Global Ecology and Conservation 57 (2025) e03389

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Unburned habitat essential for amphibian breeding persistence following wildfire

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ARTICLE INFO

Keywords:
Burn severity
Wood frog
Lithobates sylvaticus
Occupancy
Wetlands

ABSTRACT

Wildfire regimes are changing rapidly with widespread increase in the intensity, frequency, and duration of fire activity, especially in the western United States. Limited studies explore the impacts of wildfires on aquatic taxa and few focus on lentic habitats that are essential for amphibians, many of which are of conservation concern. We capitalized on existing pre-fire surveys for anuran species and resurveyed a random subset of wetlands across a gradient of soil burn severity to investigate the short-term effects of wildfire on a relict population of wood frogs in the southern Rocky Mountains. We also investigated whether maps created to support rapid post-fire emergency response activities (i.e., United States Forest Service Burned Area Emergency Response program) accurately characterize soil burn severity around small habitat features (i.e., ponds) that serve as important amphibian breeding and rearing habitat. Soil burn severity reflects fire impacts on soil and surface organic layers, including vegetation loss and changes in soil structure and function. We found that wood frog (*Lithobates sylvaticus*) breeding persistence following fires was negatively influenced by the percentage of their terrestrial habitat (100 m buffer surrounding breeding ponds) that was burned. Wood frog colonization probability of previously unoccupied ponds was low (~ 0.10) and unaffected by soil burn severity. Importantly, we found that remotely sensed data typically produced to predict flooding and erosion at broad (catchment) scales is a poor representation of the amount and variation in soil burn severity surrounding small habitat features, suggesting that additional field sampling is necessary to understand wildfire responses for species that rely on these small habitat features. Understanding short-term geographic- and species-specific variation in response to wildfires provides the basis to explore time to recovery (e.g., when wood frogs return to burned breeding sites) or to determine if declines in breeding distributions intensify over time.

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https://doi.org/10.1016/j.gecco.2024.e03389
Received 19 July 2024; Received in revised form 18 December 2024; Accepted 29 December 2024
Available online 30 December 2024

1. Introduction

Wildfire regimes are changing globally with widespread increase in the intensity, frequency, and duration of fire activity (Westerling, 2016; Ward et al., 2020; Higuera et al., 2021; Alizadeh et al., 2021). This is especially true in the western United States where the 2020 fire season marked a decades-long trend of increasing wildfire activity that nearly doubled the total area burned during the last half century in some areas (Alizadeh et al., 2021; Higuera et al., 2021). Historically, mid- and low-elevation forests in this region experienced relatively frequent, low intensity fires (Parks et al., 2015), but high-elevation subalpine forests, with typically moist, cool climates, burn less frequently, with larger, stand-replacing fires (Sibold et al., 2006; Calder et al., 2015; Higuera et al., 2021). Twenty-first century climate scenarios now suggest that fire activity in Rocky Mountain subalpine forests exceeds the range of variability previously experienced by these ecosystems and the organisms that evolved within them (Higuera et al., 2021).

Understanding the effects of large wildfire events is important, but difficult to study due to the stochastic nature of fires, and because species and community responses vary widely (e.g., Pastro et al., 2014; dos Anjos et al., 2021). Wildfire can result in a myriad of environmental change to both terrestrial (e.g., Fontaine and Kennedy, 2012) and aquatic ecosystems (e.g., Arkle and Pilliod, 2010) and affect food web structure and function across these systems (e.g., Preston et al., 2023). The number of studies evaluating wildfire effects on fauna has grown in recent years, but we still understand little about how organisms, especially those in high-elevation forests, respond to wildfire (Fontaine and Kennedy, 2012; Gomez Isaza et al., 2022). Most literature on fire effects in aquatic systems focuses on streams, with few studies on ponds and wetlands (Bixby et al., 2015). Additionally, fire effects likely depend on spatial pattern of burning, yet most studies lack important pre-fire information and rigorous probabilistic post-fire sampling to address spatial variation in fire intensity (Bixby et al., 2015). Most existing literature focused on vertebrate responses treat fire as a binary variable, comparing burned and unburned areas (Parr and Chrown, 2003; dos Anjos et al., 2021). However, fire severity, an indicator of the proportion of vegetation and soils burned (Parsons et al., 2010), is considered the most relevant metric to evaluate fire effects (Kennedy and Fontaine 2012) and it varies widely within most wildfire scars (e.g., Kolden et al., 2012; Meddens et al., 2018). Numerous reviews and meta-analyses highlight the need for fire severity metrics to better understand variation in wildlife response across sites and species (Hossack and Pilliod, 2011; Fontaine and Kennedy, 2012; dos Anjos et al., 2021).

Among vertebrate taxa, anurans are underrepresented in the fire response literature, but they are particularly relevant to an understanding of the impacts of fire. Because of their biphasic life histories, they are susceptible to fire effects in both terrestrial and aquatic habitats (Hossack and Pilliod, 2011; dos Anjos et al., 2021; Heard et al., 2023). As ectotherms, anuran physiology, behavior, and growth are governed by microhabitat conditions (e.g., temperature, humidity) that can change dramatically following fire (Hossack et al., 2009). Few studies have explored wildfire effects on anurans in the western United States (but see Rochester et al., 2010; Hossack et al., 2013b; Barrile et al., 2022) and it is uncertain how broadly studies from other ecosystems apply due to differences in fire regimes, regional climates, and species assemblages (Hossack and Pilliod, 2011). Drawing on existing literature, known life history, and species distributions, we might expect few effects of fire on anuran survival or reproduction, except for range-restricted species that rely on fire-sensitive vegetation (Hossack and Pilliod, 2011; Mahony et al., 2022). Still, predictions regarding wildfire effects on anurans vary; fire may lead to more advantageous (i.e., warmer) wetland conditions for larvae, but species using smaller, ephemeral pools may be more vulnerable (Hossack and Pilliod, 2011). Species that prefer cooler temperatures are less tolerant to desiccation, and those with limited dispersal abilities may be especially susceptible to environmental changes following wildfire (Hossack et al., 2009, Mahony et al., 2022).

In this study we capitalize on pre-fire amphibian surveys to test the effect of soil burn severity on persistence and colonization of breeding wood frogs (*Lithobates sylvaticus*), a relict, high-elevation species in the southern Rocky Mountains of North America. We stratified previously sampled ponds based on remotely sensed burn severity categories (United States Department of Agriculture 2020, Burned Area Emergency Response (BAER) Report) and resurveyed all or a random subset of ponds within each stratum during the breeding season after a large wildfire. Soil burn severity assessment includes loss of understory vegetation, woody debris, litter/duff layer, in addition to changes in soil structure and fine roots that compromise structural integrity post fire (USDA, 2020, BAER Report). Additionally, we investigated whether maps created to support rapid post-fire emergency response activities (i.e., United States Forest Service Burned Area Emergency Response (USFS BAER) program) have utility for characterizing soil burn severity surrounding small features (i.e., ponds). Such ponds serve as important amphibian breeding/rearing habitat, while the surrounding upland habitat provides critical foraging and overwintering areas for amphibian species.

2. Methods

2.1. Study area and target species

The Medicine Bow Mountains are located within the Medicine Bow National Forest in southeastern Wyoming, USA. The forest is dominated by spruce-fir (*Picea engelmannii; Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) stands that have been impacted heavily by mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (USDA, 2020, BAER Report). High-severity, stand-replacing wildfires have historically occurred at century-long intervals in these higher elevation forests (Schoennagel et al., 2004); however, due to increased drought, the frequency of wildfires has nearly doubled relative to the past two millennia (Alizadeh et al., 2021; Higuera et al., 2021).

Wood frogs occur above 2600 m in the Medicine Bow Mountains and represent one of two highly disjunct relict populations that persist in the southern Rocky Mountains after glacial retreat (Holman, 2003; Lee-Yaw et al., 2008). Wood frogs typically breed over 1–4 weeks early in the spring in fishless permanent, semi-permanent, and ephemeral water bodies (Baxter and Stone, 1980;

Hammerson, 1999). They use surrounding wet meadows, willow patches, and nearby aspen (*Populus tremuloides*) groves during summer foraging and seek hibernacula (e.g., litter, moss, small mammal burrows) near breeding wetlands in late summer and early fall (Cook, 2023). Unlike other amphibians that seek hibernacula below the surface to avoid freezing (e.g., rodent burrows), wood frogs tend to hibernate in shallow soil/duff layers because they produce cryoprotectants that allow them to survive sub-freezing temperatures (Storey and Storey, 1984; Costanzo et al., 2013). Most research and ecological knowledge of the species is based on studies in the eastern United States, which may not always translate to higher elevation habitats in the southern Rocky Mountains (Muths et al., 2005). Little is known about the species' response to fire anywhere within its range (dos Anjos et al., 2021).

In the southern Rocky Mountains, wood frogs are considered a vulnerable species due to their highly restricted range, most of which occurs on U.S. Forest Service (USFS) lands (Wyoming Game and Fish Department, 2017*;* Muths et al., 2005). Wood frogs are sensitive species in USFS Region 2 and a Tier II species of greatest conservation need in Colorado and Wyoming (Colorado Parks and Wildlife, 2015; Wyoming Game and Fish Department, 2017). Forest activities near their breeding sites are limited to actions that either benefit or have minimal adverse effects to wood frogs or their habitat. The need to improve forest health and reduce hazardous fuels are on-going priorities for land management agencies. Balancing these concerns with wood frog conservation has become a focus in the last decade.

The USFS is required to conduct surveys for sensitive species, including wood frogs, within areas proposed for vegetation management. Such surveys were conducted by USFS personnel during the two years preceding the Mullen Fire (see next section for survey details). The Mullen Fire started on September 17th, 2020 and burned 71,311 ha in southern portions of the Medicine Bow Mountains. Similar to recent wildfires in the region, the Mullen Fire burned in the fall when wood frogs are likely to be foraging or seeking hibernacula. The Mullen Fire was the largest single-start wildfire in Wyoming history, with daily runs up to 15 km. Approximately one

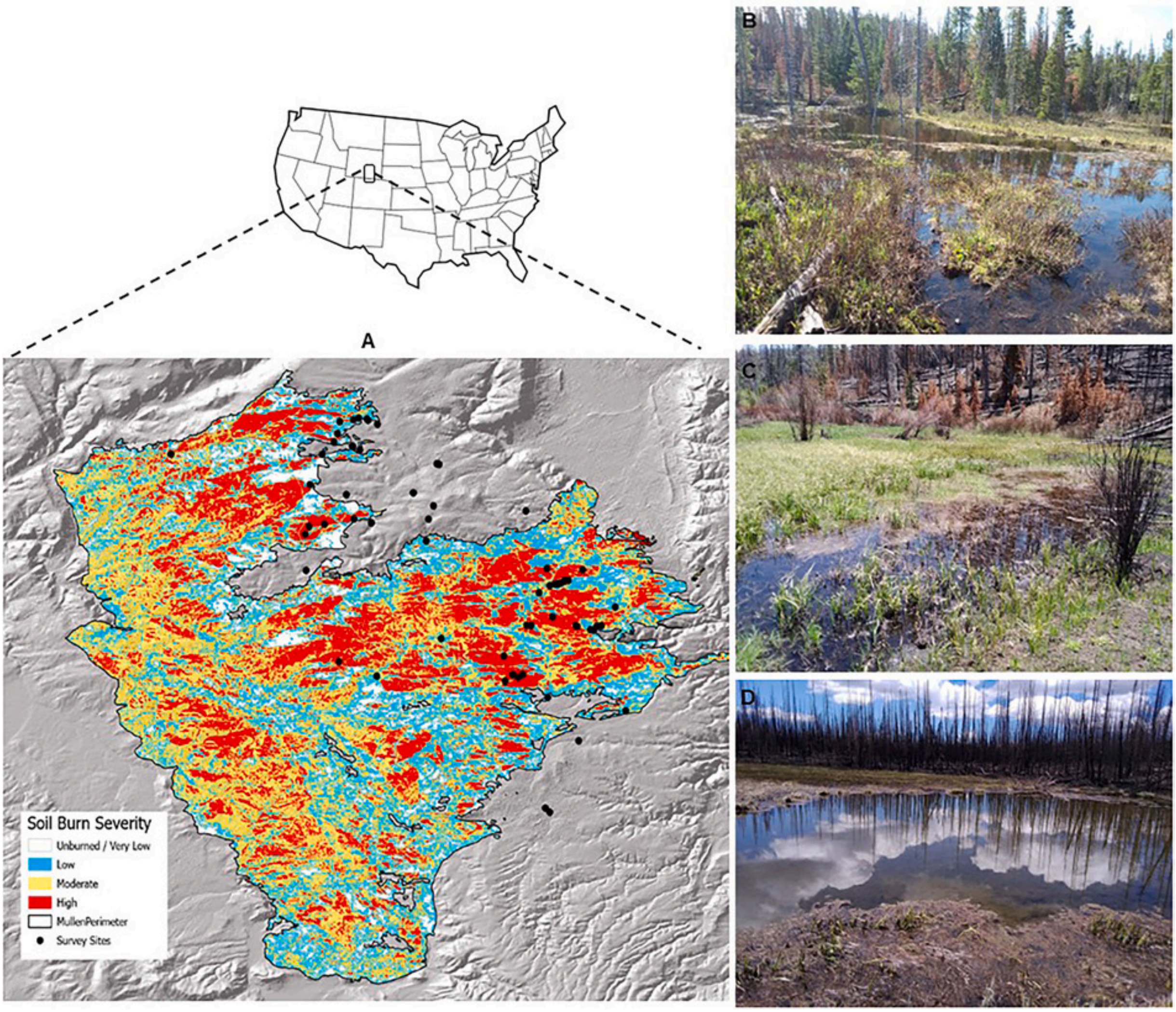

Fig. 1. A: Map displaying Mullen Fire burn perimeter, including soil burn severity categories, and sampled ponds (black circles). Examples of an unburned pond (B; 6/7/3021) and ponds with moderate soil burn severity (C; 6/8/2021) and high soil burn severity (D; 6/3/2021).

third of the known wood frog breeding sites in the Medicine Bow Mountains were within or near the area burned by the fire, providing a unique opportunity to study the short-term effects of fire on this species.

2.2. Study design

In 2019 and 2020, the USFS proposed vegetation management projects within the study area and polygons containing potential wetlands were identified via the National Wetland Inventory database (U.S. Fish and Wildlife Service, 2018). Between mid-May – September, biologists censused these polygons to locate wetlands and conducted a single visual encounter survey for amphibians at identified wetlands (i.e., ponds). Visual encounter surveys consisted of 1–3 observers slowly walking the pond perimeter searching for amphibians of any life history phase (e.g., egg masses, tadpoles, juveniles, or adults). Additional potential and known wood frog breeding sites were identified, and added to the sample frame, via a concurrent study conducted in the same area (Cook, 2023).

We used a stratified random sample to select ponds to resurvey post-fire. Specifically, we categorized all known and potential breeding ponds into three burn categories (high, moderate, or low severity), plus an unburned category. Categories were based on a soil burn severity layer developed for the Mullen Fire (Fig. 1; USDA, 2020, BAER Report; also see Section 2.4 below). These locations were further categorized based on evidence of breeding (egg masses or tadpoles) observed during pre-fire surveys (Table 1; 8 total strata). Our primary objective was to evaluate the effect of soil burn severity on persistence of wood frog breeding post-fire. To do this, we resurveyed locations with evidence of breeding in 2019–2020 (i.e., pre-fire): nearly all burned ponds and 12 randomly selected, unburned ponds (Table 1). We also resampled four burned ponds where juvenile wood frogs were observed during pre-fire surveys. Secondarily, we explored the effect of soil burn severity on wood frog 'colonization' of pond habitats as other amphibian species are known to colonize recently burned wetlands that may contain favorable thermal habitats (Hossack and Corn, 2007; Hossack et al., 2009). Accordingly, we randomly selected 6–10 potential breeding sites (ponds) within each burn strata where wood frogs were not observed during the 2019–2020 pre-fire surveys (Table 1).

2.3. Amphibian surveys

After the fire, crews resurveyed 67 ponds during wood frog breeding season when conspicuous egg masses are available for detection (Fig. 1, Table 1). Surveys took place 2–16 June 2021, using a double independent observer approach to estimate detection probability. Members of the two-person crew independently surveyed each pond for evidence of wood frog breeding (e.g., egg masses or tadpoles). Observers recorded data separately and did not discuss survey results until surveys were completed. Immediately following surveys, the crew recorded several survey- and site-specific characteristics that could influence wood frog breeding or detection probability (e.g., water temperature and depth, fish presence; Table 2). If only tadpoles were observed, 2–5 individuals were collected for identification based on tooth row characteristics visible with a dissecting microscope (McDiarmid and Altig, 1999). If identification to species could not be confirmed, the ponds were revisited 3 weeks later to identify tadpoles or metamorphic frogs. Additionally, a subset of ponds without initial egg mass or tadpole detections were also revisited, such that each pond had 2–3 independent surveys during the season.

2.4. Soil burn severity comparison: Field observations and BAER map values

USFS post-fire assessment uses remotely sensed data and local information to identify areas where high severity wildfire is likely to threaten natural resources and infrastructure (USDA, 2020, BAER Report). Remote sensing is based on differences in pre- and post-fire indices of reflectance (i.e., dNBR, van Wagtendonk et al., 2004; Cocke et al., 2005) associated with combustion of vegetation and surface soil organic matter layers (O-horizons). Field crews then verify or adjust imagery to match standard soil burn severity classes encountered throughout the burned area (Parsons et al., 2010). The information generated during this rapid data acquisition and analysis (typically within weeks of a fire) is intended for predicting erosion, flooding, debris flow, and associated resource damage at relatively broad catchment scales and short time frames (1–3 years; USDA, 2020, BAER Report). Information derived from this approach is commonly used to evaluate longer term ecosystem response and recovery (e.g., Nelson et al., 2022; Caiafa et al., 2023), but it is unclear how suitable changes calculated within 30×30 m pixels is for evaluating burned habitat around small landscape features (e.g., small wetlands).

We used a line-intercept method to evaluate the agreement between remotely sensed maps and field measures of soil burn severity near burned ponds ($n = 45$). We defined "near" as habitat within 100-m of the edge of a pond and considered this area to be the 'buffer'. Our buffer size was based on a concurrent study evaluating adult wood frog movement and habitat use (Cook, 2023); that

Table 1
Number of ponds identified and surveyed in 2019–2020 prior to the Mullen Fire. Post-fire, these ponds were distributed among eight strata based on mapped soil burn severity (4 levels) and evidence of wood frog (*Lithobates sylvaticus*) breeding (2 levels). Most burned ponds where wood frog breeding was documented before the fire were resurveyed and a random subset of 6–12 ponds were chosen from each of the other strata.

	Evidence of Wood Frog Breeding				No Evidence of Wood Frogs			
Burn Strata:	Unburned	Low	Moderate	High	Unburned	Low	Moderate	High
Ponds surveyed prior to fire (2019–2020)	24	9	10	3	107	33	39	43
Sampled ponds with potential breeding habitat post-fire	12	7	9	2	10	10	6	7

Table 2
Survey- and site-specific covariates hypothesized to influence the probability of wood frog (*Lithobates sylvaticus*) breeding persistence (conversely, local extinction ε), colonization (γ), or detection probability (*p*). 'na' indicates no hypothesized relationship.

Covariate	Range	Description	Expected effect		
			ε	γ	*p*
High Soil Burn Severity (HighBurn)	0–0.82	Percentage of 100 m buffer surrounding each pond that was severly burned based on ground cover field measurements	+	-	na
Unburned Area (Unburn)	0–1.00	Percentage of 100 m buffer surrounding each pond that was unburned based on ground cover field measurements	-	+	na
High + Moderate Soil Burn Severity (High&Mod)	0–0.93	Sum of the percentage of 100 m buffer surrounding each pond that was severly or moderately burned based on ground cover field measurements	+	-	na
Fish presence (Fish)	0,1	Denotes whether trout were detected (1) or not (0) in any of the 2–3 surveys.	+	-	na
Surface area (SArea)	0.01–3.75	Estimated surface area (ha) using maximum width and length measurements for each pond	-	+	-
Depth	< 1 m, > 1 m	Binary covariate denoting whether the pond was deep (maximum depth >1 m) or shallow (maximum depth <1 m)	-	+	-
Water temperature (Wtemp)	6.0–28.0	Water temperature (C) of the pond during each survey	na	na	+

study revealed that wood frogs in the Medicine Bow Mountains rarely use habitats more than 50–100 m from a known breeding pond during their summer foraging season. Additionally, wood frogs selected hibernacula near aquatic habitats (≤ 20 m), seldom exceeding distances of 50–120 m from known breeding ponds (Cook, 2023). In the field, we sampled four transects starting at the water edge and extending 100-m into the surrounding habitat. The orientation of the first transect was chosen randomly, and the remaining transects were oriented at 90-degree intervals from the first. Soil burn severity was assessed at 3-meter intervals (34 points) along each transect using: (1) ground cover (O-horizon, bare soil) and (2) understory vegetation (shrubs/herbaceous) and standard burn severity categories (unburned, low, moderate, and high; Parsons et al., 2010). The percentage of points in each burn category was compared with BAER mapped data for the same pond. Specifically, we created a 100 m buffer of the pond perimeter clipped to the Mullen Fire soil burn severity layer (USDA, 2020, BAER Report) to estimate the proportion of area within each buffer in the four burn severity categories (hereafter 'mapped' soil burn severity metric).

2.5. *Bland-Altman agreement analysis*

We used the Bland-Altman analysis (Altman and Bland, 1983; Bland and Altman, 1986) to evaluate agreement between field observations and mapped soil burn severity metrics for areas surrounding ponds within the burn perimeter. This analysis is commonly used to quantify agreement (i.e., concordance) between two quantitative measures of the same unknown value and detect systematic differences between the measurements (i.e., bias) or possible outliers. The approach is superior to a simple correlation because it provides measures of agreement between the two methods not simply the strength of the linear relationship between the measures (Bland and Altman, 1986).

First, we evaluated the agreement between the two field observations (vegetation and ground cover) collected via the line-intercept method. Using the percentage of sampled points (n = 136 total points) in each of four burn severity categories (low, moderate, high, and unburned), we used scatterplots, Pearson's correlation coefficients (*r*), and Bland-Altman plots to demonstrate the degree of agreement between the two field measures for each burn severity category (Appendix A). Next, we evaluated the agreement between the BAER mapped soil burn severity and one of the field observations (ground cover). Again, we used scatterplots, correlation coefficients (*r*), and Bland-Altman plots to evaluate the agreement between BAER mapped and ground cover measures of soil burn severity within 100 m buffers of each pond within the burn perimeter (Appendix B).

2.6. *Dynamic occupancy analysis*

We used a dynamic occupancy analysis to test the effects of soil burn severity and other site-specific covariates on persistence and colonization of breeding wood frogs following the Mullen Fire. Dynamic occupancy models (MacKenzie et al., 2003) consist of four types of parameters: initial, pre-fire occupancy (ψ_1), local extinction (ε) and colonization probabilities (γ), and the probability of detecting wood frog breeding (egg masses or tadpoles), given breeding occurred at the pond (*p*). Wood frog persistence is simply the complement of local extinction (1- ε), so hypotheses regarding wood frog persistence were addressed by modeling local extinction probability. In the occupancy framework, local extinction is the probability that a pond that previously supported breeding wood frogs at one time period (t) no longer supports breeding at the following time period ($t + 1$). Likewise, colonization probability is the probability that a pond that previously did not support breeding wood frogs at time t, now supports breeding at time $t + 1$.

We used detection-nondetection data from pre-fire and post-fire surveys for each of our 67 sampled ponds to fit a series of models representing *a priori* hypotheses about factors likely to influence model parameters. First, we fixed $\psi_1 = 1$ for ponds where wood frog breeding was detected during pre-fire surveys and estimated pre-fire occupancy for other ponds. Next, we explored whether wood frog persistence (or conversely, local extinction) was influenced by soil burn severity surrounding the pond. Given the lack of agreement between mapped and field soil burn severity measures (see Section 3.2 below), we used field ground cover observations to estimate the percentage of the 100 m buffer that was severely burned (HighBurn), high or moderately burned (High&Mod), and unburned

(Unburn). We modeled breeding persistence and colonization as a function of each of these burn severity covariates independently to determine which was the best predictor of these dynamic parameters. We also explored whether breeding persistence and colonization were influenced by factors other than soil burn severity. Wood frogs typically breed in wetlands that dry annually or semiannually and that lack fish (Dodd, 2023). Accordingly, we considered models where dynamic parameters were a function of fish presence (Fish), pond surface area (SArea), or differed between deep (>1 m) or shallow (<1 m) ponds (breeding persistence only; Table 2). Finally, we explored whether wood frog detection probability was influenced by water temperature (WTemp), pond surface area, or depth (Depth; Table 2).

We fit all models using the Robust Design Occupancy model in Program *MARK* (White and Burnham, 1999). We employed a secondary candidate set model building approach (Morin et al., 2020), where we fit models to test hypotheses about one focal parameter at a time (e.g., persistence, $\varphi = 1- \varepsilon$) using a null model structure for the other non-focal parameters (i.e., γ, p; Appendix C). This approach is better than other model building strategies at recovering total Akaike weights, limiting inclusion of unimportant covariates, and identifying the most parsimonious model when using model types with multiple parameters (Morin et al., 2020). We combined all supported parameter structures, with $\Delta AICc < 10$ and no correlated or uninformative covariates, into a final 'combined model set' and used model selection approaches to draw scientific inference (Burnham and Anderson, 2002).

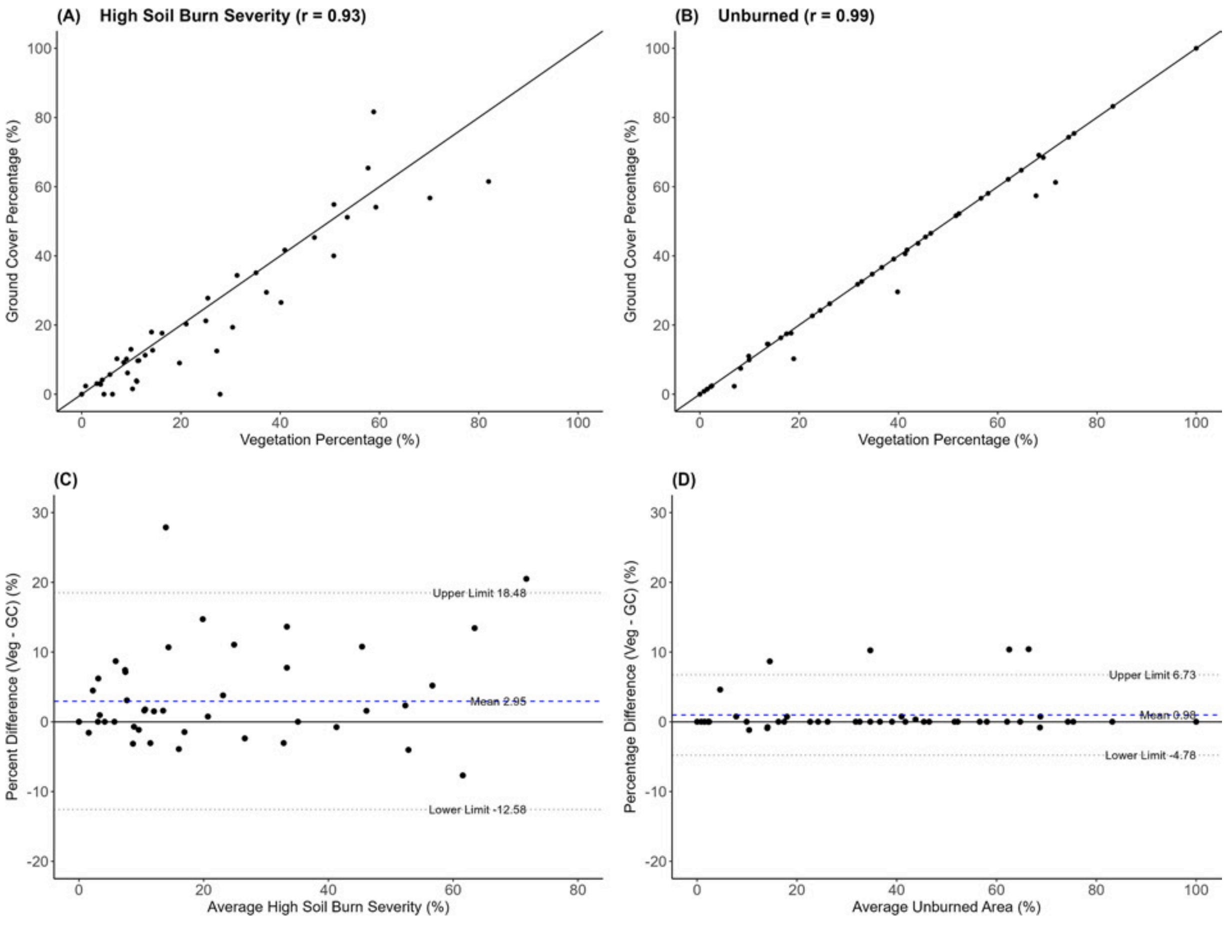

Fig. 2. Scatterplots and calculate Pearson's correlation coefficient (r) for the percentage of high soil burn severity (A) and unburned area (B) at sample points in 100 m buffers surrounding 45 ponds within the Mullen Fire based on vegetation or ground cover evaluation using a line-intercept sampling method. The Bland-Altman plot shows the difference between the percentage of sampled points with high soil burn severity (C) and unburned designation (D) based on vegetation (Veg) and ground cover (GC) field measurements. The data points in the Bland-Altman plot are close to zero and the limits of agreement are relatively low and symmetric, demonstrating good agreement between the soil burn severity based on field evaluations of vegetation and ground cover. There is no relationship between the discrepancy between vegetation and ground cover evaluations and the estimated percentage of the buffer that was severely burned (C) or unburned (D).

3. Results

3.1. Agreement analysis

There was good agreement between the two field measures (vegetation and ground cover) in their ability to categorize variation in soil burn severity within the 100 m buffer around each pond within the burn perimeter (Fig. 2; Appendix A). The two measurements produced nearly identical percentages of unburned area within pond buffers (Fig. 2B) and the mean difference in estimated percentages for any burn severity category never exceeded 5 % (Appendix A). Estimating burn severity via vegetative measures produced slightly larger percentages of high soil severity burn (mean difference: 2.95 %; Fig. 2C) and slightly lower percentages of low soil severity burn (mean difference: −4.15 %; Fig. A3.2) relative to ground cover measurements. However, the discrepancy between the two measures at a given pond rarely exceeded ± 18 % regardless of the soil burn severity category (see limits of agreement reported in Fig. 2 and Appendix A).

Our field measurements also revealed remarkable heterogeneity in soil burn severity among and within pond buffers. Soils within some buffers were severely burned (high percentages of high soil burn severity, Figs. 1 and 2A), while soils within other buffers were predominantly unburned (Fig. 2B). The estimated percentage of buffers with moderate burn severity never exceeded 40 % (Figs. A2.1 and A2.2), and most buffers contain a mosaic of soil burn severity.

In contrast, the agreement between field measures and mapped soil burn severity metrics for the pond buffers was poor. Correlation coefficients (*r*) between mapped and field ground cover measurements were never > 65 % for any soil burn severity category (Fig. 3) and the correlation was zero or negative for moderate and low soil severity burn categories, respectively (Appendix B). Mapped estimates of the amount of area burned within pond buffers was higher for all soil burn severity categories, especially high (mean

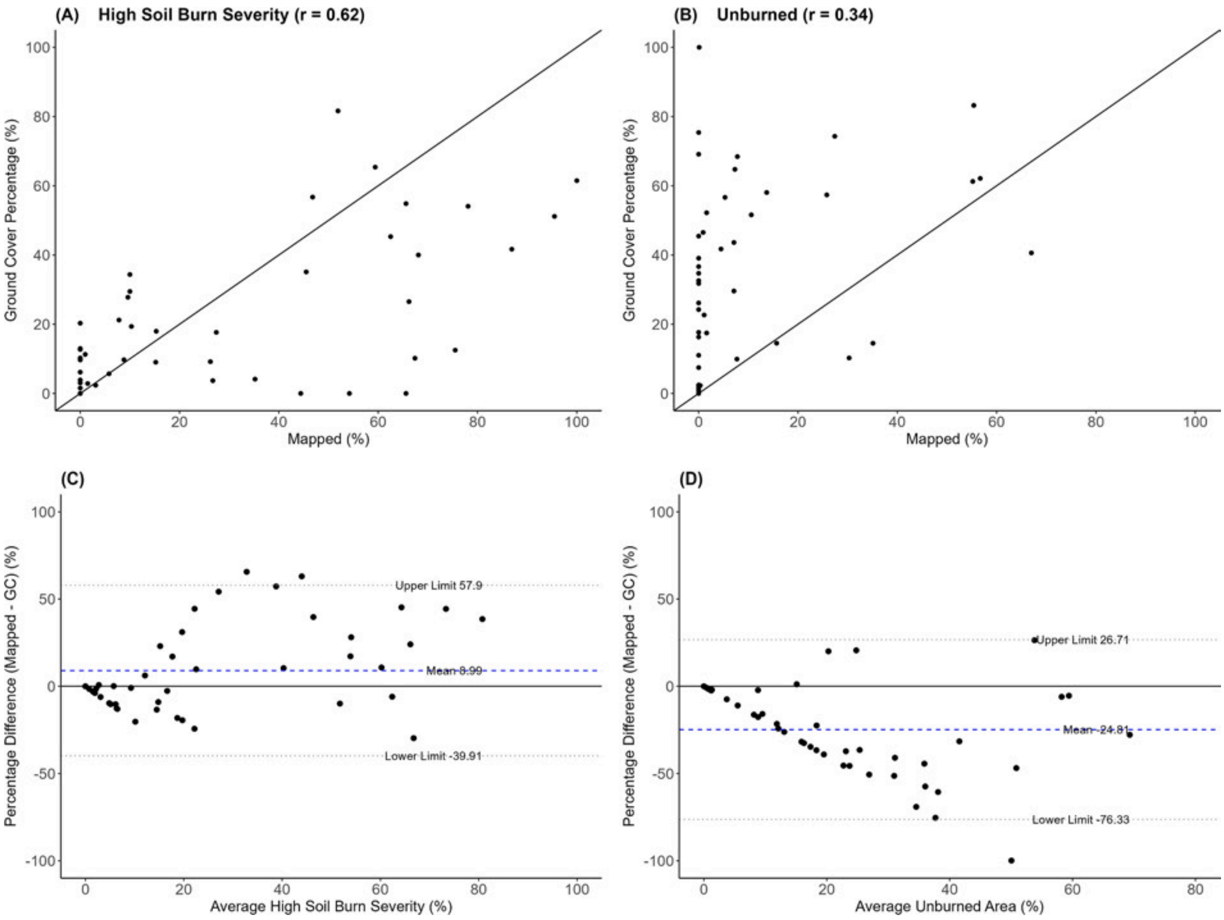

Fig. 3. Scatterplots and calculate Pearson's correlation coefficient (r) for the percentage of area categorized as high soil burn severity (A) and unburned (B) for 100 m buffers surrounding 45 ponds within the Mullen Fire perimeter based on mapped or field ground cover evaluation. The Bland-Altman plot shows the difference between the percentage of area with high soil burn severity (C) and unburned designation (D) based on Mapped and ground cover (GC) measurements. The data points in the Bland-Altman plot are not near zero, the limits of agreement are wide, and the discrepancy between mapped and field ground cover measures increases with higher percentages of the buffer that was severely burned (C) or unburned (D).

difference: 8.99 %; Fig. 3C) and moderate soil burn severity (mean difference: 14.17 %; Appendix B; Fig. B2.2). Moreover, the variation in the amount of area burned varied dramatically between mapped and field estimates, often exceeding ± 50–75 % (e.g., Fig. 3C; Appendix B). The limits of agreement were also extremely wide, especially for unburned habitat, such that 95 % of burned ponds had BAER mapped estimates of unburned habitat that were between ~75 % less than and ~25 % higher than field ground cover evaluations (Fig. 3D). Collectively, these findings suggest that BAER maps poorly represent the degree and diversity of soil burn severity around small wetland features.

3.2. Dynamic occupancy analysis

We detected evidence of wood frog breeding at 18 of the 30 ponds identified as breeding sites during pre-fire surveys (naïve occupancy/persistence = 0.60). We also detected wood frog breeding at four other ponds, one where only a juvenile was observed during pre-fire surveys and three where wood frogs had not been previously detected (naïve occupancy/colonization = 0.11).

We found good support that wood frog breeding persistence varied based on the percentage of area burned (or unburned) around ponds (Table 3, Table C.1). The amount of unburned habitat within the pond buffers was a slightly better predictor of the probability of the persistence of wood frog breeding relative to percentages of high soil burn severity or a combination of high and moderate soil burn severity. All three burn severity metrics were better at modeling variation in wood frog breeding persistence relative to other hypothesized factors (i.e., pond depth, surface area, fish presence; Table C.1). Wood frogs continued to breed at ~80 % of occupied ponds outside of the fire perimeter ($\widehat{\varphi} = 1 - \widehat{\varepsilon} = 0.80$; $\widehat{SE}(\widehat{\varphi}) = 0.11$), but persistence probabilities declined dramatically when little (< 20 %) or no unburned area remained within the pond buffer following wildfire ($\widehat{\varphi} = 0.30 - 0.40$;). Fig. 4

Unlike some other amphibian species, we found no evidence that wood frogs are more likely to colonize burned ponds and the surrounding area following wildfire. The probability that wood frogs breed in ponds that did not support breeding during pre-fire surveys was relatively low ($\widehat{\gamma} = 0.11$; $\widehat{SE}(\widehat{\gamma}) = 0.05$) and not influenced by any of our soil burn severity covariates (Table C.2). There was some evidence that breeding colonization probability was higher in ponds without trout (model averaged estimates: $\widehat{\gamma}(\text{no fish}) = 0.12$, $\widehat{SE}(\widehat{\gamma}(\text{no fish})) = 0.06$)) relative to those where trout were detected ($\widehat{\gamma}(\text{fish}) = 0.06$, $\widehat{SE}(\widehat{\gamma}(\text{no fish})) = 0.07$)). Finally, the probability that an observer detected egg masses or tadpoles at ponds that supported wood frog breeding was high (>0.80) and positively influenced by pond surface area ($\widehat{\beta} = 2.11$; $\widehat{SE}(\widehat{\beta}) = 2.70$). Larger ponds (>0.50 ha) that support wood frog breeding may have more egg masses making it easier to detect at least one egg mass or tadpole. By performing two or more independent surveys at each pond, the overall (cumulative) probability of detecting wood frog breeding was very high ($\widehat{p}_{cum} = 1 - (1 - \widehat{p})^2 \geq 0.96$).

4. Discussion

Our findings add to the limited literature on amphibian response to wildfire in subalpine forests of the western U.S. and contribute to the larger body of knowledge about the effects of wildfire on amphibians worldwide. We capitalized on existing pre-fire surveys for anuran species to investigate the short-term effects of wildfire on a relict population of wood frogs in the southern Rocky Mountains. We found that wood frog breeding persistence following fires can be high, provided unburned area is available around the breeding habitat, but persistence probabilities decline dramatically with increasing proportions of burned area in the buffer around a pond (Fig. 4). Wood frog colonization probability was low (~ 0.10) and unaffected by wildfire but may be lower at ponds with trout. We also found that mapped soil burn severity layer(s) produced following wildfire may overestimate the amount and severity of burned area around small landscape features such that field observations are likely necessary to achieve accurate burn severity metrics at small spatial scales (e.g., < 4 ha).

Our work provides a counterpoint to previous studies of short-term anuran responses to stand-replacing fires in the western United States. Hossack and colleagues investigated wildfire responses of two anurans in Montana and found no negative effects of wildfire on occurrence of Columbia spotted frog (*Rana luteiventris*) at breeding habitats 1–6 years following wildfire (Hossack and Corn, 2007), but lower occupancy in the subsequent decade (Hossack et al., 2013a). Numerous studies suggest short-term positive effects of wildfire on boreal toads (*Anaxyrus boreas boreas;* Hossack and Corn, 2007) due to improved thermal conditions (Hossack et al., 2009), higher

Table 3
Combined model set for wood frog (*Lithobates sylvaticus*) breeding dynamics pre- and post-wildlife. Models were fit to wood frog detection-nondetection data from visual encounter surveys collected 1–2 years before and 8 months after the Mullen Fire. Model names include covariate structures for local extinction (ε), colonization (γ) and detection probability (*p*). Akaike Information Criterion for small sample sizes (AICc), Δ AICc, model weights (*w*), number of parameters (K), and deviance (-2log *(*L)) are given for each model.

Model	AICc	Δ AICc	*w*	K	-2log(L)
ε(Unburn) γ(.) *p*(SArea)	138.54	0	0.18	6	125.88
ε(Unburn) γ(.) *p*(.)	138.59	0.04	0.18	5	128.12
ε(Unburn) γ(Fish) *p*(SArea)	138.68	0.14	0.17	7	123.79
ε(Unburn) γ(Fish) *p*(.)	138.69	0.15	0.17	6	126.03
ε(.) γ(.) *p*(.)	140.28	1.74	0.08	4	131.97
ε(.) γ(.) *p*(SArea)	140.31	1.76	0.08	5	129.84
ε(.) γ(Fish) *p*(.)	140.35	1.81	0.07	5	129.88
ε(.) γ(Fish) *p*(SArea)	140.41	1.87	0.07	6	127.75

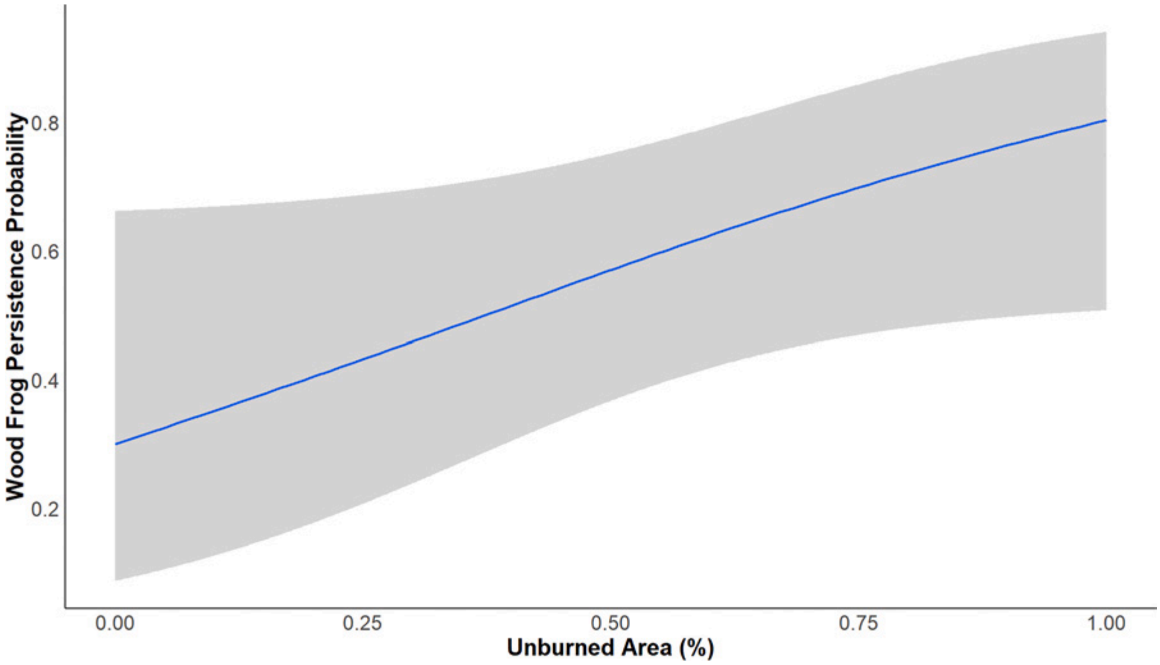

Fig. 4. Estimated wood frog (*Lithobates sylvaticus*) breeding persistence probabilities as a function of the percentage of unburned area within 100 m surrounding each pond. Shaded area represents 95 % confidence intervals.

growth rates (Barrile et al., 2022), or by providing opportunities for individuals to clear deadly fungal (*Bactachochytrium dendrobatidis*) infection via behavioral fever (Hossack et al., 2013b; Barrile et al., 2021). However, boreal toad resilience to wildfire may be unique within high-elevation amphibian communities due to their tolerance of desiccation, high thermal optima and dispersal capabilities, and propensity to use underground burrows (Hossack et al., 2009; Barrile et al., 2022). Moreover, benefits of wildfire to boreal toads may vary spatially and initial colonization following fire does not appear to result in robust, stable breeding populations (Hossack et al., 2013a). In comparison, wood frogs prefer closed canopy forests (Demaynadier and Hunter, 1998; Gibbs 1998a; Gibbs 1998b), have a lower thermal tolerance and optima (Cupp 1980; Herreid and Kinney, 1967), and are typically found near the soil surface under vegetation that burns during wildfires (e.g., clumps of grass, willow, leaf litter, and aspen groves; Constible et al., 2001; Cook, 2023). Reduced wood frog breeding persistence at ponds with little unburned area could be associated with direct mortality during the fire when wood frogs were likely moving in the upland habitat immediately adjacent to breeding ponds in search of winter hibernacula (Cook, 2023). Additionally, loss of surface O-horizons and understory vegetation at highly impacted ponds reduces soil moisture and increases surface temperatures creating inhospitable conditions for any remaining wood frogs. Wood frogs are a species that prefers cooler temperatures and are less tolerant to desiccation than other species in the region (e.g., boreal toad), making them especially susceptible to environmental changes following wildfire (Hossack et al., 2009).

Immediate declines in breeding occurrence post-fire have not been documented for other amphibian species in subalpine forests of the western U.S. (Hossack and Corn, 2007; Hossack et al., 2013a), but the combination of low persistence in severely burned areas and low colonization probabilities ($\widehat{\gamma} = 0.11$; $\widehat{SE}(\widehat{\gamma}) = 0.05$), suggest that it may take several years or decades before wood frogs return to breed in impacted (i.e., severely burned) habitats. Furthermore, initial declines may magnify over time, as seen in two other pond-breeding amphibian species (*R. luteiventris, Ambystoma macrodactulum*) whose long-term declines were a function of fire severity (Hossack et al., 2013a). Future monitoring of our study ponds will add to our knowledge of long-term effects of wildfire on anuran species in the region.

We found poor agreement between mapped and field observations of soil burn severity around small pond features. Developers emphasize that BAER data layers and the associated assessment are intended for short-term prediction of flooding and erosion at relatively broad (catchment) scales (USDA, 2020, BAER Report). Still, these data layers are often the only soil burn severity metrics available and have been used to characterize burn severity near small features (e.g., wetlands, small streams, rock outcrops) that are used by various vertebrates such as amphibians, reptiles, and small bodied fish (e.g., Hossack et al., 2013a; Preston et al., 2023). Our findings suggest that BAER data layers overstate the amount and severity of burned areas near these habitat features and misrepresent the patchy nature of unburned remnants, especially around small pond features. Importantly, our study suggests that accurate measures (i.e., field observations) of unburned habitat is the best predictor of wood frog persistence following wildfire: ponds with little to no unburned area (< 30 %) within 100 m buffers are likely to lose breeding wood frog populations ($\widehat{\varphi} < 0.40$), while ponds that retain $\geq$ 60 % unburned area have much higher persistence probabilities ($\widehat{\varphi} > 0.60$), similar to levels found at unburned ponds ($\widehat{\varphi} = 0.80$). Using soil burn severity maps that potentially misrepresent conditions around riparian and wetland features could lead to erroneous conclusions about the resilience of species in areas with overestimated levels of soil burn severity.

In addition to the major findings discussed above, our study provided several insights that inform monitoring and conservation efforts for this sensitive amphibian species. First, timing surveys to correspond to the wood frog breeding season produced excellent cumulative detection probabilities using our independent, double observer approach ($\widehat{p}_{cum} \geq 0.96$). Egg masses were available at most of our occupied ponds and the few uncertain tadpole detections were clarified via surveys timed later in the season when species identification was unambiguous. This careful survey timing allowed us to avoid using occupancy models that incorporate species uncertainty. Second, similar to birds and mammals (Fontaine and Kennedy, 2012), we show that amphibians can vary in their sensitivity to wildfire and resource managers could consider a range of strategies to maintain biodiversity. Finally, one of the strengths of our study is having species occurrence data before and after wildfire (Bixby et al. 2015). For species of conservation concern that are less resilient to wildfire (e.g., wood frogs), knowledge of breeding site locations and population core areas can inform forest treatments, fire suppression strategies, and post-fire assessments. Treatments and strategies likely to maximize unburned or intact habitat in close proximity to critical habitat (e.g., breeding sites) or that facilitate mosaics of burn severity could minimize negative impacts to these species (Jones et al. 2016).

5. Conclusions

Wood frogs are a glacial relic species with a limited distribution in the intermountain west, thus understanding how the species responds to wildfire is critical. The Mullen Fire burned approximately 1/3 of the species range in one of two mountain ranges where the species occurs in Wyoming. The decline in post-fire occupancy coupled with low colonization rates identified in this study are concerning given that wildfires in the region are predicted to be more frequent and severe. However, we acknowledge that our study only explores effects one-year post-fire and it would be useful to extend the timeframe to determine if and when recolonization occurs in severely burned areas. Such studies could also investigate the potential for lag effects seen in other amphibians in similar ecosystems where declines intensified multiple years post-fire (Hossack et al., 2013a). Longer-term studies could also include habitat dynamics to differentiate losses due to habitat change (e.g., sedimentation or desiccation events) from those due to demographic processes (e.g., survival, movement, breeding site selection; McDonald et al., 2018; Barrile et al., 2022). Additionally, our study explored only one life-history stage (breeding or reproductive effort), but fire may have different effects on larval survival and metamorphosis (e.g., Hossack and Pilliod, 2011, McDonald et al., 2018). An understanding of the effect of soil burn severity on probability of successful metamorphosis (i.e., the effect of fire on larval survival), given that breeding occurred, would be useful in predicting persistence of the species over time. This could be informed by surveys timed to detect late-stage tadpoles or recent metamorphs (e.g., Crockett, 2019; MacKenzie et al., 2011).

Human-induced climate change is the primary factor responsible for globally changing fire regimes (Jolly et al., 2015), but research on the impacts of fire on aquatic taxa is still in its infancy (Bixby et al., 2015; Gomez Isaza et al., 2022). Most existing literature focuses on streams, with few studies on fire effects on lentic habitats (Bixby et al., 2015) or the amphibians that rely on these features (Hossack and Pilliod, 2011; dos Anjos et al., 2021; Gomez Isaza et al., 2022), many of which are of conservation concern. Capitalizing on pre-fire surveys, we resurveyed a random subset of ponds across a gradient of soil burn severity and found that wood frog breeding persistence was strongly influenced by the percentage of their terrestrial habitat (100 m buffer) that was burned. Moreover, accurate representation of heterogeneity in soil burn severity at this fine scale is not captured in remotely sensed data typically used by land management agencies for predicting erosion, debris flow, and associated resource damage. Understanding short-term geographic- and species-specific variation in response to wildfires provides the basis to explore time to recovery (e.g., when wood frogs return to burned breeding sites) or to determine if declines in breeding distributions intensify over time.

Ethics

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

CRediT authorship contribution statement

Larissa L. Bailey: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Richard Henderson:** Conceptualization, Validation, Investigation, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Wendy A. Estes-Zumpf:** Conceptualization, Investigation, Resources, Writing – review & editing. **Chuck Rhoades:** Conceptualization, Methodology, Resources, Writing – review & editing. **Ellie Miller:** Investigation, Data Curation, Writing – review & editing. **Dominique Lujan:** Validation, Investigation, Data Curation, Writing – review & editing, Visualization, Supervision. **Erin Muths:** Conceptualization, Resources, Writing – review & editing.

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

Acknowledgements

We thank Maya Velaso for calculating mapped soil burn severity metrics from BAER data layers. Ryan Adams helped develop field soil burn severity sampling methods. We thank the numerous technicians from U.S. Forest Service, Wyoming Department of Fish and Game, and University of Wyoming for their field assistance. This work was supported by the U.S. Forest Service National Stream and Aquatic Ecology Center. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is contribution number 923 of the U.S. Geological Survey's Amphibian Research and Monitoring Initiative.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03389.

Data availability

The authors do not have permission to share data.

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