Forest Ecology and Management 468 (2020) 118185

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Influence of prescribed fire and forest structure on woodland salamander abundance in the central Appalachians, USA

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ARTICLE INFO

Keywords:
Amphibian
Cow Knob Salamander
George Washington National Forest
Habitat Management
Plethodon

ABSTRACT

Prescribed fire is used in the central Appalachians to promote and maintain mixed-oak and pine forests, create open forest conditions, improve habitat for wildlife, and to reduce the risk of impact of higher intensity wildfires on human development. Few studies have investigated responses of terrestrial salamander populations to habitat management using fire, and estimated responses have been neutral, negative, and positive depending on geography, species, and fire-severity. We examined woodland salamander (genus *Plethodon*) population responses to habitat management using prescribed fire on Shenandoah Mountain in the George Washington National Forest in West Virginia and Virginia, USA. We focused on responses of the Cow Knob Salamander (*P. punctatus*), a talus specialist and species of high conservation concern, but also examined responses of the Eastern Red-Backed Salamander (*P. cinereus*), a widespread habitat generalist. Three burn units were subjected to two low-severity burns and one unit was burned five times with ca. 40% tree mortality. Using a combination of nighttime visual encounter surveys and coverboard surveys, we compared terrestrial salamander abundance and body condition in unburned and burned areas. We also measured habitat characteristics at sampling sites to determine if prescribed burn histories were correlated with habitat conditions important to woodland salamanders. Mean abundance for *P. punctatus* was lower at sites that were burned, but there was not a strong burn effect for *P. cinereus*. Abundance of both species was positively correlated with canopy cover. Mean and median body condition index (BCI) score was higher for *P. punctatus* and lower for *P. cinereus* on the West Virginia side of Shenandoah Mountain, and lower in burned areas for both species. However, the most parsimonious BCI models did not contain the burn predictor. Management using prescribed fire altered microhabitat conditions that are important for woodland salamanders, such as canopy cover, leaf litter depth, and vegetation groundcover. Our study suggests that woodland salamanders in the central Appalachians can persist in forests managed using prescribed fire, but also indicates that prescribed fire can result in reduced habitat quality for some woodland salamander species.

1. Introduction

In the central Appalachian region of the eastern United States, prescribed fire is used by land managers as a tool to maintain and restore mixed-oak and pine forests, create and maintain open forest and early successional conditions, and decrease fuel loads to reduce the intensity of wildfires (Lafon et al., 2005). Mixed-oak (*Quercus* spp.) and pine (*Pinus* spp.) forests established prior to European settlement developed from low-intensity, high-frequency fires that were set by native Americans or caused by lightning strikes (Aldrich et al., 2010, 2014). During the industrial logging period in the late 19th and early 20th centuries, high-intensity, stand-replacing fires became common, followed by a period of fire suppression that began in ca. 1930 (Brose et al., 2001; Lafon et al., 2017). Massive wildfires during this period shifted public opinion to view fire as a detrimental force and fire suppression became a widespread policy and one of the first priorities for the U.S. Forest Service (USFS; Brose et al., 2001). Fire suppression allowed for succession from mixed-oak to forests dominated by shade-tolerant, fire-sensitive species, because oaks are not adapted to grow in heavily shaded forests (Brose et al., 2001). After decades of fire

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https://doi.org/10.1016/j.foreco.2020.118185
Received 14 November 2019; Received in revised form 28 March 2020; Accepted 24 April 2020

suppression, the ecological importance of fire in eastern U.S. forests became apparent, with fire serving to maintain mixed-oak and pine forests and promote diversity of vegetation communities at the landscape-scale (Nowacki and Abrams, 2008). Consequently, in the early 1970s, natural resource managers began using prescribed fire as a forest management tool in the central Appalachians, and it is now used for restoration and maintenance of fire-dependent ecosystems on public lands in the region (Lafon et al., 2005).

Prescribed fires allow for the regeneration of mixed-oak stands through removal of thin-barked shrubs and trees that compete for sunlight, reduction of leaf litter that prevents seedling establishment, decreased insect predation on acorns, and increased acorn caching by wildlife (Van Lear and Watt, 1993; Barnes and Van Lear, 1998). Further, seed banks of non-oak species often decline after prescribed burns (Schuler et al., 2010). The greatest benefits of prescribed burns for oak regeneration generally come after repeated burns and when fires occur during the oak growing season (April to October; Brose et al., 2013). Fire is also important to Table Mountain pine (*Pinus pugens*) and pitch pine (*P. rigida*), two species that are native to the southern and central Appalachians, because it opens their serotinous cones to release seeds (Elliott et al., 1999; Welch et al., 2000). Prescribed fires can also increase the diversity and abundance of understory shrubs, forbs, and grasses that provide food and cover resources for wildlife (Elliott et al., 1999; Barrioz et al., 2013).

Although the importance of fire for maintenance and restoration of oak and pine stands is well-studied, research is needed to understand how wildlife species respond to different fire regimes (i.e., fire season, intensity, size, and return interval). Species-specific research is needed because wildlife species respond differentially to fire based on their ecology. For example, some species in the Appalachian region such as Turkey (*Meleagris gallopavo*; McCord et al., 2014), White-Tailed Deer (*Odocoileus virginianus*; Lashley et al., 2011), and many reptiles (e.g. Keyser et al., 2004; Greenberg et al., 2018; Hromada et al., 2018) appear to benefit from prescribed fire, but negative impacts have been documented for other species such as the Eastern Box Turtle (*Terrapene carolina*; Howey and Roosenburg, 2013). In addition, local research is needed because the scale of inference is limited in fire-wildlife research due to variation in fire regimes, site-level habitat characteristics, and biotic interactions (e.g., Pilliod et al., 2003; Fontaine and Kennedy, 2012; Brown et al., 2014; O'Donnell et al., 2016).

The Appalachians are a global biodiversity hotspot for salamanders (Milanovich et al., 2010). Woodland salamanders (genus *Plethodon*) are an integral component of forest ecosystems. Their biomass often exceeds that of birds, small mammals, and deer (Burton and Likens, 1975). Woodland salamanders are central to forest food webs, as prey for a wide variety of vertebrates and invertebrates (reviewed by Casper, 2005), and as mid-level predators they influence invertebrate community composition and contribute to forest nutrient cycling (Semlitsch et al., 2014; Best and Welsh, 2014). Given their unique biodiversity and key ecological functions in Appalachian forests, it is important to understand salamander responses to fire in this region.

For woodland salamanders, previous investigations found a range of responses to fire that varied among species, size class, geographic region, microhabitat characteristics, and fire regime (e.g., Matthews et al., 2010; Ford et al., 2010; O'Donnell and Semlitsch, 2015; Hromada et al., 2018; Gade et al., 2019). Although the majority of previous studies did not conclude that prescribed fire significantly influenced salamander abundance, declines in abundance were apparent when multiple burns resulted in tree mortality (Matthews et al., 2010), and when prescribed fire was combined with shelterwood harvest or clearcuts (Hocking et al., 2013; Mahoney et al., 2016), suggesting prescribed fire may negatively impact salamander populations when it causes, or is combined with, a reduction in canopy cover.

The effects of fire on salamanders are likely indirect; terrestrial salamanders are fossorial, so direct mortality from fire is probably rare (Renken, 2006; O'Donnell et al., 2016). In the short-term, prescribed fires can affect microhabitat characteristics of a forest by reducing canopy cover, coarse woody debris, leaf litter, and duff, thus creating drier soil conditions and in some cases increasing soil hydrophobicity (i.e., tendency to repel water; Certini, 2005; Lafon et al., 2007; Matthews et al., 2010; Mahoney et al., 2016). Plethodontid salamanders are sensitive to changes in microhabitat characteristics that affect moisture or temperature, such as leaf litter depth and canopy cover, because they are lungless and retention of skin moisture is needed to perform cutaneous respiration for gas exchange (Maerz et al., 2009).

The majority of studies on the effects of prescribed fire on woodland salamanders have focused on the short-term effects of a single burn. However, repeated burns with relatively short fire intervals are often needed to achieve management objectives in central Appalachia (Brose et al., 2013). Thus, it is important to understand how woodland salamander populations respond to multiple prescribed burns and the resulting changes in forest structure characteristics. Additionally, population-level responses to a reduction in canopy cover can take several years to be realized. For example, Greenberg and Waldrop (2008) concluded that abundance of woodland salamanders was not affected by a mechanical fuel reduction and prescribed burn that resulted in tree mortality and reduced canopy cover; however, salamander abundance was lower at these sites a few years later following a second prescribed burn, and lower than a treatment that was burned twice with no mechanical fuel reduction (Matthews et al., 2010). In contrast, captures of total plethodontid salamanders and Northern Red Salamanders (*Pseudotriton ruber*) were not influenced by repeated prescribed burns or mechanical fuel reduction in a 14-year study in North Carolina (Greenberg et al., 2018). Gade et al. (2019) found a decline in the number of juvenile Red-Legged Salamanders (*P. shermani*) 18 months post-wildfire when compared to the same sites 6 months post-wildfire.

The purpose of this study was to examine effects of fire history and forest structure characteristics on abundance and body condition of woodland salamanders in the central Appalachian region. Specifically, we focused on the Cow Knob Salamander (*Plethodon punctatus*), a high elevation endemic species of conservation concern, and sympatric populations of the common and widely distributed Eastern Red-Backed Salamander (*Plethodon cinereus*). Most of the distribution of *P. punctatus* occurs on Shenandoah Mountain within the George Washington National Forest (GWNF; Highton, 1972), and prescribed fire is heavily used for forest vegetation management in the GWNF and adjacent Jefferson National Forest (USFS, 2014). Shenandoah Mountain occurs in the Valley and Ridge Province, one of the driest regions in the Appalachians (Lafon and Grissino-Mayer, 2007), and responses of woodland salamanders to prescribed fire in this drier region could differ from more mesic regions. Further, because *P. punctatus* is a species of high conservation concern that is projected to lose most of its climatic niche this century (Sutton et al., 2015; Jacobsen et al., 2020), it is important to understand relationships between forest structure characteristics and abundance of *P. punctatus*. If abundance is strongly correlated with forest structure, managers can use this information to maximize habitat quality for *P. punctatus*, potentially increasing resilience to climate change (Dawson et al. 2011; Jacobsen et al., 2020). We compared the abundance and body condition of *P. punctatus* and *P. cinereus* in burned and unburned plots with varying forest structure characteristics. The results of this study contribute to our understanding of woodland salamander responses to habitat management using prescribed fire, and provide managers with information that can be used to integrate vegetation-related goals with the promotion of robust salamander populations.

2. Methods

2.1. Study area

We conducted our study at high elevations (> 1075 m) on

Shenandoah Mountain in the GWNF in eastern West Virginia and western Virginia, USA (precise locations withheld due to the conservation status of *P. punctatus*). This area is in the Valley and Ridge Province, the driest region in the central Appalachians (Lafon and Grissino-Mayer, 2007). Dominant overstory trees included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. montana*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), and red maple (*Acer rubrum*). The understory consisted mostly of striped maple (*A. pensylvanicum*) and mountain laurel (*Kalmia latifolia*). Much of the study area consisted of steep talus slopes.

The USFS uses prescribed fire as a management tool on the GWNF to create open forest conditions, and to help protect the forest and wildland-urban interfaces from severe wildfires by decreasing fuel loads (USFS, 2014; Lorber et al., 2018). This management plan instructs managers to mostly avoid burning more mesic forests where oaks are not a major component, and when burning is necessary, to allow only low-intensity fires which aim to control understory vegetation growth and manage fuels (USFS, 2014). In order to achieve this goal, they have a target fire-return interval of 5–15 years in oak-dominated stands, and 3–9 years in pine-dominated stands, with ca. 4850–8100 ha burned annually (USFS, 2014). Burns are ignited by hand along perimeters and aerially within the interiors of burn units, and typically conducted at the end of the dormant season or beginning of the growing season in late April or early May (Lorber et al., 2018).

We restricted the study area to accessible locations in the GWNF within the known distribution of *P. punctatus*. We sampled 4 prescribed burn units: North New Road (NNR) was ca. 1760 ha and burned on 15 March 2012 and 10 May 2015; Little Fork (LF) was ca. 790 ha and burned on 6 April 2000 and 7 May 2008; Hone Quarry 2 (HQ2) was ca. 1010 ha and burned on 27 April 2013 and 20 April 2018; Hone Quarry (HQ) was ca. 525 ha and burned on 8 April 1999, 29 March 2002, 2 May 2010, 27 April 2013, and 20 April 2018 (Fig. 1). Sites that were burned twice (i.e., NNR, LF, HQ2) were considered low-severity fires, with minimal tree mortality and minor changes in vegetation characteristics (Lorber et al., 2018). The first HQ burn was a high severity fire that resulted in ca. 40% overstory tree mortality (Lorber et al., 2018), and this site was subsequently burned 4 times.

Within each burn unit, we chose sampling locations that were near unburned areas (i.e., areas not burned since initiation of the GWNF fire program in 1998) and similar in aspect, elevation, and talus level. After delineating the sampling locations, we selected sampling sites using a stratified random approach, where sites were at least 35 m from any roads to minimize edge effects (Semlitsch et al., 2007), no more than 100 m from roads to facilitate access, and at least 40-m apart to ensure each site was spatially independent with respect to typical woodland salamander movement distances. For example, a multi-year capture-recapture study in Virginia found the median dispersal distance for adult and juvenile *P. cinereus* was < 5 m (Ousterhout and Liebgold, 2010). We ensured that all burn units had signs of fire (e.g.., fire scars on trees or charred woody debris) within 10 m of each survey site. Each burned unit and adjacent unburned unit contained from 6 to 10 5 × 5 m survey sites, for a total of 26 unburned sites, 29 low-severity burn sites, and 6 high-severity burn sites. Time-since-burn ranged from 0 to 10 years (mean = 3.5 years). We considered sites the sampling unit for abundance estimation.

2.2. Salamander surveys

We used a combination of nighttime visual encounter surveys (VES) and nighttime coverboard surveys to sample salamanders at each site. Nighttime VES was previously found to be more effective than daytime surveys using coverboards and natural cover objects for detecting *P. punctatus* because in talus, where they are most abundant, they are typically not on the surface during the daytime (Flint, 2004; Flint and Harris, 2005). In contrast, studies have found daytime coverboard surveys to be effective for *P. cinereus* (Moore, 2005; Hesed, 2012). As such, we acknowledge coverboard surveys are potentially less effective at night, and were used here only as supplements to VES. Coverboard sampling consisted of 4 coverboards (2.5-cm thick × 15-cm wide × 30-cm long) made from untreated tulip-poplar (*Liriodendron tulipifera*). We placed coverboards flat on the soil or rock at the center of each site, usually in 2 rows with all boards spaced 2 cm apart. At talus sites, we increased spacing between boards when a board could not be placed flat on the rocks.

Each site was sampled between 2 and 5 times within a single survey year, from 22 April to 9 October 2017 or 16 May to 23 September 2018, for a total of 197 survey events. We surveyed salamanders after dusk (i.e., starting at least 30 min after civil twilight to a maximum of seven hours after dusk). All surveys took place within 24 h of a rain event to maximize the probability of salamander surface activity and thus detection probability (Grover, 1998; Flint and Harris, 2005). We employed area-constrained surveys that lasted 7–18 min (mean = 12 min), depending on groundcover and vegetation complexity (e.g., crevices in talus and vegetation for climbing). We only counted salamanders visible on the surface or under coverboards, no natural cover objects were flipped in order to preserve the integrity of the lichen and moss-covered talus used by *P. punctatus* (Flint and Harris, 2005).

2.2.1. Salamander body condition

When possible, we hand-captured and measured all detected salamanders. We recorded snout-vent-length (SVL) to the nearest 1 mm and weight to the nearest 0.1 g. We used a salamander stick to maximize accuracy of SVL measurements (Margenau et al., 2018). Capture and handling methods were approved by the West Virginia University Institutional Animal Care and Use Committee (Protocol 1612004927). We created body condition indices (BCI) for *P. punctatus* and *P. cinereus* by regressing (log) snout-vent-length (SVL) on (log) weight (Schulte-Hostedde et al. 2005); positive residuals indicate a greater than average weight for a given SVL, and vice versa. A positive BCI indicates comparatively greater energy reserves, which is associated with greater fitness (Jakob et al., 1996), and could potentially result in greater survival probability (Caruso et al., 2019). We did not include gravid females or salamanders missing portions of their tails in BCI analyses.

2.3. Model predictors

Our abundance predictors included fire history, forest structure, geological, and topographic variables. The fire history variables that we tested were burn status (burned or unburned) and time-since-burn. We measured overstory canopy cover at the center of each site using a convex spherical densiometer at chest height, with measurements taken in 4 directions and averaged. We recorded the percent groundcover of leaves, moss, and vegetation (< 1 m in height) at each site using ocular estimation. We measured leaf litter depth from the surface of the leaf litter to the top of the mineral soil, duff layer, or rocks. We took one leaf litter depth measurement in the center of each quadrant and used the mean of these values. We did not measure the duff layer because most sites did not have duff in the talus. We modified a talus ranking system that has been used previously in our study area that is based on the relative amount of rocks, soil, and spacing between rocks (Downer, 2009). We ranked talus on a scale from 0 to 5, where 0 is soil with few or no rocks present, 2.5 is a mixture of soil and rocks with some cracks and crevices present, and 5 is rocks with no soil and abundant cracks and crevices between the rocks. We also created a binary talus variable to assess whether the presence of talus is more important than the number of cracks and crevices present. Sites were classified as talus if they received a talus ranking score greater than 2.5.

We included state (i.e. West Virginia [WV] or Virginia [VA]), which corresponded to side of the mountain, as a covariate because previous research found *P. punctatus* was more abundant on the western side of the mountain (i.e., WV), likely due to wetter conditions within the

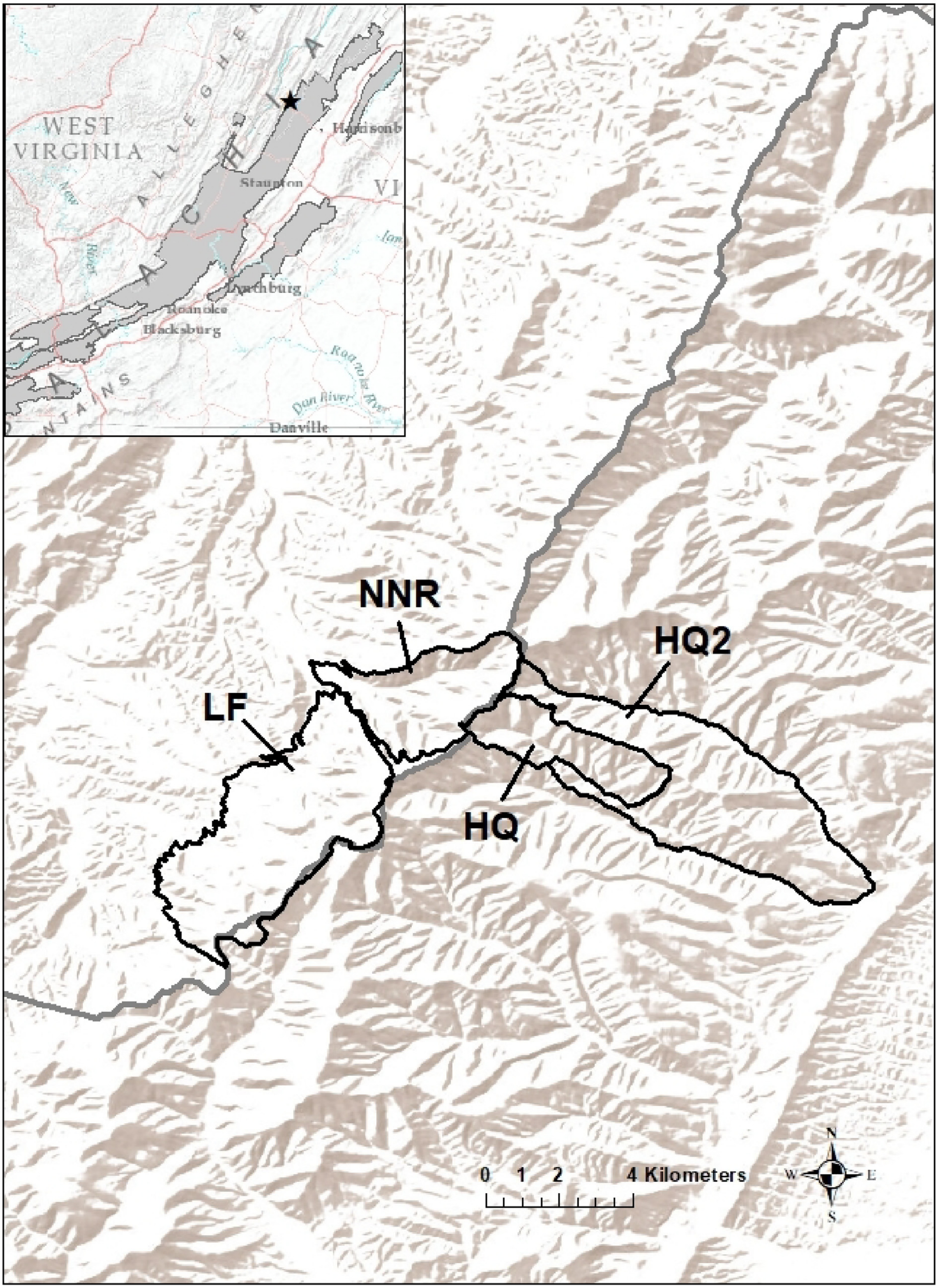

Fig. 1. Burn units included in this study investigating responses of woodland salamanders to prescribed fire management on Shenandoah Mountain in the George Washington National Forest (Gray area on inset map) in West Virginia and Virginia, USA. The dark gray line represents the border between West Virginia and Virginia. Prescribed burns were conducted in the following years: North New Road (NNR) in 2012 and 2015, Little Fork (LF) in 2000 and 2008, Hone Quarry (HQ) in 1999, 2002, 2010, 2013, and 2018, and Hone Quarry 2 (HQ2) in 2013 and 2018.

study area (Flint and Harris, 2005). Sites for burn unit NNR were located in WV, sites for unit HQ and HQ2 were located in VA, and sites for unit LF were located in both states. We obtained a 1/3 arc second (ca. 8 m^2 at 39° North) digital elevation model (DEM) from the U.S. Geological Survey National Elevation Dataset and derived 3 variables from this layer: Heat Load Index (HLI), slope, and hillshade. The HLI is a measurement of the potential heat and incident radiation a site receives due to aspect and slope (McCune and Keon, 2002). This index assigns higher values for locations with a southwest aspect because they receive higher maximum temperatures from the afternoon sun. The following equation rescales aspect to a scale from 0 for cooler northeast-facing slopes, to 1 for warmer southwest-facing slopes:

$$Heat\ \ Load\ \ Index = \frac{1 - \cos(\theta - 45)}{2}$$

where θ = aspect in degrees east of north. The HLI also accounts for the steepness of a south-facing slope because steeper slopes dry out faster (McCune and Keon, 2002).

2.4. Data analyses

2.4.1. Forest structure characteristics

We assessed relationships between fire history and forest structure characteristics using redundancy analyses (RDA). RDA is a multivariate analysis that is an extension of principal components analysis (PCA) to include explanatory variables. We chose RDA over canonical correspondence analysis (CCA) because gradient lengths were short (< 2; Legendre and Legendre, 2012). We conducted global ANOVA permutation tests to determine if forest structure characteristics differed based on burn status and time-since-burn. We used the package *vegan* (version 2.5–4) in program R (version 3.5.1) for RDA analyses.

2.4.2. Salamander abundance

For woodland salamanders, often only a small proportion of the population is active on the surface and available for detection due to their unique physiological requirements and activity patterns (Bailey et al., 2004). Thus, it is important to consider parameters that affect detectability when estimating salamander abundance (O'Donnell and Semlitsch, 2015). To estimate abundance and detectability parameters, we analyzed repeated counts using single-season, closed population *N*-mixture models (Royle, 2004). *N*-mixture models account for variations in detection probability using temporally and spatially replicated surveys.

For each species, we tested a Poisson, Zero-inflated Poisson (ZIP), and negative binomial (NB) distribution for the abundance distribution. The negative binomial models did not converge, which is a common issue when detection probabilities are low (Dennis et al., 2015). We selected the ZIP distribution because it resulted in a lower Quasi Akaike Information Criterion, corrected for small sample size ($QAIC_c$) score for both species. To assess model goodness-of-fit, we used the most complex candidate model and a 1000-replication parametric bootstrap of the Pearson chi-square statistic (Kéry and Royle, 2016). C-hat values indicated some overdispersion for both *P. punctatus* (range = 1.32–1.46) and *P. cinereus* (range = 1.73–1.88). To account for this overdispersion, we ranked candidate models using $QAIC_c$ (Symonds and Moussalli, 2011).

We used a $QAIC_c$ model selection approach to determine the most important predictors of woodland salamander abundance and detection probability (p). We first selected the most parsimonious (i.e., lowest $QAIC_c$) p submodels using weather and temporal variables collected during each survey. We tested air temperature (°C), relative humidity, time since sunset, and wind speed (kph). We retained the most parsimonious p submodel for all further analyses. We then selected the most parsimonious model for geological-topographic variables (i.e., state, talus, elevation, HLI, hillshade, slope), which were also retained for all further analyses.

For each species, we conducted two fire history model selection analyses to determine if there was an overall effect of habitat management using prescribed fire on salamander abundance. One model selection included all sites and ranked the candidate predictor burn status, and the other model selection included only burned sites and ranked the candidate predictor time-since-burn. We conducted a separate model selection analysis to determine if abundance was strongly related to the forest structure characteristics we measured. During preliminary analyses we detected model convergence issues for some variable combinations when greater than 4 abundance covariates were included, and thus we restricted model selections to include a maximum of 4 covariates.

We considered models to have some support if $\Delta QAIC_c < 7$ (Burnham et al., 2011). For the most supported models in each model selection, we assessed confidence for an effect of each variable by computing the 95% confidence intervals for their model coefficients, and considered evidence for a strong effect when confidence intervals did not overlap zero (Halsey, 2019). We also provide the estimated effect size of the variable. We conducted *N*-mixture and model selection analyses using the packages *unmarked* (version 0.12–2) and *AICcmodavg* (version 2.1–1) in program R.

2.4.3. Salamander body condition

We used linear regression models with a Gaussian distribution to assess effects of fire history and forest structure characteristics on salamander BCI (Zuur et al., 2009). We used graphical diagnostics (i.e., quantile–quantile and residual plots) to assess model fit, which indicated the data satisfied the assumptions of normality and heteroscedasticity. As with the abundance analyses, we first fit models with the most parsimonious geological-topographical variables; we then retained these variables for separate fire history and forest structure analyses. We only tested geological-topographic variables we hypothesized could have an impact on BCI, including state, talus, elevation, HLI, and hillshade.

3. Results

3.1. Forest structure characteristics

The RDA indicated a significant relationship between burn status and forest structure characteristics (F = 5.76, P < 0.001), and between time-since-burn and forest structure characteristics (F = 7.52, P < 0.001). Canopy cover, moss groundcover, leaf groundcover, and litter depth showed a strong positive correlation with unburned sites, whereas vegetation groundcover showed the opposite relationship (Fig. 2a). Canopy cover and moss groundcover were positively correlated, vegetation groundcover was negatively correlated, and litter depth and leaf groundcover were not strongly correlated with time-since-burn (Fig. 2b).

3.2. Salamander abundance

We captured a total of 296 salamanders, including 80*P. punctatus*, 213*P. cinereus*, and 3 Eastern Newts (*Notophthalmus viridescens*). We detected *P. punctatus* and *P. cinereus* at 31 and 54 sites, respectively. All locations where *P. punctatus* was found were on or within 100 m of talus. We did not find *P. punctatus* at our high severity sites, however, these sites were also not talus. No *P. punctatus* and 3.8% of *P. cinereus* were found under coverboards during the study. Detection probability increased with temperature for both *P. punctatus* and *P. cinereus* (Fig. 3). Mean estimated abundance per site was 6.1 (SD = 6.3) and 22.7 (SD = 11.8) for *P. punctatus* and *P. cinereus*, respectively (Fig. 4).

For the geological-topographic model selection, abundance of *P. punctatus* was best predicted by state and the binary talus variable, while *P. cinereus* abundance was best predicted by state (Table 1), with abundances tending to be higher on the WV side of the mountain for

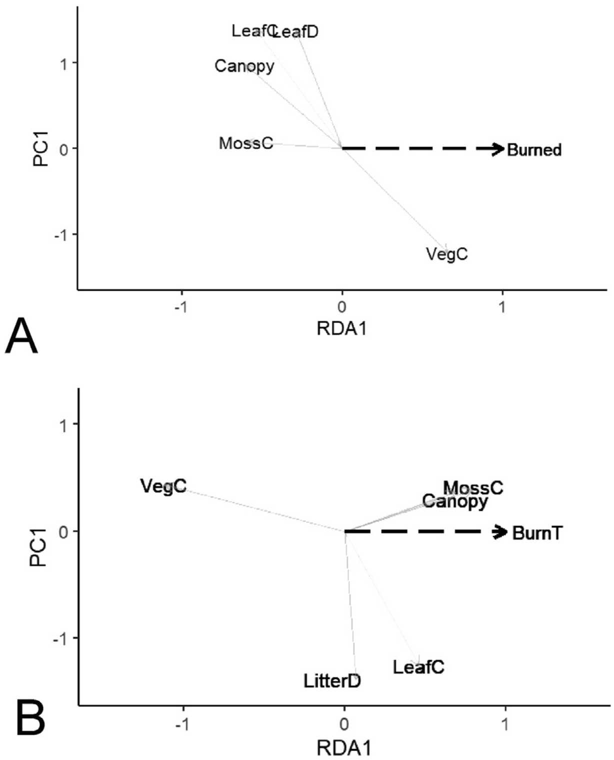

Fig. 2. Biplots from redundancy analyses (RDA) showing the relationships between forest structure characteristics and fire history variables at our woodland salamander survey plots on Shenandoah Mountain in the George Washington National Forest in West Virginia and Virginia, USA. Forest structure characteristics included canopy cover % (Canopy; mean = 81.3, range = 9.5–94.0), moss groundcover % (MossC; mean = 12.2, range = 0.0–60.0), vegetation groundcover % (VegC; mean = 34.4, range = 0.0–100), leaf groundcover % (LeafC; mean = 47.5, range = 0.0–90.0), and leaf litter depth cm (LitterD; mean = 0.2, range = 0.0–1.0). (A) Relationships between forest structure characteristics and whether a site was located in burned or unburned sites. (B) Relationships between forest structure characteristics and time-since-burn (BurnT) among the burn sites. Forest structure characteristics pointing towards the fire history variables were positively correlated, and vice versa.

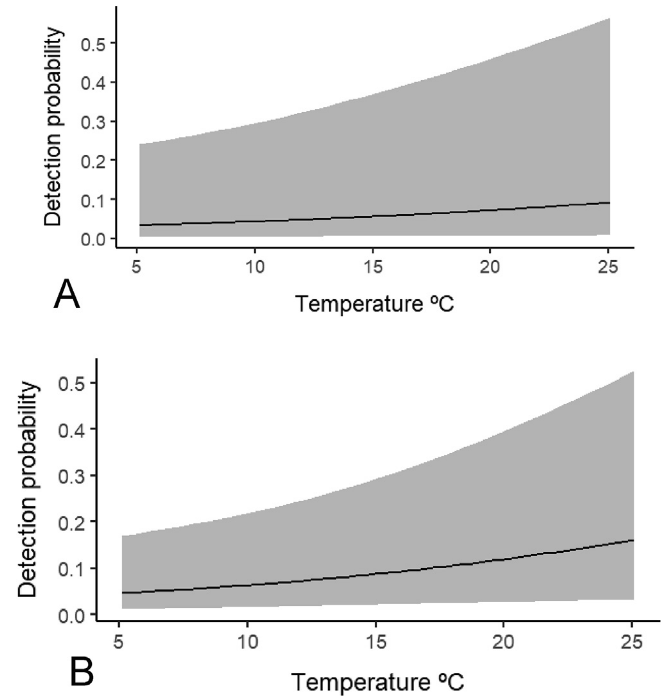

Fig. 3. Estimated relationship between air temperature and detection probability (p) for the (A) Cow Knob Salamander (*Plethodon punctatus*), and (B) Eastern Red-Backed Salamander (*Plethodon cinereus*) on Shenandoah Mountain in the George Washington National Forest, West Virginia and Virginia, USA. These p estimates are based on N-mixture models that included 197 surveys across 61 sites in 2017 and 2018. Abundance predictors for *P. punctatus* were state (West Virginia or Virginia), talus or not talus, and canopy cover (%). Abundance predictors for *P. cinereus* were state, canopy cover (%), and vegetation groundcover (%). The black line represents mean detection probability and gray areas fall within the 95% confidence interval.

both species, and higher in talus for *P. punctatus* (Fig. 4; Table 2). Our results indicated that abundances of *P. punctatus* were more than twice as high in talus habitat on the WV side of the mountain (0.41 per m^2) compared to the VA side of the mountain (0.15 per m^2; Fig. 4). For the fire history (all sites) model selection, the most parsimonious model for *P. punctatus* included burn status as a predictor of abundance (Table 1), and predicted abundance was lower at burned sites (Table 2), though the null model (i.e., the geological-topographical model only) also received some support ($\Delta QAIC_c < 7$). Our *P. punctatus* fire history model predicted that sites in WV talus had 12.1 and 22.4, whereas sites in VA there had 3.9 and 7.2 salamanders in burned and unburned areas, respectively. For *P. cinereus*, the most parsimonious model was the null model, however there was support for burn status as a predictor of abundance (Table 1), with abundance higher in unburned sites (Table 2). The *P. cinereus* fire history model predicted that WV sites had 16.5 and 19.3 salamanders, whereas sites in VA had 6.5 and 7.6 salamanders, in burned and unburned areas, respectively. For the fire history (burned sites-only) model selection, time-since-burn showed some support for both species, but was not the most parsimonious model (Table 1). Model-predicted abundances of *P. punctatus* and *P. cinereus* increased by 0.95 and 0.60 per year-since-burn, respectively.

For the forest structure characteristics model selection, canopy cover was the most supported predictor for abundance of both *P. punctatus* and *P. cinereus* (Table 1). Each percent increase in canopy cover resulted in *P. punctatus* abundance increasing by 0.4 and 0.2 in WV and VA talus sites, respectively; whereas *P. cinereus* abundance increased by 0.05 and 0.02 in WV and VA sites, respectively (Table 2, Fig. 4). Vegetation groundcover was also included in the most parsimonious forest structure model for *P. cinereus*, with a positive correlation. All forest structure variables tested had some support as predictors of abundance for both species (Table 1).

3.3. Salamander body condition

For the geological-topographic BCI model selection, the most parsimonious model for both species contained state as a predictor (Table 3), with *P. punctatus* BCI being higher, and *P. cinereus* BCI being lower, on the WV side of the mountain (Table 4, Fig. 5a). For the fire history model selection, burn status had some support for both species, but the null models received higher support (Table 3). Mean and median BCI were lower in burned areas for both species (Fig. 5b). For the forest structure model selection, the most parsimonious model included leaf groundcover for both species, and vegetation groundcover for *P. cinereus* (Table 3). BCI was negatively correlated with leaf litter depth for *P. punctatus*, and negatively correlated with leaf groundcover and vegetation groundcover for *P. cinereus* (Table 4).

4. Discussion

Mean abundance of *P. punctatus* was lower at sites that were burned, suggesting that, at least in the short-term, prescribed fires may result in reduced habitat quality for woodland salamander populations on Shenandoah Mountain. However, there was not a strong burn effect for *P. cinereus*, indicating effects are likely species-specific. In spite of the inverse relationship between canopy cover and vegetation groundcover

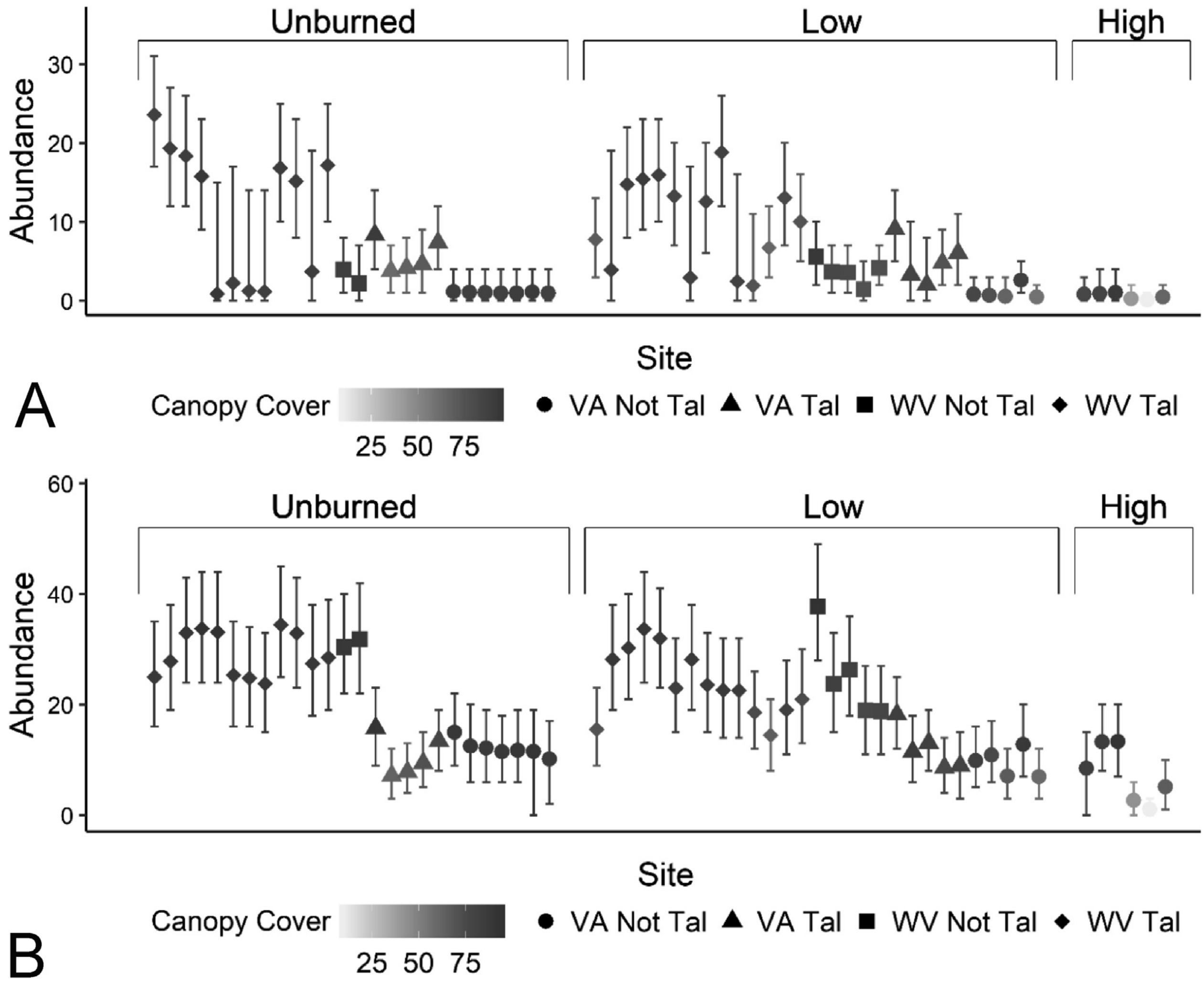

Fig. 4. Estimated abundances of (A) the Cow Knob Salamander (*Plethodon punctatus*) and (B) the Eastern Red-backed Salamander (*Plethodon cinereus*) across 61, 25 m^2 sites surveyed in 2017 or 2018 on Shenandoah Mountain in the George Washington National Forest in West Virginia and Virginia, USA. Abundance estimates are based on *N*-mixture models using geological-topographic and forest structure predictors-only, including the additive effects of state (West Virginia or Virginia), talus or not talus, and canopy cover (%) for *P. punctatus*, and state, canopy cover (%), and vegetation groundcover (%) for *P. cinereus*. Site abundances are separated by burn class (unburned, low-severity [Low], and high-severity [High]). Shapes represent the mean abundance estimate for the following sites: circles for VA not talus, triangles for VA talus, squares for WV not talus, and diamonds for WV talus. Lines represent 95% confidence intervals. Shading represents a site's canopy cover, with lighter shading represents less canopy cover and darker shading represents more canopy cover.

(Fig. 2), *P. cinereus* abundance was positively correlated with both variables, suggesting increased vegetation groundcover from prescribed fire could buffer the effects of reduced canopy cover, but additional research is needed to explicitly test this hypothesis. Based on our results and additional studies (e.g. Matthews et al., 2010; Mahoney et al., 2016), it appears that the greatest effects of prescribed fire on woodland salamander abundance occur when canopy cover is reduced.

Closed canopy forests could be an important component of climate refugia for salamanders in the study area, as *P. punctatus* is potentially one of the most vulnerable woodland salamanders (Milanovich et al., 2010; Markle and Kozak, 2018), with most or all of its climatic niche projected to be lost this century (Sutton et al., 2015; Jacobsen et al., 2020). Vertical structure may also be an important component of *P. punctatus* habitat because of terrestrial salamander behavior; salamanders can respond to drier weather conditions by climbing vegetation in order to remain active on the surface longer (McEntire and Maerz, 2019). This behavior appears to be employed by *P. punctatus* as they frequently climb on woody vegetation while foraging at night (Jacobsen et al., 2019). Additionally, they have been found climbing under the bark of a dead standing tree during the daytime (Jacobsen, Pers. obs.). Canopy cover and leaf litter could be also be particularly important for *P. punctatus* because of their talus association. The surface of talus dries out faster than areas with soil because as water percolates through the rubble, spaces between the rocks allow for air flow and quicker evaporation, and the reduced capillarity associated with coarser particles (McCune, 1977; Pérez, 1998). Reductions in canopy cover and leaf litter would increase the rate of surface drying and could limit the amount of time salamanders can be active on the surface for foraging or breeding (O'Donnell et al., 2016). The GWNF manages for mature forests in *P. punctatus* habitat by prohibiting the construction of new roads and logging on ca. 23,500 ha of land protected by an agreement with the U.S. Fish and Wildlife Service (USFS, 2014).

Potential concerns for negative effects of prescribed fire management on *P. punctatus* population viability might be eased if fire is concentrated on drier sites (i.e. lower elevation and hillshade, higher HLI), where the species is less abundant, habitat suitability is lower (Jacobsen et al., 2020), and fire was historically more common (Harper et al., 2016). Further, areas that contain high suitability habitat for *P. punctatus* could be subjected only to low-severity fires to reduce the risk of overstory tree mortality. Prescribed fire in the GWNF tended to create more canopy gaps on sites with a higher HLI (Lorber et al., 2018), meaning fire creates more canopy gaps on aspects where *P. punctatus*

Table 1
Model selection results to determine relationships between fire history and habitat characteristics on Cow Knob Salamander (*Plethodon punctatus*) and Eastern Red-backed Salamander (*Plethodon cinereus*) abundance. Geological-topographic model selection variables included state (i.e., West Virginia or Virginia), elevation (Elev), slope, hillshade (Hill), Heat Load Index (HLI), an index of talus cover (Talus), and talus or not talus (Bin_tal). Fire history – all sites model selection variables included unburned or burned (Burn Status). The fire history – burned sites model selection variable of interest was time-since-burn (Time Burn). Forest structure model selection variables included canopy cover (C%), vegetation groundcover (V%), leaf groundcover (L%), moss groundcover (M%), and litter depth in cm (LD). Model selection was based on Quasi Akaike Information Criterion corrected for small sample size ($QAIC_c$).

Plethodon punctatus				*Plethodon cinereus*			
Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Model	$QAIC_c$	$\Delta QAIC_c$	w_i
Geological-topographic				**Geological-topographic**			
Bin_tal + State	243.26	0	0.55	State	350.07	0.00	0.35
Bin_tal + Elev	244.41	1.15	0.31	State + Talus	350.34	0.27	0.30
Bin_tal	247.39	4.14	0.07	State + Slope	351.34	1.27	0.18
Talus	248.81	5.55	0.03	State + Bin_tal	352.05	1.98	0.13
Bin_tal + Slope	249.94	6.69	0.02	Hill	355.09	5.02	0.03
WV	251.03	7.77	0.01	Talus	357.71	7.64	0.01
Elev	252.81	9.55	0	Bin_tal	359.82	9.75	0.00
HLI	256.09	12.83	0	Slope	362.16	12.09	0.00
Slope	258.48	15.22	0	Elev	369.30	19.23	0.00
Hill	258.88	15.62	0	State + Elev	395.50	45.43	0.00
Fire history – all sites				**Fire history – all sites**			
Bin_tal + State + Burn Status	239.04	0	0.62	State	332.07	0.00	0.72
Bin_tal + State	240.03	1	0.38	State + Burn Status	333.39	1.86	0.28
Fire history – burned sites				**Fire history – burned sites**			
Bin_tal	141.16	0.00	0.84	Hill	163.31	0.00	0.77
Bin_tal + Time Burn	144.53	3.37	0.16	Hill + Time Burn	165.72	2.41	0.23
Forest structure				**Forest structure**			
Bin_tal + State + C%	244.57	0.00	0.30	State + C% + V%	340.95	0.00	0.24
Bin_tal + State	244.90	0.34	0.25	State + C%	341.09	0.14	0.22
Bin_tal + State + C% + V%	247.06	2.50	0.09	State + C% + LD	342.33	1.38	0.12
Bin_tal + State + C% + LD	247.18	2.61	0.08	State + C% + V % + LD	342.48	1.53	0.11
Bin_tal + State + C% + L%	247.26	2.69	0.08	State + C% + V% + M%	343.26	2.30	0.08
Bin_tal + State + LD	247.51	2.95	0.07	State + C% + M%	343.60	2.65	0.06
Bin_tal + State + L%	247.54	2.97	0.07	State + C% + L%	343.74	2.79	0.06
Bin_tal + State + V%	247.54	2.97	0.07	State + C% + V% + L%	343.78	2.83	0.06
				State	346.31	5.36	0.02
				State + LD	347.59	6.63	0.01
				State + M%	348.22	7.27	0.01
				State + L%	348.78	7.83	0.00
				State + V%	348.79	7.84	0.00

Table 2
Abundance parameter estimates (β) for the best approximating fire history and forest structure *N*-mixture models for the Cow Knob Salamander (*Plethodon punctatus*; left) and the Eastern Red-Backed Salamander (*Plethodon cinereus*; right). Variables include state (West Virginia [= 1] or Virginia), an index of talus cover (Talus), talus or not talus (Bin_tal), hillshade (Hill), canopy cover (C%), vegetation groundcover (V%), litter depth (LD), unburned or burned (Burn Status; burned = 1), and time-since-burn (Time Burn).

Plethodon punctatus				*Plethodon cinereus*			
Variable	β	SE	95% CI	Variable	β	SE	95% CI
Fire history – all sites				**Fire history – all sites**			
(Intercept)	0.899	1.257	(−1.56, 3.36)	(Intercept)	1.986	0.541	(0.92, 3.05)
Bin_tal	1.333	0.416	(0.52, 2.15)	State	0.940	0.168	(0.61, 1.27)
State	1.146	0.334	(0.49, 1.80)	Burn Status	−0.168	0.488	(−0.46, 0.12)
Burn Status	−0.612	0.264	(−1.13, −0.09)				
Fire history – burned sites				**Fire history – burned sites**			
(Intercept)	2.44	1.08	(0.33, 4.56)	(Intercept)	2.49	1.04	(0.45, 4.54)
Talus	0.48	0.24	(0.02, 0.94)	Hill	0.00	0.00	(−0.00, 0.01)
Time Burn	0.02	0.05	(−0.09, 0.14)	Time Burn	0.05	0.03	(−0.01, 0.10)
Forest structure				**Forest structure**			
(Intercept)	0.655	1.133	(−1.57, 2.88)	(Intercept)	−0.716	1.302	(−3.27, 1.84)
Bin_tal	1.439	0.421	(0.62, 2.26)	State	0.891	0.183	(0.53, 1.25)
State	0.714	0.360	(0.01, 1.42)	C%	0.036	0.010	(0.02, 0.05)
C%	0.031	0.016	(−0.00, 0.06)	V%	0.007	0.003	(0.00, 0.01)

was likely to be absent or less abundant (Buhlmann et al., 1988; USFS, 2014). However, *P. punctatus* were present at several sites on a high-elevation, south-facing talus slope. We note that some of the drier ridges of Shenandoah Mountain, which tend to be lower in elevation (Downer, 2009), are occupied by the endemic Shenandoah Mountain Salamander (*Plethodon virginia*; Highton, 1999). This species is also highly vulnerable to climate change (Sutton et al., 2015), and to our knowledge no studies have investigated effects of prescribed fire on this

Table 3
Model selection results for relationships between environmental variables and body condition index (BCI) for the Cow Knob Salamander (*Plethodon punctatus*; left) and Eastern Red-Backed Salamander (*Plethodon cinereus*; right). Geological-topographic model selection variables included state (West Virginia or Virginia), an index of talus cover (Talus), elevation (Elev), hillshade (Hill), and Heat Load Index (HLI). Fire history model selection variables included unburned or burned (Burn Status). Forest structure model selection variables included canopy cover (C%), vegetation groundcover (V%), leaf groundcover (L%), moss groundcover (M%), and litter depth (LD). Model selection was based on Quasi Akaike's Information Criterion corrected for small sample size (AIC_c).

Plethodon punctatus				*Plethodon cinereus*			
Model	AIC_c	ΔAIC_c	w_i	Model	AIC_c	ΔAIC_c	w_i
Geological-topographic				**Geological-topographic**			
State	−108.91	0.00	0.28	State	−124.14	0.00	0.28
State + HLI	−108.69	0.22	0.25	Null	−122.67	1.47	0.13
State + Talus	−107.36	1.55	0.13	State + HLI	−122.61	1.53	0.13
State + Hill	−106.77	2.14	0.10	State + Hill	−122.20	1.94	0.11
State + Elev	−106.56	2.35	0.09	State + Talus	−122.04	2.10	0.10
HLI	−106.07	2.83	0.07	State + Elev	−121.94	2.20	0.09
Null	−105.10	3.80	0.04	HLI	−121.52	2.62	0.07
Talus	−103.56	5.35	0.02	Elev	−120.57	3.57	0.05
Hill	−103.47	5.43	0.02	Talus	−120.52	3.62	0.05
Elev	−103.03	5.88	0.01				
Fire-history				**Fire history**			
State	−108.91	0.00	0.77	State	−124.14	0.00	0.64
State + Burn Status	−106.53	2.37	0.23	State + Burn Status	−123.02	1.12	0.36
Forest structure				**Forest structure**			
State + LD	−108.93	0.00	0.18	State + V% + L% + LD	−133.03	0.00	0.32
State	−108.91	0.02	0.18	State + V% + L%	−132.68	0.35	0.27
State + V%	−108.54	0.38	0.15	State + V%	−130.79	2.24	0.10
State + LD + V%	−108.44	0.48	0.14	State + V% + L% + M%	−130.73	2.30	0.10
State + Can	−107.43	1.50	0.08	State + V% + L% + C%	−130.32	2.71	0.08
State + LD + C%	−106.88	2.05	0.06	State + V% + M%	−128.69	4.33	0.04
State + L%	−106.74	2.18	0.06	State + V% + LD	−128.69	4.34	0.04
State + M%	−106.59	2.33	0.06	State + V% + C%	−128.62	4.41	0.04
State + L% + LD	−106.45	2.48	0.05	State	−124.14	8.89	0.00
State + LD + M%	−106.45	2.48	0.05	State + M%	−123.87	9.16	0.00
				State + L%	−123.22	9.80	0.00
				State + LD	−122.54	10.49	0.00

species. It is possible prescribed fire could push these areas past a dryness threshold that this species cannot tolerate. Alternatively, prescribed fire could give *P. virginia* a competitive advantage over *P. cinereus*, which prefers wetter (i.e. higher elevation) areas on Shenandoah Mountain (Downer, 2009).

Abundance estimates for this study, as well as our finding that *P. punctatus* abundance was approximately twice as high in talus on the WV side of the mountain compared to the VA side of the mountain, are congruent with a previous capture-recapture study for *P. punctatus* that was conducted on perceived optimal habitat on north-facing talus slopes (Flint and Harris, 2005). For the most-abundant *P. punctatus* sites, estimated abundances were greater than or equal to estimates reported by Flint and Harris (2005). Greater abundance of *P. punctatus* on the WV side of the mountain could be due to wetter conditions and environmental differences (Flint and Harris, 2005), which is corroborated by our estimates of greater moss groundcover on WV sites. Additionally, the WV sites tended to have more and larger talus areas, which could allow for greater habitat patch size and connectivity. Similarly, the greater BCI values for *P. punctatus* on the WV side of the mountain is also consistent with Flint and Harris (2005), indicating potentially greater prey availability or better foraging conditions. In addition, BCI tended to be higher in unburned habitat for both species (although the difference was not significant for *P. punctatus*), potentially indicating higher prey availability or better environmental conditions for foraging (e.g., higher moisture levels on surface objects).

We emphasize that, although we detected a difference in abundance based on Burn Status, our study does not indicate that burning has resulted in local extirpations of *P. punctatus*. We found *P. punctatus* at

Table 4
Parameter estimates (β) for relationships between environmental variables and body condition index (BCI) for the Cow Knob Salamander (*Plethodon punctatus*; left) and Eastern Red-Backed Salamander (*Plethodon cinereus*; right). The geological-topographic variable is state (West Virginia [= 1] or Virginia). Fire history variables include unburned or burned (Burn Status; burned = 1). Forest structure variables include vegetation groundcover (V%), leaf groundcover (L%), and litter depth (LD).

Plethodon punctatus				*Plethodon cinereus*			
Variable	β	SE	95% CI	Variable	β	SE	95% CI
Fire history				**Fire history**			
Intercept	−0.072	0.033	(−0.10, 0.30)	Intercept	0.045	0.024	(−0.00, 0.09)
State	0.083	0.034	(0.01, 0.14)	State	−0.047	0.027	(−0.10, 0.00)
Burn Status	−0.001	0.022	(−0.04, 0.04)	Burn Status	−0.025	0.024	(−0.07, 0.02)
Forest structure				**Forest structure**			
Intercept	−0.049	0.034	(−0.11, 0.02)	Intercept	0.124	0.031	(0.06, 0.18)
State	0.086	0.033	(0.02, 0.15)	State	−0.035	0.028	(−0.09, 0.02)
LD	−0.042	0.028	(−0.10, 0.01)	V%	−0.002	0	(−0.00, −0.00)
				L%	−0.002	0.001	(−0.00, −0.00)
				LD	0.094	0.058	(−0.02, 0.20)

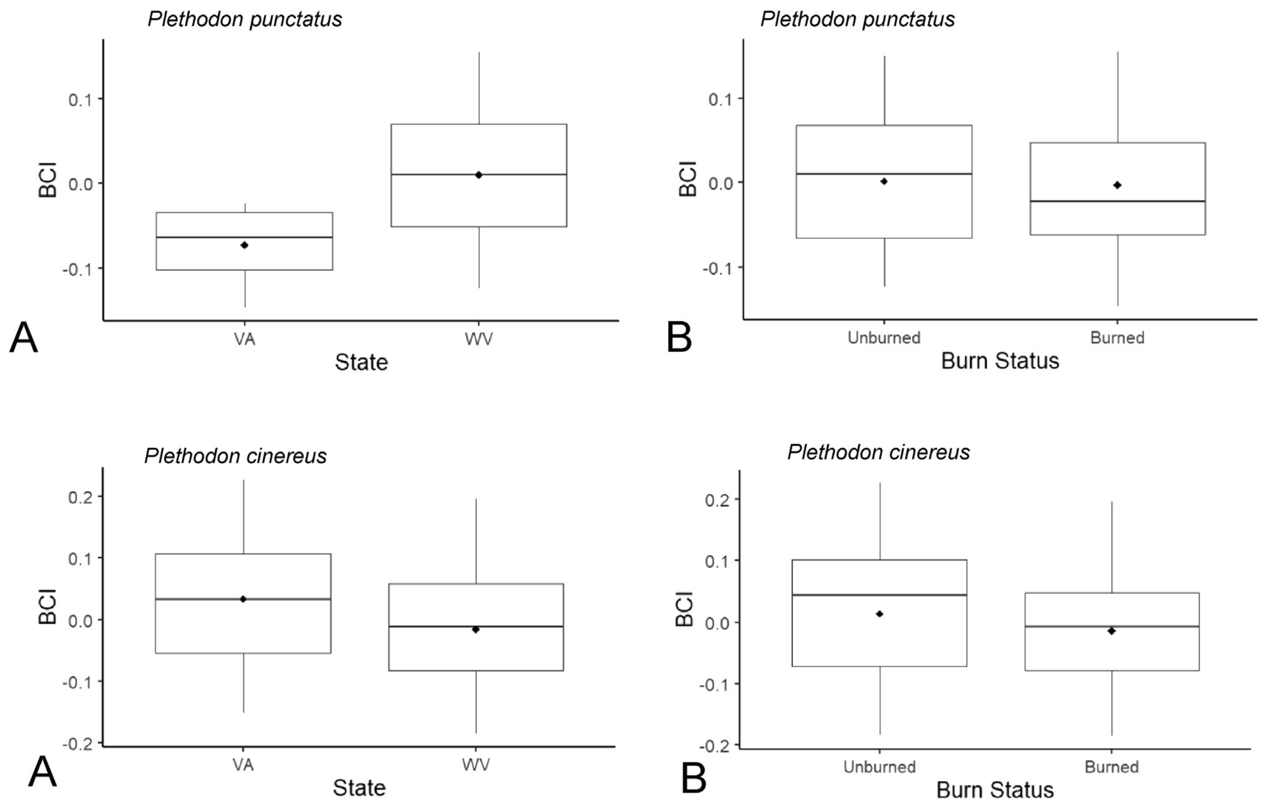

Fig. 5. Boxplot summaries of body condition index (BCI) values for the Cow Knob Salamander (*Plethodon punctatus*; n = 49; top) and the Eastern Red-Backed Salamander (*Plethodon cinereus*; n = 76; bottom) from our study investigating responses of woodland salamanders to prescribed fire management on Shenandoah Mountain in the George Washington National Forest in West Virginia and Virginia, USA.

sites that were burned 25 days to 8 years prior to sampling, indicating populations can persist with prescribed fire management. However, our study indicates that if fire results in a canopy cover reduction, habitat quality for *P. punctatus* will likely be reduced. We did not find a strong effect of time-since-burn on abundance of either species, and thus there was not a strong indication that burning had either a lagged effect on the populations or that the populations recovered from initial negative impacts. However, the fire histories included in this study were limited, and more robust studies on temporal dynamics are needed. In addition, our study sites were located in comparatively high quality habitat within the distribution of *P. punctatus* (Jacobsen et al., 2020), and thus we cannot infer potential impacts of fire to populations in more marginal habitat. We also acknowledge that our inferences are limited by the prescribed fire history in the study area. Specifically, we were only able to include one high-severity burn unit, and all of our low-severity sites were burned twice, limiting our ability to separate the effects of fire severity and fire frequency.

This study contributes to the general ecological knowledge of *P. punctatus* and *P. cinereus* by quantifying relationships between forest structure characteristics and abundance/BCI for these species. This information can be used to balance preservation of biodiversity with management actions designed to improve ecological conditions and functions, such as prescribed fire. For *P. punctatus*, this study extends the broad ecological conditions associated with occurrence that were identified in Jacobsen et al. (2020) to site-level habitat factors associated with abundance. Jointly, these manuscripts provide information that can be used to protect and manage habitat for this species of high conservation.

CRediT authorship contribution statement

Carl D. Jacobsen: Methodology, Investigation, Data curation, Writing - original draft, Formal analysis. **Donald J. Brown:** Conceptualization, Methodology, Writing - original draft, Supervision, Funding acquisition, Conceptualization, Methodology, Writing - original draft, Supervision, Funding acquisition. **William D. Flint:** Methodology, Investigation, Writing - review & editing. **Jamie L. Schuler:** Methodology, Writing - review & editing. **Thomas M. Schuler:** Conceptualization, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

Acknowledgments

This work was supported by a grant from the U.S. Forest Service Northern Research Station. We thank C. Croy, S. Croy, and U.S. Forest Service George Washington-Jefferson National Forest staff for their assistance with study design and for providing management and spatial data. We thank S. Crayton and J. Newman for assisting with surveys, and L. Rucker for help setting up field sites. We thank 3 reviewers for providing suggestions that greatly improved the quality of this manuscript. This study was approved by the West Virginia Division of Natural Resources (Permits 2017.023, 2018.09), Virginia Department of Game and Inland Fisheries (Permit 059581), and U.S. Forest Service George Washington National Forest.

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