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Multiple drivers, scales, and interactions influence southern Appalachian stream salamander occupancy

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Abstract. Understanding how factors that vary in spatial scale relate to population abundance is vital to forecasting species responses to environmental change. Stream and river ecosystems are inherently hierarchical, potentially resulting in organismal responses to fine-scale changes in patch characteristics that are conditional on the watershed context. Here, we address how populations of two salamander species are affected by interactions among hierarchical processes operating at different scales within a rapidly changing landscape of the southern Appalachian Mountains. We modeled reach-level occupancy of larval and adult black-bellied salamanders (*Desmognathus quadramaculatus*) and larval Blue Ridge two-lined salamanders (*Eurycea wilderae*) as a function of 17 different terrestrial and aquatic predictor variables that varied in spatial extent. We found that salamander occurrence varied widely among streams within fully forested catchments, but also exhibited species-specific responses to changes in local conditions. While *D. quadramaculatus* declined predictably in relation to losses in forest cover, larval occupancy exhibited the strongest negative response to forest loss as well as decreases in elevation. Conversely, occupancy of *E. wilderae* was unassociated with watershed conditions, only responding negatively to higher proportions of fast-flowing stream habitat types. Evaluation of hierarchical relationships demonstrated that most fine-scale variables were closely correlated with broad watershed-scale variables, suggesting that local reach-scale factors have relatively smaller effects within the context of the larger landscape. Our results imply that effective management of southern Appalachian stream salamanders must first focus on the larger scale condition of watersheds before management of local-scale conditions should proceed. Our findings confirm the results of some studies while refuting the results of others, which may indicate that prescriptive recommendations for range-wide management of species or the application of a single management focus across large geographic areas is inappropriate.

Key words: Appalachian Mountains; Blue Ridge; *Desmognathus quadramaculatus*; distribution; *Eurycea wilderae*; land-use change; occupancy; riparian; salamander; scale.

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INTRODUCTION

Forecasting and managing species' responses to environmental change requires understanding how local abundance or individual performance varies with integrated environmental conditions. Identifying causal relationships between environmental heterogeneity and animal distributions can be challenging due to interactions among species traits and environmental factors that vary at different scales (Turner 2005, Clark et al. 2011). At local scales, abundance may depend on how individuals respond to factors such as resource availability and predation, while larger scale processes may shape local abundances by setting background conditions for population processes such as dispersal and migration (Lima and Zollner 1996, Holland and Hastings 2008). Ultimately, the integration of local and larger scale processes affecting demography determines patterns of abundance.

Demographic responses that produce patterns of local and regional abundance highlight the need to understand mechanistically why local abundance is often governed by broad-scale factors relative to fine-scale factors (He and Gaston 2000, Hiebeler 2000, Fausch et al. 2002, Durance et al. 2006, Azaele et al. 2015). One reason that broader-scale factors may better predict local responses is because broad-scale variables integrate a suite of correlated fine-scale factors (Allan et al. 1997, Ward 1998, Huston 1999, Azaele et al. 2015). For example, local changes in stream substrate, water chemistry, and microclimates all result from land cover change occurring at the catchment scale and have been implicated as the proximate cause of declines in many aquatic organisms (Welsh and Olliver 1998, Barr and Babbitt 2002, Burcher et al. 2007). Broader-scale factors are also likely to affect demographic processes such as dispersal and migration that occur over larger spatial scales (Lima and Zollner 1996, With et al. 1997, Lowe 2002, Grant et al. 2010). For example, short stream reaches with limited riparian cover in otherwise well-forested catchments may serve locally as sink habitats (Bliss and Cecala 2015), and there may be limited dispersal among forested reaches within catchments because of behavioral reluctance of animals to move across forest gaps (Grant et al. 2010, Cecala et al. 2014). Finally, we cannot disregard the methodological effect of grain on the strength of relationships inferred from data that vary in scale. Generally, one will find weaker relationships to variables measured at finer scales than the response variable (Poff 1997, Corry and Lafortezza 2007). Further, some measures represent fine-scale snapshots in highly dynamic systems, whereas larger scale variables tend to remain stable at the temporal scale of most studies (Malcolm et al. 2004, Webster et al. 2012).

Understanding the role of human influence and heterogeneity of the natural environmental on plant and animal populations is particularly important in regions of high global biodiversity. The southern Appalachian Mountains are a temperate forest biome of exceptional plant and animal diversity that is experiencing high rates of exurban development (Stein et al. 2000, Hansen et al. 2005, Radeloff et al. 2010, Kirk et al. 2012, Terando et al. 2014). The region owes its diversity and high level of endemism to its ancient montane topography, which creates a diversity of climates and habitats, with particularly cool, wet forests at mid- and upper elevations that act as both refuge and islands for many northern temperate lineages (Kozak and Wiens 2010). The southern Appalachian Mountains are one of the most significant areas globally for salamander diversity. While salamanders compose only ~10% of known amphibian species globally, they account for 50–60% of amphibian species in North America with over 100 species occurring in the Appalachian Mountains (~17% of global salamander diversity). Salamanders occur in every terrestrial and freshwater ecosystem in Appalachia, where they are often the most abundant vertebrates and highly influential in community and ecosystem processes (Davic and Welsh 2004, Best and Welsh 2014, Semlitsch et al. 2014, Milanovich et al. 2015). Stream-associated salamanders are one group of organisms that often have little resistance or resilience to environmental changes due to their dual reliance on aquatic and terrestrial environments, limited dispersal abilities, high philopatry, and apparent susceptibility to changes in abiotic conditions resulting from their highly permeable skin (summarized in Stuart et al. 2004, Cushman 2006, but see Kerby et al. 2009). A recent review found that amphibians in North America are declining continent-wide, and amphibians in the eastern

United States are declining primarily due to habitat loss and degradation (Grant et al. 2016).

To date, few studies have addressed the interactions of multiple types of land-use change or the combined effects of environmental changes from reach to catchment scale on stream amphibians (Fig. 1; Sweeten and Ford 2016, Weaver and Barrett 2017). Most previous studies of stream-associated amphibian abundance focused on regionally significant land uses such as commercial timber harvest in the Pacific Northwest (Welsh and Hodgson 2008, Kroll et al. 2010), urban development in the Piedmont (Barrett et al. 2010, Price et al. 2012), or coal mining in central Appalachia (Price et al. 2016, Sweeten and Ford 2016). While studies of scale-dependent land-use effects collectively suggest that stream-dwelling amphibians are most sensitive to reach-level sedimentation and catchment-level loss of forests (Welsh and Olliver 1998, Crawford and Semlitsch 2007, Kroll et al. 2008), disagreement exists regarding the relative influence of these factors on population declines or distribution changes (e.g., Kroll et al. 2008, Welsh and Hodgson 2008). For example, studies examining effects of urban land use on stream salamander abundance from a single region disagree on whether changes in catchment forest cover or local riparian forest cover are the most important predictor of declines (Willson and Dorcas 2003, Price et al. 2011) though recent studies suggest that riparian forest is most important across ecoregions (Surasinghe and Baldwin 2015, Weaver and Barrett 2017). Additional disagreement exists in whether land-use legacies impact current distributions (Surasinghe and Baldwin 2014, Weaver and Barrett 2017). Moreover, many of these aforementioned studies did not measure other reach-level parameters that may have contributed to declines.

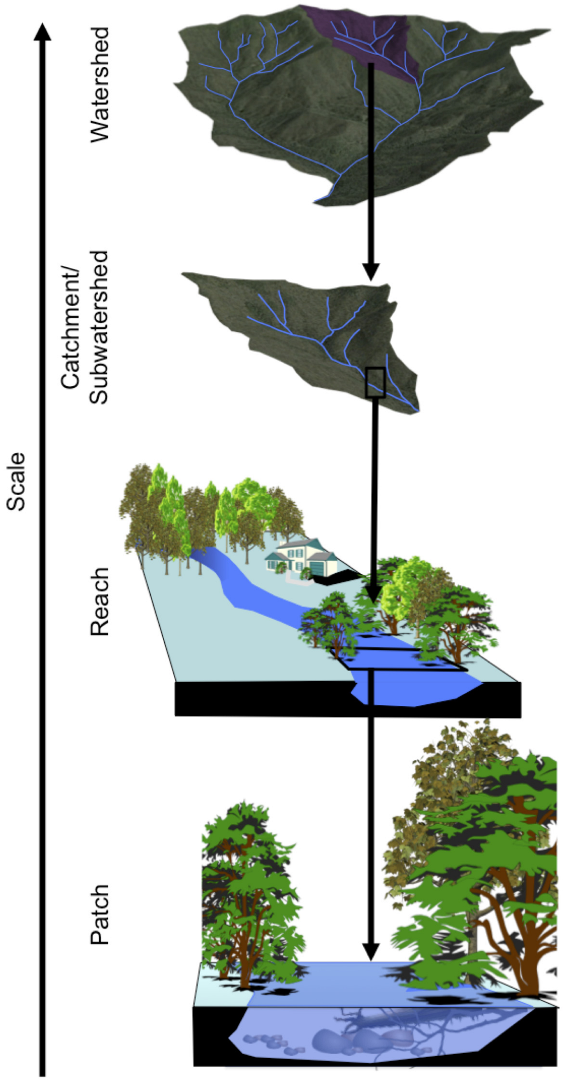

Fig. 1. Stream organisms measured at the patch scale respond to processes occurring at different scales that are nested within one another. Attention to changes at all scales is necessary to fully understand changes in animal occupancy.

Our objective is to determine how factors that are nested and vary in scale predict the abundance of stream salamanders in the southern Appalachian Mountains using a patch-occupancy approach at 37 sites within the Little Tennessee River watershed (>1100 km^2). We hypothesize that (1) catchment-scale characteristics are more important than reach-scale characteristics in predicting salamander occupancy (Fig. 1); (2) at the catchment scale, salamander occupancy will decline with increasing human activity and decreasing forest cover; and (3) salamander occupancy will be highest in stream reaches with little disturbance to reach-scale conditions.

MATERIALS AND METHODS

Study region

The southern Appalachian Mountains are undergoing rapid development as a result of its close proximity to several major metropolitan areas (Radeloff et al. 2010, Kirk et al. 2012, Terando et al. 2014). River valleys long have been used for agriculture (Gragson and Bolstad 2007), and the region also was extensively logged by the early 1900s; however, forested coves and steep slopes remained as refuge for many species (Griffith et al. 2003). The majority of the area underwent rapid recovery of plant and animal populations such that the region is now largely forested, with broad areas under federal management including the Nantahala and Chattahoochee National Forests. However, with rapid exurbanization, development is increasing on mid- and high-elevation hillslopes where most headwater streams and salamander diversity occur (Kozak and Wiens 2010, Kirk et al. 2012). This development includes the creation of roads and powerline rights-of-way throughout otherwise forested catchments. Moreover, residential development and the spread of introduced diseases (e.g., hemlock wooly adelgid) are associated with widespread alteration of riparian vegetation in forested catchments (Paul and Meyer 2001, Allan 2004, Ellison et al. 2005). As a result, the region is characterized by a mixture of catchments that differ in extent of forest, agriculture, and residential land cover creating a mosaic of catchment-, riparian-, and reach-scale conditions among streams (Webster et al. 2012). We surveyed 37 stream reaches in the Little Tennessee River watershed upstream of Fontana Lake, which encompasses 111,760 ha and spans portions of Rabun County, Georgia, and Macon County, North Carolina (Fig. 2). These sites were selected from a larger set of study locations by sampling all sites with drainage areas <1700 ha (Webster et al. 2012).

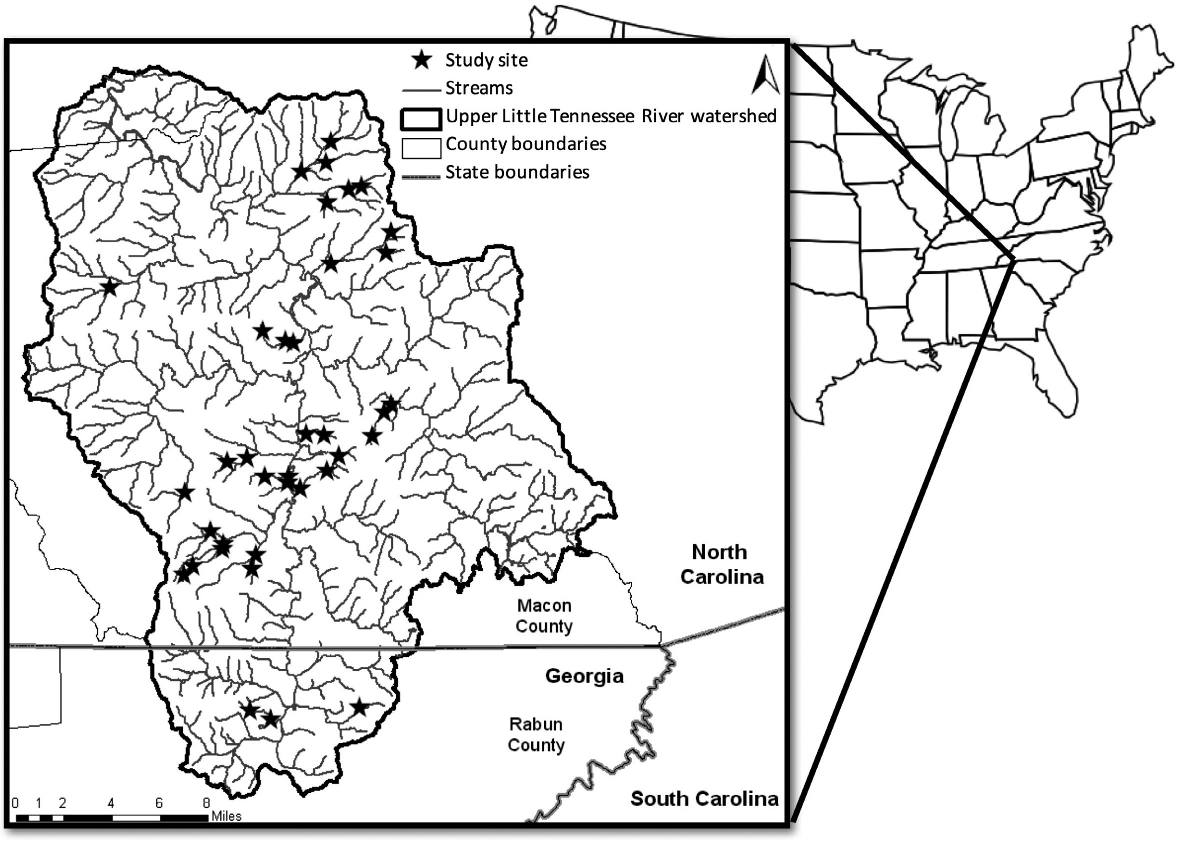

Fig. 2. Location of study sites (N = 37) throughout the upper Little Tennessee River watershed. These sites were a subset of 58 sites surveyed by Webster et al. (2012). Note that multiple sites may occur within a single catchment. We accounted for potential spatial autocorrelation by including a random effect for each catchment in our models.

Focal species

Our focal organisms in this study are two endemic salamander species that are the most abundant salamander species within forested reference streams of the region: the black-bellied salamander (*Desmognathus quadramaculatus*) and the Blue Ridge two-lined salamander (*Eurycea wilderae*; Milanovich et al. 2015). *Desmognathus quadramaculatus* are large-bodied and generally remain within the stream channel and bank throughout their lives (Kucken et al. 1994, Petranka 1998, Peterman et al. 2008). *Desmognathus quadramaculatus* spend 2–4 yr as larvae (typically 3–4 yr at our study sites) before metamorphosis (Bruce 1988, Austin and Camp 1992, Castanet et al. 1996). *Eurycea wilderae* is a small salamander that often occurs in surrounding forests far from streams from June to December before returning to streams to lay eggs (Bruce 1982*a*, Petranka 1998). The typical larval period for *E. wilderae* is 14 months (Bruce 1982*a*, *b*, Voss 1993, Petranka 1998). Both adult *D. quadramaculatus* and *E. wilderae* are lungless and completely dependent on cutaneous respiration as adults. However, larval *D. quadramaculatus* are also completely dependent on cutaneous gas exchange (their gills are not vascularized), and therefore, larvae are generally associated with forested streams and cold, fast-flowing water where dissolved oxygen is maximized (Pope 1924, Hairston 1949, Organ 1961, Davic and Orr 1987). In contrast, larval *E. wilderae* have vascularized gills that allow them to inhabit a wider range of stream conditions.

Field methods

We used a patch-occupancy approach to quantify drivers of salamander abundance among a large number of streams concurrently, while accounting for incomplete detection (Conroy et al. 2008). To sample stream salamanders, we used the approach detailed below during May–July 2009. At each site, we identified a 150-m stream reach upstream of any nearby road crossings. Within each reach, we designated thirty-one 1-m^2 plots every 5 m, and within each plot, we placed a 25 × 40 cm leaf-litter bag (Jung et al. 2000, Marsh 2009, Graeter et al. 2013). Leaf-litter bags were constructed with plastic mesh (1 cm^2) filled with leaf litter from the stream bank, or nearest upstream source, and secured in place with a rock. The design of the leaf-litter bags allowed animals to move freely in and out, and prior research suggests that bags were attractive to animals in the immediate area, but because of limited instream movement, did not attract animals into a plot (Lowe 2003, Cecala et al. 2009, Nowakowski and Maerz 2009). Bags were soaked for 48 h before our first sampling. Each leaf-litter bag was sampled once a day for three consecutive days. To sample, we placed a fine-mesh net immediately adjacent to and downstream of the leaf-litter bag. We quickly moved the leaf-litter bag into the net and transferred the bag to a large bin. We then turned cobble and debris within the plot and used a dipnet to collect salamanders. We rinsed the bag with stream water while gently agitating the net to dislodge organisms. Water in the bin was then strained through a fine-mesh dipnet, followed by identification of species and age cohort (larva or adult) of all captured individuals. Finally, we replaced the leaf-litter bag in the stream and released all animals back into the plot, taking care to ensure they were not swept away by the current. Animals were free to move in and out of the leaf-litter bag between sample events.

Predictor variable collection

We selected a series of variables collected for this study and a larger stream study (Webster et al. 2012) to predict salamander occupancy based on evidence from previous studies on salamanders and other stream-dwelling organisms (Table 1). These variables were distributed among spatial extents and categories of factors. We used a 10-m digital elevation model (DEM) to delineate catchments using our sampling points as the outlet for the catchments, which were then used as boundaries for subsequent evaluation of land-use and land cover variables. Drainage area and elevation were quantified at the downstream end of our transects (Table 1). We used the stream network derived from the DEM to estimate Shreve stream order for each stream reach. Shreve stream order describes the number of confluences occurring upstream of a sample location (Table 1).

Catchment land cover was obtained from the 2006 National Land Cover Dataset. Because land cover types within this region were correlated, we combined proportions of deciduous forest (41), evergreen forest (42), mixed forest (43), and scrub/shrub (52) to characterize forested land cover within a stream catchment. We modeled

Table 1. Hypotheses associated with each salamander occupancy predictor variable and supporting literature.

Predictor variable	Hypothesis	Direction of relationship	Support
Catchment-scale predictors			
Catchment forest	Streams integrate and process changes occurring throughout the catchment due to land cover change known to affect salamander populations	Positive	Price et al. (2011)
100-m network buffer	Network buffers can filter runoff from the catchment to reduce sedimentation and inputs of other nutrients and chemicals known to influence salamander populations	Positive	Willson and Dorcas (2003)
Catchment commercial	Commercial land use is associated with increased impervious surface which greatly affects flood frequency and magnitude that may flush salamanders from downstream study reaches	Negative	Barrett et al. (2010)
Catchment agriculture	Agricultural land use is associated with increased sedimentation, which embeds large sediments and reduces refuge availability. Furthermore, fertilizer applications from agricultural land use may alter food webs	Negative	Webster et al. (2012)
Maximum building age	The temporal scale of catchment disturbance will increase the effects of altered conditions on salamander populations through iterations of demographic processes	Negative	Harding et al. (1998)
Elevation	Elevation is negatively correlated with stream order and stream temperatures that positively influence salamander occupancy	Positive	Petranka (1998), Grant et al. (2005), Ward et al. (2008)
Drainage area	Small drainage areas are correlated with stream order. Low-order streams have low discharge and often an absence of fish known to prey on salamanders	Negative	Petranka (1998), Lowe (2005), Sepulveda and Lowe (2009)
Network	Confluences are hypothesized to increase stream populations' connectivity increasing the probability of long-term persistence by stream salamanders	Positive	Grant et al. (2009)
Reach-scale predictors			
100-m point buffer	Local conditions influence survival and dispersal of salamanders	Positive	Lowe and Bolger (2002), Lowe (2005), Price et al. (2011)
Stream substrate (ϕ)	Finer substrates reduce the availability of refuge and increase the probability of salamanders being flushed from a stream reach	Positive	Lowe et al. (2004), Barrett et al. (2010)
Riparian canopy cover	Salamanders are adapted to heavily canopied streams that regulate temperature and stream bank soil moisture to allow for successful terrestrial foraging by adults and juveniles	Positive	Ash (1997), Rieman et al. (1997), Peterman et al. (2011), Ward et al. (2008)
Mean daily stream water temperature range	Salamander movement is influenced by stream temperatures. Salamanders may be unable to tolerate large ranges in stream water temperature	Negative	Feder (1983), Marvin (2003*a*, *b*), Bernardo and Spotila (2006)
Large woody debris	Large woody debris is one type of refuge typically found in forested streams. They increase habitat heterogeneity	Positive	Kluber et al. (2009)
Percent riffle	Riffles increase water oxygenation that is important for vertebrates that respire through the skin and are areas of hyporheic water exchange where salamanders may occur when they move out of the mainstream channel	Positive	Welsh and Olliver (1998), Lowe et al. (2004), Stoddard and Hayes (2005)
Total dissolved phosphorus	Nutrient additions may stimulate production of salamander prey	Positive	Davis et al. (2010)
Sodium	Sodium from road salt contributions can be toxic to amphibians	Negative	Karraker et al. (2008)
Calcium	Desmognathan salamanders have heavily ossified skulls that require calcium for development	Positive	Petranka (1998)

relationships between salamander occupancy and estimates of forest cover at three scales: (1) the whole catchment, (2) a 100-m buffer for the entire stream network upstream of our sampling location (100-m network buffer), and (3) a 100-m buffer of our sampled reach. We used ArcGIS (v.9) to calculate land cover proportions from our delineated scales. We also included catchment land use because concurrent studies indicate that land use rather than characterization of forest loss better predicts some stream conditions (Webster et al. 2012), and land-use classifications allowed us to distinguish between different types of non-forested land cover (agriculture or commercial; Table 1). Maximum building age within each sample catchment was derived from tax records of Macon County, North Carolina. Unified records were unavailable for sites located in Rabun County (N = 3), Georgia, and mean values were used for analyses involving land use and maximum building age.

We made direct measurements of local riparian and instream conditions (Table 1). We estimated the proportion of different microhabitat types for each stream reach by measuring active channel width and depth at each plot, and classifying the channel unit types within each reach. We considered all channel units with fast-flowing water (e.g., riffle, bedrock step, rapid, and cascade) as riffle and included the percentage of the reach that was riffle in our models. For each reach, we also counted all large woody debris >10 cm and conducted a Wolman (1954) pebble count that included 100 measurements in a representative riffle. We then calculated Φ (-$\log_2$ [Sediment β-axis]) to represent the median particle size in each stream. We measured canopy cover at each plot by taking digital photographs of the canopy from one meter above the stream channel and quantifying the percent cover via visual analysis. We placed two or three HOBO Pendant temperature/light data loggers (Onset Computer, Bourne, Massachusetts, USA) at the water surface to measure surface water temperatures every 10 min for the 72 h that we sampled salamanders. We included mean reach canopy cover and mean daily variation in stream water temperature in our models (Table 1). Finally, we took three replicate grab samples for chemical analysis. Samples were filtered using a Whatman GF/F filter (0.7 μm) in the field and frozen before chemical analysis. Total dissolved phosphorus was obtained via a persulfate in-line UV digestion with a Lachat QuikChem FIA+ (Table 1; Webster et al. 2012), and calcium and sodium concentrations were obtained from an atomic absorption spectrometer (Perkin Elmer AAnalyst 300; Table 1; Webster et al. 2012).

Data analysis

To evaluate the explanatory power of our predictor variables, we estimated single-season, single-species occupancy after accounting for incomplete detection that could bias parameter estimates (MacKenzie et al. 2002) and spatial correlations among catchments that could underestimate parameter variance (Snijders and Bosker 1999). We used a hierarchical Bernoulli–binomial mixture model to describe occupancy probability (ψ) and detection probability (P; Royle and Dorazio 2008, Kéry and Schaub 2012). Random effects were introduced by allowing the intercepts to vary among watersheds to allow for spatial variation in salamander occupancy and detection. We also included a hierarchy of occurrence, whereby occurrence in a leaf-litter bag (reach prevalence) was conditional on the reach being occupied, and occurrence in a reach was conditional on the watershed being occupied (Metadata S1). This conditional hierarchy of occurrence was modeled using Bernoulli distributions, such that occurrence in a leaf-litter bag (z_{plot}) was distributed as Bernoulli($z_{\text{reach}} \times \psi_{\text{plot}}$), $z_{\text{reach}} \sim$ Bernoulli($z_{\text{watershed}} \times \psi_{\text{reach}}$), and $z_{\text{watershed}} \sim$ Bernoulli($\psi_{\text{watershed}}$). We further modeled ψ_{plot} and P for larval and adult *D. quadramaculatus* and larval *E. wilderae* based on habitat variables in logistic regression models.

The large number of identified predictor variables in these models necessitated a multi-step modeling process to identify the most predictive habitat characteristics for detection and patch occupancy and minimize the number of models evaluated (Kroll et al. 2009). For detection, we considered all instream parameters that may affect detection including streambed particle size, large woody debris, and riffle habitat proportion. For occupancy, we divided our 17 habitat variables into two groups characterized by the spatial extent of the measurement (Table 1). Within each scale, we identified variables that had greater posterior than prior support (marginal posterior inclusion probability > 0.5), and combined the supported predictor variables from each scale to construct a multi-scale model. We selected variables for the global occupancy model that varied in measurement extent and represented the current state of knowledge about habitat effects on salamander abundances and distributions (Table 1).

The relative fit of candidate models was evaluated using indicator variables on model coefficients (Kuo and Mallick 1998, Royle and Dorazio 2008, Kruschke 2015). Briefly, the indicator variable acts as a switch to turn individual habitat effects in the logistic regression models on or off. We set the prior probability for each indicator variable as Bernoulli(0.5) and used hierarchical shrinkage priors for the precision of model coefficients. The hierarchical shrinkage priors on model coefficients are useful for examining the effects of many covariates on a response because they use a *t* distribution, which allows a few covariates to have larger effects, while most covariates retain very small effects (Kruschke 2015). The hierarchical shrinkage priors also use a hyperprior for the standard deviation of the *t* distribution, which helps to integrate over the effects of prior sensitivity of model selection to the priors placed on model coefficients (Link and Barker 2010). Because all habitat variables were selected based on a priori hypotheses, and because model selection with indicator variables works well even when collinear variables are included in the same model (Kuo and Mallick 1998), we included all habitat variables in the model set for each spatial scale examined. All habitat variables were normalized for model evaluation. We calculated posterior model probabilities as the proportion of iterations each model (unique combination of predictor variables) was turned on, and evaluated the relative support of one model over another using Bayes factors (Link and Barker 2010).

Model complexity necessitated Bayesian inference, which we implemented using the software package JAGS 4.2.0 (Plummer 2015) called from R 3.4.0 (R Core Team 2017) using the package jagsUI (Kellner 2016). We used uninformative, diffuse priors for all model parameters, including beta(1, 1) for all probabilities, half-Cauchy(1) for all standard deviations, and hierarchical shrinkage priors ($t(0, \sigma_\beta, 1)$; Kruschke [2015]) for coefficients describing habitat effects on detection and occupancy probabilities. Using the Gelman and Rubin test, implemented using package CODA in program R (Gelman and Rubin 1992, Plummer et al. 2006, R Core Team 2017), and visual examination of history plots, we determined that all models converged after fitting five independent chains with 100 K Markov chain Monte Carlo iterations each after 10 K burn-in iterations and a thinning rate of 5. We assessed model fit with a Bayesian *P*-value based on the χ^2 statistic (Kéry 2010). We examined posterior distributions of supported coefficients and describe the posterior probability of the most likely directional effect and their model-averaged posterior distributions using medians and 95% credible intervals. We also calculated odds ratios for model coefficients to facilitate interpretation of the results.

RESULTS

We captured 2008 larval and adult salamanders of nine different species including 554 *Desmognathus quadramaculatus* larvae, 190 *D. quadramaculatus* adults, and 833 larval *Eurycea wilderae*. We did not evaluate adult *E. wilderae* because of limited detections (N = 23). Study sites varied considerably with respect to our predictor variables. Sites varied in elevation from 619 to 1058 m, with drainage areas between 18 and 1670 ha (Table 2). Overall, the catchments of our study sites remained largely forested with the most developed catchment retaining 29.7% forest; however, our reaches ranged from having a 100% forested buffer to a buffer with 0% forest (Table 2). Catchments with post-European anthropogenic activity had been disturbed for a maximum of 161 yr and a minimum of 41 yr (Table 2). Reach-scale variables were often correlated with one another and with catchment-scale variables, whereas catchment-scale variables were less frequently correlated with one another (Appendix S1). Mean reach occupancy for *D. quadramaculatus* larvae in a reach with an average covariate profile was median = 0.71 (95% credible interval = 0.46–0.94). Adult *D. quadramaculatus* reach occupancy (0.78 [0.51–0.97]) was similar to that of larvae, as was larval *E. wilderae* reach occupancy (0.76 [0.62–0.88]).

Models for detection probabilities of all species and life stages appeared to fit, with Bayesian *P*-values >0.13. Evaluation of the detection models indicated that after accounting for random variation among reaches, covariates had little explanatory power (Table 3). Mean trap-level

Table 2. Summary statistics for predictor variables and salamander occupancy and detection estimates quantified from surveys of 37 sites within the upper Little Tennessee River watershed.

Parameter	Code	Mean (SD)	Range	Unit
Catchment scale				
Catchment forest land cover	Forest	0.846 (0.186)	0.30 to 1.00	Proportion
100-m stream network buffer forest land cover	Network buffer	0.732 (0.250)	0.13 to 1.00	Proportion
Elevation	Elevation	693 (87)	617 to 1058	Meters
Drainage area	Drainage area	421 (398)	18 to 1670	Hectares
Shreve stream order	Network	2.78 (2.43)	0 to 9	Confluences
Age of human disturbance	Age	118 (53)	41 to 161	Years
Agricultural land use	Agriculture	0.091 (0.037)	0.00 to 0.27	Proportion
Commercial land use	Commercial	0.009 (0.006)	0.00 to 0.11	Proportion
Reach scale				
100-m point buffer forest land cover	Point buffer	0.450 (0.374)	0.00 to 1.00	Proportion
Substrate (Φ scale)	Substrate	−4.96 (0.92)	−6.43 to (−3.32)	log (mm)
Canopy cover		0.736 (0.28)	0.00 to 0.982	Proportion
Maximum daily temperature variation	Temperature	7.61 (4.6)	1.66 to 21.83	°C
Large woody debris	LWD	8.5 (14.1)	0 to 63	logs
Riffle and fast-flowing water	Percent riffle	0.61 (0.35)	0.053 to 0.994	Proportion
Total dissolved phosphorus	TDP	6.94 (3.26)	2.50 to 13.20	μg P/L
Sodium		2.06 (0.84)	0.76 to 4.74	mg Na/L
Calcium		1.50 (0.89)	0.26 to 3.15	mg Ca/L

Table 3. Posterior marginal probabilities of including predictor variables, direction of effects, parameter estimates, and odds ratios for models explaining detection probability (P) and reach-level occupancy (ψ) of stream salamanders.

Species and stage	Process	Predictor variable	Marginal probability	Direction	Parameter estimate	Odds ratio
Desmognathus quadramaculatus, larvae	P	Percent riffle	0.582	−, 0.55	−0.13 (−0.78–0.01)	0.88 (0.46–1.01)
	ψ	Forest	0.980	+, 0.98	1.75 (0.25–3.15)	5.78 (1.28–23.4)
		Elevation	0.890	+, 0.88	2.20 (0.00–5.82)	9.06 (1.00–337)
		Drainage area	0.538	−, 0.46	0.00 (−1.44–0.79)	1.00 (0.24–2.21)
		Network	0.546	−, 0.48	0.00 (−2.06 to 0.31)	1.00 (0.13–1.37)
		Agriculture	0.498			
		Point buffer	0.385			
		Canopy cover	0.340			
		Tdp	0.298			
Desmognathus quadramaculatus, adults	P	Substrate	0.496			
	ψ	Forest	0.941	+, 0.94	1.32 (0.00–2.59)	3.73 (1.00–13.28)
		Elevation	0.858	+, 0.84	2.94 (0.00–7.21)	18.9 (1.00–1350)
		Commercial	0.759	+, 0.75	0.60 (0.00–2.45)	1.82 (1.00–11.60)
		Point buffer	0.656	+, 0.63	0.67 (0.00–3.57)	1.95 (1.00–35.5)
		Canopy cover	0.275			
		Temperature	0.272			
Eurycea wilderae, larvae	ψ	Network	0.448			
		Commercial	0.512	+, 0.46	0.00 (−0.06–2.23)	1.00 (0.94–9.29)
		Percent riffle	0.570	−, 0.53	−0.07 (−0.84–0.03)	0.93 (0.43–1.03)

Notes: All predictor variables had marginal prior probabilities of 0.5. Only predictor variables with marginal posterior probabilities >0.5 are summarized, and only those predictor variables with marginal posterior probabilities >0.5 at the catchment and reach scales were included in the multi-scale model. Intermediate model results at the catchment or reach scale may be found in Appendix S2. Direction indicates the direction of the effect on the response (+ or −) and the posterior probability of that directional effect. Parameter estimates and odds ratios are model-averaged and expressed as median (0.025–0.975 quantile).

Table 4. Posterior model probabilities and Bayes factors relative to the top model for reach-level occupancy (ψ) of larval *Desmognathus quadramaculatus* using predictor variables at multiple scales.

Predictor variable										
Forest	Elevation	Drainage area	Network	Agriculture	Point buffer	Canopy cover	TDP	Catchment	Posterior probability	Bayes factor
1	1	0	1	1	0	0	0	1	0.057	1.00
1	1	1	1	1	0	0	0	1	0.031	1.81
1	1	1	0	1	0	0	0	1	0.028	1.99
0	0	0	0	0	0	0	0	0	<0.001	∞

Notes: Only models with a Bayes factor <2 or a posterior probability >0.05 and the null model are included in the table. Models are listed in order of decreasing support. A "1" indicates that the variable was included in the model; a "0" indicates that the variable was excluded from the model. "Catchment" indicates a catchment-level random intercept.

detection probability of larval *D. quadramaculatus* was 0.19 (0.12–0.27), which was greater than that of adult *D. quadramaculatus* (0.09 [0.08–0.11]), and similar to the detection probability of *E. wilderae* (0.18 [0.12–0.25]; Table 2). Model-averaged logit-scale standard deviations for reach-level variation in larval *D. quadramaculatus*, adult *D. quadramaculatus*, and larval *E. wilderae* detection probabilities were 0.84 (0.48–1.28), 0.00 (0.00–0.25), and 1.08 (0.79–1.47), respectively.

As for detection models, models for occupancy of all species and life stages appeared to fit, with Bayesian *P*-values of 0.47 for all models. For larval *D. quadramaculatus*, the best occupancy model included forest cover within the catchment, elevation, network complexity as measured by confluences within the catchment, agricultural land cover, and a random intercept for watershed (Table 4). This model was 1.8 times more likely than the next best model that included drainage area, and twice as likely as a model that included drainage area but excluded network complexity (Table 4). The best model for adult *D. quadramaculatus* occupancy contained forest cover within the catchment, elevation, commercial land cover, and forest within a 100-m point buffer (Table 5). This model was 1.1 times more likely than the next best model that dropped forest within a 100-m point buffer, and 1.6 times more likely than a model that dropped forest within a 100-m point buffer and added a random intercept for watershed (Table 5). Forest cover in the catchment and elevation were important correlates of occupancy for both larval and adult *D. quadramaculatus*, with positive effects of both variables on both life stages (Figs. 3, 4). Models suggest that with a 19% increase in catchment forest cover, occupancy should increase 5.8 (1.3–23) times for larvae but 3.7 (1.0–13) times for adults. Larvae exhibited stronger relationships with these variables, and coefficients for larvae were more precisely estimated than those for adults (Table 3; Figs. 3, 4).

The best model for larval *E. wilderae* occupancy contained percent riffle. This model was 1.3 times more likely than the next best model that

Table 5. Posterior model probabilities and Bayes factors relative to the top model for reach-level occupancy (ψ) of adult *Desmognathus quadramaculatus* using predictor variables at multiple scales.

Predictor variable								
Forest	Elevation	Commercial	Point buffer	Canopy cover	Temperature	Catchment	Posterior probability	Bayes factor
1	1	1	1	0	0	0	0.124	1.00
1	1	1	0	0	0	0	0.111	1.12
1	1	1	0	0	0	1	0.075	1.64
1	1	1	1	0	0	1	0.075	1.66
0	0	0	0	0	0	0	0.011	11.71

Notes: Only models with a Bayes factor <2 or a posterior probability >0.05 and the null model are included in the table. Models are listed in order of decreasing support. A "1" indicates that the variable was included in the model; a "0" indicates that the variable was excluded from the model. "Catchment" indicates a catchment-level random intercept.

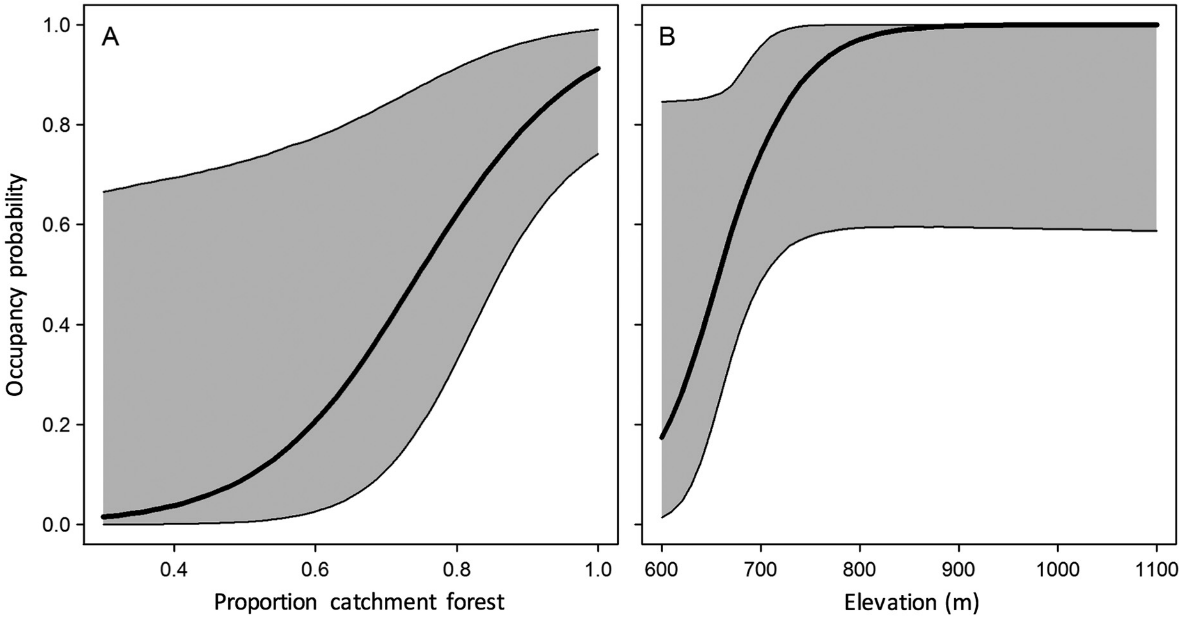

Fig. 3. Model-averaged effects of (A) proportion catchment forest land cover and (B) elevation on larval *Desmognathus quadramaculatus* reach-level occupancy. Bold lines indicate posterior medians, and gray-shaded areas and light lines represent the 95% credible intervals.

dropped the effect of percent riffle and replaced it with a random intercept for watershed, and 1.4 times more likely than a model that added commercial land cover (Table 6). No variables were strong predictors of larval *E. wilderae* occupancy (Tables 3 and 6), but they were 0.93 (0.43–1.03) times as likely to occur in a reach with a 35% increase in percent riffle.

Discussion

Hierarchical processes occurring in this landscape result in reach-level characteristics that are correlated with each other and broad-scale factors including two scales of forest cover. A key finding of our study was that salamanders occupied nearly 100% of streams with largely intact riparian forests and fully forested catchments, yet prevalence varied widely among those fully forested streams and catchments. Our salamander occupancy relationships suggest that catchment-scale factors related to forest cover throughout a catchment have larger effects on local occupancy by salamanders sensitive to forest loss and that local reach-scale factors can have smaller effects within the context of the larger landscape. Our findings also suggest that local salamander occupancy is determined by processes affected by human activities at various extents. Despite exploring a wide variety of landscape and reach characteristics known to influence stream amphibians, only a small and consistent subset of characteristics were relevant for understanding patterns of stream-amphibian occupancy at the reach scale.

Despite high natural variability in salamander occupancy among near fully forested streams, our results demonstrate that small-to-moderate regional declines in forest cover cause corresponding declines in salamander abundance. Small-to-moderate loss of forest cover within catchments was associated with the loss of sites with high salamander occupancy rates and an increased likelihood of sites where some otherwise abundant salamander species such as *Desmognathus quadramaculatus* are now absent (Figs. 3A, 4A). Between 1973 and 2012, forest cover in our study area declined from 79% to 70% (Griffith et al. 2003, Kirk et al. 2012), and our data suggest that during that period, mean *D. quadramaculatus* occupancy within stream reaches may have declined by as much as 26%

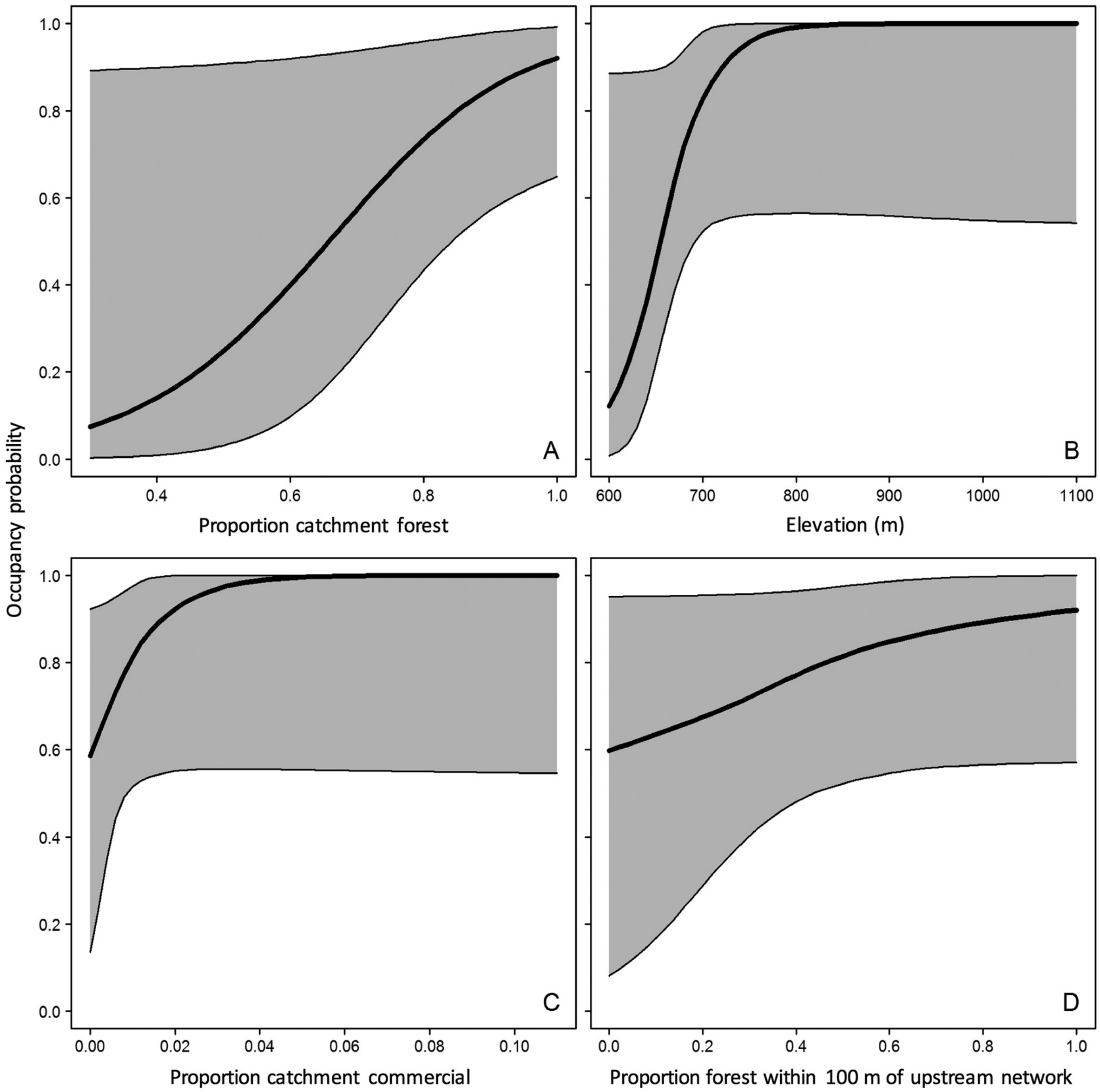

Fig. 4. Model-averaged effect of (A) proportion catchment forest land cover, (B) elevation, (C) proportion catchment commercial land cover, and (D) proportion forest within 100 m of sampled reach on adult *Desmognathus quadramaculatus* reach-level occupancy. Bold lines indicate posterior medians, and gray-shaded areas and light lines represent the 95% credible intervals.

and the probability that the species was absent from a stream reach increased by up to 8%. At an assumed constant rate of forest loss, forest cover would decline to 61% by 2030, and our data would predict that the probability of *D. quadramaculatus* being absent from a stream would increase by 22% from 1973 (Figs. 3A, 4A). We acknowledge that there are limits to extrapolating our results to contexts we could not sample. For example, human settlement patterns in this region have historically been biased to lower elevations, leaving nearly all high-elevation streams heavily forested (Kirk et al. 2012). It is possible that higher elevation reaches without riparian

Table 6. Posterior model probabilities and Bayes factors relative to the top model for reach-level occupancy (ψ) of larval *Eurycea wilderae* using predictor variables at multiple scales.

Predictor variable					
Network	Commercial	Percent riffle	Catchment	Posterior probability	Bayes factor
0	0	1	0	0.119	1.00
0	0	0	1	0.093	1.28
0	1	1	0	0.087	1.37
1	1	1	0	0.076	1.56
1	1	0	0	0.070	1.69
0	0	1	1	0.070	1.72
1	1	0	1	0.065	1.83
0	0	0	0	0.026	4.50

Notes: Only models with a posterior probability >0.063 (the prior probability for each model) and the null model are included in the table. Models are listed in order of decreasing support. A "1" indicates that the variable was included in the model; a "0" indicates that the variable was excluded from the model. "Catchment" indicates a catchment-level random intercept.

cover could continue to support salamander species not currently found in deforested reaches at lower elevations. This tendency for landscape-scale factors to covary may also explain why commercial land use was positively associated with salamander occupancy. Agricultural land-use was negatively correlated with commercial land use, suggesting that in some instances, agriculture was replaced by commercial land use particularly in mid-stem streams. These commercial uses were typically large parcels with a small commercial footprint that may have smaller stream impacts or retain more forest cover than an agricultural parcel of similar size.

Recent studies have highlighted the inherent value of understanding the range and variability in ecological conditions especially as researchers seek to understand how populations have changed and should be managed (Landres et al. 1999, Benedetti-Cecchi 2003, Fraterrigo and Rusak 2008). While there has been significant study of community structure of stream salamanders (Hairston 1987, Beachy 1993, 1994, 1997), there has been remarkably little research on natural variation in stream salamander abundance. Patch dynamics and heterogeneity including predation, competition, and resource availability all affect larval and adult salamander performance (Hairston 1987, Beachy 1993, 1994, 1997, Bernardo 1994). Few reach-level metrics were included in our final multi-scale models suggesting that variation in salamander occupancy was largely driven by large-scale interactions such as forest cover and elevation or stream network structure. In these instances, both life stages of *D. quadramaculatus* were most likely to occupy high-elevation, small, and forested streams. Describing potential interactions among landscape-scale variables is the first step toward understanding natural temporal and spatial variation in salamander occupancy to provide context for anthropogenic impacts. We recommend future studies assess how variability in salamander occupancy responds to changing catchment forest cover while constraining other landscape variables.

In the context of scale, we also caution that species' responses to environmental gradients may vary geographically and therefore cannot be generalized across a species' range. A large body of research spanning much of North America demonstrates a general negative effect of forest loss from logging, agriculture, or urban development on stream amphibians (e.g., Welsh and Ollivier 1998, Welsh and Lind 2002, Price et al. 2006, Barrett et al. 2010, Tilghman et al. 2012, Grant et al. 2016). However, the effect of forest loss does appear to vary geographically (Corn et al. 2003, Welsh and Hodgson 2008, Kroll et al. 2009, Barrett et al. 2010, Price et al. 2011, Gould et al. 2017). A recent meta-analysis also suggests that the effects of forest loss on salamanders may be stronger in warmer climates including those found at lower elevations (Tilghman et al. 2012). Our study occurred at the southern range limit for many salamander species, and evidence suggests that individuals live near the limits of their physiological tolerances (Bernardo and Spotila 2006, Bernardo et al. 2007, Strickland et al. 2016), which could explain why we observed near threshold-like responses to elevations above 800 masl. Therefore, some species may be particularly sensitive to forest loss and associated stream warming in southern Appalachia, but potentially more tolerant of warming associated with canopy cover loss in more northern portions of their range or at higher elevations (Caruso et al. 2014, Peterman et al. 2016). Though surprising that *Eurycea wilderae* larvae did not demonstrate predictable occupancy patterns in response to forest cover, it may be that the shorter larval period and less restrictive physiology of *E. wilderae* larvae minimizes development of strong habitat selection behaviors. Other studies on *E. wilderae* and closely related congeners (e.g., *Eurycea cirrigera*) also reflect their tolerance to changes in stream condition due to land-use change (Price et al. 2006, Barrett et al. 2010). Comparisons between larval and adult *E. wilderae* occupancy patterns could reveal whether larval occupancy patterns are reflective of adult breeding activity or whether they exhibit different requirements.

Similarly, at smaller scales, studies in the northeastern United States and in the southeastern Piedmont link increased sedimentation with declines in stream salamander abundance (e.g., Orser and Shure 1972, Welsh and Olliver 1998, Barr and Babbitt 2002, Lowe et al. 2004, Miller et al. 2007); however, we found no relationship between salamander occupancy and variation in substrate conditions. Our findings were consistent with Keitzer and Goforth (2012), who similarly did not find a negative relationship between increased sedimentation and larval stream salamander abundance in southern Appalachia. Further, our results suggest that *E. wilderae* in southern Appalachia are more common in habitats with slower moving water where fine sediments are more likely to settle. The reason for these apparent geographic inconsistencies is unknown. Corn and Bury (1989) suggest that sedimentation effects on stream-associated amphibians in the Pacific Northwest may vary with stream order, but that would not explain the differences between patterns observed in southern Appalachia and elsewhere. Collectively, these studies suggest that while coarse generalities about the relationships between forest loss and stream amphibians exist, the hierarchical nature of landscape and local processes, as well as variation in climate, will result in geographic variation in species responses to land-use changes.

Management implications

While designing management strategies for semi-aquatic species remains a challenge (e.g., Olson et al. 2007, Herbert et al. 2010), our study illustrates the need to carefully consider the spatial scale of management. Because of the unique hierarchical organization of streams, the scale of anthropogenic development is often different than the scale at which stream organisms operate and respond to their environments. In our study region, most conservation of streams and their associated fauna focuses solely on local stream restoration and management. Our results indicate that local stream management without consideration of the broader catchment and regional context may limit the effectiveness of management efforts. Finally, our results indicate that well-forested landscapes harbor considerable variability in salamander occupancy and that management suggestions are likely inappropriate (e.g., Tilghman et al. 2012). Acknowledging relationships among landscape-scale variables with species- and region-specific responses will improve conservation or restoration activities.

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