0.05) of salamander survival (S), temporary emigration (γ), and capture probability (p) for each grid, along with model specifications (covariates include before/after fire (BA), intercept (1), or environmental variables), AICc, weights, and deviance for each model.

Grid	S	γ	p	AICc	weight	Deviance
Bm1	~BA	~BA	~Soil Moisture	1612.283	1	2898.440
Bx1	~BA	~BA	~Soil Moisture	954.995	1	984.580
Bm2	~BA	~BA	~Soil Moisture	1406.63	1	1610.179
Bx2	~1	~1	~Season	779.471	0.913	694.982
	~1	~1	~Soil Moisture	784.179	0.087	699.691
Cm	~1	~1	~Season	616.279	0.352	1128.996
	~1	~1	~Leaf Litter	616.368	0.337	1129.085
	~1	~1	~Soil Moisture	616.522	0.312	1129.239
Cx	~1	~1	~Soil Moisture	1490.079	0.997	1781.403

to prescribed fires used in the region for forest management (e.g., Cuprewich & Saunders, in press), suggesting that prescribed fires for oak regeneration in the Midwest may have little effect on salamander populations over time frames comparable to our study.

Reducing fuel loads of leaf litter is often a key goal of prescribed fires (Pilliod et al., 2003), and our prescribed fires did lower leaf litter depth. In all prescribed fire grids except for Bx2, leaf litter also was associated with higher capture probability under higher leaf litter for two grids and lower capture probability in a third. Capture probability is associated with salamander surface activity, as salamanders are unavailable for sampling when underground; thus, reductions in capture probability may indicate lower surface activity. It is likely that repeated applications of prescribed fire over longer timeframes may further reduce leaf litter, potentially to the point of restricting salamander surface activity and affecting survival through reductions in cover for salamanders or through reductions in invertebrate prey that use or feed on leaf litter. Lower capture probability with lower leaf litter depth may also hamper monitoring efforts by increasing variation in parameter estimates, which may increase the necessary sampling effort for obtaining meaningful results. Notably, the grid that had lower capture probability with higher

Table 9
Estimates of monthly apparent survival (S) and temporary emigration (γ) from top model for each grid (Table 8), along with standard error and upper and lower 95% confidence intervals. In burn grids Bm1, Bm2, and Bx1, S and γ vary by before/after fire (B/A), while in control grids Cx and Cm and burn grid Bx2 S does not vary and γ is fixed at 0 (γ'') or 1 (γ') to model no temporary emigration.

Grid	Parameter	Before/ After Fire	Estimate	SE	Lower	Upper
Bm1	S	B	0.919	0.008	0.901	0.934
	S	A	0.905	0.009	0.885	0.922
	γ	B	0.471	0.049	0.376	0.568
	γ	A	0.191	0.057	0.103	0.327
Bx1	S	B	0.962	0.011	0.932	0.979
	S	A	0.968	0.023	0.877	0.992
	γ	B	0.298	0.102	0.140	0.525
	γ	A	0.492	0.082	0.338	0.648
Bm2	S	B	0.940	0.009	0.919	0.956
	S	A	0.949	0.018	0.901	0.974
	γ	B	0.327	0.068	0.209	0.472
	γ	A	0.465	0.078	0.321	0.616
Bx2	S		0.924	0.011	0.9	0.942
	γ	Fixed				
Cm	S		0.891	0.006	0.878	0.903
	γ	Fixed				
Cx	S		0.923	0.007	0.907	0.936
	γ	Fixed				

leaf litter was in Morgan-Monroe State Forest, while the other two were both in Yellowwood State Forest. Higher salamander populations have been seen in Morgan-Monroe than Yellowwood State Forest in this (Table 2) and previous studies (Ochs et al., 2022), despite the similarities in forest composition and location. As salamanders can be territorial (Mathis, 1990), and the effects of territoriality can increase with population density (Marvin, 1998), it is possible that salamanders in higher density areas react differently to leaf litter than in lower density areas. It is also notable that capture probabilities in the grid with the highest estimated abundance (Cm) were not substantially affected by any environmental variables.

Soil moisture affected salamander detection more than leaf litter depth, consistently increasing capture probability with increased soil moisture. As salamanders rely on cool, moist conditions and avoid surface movements when the soil is dry, this relationship is expected (Feder, 1983; O'Donnell and Semlitsch, 2015; Spotila, 1972). Soil moisture was closely related to season (Fig. 2), and models of soil moisture outperformed models of season, thus suggesting a seasonal effect driven by soil moisture. The connection between soil moisture and season is corroborated by models of seasonal effects, which had lower detection in the fall, when soil moisture is lower and soil temperatures are higher. While the mesic control grid, Cm, did not exhibit effects of soil moisture, it also demonstrated no effect of leaf litter or season, and all models were similar to the null model. Notably, Cm had the highest number of salamander captures and consistently higher populations (Fig. 1), perhaps making the grid more resilient to environmental changes than other grids on drier aspects or receiving treatment.

Aspect has been suggested to affect salamander populations (Moseley et al., 2009), and our grids were stratified by aspect, with one control grid and two burn grids each on either northeast-facing or southwest-facing slopes. However, examining estimated population abundances between grids, aspect did not appear to affect salamander population responses to our prescribed fires, nor did it affect soil moisture, leaf litter depth, or soil temperature. Soil pH was the only variable affected by aspect, and was only slightly lower on southwest-facing slopes. The influence of aspect is largely expected to act through effects on soil moisture and temperature, with southwest-facing slopes typically warmer and drier than northeast-facing slopes (Moseley et al., 2009). Previous research at the HEE demonstrated aspect effects on the abundance of *P. dorsalis*, but not *P. cinereus* (MacNeil and Williams,
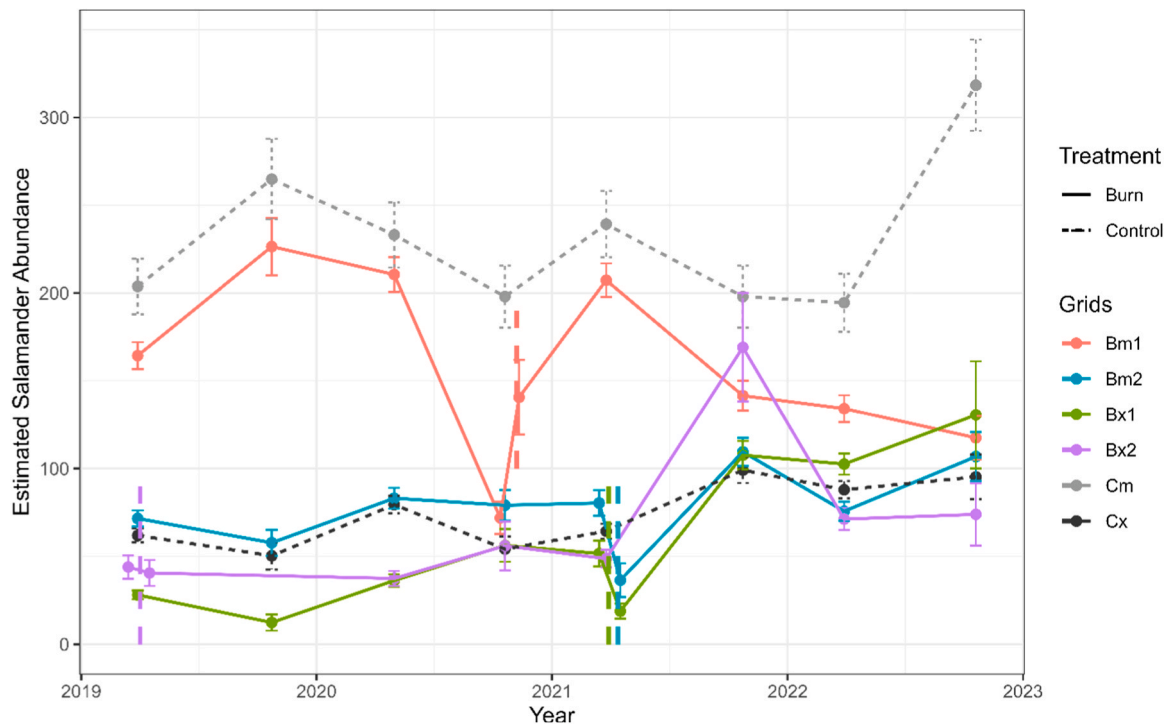
Fig. 3. *Plethodon* salamander abundance estimated by robust design models during the study. Error bars indicate standard error. Vertical dotted line segments indicate prescribed fires corresponding to grid color.

2014). Given the limited number of grids and lack of slope measures, it is possible that the aspects in our study were less defined than other areas, or that the higher captures of *P. cinereus* than *P. dorsalis* masked any potential effects of aspect on a single species.

Due to a lack of replication between treatment (prescribed fire or control) and aspect, and the distance between study grids leading to completely separate populations, we were unable to directly compare grids to each other, which limited some of the inferences from our study. Future studies should use paired control grids near prescribed fire grids for a full before-after-control-impact design (Green, 1979). While we initially hoped to use such a design, the unpredictable nature of scheduling for prescribed fires among different grids made it difficult to compare all prescribed fire grids to the few control grids, because control grids needed to be designated both before and after burn simultaneously to compare with different prescribed fires. Our study also examined only a few years post-fire and did not examine the potential impact of multiple fires at a site. Repeated fires may not only suppress leaf litter layers but may also alter invertebrate communities, affecting salamander prey abundance and foraging, a variable that was not accounted for in this study that can have strong effects on salamander abundance (O'Donnell et al., 2016) and could lead to a lagged effect of prescribed fire on salamander populations. Oak management uses a sequence of prescribed fires to slowly but dramatically shift forest composition by altering seed beds, leaf litter, and duff layers, with sequential fires differing in intensity and purpose; in the Midwest, recommendations are for three or more prescribed fires within a 15-year window (Cuprewich & Saunders, 2024), often with follow-up or concurrent thinning. More than fire intensity, the number of fires at a site, fire return intervals, or the season in which fires occur may greatly affect salamander populations. Salamander populations may take several years to respond to disturbances such as timber harvest and may face additional threats from combined disturbances from drought and management (Ochs et al., 2022). Additional research is needed to determine how prescribed fire may interact with other disturbances over a longer time scale.

5. Conclusions

Overall, we found few and small effects of prescribed fire on terrestrial salamanders. However, fire effects may indirectly affect salamanders by changes to the microclimate such as loss of leaf litter, which may affect salamanders' ability to forage and find mates on the soil surface. Independent of fire, variables such as soil moisture have sizable effects on salamander activity and may merit greater attention in case of declines in moisture or salamander populations. Further research is needed on factors that support higher salamander density between forests of similar composition to those studied here, but larger populations likely are better able to adjust to future prescribed fires and environmental changes. Long-term effects of prescribed fires and potential interactions of fire with other disturbances remain unknown. In the face of such uncertainty, supporting large salamander populations will be important when considering future forest management methods. Understanding the interplay between forest quality and forest management techniques will be critical to identifying best practices for sustaining sensitive wildlife populations including salamanders.

CRediT authorship contribution statement

Alison Ellen Ochs: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robert K. Swihart:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Michael R. Saunders:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix

Table A1

Outputs of linear mixed-effects models examining the effect of before/after fire (B/A), percent char (PC), season (fall), and aspect (southwest-facing slopes) on soil temperature, soil moisture, soil pH, and leaf litter. Coefficients, standard errors, and p-values, along with cAIC are shown for each model. P-values less than 0.05 are bolded, as are the lowest cAIC for that environmental variable. Where p values less than 0.05 occur in models with the lowest cAIC for that environmental variable, corresponding coefficients are also bolded.

		Soil											
		Temperature			Moisture			pH			Leaf Litter		
Model	Variable	Coefficient	SE	p-value	Coefficient	SE	p-value	Coefficient	SE	p-value	Coefficient	SE	p-value
(1) ~B/A	B/A	0.798	0.665	0.389	0.694	3.516	0.845	0.134	0.169	0.434	-0.883	0.183	**<0.001**
				cAIC=153.39			cAIC=272.78			cAIC=45.41			cAIC=65.06
(2) ~B/A x Season	B/A	1.281	1.351	0.351	4.266	2.724	0.127	0.199	0.263	0.456	-0.521	0.258	0.052
	Season	-1.602	1.280	0.221	19.117	2.829	**<0.001**	0.195	0.238	0.419	0.654	0.267	**0.021**
	B/A x Season	-0.854	1.752	0.630	-2.532	3.674	0.496	-0.101	0.325	0.757	-0.565	0.347	0.114
				cAIC=151.59			cAIC=227.14			cAIC=48.65			cAIC=63.50
(3) ~B/A x Aspect	B/A	0.185	1.334	0.891	1.136	5.001	0.822	0.419	0.214	0.062	-0.941	0.256	**0.001**
	Aspect	-0.542	1.395	0.701	3.936	5.592	0.487	-0.247	0.412	0.592	0.054	0.333	0.877
	B/A x Aspect	1.216	1.910	0.530	-1.955	7.291	0.790	-0.640	0.328	0.061	0.056	0.383	0.884
				cAIC=157.12			cAIC=276.21			cAIC=43.99			cAIC=67.53
(4) ~PC	PC	0.009	0.010	0.394	0.008	0.040	0.835	0.002	0.002	0.426	-0.010	0.002	**<0.001**
				cAIC=153.4			cAIC=272.77			cAIC=45.37			cAIC=64.82
(5) ~PC x Season	PC	0.014	0.015	0.362	0.049	0.031	0.120	0.002	0.003	0.438	-0.006	0.003	**0.046**
	Season	-1.613	1.280	0.218	**19.136**	2.822	**<0.001**	0.200	0.237	0.407	0.642	0.267	**0.023**
	PC x Season	-0.009	0.020	0.640	-0.029	0.042	0.492	-0.001	0.004	0.739	-0.006	0.004	0.124
				cAIC=151.64			*cAIC=227.02*			cAIC=48.59			cAIC=67.28
(6) ~PC x Aspect	PC	0.002	0.015	0.906	0.013	0.057	0.818	0.005	0.002	0.054	**-0.011**	0.003	**0.001**
	Aspect	-0.552	1.395	0.696	3.932	5.589	0.487	-0.237	0.406	0.602	0.062	0.339	0.862
	PC x Aspect	0.014	0.022	0.526	-0.023	0.083	0.790	-0.008	0.004	0.053	0.001	0.004	0.877
				cAIC=157.13			cAIC=276.21			*cAIC=43.79*			*cAIC=63.42*
(7) Season x Aspect	Season	-2.616	1.016	**0.014**	15.920	2.151	**<0.001**	0.131	0.174	0.458	0.389	0.263	0.146
	Aspect	-0.146	1.109	0.896	-0.959	2.195	0.664	-0.863	0.352	0.051	-0.070	0.271	0.801
	Season x Aspect	1.101	1.448	0.451	2.472	3.047	0.421	0.104	0.247	0.676	0.065	0.372	0.863
				cAIC=215.63			cAIC=328.56			cAIC=58.87			cAIC=116.31

References

Akaike, H., 1998. Information Theory and an Extension of the Maximum Likelihood Principle, in: Parzen, E., Tanabe, K., Kitagawa, G. (Eds.), Selected Papers of Hirotugu Akaike. Springer New York, New York, NY, pp. 199–213.

Anderson, H.E., 1982. Aids to Determining Fuel Models For Estimating Fire Behavior. Gen. Tech. Rep. 122.

Bailey, L.L., 2002. Estimating Detection Probabilities for Terrestrial Salamanders in Great Smoky Mountains National Park (Doctoral Thesis). North Carolina State University, Raleigh.

Brose, P.H., Dey, D.C., Waldrop, T.A., 2014. The Fire – Oak Literature of Eastern North America: Synthesis and Guidelines. Gen. Tech. Rep. 135.

Bury, R., Major, D., Pilliod, D., 2002. Responses of amphibians to fire disturbance in Pacific Northwest forests: a review. Role Fire Nongame Wildl. Manag. Community Restor. Tradit. Uses N. Dir. 34–42.

Bury, R.B., 2004. Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests (Special section: Wildfire and conservation in the western United States). Conserv. Biol. 18, 968–975.

Campbell, J.W., Grodsky, S.M., Keller, O., Vigueira, C.C., Vigueira, P.A., Waite, E.S., Greenberg, C.H., 2018. Response of beetles (Coleoptera) to repeated applications of prescribed fire and other fuel reduction techniques in the southern Appalachian Mountains. Ecol. Manag. 429, 294–299.

Cuprewich, S.A., Saunders, M.R., 2024. Evaluating the impact of prescribed surface fire on seedlings in the Central Hardwood Region, USA. For. Int. J. For. Res. 97, 94–106.

Feder, M.E., 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39, 291–310.

Fontaine, J.B., Kennedy, P.L., 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. Fire-prone forests. Ecol. Appl. 22, 1547–1561.

Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J., McCay, T.S., 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. Ecol. Manag. 114, 233–243.

Ford, W.M., Rodrigue, J.L., Rowan, E.L., Castleberry, S.B., Schuler, T.M., 2010. Woodland salamander response to two prescribed fires in the central Appalachians. Ecol. Manag. 260, 1003–1009.

Green, R.H., 1979. Sampling Design and Statistical Methods for Environmental Biologists. John Wiley & Sons.

Greenberg, C.H., Moorman, C.E., Raybuck, A.L., Sundol, C., Keyser, T.L., Bush, J., Simon, D.M., Warburton, G.S., 2016. Reptile and amphibian response to oak regeneration treatments in productive southern Appalachian hardwood forest. Ecol. Manag. 377, 139–149.

Greenberg, C.H., Moorman, C.E., Matthews-Snoberger, C.E., Waldrop, T.A., Simon, D., Heh, A., Hagan, D., 2018. Long-term herpetofaunal response to repeated fuel reduction treatments. J. Wildl. Manag. 82, 553–565.

Grover, M.C., 1998. Influence of cover and moisture on abundances of the terrestrial Salamanders Plethodon cinereus and Plethodon glutinosus. J. Herpetol. 32, 489–497.

Hanberry, B.B., Kabrick, J.M., He, H.S., 2014. Densification and state transition across the Missouri Ozarks landscape. Ecosystems 17, 66–81.

Hanson, E.E., 1978. The Impact of A Prescribed Burn in A Temperate Subalpine Forest upon the Breeding Bird and Small Mammal Populations. Thesis (M.S.)–Central Washington University.

Hesed, K.M., 2012. Uncovering salamander ecology: a review of coverboard design. J. Herpetol. 46, 442–450.

Hocking, D.J., Connette, G.M., Scheffers, B.R., Peterman, W.E., Conner, C.A., Pittman, S. E., Semlitsch, R.D., Scheffers, B.R., Pittman, S.E., Peterman, W.E., Semlitsch, R.D., 2012. Effects of experimental forest management on a terrestrial, woodland salamander in Missouri. Ecol. Manag. 287, 32–39.

Hromada, S.J., Howey, C.A.F., Dickinson, M.B., Perry, R.W., Roosenburg, W.M., Gienger, C.M., 2018. Response of reptile and amphibian communities to the reintroduction of fire in an oak/hickory forest. Ecol. Manag. 428, 1–13. https://doi. org/10.1016/j.foreco.2018.06.018.

Hurvich, C.M., Tsai, C.-L., 1991. Bias of the corrected AIC criterion for underfitted regression and time series models. Biometrika 78, 499–509.

Jacobsen, C.D., Brown, D.J., Flint, W.D., Schuler, J.L., Schuler, T.M., 2020. Influence of prescribed fire and forest structure on woodland salamander abundance in the central Appalachians, USA. Ecol. Manag. 468.

Kendall, W.L., Pollock, K.H., Brownie, C., 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51, 293–308.

Keyser, P.D., Sausville, D., Ford, W.M., Schwab, D.J., Brose, P.H., 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvest oak-dominated forests. Va J. Sci. 55, 159–168.

Laake, J.L., 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC processed report; 2013-01.

Landers, J.L., Crawford, R.L., 1995. A Study of Habitat Relations of Nongame Birds and Mammals in Seres of Oldfield Pinewoods following Fire Exclusion. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62, 67–118.

MacNeil, J.E., Williams, R.N., 2014. Effects of timber harvests and silvicultural edges on terrestrial salamanders. PLoS One 9.

Main, M.B., Richardson, L.W., 2002. Response of wildlife to prescribed fire in southwest Florida pine flatwoods. Wildl. Soc. Bull. 30, 213–221.

Major, D.J., 2005. Effects of fire disturbance on terrestrial salamanders in mixed-coniferous forests of the Klamath/Siskiyou region of the Pacific Northwest (PhD). Thesis (Ph.D.)–Utah State University.

Marsh, D.M., Goicochea, M.A., 2006. Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. J. Herpetol. 37, 460–466.

Marvin, G.A., 1998. Territorial behavior of the plethodontid salamander Plethodon kentucki: influence of habitat structure and population density. Oecologia 114, 133–144.

Mathewson, B., 2007. Salamanders in a changing environment on hemlock hill. Arnoldia 65, 19–25.

Mathis, A., 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. Behavior 112, 162–175.

McDade, K.A., Maguire, C.C., 2005. Comparative effectiveness of three techniques for salamander and gastropod land surveys. Am. Midl. Nat. 153, 309–320.

Mendes, D.M., Leão, R., de, F., Toledo, L.F., 2015. Drift fences in traps: theoretical evidence of effectiveness of the two most common arrays applied to terrestrial tetrapods. Nat. e Conserv. 13, 60–66.

Mitchell, J.C., 2000. Observations on amphibians and reptiles in burned and unburned forests on the upper coastal plain of Virginia. Va J. Sci. 51, 199–204.

Moseley, K.R., Castleberry, S.B., Schweitzer, S.H., 2006. Effects of prescribed fire on Herpetofauna in bottomland hardwood forests. Southeast. Nat. 2, 475–486.

Moseley, K.R., Ford, W.M., Edwards, J.W., 2009. Local and landscape scale factors influencing edge effects on woodland salamanders. Environ. Monit. Assess. 151, 425–435.

Northwest Marine Technology Inc., 2019. Visible Implant Elastomer Tags [WWW Document]. URL ⟨https://www.nmt.us/visible-implant-elastomer/⟩ (accessed 8.26.19).

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "Mesophication" of forests in the Eastern United States. Bioscience 58, 123–138.

O'Donnell, K.M., Semlitsch, R.D., 2015. Advancing terrestrial salamander population ecology: the central role of imperfect detection. J. Herpetol. 49, 533–540.

O'Donnell, K.M., Thompson, F.R., Semlitsch, R.D., 2015. Prescribed fire and timber harvest effects on terrestrial salamander abundance, detectability, and microhabitat use. J. Wildl. Manag. 79, 766–775.

O'Donnell, K.M., Thompson, F.R., Semlitsch, R.D., 2016. Prescribed fire alters surface activity and movement behavior of a terrestrial salamander. J. Zool. 298, 303–309.

Ochs, A.E., Saunders, M.R., Swihart, R.K., 2022. Response of terrestrial salamanders to the decade following timber harvest in hardwood forests. Ecol. Manag. 511, 120159.

Panek, D., Kipfmueller, K., 2021. Past, Present and Future of Fire in the Apostle Islands, in: Apostle Islands 50th Anniversary Resource Stewardship Symposium.

Pausas, J.G., Keeley, J.E., 2014. Abrupt climate-independent fire regime changes. Ecosystems 17, 1109–1120.

Pilliod, D.S., Bury, R.B., Hyde, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. Ecol. Manag. 178, 163–181.

Pollock, K.H., 1982. A capture-recapture design robust to unequal probability of capture. J. Wildl. Manag. 46, 752–757.

Pyne, S.J., 1996. Introduction to Wildland Fire, 2nd ed. ed, Wiley. New York.

R Core Team, 2022. R: A Language and Environment for Statistical Computing.

Rieman, B., Clayton, J., 1997. Wildfire and native fish: issues of forest health and conservation of sensitive species. Fisheries 22, 6–15.

Russell, K.R., Lear, D.H., Van, Guynn, D.C., Russell, K.R., Lear, D.H., Van, Guynn, D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildl. Soc. Bull. 27, 374–384.

Russell, R.E., Royle, J.A., Saab, V.A., Lehmkuhl, J.F., Block, W.M., Sauer, J.R., 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecol. Appl. 19, 1253–1263.

Saefken, B., Kneib, T., van Waveren, C.S., Greven, S., 2014. A unifying approach to the estimation of the conditional Akaike information in generalized linear mixed models. Electron. J. Stat. 8, 201–225.

Spotila, J.R., 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42, 95–125.

Sugiura, N., 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Commun. Stat. Theory Methods 7, 13–26.

Sutton, W.B., Wang, Y., Schweitzer, C.J., 2013. Amphibian and reptile responses to thinning and prescribed burning in mixed pine-hardwood forests of northwestern Alabama, USA. Ecol. Manag. 295, 213–227.

Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, G.S., Michler (editors), C.H., 2013. The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management. General Technical Report NRS-P-108. USDA Forest Service, Northern Research Station, Newtown Square, PA.

Taub, F.B., 1961. The distribution of the redbacked Salamander, Plethodon C. cinereus, within the soil. Ecology 42, 681–698.

Tiedemann, A.R., Klemmedson, J.O., Bull, E.L., 2000. Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk? Ecol. Manag. 127, 1–18.

Welsh, H.H., Droege, S., 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conserv. Biol. 15, 558–569.

Welsh, H.H., Hodgson, G.R., 2013. Woodland salamanders as metrics of forest ecosystem recovery: a case study from California's redwoods. Ecosphere 4, 1–25.

Welsh Jr, H.H., Ollivier, L.M., 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's Redwoods. Ecol. Appl. 8, 1118–1132.

White, G., Rockwell, D., McDuff, E., 2021. Embracing Indigenous Knowledge to Address the Wildfire Crisis. U.S. Department of the Interior, Office of Wildland Fire.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird. Study 46, S120–S139.

Wyman, R.L., 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodivers. Conserv 7, 641–650.

Zhang, D., 2020. Coefficients of Determination for Mixed-Effects Models. arXiv 2007, 0867.