



RESEARCH ARTICLE

# Multiple environmental gradients influence the distribution and abundance of a key forest-health indicator species in the Southern Appalachian Mountains, USA

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## Abstract

**Context** The effects of global climate change are threatening biodiversity, with particular concern for amphibians, whose survival often depends on specific abiotic conditions. To predict how future climate change will affect amphibian populations, it is first necessary to understand how patterns of abundance are shaped by multiple environmental conditions at both local and regional scales.

**Objectives** Plethodontid salamander are a group of lungless ectotherms that require cool and moist habitats to survive. While the broad elevational distribution and abundance patterns are well-understood, other important abiotic gradients exist within montane systems that are contributing to fine-scale spatial abundance patterns. We aim to assess the fine-scale spatial abundance of a plethodontid salamander across two key environmental gradients: temperature and moisture.

**Methods** We conducted area-constrained repeated point-count surveys at plots situated across

temperature and moisture gradients in western North Carolina. Each plot was surveyed on 4 occasions, and site and survey-level covariates were measured.

**Results** We found heterogeneous abundance patterns across these two gradients whereby warmer low elevations contain the greatest abundance near stream sides, where conditions are cooler and wetter than the regional landscape. At cooler, higher elevations, salamanders are distributed more uniformly across the broader landscape, likely as a result of the suitable regional climate.

**Conclusions** Fine-scale habitat associations of plethodontids are driven by temperature and moisture, and the spatial patterns of suitable microhabitats drive regional scale patterns. Incorporating multiple environmental gradients provides a more biologically relevant prediction of abundance patterns, which will help inform conservation and management strategies especially in the context of climate change.

**Keywords** Salamander · Plethodon · Bayesian binomial mixture modelling · Climate change · Environmental gradients · Montane · Abundance

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## Introduction

Understanding the distribution and abundance of organisms across the landscape is paramount not only

for attaining greater knowledge of the basic ecology of a species, but also for gaining insight into species' potential for persistence in the face of environmental change (Brown 1984). However, the scale at which we assess these relationships is a critical consideration because patterns can emerge at local scales that may be undetectable at landscape scales, while only assessing local scale relationships may neglect the broader ultimate factors influencing patterns (Miguel et al. 2016; Suárez-Castro et al. 2018). Local-scales typically represent the abiotic conditions individuals are directly experiencing, but the surrounding habitat matrix may have steep abiotic gradients that differentially influence adjacent local patches (Steen et al. 2012; Suárez-Castro et al. 2018). The hierarchical nature of different scales influencing and constraining each other is key, and integrating both landscape and local scale conditions is needed to better ascertain the drivers of spatial distribution and abundance.

The scale by which species' spatial patterns emerge is a key concern when predicting responses to climate change and developing effective conservation strategies. With climate change, temperatures are expected to rise and there will be greater spatial and temporal climate and habitat heterogeneity (Nadeau et al. 2017a, b). Thus, knowing how species relate to local abiotic features, as well as how the broader landscape gradients influence local-scale microhabitats is necessary (Lenoir et al. 2017). Often, studies use broad, macroclimate covariates to predict species vulnerability to climate change (e.g., Randin et al. 2009; Warren and Chick 2013). However, landscape-scale data overlook microhabitats embedded within a landscape, which often experience decoupled abiotic conditions from the regional conditions, and are more strongly driving spatial patterns (Nadeau et al. 2017a, b; Scheffers et al. 2014a, b). Montane systems have particularly complex topographic and climatic variation which drives a wide range of microclimatic conditions across the landscape (Ashcroft et al. 2009). As such, landscape level assessments of species distribution and abundance are often broad, spatially inaccurate generalizations of fine-scale spatial patterns (Nadeau et al. 2017b; Chase et al. 2018). To provide more biologically relevant predictions of species persistence in the face of change, we must first assess abundance relationships with local-scale environmental conditions to understand the drivers of regional scale spatial patterns (Lenoir et al. 2017).

Amphibians are an ideal taxa to consider the effect of scale and climate change because of their ubiquity across landscapes and strict abiotic requirements for survival (Blaustein et al. 2010). Because of their physiological limitations and subsequent sensitivity, amphibians have experienced unprecedented declines in the wake of climate change as a result of these requirements (Blaustein et al. 2010; Grant and al. 2016). Recent evidence suggests that amphibians have responded to climate change through shifting ranges, changes in physiology such as metabolic depressions and slowed growth, and overall reduced fitness (Bernardo and Spotila 2006; Catenazzi 2016; Muñoz et al. 2016). It is likely that amphibian's vulnerability to climate change will be exacerbated from the increased spatial and temporal habitat heterogeneity which limits physiologically suitable habitat (Milanovich et al. 2010; Nadeau et al. 2017a, b). However, many climate change impact assessments of amphibians use coarse climatic data, which may misrepresent risks relative to more local-scale assessments (Nadeau et al. 2017a, b). The fine-scale habitat associations of many amphibians, and how broader environmental gradients influence microhabitat associations are not well understood (but see Peterman and Semlitsch 2013a, b). Such lack of knowledge significantly limits our capacity to predict the effects of future climate change on species.

Terrestrial plethodontid salamanders are a group of amphibians that may be particularly sensitive to change due to their lungless anatomy and highly specialized physiological requirements (Dodd and Dorazio 2004a, b). Plethodontid distribution and abundance is strongly driven by their associations with cool and moist habitats to facilitate cutaneous respiration (Spotila 1972; Peterman and Semlitsch 2013a, b). These salamanders are widely distributed throughout the Southern Appalachian mountains, and the broad elevational distributions are generally well-documented (Dodd and Dorazio 2004a, b; Kozak and Wiens 2010; Peterman et al. 2016). However, broad scale patterns typically do not represent environmental conditions salamanders directly experience (Clark et al. 2011). Thus, examining the micro-habitat associations with local-scale environmental gradients is of utmost importance. Elevation is typically used as a proxy for temperature and precipitation, whereby low elevations exhibit warmer and drier conditions than higher elevations, which are cooler and wetter

(Barry 2008). Therefore, salamanders inhabiting low elevations may experience a more challenging climate than their high elevation conspecifics. However, there are multiple other abiotic gradients in montane systems that are likely influencing spatial patterns of salamander distribution and abundance. For example, stream sides provide a microrefugia with cool temperatures and moist conditions amenable to plethodontid habitat requirements (Petraska and Smith 2005). Salamanders inhabiting harsher regional climates such as lower elevations may be using microhabitats shaped by multiple abiotic gradients to persist in these suboptimal regions (Feder and Londos 1984; Crawford and Semlitsch 2008).

Terrestrial salamanders play a key role in ecosystem functioning and serve as forest health indicators due to their high densities, long life-span, low fecundity, and high sensitivity to disturbance (Hirston 1983; Welsh and Droege 2001). As such, it is important to garner a better understanding of their physiological constraints and habitat relationships across relevant abiotic gradients to develop effective management strategies. Herein, we assess how two abiotic gradients, temperature and moisture, across a montane landscape drives the variation in distribution and abundance of terrestrial plethodontid salamanders. We specifically focus on the red-legged salamander, *Plethodon shermani*. We hypothesized that salamanders at low elevation will be more abundant closer to streams, due to the cool and moist microhabitat provided by streams, relative to the regional climate. Conversely, salamanders at higher elevations will be less restricted to streams due to the cooler and wetter regional climate at higher elevations. By assessing fine-scale spatial patterns of *P. shermani* across these two dimensions of environmental variation, our ultimate goal is to refine our understanding of the local processes shaping landscape-scale patterns.

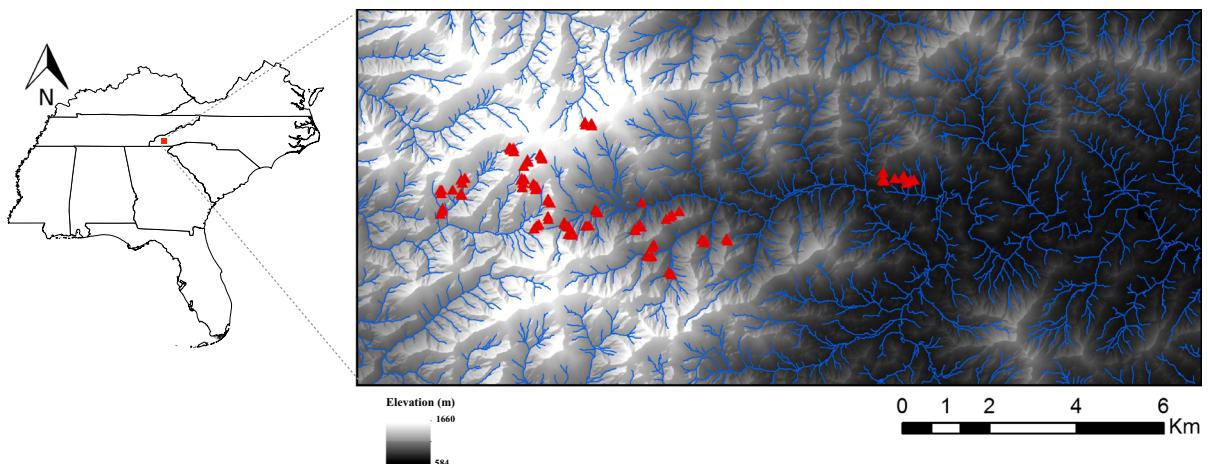
## Methods

### Field methods

Our study was conducted in the vicinity of Wayah Bald (35.158N, –83.574W) in the Nantahala National Forest in western North Carolina (Fig. 1). Forest composition consisted primarily of upland oak-hickory, cove hardwood, and northern hardwood

forest. Forest stand age ranged from 15 to 165 years, with an average age of  $78 \pm 49$  years. Eighty-seven locations were generated in ArcGIS v.10.2 in a stratified random design to incorporate the full range of available elevation and stream distances. Elevation ranged from 700 to 1600 m and distance from stream, ranging from < 5 m to ~ 300 m was used as a proxy for moisture. We incorporated elevation and stream distance to independently assess temperature and moisture. Each of the 87 plots were at least 30-m from each other to insure independence of plots (Connette and Semlitsch 2013). Once each plot location was determined in the field, a second, paired plot was established 10 m in a random direction from the original plot, to maximize survey areas due to other logistical constraints, resulting a total of 174 survey plots. Before establishing each plot, we ground-truthed the presence of streams to ensure our GIS-derived hydrological surfaces were accurate. Each plot was 3 m × 3 m in size.

Southern Appalachian plethodontid activity is restricted to the summer months when climactic conditions are optimal (Hirston 1949). As such, plots were surveyed on four separate occasions between 4 June and 2 August 2017, during peak activity time between 2130 and 0230 EST. Two observers walked through the center of each plot looking for surface active salamanders. Surveys took approximately 3–5 min and, in addition to recording the number of observed salamanders, the following environmental covariates were recorded: surface soil temperature using an infrared thermometer (Raytek MT4), soil temperature at 10 cm below the surface using a digital pocket thermometer (Thermoworks RT600), and air temperature and relative humidity using a Ketsrel 5200. We also deployed 23 environmental data loggers (HOBO U23-003 Pro v2 [n = 8] and Thermochron DS1920 iButton [n = 14]) at 23 of the survey plots ensuring that the wide range of elevation and moisture (stream distances) gradients were captured. The environmental loggers were placed ~ 12 inches from the forest floor to collect near-ground measurements realistic to those experienced by the salamanders (Riddell and Sears 2015), and continually monitored temperature and relative humidity at 30-minute intervals for the duration of the study period.



**Fig. 1** Locations of salamander survey plots (red triangles) on Wayah Mountain in the Nantahala National Forest, North Carolina, USA. Blue lines indicate streams. (Color figure online)

### Site and landscape covariates

Site-level covariates including percent canopy cover, percent ground cover, and leaf litter depth (cm) were assessed prior to nocturnal surveys to avoid effects of potential site disruption from surveys. Canopy cover and percent ground cover were collected using the iPhone app Caneopo (Patrignani and Ochsner 2015), which estimates fractional green canopy cover from a photograph taken at the center of each plot. Leaf litter depth was determined by the average of three haphazard measurements taken within each plot. Site topographic variables including elevation, slope, aspect, and topographic position index (TPI) were obtained from a  $9\text{ m}^2$ —resolution digital elevation model obtained from EarthExplorer ASTER Global DEM ([earthexplorer.usgs.gov](http://earthexplorer.usgs.gov)). TPI was calculated as the slope position relative to the surrounding 90 m, with negative values indicating ravines and positive values indicating ridges. Aspect was transformed from degrees (1–360) to two linear measures, indicating eastness and northness by taking the sine and cosine of aspect, respectively. Streams were delineated by generating a flow accumulation layer using a 450-pixel cell threshold from the  $9\text{ m}^2$  resolution DEM resulting in a 0.405 hectare drainage area. The 450-pixel cell threshold was selected as the best representation of actual stream networks based on visual inspection of the map, comparison with other maps, and ground-truthing. Stream distance was then assessed using the Euclidean distance tool in ArcGIS

v.10.2. Although not a direct part of the sampling design, we also included forest stand age as a landscape covariate using a 2018 compartment map provided by the US Forest Service.

### Temporal covariates

Because salamander detection can be highly dependent on weather conditions (Peterman and Semlitsch 2013a; Connette et al. 2015), we obtained a series of hourly temperature and precipitation data from the Wayah Bald Mountain WINE weather station using the North Carolina Climate Retrieval and Observation Network of the Southeast Database (CRONOS). The Wayah Bald Mountain WINE weather station is the closest continual weather station to our sites, with all sites at least 3 km from the top of the mountain and is the closest approximation of precipitation across our sites. We used moving window analyses to assess the total precipitation in the 24-h preceding a survey (hereafter 24-h precipitation), total precipitation in the 3 days preceding surveys (hereafter 3-day precipitation), the total number of days since rain (hereafter dry days), and average temperature over the preceding 24 h (hereafter 24-h temperature). The Julian date of each survey was also included as a detection covariate.

### Statistical analyses

To assess the repeated count observations, and to account for site-level covariates and imperfect

detection, we implemented a binomial mixture model analyzed in a Bayesian framework (Royle 2004). We included the following parameters as abundance predictors: elevation, elevation<sup>2</sup>, eastness, northness, TPI, forest stand age, canopy cover, leaf litter depth, stream distance, and the interaction of elevation and stream distance. The following parameters were included as predictors of detection probability: ground cover, 24-h precipitation, 3-day precipitation, dry days, 24-h temperature, relative humidity, surface soil temperature, belowground soil temperature, and Julian date. Plots were considered independent, but we included a random effect to account for the spatial autocorrelation between sampling plots in the abundance model. The detection model included a random effect to account for the survey night. Uninformative, normally distributed priors with a mean of zero and a precision of 0.1 were assigned to each parameter. We included all of the aforementioned parameters in a global model, and subsequently removed covariates that had < 75% of their posterior distribution having the same sign as the mean estimate (overlap zero) to create the final, reduced model (see Online Resource 1). Posterior summaries were based on 372,500 Markov Chain Monte Carlo iterations, thinned at a rate of 5 following an adaption phase of 210,000 and a burn-in of 150,000 iterations. Models were assessed, and convergence was confirmed using Gelman-Rubin statistic ( $Rhat < 1.1$ ), a calculated Bayesian  $p$  value (bpv) using the Freeman-Tukey statistic, and visual assessment of MCMC chain mixing. Analyses were conducted using the JagsUI packages in R version 3.4.1 (Plummer 2003; R Core Team 2013; Kellner 2017). Fully annotated model code is available in Online Resource 3.

We quantified the relationship of temperature and humidity across elevation and moisture gradients in our study using mixed effects models in a Bayesian framework using the brms package (Bürkner 2017). The iButton and HOBO logger data were combined, and data from 2100 to 0300 EST each night were averaged for each logger. We fit two models, one with temperature and the other with humidity as response variables. Both models used elevation, stream distance, and the interaction of elevation and stream distance as fixed effects, with the environmental logger ID number as a random effect. Both models used a Gaussian distribution with uninformative, flat priors (brms default), run for 2000 iterations after a

burn-in phase of 1000, thinned at a rate of 1. We assessed model fit based on visual inspection of MCMC chain mixing and the Gelman-Rubin statistic ( $Rhat < 1.1$ ).

After fitting the hierarchical abundance model, we projected abundance across the landscape using 500 random posterior samples generated from the reduced Jags model using R version 3.4.1 (R Core Team 2013). We only included spatial layers generated from ArcGIS v.10.2 from which abundance estimates could be spatially extrapolated, including elevation, elevation<sup>2</sup>, stream distance, northness, TPI, and the interaction of elevation and stream distance. All other covariates (leaf litter, canopy cover) were predicted at their mean value. Annotated code of the spatial projection process is available in Online Resource 4. We then generated eighteen elevation rasters each comprising of a 50-m elevation interval ranging from < 600 to > 1450 m (Table 1). We generated a multi-ring buffer with twenty-five, 10-m intervals, ranging from 10 to 250 m, extending away from streams. These buffers were intersected with each elevation raster to determine the stream distance that encompassed both 50% and 95% of the total salamander abundance across the study site (as determined from the spatial projection) at each respective 50-m elevation range.

## Results

We observed a total of 713 *P. shermani* across the four survey periods. Both the global and reduced binomial mixture models fit the data (global bpv = 0.72, reduced bpv = 0.72). All results are reported for the reduced model. The average detection rate of an individual salamander was 0.059 (SD = 0.025), while the total abundance across all sites (total area = 1566 m<sup>2</sup>) is estimated to be 6244.34 (SD = 5571.98). After correcting for imperfect detection, salamander abundance was positively associated with canopy cover and leaf litter depth, and negatively associated with northness (Table 2, Fig. 2). Abundance also showed a quadratic relationship with elevation, peaking at ~ 1350 m (Fig. 2). Further, there was a significant interactive effect between stream distance and elevation on salamander abundance (Fig. 3). Detection was negatively associated with surface soil temperature and positively related

**Table 1** The total area and salamander abundance at each elevation interval across our study area at Wayah Mountain, NC

Elevation interval (m)	Total area (hectares)	Total abundance (millions)	Abundance/m <sup>2</sup>
< 600	78.08	3.55	3.54
600–650	235.02	9.99	3.62
650–700	166.72	8.13	3.87
700–750	138.28	7.42	4.36
750–800	117.00	6.79	4.81
800–850	102.68	6.41	5.24
850–900	110.12	7.42	5.74
900–950	102.20	7.22	6.07
950–1000	88.84	6.64	6.47
1050–1100	81.44	6.45	6.93
1100–1150	73.76	6.16	7.36
1150–1200	81.48	7.14	7.76
1200–1250	94.09	8.52	8.06
1250–1300	100.21	9.28	8.26
1300–1350	95.18	9.00	8.46
1350–1400	81.58	7.49	8.62
1400–1450	59.95	5.86	8.78
> 1450	87.99	8.86	9.06

These values were used to determine the distance from a stream for which 50% and 95% of the total salamander abundance exists (Fig. 7)

**Table 2** Parameter estimates for the reduced detection and abundance hierarchical n-mixture model

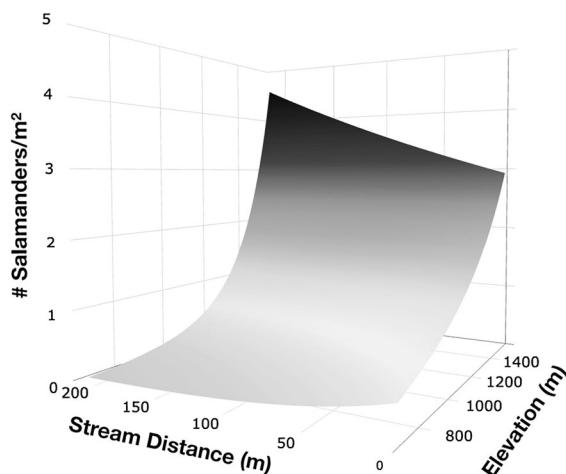
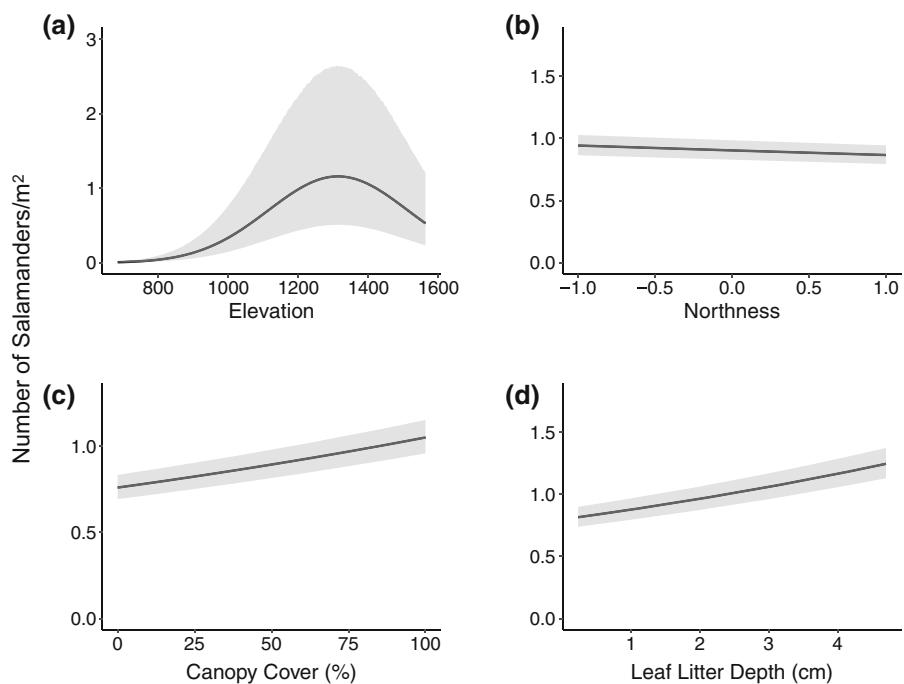
Model	Parameter	Beta	Lower CI	Upper CI	f	n effective
Detection	Intercept	− 2.949	− 4.449	− 2.123	1.00	1173
	Ground cover	0.042	− 0.068	0.151	0.78	31,794
	3-day precipitation	0.082	− 0.045	0.206	0.90	36,691
	24-h temperature	0.098	− 0.043	0.236	0.92	50,048
	Relative humidity	0.082	− 0.010	0.174	0.96	44,372
	Surface soil temperature	− 0.157	− 0.338	0.021	0.96	20,129
	Belowground soil temperature	0.089	− 0.034	0.214	0.92	52,766
Abundance	Intercept	2.098	− 2.808	4.403	0.90	1182
	Elevation	0.849	− 0.164	1.545	0.96	5768
	Elevation2	− 0.733	− 1.372	0.369	0.93	3522
	Northness	− 0.031	− 0.118	0.055	0.58	16,870
	Canopy cover	0.070	− 0.023	0.162	0.93	43,641
	Leaf litter depth	0.068	− 0.032	0.164	0.91	172,474
	Stream distance	− 0.321	− 0.561	− 0.029	0.98	26,000
	Elevation × stream distance	0.294	− 0.123	0.590	0.93	46,257

N effective refers to the effective sample size from posterior samples (total = 178,000) and f refers to the proportion of the posterior with the same sign as the mean

with belowground soil temperature, ground cover, relative humidity, 24-hour temperature and 3-day precipitation (Table 2, Fig. 4).

The mixed effect models of temperature and humidity showed adequate convergence (all Rhat = 1.00). Temperature was inversely related to elevation ( $\beta = -0.96$ , CRI =  $-1.32, -0.59$ ), and positively

**Fig. 2** Marginal effect plots ( $\pm$  CI) showing the relationship between salamander abundance and **a** elevation, **b** northness, **c** percent canopy cover, **d** leaf litter depth



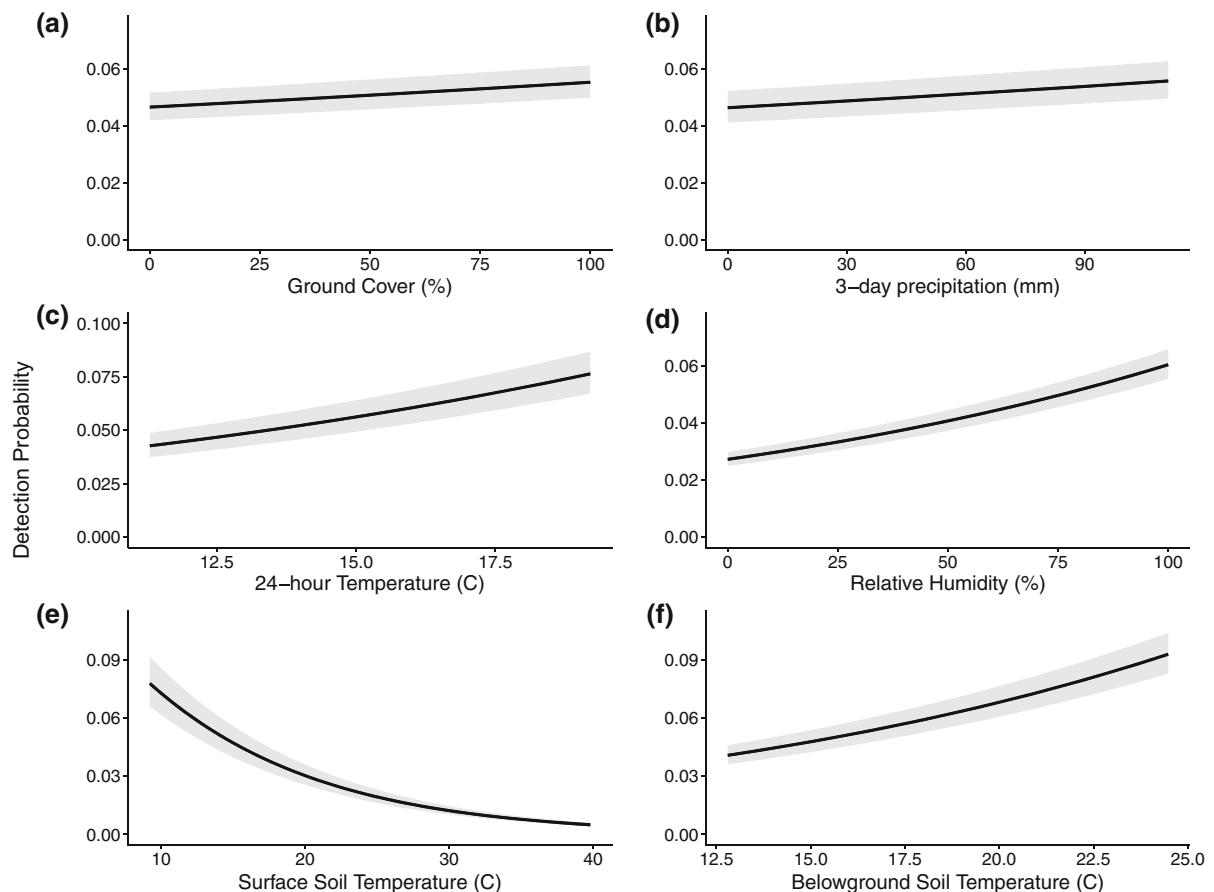
**Fig. 3** Interaction plot showing the relationship between elevation (m), stream distance (m), and abundance

associated with stream distance ( $\beta = 0.27$ , CRI =  $-0.13$ ,  $0.65$ ) (Fig. 5). There was no relationship between temperature and the interaction of stream distance and elevation ( $\beta = 0.001$ , CRI =  $-0.38$ ,  $0.35$ ). Relative humidity showed a significant negative relationship with stream distance ( $\beta = -3.60$ , CRI =  $-7.84$ ,  $0.55$ ) (Fig. 5) and non-significant negative relationship with elevation ( $\beta = -1.34$ , CRI =  $-5.18$ ,  $2.58$ ). We also found that salamander

abundance varied across the landscape in relation to elevation and stream distance (Fig. 6). At the lowest elevations (< 650 m), 50% of the total abundance is predicted to be within 35 m of streams, and 95% of the abundance is predicted to be within 120 m from streams (Fig. 7). Higher elevations (> 1100 m) reach 50% of the total salamander abundance at > 80 m from a stream and 95% of the total abundance > 220 m away from streams (Fig. 7).

## Discussion

The prevailing threat of climate change endangers the persistence and survival of many species, most especially those dependent on specific abiotic conditions. Understanding the relationship between abundance and environmental gradients at the finest possible scale is a critical first step in understanding the potential species responses to such change. By incorporating both fine-scale habitat associations as well as broader landscape-scale gradients, we provide a better understanding of spatial abundance patterns of terrestrial salamanders, and our results provide strong evidence showing variable distribution and abundance patterns across elevation and moisture gradients.

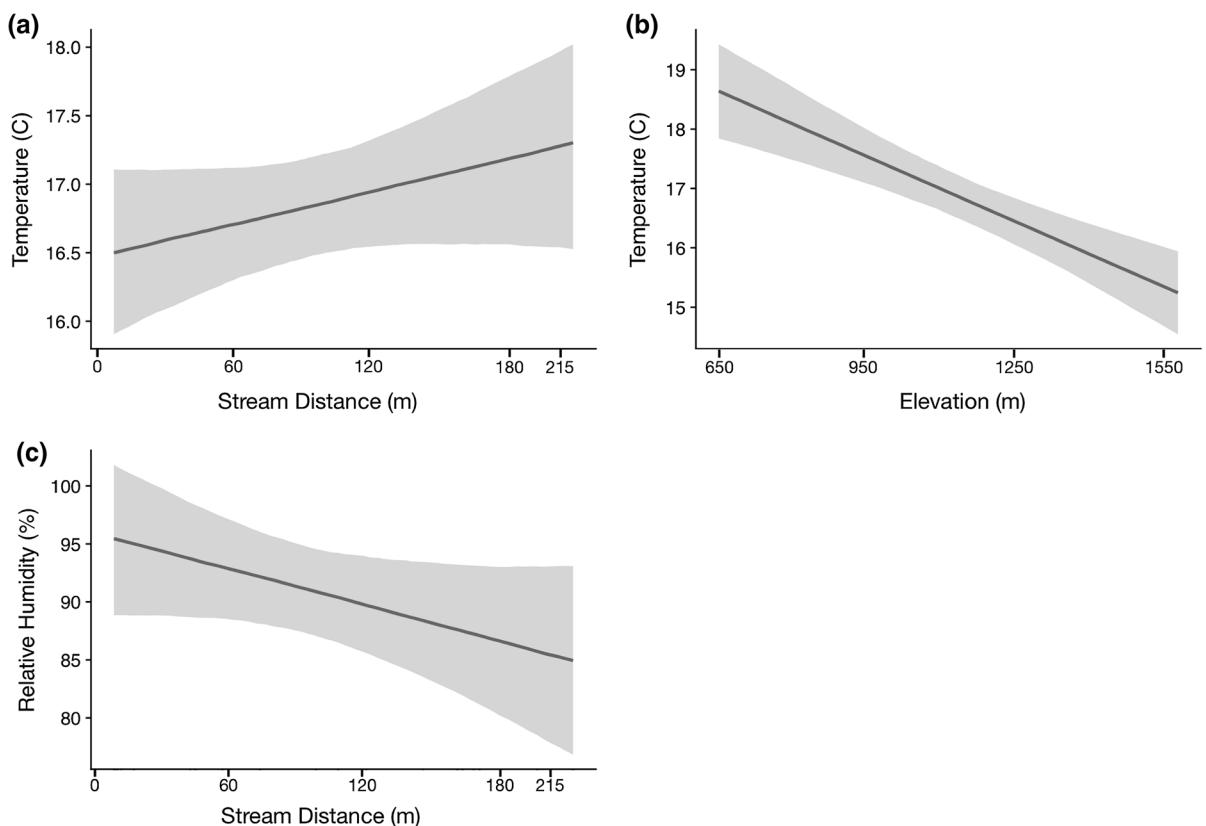


**Fig. 4** Marginal effect ( $\pm$  CI) of the relationship between detection probability and **a** percent ground cover, **b** 3-day precipitation, **c** 24-h temperature, **d** relative humidity, **e** surface soil temperature, and **f** belowground soil temperature

Plethodontid salamanders are generally known to be associated with cool and moist regions (Feder 1983; Grover 2000; Peterman and Semlitsch 2013a, b). Our study demonstrates that these patterns are consistent in montane habitats, as well as showing predictable and repeatable patterns across various environmental gradients, emphasizing the importance of assessing multiple abiotic gradients relevant to the organism. Our results highlight the interaction between stream distance and elevation as a strong driver of the spatial patterns of *P. shermani*, particularly at low elevations where 50% of abundance is contained within 35 m of a stream (Fig. 7). Higher elevations appear to support higher salamander abundance at greater distances from streams with a more uniform distribution, likely as a result of more optimal temperature and moisture conditions across the broader landscape. Our fitted models indicate that areas farthest from streams at

high elevations support the highest abundance of salamanders (Fig. 3). However, this result is likely due to model extrapolation. It should be noted that the uncertainty in estimated abundance was greatest at high elevation in areas far from streams (Fig. 6b).

Temperatures along streams are consistently decoupled from the regional climate and have historically experienced more stable temperature relative to other parts on the landscape (Fridley 2009; Scheffers et al. 2014b; Lesser and Fridley 2016; Caruso and Rissler 2018). Our results suggest that temperature increases and relative humidity decreases as the distance from a stream-side increases (Fig. 5). Thus, regions close to streams at low elevation likely provide valuable microhabitat for salamanders, which experience hotter and drier conditions than salamanders at higher elevations (Barry 2008). Our results showed a weak inverse relationship between relative humidity



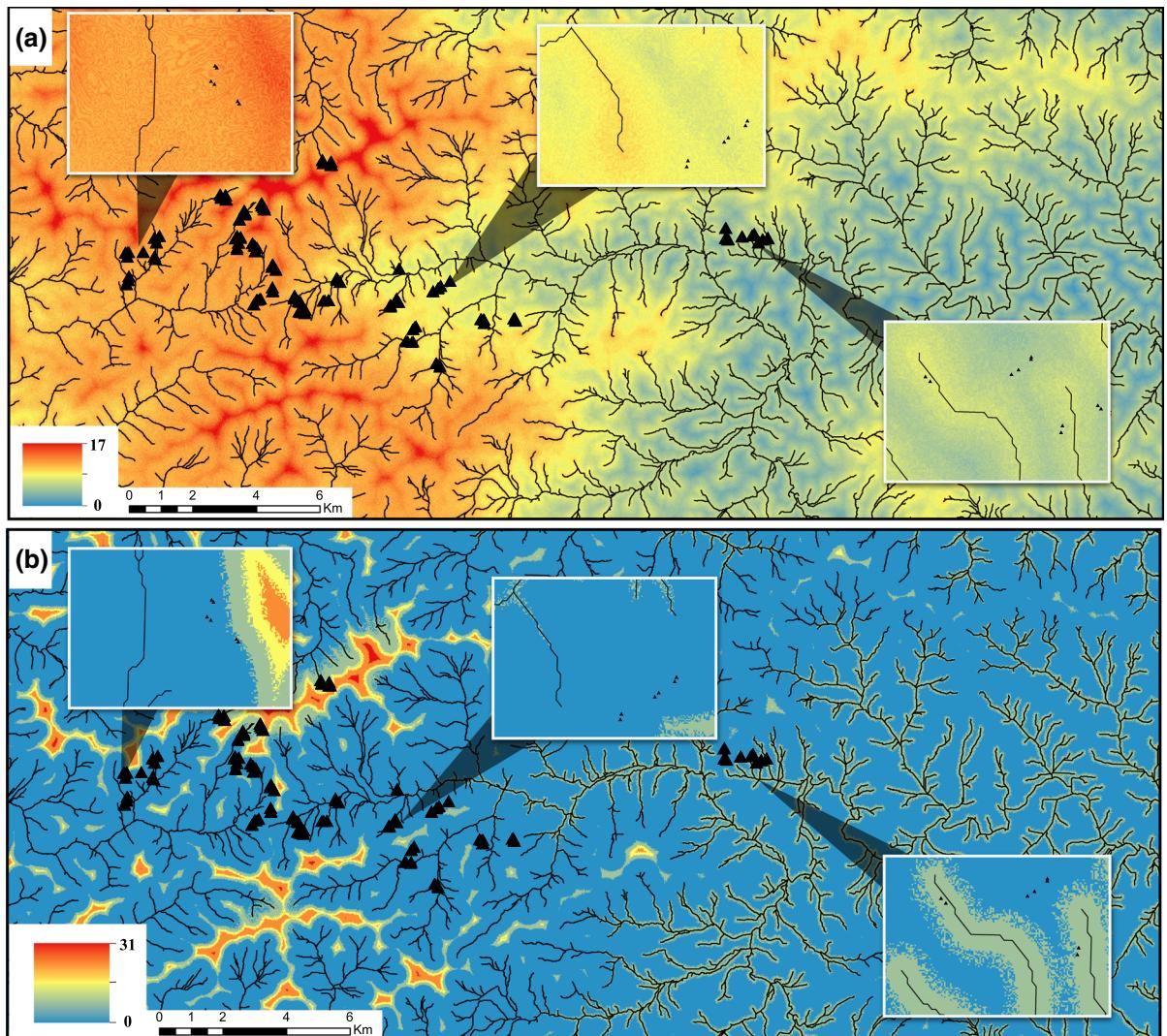
**Fig. 5** Marginal effects plots ( $\pm$  CI) of the mixed effect model showing the predicted relationship between temperature and **a** stream distance and **b** elevation, as well as between relative humidity and **c** stream distance

and elevation. Other studies of the Southern Appalachian region, as well as other mountainous regions, have failed to identify a consistent pattern between humidity and elevation, likely as a result of the uniformly high humidity across the region (Busing et al. 2005; Duane et al. 2008; Fridley 2009). Further, montane regions often exhibit winds that cause an upslope moisture transport during the day, and down-slope moisture transport at night (Barry 2008; Duane et al. 2008). We used temperature and humidity data from only a short nocturnal window, which may be capturing such patterns. Overall, we show that at a fine spatial scale, salamander abundance is linked to cool and moist microhabitats, but these microhabitats vary across a landscape given the abiotic gradients present.

We found salamander abundance to be highest in areas with greater canopy coverage and deeper leaf litter which are factors that influence soil moisture, temperature, and foraging opportunities, subsequently leading to suitable salamander habitat (Crawford and

Semlitsch 2008; Suggitt et al. 2011). *Plethodon shermani* were also marginally more abundant on south-facing slopes, a trend consistent with other observations (Connette and Semlitsch 2013). Previously, forest stand age was identified as an important covariate affecting salamander abundance (Dupuis et al. 1995; Connette and Semlitsch 2013). For example, Connette and Semlitsch (2013) found greater salamander abundance in older forests, and peak abundance was not reached until 100 years post-timber harvest. Although we included forest stand age in our global model, it was ultimately removed as it did not have a strong effect on abundance (see Online Resource 1). Our sampling design was focused on capturing elevation and moisture gradients without specific attention to stand age, potentially leading to the small effect of stand age on abundance in our model (see Online Resource 2).

Terrestrial salamanders vertically migrate between belowground refugia and the surface depending on the

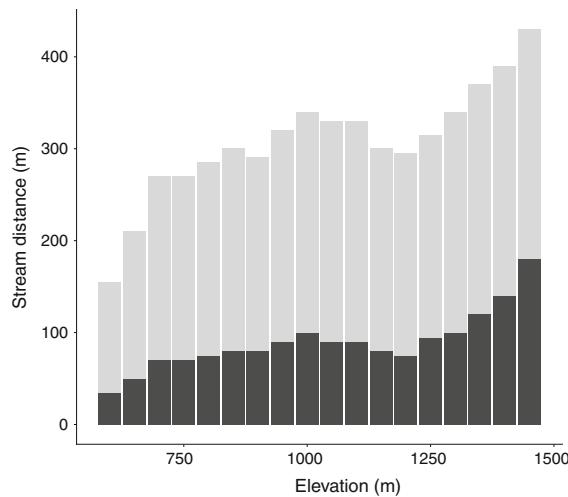


**Fig. 6** **a** Spatial estimate of mean salamander abundance across the Wayah Mountain region of the Nantahala National Forest  
**b** Standard deviation of the mean salamander abundance.

Greater abundance is indicated with warmer colors. Inset maps are at a 120 m scale

available climate conditions during their active summer season (Spotila 1972; Feder and Londos 1984). Our study adds additional evidence that including survey-level environmental measures increases the precision of abundance estimates by accounting for variable detection probability based on environmental conditions (Dodd and Dorazio 2004a, b; Connette et al. 2015). Additionally, we found that detection increases with increasing ground cover. It is possible this relationship is due to plethodontid salamander's propensity to climb on top of vegetation (McEntire 2016), subsequently becoming more detectable. It is

also possible that increased ground cover has a buffering capacity on temperature and humidity creating more favorable conditions for salamanders (Frey et al. 2016; Davis et al. 2018). Further, we found a positive effect of the total 3-day precipitation on detection probability (Fig. 4). Higher rates of precipitation create conditions more suitable for salamander activity, which provides more foraging opportunities, likely leading to greater detectability (Petraska and Murray 2001; Connette and Semlitsch 2013; Peterman and Semlitsch 2013a).



**Fig. 7** Depiction of the distance away from a stream at which 50% (black) and 95% (grey) of the total abundance of *P. shermani* is reached across an elevational gradient on Wayah Mountain, NC

Physiological constraints of plethodontid salamanders have been shown to be a primary mechanism driving abundance (Peterman and Semlitsch 2014). The requirement of salamanders to cutaneously respire limits the suitable habitat available to individuals, however despite such limitations, our study does not assess salamander physiology, body condition, or fitness in each habitat. As such, areas with greater abundance may not indicate greater habitat quality or relate to individual fitness. However, there are numerous interactions between climate conditions and salamander distribution, abundance, and demography. For example, salamander growth rates have been shown to increase with elevation and precipitation (Connette et al. 2015; Caruso and Rissler 2018), and higher temperatures are linked with higher energy assimilation and survival rates, but only to an optimal temperature, that when surpassed, results in declining rates (Clay and Gifford 2016; Caruso and Rissler 2018). Yet, these patterns were examined across broad elevation gradients, neglecting other abiotic gradients across the landscape. Our results show that incorporating fine-scale temperature and moisture gradients could be an important consideration that may affect local demographic rates of salamanders. For example, although it has been shown that growth rates increase with increasing elevation (Caruso and Rissler 2018), salamanders at low elevations in close proximity to streams may experience similar microclimate

conditions to salamanders at higher elevation, and therefore experience similar growth rates. The interactions of key demographic rates with multiple abiotic gradients across local and landscape spatial scales are an increasingly important consideration to fully understanding the responses and resilience of wildlife to climate change. Going forward, it will be important to assess direct measurements of individual fitness, behavior, and physiology in the environment including reproductive output, physiological stress, and overall survival (Ellis et al. 2012).

Relating abundance to local-scale abiotic factors will be most informative in accurately predicting the potential resilience of plethodontids to climate change (Ashcroft et al. 2009; Seo et al. 2009). For example, Gillingham et al. (2012) modeled habitat suitability for ground beetles in Wales under various warming scenarios at both fine ( $5\text{ m}^2$ ) and coarse ( $1\text{ km}^2$ ) resolution, and found that coarse resolutions underestimated suitable landscape relative to the fine scale assessment. However, the landscape-level gradients that influence microhabitats must also be considered to more completely ascertain drivers of spatial patterns. On a global scale, McCain and Colwell (2011) showed that extirpation risk of over 800 vertebrates increases ten-fold when precipitation gradients are included in models that previously only considered temperature. With species that are restricted to specific abiotic conditions and limited in movement and dispersal such as plethodontid salamanders, the incorporation of multiple relevant gradients, as well as local-scale conditions will provide the most biologically relevant information in assessing vulnerabilities and responses to climate change (Lenoir et al. 2017; Nadeau et al. 2017a, b). Our results show that previous accounts of plethodontid distribution have been overgeneralized, therein highlighting the importance of including numerous relevant abiotic gradients at the finest possible scale when assessing species distribution and abundance, especially in the context of assessing responses to global change.

The results from our study show that salamander abundance increases with elevation (Table 1), a trend consistent with other studies (Dodd and Dorazio 2004a, b). However, we show that abundance varies with stream distances across elevational gradients (Fig. 7). Such results lead to important implications for habitat management. Previous studies have offered habitat management recommendations for amphibians

(Petraska et al. 1994; Demaynadier and Hunter 1995; Semlitsch and Bodie 2003; Crawford and Semlitsch 2007). For example, Semlitsch and Bodie (2003) recommended a 3-tiered model for conserving herpetofaunal biodiversity around wetland and riparian habitat whereby the region immediately adjacent to the wetland/riparian zone is fully protected, the area of core habitat extending beyond the first zone is conserved, and a buffer outside the core habitat to protects the wetland/riparian zone from surrounding land use is implemented (Semlitsch and Bodie 2003). We support the recommendation of conserved buffer regions surrounding riparian habitats. However, our results allow us to add a more dynamic management strategy in montane systems with respect to the incorporation of elevation gradients. For example, in low elevation (< 900 m) regions, 50% of salamander abundance is found within 90 m of a stream, indicating a 90 m conservation buffer is of the utmost importance. At elevations > 900 m, and the majority of salamander abundance is not constrained to riparian regions. Therefore, at higher elevation habitats, immediate riparian conservation may be of less concern for terrestrial plethodontids, and instead managers can focus on promoting spatial habitat heterogeneity across the broader region (Petraska et al. 1994). Managing forests in the Southern Appalachians for terrestrial salamanders, while likely a low priority of forest managers, will provide benefit to the forest ecosystem as a whole and promote the integrity of such systems due to the critical role salamanders play to ecosystem function (Demaynadier and Hunter 1995; Welsh and Droege 2001; Semlitsch et al. 2014a, b). Forest managers should consider the interactions between distance from stream and elevation when making decisions, especially in the context of changing climates.

The conservation of plethodontids is critical, as they contribute to nutrient cycling and storage, leaf-litter decomposition, and ultimately serve as indicators of forest health (Welsh and Droege 2001; Semlitsch et al. 2014). Herein, we showed that across a montane landscape, salamanders are tightly linked to cool and moist regions, leading to heterogeneous yet predictable patterns of abundance across the landscape. Evaluating the patterns of species' distribution and abundance in relation to local-scale habitat and climate variation can reveal critical relationships that may have been missed by assessing only landscape-scale

patterns. We emphasize the importance of evaluating how key environmental gradients interact to create local-scale microhabitats that are critical to understanding spatial variation in abundance patterns. It will be important to consider the dynamics of numerous abiotic gradients when making decisions for conserving biodiversity and ecosystem function in the context of climate change.

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#### Compliance with ethical standards

**Conflict of interest** The authors have no conflicts of interest to declare.

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