

Article

Microhabitat Associations for the Threatened Cheat Mountain Salamander in Relation to Early-Stage Red Spruce Restoration Areas

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Abstract

The Central Appalachian Spruce Restoration Initiative was formed to promote restoration of red spruce *Picea rubens* forests in Central Appalachia. One goal of the initiative is to increase availability and enhance quality of habitat for wildlife, including the threatened Cheat Mountain salamander *Plethodon nettingi*. The purpose of this research was to compare microhabitat characteristics between an occupied Cheat Mountain salamander site and early-stage spruce restoration sites, and between four occupied sites and proximal nondetection sites. We found that soil pH was higher and soil moisture was lower at spruce restoration sites compared with the occupied site, and that light intensity, subcanopy air temperature, and ground-level air temperature were higher in spruce restoration sites with reduced canopy cover. We found that soil moisture was higher at occupied sites compared with proximal nondetection sites, but soil pH was not significantly different. Our study suggests that Cheat Mountain salamanders are associated with low soil pH and high soil moisture, and thus spruce restoration could enhance habitat quality for this species in the long-term.

Keywords: forest; mineland; pH; moisture; *Plethodon nettingi*; soil; West Virginia

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Introduction

Prior to European settlement, red spruce *Picea rubens* was a prominent tree species in high-elevation forests of eastern West Virginia (Mayfield and Hicks 2010; Thomas-Van Gundy and Strager 2012). As a consequence of broad-scale clearcutting and wildfires in the late 1800s and early 1900s, occurrence of red spruce-dominated forests in West Virginia may have been reduced by up to 95% (Nowacki and Wendt 2010; Beane et al. 2013). In response, the Central Appalachian Spruce Restoration Initiative (CASRI) was formed to promote restoration of red spruce forests in the Central Appalachian region (CASRI Strategy Committee 2010). Since 2007, CASRI has completed forest restoration projects across thousands of hectares of land and planted approximately one million trees (K. Barlow, The Nature Conservancy, personal communication), with a strong focus on the Monongahela National Forest (MNF) in eastern West Virginia.

Several red spruce restoration prescriptions are being implemented on the MNF (U.S. Forest Service 2016). Former mined land is being restored using a deep ripping technique to loosen the compacted soil, followed by planting of spruce and other native vegetation. In areas that were dominated by red spruce prior to the industrial logging era (late 1800s to early 1900s), increased prevalence of spruce is being promoted using strategic application of herbicides, tree felling, mulching, and young spruce planting. Thinning of dense young spruce patches is being performed to promote growth and maturation of naturally regenerating red spruce.

One goal of CASRI is to increase availability and enhance quality of habitat for wildlife species of conservation concern, including the Cheat Mountain salamander *Plethodon nettingi* (CMS; Figure 1), which was listed as threatened under the U.S. Endangered Species Act in 1989 (ESA 1973, as amended; USFWS 1989). The CMS is currently restricted to approximately 80 geographically isolated populations in eastern West Virginia, primarily on the MNF (Pauley 2008). This species is strongly associated with mature high-elevation forests (> 800 m) containing a red spruce or eastern hemlock *Tsuga canadensis* component (Pauley and Pauley 1997; Pauley 2007, 2008). Thus, restoration of spruce stands adjacent to forest patches currently occupied by CMS could facilitate connectivity and enhance long-term viability of populations.

Although we have a good understanding of forest structural characteristics associated with occurrence of CMS and the general geographical distribution of the species (e.g., Pauley 2007, 2008; Dillard et al. 2008), little research has been conducted to quantify microhabitat characteristics of occupied forest patches or spruce restoration sites. This information is needed to develop microhabitat quality targets, and to assess and monitor changes in suitability of spruce restoration sites for the CMS. The purpose of this research was to quantify and compare microhabitat characteristics of early-stage spruce restoration sites in relation to microhabitat



Figure 1. Cheat Mountain salamander *Plethodon nettingi* photographed on 25 August 2017 in the Monongahela National Forest, Randolph County, West Virginia. Photo credit: Lacy Rucker

associations for the CMS. We assessed differences between an occupied site and spruce restoration sites for five microhabitat variables, including soil pH, soil moisture, subcanopy air temperature and light intensity, and ground-level air temperature (hereafter, restoration site study). We also assessed whether soil pH and soil moisture differed between four occupied sites and proximal nondetection sites to determine whether these microhabitat characteristics were strongly associated with occurrence (hereafter, CMS site study). In addition to improving our understanding of CMS habitat associations, this study provides baseline data that will be useful for monitoring long-term temporal dynamics in microhabitat conditions at spruce restoration sites.

Methods

Study area

Restoration site study. All study sites were located on the MNF in eastern West Virginia. Spruce restoration sites were located on the Mower Tract, a former industrial logging and surface mining area in Randolph and Pocahontas counties that was acquired by the MNF in 1987 (U.S. Forest Service 2016; Figure 2a). The portion of the Mower Tract designated for spruce restoration encompasses 13,757 ha, 97% of which is on the MNF (U.S. Forest Service 2016). The occupied site occurred on Gaudineer Knob (Shavers Mountain) within 10 km of all spruce restoration sites on the Mower Tract (Figure 3a; specific location withheld on account of the conservation status of CMS).

Spruce restoration sites included three restoration prescriptions on the Mower Tract: mineland restoration, young red spruce thinning, and hardwood thinning. The mineland restoration site was open-canopied and consisted primarily of herbaceous vegetation and shrubs with interspersed young red spruce (Figure 3b). The

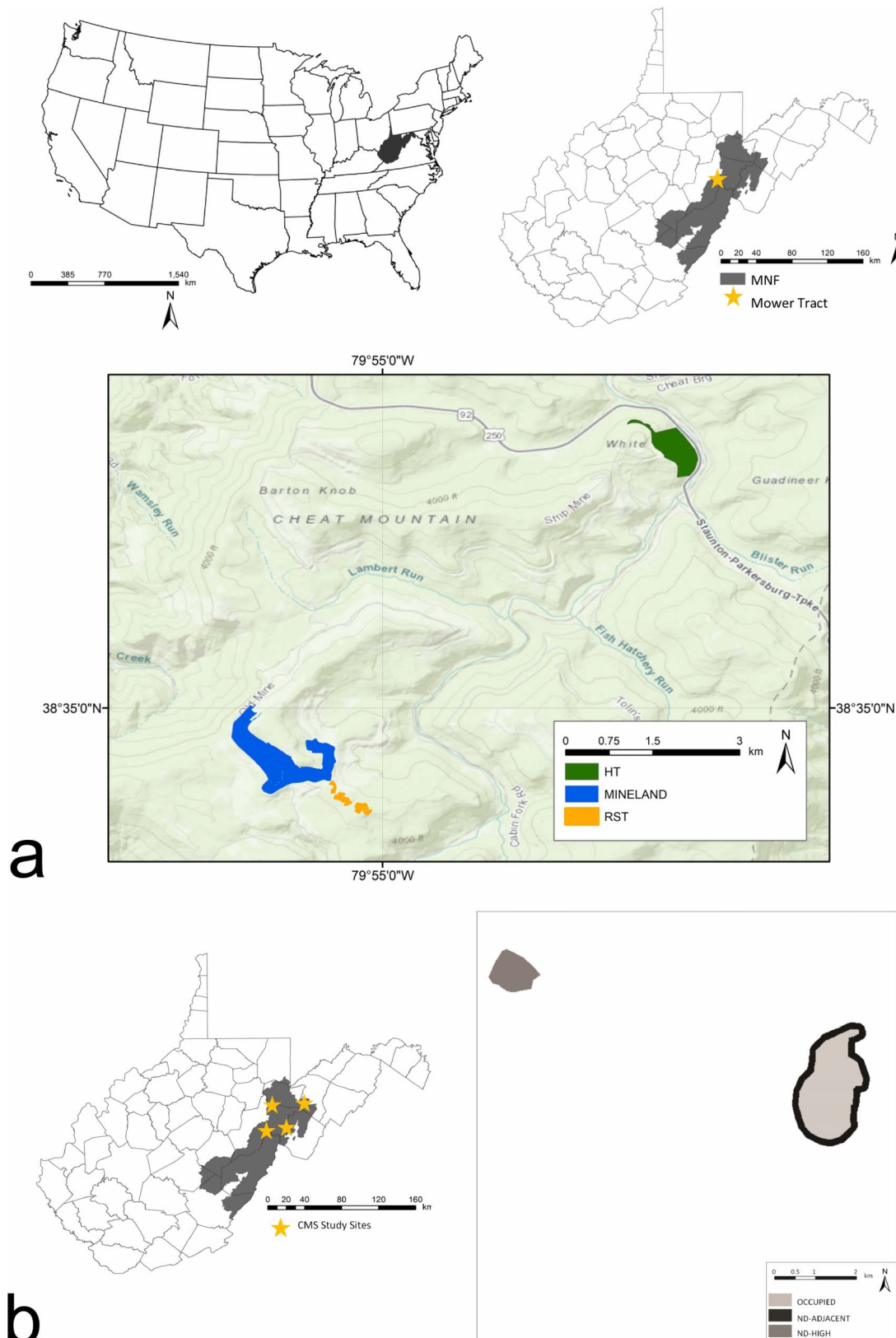


Figure 2. Locations of (a) red spruce *Picea rubens* restoration study sites and (b) Cheat Mountain salamander *Plethodon nettingi* study sites. All sites were located in the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. Spruce restoration sites were located on the Mower Tract in Randolph and Pocahontas counties, and prescriptions included mineland restoration (MINELAND), red spruce thinning (RST), and hardwood thinning (HT). Cheat Mountain salamander study sites were located on Dolly Sods (Tucker County), Gaudineer Knob (Pocahontas County), Spruce Knob (Pendleton County), and Stuart Knob (Randolph County), and categories included occupied sites (OCCUPIED), adjacent nondetection sites (ND-ADJACENT), and seemingly high-quality habitat nondetection sites (ND-HIGH). An example study area is included in the figure. For analyses, reference sites were further classified as interior forest or road-trail edge.





Figure 3. Sites included in this study investigating differences in microhabitat characteristics between an occupied Cheat Mountain salamander *Plethodon nettingi* site (a) and early-stage red spruce *Picea rubens* restoration sites (b–g). All study sites were located on the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. Spruce restoration prescriptions included mineland restoration (b), red spruce thinning—thinned and mulched area (c), red spruce thinning—forest edge (d), red spruce thinning—forest interior (e), hardwood thinning—high understory red spruce density (f), and hardwood thinning—low understory red spruce density (g).

young red spruce thinning site was also open-canopied, but it contained extensive mulch and coarse woody debris from the removed trees and was adjacent to a hardwood-dominated stand. For this site, we sampled within the thinned and mulched area (≥ 5 m from the forest edge; Figure 3c) and within the adjacent forest (0–10 m [Figure 3d] and > 30 m from the edge [Figure 3e]). The hardwood thinning site consisted of mixed hardwoods and spruce, with primarily midstory and codominant overstory hardwoods treated with herbicides. The herbicide application occurred near the end of the

sampling period (i.e., late July), and thus the study data for this site represent baseline conditions prior to tree mortality. Within the hardwood thinning site, we separately sampled treatment areas with high (Figure 3f) and low (Figure 3g) densities of young red spruce.

Cheat Mountain salamander site study. All study sites were located on the MNF in eastern West Virginia. We sampled four occupied sites, located on Dolly Sods (Allegheny Front, Tucker County), Gaudineer Knob (Shavers Mountain, Pocahontas County), Spruce Knob (Spruce Mountain, Pendleton County), and Stuart Knob

(Shavers Mountain, Randolph County; specific locations withheld because of the conservation status of CMS). The sites were originally selected to assess differences in CMS abundance in (recently) undisturbed microhabitat patches compared with microhabitat patches adjacent to gated forest roads and hiking trails and were subsequently used for periodic long-term monitoring by the MNF (USFWS 2009). Each monitoring site consisted of 12 monitoring points in interior forest, and either 12 or 24 monitoring points adjacent to forest roads or trails, with salamanders sampled using coverboard sets at each point. We retained the monitoring point locations as occupied site sampling points for this study, except for four points that could not be located on account of coverboard degradation.

We paired each of the occupied sites with adjacent forest where CMS has not been detected (hereafter, ND-ADJACENT) and is presumed to be absent based on extensive past searching efforts by one of the authors (TKP; Pauley 2007). Specifically, we placed a 50-m buffer around the spatially delineated zone of occupancy and selected random sampling points within the buffer. In addition, we paired each of the monitoring sites with nearby forest patches that represented seemingly high-quality habitat based on the expert opinion of one of the authors (TKP), but where the species has not been detected (hereafter, ND-HIGH; Figure 2b). Specifically, we first identified all past search areas within seemingly high-quality habitat where the species was not found ($n = 14$). For each reference site, we then restricted candidate ND-HIGH sites to areas that were located within 200 m elevation, were similar in aspect, and had similar tree species composition to the occupied site. For the remaining candidate ND-HIGH sites, we sampled the site that was nearest to the occupied site (mean = 4.56 km, range = 1.88–6.83 km).

Data collection

Restoration site study. Sampled site categories included an occupied CMS site, mineland restoration (MINELAND), red spruce thinning—thinned and mulched area (RST-MULCH), red spruce thinning—forest edge (RST-EDGE), red spruce thinning—forest interior (RST-INTERIOR), hardwood thinning—high understory and midstory red spruce density (HT-HIGH), and hardwood thinning—low understory and midstory red spruce density (HT-LOW). At five randomly selected locations within each site category, we computed elevation (m) and aspect (compass direction) using a geographic information system (ArcGIS, ESRI, Redlands, CA), and estimated several forest structural characteristics. We estimated overstory canopy cover (%) using a densitometer (Geographic Resource Solutions, Arcata, CA). We measured diameter at breast height of all trees > 10 cm diameter at breast height within variable radius plots (Basal Area Factor of 10 using an angle gauge [Cruz-All]), and estimated basal area by multiplying the tallied “in” trees by the basal area conversion factor and standard-

izing to m^2/ha . We also counted red spruce stems of overstory, midstory, understory, and seedling trees using a 0.004-ha (1/247th-ha, 1/100th-acre) fixed-radius plot.

We used a random sampling approach to select microhabitat sampling locations ($n = 24\text{--}26$) within each site category, with random points restricted to between 30 m and 200 m of access roads, and to > 15 m from the nearest sampling point. We collected one soil sample from each sampling point (depth = 20 cm) between 11 June and 10 September 2019, and estimated soil pH using the Natural Resources Conservation Service soil pH protocol (Soil Survey Staff 2014). Specifically, we mixed 25-g soil samples with distilled water at a 1:1 ratio, with soil stirred for 1 min over three 10-min intervals, and we measured the pH of the aqueous mixture using a pH meter (Oakton pH Testr 30, Vernon Hills, IL). We measured soil moisture (% volumetric water content) at sampling points on either 30 September 2020 or 1 October 2020 using a soil moisture meter (General Tools DSMM500, Melrose Aurora, MA), with the probe inserted to 10 cm. For soil moisture, we excluded four sampling points for RST-EDGE and three sampling points for RST-INTERIOR because these points were thinned and mulched in summer 2020 prior to sampling.

At each sampling point, we measured air temperature ($^{\circ}\text{C}$) and light intensity (lux) at the subcanopy level using HOBO 8K Pendant data loggers (model UA-002-08; Onset Computer Corporation, Bourne, Massachusetts) mounted on U-posts at chest height, and air temperature ($^{\circ}\text{C}$) at ground level using iButton data loggers (model DS1923-F5#; Maxim Integrated, San Jose, California). For these variables, we sampled each site at 15-min intervals from mid-June to mid-September 2019. Funding constraints limited us to one of each sampling device per study site, and thus we were unable to have joint spatial-temporal replication within study sites. To maximize spatial representation, we sampled across 24–26 random points within each site category, with each point sampled for a mean of 86.1 h. We downloaded data and reset the loggers during each movement event to minimize loss of data in the event of logger failure. To create complete temporal sampling comparability among site categories, we reduced the data set to the timeframe when every category was sampled (14 June to 8 September 2019), which included 8,223 temporal samples per category. We computed 24-h daily means for each variable (hereafter, daily mean), as well as 12-h means representing the warmest and coolest half of the day (hereafter, daytime and nighttime mean, respectively). To define the daytime and nighttime periods, we computed the mean air temperature by hour across all site categories over the entire sampling period and chose the warmest 12 h for the daytime period (0900–2000 hours). Microhabitat variable sample sizes used for statistical analyses are shown in Table 1.

Cheat Mountain salamander site study. We sampled all sites in the four study areas between 23 April 2019 and 4 May 2019, including occupied sites—interior forest



Table 1. Microhabitat variable data analysis sample sizes (*n*) for comparisons of early-stage red spruce *Picea rubens* restoration sites to an occupied Cheat Mountain salamander *Plethodon nettingi* (CMS) site (OCCUPIED; restoration site study), and for comparisons of occupied sites and proximal mature forest nondetection sites (CMS site study). All study sites were located on the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. For the restoration site study, spruce restoration prescriptions included hardwood thinning with low (HT-LOW) and high (HT-HIGH) levels of spruce in the midstory and understory, mineland restoration (MINELAND), and red spruce thinning (RST), with sampling in the thinned and mulched area (RST-MULCH), near the adjacent forest edge (RST-EDGE), and within the adjacent forest interior (RST-INTERIOR). The CMS site study included occupied sites—interior forest (OCCUPIED-INTERIOR), occupied sites—road or trail edge (OCCUPIED-EDGE), adjacent nondetection sites (ND-ADJACENT), and seemingly high-quality habitat nondetection sites (ND-HIGH).

Restoration site study								
Site	Soil pH	Soil moisture	Subcanopy air temperature	Ground-level air temperature	Light intensity			
OCCUPIED	26	26	87	87	87			
HT-HIGH	24	27	87	87	87			
HT-LOW	24	27	87	87	87			
MINELAND	25	26	87	87	87			
RST-MULCH	25	26	87	87	87			
RST-EDGE	26	19	87	87	87			
RST-INTERIOR	26	23	87	87	87			
CMS site study								
Site category	Soil pH				Soil moisture			
	Dolly Sods	Gaudineer Knob	Spruce Knob	Stuart Knob	Dolly Sods	Gaudineer Knob	Spruce Knob	Stuart Knob
OCCUPIED-INTERIOR	12	11	11	12	12	11	11	12
OCCUPIED-EDGE	23	11	24	24	23	11	24	24
ND-ADJACENT	12	12	12	12	12	12	12	12
ND-HIGH	12	12	12	12	12	12	12	12

(OCCUPIED-INTERIOR), occupied sites—road or trail edge (OCCUPIED-EDGE), adjacent nondetection sites (ND-ADJACENT), and seemingly high-quality habitat nondetection sites (ND-HIGH). We randomly selected 12 sampling points within each paired ND-ADJACENT and ND-HIGH site. At each location, we sampled soil pH 1 m from center of the sampling point in a random cardinal direction, and soil moisture 1 m from the center of the sampling point in each cardinal direction. We estimated soil pH and soil moisture using the same protocol as the restoration site study. For soil moisture, we used the mean of the four samples to represent each sampling point. For the OCCUPIED-INTERIOR and OCCUPIED-EDGE sites, we also measured soil temperature (°C) at each monitoring point during concurrent CMS surveys using a soil thermometer (Acurite Stainless Steel Soil Thermometer, Lake Geneva, WI). Microhabitat variable sample sizes used for statistical analyses are shown in Table 1.

Data analyses

Logger data. For small portable weather data loggers placed in field conditions, occurrence of anomalous measurement values and periodic logger malfunctioning is common (e.g., Reusser and Zeje 2011; Roznik and Alford 2012). We used bagplots (i.e., bivariate boxplots) to screen the logger data for outliers (Rousseeuw et al. 1999). We created bagplots for each variable combination within each site category and removed extreme outlier values from the data set. We then estimated the missing values using either a bivariate regression

(temperature variables only) or a local averaging smoother (Friedman's super smoother; Friedman 1984). Data screening resulted in removal and re-estimation of 3.65% of the measurement values.

Restoration site study. We used Principal Response Curves to visually assess differences in repeated-sampling microhabitat characteristics (i.e., light intensity, subcanopy air temperature, and ground-level air temperature) between spruce restoration site categories and the occupied site across the sampling period. This analysis is an extension of Redundancy Analysis to allow for visualization of differences in continuous variables among categories (e.g., sites) over time (Van den Brink and Ter Braak 1999; Van den Brink et al. 2009). We used the daily time series for this analysis, and standardized the response data (mean = 0, standard deviation = 1) because the variables had different units and scales.

We used linear regression models to quantify differences between spruce restoration site categories and the occupied site for the means of individual variables. Soil pH and soil moisture contained one estimate per sampling plot, and thus we used standard linear regressions. During preliminary analyses we found that converting from the pH scale to H^+ (mol/L) did not influence the results, and thus we used the pH scale for the final analyses to enhance interpretability. For the repeated-sampling microhabitat characteristics, we accounted for nonindependence of residuals by including a continuous autoregressive term (corAR1)

Table 2. Elevation, aspect, and forest structural characteristics of early-stage red spruce *Picea rubens* restoration sites relative to an occupied Cheat Mountain salamander *Plethodon nettingi* (CMS) site (OCCUPIED). All study sites were located on the Monongahela National Forest in eastern West Virginia, and sampling of forest structural characteristics occurred in 2019. Spruce restoration sites were located on the Mower Tract, a former industrial logging and surface mining area, and the occupied CMS site occurred on Gaudineer Knob (Shavers Mountain) within 10 km of all spruce restoration sites on the Mower Tract. Spruce restoration prescriptions included hardwood thinning with low (HT-LOW) and high (HT-HIGH) levels of spruce in the midstory and understory, mineland restoration (MINELAND), and red spruce thinning (RST), with sampling in the thinned and mulched area (RST-MULCH), near the adjacent forest edge (RST-EDGE), and within the adjacent forest interior (RST-INTERIOR). At five randomly selected locations within each site category, we computed elevation (m) and aspect (compass direction) using a geographic information system, measured overstory canopy cover (%), measured diameter at breast height (DBH) of all trees > 10 cm DBH within variable-radius plots and estimated basal area (standardized to m²/ha), and counted red spruce stems of overstory, midstory, understory, and seedling trees using a 0.004-ha; 1/247th-ha, 1/100th-acre) fixed-radius plot. Values represent the mean among the five sampling points.

Site	Elevation	Aspect	Canopy cover (%)	Basal area (m ² /ha)	Red spruce stems			
					Overstory	Midstory	Understory	Seedling
OCCUPIED	1,290	44 (NE)	74.0	26.68	4.6	1.8	10.8	31.4
HT-HIGH	1,103	48 (NE)	84.4	20.70	0.6	10.8	12.2	3.4
HT-LOW	1,115	52 (NE)	86.0	17.94	0	1.8	3.6	0.8
MINELAND	1,276	254 (W)	0.00	0.00	0	0	3.8	0
RST-MULCH	1,315	222 (SW)	5.0	1.84	0	0.4	0.2	0.6
RST-EDGE	1,315	267 (W)	83.0	17.25	0	12.4	0	0
RST-INTERIOR	1,309	220 (SW)	91.4	26.83	0.2	10.4	5.2	0.2

within each site (Zuur et al. 2009), and analyzed the daily, daytime, and nighttime time series. For each model, we determined whether site was a supported predictor using likelihood-ratio tests ($\alpha = 0.05$; Zuur et al. 2009). In addition, we computed Pearson's correlation coefficients (r) between canopy cover and soil pH, and canopy cover and soil moisture, using the randomly selected locations within each site where all three variables were measured ($n = 35$ and 33 locations for soil pH and moisture, respectively). The purpose of this analysis was to determine whether soil pH and moisture were strongly correlated with canopy cover, independent of restoration prescription. We computed 95% confidence intervals (CI) for r using a 1,000-replication bootstrap (Legendre and Legendre 2012) and considered the correlations to be supported if the CI did not overlap zero (Halsey 2019).

Cheat Mountain salamander site study. We used linear mixed-effects models to determine whether soil pH and soil moisture differed between the OCCUPIED-INTERIOR site category and the OCCUPIED-EDGE, ND-ADJACENT, and ND-HIGH site categories (Zuur et al. 2009). We treated soil pH and soil moisture as response variables, site category as a fixed effect, and study area as a random effect to control for geographic variation in the response variables independent of site category. We determined whether site category was a supported predictor of soil pH and soil moisture using likelihood-ratio tests (Zuur et al. 2009). We also tested whether soil pH, soil moisture, and soil temperature differed among occupied sites in the four study areas using one-way analysis of variance tests with Type II sums of squares ($\alpha = 0.05$; Langsrud 2003).

For supported regression models, we estimated site-specific beta coefficients and 95% CIs, with the OCCUPIED-INTERIOR site category treated as the model

intercept. We considered evidence for a strong effect for regression and analysis of variance models when coefficient CIs did not overlap zero (Halsey 2019). We assessed assumptions of normality using quantile-quantile plots and homoscedasticity using residual plots (Zuur et al. 2009, 2010). To satisfy model assumptions, we $\log_{10}$ -transformed light intensity, and removed a total of 58 data points across the 10 univariate models. We conducted all analyses using Program R (version 3.6.3). We manipulated data using the package 'dplyr' (version 0.8.4), created Principal Response Curve models using the package 'vegan' (version 2.5-6), created autoregressive and linear mixed-effects regression models using the package 'nlme' (version 3.1-149), computed Type II sums of squares for analysis of variance models using the package 'car' (version 3.0-6), performed model diagnostics using the package 'predictmeans' (version 1.0.4), performed likelihood-ratio tests using the package 'lmerTest' (version 0.9-38), and performed bootstrapping using the package 'boot' (version 1.3-28).

Results

Restoration site study. Mean elevation was similar among sites, ranging from 1,103 to 1,315 m (Table 2). The occupied and HT sites had northeasterly aspects, whereas the MINELAND and RST sites had southwest and westerly aspects (Table 2). Overstory canopy cover and basal area were lowest at the MINELAND site and highest at the RST-INTERIOR site (Table 2). The occupied site had the greatest number of overstory and seedling red spruce stems, but the HT-HIGH site had more understory and midstory stems, and the RST-EDGE and RST-INTERIOR sites had greater midstory stems (Table 2). Data for individual sampling points are available in Data

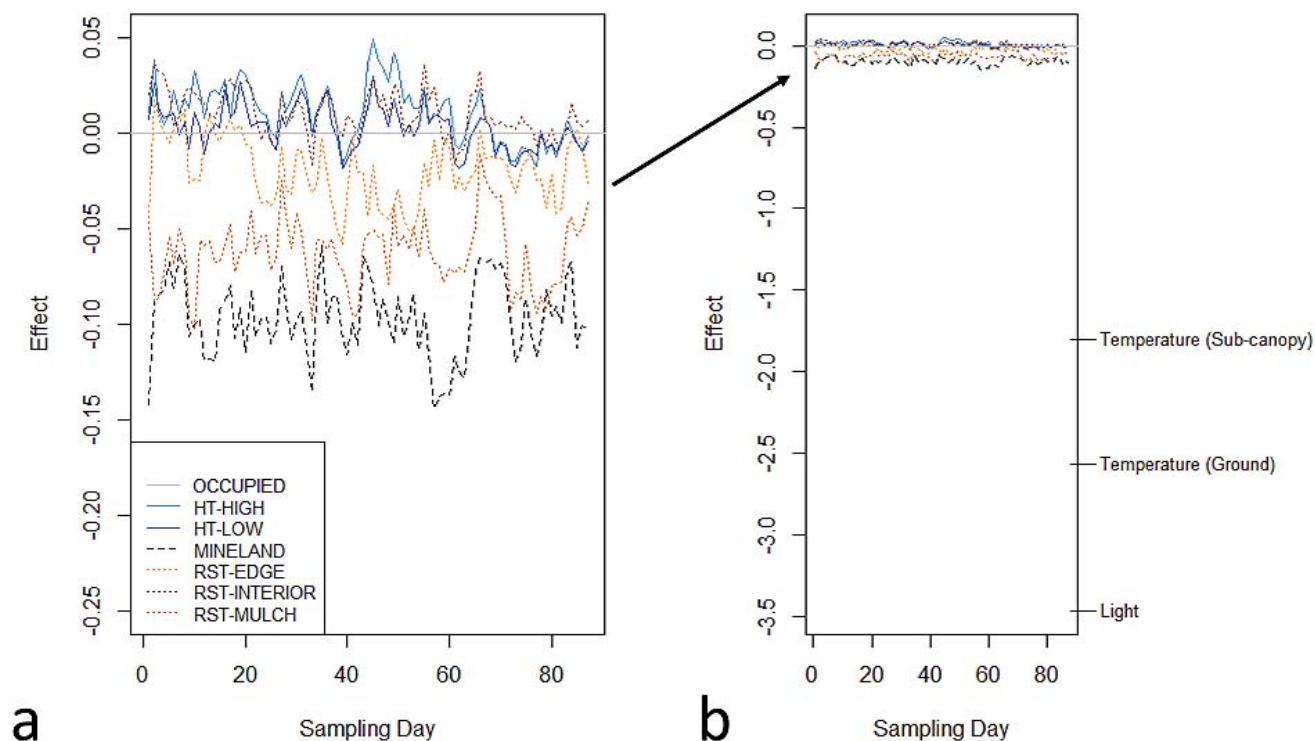


Figure 4. Principal Response Curves showing differences among early-stage red spruce *Picea rubens* restoration sites relative to an occupied Cheat Mountain salamander *Plethodon nettingi* site (OCCUPIED; **a**), and strength of effect for individual microhabitat variables (**b**). All study sites were located on the Monongahela National Forest in eastern West Virginia. Spruce restoration prescriptions included hardwood thinning with low (HT-LOW) and high (HT-HIGH) levels of spruce in the understory, mineland restoration (MINELAND), and red spruce thinning (RST), with sampling in the thinned and mulched area (RST-MULCH), near the adjacent forest edge (RST-EDGE), and within the adjacent forest interior (RST-INTERIOR). We sampled each site at 15-min intervals from 14 June 2019 to 8 September 2019 and used the daily (24-h) mean for this analysis.

S1 (Supplemental Material). The Principal Response Curve indicated that microhabitat differences among sites were fairly consistent across the sampling period, with MINELAND, RST-MULCH, and RST-EDGE differing substantially from the occupied site, while RST-INTERIOR, HT-LOW, and HT-HIGH were similar to the occupied site (Figure 4a). For the repeated-sampling microhabitat characteristics, light intensity had the greatest variation among sites, followed by ground-level temperature (Figure 4b).

Site was a supported predictor for all univariate models ($P < 0.05$) except for nighttime subcanopy air temperature ($\chi^2_6 = 10.839$, $P = 0.093$). Mean daily subcanopy and ground-level air temperatures were higher for the MINELAND site compared with the occupied site (Table 3, Table S1, Supplemental Material). Mean daytime subcanopy and ground-level air temperatures were higher for the MINELAND and RST-MULCH sites, but mean nighttime ground-level air temperature was only higher for the MINELAND site (Table S1, Supplemental Material). Mean daily, daytime, and nighttime light intensities were higher for the MINELAND, RST-MULCH, and RST-EDGE sites (Table 3, Table S1, Supplemental Material). Soil pH was higher at all spruce restoration sites except for RST-EDGE, where the lower CI narrowly overlapped 0 (Table 3, Table S1, Supplemental Material). Soil moisture was lower at all spruce

restoration sites except for RST-MULCH, where the upper CI narrowly overlapped 0 (Table 3, Table S1, Supplemental Material). Data for individual sampling days are available in Data S1 (Supplemental Material). Across sampling sites, soil pH was negatively associated with overstory canopy cover ($r = -0.67$, CI = -0.84 to -0.43), but soil moisture was not strongly associated with canopy cover ($r = -0.03$, CI = -0.41 – 0.37).

Cheat Mountain salamander site study. Site category was a supported predictor for soil pH ($\chi^2_3 = 9.598$, $P = 0.0223$) and soil moisture ($\chi^2_3 = 18.712$, $P = 0.0003$). Compared with OCCUPIED-INTERIOR sites, mean soil pH was lower at OCCUPIED-EDGE ($\beta = -0.10$) and ND-ADJACENT ($\beta = -0.06$) sites, and higher at ND-HIGH sites ($\beta = 0.08$; Table 3). However, the coefficient CI overlapped 0 for all three site categories (Table S1, Supplemental Material). Mean soil moisture at the time of sampling was lower at ND-ADJACENT ($\beta = -0.10$) and ND-HIGH ($\beta = -0.06$) sites, and higher at OCCUPIED-EDGE sites ($\beta = 0.08$; Table S1, Supplemental Material). The coefficient CI largely overlapped 0 for OCCUPIED-EDGE sites and did not overlap 0 for ND-ADJACENT or ND-HIGH sites (Table S1, Supplemental Material). Data for individual sampling points are available in Data S1 (Supplemental Material).

Table 3. Summary statistics for microhabitat variables measured in early-stage red spruce *Picea rubens* restoration sites and an occupied Cheat Mountain salamander *Plethodon nettingi* (CMS) site (OCCUPIED), and in four occupied sites and proximal mature forest nondetection sites (CMS site study). All study sites were located on the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. For the restoration site study, spruce restoration prescriptions included hardwood thinning with low (HT-LOW) and high (HT-HIGH) levels of spruce in the midstory and understory, mineland restoration (MINELAND), and red spruce thinning (RST), with sampling in the thinned and mulched area (RST-MULCH), near the adjacent forest edge (RST-EDGE), and within the adjacent forest interior (RST-INTERIOR). The CMS site study included occupied sites—interior forest (OCCUPIED-INTERIOR), occupied sites—road or trail edge (OCCUPIED-EDGE), adjacent nondetection sites (ND-ADJACENT), and seemingly high-quality habitat nondetection sites (ND-HIGH). Summary statistics for microhabitat variables include the mean (SD) of point measurements of soil pH and soil moisture (% volumetric water content), and of the daily (i.e., 24-h) means derived from continuous monitoring of subcanopy air temperature (°C), ground-level air temperature (°C), and light intensity (lux) using data loggers (restoration site study only). Note that soil pH and soil moisture were measured at different times between the restoration site study and CMS site study, and thus comparisons between studies should be made with caution.

Site	Soil pH	Soil moisture	Subcanopy air temperature	Ground-level air temperature	Light intensity
Restoration site study					
OCCUPIED	3.42 (0.30)	10.28 (2.16)	17.0 (2.40)	16.7 (2.18)	284.59 (162.20)
HT-HIGH	3.75 (0.29)	5.19 (2.49)	16.7 (2.35)	16.1 (1.97)	187.89 (66.54)
HT-LOW	3.60 (0.25)	4.67 (3.27)	16.8 (2.30)	16.4 (1.89)	259.06 (97.28)
MINELAND	4.84 (0.54)	3.48 (2.39)	20.4 (2.73)	21.3 (3.16)	4,469.60 (1,508.83)
RST-MULCH	3.71 (0.31)	8.82 (3.67)	18.6 (2.39)	19.1 (2.02)	2,433.25 (1,267.86)
RST-EDGE	3.57 (0.31)	5.25 (3.42)	17.3 (2.44)	17.1 (2.43)	702.84 (486.04)
RST-INTERIOR	3.73 (0.28)	7.27 (1.96)	16.9 (2.29)	16.0 (2.09)	195.86 (92.03)
CMS site study					
OCCUPIED-INTERIOR	3.78 (0.36)	7.91 (3.19)	—	—	—
OCCUPIED-EDGE	3.68 (0.35)	8.03 (2.14)	—	—	—
ND-ADJACENT	3.71 (0.27)	6.50 (1.91)	—	—	—
ND-HIGH	3.93 (0.49)	6.61 (2.51)	—	—	—

For the occupied sites, mean soil moisture at the time of sampling was 8.34% (Dolly Sods), 8.82% (Gaudineer Knob), 6.99% (Spruce Knob), and 8.05% (Stuart Knob), and differed among the sites ($F_{3,124} = 2.937$, $P = 0.0360$). Based on the CIs, Gaudineer Knob had higher soil moisture than Spruce Knob, but the other site pairs did not significantly differ. Mean soil pH was 3.72 (Dolly Sods), 3.61 (Gaudineer Knob), 3.68 (Spruce Knob), and 3.82 (Stuart Knob), and did not significantly differ among the sites ($F_{3,124} = 4.909$, $P = 0.01316$). Mean soil temperature at the time of sampling was 11.24°C (Dolly Sods), 10.66°C (Gaudineer Knob), 10.37°C (Spruce Knob), and 10.75°C (Stuart Knob), and did not significantly differ among the sites ($F_{3,124} = 0.885$, $P = 0.4512$). Data for individual sampling points are available in Data S1 (Supplemental Material).

Discussion

We found that several microhabitat characteristics differed between early-stage spruce restoration sites and the occupied CMS site. Consistent with other forest systems (e.g., Delgado et al. 2007; Abdallah and Chaieb 2012), air temperature and light intensity were higher at restoration sites with low canopy cover. However, air temperature was similar between the occupied site and interior forest sites, which is consistent with most previous observations of occupied and proximal unoccupied CMS sites (Calise 1978; Santiago 1999; but see Pauley 1998). Air temperature could be an important factor influencing the lower elevational limit of CMS, but

it does not appear to be a particularly strong predictor of occurrence across mature forest patches in close proximity.

Soil pH was a useful variable for separating spruce restoration sites from the occupied site. Red spruce soils are naturally acidic, particularly the O horizon (Johnson et al. 1991; David and Lawrence 1996), and acidity can continue to increase as stands age (Joslin et al. 1992). Thus, we would expect soil pH at the occupied site (i.e., a mature red spruce stand) to be more acidic than at the MINELAND and hardwood-dominated sites. Our finding that soil pH was negatively correlated with canopy cover provides evidence that spruce forest maturity influences pH dynamics, which has been documented in other regions and species (e.g., Orlova et al. 2016; Setälä et al. 2016; Yin et al. 2021).

Cheat Mountain salamanders can tolerate acidic soils; however, most plethodontid salamanders exhibit negative physiological effects in highly acidic soils, so it is unlikely that soil acidification improves habitat quality for the species (Wyman 1988; Frisbie and Wyman 1991). However, acidic soils could give CMS a competitive advantage over salamanders that are less tolerant of acidic soils. For example, the eastern red-backed salamander *Plethodon cinereus* (RBS) is a major competitor of CMS (Pauley 1981; Kroschel et al. 2014). Wyman and Hawksley-Lescault (1987) found that RBS occupancy of survey plots was significantly greater when soil pH exceeded 3.7. In a laboratory experiment, soil pH was more important than soil moisture and light intensity for habitat selection of RBS, with salamanders showing a strong preference for higher pH soils (pH 7.0–7.5 vs. 3.0–



3.5; Sugalski and Claussen 1997). However, an experimental field study in West Virginia did not find that soil pH strongly influenced surface abundance of RBS (Pauley et al. 2006), and thus further research is warranted in areas where CMS and RBS are sympatric.

Soil moisture was also a useful variable for separating spruce restoration sites from the occupied site, and importantly, for separating occupied sites from ND-ADJACENT and ND-HIGH sites. Several field studies have noted that CMS appear to be associated with high-moisture environments (e.g., Brooks 1948; Pauley 2007; Dillard et al. 2008), and a laboratory study indicated the species had a lower tolerance for dehydration than did RBS (Pauley 1998). Furthermore, occurrence of CMS is strongly associated with occurrence of the liverwort *Bazzania trilobata* (Pauley 2007), which grows in high-moisture areas (Sollows et al. 2001; Cleavitt et al. 2007). Thus, soil moisture could be a useful variable for fine-scale habitat delineation, and for monitoring changes in suitability of spruce restoration sites for CMS. Interestingly, soil moisture was not correlated with canopy cover across spruce restoration areas. This is likely due to the mulch and woody debris in the RST-MULCH prescription positively influencing soil moisture despite very low levels of overstory canopy cover (Rhoades et al. 2012; Wang et al. 2021). In the absence of mulch, mean soil moisture was higher in mature red spruce patches, and thus we would expect that as restored spruce stands mature, soil moisture will increase.

Annual acreages of spruce restoration through CASRI have steadily increased over the past decade, and we expect this trend will continue in the next decade. There is currently a strong management interest in restoring spruce ecosystems in the vicinity of occupied sites to enhance habitat availability and connectivity in the long-term. Our study indicates that restoration prescriptions that decrease canopy cover could negatively affect habitat quality for the species in the short-term, and thus these prescriptions are most suitable for currently unoccupied patches. However, planting understory red spruce trees in occupied mature forest patches could help maintain or improve habitat quality for the species in the long term by decreasing light penetration and increasing organic matter, which could increase soil moisture levels (Pearson 1930; Redding et al. 2003), and potentially by increasing soil acidity, which could reduce competition from RBS (Wyman and Hawksley-Lescault 1987). Occupied patches with an eastern hemlock component are particularly strong candidates for spruce restoration because of the potential for widespread eastern hemlock mortality caused by the exotic invasive insect hemlock woolly adelgid *Adelges tsugae* (Fitzpatrick et al. 2012).

In conclusion, our study indicates that for the microhabitat variables we measured, soil moisture appears to be most strongly associated with CMS occurrence. While our results are encouraging, a more spatially and temporally robust study of soil moisture patterns in occupied and unoccupied areas is needed to confirm that soil moisture is indeed a strong predictor of fine-scale occurrence, and to quantify spatial and

temporal dynamics. Additional research investigating the influence of soil pH on CMS and RBS density in sympatric areas is also needed because increasing soil acidity could potentially reduce competitive pressure from RBS (Wyman and Hawksley-Lescault 1987). Other microhabitat variables, particularly those associated with soil and surface characteristics (e.g., soil organic matter content, soil depth to rock, and emergent rocks), also have been suggested as playing an important role in habitat quality for CMS (Dillard et al. 2008; Pauley 2008). We recommend that future studies incorporate these additional microhabitat variables to further inform CMS habitat conservation and associated spruce and spruce-hardwood ecosystem restoration efforts throughout the species' range.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Forest structure and microhabitat variable data used for comparisons of early-stage red spruce *Picea rubens* restoration sites to an occupied Cheat Mountain salamander *Plethodon nettingi* (CMS) site (restoration site study), and for comparisons of four occupied sites and proximal nondetection sites (CMS site study). All study sites were located on the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. Forest structure data include canopy cover (%), red spruce stem counts (overstory, midstory, understory, seedling), red spruce basal area, and total basal area. Microhabitat data include subcanopy air temperature (°C) and light intensity, ground-level air temperature (°C), soil moisture (% volumetric water content), and soil pH.

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Table S1. Parameter estimates (β) and 95% confidence intervals (CI) for mean differences in microhabitat variable values between occupied Cheat Mountain salamander *Plethodon nettingi* (CMS) sites (OCCUPIED), red spruce *Picea rubens* restoration sites (restoration site study), and proximal nondetection sites (CMS site study). All study sites were located on the Monongahela National Forest in eastern West Virginia, and microhabitat sampling occurred in 2019 and 2020. The restoration site study included the following site categories: hardwood thinning—high understory red spruce density (HT-HIGH), hardwood thinning—low understory red spruce density (HT-LOW), mineland restoration (MINE-LAND), red spruce thinning—thinned and mulched area (RST-MULCH), red spruce thinning—forest edge (RST-EDGE), and red spruce thinning—forest interior (RST-INTERIOR). The CMS site study included the following site categories: occupied sites—interior forest (OCCUPIED-INTERIOR), occupied sites—road or trail edge (OCCUPIED-EDGE), adjacent nondetection sites (ND-ADJA-



CENT), and seemingly high-quality habitat nondetection sites (ND-HIGH). Microhabitat variables measured for both the restoration site study and CMS site study included soil pH and soil moisture (% volumetric water content). Additional microhabitat variables measured for the restoration site study included daily (24 h), daytime (0900–2000 hours), and nighttime subcanopy air temperature (°C), ground-level air temperature (°C) and light intensity (lux, log₁₀-transformed). The OCCUPIED and OCCUPIED-INTERIOR sites represent the model intercepts for the restoration site study and CMS site study, respectively, and β coefficients represent modelled deviation from the intercept (with 95% confidence intervals [CI]).

Available: <https://doi.org/10.3996/JFWM-21-042.S2> (39 KB DOCX)

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