



Habitat-dependent responses of terrestrial salamanders to wildfire in the short-term



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ABSTRACT

Wildfire is an important natural disturbance event that promotes landscape heterogeneity and regulates many wildlife communities. The compounding effects of fire suppression and climate change have increased the frequency and severity of wildfire, but the responses of many organisms to wildfire is unknown. Landscape heterogeneity, specifically microhabitats, may mediate and buffer the effects of wildfire, and evaluating variable responses to wildfire given habitat is key to developing a more cohesive understanding of population responses. Terrestrial plethodontid salamanders are likely disproportionately affected by wildfire events because of their lungless anatomy and reliance on cool and moist habitats. Our knowledge of salamander responses to wildfire in the short-term is limited due to the inherent challenge of opportunistically studying post-wildfire events. We capitalized on a wildfire event in western North Carolina, USA to determine the short-term (6–18-month post-fire) habitat-mediated responses of salamanders to wildfire using body size measurement and repeated count surveys. We observed precipitous declines of the red-legged salamander, *Plethodon shermani*, in exposed upland forests, but no apparent negative effects in riparian forests 18-months post-fire relative to unburned sites. We also observed a loss of juvenile size classes in the upland burned forest with only the largest adult individuals remaining 18-months post-fire. There were no size class differences in the riparian forests. Our results suggest riparian forests may be buffered from the effects of wildfire because canopy cover, vegetation, and soil duff layer are retained following a wildfire event. Salamander populations inhabiting riparian forests may be at less risk of declining than those in exposed habitats. Our results underscore the need to assess wildfire effects in all habitat types to fully determine the effects of disturbance to populations.

1. Introduction

Wildfire is an important natural disturbance event that promotes landscape heterogeneity and regulates and maintains many wildlife communities (Agee, 1996; Hutto, 2008). However, fire suppression, compounded by the effects of climate change, is expected to increase wildfire frequency and intensity (Liu et al., 2010; Sommerfeld et al., 2018), the effects of which are largely unknown for many wildlife species. Wildlife dependent on specific microhabitats and sensitive to habitat alteration, such as amphibians, may be disproportionately impacted by unpredictable severe wildfires (Hossack and Pilliod, 2011), underscoring the importance of understanding wildlife responses to disturbance events.

Terrestrial woodland salamanders in the family Plethodontidae are amphibians with unique physiological requirements because of their lungless anatomy (Feder, 1983). Lunglessness restricts salamanders to cool and moist microhabitats (Feder and Londos, 1984), habitats that

could be severely altered by wildfire events. Plethodontids are often used as forest health indicators because of their high densities and sensitivity to change (Davic and Welsh, 2004; Hairston, 1983; Welsh and Droegge, 2001), and are important to overall forest ecosystem function as they aid in leaf litter decomposition, contribute to nutrient cycling, and serve as a vital food web connection (Best & Welsh, 2014). Despite salamanders' importance to terrestrial forest ecosystems, there is a significant gap in understanding their responses to severe wildfire, both short term and long term.

Much of the work on fire effects and salamanders has focused on prescribed fires (Mahoney et al., 2016; O'Donnell et al., 2015; Russell et al., 1999). Prescribed fires are used across the United States as a forest management tool to control fuel loads and reintroduce fires to historically fire-dependent ecosystems (Pyne et al., 1996). Although it is vital to understand how salamanders respond to a commonly used forest management tool, prescribed fires are often not a proxy for the ecological disturbance events of severe wildfires because most

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prescribed fires burn with less intensity and often do not eliminate canopy cover, coarse woody debris, or penetrate the duff layer of soil like severe wildfires (Arkle and Pilliod, 2010; Greenberg et al., 2018). Further, with climate change threatening more severe wildfires (Sommerfeld et al., 2018), current knowledge of amphibian responses to moderate-severity wildfires will not accurately reflect effects following severe wildfire. Plethodontids may be unable to maintain their physiological requirements following severe wildfires because of the loss of critical habitat features that moderate cool and moist refuge, and be at risk of decline (Feder and Londos, 1984; Feder and Lynch, 1982). Uncovering how salamanders respond in the short-term following a severe wildfire is the first step to understanding long-term population persistence and key to developing effective management and conservation strategies for future disturbance events.

Plethodontid salamanders exploit microhabitats across the landscape characterized by cool and moist conditions. At high elevations, where regional climate is both cool and wet, salamanders are found in both riparian forests and upland habitats (Gade and Peterman, 2019). Across the Southern Appalachians many mountain summits are naturally treeless and instead covered with grasses and shrubs (Lindsay and Bratton, 1979). These areas, called balds, are topographically exposed and experience high rain intensity, low temperatures, high wind velocity, and deeper snowpack (Mark, 1958). While plethodontids do inhabit balds, likely as a result of the regional wet and cool climate and abundance of cover objects, any alterations to this already exposed habitat could be catastrophic for populations. Further, plethodontids are found in high abundance in riparian regions throughout Southern Appalachia (Gade and Peterman, 2019), where fire impacts are often more mild (Pettit and Naiman, 2007). When fire does encroach these areas, often only understory vegetation and some leaf litter ignite, providing an ideal refugia from the effects of fires (Ford et al., 1999; Pearson, 1994). However, if a severe fire does infiltrate riparian areas, salamanders could be severely influenced due to the loss of their mesic microhabitats (Ford et al., 1999). Given plethodontids propensity to inhabit both upland and riparian habitats which may be differentially impacted by wildfire, determining the breadth of response of salamanders is a fundamental consideration for mitigating fire impacts.

Assessing wildfire effects is inherently challenging due to their unpredictability and logistical challenges in consistently studying their effects. Therefore, wildfire studies are often opportunistic and occur as a result of researchers being in the “right place at the right time” (Smucker et al., 2005). In the Fall of 2016, the Southeastern Appalachian region of the United States experienced unprecedented numbers of wildfire outbreaks. Drought, lightning, arson, and accidental human activity are credited with igniting 28 significant wildfires, burning over 25,000 ha and costing taxpayers upwards of \$55 million in Western North Carolina alone (USFS, 2017). These fires ignited across a region of high plethodontid salamander abundance and diversity already being monitored, providing a unique opportunity to assess the effects on salamanders.

The goals of the present study were to determine the short term (6–18-months) effects of severe wildfire in different habitats on a terrestrial salamander in western North Carolina. We combined two complimentary studies to achieve these goals. First, we used mark-recapture data to assess body condition and density changes during the first two active seasons following a severe wildfire event on a mountain bald. We also used repeated count data from a riparian region with similar burn severity at comparable high elevation to detect density differences between the two active seasons.

2. Methods

2.1. Study organism

The red-legged salamander, *Plethodon shermani*, is a direct developing terrestrial salamander found in high elevation (900–1600 m)

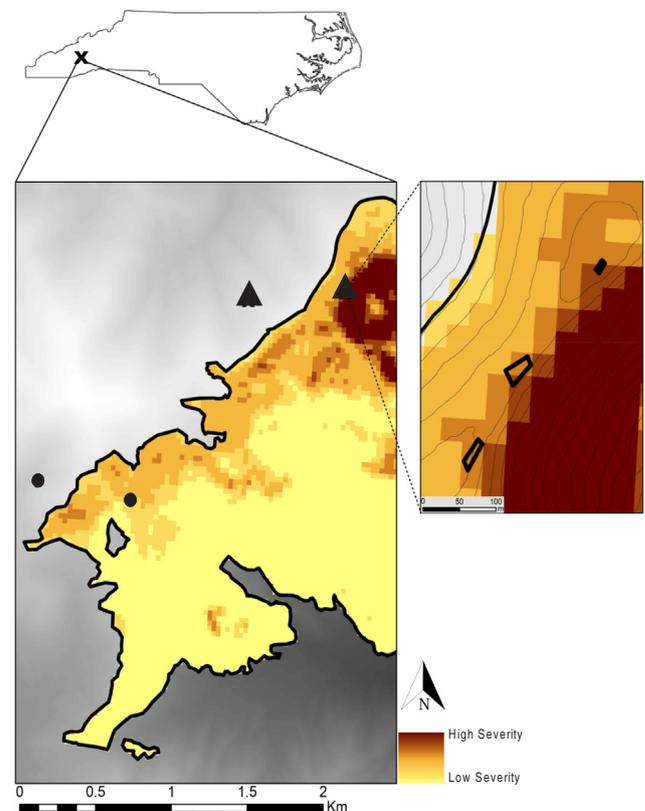


Fig. 1. Sampling sites at Wayah Bald in western North Carolina. The Camp Branch Fire outline is in black and dNBR fire severity is indicated with warmer colors indicating higher severity. Upland sites are denoted with triangles, and riparian sites are denoted with circles. Inset map delineates the three sampling areas at Wayah Bald. Contour lines are 10 m.

mesic hardwood forests in western North Carolina and some parts of south east Tennessee and northern Georgia. This species is large bodied (SVL: 85–185 mm) and long lived, with maximum life-span estimates averaging approximately 10 years (Staub 2016). Male *P. shermani* reach maturity at 2–3 years and females mature at or after 3 years (Connette, 2014). Female *P. shermani* are less fecund than many other amphibian species, only producing 10–12 eggs per clutch on a biannual basis (Connette, 2014; Hairston 1983). Plethodontids are known to be highly philopatric and have short dispersal movements of < 10 m in *P. shermani* (Connette, 2014).

2.2. Study site

Wayah Mountain is located in the Nantahala National Forest in western North Carolina, USA (35.178145, –83.562236). The forest is primarily composed of upland oak-hickory and cove hardwood, and there is a natural heath bald at its summit. On 23 November 2016, the Camp Branch wildfire ignited and burned over 1300 ha of the mountain (Fig. 1). While much of the burn was considered low to moderate severity, some regions, including the bald and high elevation riparian habitats experienced severe burning, characterized by overstory canopy trees and understory vegetation loss, and consumption of surface leaf litter and soil organic layer (Keeley, 2009). Wildfire severity was quantified using the difference Normalized Burn Ratio index (dNBR) generated from Landsat 8 satellite imagery downloaded from earthexplorer.usgs.gov. dNBR calculates the reflectance of surface vegetation from pre-fire and post-fire periods using near infrared and shortwave infrared waves to quantify canopy and vegetation loss. We validated the dNBR severity indication from our map (Fig. 1) in the field and selected four sites encompassing both upland and riparian

Table 1
Physical and topographic characteristics of the four sites sampled across upland and riparian burn and control regions.

| Habitat | Treatment | Total Search Area (m ²) | Elevation (m) | Slope (degrees) | Aspect | Stand Age (years) |
|----------|-----------|-------------------------------------|---------------|-----------------|--------|-------------------|
| Upland | Burn | 460 | 1615 | 16.7 | 108 | 190 |
| Upland | Control | 200 | 1556 | 19.7 | 305 | 197 |
| Riparian | Burn | 400 | 1350 | 16.4 | 171 | 139 |
| Riparian | Control | 400 | 1430 | 26.7 | 294 | 170 |

regions, each with a burned and unburned (control) site. Topographic characteristics of each site are summarized in Table 1.

2.3. Upland

In summer 2017, we established a mark-recapture study on all accessible and searchable areas of Wayah Bald that were severely burned. Because of a large paved parking area and road, and steep southerly slopes, the searchable area was limited and disjunct. We sampled three primary areas totaling approximately 460 m² of searchable terrain (Fig. 1). We sampled the bald three times from May to August in both 2017 and 2018 between 21:00 and 22:00. Survey nights occurred within 24 h of a rain event, to reflect favorable conditions for salamander surface activity (Peterman et al., 2016). During each sampling event, at least two observers exhaustively searched for surface active salamanders along five transects that covered the total searchable area. Salamanders were hand captured and placed in a sealable bag containing moist leaf litter and transported to Highlands Biological Station (HBS) approximately 60 km away for processing. At HBS, salamanders were anesthetized using 1 g/L of Orajel © solution and uniquely marked with visual implant elastomer (Northwest Marine Technologies). Snout-vent length (SVL) was measured to the nearest 0.01 mm using digital calipers and mass was obtained to the nearest 0.01 g. Following processing, salamanders were returned to their exact capture location on the bald within 48 h after capture.

We also established mark-recapture plots (two plots, each 10 m²) in an unburned hardwood forest at a similar elevation to the upland burn site to serve as a control. While this is not a direct comparison to the bald because it was located in continuous forest in less topographically exposed area, it was located less than 500 m from the bald (straight-line distance), in an upland region, and provided the most reasonable unburned comparison to the bald. We sampled each upland control plot three times in 2017 in 2018 on the same nights we sampled the burn sites. We uniformly searched the entire area with at least two observers, and capture and processing details were identical to the above methodology.

2.4. Riparian

We conducted a repeated count study in riparian areas that experienced similar intensity burns as the bald and unburned, control sites (Table 1). At each site, we established paired transects, at least 10 m from each other, 50 m × 4 m in length extending perpendicular from the stream bank. At least two observers counted all surface-active salamanders along the transects over three sampling periods from May to August in 2017 and two sampling periods from May to August in 2018. We identified species and life-stage (juvenile or adult) of each observation. Life stage was determined by sight, estimating the SVL of each individual (juveniles < 50 mm and adults > 50 mm).

2.5. Statistical analysis

Body Condition (from mark-recapture) – We used the standard mass index (SMI), which standardized body mass to body size using body mass (g) as the mass parameter and SVL (mm) as the linear body measurement (Peig and Green 2009), to assess body condition. To

determine difference between SVL and SMI between years within each treatment (burn/control), we used a paired one-sample *t*-tests generated from resampled, bootstrapped data in the following steps: For each treatment, equal numbers of individuals across years, dictated by the year where fewer individuals were tagged (i.e. 14 individuals in the upland burn in 2018, 35 individuals in upland control plots in 2018; see Section 3) were resampled 1000 times with replacement. Paired one-sample *t*-tests were conducted on each resampled dataset, and the proportion of significantly different tests ($\alpha = 0.05$) were determined. We conducted bootstrapped *t*-tests for differences of SVL and SMI between years at the burn and between years at the control site. We evaluated significance by averaging *t*-values (denoted as $\bar{t} \pm SD$) and determining the percentage of iterations where $p < 0.05$ (denoted as %p*) across the 1000 iterations. We excluded recaptured individuals in 2018 at the control since we did not recapture any individuals in 2018 at the bald (see Section 3).

Density and Size Class – We determined observed density by dividing the total number of salamander counts per transect by the total searched area of a given site. We determined the size class breakdown at each site, counting adults as individuals > 50 mm SVL and sub-adults and juveniles < 50 mm SVL (Connette et al., 2015). To estimate the effects of year and burn on density across habitat types, we used a generalized linear model using density as the response variable, and habitat type (riparian or upland), treatment (burn or unburned), and year (2017 or 2018) and the three-way interactions of habitat, treatment, and year as explanatory variables.

3. Results

3.1. Observed density

At the upland burn site we observed densities of 0.26 individuals/m² in 2017 and 0.03 individuals/m² in 2018, while observed densities at the upland control were 0.27 and 0.37 individuals/m² in 2017 and 2018, respectively. At the riparian burn site, observed densities were 0.07 individuals/m² and 0.14 individuals/m², in 2017 and 2018 respectively. In the riparian unburned site, observed densities were 0.10 and 0.21 individuals/m² in 2017 and 2018 respectively (Fig. 2).

Density did not differ between habitat types ($\beta = 0.073$, $t_{23} = 1.613$, $p > 0.050$) but significantly differed between the interaction of habitat and burn treatment (i.e. burned or unburned; $\beta = 0.173$, $t_{23} = 2.685$, $p = 0.020$). Between 2017 and 2018, density significantly increased ($\beta = 0.075$, $t_{23} = 3.34$, $p = 0.004$), although the change in density between years was significantly lower in upland habitat ($\beta = -0.086$, $t_{23} = -3.005$, $p = 0.008$). There was also a significant negative interaction between upland habitat, burn treatment, and year ($\beta = -0.104$, $t_{23} = -2.500$, $p = 0.020$), accounting for all of the declines in density observed in upland habitat in 2018 (Fig. 2).

3.2. Body condition and size class

In 2017 at the upland burn site, we captured and marked 119 unique individual *P. shermani*, recapturing 5 individuals, while in 2018, we captured 14 unique individuals, recapturing 1 individual. We did not recapture any individuals in 2018 that were captured in 2017. Due

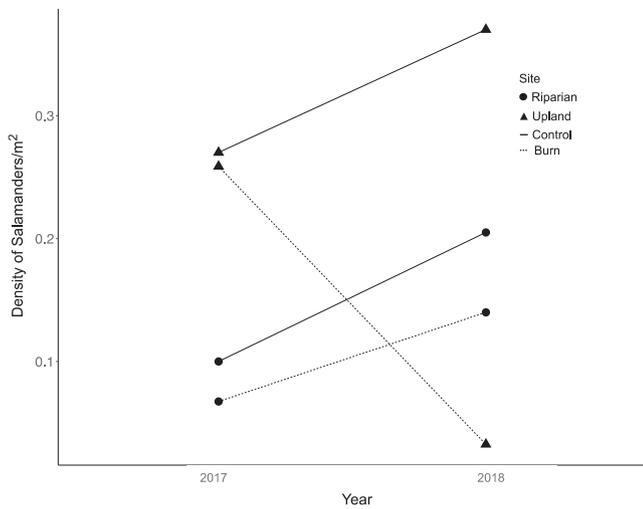


Fig. 2. Salamanders density (m²) between upland burn and unburned sites and riparian burned and unburned sites between years.

to the lack of between-year recapture rates, we do not report any mark-recapture metrics, and instead use body size data, with confidence in the independence of individuals.

We saw a decline in the density of surface-active salamanders over the active season in 2017 (Fig. 3). There was a significant difference in SVL (%p* = 97.5, $\bar{i} = -4.21 \pm 1.19$) between years in the upland burn such that those in year 2 were larger (Fig. 4). There was no difference in SMI between years at the upland burn (%p* = 23.1, $\bar{i} = -0.91 \pm 1.01$). In 2018 at the upland burn site, there was a shift in size classes, excluding juveniles and subadults which was not seen in the control plot (Fig. 5). There was no difference in the proportion of juvenile and adult salamander at the riparian burned and unburned sites (Fig. 6).

At the upland control sites in 2017, we captured and marked 40 unique individuals, recapturing 3 individuals, while in 2018 we captured 35 unique individuals, recapturing 21. We recaptured 8

salamanders in 2018 originally marked in 2017. Between years at the control site there was no significant difference between SVL (% p* = 20.1, $\bar{i} = -1.08 \pm 1.04$) or SMI (%p* = 13.7, $\bar{i} = -2.25 \pm 0.090$; Fig. 4).

4. Discussion

Terrestrial plethodontid salamanders in the Wayah Mountain region of western North Carolina show differential impacts by a wildfire event depending on their habitat. Exposed upland habitats experienced more severe declines in observed density, and the salamanders that were detected had large body sizes. Wildfire did not appear to negatively affect salamander density or size classes in riparian forests, suggesting a buffering effect from wildfire.

Although we cannot make inference on pre-fire and post fire numbers, we were able to assess salamander response in their first active season after a fire. Often, amphibians can avoid direct mortality from fire by retreating underground or seeking moist refuge (Friend, 1993; Pilliod et al., 2003; Vogl, 1973). Plethodontids remain underground during their inactive season (September–May; Feder and Londos, 1984), and likely avoided direct mortality from the November ignition of Camp Branch fire. We began our sampling near the beginning of the salamander active season directly following the fire event, therefore likely sampling portions of the ‘pre-fire’ population. As the first active season following the fire progressed in 2017, however, we observed overall declines in surface-active salamanders, a pattern not detected in the control sites (Fig. 3). Loss of sub-canopy vegetation, dead woody debris, declines in soil nutrients, and invertebrate biomass have been reported following fire events, and may have disturbed the moist, cool, and productive conditions required for salamanders contributing to the observed declines in surface-active salamander density (Cummer and Painter, 2007; Pilliod et al., 2003; Verble-Pearson and Yanoviak, 2014). Such conditions may have also increased salamander exposure to bird and small mammal predators (Cummer and Painter, 2007). Further, across all other sites (upland control, riparian burn, and riparian control), we observed an overall increase in salamander density (Fig. 2), indicating post-fire conditions in riparian areas in 2018 were not

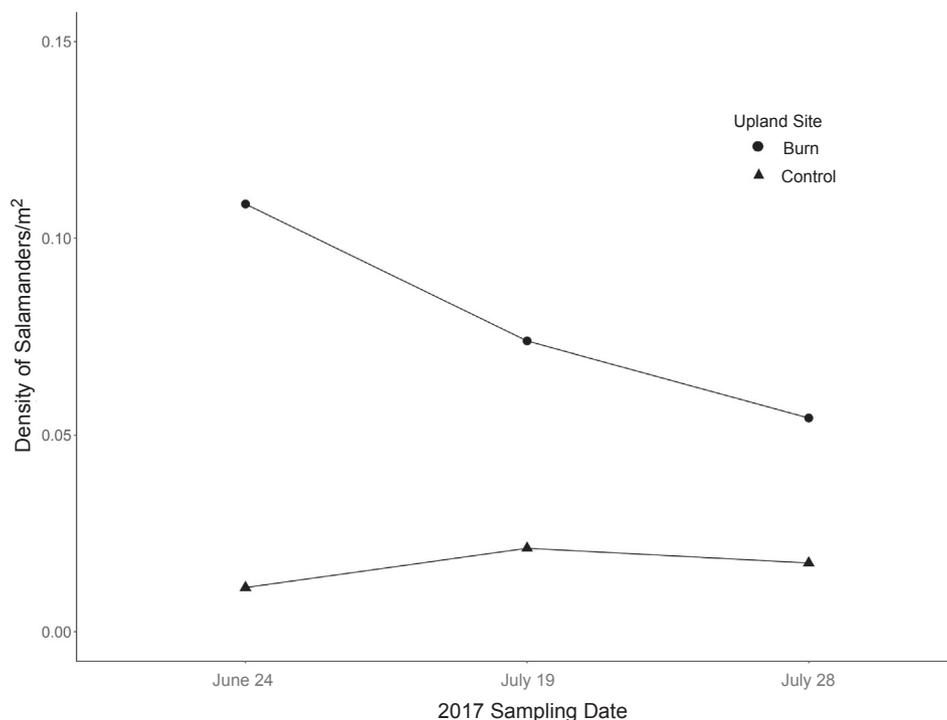


Fig. 3. Surface-active salamander density during each sampling occasion in 2017 at the upland burn (circles) and upland control site (triangles).

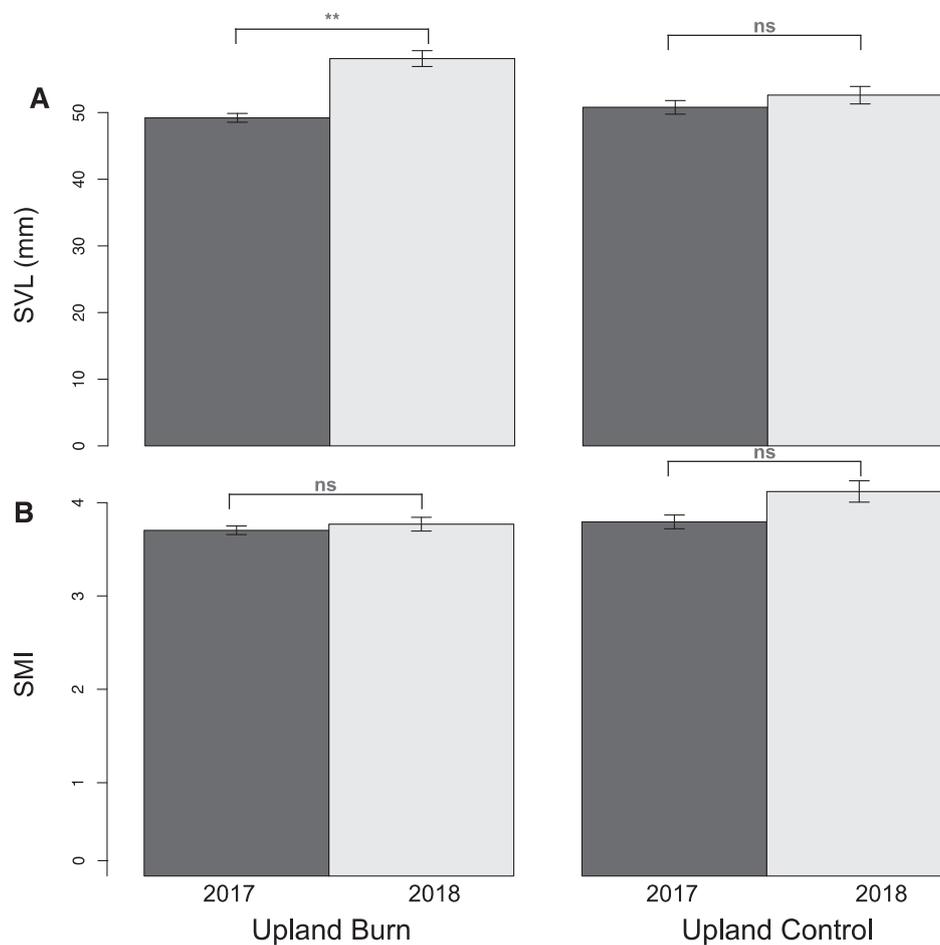


Fig. 4. Mean differences in (A) SVL (mm) (B) SMI between upland burn and control plots between years (2017 in black, and 2018 in grey).

unfavorable for *P. shermani*.

We cannot determine the exact mechanism of decline at the upland bald, whether it be a result of indirect mortality via desiccation, predation, starvation, or a combination of factors. It is also possible that individuals evacuated from the bald into more optimal conditions, an event observed in pond breeding salamanders following timber clear-cuts (Semlitsch et al., 2008) and stream breeding salamanders in riparian habitats following logging events (Peterman et al., 2011). Salamanders are capable of moving away from intensive disturbance events and may be an alternative hypothesis to the declines we observed at the upland bald.

The effects of wildfire on salamander density were not consistent among habitats across years, and we detected no decline in the density of surface-active salamander between 2017 and 2018 in the riparian areas. Riparian forests generally have higher relative humidity, more consistent temperature regimes, and are less exposed relative to upland habitats (Arkle and Pilliod, 2010; Gregory et al., 1991). In burned riparian sites, counts were similar to those in control riparian habitat (Fig. 2), suggesting riparian regions may act as a buffer from severe fire. Much of the current literature exploring the effects of fire on amphibians in riparian areas found no difference in abundance between burned and unburned forests (Ford et al., 1999; Greenberg and Waldrop, 2008; Keyser et al., 2004; Mahoney et al., 2016; O'Donnell et al., 2015; Schurbon and Fauth, 2003). For example, Ford et al. (1999) found no difference in abundance of woodland salamanders between prescribed burn and control riparian regions, and Arkle and Pilliod (2010) detected no immediate or delayed effects on the density of Rocky Mountain tailed frogs (*Ascaphus montanus*) and Idaho giant salamanders (*Dicaptodon aterrimus*) following a prescribed fire in Idaho.

Although these studies look at the effects of prescribed fire, which are not always ecological surrogates for severe wildfire disturbance (Arkle and Pilliod, 2010), they do highlight the reduced effect of fire in riparian regions. Our results add to the growing consensus that riparian regions are less susceptible to effects of fire, at least in the short-term.

We also saw differences in body size and size classes in our upland burned site relative to the unburned upland site. In 2018, only the largest individuals remained in the upland burn (Fig. 4). Large body size likely affords salamanders an advantage in surviving unfavorable conditions, due to greater lipid reserves to buffer starvation (Hairston et al., 1987; Riddell et al., 2018), and physiological advantages because of their low surface area-to-volume ratio and higher resistance to water loss (Hairston et al., 1987; Riddell and Sears, 2015; Rohr and Palmer, 2013). Interestingly, there was no difference in the body condition index (Fig. 4), suggesting body size alone, and not condition, is a more important factor to persisting after a fire. The salamanders found in 2018 were not recaptured from 2017 and we cannot ascertain whether those captured in 2018 persisted through the wildfire, were recent immigrants, or were migrating individuals. For example, it is possible that large-bodied salamanders moved into the burned site to avoid resources competition from the decreased conspecific density (Cote et al., 2008). Continued long-term monitoring of this population will be required to assess such alternative hypotheses.

We saw a shift in size class in the second year at the upland burn site, where the remaining individuals were only of the adult size class (> 50 mm SVL; Fig. 5). The presence of juvenile size classes indicates that recruitment is occurring (Connette et al., 2015), and a loss of the smallest individuals will lead to declines in recruitment and ultimately, population collapse (but see Cummer and Painter, 2007). Species that

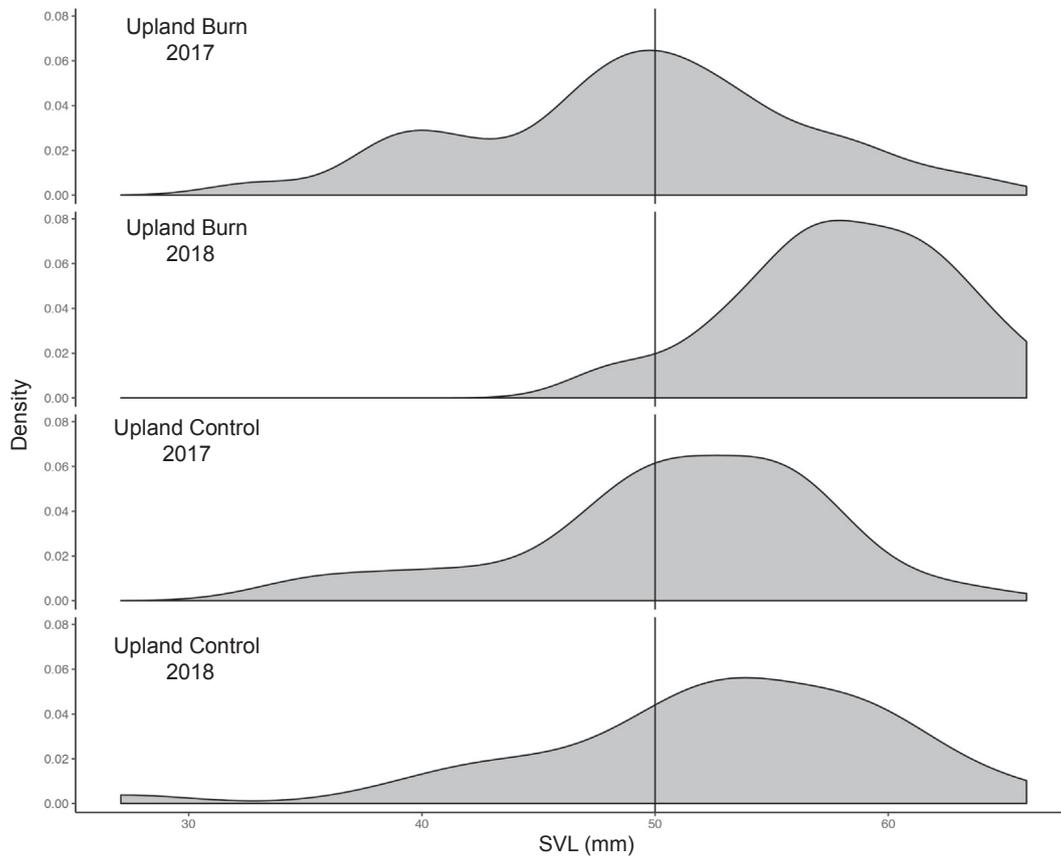


Fig. 5. Size class density histograms between upland burn and control plots between 2017 and 2018. The vertical line at 50 mm SVL indicates the size at which individuals reach maturity and are considered adults.

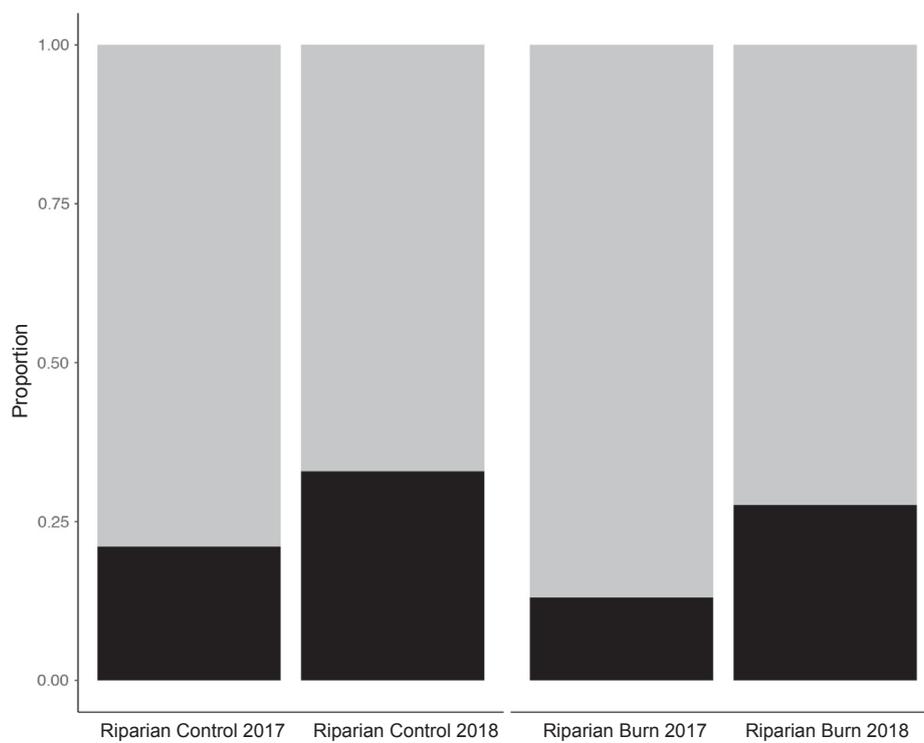


Fig. 6. Relative proportion of juvenile (black) and adult (grey) salamanders counted at the riparian burned and unburned sites.

are prolific breeders and good dispersers are often most resilient to disturbance (reviewed in Moritz and Agudo, 2013). However, *P. shermani* are relatively poor dispersers (Connette and Semlitsch, 2013b), long-lived, and reproduce on a biannual basis, producing small clutch sizes (Staub, 2016). These life history traits and observed loss of juvenile size class suggest a high probability of population decline following disturbance events and unlikely persistence in the future. In contrast to the upland sites, we detected no discernable difference between juvenile and adult proportions in the riparian areas (Fig. 6). While we did not obtain exact SVL measurements in the riparian sites, and instead estimated adult or juvenile status based on observer knowledge, we still saw a clear trend of consistent size classes at both unburned and burned riparian sites further suggesting the buffering effects of riparian regions.

Our study only assessed salamander response after the first 18-months following a wildfire, representing two salamander active seasons, therefore limiting our inference potential long-term effects. There is evidence of a time-lagged response to wildfire in plethodontids in Western North America, whereby salamander occupancy only declined after 7–21 years post-fire (Hossack et al., 2013). Time lag effects may result from decreased vital rates in response to changes in habitat quality, reduced dispersal and survival, or increased daily movement resulting in increased energy costs and predator exposure (Connette and Semlitsch, 2013a; Hossack et al., 2013; O'Donnell et al., 2016). Thus, continued monitoring following a wildfire and studies focused on quantifying critical demographic parameters will facilitate a mechanistic understanding of population decline and will provide valuable insight into amphibian responses to wildfire.

5. Conclusions

Wildfires are expected to become more frequent and more severe in the southern Appalachians, as a result of global climate change (Liu et al., 2010). It is therefore important to understand the responses of individuals and populations of wildlife sensitive to habitat perturbation so management and conservation strategies can be developed to best protect these animals. Given the high density and importance of salamanders to ecosystem health, our understanding of their responses will better inform conservation and management mitigation practices. Our results indicate context-dependent response of salamanders to wildfire suggesting that forest managers should focus on managing upland habitats to most effectively conserve salamander and other wildlife populations from the effects of wildfire. Riparian areas appear to buffer the effects of wildfire, and should be managed to retain the inherent value, but concentrating wildfire management effort on upland habitats will most efficiently and effectively protect vulnerable populations.

Declaration of Competing Interest

The authors have no conflicting interest to declare.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117479>.

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