Biogeographical factors affecting the distribution of stream salamanders on the Cumberland Plateau, USA

P.R. Gould [a,1], K.K. Cecala [a,*], S.S. Drukker [a], B.A. McKenzie [a], C. Van de Ven [b]

[a] Department of Biology, University of the South, Sewanee, TN 37383, USA
[b] Earth and Environmental Systems Department, The University of the South, Sewanee, TN 37383, USA

HIGHLIGHTS

- Stream amphibians are good stream bioindicators.
- Stream amphibian distributions are typically driven by forest loss.
- Context can change biological responses to alternative human land-uses.
- Complex topography can drive stream characteristics more than forest loss.
- Regional topography drive stream amphibian distributions more than forest loss.

GRAPHICAL ABSTRACT
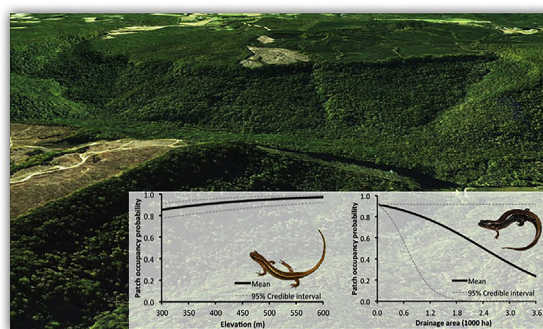
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ABSTRACT

Geophysical and climate conditions play an important role in the distribution of organisms at both fine and broad scales. Headwater streams integrate changes at broad geographical scales and serve as important regions of nutrient processing and support high biodiversity. Stream salamanders are important members of headwater aquatic communities as both predators and prey. Combined with their biphasic life histories and physiological requirements, stream amphibians may serve as indicators for headwater stream conditions. We surveyed 50 streams for salamander occupancy, across eight counties of the southern Cumberland Plateau in Tennessee for which we are unaware of any stream amphibian distribution data. Our objective was to determine what variables best-predicted stream amphibian occupancy among species with variable life histories and habitat needs. Models were generated to determine the effects of elevation, catchment forest cover, and total catchment size as indicators of stream condition. We found species showed no significant responses to forest cover. Though forest cover has previously been the primary predictor of stream amphibian occupancy in streams across the United States, stream amphibian occupancy of the southern Cumberland Plateau was most closely associated with elevation and catchment size. Thus, the unique topography of the southern Cumberland Plateau may instead be the more important factor driving occupancy patterns. Despite limited evidence in this study for negative human impacts on salamander occupancy, low occupancy and abundance relative to other ecoregions suggests either poor quality habitat or large historic impacts. Developing a more comprehensive understanding of regional stream salamander occupancy patterns is necessary to ensure effective management and habitat conservation in a region with limited description of stream ecology.

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* Corresponding author at: 735 University Avenue, University of the South, Sewanee, TN 37383, USA.
  E-mail address: kkcecala@sewanee.edu (K.K. Cecala).
[1] Present address: School of Environment and Natural Resources, The Ohio State University, Columbus, OH 43210.

1. Introduction

Understanding how and why species are distributed across landscapes is important to adequately predict species responses to environmental change (Beaumont et al., 2007; Williams et al., 2012). Biotic factors, including competition and predator-prey interactions, and abiotic factors such as resource availability, temperature, and geochemical traits, combine to determine whether species occupy certain areas (Brown, 1984; Skelly, 2001; Bailey et al., 2004; Munzbergova, 2004). These factors influence species occupancy at both the local and landscape scale, affecting distribution patterns of organisms (Kashian and Barnes, 2000; Minchinton, 2001; Lowe and Bolger, 2002; Knapp et al., 2003; Gould et al., 2012). Evaluating patterns of occupancy is particularly important for freshwater organisms, as freshwater habitats tend to be highly diverse but underrepresented in protected landscapes (Skelton et al., 1995; Knapp and Matthews, 2000; Lowe and Likens, 2005). Furthermore, headwater streams rarely receive protection at the state or federal levels, yet this habitat represents the majority of stream length (Lowe and Likens, 2005; Clean Water Act 33 USC -1258; but see Pressey, 1994).

Stream breeding amphibians are one group restricted to low-order, stream ecosystems, where they are often the top vertebrate predators and exhibit high biomass that contributes to ecosystem functions (Petranka, 1998; Petranka and Murray, 2001; Whiles et al., 2006; Peterman et al., 2008). Recently, documented declines of stream dwelling salamanders appear to be the result of declining forest cover (e.g. Lowe and Bolger, 2002; Willson and Dorcas, 2003; Petranka and Smith, 2005). Forest removal itself may have local impacts, but the effects of forest removal and alternate land uses can propagate downstream and impact ecosystems far from the point of disturbance (Richards et al., 1996; Willson and Dorcas, 2003; Allan, 2004). Forest removal may affect downstream communities via changes in erosion and sedimentation patterns, increases in water temperature, lowered humidity, and changing hydrologic regimes (e.g. Johnson and Jones, 2000; Caissie, 2006; Peckarsky et al., 2014). Each of these proximal changes may be associated with a different mechanism by which stream amphibians decline, and responses to one change may make individuals more susceptible to other stressors (Tilghman et al., 2012).

Stream amphibians repeatedly demonstrate strong, negative responses to ecosystem disturbance and human-caused habitat degradation (Delis et al., 1996; Kloas et al., 1999; Welsh and Droege, 2001; Hayes et al., 2002), though these responses vary among taxa. Species often respond differently depending on their tolerance of high temperatures, sedimentation, and high flows (Price et al., 2006, 2011; Barrett et al., 2010). Tolerance may be determined by their larval periods, larval size, and adult terrestriality (Barr and Babbitt, 2002; Price et al., 2011). For example, studies have found variable intraspecific sensitivity to diminished forest cover relative to their distribution (Welsh and Lind, 2002; Kroll et al., 2008; Barrett et al., 2010; Price et al., 2011). Hypotheses about these differences in sensitivity to forest loss include other secondary stressors such as climate or historic disturbance (Surasinghe and Baldwin, 2015). While this could limit the viability of using stream amphibians as indicators of ecosystem health, it suggests that species distributions are geographically dependent on local context.

Although salamander distributions have been well studied in areas of the southeastern United States (e.g., the Piedmont or Appalachian Mountains), the southern Cumberland Plateau remains an understudied region of the southern highlands, despite being identified as a landscape in need of protection (Jenkins et al., 2015). The southern Cumberland Plateau of Tennessee and Alabama is characterized by a dry, warm and flat plateau top, with cool, humid and deep coves bordering the plateau. Habitat on top of the plateau is characterized by shallow, acidic soils, and oak-hickory forests. Cove habitats are characterized by nutrient-rich soils, and mixed mesophytic forest communities. Sandstone layers on top of the plateau result in flashy and often intermittent streams, shown to negatively affect some macroinvertebrate communities (McGrath et al.,

2004; Grubbs, 2011); whereas limestone in coves results in extensive subterranean flow and a reduction of perennial surface streams (Arnwine et al., 2006; Knoll et al., 2015). This deeply dissected landscape results in a mosaic of streams that begin as shallow sloped, sandy streams that drop into coves (Arnwine et al., 2006). Until streams reach the valley floor, they are often steep with bedrock substrate and waterfalls (Knoll et al., 2015). The cove-plateau dichotomy likely plays a large role in the distribution of stream salamander species in this region yet has not been evaluated.

The southern Cumberland Plateau is predominantly privately owned and was formerly a hotspot for timber harvesting activities (McGrath et al., 2004; Arnwine et al., 2006). The region was recently highlighted as an underprotected landscape underscoring the need to understand biodiversity patterns in the region (Jenkins et al., 2015). Despite current and historic threats to the region little is known about the ecology and distribution of stream amphibians in the area. Understanding to what degree their current distributions are a result of human activities versus characteristics of the physiographic region is made more important by the Cumberland Plateaus' proximity to areas of herpetofaunal conservation interest and a potential climate refuge (Stein et al., 2000; Graham et al., 2010; Barrett et al., 2014). Our objective was to assess predictors of stream amphibian occupancy on the southern Cumberland Plateau to evaluate (1) human impacts on streams, (2) topographical influences on headwater stream communities, and (3) develop a baseline for understanding future change.

2. Materials and methods

2.1. Study community

The southern Cumberland Plateau has a diverse array of amphibians that occupy the region. Of the desmognathan taxa, three species occur in the area that include species associated with a small, high elevation distribution (*Desmognathus abditus*) and species associated with larger distributions (*D. conanti* and *D. monticola*; Anderson and Tilley, 2003; Petranka, 1998). All three species are stream-side salamanders occupying the stream and are rarely found away from stream channels (Petranka, 1998). They also have short larval periods that coincide with resumption of flow in the spring for intermittent streams in the region. In addition, three species from the genus *Eurycea* are found on the southern Cumberland Plateau and have variable ranges and habitat preferences. *Eurycea wilderae* is associated with high elevations in the southern U.S. while *E. longicauda* is found throughout the eastern and central United States, but *E. lucifuga* is most closely associated with karst areas (Petranka, 1998). Larval periods for these species range from only a few months to over a year with adults spending significant time away from stream habitat in either terrestrial or subterranean refugia (Petranka, 1998). *Pseudotriton ruber* and *Gyrinophilus porphyriticus* achieve large adult sizes and have a 2–4 year larval period that restricts successful breeding to permanent streams (Petranka, 1998). Likewise, in the larval stage, both are known to prey upon other larval salamanders, though *G. porphyriticus* is known as a salamander specialist throughout its life (Petranka, 1998). *Pseudotriton ruber* make extensive terrestrial movements that may make them more susceptible to changes in land-use at a large scale, similar to *Eurycea* spp. and are known to use subterranean habitat for nesting (Petranka, 1998). Recent estimates of population density of *D. conanti*, *E. wilderae*, and *P. ruber* suggest that these species occur at lower densities on the Cumberland Plateau than in other ecoregions of the southeastern United States (Kirchberg et al., 2016).

2.2. Study design

We surveyed a total of 50 haphazardly selected streams in a range of upland and cove locations along the southern Cumberland Plateau in Tennessee from May–July 2015 (Fig. 1).
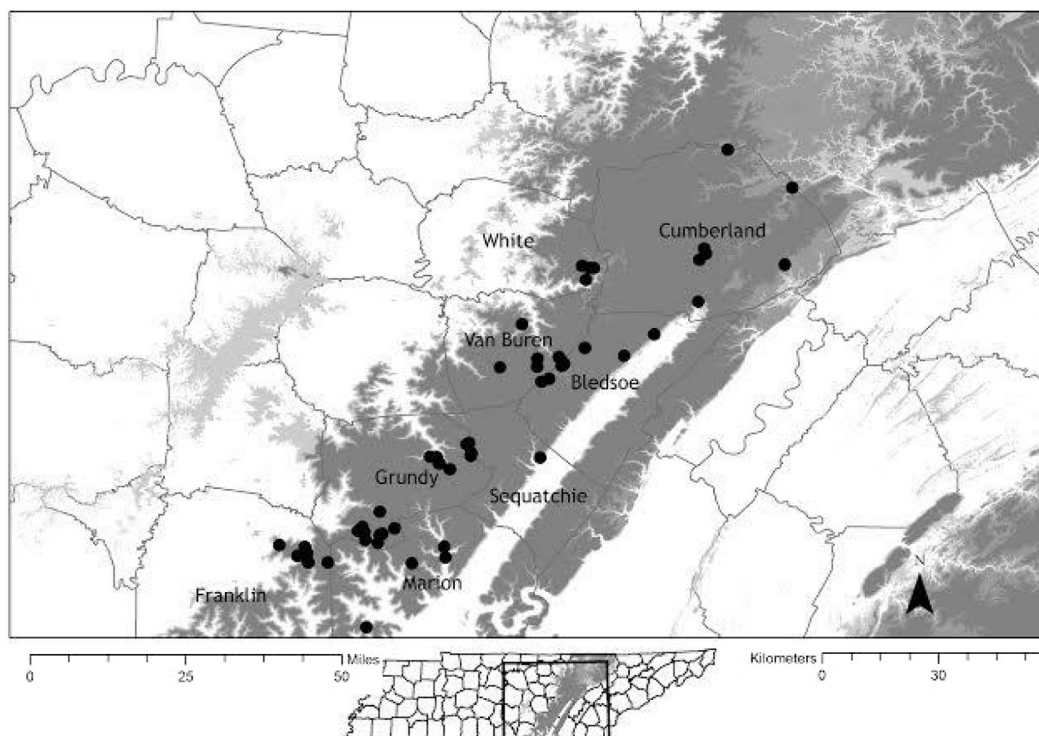
Fig. 1. Elevation of the study area on the southern Cumberland Plateau of Tennessee darker values indicating higher elevation and black dots representing study sites. The lowest elevations (white) are 300 m, and the highest elevations (dark grey) are 580 m above sea level.

We selected sites along a north to south gradient and a forest cover gradient. We prioritized sites for which access could be easily obtained, such as state-owned property. At each site, we established 150 m transects that included 15 five-meter plots located 5 m from one another. We surveyed sites on three consecutive days to account for imperfect detection (MacKenzie et al., 2003). Larval and adult salamander presence or absence were assessed by dip-netting through leaves and silt and by flipping all cover material in the plot and within 1 m of the stream edge. In areas where rock crevices were present, we used a flashlight to visually inspect all crevices. We captured salamanders by hand or net and salamanders were identified to species and life stage, measured for morphological information including snout-vent length (SVL), total length (TL), mass (g), and tail loss, and released at their capture location attempting to minimize downstream transport upon release.

We quantified site variables that represented known influences on stream amphibian success (Table 1). During surveys, we noted the presence or absence of fish and hemlock. We also described the dominant substrate of each transect including sand/mud, pebble, cobble, bedrock, and large rocks/boulders (Wolman, 1967). Analyses of substrate were conducted on ranks of substrate size from 0 to 4 moving from the smallest particles to the largest. On the first day of sampling, we also set HOBO pendant data loggers to record stream temperature every 15 min. We collected data loggers at the end of the third day and evaluated the mean daily temperature range in analyses to describe stream thermal regimes. Though three days of data may not adequately characterize the thermal regime of a site, relative differences between minimum and maximum temperatures should provide an index of forest removal in the riparian corridor (Caissie, 2006; Cecala et al., 2017).

We used additional geospatial data in ArcGIS to characterize the geographical properties of each site. Specifically, we used 10-m digital elevation models (DEM) to estimate aspect, stream slope of transects, and elevation of the downstream end of transects. Using the Watersheds and Flow Direction tools in the Hydrology toolbox (ESRI Spatial Analyst,

Table 1
Mean covariate values across all 50 sites with standard error (SE) and maximum range. Temperature range represents the range between average daily maximum and average daily minimum temperatures.

Covariate	Mean	SE	Range	Observed	Expected	SD	p	Hypothesis	Citation
Substrate	1.54	0.15	4	0.120	−0.020	0.055	0.011	Fine substrates fill interstitial spaces to minimize refugia availability.	Smith and Grossman, 2003
Fish presence	0.28	0.06	1	−0.024	−0.02	0.069	0.958	Fish are salamander predators.	Sepulveda and Lowe, 2009
Slope (%)	3.28	0.55	15	0.120	−0.020	0.056	0.012	Slope drives physical characteristics of streams.	Vannote et al., 1980
Elevation (m)	507	8.1	262	0.041	−0.020	0.057	0.279	Elevation drives local climate.	Knoll et al., 2015
Latitude (decimal degrees)	35.52	0.04	1.1	0.061	−0.020	0.069	<0.001	The Cumberland Plateau becomes more dissected in the south relative to the north.	Knoll et al., 2015
Temperature range (°C)	2.68	0.2	5.56	0.008	−0.020	0.056	0.611	Higher temperature fluctuation may exceed salamander thermal tolerances.	Grant et al., 2016
Forest cover (%)	67.3	3.8	100	0.035	−0.020	0.057	0.330	Lower catchment forest cover causes habitat degradation.	Grant et al., 2016
Catchment size (ha)	571	118	3572	0.131	−0.020	0.054	0.005	Larger catchments have more predators and higher flows.	Vannote et al., 1980
Shreve stream order	31	6.79	218	0.027	−0.020	0.054	0.381	Confluences offer high quality habitat and population connectivity.	Grant et al., 2009

ESRI, 2015) in ArcGIS, we used the DEM to delineate the catchment for each site to calculate catchment area and the Shreve stream order for each location by quantifying the number of upstream confluences. We used 2011 NLCD data (Fry et al., 2011) to assess catchment forest cover including hardwood forest (41), pine forest (42), and mixed forest (43) as forest.

2.3. Analysis

We used single-species, single-season occupancy models to predict patch occupancy probabilities after accounting for imperfect detection and spatial correlations (MacKenzie et al., 2003). Hierarchical models included submodels to describe the observation process (detection) and the ecological process (occupancy) as functions of habitat covariates. We used a Bernouli-Bernouli mixture model with logistic regression to describe each process. Random intercepts were allowed to vary among catchments to allow for spatial autocorrelations (Royle and Dorazio, 2009). We repeated the modeling process described below for all species captured in at least 10% of sites. Life stages were pooled for each species.

Models were implemented using Bayesian inference in WinBUGS (Lunn et al., 2000) using uninformative and diffuse priors following a uniform distribution for random effects and a normal distribution for derived parameters. We used the Gelman and Rubin test implemented in R using the package CODA to evaluate model convergence (Gelman and Rubin, 1992). Models were determined to have converged and have limited autocorrelation with 30 K iterations used as our burn in period and a thinning rate of 15. We discarded the burn in iterations and estimated mean parameter values and 95% credible intervals from 300 K iterations.

To prevent overfitting models (Anderson et al., 1998), we used a Spearman rank correlations implemented in R because of non-normal distributions of predictor variables. Any significantly correlated variables were excluded from co-occurrence in models (Burnham and Anderson, 2002). We also evaluated spatial correlations using Moran's I using R package gstat (Pebesma, 2004; Gräler et al., 2016). For spatially correlated variables, we plotted smoothed point pattern data and evaluated any spatial co-variance visually using R package spatstat (Baddeley et al., 2015). Using information from the correlation matrix, we selected elevation, percent forest cover, and catchment size as the three dominant predictors because they were uncorrelated with one another and correlated with one or more other habitat variables and represent variables that could be extrapolated using spatial models (Table 1). Catchment size was the only variable included in our occupancy models that was spatially dependent (Table 1). In our detection model, we included sampling day to allow for capture-shy behaviors and substrate as a known influence on detection probability (Kroll et al., 2008; Cecala et al., 2013; substrate was also spatially correlated; Table 1). Habitat variables were determined to be biologically significant if at least 75% of the 95% Bayesian credible interval fell above or below zero. Bayesian credible intervals represent 95% of the posterior distribution of estimates of a parameter given the data. We performed posterior predictive checks to evaluate model fit for each species (Gelman, 2003).

3. Results

3.1. Survey data

We found 1011 individuals of six species of stream salamanders including limited detections of *D. abditus* and *G. porphyriticus*. We found four species at >10 sites and only evaluated their distributions (*D. conanti* [32 sites], *E. longicauda* [12 sites], *E. wilderae* [34 sites], and *P. ruber* [21 sites]). At 14% of sites (7 sites) we failed to detect any salamanders. Study sites varied significantly with respect to occupancy predictors. Overall, our study sites were well forested with catchments having on average 67.2 ± 3.8% forest cover (range: 0–100%; Table 1). Elevation at our sites ranged from 323 to 585 m (Table 1). Total catchment area ranged considerably among sites (0.1–3572 ha; Table 1). Several of our site covariates were correlated with one another. Specifically, sampling elevation was correlated with slope and latitude (Table 2). Catchment forest land-cover was correlated with temperature variation, and catchment area was correlated with slope and Shreve stream order (Table 2). Substrate, slope, latitude, and catchment size were all spatially correlated. Though substrate and catchment size were spatially correlated and both included in our models, visual evaluation did not reveal any co-varying patterns (Appendix A).

3.2. Model results

Posterior predictive checks indicated fit of models to *D. conanti* (p = 0.538) and *E. wilderae* (0.677) data but lack of fit for *E. longicauda* (p < 0.001) and *P. ruber* (p = 0.929). Detection rates were similar across all species assessed in this analysis (maximum 95% credible interval for all species, 0.50–0.55). Larger substrates had a small positive influence on detection probability for each species (Table 3). Elevation was positively associated with occupancy by *E. longicauda*, *E. wilderae*, and *P. ruber* though elevation may not have a biologically significant effect on *P. ruber* occupancy (Table 4; Fig. 2). Within catchment forested land-cover had no significant effect on occupancy of any of the species (Table 4, Fig. 3). Catchment size was negatively associated with occupancy of *D. conanti*, *E. longicauda*, and *E. wilderae* (Table 4, Fig. 4). Elevation was the most important predictor for *E. longicauda* and *E. wilderae* with a 100 m increase in elevation associated with a 0.056 ± 0.001 increase in occupancy probability for *E. longicauda* and an increase of 0.058 ± 0.002 for *E. wilderae* (Fig. 2). Catchment forested land-cover was most important for predicting *P. ruber* occupancy with every 10% increase in forest associated with a decline of 0.048 ± 0.002 in occupancy probability (Fig. 3). Finally, catchment size was the most important predictor for *D. conanti* with a 0.017 ± 0.001 decrease in occupancy with every 100 ha increase in catchment size.

4. Discussion

Stream salamanders on the southern Cumberland Plateau occupy the region at lower rates than other southeastern regions (e.g. Price et al., 2011; Surasinghe and Baldwin, 2015; Kirchberg et al., 2016), which may also have resulted in limited sample sizes that contributed to lack of model fit for less common species. Our study failed to find a positive association between salamander occupancy and forest cover,

Table 2
Results of Spearman correlations (ρ) and p-values in parentheses for site covariates. Significance was used to identify covarying predictors and are indicated in bold.

	Slope	Elevation	Latitude	Temperature range	Forest cover	Catchment size	Stream order
Slope	–	−**3.41** (**0.016**)	−0.176 (0.222)	−0.084 (0.561)	0.151 (0.294)	−**0.211** (**0.048**)	−**0.275** (**0.035**)
Elevation		–	−**0.439** (**0.001**)	0.117 (0.416)	0.030 (0.834)	−0.001 (0.996)	−0.041 (0.777)
Latitude			–	−0.194 (0.178)	−0.189 (0.190)	0.040 (0.785)	−0.006 (0.962)
Temperature range				–	**0.216** (**0.013**)	−0.031 (0.830)	−0.078 (0.592)
Forest cover					–	−0.045 (0.755)	−0.147 (0.308)
Catchment size						–	**0.902** (<**0.001**)
Stream order							–

Table 3

Parameter estimates, standard deviation, and 95% credible intervals for the effects of substrate on species detection rates. Overall, species were easier to detect where larger substrates were present. Asterisks represent biologically significant relationships.

	Estimate	Standard deviation	2.5% CI	97.5% CI
Desmognathus conanti	0.027*	0.025	0.0073	0.093
Eurycea longicauda	0.048*	0.041	0.0010	0.151
Eurycea wilderae	0.023*	0.020	6.54E-04	0.076
Pseudotriton ruber	0.018*	0.017	4.80E-04	0.064

which was unexpected given our current understanding that salamanders tend to occupy more forested regions (Welsh and Ollivier, 1998; Lowe and Bolger, 2002; Price et al., 2006; Crawford and Semlitsch, 2008; Peterman and Semlitsch, 2009; Grant et al., 2016). Even closely related species exhibit significant negative responses to forest cover loss in the southern Appalachians and the Piedmont (Price et al., 2011; Barrett et al., 2014). Despite the consistency between two large southeastern ecoregions, salamanders occupying the southern Cumberland Plateau exhibit different patterns suggesting context-specific associations with forest cover.

Several factors may influence salamanders' responses to loss of forest cover, allowing them to persist in catchments with less forested area. One possible driver of this response is the spatial arrangement of current forested areas (Olson et al., 2007). Previous studies demonstrate positive effects of forested riparian zones on stream salamander occupancy (e.g. Jackson et al., 2007; Olson et al., 2007; Peterman et al., 2011; Surasinghe and Baldwin, 2015). Our assessment of forest cover did not assess proximity to stream or riparian forest cover. If the majority of streams in these catchments have sufficient riparian buffers, the negative effects of total catchment deforestation may be reduced (Olson et al., 2007). On the Cumberland Plateau, conversion of forest to exurban areas may also serve to stabilize stream flow regimes (i.e. lower variance; Davis, unpublished data; Grubbs, 2011; Knight et al., 2012). The development of lawns in exurban areas appears to moderate storm flow peaks and maintain higher base flows (Grubbs, 2011). Minimization of floods and increases in stream permanence provides essential habitat for species like *P. ruber* with multi-year aquatic larvae (Petranka, 1998) though a recent study did not find that *P. ruber* density was positively influenced by the presence of small dams that increase stream permanency (Kirchberg et al., 2016). This increase in available larval habitat may partially account for *P. ruber* preferring streams in less forested catchments though lack of fit of *P. ruber* models prevents us from concluding whether they have a negative relationship with forest cover. Low numbers of occupied sites combined with 2 sites with no native forest cover where they were present may have driven this relationship.

Table 4

Parameter estimates, standard deviation, and 95% credible interval for each species. Bayesian p-values assessing model goodness-of-fit are indicated in parentheses for each species. Values further from 0.5 indicate lack of fit.

|	Estimate	Standard deviation	2.5% CI	97.5% CI
Desmognathus conanti (p = 0.538)				
Elevation	−0.30	1.19	−3.09	2.04
Forest	1.18	2.37	−2.95	5.85
Catchment size	−0.99*	1.07	−3.56	−6.24E-06
Eurycea longicauda (p < 0.001)				
Elevation	1.64*	1.04	0.14	4.00
Forest	−0.008	1.645	−3.232	3.219
Catchment size	−0.65*	0.49	−1.88	−0.05
Eurycea wilderae (p = 0.677)				
Elevation	1.79*	0.34	1.25	2.35
Forest	0.002	1.644	−3.226	3.222
Catchment size	−1.15*	0.22	−1.51	−0.81
Pseudotriton ruber (p = 0.929)				
Elevation	3.73E-07*	4.08E-07	−7.40E-08	1.27E-06
Forest	−2.75*	2.27	−7.70	0.83
Catchment size	0.003	2.238	−4.375	4.392
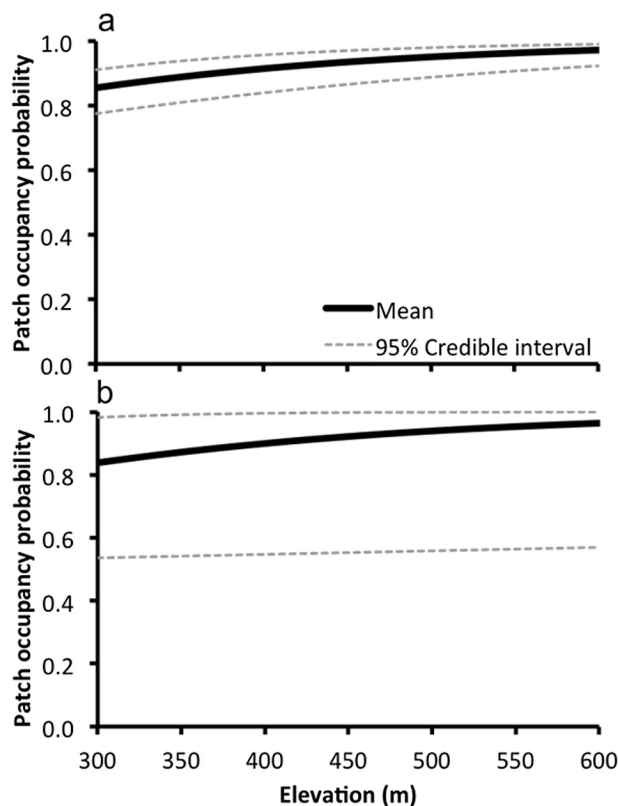
Fig. 2. *Eurycea longicauda* (a) and *E. wilderae* (b) patch occupancy probability (with 95% credible interval) was positively associated with elevation on the southern Cumberland Plateau.

While we assessed percent forest cover, we did not quantify agriculture or exurban land use in study catchments. The degree to which increases or decreases in agricultural land use influences stream salamander occupancy the Cumberland Plateau is unknown, though it has been shown to negatively impact freshwater communities in other areas of the southeastern United States (Harding et al., 1998; Surasinghe and Baldwin, 2014). Proper riparian zone management has been shown to effectively buffer freshwater systems from the negative effects of agricultural land use (Muenz et al., 2006). Future studies should seek to identify the influence agriculture and exurban development has on aquatic salamander communities in this region. Apart from agriculture and exurban land use, commercial forestry is also prevalent across much of the study region. The southern Cumberland Plateau was subjected to intense commercial logging activity from 1981 to 2000, resulting in regional declines in freshwater macroinvertebrate
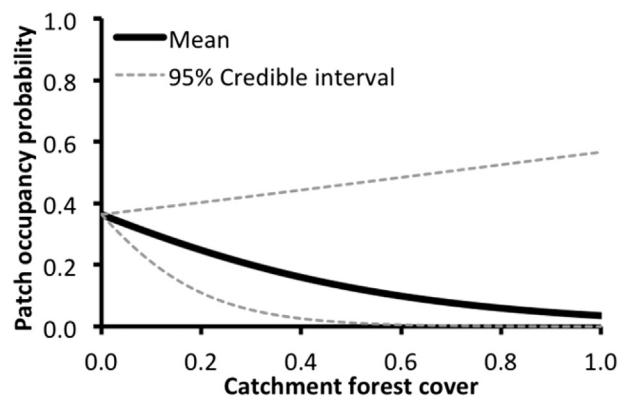

Fig. 3. *Pseudotriton ruber* patch occupancy probability (with 95% credible interval) was not positively associated with increasing forest cover within a stream's catchment.
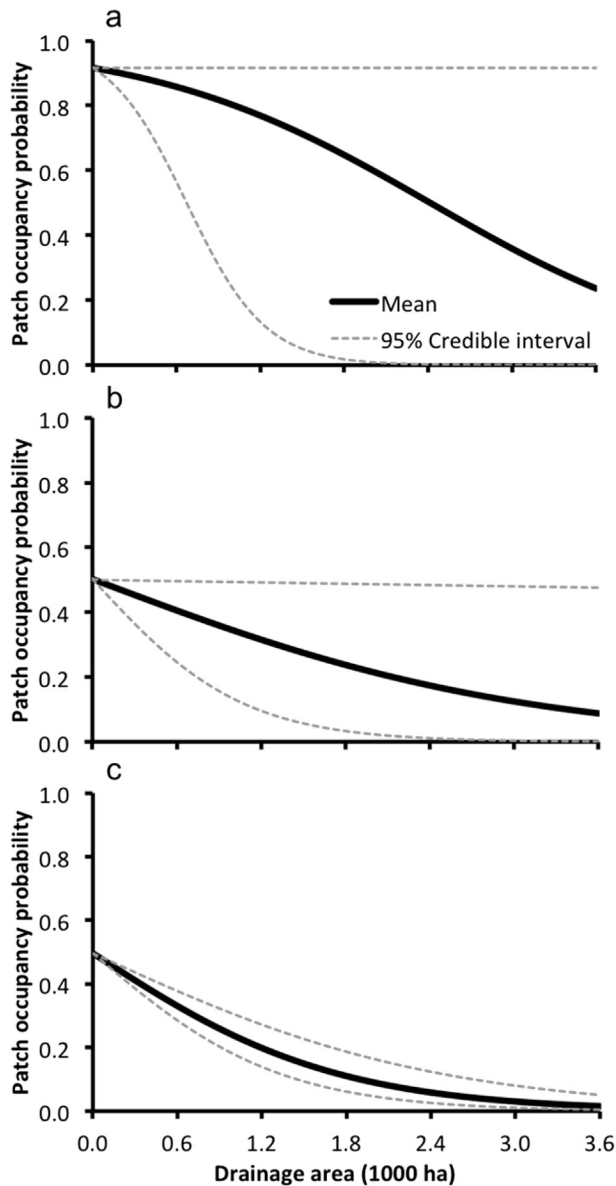
Fig. 4. Patch occupancy probabilities (with 95% credible interval) of *Desmognathus conanti* (a), *Eurycea longicauda* (b), and *E. wilderae* (c) were negatively associated with catchment size.

of slow moving water that lacks large flood pulses (Wolman, 1967). Because larvae of some stream amphibians are displaced downstream at high flow rates, streams with less variable flow regimes may promote the maintenance of larvae in upstream reaches (Barrett et al., 2010; Kirchberg et al., 2016). Similarly, if streams with larger catchment sizes are presumed to have higher annual flow and water permanence (Vannote et al., 1980), we would anticipate positive associations of *P. ruber* with increasing catchment sizes, yet we found no relationship though we again acknowledge that lack of model fit may have resulted in this neutral relationship with catchment size. We suggest that the relationship of *P. ruber* occupancy with catchment size could be non-linear. At the smallest catchment sizes, streams are likely intermittent and unsuitable for long-term larval development by *P. ruber*, but at the larger catchment sizes, streams are more likely to encounter geologic discontinuity that either result in transitions to steep slopes or subsurface flow.

Although small catchment sizes are typically associated with higher elevations, we found no correlation between these habitat covariates on the southern Cumberland Plateau. This relationship may result from large drainages that occur on top of the plateau and are responsible for dissection and erosion of large coves (Arnwine et al., 2006). This region also includes smaller streams that descend into larger coves resulting in small catchments at lower elevations (Knoll et al., 2015). Unlike *Eurycea* spp., we found that *D. conanti* tended to occupy smaller streams at lower elevations in the coves. Despite being unable to assess occupancy drivers of other species such as *D. abditus* or *G. porphyriticus*, we found these species exclusively in cove streams. Elevation was positively correlated with stream temperatures resulting in the warmest streams occurring on top of the plateau. A recent study suggests that *D. abditus* is sensitive to high temperatures and therefore may select cove streams as a mechanism to avoid high temperatures on the top of the plateau (Liles et al., 2017). Other species found on the Cumberland Plateau but not detected in our study include *D. monticola* and *D. welteri* that may also exhibit low tolerances to warm temperatures or their distributions may be overstated for the region (Bernardo et al., 2007). Similarly, cool microclimates in coves may buffer streams in these areas from higher temperatures associated with forest removal on the plateau. More surveys of cove streams appear to be necessary to assess the distributions of desmognathine salamanders on the Cumberland Plateau.

One challenge associated with using models to describe occupancy of stream organisms on the Cumberland Plateau is the non-linear nature of streams in the ecoregion. Physical discontinuities make streams on the Cumberland Plateau a good natural example of the serial discontinuity concept that was developed to explain non-linear changes in rivers associated with confluences, dams, or major changes in channel morphology (Ward and Stanford, 1995; Poole, 2002; Stanford and Ward, 2001). For example, the transition of streams between different underlying geologic layers can cause shifts in hydrology and morphology that are non-linear. Over sandstone, streams have flow regimes characterized by high variance versus downstream areas unique for having surface discontinuities associated with limestone dissolution (Smith et al., 2003). Similarly, stream substrate tends to decrease in size with increasing catchment size (Charlton, 2007), but because of the sharp transition between the plateau and the cove, downstream reaches often have bedrock, colluvium, and steep slopes typical of headwaters at high elevations. In other physiographic provinces, semi-aquatic species with short larval periods (e.g. *Desmognathus* spp.) are often found further upstream in more intermittent streams whereas species with longer larval periods are found further downstream (e.g. *Eurycea* spp., *Pseudotriton* spp.; Hairston, 1987; Bruce, 2007). In the southern Cumberland Plateau region, we observed a reversal of this pattern with *Eurycea* spp. and *P. ruber* occupying streams on top of the plateau and *D. conanti* occupying the same streams at lower elevations in the coves. Overall, it is challenging to assess relationships among habitat predictors (e.g. watershed size, elevation), and species occupancy

communities (McGrath et al., 2004). The degree to which the effects are still observed today is unknown, however, land-use histories must be considered to fully understand current species habitat preferences (Harding et al., 1998; Apodaca and Godwin, 2015). We hypothesize that this may be one reason for low occupancy observed in this study.

Despite forested land-cover being largely unrelated to occupancy patterns of stream amphibians on the southern Cumberland Plateau, we found associations between salamander occupancy and geographical features of elevation and catchment size. Catchment area was positively associated with the presence of fish, substrate, and stream order while being negatively correlated with slope (Table 2). Streams on the Cumberland Plateau develop larger and rockier substrates with larger catchment sizes, suggesting a deviation from patterns described by the river continuum concept (Vannote et al., 1980). In particular, small headwater streams located at high elevations had higher rates of *Eurycea* spp. occupancy where streams were more likely to have sandy and silty substrates. This pattern is consistent with other studies suggesting that *Eurycea* spp. are tolerant of sedimentation (Keitzer and Goforth, 2012). Settlement of fine sediments can also be indicative

when the underlying habitat does not change in predictable or linear ways, though finer-scale variables (e.g. temperature) may be more useful in these scenarios. We suggest that evaluations of climate envelope models could be explanatory of patterns observed on the Cumberland Plateau and recommend this as an area of future study.

Despite consistent patterns in drivers of stream amphibian occupancy from multiple ecoregions (Delis et al., 1996; Kloas et al., 1999; Welsh and Droege, 2001; Hayes et al., 2002), our study highlights the context-specific nature of these relationships. Non-linear stream characteristics, historic land-use, and/or highly variable hydrologic regimes are all common to this region and may to play a role in influencing current stream amphibian distributions. In particular, studies are necessary to determine the degree of similarity between cove and plateau stream communities and to evaluate whether drivers of geographical distributions depend on species preferences for either cove or plateau streams. Because stream amphibians occur at lower densities on the Cumberland Plateau relative to other southeastern ecoregions, determining drivers of stream amphibian occupancy is particularly important for landscape management (Kirchberg et al., 2016). We conclude that preservation of stream salamander communities dominated by *Eurycea* spp. and *Pseudotriton* spp. requires attention to preserving low streamflow variation in streams on top of the Cumberland Plateau. Further research aimed at understanding species responses to land use and management is required to better preserve headwater stream communities on the Cumberland Plateau.
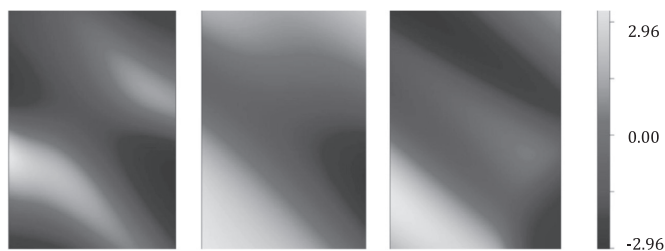
Appendix A. Significant spatial correlations of potential z-scored predictor variables including (a) catchment area, (b) substrate, and (c) slope

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