



Long-term occupancy dynamics of the threatened Cheat Mountain salamander and its competitors in relation to linear habitat fragmentation

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ABSTRACT

Amphibians are declining globally and while many factors are contributing to this decline, habitat loss and degradation caused by climate and land use changes are among the most critical. Habitat degradation and increased interspecific competition are both concerns for long-term viability of the federally-threatened Cheat Mountain salamander (*Plethodon nettingi*) which is endemic to high elevations in West Virginia. In this study, we quantified the impacts of linear habitat fragmentation (i.e., a linear forest clearing for creation of a ski slope) on local colonization and extinction probabilities in adjacent forested habitat for the Cheat Mountain salamander and two co-occurring competitor species, eastern red-backed salamander (*Plethodon cinereus*) and Wehrle's salamander (*Plethodon wehrlei*). We also quantified long-term changes in total occupancy of the species within the high elevation study area. We surveyed the salamander community annually from 1988 to 2021 using diurnal natural cover object searches at 43 plots, with 1988 representing three years following linear habitat fragmentation. For each species, we used dynamic occupancy models to identify and model influential covariates for initial occupancy, colonization, extinction, and detection probability. We found that distance to fragmentation was positively correlated with colonization probability for Cheat Mountain salamanders, indicating negative edge effects of the linear forest clearing. Distance to fragmentation was negatively correlated with colonization probability for eastern red-backed salamanders, potentially indicating this species benefited from increased solar radiation or reduced competition from Cheat Mountain salamanders. Predicted occupancy of eastern red-backed salamanders and Wehrle's salamanders increased over the 34 year monitoring period, indicating potential for increased competitive interactions. Our study suggests that extensive linear habitat fragmentation could result in degraded habitat for Cheat Mountain salamanders in the adjacent forest, and that potential for interactions with competitor species is increasing in high elevation forest stands.

1. Introduction

Amphibian population declines and species extinctions are occurring at a global scale (Semlitsch et al., 1996; Collins and Storfer, 2003; Beebee and Griffiths, 2005). Several factors are thought to be contributing to this widespread decline, with habitat loss and degradation among the most critical (Sodhi et al., 2008). Linear fragmentation of mature forests is a common practice that occurs worldwide for installation and maintenance of transportation, energy, and recreation corridors and infrastructure (Riitters et al., 2004; Goosem, 2007; Monz et al., 2010; Jones et al., 2015). For example, development associated

with the unconventional oil and gas industry in the central Appalachian region of the eastern United States is resulting in extensive linear forest fragmentation (Brittingham et al., 2014; Langlois et al., 2017). Drohan et al. (2012) estimated that 54% of existing shale-gas well pads in Pennsylvania occurred in forests, with 23% in core forests. The infrastructure associated with shale development has the potential to negatively impact plethodontid salamanders in the region (Brand et al., 2014). The Appalachian region is a global biodiversity hotspot for woodland salamanders (genus *Plethodon*; Kozak et al., 2009; Milanovich et al., 2010), and there is broad concern for impacts of habitat loss and fragmentation on these species (Barrett et al., 2014; Sutton et al., 2015).

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Woodland salamanders have low vagility (Marvin, 1998; Gillette, 2003; Cabe et al., 2006) and strict microclimate requirements for cutaneous respiration (Spotila, 1972), and thus linear fragmentation of forests over long distances could potentially reduce or eliminate population connectivity (deMaynadier and Hunter, 2000; Marsh et al., 2005). In addition, edge effects can result in habitat degradation of adjacent forested habitat. For example, Marsh and Beckman (2004) found abundance of eastern red-backed salamanders (RBS; *Plethodon cinereus*) was reduced up to 20 m from road edges, and deMaynadier and Hunter (1998) estimated interior edge effects from clearcuts extended 25–35 m for RBS. Wood and Williams (2013) found that salamander abundance was highest 75 m from the forest edge, with few captures occurring within edge treatments. However, Moseley et al. (2009) found RBS could occupy sites within 20 m of edges if sufficient refugia were available. Thermal tolerances are species-specific (Markle and Kozak, 2018), and some woodland salamander species could benefit from exposure to increased solar radiation at locations near their lower thermal tolerance limit (Huheey and Brandon, 1973).

In addition to impacting habitat availability and quality, fragmentation could alter interspecific competition dynamics. Interspecific competition appears to influence distribution and abundance of some montane salamanders, as individuals compete for limited resources or optimal habitat (Jaeger, 1970; Fraser, 1976; Griffis and Jaeger, 1998; Reichenbach and Kniewski, 2009; Amburgey et al., 2019). In particular, previous studies have suggested strong competition between RBS and many woodland salamanders of conservation concern. For example, densities of Peaks of Otter salamanders (*Plethodon hubrichti*) were reduced in areas of sympatry with RBS, and RBS densities are increasing in areas that were historically dominated by Peaks of Otter salamanders (Reichenbach and Kniewski, 2009). Valley and Ridge salamanders (*Plethodon hoffmani*) and RBS compete for space, particularly nest sites, in areas of sympatry (Fraser, 1976). Shenandoah salamanders (*Plethodon shenandoah*) often appear to be restricted to suboptimal habitats in areas of sympatry with RBS (Jaeger, 1970, 1980; Griffis and Jaeger, 1998). Thus, changes in competing species distributions could be an important factor for long-term population viability of salamanders that are endemic to high elevations.

The Cheat Mountain salamander (CMS; *Plethodon nettingi*) is a federally threatened species whose entire range falls within the high Allegheny Mountains of eastern West Virginia, primarily within the Monongahela National Forest (Pauley, 2008). This high-elevation endemic salamander is strongly associated with northern hardwood forests with a red spruce (*Picea rubens*) or eastern hemlock (*Tsuga canadensis*) component (Pauley, 2007, 2008). Broad-scale clearcutting and wildfires in the late-1800s and early-1900s resulted in a reduction of red spruce-dominated forest in West Virginia from $\geq 190,000$ ha to $< 10,000$ ha (reviewed by Beane et al., 2013), and today the Cheat Mountain salamander is limited to approximately 80 geographically isolated populations (Pauley, 2008). Potential contemporary threats identified for the species include additional habitat loss, fragmentation, and degradation, increased competition and predation, and disease (U.S. Fish and Wildlife Service, 2009). Increased interspecific competition is of particular concern, with a previous study finding that occupancy of sympatric CMS and RBS populations decreased and increased, respectively, between 1978 and 2011 (Kroschel et al., 2014).

The purpose of this study was to quantify long-term (i.e., 34-year) occupancy dynamics of CMS and two competitor species (RBS and Wehrle's salamander [WES; *Plethodon wehrlei*]) in relation to linear forest clearing. We investigated if occupancy of CMS and its competitors was influenced by distance to forest edge, and if occupancy of the species within the study area has changed over time. Estimating the long-term impacts of historical linear forest fragmentation on this woodland salamander community will provide valuable insights into potential responses to future fragmentation for high-elevation endemic salamanders of conservation concern.

2. Methods

2.1. Study area

We conducted this study at a ski resort partially located within the Monongahela National Forest (MNF) in Tucker County, West Virginia (Fig. 1; specific location withheld due to the conservation status of CMS). Since its inaugural season in 1986, 41 ski trails have been established across the property. Our study area consisted of a 4-ha mature forest patch near the mountain peak (survey site elevation = 1193–1250 m), and adjacent to a ski trail (hereafter linear forest clearing) with an average width of 19 m that was established in 1986. The study area consisted of shallow soil composed primarily of inceptisols and spodosols (Gilliam, 2002). Dominant tree species included red spruce, yellow birch (*Betula alleghaniensis*), and American mountain ash (*Sorbus americana*), with 44% of monitoring plots having 50% or more of the canopy comprised of mature red spruce. Monitoring plots had mainly north-northeast-east aspects, with one plot having a northwest aspect. Annual average precipitation and air temperature in this area is approximately 147 cm and 8.8 °C, respectively (U.S. Forest Service, 2006). In addition, a sprinkler system was installed in 2012 to improve habitat quality (i.e., increase soil moisture) for CMS within the study area.

2.2. Field data collection

We delineated 43 survey plots within the study area to monitor long-term occupancy dynamics of CMS and co-occurring salamander species in relation to the linear forest clearing. We used a systematic sampling approach, with 10 plots placed at the edges of the linear forest clearing (plot centers located ca. 4 m from the edge), and the remaining plots placed within the adjacent forest at approximately 20 m intervals from the edge plots, resulting in an even distribution of plots throughout the 4-ha monitoring area and plot distances of up to 80 m from the clearing.

We conducted visual encounter surveys annually from 1988 to 2021 (excluding 2019). We excluded two pilot survey years conducted prior to 1988 (1986–1987), because the sampling protocol was still being developed and detections for all species were unusually low relative to the other sampling years. Surveys consisted of diurnal area-constrained natural cover object searches. All moveable rocks and coarse woody debris > 6 cm in diameter within each plot were searched. We primarily conducted surveys within 48 h of a rain event and during warm months (May–September, typically in spring and fall) to maximize probability of availability of the focal species, as surface activity of woodland salamanders is highly influenced by environmental hydric and thermal conditions (Spotila, 1972; Feder, 1983; Stuczka et al., 2016). We conducted surveys once ($n = 17$), twice ($n = 15$), or three times ($n = 1$) per year. For years with repeated samples, the median number of days between surveys was 108 (minimum = 4, maximum = 131). Detected salamanders were identified to species.

2.3. Habitat data

We used weather data to assess if climatic conditions changed across the study period, as well as to account for effects of daily weather conditions on salamander detection probability. We obtained annual historical weather data (precipitation and minimum temperature) from 1980 to 2020 for the study area from Daymet Daily Surface Weather and Climatological Summaries (Thornton et al., 2018). Because Daymet has a four-month latency, weather data for 2021 salamander surveys was derived from a nearby weather station located in Davis, West Virginia (39.0980° N, 79.4322° W).

We used a 3×3 m digital elevation model (DEM; 1:4,800 scale elevation data) to derive several environmental variables, including heat load index (HLI), integrated moisture index (IMI), landform, slope position, and percent slope for each plot using ArcMAP (v. 10.5,

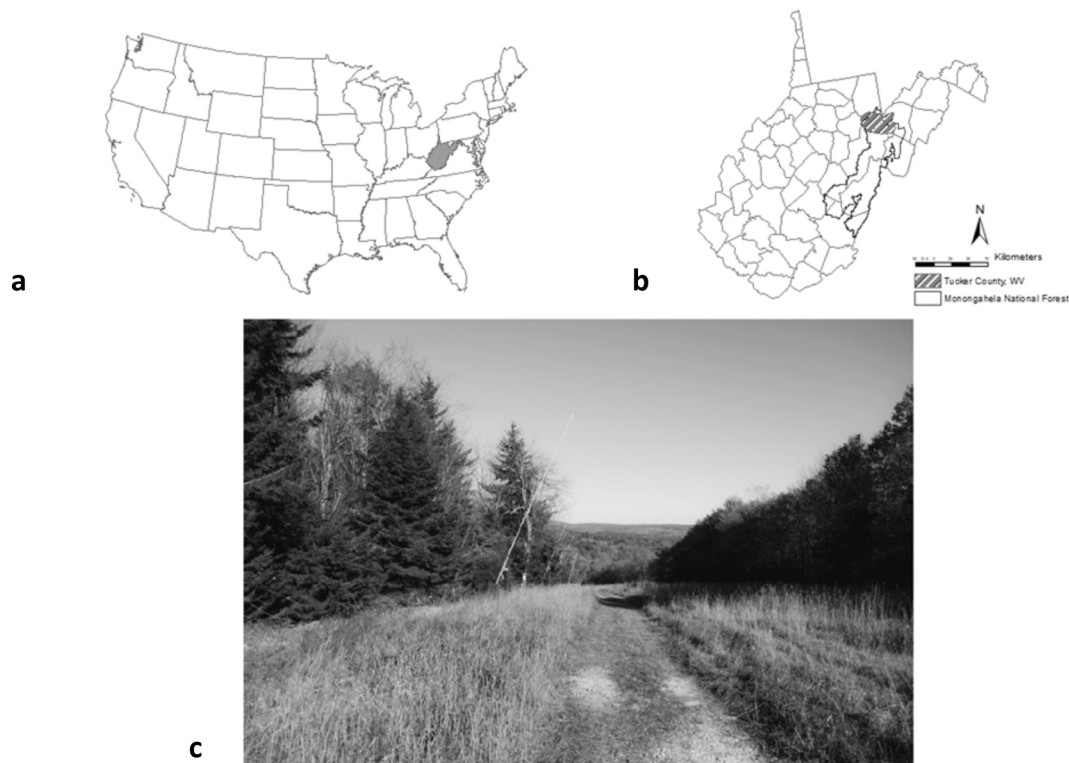


Fig. 1. Location of this study assessing impacts of linear habitat fragmentation on a high elevation salamander community in West Virginia, USA (a). The study area was located on a ski resort in Tucker County (b), within the boundary of the Monongahela National Forest (specific location withheld due to the conservation status of the Cheat Mountain salamander [*Plethodon nettingi*]). The study area consisted of a 4-ha mature forest patch that was adjacent to a ski slope with an average width of 19 m (c).

Environmental Systems Research Institute, Inc., Redlands, CA, USA). The HLI is an index representing temperature associated with aspect of plots, with higher scores indicating higher heat loads (McCune and Keon, 2002). We calculated HLI using the following equation:

$$HLI = 0.039 + [0.808 * \cos(l) * \cos(\theta)] - [0.196 * \sin(\theta)] - [0.482 * \cos(f(\alpha)) * \sin(f(\alpha))]$$

where l represents latitude of an area of interest, θ represents the slope of an area of interest, and $f(\alpha)$ represents the folded slope of an area of interest (McCune and Keon, 2002). Aspect can be an important factor for woodland salamander habitat quality (Briggler and Prather, 2006; Dillard et al., 2008; MacNeil and Williams, 2013; Jacobsen et al., 2020), as southern aspects usually have higher temperatures and less moisture because these aspects receive more direct sunlight (Harper and Guynn, 1999; Mohammad, 2008). The IMI, which is a relative rating of available moisture on the landscape, ranges from 0 to 100 with higher scores indicating higher moisture levels on the landscape (Iverson et al., 1997). The IMI model has been used as a predictive tool for several ecosystem attributes ranging from vegetation composition to bird distributions (Iverson et al., 1997). The IMI was calculated using the following equation (Iverson et al., 1997):

$$IMI = [\text{hillshade} * 0.5] + [\text{curvature}(\theta) * 0.15] + [\text{FlowAccumulation} * 0.35]$$

Landform describes the surface curvature of a landscape, specifically the concavity and convexity index based on landscape features (McNab, 1993). Slope position was defined using the Topographical Positional Index tool, and calculates a scalable slope position by comparing average neighboring values on the landscape from a focal position (Guisan et al., 1999). Positive values indicate that the focal point is on a higher slope position than neighbor averages, and negative values indicated the focal point is lower (Guisan et al., 1999). This differs from landform values in that this metric delineates the focal points position

topographically on the landscape. We measured percent slope because previous research found that slope can influence CMS occurrence (Dillard et al., 2008). Distance from edge of the ski slope (m) was measured from each survey plot center using geo-referenced aerial photography.

2.4. Data analysis

To assess whether climatic conditions are changing in the study area, we determined if there were significant temporal trends in temperature and precipitation between 1980 and 2020 using Mann-Kendall tests (Mann, 1945; Kendall, 1975). This non-parametric test is widely used to detect monotonic trends in environmental data (e.g., Burn and Hag Elnur, 2002; Linares et al., 2011; Westra et al., 2013). The Mann-Kendall test estimates test distributions using a permutation approach, where a large number of random orderings of the data set are created and a test statistic is calculated for each permutation (Burn and Hag Elnur, 2002). A significant p -value indicates a trend is present within the data tested, and a τ value specifies the direction and magnitude of the trend. We tested for annual trends in mean daily minimum and maximum temperature during the warmest and coldest quarter (July–September and January–March respectively), and monthly total precipitation. We conducted climatic analyses using the package *Kendall* (version 2.2) in program R.

We used dynamic occupancy models to quantify species-specific changes in occupancy from 1988 to 2021 in relation to time and distance from edge (MacKenzie et al., 2003, 2017). We considered survey plots to be closed within-years and used within-year survey replications to estimate detection probability (p). Detection probabilities in years with a single survey were informed by the estimated p using the full data set. We tested several covariates as predictors of p and initial occupancy (Ψ). For p , we tested survey season (spring [April–May] and fall [September–October]), weather conditions the day of the survey (i.e., precipitation and minimum temperature), and weather conditions prior

to the survey (i.e., 3-day cumulative precipitation and 7-day cumulative precipitation). For initial occupancy, we tested HLI, IMI, landform, slope position, and percent slope.

Our focal covariates for dynamic occupancy were year (specified as a continuous variable) and plot distance to linear forest clearing (hereafter distance to edge). We also tested absence (1988–2011)/presence (2012–2021) of the sprinkler system as a yearly colonization (γ) and extinction (ϵ) covariate to assess if this management prescription is having clear impacts on occupancy for CMS or its competitors. We did not model the sprinkler system as a plot-level covariate because sprinkler lines were placed throughout the study area.

We used a step-wise model selection approach to identify important predictors because of the large number of potential candidate models (Table 1). For each species, we first determined the most parsimonious p model (based on Akaike Information Criterion, corrected for small sample size [AIC_c]; Burnham et al., 2011), and then determined the most parsimonious Ψ model. Due to sample size limitations, we restricted the p and Ψ model selections to single variable models. We retained the top p and Ψ model as the null models for the focal colonization and extinction analyses, unless model convergence could not be achieved when these variables were included. We centered and scaled all continuous covariates prior to analysis.

For CMS, we tested all combinations of distance from edge, year, and distance from edge + year as predictors of γ and ϵ for CMS (Supplemental Material Table S1). For all species, we tested presence or absence of the sprinkler as a predictor of γ and ϵ . Finally, we derived annual predicted occupancy across the study period for each species based on model-estimated p , Ψ , and ϵ , and year as a predictor of γ and ϵ . We considered models to have strong support if $\Delta\text{AIC}_c < 2$ (Burnham and Anderson, 2004; Burnham et al., 2011). For models with strong support, we assessed confidence for an effect of each variable by computing the 85% profile likelihood confidence intervals (CI) of the beta coefficients (Arnold, 2010) and considered evidence for a strong effect when CIs did not overlap zero (Halsey, 2019). We assessed model fit using a parametric bootstrap based on Pearson's chi-square with 1000 simulations (Kéry and Royle, 2015). The \hat{C} values indicated only minor overdispersion for the models (range = 1.49–1.87), and thus we proceeded with the analyses. We conducted occupancy and model selection analyses using the packages *unmarked* (version 0.12-2) and *AICcmodavg* (version 2.1-1), respectively, in program R (version 3.6.3). We calculated the Relative Variable Importance (RVI) for predictors of γ and ϵ (Table 1) using the package *MuMIn* (version 1.43.17). We included models in the RVI if $\Delta\text{AIC}_c \leq 4$.

Table 1

Relative Variable Importance (RVI) for focal parameter (colonization [γ] and extinction [ϵ]) with a $\Delta\text{AIC}_c \leq 4$ for the Cheat Mountain salamander (*Plethodon nettingi*), eastern red-backed salamander (*P. cinereus*), and Wehrle's salamander (*P. wehrlei*) in Tucker County, West Virginia, USA. These models are considered to have some support. We sampled salamanders 1–3 times annually using area-constrained diurnal cover object searches at 5 m radius plots.

Species	Parameter	Sum of Weights	Number of models ≤ 4
<i>P. nettingi</i>	γ (Year)	0.59	6
	γ (Distance from edge)	0.68	6
	ϵ (Year)	0.15	3
	ϵ (Distance from edge)	0.16	3
<i>P. cinereus</i>	γ (Year)	1.00	4
	γ (Distance from edge)	0.54	2
	ϵ (Distance from edge)	0.26	2
<i>P. wehrlei</i>	γ (Year)	0.38	4
	γ (Sprinkler)	0.16	1
	γ (Distance from edge)	0.09	2
	ϵ (Year)	0.12	2
	ϵ (Sprinkler)	0.10	1

3. Results

3.1. Climate change

From 1980 to 2020, positive trends were detected for mean daily minimum temperature in the warmest quarter ($p = 0.0007$, $\tau = 0.370$; Fig. 2a) and total monthly precipitation ($p = 0.006$, $\tau = 0.087$; Fig. 2b). We did not detect a significant trend for mean daily maximum temperature in the warmest quarter ($p = 0.357$) or coolest quarter ($p = 0.307$) or mean daily minimum temperature in the coldest quarter ($p = 0.096$).

3.2. Salamander responses

In total, 1892 detections of 4 salamander species occurred during the study, including 1633 CMS, 106 RBS, 106 WES, and 47 Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*). We were unable to include Allegheny Mountain dusky salamanders in the study due to lack of model convergence caused by the low occurrence rates. Annual naïve (observed) occupancy ranged from 0.23 to 0.84 for CMS, 0.00–0.19 for RBS, and 0.00–0.37 for WES (Fig. 3). The most parsimonious p model was minimum temperature on the day of the survey for CMS, the null model for RBS, and the survey season model for WES (Table S1). Estimated p (SE) was 0.582 (0.018) for CMS at the median temperature for the study period, 0.147 (0.024) for RBS, and 0.165 (0.022) and 0.039 (0.011) for WES during spring and fall, respectively. The most parsimonious Ψ model was the null model for CMS, the IMI model for RBS, and the HLI model for WES. Initial occupancy was positively correlated with IMI for RBS and negatively correlated with HLI for WES. For the focal analyses, we included HLI for the WES models, but we were unable to include IMI in the RBS models due to lack of model convergence.

For CMS, the most parsimonious focal analysis model contained year and distance from edge for γ (Table S1). This was the most complex model with strong support, and coefficient confidence intervals (CIs) did not overlap 0 (Table 2). Between the first and last study year, predicted occupancy of plots increased from 0.76 to 0.85 (Fig. 3a). Colonization probability (γ) increased from 0.22 to 0.39 at year 0, and 0.42–0.65 at year 33 with increasing distance from edge (Fig. 4a).

For RBS, the most parsimonious focal analysis model also contained year and distance from edge for γ (Table S1). This was the most complex model with strong support, and coefficient CIs did not overlap 0 (Table 2). Between the first and last survey year, predicted occupancy of plots increased from 0.03 to 0.53 (Fig. 3b). Colonization probability decreased from 0.02 to 0.01 at year 0, and 0.29–0.10 at year 33 with increasing distance from edge. Distance from edge also had some support as an ϵ predictor (in conjunction with year as a γ predictor), with ϵ probability increasing from 0.04 to 0.15 with increasing distance from edge. However, there was low support for the estimate, with the coefficient CI broadly overlapping 0 (-0.12, 1.18). The sprinkler model received lower support than the null model as a predictor of γ and ϵ . For WES, the most parsimonious model contained year for γ (Table S1). Between the first and last study year, predicted occupancy of plots increased from 0.34 to 0.63 (Fig. 3c). Colonization probability increased from 0.005 at year 0 to 0.08 at year 33 (Fig. 4c).

The calculated RVIs for models with CMS show that both distance and year were important γ predictors, with distance returned as the highest relative importance (0.68; Table 1). For ϵ , year and distance returned relative importance values of 0.15 and 0.16 respectively. For RBS, both year and distance were important predictors of γ , receiving relative importance values of 1.00 and 0.54, respectively (Table 1). For ϵ , distance from edge returned a RVI of 0.26. For WES, year, distance from edge, and the sprinkler were all important predictors of γ with RVI values of 0.38, 0.09, and 0.16, respectively. For ϵ , year and the sprinkler were important predictors with RVI values of 0.12 and 0.10, respectively.

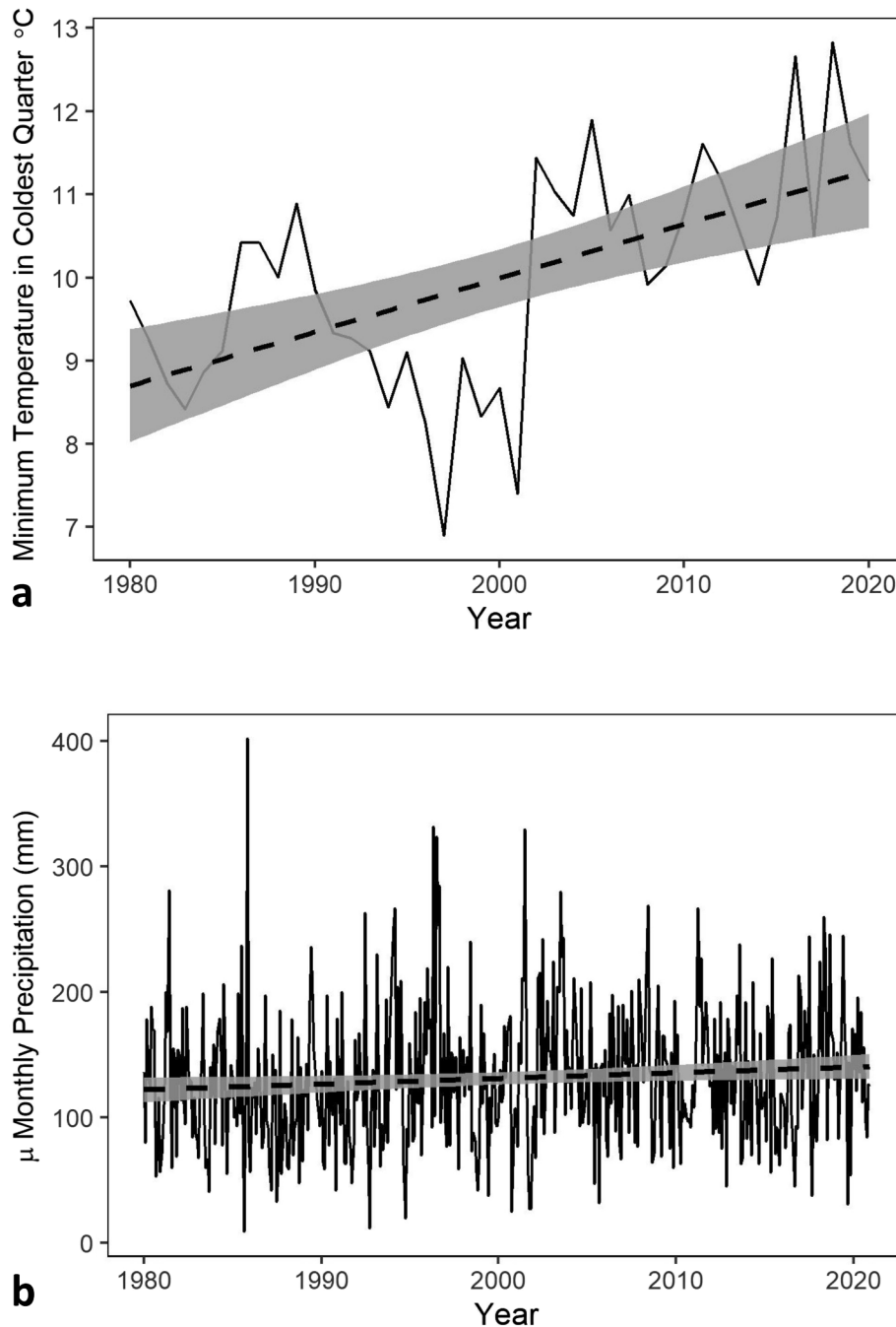


Fig. 2. Observed weather conditions from 1980 to 2020 in a high elevation forest adjacent to a ski slope in Tucker County, West Virginia, USA. Positive trends were detected for mean daily minimum temperature in the warmest quarter (July–September; a) and monthly total precipitation (b), but not for mean daily minimum or maximum temperature in the coolest quarter, or for maximum temperature in the warmest quarter. We obtained weather data from Daymet Daily Surface Weather and Climatological Summaries (<https://daymet.ornl.gov/>). Dashed lines represent a least squares line of best fit, with slopes of 0.03558 and 0.0012 for minimum temperature and monthly precipitation, respectively.

4. Discussion

Our results suggest that linear fragmentation of a high elevation forest in Central Appalachia could be influencing salamander occupancy dynamics in the adjacent mature forest. We acknowledge that our study lacked a true control, and thus our inferences are restricted to temporal and spatial variation within a fragmented forest patch. It is well documented that fragmentation of mature forests influences microclimatic conditions near the forest edge, often resulting in more extreme air and soil temperature fluctuations, lower humidity, and decreased soil moisture (Chen et al., 1995; Gehlhausen et al., 2000; Ewers and Banks-Leite, 2013; Arroyo-Rodríguez et al., 2017). Our results indicate that forest fragmentation negatively impacted microhabitat quality adjacent to the forest edge for the threatened CMS, which is consistent with previous work that found CMS occurrence was associated with interior

forest conditions, including lower air temperature and higher humidity (Pauley, 1980a). Further, our results indicate that linear forest removal either increased microhabitat quality for RBS or allowed this species to capitalize on reduced competition from CMS near the forest edge. For WES, our results indicate that this species has increased their occupancy of the study site across years, possibly in response to the changing climate in the study area.

Physiological traits influence the ability of species to colonize and persist in areas subjected to major disturbances (Sousa, 1984; Hendry et al., 2011; Lankau et al., 2011). Woodland salamanders are particularly sensitive to microclimatic conditions because they require cutaneous respiration for gas exchange (Spotila, 1972). However, species and populations vary in their moisture and thermal tolerances and acclimation abilities (Spotila, 1972; Pauley, 1978; Muñoz et al., 2016; Markle and Kozak, 2018). Markle and Kozak (2018) studied thermal

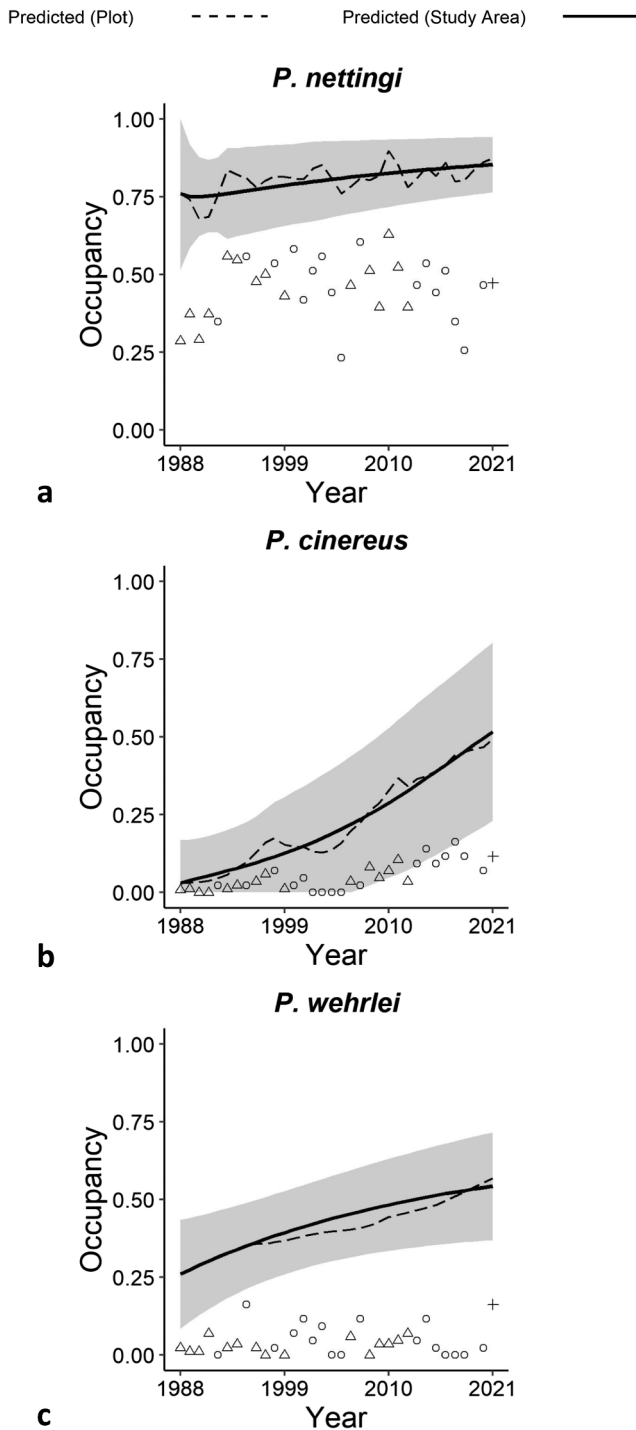


Fig. 3. Naïve (symbols) and predicted occupancy for the Cheat Mountain salamander (*Plethodon nettingi*; a), eastern red-backed salamander (*P. cinereus*; b), and Wehrle’s salamander (*P. wehrlei*; c) from 1988 to 2021 in a high elevation forest adjacent to a ski resort in Tucker County, West Virginia, USA. Mean proportion of occupied plots (naïve occupancy) is based on one (circles), two (triangles), or three (crosses) surveys conducted annually using area-constrained diurnal natural cover object searches in 5 m radius plots. These dynamic occupancy models included year as a continuous variable for colonization (γ). Gray bands represent 95% confidence intervals for the predicted (study area) occupancy based on a 1000 replication bootstrap.

Table 2

Model coefficient 85% confidence intervals (CI) of the most complex strongly supported dynamic occupancy models for the Cheat Mountain salamander (*Plethodon nettingi*) and eastern red-backed salamander (*P. cinereus*) in relation to distance from linear forest clearing (distance from edge; 4–80 m) and year (1988–2021) in Tucker County, West Virginia, USA. We sampled salamanders 1–3 times annually using area-constrained diurnal cover object searches at 5 m radius plots.

Species	Parameter	Estimate	CI (lower)	CI (upper)
<i>P. nettingi</i>	$\Psi(\cdot)$	1.060	0.440	1.816
	γ (Year)	0.032	0.007	0.060
	γ (Distance from edge)	0.269	0.053	0.505
	$\epsilon(\cdot)$	-2.290	-2.616	-2.005
	$p(\text{Temperature})$	0.172	0.097	0.248
<i>P. cinereus</i>	$\Psi(\cdot)$	-3.46	-5.362	-2.251
	γ (Year)	0.089	0.049	0.127
	γ (Distance from edge)	-0.389	-0.720	-0.081
	$\epsilon(\cdot)$	-1.920	-3.419	-0.878
	$p(\cdot)$	-1.360	-1.762	-0.921
<i>P. wehrlei</i>	$\Psi(\cdot)$	-0.625	-1.315	0.065
	γ (year)	0.087	0.007	0.166
	$\epsilon(\cdot)$	-4.390	-5.629	-3.159
	$p(\text{Season}_b)$	-1.580	-2.007	-1.148

capacities of 16 plethodontid species and found that size of geographic range was positively correlated with capacity to acclimate to increased temperatures. Further, RBS had the greatest thermal acclimation capacity of the 10 *Plethodon* species tested. Many field studies indicate that RBS populations are negatively impacted by timber harvest, but that the populations are also capable of persisting in the resulting suboptimal environments (e.g., Pough et al., 1987; Duguay and Wood, 2002; Hocking et al., 2013; Homyack and Haas, 2013). Little previous research has been conducted on responses of WES and CMS populations to timber harvest. However, the leading hypothesis for why CMS is currently only found in geographically small, isolated populations is that the species was unable to persist through historical clear-cutting activities and associated wildfires except in exceptionally rocky substrates (Pauley, 2008).

Our study area is somewhat unusual in that RBS is not the dominant woodland salamander, and it was rarely encountered during the early years of the study (i.e., RBS was detected in zero or one of the 43 survey plots annually from 1988 to 1995). In addition to linear forest clearing likely reducing competition from CMS, it is possible that the increasing trend in precipitation or minimum temperature in summer is increasing climatic suitability for competitors of the Cheat Mountain salamander. Given that most previous research indicates CMS selects for cooler, moister environments (Jaeger, 1971; Downer, 2009; Farallo and Miles, 2016), we speculate that if climate change is increasing habitat quality for RBS and WES in our study area, it is likely through increased precipitation, which is expected to continue increasing in this region (Fernandez and Zegre, 2019). Prevalence of RBS is also increasing at other high elevation locations where CMS and RBS are sympatric (Kroschel et al., 2014), indicating this is a general pattern independent of linear forest clearing.

There is concern that interspecific competition is a threat to long-term viability of CMS populations (Highton, 1972; Pauley, 1980b; U.S. Fish and Wildlife Service, 2009), particularly because occurrence of CMS at some monitoring sites has decreased in conjunction with an increase in RBS (Kroschel et al., 2014). While the results of this study do not indicate that CMS is declining at our study area, continued monitoring is needed due to the increasing occupancy trends for RBS and WES. Further, we encourage an increase in within-year survey replication effort to increase precision of model estimates as well as allow for use of more complex and informative models, such as multi-state and species interaction models (e.g., MacKenzie et al., 2009; Richmond et al., 2010; Rota et al., 2016).

Our findings indicate that for the threatened CMS, negative effects of

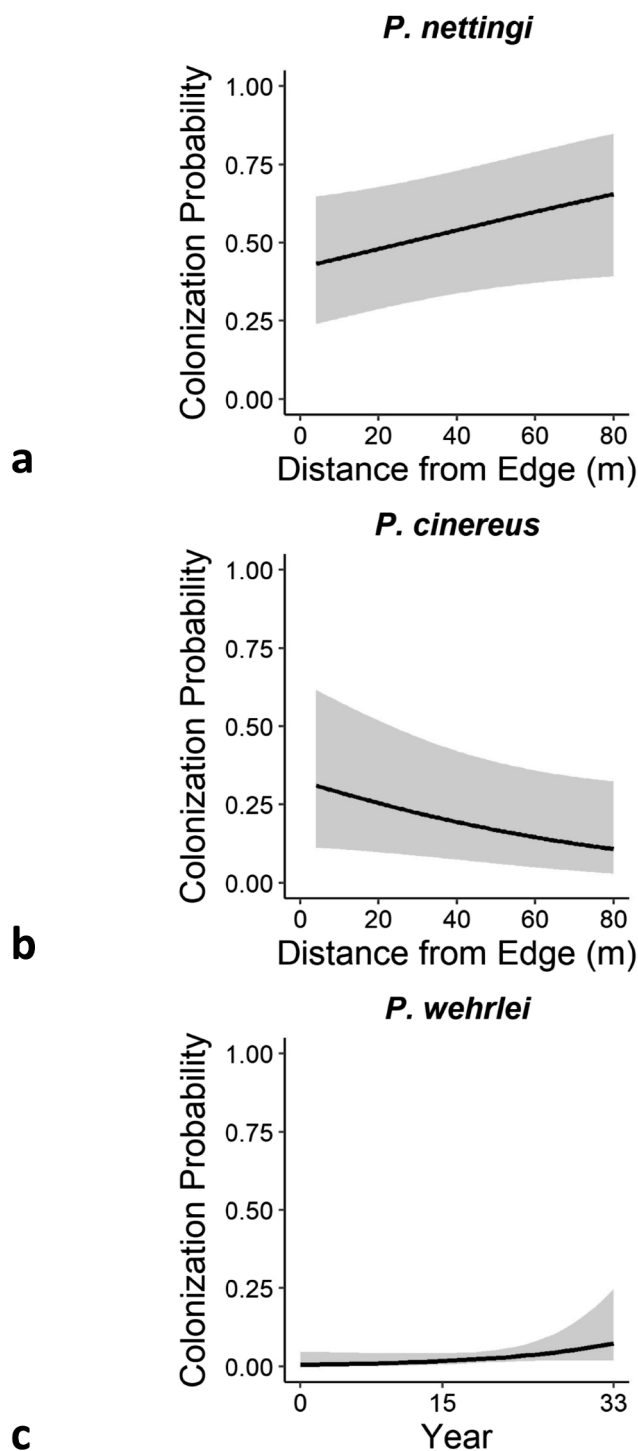


Fig. 4. Colonization (γ) probabilities for the Cheat Mountain salamander (*Plethodon nettingi*; a) eastern red-backed salamander (*Plethodon cinereus*; b), and Wehrle's salamander (*P. wehrlei*; c) in a high elevation forest stand adjacent to a ski slope in Tucker County, West Virginia, USA. We sampled salamanders 1–3 times annually from 1988 to 2021 using area-constrained diurnal cover object searches at 5 m radius plots Cheat Mountain salamander and eastern red-backed salamander. γ probability was influenced by distance from the linear forest clearing (distance from edge; 4–80 m) and survey year (0–33), and Wehrle's salamander γ probability was influenced by survey year. For the Cheat Mountain salamander and eastern red-backed salamander plots, survey year was fixed at 33 (i.e., 2021). Gray bands represent the 85% confidence intervals based on a 1000 replication bootstrap.

linear habitat fragmentation extend well beyond the impact boundary. This result is commonly observed for woodland salamanders (e.g., DeGraff and Yamasaki, 2002; MacNeil and Williams, 2013), and can persist for at least as long as the forest clearing remains (Semlitsch et al., 2007). Previous work has shown that aspect influences intensity of edge effects for woodland salamanders, with the most pronounced effects on dryer southerly aspects (Moseley et al., 2009; MacNeil and Williams, 2013). However, our study indicates that CMS is also vulnerable to edge effects on northerly aspects. Thus, even if the species is not directly impacted within the zone of linear forest clearing, adjacent forest populations could be impacted. This result has implications for possible future linear forest clearing near known and potential CMS populations, such as for electricity powerlines and natural gas pipelines.

Many studies provide concerning projections for the impacts of continued anthropogenic land use changes and contemporary climate changes on the long-term viability of amphibians in Appalachia and across North America, particularly for range-restricted and high-elevation endemic species (McCallum, 2007; Milanovich et al., 2010; Barrett et al., 2014; Bonetti and Wiens, 2014; Sutton et al., 2015; Struecker and Milanovich, 2017). Additional research indicates the capacity of amphibians to adapt to rapid climate change may be greater than previously perceived (Urban et al., 2014; Ficetola et al., 2016; Lyons and Kozak, 2020). What is clear is that maintaining and restoring high quality habitats for vulnerable species is key to maximizing their capacity for resilience to climate change (Hulme, 2005; Mawdsley et al., 2009; Hole et al., 2011). Our study suggests that linear forest clearing could have negative effects on adjacent populations of the threatened CMS. Thus, restricting future fragmentation in areas with known and potential CMS populations is likely an important management consideration for this species.

CRedit authorship contribution statement

Lacy E. Rucker: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Donald J. Brown:** Conceptualization, Resources, Writing – review & editing, Visualization, Supervision. **Mark B. Watson:** Data curation. **Thomas K. Pauley:** Conceptualization, Methodology, Resources, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119847>.

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