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Impacts of Wildfire Burn Severity on Plethodontid Salamander Populations of Great Smoky Mountains National Park

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Abstract: Wildfire is an increasingly common disturbance in forested landscapes that can drastically alter local habitats. Under current climate change predictions, wildfires are likely to become more frequent and severe. In regions and ecosystems that have historically infrequent fire return intervals, there is little known about how organisms will respond to the more severe and frequent wildfires predicted under climate change. In the southern Appalachian Mountains, USA, fire has been suppressed and severe burns are historically uncommon. This region boasts immense biodiversity and is considered a biological hot spot for diversity in the salamander family Plethodontidae. These species rely upon cool, moist microclimates that may be impacted more by severe fire than by low-intensity wild or prescribed fire. In 2016, the Chimney Tops Two wildfire burned >6000 ha of Great Smoky Mountains National Park, USA, and left a mosaic of burn severity across the landscape. This presented an opportunity to examine how five plethodontid salamander species respond to and recover from a range of burn severity. Even though the landscape had been recovering for 5 yr at the time of study, populations of *Plethodon jordani*, *Plethodon glutinosus* spp., *Desmognathus wrighti*, *Desmognathus imitator*, and *Eurycea wilderae* within the burn boundary had lower abundance than those in unburned habitat. In addition, there was a trend of even lower abundances in more severely burned habitat. Evidence of recovery, as indicated by a relationship between population abundance and distance from the burn boundary, was only present for *D. imitator*. Finally, body size distributions were different between burned and unburned sites for three of the five species and individuals were larger, on average, in burned sites. This work provides insights into how terrestrial salamander populations may respond to the more severe and frequent wildfires predicted under climate change for the southern Appalachian Mountains region.

Key words: Disturbance; Hierarchical model; Plethodon; Wildfire

Disturbance is a fundamental driver of ecological change, and understanding how it alters landscapes and changes wildlife population sizes is critical for conservation. Disturbances such as floods (Coyle et al. 2017), wind events (Nelson et al. 2008; Bernardes and Madden 2016), anthropogenic land use, and fires (Parkins et al. 2018; Giorgis et al. 2021) have direct and indirect consequences for floral and faunal populations through direct mortality and promotion of disturbance-dependent species (Gogol-Prokurat 2011) or by changing habitat suitability (Banks et al. 2013; Carman and Jenkins 2016). Wildfire is an increasingly common form of disturbance and is predicted to become even more common and severe under climate change (Miller et al. 2012; Jolly et al. 2015; Harvey et al. 2016; Stevens-Rumann et al. 2018); therefore, understanding the effects of wildfires on ecosystems is of pressing conservation concern (McLauchlan et al. 2020).

Wildfire can have varied effects on ecosystems, depending on ecological context and severity. In some ecosystems, wildfire is important for maintenance. For example, pine savannah ecosystems rely on frequent low-intensity burns to maintain a host of endemic, fire-resistant species (Fill et al. 2015). In other systems, fire provides spatial and temporal variability that can increase biodiversity on a regional scale (Pausas and Ribeiro 2017; Kelly et al. 2020). However, wildfire may have drastic impacts in habitats where fire return intervals are historically infrequent, such as those in the Southern Appalachian Mountains, USA. The Southern Appalachians have long intervals between fires, >100 yr in some areas, and native wildlife may be particularly vulnerable to changing fire regimes predicted under climate change (Mitchell et al. 2014; Syphard et al. 2018).

The Southern Appalachians are a hot spot of biodiversity, harboring many endemic species within a relatively small geographic extent due to the varied topography and local climate (Reid 1998; Duellman 1999; Hodkinson 2010; Kozak 2017). A central component of the ecosystems in Southern Appalachia are salamanders within the family Plethodontidae. Plethodontid salamanders exist in high numbers across a wide elevational range (Hocking et al. 2021), represent a considerable biomass in many forest ecosystems (Burton and Likens 1975; Peterman et al. 2008; Milanovich and Peterman 2016), assist with nutrient cycling and cross-scale nutrient transfer (Hocking and Babbitt 2014), and act as a reservoir of energy within the ecosystem due to their highly efficient physiology (Fitzpatrick 1973). It is valuable to understand how plethodontid salamanders in the Southern Appalachians may respond to wildfires as they may become more common or severe in the future (Stevens-Rumann et al. 2018). However, most of our understanding on how plethodontid salamanders respond to fire comes from studies on prescribed fire, low-intensity wildfire, or plethodontids in other regions. There is little known about how plethodontids of the Southern Appalachians respond to a range of wildfire severity.

There is consensus that plethodontid salamanders are not highly affected by prescribed fire (Russell et al. 1999; Greenberg and Waldrop 2008; O'Donnell 2014; O'Donnell et al. 2015; Mahoney et al. 2016); however, some evidence exists that plethodontid salamander population sizes respond negatively to prescribed fire but that this loss is small and species dependent (Jacobsen et al. 2020). Our understanding of how plethodontids of the Southeast respond to wildfire is relatively limited, but in the case of low-severity burns, populations may be depressed in the year following

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burn and recover after an additional year (Gade et al. 2019; Gould et al. 2022). This response may be mediated by habitat and appears to be species dependent. Our understanding of how plethodontid salamanders respond to more intense wildfire is based on a single species from the desert southwest. A population of *Plethodon neomexicanus* had greater proportions of juveniles 1 yr after a burn and a decrease in observed adults 2 yr after a burn (Cummer and Painter 2007). Cummer and Painter (2007) also examined a different set of populations of *P. neomexicanus* persisting after the same burn and found no relationship between burn severity and the percentage of surveys where salamanders were present; however, their study design confounded detection probability and occupancy and did not test for differences in counts or estimate abundances. All of these studies focused on either one species or only on low-severity burns and did not examine relationships between population abundance and wildfire severity. Understanding how plethodontid populations are affected by heterogeneous wildfire severity and how they recover after a burn can provide information on responses to potential future fire.

In this study, we examined the abundance and body size distributions of five plethodontid salamander species in Great Smoky Mountains National Park, USA, that were affected by the Chimney Tops Two (CT2) wildfire. To gain a more holistic view of the effects of the wildfire, we compared abundance and body size distributions between salamander populations persisting across the range of burn severity created by the fire and those in unburned habitat. We predicted that populations persisting in burned habitat, if present, would have lower abundance than those in similar, unburned habitat. Furthermore, we predicted that salamander population abundance in more severely burned areas would be lower than those in less severely burned areas. Because larger bodied individuals would be at lesser risk of desiccation in warmer, drier habitats such as those created after a wildfire, we hypothesized that individuals found in burned habitat would be larger than those found in unburned habitat. Finally, we hypothesized that salamander populations located in burned areas closer to the burn boundary would have higher abundances than those closer to the core of the burn due to immigration from sites that were not burned.

Materials and Methods

Study System and Sampling

Our study took place in Great Smoky Mountains National Park and focused on the CT2 fire boundary and a surrounding 7.5-km-radius buffer (Fig. 1). This fire started in November 2016 during one of the most intense droughts that the region had experienced in the past century (Reilly et al. 2022). Dry conditions and unpredicted changes in weather caused the fire to spread rapidly. By the time the fire was extinguished, >6000 ha of land had burned at varying severities. To adequately cover the variance in burn severity and elevation present on the landscape, we used generalized random tessellated sampling, a method to generate spatially balanced sampling locations across categorized landscapes. Elevation ranged from 337 to 1656 m and was categorized into five equal intervals of 264 m. Burn severity, as represented by the relative differenced normalized burn ratio (RdNBR) index (Miller et al. 2009), ranged from −0.47 to 1.22 within our study area and we categorized it into five equal intervals of 0.338. RdNBR is a remote-sensing metric acquired by first calculating NBRs (Key and Benson 2006) from imagery before and after a fire, differencing them to get dNBR, and finally dividing dNBR by prefire NBR to account for prefire bias. The metric ranges from a theoretical minimum of 0 to an approximate maximum of 1.3, but we retained negative values of RdNBR because they may be interpreted as enhanced regrowth and we sought to characterize the entire range of observed values.

To control for variation in elevation and burn severity when randomly placing sampling sites, we identified polygons for each severity-by-elevation combination. We then clipped these polygons to a 30-m buffer around established trails and used the R package spsurvey (Dumelle et al. 2023) to identify sampling locations. This ensured our sampling sites were balanced across all elevation/burn-severity combinations, but were still randomly located within the area covered by each. We generated five samples per elevation-by-severity combination that were accessible via trails within the park. In addition, we tried to identify similar, unburned sites outside of the burn boundary by creating a random sample of 20,000 points along all trails within 1 km of the burn boundary and then comparing the physiographic attributes of the sample sites within the burn to this random sample. We matched unburned sites to burned sites by elevation, distance from stream, slope, and Beers transformed aspect (Beers et al. 1966) to account for additional physiographic features that could not be controlled when identifying sample locations. Paired sites had to be within 25-m elevation, 5% slope, 30 m distant from streams, and 0.15 units of Beers transformed aspect of one another to be considered approximately equivalent. We identified 35 burned sites in total from 19 of the 25 possible burn-by-elevation combinations that were accessible and covered a range of burn severities as assessed by RdNBR values (Fig. 2) and 35 paired, unburned sites. We included an additional 30 unburned sites for the analysis, each sampled using the same protocol but identified for another project and included to cover potential variability introduced through historical land use.

At each site, we laid two 25-m transects along an established trail, and each were split into five 5-m subplots (Milanovich et al. 2015). We measured habitat variables at each 5-m subplot during May 2021 and included canopy cover, leaf litter depth, and a visual estimate of percent vegetative cover. We conducted nocturnal visual encounter surveys from late May to early August 2021, and each site was visited at least three times. During the survey, we recorded survey-specific weather conditions thought to alter plethodontid surface activity including relative humidity, air temperature, soil surface temperature, and subsurface soil temperature (Baecher and Richter 2018; Gade and Peterman 2019; Hocking et al. 2021). We identified the species of all salamanders encountered and assigned a total length size category by using a ruler with equal intervals of 3 cm (i.e., $0 < x \leq 3$ cm = Category 1, $3 < x \leq 6$ cm = Category 2, etc.). For analysis, we examined five species: *Plethodon jordani*, *Plethodon glutinosus* spp., *Desmognathus wrighti*, *Desmognathus imitator*, and *Eurycea wilderae*. These species were chosen because they represent a range of life-history traits and habitat preferences (Dodd 2004).

Analysis

We fit N-mixture models (Royle 2004) to estimate abundance for each of the five species by using the ubms package

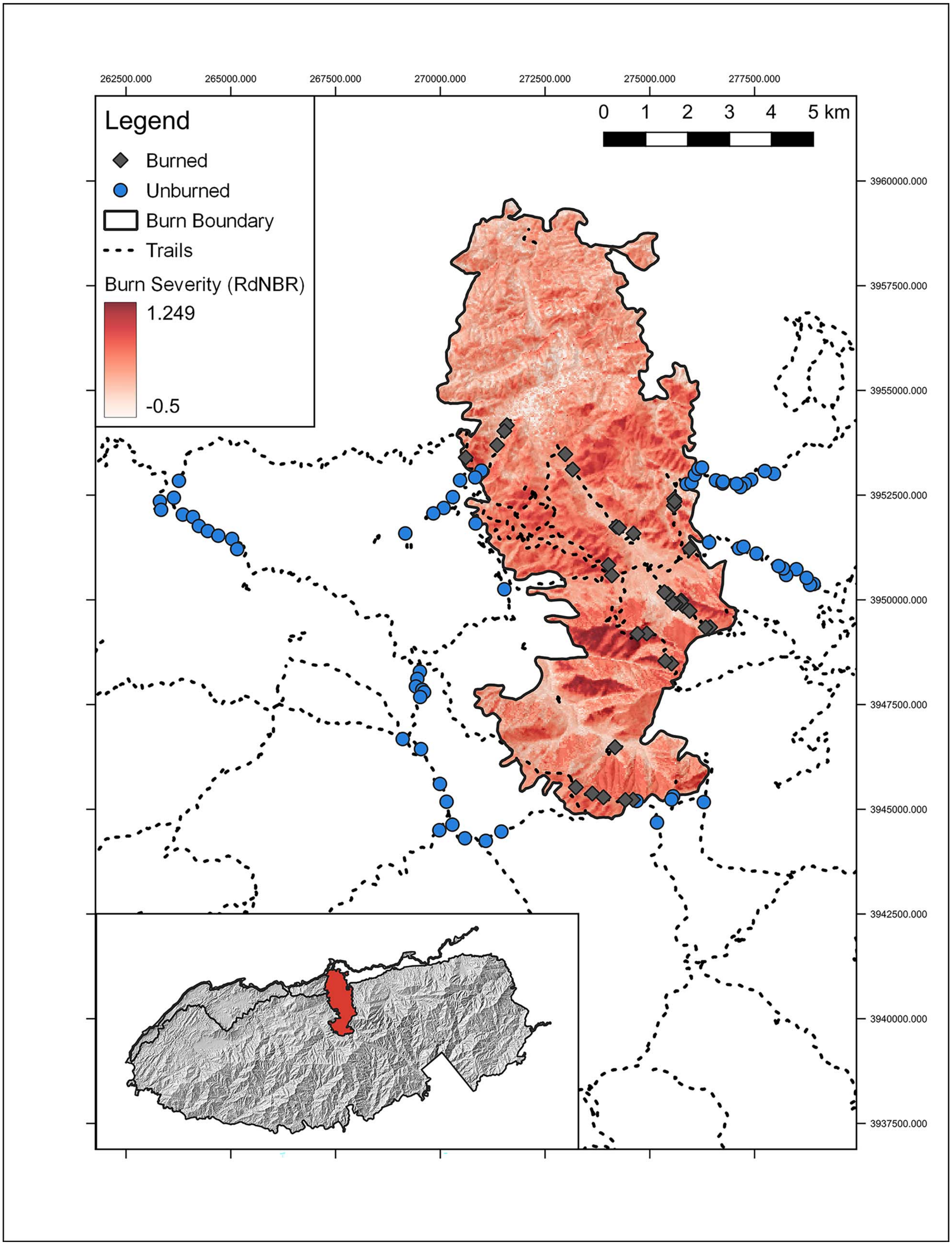

Fig. 1.—Map of site locations and burn severity of the CT2 wildfire. The inset shows the burn contextualized within the boundary of Great Smoky Mountains National Park. In total, 35 burned and 65 unburned sites were identified and sampled. The burned sites covered a range of severity, and each had an analogous unburned site matched using elevation, distance from nearest stream, Beers transformed aspect, and slope. The remaining 30 sites were sampled identically for a different project, but were included for analysis.

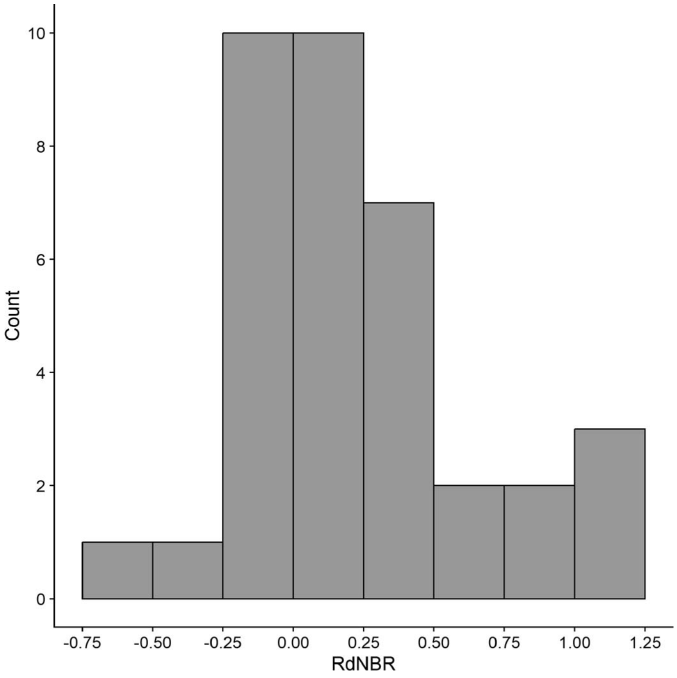

FIG. 2.—Histogram of burn severity as measured by RdNBR from burned sites.

(Kellner et al. 2022) in R v4.1 (R Core Team 2020). Our models assumed that latent abundance (λ) at a site (*i*) followed (∼) a Poisson distribution (Equation 1) linked to environmental covariates with a logarithmic function (Equation 2):

$$N_i \sim \text{Poisson}(\lambda_i) \qquad [1]$$

$$\begin{aligned}\log_e(\lambda_i) \sim\ & \alpha + \beta_1\text{Elev}_i + \beta_2\text{Elev}_i^2 + \beta_3\text{Beers}_i \\ & + \beta_4\text{Stream}_i + \beta_5\text{Elev}_i \times \text{Stream}_i \\ & + \beta_6\text{Unburned}_i + \beta_7\text{RdNBR}_i \\ & + \beta_8\text{Unburned}_i \times \text{RdNBR}_i \\ & + \beta_9\text{Disturbance}_i. \qquad [2]\end{aligned}$$

In addition, the models assumed that the count of observed individuals during any given survey (*j*) was the result of a binomial process that sampled the latent population (λ_i) and incorporated site-survey–specific individual detection probability (p_{ij}; Equation 3). Individual detection probability was linked to site-survey variables by using a logit equation (Equation 4):

$$\text{Count}_{ij} \sim \text{Binomial}(N_i,\ p_{ij}) \qquad [3]$$

$$\begin{aligned}\text{logit}(p_{ij}) \sim\ & \alpha +\ \beta_1\text{Temp}_{ij} + \beta_2\text{Temp}_{ij}^2 + \beta_3\text{Humidity}_{ij} \\ & +\ \beta_4\text{Precipitation}_{ij}. \qquad [4]\end{aligned}$$

To estimate latent abundance, we used the physiographic variables of Beers transformed aspect, a quadratic of elevation (meters), distance from stream (meters), an interaction between distance from stream and elevation, historical disturbance category, and RdNBR for sites that were burned. Topographic data were derived from a 10-m-resolution digital elevation model retrieved from the National Parks Service Integrated Resource Management Applications portal, and RdNBR was retrieved from the Monitoring Trends in Burn Severity database (Eidenshink et al. 2007; Finco et al. 2012; Picotte et al. 2020). We chose not to include local habitat variables in the analysis to reduce model complexity.

To estimate survey-specific detection probabilities, we used precipitation sums (millimeters) for the 3 d before sampling, relative humidity (percent), and a quadratic of air temperature (Celsius) as all of these covariates have been shown to influence plethodontid surface activity (Gade and Peterman 2019; Sanchez et al. 2020; Hocking et al. 2021). All covariates were scaled and centered before analysis.

For each species and covariate used, we created informed prior distributions based on published estimates for the species or from congenerics when estimates could not be found (Table 1). In instances where priors were taken directly from published values for a species, SDs were increased by 10%. When the prior distributions were taken from studies on congenerics, SDs were increased by 25%. If there were no published data on covariate effects for a species or congenerics, diffuse normal priors with a mean of 0 and a SD of 1.96 were used. The models were run using 10,000 sampling iterations on eight chains, and the first half (5000 iterations) were discarded as warmup for a total of 40,000 draws characterizing the posterior. We examined chains for proper mixing by evaluating Rhat values and ensuring they were all $<$1.1. We characterized the posterior and evaluated the effect of burn and burn severity by using probability of direction and practical significance generated from the *bayestestR* package (Makowski et al. 2019). Probability of direction indicates the proportion of a posterior estimate that lies to one side of zero, whereas practical significance represents the proportion of a posterior that lies to one side of the region of practical equivalence (ROPE). We used $\pm 0.1 \times$ SD of the covariate to identify ROPE boundaries (Kruschke 2018).

We tested for a difference between the body size distributions for burned and unburned sites by using one-sided Mann–Whitney *U*-tests (Mann and Whitney 1947). We used Mann–Whitney *U*-tests rather than *t*-tests because the data collected on body size are best considered as ordinal rather than continuous. We used a threshold of $\alpha = 0.05$ to evaluate the significance of any differences observed.

We also examined the potential relationship between estimated abundance at burn sites and distance from the burn boundary. To account for the variability in abundance estimates, we used 2000 draws from the posterior of the abundance model to create 2000 sets of abundance predictions. These prediction sets were then used to build a linear model where abundance was predicted by distance from burn edge by using the brms package (Bürkner 2017). Each of the 2000 models was run on four chains for 2000 iterations, where the first half (1000) were discarded as warmup, resulting in 4000 posterior draws. We then combined the posteriors from each of these 2000 models to form a single, grand

TABLE 1.—Means and SDs provided to inform prior distributions for each salamander species. Means were taken directly from published literature where applicable, estimated based on expert knowledge, or left at zero. SDs were taken from the literature and were increased by 10 or 25% depending on whether the values were published for a species or a congeneric, respectively.

	Species				
Parameter	*Plethodon jordani*	*Plethodon glutinosus* spp.	*Desmognathus wrighti*	*Desmognathus imitator*	*Eurycea wilderae*
Detection					
3-day precipitation (mm)	0.082 ± 0.079	0.082 ± 0.079	0.082 ± 1.96	0.1 ± 1.96	0.2 ± 1.96
Relative humidity (%)	0.109 ± 0.062	0.082 ± 0.059	0.930 ± 0.286	0.1 ± 1.96	0.684 ± 0.190
Air temperature (°C)	0.216 ± 0.104	0.216 ± 0.118	−0.120 ± 0.397	0 ± 1.96	0.125 ± 0.235
Air temperature^2	−0.13 ± 0.068	−0.130 ± 0.073	−0.285 ± 0.230	0 ± 1.96	−0.478 ± 0.183
Abundance					
Burn binary	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
RdNBR	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
RdNBR × burn binary	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Elevation (m)	2.467 ± 0.410	−0.5 ± 1.96	2.503 ± 1.133	2 ± 1.96	0.796 ± 0.374
Elevation^2	−1.658 ± 0.372	0 ± 1.96	−0.375 ± 0.753	0 ± 1.96	−0.478 ± 0.326
Beers index	0.250 ± 1.96	0.25 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Distance from stream (m)	−0.321 ± 0.186	−0.321 ± 0.186	0 ± 1.96	0 ± 1.96	0 ± 1.96
Distance from stream × elevation	0.294 ± 0.189	0.294 ± 0.189	0 ± 1.96	0 ± 1.96	0 ± 1.96
Light cut	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Selective cut	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Commercial logging	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Settlement	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96	0 ± 1.96
Source	Baecher and Richter 2018; Gade and Peterman 2019; Hocking et al. 2021	Baecher and Richter 2018; Gade and Peterman 2019; Hocking et al. 2021	Gade and Peterman 2019; Hocking et al. 2021	Hocking et al. 2021	Hocking et al. 2020

posterior with a total of 8,000,000 samples to characterize the possible relationship between abundance and distance from burn boundary. We used the *bayestestR* package to estimate the probability of distance from edge affecting abundance estimates by characterizing the grand posterior for each species and calculating probability of direction, the region of probable equivalence, and the practical significance.

RESULTS

We observed 1832 salamanders of 12 species. The most frequently observed species were *P. jordani* followed by *P. glutinosus* spp., with 991 and 284 captures, respectively. The other species examined for this study, *D. imitator*, *D. wrighti*, and *E. wilderae*, had 111, 85, and 247 counts, respectively. Burn status had strong negative effects on abundance across all species (Fig. 3; Table 2), and there was a 100% probability of negative effect for each species. Burn severity also had negative effects on each species' abundance (Table 2), but the probability of an effect being present was less clear and was never >82% (*P. jordani*, 82%; *D. imitator*, 75%; *D. wrighti*, 71%; *P. glutinosus* spp., 70%; and *E. wilderae*, 68%). For all species except *E. wilderae*, the uncertainty around predictions of abundance for sites with negative RdNBR values (i.e., indicating regrowth) was much greater than those with positive RdNBR values (i.e., moderate- to high-severity burns; Fig. 3). This indicates that populations may be persisting within the burn boundary in areas that saw enhanced regrowth at abundances similar to unburned habitat.

Body size distributions significantly differed between burned and unburned sites for *P. jordani* ($U_{385,602} = 100{,}648.5$; $P < 0.001$), *D. wrighti* ($U_{30,54} = 735$; $P = 0.045$), and *D. imitator* ($U_{27,84} = 808.5$; $P = 0.006$). However, there were no significant differences in body size distributions for *P. glutinosus* spp. ($U_{5,275} = 461$; $P = 0.091$) or *E. wilderae* ($U_{46,200} = 4342$; $P = 0.264$). Body size distribution in burned habitat trended toward a prevalence of larger individuals for all species when a significant difference was found (Table 3).

There were unclear relationships between distance from burn boundary and local abundance in burned sites. When using the probability of direction as an evaluation metric, all species had >50% probability of a negative relationship between abundance and burn boundary (i.e., populations within the burn, closer to the boundary would have greater abundance than those farther into the burn). Three species even had >90% probability of a negative relationship by using this metric (Table 4). However, there were not consistent trends about the presence of an effect after excluding the ROPE and using the practical significance. After excluding the ROPE, only *D. imitator* populations had >90% probability of a negative relationship.

DISCUSSION

Our study examined the effects of wildfire severity on plethodontid salamander abundances of the Southern Appalachian Mountains and changes in body size distributions of salamanders between burned and unburned habitats. Populations in burned habitat had drastically lower abundances than those in unburned habitat, and there was a nonsignificant trend of more severe fire causing greater reductions. The relationship with burn severity was less pronounced than hypothesized, but the lack of relationship may be a result of highly depressed abundance even at sites that experienced low-severity burns. Body size distributions were different between burned and unburned sites for three of the five species, and individuals were larger, on average, in burned sites. Finally, only *D. imitator* exhibited a relationship between abundance and distance from burn edge at burned sites. This indicates that *D. imitator* populations may have received meaningful numbers of immigrants since the CT2 fire, whereas other poluations have not.

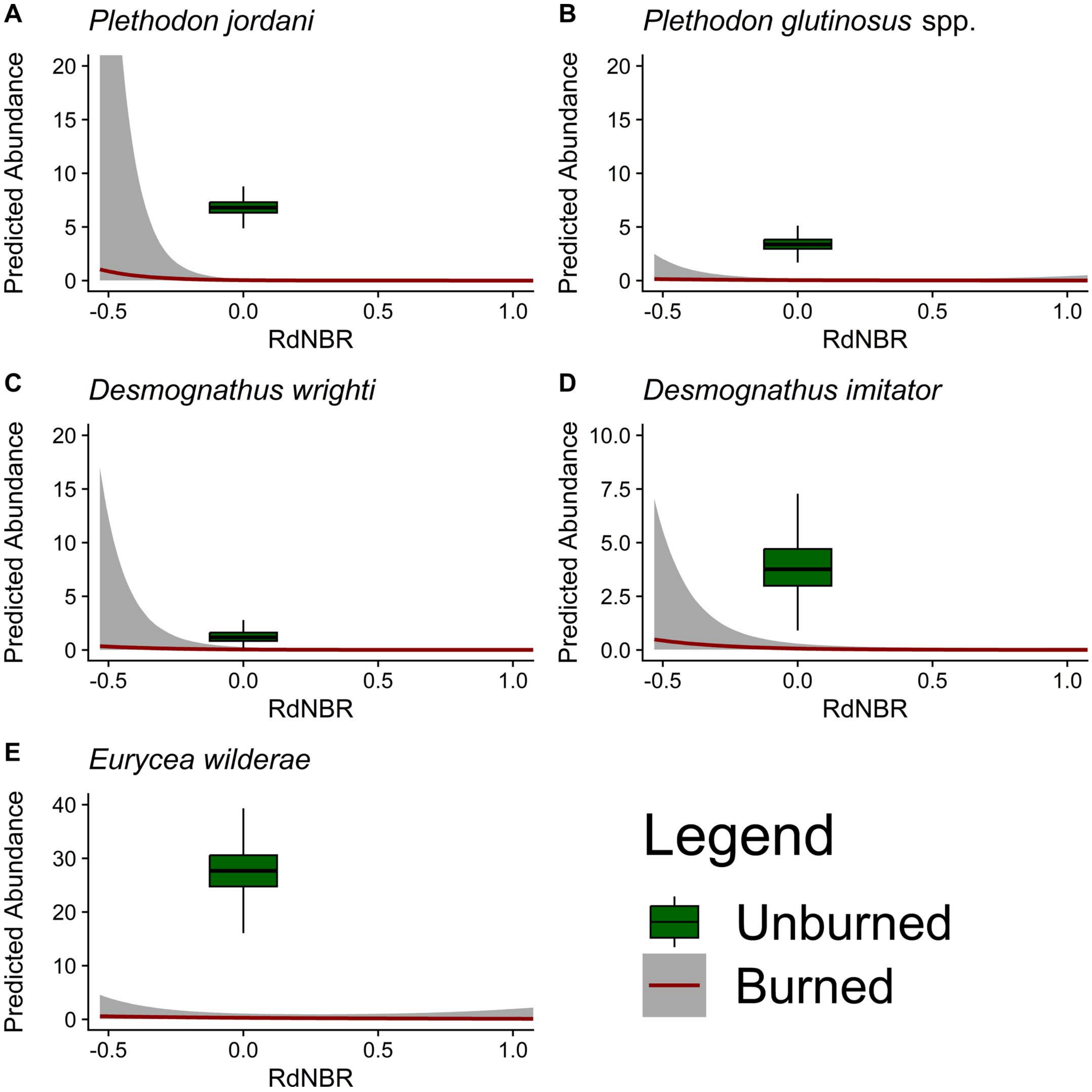

FIG. 3.—Marginal effects of RdNBR compared with estimates from unburned areas. Boxplots represent the predicted population abundance (individuals per site) in unburned areas, whereas the curves show predicted abundance across a range of burn severities. Shaded areas represent 95% credible interval. Marginal effects were predicted for hypothetical sites at 1000-m elevation.

Most knowledge about plethodontid responses to fire are based on studies from prescribed fire or examining low-intensity wildfire that are not comparable to high-severity wildfire. In response to prescribed fire, plethodontid salamander populations were not affected (Ford et al. 1999; Greenberg and Waldrop 2008; Mahoney et al. 2016) or had slight reductions in abundance (Jacobsen et al. 2020). Plethodontid populations affected by low-intensity wildfire showed slight reductions in abundance, followed by recovery within 3 yr (Gade et al. 2019). However, a site merely being within the burn boundary of the higher intensity CT2 fire had significant, negative impacts on local abundance, regardless of burn severity. These results emphasize that moderate- to high-severity burns impact plethodontid populations more severely than prescribed fire or low-severity wildfire. Using prescribed fire to mitigate the chance of high-severity wildfires is justified, despite the potential negative effects on plethodontid populations.

Despite showing that plethodontid populations burned by the CT2 fires had meaningful declines in abundance compared

TABLE 2.—Parameter estimates from N-mixture models. Mean estimates and 95% credible intervals are provided for each salamander species. Bolded values with an asterisk (*) indicate when the entire credible interval follows the same direction of effect as the mean estimate.

Variable	*Plethodon jordani*	*Plethodon glutinosus* spp.	*Desmognathus wrighti*	*Desmognathus imitator*	*Eurycea wilderae*
State					
Intercept (state)	0.79 (−0.11 to 1.69)	1.15 (0.25–2.05)	−0.48 (−1.88 to 0.89)	0.76 (−0.32 to 1.84)	3.38 (2.54–4.21)
Burned	**−5.37 (−7.79 to −3.49)***	**−4.51 (−7.15 to −2.44)***	**−3.52 (−6.46 to −1.20)***	**−4.12 (−6.48 to −2.21)***	**−4.58 (−6.86 to −2.75)***
RdNBR	−1.55 (−4.68 to 1.54)	−0.91 (−3.96 to 2.11)	−0.97 (−4.12 to 2.14)	−1.05 (−3.88 to 1.74)	−0.77 (−3.53 to 1.99)
Elevation	**2.48 (2.01–2.97)***	0.14 (−0.48 to 0.76)	**1.41 (0.27–2.68)***	**1.04 (0.29–1.90)***	**−0.75 (−1.21 to −0.29)***
Elevation^2	**−0.29 (−0.54 to −0.05)***	**−2.78 (−3.68 to −1.96)***	−0.49 (−1.49 to 0.35)	−0.36 (−0.86 to 0.06)	**−0.84 (−1.19 to −0.50)***
Beers index	**−0.29 (−0.42 to −0.17)***	−0.03 (−0.19 to 0.14)	−0.20 (−0.57 to 0.16)	−0.21 (−0.45 to 0.03)	0.07 (−0.07 to 0.21)
Distance from stream (m)	**−0.43 (−0.76 to −0.11)***	**0.60 (0.31–0.88)***	**−1.02 (−1.79 to −0.29)***	0.19 (−0.58 to 0.95)	**−0.49 (−0.89 to −0.12)***
Light cut	**−1.09 (−1.38 to −0.80)***	**0.52 (0.23–0.81)***	**0.98 (0.05–1.95)***	**−3.59 (−5.90 to −1.82)***	**−1.33 (1.97 to −0.71)***
Selective cut	−0.02 (−0.36–0.32)	0.33 (−0.01 to 0.66)	−2.19 (−4.93 to 0.07)	**−2.49 (−5.15 to −0.42)***	**−3.22 (−4.66 to −2.03)***
Commercial logging	**0.43 (0.12–0.74)***	−0.66 (−1.48 to 0.09)	−0.73 (−2.10 to 0.56)	−0.52 (−1.43 to 0.32)	**−0.94 (−1.44 to −0.44)***
Settlement	**−1.99 (−3.23 to −0.97)***	0.4 (−0.19 to 0.98)	−1.58 (−3.38 to 0.03)	−0.16 (−2.69 to 0.93)	**−1.76 (−2.41 to −1.16)***
RdNBR × burn binary	−0.02 (−3.11 to 3.03)	0.36 (−2.62 to 3.37)	−0.03 (−3.05 to 3.05)	0.16 (−2.69 to 3.01)	0.46 (−2.29 to 3.25)
Elevation × distance from stream	−0.19 (−0.47 to 0.08)	**1.18 (0.58–1.82)***	0.39 (−0.49 to 1.19)	0.08 (−0.44 to 0.62)	0.35 (−0.20 to 0.85)
Detection					
Intercept (detection)	−0.04 (−0.29 to 0.21)	**−0.64 (−0.97 to −0.29)***	**−2.06 (−3.14 to −1.12)***	**−1.77 (−2.40 to −1.09)***	**−3.02 (−3.44 to −2.60)***
3-day precipitation sum	0.11 (−0.02 to 0.24)	**0.21 (0.10–0.31)***	**1.23 (0.69–1.86)***	0.27 (−0.16 to 0.73)	**0.57 (0.38–0.77)***
Relative humidity (%)	**0.11 (0.03–0.19)***	0.01 (−0.09 to 0.11)	**1.17 (0.74–1.61)***	**0.3 (0.01–0.62)***	**0.61 (0.41–0.83)***
Air temperature (°C)	0.09 (−0.06 to 0.25)	**0.33 (0.15–0.52)***	0.04 (−0.56 to 0.62)	−0.39 (−0.94 to 0.14)	**−0.61 (−0.89 to −0.34)***
Air temperature^2	−0.08 (−0.18 to 0.03)	−0.08 (−0.21 to 0.04)	−0.05 (−0.45 to 0.36)	0.10 (−0.35 to 0.53)	0.19 (−0.04 to 0.42)

TABLE 3.—Counts of each salamander species according to burn status and the relative proportions of salamanders that fell into each total length size category. Overall, larger size categories accounted for greater proportions of all salamanders seen in burned habitat. In total, 65 unburned sites and 35 burned sites were sampled.

		Size range (cm)					
Species	Count	0–3	3–6	6–9	9–12	12–15	15–18
Desmognathus imitator							
Unburned	84	0.01	0.39	0.51	0.08	0	0
Burned	27	0	0.11	0.78	0.11	0	0
Desmognathus wright							
Unburned	54	0.09	0.91	0	0	0	0
Burned	30	0	1	0	0	0	0
Eurycea wilderae							
Unburned	200	0.01	0.42	0.31	0.26	0	0
Burned	46	0	0.3	0.52	0.17	0	0
Plethodon glutinosus spp.							
Unburned	275	0.01	0.07	0.2	0.45	0.24	0.04
Burned	5	0	0	0.2	0.2	0.4	0.2
Plethodon jordani							
Unburned	602	0.01	0.06	0.35	0.46	0.11	0.01
Burned	385	0	0.05	0.26	0.5	0.18	0.01

with unburned sites, the mechanism of loss is still unknown. The context of other environmental conditions co-occurring with the CT2 burn must be considered when examining its effects on plethodontid populations. The observed losses may possibly be explained by indirect effects of reduced habitat suitability following burn (Gade et al. 2019) or direct effects such as mortality during the burn (Jolly et al. 2022).

An example of important co-occurring conditions that may influence the impact of fire on plethodontid populations is the time of year that a burn takes place. The CT2 fire burned during the winter, a season in which plethodontid salamanders would likely be in underground refugia for the winter torpor (Feder and Burggren 1992; Lannoo 2005). In addition, the fire started during one of the most severe droughts that the region had experienced in the past century (Reilly et al. 2022). Drought effects may have acted in tandem with the winter to drive plethodontids into underground refugia, thereby potentially escaping direct mortality from the fire. However, the drought may have reduced the foraging potential of these populations during the fall when individuals were preparing for torpor. Reduced foraging potential may have led to reduced body condition going into a season where they rely on energy storage to survive and putting them at greater risk of indirect mortality after emerging to a burned landscape in the spring.

Wildfire can dramatically alter local habitat suitability depending on its severity, which may lead to indirect mortality. In many burned areas, leaf litter and the duff layer can be fully or partially removed and soil properties may be altered (Thompson et al. 2019). In the most severe instances, wildfire can burn forest floors down to mineral soil and remove canopy cover. The range of severity covered in this study is large: some sites were reduced to little more than mineral soil, gravel, and burnt stumps, whereas others were nearly indistinguishable from unburned habitat after 5 yr of recovery.

The changes in local habitat may have cascading effects on plethodontid populations. First, decreased leaf litter throughout burned areas and loss of canopy cover in others will alter soil moisture and temperature regimes (Ice et al. 2004; Cardenas and Kanarek 2014) and reduce the short-term

TABLE 4.—Relationship between salamander abundance and distance from burn edge (m) at burned sites. Median parameter estimates and 95% credible intervals (CIs) are shown. Probability of direction indicates the proportion of the posterior that lies to one side of zero. Percent in the region of practical equivalence (ROPE) represents the proportion of the posterior that falls within 0 ± (0.1 × SD) of the variable. Practical significance indicates the proportion of the posterior that lies to one side of zero and outside of the ROPE and can be interpreted as the percent probability of a direction of effect consistent with the median parameter estimate.

Species	Distance from burn boundary (CI)	Probability of direction (%)	% in ROPE	Practical significance (%)
Desmognathus imitator	−0.02 (−0.15 to 0.0)	96.22	4.91	92.50
Desmognathus wrighti	−0.02 (−0.15 to 0.0)	95.42	32.17	66.93
Eurycea wilderae	0.0 (−0.08 to 0.10)	62.3	2.10	61.26
Plethodon glutinosus spp.	0.0 (−0.05 to 0.04)	56.93	21.3	45.66
Plethodon jordani	−0.03 (−0.14 to 0.0)	98.92	21.25	77.32

density of arthropod populations (Vasconcelos et al. 2009), the primary food source of plethodontid salamanders (Holomuzki 1980; Walton et al. 2006). Second, plethodontid salamanders respire cutaneously and require stable, cool, moist microclimates to persist (Peterman and Semlitsch 2014), conditions that may be lost with the decrease in leaf litter and canopy cover. The short-term alterations in microclimate and food source because of wildfire may make some areas within burns unsuitable. Salamanders that survived the initial burn may perish or attempt to emigrate as a result. However, it is unknown what constitutes habitat changes severe enough to cause emigration or indirect mortality.

Conversely, it is possible that the fire increased soil temperatures to fatal levels for salamanders despite their shelter, especially in more severely burned areas. The unknown depth at which plethodontid salamanders retreat during the winter and what soil temperatures were reached during the CT2 fire leave the magnitude of direct mortality as speculation and a possible route for future research.

Another potential reason for the decrease in population estimates in burn areas is drastic alteration in surface activity patterns. There is some evidence that plethodontid salamanders reduce their surface activity levels in postburn habitat (J.C. Maerz, personal observation). Because our study examined populations in both burned and unburned habitats under a variety of survey conditions, the alterations in activity level would need to be severe for salamanders to be absent from surveys of burned habitat and to have the models estimate such differences in abundance. Although there is little evidence of this in the literature, this hypothesis warrants further study.

In addition to changes in population density, the CT2 wildfire altered plethodontid salamander body size distributions similarly to what has been shown in lower severity burns where remaining salamanders are larger (Cummer and Painter 2007; Gade and Peterman 2019). The difference in size distributions between burned and unburned sites may be related to the change in habitat suitability and local microclimate postburn. Burned areas are warmer and drier, conditions that cause greater vapor pressure deficits and increased desiccation risk. Larger bodied individuals have a lower desiccation risk because they have a lower surface area-to-volume ratio (Baken et al. 2020) and therefore are better able to persist in drier habitats compared with small-bodied individuals. However, there is a possibility that observed differences in body size estimates is an artifact of sampling bias from survey-specific weather conditions (Connette et al. 2015). The changes in body size distributions may be indicative of a change in age structure that could have implications for survivorship and reproduction rate, and monitoring for changes in these parameters postfire is an area of further study.

After 5 yr of recovery, populations in burned habitat (RdNBR values > 0) had significantly fewer salamanders than those in unburned habitat (≤1/10). Furthermore, only one species displayed evidence of a relationship between proximity to the burn boundary and abundance in burned habitat. This indicates that mortality or emigration has occurred in all burned habitats surveyed and that population recovery has not occurred in the 5 yr since the fire. However, it is unknown whether the reductions and losses of populations in these habitats are a direct result of the fire or whether sublethal effects such as altered habitat suitability have caused mortality or emigration. Some areas, especially in high-intensity burn sites where the surface was burned down to mineral soils, may require a long recovery to reestablish because plethodontid populations require leaf litter and organic horizons to thrive (Gade and Peterman 2019; Wilk et al. 2020; Hocking et al. 2021). There is no reliable way to estimate when these populations may recover because it will rely on a combination of immigration, reproduction, and habitat regaining suitability to host these species. As such, we advocate for continued monitoring of these and additional sites to examine long-term responses of plethodontid salamanders to wildfire.

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