



Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests



Jacquelyn Guzy^{a,*}, Kelly Halloran^a, Jessica Homyack^b, John D. Willson^a

^a Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

^b Weyerhaeuser Company, 505 North Pearl St., Centralia, WA 98531, USA

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ABSTRACT

Streamside management zones (SMZs), buffers of forest retained along streams when adjacent areas are harvested, are a primary tool for maintaining ecological functions in managed forests. However, few studies have examined the influence of SMZs on salamanders, and none have examined variation in salamander occupancy, species richness, and abundance across a gradient of SMZ widths at a large spatial scale. Further, because previous studies had limited ability to detect responses of uncommon species, little is known about interspecific variation in salamander responses or whether SMZs serve as refuges for terrestrial species during harvesting. To evaluate the role of SMZs in maintaining salamander species, we conducted four replicate surveys at 102 headwater stream sites, spanning a gradient of SMZ widths and adjacent forest stand ages, within the Ouachita Mountains, Arkansas, USA. We used a hierarchical Bayesian community occupancy model to estimate salamander species richness and species-specific occupancy responses to SMZ and overstory characteristics, while accounting for variation in occupancy and detection attributable to site and sampling covariates. Additionally, we used Bayesian binomial mixture models to examine the influence of SMZ width and surrounding stand age on abundance of two stream-associated salamanders [Ouachita dusky salamander (*Desmognathus brimleyorum*) and many-ribbed salamander (*Eurycea multiplicata*)] and three terrestrial salamanders [red-backed salamander (*Plethodon serratus*), slimy salamander (*P. glutinosus* complex), and Caddo Mountain salamander (*P. caddoensis*)]. Occupancy, species richness, and abundance increased with increasing SMZ width, but the strength of responses varied among species. Occupancy of uncommon species was highest at sites with wide SMZs, likely because of the need for specific habitat elements (e.g., wetlands, rocky talus). Richness was lowest in SMZs dominated by pine overstory, and lowest in mid-aged stands, consistent with a lagged decrease in richness within SMZs following harvest. Finally, we documented patterns of abundance consistent with the evacuation hypothesis, indicating that salamanders may leave recently harvested areas seeking more suitable habitat and microclimate within SMZs. Collectively, results indicate that SMZs in intensively managed forests can support robust salamander communities, provided managers continue to retain wide SMZs at some key sites across the landscape (i.e., ≥ 55 m on each side of the stream), a value larger than current Forestry BMP guidelines.

1. Introduction

Headwater streams account for approximately three-fourths of total stream channel length in the United States (Leopold et al., 1964, Meyer and Wallace, 2001) and are an important habitat type for many species. Because detrital inputs provide streams with dissolved nutrients and particulate matter that influence stream productivity, biotic diversity, and physical and chemical conditions (Likens and Bormann, 1974, Wallace et al., 1997), forests surrounding headwater streams are critical to stream ecosystem function (Wallace et al., 1997). Consequently, headwaters are sensitive to natural and anthropogenic disturbance of

surrounding uplands (Lowe and Likens, 2005). A major land use influencing riparian areas is timber harvest, which can alter stream metabolism and influence wildlife habitat and communities (Broadmeadow and Nisbet, 2004, Moore et al., 2005).

Forested buffers (i.e., streamside management zones; SMZs) often are maintained along streams and are implemented widely within managed forests under either regulatory or non-regulatory best management practices (BMPs), or regulatory programs (Lee et al., 2004, Cristan et al., 2018). Streamside management zones moderate air and water temperatures, maintain soil moisture (Broszofske et al., 1997, Swank et al., 2001, Wilkerson et al., 2006), and protect water quality

* Corresponding author.

E-mail address: jackieguzy@gmail.com (J. Guzy).

and stream microhabitat by reducing sediment delivery (Aust and Blinn, 2004, Cristan et al., 2016). Riparian buffers also support natural stream processes by providing shade, inputs of detritus, and exchange of nutrients between terrestrial and aquatic systems (Boothroyd and Langer, 1999, Parkyn, 2004). Retention of SMZs has been recommended for conserving invertebrate, fish, bird, mammal, and vegetative communities (Lee et al., 2004). However, SMZs also may provide habitat for other semi-aquatic species such as salamanders, and may provide movement corridors or refugia for terrestrial species during intensive forestry operations.

In many forest ecosystems, salamanders are the most abundant vertebrates (Peterman et al., 2008, Semlitsch et al., 2014). Salamanders play critical roles as predators and prey (Davic and Welsh, 2004) and are particularly abundant within headwater streams, where densities can exceed $18,400 \text{ ha}^{-1}$ (Petranka and Murray, 2001). Both stream and forest salamanders can influence forest food web dynamics, nutrient cycling, and litter decomposition (Wyman, 1998, Best and Welsh, 2014, Milanovich et al., 2015). Understanding the roles of salamanders in forest and stream ecosystems is particularly relevant, given that millions of hectares of US forests are managed for timber production (Oswalt et al., 2014), and many salamanders are forest-associated (Petranka, 1998) and sensitive to ecosystem perturbations such as harvesting overstory trees (Welsh et al., 2008, Homyack and Haas, 2009). Thus, forest management activities that influence salamander abundance or diversity may affect forest productivity and ecological functions.

Although a broad body of research has examined the influence of forest management on salamanders, most studies have focused on terrestrial (Tilghman et al., 2012) or pond-breeding species (e.g., Semlitsch et al., 2008), with comparatively little research on stream-associated salamanders. Of studies examining stream-associated salamander populations in SMZs, most compared responses across 2–4 buffer widths to unharvested controls at a small number of streams (typically 5–15; Johnston and Frid, 2002, Perkins and Hunter, 2006, Jackson et al., 2007, Peterman and Semlitsch, 2009, Peterman et al., 2011, Maigret et al., 2014). Such categorical study designs have limited ability to reveal thresholds where responses occur, and likewise, small sample sizes have limited ability to detect responses of rarer species. In addition, little is known about interspecific variation in salamander responses or whether riparian buffers serve as refuges for terrestrial species negatively affected by upland harvesting. Further, no studies have rigorously evaluated community-level responses of salamanders to riparian buffer characteristics. Previous studies of stream salamanders in managed forests are restricted to the U.S. Pacific Northwest (e.g., Kroll, 2009) and Appalachian Mountain region (e.g., Petranka and Smith, 2005, Crawford and Semlitsch, 2007, Peterman and Semlitsch, 2009), leaving a large knowledge gap for the biodiversity hotspot of the Ozark/Ouachita Mountains of the central United States.

To evaluate the role of SMZs in maintaining salamander biodiversity within managed forests, we examined abundance and species richness across 102 headwater stream sites that spanned a wide and continuous gradient of SMZ buffer widths and surrounding stand ages. We used a hierarchical Bayesian community occupancy model to estimate salamander species richness and species-specific occupancy responses to SMZ and overstory characteristics along with Bayesian binomial mixture models to examine abundance relationships. We predicted that salamander species richness and abundance would be greatest within the widest SMZs and at sites surrounded by the oldest timber stands. However, we expected variation in the magnitude of species responses to SMZ characteristics, with terrestrial species (i.e., *Plethodon* spp.) being more sensitive than stream-associated species to width and overstory composition.

2. Methods

2.1. Study sites

This study occurred in even-aged loblolly pine (*Pinus taeda*) stands

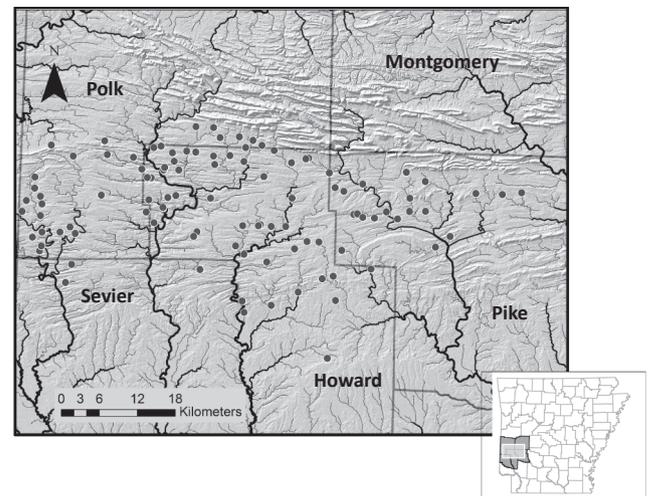


Fig. 1. Location of study sites. Map inset: Ouachita Mountains Ecoregion of west-central Arkansas, USA. Main map: distribution of study sites ($n = 102$) located in Howard, Polk, Pike, and Sevier counties, Arkansas.

managed by Weyerhaeuser Company, and located on the Athens Plateau (Woods et al., 2004), the southernmost subdivision of the Ouachita Mountains in west-central Arkansas, USA (Fig. 1). The Ouachita Mountains run east-west and the Athens Plateau is characterized by low ridges and hills underlain by shale. Much of this region is managed intensively for timber production (Woods et al., 2004) and supports a rich diversity of salamander species (Trauth et al., 2004), including several endemic woodland and stream-breeding Plethodontids (Petranka, 1998).

Using a preliminary analysis of watershed spatial characteristics and field surveys for salamanders, we determined that streams draining $< 3.0 \text{ km}^2$ watersheds had a sufficient hydroperiod to support regional species pools of salamanders but not large populations of predatory fish. Using a GIS (ArcGIS 10.0; Environmental Systems Research Institute, Redlands, CA, USA) and Geodata Crawler (Leasure, 2014), we identified 1854 potential study sites located within managed forests and draining $< 3.0 \text{ km}^2$, and at the watershed-level we classified these sites based on stand age and average width of the SMZ upstream of the sampling location. We determined average SMZ width by measuring riparian buffer boundaries in GIS. Measurements began at the most downstream sampling point for each stream, and moved upstream in 20 m increments; we measured the perpendicular distance from the edge of the buffer to the center of the stream. We took measurements on each side of the stream, such that reported SMZ values represent average width on each side of the stream; SMZ width was relatively consistent on both sides. We verified riparian buffer width by ground-truthing SMZ width during each of four salamander surveys. We then selected the 102 sites across a study area size of 2312 km^2 (Fig. 1) with the most uniform age of upstream forest stands (i.e., watershed upstream of the sampling point on either side of the SMZ comprised of a single stand or similarly aged stands) and that spanned a wide gradient of average SMZ buffer widths (0–55 m; mean = 21.23 m, SD = 10.06 m; Appendix 1a). State forestry BMP guidelines recommend minimum buffers of 11–24 m, depending on slope (Arkansas Forestry Commission, 2002). Upstream forest stands varied in age from 2 to 35 years (mean = 18 years, SD = 10.15 years; Appendix 1b). Common silvicultural practices for the study area included: clearcutting mature stands (25–35 years old), followed by mechanical and/or chemical site preparation, planting of loblolly pine seedlings (~ 1100 trees/ha), fertilization, and typically one commercial thin after ~ 15 years. All sites were headwater streams with 0.08 km^2 to 1.71 km^2 (mean = 0.62 km^2 ; SD = 0.31 km^2) watersheds upstream of the most downstream sampling location. Elevation varied from 138 to 354 m (mean = 241 m; SD = 50 m).

2.2. Data collection

During April – June 2014, 2015, and 2016 we sampled salamanders with repeated, time- and area-constrained surveys in SMZs across the 102 first-order headwater stream sites (Fig. 1). We surveyed each site four times and each survey occurred over a different 15-m stream transect, with transects closely spaced, and positioned at the downstream end of each headwater stream. Surveys consisted of a single observer opportunistically dipnetting and flipping cover objects for 30 min, split between 10 min in the stream channel, 10 min along stream edges, and 10 min in terrestrial habitat within the SMZ. All salamanders captured or observed were identified to species and life stage, counted, photographed, and released at the end of the survey.

During each survey we measured the following variables: air and water temperature, average water depth, average soil moisture, humidity, barometric pressure, dissolved oxygen, conductivity, percent canopy closure, substrate composition, amount of upland cover objects (i.e., upland cover score), and SMZ overstory composition. To estimate percent canopy closure, we used a concave spherical densitometer (Lemmon, 1956) standing at the center of the stream, at the center point of the stream transect, and averaged measurements taken at the 4 cardinal directions. We estimated substrate composition for each survey by dividing the 15-m transect into four sections, and visually estimating percent cover of stream substrate (i.e., bedrock, boulders, cobble, gravel, fine gravel, sand, and silt) following the Wentworth scale of grain size (Wentworth, 1922). The indicator of amount of upland cover objects, ‘upland cover score,’ was determined during each 10-min upland survey, and consisted of a 1–5 scale relating the availability of additional cover objects (i.e., rocks, logs, etc.) to time remaining in 2 min increments (i.e., a score of 1 indicated that after 2 min of searching, no additional cover objects could be located, a score of 2 indicated that after 4 min, no additional cover objects could be located, etc). We visually estimated SMZ overstory composition; ‘Pine’ sites were > 75% pine basal area; ‘Mixed’ sites were 25%–75% pine, and ‘Deciduous’ sites were < 25% pine.

We predicted a nonlinear response of salamander occupancy and abundance to surrounding forest stand age, because mid-rotation thinning is a second disturbance during the approximate 30-year rotation that may influence salamanders (Grialou et al., 2000). Thus, we incorporated age of the adjacent stand(s) as a categorical variable based on years since overstory harvest (clearcutting or thinning). Categories included ‘Young pre-thin’ (stands 0–5 years old, un-thinned), ‘Mid pre-thin’ (6–13 years old, un-thinned), ‘Post-thin’ (13–22 years old, 1–6 years since thinning), and ‘Old Post-thin’ (22–35 years old, 8–17 years since thinning). Finally, we calculated latitude, elevation, watershed area, and average SMZ width using a GIS.

2.3. Data analyses

Because of the large number of site and sampling variables, we used principal components analysis (PCA) in PRIMER 6.0 (Clarke and Gorley, 2006) to reduce dimensionality of data (Clarke, 1993). We performed a PCA on a subset of both site and sampling covariates and used the principal component scores from each of the first two PC axes as site and sampling covariates in occupancy analyses (Appendix 2). To isolate the effects of SMZ width and forest stand age, we did not include them in the PCA; exploratory analyses suggested that they were not strongly correlated with other site or sampling covariates.

2.4. Salamander occupancy

We used a multi-species, hierarchical Bayesian model developed by Zipkin et al. (2009) and modified by Hunt et al. (2013) to estimate species-specific occupancy responses to site-specific covariates (average SMZ width, stand age categories, SMZ composition, Site PC1, and Site PC2) and sampling covariates (PC1 and PC2). This hierarchical

approach incorporates species-specific and assemblage-level (i.e., all salamander species) attributes into the same modeling framework by providing separate estimates for species-specific occurrence and detection probabilities (Dorazio and Royle, 2005, Zipkin et al., 2009) while also accounting for imperfect detection because non-detection does not necessarily indicate species absence (Dorazio et al., 2006, Kéry et al., 2009). Further, because individual species-level estimates are a combination of the single species and the average estimate of those parameters for the entire community (Pacifi et al., 2014), individual parameter estimates, particularly for rare species, are more precise and less likely to be biased (Sauer and Link, 2002).

We generated species-specific observance matrices for four sampling occasions at each site, where detection was represented as 1, and non-detection as 0. Thus, the data provided a three dimensional matrix $x(i,j,k)$ for species i at site j for the k th sampling occasion. We related species-specific salamander covariate parameters (α and β values, described below) and occupancy and detection probabilities (Ψ_{ij} and Θ_{ijk} respectively) with the model below.

- $\text{logit}(\Psi_{ij}) = u_i + \alpha 1_i \text{ SMZ width }_j + \alpha 2_i \text{ Young pre-thin }_j + \alpha 3_i \text{ Mid pre-thin }_j + \alpha 4_i \text{ Post-thin }_j + \alpha 5_i \text{ Staggered harvest }_j + \alpha 6_i \text{ Pine SMZ }_j + \alpha 7_i \text{ Mixed SMZ }_j + \alpha 8_i \text{ No SMZ }_j + \alpha 9_i \text{ Site PC1 }_j + \alpha 10_i \text{ Site PC2 }_j$

We modeled detection probabilities for each species with the following equation, within the model described above:

- $\text{logit}(\Theta_{ijk}) = v_i + \beta 1_i \text{ Sampling PC1 }_j + \beta 2_i \text{ Sampling PC2 }_j$

Parameters $\alpha 2$ – $\alpha 5$ were effects of the categorical predictor variable “stand age”, with “Old post-thin” as the reference category, and parameters $\alpha 6$ – $\alpha 8$ were effects of the categorical predictor variable “SMZ Composition”, with “Deciduous” as the reference category. The u_i parameter is the mean community response (across species) to each α parameter listed above. For example $u_{\alpha 1}$ is the mean community response to the SMZ width covariate. The ‘SMZ width’ covariate was defined as the z-score of the average width of the SMZ surrounding each study stream, upstream of the most downstream sampling location (i.e., site’s SMZ value - mean/SD). Stand age categories (i.e., Young and Mid pre-thin, Post and Old post-thin) and SMZ composition (i.e., Pine, Mixed, Deciduous, or No SMZ) were categorical variables. We defined ‘Site PC1’ and ‘Site PC2’ covariates as the respective z-score of principal component scores from each of the first two site-PC axes (Appendix 2a). Because seven sites were harvested unevenly (i.e., harvest on one side of the stream occurred 5–10 years after the other side; “Staggered”) we included them as a separate stand age category in the model, but excluded them from subsequent comparisons. Finally, when modeling detection probability, the ‘Sampling PC1’ and ‘Sampling PC2’ covariates were defined as the respective z-score of principal component scores from each of the first two sample-specific-PC axes (Appendix 2b).

The model contained 14 species-specific parameters ($u_i, \alpha 1_i, \alpha 2_i, \alpha 3_i, \alpha 4_i, \alpha 5_i, \alpha 6_i, \alpha 7_i, \alpha 8_i, \alpha 9_i, \alpha 10_i, v_i, \beta 1_i, \beta 2_i$). Standardized covariates allowed us to estimate Ψ and Θ at mean site and survey covariates (where the z-score equals zero) from model-generated estimates of u_i and v_i and allowed direct comparison of model coefficients as effect sizes relative to variation in each covariate. We organized all data in Program R (3.3.2) (R Development Core Team, 2015) and executed analyses in WinBUGS (Spiegelhalter et al., 2003) using R2WinBUGS (Sturtz et al., 2005). This model, and abundance models (see below; Abundance) were implemented in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in WinBUGS to generate samples from the posterior distribution (Lunn et al., 2012).

We estimated species richness at sampled sites by summing indicator variables for occupancy for each species at each site, and simulated species richness at hypothetical sites with SMZ width ranging from 0 m to 55 m for each model iteration to generate a posterior

Table 1

Summary of species captured, with model-estimated occupancy and detection probabilities and 95% credible intervals, for salamanders within streamside management zones in managed forests in the Ouachita Mountains, Arkansas, USA.

Common name	Scientific name	Captures	# of sites	Occupancy			Detection		
				Mean	(95% posterior interval)		Mean	(95% posterior interval)	
Ringed salamander	<i>Ambystoma annulatum</i>	2	2	0.03	0.01	0.37	0.08	0.00	0.67
Spotted salamander	<i>Ambystoma maculatum</i>	25	4	0.07	0.01	0.80	0.03	0.00	0.18
Marbled salamander	<i>Ambystoma opacum</i>	1	1	0.05	0.01	0.87	0.02	0.00	0.26
Ouachita dusky salamander	<i>Desmognathus brimleyorum</i>	550 ⁺	60 ⁺	0.59	0.36	0.78	0.69	0.63	0.75
Many-ribbed salamander	<i>Eurycea multiplicata</i>	502 ⁺	89 ⁺	0.97	0.89	0.99	0.60	0.54	0.65
Four-toed salamander	<i>Hemidactylium scutatum</i>	2	2	0.06	0.01	0.83	0.03	0.00	0.22
Caddo Mt. salamander	<i>Plethodon caddoensis</i>	27	8	0.03	0.01	0.11	0.27	0.11	0.50
Slimy salamander	<i>Plethodon glutinosus</i> [#]	73	34	0.53	0.29	0.79	0.26	0.18	0.36
S. red-backed salamander	<i>Plethodon serratus</i>	189	39	0.41	0.22	0.64	0.30	0.21	0.40
Lesser siren	<i>Siren intermedia</i>	1	1	0.06	0.01	0.87	0.02	0.00	0.25

⁺Captures (Adults: 432, Larva: 118), # of sites (Adults: 58, Larva: 43).

*Captures (Adults: 106, Larva: 396), # of sites (Adults: 46, Larva: 84).

[#]*P. glutinosus* complex.

predictive distribution for species richness as a function of SMZ width. We used uninformative priors for the hyper-parameters (i.e., $U(-3$ to $3)$ for μ_α and μ_β parameters and $U(0, 5)$ for all σ parameters; species-specific model coefficients were truncated at ± 5 from μ to avoid traps). Three parallel chains were run in WinBUGS for each model so that convergence could be assessed via the Gelman-Rubin diagnostic. For all monitored parameters in the study, this value was at or below 1.02 (Gelman and Rubin, 1992). Each chain was run for 70,000 iterations in total, the first 20,000 were removed as burn-in, and remainder were thinned by a factor of 3. Across the three chains, this provided a total of 50,000 samples to approximate posterior summary statistics for each model parameter including mean, standard deviation, and 2.5% and 95% percentiles of the distribution, which represent 95% Bayesian credible intervals. Credible intervals (CIs) are defined by quantiles of the posterior distribution, and we inferred strong support for continuous covariates when intervals did not contain zero. Some covariates were treated categorically, and in this case, we inferred strong support by generating posterior summary statistics including the mean difference in species richness between categorical covariates, which was further examined using Bayesian t-tests (Kéry, 2010). Species-specific occupancy and detection estimates were derived using the inverse logit transformation (i.e. $(\exp(\alpha)/(1 + \exp \alpha))$).

Finally, to evaluate whether greater upland survey area within the widest SMZs influenced salamander occupancy or richness relationships, we conducted an identical analysis including only in-stream and riparian survey captures, for which survey area was similar for all sites, and was not influenced by SMZ width. We then qualitatively compared these results to those from analyses including upland surveys to examine whether strong relationships (i.e., credible intervals that don't contain zero) changed.

2.5. Salamander abundance

We used binomial mixture models (Royle, 2004) to examine effects of forest (i.e., SMZ width and composition, age of the surrounding stand) and habitat covariates on abundance of common salamander species. We conducted four replicate count surveys at 102 spatially distinct sites (*i*) during temporally indexed surveys (*j*), denoted as c_{ij} (Royle and Dorazio, 2008). Under this framework, counts were modeled as independent outcomes of binomial sampling with index N_i and detection probability p_i . Abundances (λ) at the local-level were modelled with a Poisson distribution and heterogeneity in abundance among populations due to habitat covariates (x_i) were modelled using a Poisson-regression formulation of local mean abundances, given by $\log(\lambda_i) = \beta_0 + \beta_1 x_i$. Sources of heterogeneity in detection were identified by modelling associations between sampling covariates and p_i such that $\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{ij}$. See Price et al. (2013) for further model

description.

We first separated salamander count data by site ($n = 102$) and species, and for the two most common species, *D. brimleyorum* and *E. multiplicata*, by age class (i.e. adult vs. larva). Low sample sizes of three Ambystomatid species, *H. scutatum* and *S. intermedia* (Table 1) prevented abundance analyses for these species. Finally, because *P. caddoensis* inhabits a geologically distinct area of the Ouachita Mountains (Trauth and Wilhide, 1999), we analysed counts for a subset of sites where the species occurred ($n = 8$ sites) and simplified the model by only using SMZ width as the site covariate, and date as the sample-specific detection covariate. In total, we had seven separate groups of salamanders [*D. brimleyorum* (adults, larva), *E. multiplicata* (adults, larva), *P. glutinosus*, *P. serratus*, and *P. caddoensis*].

We specified salamander abundance with the model below. Parameters $\beta_2 - \beta_5$ were the effects of the categorical predictor variable “stand age”, with “Old post-thin” as the reference category.

- $N_i | \lambda_i \sim \text{Poi}(\lambda_i)$
 $\log(\lambda_i) = \beta_0 + \beta_1 \text{SMZ width} + \beta_2 \text{Young pre-thin} + \beta_3 \text{Mid pre-thin} + \beta_4 \text{Post-thin} + \beta_5 \text{Staggered harvest} + \beta_6 \text{Site PC1} + \beta_7 \text{Site PC2}$

Heterogeneity in detection probability was modelled for each species, with the following equation included within the model described above:

- $c_{ij} | N_i \sim \text{Bin}(N_i, p_{ij})$
 $\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 \text{Sampling PC1}$

Site (i.e., average SMZ width, Site PC1, and Site PC2) and sampling (Sampling PC1) covariates were standardized by z-score. Models used uninformative priors; specifically, we assumed $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7 \sim N(0, 10^2)$, $\alpha_0 \sim N(0, 1.6^2)$ and $\alpha_1 \sim N(0, 10^2)$. The α_0 prior approximates a $U(0,1)$ prior for $\text{expit}(\alpha_0)$, where expit represents the inverse logit function (i.e., $\exp(\alpha)/(1 + \exp(\alpha))$). Posterior summaries for each parameter were based on 150,000 Markov chain Monte Carlo iterations with a 20,000 sample burn-in and a thinning rate of 3. This provided a total of 130,000 samples from which we approximated posterior summary statistics for each of the model parameters including the mean, standard deviation, and 2.5% and 95% percentiles of the distribution, which represent 95% Bayesian credible intervals. As with occupancy analysis (above) we used Bayesian t-tests (Kéry, 2010) to infer significance for categorical covariates and assessed convergence via the Gelman-Rubin diagnostic (i.e., all monitored parameters at or below 1.02 (Gelman and Rubin, 1992).

As with occupancy analyses, we conducted a second analysis with only stream and riparian surveys, for which survey area was similar

across sites, to evaluate whether greater survey area within the widest SMZs influenced abundance relationships. We conducted these analyses for the four most common species (*D. brimleyorum*, *E. multiplicata*, *P. serratus*, and *P. glutinosus*).

3. Results

We captured 1372 salamanders of 10 species across four replicate surveys at each of 102 first-order stream sites (Table 1). Captures were dominated by two stream-breeding species, the Ouachita dusky (*Desmognathus brimleyorum*, 40%) and many-ribbed salamander (*E. multiplicata*, 37%), followed by two terrestrial species, the southern red-backed (*Plethodon serratus*, 14%) and slimy salamander (*P. glutinosus* complex; 5%, Table 1). The *P. glutinosus* complex has been split into many independent lineages, and the predominant species in the region is *P. albagula* (Petranka, 1998). However, because several other non-morphologically distinguishable species may occur in the study area, we refer to this complex collectively as *P. glutinosus*. The six remaining species included the Caddo Mountain salamander (*P. caddoensis*), a terrestrial species narrowly endemic to the study region, the uncommon four-toed salamander (*Hemidactylum scutatatum*), three pond-breeding species (ringed [*Ambystoma annulatum*], spotted [*A. maculatum*], and marbled [*A. opacum*] salamanders), and the fully aquatic lesser siren (*Siren intermedia*).

The first two site-covariate PC axes explained 31.0 and 15.5% of the variance, respectively (Appendix 2a). Site PC1 had a high positive factor loading for latitude (0.40), which likely drives patterns in the remaining stream characteristic scores of Site PC1 [high elevation (0.34), low sand substrate coverage (−0.36), cool water temperature (−0.43), and low conductivity (−0.34)]. Thus, we considered Site PC1 as a general index of northerly geographic position within the southern tier of the Ouachita Mountains. Site PC2 had a high positive factor loading for watershed area (0.35) and negative factor loading for elevation (−0.40), likely driving patterns in the remaining stream characteristic scores of Site PC2 [more boulder/cobble (0.51), less sand (−0.38), and less canopy cover (−0.38)].

The first two sampling-covariate PC axes explained 33.8 and 20.0% of the variance, respectively (cumulative 53.8%; Appendix 2b). The first sampling-covariate axis (Sampling PC1) had high positive factor loadings for date (0.51), water temperature (0.58) and air (0.49) temperature, and a negative factor loading for soil moisture (−0.34); thus high Sampling PC1 scores reflected later date, warmer weather, and drier soil. The second sampling-covariate axis (Sampling PC2) had negative factor loadings for date (−0.35), humidity (−0.70), water depth (−0.31) and soil moisture (−0.45), and a positive factor loading for air temperature (0.29); thus high Sampling PC2 scores reflected drier conditions with lower humidity and shallower water. These conditions were negatively correlated with date, likely due to unusually wet summers in 2014–2016.

3.1. Occupancy, detection, and species richness

Across the entire species assemblage, mean salamander occupancy response to SMZ width was positive ($u_{\alpha 1}$: 1.08; 95% CI 0.47 to 1.80), indicating a positive relationship between occupancy and increasing SMZ width. Mean estimated occupancy probability varied from 6.03% (95% CI 0.44 to 25.90%) at SMZ widths < 1 m, to 87.00% (95% CI 45.80 to 99.58%) at SMZ widths averaging > 55 m on each side of the stream (Fig. 2a). Furthermore, the across-species standard deviation ($\sigma = 0.56$, 95% CI 0.03 to 1.42) for the SMZ covariate effect was less than the corresponding mean (μ) covariate estimate ($CV_{\alpha 1} = 0.52$), indicating that the occupancy response to increasing SMZ width was consistently positive across species (Fig. 3; Appendix 3). Results of this model also indicated a positive occupancy response of the salamander assemblage to Site PC1 ($u_{\alpha 9}$: 0.66, 95%CI 0.13 to 1.20; Appendices 3 and 4a) that was consistently positive across species ($CV_{u_{\alpha 9}} = 0.76$).

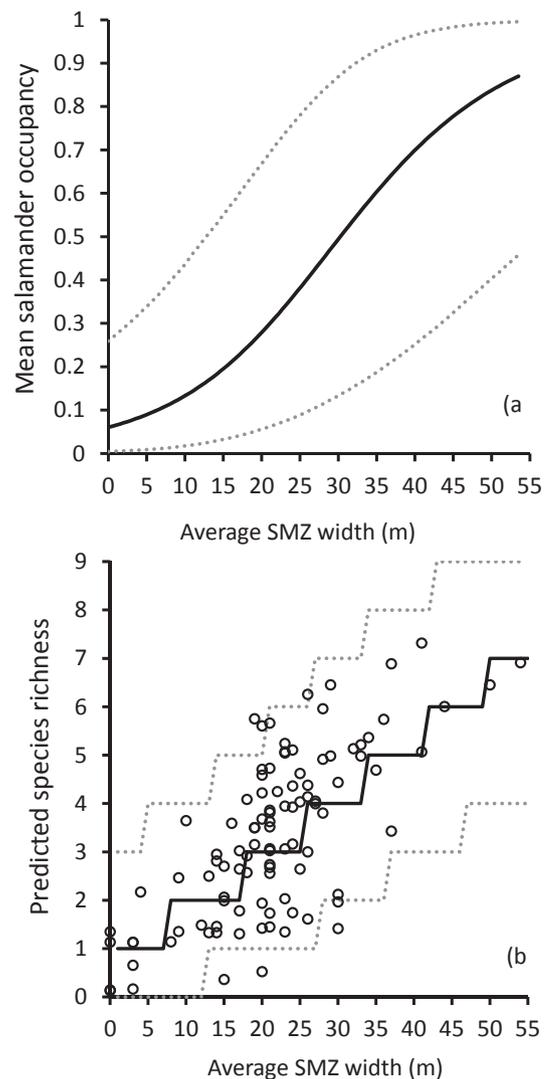


Fig. 2. Relationship between streamside management zone (SMZ) width and a) mean occupancy probability and b) median estimated species richness of salamanders within streamside management zones of the Ouachita Mountains, Arkansas, USA. Solid lines represent the posterior mean and dashed lines represent a) the 95% credible interval and b) 95% predictive interval of species richness at hypothetical sites. Circles are site-specific mean richness estimates.

Thus, salamander occupancy was greater at sites located at higher latitude and elevation, which also tended to have less sand and silt, cooler water, and lower conductivity. We did not detect a relationship between assemblage occupancy and Site PC2.

The community response to the Sampling PC1 covariate (i.e., $\mu_{\beta 1}$ PC1) indicated that detection probability was greater at earlier dates, which also had cooler temperatures and moister soils ($\mu_{\beta 1}$: −0.49; 95% CI −1.04 to −0.01; Appendix 4b). We did not detect evidence for a relationship between mean detection probability and Sampling PC2.

3.1.1. Species-specific occupancy responses to increasing SMZ width

Across all species, there was a positive occupancy response to increasing SMZ width, but the magnitude of the relationship varied among species. Specifically, wide SMZs strongly influenced (i.e., non-overlapping credible intervals) *A. maculatum*, *A. opacum*, *D. brimleyorum*, *E. multiplicata*, *H. scutatatum*, *P. glutinosus*, and *P. serratus* (Fig. 3; Appendix 3). When examining patterns among individual species, three groups were evident: (1) high occupancy, even at sites with narrow SMZs (*E. multiplicata*), (2) low occupancy within narrow SMZs, high occupancy within wide SMZs (*D. brimleyorum*, *P. serratus*, and *P.*

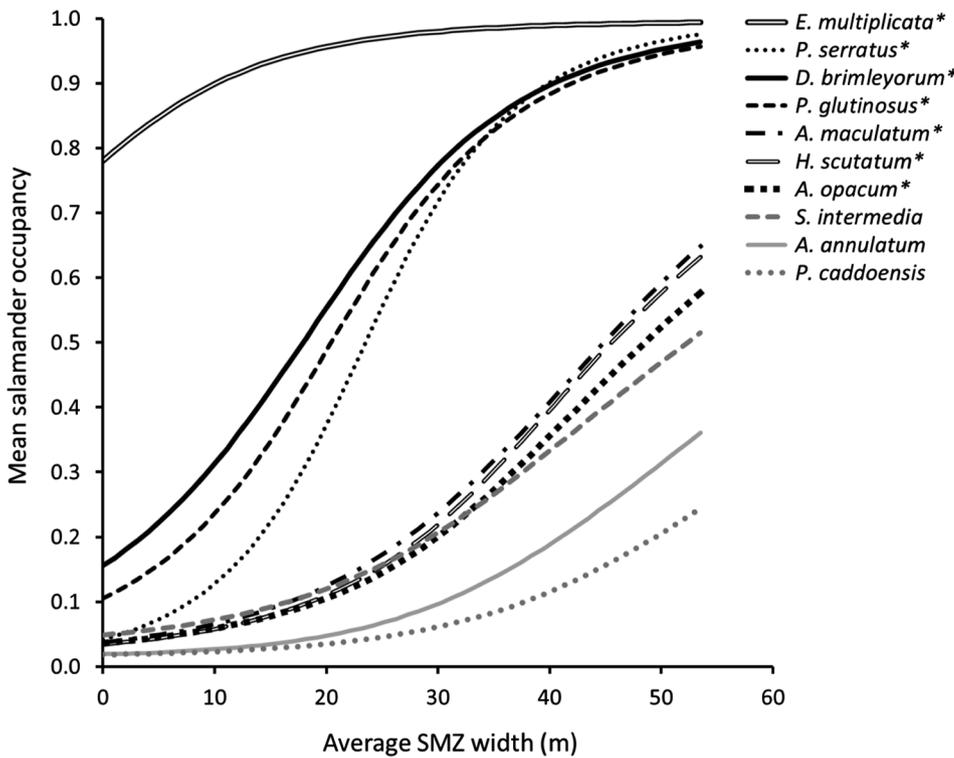


Fig. 3. Relationship between mean species-specific occupancy probability and streamside management zone (SMZ) width for salamanders within SMZs of the Ouachita Mountains, Arkansas, USA. Credible intervals are omitted for clarity, and asterisks indicate species for which the SMZ parameter estimate (α_{1i}) did not overlap zero.

glutinosus), and (3) species found within wide SMZs, but with low occupancy probability (*A. annulatum*, *A. maculatum*, *A. opacum*, *H. scutatum*, *P. caddoensis*, and *S. intermedia*) (Table 1; Fig. 3; Appendix 3)

3.1.2. Species richness: SMZ characteristics and stand age

Estimated salamander species richness was strongly influenced by increasing SMZ width. Assuming average values of other site and sampling covariates, estimated species richness per site varied from 1 species (95% CI 0 to 3) at sites with narrow SMZs to 7 species (95% CI 4 to 9; Fig. 2b) at sites with the widest (> 50 m on each side of the stream) SMZs. Estimated species richness increased with increasing SMZ width, with a richness of at least 4 out of 7 estimated species not predicted until SMZ width was > 27 m, and maximum species richness reached when SMZ widths exceeded 50 m on each side of the stream (Fig. 2b).

We found strong support for differences in estimated salamander species richness among Stand Age categories, with richness highest in Old Post-thin sites (4.45), lowest in Mid Pre-thin sites (2.23), and intermediate at Young Pre-thin (3.18) and Post-thin sites (4.08) (Fig. 4a, Appendix 5a). Estimated richness was twice as high (~4 species) in SMZs comprised of Mixed or Deciduous overstory, compared to Pine (~2 species; Fig. 4b and Appendix 5b).

3.1.3. Occupancy analysis excluding upland surveys

Analysis including only stream and riparian data did not alter the mean salamander community occupancy response to increasing SMZ width (u_{α_1} 1.34; 95% CI 0.48 to 2.17), and likewise, species-specific occupancy responses to increasing SMZ width remained strongly positive (i.e., non-overlapping credible intervals) for *A. maculatum*, *A. opacum*, *D. brimleyorum*, *E. multiplicata*, *P. glutinosus*, and *P. serratus*. One species, *H. scutatum*, was not analyzed because it was only detected during upland surveys. Further, the richness relationship with SMZ width did not change when upland surveys were removed; estimated species richness per site varied from 1 species (95% CI 0 to 4) at sites with narrow SMZs to 8 species (95% CI 5 to 9; Fig. 2b) at sites with the widest SMZs.

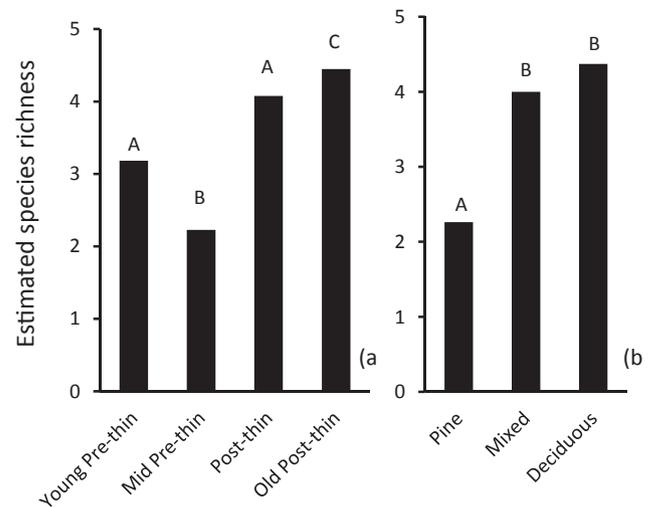


Fig. 4. Estimated mean salamander species richness among (a) stand age and (b) overstory composition categories of streamside management zones (SMZs) within the Ouachita Mountains, Arkansas, USA. Columns that do not share a letter are statistically different from each other (i.e., credible interval does not contain zero). Stand age categories are defined as ‘Young pre-thin’ (stands 0–5 years old, un-thinned), ‘Mid pre-thin’ (6–13 years old, un-thinned), ‘Post-thin’ (13–22 years old, 1–6 years since thinning), and ‘Old Post-thin’ (22–35 years old, 8–17 years since thinning).

3.2. Abundance

We found strong support for the influence of Site PC1 on mean estimated abundance of *D. brimleyorum* (adults and larva), *P. glutinosus*, and *P. serratus* (Appendix 6) indicating that abundance for these species increased with increasing latitude and elevation (Appendix 2b). Mean estimated abundances of *D. brimleyorum* (adults and larva) and *P. glutinosus* were positively associated with ‘Site PC2’ (Appendix 6) indicating that abundance of these species increased with stream size (i.e., larger watersheds; Appendix 2b). Finally, detection probabilities

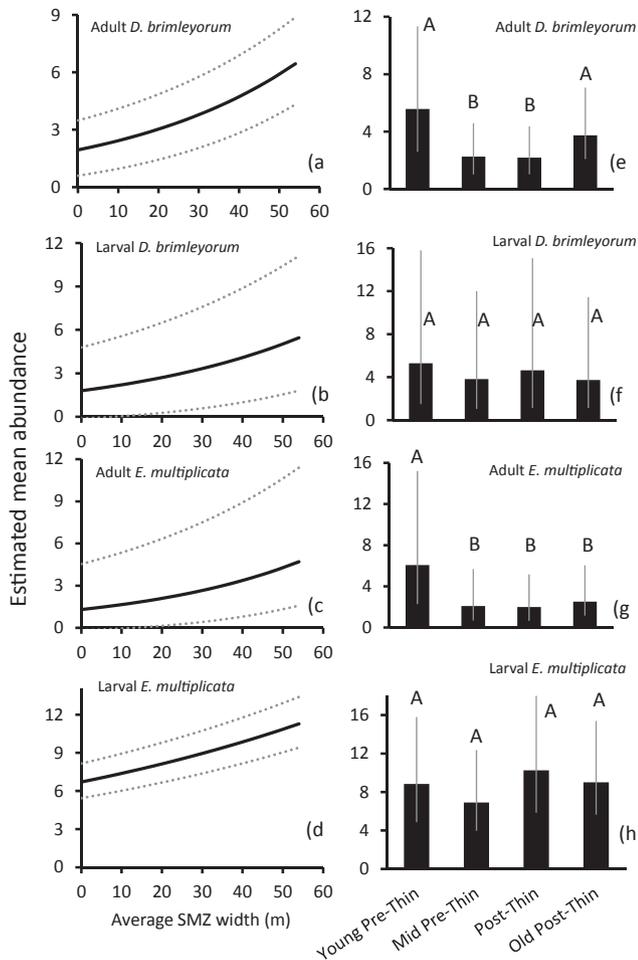


Fig. 5. Estimated mean abundance by age class of *Desmognathus brimleyorum* and *Eurycea multiplicata* in relation to (a-d) streamside management zone (SMZ) width and (e-h) stand age within the Ouachita Mountains, Arkansas, USA. Solid lines represent the posterior mean and dashed lines represent the 95% credible interval.

of larval and adult *D. brimleyorum*, larval and adult *E. multiplicata*, and *P. serratus* were negatively associated with ‘Sampling PC1’ (Appendix 6), indicating that detection decreased at later dates when temperature was warmer and soils were drier (Appendix 2b).

3.2.1. SMZ width

Increasing SMZ width strongly influenced estimated abundance of *D. brimleyorum*, *E. multiplicata*, *P. caddoensis*, and *P. serratus* (β_1 (*D. brimleyorum*) = 0.40; 95% CI 0.28 to 0.52; β_1 (*E. multiplicata*) = 0.22; 95% CI 0.10 to 0.33), β_1 (*P. caddoensis*) = 0.38; 95% CI 0.00 to 0.73), and β_1 (*P. serratus*) = 0.50; 95% CI 0.31 to 0.70; Appendix 6). Mean estimated abundance of adult *D. brimleyorum* varied from 1.94 (95% CI 0.60 to 3.48) per 15 m transect, at SMZ widths of < 1 m to 6.44 (95% CI 4.31 to 8.88) at SMZ widths > 55 m and the relationship was similar for larva (Fig. 5 a-b). Mean estimated abundance of adult *E. multiplicata* varied from 1.3 (95% CI -0.18 to 4.53) at SMZ widths of < 1 m to 4.70 (95% CI 1.58 to 11.39) at SMZ widths > 55 m and the relationship was similar for larva (Fig. 5c-d). Mean estimated abundance of *P. serratus* varied from 0.96 (95% CI -0.18 to 2.13) at SMZ widths of < 1 m to 4.30 (95% CI 2.26 to 6.38) at SMZ widths > 55 m (Fig. 6a). There was no relationship between *P. glutinosus* abundance and SMZ width (Fig. 6b; Appendix 6). Abundance of *P. caddoensis* varied from to 5.93

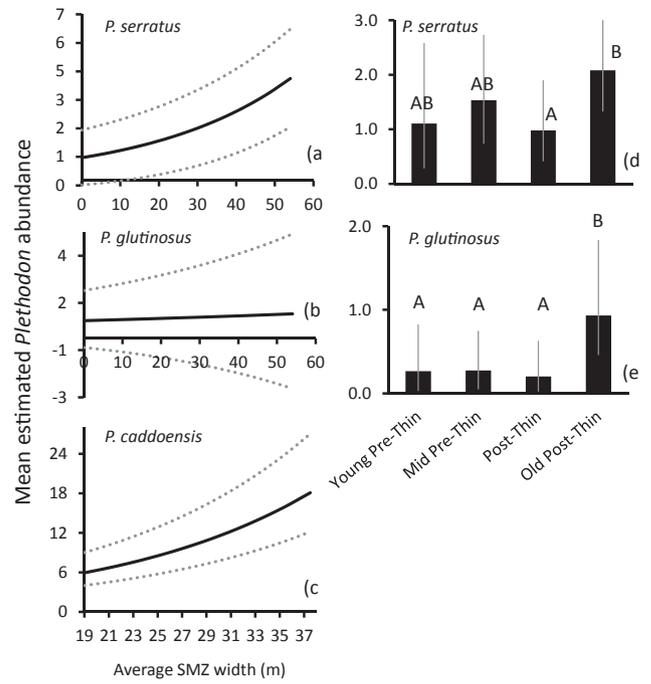


Fig. 6. Estimated mean abundance of (a) *Plethodon serratus*, (b) *P. glutinosus* complex, and (c) *P. caddoensis* in relation to streamside management zone (SMZ) width, and mean abundance of (d) *P. serratus* and (e) *P. glutinosus* complex in relation to stand age within the Ouachita Mountains, Arkansas, USA. Solid lines represent the posterior mean and dashed lines represent the 95% credible interval. Analyses for *P. caddoensis* were restricted to the subset of 8 sites where the species occurred.

(95% CI 4.00 to 9.02) at SMZ widths of 19 m to 18.08 (95% CI 12.15 to 27.04; Fig. 5c) at SMZ widths of 37 m.

3.2.2. Analysis excluding upland surveys

Analysis including only stream and riparian data did not alter salamander abundance relationships; specifically, increasing SMZ width strongly influenced estimated abundance of *D. brimleyorum*, *E. multiplicata*, and *P. serratus* (β_1 (*D. brimleyorum*) = 0.42; 95% CI 0.30 to 0.53; β_1 (*E. multiplicata*) = 0.23; 95% CI 0.11 to 0.34), and β_1 (*P. serratus*) = 0.52; 95% CI 0.20 to 0.83).

3.2.3. Stand age

Across our stand age categories, young stands prior to thinning and older stands after thinning had the highest estimated abundances of adult *D. brimleyorum*, with 5.58 individuals (95% CI 2.58–11.34) and 3.73 (95% CI 2.08–7.07) individuals per 15 m transect, respectively. Estimated abundance of Mid-rotation age sites (Mid Pre-Thin and Post-Thin) was approximately half that of recently harvested and old sites (Fig. 5e; Appendix 7a). However, there was no difference among stand age categories in abundance of larval *D. brimleyorum* (Fig. 5f; Appendix 7b).

Estimated abundances of adult *E. multiplicata* were similar (2.00–2.51 per 15 m transect) at Mid pre-thin, Post-thin, and Old post-thin sites, but were three-fold higher in streams embedded in Young Pre-thin sites (6.06; 95% CI 2.28–15.21) (Fig. 5g; Appendix 7c). Mean abundance of larval *E. multiplicata* was similar across Stand Age categories (6.92–10.26 individuals per 15 m transect; Fig. 5h; Appendix 7d).

Mean abundance of *P. serratus* was highest at Old post-thin sites (2.08 per 15 m transect; 95% CI 1.33–3.19), corresponding to

approximately twice as many individuals as in Post-thin (mid-age) sites (Fig. 6d; Appendix 7e). Abundances were similar among remaining Stand Age categories. Old post-thin sites had an estimated 0.93 *P. glutinosus* per 15 m transect (95% CI 0.46–1.84), corresponding to approximately 3–4 times as many individuals as in Young, Mid, and Post-thin sites (Fig. 6e; Appendix 7f).

4. Discussion

We investigated variation in salamander abundance and species richness across > 100 headwater stream sites embedded in an intensively managed forest landscape at a large spatial-scale. We documented all stream and terrestrial plethodontid salamander species potentially occurring in the region, and several additional species associated with lentic habitat types. Across the salamander community, occupancy, species richness, and abundance were positively related to increasing SMZ width, with maximum estimated richness of 7–9 species occurring at sites with buffers extending 55 m on either side of the stream. Sites with deciduous or mixed deciduous-pine SMZs had nearly twice as many species as those with a pine-dominated canopy. Patterns of species richness and abundance across stand ages were variable, with some patterns suggesting lagged responses to harvesting (i.e., lowest richness within mid-age stands) or potential concentrations of individuals near streams following harvest. Collectively, results indicate that SMZs surrounding first-order streams embedded in intensively managed forest can support robust salamander communities and enhance biodiversity of managed landscapes.

4.1. SMZ width

Riparian buffers are one of the primary tools implemented to mitigate effects of forestry operations on water quality in the United States (Cristan et al., 2018). Recommended width of SMZs varies across jurisdictions and can either be a fixed distance determined by slope or type of water body, or a variable width, based on specific site conditions (e.g., local hydrology or geomorphology; Phillips et al., 2000). The fixed-width approach is most common, and a minimum buffer width of 15–30 m on either side of the stream is typical in many U.S. jurisdictions (Blinn and Kilgore, 2001, Lee et al., 2004, Marczak et al., 2010). Previous studies tracking riparian habitat use by salamanders in undisturbed forests have suggested buffers of 42–79 m on either side of the stream are needed to protect core habitat used by salamanders, with an additional 50 m needed to avoid edge effects (Crawford and Semlitsch, 2007, Connette et al., 2016). Experimental manipulation of SMZ width, using ~2–3 different width treatments (i.e., a categorical experimental design) have documented the importance of SMZs to salamander population parameters. However, because these studies did not examine continuous variation in buffer widths and had relatively small sample sizes, (Maigret et al., 2014, Peterman and Semlitsch, 2009, Johnston and Frid, 2002, Jackson et al., 2007, Perkins and Hunter, 2006) they had a limited ability to detect threshold responses or evaluate differential responses among species. We demonstrate that salamander occupancy, abundance, and species richness increased linearly with increasing SMZ width and was highest at the maximum sampled buffer width (55 m).

Forestry BMP guidelines for the study region recommend minimum buffers of 11–24 m and 11–15 m, for Arkansas and Oklahoma, respectively (Arkansas Forestry Commission, 2002, Oklahoma Forestry Services, 2016). While average buffer width across 102 sites was 21 m, corresponding to an estimated richness of 1–5 salamander species (mean = 3), wider SMZs do occur throughout the managed forest landscape. Although forestry BMP guidelines for riparian buffer width

were developed to protect water quality, SMZs can also benefit riparian-associated and aquatic wildlife (Warrington et al., 2017), and our results extend these benefits to salamander communities. However, to maintain the entire salamander community, implementation of wide buffers at a subset of streams across the landscape should continue.

Previous studies of the effects of forestry on stream salamanders have generally focused on 1–2 focal species, but a multi-species hierarchical occupancy approach allowed us to understand relationships for the entire salamander community, including uncommon species. Salamanders exhibited strong interspecific variation in responses, which likely drives the strong positive relationship we observed between SMZ width and species richness. For example, occupancy probability and estimated abundance of *D. brimleyorum* strongly increased with increasing SMZ width, whereas occupancy of *E. multiplicata* was high across all sites, even those with narrow SMZs. *Desmognathus brimleyorum* may be more sensitive to local habitat conditions and therefore require wider buffers to persist in managed stands. Our findings that *D. brimleyorum* are sensitive to narrow SMZs is especially notable because previous research on congeners (*D. quadramaculatus*, *D. ocoee*, *D. monticola*) has found many species to be associated with the stream channel, and primarily found within 15 m of headwater streams (Crawford and Semlitsch, 2007, Peterman et al., 2008), suggesting that *Desmognathus* spp. may be resilient to immediate effects of stand harvest (Peterman and Semlitsch, 2009).

As with *D. brimleyorum*, occupancy of two terrestrial, direct-developing species, *P. serratus* and *P. glutinosus*, was strongly tied to wider SMZs, with estimated occupancy increasing from 35% within SMZs < 15 m wide to nearly 100% at sites with the widest SMZs. Abundance of *P. serratus* was also positively related to SMZ width, and this relationship was consistent when analyses excluded upland surveys; thus, the positive relationship between SMZ width and occupancy and abundance likely reflects suitable microhabitat conditions in wider SMZs rather than greater area (Wilson and MacArthur, 1967; Simberloff and Wilson, 1969). In general, counts of terrestrial salamanders are reduced following clearcut harvesting (Petranka et al., 1994, Ash, 1997, Herbeck and Larsen, 1999, Knapp et al., 2003, Hocking et al., 2013), in part because these species are sensitive to environmental disturbances that modify temperature, humidity, or soil moisture. For example, eastern red-backed salamanders (*Plethodon cinereus*) exhibit strong avoidance of edge habitats (DeGraaf and Yamasaki, 1992, deMaynadier and Hunter, 1998, Gibbs, 1998) and this effect can extend from 20 m up to 80 m in a dry year (Marsh and Beckman, 2004) because of alterations to abiotic and biotic conditions at harvest boundaries. Therefore, wider SMZs may buffer against edge effects occurring at harvest boundaries, and may provide refuges for *Plethodon* species to persist after upland silvicultural activities (deMaynadier and Hunter, 1995, Tilghman et al., 2012). Use of SMZs by terrestrial salamanders suggests that these areas may provide important corridors that promote connectivity between managed forest stands, allowing individuals to move into harvested stands as they regenerate.

High salamander species richness at sites with wide SMZs was driven by uncommon species that had low overall occupancy and generally only occurred at sites with wide SMZs, and this pattern held when analyses excluded upland surveys. These species included the endemic *P. caddoensis* and *A. annulatum*, along with *H. scutatum*, *A. maculatum*, *A. opacum*, and *S. intermedia*. Salamanders in this group are generally uncommon and have specific habitat requirements, such as preference for rocky talus (*P. caddoensis*) or use of lentic habitats for breeding and larval development (*Ambystoma* spp. and *S. intermedia*). In this study, greater habitat diversity likely positively influences species richness. This conclusion is supported by the presence of salamanders with specific habitat requirements in large SMZs, and by analyses aimed

at identifying whether greater area of salamander habitat (Wilson and MacArthur, 1967; Simberloff and Wilson, 1969) played a role in species richness relationships.

4.2. SMZ composition

Estimated salamander species richness was approximately two times greater in SMZs with deciduous-dominated overstories, compared to those dominated by pine. Higher salamander richness in hardwood forests has been attributed to conditions favoring production of terrestrial and aquatic macroinvertebrate prey, including a more speciose leaf litter resource base (Swan and Palmer, 2006, Willacker et al., 2009), deeper leaf litter and higher soil pH (DeGraaf and Rudis, 1990, Wyman and Jancola, 1992), and higher litter nutrient quality and decomposition rates (Taylor et al., 1989, Klemmedson, 1992, Whiles and Wallace, 1997). Silvicultural practices that maintain a diverse overstory in riparian buffers, or prioritize deciduous species, may positively influence salamander richness. Because the primary crop trees within managed forests are pine species, maintaining deciduous SMZs is particularly important to increasing heterogeneity at the landscape scale.

4.3. Stand age

Estimated salamander richness within SMZs was highest (~5 species) at sites surrounded by the oldest stands (i.e., 22–35 years old, 8–17 years post-thinning). This finding is consistent with previous studies indicating salamander richness and abundance is low within recently clearcut stands (> 10 years) and highest in mature stands (50–120 years; Petranka et al., 1993, 1994; Herbeck and Larsen, 1999). Observational studies suggest recovery of salamander populations to pre-disturbance levels varies between 25 years and 100+ years (Ash, 1997, Petranka et al., 1993, Ashton et al., 2006, Herbeck and Larsen, 1999) and likewise, experimental research indicates > 60 years may be necessary (Homyack and Haas, 2009), with recovery times varying by species.

Contrary to expectations, estimated salamander richness was lowest at sites within SMZs adjacent to mid-age stands (~2 species), rather than recently harvested stands. This pattern may be explained by a lagged effect of harvesting on salamander richness. Declines in richness may be delayed because of sublethal effects that reduce body condition, survival, or reproduction, ultimately leading to declines in abundance and eventual loss of species from sites. For example, Peterman et al. (2011) found that *D. ocoee* within narrow buffers (0 and 9 m) lost body mass, whereas salamanders in non-harvested areas gained weight. Further, Homyack and Haas (2009) reported reduced reproduction of *P. cinereus* at 7–13 years after clearcut harvest relative to unharvested controls. Alternatively, compared to other stand ages, habitat conditions of mid-aged stands may be poorest. For example, abundant woody debris or arthropod prey following harvest may act as refugia or mitigate canopy loss in young stands; but this effect may decline as stands age and debris becomes degraded or scarce (Moore et al., 2002, McKenny et al., 2006, Rittenhouse et al., 2008).

Although species richness was lowest in SMZs within mid-aged stands (i.e., ~15 years), abundance of two stream-associated species was highest in SMZs surrounded by recently harvested stands. Specifically, we estimated approximately six adult *D. brimleyorum* and *E. multiplicata* per 15 m linear stretch of stream at young pre-thin sites, compared to ~2–4 individuals within other stand age categories. One explanation for this pattern is that salamanders leave harvested areas (i.e., uplands) seeking habitat within the SMZ, rather than retreating underground or dying as a result of desiccation or starvation (i.e., evacuation hypothesis; Semlitsch et al., 2008). Although these species are semi-aquatic, they can be found away from streams, and perhaps

these individuals evacuate to the stream during and immediately after harvest. In a study evaluating the impacts of riparian timber harvest on stream-breeding salamanders, Peterman et al. (2011) found that following intensive riparian logging, salamanders at sites with small buffers (i.e., 0 and 9 m) evacuated the modified riparian forest and entered the respective streams. Alternatively, high abundance of salamanders at SMZs within in young stands could reflect an increase in individual detection probability of salamanders following harvest. For example, harvest of the surrounding stand might concentrate salamanders within the stream where they are easily detected under riparian cover objects. In a concurrent capture-recapture study at two streams in this region, we observed increased in-stream movement of *D. brimleyorum* following timber harvest, but no reduction in survival or individual capture probability up to 2 years post-harvest (Halloran, 2017), lending support to the evacuation hypothesis as a mechanism for the abundance patterns we observed. Thus, our findings corroborate those of Peterman et al. (2011). Further, this result supports the idea that streams and their associated SMZs, along with stringers (i.e., vegetated buffers retained along ephemeral drainages/gullies; Parrish et al., 2017), may be important as refugia for species negatively affected by forest harvest. Similar larval abundances across stand age categories suggest that reproduction was not strongly influenced by stand age or mid-rotation silvicultural treatments including commercial thinning. Conversely, reduced abundance of adult *D. brimleyorum* at sites located in mid-age stands could result from either a lagged decrease in adult survival or dispersal of adults away from the stream as adjacent stand ages and canopy-closure is achieved.

Contrary to stream-associated salamanders, terrestrial salamander species, *P. serratus*, and especially *P. glutinosus*, were most abundant in SMZs surrounded by the oldest stands, and as such, this study supports long recovery periods for *Plethodon* salamanders. Because terrestrial salamanders typically have very small home ranges (Kleeberger and Werner, 1982, Marvin, 1998), the local effects of recent harvesting, even outside of SMZs, may precipitate unsuitable microhabitat changes such as increased light and temperature which extend into the SMZ. Thus, potential edge effects may be important in mediating the suitability of SMZs.

4.4. Landscape factors

Several landscape and local habitat factors also were important drivers of salamander occupancy, abundance, and detection. Salamander occupancy declined with decreasing latitude and elevation, likely reflecting the position of study sites in the southern tier of the Ouachita Mountains Ecoregion and suggesting that conservation practices aimed at salamanders should focus on higher elevation sites in the region. Salamander abundance and proportional use of terrestrial habitat increase with elevation (Hairston, 1987, Ford et al., 2002, Russell et al., 2004, Petranka and Smith, 2005), in part because high elevation sites can provide cooler, wetter conditions preferred by many salamanders (Petranka and Smith, 2005). Detection probability was higher at earlier dates with cooler temperatures and wetter soil conditions, suggesting that spring may be the optimal season for salamander sampling. These findings lend continued support for rigorous consideration of site and sampling variables that influence occupancy and detection. If not accounted for, these factors could confound relationships of interest or reduce precision of parameter estimates.

5. Conclusions and management recommendations

This study demonstrates that SMZs extend beyond protection of water quality; they provide critical habitat for semi-aquatic and terrestrial amphibians and are effective for conserving salamander

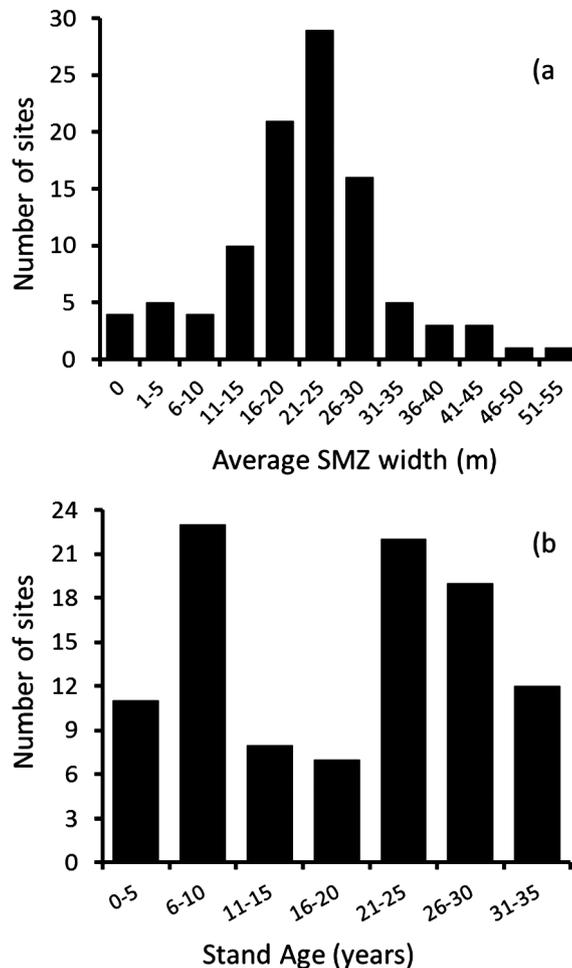
populations and communities in managed forests. Across the managed forest landscape of the southern Ouachita Mountains, average SMZ width generally follows Forestry Best Management Practice guidelines (11–24 m), although wider buffers occur, and up to 18% of the landscape is preserved through riparian SMZs and stringers (Parrish et al. 2017). We estimate that 1–5 (mean = 3) salamander species will occur within SMZs of the width recommended by local BMP guidelines; therefore, current BMPs are effective for maintaining occupancy of common species. At sites with very narrow, or no SMZ altogether, only one stream-associated species is predicted to occur, at reduced abundances. Therefore, to conserve the complete community of up to 10 salamander species found in the region, retaining buffers of ≥ 55 m on either side of streams at some sites should continue as these areas preserve occupancy of uncommon species, some of which are endemic or of high conservation concern. Thus, BMP guidelines for SMZ width should continue to be viewed as a minimum buffer requirement. Further, when planning harvests and silvicultural activities, forest managers should consider using variable-width riparian buffers, aimed at providing wider buffers at sensitive areas (Marczak et al., 2010, Kuglerova et al., 2014) such as headwaters and streams associated with ephemeral water bodies and/or rocky talus. Finally, to positively influence salamander richness, managers should maintain diverse overstory composition within SMZs, prioritizing inclusion of deciduous

species. Studies at a large spatial-scale and hierarchical analyses show great promise for elucidating complex responses of secretive wildlife to forest management and indicate that SMZs surrounding small first-order streams within intensively managed forest can support diverse salamander communities.

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Appendix 1. Frequency histogram of (a) streamside management zone (SMZ) width and (b) stand age surrounding SMZs across 102 study sites within the Ouachita Mountains, Arkansas, USA.



Appendix 2. Factor loadings and percentage of variance explained by the first two principal component (PC) axes for (a) site-specific variables and (b) sample-specific variables expected to influence salamander occupancy and detection, respectively, within streamside management zones of the Ouachita Mountains, Arkansas, USA. Bold figures indicate variables with the highest loadings.

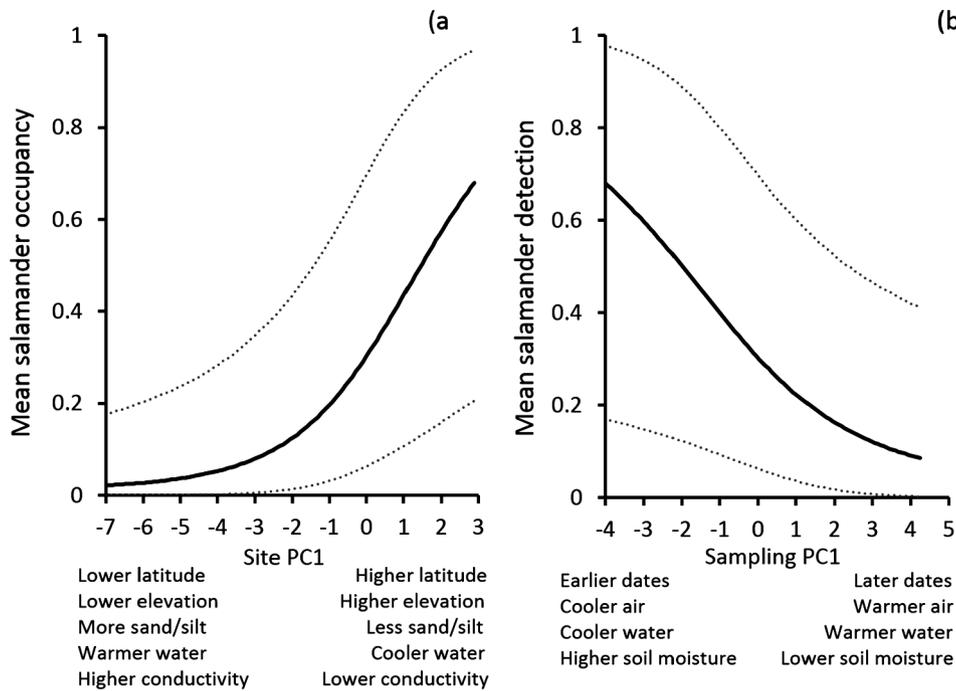
Site Covariates Principal Components	1		2		Sampling Covariates	1		2	
	1	2	1	2		1	2	1	2
Eigenvalues	3.75	1.88				2.37	1.41		
% of Variation	31.0	15.5				33.8	20.0		
Cum. % of Variation	31.0	46.5				33.8	53.8		
Variable (Eigenvectors*)	PC1	PC2				PC1	PC2		
Latitude	0.40	-0.27			Date	0.51	-0.35		
Watershed area	-0.16	0.35			Air temperature	0.49	0.29		
Elevation	0.34	-0.40			Barometric pressure	0.14	-0.08		
% Bedrock	0.09	0.18			Humidity	0.13	-0.70		
% Boulder and cobble	0.25	0.51			Water depth	-0.07	-0.31		
% Sand and silt	-0.36	-0.38			Water temperature	0.58	-0.06		
Water temperature	-0.43	-0.02			Soil moisture	-0.34	-0.45		
Water depth	-0.24	0.05							
Dissolved oxygen	0.19	-0.05							
Conductivity	-0.34	-0.12							
Amount of upland cover objects	0.16	0.20							
% Open canopy	0.29	-0.38							

Appendix 3. Summary of species-specific occupancy (SMZ, Site PC1, Site PC2) and detection (Sampling PC1 and 2) parameter estimates, and 95% credible intervals, for salamanders within streamside management zones in the Ouachita Mountains, Arkansas, USA.

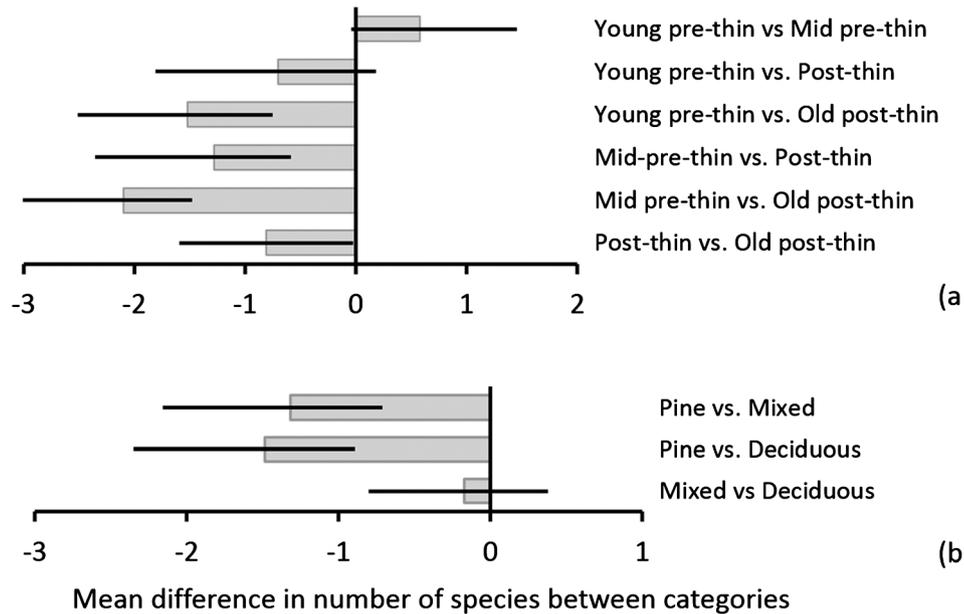
Latin name	Parameter	Mean	2.5% CRI	Median CRI	97.5% CRI	SD
<i>Ambystoma annulatum</i>	SMZ	0.87	-0.39	0.90	2.12	0.60
	Site PC1	0.55	-0.41	0.56	1.50	0.47
	Site PC2	0.09	-0.61	0.04	1.05	0.41
	Sampling	-0.63	-1.83	-0.58	0.26	0.52
	Sampling	-0.05	-1.09	0.01	0.73	0.44
<i>Ambystoma maculatum</i>	SMZ	1.14	0.24	1.10	2.24	0.49
	Site PC1	0.67	-0.24	0.65	1.81	0.49
	Site PC2	0.17	-0.50	0.09	1.21	0.43
	Sampling	-0.91	-2.05	-0.85	-0.14	0.48
	Sampling	0.35	-0.20	0.28	1.24	0.37
<i>Ambystoma opacum</i>	SMZ	1.19	0.05	1.13	2.57	0.61
	Site PC1	0.21	-1.18	0.30	1.19	0.61
	Site PC2	0.16	-0.57	0.08	1.28	0.46
	Sampling	-0.69	-1.91	-0.64	0.21	0.52
	Sampling	-0.06	-1.05	-0.01	0.62	0.41
<i>Desmognathus brimleyorum</i>	SMZ	1.08	0.45	1.06	1.81	0.34
	Site PC1	1.01	0.57	1.00	1.56	0.26
	Site PC2	-0.20	-0.62	-0.18	0.16	0.20
	Sampling	-0.18*	-0.37	-0.18	0.01	0.10
	Sampling	0.13	-0.09	0.13	0.37	0.12
<i>Eurycea multiplicata</i>	SMZ	0.89	0.02	0.90	1.71	0.42
	Site PC1	0.43*	-0.05	0.43	0.91	0.25
	Site PC2	-0.17	-0.79	-0.14	0.34	0.28
	Sampling	-0.12*	-0.26	-0.12	0.02	0.07
	Sampling	0.14*	-0.04	0.13	0.32	0.09
<i>Hemidactylum scutatum</i>	SMZ	1.24	0.19	1.17	2.58	0.58
	Site PC1	0.62	-0.41	0.62	1.73	0.51
	Site PC2	0.22	-0.45	0.13	1.33	0.45
	Sampling	-0.32	-1.29	-0.31	0.58	0.46
	Sampling	0.35	-0.23	0.27	1.34	0.39

<i>Plethodon caddoensis</i>	SMZ	0.61	-0.31	0.64	1.38	0.44
	Site PC1	1.16	0.50	1.13	2.03	0.41
	Site PC2	-0.03	-0.57	-0.03	0.53	0.27
	Sampling	-0.82	-1.65	-0.79	-0.17	0.38
	Sampling	0.10	-0.36	0.09	0.57	0.23
<i>Plethodon glutinosus complex</i>	SMZ	1.26	0.42	1.20	2.46	0.50
	Site PC1	0.68	0.17	0.66	1.37	0.30
	Site PC2	-0.20	-0.74	-0.18	0.25	0.25
	Sampling	-0.26	-0.50	-0.26	-0.03	0.12
	Sampling	-0.26*	-0.60	-0.26	0.08	0.17
<i>Plethodon serratus</i>	SMZ	1.58	0.75	1.51	2.72	0.52
	Site PC1	0.66	0.21	0.65	1.13	0.23
	Site PC2	0.17	-0.24	0.15	0.66	0.23
	Sampling	-1.10	-1.52	-1.09	-0.72	0.20
	Sampling	0.19*	-0.08	0.18	0.49	0.15
<i>Siren intermedia</i>	SMZ	0.97	-0.39	0.98	2.35	0.65
	Site PC1	0.66	-0.40	0.66	1.87	0.54
	Site PC2	-0.20	-1.27	-0.14	0.57	0.44
	Sampling	0.12	-0.77	0.06	1.37	0.54
	Sampling	-0.08	-1.10	-0.01	0.60	0.41

Appendix 4. Factors influencing occupancy and detection of the salamander community within streamside management zones of the Ouachita Mountains, Arkansas, USA. Mean a) occupancy of the salamander community in relation to Site PC1 and b) detection probability of the salamander community in relation to Sampling PC1. Solid lines represent the posterior mean community response and dashed lines represent 95% credible intervals.



Appendix 5. Mean differences in salamander species richness between pairs of a) stand age categories and b) streamside management zone (SMZ) overstory composition, including 95% credible intervals, within SMZs of the Ouachita Mountains, Arkansas, USA. The mean difference in number of species is derived from calculations at each iteration of respective models.

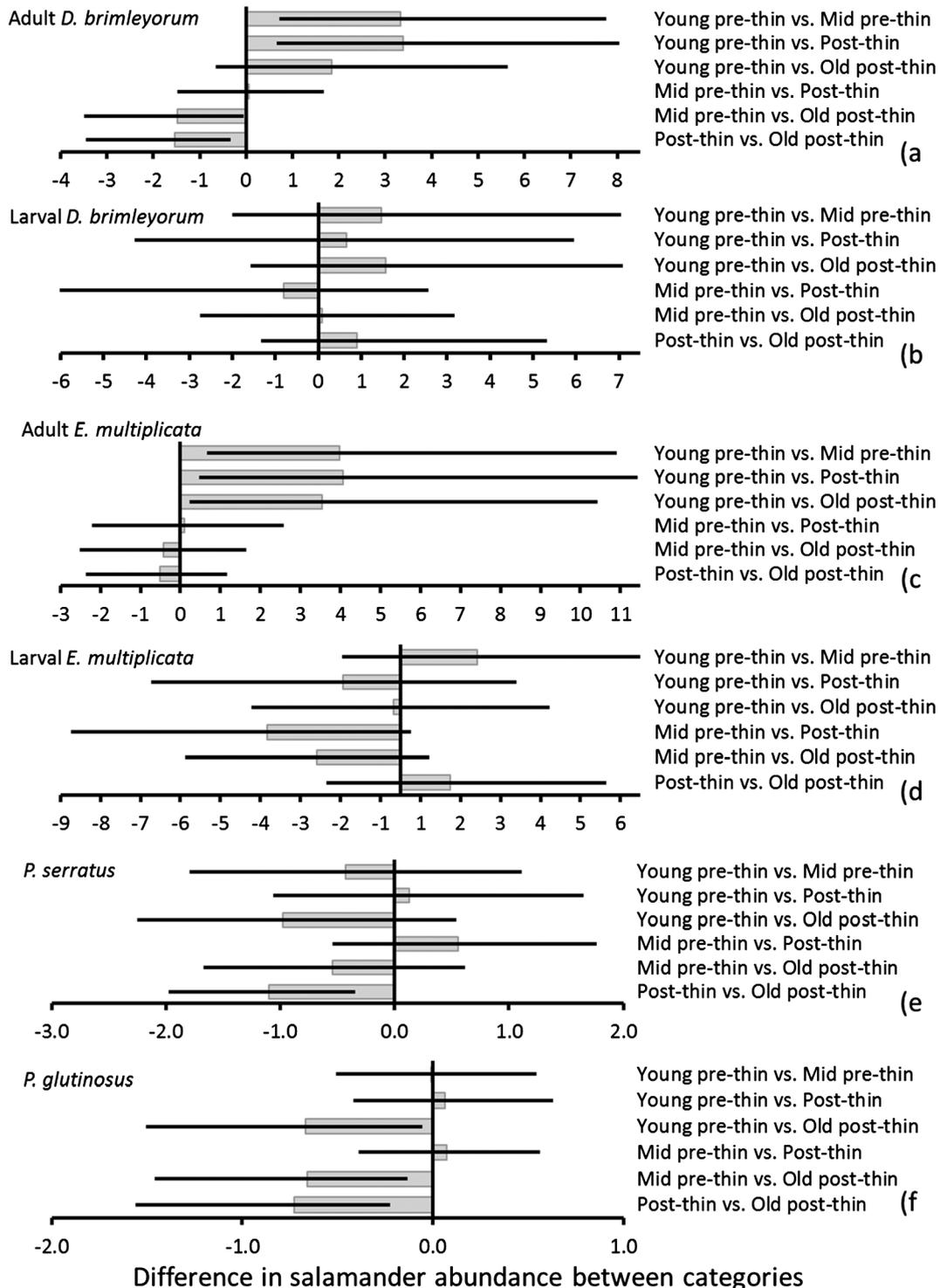


Appendix 6. Summary of species-specific abundance parameter estimates, and 95% credible intervals, for salamanders within streamside management zones in the Ouachita Mountains, Arkansas, USA. Covariates influencing detection probability include Sampling PC1 and 2.

Genus	species	Age Class	Parameter	Mean	2.5% CRI	Median CRI	97.5% CRI
<i>Desmognathus</i>	<i>brimleyorum</i>	All	SMZ	0.40	0.28	0.40	0.52
			Site PC1	0.53	0.43	0.53	0.62
			Site PC2	0.22	0.11	0.22	0.33
			Sampling PC1	-0.04	-0.11	-0.04	0.03
		Adult	SMZ	0.40	0.25	0.40	0.56
			Site PC1	0.63	0.49	0.63	0.76
			Site PC2	0.19	0.05	0.19	0.33
			Sampling PC1	-0.11	-0.20	-0.11	-0.01
		Larva	SMZ	0.37	0.16	0.37	0.59
			Site PC1	0.40	0.23	0.40	0.58
			Site PC2	0.40	0.19	0.40	0.61
			Sampling PC1	-0.32	-0.48	-0.31	-0.16
<i>Eurycea</i>	<i>multiplicata</i>	All	SMZ	0.22	0.10	0.22	0.33
			Site PC1	-0.03	-0.09	-0.03	0.04
			Site PC2	0.07	-0.02	0.07	0.16
			Sampling PC1	-0.04	-0.11	-0.04	0.03
		Adult	SMZ	0.43	0.18	0.43	0.68
			Site PC1	-0.06	-0.21	-0.06	0.10
			Site PC2	-0.08	-0.27	-0.08	0.12
			Sampling PC1	-0.68	-0.92	-0.68	-0.46
		Larva	SMZ	0.17	0.04	0.18	0.30
			Site PC1	-0.02	-0.10	-0.02	0.05
			Site PC2	0.10	0.00	0.10	0.19
			Sampling PC1	0.09	0.02	0.09	0.17
<i>Plethodon</i>	<i>caddoensis</i>	-	SMZ	0.38	0.00	0.38	0.73
		-	date	-0.02	-0.43	-0.02	0.38
<i>Plethodon</i>	<i>glutinosus complex</i>	-	SMZ	0.11	-0.23	0.11	0.44
		-	Site PC1	0.36	0.10	0.35	0.62
		-	Site PC2	0.35	0.07	0.35	0.64
		-	Sampling PC1	-0.17*	-0.38	-0.17	0.03

<i>Plethodon</i>	<i>serratus</i>	–	SMZ	0.50	0.31	0.50	0.70
		–	Site PC1	0.35	0.20	0.35	0.51
		–	Site PC2	–0.04	–0.21	–0.04	0.13
		–	Sampling PC1	–0.74	–0.94	–0.74	–0.56

Appendix 7. Mean differences in salamander abundance by age class between pairs of stand age categories, including 95% credible intervals, within streamside management zones of the Ouachita Mountains, Arkansas, USA. The mean difference in number of species is derived from calculations at each iteration of respective models. (a) adult *Desmognathus brimleyorum*, (b) larval *Desmognathus brimleyorum*, (c) adult *Eurycea multiplicata*, (d) larval *Eurycea multiplicata*, (e) *Plethodon serratus*, and (f) *Plethodon glutinosus* complex.



Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.10.006>.

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