5-2019

Amphibian and Reptile Community Responses to Forest and Riparian Disturbance

Jacquelyn Christine Guzy
University of Arkansas, Fayetteville

Recommended Citation

Guzy, Jacquelyn Christine, "Amphibian and Reptile Community Responses to Forest and Riparian Disturbance" (2019). *Theses and Dissertations*. 3212.
https://scholarworks.uark.edu/etd/3212

Amphibian and Reptile Community Responses to Forest and Riparian Disturbance

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

Jacquelyn Guzy
University of Tampa
Bachelor of Science in Biology, 2005
University of South Florida
Master of Science in Biology, 2010

May 2019
University of Arkansas

This dissertation is approved for recommendation to the Graduate Council.

John David Willson, PhD
Dissertation Director

Michelle Evans-White, PhD
Committee Member

Dan Magoulick, PhD
Committee Member

Jessica Homyack, PhD
Committee Member

Abstract

Riparian zones are transitional, semi-terrestrial areas regularly influenced by freshwater. These areas serve as dispersal corridors for many animal and plant species and ultimately function as important reservoirs of biodiversity in altered landscapes. While much of the riparian habitat in the United States has been affected by anthropogenic activities, management actions may mitigate potentially negative influences of these activities. For example, Streamside Management Zones (i.e., riparian buffers; SMZs) are commonly implemented within managed forests to protect water quality, but may also provide habitat for riparian-associated wildlife. Yet, little research has rigorously addressed the value of SMZs for wildlife, particularly cryptic species such as amphibians and reptiles. Previous studies of herpetofauna within SMZs have focused on one or a few stream-associated species, and questions remain regarding variation among species or guilds and what role SMZs serve toward conservation of herpetofaunal diversity in managed forests. However, recent statistical advances have improved our ability to analyze large multi-species presence-absence datasets, accounting for low detection rates typical for some herpetofaunal species. This study represents an extensive landscape-scale examination of herpetofaunal communities within SMZs using a multi-species occupancy approach within the Ouachita Mountains, Arkansas, and along the Broad River in South Carolina, USA. We used a hierarchical Bayesian community occupancy model to estimate species richness and species-specific occupancy responses to SMZ and overstory characteristics. In addition to this landscape-scape investigation, we also examined the effect of harvesting on individual growth of the Ouachita dusky salamander (*Desmognathus brimleyorum*). We used intensive capture-mark-recapture at three headwater streams embedded in intensely managed pine forests of west-central Arkansas, employing a Before-After-Control-Impact (BACI) design. Collectively, our results indicate that SMZs surrounding small first-order streams in intensively managed forests not only protect water quality, but also can support diverse amphibian and reptile communities.

Acknowledgements

Many people have contributed a great deal to this dissertation, and my sincerest thanks go out to each of you. In particular, I thank my advisor, the inimitable J.D. Willson, for providing this incredible opportunity, along with fantastic feedback every step of the way, great ideas, and elegant long-term vision. I have learned so much from you and the experience was made even richer by 31,862 miles of amazing cross-country adventures. To Jessica Homyack, who secured the bulk of the funding for this dissertation, I am eternally grateful. It has been a pleasure to benefit from your expertise; this project would not exist without you. For years of support and great ideas, I thank my long-term collaborators Steven Price and Brian Halstead along with Jamie Thornton-Frost; you have taught me so much and given me the foundation to build this dissertation, and I could not have completed this PhD without you. To Jennifer Mortensen and Teofil Nakov for your patience and many innovative ways to manipulate and analyze data; I am profoundly grateful. I also must thank Paula Szczerba for tremendous logistical support in gaining site access and Shane Szczerba for introducing me to the wonders of Avenza PDF Maps—it was a game changer for navigating the wilds of remote pine plantations. Additionally, I am extremely grateful to my funding sources: Weyerhaeuser Company, the National Council for Air and Stream Improvement, the Arkansas Science and Technology Authority, and the University of Arkansas. And finally, to Kelly Halloran, who said it best: “We make an amazing team”. I extend my deepest gratitude for the great adventures we had as you accompanied me on hundreds of surveys. I was so lucky to have you through this process; I hope we can do it again someday.

Table of Contents

Chapter 1:Herpetofaunal responses to riparian buffer characteristics in managed forests: synthesis and future directions 1
  Streamside Management Zones (SMZs) 1
  Herpetofaunal research in SMZs 3
  Buffer Width 5
  Mechanisms 7
  Towards Demographic Endpoints 7
  Towards Ecological Mechanisms 9
  Future Directions 11
  Literature Cited 15
  Tables and Figures 21
Chapter 2: Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests 22
  Abstract 23
  Introduction 24
  Methods 27
    Study Sites 27
    Data Collection 28
    Data Analyses 30
      Salamander Occupancy 30
      Salamander Abundance 33
  Results 35
    Occupancy, Detection, and Species Richness 37
      Species-Specific Occupancy Responses to Increasing SMZ Width 38
      Species Richness: SMZ Characteristics and Stand Age 38
      Occupancy Analysis Excluding Upland Surveys 39
    Abundance 39
    SMZ Width 39
      Abundance Analysis Excluding Upland Surveys 40

Stand Age 40
Discussion 41
SMZ Width 42
SMZ Composition 45
Stand Age 46
Landscape Factors 48
Conclusions and Management Recommendations 49
Acknowledgements 50
Literature Cited 50
Figures and Tables 59
Appendices 66
Chapter 3: Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests 76
Abstract 77
Introduction 78
Methods 81
Study Sites 81
Data Collection 82
Data Analyses 83
Results 87
Species Richness Across the Entire Herpetofaunal Assemblage 88
Salamander Occupancy and Richness 89
Reptile Occupancy and Richness 91
Anuran Occupancy and Richness 92
Discussion 94
Streamside Management Zone Width 95
Stand Age and SMZ Composition 97
Landscape Factors 98
Conclusions and Management Recommendations 99
Acknowledgements 100
Literature Cited 101

- Figures and Tables ... 110
- Appendices ... 119

Chapter 4: Effects of forest harvesting on growth rates of stream salamanders ... 128

- Abstract ... 129
- Introduction ... 130
- Methods ... 133
  - Study Sites ... 133
  - Study Design ... 133
  - Field Methods ... 134
  - Data Analysis ... 135
- Results ... 136
- Discussion ... 137
- Conclusions ... 143
- Acknowledgements ... 144
- Literature Cited ... 144
- Figures and Tables ... 152

Chapter 5: Influence of Damming on Anuran Species Richness in Riparian Areas: A Test of the Serial Discontinuity Concept. ... 155

- Abstract ... 156
- Introduction ... 157
- Methods ... 159
  - Study Sites ... 159
  - Data Collection ... 161
  - Data Analysis ... 161
- Results ... 164
  - Site Characteristics ... 164
  - Anuran Detections ... 164
  - Community-Level Summary ... 165
  - Occupancy and Species Richness Responses to Downstream Distance from Dam ... 166
- Discussion ... 166
  - Caveats and Limitations ... 171

  Management Recommendations 172
Acknowledgements 173
Literature Cited 173
Figures and Tables 180

List of Published Papers

Published

Chapter 2

Guzy, J. C., Halloran, K. M., Homyack, J. A., and Willson, J. D. 2019. Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests. Forest Ecology and Management 432:868-883.

Chapter 5

Guzy, J. C., Eskew, E. A., Halstead, B. J., and Price, S. J. 2018. Influence of damming on anuran species richness in riparian areas: A test of the serial discontinuity concept. Ecology and Evolution. 2018:00:1–12.

Under Review

Chapter 3

Guzy, J.C., Halloran, K.M., Thornton, J.A., Homyack, J., and Willson, J.D. *In review*. Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests. Ecological Applications.

Chapter 4

Guzy, J.C., Halloran, K.M., Halstead, B.J., Homyack, J.A., and Willson, J.D. *In Review*. Stream salamander growth before and after clearcut harvesting in a managed forest. Freshwater Biology.

Chapter 1:

Herpetofaunal responses to riparian buffer characteristics in managed forests: synthesis and future directions

Streamside Management Zones (SMZs)

Forestry best management practices (BMPs) are widely implemented within managed forests (Cristan et al. 2018) to minimize adverse impacts from forest operations to aquatic environments (Aust and Blinn 2004). A cornerstone of most BMP programs is the inclusion of forested riparian buffers along streams known as Streamside Management Zones (SMZs). Research indicates that SMZs moderate air and water temperatures and protect water quality and stream microhabitat by reducing sediment delivery (Aust and Blinn 2004, Clinton 2011, Cristan et al. 2016). Considerable variation in buffer width guidelines exists among jurisdictions (Blinn and Kilgore 2001, Lee et al. 2004), with recommendations for buffer widths along intermittent streams in the northwestern United States being twice as wide as those for the Southeast (~50 m vs. 24 m on each side of the stream; (Lee et al. 2004).

Although SMZs primarily were implemented to protect water quality, they may provide additional benefits to non-aquatic species by acting as movement corridors and habitat for semi-aquatic and terrestrial wildlife during and following forestry operations on upland areas (Rudolph and Dickson 1990, Spackman and Hughes 1995, Machtans et al. 1996, Perkins and Hunter 2006, Perry et al. 2011, Peterman et al. 2011, Pearson et al. 2015). Streamside Management Zones may be particularly beneficial to wildlife because they provide diversity of habitat types (e.g., waterbodies, coarse woody debris, snags, tree cavities, rocks, leaf litter; (Homyack and Kroll 2014, Warrington et al. 2017) that may be reduced in intensively managed forest. However, BMP recommended widths for SMZs were not designed to conserve terrestrial wildlife species associated with riparian ecosystems. Further, SMZ characteristics important to a taxa may vary depending on the hydrology, geology, and vegetative structure of a particular location (Foley 1994, deMaynadier and Hunter 1995). Notably, most studies of SMZs focus on a few species or one group, yet substantial variation has been reported in response to riparian buffer characteristics among taxonomic groups (i.e., birds, amphibians, reptiles, small mammals, and invertebrates; (Marczak et al. 2010, Greene et al. 2016) and among species within groups (Guzy 2019).

Riparian buffers may be particularly important for amphibians and reptiles. Many herpetofaunal species depend on both terrestrial and aquatic habitat types to meet life history needs (e.g., reproduction, larval development, estivation, foraging; Gibbons 2003). Thus, both aquatic waterbodies, terrestrial habitats, and the corridors that link them are important for population persistence (Marsh and Trenham 2001). Additionally, relative to other vertebrates, herpetofauna are generally characterized by limited mobility and high philopatry (e.g., amphibians), relatively narrow habitat tolerances, and specific breeding requirements (deMaynadier and Hunter 1995, Gibbons and Buhlmann 2001, Cushman 2006). Further, habitat modification (e.g., canopy cover reduction) can substantially alter the amount and distribution of thermally suitable habitat, with high local temperatures rendering some land-cover types uninhabitable for some herpetofauna (Rittenhouse et al. 2008, Frishkoff et al. 2015, Nowakowski et al. 2015, Nowakowski et al. 2017). Narrow thermal optima of lizards and amphibians and high evaporative water loss rates of amphibians have been associated with increased sensitivity to habitat modification (Nowakowski et al. 2018). Because of this, many herpetofaunal species are sensitive to habitat alteration (Gibbons et al. 2000, Cushman 2006) and consequently, negative effects of timber harvest have been documented for many groups and species (Russell et al. 2004). Thus, SMZs have great potential to conserve herpetofaunal biodiversity. Our objectives were to 1) review herpetofaunal research in SMZs, 2) discuss typical study designs, 3) examine ecological mechanisms potential responsible for observed patterns, and 4) propose future research directions.

Herpetofaunal research in SMZs

One common approach to assessing SMZ widths required by herpetofauna has been to measure extent of terrestrial habitats used (i.e., ‘core upland habitat’) by semiaquatic species, particularly amphibians, in unharvested forest areas. Semlitsch and Bodie (2003) summarized migration distances (i.e., use of terrestrial habitats) of 65 species of amphibians and reptiles from wetlands and streams, and found core terrestrial habitat ranged from 159-200 m from wetlands. Similarly, in studies of stream plethodontids (i.e., *D. monticola*, *D. ocoee*, *D. quadramaculatus*, *E. wilderae*), researchers investigating riparian habitat use by salamanders in undisturbed forests of the Appalachian Mountains have suggested that riparian buffers of 42 – 79 m on either side of a stream are needed to protect core habitat, with an additional 50 m buffer needed to protect against alterations in temperature, humidity, and soil moisture (i.e., edge effects) extending from disturbed areas into the forest (Crawford and Semlitsch 2007, Connette et al. 2016). In a review of riparian forest management approaches in the U.S. Pacific Northwest Pacific Northwest, Olson et al. (2007) suggest that for amphibian persistence, wide riparian buffers (40–150 m) along headwater streams in key areas are necessary to accommodate terrestrial life history functions of stream/riparian associated amphibians. Measuring migration distance via methods such as drift fences is an effective way to determine terrestrial habitat use for many species when costly methods such as radio-tracking are impractical. However, this method only determines how far herpetofauna travel before settling, and does not measure responses to alterations in habitat, or determine precisely how much terrestrial habitat is necessary for population persistence.

Most studies evaluating responses of herpetofauna to riparian buffer characteristics are limited in their inferential scope by focusing on a limited number of stream-associated species, and few address whether SMZs provide habitat for terrestrial amphibians or reptiles (Table 1). Additionally, most research has focused on the U.S. Pacific Northwest and Appalachian Mountain regions (Table 1), leaving a large knowledge gap for the southern United States, a region that contains extensive managed forest and high herpetofaunal diversity (Greenberg 2001, Russell et al. 2002, Owens et al. 2008, Homyack et al. 2016). These studies typically are structured as retrospective, observational studies where data is collected at sites that have been harvested but retain riparian buffers (e.g., natural experiment; Table 1). Alternatively, other studies directly manipulate SMZ width and collect data on herpetofaunal responses before and after harvesting occurs, with comparisons to unharvested controls (e.g., BACI designs; Table 1). Due to logistical challenges of landscape-scale studies and intensive sampling needed to overcome the low detectability of many species, the scope of most herpetofaunal studies within SMZs has been restricted to comparisons across a few buffer widths at a small number of streams (typically 5-15 streams; Table 1). Such categorical study designs have limited ability to reveal thresholds where responses occur and small sample sizes have limited ability to estimate responses of rarer species. Further, even when strong responses to riparian buffer width have been identified, considerable unexplained variation frequently exists because of the complex nature of geography, topography, and hierarchical stream network structure acting at multiple spatial scales. Substantial replication at the site level is needed to examine mechanisms for variation among sites.

Buffer Width

Some studies have examined salamander responses to experimental manipulation of a few different SMZ widths (i.e., a categorical approach). For example, Maigret et al. (2014) suggested that a 7.6 m buffer protected the abundance of terrestrial *P. glutinosus* along with aquatic *Desmognathus* spp., whereas Peterman and Semlitsch (2009) found 30 m buffers protected *E. bislineata* abundance (n=413), and 9 m buffers did not (n=~72). Similarly, Johnston and Frid (2002) found that *Dicamptodon tenebrosus* exhibited reduced terrestrial movement at streams without buffers compared to those with buffers, consistent with desiccation avoidance. Other experimental studies with categorical SMZ buffer treatments indicate a short-term (i.e., 2 years) negative effect of harvesting on *D. tenebrosus* abundance at streams with narrow buffers (~10 m) (Jackson et al. 2007) or equivocal support for positive effects of 11-34 m buffers for *E. bislineata* (Perkins and Hunter 2006), compared to clearcut areas.

While most experimental studies manipulating SMZ width generally conclude that buffers are important conservation measures for streamside salamanders, categorical study designs have limited ability to detect threshold responses (e.g., abrupt change in occupancy along a continuous scale) or evaluate differential responses among species. Guzy et al. (2019) have begun to extend the scope of herpetofaunal studies toward a landscape-scale approach spanning >100 first order streams that encompass a continuous gradient of SMZ buffer widths. Using a hierarchical Bayesian community occupancy model the authors estimate herpetofaunal species richness and species-specific occupancy responses to SMZ and overstory characteristics, documenting high herpetofaunal richness (37 species) within SMZs (Guzy 2019). Results indicated that across the herpetofaunal community, occupancy and species richness were consistently positively associated with SMZ width, with maximum predicted richness of 30 species occurring at sites with the largest buffers present in the sample (51 m on either side of the stream; Guzy 2019).

However, substantial variation in species' associations with SMZ width occurred within taxonomic groups. Among the 10 salamander species detected, three groups were evident: 1) tolerant species with high occupancy, even at sites with narrow SMZs (*E. multiplicata*), 2) species with low occupancy within narrow SMZs, high occupancy within wide SMZs (*D. brimleyorum*, *P. serratus*, and *P. 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*). The latter pattern was attributed to these species having 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*; Guzy 2019). Additionally, considerable variation among taxonomic groups was documented, with reptile predicted richness increasing more rapidly up to SMZs of ~35 m, whereas maximum amphibian predicted richness was not seen until a SMZs width of 50-55 m (Guzy 2019). Compared to salamanders, estimated anuran occupancy reached maximum values at narrower SMZs, and a greater proportion of species were tolerant of more narrow SMZs. Some of the variation among taxonomic groups was partially attributed to guild specific responses to landscape and habitat characteristics such as latitude and elevation (Guzy 2019). While occupancy of only one salamander species (*E. multiplicata*) was not strongly influenced by wider SMZs, several anurans (*H. chrysoscelis*, *P. fouquettei*, *L. sphenocephalus*, *L. clamitans*) exhibited high probability of occupancy (~0.5-0.75) at sites with very narrow SMZs. Unlike salamanders, some anuran species may be considered early successional or edge species during reproduction (e.g., treefrogs, chorus, and leopard frogs; Lannoo 2005), because eggs and larva can benefit from increased temperature and primary productivity in open canopy aquatic conditions (Hocking and Semlitsch 2007, Semlitsch et al. 2009). Conversely, variation among mean reptile association to SMZ width was minimal (Guzy 2019). The authors conclude that greater habitat diversity likely positively influences species richness, and to our knowledge this study is the only one to address reptile or anuran community responses to SMZ characteristics (Guzy 2019).

Mechanisms

Although studies of herpetofauna within SMZs are limited, most research indicates that SMZs are beneficial to herpetofauna, with wider buffers tending to provide greater benefits relative to narrower buffers. However, the strength of these findings varies among species and there is debate about how wide buffers need to be (Rudolph and Dickson 1990, Johnston and Frid 2002, Vesely and McComb 2002, Perkins and Hunter 2006, Jackson et al. 2007, Peterman and Semlitsch 2009, Marczak et al. 2010, Pollett et al. 2010, Hawkes and Gregory 2012, Maigret et al. 2014, Olson et al. 2014, Guzy et al. 2019). Importantly, most studies measure changes in herpetofaunal occupancy or abundance. Thus, researchers should seek to understand mechanisms driving changes in population parameters such as abundance, along with underlying variation among species' responses to riparian buffer characteristics. Importantly, both demographic and ecological studies can inform these mechanisms. Demographic studies target species and use capture-mark-recapture approaches to compare vital rates among sites or treatments. However, even when a population response to disturbance such as harvesting is identified, ecological studies are needed to further determine ecological factors responsible for the population response, such as changes in resource availability or habitat quality. Below we propose several non-mutually-exclusive mechanisms underlying herpetofaunal response to riparian buffer characteristics, describe the current knowledge, and suggest avenues to elucidate mechanisms.

Towards Demographic Endpoints

To understand mechanisms driving population and community responses to forest management practices, researchers must identify vital rates (e.g., survival, growth, reproduction, immigration, emigration) that drive changes in abundance, occupancy, and ultimately species richness and diversity. Currently, limited information on vital rates of herpetafauna in response to SMZ characteristics or manipulation of upland habitat types is available. Johnston and Frid (2002) found that Pacific giant salamander (*D. tenebrosus*) movements in riparian buffer zones (40-60 m) were similar to unharvested forested, but salamanders in clearcut sites without SMZs stayed closer to streams, spent more time in refuges, and had smaller home ranges. The authors monitored movement in conjunction with surface and soil temperatures of riparian buffers and found microclimates of SMZs to be less extreme and variable than clearcuts, suggesting that SMZs mitigate some of the negative effects of clearcuts on salamander movement (Johnston and Frid 2002). Halloran (2017) estimated movement and survival of Ouachita dusky salamanders (*Desmognathus brimleyorum*) within SMZs (14 and 21 m on each side) before and after harvest in Arkansas. Relative to in-stream movements at an unharvested control, salamander movement increased at two headwater streams after harvest, but there was no detectable reduction in survival or individual capture probability two years post-harvest, suggesting that buffers were sufficient to avoid mortality (Halloran 2017). Increased movement by individual salamanders may indicate increased dispersal, or be associated with higher energetic costs, indirectly affecting long-term survival and/or reproduction (Keen and Reed 1985, Schmidt et al. 2007). Working in the same BACI experimental framework adult salamander abundances (*D. brimleyorum*, *E. multiplicata*) increased within SMZs surrounded by recently harvested stands, compared to older stands without a timber harvest during the study period. This pattern was consistent with the evacuation hypothesis (see Peterman et al. 2011), an alternative mechanism explaining changes in abundance, that postulates adult salamanders leave recently harvested areas seeking more suitable habitat and microclimate within SMZs (Guzy et al. 2019). Conversely, larval abundances across stand age categories (i.e., 0-5, 6-13, 13-22, and 22-35 years old) were similar, suggesting that reproduction was not strongly influenced by the stand age surrounding SMZs, or by mid-rotation silvicultural treatments including commercial thinning (Guzy et al. 2019). Another study measured *D. ocoee* body condition before and after harvest within two narrow SMZs sites (<9m), and documented significantly reduced body conditions relative to an unharvested control, presumably linked to a reduction in leaf litter and subsequent decrease in available invertebrate prey (Peterman et al. 2011). However, at two streams with larger SMZs (14 and 21 m), juvenile *D. brimleyorum* growth rate increased following harvest of the surrounding watershed, possibly because of post-harvest resource pulses resulting from a shift in the quality, quantity, or composition of invertebrate prey available. Thus, a logical but difficult direction for future studies is to experimentally study demographic parameters of several species with varying life histories, within SMZs before and after harvest, with extended monitoring post-harvest.

Towards Ecological Mechanisms

Studies have begun to address the ecological aspects of SMZs that are responsible for observed benefits to herpetofauna. Of particular interest is determining why wider SMZs are more beneficial, but it is also important to determine why variation in herpetofaunal responses exist among sites with similarly wide SMZs. Several studies of amphibians suggest that retaining canopy trees around headwater streams mediate changes to microclimate (i.e., temperature, humidity, and soil moisture) known to be important to this group (Peterman et al. 2009, Olson et al. 2014, Johnston and Frid 2002, Vesley and McComb 2002, Guzy et al. 2019) and reduce sediment delivery (Peterman et al. 2009, Maigret et al. 2014, Dupuis and Steventon 1999) and buffer stream water temperatures (Pollett et al. 2010). In Arkansas, wide SMZs (50-55m) supported greater species richness of salamanders and anurans, while most reptile species were present within mid-sized SMZs (>35 m). More specifically, high salamander species richness at sites with wide SMZs was driven by species that had low overall occupancy and generally only occurred at sites with wide SMZs (i.e., *P. caddoensis*, *A. annulatum*, *H. scutatum*, *A. maculatum*, *A. opacum*, *S. intermedia;* Guzy 2019). 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*). Conversely, most reptiles are less sensitive to environmental disturbances that modify temperature and humidity, and may act as habitat generalists that use edges and early successional vegetation for foraging and thermoregulation (Ross et al. 2000, Greenberg 2001, Crosswhite et al. 2004). Thus for amphibians, wider buffer requirements may be driven by greater sensitivity to edge effects (e.g., Brosofske et al 1997; Tilghman et al. 2012) relative to reptiles, along with more specialized microhabitat requirements (Guzy 2019).

In addition to consistently positive responses to wider buffers, Guzy et al (2019) found that estimated salamander richness was highest within SMZs comprised of a deciduous or mixed overstory compared to pine, but anuran and reptile richness did not vary by overstory composition. Deciduous SMZs may better support production of macroinvertebrate prey and more suitable soil pH conditions that benefit salamanders (Taylor et al. 1989, Klemmedson 1992, Whiles and Wallace 1997). Conversely, some anuran and reptile species are habitat generalists, associated with either mixed or pine forest, and some are considered upland pine specialists. Guzy (2019) suggest silvicultural practices that maintain a diverse overstory within SMZs, or prioritize deciduous species, may positively influence herpetofaunal richness across the landscape. Notably, in managed forest landscapes, it can be difficult to disentangle effects of SMZ width from overstory composition because SMZs are typically different from surrounding stands. For example, at streams with narrow deciduous buffers, determining if benefits to herpetofauna derive from presence of a riparian buffer, or from an overstory that is deciduous compared to the surrounding coniferous timber stands can be challenging.

Future Directions

More work is needed to explicitly determine how SMZs act to conserve biodiversity in managed forests. Are wider buffers beneficial to amphibians and reptiles because they provide undisturbed habitat that buffers against edge effects, or because they protect a greater variety of uncommon habitat elements important to particular species or life stages? Alternatively, wide SMZs may be more likely to occur where forest harvesting is more difficult, such as low lying floodplain or steep mountainous locations, and these areas may have diverse habitat; this problem is difficult to address with natural experiment study designs used in most studies to date. Important avenues for future research should include closer examination of how abiotic conditions and resource availability change with inclusion of wide riparian buffers, and how amphibians and reptiles respond to these changes. For example, similar to Guzy et al. (2019), a retrospective, observational study could include a random selection of a large number (>50) of wide (relative to BMPs) riparian buffers (e.g., ~ 30-50 m) in recently (<10 years) harvested stands where the overstory composition (e.g., deciduous or mixed-coniferous), microhabitat, and microclimate is quantified throughout each buffer, with variation among these parameters related to herpetofaunal species richness. Studies such as these are needed in different regions of the United States and Canada, as well as other timber-producing regions world-wide. A higher degree of microhabitat elements (e.g., aquatic waterbodies, rocky talus) and/or greater variation in microclimate throughout buffers may support higher herpetofaunal richness. Importantly, wider buffers may occur for logistical reasons, such as floodplains or steep mountainous slopes which limit harvest opportunities, and these locations may tend to have diverse habitat types. In cases such as this, where there are confounding aspects of buffer width, alternative study designs are necessary to tease out mechanisms. These could include an experimental approach where buffer widths are randomly applied, irrespective of topography, or a natural experiment where sites explicitly include buffers spanning a gradient of SMZ width and topography. Other difficult, but invaluable study designs, should include experimental manipulations of SMZ width, replicated across a wide geographic area, similar to that of Semlitsch et al. (2009), which has been invaluable in identifying mechanisms responsible for responses by pond-breeding amphibians to different timber harvest treatments.

Notably, habitat use along the aquatic-terrestrial gradient is species specific, with some species exclusively using the stream itself (fully aquatic species), others restricted to the riparian area (e.g., stream-associated salamanders), and other species making extensive use of the adjacent upland forested habitat outside of riparian buffers (e.g., woodland salamanders, some snakes, box turtles) or edges and early successional vegetation (e.g., lizards). Thus, future studies may seek to determine whether stream-associated herpetofauna are necessarily less sensitive to buffer width compared to more terrestrial species, to better tailor conservation when prioritization of areas for management must be focused on the needs of a set of target species. Other challenges with regard to future studies aimed at conservation of herpetofaunal biodiversity within SMZs include more explicit consideration of species that are uncommon where they occur (low detection probability) compared to those that are rare across the landscape (low occupancy probability). In these cases, different study designs are necessary to effectively sample these species. For example, the Caddo Mountain salamander (*Plethodon caddoensis*) is a terrestrial species inhabiting a geologically distinct area of western Arkansas that is uncommon across the landscape; however, where they occur in the Caddo and Cossatot Mountains, they are fairly easy to detect (Trauth and Wilhide 1999), and provided repeat surveys are conducted carefully, researchers can be relatively confident these salamanders are not occupying sites where they are undetected. Conversely, several mole salamander species (*Ambystoma* spp.) are much more common across the landscape, but due to a fossorial behavior, have lower detection probabilities conditional on seasonal activity, and thus researchers are necessarily less confident these species are absent when they are undetected during surveys. Thus, study designs measuring occupancy probability are most useful for uncommon species (e.g., Mackenzie and Royle 2005), and implementing hierarchical community occupancy models improve our ability to assess uncommon species (Pacifici et al. 2014, Guzy et al. 2019). Other useful approaches include studies implementing abundance estimation with binomial mixture models, popular because they incorporate factors influencing detection probability without individually marking animals (Royle 2004). Although the usefulness of binomial mixture models as indicators of true density is controversial (Barker et al. 2018), they allow researchers to examine variation in abundance across a large number of sites, thus providing a valuable relative index of abundance.

Other aspects of riparian buffers should be more closely examined, including mechanistic studies to determine how riparian buffers influence stream salamander growth. For example, Guzy (2019) determined that juvenile *D. brimleyorum* growth rate was higher post-harvest at two streams with moderate riparian buffers (14 and 21 m). Future research should determine mechanisms responsible for increased post-harvest growth rates. For example, juvenile salamanders may have different behavioral responses to harvesting or be able to better capitalize on post-harvest resource pulses resulting from a shift in the quality, quantity, or composition of invertebrate prey available. Additionally, changes to metabolism as a result of potentially increased air and water temperatures post-harvest may favor increased juvenile growth or result in a slightly extended activity season during cooler months. Thus, studies that quantify the macroinvertebrate prey community, nutrient levels, and water temperatures, along with salamander growth, should be high priority. A first step may include determining whether increased light, nutrients, or both, are responsible for increased salamander growth post-harvest; experimental studies that manipulate canopy cover without harvesting the watershed (and thus potentially altering nutrient inputs to streams) could accomplish this. Further, we have no information on how salamander growth responds to harvesting without inclusion of riparian buffers, and given that studies suggest body condition is reduced within narrow buffers (Peterman et al. 2011), we may expect growth to likewise be reduced.

In conjunction with considerations of buffer width, the landscape context of SMZs undoubtedly deserves further evaluation. When attempting to conserve stream-affiliated herpetofauna, future research should not only consider how wide riparian buffers are, but also how SMZs can act to increase habitat connectivity along stream networks, and ultimately act to preserve biological diversity within habitat reserves. Both longitudinal and lateral connectivity of habitats is likely important for long-term persistence of aquatic–riparian species and assemblages. As such, future studies should examine whether riparian buffers can act as corridors between habitat patches that reduce fragmentation and facilitate dispersal among herpetofaunal populations. For example, research indicates that stream salamanders exhibit a surprisingly high rate of overland dispersal to adjacent headwater streams, suggesting that connectivity among neighboring drainages may be important to their population dynamics (Grant et al. 2010). Similarly, Lowe and Bolger (2002) found the abundance of spring salamanders (*Gyrinophilus porphyriticus*) was greater in paired streams linked by a downstream tributary compared to isolated streams, suggesting that landscape connectivity confers resilience to habitat disturbance. Olson et al. (2007) outlined a combination of seven riparian and upslope forest management approaches that would retain all habitat used by amphibians for breeding, foraging, overwintering, and dispersal. These approaches range from inclusion of narrow buffer zones to be used where headwater amphibian occurrences or habitat quality are low, up to the most conservative approaches where forest patch reserves, partial harvest, and leave islands are included to provide connectivity between watersheds and across ridgelines to adjacent drainages.

This ‘‘spaghetti and meatball’’ approach (Olson et al. 2007) of linear stream buffers (spaghetti reserves) and patch reserves (meatballs), either along streams or upslope has yet to be experimentally tested, but shows promise for the potential of SMZs to conserve herpetofauna.

Literature Cited

Aust, W. M. and C. R. Blinn. 2004. Forestry best management practices for timber harvesting and site preparation in the eastern United States: An overview of water quality and productivity research during the past 20 years (1982–2002). Water, Air and Soil Pollution: Focus **4**:5-36.

Barker, R. J., M. R. Schofield, W. A. Link, and J. R. Sauer. 2018. On the reliability of N-mixture models for count data. Biometrics **74**:369-377.

Blinn, C. R. and M. A. Kilgore. 2001. Riparian management practices: a summary of state guidelines. Journal of Forestry **99**:11-17.

Brosofske, K. D., J. Q. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Clinton, B. D. 2011. Stream water responses to timber harvest: Riparian buffer width effectiveness. Forest Ecology and Management **261**:979-988.

Connette, G. M., M. S. Osbourn, and W. E. Peterman. 2016. The Distribution of a Stream-breeding Salamander, Desmognathus ocoee, in Terrestrial Habitat Suggests the Ecological Importance of Low-order Streams. Copeia **104**:149-156.

Crawford, J. A. and R. D. Semlitsch. 2007. Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. Conservation Biology **21**:152-158.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, and J. F. Munsell. 2018. National status of state developed and implemented forestry best management practices for protecting water quality in the United States. Forest Ecology and Management.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, J. F. Munsell, and E. Schilling. 2016. Effectiveness of forestry best management practices in the United States: Literature review. Forest Ecology and Management **360**:133-151.

Crosswhite, D. L., S. F. Fox, and R. E. Thill. 2004. Herpetological habitat relations in the Ouachita Mountains, Arkansas. Pages 273-282 in Tech. Rep. SRS-74. Ouachita and Ozark Mountains Symposium: Ecosystem Management Research. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation **128**:231-240.

deMaynadier, P. G. and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3**:230-261.

Dupuis L., and D. Steventon. 1999. Riparian management and the tailed frog in northern coastal forests. Forest Ecology and Management, 124(1), 35-43.

Foley, D. H. 1994. Short-term response of herpetofauna to timber harvesting in conjuction with streamside-management zones in seasonally-flooded bottomland-hardwood forests of southeast Texas. Texas A&M University.

Frishkoff, L. O., E. A. Hadly, and G. C. Daily. 2015. Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. Global change biology **21**:3901-3916.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands **23**:630-635.

Gibbons, J. W. and K. A. Buhlmann. 2001. Reptiles and Amphibians. Wildlife of Southern Forests: Habitat and Management. Hancock House Publishers, Blaine, WA **552**:372-390.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience **50**:653-666.

Grant, E. H. C., J. D. Nichols, W. H. Lowe, and W. F. Fagan. 2010. Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. Proceedings of the National Academy of Sciences, 107(15), 6936-6940.

Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management **148**:135-144.

Greene, R. E., R. B. Iglay, K. O. Evans, D. A. Miller, T. B. Wigley, and S. K. Riffell. 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests—opportunities for open pine conservation. Forest Ecology and Management **360**:30-39.

Guzy, J. C., K. M. Halloran, J. A. Homyack, and J. D. Willson. 2019. Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests. Forest Ecology and Management **432**:868-883.

Guzy, J. C. 2019. Amphibian and Reptile Community Responses to Forest and Riparian Disturbance. Dissertation. University of Arkansas.

Halloran, K. M. 2017. Population Dynamics of Ouachita Dusky Salamanders (*Desmognathus brimleyorum*) in a Managed Forest Landscape. Thesis. University of Arkansas.

Hawkes, V. C. and P. T. Gregory. 2012. Temporal changes in the relative abundance of amphibians relative to riparian buffer width in western Washington, USA. Forest Ecology and Management **274**:67-80.

Hocking, D. J. and R. D. Semlitsch. 2007. Effects of timber harvest on breeding-site selection by gray treefrogs (*Hyla versicolor*). Biological Conservation **138**:506-513.

Homyack, J. A. and A. J. Kroll. 2014. Slow lives in the fast landscape: conservation and management of Plethodontid salamanders in production forests of the United States. Forests **5**:2750-2772.

Homyack, J. A., C. J. O’Bryan, J. E. Thornton, and R. F. Baldwin. 2016. Community occupancy of herpetofauna in roadside ditches in a managed pine landscape. Forest Ecology and Management **361**:346-357.

Jackson, C., D. P. Batzer, S. S. Cross, S. M. Haggerty, and C. A. Sturm. 2007. Headwater streams and timber harvest: channel, macroinvertebrate, and amphibian response and recovery. Forest Science **53**:356-370.

Johnston, B. and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). Canadian journal of zoology **80**:2170-2177.

Keen, W. H. and R. W. Reed. 1985. Territorial defence of space and feeding sites by a plethodontid salamander. Animal behaviour **33**:1119-1123.

Klemmedson, J. O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. Forest Ecology and Management 47:349-361.

Lannoo, M. 2005. Amphibian Declines: the Conservation Status of United States Species. University of Califronia Press.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management **70**:165-180.

Lowe, W. H. and D. T. Bolger. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183-193.

Machtans, C. S., M. A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology **10**:1366-1379.

Mackenzie, D. I. and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105-1114.

Maigret, T. A., J. J. Cox, D. R. Schneider, C. D. Barton, S. J. Price, and J. L. Larkin. 2014. Effects of timber harvest within streamside management zones on salamander populations in ephemeral streams of southeastern Kentucky. Forest Ecology and Management **324**:46-51.

Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications **20**:126-134.

Marsh, D. M. and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology **15**:40-49.

Nowakowski, A. J., M. Veiman-Echeverria, D. J. Kurz, and M. A. Donnelly. 2015. Evaluating connectivity for tropical amphibians using empirically derived resistance surfaces. Ecological Applications **25**:928-942.

Nowakowski, A. J., J. I. Watling, M. E. Thompson, G. A. Brusch IV, A. Catenazzi, S. M. Whitfield, D. J. Kurz, Á. Suárez-Mayorga, A. Aponte-Gutiérrez, and M. A. Donnelly. 2018. Thermal biology mediates responses of amphibians and reptiles to habitat modification. Ecology Letters **21**:345-355.

Nowakowski, A. J., J. I. Watling, S. M. Whitfield, B. D. Todd, D. J. Kurz, and M. A. Donnelly. 2017. Tropical amphibians in shifting thermal landscapes under land-use and climate change. Conservation Biology **31**:96-105.

Olson, D. H., P. D. Anderson, C. A. Frissell, H. H. Welsh Jr, and D. F. Bradford. 2007. Biodiversity management approaches for stream–riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. Forest Ecology and Management **246**:81-107.

Olson, D. H., J. B. Leirness, P. G. Cunningham, and E. A. Steel. 2014. Riparian buffers and forest thinning: Effects on headwater vertebrates 10 years after thinning. Forest Ecology and Management **321**:81-93.

Owens, A. K., K. R. Moseley, T. S. McCay, S. B. Castleberry, J. C. Kilgo, and W. M. Ford. 2008. Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. Forest Ecology and Management **256**:2078-2083.

Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry, and A. DeWan. 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecology and Evolution **4**:877-888.

Pearson, S. F., J. Giovanini, J. E. Jones, and A. J. Kroll. 2015. Breeding bird community continues to colonize riparian buffers ten years after harvest. PloS one **10**:e0143241.

Perkins, D. W. and M. L. Hunter. 2006. Use of amphibians to define riparian zones of headwater streams. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:2124-2130.

Perry, R. W., T. B. Wigley, M. A. Melchiors, R. E. Thill, P. A. Tappe, and D. A. Miller. 2011. Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds. Biodiversity and conservation **20**:625-642.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2011. Effects of even-aged timber harvest on stream salamanders: Support for the evacuation hypothesis. Forest Ecology and Management **262**:2344-2353.

Peterman, W. E. and R. D. Semlitsch. 2009. Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. Forest Ecology and Management **257**:8-14.

Pollett, K. J., J. G. Maccracken, and J. A. MacMahon. 2010. Stream buffers ameliorate the effects of timber harvest on amphibians in the Cascade Range of Southern Washington, USA. Forest Ecology and Management **260**:1083-1087.

Rittenhouse, T. A., E. B. Harper, L. R. Rehard, and R. D. Semlitsch. 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak–hickory forest. Copeia **2008**:807-814.

Ross, B., T. Fredericksen, E. Ross, W. Hoffman, M. L. Morrison, J. Beyea, M. B. Lester, B. N. Johnson, and N. J. Fredericksen. 2000. Relative Abundance and Species Richness of Herpetofauna in Forest Stands in Pennsylvania. Forest Science 46:139-146.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics **60**:108-115.

Rudolph, D. C. and J. G. Dickson. 1990. Streamside zone width and amphibian and reptile abundance. The Southwestern Naturalist **35**:472-476.

Russell, K. R., D. C. Guynn Jr, and H. G. Hanlin. 2002. Importance of small isolated wetlands for herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South Carolina. Forest Ecology and Management **163**:43-59.

Russell, K. R., T. B. Wigley, W. M. Baughman, H. G. Hanlin, and W. M. Ford. 2004. Responses of southeastern amphibians and reptiles to forest management: a review. In: Gen. Tech. Rep. SRS–75. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station. Chapter 27. p. 319-334.

Schmidt, B. R., M. Schaub, and S. Steinfartz. 2007. Apparent survival of the salamander *Salamandra salamandra* is low because of high migratory activity. Frontiers in Zoology **4**:19.

Semlitsch, R. D. and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology **17**:1219-1228.

Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. K. Calhoun, J. W. Gibbons, J. P. Gibbs, G. J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter, D. A. Patrick, T. A. G. Rittenhouse, and B. B. Rothermel. 2009. Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments. BioScience **59**:853-862.

Spackman, S. C. and J. W. Hughes. 1995. Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation **71**:325-332.

Taylor, B. R., D. Parkinson, and W. F. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97-104.

Tilghman, J. M., S. W. Ramee, and D. M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation 152:1-9.

Trauth, S.E., J.D. Wilhide. 1999. Status of three plethodontid salamanders (Genus Plethodon) from the Ouachita National Forest of southwestern Arkansas. Journal of the Arkansas Academy of Science 53:125-137.Vesely, D. G. and W. C. McComb. 2002. Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon Coast Range. Forest Science **48**:291-297.

Warrington, B. M., W. M. Aust, S. M. Barrett, W. M. Ford, C. A. Dolloff, E. B. Schilling, T. B. Wigley, and M. C. Bolding. 2017. Forestry Best Management Practices Relationships with Aquatic and Riparian Fauna: A Review. Forests **8**:331.

Whiles, M. R., and Wallace, J. B. 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. Hydrobiologia, 353:107-119.

Tables and Figures

Table 1. Studies examining herpetofaunal responses to inclusion of Streamside Management Zones (SMZs)

				Study Design				# Sites in Experimental Units						# Species in SMZ Analyses			
Citation	Year	State	Location	Design	Approach	# of Sites	# of Categories	Control	Clear Cut No SMZ	Other	SMZ [# of Sites (width-in m)]	Random SMZ Treatments	Measured Parameters	Salamanders	Anurans	Reptiles	Total
Olson et al.	2014	OR	Pacific NW	Categorical	Before After Control	45	4	12	-	-	10(6), 14(15), 9(70-145)	Partial*	Counts	9	3	-	12
Perkins & Hunter	2006	ME	Northeast US		Before After Control Impact	15	5	3	3	3	3(11), 3(23)	Yes	Abundance	2	2	-	4
Jackson et al.	2007	WA	Pacific NW			15	3	4	6	-	4(8-10)	No	Density	2	1	-	3
Hawks & Gregory	2012	WA	Pacific NW			18	3	6			6(~7.5), 6(~7.5 + reserve trees)	No	Abundance	2	1	-	3
Maigret et al.	2014	KY	Appalachians			11	3	4	3	-	4(7.6)	Yes	Abundance	5	-	-	5
Halloran	2017	AR	Ouachita Mts			3	2	1	-	-	1(14), 1(21)	No	Abundance, Survival, Movement	1	-	-	1
Guzy et al.	2019	AR	Ouachita Mts			3	2	1	-	-	1(14), 1(21)	No	Growth rate, body size	1	-	-	1
Rudolph & Dickson	1990	TX	Western US		Observational Study	6	3	-	-	-	2(0-25), 2(30-40), 2(50-95)	No	Abundance	-	7	21	28
Dupuis & Steventon	1999	BC	Eastern Canada			54	3	18	18	-	18(5-60)	No	Density	-	1	-	1
Johnston & Frid	2002	BC	Eastern Canada			12	3	7	3	-	1(20), 1(30)	No	Individual movement	1	-	-	1
Peterman & Semlitsch	2009	NC	Appalachians			5	4	2	1	-	1(9), 1(30)	No	Abundance	2	-	-	2
Pollett et al.	2010	WA	Pacific NW			41	4	9	10	10	12(5-23)	No	Density	2	1	-	3
Peterman et al.	2011	NC	Appalachians			5	4	2	1	-	1(9), 1(30)	No	Abundance, Density, Distance from stream	3	-	-	3
Vesley & McComb	2002	OR	Pacific NW	Continuous		29	-	12	-	-	17(0-64)	No	Richness, Abundance, Occurrence	6	-	-	6
Guzy et al.	2019	AR	Ouachita Mts			102	-	-	-	-	102(0-55)	No	Occupancy, Abundance	10	-	-	10
Guzy	2019	AR	Ouachita Mts			102	-	-	-	-	102(0-55)	No	Occupancy	10	11	16	37

Chapter 2:

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

Jacquelyn C. Guzy[1], Kelly M. Halloran[1], Jessica A. Homyack[2], and John D. Willson[1]

[1]Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701

[2] Weyerhaeuser Company, 505 North Pearl Street, Centralia, WA 98531

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 back-ed 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., ≥ 55m on each side of the stream), a value larger than current Forestry BMP guidelines.

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 (Brosofske et al. 1997, Swank et al. 2001, Wilkerson et al. 2006), and protect water quality 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 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 and Hodgson 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.

Methods

Study Sites

This study occurred in even-aged loblolly pine (*Pinus taeda*) stands 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 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 1,854 potential study sites located within managed forests and draining < 3.0 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 2,312 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 138-354 m (mean = 241m; SD = 50m).

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 steam, 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 minute increments (i.e., a score of 1 indicated that after 2 minutes of searching, no additional cover objects could be located, a score of 2 indicated that after 4 minutes, 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.

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.

Salamander Occupancy

We used a multi-species, hierarchical Bayesian model developed by Zipkin et al. (2009) and modified by Hunt et al. (2012) 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 (Pacifici 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 kth 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.

- $\text{logit}(\Psi_{ij}) = u_i + \alpha1_i\,\text{SMZ width}_j + \alpha2_i\,\text{Young pre-thin}_j + \alpha3_i\,\text{Mid pre-thin}_j + \alpha4_i\,\text{Post-thin}_j + \alpha5_i\,\text{Staggered harvest}_j + \alpha6_i\,\text{Pine SMZ}_j + \alpha7_i\,\text{Mixed SMZ}_j + \alpha8_i\,\text{No SMZ}_j + \alpha9_i\,\text{Site PC1}_j + \alpha\,10_i\,\text{Site PC2}_j$

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

- $\text{logit}(\Theta_{ijk}) = v_i + \beta1_i\,\text{Sampling PC1}_j + \beta2_i\,\text{Sampling PC2}_j$

Parameters α2 – α5 were effects of the categorical predictor variable “stand age”, with "Old post-thin" as the reference category, and parameters α6 – α8 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 $u_{\alpha1}$ 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 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 (α)/(1+ exp α)).

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.

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. glutinousus*, *P. serratus*, and *P. caddoensis*].

We specified salamander abundance with the model below. Parameters β2 – β5 were the effects of the categorical predictor variable “stand age”, with "Old post-thin" as the reference category.

- $N_i|\lambda_i \sim \text{Poi}(\lambda_i)$

  $\log(\lambda_i) = \beta_0 + \beta_1$ SMZ width + β_2 Young pre-thin + β_3 Mid pre-thin + β_4 Post-thin + β_5 Staggered harvest + β_6 Site PC1 + β_7 Site PC2

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

- $c_{ij}|N_i \sim \text{Bin}(N_i, p_{ij})$

  $\text{logit}(p_{ij}) = \alpha_0 + \alpha_1$ 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 expit(α_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*).

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 scutatum*), 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.

Occupancy, Detection, and Species Richness

Across the entire species assemblage, mean salamander occupancy response to SMZ width was positive ($u_{\alpha1}$: 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 (σ=0.56, 95% CI 0.03 to 1.42) for the SMZ covariate effect was less than the corresponding mean (μ) covariate estimate ($CV\alpha1 = 0.52$), 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 ($u_{\alpha9}$: 0.66, 95%CI 0.13 to 1.20; Appendix 3 and 4a) that was consistently positive across species ($CVu_{\alpha9} = 0.76$). 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., $\mu_{\beta1}$ PC1) indicated that detection probability was greater at earlier dates, which also had cooler temperatures and moister soils ($\mu_{\beta1}$: -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.

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. scutatum*, *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. 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).

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 (> 55 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).

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 ($u_{\alpha 1}$ 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.

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 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).

SMZ Width

Increasing SMZ width strongly influenced estimated abundance of *D. brimleyorum*, *E. multiplicata*, *P. caddoensis*, and *P. serratus* ($\beta_{1\,(D.\ brimleyorum)} = 0.40$; 95% CI 0.28 to 0.52; $\beta_{1\,(E.}$

$_{multiplicata)}$ = 0.22; 95% CI 0.10 to 0.33), $\beta_{1(P.\ caddoensis)}$ = 0.38; 95% CI 0.00 to 0.73), and $\beta_{1(P.\ serratus)}$ = 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. 5 c-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 (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.

Abundance 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* ($\beta_{1\ (D.\ brimleyorum)}$ = 0.42; 95% CI 0.30 to 0.53; $\beta_{1\ (E.\ multiplicata)}$ = 0.23; 95% CI 0.11 to 0.34), and $\beta_{1(P.\ serratus)}$ = 0.52; 95% CI 0.20 to 0.83).

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).

*E*stimated 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).

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.

Additionally, 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.

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.

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.

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 9m) 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.

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.

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 (11-24m), 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.

Acknowledgements

Funding for this study was provided by Weyerhaeuser Company, the National Council for Air and Stream Improvement, the Arkansas Science and Technology Authority, and the University of Arkansas. We are grateful to Brian Halstead and Steven Price for assistance implementing the data analysis approach and to Doug Leasure for assistance with geospatial analyses. T. Bentley Wigley provided valuable input on project design and management and comments that improved this manuscript. We thank Paula Szczerba and Shane Szczerba at Weyerhaeuser for providing extensive logistical support during data collection. We thank Meredith Swartwout and Dustin Lynch for assistance with stream surveys. For project guidance and comments on the manuscript, we thank Michelle Evans-White and Dan Magoulick. We thank two anonymous reviewers for comments that improved this manuscript.

Literature Cited

Arkansas Forestry Commission. 2002. Best Management Practices for Water Quality Protection. www.forestry.state.ar.us

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11:983-989.

Ashton, D. T., S. B. Marks, and H. H. Welsh. 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. Forest Ecology and Management 221:183-193.

Aust, W. M., and C. R. Blinn. 2004. Forestry best management practices for timber harvesting and site preparation in the eastern United States: An overview of water quality and productivity research during the past 20 years (1982-2002). Water, Air, and Soil Pollution: Focus 4:5-36.

Best, M. L., and H. H. Welsh Jr. 2014. The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. Ecosphere 5:1-19.

Blinn, C. R., and M. A. Kilgore. 2001. Riparian management practices: a summary of state guidelines. Journal of Forestry 99:11-17.

Boothroyd, I. K. G., and E. R. Langer. 1999. Forest harvesting and riparian management guidelines. National Institute of Water and Atmospheric Research. Technical Report 56.

Broadmeadow S., and T. R. Nisbet. 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. Hydrology and Earth System Sciences Discussions 8:286-305.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Connette, G. M., M. S. Osbourn, and W. E. Peterman. 2016. The distribution of a stream-breeding salamander, (*Desmognathus ocoee*), in terrestrial habitat suggests the ecological importance of low-order streams. Copeia 2016:149-156.

Crawford, J. A., and R. D. Semlitsch. 2007. Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. Conservation Biology 21:152-158.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, J. F. Munsell, and E. Schilling. 2016. Effectiveness of forestry best management practices in the United States. Forest Ecology and Management 360:133-151.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, and J. F. Munsell. 2018. National status of state developed and implemented forestry best management practices for protecting water quality in the United States. Forest Ecology and Management 418:73-84.

Davic, R. D., and H. H. Welsh Jr. 2004. On the ecological roles of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405-434.

Degraaf, R. M., and D. D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. Forest Ecology and Management 32:155-165.

Degraaf, R. M., and M. Yamasaki. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. Wildlife Society Bulletin 20:260-264.

deMaynadier, P. G., and M. L. Hunter Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230-261.

deMaynadier, P. G., and M. L. Hunter. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12:340-352.

Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association 100:389-398.

Dorazio, R. M., J. A. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842-854.

Ford, W. M., M. A. Menzel, and R. H. Odom. 2002. Elevation, aspect, and cove size effects on southern Appalachian salamanders. Southeastern Naturalist 1:315-324.

Gelman, A., and D. B. Rubin. 1992 Inference from iterative simulation using multiple sequences. Statistical Science 7:457-472.

Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. The Journal of Wildlife Management 1998:584-589.

Grialou, J. A., West, S. D., and Wilkins, R. N. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. The Journal of Wildlife Management 64:105-113.

Hairston, N. G. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge, U.K.

Halloran, K.M. 2017. Population dynamics of Ouachita Dusky Salamanders (*Desmognathus brimleyorum*) in a managed forest landscape Thesis. University of Arkansas. Fayetteville.

Herbeck, L. A., and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark Forests. Conservation Biology 13:623-632.

Hocking, D. J., G. M. Connette, C. A. Conner, B. R. Scheffers, S. E. Pittman, W. E. Peterman, and R. D. Semlitsch. 2013. Effects of experimental forest management on a terrestrial, woodland salamander in Missouri. Forest Ecology and Management 287:32-39.

Homyack, J. A., and C. A. Haas. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation 142:110-121.

Hunt, S. D., J. C. Guzy, S. J. Price, B. J. Halstead, E. A. Eskew, and M. E. Dorcas. 2013. Responses of riparian reptile communities to damming and urbanization. Biological Conservation 157:277-284.

Jackson, C. R., D. P. Batzer, S. S. Cross, S. M. Haggerty, and C. A Sturm. 2007. Headwater streams and timber harvest: channel, macroinvertebrate, and amphibian response and recovery. Forest Science 53:356-370.

Johnston, B., and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus*). Canadian Journal of Zoology 80:2170-2177.

Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90:1279-1290.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press.

Kleeberger, S. R., and J. K. Werner. 1982. Home range and homing behavior of Plethodon cinereus in northern Michigan. Copeia 1982:409-415.

Klemmedson, J. O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. Forest Ecology and Management 47:349-361.

Knapp, S. M., C. A. Haas, D. N. Harpole, and R. L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silivicultural practices on terrestrial salamander abundance. Conservation Biology 17:752-762.

Kroll, A. J. 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. Forest Ecology and Management 257:1188-1199.

Kuglerová, L., A. Ågren, R. Jansson, and H. Laudon. 2014. Towards optimizing riparian buffer zones: ecological and biogeochemical implications for forest management. Forest Ecology and Management 334:74-84.

Leasure, D. R. 2014. Applications of a new geodata crawler for landscape ecology: from mapping natural stream hydrology to monitoring endangered beetles. Dissertation. University of Arkansas.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Forest Ecology and Management 70:165-180.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial Processes in Geomorphology. San Francisco, California, Freeman. Pp.135-163.

Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. BioScience 24:447-456.

Lowe, W. H., and G. E. Likens. 2005. Moving headwater streams to the head of the class. BioScience 55:196-197.

Lunn, D., Jackson, C., Best, N., Spiegelhalter, D., and Thomas, A. The BUGS book: A practical introduction to Bayesian analysis. Chapman and Hall/CRC.

Maigret, T. A., J. J. Cox, D. R. Schneider, C. D. Barton, S. J. Price, and J. L. Larkin. 2014. Effects of timber harvest within streamside management zones on salamander populations in ephemeral streams of southeastern Kentucky. Forest Ecology and Management 324:46-51.

Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications 20:126-134.

Marsh, D. M., and N. G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14:1882-1891.

Marvin, G. A. 1998. Territorial behavior of the plethodontid salamander Plethodon kentucki: influence of habitat structure and population density. Oecologia 114:133-144.

McKenny, H. C., W. S. Keeton, T. M. Donovan. 2006. Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. Forest Ecology and Management 230:186-196.

Meyer, J. L., and J. B. Wallace. 2001. “Lost Linkages and Lotic Ecology: Rediscovering Small Streams,” In: M. C. Press, N. J. Huntly and S Levin, Eds., Ecology: Achievement and Challenge, Blackwell Scientific, Oxford, pp. 295-317.

Milanovich, J. R., J. C. Maerz, and A. D. Rosemond. 2015. Stoichiometry and estimates of nutrient standing stocks of larval salamanders in Appalachian headwater streams. Freshwater Biology 60:1340-1353.

Moore, J-D, R. Ouimet, C. Camiré, and D. Houle. 2002. Effects of two silvicultural practices on soil fauna abundance in a northern hardwood forest, Québec, Canada. Canadian Journal of Soil Science, 82: 105-113.

Moore, R., D. L. Spittlehouse, and A. Story. 2005. Riparian microclimate and stream temperature response to forest harvesting: a review. Journal of the American Water Resources Association, 41: 813-834.

Oklahoma Forestry Services. 2016. Oklahoma's Best Management Practices for Water Quality. forestry.ok.gov

Oswalt, S. N., W. B. Smith, P. D. Miles, and S. A. Pugh. 2014. Forest Resources of the United States, 2012: a technical document supporting the Forest Service 2010 update of the RPA Assessment.

Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry, and A. DeWan. 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecology and Evolution 4:877-888.

Parkyn, S. 2004. Review of riparian buffer zone effectiveness. Wellington, New Zealand: Ministry of Agriculture and Forestry. Volume 2005.

Parrish, M. C., S. Demarais, A. W. Ezell, T. B. Wigley, P. D. Jones, and S. K. Riffell. 2017. Retained vegetation density of streamside management zones and stringers in southern intensively managed pine forests. Forest Ecology and Management 397:89-96.

Perkins, D. W., and M. L. Hunter Jr. 2006. Effects of riparian timber management on amphibians in Maine. Journal of Wildlife Management 70:657-670.

Peterman, W. E., and R. D. Semlitsch. 2009. Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. Forest Ecology and Management 257:8-14.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). Freshwater Biology 53:347-357.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2011. Effects of even-aged timber harvest on stream salamanders: support for the evacuation hypothesis. Forest Ecology and Management 262:2344-2353.

Petranka, J. W., and S. S. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. Journal of Herpetology 2001:36-44.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7:363-370.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Washington: Smithsonian Institution Press. 587pp.

Petranka, J. W., and C. K. Smith. 2005. A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. Forest Ecology and Management 210:443-454.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Phillips, M. J., W. Lloyd Jr., and C. R. Blinn. 2000. Best management practices for riparian areas. In: Verry, Elon S.; Hornbeck, James W.; Dolloff, C. Andrew, eds. Riparian management in forests of the continental Eastern United States. Boca Raton, FL: Lewis Publishers, CRC Press LLC: 273-286.

Price, S. J., J.C. Guzy, L. Witczak, and M.E. Dorcas. 2013. Do ponds on golf courses provide suitable habitat for wetland-dependent animals in suburban areas? An assessment of turtle abundances. Journal of Herpetology 47:243-250.

R Development Core Team. 2015 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rittenhouse, T. A., E. B. Harper, L. R. Rehard, and R. D. Semlitsch. 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak-hickory forest. Copeia 2008:807-814.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities. Academic Press, New York, NY.

Russell, K. R., T. J. Mabee, and M. B. Cole. 2004. Distribution and habitat of Columbia torrent salamanders at multiple spatial scales in managed forests of northwestern Oregon. Journal of Wildlife Management 68:405-417.

Sauer, J. R. and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. Ecology 86:1743-1751.

Semlitsch, R. D., C. A Conner, D. J. Hocking, T. A. Rittenhouse, and E. B. Harper. 2008. Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. Ecological Applications 18:283-289.

Semlitsch, R. D., K. M. O’Donnell, and F. R. Thompson III. 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. Canadian Journal of Zoology 92:997-1004.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278-296.

Spiegelhalter, D. J., A. Thomas, N. G. Best, and D. Lunn. 2003. WinBUGS Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge, UK.

Sturtz, S., U. Ligges, and A. E. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software 12:1-16.

Swan, C. M., and M. A. Palmer. 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia 147:469-478.

Swank, W. T., J. M. Vose, and K. J. Elliott. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and Management 143:163-178.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97-104.

Tilghman, J. M., S. W. Ramee, and D. M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation 152:1-9.

Trauth, S. E., H. W. Robison, and M. V. Plummer. 2004. Amphibians and reptiles of Arkansas. The University of Arkansas Press. Fayetteville, Arkansas, USA.

Trauth, S.E., J.D. Wilhide. 1999. Status of three plethodontid salamanders (Genus Plethodon) from the Ouachita National Forest of southwestern Arkansas. Journal of the Arkansas Academy of Science 53:125-137.

Wallace, J. B., Eggert, S. L., Meyer, J. L., and Webster, J. R. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science, 277:102-104.

Warrington, B. M., W. M. Aust, S. M. Barrett, W. M. Ford., C. A. Dolloff, E. B. Schilling, T. B. Wigley, and M. C. Bolding. 2017. Forestry Best Management Practices Relationships with Aquatic and Riparian Fauna: A Review. Forests 8:331-346.

Welsh Jr, H.H., and G.R. Hodgson. 2008. Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, USA. Freshwater biology 53.7 (2008): 1470-1488.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology, 377-392.

Whiles, M. R., and Wallace, J. B. 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. Hydrobiologia, 353:107-119.

Willacker Jr, J. J., W. V. Sobczak, and E. A. Colburn. 2009. Stream macroinvertebrate communities in paired hemlock and deciduous watersheds. Northeastern Naturalist 16:101-112.

Wilkerson, E., Hagan, J. M., Siegel, D., and Whitman, A. A. 2006. The effectiveness of different buffer widths for protecting headwater stream temperature in Maine. Forest Science, 52:221-231.

Wilson, E. O., and R. H. MacArthur. 1967. The theory of island biogeography. Princeton, NJ.

Woods A.J., Foti, T.L., Chapman, S.S., Omernik, J.M., Wise, J.A., Murray, E.O., Prior, W.L., Pagan, J.B., Jr., Comstock, J.A., and Radford, M., 2004, Ecoregions of Arkansas (color poster with map, descriptive text, summary tables, and photographs: Reston, Virginia, U.S. Geological Survey (map scale 1:1,000,000). ftp://ftp.epa.gov/wed/ecoregions/ar/ar_front.pdf

Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation 7:641-650.

Wyman, R. L., and Jancola, J. 1992. Degree and scale of terrestrial acidification and amphibian community structure. Journal of Herpetology, 392-401.

Zipkin, E.F., Dewan, A., and Royle, J.A. 2009 Impacts of forest fragmentation on species richness: a hierarchical approach to community modeling. Journal of Applied Ecology, 46:815-822.

Figures and Tables

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.

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

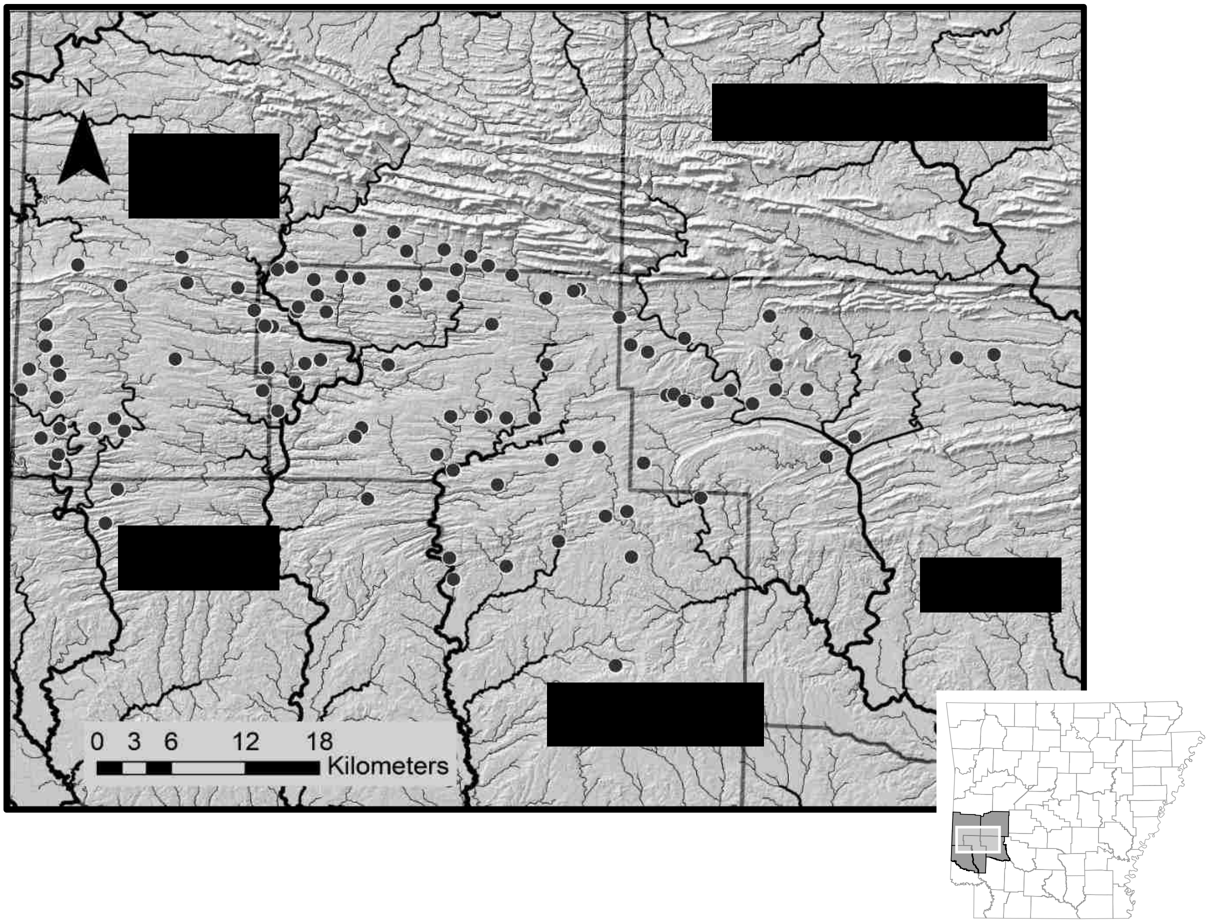


Figure 1. Location of study sites. Map inset: Ouachita Mountains Ecoregion of west-central Arkansas, USA. Main map: distribution of study sites (n=102) located in Howard, Polk, Pike, and Sevier counties, Arkansas.

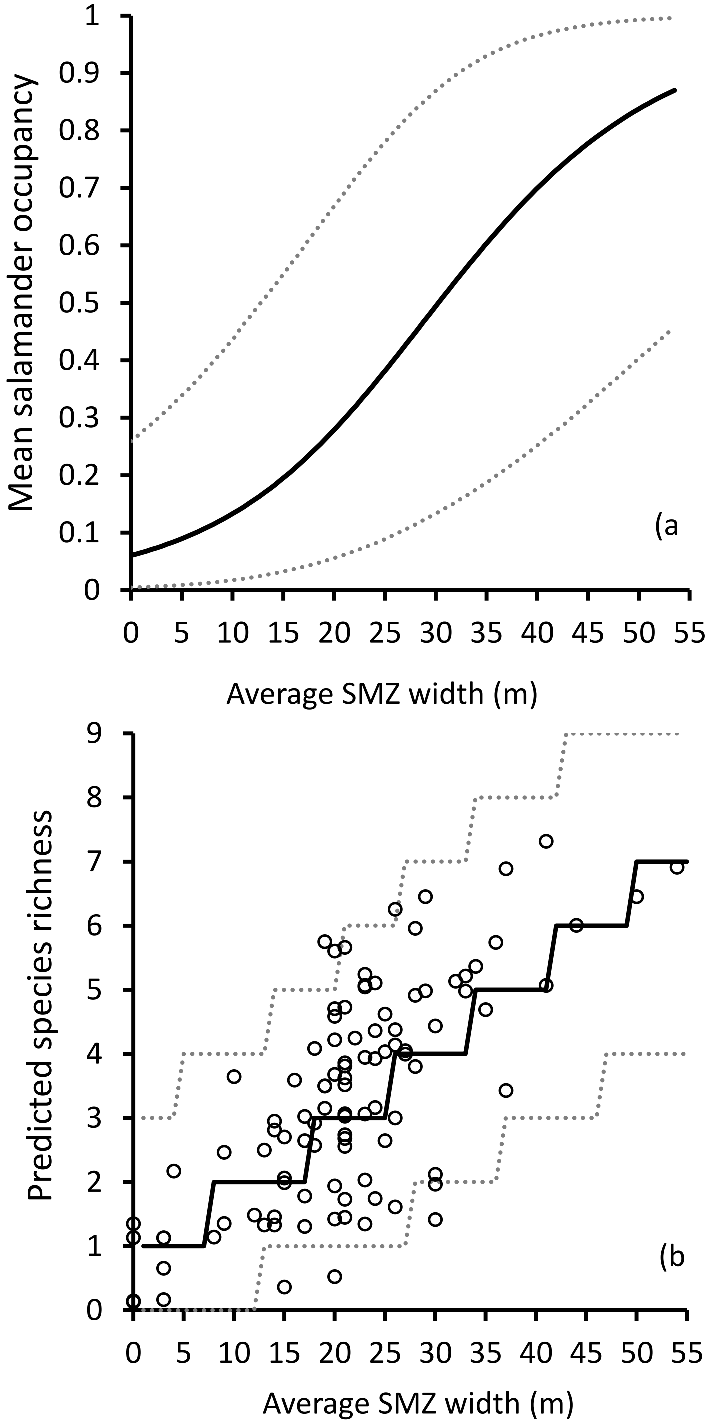


Figure 2. Relationship between streamside management zone (SMZ) width and a) mean occupancy probability and b) median estimated species richness of salamanders within streamside management zones of the Ouachita Mountains, Arkansas, USA. Solid lines represent the posterior mean and dashed lines represent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

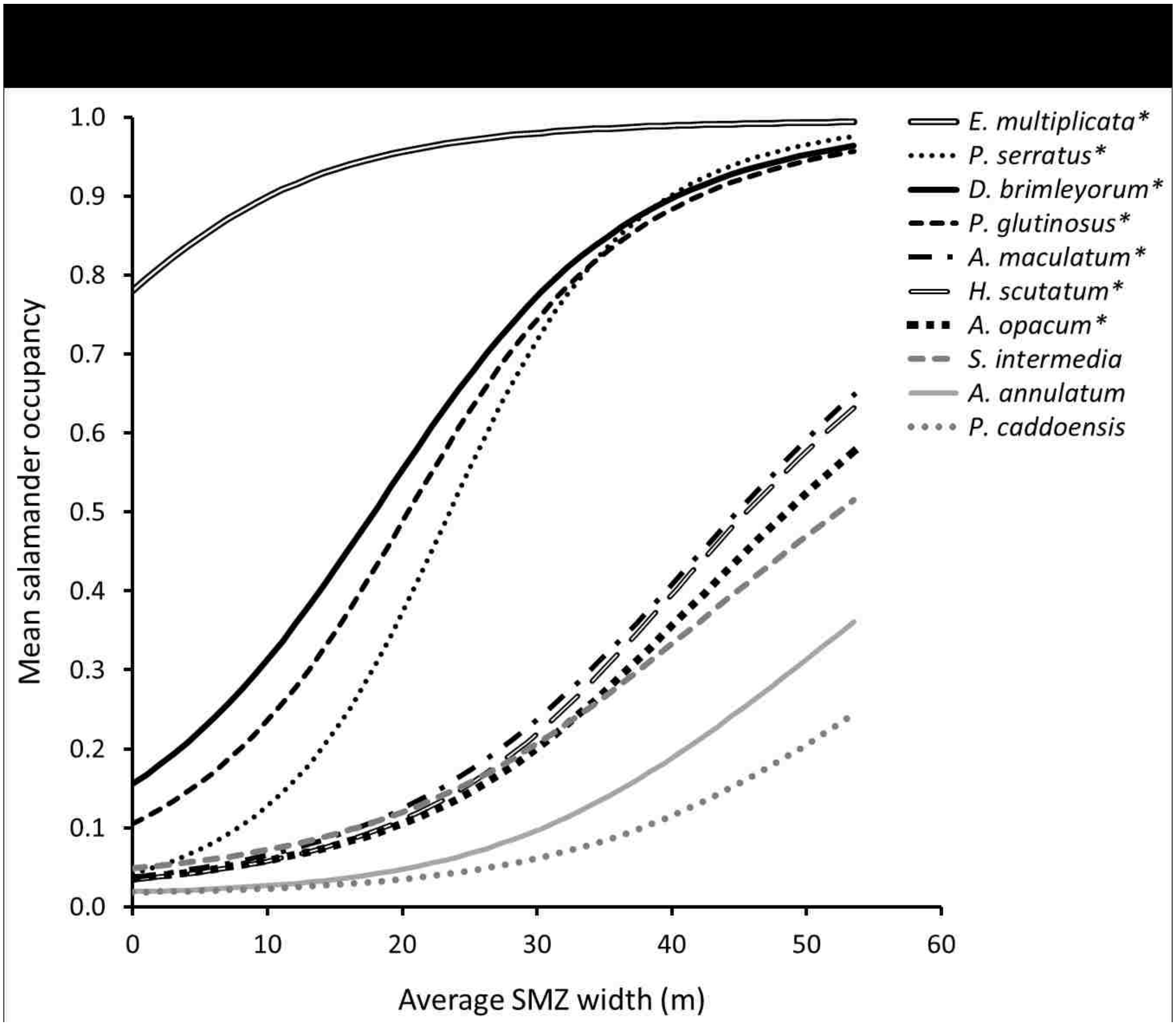


Figure 3. Relationship between mean species-specific occupancy probability and streamside management zone (SMZ) width for salamanders within SMZs of the Ouachita Mountains, Arkansas, USA. Credible intervals are omitted for clarity, and asterisks indicate species for which the SMZ parameter estimate (α1i) did not overlap zero.

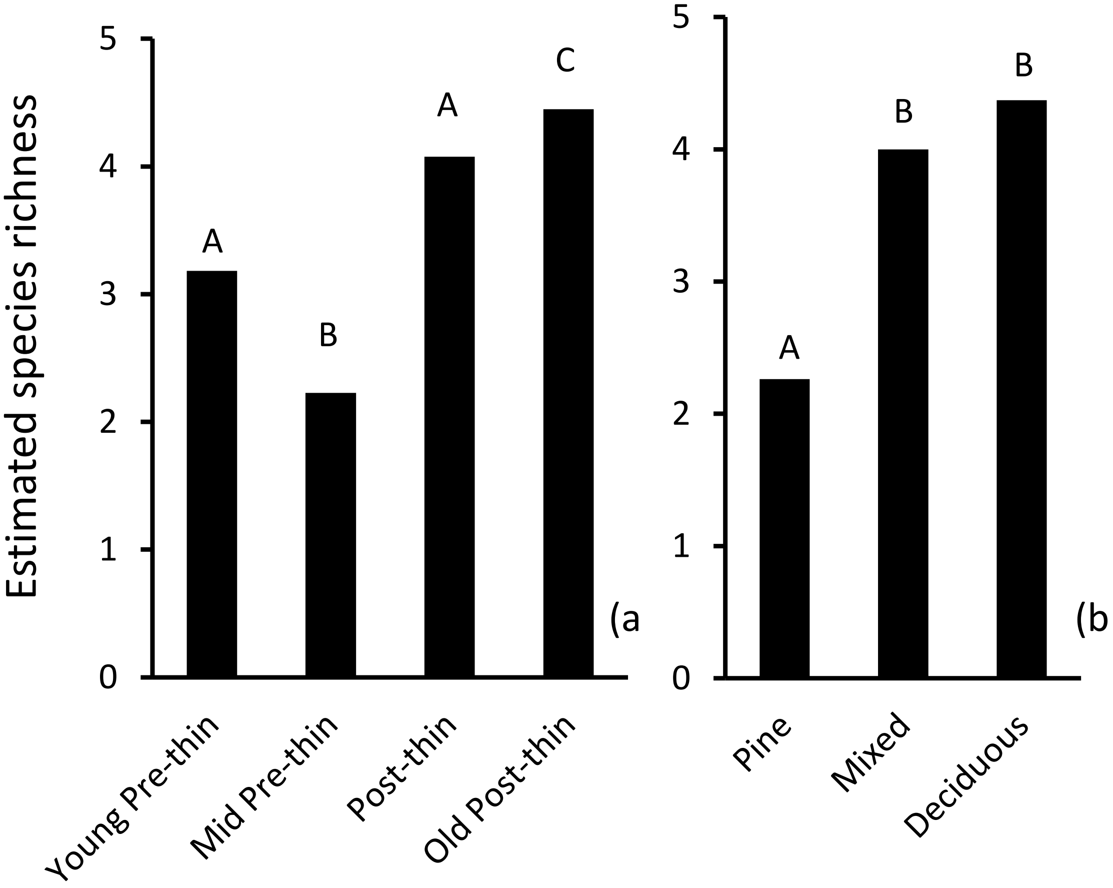


Figure 4. Estimated mean salamander species richness among a) stand age and b) overstory composition categories of streamside management zones (SMZs) within the Ouachita Mountains, Arkansas, USA. Columns that do not share a letter are statistically different from each other (i.e., credible interval does 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' (13-22years old, 1-6 years since thinning), and 'Old Post-thin' (22-35 years old, 8-17 years since thinning).

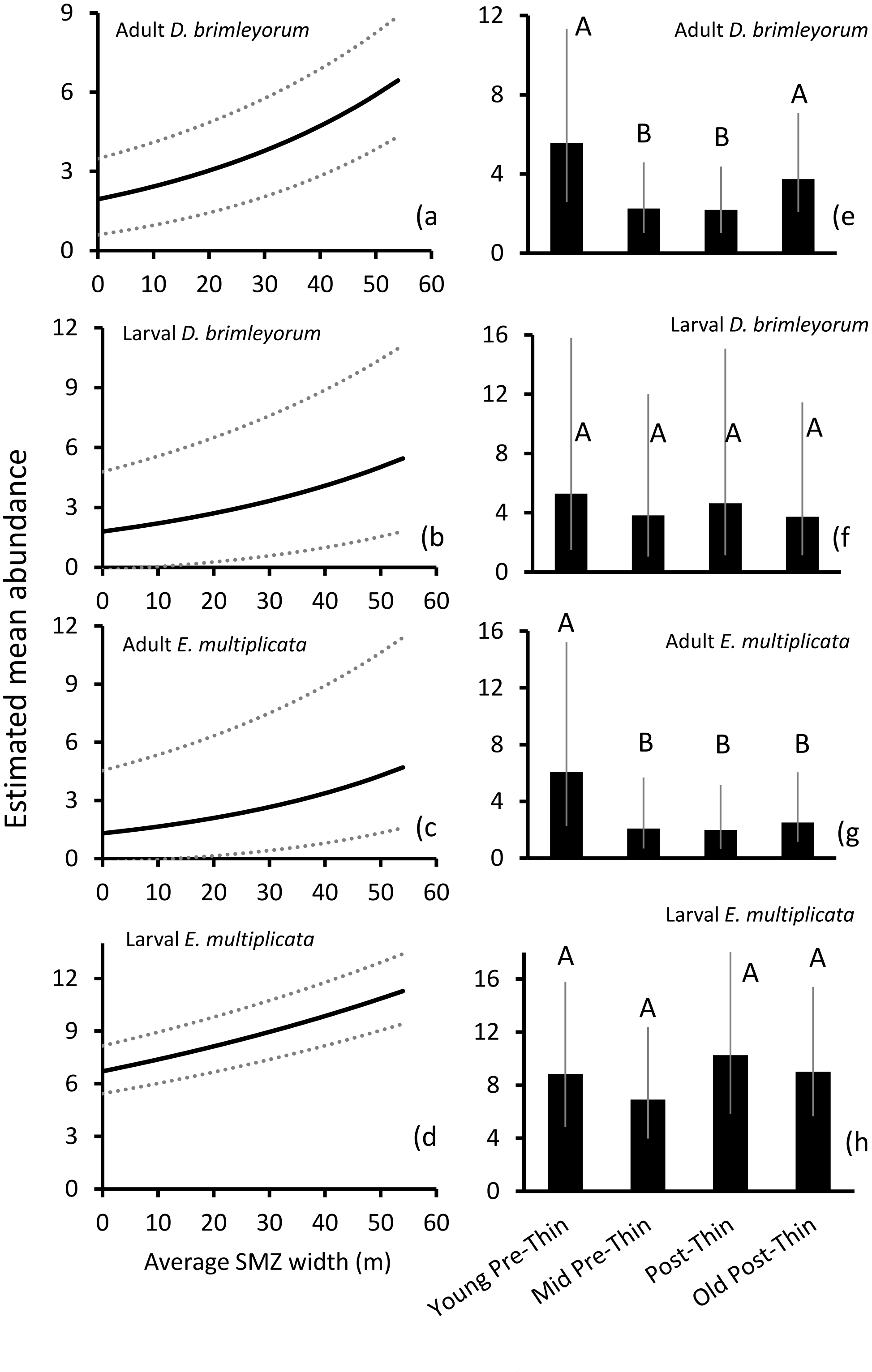


Figure 5. Estimated mean abundance by age class of *Desmognathus brimleyorum* and *Eurycea multiplicata* in relation to a-d) streamside management zone (SMZ) width and e-h) stand age within the Ouachita Mountains, Arkansas, USA. Solid lines represent the posterior mean and dashed lines represent the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

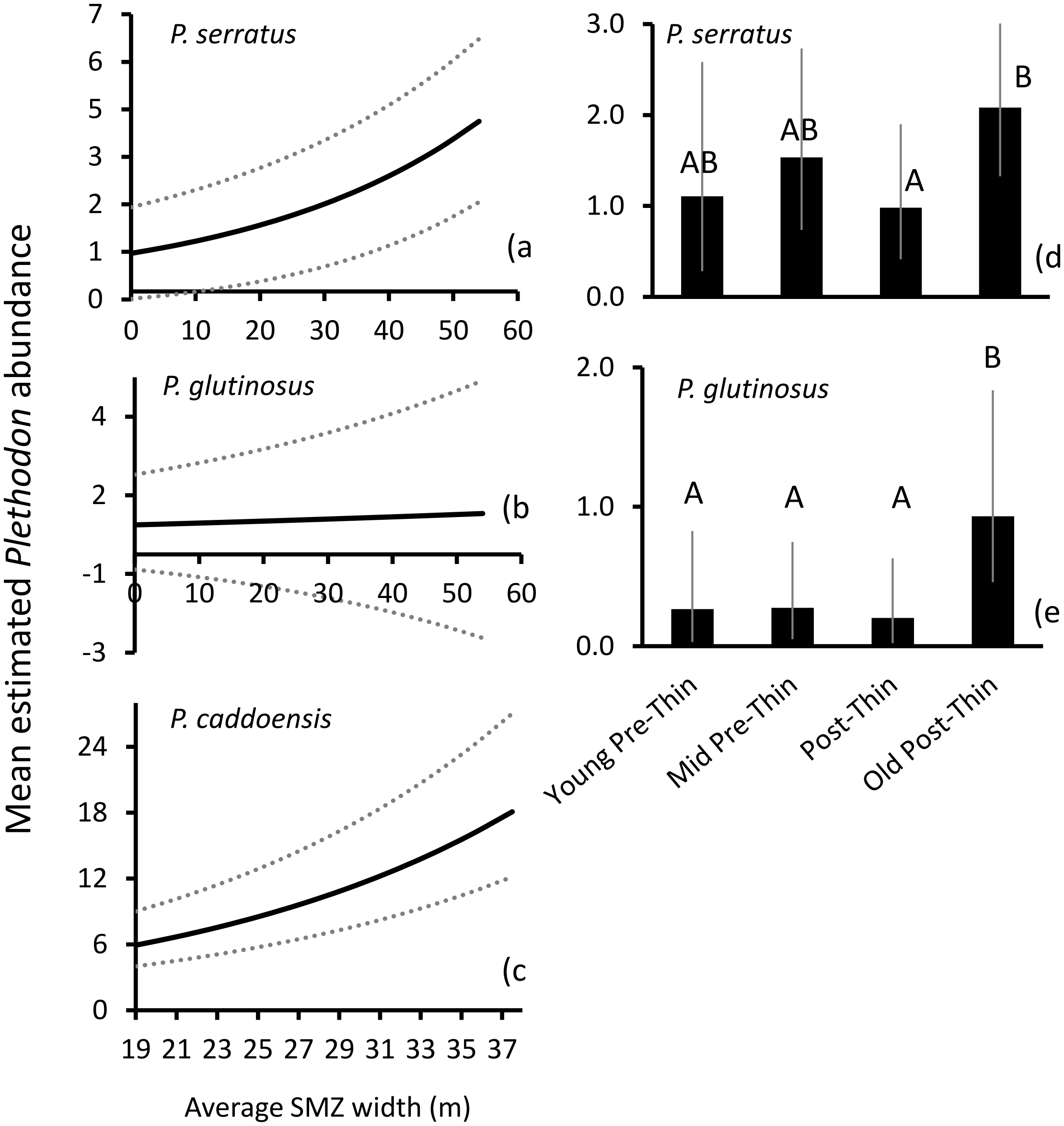
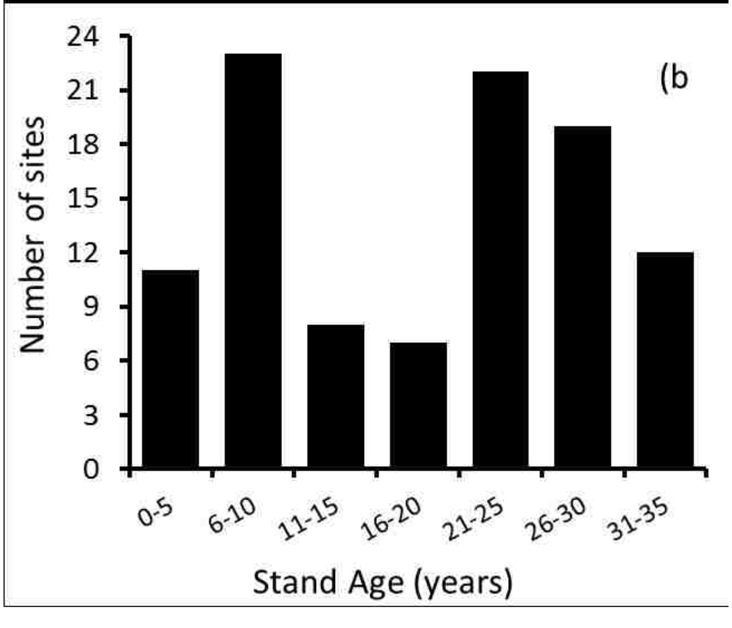


Figure 6. Estimated mean abundance of a) *Plethodon serratus*, b) *P. glutinosus* complex, and c) *P. caddoensis* in relation to streamside management zone (SMZ) width, and mean abundance of d) *P. serratus* and e) *P. glutinosus* complex in relation to stand age within the Ouachita Mountains, Arkansas, 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.

Appendices

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.

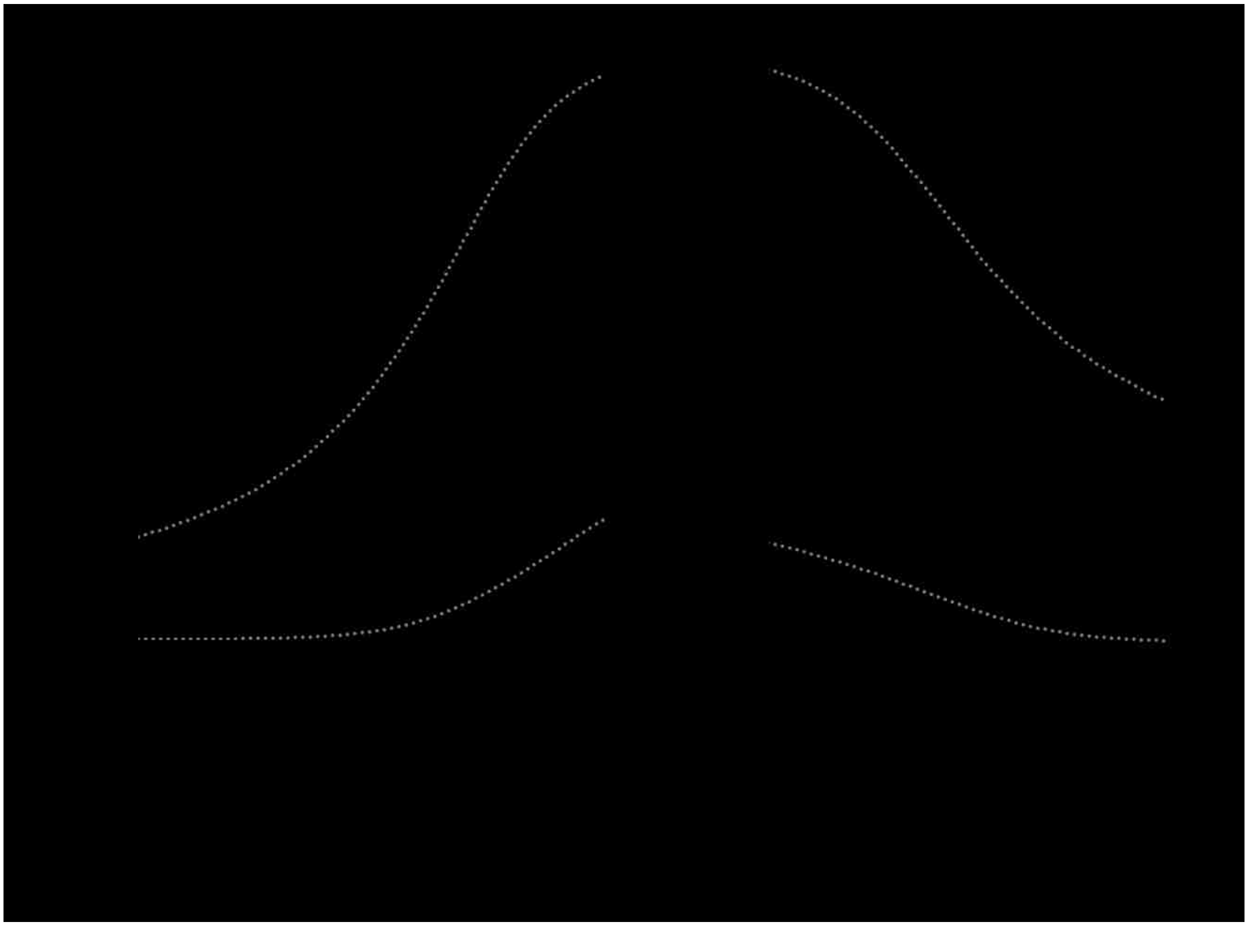
Site Covariates		
Principal Components	1	2
Eigenvalues	3.75	1.88
% of Variation	31.0	15.5
Cum. % of Variation	31.0	46.5
Variable (Eigenvectors*)	PC1	PC2
Latitude	**0.40**	-0.27
Watershed area	-0.16	**0.35**
Elevation	**0.34**	**-0.40**
% Bedrock	0.09	0.18
% Boulder and cobble	0.25	**0.51**
% Sand and silt	**-0.36**	**-0.38**
Water temperature	**-0.43**	-0.02
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**

Sampling Covariates		
	1	2
	2.37	1.41
	33.8	20.0
	33.8	53.8
	PC1	PC2
Date	**0.51**	**-0.35**
Air temperature	**0.49**	**0.29**
Barometric pressure	0.14	-0.08
Humidity	0.13	**-0.70**
Water depth	-0.07	**-0.31**
Water temperature	**0.58**	-0.06
Soil moisture	**-0.34**	**-0.45**

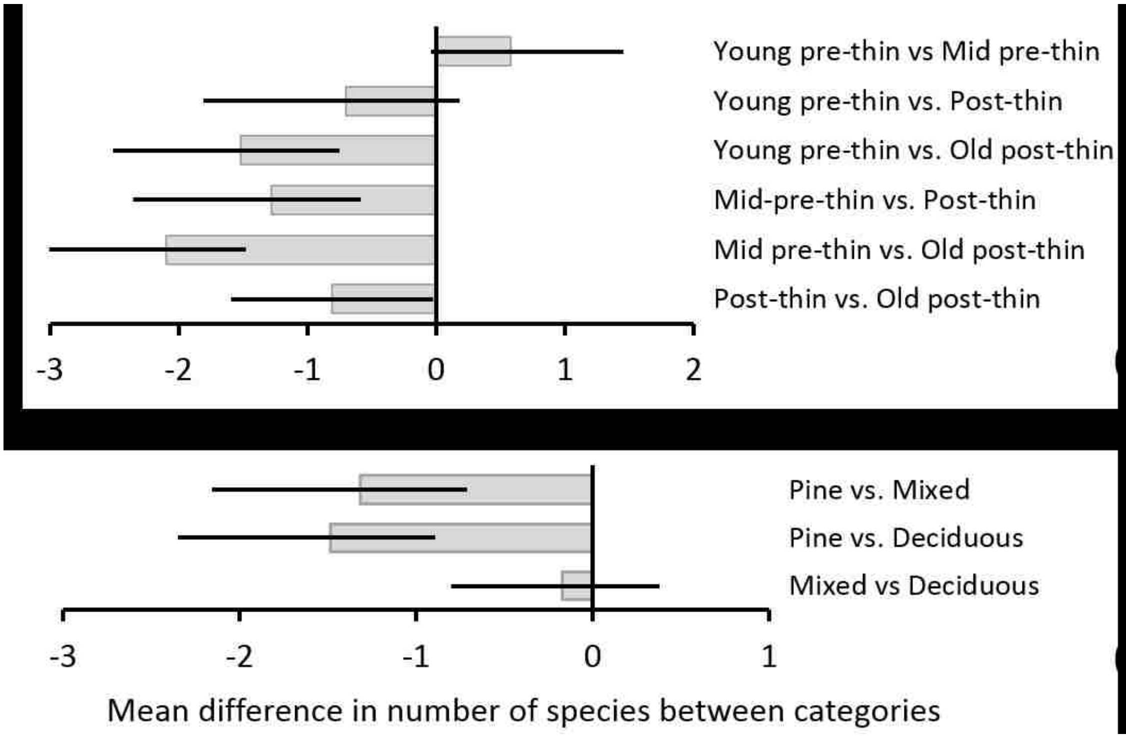
Appendix 3. Summary of species-specific occupancy (SMZ, Site PC1, Site PC2) and detection (Sampling PC1-2) parameter estimates, and 95% credible intervals, for salamanders within streamside management zones in the Ouachita Mountains, Arkansas, USA.

Latin name	Parameter	Mean	2.5 % CRI	Median CRI	97.5 % CRI	SD
Ambystoma annulatum	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 PC1	-0.63	-1.83	-0.58	0.26	0.52
	Sampling PC2	-0.05	-1.09	0.01	0.73	0.44
Ambystoma maculatum	**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 PC1	**-0.91**	-2.05	-0.85	-0.14	0.48
	Sampling PC2	0.35	-0.20	0.28	1.24	0.37
Ambystoma opacum	**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 PC1	-0.69	-1.91	-0.64	0.21	0.52
	Sampling PC2	-0.06	-1.05	-0.01	0.62	0.41
Desmognathus brimleyorum	**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 PC1	-0.18*	-0.37	-0.18	0.01	0.10
	Sampling PC2	0.13	-0.09	0.13	0.37	0.12
Eurycea multiplicata	**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 PC1	-0.12*	-0.26	-0.12	0.02	0.07
	Sampling PC2	0.14*	-0.04	0.13	0.32	0.09
Hemidactylum scutatum	**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 PC1	-0.32	-1.29	-0.31	0.58	0.46
	Sampling PC2	0.35	-0.23	0.27	1.34	0.39
Plethodon caddoensis	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 PC1	**-0.82**	-1.65	-0.79	-0.17	0.38
	Sampling PC2	0.10	-0.36	0.09	0.57	0.23
Plethodon glutinosus complex	**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 PC1	**-0.26**	-0.50	-0.26	-0.03	0.12
	Sampling PC2	-0.26*	-0.60	-0.26	0.08	0.17
Plethodon serratus	**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 PC1	**-1.10**	-1.52	-1.09	-0.72	0.20
	Sampling PC2	0.19*	-0.08	0.18	0.49	0.15
Siren intermedia	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 PC1	0.12	-0.77	0.06	1.37	0.54
	Sampling PC2	-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 to Sampling PC1. Solid lines represent the posterior mean community response and dashed lines represent 95% credible intervals.



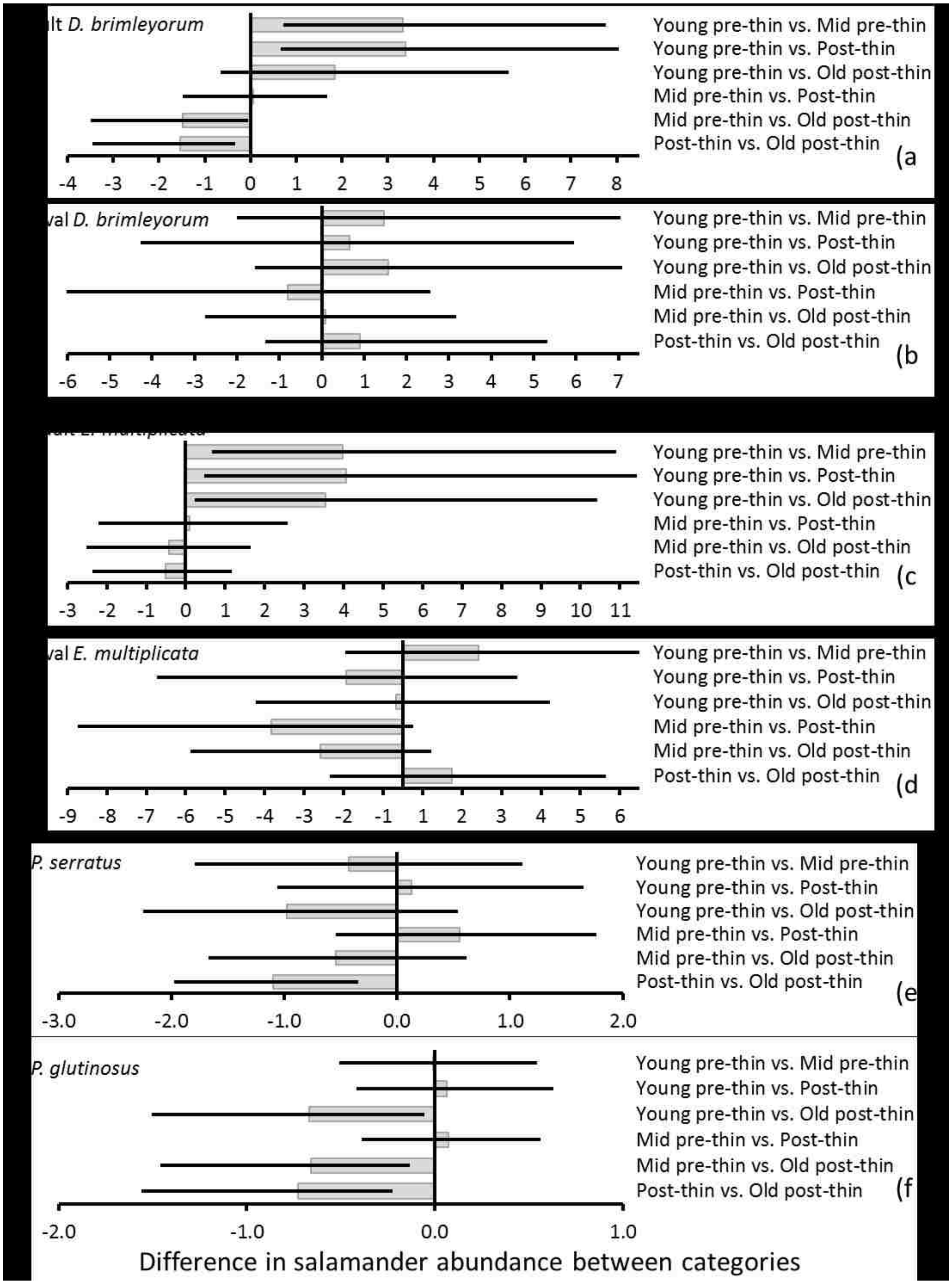
Appendix 5. Mean differences in salamander species richness between pairs of a) stand age categories and b) streamside management zone (SMZ) overstory composition, including 95% credible intervals, within SMZs of the Ouachita Mountains, Arkansas, USA. The mean difference in number of species is derived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



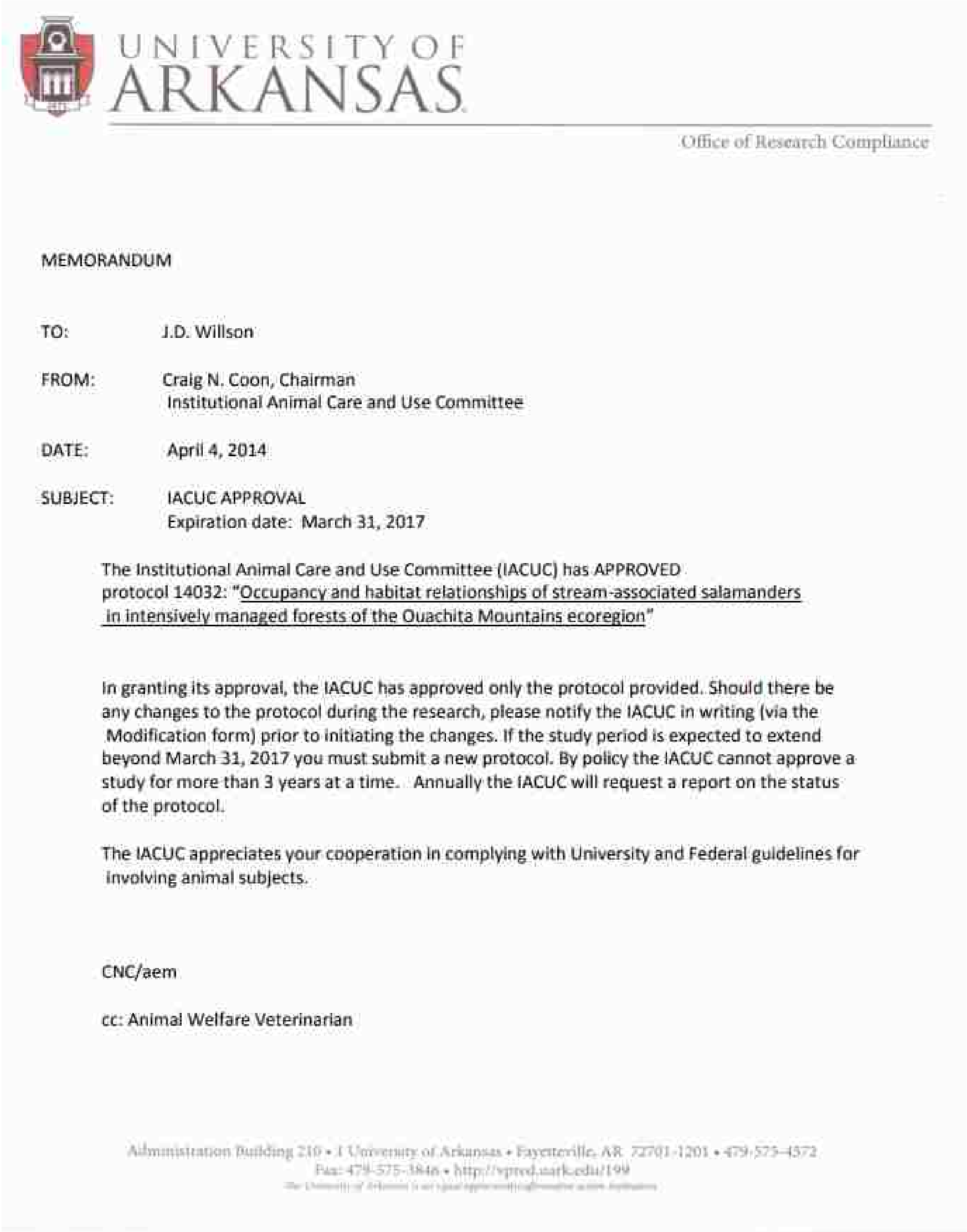
Appendix 6. Summary of species-specific abundance parameter estimates, and 95% credible intervals, for salamanders within streamside management zones in the Ouachita Mountains, Arkansas, USA. Covariates influencing detection probability include Sampling PC1 and 2.

Genus	species	Age Class	Parameter	Mean	2.5 % CRI	Median CRI	97.5 % CRI
Desmognathus	*brimleyorum*	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
Eurycea	*multiplicata*	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
Plethodon	*caddoensis*	-	**SMZ**	**0.38**	0.00	0.38	0.73
		-	date	-0.02	-0.43	-0.02	0.38
Plethodon	*glutinosus complex*	-	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
Plethodon	*serratus*	-	**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 8. IACUC Approval documents



UNIVERSITY OF
ARKANSAS
Office of Research Compliance

MEMORANDUM

TO: J.D. Willson

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee

DATE: April 4, 2014

SUBJECT: IACUC APPROVAL
Expiration date: March 31, 2017

The Institutional Animal Care and Use Committee (IACUC) has APPROVED protocol 14032: "Occupancy and habitat relationships of stream-associated salamanders in intensively managed forests of the Ouachita Mountains ecoregion"

In granting its approval, the IACUC has approved only the protocol provided. Should there be any changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond March 31, 2017 you must submit a new protocol. By policy the IACUC cannot approve a study for more than 3 years at a time. Annually the IACUC will request a report on the status of the protocol.

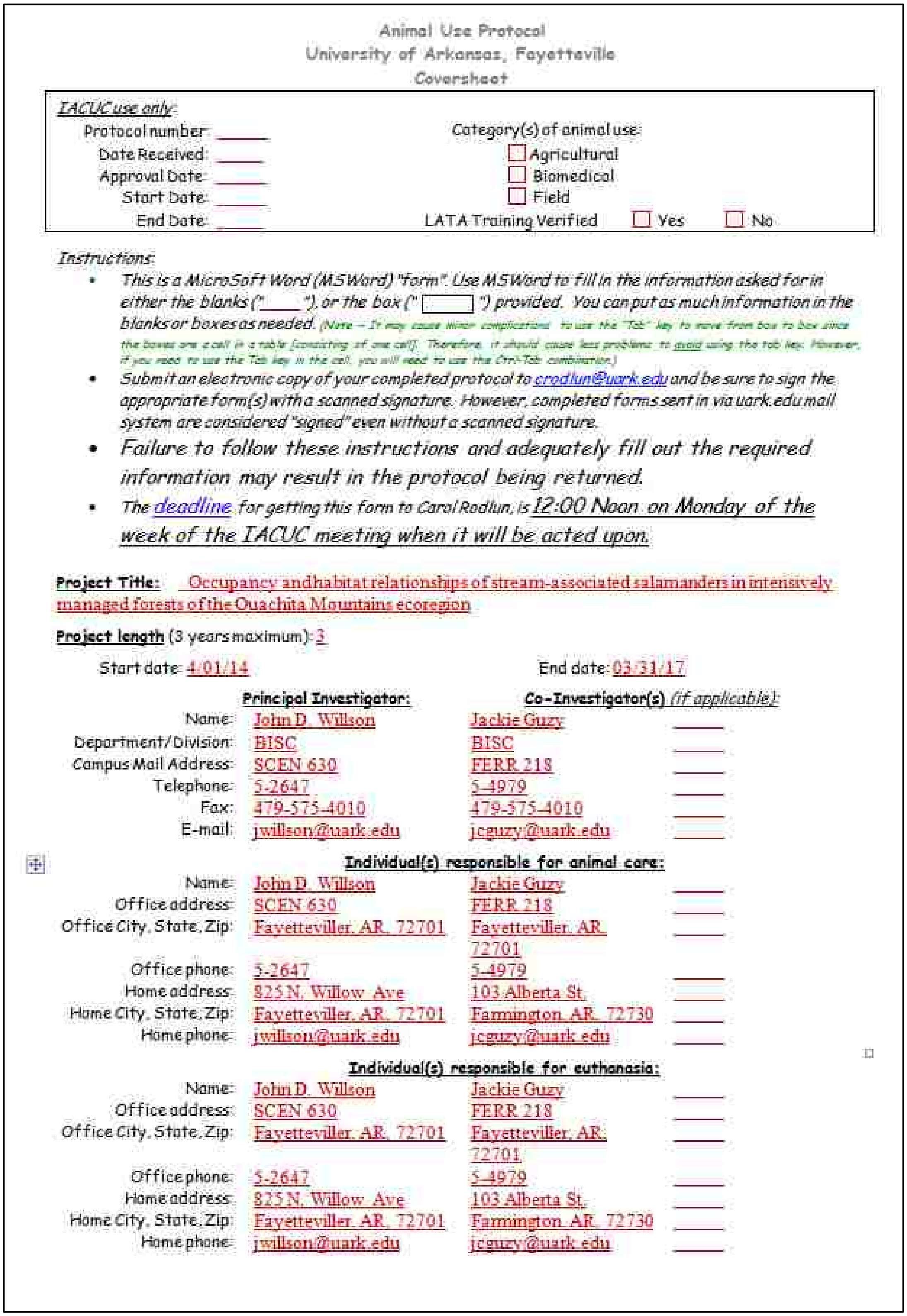
The IACUC appreciates your cooperation in complying with University and Federal guidelines for involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

Administration Building 210 • 1 University of Arkansas • Fayetteville, AR 72701-1201 • 479-575-4572
Fax: 479-575-3846 • http://vpred.uark.edu/199

Appendix 8 (*continued*). IACUC Approval documents



Animal Use Protocol
University of Arkansas, Fayetteville
Coversheet

IACUC use only:

Protocol number: ____
Date Received: ____
Approval Date: ____
Start Date: ____
End Date: ____

Category(s) of animal use:
☐ Agricultural
☐ Biomedical
☐ Field

LATA Training Verified ☐ Yes ☐ No

Instructions:

- *This is a MicroSoft Word (MSWord) "form". Use MSWord to fill in the information asked for in either the blanks ("____"), or the box (" ☐ ") provided. You can put as much information in the blanks or boxes as needed.* (Note – It may cause minor complications to use the "Tab" key to move from box to box since the boxes are a cell in a table [consisting of one cell]. Therefore, it should cause less problems to avoid using the tab key. However, if you need to use the Tab key in the cell, you will need to use the Ctrl-Tab combination.)
- *Submit an electronic copy of your completed protocol to crodlun@uark.edu and be sure to sign the appropriate form(s) with a scanned signature. However, completed forms sent in via uark.edu mail system are considered "signed" even without a scanned signature.*
- *Failure to follow these instructions and adequately fill out the required information may result in the protocol being returned.*
- *The deadline for getting this form to Carol Rodlun, is 12:00 Noon on Monday of the week of the IACUC meeting when it will be acted upon.*

Project Title: Occupancy and habitat relationships of stream-associated salamanders in intensively managed forests of the Ouachita Mountains ecoregion

Project length (3 years maximum): 3

Start date: 4/01/14 End date: 03/31/17

	Principal Investigator:	**Co-Investigator(s)** *(if applicable):*	
Name:	John D. Willson	Jackie Guzy	____
Department/Division:	BISC	BISC	____
Campus Mail Address:	SCEN 630	FERR 218	____
Telephone:	5-2647	5-4979	____
Fax:	479-575-4010	479-575-4010	____
E-mail:	jwillson@uark.edu	jcguzy@uark.edu	____

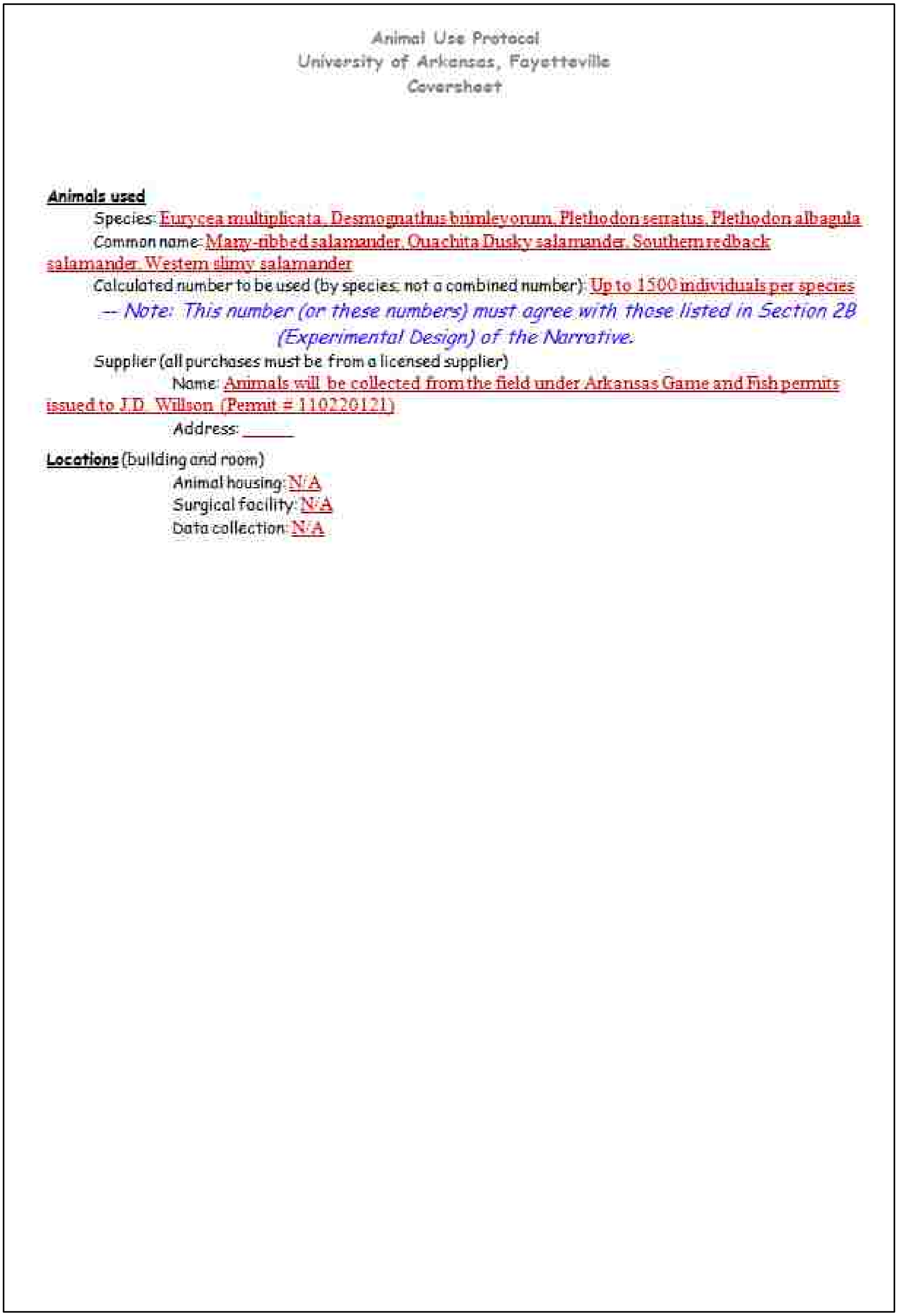
Individual(s) responsible for animal care:

Name:	John D. Willson	Jackie Guzy	____
Office address:	SCEN 630	FERR 218	____
Office City, State, Zip:	Fayetteviller, AR, 72701	Fayetteviller, AR, 72701	____
Office phone:	5-2647	5-4979	____
Home address:	825 N. Willow Ave	103 Alberta St.	____
Home City, State, Zip:	Fayetteviller, AR, 72701	Farmington, AR, 72730	____
Home phone:	jwillson@uark.edu	jcguzy@uark.edu	____

Individual(s) responsible for euthanasia:

Name:	John D. Willson	Jackie Guzy	____
Office address:	SCEN 630	FERR 218	____
Office City, State, Zip:	Fayetteviller, AR, 72701	Fayetteviller, AR, 72701	____
Office phone:	5-2647	5-4979	____
Home address:	825 N. Willow Ave	103 Alberta St.	____
Home City, State, Zip:	Fayetteviller, AR, 72701	Farmington, AR, 72730	____
Home phone:	jwillson@uark.edu	jcguzy@uark.edu	____

Appendix 8 (*continued*). IACUC Approval documents



Animal Use Protocol
University of Arkansas, Fayetteville
Coversheet

Animals used

Species: Eurycea multiplicata, Desmognathus brimleyorum, Plethodon serratus, Plethodon albagula

Common name: Many-ribbed salamander, Ouachita Dusky salamander, Southern redback salamander, Western slimy salamander

Calculated number to be used (by species: not a combined number): Up to 1500 individuals per species

-- Note: This number (or these numbers) must agree with those listed in Section 2B (Experimental Design) of the Narrative.

Supplier (all purchases must be from a licensed supplier)

Name: Animals will be collected from the field under Arkansas Game and Fish permits issued to J.D. Willson (Permit # 110220121)

Address: ______

Locations (building and room)

Animal housing: N/A

Surgical facility: N/A

Data collection: N/A

Chapter 3:

Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests

Jacquelyn C. Guzy[1], Kelly M. Halloran[1], Jessica A. Homyack[2], Jamie E. Thornton-Frost[3], and

John D. Willson[1]

[1] Department of Biological Sciences, University of Arkansas, Fayetteville, AR, 72701, USA

[2] Weyerhaeuser Company, 505 North Pearl St., Centralia, WA 98531, USA

[3] Weyerhaeuser Company, 220 Occidental Ave South, Seattle, WA 98104, USA

Abstract

Streamside management zones (i.e., riparian buffers; SMZs) are commonly implemented within managed forests to protect water quality, but may also provide habitat for riparian-associated wildlife. Yet, little research has rigorously addressed the value of SMZs for wildlife, particularly cryptic species such as amphibians and reptiles. Previous studies of herpetofauna within SMZs have focused on one or a few stream-associated species, and questions remain regarding variation among species or guilds and what role SMZs serve toward conservation of herpetofaunal diversity in managed forests. However, recent statistical advances have improved our ability to analyze large multi-species presence-absence datasets, accounting for low detection rates typical for some herpetofaunal species. Our study represents an extensive landscape-scale examination of herpetofaunal communities within SMZs using a multi-species occupancy approach. We conducted four replicate surveys at 102 headwater streams, 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 species richness and species-specific occupancy responses to SMZ and overstory characteristics, accounting for variation in occupancy and detection attributable to site and sampling covariates. We documented high richness (37 species) within SMZs. Across the herpetofaunal community, occupancy and species richness were consistently positively associated with SMZ width, with maximum predicted richness of 30 species occurring at sites with buffers extending 51 m on either side of the stream. However, we documented considerable variation among groups and among species within groups, underscoring the potential for different responses to forest management among taxa. Reptile predicted richness increased more rapidly up to SMZs of ~35 m, whereas maximum salamander predicted richness was not seen until a SMZ width of 55 m. Estimated salamander richness was highest within SMZs embedded in mature managed pine

stands and was higher in SMZs comprised of a deciduous or mixed overstory versus pine. Compared to salamanders, more anuran species showed high mean estimated occupancy (>75%) at narrower SMZs (<30 m). Collectively, our results indicate that SMZs surrounding small first-order streams in intensively managed forests not only protect water quality, but also can support diverse amphibian and reptile communities.

Introduction

Forested riparian buffers (i.e., streamside management zones; SMZs) are used to protect aquatic environments from terrestrial disturbances, such as timber harvesting operations (Blinn and Kilgore 2001). Streamside management zones are a particularly important component of many Best Management Practice (BMP) programs (Warrington et al. 2017), and consequently, are widely implemented within managed forests (Lee et al. 2004) to minimize physical and chemical changes to streams, maintain soil moisture in riparian areas (Brosofske et al. 1997, Swank et al. 2001, Wilkerson et al. 2006), and reduce sediment delivery (Aust and Blinn 2004). Riparian buffers also support ecological processes including resource subsidies (e.g., allochthonous inputs of detritus and large and small wood; (Boothroyd and Langer 1999, Parkyn 2004). Increasingly, SMZs are recommended to help conserve habitat for stream-affiliated species such as aquatic macroinvertebrates (Newbold et al. 1980, Noel et al. 1986, Davies and Nelson 1994, Quinn et al. 2004), fish (Moring 1982, Jones et al. 1999, Young et al. 1999, Allan et al. 2003), mussels (Morris and Corkum 1996, Poole and Downing 2004), and crayfish (Parkyn and Collier 2004, Adams et al. 2018).

Although SMZs are designed to protect water quality (Aust and Blinn 2004, Cristan et al. 2016), they may also provide movement corridors and habitat for semi-aquatic and terrestrial species during forestry operations within upland areas of forest stands (Perry et al. 2011, Peterman et al. 2011). Within managed forests, SMZs may be particularly beneficial to wildlife because, compared to the surrounding landscape, they provide diverse vegetation conditions and microtopography (e.g., waterbodies, coarse woody debris, snags, tree cavities, rocks, leaf litter; (Homyack and Kroll 2014, Warrington et al. 2017). Further, SMZ characteristics may vary across the landscape depending on hydrology, geology, and vegetative structure of a particular location (Foley 1994, deMaynadier and Hunter 1995). Although SMZs are generally not designed to conserve terrestrial wildlife associated with riparian ecosystems, they likely provide this secondary benefit for many species. Notably, most studies of SMZs focus on a few species or a single functional group, yet variation has been reported among species responses (i.e., birds, amphibians, reptiles, small mammals, and invertebrates) to riparian buffer characteristics (Marczak et al. 2010, Greene et al. 2016).

Amphibians and reptiles are critical components of forest ecosystems and are involved in a myriad of dynamic interactions as predators and prey, making them functionally important to flow of energy and nutrients within food webs. Further, semi-aquatic herpetofauna use aquatic, riparian, and terrestrial environments and transfer significant amounts of energy and nutrients among these areas (Burton and Likens 1975, Regester et al. 2006, Willson and Winne 2016). Many herpetofaunal species depend on terrestrial and aquatic habitat types to meet life history needs (e.g., reproduction, larval development, hibernation, foraging; (Gibbons 2003), therefore alterations to these areas from forest-harvesting activities have the potential to influence reptile and amphibian populations. While previous studies within managed forests have focused on stream-associated salamander responses to riparian buffer characteristics (Johnston and Frid 2002, Perkins and Hunter 2006, Peterman and Semlitsch 2009, Maigret et al. 2014, Olson et al. 2014, Guzy et al. 2019), few have addressed whether SMZs support occupancy of reptiles or semi-aquatic and upland amphibians.

Various challenges exist that complicate rigorous community-level research on herpetofauna (Walls 2014), and may partially explain why there are so few studies focusing on the role of SMZs in supporting herpetofaunal communities. Species in this group are notoriously difficult to study due to their secretive behaviors, cryptic coloration, frequent inactivity due to low metabolic demands, and seasonal behavior patterns which often place them in inaccessible (e.g., subterranean, arboreal, or aquatic) locations (Bailey et al. 2004, Durso et al. 2011, Guzy et al. 2014, Walls 2014). As a result, detection probabilities of amphibians and reptiles are often extremely low (Durso et al. 2011). In conjunction with low detection, is the challenge of achieving sufficient site-level replication to account for variation that may confound assessments of SMZ characteristics on reptile and amphibian communities. However, recent statistical advances (Zipkin et al. 2009) have improved our ability to analyze large multi-species presence-absence datasets and account for low detection rates, thereby allowing landscape-scale studies that facilitate understanding factors influencing herpetofaunal community occupancy within managed forests.

To better understand conservation value of SMZs for herpetofauna, we used multi-species occupancy and species richness estimation to examine the herpetofaunal community relationship with SMZ width and forest stand characteristics, including taxa specific (i.e., salamanders, anurans, and reptiles) analyses. Our surveys spanned a continuous gradient of SMZ buffer widths and stand ages across 102 first order stream sites, permitting us to examine relationships of both terrestrial and semi-aquatic species to SMZ characteristics. We predicted that herpetofaunal richness would be greatest within the widest SMZs. However, we expected variation in the strength of responses among taxonomic groups, with salamanders exhibiting stronger responses than reptiles based on their sensitivity to forestry activities (Tilghman et al.

2012). Conversely, we expected weaker responses of reptiles because they are primarily habitat-generalists that use edges and early successional vegetation (Moorman et al. 2011).

Methods

Study Sites

This study was located on the Athens Plateau (Woods et al. 2004), the southernmost subdivision of the Ouachita Mountains in west-central Arkansas, USA, within a landscape of primarily even-aged loblolly pine (*Pinus taeda*) stands managed by Weyerhaeuser Company (Fig. 1). We focused site selection on headwater streams because of their importance to amphibians (Peterman et al. 2008) and because delineating stream watersheds allowed us to select sites with uniform forestry characteristics (e.g., stand age). Using a GIS (ArcGIS 10.0; Environmental Systems Research Institute, Redlands, CA, USA) and Geodata Crawler (Leasure 2014), we identified 1,854 potential study sites that drained < 3.0 km^2. At the watershed-level, we classified sites based on stand age and average width of SMZs upstream of sampling locations. We determined sampling locations starting at most downstream position within each focal stand. We quantified SMZ width using delineated SMZ shapefiles overlain on digital ortho quad county mosaic imagery (https://datagateway.nrcs.usda.gov/). For each site, we measured SMZ width incrementally along the entire length of each study stream and then averaged and ground-truthed them. More specifically, we began measurements at the most downstream sampling point for each stream and we moved upstream in 20 m increments, where we measured the perpendicular distance from the edge of the buffer to the stream center. We measured 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. For our survey sampling, we then selected all available sites (n=102) 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 = 21.41 m, SD = 10.09 m; Appendix 1a). We verified riparian buffer width by ground-truthing during each of four occupancy surveys (see below). Arkansas 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 138-354 m (mean = 241m; SD = 50m).

Data Collection

We sampled amphibians and reptiles with repeated, time, and area-constrained surveys within SMZs during April – June 2014, 2015, and 2016. We surveyed each site with four spatial repeats and each survey occurred over a different 15-m stream transect, proceeding upstream from the previous transect. Surveys consisted of a single observer opportunistically dip-netting and flipping cover objects for 30 min (i.e., 10 min in stream channel, 10 min along stream edges, and 10 min in terrestrial locations within the SMZ); we pooled data from these locations for each survey. We counted, photographed, identified to species, and released at the end of the survey all amphibians and reptiles encountered.

During each survey, we measured several variables (*environmental*: air temperature, humidity, barometric pressure; *stream*: water temperature, average depth, dissolved oxygen, conductivity; *upland areas*: average soil moisture, canopy closure, substrate composition, availability of upland cover objects [i.e., ‘upland cover score’], and SMZ overstory composition). We estimated percent canopy closure by averaging measurements taken at 4 cardinal directions, using a hand-held, concave spherical densitometer at the center of each stream transect (Lemmon 1956). We estimated substrate composition for each survey by dividing the 15-m transect into four sections and visually estimating percent cover of stream substrate following the Wentworth scale of grain size (Wentworth 1922). Our indicator of amount of upland cover objects, 'upland cover score,' was determined during each 10-min upland survey, and consisted of a 1 to 5 scale (i.e., fewest to highest). We visually estimated SMZ overstory composition: 'Pine' sites were > 75% pine basal area, 'Mixed' sites were 25%-75% pine, "Deciduous" sites were < 25% pine, and "No SMZ" sites contained no overstory. We incorporated age of adjacent stand(s) as categorical variables 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, using a GIS we calculated latitude, elevation (m), watershed area (km^2), and SMZ width for each site. For further details on data collection see Guzy et al. (2019).

Data Analyses

We used principal components analysis (PCA) in PRIMER 6.0 (Clarke and Gorley 2006) to reduce dimensionality of our data (Clarke 1993) and the large number of site and sampling variables. We performed a PCA on a subset of site and sampling covariates and used the principal component scores from each of the first two PC axes as site and sampling covariates in our occupancy analyses (Appendix 2). To isolate 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 or PCs.

We used a hierarchical Bayesian community occupancy model (Dorazio and Royle 2005, Homyack et al. 2016) to estimate species-specific occupancy and detection probability as a function of site-specific covariates (average SMZ width, stand age categories, SMZ composition, Site PC1, and Site PC2) and sampling covariates (Sampling-PC1 and Sampling-PC2). This hierarchical approach incorporates species-specific and assemblage-level (i.e., salamander, reptile, or anuran groups) covariate effects into the same modeling framework, thus allowing estimation of species-specific occurrence and detection probabilities and site-specific species richness while also accounting for imperfect detection (Dorazio and Royle 2005, Zipkin et al. 2009). Using this modeling approach, species-specific parameter estimates, particularly for rare species, are more precise as they are considered in the context of the larger community (Sauer and Link 2002, Zipkin et al. 2009, Pacifici et al. 2014).

We generated species-specific observance matrices for four sampling occasions at each site, where detection was represented as 1, and non-detection as 0. We let $z_{i,j}$ denote true occupancy status such that $z_{i,j} = 1$ if species *i* occupies site *j*, otherwise $z_{i,j} = 0$. Based on longevity and strong philopatry of most herpetofauna, we assumed that the occupancy status of each site was constant across all surveys in our study. The occupancy state is considered to be a Bernoulli random variable, $z_{i,j} \sim Bern(\Psi_{i,j})$, where $\Psi_{i,j}$ is the probability that species *i* occupies site *j*. Similarly, we modeled species detection as a Bernoulli random variable: $y_{i,j,k} \sim Bern(p_{i,j,k} * z_{i,j})$, where $y_{i,j,k}$ is 1 if species *i* is detected at site *j* during survey *k*, or 0 otherwise and $p_{i,j,k}$ is the probability that species i is detected at site j during survey k. Note that if species i was not present at site j (i.e. $z_{i,j} = 0$) then no detections of species i were possible as $(p_{i,j,k} * z_{i,j}) = 0$.

We assumed species-specific occupancy probability ($\Psi_{i,j}$) followed a linear-logit function of the model covariates:

$$logit(\Psi_{i,j}) = \alpha_{0i} + \alpha_{1i} * SMZ\ width_j + \alpha_{2i} * I(Young\ pre - thin_j = 1) + \alpha_{3i} * I(Mid\ pre - thin_j = 1) + \alpha_{4i} * I(Post - thin_j = 1) + \alpha_{5i} * I(Staggered\ harvest_j = 1) + \alpha_{6i} * I(Pine\ SMZ_j = 1) + \alpha_{7i} * I(Mixed\ SMZ_j = 1) + \alpha_{8i} * I(No\ SMZ_j = 1) + \alpha_{9i} * Site\ PC1_j + \alpha_{10i} * Site\ PC2_j + \gamma_j$$

Where $I(.)$ is an indicator function taking the value of 1 if the arguments is true and 0 otherwise. γ_j is a random intercept for site j, where $\gamma_j \sim N(0, \sigma_\gamma^2)$.

Species-specific detection probabilities also followed a linear-logit function of the model covariates:

$$logit(p_{i,j,k}) = \beta_{0i} + \beta_{1i} * Sampling\ PC1_{j,k} + \beta_{2i} * Sampling\ PC2_{j,k}$$

Parameters α2 – α5 are interpreted as contrasts of the categorical predictor variable “stand age” (i.e., Young and Mid pre-thin, Post and Old post-thin) with "Old post-thin" as the reference category. Likewise, parameters α6 – α8 are contrasts of the categorical predictor variable “SMZ Composition” (i.e., Pine, Mixed, Deciduous, or No overstory) with "Deciduous" as the reference category. The ‘SMZ width’ covariate was defined as the average width of the SMZ surrounding each study stream, upstream of the most downstream sampling location, these values were centered and scaled (i.e., [site’s SMZ value - mean]/SD). We defined ‘Site PC1’ and ‘Site PC2’ covariates as the respective z-score (i.e. centered and scaled to a mean of 0 and sd of 1) 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, we defined the ‘Sampling PC1’ and ‘Sampling PC2’ covariates as the respective z-score of principal component scores from each of the first two sample-specific-PC axes (Appendix 2b).

We estimated species richness (N) for 102 sites by summing estimated occupancy for each of the 37 observed species. Species richness for site j was defined as:

$$\widehat{N}_j = \sum_{i=1}^{37} \hat{z}_{i,j}$$

where $\hat{z}_{i,j}$ is the estimated occupancy of species *i* at site *j*.

One advantage of using community occupancy models is that estimates for data poor species with few detections are more precise because they can borrow information from data-rich species, or those with many detections (Pacifici et al. 2014). However, borrowing information may only be appropriate if the species that are sharing information have some degree of relatedness (Pacifici et al. 2014). To increase the degree of relatedness among our species, we divided our 37 species of interest into 3 groups: (1) salamanders, (2) reptiles, and (3) anurans. We drew species-specific effects from group normal distributions e.g., $\alpha_{d,i} \sim N(\mu_{d,h}, \sigma^2_{d,h})$ for parameter α_d of species *i* in group h or $\beta_{d,i} \sim N(\mu_{d,h}, \sigma^2_{d,h})$ for parameter β_d of species *i* in group h, where the mean and variance of the normal distribution are group level hyper-parameters. We used a N(0,2) (mean, variance) prior for all group mean parameters and U(0.1,3) for all group standard deviation parameters.

We fit the model using JAGS (Plummer 2003) called from R (3.4.4) (R Core Team 2018) and executed using the ‘‘jags’’ function from package ‘R2jags’ (Su and Yajima 2015). We implemented this model in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in JAGS to generate samples from the posterior distribution (Lunn et al. 2000). We used 3 Markov chains, each of length 200,000; the first 100,000 were removed as burn-in, and remainder were thinned by a factor of 50. Across the three chains, this provided 6,000 samples to approximate posterior summary statistics for each model parameter including mean, standard deviation, and 2.5% and 97.5% percentiles of the distribution, which represent 95% Bayesian credible intervals. We assessed model convergence via the Gelman-Rubin diagnostic and a visual inspection of chains, with both measures indicating a reasonable assumption of convergence. For all monitored parameters in our study, the Gelman-Rubin statistic value was at or below 1.02 (Gelman and Rubin 1992). A posterior predictive check did not indicate any problems with the fitted model (Appendix 6). Code to implement this model is provided in Appendix 7.

Results

We obtained 2,010 captures of 37 species [anurans (n=11), salamanders (n=10), and reptiles (n=16: turtles (n=1), lizards (n=4), snakes (n=11)] across four replicate surveys at each of 102 first-order stream sites (Table 1). Notable species include three listed as Species of Greatest Conservation Need by the state of Arkansas: the Caddo Mountain salamander (*Plethodon caddoensis*), four-toed salamander (*Hemidactylium scutatum*), and ringed salamander (*Ambystoma annulatum*; Table 1). Although we observed two different skink species (*Plestiodon laticeps* and *P. fasciatus*) and two different toad species (*Anaxyrus americanus* and *A. fowleri*), we pooled these species in our analyses because species-specific identifications were not always possible. In addition, although the predominant slimy salamander in our region is *P. albagula*, we use *P. glutinosus* complex because several non-morphologically distinguishable species may occur in our study area.

The first two site-covariate principal components explained 31.0 and 15.5% of the total variance, respectively (cumulative 46.5%; Appendix 2a). Site PC1 was an index of northerly geographic position within the southern tier of the Ouachita Mountains, as indicated by strong factor loadings for latitude (+), elevation (+), sand substrate coverage (-), water temperature (-), and conductivity (-). Site PC2 had a high positive factor loading for watershed area and negative factor loading for elevation, likely driving patterns of high boulder/cobble substrate, less sand, and less canopy cover.

The first two sampling-covariate principal components explained 33.8 and 20.0% of the total variance, respectively (cumulative 53.8%; Appendix 2b). Sampling PC1 was an index of later dates (i.e., warmer temperatures and drier soils) as indicated by high positive factor loadings for date, water temperature, and air temperature, and a negative factor loading for soil moisture. Sampling PC2 had negative factor loadings for date, humidity, water depth, and soil moisture, and a positive factor loading for air temperature, reflecting drier conditions with lower humidity and shallower water. For further detail on Site and Sampling covariate results see Guzy et al. (2019).

Species Richness Across the Entire Herpetofaunal Assemblage

Results of our fitted model indicated that herpetofaunal species richness was positively associated with SMZ width (Fig. 2). More specifically, assuming average values of other site and sampling covariates, predicted species richness per site increased from a median of 8 species (95% CI 3 to 16) at sites with narrow SMZs to 30 species (95% CI 24 to 35; Fig. 2a) at sites with the widest SMZs (55 m). Predicted richness was similar across stand age categories and among SMZ overstory categories.

Salamander Occupancy and Richness

When examining salamanders as an assemblage, the mean SMZ width coefficient estimate was positive ($\mu\alpha1_{(\text{Salamanders})}$: 1.04; 95% CI 0.47 to 1.67, Appendix 3), indicating support for a positive relationship between mean occupancy probability and SMZ width (Fig. 3). Mean estimated salamander occupancy probability varied from 4.3% (95% CI 0.38 to 17.38%) at SMZ widths of less than 1 m, to 83.2% (95% CI 38.59 to 99.27%) at an SMZ width of 55 m (Fig. 3). Furthermore, the species-specific estimates of effect of SMZ width on occupancy probability were consistently positive (Appendix 4). Results of this model also indicated a positive association between the salamander assemblage and Site PC1 ($\mu\alpha10_{(\text{Salamanders})}$: 0.71, 95%CI 0.22 to 1.20; Appendix 3) and the species-specific Site PC1 coefficient estimates were consistently positive (Appendix 4). Thus, salamander occupancy was estimated to be greater at sites with higher latitude and elevation, and sites with less sand and silt, cooler water, and lower conductivity (Fig. 5a). However, because we sampled a different transect for each survey, we cannot separate spatial effects from environmental sampling covariates. We did not detect evidence for a relationship with assemblage occupancy and Site PC2 (Appendix 3).

The estimated community response to the Sampling PC1 covariate indicated that detection probability was greater when sampling occurred at earlier dates, during periods with cooler temperatures and moister soil ($\beta1$: -0.47; 95% CI -0.97 to -0.02; Fig. 5b; Appendix 3 and 5). We did not detect clear evidence for a positive or negative relationship between detection probability across the salamander community and Sampling PC2 (Appendix 3 and 5).

Across salamander species, we estimated a positive association between mean occupancy probability and SMZ width (Appendix 3 and 4), but the magnitude of the relationship varied among species (Fig. 4a). One species, *E. multiplicata*, maintained high occupancy probability across all surveyed sties. Three species (*D. brimleyorum*, *P. glutinosus*, and *P. serratus*) only attained high mean occupancy probability (>75%) at sites with relatively wide SMZs (>30m; Fig. 4a). Conversely, mean occupancy probability of *A. maculatum*, *A. opacum*, and *H. scutatum*, was low across all sites (0.19-0.23; Table 1), despite all these species showing evidence of a positive association with SMZ width (i.e., credible intervals do not contain zero).

Estimated salamander species richness was positively associated with increasing SMZ width (Fig. 2b). Assuming average values of other site and sampling covariates and averaging across overstory and stand age categories relative to their prevalence in our sample, predicted salamander species richness per site varied from a median of 1 species (95% CI 0 to 3) to 7 species (95% CI 4 to 9; Fig. 2b) with increasing SMZ width up to 55 m. A median richness of 3 species is predicted at the average SMZ width across our sites (21m). Maximum species richness was not reached until SMZ widths reach 55 m (Fig. 2b).

Category-specific estimates of richness were determined by averaging species richness estimates over sites that fell into each stand age or overstory category. Categorizing our 102 observed sites by Stand Age category indicated that mean estimated richness was lower at younger sites and highest at oldest sites, with Old post-thin sites (n=49; mean 4.20, 95% CI 3.22 to 5.86) containing 2 more species on average than Mid pre-thin sites (n=22; mean 2.09, 95% CI 1.55 to 3.23; Fig. 6c, 6d). Although confidence intervals were wide, Old post-thin sites consistently had greater estimated richness than younger sites (Fig. 6d). Examining sites by overstory category, we observed that estimated species richness at sites with SMZs comprised of Mixed or Deciduous overstory was higher on average than at sites with SMZs comprised of Pine overstory (Fig 7c, 7d). Pine overstory sites (n=19) had an average estimated species richness of 2.37 (95% CI 1.74 to 3.68) while Mixed and Deciduous sites (n=35, 43 respectively) had an average estimated species richness of 3.72 (95% CI 2.86 to 5.23) and 3.86 (95% CI 2.91 to 5.49), respectively.

Reptile Occupancy and Richness

When examining reptiles as an assemblage, the mean SMZ width coefficient estimate was positive ($\mu\alpha 1_{(Reptiles)}$: 1.45; 95% CI 0.52 to 2.64; Appendix 3), indicating support for a positive relationship between mean occupancy probability and SMZ width (Fig. 3). Mean estimated occupancy probability varied from 16.90% (95% CI 1.15 to 65.33%) at SMZ widths of less than 1 m, to 98.01% (95% CI 83.77 to 100.00%) at an SMZ width of 55m (Fig. 3). Furthermore, the species-specific estimates of effect of SMZ width on occupancy probability were consistently positive (Appendix 4). We did not detect clear evidence for a positive or negative relationship with assemblage occupancy and Site PC1 or Site PC2 (Appendix 4).

A weakly positive community association to the Sampling PC1 covariate indicated that detection probability was greater when sampling occurred at later dates, when temperatures are warmer and soils are drier ($\beta 1_{(Reptiles)}$: 0.13; 95% CI -0.07 to 0.32; Appendix 3). Similarly, the weakly positive community response to the Sampling PC2 covariate indicated that detection probability was greater with lower humidity and shallower water $\beta 2_{(Reptiles)}$: 0.17; 95% CI -0.05 to 0.38; Appendix 3). However, for these covariates, we observed high variation among species responses (Appendix 5). Additionally, because we sampled a different transect for each survey, we cannot separate spatial effects from environmental sampling covariates.

Mean occupancy probability estimates of reptiles across our observed sites was high, and varied from 46.71% to 82.08%, however these estimates were accompanied by wide credible intervals, particularly for snake species (Table 1). Across all reptile species, there was a positive association between occupancy probability and SMZ width (Fig. 3). Reptiles appeared to be more tolerant of smaller SMZs than salamanders (Fig. 4). Specifically, most reptile species reach an estimated 75% occupancy probability at SMZs ~30m wide (Fig. 4b). Species exhibiting a positive association with SMZ width (i.e., credible intervals do not contain zero) include *A.*

contortrix, *N. erythrogaster*, *P. obsoletus*, *Plestiodon* spp., *S. lateralis*, *S. occipitomaculata*, and *T. carolina* (Fig. 4b; Appendix 4).

Assuming average values of other site and sampling covariates and averaging over overstory and stand age categories relative to their prevalence in our sample, predicted reptile species richness per site varied from 4 species (95% CI 0 to 10) to 16 species (95% CI 11 to 16) with increasing SMZ width from 0 to 55 m (Fig. 2c). A median richness of 10 species was predicted at the average SMZ width across our sites (21m; Fig. 2c). Although maximum species richness was not reached until SMZ width equaled 55 m, predicted reptile richness rose rapidly between 5 and 30 m and began to plateau at widths >35 m (Fig. 2c). We found no clear evidence for a difference in reptile species richness among Stand Age categories (Fig. 6 e and f) or among SMZ overstory categories (Fig. 7e and f). More specifically, mean estimated species richness ranged from 8.22 at Mid pre-thin sites (95% CI 4.45 to 11.95) to 10.84 at Post thin sites (95% CI 6.38 to 14.62; Fig. 6 e and f), and ranged from 9.86 at Pine sites (95% CI 5.32 to 14.00) to 10.37 at Deciduous sites (95% CI 6.30 to 13.63; Fig. 7e and f).

Anuran Occupancy and Richness

When examining anurans as an assemblage, the mean SMZ width coefficient estimate was positive ($\mu\alpha1_{(\mathrm{Anurans})}$: 0.81; 95% CI 0.13 to 1.61; Appendix 3), indicating support for a positive relationship between mean occupancy probability and SMZ width (Fig. 3). Mean estimated occupancy probability varied from 19.39% (95% CI 2.05 to 62.28%) at SMZ widths of less than 1 m, to 87.83% (95% CI 47.68 to 99.77%) at an SMZ width of 55 m (Fig.3). Furthermore, species-specific estimates of effect of SMZ width on occupancy probability were consistently positive (Fig. 4c; Appendix 4). Results of this model also indicated a negative association between the anuran assemblage and Site PC1 ($\mu\alpha10_{(\mathrm{Anurans})}$: -0.80, 95%CI -1.49 to -0.24; Appendix 3) and the species-specific Site PC1 coefficient estimates were consistently negative (Appendix 4). Thus, anuran occupancy was estimated to be greater at sites with lower latitude and elevation, and sites with more sand and silt, warmer water, and higher conductivity (Fig. 5c). However, because we sampled a different transect for each survey, we cannot separate spatial effects from environmental sampling covariates. We did not detect clear evidence for a positive or negative relationship with assemblage occupancy and Site PC2 (Appendix 3). Likewise, we did not detect evidence for a relationship with assemblage detection and the Sampling PC1 or Sampling PC2 covariates (Appendix 3).

Across all anuran species, there was a positive association between occupancy probability and SMZ width, but the magnitude of the relationship varied among species (Fig. 4c). A subset of species (*H. chrysoscelis*, *L. sphenocephalus*, *P. fouquettei*, *L. clamitans*, *L. palustris*, and *A. blanchardi*) had high mean occupancy probabilities across our observed sites, varying from 58.49% - 72.79%, whereas *P. crucifer* and *L. catesbeianus* had low mean occupancy across observed sites, 22.80% and 10.96%, respectively (Table 1). As with salamanders, the minimum SMZ width necessary to attain 75% occupancy varied greatly by species (Fig. 4c). Species exhibiting a positive association with SMZ width (i.e., credible intervals do not contain zero) include *A. blanchardi*, *A. americanus*, and *L. catesbeianus* (Appendix 4).

Estimated anuran species richness was positively associated with increasing SMZ width. Assuming average values of other site and sampling covariates and averaging over overstory and stand age categories relative to their prevalence in our sample, predicted anuran species richness per site varied from 3 species (95% CI 1 to 7) to 9 species (95% CI 5 to 11; Fig. 2d) with increasing SMZ widths from 0 to 55 m. At the average SMZ width across our sites (21m), median estimated richness was 6 species. Maximum predicted species richness was not reached until SMZ widths exceeded 50 m (Fig. 2d). We found no clear evidence for a difference in estimated anuran species richness among Stand Age categories (Fig. 6g and h) or among SMZ overstory categories (Fig.7g and h). More specifically, estimated species richness ranged from 4.96 at Old post-thin sites (95% CI 3.55 to 6.67) to 6.18 at Young pre-thin sites (95% CI 4.18 to 8.73; Fig. 6g and h), and ranged from 4.73 at Pine sites (95% CI 3.16 to 6.63) to 5.68 at Mixed overstory sites (95% CI 4.09 to 7.63; Fig.7g and h).

Discussion

Despite previous research demonstrating the value of SMZs as wildlife habitat (Wigley and Melchiors 1994), most prior studies of herpetofauna have focused on a few species of stream-associated amphibians (e.g., (Vesely and McComb 2002, Jackson et al. 2007, Peterman and Semlitsch 2009, Pollett et al. 2010). Thus, comprehensive understanding of how retaining overstory trees in the dynamic aquatic-terrestrial interface influences diversity and occupancy of amphibians and reptiles in managed forests is lacking and restricts future management options based on empirical knowledge. While our study's scope is limited to the sites we observed, ours is the first landscape-scale study of herpetofaunal communities within SMZs and our findings extend previous work on stream-associated species to the entire herpetofaunal community. We documented high herpetofaunal richness (37 species) within SMZs embedded in a managed forest landscape. Notably, the number of species we observed was comparable with or exceeded that from other managed forests across the southeastern United States known for high herpetofaunal diversity (Greenberg 2001, Russell et al. 2002a, Owens et al. 2008, Homyack et al. 2016). Across the herpetofaunal community, occupancy and species richness were consistently positively associated with SMZ width, with maximum estimated richness of 30 species occurring at sites with buffers extending 51 m on either side of the stream. However, we documented considerable variation among taxonomic groups and among species within taxonomic groups, underscoring the potential for differential responses to forest management among taxa. Reptile richness increased rapidly up to SMZs of ~30m, whereas salamanders tended to require wider

SMZs to attain highest richness and were associated more strongly with surrounding stand age characteristics. Specifically, salamander richness was highest within SMZs embedded in mature managed pine stands and was observed to be higher in SMZs comprised of a deciduous or mixed overstory versus a pine overstory. Compared to salamanders, anurans were more tolerant of narrower SMZs. Taken together, our results indicate that SMZs surrounding small first-order streams within our sample of sites in intensively managed forests not only protect water quality (Aust and Blinn 2004), but also support diverse amphibian and reptile communities. These results are particularly significant given that protected areas are likely to become increasingly limited and underscore the value of managed forests in conserving biodiversity (Demarais et al. 2017).

Streamside Management Zone Width

We documented positive occupancy probability association with SMZ width across all 37 amphibian and reptile species and found that predicted herpetofaunal richness peaked near the maximum sampled buffer width (55 m). However, we observed considerable variation among taxonomic groups (i.e., salamanders, anurans, and reptiles) in association with SMZ width. Predicted salamander and anuran species richness increased approximately linearly with increasing SMZ width up to widths of 55 m and 50 m respectively, whereas reptile richness exhibited a threshold relationship, with predicted richness nearing the maximum possible group richness (N=16) at SMZs > 35 m wide. Thus, we observed the widest SMZs supporting occupancy of a greater community of amphibians, while most reptiles are present within mid-sized SMZs. Because amphibians generally require cool, moist conditions to maintain respiratory function and positive energy balances, most species are forest-associated and need closed-canopy conditions that moderate temperature, humidity, and soil moisture (deMaynadier and Hunter 1995). This is particularly true for Plethodontid salamanders, which are lungless and therefore rely on cutaneous respiration (Petranka 1998). Therefore, wider SMZs may buffer against edge effects (i.e., altered microclimate) extending from harvested areas into SMZs (Tilghman et al. 2012). Salamander species richness at study sites with the widest SMZs was driven by uncommon species (e.g., *P. caddoensis*, *A. annulatum*, *A. maculatum*, *A. opacum*, *H. scutatum*, and *S. intermedia*) with low overall occupancy and specific habitat requirements (i.e., wetlands, rock talus) likely only present within wider SMZs (Guzy et al. 2019). Conversely, most reptiles are less sensitive to environmental disturbances that modify temperature and humidity, and many lizard and snake species in our study area are habitat generalists or use edges and early successional vegetation for foraging and thermoregulation (Ross et al. 2000, Greenberg 2001, Crosswhite et al. 2004).

Along with variation in occupancy among taxonomic groups, we documented substantial variation in species' associations with SMZ width within taxonomic groups. This variation is particularly notable given that many studies focus on 1-2 focal taxa when examining herpetofaunal responses to forest management practices (e.g., Johnston and Frid 2002, Jackson et al. 2007, Pollett et al. 2010), making inference about herpetofauna communities difficult. For example, while occupancy of only one salamander species (*E. multiplicata*) was not strongly influenced by wider SMZs (Guzy et al. 2019), several anurans (*H. chrysoscelis*, *P. fouquettei*, *L. sphenocephalus*, *L. clamitans*) exhibited high probability of occupancy (~0.5-0.75) at sites with very narrow SMZs. Unlike salamanders, some anuran species may be considered early successional or edge species during reproduction (e.g., treefrogs, chorus, and leopard frogs; Lannoo 2005), because eggs and larva can benefit from increased temperature and primary productivity in open canopy aquatic conditions (Hocking and Semlitsch 2007, Semlitsch et al. 2009). Conversely, variation among mean reptile association to SMZ width was minimal, possibly as a consequence of limited sample sizes. Our hierarchical multispecies model incorporates a ‘group effect’ permitting the borrowing of information across species with similar life-histories (e.g., salamanders, reptiles, anurans) such that individual species-level estimates are a combination of single species and average parameter estimates of the group. Thus, we were able to estimate species-specific covariates for herpetofauna that are rarely detected, and would otherwise not be estimable (Sauer and Link 2002, Russell et al. 2009). As such, we can detect taxonomic group-level trends to forest management practices, within our sample of sites, in ways that previous studies have not. However, for reptiles, we have little insight on interspecific variation in responses, particularly for uncommon species. Virtually no studies have examined reptile responses to SMZs (but see (Rudolph and Dickson 1990), likely because of the difficulties related to their cryptic morphology and behavior (Durso et al. 2011). Therefore, further insight on interspecific variation in reptile responses to SMZs will require research using methods aimed at increasing reptile detection probability (e.g., greater effort per sample, drift fences, traps, coverboards; e.g., (Crosswhite et al. 1999) or focal studies (e.g., mark-recapture, radiotelemetry) on individuals.

Stand Age and SMZ Composition

Although there was a pattern of higher salamander richness in SMZs within older stands, overall herpetofaunal richness was similar across surrounding stand ages. This is in contrast to previous studies of salamanders (Petranka et al. 1993, Petranka et al. 1994, Herbeck and Larsen 1999) and may be driven by different habitat requirements of anurans and reptiles. For example, anurans are less sensitive to even-aged harvesting and associated edge effects than salamanders (Demaynadier and Hunter 1998, Gibbs 1998, Hager 1998, Russell et al. 2002b), presumably because of higher operating and tolerance temperatures (Stebbins and Cohen 1995). Additionally, several reptile species prefer open-canopy habitats and may be attracted to recently harvested areas for basking and foraging (Crosswhite et al. 2004, Loehle et al. 2005); others are associated with structurally complex forests (e.g., arboreal lizards; Pianka 1973). Therefore, provided SMZs are present, our results suggest surrounding forest age may be less important to anurans and reptiles, and a mixture of stand ages across the landscape may help maintain local and regional herpetofaunal species richness across managed forest landscapes (Loehle et al. 2005, Johnson et al. 2016).

Additionally, although herpetofaunal richness was similar within deciduous, mixed, and pine-dominated SMZs, we noted a trend suggesting pine-dominated SMZs contained ~2 fewer species on average, that was driven by salamanders (Guzy et al. 2019). Hardwood forests may favor bottom up production of terrestrial and aquatic macroinvertebrate prey and more suitable soil pH conditions that promote salamander diversity (Taylor et al. 1989, Klemmedson 1992, Whiles and Wallace 1997). Richness of anurans and reptiles, however, did not differ with overstory composition. Although anurans may be more abundant in hardwood compared to coniferous forests (Degraaf and Rudis 1990, Mitchell et al. 1997), some anurans and reptiles in our study were habitat generalists and associated with either mixed or pine forest. Our study suggests silvicultural practices that maintain a diverse overstory within SMZs, or prioritize deciduous species, may positively influence herpetofaunal richness across the landscape.

Landscape Factors

Our results indicated that landscape and local habitat factors influenced herpetofaunal occupancy and detection across our managed forest landscape. Specifically, salamander occupancy declined with decreasing latitude and elevation, likely because high elevation sites provide cooler, wetter conditions preferred by many salamanders (Petranka and Smith 2005). Conversely, anuran occupancy was greater at sites with lower latitude and elevation, reflecting the higher anuran richness in the Gulf Coastal Plain (Trauth et al. 2004), just south of our study region. Likewise, variation in herpetofaunal physiology underscores the influence of sampling conditions on detection. Salamander detection probability was higher for samples taken at earlier dates with cooler temperatures and wetter soil conditions, whereas there was some support for increased reptile detection with later sampling dates and warmer, drier conditions, when heliophilic species are most active (Gibbons and Semlitsch 1987, Spence-Bailey et al. 2010). Therefore, herpetofaunal sampling should consider conditions expected to influence occupancy and detection of particular species or taxonomic groups, to maximize precision of estimated parameters.

Conclusions and Management Recommendations

Although riparian buffers were designed to mitigate effects of forestry operations on water quality (Cristan et al. 2018), our study examining the empirical relationships between SMZs and semi-aquatic amphibian and terrestrial reptile communities suggests SMZs may also serve to support species diversity. Because our study was observational, there may be environmental factors that we were unable to account for which influence our study species and the width of the SMZs among our sites. However, we believe our study offers some unique insights to how SMZs may influence species diversity within managed forests.

Among our survey sties, we documented high herpetofaunal richness (37 species) in SMZs, demonstrating the value SMZs embedded in managed pine landscapes may provide for supporting diverse wildlife communities. Although all species were positively associated with increasing SMZ width, we observed substantial variation among taxonomic groups and species. Thus, it is critical to consider the entire herpetofaunal community when examining the influence of forestry, as management actions may differentially affect taxonomic groups and species. Notably, in our study, amphibian predicted species richness did not reach its maximum value until a SMZ width of 55m, while reptile predicted species richness approached its maximum value within mid-sized SMZs (~35 m). Forestry best management practices (BMP) for our 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). Buffer widths in our study reflected this and were on average 21 m on either side of the stream, with a few sites exhibiting much larger buffers (up to 55 m). Our study indicates that current BMP guidelines for SMZ width in our study region may be sufficient to support relatively high overall species richness (i.e., at SMZs 11-24 m we estimate a mean of 13-21 species) and to conserve most reptiles. However, the practice of retaining buffers of ≥50 m at some sites may be beneficial to the regional species pool as we predicted the highest species richness among these buffers. Additionally, wide buffers may benefit uncommon salamanders, many of which require specific aquatic and terrestrial habitat types (Semlitsch and Bodie 2003). Our study design and analytical approach allowed for insight across a much broader spectrum of species than has previously been possible and suggests that SMZs show great promise for promoting biodiversity in managed forest landscapes.

Acknowledgements

This study was funded by Weyerhaeuser Company, the National Council for Air and Stream Improvement, the Arkansas Science and Technology Authority, and the University of Arkansas. We thank Paula Szczerba and Shane Szczerba for logistical support during data collection, and Meredith Swartwout for assistance with data collection. We are grateful to Doug Leasure for advice on geospatial analyses and to Teofil Nakov for assistance creating figures. For comments which improved this manuscript we thank Aaron Springford, Jay Jones, Greg Johnson, and Julio Rojas. For input of project design and management we thank Michelle Evans-White, Dan Magoulick, Darren Miller, and T. Bently Wigley.

Literature Cited

Adams, S. B., B. A. Davis, and D. A. Miller. 2018. *Hobbseus yalobushensis*, a Crayfish of Intermittent Streams: Biotic and Habitat Associations, Life History Characteristics, and New Localities. The American Midland Naturalist **179**:126-149.

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences **60**:309-320.

Arkansas Forestry Commission, A. 2002. Best Management Practices for Water Quality Protection.

Aust, W. M. and C. R. Blinn. 2004. Forestry best management practices for timber harvesting and site preparation in the eastern United States: An overview of water quality and productivity research during the past 20 years (1982–2002). Water, Air and Soil Pollution: Focus **4**:5-36.

Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications **14**:692-702.

Blinn, C. R. and M. A. Kilgore. 2001. Riparian management practices: a summary of state guidelines. Journal of Forestry **99**:11-17.

Boothroyd, I. and E. Langer. 1999. Forest harvesting and riparian management guidelines. National Institute of Water and Atmospheric Research. Technical Report 56.

Brosofske, K. D., J. Q. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications **7**:1188-1200.

Burton, T. M. and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in Hubbard Brook Experimental Forest, New Hampshire. Ecology **56**:1068-1080.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clarke, K. R. and R. N. Gorley. 2006. PRIMER-E® (v6): User Manual/Tutorial. PRIMER-E Ltd, Plymouth, UK. .

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, and J. F. Munsell. 2018. National status of state developed and implemented forestry best management practices for protecting water quality in the United States. Forest Ecology and Management.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, J. F. Munsell, and E. Schilling. 2016. Effectiveness of forestry best management practices in the United States: Literature review. Forest Ecology and Management **360**:133-151.

Crosswhite, D. L., S. F. Fox, and R. E. Thill. 1999. Comparison of methods for monitoring reptiles and amphibians in upland forests of the Ouachita Mountains. Proceedings of the Oklahoma Academy of Science **79**:45-50.

Crosswhite, D. L., S. F. Fox, and R. E. Thill. 2004. Herpetological habitat relations in the Ouachita Mountains, Arkansas. Pages 273-282 *in* Tech. Rep. SRS-74. Ouachita and Ozark Mountains Symposium: Ecosystem Management Research. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

Davies, P. and M. Nelson. 1994. Relationships between riparian buffer widths and the effects of logging on stream habitat, invertebrate community composition and fish abundance. Marine and Freshwater Research **45**:1289-1305.

Degraaf, R. M. and D. D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. Forest Ecology and Management **32**:155-165.

Demarais, S., J. P. Verschuyl, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the US. Forest Ecology and Management **385**:308-330.

deMaynadier, P. G. and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3**:230-261.

Demaynadier, P. G. and M. L. Hunter. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology **12**:340-352.

Dorazio, R. M. and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association **100**:389-398.

Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation **144**:1508-1515.

Foley, D. H. 1994. Short-term response of herpetofauna to timber harvesting in conjuction with streamside-management zones in seasonally-flooded bottomland-hardwood forests of southeast Texas. Texas A&M University.

Gelman, A. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science **7**:457-472.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands **23**:630-635.

Gibbons, J. W. and R. D. Semlitsch. 1987. Activity patterns. Pages 396-421 *in* R. A. Seigel, J. T. Collins, and S. S. Novak, editors. Snakes: Ecology and Evolutionary Biology. The Blackburn Press, Caldwell, New Jersey.

Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management **62**:584-589.

Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management **148**:135-144.

Greene, R. E., R. B. Iglay, K. O. Evans, D. A. Miller, T. B. Wigley, and S. K. Riffell. 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests—opportunities for open pine conservation. Forest Ecology and Management **360**:30-39.

Guzy, J. C., K. M. Halloran, J. A.Homyack, and J. D. Willson. 2019. Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests. Forest Ecology and Management **432**:868-883.

Guzy, J. C., S. J. Price, and M. E. Dorcas. 2014. Using multiple methods to assess detection probabilities of riparian-zone anurans: implications for monitoring. Wildlife Research **41**:243-257.

Hager, H. A. 1998. Area-sensitivity of reptiles and amphibians: Are there indicator species for habitat fragmentation? Ecoscience **5**:139-147.

Herbeck, L. A. and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology **13**:623-632.

Hocking, D. J. and R. D. Semlitsch. 2007. Effects of timber harvest on breeding-site selection by gray treefrogs (*Hyla versicolor*). Biological Conservation **138**:506-513.

Homyack, J. A. and A. J. Kroll. 2014. Slow lives in the fast landscape: conservation and management of Plethodontid salamanders in production forests of the United States. Forests **5**:2750-2772.

Homyack, J. A., C. J. O'Bryan, J. E. Thornton, and R. F. Baldwin. 2016. Community occupancy of herpetofauna in roadside ditches in a managed pine landscape. Forest Ecology and Management **361**:346-357.

Jackson, C., D. P. Batzer, S. S. Cross, S. M. Haggerty, and C. A. Sturm. 2007. Headwater streams and timber harvest: channel, macroinvertebrate, and amphibian response and recovery. Forest Science **53**:356-370.

Johnson, B. A., J. A. Homyack, K. Barrett, and R. F. Baldwin. 2016. Factors influencing herpetofaunal assemblages of aquatic systems in a managed pine forest. Forest Ecology and Management **379**:124-132.

Johnston, B. and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). Canadian journal of zoology **80**:2170-2177.

Jones, E., G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology **13**:1454-1465.

Klemmedson, J. O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. Forest Ecology and Management **47**:349-361.

Lannoo, M. 2005. Amphibian Declines: the Conservation Status of United States Species. University of Califronia Press.

Leasure, D. R. 2014. Applications of a new geodata crawler for landscape ecology: from mapping natural stream hydrology to monitoring endangered beetles. University of Arkansas.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management **70**:165-180.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science **2**:314-320.

Loehle, C., T. B. Wigley, P. A. Shipman, S. F. Fox, S. Rutzmoser, R. E. Thill, and M. A. Melchiors. 2005. Herpetofaunal species richness responses to forest landscape structure in Arkansas. Forest Ecology and Management **209**:293-308.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing **10**:325-337.

Maigret, T. A., J. J. Cox, D. R. Schneider, C. D. Barton, S. J. Price, and J. L. Larkin. 2014. Effects of timber harvest within streamside management zones on salamander populations in ephemeral streams of southeastern Kentucky. Forest Ecology and Management **324**:46-51.

Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications **20**:126-134.

Mitchell, J. C., S. C. Rinehart, J. F. Pagels, K. A. Buhlmann, and C. A. Pague. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management **96**:65-76.

Moorman, C. E., K. R. Russell, and C. H. Greenberg. 2011. Reptile and amphibian response to hardwood forest management and early successional habitats. Pages 191-208. Sustaining Young Forest Communities. Springer.

Moring, J. 1982. Decrease in stream gravel permeability after clear-cut logging: an indication of intragravel conditions for developing salmonid eggs and alevins. Hydrobiologia **88**:295-298.

Morris, T. J. and L. D. Corkum. 1996. Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. Journal of the North American Benthological Society **15**:576-586.

Newbold, J., D. Erman, and K. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences **37**:1076-1085.

Noel, D. S., C. W. Martin, and C. A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. Environmental Management **10**:661-670.

Oklahoma Forestry Services. 2016. Oklahoma's Best Management Practices for Water Quality.

Olson, D. H., J. B. Leirness, P. G. Cunningham, and E. A. Steel. 2014. Riparian buffers and forest thinning: Effects on headwater vertebrates 10 years after thinning. Forest Ecology and Management **321**:81-93.

Owens, A. K., K. R. Moseley, T. S. McCay, S. B. Castleberry, J. C. Kilgo, and W. M. Ford. 2008. Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. Forest Ecology and Management **256**:2078-2083.

Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry, and A. DeWan. 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecology and Evolution **4**:877-888.

Parkyn, S. 2004. Review of riparian buffer zone effectiveness. Citeseer.

Parkyn, S. M. and K. J. Collier. 2004. Interaction of press and pulse disturbance on crayfish populations: flood impacts in pasture and forest streams. Hydrobiologia **527**:113-124.

Perkins, D. W. and M. L. Hunter. 2006. Use of amphibians to define riparian zones of headwater streams. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:2124-2130.

Perry, R. W., T. B. Wigley, M. A. Melchiors, R. E. Thill, P. A. Tappe, and D. A. Miller. 2011. Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds. Biodiversity and conservation **20**:625-642.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). Freshwater Biology **53**:347-357.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2011. Effects of even-aged timber harvest on stream salamanders: Support for the evacuation hypothesis. Forest Ecology and Management **262**:2344-2353.

Peterman, W. E. and R. D. Semlitsch. 2009. Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. Forest Ecology and Management **257**:8-14.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian, Washington, D.C.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management **67**:135-147.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology **7**:363-370.

Petranka, J. W. and C. K. Smith. 2005. A functional analysis of streamside habitat use by southern Appalachian salamanders: Implications for riparian forest management. Forest Ecology and Management **210**:443-454.

Pianka, E. R. 1973. The structure of lizard communities. Annual review of ecology and systematics **4**:53-74.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.*in* Proceedings of the 3rd international workshop on distributed statistical computing. Vienna, Austria.

Pollett, K. J., J. G. Maccracken, and J. A. MacMahon. 2010. Stream buffers ameliorate the effects of timber harvest on amphibians in the Cascade Range of Southern Washington, USA. Forest Ecology and Management **260**:1083-1087.

Poole, K. E. and J. A. Downing. 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. Journal of the North American Benthological Society **23**:114-125.

Quinn, J. M., I. K. Boothroyd, and B. J. Smith. 2004. Riparian buffers mitigate effects of pine plantation logging on New Zealand streams: 2. Invertebrate communities. Forest Ecology and Management **191**:129-146.

R Core Team. 2018. R: A language and environment for statistical computing., Vienna, Austria.

Regester, K. J., K. R. Lips, and M. R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia **147**:303-314.

Ross, B., T. Fredericksen, E. Ross, W. Hoffman, M. L. Morrison, J. Beyea, M. B. Lester, B. N. Johnson, and N. J. Fredericksen. 2000. Relative Abundance and Species Richness of Herpetofauna in Forest Stands in Pennsylvania. Forest Science **46**:139-146.

Rudolph, D. C. and J. G. Dickson. 1990. Streamside zone width and amphibian and reptile abundance. The Southwestern Naturalist **35**:472-476.

Russell, K. R., D. C. Guynn Jr, and H. G. Hanlin. 2002a. Importance of small isolated wetlands for herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South Carolina. Forest Ecology and Management **163**:43-59.

Russell, K. R., H. G. Hanlin, T. B. Wigley, and D. C. Guynn Jr. 2002b. Responses of isolated wetland herpetofauna to upland forest management. The Journal of wildlife management:603-617.

Russell, R., J. Royle, V. Saab, W. Block, J. Lehmkuhl, and J. Sauer. 2009. Modeling the response of wildlife communities to environmental disturbance: quantifying the effect of prescribed fire treatments on avian communities in a coniferous forest in Washington. Ecological Applications **19**:1253-1263.

Sauer, J. R. and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. Ecology **86**:1743-1751.

Semlitsch, R. D. and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology **17**:1219-1228.

Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. K. Calhoun, J. W. Gibbons, J. P. Gibbs, G. J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter, D. A. Patrick, T. A. G. Rittenhouse, and B. B. Rothermel. 2009. Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments. BioScience **59**:853-862.

Spence-Bailey, L. M., D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2010. Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success. Wildlife Research **37**:104-115.

Stebbins, R. and N. Cohen. 1995. A Natural History of Amphibians. Princeton University Press: Princeton, NJ.

Su, Y.-S. and M. Yajima. 2015. R2jags: A Package for Running jags from R. R package version 0.03-08, URL http://CRAN. R-project. org/package= R2jags.

Swank, W. T., J. Vose, and K. Elliott. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and Management **143**:163-178.

Taylor, B. R., D. Parkinson, and W. F. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology **70**:97-104.

Tilghman, J. M., S. W. Ramee, and D. M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation **152**:1-9.

Trauth, S. E., H. W. Robison, and M. V. Plummer. 2004. The Amphibians and Reptiles of Arkansas. University of Arkansas Press, Fayetteville, AR.

Vesely, D. G. and W. C. McComb. 2002. Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon Coast Range. Forest Science **48**:291-297.

Walls, S. C. 2014. Identifying monitoring gaps for amphibian populations in a North American biodiversity hotspot, the southeastern USA. Biodiversity and conservation **23**:3341-3357.

Warrington, B. M., W. M. Aust, S. M. Barrett, W. M. Ford, C. A. Dolloff, E. B. Schilling, T. B. Wigley, and M. C. Bolding. 2017. Forestry Best Management Practices Relationships with Aquatic and Riparian Fauna: A Review. Forests **8**:331.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology **30**:377-392.

Whiles, M. R. and J. B. Wallace. 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. Hydrobiologia **353**:107-119.

Wigley, T. B. and M. A. Melchiors. 1994. Wildlife habitat and communities in streamside management zones: a literature review for the eastern United States. Pages 100-121 *in* Proceeding of the Conference on Riparian Ecosystems in the Humid US: Functions, Values and Management, National Association of Conservation Districts, Washington, DC.

Wilkerson, E., J. M. Hagan, D. Siegel, and A. A. Whitman. 2006. The effectiveness of different buffer widths for protecting headwater stream temperature in Maine. Forest Science **52**:221-231.

Willson, J. D. and C. T. Winne. 2016. Evaluating the functional importance of secretive species: A case study of aquatic snake predators in isolated wetlands. Journal of Zoology **298**:266-273.

Woods, A., T. Foti, S. Chapman, J. Omernik, J. Wise, E. Murray, W. Prior, J. Pagan, J. Comstock, and M. Radford. 2004. Ecoregions of Arkansas (color poster with map, descriptive text, summary tables, and photographs). US Geological Survey.

Young, K. A., S. G. Hinch, and T. G. Northcote. 1999. Status of Resident Coastal Cutthroat Trout and Their Habitat Twenty-Five Years after Riparian Logging. North American Journal of Fisheries Management **19**:901-911.

Zipkin, E. F., A. DeWan, and J. Andrew Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. Journal of Applied Ecology **46**:815-822.

Figures and Tables

Table 1. Summary of species captured, with model-estimated mean occupancy and detection probabilities and 95% credible intervals, for herpetofauna within streamside management zones of the Ouachita Mountains, Arkansas, USA.

					Occupancy			Detection		
Common name	Scientific name	Figure code name	Sum	# of sites	Mean	95% posterior interval		Mean	95% posterior interval	
Blanchard's cricket frog	*Acris blanchardi*	Acr.bla	119	44	0.63	0.45	0.89	0.14	0.11	0.18
American toad	*Anaxyrus americanus*	Ana.ame	40	13	0.37	0.14	0.78	0.03	0.02	0.05
Eastern narrow-mouthed toad	*Gastrophryne carolinensis*	Gas.car	6	2	0.36	0.04	0.89	0.01	0.00	0.02
Cope’s gray treefrog	*Hyla chrysoscelis*	Hyl.chr	108	56	0.71	0.58	0.87	0.18	0.14	0.21
Green treefrog	*Hyla cinerea*	Hyl.cin	7	7	0.33	0.11	0.72	0.02	0.01	0.03
American bullfrog	*Lithobates catesbeianus*	Lit.cat	2	1	0.11	0.01	0.57	0.00	0.00	0.01
Green frog	*Lithobates clamitans*	Lit.cla	12	11	0.65	0.24	0.98	0.03	0.01	0.04
Pickerel frog	*Lithobates palustris*	Lit.pla	8	7	0.58	0.16	0.97	0.02	0.01	0.03
Southern leopard frog	*Lithobates sphenocephalus*	Lit.sph	33	23	0.73	0.40	0.97	0.06	0.04	0.08
Spring peeper	*Pseudacris crucifer*	Pse.cru	3	3	0.23	0.04	0.68	0.01	0.00	0.02
Cajun chorus frog	*Pseudacris fouquettei*	Pse.foq	34	22	0.73	0.48	0.98	0.06	0.04	0.08
Ringed salamander	*Ambystoma annulatum*	Amb.ann	2	1	0.05	0.00	0.37	0.00	0.00	0.01
Spotted salamander	*Ambystoma maculatum*	Amb.mac	25	4	0.21	0.03	0.74	0.01	0.00	0.02
Marbled salamander	*Ambystoma opacum*	Amb.opa	1	1	0.20	0.00	0.84	0.00	0.00	0.01
Ouachita dusky salamander	*Desmognathus brimleyorum*	Des.bri	595	61	0.59	0.52	0.66	0.41	0.38	0.45
Many-ribbed salamander	*Eurycea multiplicata*	Eur.mul	550	89	0.90	0.84	0.95	0.53	0.49	0.58
Four-toed salamander	*Hemidactylum scutatum*	Hem.scu	2	2	0.19	0.01	0.76	0.01	0.00	0.01
Caddo Mt. salamander	*Plethodon caddoensis*	Ple.cad	33	8	0.10	0.05	0.16	0.04	0.03	0.05
Slimy salamander	*Plethodon glutinosus* complex	Ple.glu	76	36	0.48	0.35	0.64	0.13	0.11	0.16
Southern red-backed salamander	*Plethodon serratus*	Ple.ser	196	35	0.43	0.34	0.53	0.19	0.16	0.21
Lesser siren	*Siren intermedia*	Sir.int	1	1	0.23	0.01	0.84	0.00	0.00	0.01
Eastern box turtle	*Terrapene carolina*	Ter.car	15	14	0.58	0.29	0.90	0.04	0.02	0.06
Green anole	*Anolis carolinensis*	Ano.car	4	4	0.70	0.27	0.97	0.01	0.00	0.02
Skink (Broad-headed/Five-lined)	*Plestiodon sp. (fasiatus/laticeps)**	Ple.spp	43	31	0.70	0.46	0.93	0.07	0.05	0.10
Eastern fence lizard	*Sceloporus undulatus*	Sce.und	11	11	0.82	0.44	0.99	0.02	0.01	0.04
Little brown skink	*Scincella lateralis*	Sci.lat	38	29	0.78	0.56	0.96	0.07	0.05	0.10

Table 1 (*continued*). Summary of species captured, with model-estimated mean occupancy and detection probabilities and 95% credible intervals, for herpetofauna within streamside management zones of the Ouachita Mountains, Arkansas, USA.

					Occupancy			Detection		
Common name	Scientific name	Figure code name	Sum	# of sites	Mean	95% posterior interval		Mean	95% posterior interval	
Eastern copperhead	*Agkistrodon contortrix*	Agk.con	2	2	0.57	0.12	0.95	0.01	0.00	0.02
Northern cottonmouth	*Agkistrodon piscivorus*	Agk.pis	20	17	0.75	0.35	0.99	0.05	0.03	0.07
North American racer	*Coluber constrictor*	Col.con	2	2	0.63	0.15	0.96	0.01	0.00	0.02
Ring-necked snake	*Diadophis punctatus*	Dia.pun	9	7	0.63	0.18	0.97	0.02	0.01	0.04
Eastern hog-nosed snake	*Heterodon platirhinos*	Het.pla	1	1	0.54	0.06	0.96	0.00	0.00	0.01
Eastern milksnake	*Lampropeltis triangulum*	Lam.tri	1	1	0.54	0.05	0.96	0.00	0.00	0.01
Plain-bellied watersnake	*Nerodia erythrogaster*	Ner.ery	3	2	0.50	0.06	0.94	0.01	0.00	0.02
Rough greensnake	*Opheodrys aestivus*	Oph.aes	1	1	0.61	0.08	0.96	0.00	0.00	0.01
Western rat snake	*Pantherophis obsoletus*	Pan.obs	3	3	0.47	0.09	0.91	0.01	0.00	0.02
Pygmy rattlesnake	*Sistrurus miliarius*	Sis.mil	1	1	0.61	0.06	0.97	0.00	0.00	0.01
Red-bellied snake	*Storeria occipitomaculata*	Sto.occ	2	2	0.52	0.07	0.95	0.01	0.00	0.01

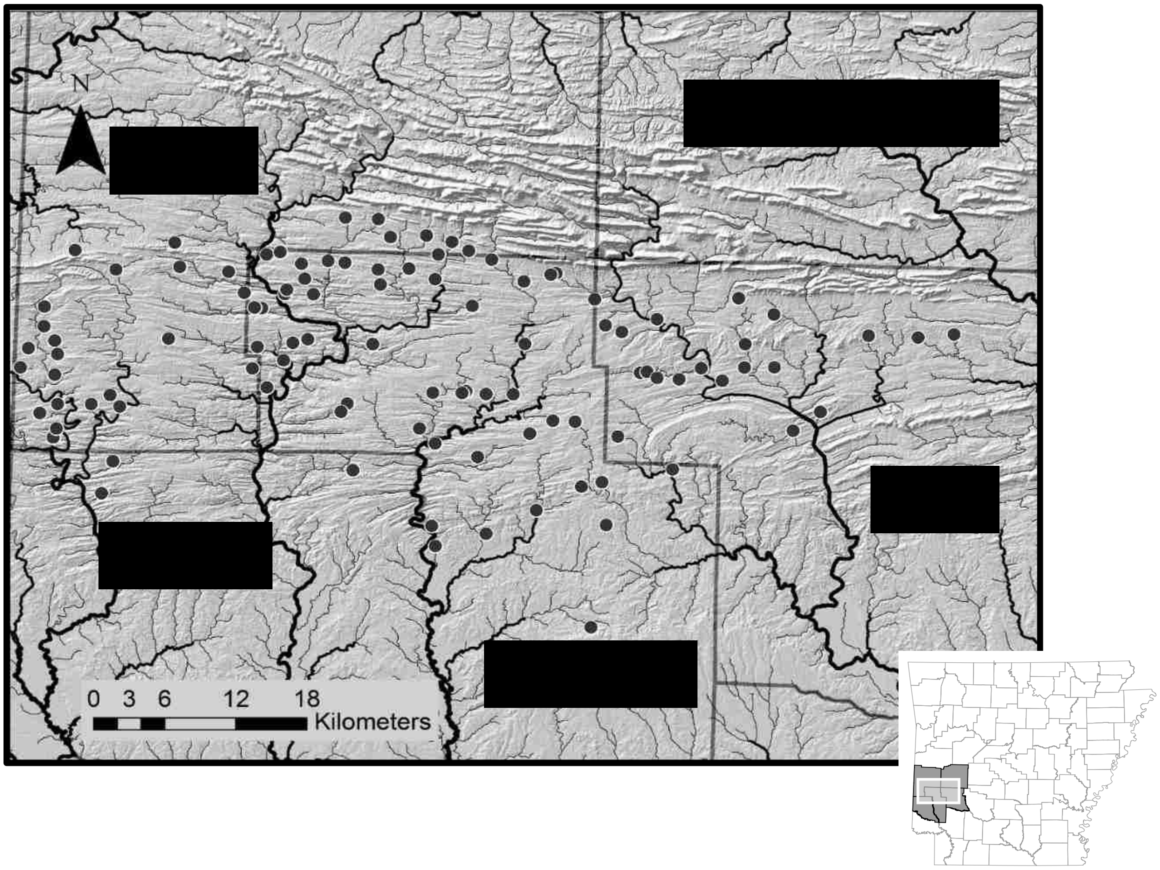


Figure 1. Location of study sites. Map inset: region on the Athens Plateau of the Ouachita Mountains Ecoregion of west-central Arkansas, USA. Main map: distribution of study sites (n=102) located in Howard, Polk, Pike, and Sevier counties, Arkansas.

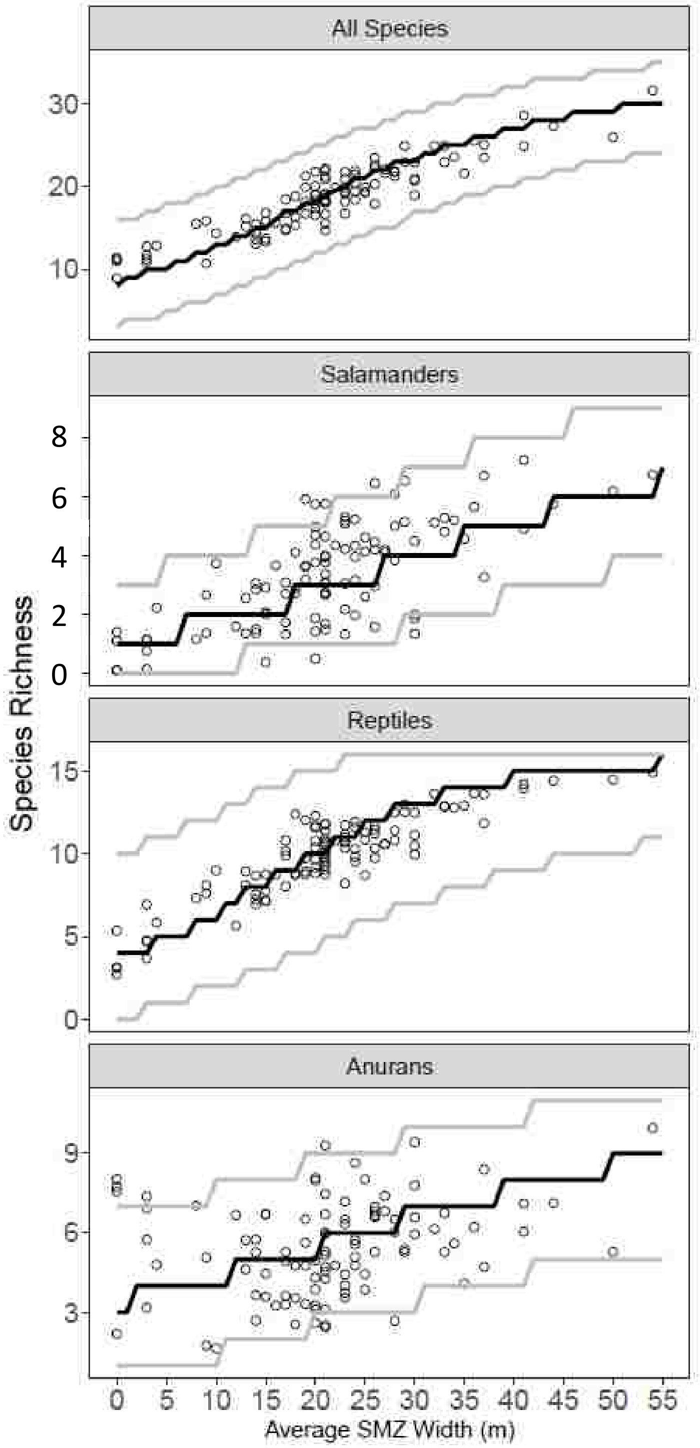


Figure 2. Relationship between streamside management zone (SMZ) width and median estimated species richness of a) all herpetofaunal species, b) salamanders, c) reptiles, and d) anurans within streamside management zones of the Ouachita Mountains, Arkansas, USA. Solid line represents the median predicted site richness and grey lines represent the 95% credible intervals calculated using average Site PC1 and Site PC2 values and a weighted average of overstory and stand age categories according to their prevalence in our sample. Circles are site-specific mean richness estimates using observed values of model covariates.

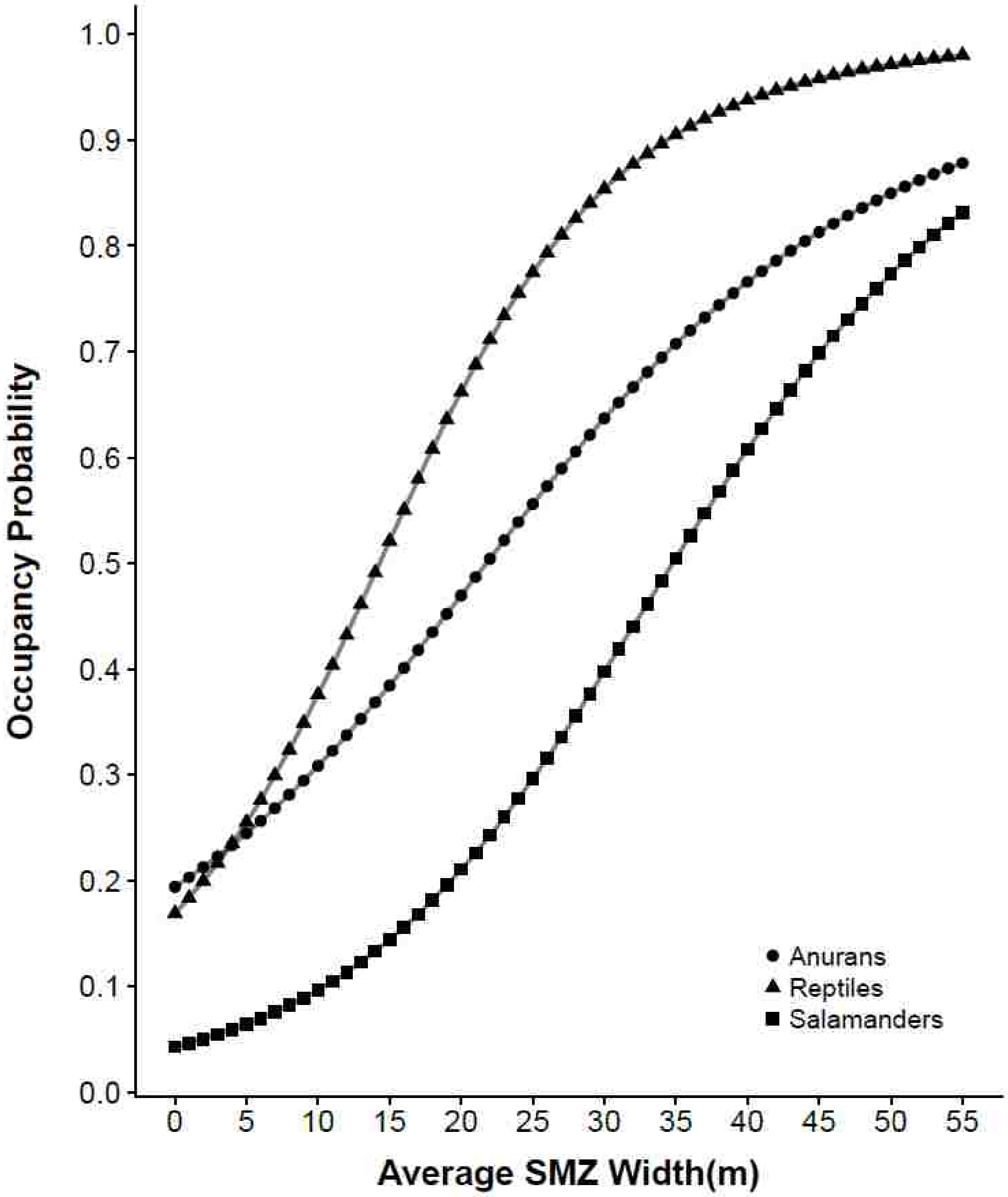


Figure 3. Relationship between streamside management zone (SMZ) width and group-specific mean occupancy probability for species within streamside management zones of the Ouachita Mountains, Arkansas, USA. Calculated using average Site PC1 and Site PC2 values and a weighted average of overstory and stand age categories according to their prevalence in our sample.

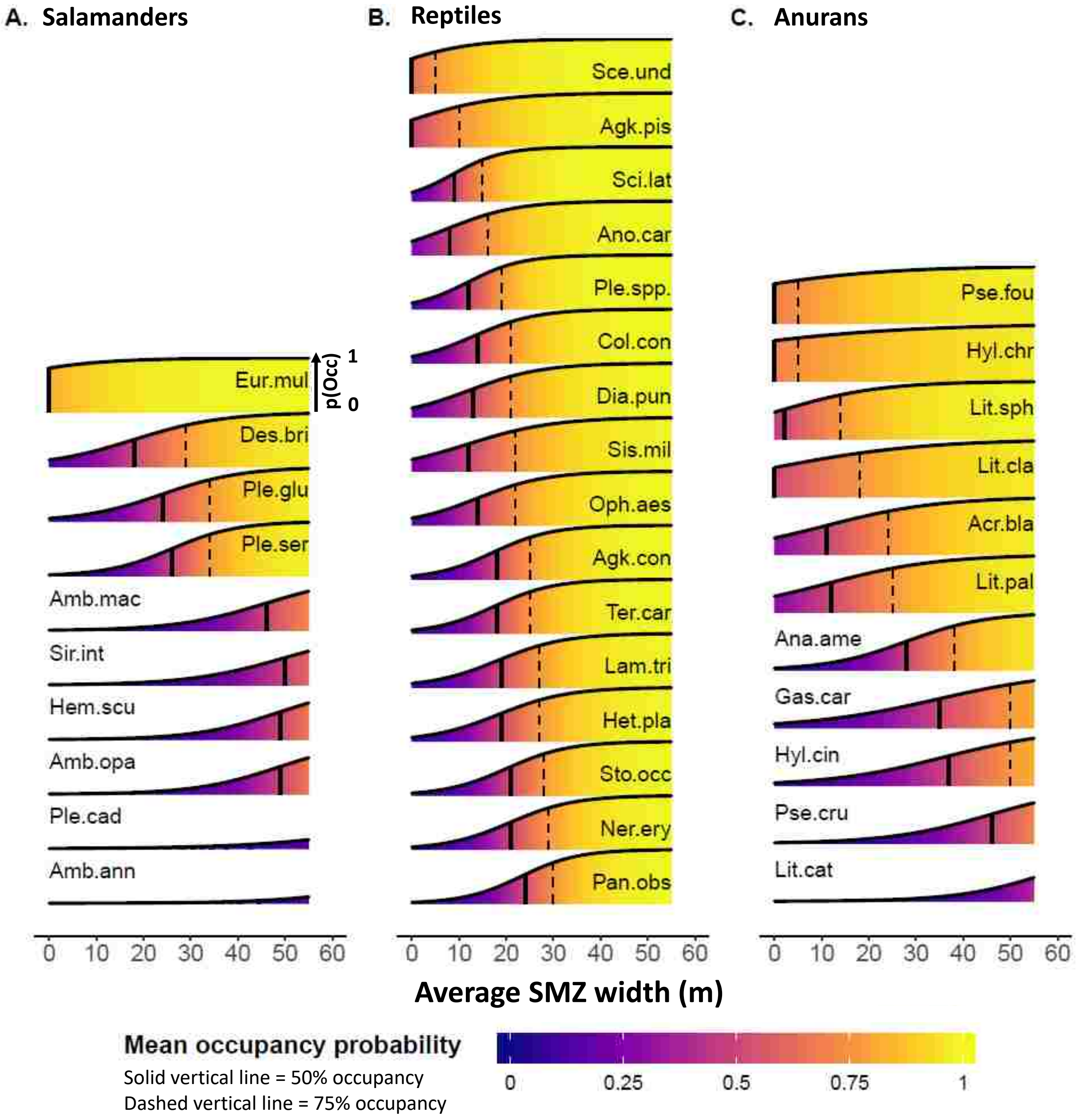


Figure 4. Relationship between mean species-specific occupancy probability and streamside management zone (SMZ) width for a) salamanders, b) reptiles, and c) anurans, within managed forests in the Ouachita Mountains, Arkansas, USA. Values were calculated using average Site PC1 and Site PC2 values and a weighted average of overstory and stand age categories according to their prevalence in our sample. For each species, shading under the line moving left to right indicates the mean occupancy probability, with darker colors (e.g., blue) indicating the lowest values, and lighter colors (e.g., yellow) indicating the highest value (i.e., 100%). Solid vertical and dashed lines within species graphs indicate 50% and 75% occupancy probability, respectively. See Table 1 for species code definitions.

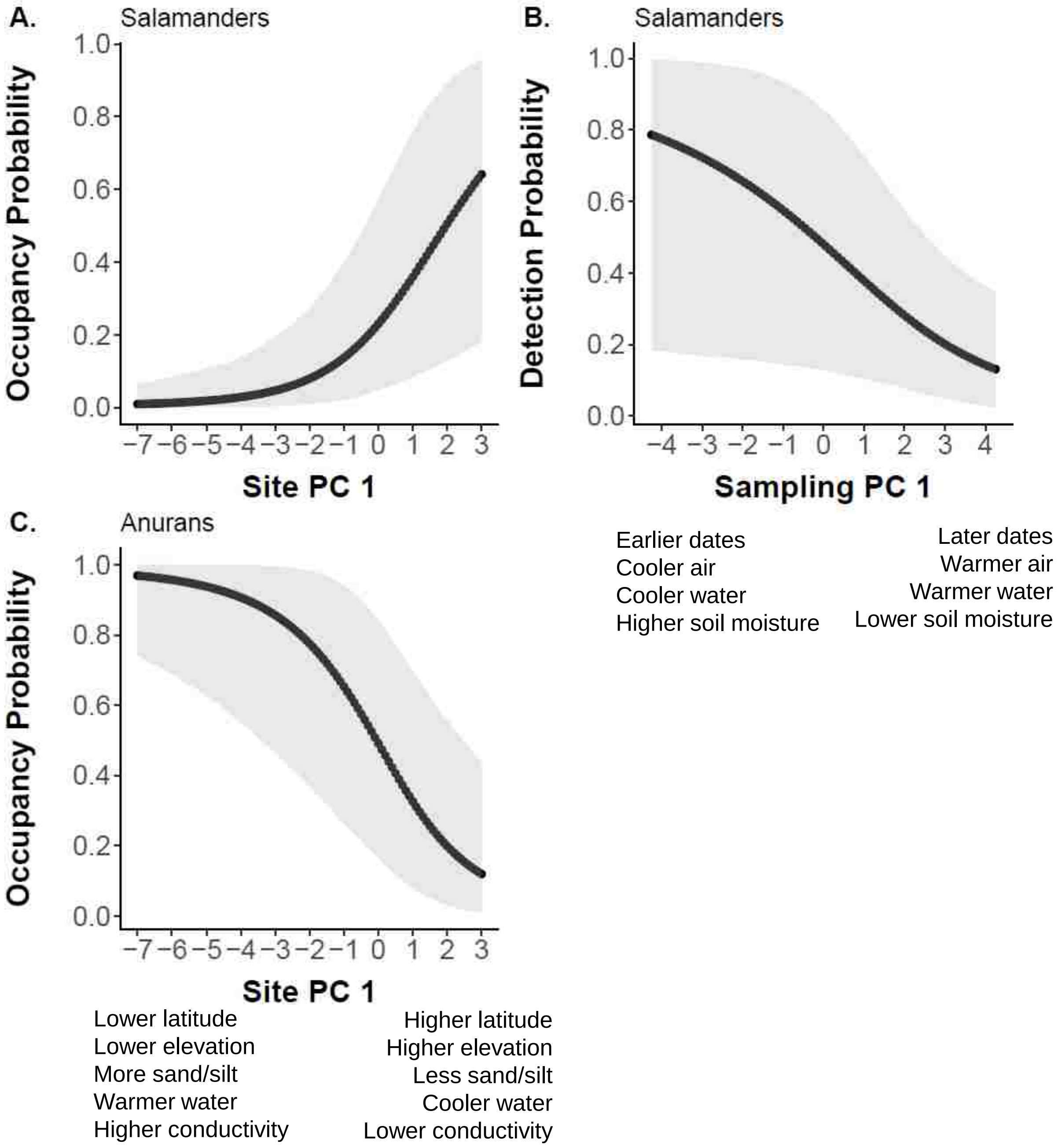


Figure 5. Factors influencing occupancy and detection of the amphibian community within streamside management zones of the Ouachita Mountains, Arkansas, USA. Calculated using average SMZ width, Site PC2 values, a weighted average of overstory and stand age categories according to their prevalence in our sample, and average Sampling PC2 values. Mean salamander a) occupancy of the community in relation to Site PC1, b) detection probability in relation to Sampling PC1, and c) occupancy of the anuran community in relation to Site PC1. Solid lines represent the posterior mean community response and grey shading represents 95% credible intervals.

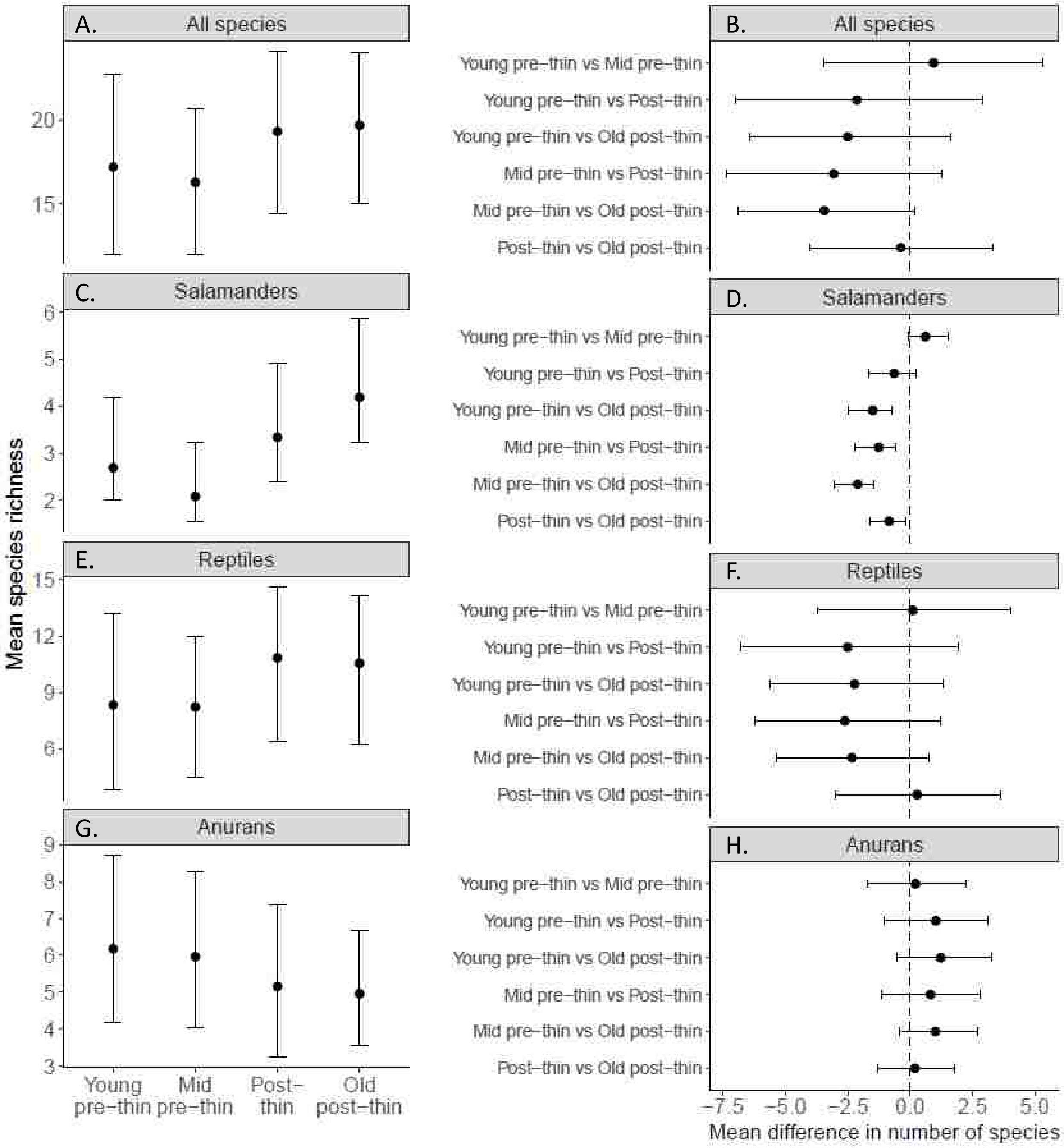


Figure 6. Estimated mean species richness and mean difference in species richness between pairs of stand age categories within streamside management zones (SMZs) for a-b) all species, c-d) salamanders, e-f) reptiles, and g-h) anurans within the Ouachita Mountains, Arkansas, USA. Error bars reflect 95% credible intervals. 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’ (13-22years old, 1-6 years since thinning), and ‘Old Post-thin’ (22-35 years old, 8-17 years since thinning). The mean difference in species richness is derived from category specific mean species richness estimates calculated at each iteration of the model.

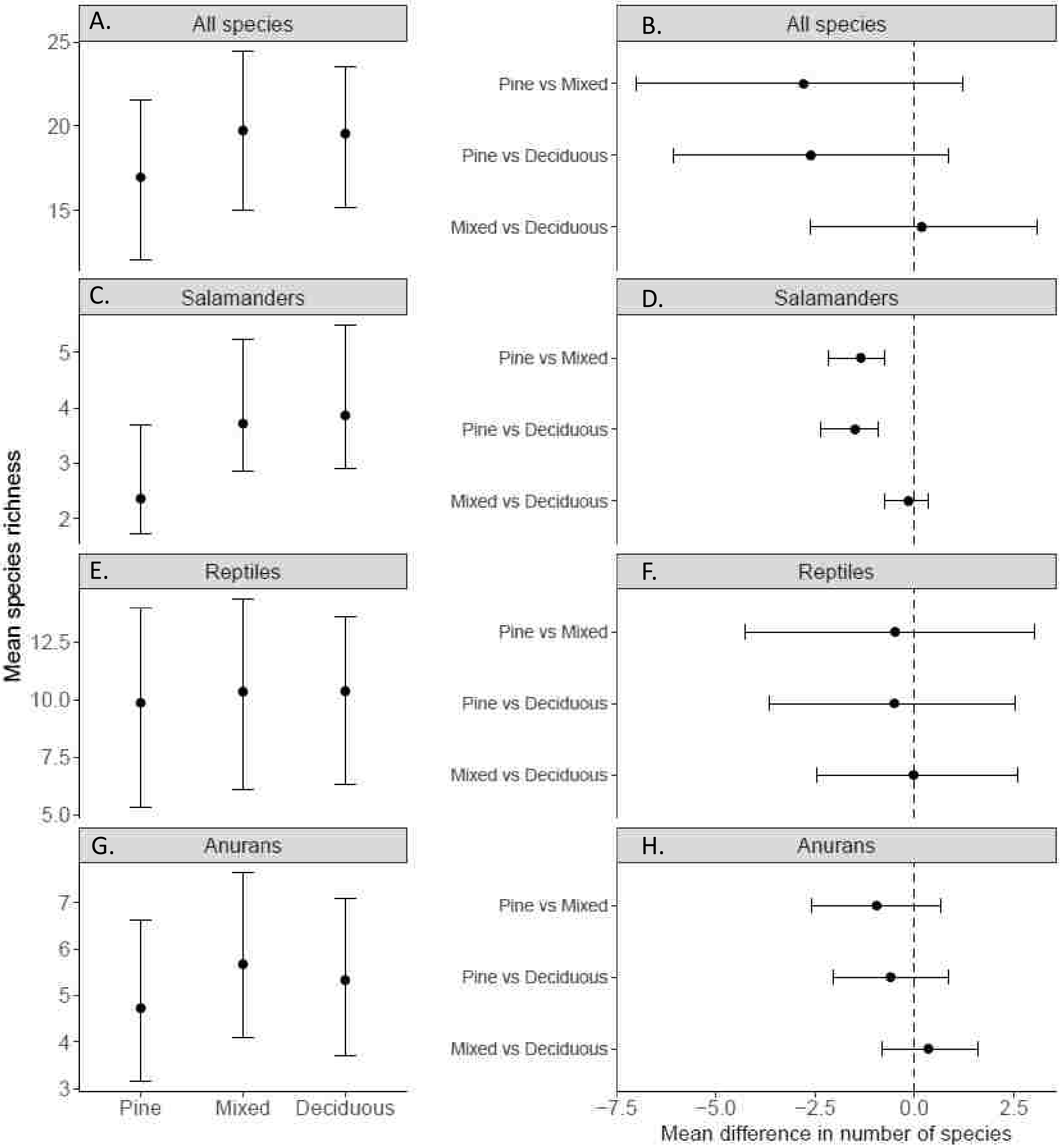
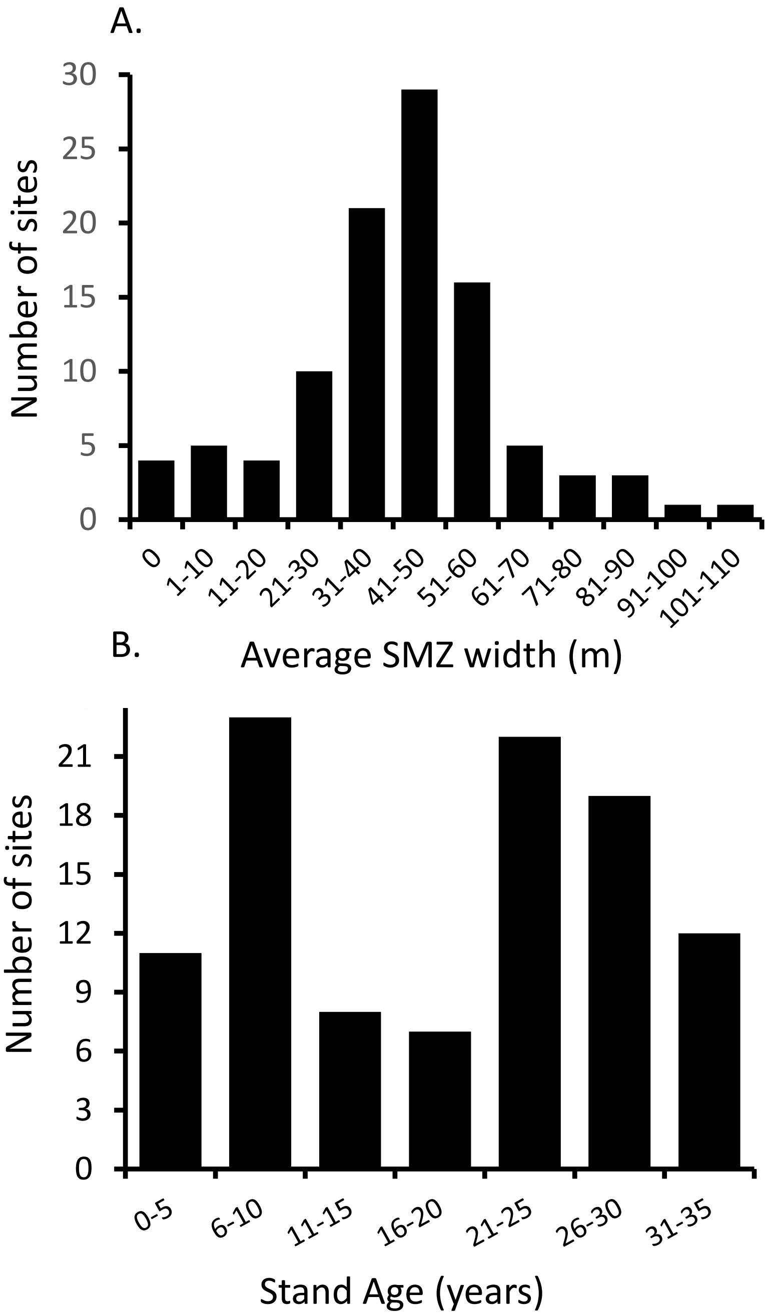


Figure 7. Estimated mean species richness and mean difference in species richness between pairs of SMZ overstory categories within streamside management zones (SMZs) for a-b) all species, c-d) salamanders, e-f) reptiles, and g- h) anurans within the Ouachita Mountains, Arkansas, USA. Error bars reflect 95% credible intervals. The mean difference in species richness is derived from category specific mean species richness estimates calculated at each iteration of the model.

Appendices

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.

A.

Site Covariates		
Principal Components	1	2
Eigenvalues	3.75	1.88
% of Variation	31.0	15.5
Cum. % of Variation	31.0	46.5

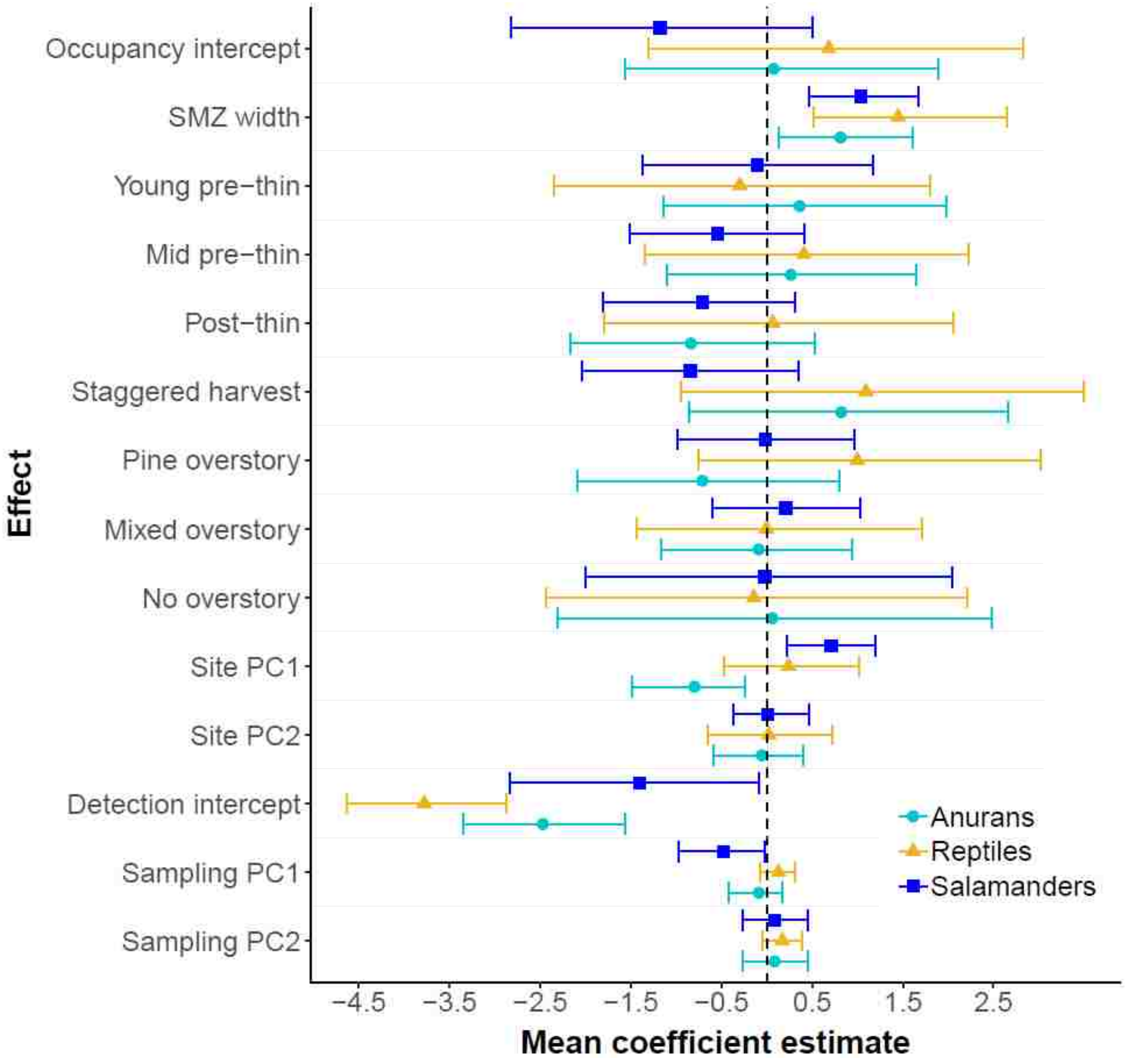
Variable (Eigenvectors*)	PC1	PC2
Latitude	**0.40**	-0.27
Watershed area	-0.16	**0.35**
Elevation	**0.34**	**-0.40**
% Bedrock	0.09	0.18
% Boulder and cobble	0.25	**0.51**
% Sand and silt	**-0.36**	**-0.38**
Water temperature	**-0.43**	-0.02
Water depth	-0.24	0.05
Dissolved oxygen	0.19	-0.05
Conductivity	**-0.34**	-0.12
Amount of upland cover objects	0.16	0.20
% Open canopy	0.29	**-0.38**

B.

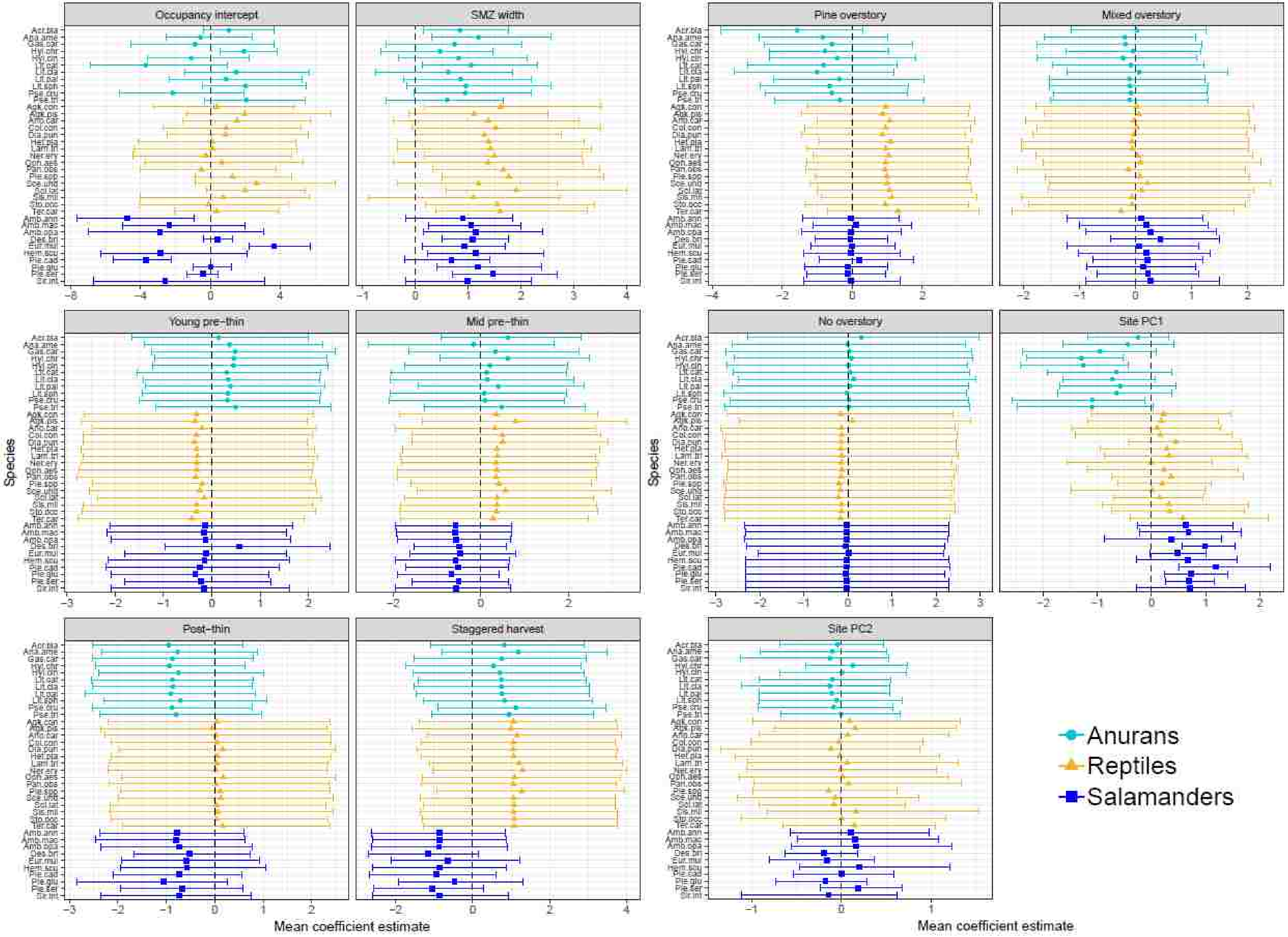
Sampling Covariates		
	1	2
	2.37	1.41
	33.8	20.0
	33.8	53.8

	PC1	PC2
Date	**0.51**	**-0.35**
Air temperature	**0.49**	**0.29**
Barometric pressure	0.14	-0.08
Humidity	0.13	**-0.70**
Water depth	-0.07	**-0.31**
Water temperature	**0.58**	-0.06
Soil moisture	**-0.34**	**-0.45**

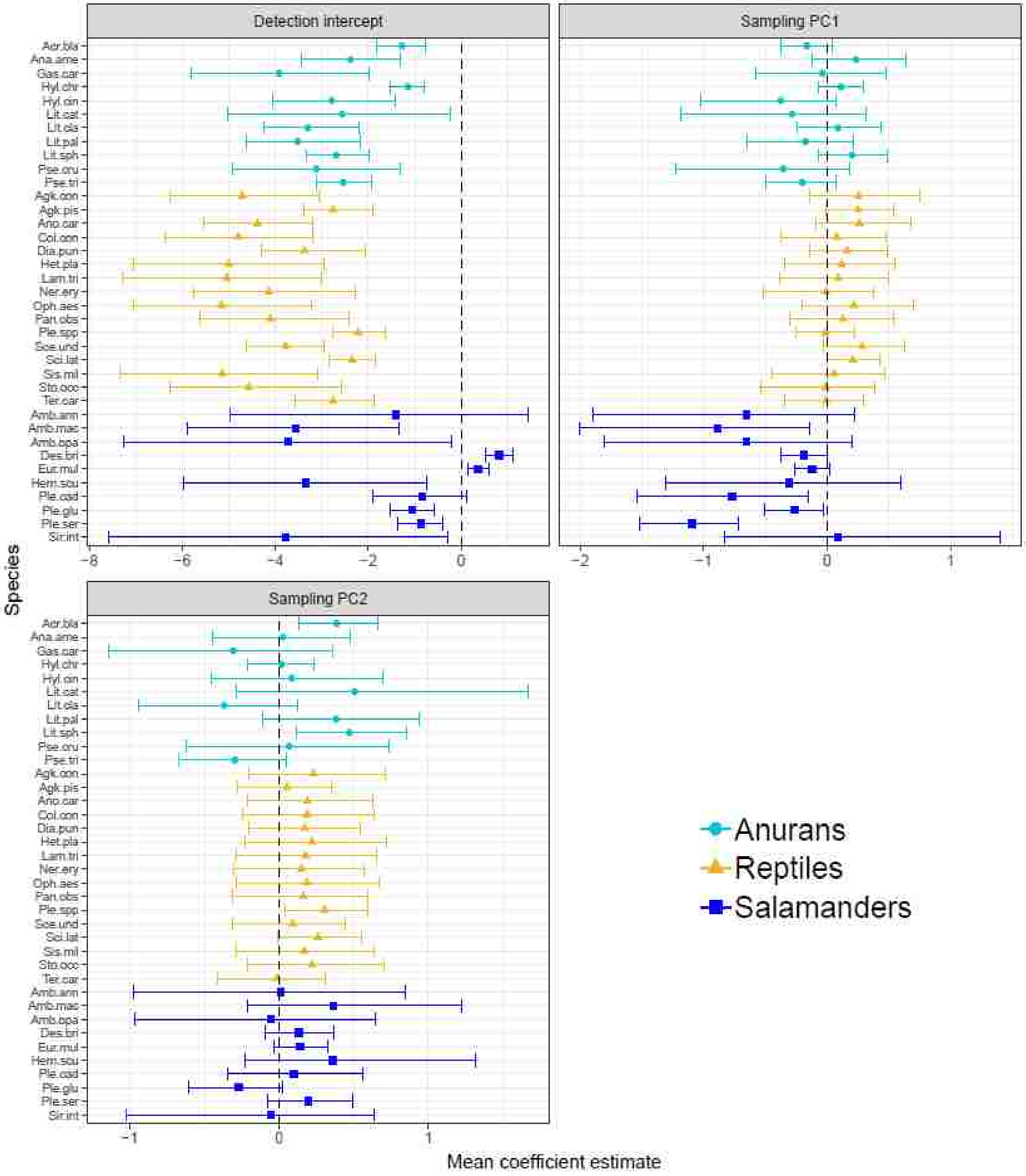
Appendix 3. Summary of hyper-parameters (i.e., mean assemblage response) with 95% Bayesian credible intervals for occupancy and detection covariates for amphibians and reptiles within the Ouachita Mountains, Arkansas, USA.



Appendix 4. Estimates of occupancy coefficients with 95% Bayesian credible intervals for herpetofaunal species. See Table 1 for species code definitions.



Appendix 5. Estimates of detection coefficients with 95% Bayesian credible intervals for herpetofaunal species. See Table 1 for species code definitions.



Appendix 6. Posterior predictive check for hierarchical community model to evaluate the empirical relationships between SMZ width and herpetofauna community.

To assess goodness of fit for our Bayesian model, we calculated a discrepancy measure, D. For a randomly selected posterior sample, s, we can calculate D and D_{sim} as follows:

$$D^{(s)} = \sum_{ijk} \left(y_{ijk} - \hat{z}_{ij}^{(s)} \hat{p}_{ijk}^{(s)} \right)^2$$

$$D_{sim}^{(s)} = \sum_{ijk} \left(\hat{y}_{ijk}^{(s)} - \hat{z}_{ij}^{(s)} \hat{p}_{ijk}^{(s)} \right)^2$$

Where y_{ijk} is the true observed occupancy of species i at site j in visit k. $\hat{z}_{ij}^{(s)}$ is the latent estimated occupancy for the sth posterior sample for species i at site j. $\hat{p}_{ijk}^{(s)}$ is the estimated detection probability for the sth posterior sample for species i at site j in visit k. $\hat{y}_{ijk}^{(s)}$ is the estimated observed occupancy for the sth posterior sample where $\hat{y}_{ijk} \sim Bernoulli(\hat{z}_{ij}^{(s)} \hat{p}_{ijk}^{(s)})$.

For each posterior sample, s, we compare $D^{(s)}$ to $D_{sim}^{(s)}$. If the model is adequately fitting the data we would expect that $D^{(s)} > D_{sim}^{(s)}$ approximately 50% of the time while $D^{(s)} < D_{sim}^{(s)}$ approximately 50% of the time. If $D^{(s)} > D_{sim}^{(s)}$ more than 95% of the time or less than 5% of the time that would be a sign that the model does not adequately represent the observed data.

For a sub-sample of 1000 of the 6000 saved posterior samples we calculated the proportion of $D^{(s)} > D_{sim}^{(s)}$ and found that $D^{(s)}$ is greater than $D_{sim}^{(s)}$ approximately 54% of the time. This indicates that our model does an adequate job fitting observed data and we have no goodness of fit concerns.

Appendix 7. R Code to run species richness model for this study.

```
library(R2jags)
load.module("glm")

## Set Loop Sizes
n.groups<-3
n.species<-37
n.sites<-102
n.visits<-4

######################
## Specify the model ##
######################
Weyer.group.occ<-function(){
  #Prior distributions on group level parameters
  for(h in 1:n.groups){
    mu.a.0[h]~dnorm(0,0.5)
    mu.a.SMZ[h]~dnorm(0,0.5)
    mu.a.Pine[h]~dnorm(0,0.5)
    mu.a.Mixed[h]~dnorm(0,0.5)
    mu.a.NoSMZ[h]~dnorm(0,0.5)
    mu.a.PCA1[h]~dnorm(0,0.5)
    mu.a.PCA2[h]~dnorm(0,0.5)
    mu.a.YoungPreThin[h]~dnorm(0,0.5)
    mu.a.MidPreThin[h]~dnorm(0,0.5)
    mu.a.PostThin[h]~dnorm(0,0.5)
    mu.a.half[h]~dnorm(0,0.5)

    mu.b.0[h]~dnorm(0,0.5)
    mu.b.pc1[h]~dnorm(0,0.5)
    mu.b.pc2[h]~dnorm(0,0.5)

    sig.a.0[h]~dunif(0.1,3)
    sig.a.SMZ[h]~dnorm(0.1,3)
    sig.a.Pine[h]~dnorm(0.1,3)
    sig.a.Mixed[h]~dnorm(0.1,3)
    sig.a.NoSMZ[h]~dnorm(0.1,3)
    sig.a.PCA1[h]~dnorm(0.1,3)
    sig.a.PCA2[h]~dnorm(0.1,3)
    sig.a.YoungPreThin[h]~dnorm(0.1,3)
    sig.a.MidPreThin[h]~dnorm(0.1,3)
    sig.a.PostThin[h]~dnorm(0.1,3)
    sig.a.half[h]~dnorm(0.1,3)

    sig.b.0[h]~dunif(0.1,3)
    sig.b.pc1[h]~dunif(0.1,3)
    sig.b.pc2[h]~dunif(0.1,3)

    tau.a.0[h]<-(1/(sig.a.0[h]*sig.a.0[h]))
    tau.a.SMZ[h]<-(1/(sig.a.SMZ[h]*sig.a.SMZ[h]))
    tau.a.Pine[h]<-(1/(sig.a.Pine[h]*sig.a.Pine[h]))
    tau.a.Mixed[h]<-(1/(sig.a.Mixed[h]*sig.a.Mixed[h]))
    tau.a.NoSMZ[h]<-(1/(sig.a.NoSMZ[h]*sig.a.NoSMZ[h]))
    tau.a.PCA1[h]<-(1/(sig.a.PCA1[h]*sig.a.PCA1[h]))
    tau.a.PCA2[h]<-(1/(sig.a.PCA2[h]*sig.a.PCA2[h]))
    tau.a.YoungPreThin[h]<-(1/(sig.a.YoungPreThin[h]*sig.a.YoungPreThin[h]))
    tau.a.MidPreThin[h]<-(1/(sig.a.MidPreThin[h]*sig.a.MidPreThin[h]))
    tau.a.PostThin[h]<-(1/(sig.a.PostThin[h]*sig.a.PostThin[h]))
    tau.a.half[h]<-(1/(sig.a.half[h]*sig.a.half[h]))
```

```
    tau.b.0[h]<-(1/(sig.b.0[h]*sig.b.0[h]))
    tau.b.pc1[h]<-(1/(sig.b.pc1[h]*sig.b.pc1[h]))
    tau.b.pc2[h]<-(1/(sig.b.pc2[h]*sig.b.pc2[h]))
  }

  #Site level Random Effects
  sig.a.site~dunif(0.1,3)
  tau.a.site<-(1/(sig.a.site*sig.a.site))
  for(l in 1:n.sites){
    zza.site[l]~dnorm(0,tau.a.site)
  }

  #Priors for species level effects
  for(i in 1:n.species){
    a.0[i]~dnorm(mu.a.0[species.group[i]],tau.a.0[species.group[i]])
    a.SMZ[i]~dnorm(mu.a.SMZ[species.group[i]],tau.a.SMZ[species.group[i]])
    a.Pine[i]~dnorm(mu.a.Pine[species.group[i]],tau.a.Pine[species.group[i]])
    a.Mixed[i]~dnorm(mu.a.Mixed[species.group[i]],tau.a.Mixed[species.group[i]])
    a.NoSMZ[i]~dnorm(mu.a.NoSMZ[species.group[i]],tau.a.NoSMZ[species.group[i]])
    a.PCA1[i]~dnorm(mu.a.PCA1[species.group[i]],tau.a.PCA1[species.group[i]])
    a.PCA2[i]~dnorm(mu.a.PCA2[species.group[i]],tau.a.PCA2[species.group[i]])
    a.YoungPreThin[i]~dnorm(mu.a.YoungPreThin[species.group[i]],tau.a.YoungPreThin[species.group[i]])
    a.MidPreThin[i]~dnorm(mu.a.MidPreThin[species.group[i]],tau.a.MidPreThin[species.group[i]])
    a.PostThin[i]~dnorm(mu.a.PostThin[species.group[i]],tau.a.PostThin[species.group[i]])
    a.half[i]~dnorm(mu.a.half[species.group[i]],tau.a.half[species.group[i]])

    b.0[i]~dnorm(mu.b.0[species.group[i]],tau.b.0[species.group[i]])
    b.pc1[i]~dnorm(mu.b.pc1[species.group[i]],tau.b.pc1[species.group[i]])
    b.pc2[i]~dnorm(mu.b.pc2[species.group[i]],tau.b.pc2[species.group[i]])

    #Loop to estimate true occupancy
    # i=species, j=site, k=visit
    for(j in 1:n.sites){
      logit(psi[j,i])<- a.0[i] + zza.site[site.num[j]] + a.SMZ[i]*SMZ[j] +
        a.Pine[i]*Pine[j] + a.Mixed[i]*Mixed[j] + a.NoSMZ[i]*NoSMZ[j] +
        a.PCA1[i]*PCA1[j] + a.PCA2[i]*PCA2[j] +a.YoungPreThin[i]*YoungPreThin[j] +
        a.MidPreThin[i]*MidPreThin[j] + a.PostThin[i]*PostThin[j] + a.half[i]*half[j]

      #limits to keep occupancy probability away from 0 or 1
      zzmu.psi[j,i]<-min(0.999,max(psi[j,i],0.001))

      z[j,i]~dbern(zzmu.psi[j,i])

      #Detection Probability
      for(k in 1:n.visits){
        logit(p[i,j,k])<- b.0[i] + b.pc1[i]*pc1[j,k] + b.pc2[i]*pc2[j,k]

        #limits to keep detection probability away from 0 or 1
        zzmu.p[i,j,k]<-min(0.999, max(p[i,j,k],0.001))*z[j,i]

        X[i,j,k]~dbern(zzmu.p[i,j,k])
      }
    }
  }

  #Richness for each site
  for(e in 1:n.sites){
    SiteRichness[e]<-sum(z[e,]) #sum over 37 species at each site
  }

}
```

```
#Write text file of model
write("model{Weyer.group.occ}","Weyer.group.occ.txt")
model.file<-"Weyer.group.occ.txt"

#Specify initial values
zinits<-matrix(NA,nrow=n.sites, ncol=n.species)
for(i in 1:n.species){
  for(j in 1:n.sites){
    zinits[j,i]<-max(X[i,j,],na.rm=TRUE)
  }
}

#Coefficient Initial Values
inits.Weyer=function(){
  list(a.0=rnorm(n.species,0),a.SMZ=rnorm(n.species,0),a.Pine=rnorm(n.species,0),
       a.Mixed=rnorm(n.species,0),a.NoSMZ=rnorm(n.species,0),a.PCA1=rnorm(n.species,0),
       a.PCA2=rnorm(n.species,0),a.YoungPreThin=rnorm(n.species,0),a.MidPreThin=rnorm(n.species,0),
       a.PostThin=rnorm(n.species,0),a.half=rnorm(n.species,0),b.0=rnorm(n.species,0),
       b.pc1=rnorm(n.species,0),b.pc2=rnorm(n.species,0),z=zinits)
}

data.Weyer<-list(n.groups=n.groups, n.sites=n.sites, n.species=n.species,
                 n.visits=n.visits, species.group=species.group, site.num=site.num,

                 SMZ=smz.scaled, Pine=SiteCovs$Pine,
                 Mixed=SiteCovs$Mixed, NoSMZ=SiteCovs$NoSMZ, PCA1=SiteCovs$PCA1, PCA2=SiteCovs$PCA2,
                 YoungPreThin=SiteCovs$YoungPreThin, MidPreThin=SiteCovs$MidPreThin,
                 PostThin=SiteCovs$PostThin, half=SiteCovs$half,

                 pc1=pc1, pc2=pc2,

                 X=X)

params.Weyer<-c("a.0","a.SMZ","a.Pine","a.Mixed","a.NoSMZ","a.PCA1","a.PCA2","a.YoungPreThin",
                "a.MidPreThin","a.PostThin","a.half",
                "b.0","b.pc1","b.pc2",

                "mu.a.0","mu.a.SMZ","mu.a.Pine","mu.a.Mixed","mu.a.NoSMZ","mu.a.PCA1",
                "mu.a.PCA2","mu.a.YoungPreThin","mu.a.MidPreThin","mu.a.PostThin","mu.a.half",
                "mu.b.0","mu.b.pc1","mu.b.pc2",

                "sig.a.0","sig.a.site","sig.a.SMZ","sig.a.Pine","sig.a.Mixed","sig.a.NoSMZ","sig.a.PCA1",
                "sig.a.PCA2","sig.a.YoungPreThin","sig.a.MidPreThin","sig.a.PostThin","sig.a.half",
                "sig.b.0","sig.b.pc1","sig.b.pc2",

                "SiteRichness","z", "zza.site", "zzmu.psi", "zzmu.p"
)

Weyer<-jags(data=data.Weyer,inits=inits.Weyer,parameters.to.save=params.Weyer,model.file=Weyer.group.occ,
            n.chains=3,n.iter=200,n.burnin=100,n.thin=5,
            DIC=TRUE, working.directory=NULL,
            refresh = 40, progress.bar = "text", digits=5)
```

Chapter 4:

Effects of forest harvesting on growth rates of stream salamanders

Jacquelyn C. Guzy[1], Kelly M. Halloran[1], Brian J. Halstead[2], Jessica A. Homyack[3], and John D. Willson[1]

[1]Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701
[2]Western Ecological Research Center, U.S. Geological Survey, Dixon, CA, 95620, USA
[3]Weyerhaeuser Company, 505 North Pearl Street, Centralia, WA 98531

Abstract

Timber harvesting can influence headwater streams by altering stream productivity, with subsequent cascading effects on the food web including predators such as stream salamanders. Currently, limited information exists on whether individual salamander growth rates change in response to timber harvesting. Examining growth may document potential sublethal effects of harvesting, compared to more typical endpoints documenting changes in abundance or body condition. To examine the effect of harvesting on growth of the Ouachita dusky salamander (*Desmognathus brimleyorum*), we used intensive capture-mark-recapture at three headwater streams embedded in intensely managed pine forests. Streams were located in west-central Arkansas and were surveyed from May 2014-October 2016 using a Before-After-Control-Impact (BACI) design. The pine stands surrounding two of the streams were harvested, with retention of a 14 and 21 m wide forested stream buffer on each side of the stream, congruent with forestry Best Management Practices. We assessed growth of post-metamorphic salamanders by fitting a hierarchical von Bertalanffy linear regression model of growth rate on SVL, modified from van Devender (1978). Newly-metamorphosed salamanders were 5.7 and 4.0 mm larger post-harvest compared to pre-harvest measurements at the two treatment sites. Using measurements from 914 individual *D. brimleyorum* recaptured between 1 and 6 times (total recaptures n=1229) we found that at the two harvested sites, there were higher growth rates of smaller (<45 mm; <2 yrs old) *D. brimleyorum* up to two years post-harvest, whereas larger salamanders (> 55 mm; >3 years) grew more slowly post-harvest. Our study is among the first to examine individual stream salamander responses to timber harvesting and we discuss several mechanisms that may be responsible for this pattern. Our results suggest retention of a riparian buffer (i.e., Streamside Management Zone) may have short term positive effects on juvenile stream salamanders, increasing growth

rates and thus potentially reducing predation risk and offsetting other potential negative sublethal effects associated with harvest.

Introduction

Managed forests provide important wildlife habitat and ecosystem services (Hansen et al. 1991, Miller et al. 2009, Demarais et al. 2017); thus it is important to understand how forest integrity can best be maintained during timber harvest. Periodically, forest management practices introduce disturbances from harvesting and thinning operations. Following canopy removal, forests typically have reduced leaf litter and coarse woody debris, changes in nutrient concentrations of soil and water, and increased light penetration resulting in higher soil temperatures and increased evaporation from the soil and understory (Likens et al. 1970, Blair and Crossley Jr 1988, Keenan and Kimmins 1993).

Headwater streams are strongly influenced by harvesting of the surrounding watershed (reviewed in (Webster et al. 1992)). The most evident direct effect of harvesting on forest streams is the removal of shading vegetation, altering stream microclimates (reviewed in Olson et al. 2007) and resulting in both increased average stream temperatures (Swift Jr and Messer 1971), and a reduction in allochthonous inputs (i.e., leaf litter;(Webster and Waide 1982). Consequently, following harvest, streams are less light-limited and filamentous green algae often increase in abundance (Lowe et al. 1986), increasing total primary production (Webster et al. 1983). Accompanying this shift in the stream energy base is often a switch in dominant benthic invertebrates (Gurtz and Wallace 1984, Wallace and Gurtz 1986, Wallace 1988) from shredders to scrapers and collectors that feed on algae (Webster et al. 1992, Wallace et al. 1997). Other potential effects of forest harvesting include short-term increases in stream flow with less evapotranspiration, high sediment delivery to streams, and alterations to nutrient processing (i.e., nitrogen and phosphorus loss; Webster et al. 1992).

Salamanders are often a primary vertebrate predator within headwater streams (Lowe and Bolger 2002, Johnson and Wallace 2005, Peterman et al. 2008). Stream salamanders are prominent consumers of both aquatic and terrestrial invertebrate detritivores (Southerland et al. 2004), and can attain extremely high densities and biomass within headwater streams (e.g., 11,294 salamanders/ha^{-1}; (Peterman et al. 2008). As such, they can exert direct and indirect biotic control of prey species and influence ecosystem processes along grazer and detrital pathways (reviewed in (Davic and Welsh 2004). These trophic associations may ultimately influence the breakdown of leaf litter and transfer of nutrients (Wyman 1998, Davic and Welsh 2004, Walker et al. 2018), and importantly, can be influenced by harvesting, particularly when allonchtonous inputs of leaf litter is reduced (Wallace et al. 1997, Johnson and Wallace 2005).

Numerous studies across North America report that salamander populations decline for a period of time after timber harvesting (e.g., (Petranka et al. 1994, Ash 1997, Herbeck and Larsen 1999, Reichenbach and Sattler 2007, Connette and Semlitsch 2015). However, recent research has suggested that forestry Best Management Practices (BMPs), specifically implementation of riparian buffers (referred to as Streamside Management Zones/SMZs in some U.S. regions; Lee et al. 2004) may ameliorate negative effects on salamander movement (Johnston and Frid 2002), abundance (Perkins and Hunter 2006, Peterman and Semlitsch 2009, Maigret et al. 2014, Halloran 2017), and species richness and occupancy (Guzy et al. 2019). Yet, it is unclear whether harvesting can affect fitness surrogates such as salamander growth and reproduction. Little research has examined salamander response to forestry activities at the individual level (but see (Chazal and Niewiarowski 1998, Cecala et al. 2014, Connette and Semlitsch 2015) and to our knowledge, none have examined changes in individual salamander growth rate as a response to timber harvesting, either for woodland or stream-associated salamanders. Although a few studies have explored the influence of forest management on endpoints such as body condition (Karraker and Welsh 2006, Homyack et al. 2011, Hocking et al. 2013), examining growth at the individual level is necessary examine alternative explanations for changes in body size such as size-biased mortality.

Measuring salamander growth as a potential response to harvest is particularly important because body size influences survival and fecundity, and thus contributes to the fitness of individuals in a population (Tilley 1968). Energetic requirements of salamanders may vary with differences in the thermal environment of harvested areas (Homyack et al. 2011), influencing metabolic rates and growth, and ultimately body size. Similarly, because stream salamander growth has been correlated with prey biomass (Johnson and Wallace 2005, Huntsman et al. 2011), changes in the stream invertebrate community from harvesting within the watershed may influence salamander growth and body size (e.g., Bumpers et al. 2017).

In this study, we used intensive capture-mark-recapture at three streams to examine the effect of harvesting on growth of a stream salamander species, the Ouachita dusky salamander (*Desmognathus brimleyorum*). To reduce the influence of stochastic differences among sites and years, we used a before-after control-impact (BACI) design, which allowed for comparisons within the same sites before and after harvest, as well as comparisons with a designated control site through time. Although our streams contained riparian buffers (SMZs), because of a potential for increased productivity resulting from canopy reduction or nutrient runoff, we predicted stream salamander growth rate would be faster immediately post-harvest relative to a control site.

Methods

Study Sites

This study was conducted in northeast Howard County, in west-central Arkansas, USA, within the southernmost subdivision of the Ouachita Mountains (Fig. 1), and occurred within even-aged loblolly pine (*Pinus taeda*) forest managed by Weyerhaeuser Company. To assess the influence of timber harvest on the stream-dwelling Ouachita dusky salamander (*Desmognathus brimleyorum*), we selected three 1st order, headwater streams based on similar size, morphology, and silvicultural history. All three sites were located within 16 km of each other in the Little Missouri River Watershed, with elevations ranging from 190 to 300m above sea level. Each stream drained a small watershed (0.41-1.15 km^2) within a mature (29-35 years old) loblolly pine (*P. taeda*) stand.

Study Design

We used a BACI study design to examine the effects of timber harvest on salamander body size. Specifically, we conducted intensive capture-mark-recapture of salamanders at one “Control” (unharvested) site and two before-after sites (hereafter “BA1” and “BA2”), that were clear-cut harvested during the study, with an SMZ retained along each stream. We conducted salamander surveys at the Control and BA1 sites from 2014 to 2016, during March, June, and October of each year; during each month, each site was sampled three times (approximately one week apart; Fig. 1). The same survey schedule was implemented for BA2, however surveys began one year later in March 2015. At each site, we established a 200 m stream transect at the most downstream section of each stream. The BA1 and BA2 sites were clear-cut harvested in Jan

2015 and Jan 2016, respectively, with a 28 m and a 42 m SMZ retained along the length of the stream (Fig. 1). In concordance with BMPs, some overstory pine trees were harvested from the SMZ of BA1to promote hardwood regeneration. The SMZ at BA2 along with the riparian forest surrounding the Control site were comprised of an oak-hickory (*Quercus* and *Carya* spp.) overstory with a cedar (*Juniperus virginana*) and holly (*Ilex opaca*) understory. The SMZ of the BA1 site was dominated by loblolly pine in the overstory and holly, musclewood (*Carpinus caroliniana*) and hophornbeam (*Ostrya virginiana*) in the understory. Based on 16 – 28 measures of canopy cover taken with a concave spherical densitometer (Lemmon 1956) in the center of each stream transect before and after harvest after leaf-out (i.e., May), canopy cover decreased by 18% at BA1 (100 vs. 82%) and by 24% (99 vs. 75%) at BA2 following harvesting, but remained constant at 98.9-100% at the Control site.

Field Methods

Each salamander survey began approximately one hour after sunset and consisted of a thorough visual search (i.e., turning over rocks and debris) of the streambed for the length of each 200m transect. Post-metamophic *Desmognathus brimleyorum* were captured using dip-nets and placed in separate containers and each individual's location was marked with a flag. The following day we processed captured salamanders in the lab by anesthetizing each individual with a solution of 1 g Orajel-20% Benzocaine/1 liter of de-chlorinated tap water (Cecala et al. 2007) and recording body metrics using a digital scale and calipers [i.e., mass (g), total length (mm), snout-vent length (SVL; mm)]. Following measurement, each newly captured individual was given a unique identification mark using a subcutaneous injection of visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA; Grant 2008). We ventrally marked individuals using a combination of 4 colors (pink, orange, blue, yellow) and 6 marking locations (posterior to each limb, and anterior to each hind limb) with a 0.5mL Micro-Fine insulin syringe (28-gauge/0.35mm). To ensure reliable identification, each salamander was marked at a minimum of two positions using at least two colors. Any recently metamorphosed individuals (less than a year since metamorphosis; < 45 mm SVL) were labeled as juveniles and were not given marks anterior to each hind limb, as we have observed the cutaneous layers in this region tend to be too thin to reliably hold marks in place. Salamanders were returned to their exact capture location within ~2 days after capture, but occasionally salamanders were held up to 5 days to avoid releasing during unusually high flow events. For more details on sampling see Halloran (2017).

Data Analysis

We assessed growth of post metamorphic *D. brimleyorum* by fitting a hierarchical linear regression model of growth rate (ΔSVL / Δt) on SVL, as assumed by the von Bertalanffy growth model (van Devender 1978). The final dataset excluded captures <21 days apart (within primary sampling intervals), as we assumed growth to be negligible within this time interval. We used the model of van Devender (1978), but expanded it by including random intercepts for site and year to account for spatial and temporal differences in growth rate, and a random intercept for individual salamanders to allow for differences in growth rate among salamanders. We further expanded the model to estimate the effect of harvest on growth rate using a binary indicator for harvest (0 = pre-harvest, 1 = post-harvest). To allow for a different effect of harvest on salamanders of different size classes, we included an interaction between SVL and harvest. We used vague priors for all model parameters: *normal(mean = 0, SD = 10)* for intercepts and coefficients and *half-Cauchy(scale = 1)* for all standard deviations. For growth intervals that spanned both pre-and post-harvest conditions, we specified the harvest covariate as missing, and gave the missing data a *Bernoulli(probability = 0.5)* prior. Similarly, for intervals that spanned multiple years, we integrated model results over the multiple years by drawing missing years from a categorical distribution with equal probability given to each year spanned by the interval between captures. To assess model fit, we used a posterior predictive check by simulating data under the model and calculating a Bayesian *P*-value using sum-of-squares for the observed and simulated data (Kéry 2010). We implemented the model in a Bayesian framework using the software Just Another Gibbs Sampler version 4.3.0 (JAGS; Plummer 2015) as called from R version 3.5.1 (R Core Team 2018) using the package 'jagsUI' (Kellner 2016). We sampled from the posterior distribution using 5 independent chains of 200,000 iterations each after a burn-in period of 50,000 iterations, and thinned chains by a factor of 10 to base inference on 100,000 samples from the posterior distribution. We used the Gelman and Rubin statistic (Gelman and Rubin 1992) and examination of history plots to assess convergence; we observed no evidence for lack of convergence (all $\hat{R} < 1.07$ and history plots appeared well-mixed with no trends). Unless indicated otherwise, posterior distributions are summarized as median (0.025 quantile – 0.975 quantile).

Results

We estimated salamander growth before and after clearcut timber harvest using measurements from 914 individual *D. brimleyorum* recaptured between 1 and 6 times (total recaptures n=1229). Based on raw data for June of each year, shortly after metamorphosis, mean body sizes of recently-metamorphosed *D. brimleyorum* were greater in all three post-harvest site-years, than in the five pre/control site-years (Fig. 2). On average, salamanders were 5.7 and 4.0 mm larger post-harvest at BA1 and BA2, respectively (Fig. 2).

The hierarchical linear model fit our growth data well, with a Bayesian *P*-value of 0.50. An interaction between harvest and SVL was supported (median $\beta_{\text{harvest} \times \text{SVL}} = -4.6 \times 10^{-4}$ [95% credible interval = -7.9×10^{-4} to -1.3×10^{-4}]), indicating that smaller salamanders (i.e., <45 mm) grew faster following harvest, whereas larger salamanders (i.e., >55 mm) grew more slowly (Fig. 3). Based on the model, a 30 mm SVL salamander at an average site in an average year prior to harvest grew 0.066 (-0.068 to 0.20) mm/d, and following harvest, grew 0.074 (-0.060 to 0.21) mm/d. Conversely, a 60 mm SVL salamander under the same conditions grew 0.031 (-0.10 to 0.17) mm/d prior to harvest, and following harvest grew 0.026 (-0.11 to 0.16) mm/d. Variation was similar among sites ($\sigma_{\text{site}} = 0.017$ [0.0047 to 0.23]) and years ($\sigma_{\text{year}} = 0.023$ [0.0066 to 0.31]), but much less among individual salamanders (0.0021 [1.3×10^{-4} – 0.0059]). Asymptotic size at the Control site was estimated to be 75 (72 to 79) mm, and asymptotic size at BA1 following harvest was estimated to be 66 (62 to 70) mm. Pre-harvest captures were too sparse to estimate asymptotic size at BA1, and asymptotic size estimates for BA2 were too large and imprecise to be considered reliable.

Discussion

We conducted a three-year capture-mark-recapture study examining growth of ~1,000 *D. brimleyorum*, before and after clearcut timber harvesting. Our study is among the first to examine stream salamander responses to timber harvesting at the individual level, an approach that is particularly notable given the important sublethal effects harvesting may have on salamander population dynamics. At the two harvested sites, we documented higher growth rates of smaller (<45 mm; <2 yrs old) *D. brimleyorum* within SMZs up to two years post-harvest, whereas larger salamanders (> 55 mm; >3 years) grew more slowly post-harvest. More specifically, model predictions indicated that 1-yr old salamanders (~30 mm SVL) grew an estimated ~0.008 mm/day faster post-harvest, whereas ~ 4-yr old salamanders (~60 mm SVL) grew an estimated ~0.005 mm/day faster before harvest. Increased growth rates of smaller salamanders (<2 yrs old) post-harvest may influence *D. brimleyorum* populations in several ways. Within and among *Desmognathus* species, body size and egg production are positively correlated, such that larger individuals are more fecund (Tilley 1968), a relationship common among salamanders (Salthe 1969, Kaplan and Salthe 1979). Salamanders with faster growth rates could reach sexual maturity earlier or have higher fecundity at first reproduction, which may have diverse but significant effects on individual fitness and emergent population dynamics (Tilley 1977, 1980, Bernardo 1993). Additionally, *Desmognathus* salamanders are territorial, prone to cannibalism, and their assemblages are often structured by competition and intraguild predation (Hairston Sr 1986, Camp and Lee 1996). Finally, increased growth rates may reduce predation risk, as many important predators of salamanders (e.g., fish, frogs, snakes, other salamanders) are gape-limited.

Several non-mutually exclusive factors may explain increased growth of smaller (i.e., younger) *D. brimleyorum* following harvest of the surrounding stand. In conjunction with faster juvenile growth rates post-harvest (Fig. 3), we found that average body size (SVL) of newly-metamorphosed salamanders in June were ~4-5 mm longer post-harvest compared to pre-harvest (Fig. 2), suggesting variation in growth is partially occurring during the larval stage. One mechanism known to affect larval salamander growth rates is density of conspecifics. Previous work has documented decreased larval growth when density, and thus competition for resources, is high (e.g., Morin et al. 1983, Petranka and Sih 1986, Semlitsch 1987). However, timber harvest did not have a negative effect on abundance or apparent survival of *D. brimleyorum* at either treatment site during the timeframe of our study (Halloran 2017). Thus, release from intraspecific competition is not likely to be the primary mechanism driving the differences in growth rate we observed.

Alternatively, a likely mechanism driving increased growth rates may be a shift in the quality, quantity, or composition of invertebrate prey available. At our treatment sites, canopy cover decreased ~20% post-harvest. Following overstory harvest there is typically an increase in light, stimulating primary production in streams (Webster et al. 1983), and thus increasing productivity of grazer macroinvertebrate assemblages that feed on algal growth (Murphy et al. 1981, Silsbee and Larson 1983, Duncan and Brusven 1985, Wallace and Gurtz 1986, Murphy 1998, Price et al. 2003). In headwater streams, scraper and collector–gatherer functional feeding groups (i.e., biofilm consumers) are typically higher in nutrient content than are shredder taxa, although this pattern is highly variable (Cross et al. 2003, Frost et al. 2006). Importantly, algae are the primary source of fatty acids in aquatic food webs, thus increases in biofilm consumers could lead to increased intake of essential fatty acids (Brett and Muller-Navarra 1997, Ballantyne et al. 2003) important for salamander growth (Fitzpatrick 1976). Additionally, chitin content of macroinvertebrates varies (Cauchie 2002), and prey may be assimilated differently depending on digestibility. Thus, it is possible that post-harvest conditions favor production of invertebrate prey that are easier to assimilate (i.e., more energy dense and/or easier to digest), contributing to increased salamander growth rates.

Increased invertebrate prey quantity may also be responsible for increased salamander growth rates post-harvest. Studies have shown that macroinvertebrate abundance and density increases immediately post-harvest (Kiffney et al. 2003, Haggerty et al. 2004, Wallace and Ely 2014), even at sites with riparian buffers (Kiffney et al. 2003). Local resource levels are a primary driver of growth in many populations, and greater prey availability has been linked to increased salamander growth in several studies (Tilley 1974, Bernardo 1994, Bernardo and Agosta 2003). Bumpers et al. (2017) documented increased *Desmognathus quadramaculatus* growth due to increased abundance of invertebrate prey, as a result of experimental enrichment of phosphorus in headwater streams. Following timber harvesting, the amount of dissolved nutrients leached from soil to the stream often increases until vegetation becomes reestablished (Swank 1988, Webster et al. 1992, Swank et al. 2001). Post-harvest application of fertilizer to newly planted stands may further increase nutrient inputs to streams (Binkley et al. 1999), although inclusion of riparian buffers can minimize inputs (Kastendick et al. 2012, Secoges et al. 2013). Thus, it is likely that nutrient enrichment was a least partially responsible for the effects we observed and there is potential for this effect to be magnified under management regimes that include fertilization of newly-planted timber stands.

Because salamanders are ectothermic, a possible mechanism driving increased growth rates post-harvest may be changes to metabolism as a result of increased air and water temperatures. Numerous studies have established that harvesting of riparian vegetation increases stream temperature (Johnson and Jones 2000, Herunter et al. 2004, Wilkerson et al. 2006). However, the magnitude of stream temperature response to harvest may vary with inclusion of riparian buffers. Riparian buffers at our treatment sites were 14 and 21 m wide, and studies of streams in British Columbia with similar buffer widths documented 1-4 °C increases in stream temperatures following harvest of the surrounding stand (Kiffney et al. 2003, Macdonald et al. 2003, Herunter et al. 2004). At streams with riparian buffers, increased stream temperatures following harvest have been observed to persist for 5 years (Macdonald et al. 2003). It is important to consider the potential biological consequences of even small changes in thermal regime, as temperature influences nearly every aspect of the physiology of ectotherms, including salamanders (Rome et al. 1992). Specifically, several temperature-sensitive processes are involved in salamander energy assimilation, including activity (Leclair et al. 2008), foraging (Moreno 1989), digestive rate (Feder et al. 1984), and assimilation efficiency (Bobka et al. 1981). While salamander energy assimilation has been shown to increase with increasing temperatures, it may also increase indirectly because of changes in other physiological processes (Clay and Gifford 2018). At higher temperatures, salamander digestive efficiency decreases and energetic demands increase (Homyack et al. 2010); thus, at warmer temperatures, salamanders may reduce foraging and mating, or trade-off growth or reproduction for increased maintenance costs (Homyack et al. 2011). However, within streams, potentially negative consequences of increased metabolic demands at warmer temperatures may be offset by benefits of consistent moisture availability during foraging (Feder and Londos 1984), facilitating increased digestive turnover and thus increased salamander growth. Additionally, warmer temperatures can influence seasonal activity of *Desmognathus* salamanders (Shealy 1975), resulting in a slightly extended activity season during cooler months, which may increase juvenile salamander growth rates following harvest.

The interaction between size (SVL) and *D. brimleyorum* growth rate was unexpected. Although our study was not designed to explicitly evaluate the mechanisms driving shifts in growth rates, we suggest potential mechanisms that might be responsible for apparently reduced adult growth rate post-harvest. Harvesting occurred at both treatment sites during January, and larval *D. brimleyorum* typically metamorphose during summer and enter torpor during winter (Trauth et al. 1990, Means 2005). Thus, most small salamanders at post-harvest sites during the timeframe of our study (1-2 years post-harvest) were new recruits immediately following harvesting, whereas large salamanders at post-harvest sites were >1 year old when harvesting occurred. Thus, slower growth rates of large salamanders post-harvest may have occurred because these individuals were disturbed by harvesting. Adult *Desmognathus quadramaculatus* defend a territory of refugia along riparian edges of the stream (Camp and Lee 1996), and likewise, adult *D. brimleyorum* are thought to be territorial (Means 2005). Additionally, a concurrent study of *D. brimleyorum* at our treatment sites documented increased within-stream movement after harvesting, which may indicate disturbance and/or increased energetic costs (Halloran 2017). Thus, harvesting of upland areas, even with a riparian buffer retained, may have disturbed typical adult behaviors, reducing growth rates. Conversely, new recruits may be less disturbed by harvesting as they have yet to establish a territory. For example, Camp and Lee (1996) found that juvenile (< 50 mm) *D. quadramaculatus* spent more time wandering streams, whereas adults remained in refugia. Alternatively, post-harvest resource pulses may initially favor production of smaller invertebrate prey that larvae and juvenile salamanders capitalize on, and which may take time to cascade through the food web and affect larger prey preferred by adults. Additionally, the interaction between juvenile and adult growth rate may be an artifact of the constraints of the von Bertalanffy growth model, which assumes a linear relationship between SVL and growth rate, and may be violated if harvesting disrupts the mean growth trajectory of salamanders. More sophisticated models and longer term dataset would be required to examine this possibility. Finally, the asymptotic size estimated by our models at the Control site (75 mm) was substantially larger than that of the BA1 following harvest (66 mm). As with most potential mechanisms we have outlined, determining if salamanders simply grow more slowly towards the same asymptotic size at BA1, or if they never get as large as individuals at the Control site would require longer-term studies. Addressing these potential mechanisms was beyond the scope of the study, however our results suggest that harvesting may have short term positive effects on stream salamanders, provided riparian buffers are maintained along the stream.

Conclusions

Our study is among the first to examine individual stream salamander responses to timber harvesting. We documented higher growth rates of smaller (<45 mm; <2 yrs old) *D. brimleyorum* up to two years post-harvest compared to pre-harvest, whereas larger salamanders (> 55 mm; >3 years) grew more slowly post-harvest compared to pre-harvest. Several mechanisms may be responsible for the pattern we observed, however given that timber harvesting did not have a negative effect on abundance or apparent survival (Halloran 2017), a release from intraspecific competition is not likely to be the primary mechanism driving this effect. Alternatively, juvenile salamanders may have different behavioral responses to harvesting or be able to better capitalize on post-harvest resource pulses resulting from a shift in the quality, quantity, or composition of invertebrate prey available. Additionally, changes to metabolism as a result of potentially increased air and water temperatures post-harvest may favor increased juvenile growth or result in a slightly extended activity season during cooler months. Addressing these potential mechanisms was beyond the scope of this study, however our results suggest that harvesting may have short-term positive effects on growth, and thus potentially reducing predation risk and other negative sublethal effects associated with harvest. However this conclusion is predicated on the fact that ~20 m riparian buffers (i.e., SMZs) were retained along each side of our streams. Forestry best management practices (BMP) for our study region recommend minimum buffers of 11-24 m (Arkansas Forestry Commission 2002) to protect water quality (Cristan et al. 2016). To develop more focused and efficient management approaches, future studies should seek to determine the mechanistic relationships driving growth rates post-harvest, which could include targeted studies of the invertebrate community before and after harvest in conjunction with examining salamander diets.

Acknowledgements

This study was funded by Weyerhaeuser Company, the National Council for Air and Stream Improvement, the Arkansas Science and Technology Authority, and the University of Arkansas. We thank Paula Szczerba and Shane Szczerba for logistical support during data collection, and Meredith Swartwout, Chelsea Kross, Jennifer Mortensen, Logan Estes, Mitchell Pruitt, Brittany Furtado, and Philip Vogrinc for assistance with data collection. We are grateful to Jennifer Mortensen and Teofil Nakov for assistance with data manipulation, and to Doug Leasure for advice on geospatial analyses. For input of project design and management we thank Michelle Evans-White, Dan Magoulick, Darren Miller, and T. Bently Wigley. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Arkansas Forestry Commission, A. 2002. Best Management Practices for Water Quality Protection.

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11:983-989.

Ballantyne, A. P., M. T. Brett, and D. E. Schindler. 2003. The importance of dietary phosphorus and highly unsaturated fatty acids for sockeye (*Oncorhynchus nerka*) growth in Lake Washington a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 60:12-22.

Bernardo, J. 1993. Determinants of maturation in animals. Trends in Ecology & Evolution 8:166-173.

Bernardo, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. The American Naturalist 143:14-38.

Bernardo, J. and S. J. Agosta. 2003. Determinants of clinal variation in life history of dusky salamanders (*Desmognathus ocoee*): prey abundance and ecological limits on foraging time restrict opportunities for larval growth. Journal of Zoology 259:411-421.

Binkley, D., H. Burnham, and H. L. Allen. 1999. Water quality impacts of forest fertilization with nitrogen and phosphorus. Forest Ecology and Management 121:191-213.

Blair, J. M. and D. Crossley Jr. 1988. Litter decomposition, nitrogen dynamics and litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. Journal of Applied Ecology:683-698.

Bobka, M. S., R. G. Jaeger, and D. C. McNaught. 1981. Temperature dependent assimilation efficiencies of two species of terrestrial salamanders. Copeia:417-421.

Brett, M. and D. Muller-Navarra. 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biology (United Kingdom).

Bumpers, P. M., A. D. Rosemond, J. C. Maerz, and J. P. Benstead. 2017. Experimental nutrient enrichment of forest streams increases energy flow to predators along greener food-web pathways. Freshwater Biology 62:1794-1805.

Camp, C. D. and T. P. Lee. 1996. Intraspecific spacing and interaction within a population of *Desmognathus quadramaculatus*. Copeia:78-84.

Cauchie, H.-M. 2002. Chitin production by arthropods in the hydrosphere. Hydrobiologia 470:63-95.

Cecala, K. K., W. H. Lowe, and J. C. Maerz. 2014. Riparian disturbance restricts in-stream movement of salamanders. Freshwater Biology 59:2354-2364.

Cecala, K. K., S. J. Price, and M. E. Dorcas. 2007. A comparison of the effectiveness of recommended doses of MS-222 (tricaine methanesulfonate) and Orajel®(benzocaine) for amphibian anesthesia. Herpetological Review 38:63.

Chazal, A. C. and P. H. Niewiarowski. 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. Ecological Applications 8:1133-1143.

Clay, T. A. and M. E. Gifford. 2018. Energy Assimilation in a Polymorphic Salamander, Plethodon angusticlavius. Journal of Herpetology 52:269-272.

Connette, G. M. and R. D. Semlitsch. 2015. A multistate mark–recapture approach to estimating survival of PIT-tagged salamanders following timber harvest. Journal of Applied Ecology 52:1316-1324.

Cristan, R., W. M. Aust, M. C. Bolding, S. M. Barrett, J. F. Munsell, and E. Schilling. 2016. Effectiveness of forestry best management practices in the United States: Literature review. Forest Ecology and Management 360:133-151.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. Bruce Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecology Letters 6:721-732.

Davic, R. D. and H. H. Welsh. 2004. On the ecological roles of salamanders. Annual Review of Ecology Evolution and Systematics 35:405-434.

Demarais, S., J. P. Verschuyl, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the US. Forest Ecology and Management 385:308-330.

Duncan, W. F. and M. A. Brusven. 1985. Benthic macroinvertebrates in logged and unlogged low-order southeast Alaskan streams. Freshwater Invertebrate Biology 4:125-132.

Feder, M. E., A. G. Gibbs, G. A. Griffith, and J. Tsuji. 1984. Thermal acclimation of metabolism in salamanders: Fact or artefact? Journal of Thermal Biology 9:255-260.

Feder, M. E. and P. L. Londos. 1984. Hydric constraints upon foraging in a terrestrial salamander, *Desmognathus ochrophaeus* (Amphibia: Plethodontidae). Oecologia 64:413-418.

Fitzpatrick, L. C. 1976. Life history patterns of storage and utilization of lipids for energy in amphibians. American Zoologist 16:725-732.

Frost, P. C., J. P. Benstead, W. F. Cross, H. Hillebrand, J. H. Larson, M. A. Xenopoulos, and T. Yoshida. 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. Ecology Letters 9:774-779.

Gelman, A. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457-472.

Grant, E. H. C. 2008. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. Journal of Wildlife Management 72:1247-1252.

Gurtz, M. E. and J. B. Wallace. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65:1556-1569.

Guzy, J. C., K. M. Halloran, J. A. Homyack, and J. D. Willson. 2019. Influence of riparian buffers and habitat characteristics on salamander assemblages in headwater streams within managed forests. Forest Ecology and Management 432:868-883.

Haggerty, S., D. Batzer, and C. Jackson. 2004. Macroinvertebrate response to logging in coastal headwater streams of Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 61:529-537.

Hairston Sr, N. G. 1986. Species packing in Desmognathus salamanders: experimental demonstration of predation and competition. American Naturalist:266-291.

Halloran, K. M. 2017. Population Dynamics of Ouachita Dusky Salamanders (*Desmognathus brimleyorum*) in a Managed Forest Landscape. Thesis. University of Arkansas.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41:382-392.

Herbeck, L. A. and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology 13:623-632.

Herunter, H., J. MacDonald, and E. MacIsaac. 2004. Effectiveness of variable-retention riparian buffers for maintaining thermal regimes, water chemistry, and benthic invertebrate communities of small headwater streams in central British Columbia. Pages 105-113 in Forest Land-fish Conference II—Ecosystem Stewardship through Collaboration, Proc. Forest-Land-Fish Conf. II.

Hocking, D. J., G. M. Connette, C. A. Conner, B. R. Scheffers, S. E. Pittman, W. E. Peterman, and R. D. Semlitsch. 2013. Effects of experimental forest management on a terrestrial, woodland salamander in Missouri. Forest Ecology and Management 287:32-39.

Homyack, J. A., C. A. Haas, and W. A. Hopkins. 2010. Influence of temperature and body mass on standard metabolic rate of eastern red-backed salamanders (*Plethodon cinereus*). Journal of Thermal Biology 35:143-146.

Homyack, J. A., C. A. Haas, and W. A. Hopkins. 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. The Journal of wildlife management 75:1267-1278.

Huntsman, B. M., M. P. Venarsky, J. P. Benstead, and A. D. Huryn. 2011. Effects of organic matter availability on the life history and production of a top vertebrate predator (Plethodontidae: *Gyrinophilus palleucus*) in two cave streams. Freshwater Biology 56:1746-1760.

Johnson, B. R. and J. B. Wallace. 2005. Bottom-up limitation of a stream salamander in a detritus-based food web. Canadian Journal of Fisheries and Aquatic Sciences 62:301-311.

Johnson, S. L. and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57:30-39.

Johnston, B. and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). Canadian journal of zoology 80:2170-2177.

Kaplan, R. H. and S. N. Salthe. 1979. The allometry of reproduction: an empirical view in salamanders. The American Naturalist 113:671-689.

Karraker, N. and H. Welsh. 2006. Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California. Biological Conservation 131:132-140.

Kastendick, D. N., E. K. Zenner, B. J. Palik, R. K. Kolka, and C. R. Blinn. 2012. Effects of harvesting on nitrogen and phosphorus availability in riparian management zone soils in Minnesota, USA. Canadian Journal of Forest Research 42:1784-1791.

Keenan, R. J. and J. Kimmins. 1993. The ecological effects of clear-cutting. Environmental Reviews 1:121-144.

Kellner, K. 2016. jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS'Analyses. Version 1.4. 2.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40:1060-1076.

Leclair, M. H., M. Levasseur, and R. Leclair Jr. 2008. Activity and reproductive cycles in northern populations of the Red-Backed Salamander, Plethodon cinereus. Journal of Herpetology 42:31-38.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165-180.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecological monographs 40:23-47.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

Lowe, W. H. and D. T. Bolger. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183-193.

Macdonald, J., E. MacIsaac, and H. Herunter. 2003. The effect of variable-retention riparian buffer zones on water temperatures in small headwater streams in sub-boreal forest ecosystems of British Columbia. Canadian Journal of Forest Research 33:1371-1382.

Maigret, T. A., J. J. Cox, D. R. Schneider, C. D. Barton, S. J. Price, and J. L. Larkin. 2014. Effects of timber harvest within streamside management zones on salamander populations in ephemeral streams of southeastern Kentucky. Forest Ecology and Management 324:46-51.

Means, D. B. 2005. Desmognathus brimleyorum Stejneger, 1895 Ouachita Dusky Salamander. Pages 701-703 in M. J. Lannoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley and Loss Angeles, California.

Miller, D. A., T. B. Wigley, and K. V. Miller. 2009. Managed forests and conservation of terrestrial biodiversity in the southern United States. Journal of Forestry 107:197-203.

Moreno, G. 1989. Behavioral and physiological differentiation between the color morphs of the salamander, Plethodon cinereus. Journal of Herpetology:335-341.

Morin, P. J., H. M. Wilbur, and R. N. Harris. 1983. Salamander predation and the structure of experimental communities: responses of Notophthalmus and microcrustacea. Ecology 64:1430-1436.

Murphy, M. L. 1998. Primary production. River ecology and management. Springer-Verlag, New York:144-168.

Murphy, M. L., C. P. Hawkins, and N. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American fisheries society 110:469-478.

Olson, D. H., P. D. Anderson, C. A. Frissell, H. H. Welsh Jr, and D. F. Bradford. 2007. Biodiversity management approaches for stream–riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. Forest Ecology and Management 246:81-107.

Perkins, D. W. and M. L. Hunter. 2006. Use of amphibians to define riparian zones of headwater streams. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 36:2124-2130.

Peterman, W. E., J. A. Crawford, and R. D. Semlitsch. 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). Freshwater Biology 53:347-357.

Peterman, W. E. and R. D. Semlitsch. 2009. Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. Forest Ecology and Management 257:8-14.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Petranka, J. W. and A. Sih. 1986. Environmental instability, competition, and density-dependent growth and survivorship of a stream-dwelling salamander. Ecology 67:729-736.

Plummer, M. 2015. JAGS Version 4.0. 0 User Manual. See https://sourceforge. net/projects/mcmc-jags/files/Manuals/4. x.

Price, K., A. Suski, J. McGarvie, B. Beasley, and J. S. Richardson. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. Canadian Journal of Forest Research 33:1416-1432.

R Core Team. 2018. R: A language and environment for statistical computing., Vienna, Austria.

Reichenbach, N. and P. Sattler. 2007. Effects of timbering on *Plethodon hubrichti* over twelve years. Journal of Herpetology 41:622-629.

Rome, L., E. D. Stevens, and H. John-Alder. 1992. The influence of temperature and thermal acclimation on physiological function. Environmental physiology of the amphibians:205-205.

Salthe, S. N. 1969. Reproductive modes and the number and sizes of ova in the urodeles. American Midland Naturalist:467-490.

Secoges, J. M., W. M. Aust, J. R. Seiler, C. A. Dolloff, and W. A. Lakel. 2013. Streamside management zones affect movement of silvicultural nitrogen and phosphorus fertilizers to Piedmont streams. Southern Journal of Applied Forestry 37:26-35.

Semlitsch, R. D. 1987. Density-dependent growth and fecundity in the paedomorphic salamander Ambystoma talpoideum. Ecology 68:1003-1008.

Shealy, R. M. 1975. Factors influencing activity in the salamanders *Desmognathus ochrophaeus* and *D. monticola* (Plethodontidae). Herpetologica:94-102.

Silsbee, D. G. and G. L. Larson. 1983. A comparison of streams in logged and unlogged areas of Great Smoky Mountains National Park. Hydrobiologia 102:99-111.

Southerland, M. T., R. E. Jung, D. P. Baxter, I. C. Chellman, G. Mercurio, and J. H. Vølstad. 2004. Stream salamanders as indicators of stream quality in Maryland, USA. Applied Herpetology 2:23-46.

Swank, W. T. 1988. Stream chemistry responses to disturbance. Pages 339-357 Forest Hydrology and Ecology at Coweeta. Springer.

Swank, W. T., J. Vose, and K. Elliott. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and Management 143:163-178.

Swift Jr, L. W. and J. B. Messer. 1971. Forest cuttings raise temperatures of small streams in the southern Appalachians. Journal of soil and water conservation 26:111-116.

Tilley, S. G. 1968. Size-fecundity relationships and their evolutionary implications in five desmognathine salamanders. Evolution 22:806-816.

Tilley, S. G. 1974. Structures and dynamics of populations of the salamander *Desmognathus ochrophaeus* Cope in different habitats. Ecology 55:808-817.

Tilley, S. G. 1977. Studies of life histories and reproduction in North American plethodontid salamanders. Pages 1-41 The reproductive biology of amphibians. Springer.

Tilley, S. G. 1980. Life histories and comparative demography of two salamander populations. Copeia:806-821.

Trauth, S. E., R. L. Cox Jr, B. P. Butterfield, D. A. Saugey, and W. E. Meshaka Jr. 1990. Reproductive phenophases and clutch characteristics of selected Arkansas amphibians. Journal of the Arkansas Academy of Science 44:107-113.

van Devender, R. W. 1978. Growth ecology of a tropical lizard, *Basiliscus basiliscus*. Ecology 59:1031-1038.

Walker, D. M., C. M. Murray, D. Talbert, P. Tinker, S. P. Graham, and T. W. Crowther. 2018. A salamander's top down effect on fungal communities in a detritivore ecosystem. FEMS microbiology ecology 94:fiy168.

Wallace, J. 1988. Aquatic invertebrate research. Pages 257-268 Forest hydrology and ecology at Coweeta. Springer.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Wallace, J. B. and D. Ely. 2014. Stream macroinvertebrate response to clearcut logging. Long-term response of a forest watershed ecosystem: Clearcutting in the southern Appalachians:177-193.

Wallace, J. B. and M. E. Gurtz. 1986. Response of Baetis mayflies (Ephemeroptera) to catchment logging. American Midland Naturalist:25-41.

Webster, J., S. Golladay, E. Benfield, J. Meyer, W. Swank, and J. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. River conservation and management 15:232-253.

Webster, J., M. Gurtz, J. Hains, J. Meyer, W. Swank, J. Waide, and J. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 Stream ecology. Springer.

Webster, J. R. and J. B. Waide. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331-344.

Wilkerson, E., J. M. Hagan, D. Siegel, and A. A. Whitman. 2006. The effectiveness of different buffer widths for protecting headwater stream temperature in Maine. Forest Science 52:221-231.

Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity and conservation 7:641-650.

Figures and Tables

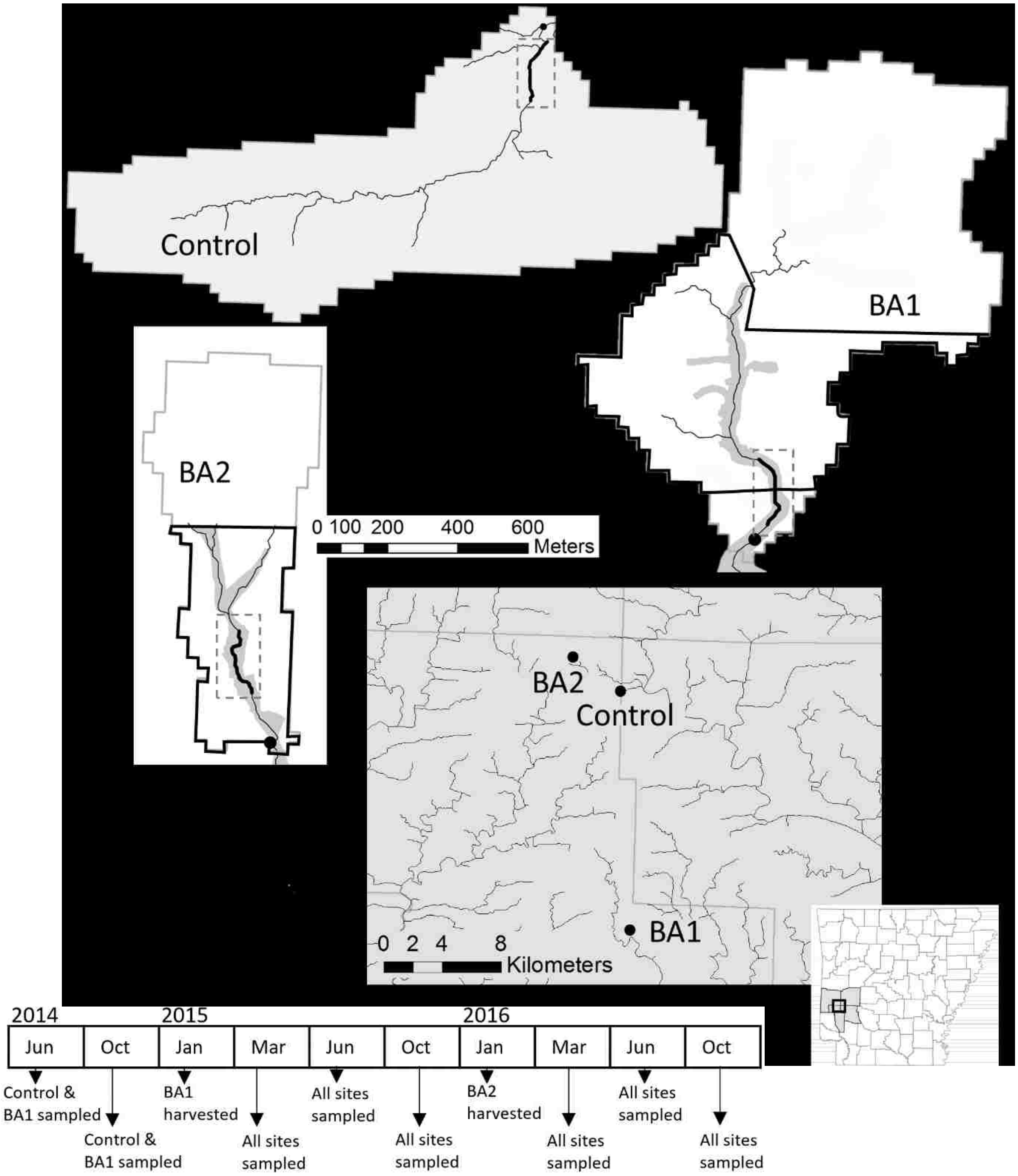


Figure 1. Location of study sites in northeast Howard County, Arkansas, USA and timeline of timber harvest and sampling schedule. Stream watersheds are outlined in grey. Approximate SMZs boundary for treatment sites (BA1, BA2) are shaded in grey. Bold black lines enclosed in a dashed box indicate the 200 m sampling transect where salamanders were sampled. At before-after sites, the harvested section of the watershed is outlined in black.

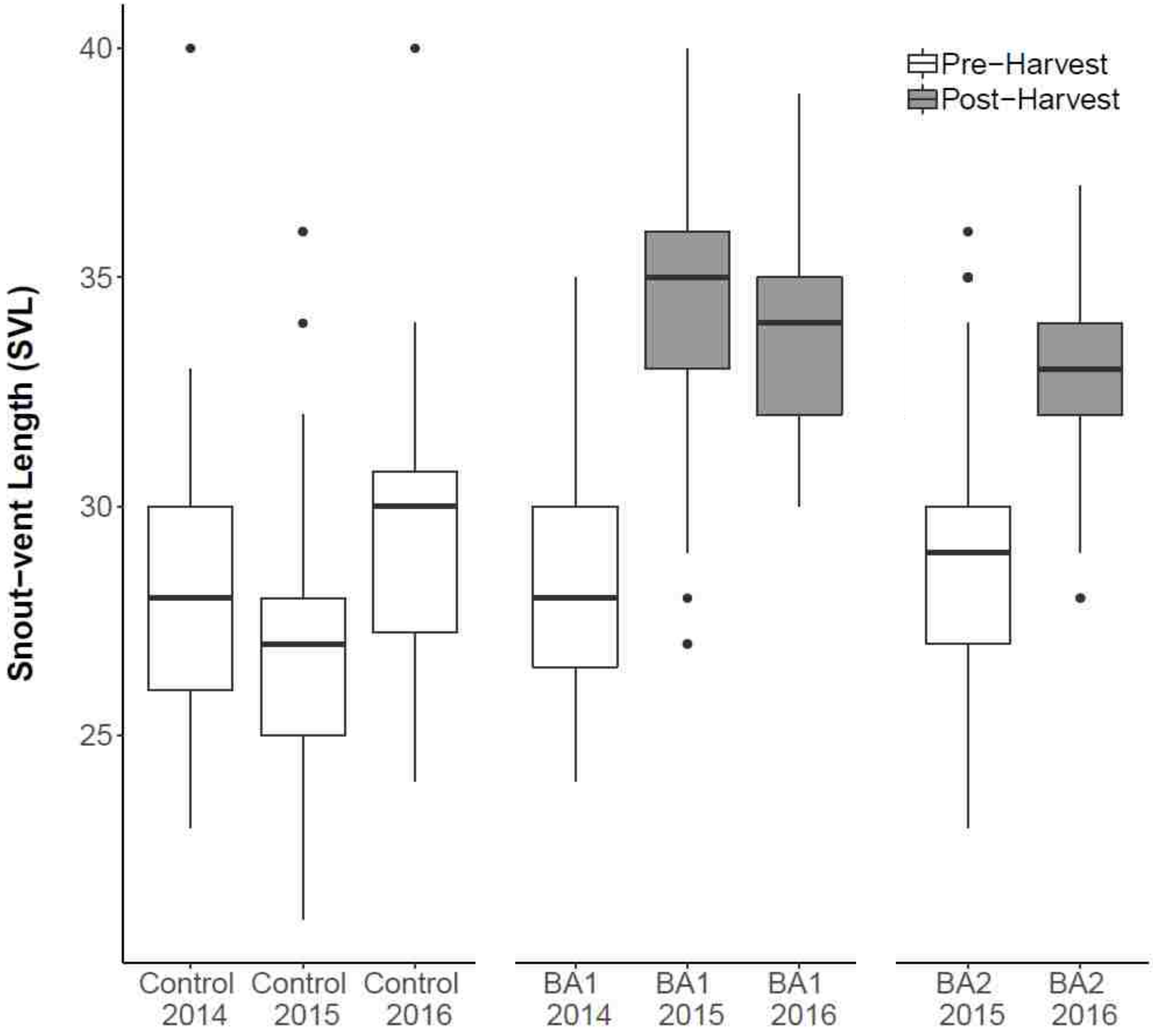
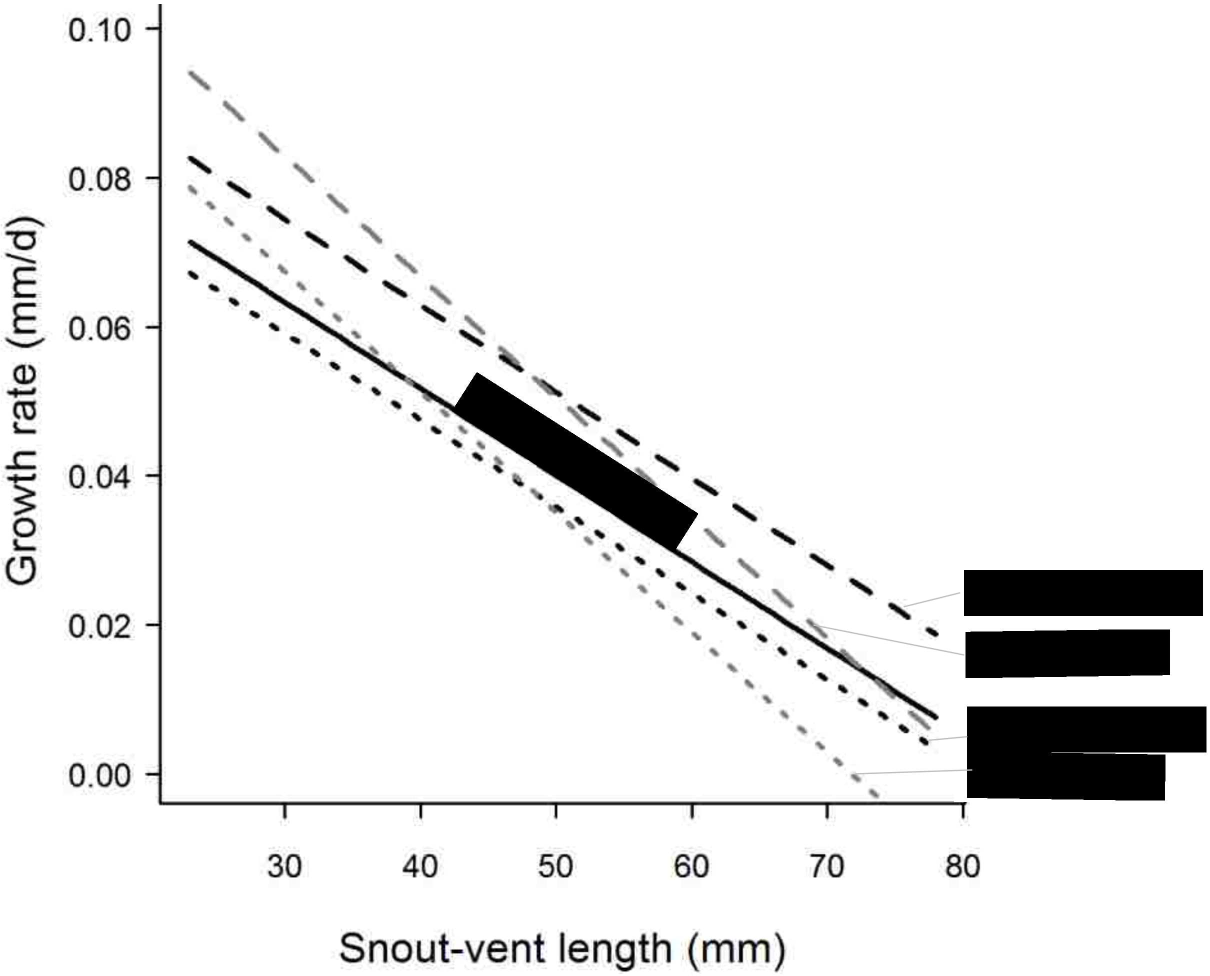


Figure 2. Pre- and post-harvest raw mean body size (snout-vent length) for recently-metamorphosed *Desmognathus brimleyorum* at control and treatment sites, each year. In each box plot, the horizontal bar is the median, boxes correspond to the first and third quartiles, and whiskers extend to the highest value within 1.5*interquartile range; data beyond the whiskers are plotted as points.



[redacted]

[redacted]

[redacted]

[redacted]

[redacted]

Figure 3. Relationship between growth rate and snout-vent length of *Desmognathus brimleyorum* for control and treatment sites, before and after harvest. The solid line represents the control site, and dashed and dotted lines represent individual treatment sites. Black lines are pre-harvest or no harvest, and gray lines are post-harvest. All lines represent posterior medians; credible intervals omitted for clarity.

Chapter 5:

Influence of Damming on Anuran Species Richness in Riparian Areas: A Test of the Serial Discontinuity Concept

Jacquelyn C. Guzy[1, 6], Evan A. Eskew[2, 3], Brian J. Halstead[4], Steven J. Price[5]

[1]Department of Biology, University of Arkansas, Fayetteville, AR, 72701

[2]Graduate Group in Ecology, University of California - Davis, Davis, CA, 95616

[3]EcoHealth Alliance, New York, NY, 10001

[4]Western Ecological Research Center, U.S. Geological Survey, Dixon, CA, 95620

[5]Department of Forestry and Natural Resources, University of Kentucky, Lexington, KY, 40546

Abstract

Almost all large rivers worldwide are fragmented by dams, and their impacts have been modelled using the serial discontinuity concept (SDC), a series of predictions regarding responses of key biotic and abiotic variables. We evaluated the effects of damming on anuran communities along a 245-km river corridor by conducting repeated, time-constrained anuran calling surveys at 42 locations along the Broad and Pacolet Rivers in South Carolina, USA. Using a hierarchical Bayesian analysis, we test the biodiversity prediction of the SDC (modified for floodplain rivers) by evaluating anuran occupancy and species diversity relative to dams and degree of urbanized land-use. The mean response of the anuran community indicated that occupancy and species richness were maximized when sites were farther downstream from dams. Sites at the farthest distances downstream of dams (47.5 km) had an estimated ~ 3 more species than those just below dams. Similarly, species-specific occupancy estimates showed a trend of higher occupancy downstream from dams. Using empirical estimation within the context of a 245-km river riparian landscape, our study supports SDC predictions for a meandering river. We demonstrate that with increasing distance downstream from dams, riparian anuran communities have higher species richness. Reduced species richness immediately downstream of dams is likely driven by alterations in flow regime that reduce or eliminate flows which sustain riparian wetlands that serve as anuran breeding habitat. Therefore, to maintain anuran biodiversity, we suggest that flow regulation should be managed to ensure water releases inundate riparian wetlands during amphibian breeding seasons and aseasonal releases, which can displace adults, larvae, and eggs, are avoided. These outcomes could be achieved by emulating pre-dam seasonal discharge data, mirroring discharge of an undammed tributary within the focal watershed, or by basing real-time flow releases on current environmental conditions.

Introduction

Abiotic and biotic conditions in uninterrupted river systems change predictably along a gradient from headwaters to downstream reaches as channel dimensions and canopy openings increase (i.e., the river continuum concept; Vannote, 1980). In natural rivers, this gradient is gradual (Ward & Stanford, 1983). However, almost all large rivers worldwide are fragmented by dams (Poff *et al*., 2007), which disrupt the natural continuum. To describe this phenomenon, Ward & Stanford (1983) proposed the serial discontinuity concept (SDC), which is a series of predictions regarding responses of biotic and abiotic variables to dams. These variables include thermal and flow regimes, water quality, substrate, periphyton, organic matter, and planktonic drift, and their recovery depends on dam size, position along the river, and tributary inputs (Ward & Stanford, 1983).

Specifically, the SDC predicts reduced invertebrate species diversity below impoundments because of the disruption to detrital transport, organic matter inputs, nutrient spiraling, and thermal regimes. The SDC also predicts a gradual increase in biodiversity downstream (Ward & Stanford, 1983), although recovery gradients of biota below dams are rarely examined (Ellis & Jones, 2013). The few studies that have examined recovery gradients indicate reduced species richness downstream of dams. More specifically, because of altered thermal conditions and lower habitat diversity, benthic macroinvertebrate diversity is reduced below dams irrespective of dam location and operation (see review by Ellis & Jones, 2013), and species richness recovers with increasing distance downstream of dams (Tiemann *et al*., 2004; Ellis & Jones, 2013). Similar patterns occur for freshwater mussels (Vaughn & Taylor, 1999; Randklev *et al*., 2015), fish (Gehrke *et al*., 1995; Gehrke & Harris, 2001; Cumming, 2004), and riparian vegetation (Merritt & Whol, 2006).

Because riparian zones are not as consistently subjected to flow regulation as rivers, the predictions of the SDC as it pertains to floodplains (e.g., Ward & Stanford, 1995a) have not been well tested (Kingsford, 2000). Headwater riparia are thought to have low invertebrate biodiversity because they are limited by low light, reduced nutrient levels, and a lack of spatio-temporal flow predictability. Flow regulation of headwaters is expected to further decrease biodiversity of riparian zones by reducing detrital transport (Ward & Stanford, 1995a). Mid-order river riparia are thought to have generally low biodiversity because of the overriding negative influence of bank instability; however, almost no data are available to suggest how river regulation influences biodiversity in mid-order reaches (Ward & Stanford, 1995a). The highest riparian biodiversity is predicted for meandering, high-order rivers (i.e., those with lotic, lentic, and semi-lotic habitats), and river regulation on meandering rivers is expected to be most detrimental to species richness because of floodplain isolation below impoundments, with biotic recovery occurring farther downstream of dams (Ward & Stanford, 1995a).

Floods and lateral connections to rivers are important drivers of ecological processes in riparian zones (i.e., the Flood Pulse Concept; Junk et al., 1989). These processes are disrupted by dams, which capture the flood pulse and subsequently reduce floodplain connectivity (Ward & Stanford, 1995a). Consequences of this disruption may be severe for amphibians because riparian wetlands represent critical habitat for many species (Semlitsch & Bodie, 2003). Thus, alteration of rivers through damming can influence semi-aquatic amphibian populations. For example, the foothill yellow-legged frog (*Rana boylii*) is more likely to be absent downstream of large dams than in free-flowing rivers (Kupferberg *et al*., 2012), and distance downstream from dams is positively correlated with both occupancy and abundance of several anuran species (Eskew *et al*., 2012). In addition, variability in seasonal flows along regulated rivers has been linked with high mortality of both *R. boylii* and the California red-legged frog (*R. draytonii*; Kupferberg *et al*., 2012). Riparian amphibian species distributions can be altered by flow regulation (Wassens & Maher, 2011) because they are sensitive to changes in temperature (Catenazzi & Kupferberg, 2013), unseasonable or strongly variable flows (Lind *et al*., 1996; Kupferberg *et al*., 2011), reduced downstream flows (Bateman *et al*., 2008), and breeding habitat loss (Lind *et al*., 1996). However, the predictions of the SDC have yet to be explicitly examined in relation to riparian amphibian communities which are those occupying habitat adjacent to main river channels.

In this study, we evaluated the effects of damming on amphibian communities along a 245-km river corridor in South Carolina, USA. Our objectives were to test the predictions of the SDC (modified for floodplain rivers; Ward & Stanford, 1995a) using anuran occupancy and species richness data. More specifically, we compare anuran distributions along the Broad and Pacolet Rivers relative to distance upstream and downstream of dams and also evaluate the effects of urbanized land-use surrounding each riparian wetland. While the modified SDC predicts alterations in invertebrate species richness as a result of damming, our focus is on anurans.

Methods

Study Sites

We used a geographic information system (ArcGIS 10.0; Environmental Systems Research Institute, Redlands, CA, USA), with 30-m resolution data layers from the National Wetland Inventory (http://www.fws.gov/wetlands/) and the 2006 National Land Cover Database (https://www.mrlc.gov/nlcd2006.php; Fry *et al.*, 2011) to select study wetlands located within the riparian zone of the Broad and Pacolet Rivers, two meandering, high-order rivers in the Piedmont region of north-central South Carolina (Fig. 1). We define the riparian zone to be any area adjacent to the main river channel or very nearby, but not within the main river bank, with semi-regular inundation from the river and its tributaries. After locating and ground-truthing approximately 200 riparian areas as close to the river channel as possible, we eliminated non-accessible sites and were left with 80 potential study locations. We then generated a circular buffer (1-km radius) around each site to delineate the distance encompassing the majority of core terrestrial habitat used by most anuran species (Semlitsch & Bodie, 2003). Our final 42 study sites were selected on the basis of spatial independence (i.e., non-overlapping 1-km radius circular buffers).

We used aerial photos taken in 2006 to visually identify sixteen dams within our study reach (Fig. 1). On the Broad River, we identified nine dams (seven used for hydroelectricity, one as a coal plant cooling reservoir, and one textile mill relic), and on the Pacolet River we identified seven dams (two for water reservoirs and five originally used in mills). Although the biophysical impacts of a dam vary according to its size and type, we considered the effects of all dams in our analyses because even small dams can influence amphibians (Kirchberg *et al.*, 2016), and in preliminary analyses where small dams were removed, our results did not change. Tracing the centerline of the river, we quantified the distance upstream and downstream from each survey site to the nearest dam using the linear referencing tool in ArcGIS. We used the National Land Cover Database (Fry *et al.*, 2011) in ArcGIS to determine percent of urban land cover (i.e., “Developed” land cover classes with low, medium, or high intensity designations) in the 1-km buffer zone around each site. Use of buffer zones resulted in quantification of urbanization not only in the riparian zone but also in the nearby upland habitats, which are important for anuran species (Semlitsch & Bodie, 2003). In addition, we used a digital elevation model (1:24,000–scale; 30-m resolution) obtained from the U.S. Geological Survey to calculate differences in mean elevation (within a 50-m buffer) between each study wetland and the nearest corresponding bank-full height of the main river channel. Finally, using ArcGIS, we summarized the number of tributaries intersecting the Broad or Pacolet Rivers for each site. More specifically, we quantified the number of tributaries accumulated between each site and its nearest upstream dam. For simplicity, each tributary intersection with the river was counted as "1" regardless of the number of branches feeding the tributary, and we used a Spearman rank correlation in Program R (2.14.0; R Development Core Team, 2015) to establish a relationship between distance downstream of dams and the number of tributaries.

Data Collection

We sampled each site nine times using manual calling surveys (Dorcas *et al*., 2010) to document all species of calling anurans. Surveys lasted for five minutes and were conducted by two experienced anuran surveyors listening independently, recording all species heard, and reconciling any differences before leaving the site. Provided multiple surveys per site and season are conducted, as in our study, surveys of this duration are sufficient for detecting breeding anurans during a given survey occasion (Gooch *et al*., 2006). All surveys were conducted between 1845 and 0130 during seasons corresponding with the peak breeding windows for species in our study: spring 2010 (April 13-May 8), summer 2010 (June 8-24), and winter 2011 (Feb 21-March 24). Each site was surveyed three times within each calling window (5-18 days apart), for a total of nine surveys.

Data Analysis

We used a hierarchical Bayesian model to estimate anuran species richness and species-specific occupancy responses to three site-specific covariates (distance downstream from dam, distance upstream from dam, and percent urbanization) and a survey-specific covariate (day of year). More specifically, we implemented the species richness model used by Hunt *et al*. (2013)

as modified from Zipkin *et al*. (2009). This hierarchical approach treated species-specific mean occupancy and responses to covariates as originating from an assemblage-level (i.e., all anuran species together) distribution and thereby estimated both species-specific and assemblage-level responses in the same model (Dorazio & Royle, 2005; Zipkin *et al*., 2009). Our analysis of species richness accounted for imperfect detection of individual species; we therefore did not assume all species were present at every site or that non-detection represented species absence (Dorazio & Royle, 2005). See Hunt *et al*. (2013) for a detailed description of this model.

We used the following equations to relate species-specific coefficients (α and β values) to occupancy and detection probabilities (Ψ_{ij} and Θ_{ijk}, respectively) to our model:

$$\text{logit}\ (\Psi_{ij}) = u_i + \alpha 1_i\, downdistance_j + \alpha 2_i\, updistance_j + \alpha 3_i\, percenturban_j$$

$$\text{logit}\ (\Theta_{ijk}) = v_i + \beta 1_i\, cumulativeday_{jk} + \beta 2_i\, cumulativeday^2{}_{jk},$$

where *i* references species, *j* references sites, *k* references surveys, *downdistance* was a site's distance downstream from the nearest dam, *updistance* was a site's distance upstream from the nearest dam, *percenturban* was the percent of a site's buffer zone containing urban land use, and *cumulativeday* was defined as days since January 1st, 2010. We also included $cumulativeday^2$ because anuran species have distinct seasonal calling windows such that a non-linear trend in detection might be expected (Guzy *et al*., 2014). All covariates were standardized by converting them to z-scores prior to analysis, and data for the Broad and Pacolet Rivers were combined for inference along a 245-km river corridor.

The model contained the following parameters, specific to each species: u_i, $\alpha 1_i$, $\alpha 2_i$, $\alpha 3_i$, v_i, $\beta 1_i$, and $\beta 2_i$. A final component of the model estimated community summaries (designated with μ), assuming that the species-specific parameters were random effects, each governed by a community-level hyper-parameter. For instance, $\alpha 1_i \sim N\ (\mu_{\alpha 1}, \sigma_{\alpha 1})$, where $\mu_{\alpha 1}$ is the mean community response (across species) to *downdistance* and $\sigma_{\alpha1}$ is the standard deviation in $\alpha1$ across species (Kéry *et al*., 2009). Because some sites were closer together relative to others, we tested for spatial autocorrelation in our model and found no effect of latitude or longitude on species richness or occupancy and therefore excluded these covariates from our modeling framework.

Our model used uninformative priors for the hyper-parameters (i.e., U(-5, 5) for α and β, U(0, 10) for σ, and U(-10, 10) for μ parameters), and species-specific model coefficients were truncated at ± 5 from μ to avoid traps. The mean and standard deviation of the model coefficients were calculated, along with the 2.5 and 97.5 percentiles of the posterior distribution, which represent a 95% Bayesian credible interval (CI). We inferred significance for continuous covariates when CIs did not contain zero. Species-specific occupancy and detection probabilities were derived using the inverse logit transformation. 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 from 0.5 to 47.5 km downstream of dams at each model iteration to generate a posterior predictive distribution for species richness as a function of distance downstream of dams.

We organized our data in program R (2.14.0; R Development Core Team, 2015) and executed data analysis in the software program WinBUGS (Lunn *et al*., 2000) using R2WinBUGS (Sturtz *et al*., 2005). The model was run on three independent chains of 300,000 iterations each, after a burn-in period of 30,000 iterations. Output was thinned by a factor of three, so inference was based upon 300,000 samples from the stationary posterior distribution. Evidence for lack of convergence was assessed by examining history plots and the Gelman and

Rubin statistic (Gelman & Rubin, 1992); we found no evidence for lack of convergence (Gelman and Rubin statistic < 1.02 for all monitored parameters).

Results

Site Characteristics

Our study sites were 0.05 – 47.51 km downstream from the nearest dam (mean = 13.47, SD = 13.55) and 0.30 – 50.69 km upstream from the nearest dam (mean = 16.61, SD = 14.01). Urban land cover in the 1-km radius buffer surrounding sites was 0 – 49.33% (mean = 9.97, SD = 12.48). Study sites were 0 – 550 m from the edge of the river channel (mean = 95.54, SD = 127.81) and 2.06 – 20.47 river-km from each other (mean = 6.42, SD = 4.01). The difference in elevation between our wetlands and the bank-full height of the river channel ranged from -9.77 – 29.69 m (mean = 10.13, SD = 10.19). Among our study sites, the number of tributaries increased farther downstream of dams, and this correlation was highly significant (Spearman's $r_s = 0.98$, $n = 42$, $p = < 0.01$).

Anuran Detections

We observed 13 anuran species among all sites (Table 1), and each species' distribution encompasses our entire study area of north-central South Carolina, and more broadly, much of the southeastern United States (Powell *et al*., 2016). Raw counts of anuran richness per site ranged from two to 12 species. Our median model-estimated number of species per site ranged from 5 species (95% CI 3 to 8) to 13 species (95% CI 12 to 13). Our model indicated variable occupancy among species, with mean estimated occupancy probabilities ranging from 0.44 (95% CI 0.25 to 0.69) for *Lithobates sphenocephalus* to 0.96 (95% CI 0.86 to 0.99) for *Anaxyrus fowleri* (Table 1). Mean estimated species detection probabilities were also highly variable (Table 1).

Community-Level Summary

When all anurans were considered together, mean response to distance downstream from dam ($\mu_{\alpha 1}$) was positive with a probability of 0.967 (mean parameter estimate: 0.56; 95% CI -0.02 to 1.27; Table 2), indicating that anurans occurred more frequently farther downstream from dams. Individual species' responses to the downstream covariate varied somewhat in magnitude as indicated by the across-species standard deviation ($\sigma_{\alpha 1} = 0.79$), which was larger than the corresponding mean ($\mu_{\alpha 1}$) covariate estimate (Table 2). Thus, our model indicated that the mean occupancy response to increasing distance downstream from dams was positive but not consistent across species.

The anuran response to $\mu_{\alpha 2}$, distance upstream from dam, was very close to zero (mean parameter estimate: -0.04; 95% CI -0.38 to 0.31), and the response to $\mu_{\alpha 3}$, percent urbanization, was negative with a probability of 0.87 (-1.43; 95% CI -3.69 to 1.10; Table 2), suggesting anurans exhibited essentially no response to upstream distance from dams and occurred less frequently at more urbanized locations.

The community response to detection covariates ($\mu_{\beta 1}$, cumulative day linear term, and $\mu_{\beta 2}$, cumulative day squared term) indicated a weak response (mean parameter estimates: 0.77 (95% CI -0.68 to 2.24) and -1.85 (95% CI -3.75 to 0.18), respectively; Table 2) as both contained positive and negative values in the 95% CI, reflecting uncertainty in the mean community responses. This weak response to cumulative day is not unexpected considering the species we observed have different calling windows (Guzy *et al.*, 2014). Furthermore, there was considerable variation among species' responses to these detection covariates (Table 2; $\sigma_{\beta 1} = 2.24$, $\sigma_{\beta 2} = 3.13$).

Occupancy and Species Richness Responses to Downstream Distance from Dam

We observed a positive mean occupancy response across anuran species to increased distance downstream from nearest dam (Fig. 2). Mean estimated occupancy across species increased farther downstream from dams, varying from 0.62 (95% CI 0.36 to 0.83) at a distance of 0.05 km downstream from a dam to 0.90 (95% CI 0.66 to 0.99; Fig. 2) at a distance of 47.5 km downstream from a dam. We observed consistent, positive estimates of species-specific responses to the distance downstream covariate (Fig. 3). Similarly, median predicted species richness increased farther downstream from dams, varying from 8 (95% predictive interval 4 to 11) species at a distance of 0.05 km downstream from a dam to 11 (95% predictive interval 8 to 13; Fig. 4) species 47.5 km downstream from a dam.

Discussion

At the spatial extent of our study, which included 42 sites, 16 dams, and approximately 245 km of river, we found a strong downstream effect of damming on riparian anurans, with estimated anuran species richness increasing from 8 species just below impoundments up to 11 species 47.5 km downstream of dams. The threshold length required to achieve maximum species richness was ~ 40 km. Our results agree with the general predictions of the floodplain-modified SDC (i.e., species richness is reduced immediately downstream of dams and increases with distance downstream of dams). These findings suggest that river stretches immediately downstream of dams may not provide suitable habitat for some anuran species.

For anurans in our system, the most important consequence of damming is likely its tendency to isolate the river channel from its floodplain. In riparian zones, because of varying water levels, the availability of amphibian breeding habitat is variable from year to year (e.g., Lind *et al*., 1996). Riparian wetlands are sustained by interactive pathways, including sediment and nutrient deposition occurring during seasonal inundation, when flood pulses form a moving shoreline across the floodplain (Ward & Stanford, 1995b). During these flood pulses, rivers flood their banks, facilitating high levels of aquatic productivity and enhancing connectivity. However, flow regulation by dams reduces connectivity and flood peaks such that river reaches downstream from dams have reduced lateral water flows (Ward & Stanford, 1995b; Kingsford 2000), which may result in a reduction in area or elimination of riparian-zone wetlands that provide critical breeding habitat for anurans. During years when flow is lower than average, as in our study, the disconnection of the floodplain from the river is further exacerbated. For example, one study found that toad abundance along a regulated river was low except during the year a flood pulse was released from a local dam, reconnecting riparian-zone breeding habitats (Bateman *et al.*, 2008). These water releases are beneficial when timed to occur during anuran breeding seasons, and importantly, provide the greatest benefit to anurans when they mimic natural patterns of daily, seasonal, and annual variation in river flow (Kupferberg *et al.*, 2012).

The greatest reductions in connectivity by river regulation are expected to occur in meandering rivers, such as the Broad River, where a multitude of dynamic interactive pathways link the river channel to the riparian habitat (Ward & Stanford, 1995b). Because there are no undammed mid- to high-order rivers in the Piedmont region of the USA, data on reference conditions (i.e., anuran species richness of undammed rivers) are unavailable; thus we cannot provide information on anuran recovery gradients in our study system. However, we do provide evidence for a strong downstream damming effect, with species richness peaking 47.5 km downstream of dams. At this downstream distance, tributaries and lateral connections to the floodplain may begin to accumulate, restoring flow and sediment transport (Ward & Stanford, 1995b) such that the riparian habitats become more diverse (i.e., extensive vegetation along the river's edge, isolated pools, and ephemeral wetlands). Although not measured in our study, we suggest that increases in habitat heterogeneity facilitate increases in anuran richness downstream of dams. For example, floodplains facilitate the creation and maintenance of a variety of waterbodies with varying degrees of connectivity to the main river channel (Ward and Stanford, 1995b) that are favorable for amphibians (Indermaur *et al*., 2010). This diversity of waterbodies is particularly important for anurans because they vary in their breeding habitat requirements and are influenced by wetland depth, vegetation structure, canopy cover, and amount of woody debris (e.g., Grant *et al*., 2015). Perhaps most importantly, some species breed in wetlands while others utilize the riparian edge of the river channel (Peterman *et al*., 2014). Such a degree of habitat variability generally does not occur immediately downstream of dams.

Increases in river-floodplain connectivity can be driven by an increase in the number of tributaries farther downstream of dams, which reset ecological conditions toward natural or unregulated conditions (Stanford & Ward, 2001). Among our study sites, the number of tributaries increased farther downstream of dams. Tributaries support important ecological functions (e.g., they supply water, sediment, and organic matter) and provide unique habitats to support amphibians (Rice *et al*., 2008). For example, tributaries may be exploited by mobile species (Power & Dietrich, 2002), such as *R. boylii*, a species that spends much of its time in tributary streams but uses the river-tributary confluence and main stem rivers primarily for breeding (Kupferberg, 1996).

Additionally, riparian anuran communities immediately downstream of dams can be negatively influenced by disruption of the predictable annual flood-drought cycles with which they evolved (Bunn & Arthington, 2002; Lytle & Poff, 2004). Hydrologic alteration was associated with decreases in the distribution and abundance of *R. boylii* and *R. draytonii*, likely in response to disruption of the seasonal synchrony between stable low-flow conditions and reproduction (Kupferberg *et al*., 2012). Reproduction in many taxonomic groups is timed to avoid flow fluctuations in rivers with seasonally predictable flooding. However, immediately downstream of dams, the potential for anurans to adjust reproductive behaviors may be constrained by a lack of environmental cues. Seasonal cues (e.g., day length, temperature) that trigger migration, and in-stream cues (e.g., stream depth, velocity) that influence oviposition site-selection (Kupferberg, 1996; Grabowski & Isely, 2007) can become decoupled from the conditions offspring may experience, with the result that there may be no indication of a water release or drawdown prior to its occurrence. For example, if a threshold temperature or water level is required before frogs can initiate breeding and these conditions occur just prior to a high-flow release, egg masses or larvae are likely to be lost (Lind *et al*., 1996).

In a concurrent study of the same 13 species examined here, Eskew *et al*. (2012) found that occupancy of two anuran species (*Acris crepitans* and *Lithobates sphenocephalus*) increased with increasing distance downstream of dams, and a similar pattern was observed for abundance of six species. Our main objective was to test the SDC through the examination of species richness, which allowed us to incorporate all species into the analysis. We observed increased anuran species richness farther downstream from dams. Species least influenced by downstream distance from dams included two toad species (*Anaxyrus fowleri* and *A. americanus*) along with *L. catesbeianus*, *Gastrophryne carolinensis*, and *Hyla chrysoscelis*, species that may be considered less reliant on a natural flow regime and the variety of floodplain wetlands it supports. These two toad species are very terrestrial compared to the rest of our anuran assemblage and can use more permanent waterbodies for reproduction (Lannoo 2005; Table 1). Similarly, while *H. chrysoscelis* and *G. carolinensis* generally use more ephemeral waterbodies for reproduction (Table 1), they will often breed in marginal habitats such as roadside ditches and retention ponds (Dorcas and Gibbons, 2008) or at the edges of permanent lentic habitats (Lannoo 2005). *Lithobates catesbeianus* breeds in permanently inundated aquatic sites that are relatively unaffected by flow alteration (Fuller *et al*., 2011), which may explain why their response was not as striking as other anurans in our study. Conversely, several species (i.e., *Acris crepitans*, *Anaxyrus terrestris*, *H. cinerea*, *Pseudacris crucifer*, *P. feriarum*, *L. clamitans*, *L. palustris*, *L. sphenocephalus*) were relatively sensitive to increasing distance downstream of dams, and these species tend to prefer ephemeral, relatively shallow breeding sites that hold enough water to host emergent aquatic vegetation but exclude fish predators (Butterfield *et al*., 2005; Gray *et al*., 2005; Lannoo 2005; Moriarty & Lannoo, 2005; Table 1). These specific requirements are less likely to occur in riparian zones that have reduced flooding frequency, particularly if the floodplain does not experience a strong enough hydrological connection to the river to sustain ephemeral water bodies. However, moving farther downstream of dams might allow tributaries to begin accumulating, thereby increasing habitat available for ephemeral breeders.

Urbanization is a pervasive source of habitat degradation that threatens anuran species (Knutson *et al*., 1999; Gibbs *et al*., 2005; Hamer & McDonnell, 2008; Guzy *et al*., 2012). In a review of 32 urban studies investigating 40% of North American anuran species, Scheffers and Paszkowski (2012) found that amphibians as a whole respond negatively to urbanization, although responses may differ by species (e.g., Rubbo & Kiesecker, 2005; Guzy *et al.*, 2012). Because urban wetlands tend to have less surrounding forest and longer hydroperiods that support fish predators, anuran species richness and abundance is often reduced, with the exclusion of ephemeral forest breeders (Rubbo & Kiesecker, 2005; Gagné & Fahrig, 2007) or species requiring forested uplands (Pillsbury & Miller, 2008). Urban watersheds alter microhabitats and facilitate the spread of exotic species that change prey communities and potentially outcompete native anurans (Riley *et al.*, 2005). Furthermore, the negative effects of urbanization can be exacerbated in high-traffic locations (Pellet *et al.*, 2004; Bee & Swanson 2007). However, anuran species associated with riparian zones can persist even in urbanized areas (Dorcas & Gibbons, 2008) if natural habitat buffers are present (Hamer & McDonnell, 2010; Price *et al*., 2014) and connectivity with terrestrial habitat is maintained (McCarthy & Lathrop, 2011). Our results are consistent with previous research (Scheffers & Paszkowski, 2012) and suggest that anuran occupancy decreases when there is more urbanization surrounding study sites; however, our estimated mean community response to urbanization parameter distribution also included non-trivial support for positive values (95% CI -3.69 to 1.10). Variable anuran occupancy responses may have diluted the community response to urbanization. In addition, the urbanization response might have been poorly estimated relative to the influence of dams because the anuran community has had less time to be affected by urbanization pressure (Grummer & Leaché, 2017). In our study, dams were constructed in the 1800's and early 1900's, whereas significant urbanization pressure has only existed in recent decades. Finally, many of our sites were located along a State Scenic River, and our most urbanized study site only contained 49.3% urban land use, so our findings may not apply in landscapes with greater urbanization.

Caveats and Limitations

We observed a strong relationship between increasing distance downstream of dams and anuran species richness, perhaps driven by impairment of flood plain inundation by flow regulation. However, downstream distance is likely a proxy measurement correlated with various structural or hydrological changes that accumulate farther downstream of dams (e.g., tributary accumulation; Ward & Stanford, 1995b), and because we cannot provide insight into specific mechanisms, it is important for natural resource managers to apply our findings cautiously. For example, changes in water temperature and chemistry, sediment accumulation, and channel incision might occur along a gradient downstream of dams, driven in part by peak stream-flow discharge, dam height, hydraulic residence time of impoundments, and type of dam operation (Ligon *et al*., 1995; Collier *et al*., 1996; Pringle *et al*., 2000; Poff & Hart, 2002). Therefore, determining connectivity of a river and its floodplain wetlands would benefit from information on daily discharge volume for each dam, in combination with measurements of overbank flows, rainfall, and consideration of structural components such as river gradient, width, and floodplain area.

Management Recommendations

Our study supports SDC predictions for a meandering river and expands the SDC to include the riparian landscape. Distance downstream from dams is an important factor influencing anuran species richness, a pattern previously documented in fish (Cumming, 2004), riparian vegetation (Merritt & Whol, 2006), and invertebrates (Ellis & Jones, 2013). Sites at the farthest distances downstream of dams (~ 50 km) had an estimated ~ 3 more species than those just below dams, a finding that is important for understanding ecological relationships in regulated rivers. Managing flows to ensure that riparian zones are inundated during amphibian winter and summer breeding seasons would likely benefit riparian amphibian communities. Such management will also increase connectivity of the riparian zone to the river channel, resulting in increased habitat heterogeneity that will benefit both aquatic and semi-aquatic animals. Furthermore, avoiding aseasonal releases, which can displace adults, larvae, and/or eggs, would also benefit riparian amphibian communities. This could be achieved by using pre-dam seasonal discharge data to identify an average discharge rate for each season, matching the discharge from an undammed tributary within the focal watershed to discharge below dams, and most importantly, basing real-time alterations to flow releases on current environmental conditions such as increasing flow releases during current rain events (Lind *et al.*, 1996). In addition, future studies should seek to elucidate mechanisms driving the patterns we observed, including the interactions between dams and number/size of tributaries and flow variation, as these may be important drivers structuring anuran assemblages along regulated rivers.

Acknowledgements

M. Dorcas was instrumental in the execution of this study. We thank L. Witczak, C. Williams, A. Domske, D. Millican, M. Kern, C. Oldham, R. Bauer, C. Ruder, and B. Abbuhl for field assistance. G. Vaughan, S. Bennett, B. Perry, and V. Vejdani assisted with logistics. Funding was provided by the Duke Endowment through the Davidson Research Initiative, the Davidson College Department of Biology, and the Broad River Mitigation Trust Fund administered through the South Carolina Department of Natural Resources. We thank three anonymous reviewers for comments that improved this manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is contribution 609 of the U.S. Geological Survey Amphibian Research and Monitoring Initiative. This work is supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, McIntire-Stennis project number 1001968.

Literature Cited

Bateman, H.L., Harner M.J., & Chung-MacCoubrey, A. (2008) Abundance and reproduction of toads (*Bufo*) along a regulated river in the southwestern United States: importance of flooding in riparian ecosystems. *Journal of Arid Environments*, **72**, 1613-1619.

Bee, M.A., & Swanson, E.M. (2006) Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, **74**, 1765-1776.

Bunn, S.E., & Arthington, A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492-507.

Butterfield, B.P., Lannoo, M.J., & Nanjappa, P. (2005) *Pseudacris crucifer*. In: *Amphibian Declines: The Conservation Status of United States Species* (Ed. M. Lannoo) pp. 472-474. University of California Press, Berkeley, California.

Catenazzi, A., & Kupferberg, S.J. (2013) The importance of thermal conditions to recruitment success in stream-breeding frog populations distributed across a productivity gradient. *Biological Conservation*, **168**, 40-48.

Collier, M., R. H. Webb, & J. C. Schmidt. (1996) Dams and rivers: Primer on the downstream effects of dams. Reston (VA): US Geological Survey. Circular no. 1126

Cumming, G.S. (2004) The impact of low-head dams on fish species richness in Wisconsin, USA. *Ecological Applications*, **14**, 1495-1506.

Davic, R.D., & Welsh, H.H. Jr. (2004) On the ecological roles of salamanders. *Annual Review of Ecology Evolution and Systematics*, **35**, 405–434.

Dorazio, R.M., & Royle, J.A. (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, **100**, 389-398.

Dorcas, M.E., & Gibbons, J.W. (2008) *Frogs and Toads of the Southeast*. The University of Georgia Press, Athens, Georgia.

Dorcas, M.E., Price, S.J., Walls, S.C., & Barichivich, W.J. (2010) Auditory monitoring of anuran populations. In: *Amphibian Ecology and Conservation: A Handbook of Techniques* (Ed. C.K. Dodd, Jr.), pp. 281-298. Oxford University Press, Oxford, United Kingdom.

Ellis, L.E., & Jones, N.E. (2013) Longitudinal trends in regulated rivers: a review and synthesis within the context of the serial discontinuity concept. *Environmental Reviews*, **21**, 136-148.

Eskew, E.A., Price, S.J., & Dorcas, M.E. (2012) Effects of river-flow regulation on anuran occupancy and abundance in riparian zones. *Conservation Biology*, **26**, 504-512.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., and Wickham, J., (2011). Completion of the 2006 National Land Cover Database for the Conterminous United States, PE&RS, Vol. 77(9):858-864.

Fuller, T.E., Pope, K.L., Ashton, D.T., & Welsh, H.H. Jr. (2011) Linking the distribution of an invasive amphibian (*Rana catesbeiana*) to habitat conditions in a managed river system in northern California. *Restoration Ecology*, **19**, 204–213.

Gagné, S.A., & Fahrig, L. (2007) Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. *Landscape Ecology*, **22**, 205-215.

Gehrke, P.C., & Harris, J.H. (2001) Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regulated Rivers: Research and Management*, **17**, 369-391.

Gehrke, P.C., Brown, P., Schiller, C.B., Moffatt, D.B., & Bruce, A.M. (1995) River regulation and fish communities in the Murray-Darling river system, Australia. *Regulated Rivers: Research & Management*, **11**, 363-375.

Gelman, A., & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457-472.

Gibbons, J.W., Winne, C.T., Scott, D.E., Willson, J.D., Glaudas, X., & Andrews, K.M. (2006) Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. *Conservation Biology*, **20**, 1457–1465.

Gibbs, J.P., Whiteleather, K.K., & Schueler, F.W. (2005) Changes in frog and toad populations over 30 years in New York state. *Ecological Applications*, **15**, 1148–1157.

Gooch, M.M., Heupel, A.M., Price, S.J., & Dorcas, M.E. (2006) The effects of survey protocol on detection probabilities and site occupancy estimates of summer breeding anurans. *Applied Herpetology*, **3**, 129-142.

Grabowski, T.B., & Isely, J.J. (2007) Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist*, **6**, 471–478.

Grant, T.J., Otis, D.L., & Koford, R.R. (2015). Short-term anuran community dynamics in the Missouri River floodplain following an historic flood. *Ecosphere*, **6**, 1-16.

Gray, R.H., Brown, L.E., & Blackburn, L. (2005) *Acris crepitans*. In: *Amphibian declines: the conservation status of United States species*. (Ed. M. Lannoo), pp. 441–443, University of California Press, Berkeley, California.

Grummer, J.A., & Leaché, A.D. (2017). Do dams also stop frogs? Assessing population connectivity of coastal tailed frogs (*Ascaphus truei*) in the North Cascades National Park Service complex. *Conservation Genetics*, **18**, 439-451.

Guzy, J.C., McCoy, E.D., Deyle, A.C., Gonzalez, S.M., Halstead, N., & Mushinsky, H.R. (2012) Urbanization interferes with the use of amphibians as indicators of ecological integrity of wetlands. *Journal of Applied Ecology*, **49**, 941-952.

Guzy, J.C., Price, S.J., & Dorcas, M.E. (2014) Using multiple methods to assess detection probabilities of riparian-zone anurans: implications for monitoring. *Wildlife Research*, **41**, 243-257.

Hamer, A.J., & McDonnell, M.J. (2008) Amphibian ecology and conservation in the urbanising world: a review. *Biological Conservation*, **141**, 2432-2449.

Hamer, A.J., & McDonnell, M.J. (2010) The response of herpetofauna to urbanization: inferring patterns of persistence from wildlife databases. *Austral Ecology*, **35**, 568-580.

Hunt, S.D., Guzy, J.C., Price, S.J., Halstead, B.J., Eskew, E.A., & Dorcas, M.E. (2013) Responses of riparian reptile communities to damming and urbanization. *Biological Conservation*, **157**, 277-284.

Indermaur, L., Schmidt, B.R., Tockner, K., & Schaub, M. (2010) Spatial variation in abiotic and biotic factors in a floodplain determine anuran body size and growth rate at metamorphosis. *Oecologia*, **163**, 637–649.

Junk, W.J., Bayley, P.B., & Sparks, R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **106**, 110-127.

Kéry, M., Royle, J.A., Plattner, M., & Dorazio, R.M. (2009) Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, **90**, 1279-1290.

Kingsford, R.T. (2000). Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology*, **25**, 109-127.

Kirchberg, J., Cecala, K.K., Price, S.J., White, E.M., & Haskell, D.G. (2016). Evaluating the impacts of small impoundments on stream salamanders. A*quatic Conservation: Marine and Freshwater Ecosystems*, **26**, 1197-1206.

Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., & Lannoo, M.J. (1999) Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. *Conservation Biology*, **13**, 1437–1446.

Kupferberg, S.J. 1996. Hydrologic and geomorphic factors affecting reproduction of the foothill yellow-legged frog (*Rana boylii*). *Ecological Applications*, **6**, 1332–1344.

Kupferberg, S.J., Lind, A.J., Thill, V., & Yarnell, S.M. (2011) Water velocity tolerance in tadpoles of the foothill yellow-legged frog (*Rana boylii*): swimming performance, growth, and survival. *Copeia*, **2011**, 141-152.

Kupferberg, S.J., Palen, W.J., Lind, A.J., Bobzien, S., Catenazzi, A., Drennan, J.O.E., *et al*. (2012) Effects of flow regimes altered by dams on survival, population declines, and range-wide losses of California River-breeding frogs. *Conservation Biology*, **26**, 513-524.

Lannoo, M. 2005. Amphibian Declines: The Conservation Status of United States Species. University of California Press. Berkeley, CA.

Lind, A.J., Welsh, H.H., Jr., & Wilson, R.A. (1996) The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in Northwestern California. *Herpetological Review*, **27**, 62-66.

Ligon, F.K., Dietrich, W.E., & Trush, W.J. (1995) Downstream ecological effects of dams. *BioScience*, **45**, 183–192

Lunn, D.J., Thomas, A., Best, N., & Spiegelhalter, D. (2000) WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325-337.

Lytle, D.A., & Poff, N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, **19**, 94-100.

McCarthy, K., & Lathrop, R. G. (2011) Stormwater basins of the New Jersey coastal plain: subsidies or sinks for frogs and toads? *Urban Ecosystems*, **14**, 395-413.

Merritt, D.M., & Wohl, E.E. (2006) Plant dispersal along rivers fragmented by dams. *River Research and Applications*, **22**, 1-26.

Moriarty, E., & Lannoo, M.J. (2005) *Pseudacris triseriata* complex. In: *Amphibian Declines: The Conservation Status of United States Species*. (Ed. M. Lannoo), pp. 485-488, University of California Press, Berkeley, California.

Pellet, J., Guisan, A., & Perrin, N. (2004) A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. *Conservation Biology*, **18**, 1599-1606.

Peterman, W.E., Anderson, T.L., Drake, D.L., Ousterhout, B.H., & Semlitsch, R.D. (2014) Maximizing pond biodiversity across the landscape: a case study of larval Ambystomatid salamanders. *Animal Conservation*, **17**, 275-285.

Pillsbury, F.C., & Miller, J.R. (2008) Habitat and landscape characteristics underlying anuran community structure along an urban–rural gradient. *Ecological Applications*, **18**, 1107-1118.

Poff, N. L., & Hart, D. D. (2002) How dams vary and why it matters for the emerging science of dam removal. *BioScience*, **52**, 659-668.

Poff, N.L., Olden, J.D., Merritt, D.M., & Pepin, D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States*, **104**, 5732-5737.

Powell, R., Conant, R., & Collins, J.T (2016) A field guide to reptiles & amphibians: eastern and central North America. Houghton Mifflin Harcourt.

Power, M.E., & Dietrich, W.E. (2002) Food webs in river networks. *Ecological Research*, **17**, 451-471.

Price, S.J., Snodgrass, J.L., & Dorcas, M.E. (2014) Managing aquatic habitats for wildlife in urban areas. In: *Urban Wildlife Science: Theory and Practice*. (Eds R. McCleery, C. Moorman, & N. Peterson), pp 361-388, Springer, USA.

Pringle, C. M., M. C. Freeman, & B. J. Freeman. (2000) Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical–temperate comparisons. *BioScience*, **50**, 807–823

R Development Core Team (2015) R: a language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Randklev, C.R., Ford, N., Wolverton, S., Kennedy, J.H., Robertson, C., Mayes, K., *et al*. (2015) The influence of stream discontinuity and life history strategy on mussel community structure: a case study from the Sabine River, Texas. *Hydrobiologia*, **770**, 1-19.

Rice, S.P., Kiffney, P., Greene, C., & Pess, G.R. (2008) The ecological importance of tributaries and confluences. *River Confluences, Tributaries and the Fluvial Network* (eds S. Rice, A. Roy & B. Rhoads), pp. 209–242. John Wiley & Sons Ltd., West Sussex, England.

Riley, S.D., Busteed, G.T, Kats, L.B., Vandergon, T.L., Lee, L.S., Dagit, R.G., Kerby, J.L., Fisher, R.N., & Sauvajot, R.M. (2005) Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. *Conservation Biology*, **19**, 1894-1907.

Rubbo, M.J., & Kiesecker, J.M. (2005) Amphibian breeding distribution in an urbanized landscape. *Conservation Biology*, **19**, 504-511.

Scheffers, B.R., & Paszkowski, C. A. (2012) The effects of urbanization on North American amphibian species: identifying new directions for urban conservation. *Urban Ecosystems*, **15**, 133-147.

Semlitsch, R.D., & Bodie, J.R. (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology*, **17**, 1219-1228.

Stanford, J.A., & Ward, J.V. (2001) Revisiting the serial discontinuity concept. *River Research and Applications*, **17**, 303-310.

Sturtz, S., Ligges, U., & Gelman, A.E. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software*, **12**, 1-16.

Tiemann, J.S., Gillette, D.P., Wildhaber, M.L., & Edds, D.R. (2004) Effects of lowhead dams on riffle-dwelling fishes and macroinvertebrates in a midwestern river. *Transactions of the American Fisheries Society*, **133**, 705-717.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., & Cushing, C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.

Vaughn, C.C., & Taylor, C.M. (1999) Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology*, **13**, 912–920.

Ward, J.V., & Stanford, J.A. (1983) The serial discontinuity concept of lotic ecosystems. *Dynamics of Lotic Ecosystems*, **10**, 29-42.

Ward, J.V., & Stanford, J.A. (1995a) The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research & Management*, **10**, 159-168.

Ward, J.V., & Stanford, J.A. (1995b) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management*, **11**, 105-119.

Wassens, S., & Maher, M. (2011) River regulation influences the composition and distribution of inland frog communities. *River Research and Applications*, **27**, 238-246.

Zipkin, E.F., Dewan, A., & Royle, J.A. (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modeling. *Journal of Applied Ecology*, **46**, 815–822.

Figures and Tables

Table 1. Summary of species observed within riparian zones of the Broad and Pacolet Rivers, South Carolina, USA and their predominant breeding habitat (Lannoo, 2005). Model-estimated occupancy and detection probabilities, calculated at mean values of upstream distance from dam, downstream distance from dam, percent urbanization, and cumulative day, are included along with 95% credible intervals for each estimate.

	Occupancy Probability			Detection Probability			General Breeding Habitat (Lannoo, 2005)	
Species	Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI	Predominant Hydroperiod	Preferred Waterbodies may include:
Acris crepitans	0.53	0.34	0.73	0.81	0.34	0.96	Permanent or Ephemeral	Lakes, ponds, wetlands, ditches, potholes, floodplains, flooded pastures, canals, river backwaters, sloughs, streams
Anaxyrus americanus	0.83	0.56	0.98	0.01	0.00	0.25		
Anaxyrus fowleri	0.96	0.86	0.99	0.89	0.61	0.97		
Anaxyrus terrestris	0.58	0.15	0.97	0.06	0.00	0.62		
Gastrophryne carolinensis	0.83	0.44	0.98	0.43	0.08	0.81	Ephemeral	Meadows, marshes, bottomland swamps, vernal pools, flooded pastures, ditches, sloughs, ponds
Hyla chrysoscelis	0.91	0.75	0.99	0.64	0.20	0.90		
Hyla cinerea	0.60	0.40	0.78	0.89	0.64	0.96		
Pseudacris crucifer	0.86	0.68	0.96	0.01	0.00	0.02		
Pseudacris feriarum	0.87	0.72	0.96	0.07	0.00	0.56		
Lithobates catesbeianus	0.53	0.36	0.70	0.61	0.15	0.92	Permanent	Lakes, streamsides, and permanent wetlands
Lithobates clamitans	0.61	0.39	0.82	0.80	0.38	0.94		
Lithobates palustris	0.82	0.36	0.99	0.00	0.00	0.20	Permanent or Ephemeral	Ponds, pools, floodplain wetlands, marshes, streamsides
Lithobates sphenocephalus	0.45	0.25	0.69	0.04	0.00	0.58	Ephemeral	Shallow, non-flowing waterbodies

Table 2. Summary of hyper-parameters for occupancy (α) and detection (β) covariates for anurans within riparian zones of the Broad and Pacolet Rivers, South Carolina, USA. The symbol μ indicates a mean community response, while σ indicates the standard deviation in the response to the covariate across species.

	Community level hyper-parameter	Mean	Standard Deviation	Lower 95% CI	Upper 95% CI
$\mu_{\alpha 1}$	Downstream from dam	0.56	0.33	-0.02	1.27
$\sigma_{\alpha 1}$	Downstream from dam	0.79	0.36	0.20	1.63
$\mu_{\alpha 2}$	Upstream from dam	-0.04	0.18	-0.39	0.31
$\sigma_{\alpha 2}$	Upstream from dam	0.21	0.18	0.01	0.66
$\mu_{\alpha 3}$	Percent Urban	-1.43	1.23	-3.67	1.09
$\sigma_{\alpha 3}$	Percent Urban	1.34	0.92	0.06	3.43
$\mu_{\beta 1}$	Day of Year (linear term)	0.79	0.74	-0.66	2.25
$\sigma_{\beta 1}$	Day of Year (linear term)	2.25	0.65	1.25	3.79
$\mu_{\beta 2}$	Day of Year (squared term)	-1.87	0.98	-3.75	0.14
$\sigma_{\beta 2}$	Day of Year (squared term)	3.12	0.83	1.90	5.12

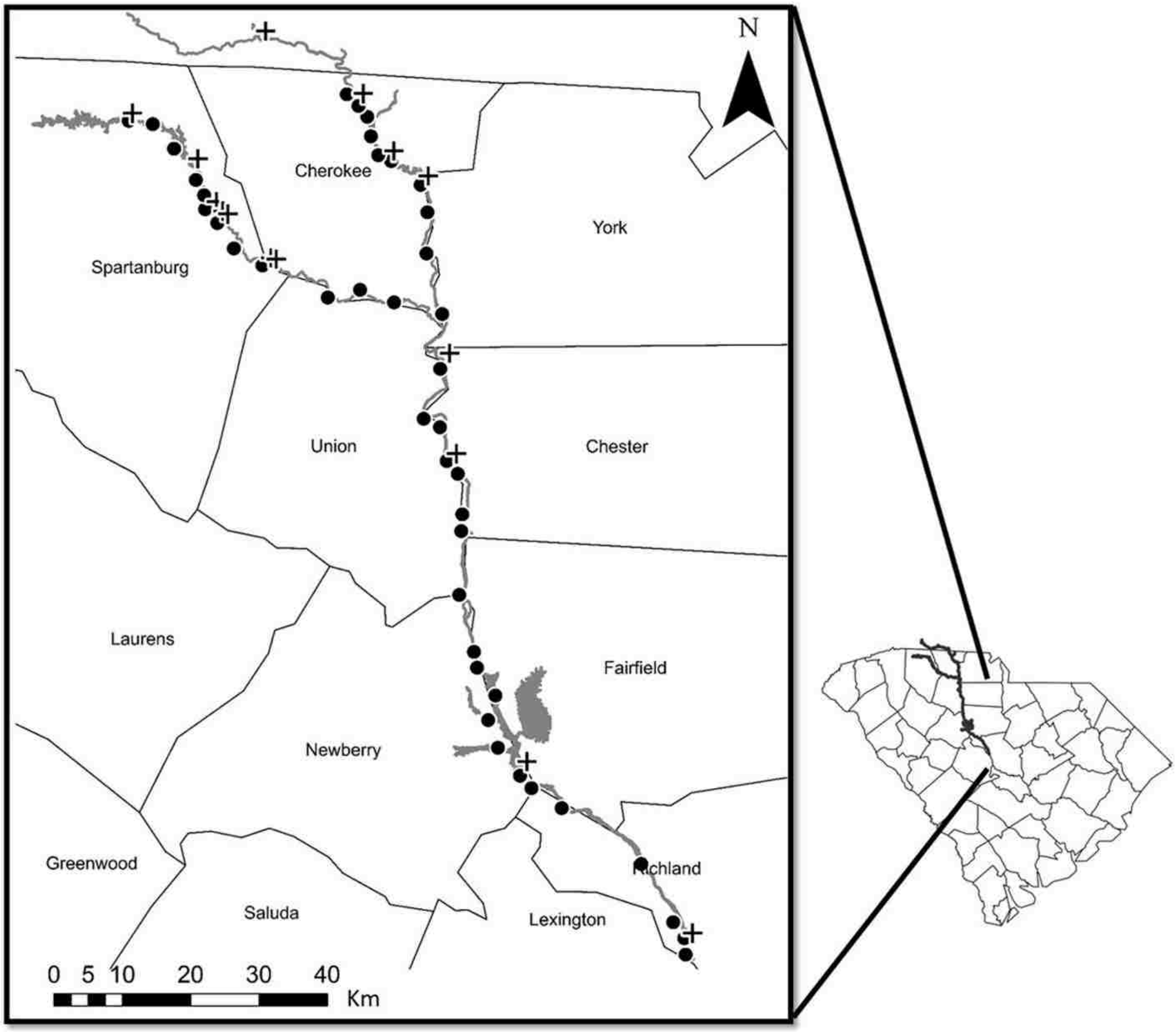


Figure 1. Locations of each anuran study site along both the Pacolet (upper left fork) and Broad Rivers in South Carolina, USA. County boundaries are delineated on the South Carolina outline and are labeled on the inset map. Study sites are shown as black circles, and locations of dams are shown as black crosses. Some of the crosses are obscured because of the proximity of the dams and the scale of the study area. For clarity, the final dam is located downstream of the southernmost site and is not depicted.

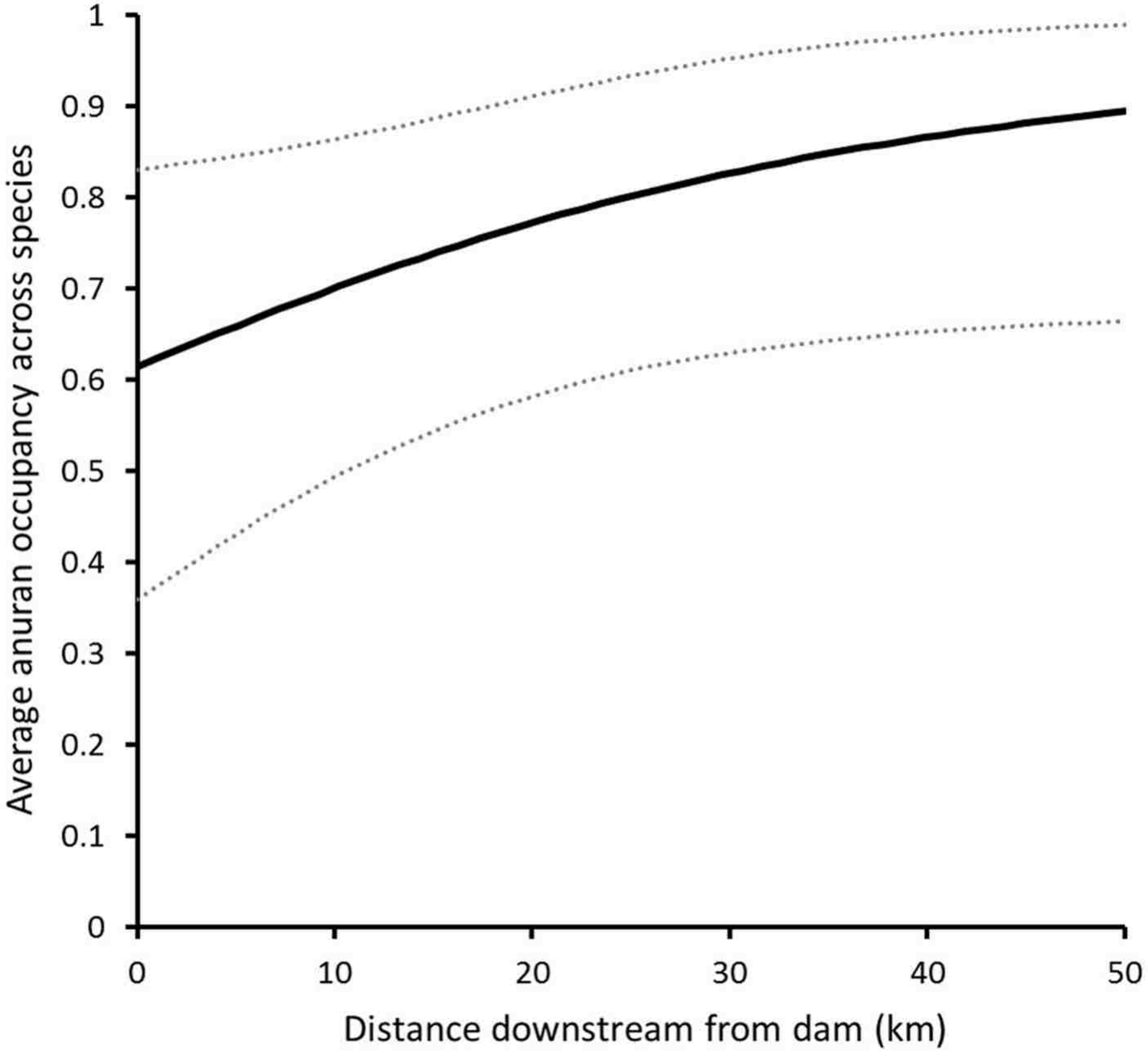


Figure 2. Relationship between mean anuran occupancy probability and distance downstream from a dam in the Broad and Pacolet Rivers, South Carolina, USA. Solid line represents the posterior mean community response and dashed lines represent a 95% credible interval. Occupancy probabilities were calculated at mean values of upstream distance from dam and percent urbanization.

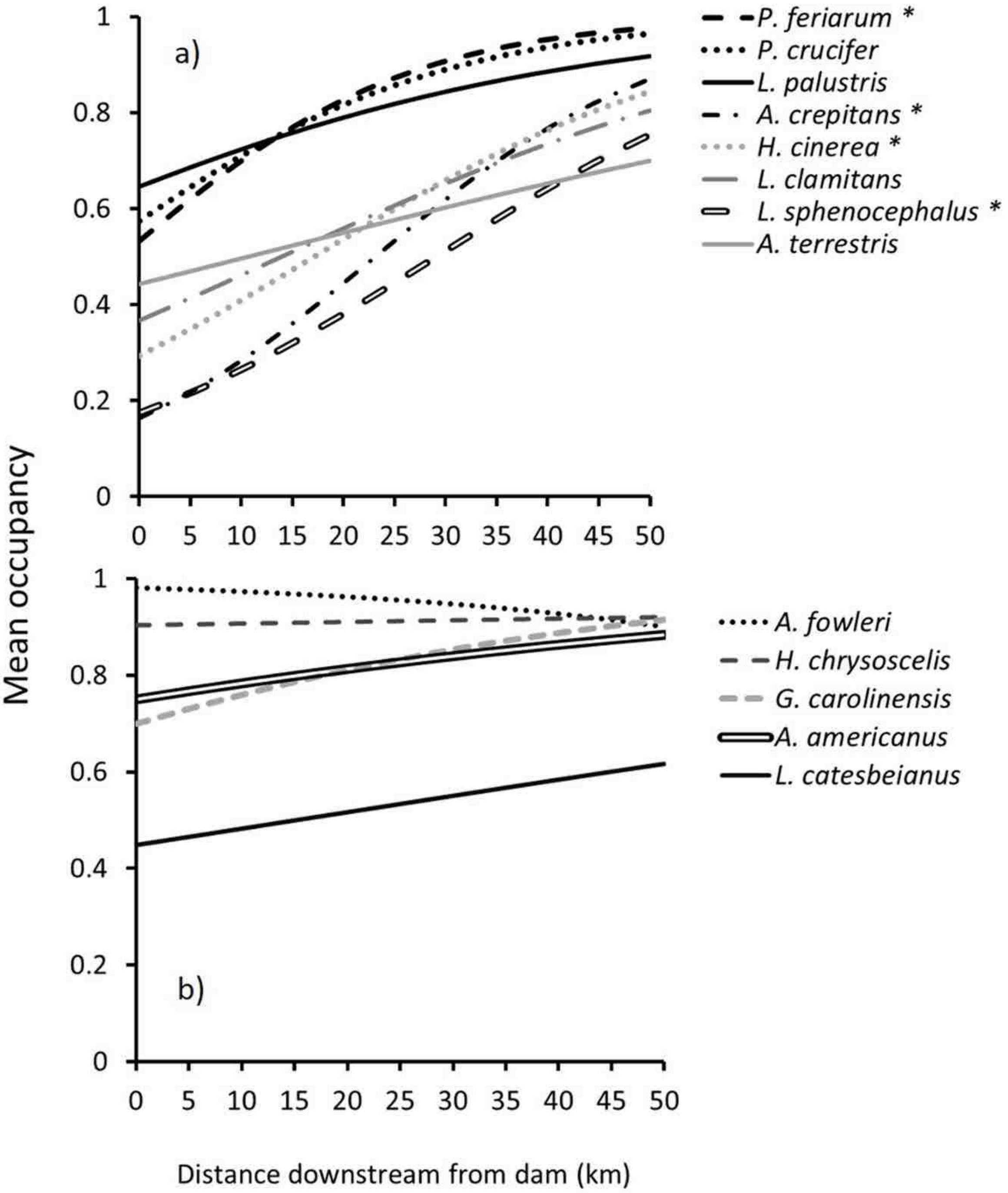


Figure 3. Relationship between mean species-specific anuran occupancy probability for a) dam-sensitive and b) dam-insensitive species, and distance downstream from a dam in the Broad and Pacolet Rivers, South Carolina, USA. Occupancy probabilities were calculated at mean values of upstream distance from dam and percent urbanization. Credible intervals are omitted for clarity, and asterisks indicate species for which the downstream distance from dam covariate parameter ($\alpha 1_i$) estimate did not overlap zero.

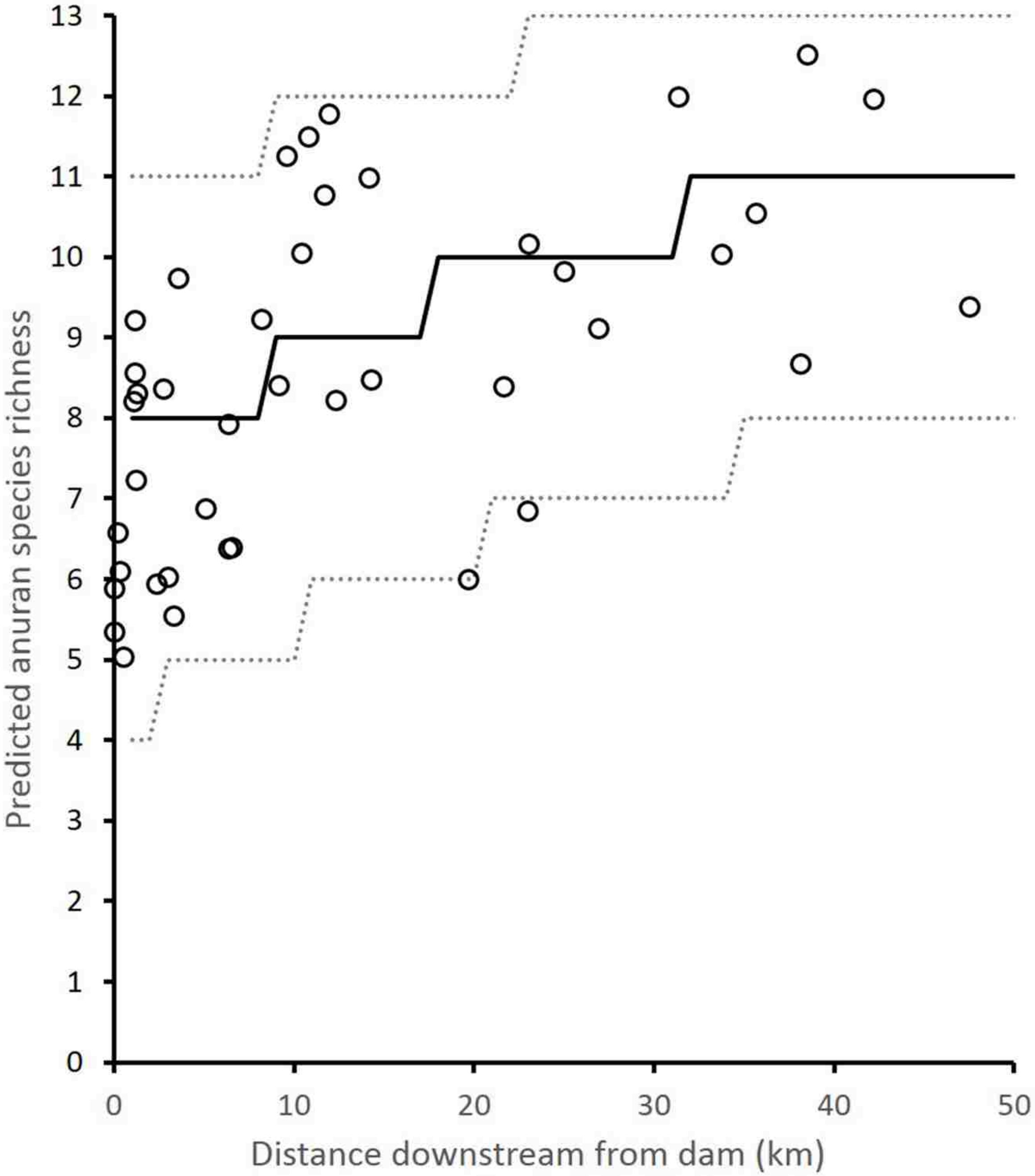


Figure 4. Estimated anuran species richness in riparian zones of the Broad and Pacolet Rivers, South Carolina, USA, in relation to distance downstream from dams. Solid line represents the posterior mean, circles are site-specific mean richness estimates, and the dashed lines represent a 95% predictive interval of species richness at hypothetical sites.