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INFLUENCES OF RIPARIAN LAND-USES ON HABITAT USE AND INTERSPECIFIC COMPETITION OF STREAM-DWELLING SALAMANDERS: EVIDENCE FROM BLUE RIDGE & PIEDMONT

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INFLUENCES OF RIPARIAN LAND-USES ON HABITAT USE AND
INTERSPECIFIC COMPETITION OF STREAM-DWELLING SALAMANDERS:
EVIDENCE FROM BLUE RIDGE & PIEDMONT

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Wildlife and Fisheries Biology

by
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ABSTRACT

Human-induced disturbances can result in persistent influences on ecosystems, including habitat loss and biogeographical changes. Global amphibian decline, a consequence of habitat degradation, is among prime conservation concerns. To better understand causes of the amphibian crisis, investigations a multiple levels of biological organization – behavior, communities, and landscapes - is imperative. I investigated the responses of stream-associated Plethodontid salamanders of the Blue Ridge and Piedmont of the Southeastern US to historical and current land uses in the riparian zone and watershed to determine, (1) change in the community structure and mechanisms driving the change and uses operating at different spatial-temporal scales; (2) competition between two sympatric species with different body sizes, natural histories, and differential sensitivity for habitat alterations (black-bellied and northern dusky salamanders) in the context of riparian land uses.

I surveyed low-order streams for salamanders, estimated 15 habitat variables and current and historical land-cover at riparian and watershed scale for each sampling site. Forested streams were more diverse than non-forested streams. Two assemblages were evident: disturbance avoiders (forest-dependent, large-bodied, disturbance-sensitive species) and disturbance tolerators (cosmopolitan, small-bodied, disturbance-resistant species); each assemblage composed of 80% and 20% of the regional species pool, respectively. Riparian zone characteristics (canopy cover, canopy height, leaf-litter cover) and stream geomorphology (bank complexity, stream substrate heterogeneity, sedimentation) were dramatically altered by land uses, rendering streams unsuitable for

most salamanders. Historical land uses at both riparian- and watershed-scale influenced current populations and community structure of salamanders. Piedmont protected areas with crop-farming legacies were the most species-deprived since intensive agriculture can lead to lasting effects including soil erosion, sedimentation, increased discharge, and destabilization of stream banks. My experiment on competition revealed marked differences in microhabitat associations of focal species across riparian land uses. Black-bellied salamanders competitively dominated the use of stream channel over northern dusky salamanders in forested and agricultural streams. Northern dusky salamanders competitively displaced black-bellied salamanders from stream banks in urban streams. Riparian anthropogenic disturbances negatively affected the large-bodied habitat specialists and favored small-bodied habitat generalists.

Terrestrial anthropogenic disturbances can modify stream habitats and, result in the exclusion of disturbance-sensitive species, ultimately leading to biotic homogenization. Conservation of stream salamander community should be strengthened with protection and restoration of riparian forests and degraded stream habitats; land-use regulations at the watershed scale; establishment of connectivity among riparian forests; and introduction of Best Management Practices for farmlands and timberlands.

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TABLE OF CONTENTS

	Page
TITLE PAGE	i
ABSTRACT	ii
ACKNOWLEDGMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
 CHAPTER	
ECOLOGY AND CONSERVATION NEEDS OF AMPHIBIANS: SALAMANDERS AND FRESHWATER ECOSYSTEMS OF THE SOUTHEASTERN UNITED STATES	1
Global biodiversity crisis	1
Systematics and biogeography of amphibians	2
Natural history of amphibians	3
Stream ecosystems as amphibian habitats	5
Ecological importance of amphibians	6
Amphibian crisis: threats and conservation issues	8
Land-use changes and anthropogenic disturbances	11
Land-use practices and stream ecosystems	13
Southeastern United States: Blue Ridge and Piedmont ecoregions	14
Conservation of amphibian fauna	16
 IMPORTANCE OF RIPARIAN FOREST BUFFERS IN CONSERVATION OF STREAM BIODIVERSITY: EVIDENCE FROM ECOLOGICAL RESPONSES TO LAND-USES BY STREAM-ASSOCIATED SALAMANDERS	20
Introduction	20
Methods	22
Results	26
Discussion	31

Table of content (Continued)	Pages
RIPARIAN LAND-USE CONDITIONS INFLUENCE COMPETITION FOR MICROHABITATS AND SPACE BETWEEN A GENERALIST AND SPECIALIST SALAMANDER IN A STREAM ECOSYSTEM	47
Introduction.....	47
Methods.....	51
Results.....	59
Discussion	63
Conclusion	71
IMPORTANCE OF CURRENT AND HISTORICAL LAND-USE IN STRUCTURING THE COMMUNITY: EVIDENCE FROM SALAMANDER OCCUPANCY IN STREAMS OF BLUE RIDGE AND PIEDMONT ECOREGIONS.....	79
Introduction.....	79
Methods.....	82
Results.....	86
Discussion	90
Conclusive Remarks	96
REFERENCES	102

LIST OF TABLES

Table	Page
2.1: Habitat variables estimated in the wet channel, riparian zone and the methods of estimations.	40
2.2: Response of adult and larval stream Plethodontids to four riparian land-uses and percentage relative abundance of each species across the four land-uses	41
2.3: Model parameters chosen from the stepwise multiple regression analyses on the Principle Components	42
2.4: Degree of protection provided by national protected area network (USGS Protected Area Database) to stream buffer zones of different widths	43
3.1: Abundance of the black-bellied and northern dusky salamanders at three riparian land-uses and percent occurrence of each focal species at different stream microhabitat types.	73
3.2: Average distance to the nearest heterospecific (DNN) between black-bellied salamanders and northern dusky salamanders in three differential artificial stream types with simulated riparian land-use and land cover types	74
4.1: A brief description of the four spatial and temporal scales under which different land-use and land cover types were categorized	97
4.2. Results of the factor analyses and representation of each factor to the land-use variables based on loadings and eigenvalues	98
4.3. Results of the multiple stepwise regression to predict the species richness and Simpson index of stream salamander community in response to historical and current land-uses at riparian and watershed scale	99

LIST OF FIGURES

Figure	Page
2.1: Species accumulation curves	44
2.2: NMDS ordinations of salamander assemblages at Blue Ridge and Piedmont Ecoregions.....	45
2.3: The study site and the salamander response groups	46
3.1: The design for the artificial stream experiment with all 3 phases of a single replication	75
3.2: The top view of the artificial streams with the perimeter of the artificial streams calibrated in centimeters producing a Cartesian grid to record the point occurrences of salamanders during each observation session.....	76
4.1: Study area: Blue Ridge and Piedmont ecoregions of the southeastern US. The field survey was limited to the states of North Carolina, South Carolina, and Georgia	100
4.2: Ordination plots for redundancy analyses (RDA) for (a) Blue Ridge and (b) Piedmont	101

CHAPTER ONE

ECOLOGY AND CONSERVATION NEEDS OF AMPHIBIANS: SALAMANDERS AND FRESHWATER ECOSYSTEMS OF THE SOUTHEASTERN UNITED STATES

Global biodiversity crisis

Global biodiversity loss is an important environmental issues given the status of the world's biological resources on which human life depends (Pimm & Raven 2000; Millennium Ecosystem Assessment 2005; Baillie et al. 2008). Rate of extinction during the Holocene Epoch has been two to three orders of magnitude greater than the background extinction rate, leading to a sixth mass extinction (Wilson 1988, 1989; World Health Organization 2005; Kumar & Khanna 2006; McKinney et al. 2009; Soberon & Peterson 2009). Habitat loss and fragmentation, overexploitation, loss of keystone species, introduction of invasive species, increased prevalence of pathogens and parasites, environmental pollution, and global climate change are considered the key causes of global biodiversity degradation (Allan & Flecker 1993; Taylor et al. 1994; Mittermeier et al. 1998; Bengtsson et al. 2000; Myers et al. 2000; Veitch & Clout 2002; Parmesan & Yohe 2003; Clavero & Garcia-Berthou 2005; Ebenman & Jonsson 2005; Brooks et al. 2006; Hof et al. 2011). Among a multitude of unsustainable human activities, land development presents the most imperilment to biodiversity which results in cascading ecological catastrophes culminating in biodiversity degradation regionally and globally. This manifests as dramatic population declines of many species; destruction of critical breeding habitats; reduced landscape permeability due to habitat fragmentation;

destabilization and loss of ecosystem functions; and alteration of ecosystem structure (Soulé 1991; Malmqvist & Rundle 2002; Dobson et al. 2006; Dudgeon et al. 2006).

Urbanization, expansion of human settlements, unsustainable agriculture, and infrastructure development are the primary forces that drive habitat loss (Czech et al. 2000; Blair 2001; Maestas et al. 2003). A globally-increasing and expanding human population accentuates rate of habitat transformation and unsustainable use of natural resources to fulfill fundamental needs (Sanderson et al. 2002; Hepinstall et al. 2008; Schipper et al. 2008). Consequently, the extent of relatively undisturbed habitats that are suitable for wildlife is declining (Noss 1991; Rouget et al. 2003; Radeloff et al. 2005). Urbanization, residential development, and infrastructure development exert a persistent impact on native biodiversity and historical disturbance regimes without any substantial recovery of the original biodiversity or ecosystems processes (McKinney 2002a). Intensive crop-farming, livestock ranching, and commercial-scale animal husbandry can also have lasting effects on ecosystem structure and services resulting in to poor soil conditions, erosion, sedimentation, altered nutrient dynamics and modified historical disturbance regimes (Foster et al. 1998; Harding et al. 1998; Foster 2006; Schipper et al. 2008). Post-disturbance recovery may be delayed and the resultant communities can be species-poor and may not resemble the original communities (McKinney 2002a).

Systematics and biogeography of amphibians

Amphibians represent a unique group of vertebrates containing over 7,140 described species worldwide that demonstrate an intrinsic aspect of evolution, niche

segregation and natural history (Frost et al. 2006; Amphibiaweb 2013). The evolutionary and phylogenetic history of amphibians goes approximately 365 million years back (Carroll 1992). Amphibians evidently evolved from either the lobe-fin fishes (Crossopterygii) or the lungfishes (Dipnoi) in the early Devonian Period and represent a transition step in the evolution of terrestrial life (Carroll et al. 1999; Carroll 2009). Since then, amphibians were shaped and reformed under multiple selective environmental pressures, radiating them into distinct life styles and body forms (Wells 2007). Multiple extinction events occurred through the evolutionary process of amphibians in the Carboniferous, Permian, and early Jurassic Periods, ultimately leaving a handful of evolutionary relics and modern amphibians (Carroll 2009). Modern amphibians have diverged into three orders with distinct anatomical features: Urodela (salamanders), Anura (frogs and toads) and Gymnophiona (caecilians, limbless amphibians). Among all amphibians, anurans have the widest distribution across many biogeographical realms with the highest diversity in the oriental, neotropical and afrotropical regions; diversity of urodelans is prominent in the nearctic and neotropical realms; caecilians are restricted to tropical wet biomes and mostly diverse in the oriental and neotropical regions (Duellman 1999; Duellman & Sweet 1999).

Natural history of amphibians

Amphibians are dependent on moist conditions and high relative humidity. Therefore, amphibian diversity is highest in regions with high precipitation and/or lower evaporative water loss (Duellman & Trueb 1994). Many require freshwater habitats to

breed and develop into the adulthood. A few amphibian clades have independently evolved to breed in foam nests constructed outside aquatic habitats; Some clades have completely lost their larval stages and lend a completely terrestrial mode of life (Beebee 1996; Wells 2007). Amphibians have radiated into terrestrial, aquatic (streams, cascades, and wetlands), scansorial (arboreal, phytotelms, rock outcrops) and fossorial (leaf litter, organic top soil) niches in both the old and the new worlds; they are also found throughout the elevation gradients in both tropical, subtropical and temperate biomes with considerable niche diversification at different ranges of altitude (Duellman 1999; Wells 2007). Thirty-nine modes of reproduction and development have been recorded among amphibians, including parental care, viviparity, and terrestrial direct development (Wells 2007). Most amphibians are generalist insectivores although a few species are known to be specialist predators of gastropods, earthworms, ants and termites. For most non-tropical amphibians, prey selection is season dependent (Duellman & Trueb 1994). Being poikilotherms and having a metamorphic lifecycle with an aquatic larval stage, they encounter a wide range of environments and habitats, each with different physiological constraints. Environmental and climatic parameters such as temperature, access to water, availability of microhabitat refugia, humidity, vegetation cover, and insect prey distribution affect their biological activities such as reproduction, foraging, local migration, and distribution (Gibbs 1998; Beebee & Griffiths 2005; Semlitsch et al. 2009). The optimal conditions of the above environmental parameters preferred by amphibians mostly prevail in relatively undisturbed forested habitats and aquatic habitats with

substantial forested buffer zones. However, there is a handful of amphibians that can tolerate long, cold winters and hot, dry summers (Duellman 1999).

Stream ecosystems as amphibian habitats

Amphibians occupy a broad spectrum of terrestrial, aquatic and semi-aquatic habitats. These include freshwater marshes, riparian wetlands, ephemeral forest pools, tropical rainforests, temperate hardwood forests, streams and riparian forests (Beachy & Bruce 1992; Wallace et al. 1992; Griffiths 1997; Bruce et al. 2000; Baldwin 2005; Beebee & Griffiths 2005; Baldwin et al. 2006; Surasinghe 2007, 2009). Among those, streams are a unique ecosystem since they are primarily driven by allochthonous production and fluvial processes, have inverted biomass pyramids, and undergo nutrient spiraling (Dodds 2002). Further, evolution of certain groups of amphibians (Plethodontidae, Sirenidae, Amphiumidae, Dicamptodontidae, Cryptobranchidae) started in stream ecosystems as evident in their synapomorphic features (Bruce et al. 2000; Dodd 2010; Mitchell & Gibbons 2010). Multiple terrestrial and hydrologic factors influence the habitat structure, habitats quality, ecosystem integrity, and communities of stream ecosystems: watershed and riparian characteristics, local and landscape-scale vegetation cover, stream order, geology, soil conditions, regional topography, geography and regional climate (Poff & Ward 1989; Allan & Flecker 1993; Allan 1995; Roth et al. 1996; Poff 1997; Lammert & Allan 1999; Allan 2004; Allan & Castillo 2007). These factors will change significantly from the headwaters to the lower reaches of a stream, even without any anthropogenic influences (Vannote et al. 1980).

Watershed characteristics such as watershed size, terrestrial vegetation structure, forest age, dominant vegetation type, canopy cover, watershed topography, edaphic characteristics and precipitation are responsible for nutrient and allochthonous energy input to the stream channel (Turner & Rabalais 2003). Geomorphic and physiographic features such as bedrock characteristics, parental rock types, outcrop formations, and stream flow pattern (meandering-flow or braided-flow) produce a continuous variation of stream channels comprising of pools, riffles, runs, deep undercut banks, and shallow shores; each of those sections serving as distinct habitat type (Cianfrani et al. 2009). Furthermore, altitude, surface runoff, groundwater feeds, geological substrates, and channel morphology determine stream discharge and dynamic flow regimes; both are critical hydrological parameters that govern the stream habitat structure (Dodds 2002; Allan 2004; Allan & Castillo 2007). The variation in the above determinants along the course of a stream drives alterations in species composition of biota and functional ecology of the stream (Roth et al. 1996).

Ecological importance of amphibians

Amphibians have a vital role in food webs and nutrient dynamics: regulation of insect and other invertebrate communities through predation; serving as a prey-base for many predators; and maintenance of plankton and vegetation biomass in freshwater habitats (Bury 1988; Davis 1996; Poulin et al. 2001; Davic & Welsh 2004; Kroll et al. 2009). Amphibians are middle-level consumers and herbivores of food chains, and thereby control species diversity and ecosystem processes along grazer and detritus

pathways (Kupferberg 1997; Altig et al. 2007). Furthermore, they are a prey-base for avian, terrestrial, and aquatic vertebrates as well as for a few invertebrate taxa (Harris 1995; Finlay et al. 2002). Aquatic and semi-aquatic amphibians migrate constantly between land and water which establishes a bidirectional flow of energy and matter between aquatic and terrestrial ecosystems (Davic & Welsh 2004; Regester et al. 2006). Fossorial activities of amphibians, i.e., construction and dwelling in underground burrow systems, contribute to soil and leaf litter dynamics (Beard et al. 2002). Therefore, loss of amphibians may have deleterious ecological consequences. The greatest impacts of amphibian decline are expected to occur in inland wetlands, montane streams and tropical rainforests, where the greatest amphibian diversity is recorded (Gibbons & Bennett 1974; Meegaskumbura et al. 2002; Pethiyagoda et al. 2006; Whiles et al. 2006).

Finally, Amphibians are excellent indicators of the overall environment health, ecological integrity, and habitat quality, as they are sensitive to perturbations in ecosystems. Given their complex life history, physiology, and unique habitat requirements, amphibians are representative of biological integrity of both terrestrial, aquatic and wetland ecosystems. Highly-permeable skin, imperfect osmoregulation and homeostasis, poikilothermy, cutaneous respiration, seasonal migrations and dispersal, bi-phasic life cycle, and association of multiple habitat types make them susceptible to environmental stressors and climate change; hence, precipitous declines in amphibian populations accompany serious environmental degradation (Blaustein & Wake 1990; Blaustein et al. 1994; Blaustein & Wake 1995; Blaustein et al. 2001; Blaustein et al. 2003; Young et al. 2005; Blaustein & Dobson 2006; Blaustein & Bancroft 2007; Baillie

et al. 2008). Amphibians are considered ecological sentinels across diverse biogeographic realms that indicate adverse impacts of climate change and gradients of human disturbance (Welsh & Ollivier 1998; Welsh & Droege 2001; Davic & Welsh 2004). Indices of biotic integrity have been developed for amphibians, particularly stream salamanders to evaluate the stream health and water quality (Southerland et al. 2004).

Amphibian crisis: threats and conservation issues

Most amphibians are not adapted to occupy non-natural land-cover types and anthropogenic habitats; only a few are tolerant of human-induced disturbances (Young et al. 2001; Stuart et al. 2005; Young et al. 2005). Compared to other vertebrates, a high proportion (32 %) of amphibians are redlisted under the top three threat categories: critically endangered, endangered, and vulnerable. This figure is significantly greater than the analogous numbers for birds (12 %) and mammals (23 %). Disproportionate and non-random extinction encountered by amphibians is evident in the comparison of critically endangered species in all vertebrate taxa: 7.4 % of amphibians are listed as critically endangered compared with 3.9% of fish, 1.8 % of birds, and 3.8 % of mammals (Baillie et al. 2004; Stuart et al. 2004; Baillie et al. 2008; IUCN 2012; IUCN et al. 2012). Given the paucity of ecological and population-level data on amphibians, particularly in the tropical regions where the overall diversity of amphibians is largely unknown, the current assessments on the amphibian conservation status is uncertain; in these regions amphibians could disappear before taxonomic and phylogenetic research make them

known to the science (Baillie et al. 2004; Meegaskumbura & Manamendra-Arachchi 2005; Meegaskumbura 2007).

During the previous two decades (1990-2010), there has been an increase in records of massive population declines of amphibians and extinction events. Most recent conservation assessments state nearly 50% of amphibians are undergoing population declines worldwide (Alford et al. 2001; Stuart et al. 2004; Andreone et al. 2005; Allentoft & O'Brien 2010; Bickford et al. 2010). This suggests that more extinctions are inevitable in the absence of intensified conservation actions. Amphibian diversity is highest in the tropics, particularly in the tropical rainforests. However, some temperate areas including southeastern United States are also considered a global hotspot for amphibian diversity, particularly for being an epicenter for evolution of certain amphibian clades (Hackney et al. 1992a; Martin et al. 1993; Donovan et al. 2000; Graham et al. 2010). The population decline and threats on amphibians are disproportionately high in such diversity-rich localities.

Habitat loss and degradation is the most detrimental factor responsible for the global amphibian crisis (Wake 1991). Amphibians mostly prefer habitats where natural disturbance regimes dominate, such as old-growth forests and vegetated inland wetlands, primarily because of high niche diversity in such ecosystems (Bennett et al. 1980; Pechmann & Wilbur 1994; Mendelson et al. 2006). High humidity, high availability of surface water, thick leaf litter, and continuous canopy cover present in relatively undisturbed forests help prevent desiccation in amphibians and provide optimal food resources (Young et al. 2001). Nevertheless, alarming declines have occurred even in

protected areas and in relatively pristine habitats. The parasitic pathogenic fungus, *Batrachochytrium dendrobatidis* is regarded a primary cause for such plights (Lips 1998; Lips et al. 2005a, b; Lips et al. 2006). The parasitic trematode genus *Ribeiroia* and ranavirus are pathogens that have caused significant impacts to amphibian populations as well (Mao et al. 1997; Hyatt et al. 2000; Johnson et al. 2002; Kiesecker 2002). Additionally, global climate change may compound other stresses to amphibians, accentuating their population decline and extinction risk (Beebee 2002; Corn 2003; Parmesan & Yohe 2003; Pearson & Dawson 2003). Introduction of invasive species (Vredenburg 2004), overexploitation for food-trade and international pet-trade (Abdulali 1985; Fitzgerald et al. 2004), increased exposure to UV-B radiation and environmental pollution (de Solla et al. 2002a; de Solla et al. 2002b; Roy 2002) are other human-induced factors responsible for amphibian declines. It is hypothesized that amphibian declines are due to synergistic effects of many adverse ecological impacts (Kiesecker et al. 2001; Blaustein & Kiesecker 2002; Beebee & Griffiths 2005).

Most biodiversity conservation and species management programs are focused on game species and charismatic megafauna (Kerley et al. 2003; Sergio et al. 2006). Conservation of nongame species such as small vertebrates and ecologically cryptic species have received little attention in the history of wildlife conservation and habitat management (Bickford et al. 2007). However, the time of the global amphibian assessment (2004) and the recent meetings of the World Congress of Herpetology (2004-2012) have underscored the importance of amphibian conservation; consequently, amphibians have received a significantly greater attention in wildlife conservation and

landscape-scale habitat management (Semlitsch & Jensen 2001; Semlitsch 2002; Semlitsch & Bodie 2003; Baldwin 2005; Baldwin et al. 2006; Semlitsch et al. 2007; Baldwin & Demaynadier 2009; Baldwin et al. 2009; Mackey et al. 2010; Howard et al. 2012; Surasinghe et al. 2012). There is a need for research on conservation issues and to plan for conservation of less-studied species such as amphibians. If amphibians are to be conserved, there also need to be effective management and conservation plans with the involvement of governments, local communities, and research and academic institutes.

Land-use changes and anthropogenic disturbances

Species diversity and distribution of a given area are often governed by multiple biogeographic filters operating at different spatial scales with unique biochemical, physiographical, and geo-climatic characteristics including regional species pool, geographic and hydrologic dispersal barriers and dispersal corridors, regional climate, habitat complexity, and evolutionary selective forces (Frissell et al. 1986; Poff 1997; Davies et al. 2000). Within a biome or an ecoregion, species distribution and community structure can be governed by community interactions, ecosystem functions, habitat quality and availability, distribution and structure of refugia, microclimate, habitat heterogeneity, and resource distribution; all these elements can be dramatically influenced by land-uses and transformations of natural land-cover (Morton & James 1988; Naiman et al. 1993; Tews et al. 2004). This is applicable to many taxa, both vertebrates and invertebrates associating aquatic, terrestrial, arboreal, aerial and transitional habitats along the aquatic-terrestrial gradient (Blair & Launer 1997; Scott &

Hall 1997; Blair 2001; Scott & Helfman 2001; Scott et al. 2002; Blair 2004; Blair 2008). Ecological impacts of land-uses and other anthropogenic disturbances that are functionally analogous to or associated with land-uses have been studied with respect to different species and taxa, communities and species assemblies, habitats and landscapes, and ecosystems; however, most such studies focused on alterations of community composition among terrestrial species along land-use gradients (Noss 1983, 1990, 1991, 1996; McKinney & Lockwood 1999; Lockwood et al. 2001). It has been documented that only a handful of species such as habitat generalists, cosmopolitan species, human commensals, edge species, weedy species and invasive can survive in altered habitats and non-natural land-cover types (Naaf & Wulf ; Scott 2006; Hepinstall et al. 2008; Scott 2009).

Land-use changes are a result of dynamic, multidirectional interactions among social, economic, and political processes and decisions operating on an environmental framework in the midst of a multitude ecological processes and entities such as climate, geomorphology and geochemistry, hydrodynamics, a variety of habitat and ecosystem templates, and interacting biota (Urban 2006). Land development results in a series of drastic modifications in structure and function of ecosystems, including changes in vegetation regimes, topography, local- and landscape-scale geomorphology, perturbations in natural successions, alterations in historical disturbance regimes, and modifications in hydrology (Filloy et al. ; Black et al. 1998; Sisk 1998; Herremans & Herremans-Tonnoeyr 2000; Fausch et al. 2002; Turner 2005b, a; Kaye et al. 2006; Zhao et al. 2006; Vera et al. 2011). Many species, through natural selection, have adapted to natural

processes and unique ecological conditions in their native range; a rapid change in these conditions due to human-induced disturbances could render such specializations a liability for survival and successful reproduction (Scott 2006; Scott 2009) . Selection pressure generated by human activities may extirpate habitat specialists, geographical and evolutionary relict species, range-restricted species, and rare species whereas habitat generalists, exotic species, and cosmopolitan “weedy” species readily colonize altered habitats in the absence of competition. With increasing frequency and magnitude of human disturbances, substitution of the aforementioned species will prevail endangering the native biodiversity and ecosystem complexity; a process termed biotic homogenization (Webster et al. 1992; Rahel 2000; Larson et al. 2001; Lockwood & McKinney 2001; Wijesinghe & de L. Brooke 2005; Ekness & Randhir 2007; Floren et al. 2008; Urquiza-Haas et al. 2009).

Land-use practices and stream ecosystems

Degradation of freshwater biodiversity is considered a global environmental issue and is rapidly aggravating in both developed and developing nations (Angermeier 2000; Baron et al. 2002; Dudgeon 2003; Dudgeon et al. 2006). Stream ecosystems are intricately linked with terrestrial habitats through processes such as surface runoff, sedimentation, nutrient loading, erosion and the movement of biota (Fisher 1997; Ward 1998; Clinton & Vose 2006). The river continuum concept and the flood pulse concept link lotic and terrestrial ecosystems (Poole 2002; Allan & Castillo 2007). The river continuum concept states that lotic bodies are open ecosystems that constantly interact

with the riparian zone; physical and chemical parameters change continuously throughout the flow from headwaters to the river mouth and deltas including flow of matter and energy; temperature, thermal regimes and other temperature-driven processes; stream geomorphology such as width, depth, and bank characteristics; hydrodynamics such as flow regimes and discharge; all of which ultimately lead to change in the water quality, biota and ecosystem functions (Vannote et al. 1980). Similarly, the flood pulse concept states that periodic flooding events expand lateral limits of a stream channel, allowing interactions between the main channel and the floodplain (Junk et al. 1989).

Disturbance in the natural land cover can modify the stream communities (Scott et al. 2002; Scott 2009). For instance, diversity of endemic freshwater fish and species richness of EPT insect taxa (Ephemeroptera, Plecoptera, Trichoptera) are known to decline in streams with increasing disturbances in riparian areas and watersheds (Walsh 2004; Heino et al. 2007). The effect of land-use on biotic integrity of streams may persist after recovery of the original forest cover (Delcourt & Delcourt 1998). Harding et al. (1998) stated that historical land-use activities create long-lasting alterations in stream biodiversity and stream habitat structure, sedimentation and siltation, despite rebound of native terrestrial vegetation.

Southeastern United States: Blue Ridge and Piedmont ecoregions

The southeastern United States is highly diverse in geomorphology, altitudinal variation, and hydrology which result in a high heterogeneity in the habitat template increasing the regional biodiversity (Hackney et al. 1992b; Kirkman et al. 1999; Donovan

et al. 2000; Estill & Cruzan 2001; Graham et al. 2010). According to the Level III classifications of the Environmental Protection Agency (EPA), eight ecoregions fall within the southeastern United States: Blue Ridge, Piedmont, Southern Coastal Plains, Mid-Atlantic Coastal Plains, Southeastern Plains, Ridge and Valley, Southwestern Appalachians, and Central Appalachians (US Environmental Protection Agency 2002). Among watersheds of the southeastern United States, some (Saluda–Reedy) are recognized as critically imperiled by the Environmental Protection Agency (Ulbrich 2007). The high diversity of fauna and flora in this region has been attributed to many ecological and biogeographical factors, i.e., monophyletic speciation due to vicariance processes where formerly wide-spread populations radiated into many distinct clades (Croizat et al. 1974; Mayden 1987b, a; Pearson et al. 1999); climate zoning (Kozak & Wiens 2007); adaptive radiation and habitat specialization as a result of niche divergence (Bermingham & Avise 1986; Bernardo 2007); niche conservatism upon historical climate change (Highton 1995; Kozak & Wiens 2006; Kozak & Wiens 2010); and higher intraspecific competition exceeding the intensity of interspecific competition leading to co-existence of species (Clark 2010).

The southeastern US and Appalachian highlands possess a rich diversity and exceptionally high degree of endemism among many native taxa: woody plants (Estill & Cruzan 2001), freshwater fish (Warren et al. 2000), freshwater molluscs (Neves et al. 1997) and herpetofauna (Petranka 1998; Lannoo 2005). Further, the degree of glaciation and sea-level rise in the southeastern US were limited compared to the other regions of the Nearctic realm; thereby, the southeastern United States has served as a biodiversity

refugia, and salvaged the regional biota from climate extremities and natural catastrophes (Martin & Harrell 1957).

Being a region with a rapid rate of urbanization, the Southeastern United States encounters a great predicament over loss of exceptionally rich, endemic biodiversity; since the late nineteenth century, anthropogenic activities have drastically changed the natural landscape, jeopardizing the native biodiversity. (Lydeard & Mayden 1995; Noss et al. 1995; Burkhead et al. 1997; Dobson et al. 1997b; Leidner & Neel 2011). Between 1800 and the mid-19th century, this region was extensively used for cotton farming; today, the Southeastern US is among the areas with the most extensive wildland-urban interfaces, where land development intermingles among natural habitats (Jackson et al. 2005; Radeloff et al. 2005). For example, in upstate SC, a human population density is $>80 \text{ km}^{-2}$, with a population growth rate of 15% between 2000-2010; the acreage of developed lands doubled in upstate SC between 1990 and 2000 (Allen et al. 2006a; Campbell et al. 2007).

Conservation of amphibian fauna

Non-point source pollution, rising demand for natural resources, needs for spatially extensive habitat connectivity make the existing protected lands inefficient as the sole conservation strategy within the southeastern US. Modern day conservation should take place among sustainable land-use activities by a holistic, proactive approach that integrates the existing protected area network, recognition of gaps in conservation lands, conservation-oriented land management strategies, and species and ecosystem

management action plans; all of which needs to be strengthened by science-based knowledge on ecology and conservation biology, formal and informal education, and conservation-driven research built upon the theory and practice of ecology (Scott et al. 1993; Miller & Hobbs 2002; Brooks et al. 2004; Rodrigues et al. 2004; Brooks et al. 2006; Miller et al. 2006). It is imperative that conservation of amphibians be integrated with other conservation efforts targeting other forms of biodiversity and natural resources including ecosystems and landscapes, threatened and endangered species, charismatic megafauna and game species, and lands with aesthetic and recreational value.

In-depth knowledge about amphibians and their habitats including community ecology, landscape ecology, life and natural histories, regional and local biodiversity, evolutionary trends, is immensely important in long-term conservation planning. Such research-based knowledge is required by conservation agencies (both federal and state level), community-based organizations, and other non-governmental organizations with motivated towards wildlife and natural resources conservation. Research studies can the foundation for decision makers, resource managers, land-use planners, land developers, conservation authorities, and private landowners for making policy decisions and establishing management actions to mitigate habitat degradation and to preserve the ecological integrity of the ecosystems that are essential for persistence of amphibian communities, beta diversity, and to sustain their metapopulation dynamics (Margules & Pressey 2000; Groves et al. 2002; Pressey et al. 2007).

Worldwide, there is a growing consensus regarding the need to mitigate threats to biodiversity and to promote landscape-scale trans-boundary conservation; and

amphibians have attracted a greater attention among conservation biologists. One of the most critical problems in biodiversity conservation is efficient allocation of limited financial, logistic, and intellectual resources among different proposed conservation lands; therefore, it is essential to develop concepts, principles and tools for the robust and effective site selection for biodiversity conservation (Turner et al. 2001; Crooks & Sanjayan 2006; Trombulak & Baldwin 2010). Decision makers are concerned about economy and efficiency; they face an inevitable challenge to optimize biodiversity conservation by using minimal land acreage while allowing alternative anthropocentric land-uses (Sarkar et al. 2006; Fuller et al. 2007). A number of biodiversity prioritization schemes have been developed to identify optimal sites to establish conservation lands and management regimes; many of these prioritization methods can be applied to amphibians with some modifications: criteria to recognize hotspots, megadiversity sites, centers of endemism, and taxon-specific locales, ecoregion concepts, global biome concepts, and complementarity-based site selection (Mittermeier et al. 1998; Mittermeier et al. 2000; Myers et al. 2000; Mittermeier 2002; Mittermeier et al. 2005; Pawar et al. 2007; Moilanen et al. 2008; Leathwick et al. 2010).

Future research on amphibian conservation in the southeastern US should focus on: revision of knowledge on species natural history with respect to the changing environment, land-use gradients and anthropogenic disturbance gradients; identifying gaps in the current protected area network for long-term occupancy, short-term use, stepping stones, dispersal and migratory corridors; modifications in amphibian community interactions in response to the environmental change; macro- and micro-scale

habitat management and restoration of degraded habitats with special focus on amphibians; ex-situ conservation and combining ex-situ conservation efforts with head-starts, re-introductions, repatriations and translocations.

CHAPTER TWO

IMPORTANCE OF RIPARIAN FOREST BUFFERS IN CONSERVATION OF STREAM BIODIVERSITY: EVIDENCE FROM ECOLOGICAL RESPONSES TO LAND-USES BY STREAM-ASSOCIATED SALAMANDERS

Introduction

Amphibian decline is a global environmental concern that has generated a number of conservation solutions ranging from global analyses of patterns and causes, to prescriptions for local habitat conservation plans (Houlahan et al. 2000; Ficetola & De Bernardi 2004). Human actions have led to the extinction of one-third of global amphibian species and decline of 50% of their populations making amphibians among the most imperiled vertebrate taxa (Stuart et al. 2004). In North America, the amphibian crisis is disproportionately weighted against salamanders; 50% of salamander species are considered threatened (Stuart et al. 2004). Salamanders account for 60-80% of the animal biomass in headwaters and vernal pools (Burton & Likens 1975; Windmiller 1996). They drive nutrient cycles, sustain food web dynamics, transport energy between aquatic and terrestrial habitats and indicate environmental degradation (Welsh & Ollivier 1998; Homyack et al. 2010). Given ecological roles salamanders play, their decline may have ecological consequences.

Multiple physiological and behavioral features, e.g., highly permeable skin, poikilothermy, and requirements for aquatic and terrestrial habitats predispose salamanders to anthropogenic disturbance (Davic & Welsh 2004). Habitat loss and fragmentation owing to conversion of landscapes to human settlements, agriculture, and

infra-structure are primary causes of biodiversity loss; salamanders are highly susceptible to the same causes of biodiversity degradation (Gallant et al. 2007). Land-uses may negatively influence stream ecosystems which are linked with terrestrial habitats through surface runoff, nutrient loading, and network connectivity (Vannote et al. 1980; Allan 2004). Urbanization has resulted in severe degradation of watersheds leading to loss of freshwater biodiversity (Riley et al. 2005). Previous studies have documented declining species richness of terrestrial and wetland salamanders with urbanization and agriculture (Hicks & Pearson 2003; Loehle et al. 2005). However, most published research focused on one or a few species and were limited in geographical extent; hence there is a scarcity of community level, landscape-scale investigations on salamander occupancy in stream habitats across land-use gradients and ecoregions (Riley et al. 2005). To fill these gaps, we investigated the effects of riparian land-use activities with different intensities across two ecoregions, on species composition of stream salamanders.

Amphibian conservation cannot be achieved solely by fortress conservation; instead it can be strengthened with regulatory and management actions in human-dominated landscapes based on detailed ecological information on current status and distribution in comparison to protected lands (Ficetola & De Bernardi 2004; Baldwin & Demaynadier 2009). To contribute to ongoing efforts, we studied ecological responses of stream-dwelling salamanders to four land-use settings of the riparian zone (residential, urban, agricultural, and forest) in two ecoregions (Blue Ridge and Piedmont). We focused our research on aquatic Plethodontid salamanders since they are highly diverse in our study region. Our specific objectives were to examine the following responses across

the riparian land use gradient and ecoregions: (1) variation of salamander diversity, (2) species-specific responses including how the responses drive habitat associations of distinct assemblages, (3) determine fundamental environmental variables that shape habitat associations of stream salamanders, (4) assess currently protected riparian forest cover and recommend alternative conservation actions that could influence salamander conservation, including targeted land management, easement purchases, policy enactments, and improved regulatory actions and land-use practices as related to stream and watershed management.

Methods

Study site

The Blue Ridge and Piedmont (Fig. 3a, b) of the Southeastern US include a diverse array of landforms, land-cover types and possesses a rich diversity (102 species) of salamanders (Tuberville et al. 2005; Graham et al. 2010). The Blue Ridge is a global hotspot for salamander diversity (approximately- 25 aquatic plethodontids, 10 other aquatic salamanders, and 25 terrestrial plethodontids) and a center of plethodontid evolution (Bruce et al. 2000). Between early-19th and mid-20th centuries, the Piedmont was extensively used for cotton farming, an intensive land-use that altered stream geomorphology (Galang et al. 2007). The Blue Ridge experienced extensive deforestation during the late 19th and early 20th centuries but forests rapidly returned following land abandonment and conservation action (Bolgiano 1998). An amenity-based housing boom

created an extensive wildland-urban interface throughout the region, in recent decades (Radeloff et al. 2005; Theobald & Romme 2007). While the agricultural lands in the Piedmont reverted to forest, extensive urban and exurban growth has nearly connected a mega-urban corridor from Atlanta through Washington DC (Brown et al. 2005).

Sampling Design

Our sampling sites consisted of 101 low-order stream reaches with watersheds $<25\text{Km}^2$, blocked across two ecoregions, in association with four riparian land-uses: forested, agricultural, residential and urban (commercial and industrial development). We used a VisualBasic query to examine all potential sampling sites within the same drainage for spatial autocorrelation (SC Department of Natural Resources; ArcGIS 10, ESRI) to select spatially independent sampling points. We selected sites that shared no more than half of the same drainage.

At each sampling point, we selected a 100m-stream segment and, during three, upstream repeat passes over the same segment, surveyed the wet channel and undercut banks for adult and larval salamanders. The survey involved dip netting, overturning movable rocks and logs and searching their surfaces, examining in crevices, and scrutinizing surfaces of large rocks and woody debris. We likewise conducted three repeat surveys of stream banks to a distance of 1m from the wet channel where we overturned all movable rocks and logs and searched through leaf litter, moss, and understory vegetation (Heyer et al. 1994; Dodd 2010). We conducted surveys daily from 0800 to 1800 for 55 sampling days during early April to mid-July for two consecutive

years (2010, 2011). Sampling was only conducted in clear-sky, non-rainy days to keep species detection consistent. We identified all captured adult and larval salamanders, recorded the species name, relative abundance, and released back to the sampling site. We assessed 15 habitat variables of the wet channel and the riparian zone at each sampling site (Table 1). Variable selection was based on stream ecology and natural history of Plethodontids. Use of multiple passes to capture salamanders and a well-trained field crew contributed to increased detection probability. We plotted species accumulation curves of larvae and adults found at the four riparian land-use types within both ecoregions (Fig. 1)

Statistical Analyses

We used an arcsine and squareroot transformations to approximate normality for univariate and multivariate analyses, respectively. We used R 2.15.1 (R Development Core Team 2012) and JMP 9.0 (SAS Institute Inc. 2012) for statistical analyses (level of significance, $\alpha > 0.05$).

Variation in the salamander diversity at the four riparian land-use types

We calculated Simpson Index (SI) and species richness at each riparian land-use type and performed a one-way ANOVA to determine significant differences among land-uses for above indices, followed by an LSMeans contrast test to determine whether above indices were significantly higher for forested streams than other land-uses. We performed a MANOVA (response variable: species identity) to reveal significant differences for

species composition among riparian land-uses, followed by an LSMeans contrast test to determine whether forested streams were comparatively richer in species composition.

Identifying species-specific responses and habitat associations

We performed Nonmetric Multidimensional Scaling (NMDS) to identify species assemblages that segregate in response to four land-uses (Bray-Curtis dissimilarity matrix, 50 random starting configurations, two-dimension ordinations), followed by a Monte Carlo simulation (1,000 iterations). Based on the ordinations, we classified species into three functional groups (Fig. 2c, (McKinney 2002b)): disturbance avoiders (species predominantly associated with forested streams), disturbance tolerators (species mostly associated with non-forest riparian land-uses, but also occurred in forested streams) and disturbance exploiters (species exclusively associated with non-forest riparian land-uses).

Environmental correlates of land use types

We performed a principal component analysis (PCA) on the correlation matrix of habitat variables. We selected all PCs that cumulatively explained 80% of the variability and ran Pearson correlations among all selected PCs and habitat variables to verify environmental correlates of derived PCs. We conducted a stepwise regression via a mixed model using species richness and SI of diversity (1-SI) as response variables and selected PCs as model parameters. Using parameters of the optimal model and natural history of focal species, we identified potential ecological mechanisms of species responses to riparian land-use.

Determining the protected area coverage for riparian zone buffers and estimating area for conservation actions

We generated 140m (Olson et al. 2007) and 240m (Semlitsch & Bodie 2003) riparian zones (ArcGIS 10) around streams (National Hydrography Dataset) within the Blue Ridge and Piedmont ecoregions. We calculated the extent of buffers located inside and outside mapped protected areas (Protected Area Database of the US; PADUS Version 1.3) and the protection level (USGS national Gap Analyses Program) of riparian zones falling within protected areas buffers. We also calculated the area of riparian habitat that would be subject to improved regulatory and management actions, and catalog several examples of regulatory and management actions.

Results

Variation of stream salamander diversity across riparian land-use types

Species distribution differed by ecoregion. We found all the 11 species of stream-associated Plethodontid salamanders known to occur in Blue Ridge ecoregion, and 7 that have been historically recorded in Piedmont (Table 2). Our species accumulation curves reached the asymptote with the first few sampling sites indicating that our detectability was similar which suggested high rate of detectability (Fig. 2). Blue Ridge forested streams fully represented regional Plethodontid diversity (100% of known diversity for the region); 85% of surveyed streams hosted all 11 species we detected. We

recorded a total of 7 species in forested Piedmont streams, which is 80% of those expected to occur; only 10% of those streams harbored all 7 species we detected. Agricultural streams were the lowest in cumulative species richness (Blue Ridge:3; Piedmont:4). Residential (Blue Ridge:5; Piedmont:4) and urban streams were also substantially species-poor (4;Fig. 1).

Richness was greatest in forested streams. The average species richness differed significantly among the riparian land-uses when pooled across ecoregions for both adults (One-way ANOVA- $F = 17.10$, $p < 0.05$), and for larvae ($F = 14.28$, $p < 0.05$). Blue Ridge forested streams had significantly greater species richness of adults (LSMeans Contrast- $F = 25.31$, $p < 0.05$), and larvae ($F = 21.82$, $p < 0.05$) than in non-forest Blue Ridge streams. Blue Ridge forested streams likewise had greater diversity and evenness than non-forest streams; the SI was significantly lower in forested compared to non-forest streams (adults: $F = 11.60$, $p < 0.05$; larvae: $F = 4.97$, $p < 0.05$), suggesting a dominance effect. Richness and diversity across land uses in the Piedmont ecoregion differed by life stage, with no differences found for adults when comparing richness and SI in forest vs. non-forest streams (species richness: $F = 2.20$, $p > 0.05$; SWI: $F = 1.57$, $p > 0.05$; SI: $F = 0.52$, $p > 0.05$). Larvae in Piedmont streams did show differences; richness was significantly greater in forested vs. non-forest streams ($F = 5.01$, $p < 0.05$). By contrast, SI was significantly lower for larvae in the forested Piedmont streams ($F = 4.97$, $p < 0.05$).

Species-specific responses of stream salamanders to riparian land-uses

Most (9) of the 11 salamander species appeared to be sensitive to type of riparian land use; 2 (*D. fuscus* and *E. cirrigera*) were cosmopolitan, and *E. guttolineata* was relatively so. Larvae showed similar trends as adults, where diversity measures of all but *D. fuscus* and *Eurycea spp.* varied significantly among riparian land-uses (Table 3).

NMDS ordinations suggested two types of habitat associations for salamanders in the Blue Ridge ecoregion: disturbance avoiders and disturbance tolerators (Fig. 2a, 2b; stress from two-dimensional solution, adults: 0.076, larvae: 0.096, Monte Carlo stress after 1,000 iterations for adults: 0.270, larvae: 0.250). Among adults, 8 species (73%) were disturbance avoiders: *D. marmoratus*, *D. monticola*, *D. ocoee*, *D. quadramaculatus*, *E. wilderae*, *P. ruber*, *P. montanus*, and *G. porphyriticus*. Disturbance tolerator group was comprised of three species: *E. cirrigera*, *E. guttolineata* and *D. fuscus*. Among larvae, five species (71%) were disturbance avoiders: *D. marmoratus*, *D. monticola*, *D. quadramaculatus*, *Pseudotriton*, *G. porphyriticus*); the rest (all *Eurycea* and *D. fuscus*) were disturbance tolerators.

The NMDS ordinations for the Piedmont ecoregion suggested the same two functional groups but with different species compositions than in the Blue Ridge (Fig. 2c, 2d; stress from two-dimensional solution, adults: 0.098, larvae: 0.09, Monte Carlo stress after 1,000 iterations for adults: 0.267, larvae: 0.262). Disturbance avoiders were *P. ruber* and *P. montanus*. Disturbance tolerators consisted of *D. quadramaculatus*, *D. fuscus*, *E. cirrigera*, *E. guttolineata* and *G. porphyriticus*. The ordination segregated the larvae of *D. marmoratus*, *D. monticola*, and *D. quadramaculatus* with forested streams

and hence they were considered disturbance avoiders whereas the rest (*D. fuscus*, *G. porphyriticus*, *Eurycea* and *Pseudotriton*) did not show distinctive segregation patterns and were regarded as disturbance tolerators.

Environmental correlates of land use types and richness

A number of habitat variables showed substantial variation among different riparian land-uses. Water chemistry parameters (dissolved Oxygen- DO, turbidity, and conductivity) showed notable variation among different land-use types of the Blue Ridge. Stream substrate particle size, streambed heterogeneity, substrate composition, stream bank complexity, and riparian features were pronouncedly different between forested and non-forest streams. The variability of habitat features across land-uses was more prominent in the Blue Ridge than in the Piedmont.

From the PCA on the habitat variables of Blue Ridge streams, we extracted the first 7 PCs that cumulatively explained 90% variability of the habitat features (PC1: 51%, PC2: 12%, each PC 3-7: 4-7%, SS 3). PC 1 showed significantly strong positive correlations with streambed heterogeneity, percent CWD, topsoil depth, canopy cover, canopy height, litter cover, and bank complexity, and negative correlations with streambed embeddedness and percent sand. These habitat variables represented the stream channel morphology and the structure of the riparian zones. PC 2 positively correlated significantly with discharge-related variables such as depth variation, velocity variation, and negatively correlated with conductivity. PCs 3-7 were related to stream substrates and physical attributes of water. For Piedmont streams, we extracted the first 10 PCs that

cumulatively explained 80% of the habitat variability (PC1: 18%, PC2: 10%, each PC 3-10: 4-9%). PC 1 correlated positively with habitat variables that govern the stream channel morphology, i.e., stream bank complexity, inorganic substrate size, and streambed heterogeneity and negatively with stream embeddedness. PC 1 also represented variables that characterized the riparian zone such as topsoil thickness and percent litter cover. PC 2 showed significant, strong correlations with velocity and percent rock. PCs 3-10 were related to stream substrate diversity, composition and water chemistry.

The stepwise regression (Table 3) for the Blue Ridge showed that PCs 1, 3, 5, 6 and 8 as best model parameters of the optimum models to predict species richness and SWI of adults and larvae. PC 2 appeared in all the models except in larval SWI model. For Piedmont, only PC 1 appeared in all the optimum models. PCs 2 and 8 were model components in larval SWI model. PCs 4 and 11 were eliminated only from the adult SWI models.

Protected area coverage of riparian zones

The conservation lands of the US only protect 30% of the Blue Ridge riparian buffers (Table 4). This situation worsens in the Piedmont where the unprotected extent of stream buffers is 96%. Nearly 80% of the protected Blue Ridge stream buffers are located within federal lands and another 10% protected by state and local governmental agencies. Similarly, 55% and 13 % of the protected Piedmont buffers fall within federal and state protected areas, respectively. In both ecoregions, 60% of protected buffer zones are

subjected my multiple uses; only 11-12% of protected buffer zones sustain historical disturbance regimes.

Discussion

Differential species diversity at different riparian land-uses

Our results suggested that Blue Ridge forested streams were most diverse with high heterogeneity in distribution. Streams associated with anthropogenic riparian land-uses were species depauperate (Fig. 2). Our general findings agreed with several other studies on amphibian responses to habitat conversion (Price et al. 2006; Barrett & Guyer 2008; Price et al. 2011). Species rich salamander community in the Blue Ridge forested streams can be attributed to high streambed heterogeneity, shaded by mature mixed mesic hardwood forests and fast-flowing highly-oxygenated, cold water (Hairston 1949; Bruce et al. 2000; Kozak & Wiens 2010).

Agricultural and residential streams undergo impellent changes in biogeochemistry, thermal regimes, microclimate, hydrodynamics, and microhabitat structure (Grimm et al. 2008; Gardiner et al. 2009). The land development in Blue Ridge is relatively patchy due to amenity-based establishments such as secondary homes, vacation cities, and golf courses (Semlitsch et al. 2007). Such habitat alterations produce highly-fragmented landscapes and extensive urban-rural interfaces where forested streams are embedded in a mosaic of land-uses with impeded habitat connectivity (Becker et al. 2007). Residential and agricultural land-uses are sources of agrochemicals,

fine sediments, and organic wastes that dramatically alter the trophic status of streams and ultimately suppress growth, reproduction, and survival of salamanders (Scott et al. 2002; Barrett et al. 2011). Low diversity of salamanders in the Piedmont across all riparian land-uses may be attributed to historical (1820-1940) cotton farming (Harding et al. 1998) and timber industries (Wear 2002). Despite post-farming forest regeneration, sediment influx from erosion gullies into streams exceeds the exportation leading to net streambed sedimentation decreasing microhabitat and resource availability (Jackson et al. 2005; Galang et al. 2007). Early European settlements substantially altered the landscape structure leaving unstable, eroded stream banks, mobile sand layers overlying streambeds, and high silt content in most Piedmont streams (Brender 1974). High degree of siltation and sedimentation are often associated with egg mortality and reduced growth stream salamanders (Willson & Dorcas 2003; Hamer & McDonnell 2008).

Surprisingly, the larval assemblages were more diverse in Piedmont non-forest streams compared to adults which could be a result of passive drift subsequent to storms with increased discharge from the Blue Ridge (Barrett et al. 2010b). Due to lack of suitable in-stream habitats, larvae may not survive to adulthood in Piedmont streams. Discontinuity of riparian forests may prevent active dispersal between Blue Ridge and Piedmont (Lannoo 2005). Species-rich Piedmont streams in our survey were located at Blue Ridge foothills where such movements are facilitated through continuous forested corridors to establish metapopulation dynamics (Grant et al. 2010). Inimical effects of land development have been recorded for multiple taxa in aquatic ecosystems. Multitude of evidence has reported decline in stream fish assemblage composition (Pease 2011),

macroinvertebrate diversity (Moore & Palmer 2005), and Biotic Integrity Index (Helms et al. 2005) preceding urban development in the watershed.

Species-specific responses to riparian land-uses

Most of the disturbance avoiders in the Blue Ridge were large (SVL 70-120mm) or medium (SVL 45-55mm) sized, and are specialists in microhabitat use (Lannoo 2005). Desmognathines and *Gyrinophilus* select large interstitial spaces underneath large rocks, boulders in the wet channel and undercut banks as their preferred microhabitats whereas other Spelerpines choose woody debris (CWD, LWD) as their preferred stream refuge (Mitchell & Gibbons 2010), and oviposit in rocky interstices and woody debris (Petranka 1998; Bruce 2003). Given their habitat selectivity, disturbance avoiders are vulnerable to siltation, low pH, and urban effluvia (Lannoo 2005). The food-base of salamanders is composed of terrestrial (lepidopeterans) and aquatic insect larvae (ephemeropterans and trichopterans) that are themselves sensitive to habitat quality (Wells 2007). When terrestrially active, disturbance-avoiders require protection from desiccation, high humidity, low temperature, deep leaf litter and LWD as terrestrial refugia and foraging grounds; these conditions can be provisioned by intact riparian forest canopy (Petranka 1998). Disturbance avoiders have great investments for long-term reproductive success: prolonged growth (5-6 yrs), delayed sexual maturity, longer (>1 yr) larval periods (Bruce & Hairston 1990; Lannoo 2005). These life history strategies may become a liability under anthropogenic stresses, such as riparian land development, since species could demise during sensitive prolonged larval stages or before sexual reproduction (Semlitsch

et al. 1988). Large-bodied species have extensive home ranges, greater resource needs and higher energy demands. These requirements make large-sized species susceptible to habitat alterations (Petranka 1998).

Disturbance tolerators are small bodied (SVL 30-40mm), have a slender morphology (Petranka 1998; Semlitsch et al. 2007), and are generalists in microhabitat section. Their larval and adult microhabitats comprised a broader variety of refugia in-stream and uplands such as cobbles, pebbles, gravel beds, woody debris, and crevices in the bank, and use the same microhabitats for oviposition (Wells 2007). Small body size does not require large interstices allowing them to tolerate some degree of sedimentation. Their terrestrial activities are not dependent on intact riparian vegetation (Bruce 2005). Gut content analyses revealed diverse prey preference, including pollution-tolerant invertebrates such as oligochaetes, hymenopterans, hemipterans, odonates, and chironomids (Lannoo 2005). Substantial population declines were not observed among disturbance-tolerant species elsewhere in North America that underwent notable land-cover transformation (Lannoo 2005).

Land-use associations of *D. quadramaculatus* and *G. porphyriticus* at the Piedmont were markedly different from those at the Blue Ridge. We recorded both above species across forest and non-forest riparian land-uses in the Piedmont (Fig. 3). Both species could be passively translocated to non-forest streams from forested streams during high stream discharge where dislocated salamanders were unable to migrate upstream due to inadequacy of in-stream refugia and riparian canopy cover (Bruce 1986). When *D. quadramaculatus* were translocated between two sites of same stream separated

by canopy gaps, they failed to return to the original location (Cecala 2012). As riparian disturbances appear to disproportionately affect competitively dominant large-bodied Desmognathines, small-bodied plethodontids (*D. fuscus*, *E. ciirrgera* and *E. gluttolineata*) are released from the competitive pressure, allowing them to monopolize scarce resources in non-forest streams such as microhabitats and food (Barrett et al. 2010a; Barrett et al. 2010c). These species have shorter larval periods (0.5-2 yrs), faster growth and reach early reproductive maturity, allowing a faster generation time; a great advantage ensuring reproductive success under stressful conditions (Petranka 1998; Wells 2007).

Environmental variables governing species responses to riparian land-use

The PCA and stepwise multiple regression identified the primary habitat associations of stream-dwelling salamanders. Our optimal stepwise regression models emphasized the importance of undercut banks, heterogeneous streambed, fast-flowing cold water, deep top soil, and mature riparian canopy. These features are characteristic of forested streams and sustain physiological optima for highly-diverse salamander communities (Hicks & Pearson 2003). Highly-heterogeneous stream substrates enriched with woody debris provide interstitial refugia necessary for cover, foraging, refuge for hibernation and aestivation, and reproduction. High velocity maintains high DO and removes sediments (Wells 2007). Our findings on the importance of protecting the riparian habitats align with other studies that underscored the necessity to conserve

terrestrial uplands associated with wetlands (Semlitsch & Bodie 2003; Baldwin et al. 2006; Howard et al. 2012).

Our models highlighted the impacts of soil erosion and nutrient-rich runoff on salamanders. High degree of sedimentation smothers interstices, destroys eggs, and prevents recruitment of macroinvertebrates (Bruce 1986; Petranka 1998). Plethodontids are intolerant to high temperatures and suffer mortality, reduced growth, and decreased activities (Welsh & Ollivier 1998). Human-impacted riparian zones have high volume-runoff contaminated with nutrients and pollutants, such as agro-chemicals, whereas forest-floor runoff is low in volume, less erodible, and low in nutrient levels (Collins & Storfer 2003; Clinton & Vose 2006). Forest cover along stream ecosystems is relatively extensive in the Blue Ridge and less impacted by historical land-use (Brown et al. 2005), hence providing suitable habitats plethodontids.

Conclusions and recommended conservation actions

Our findings emphasized the dependency of stream salamanders on conservation of riparian forests; streams in altered landscapes and those with longer histories of intensive land use may develop simplified salamander assemblages. Our results support those of recent studies, and expand inference to ecoregional differences. Piedmont streams exist in landscapes with longer and more intensive land uses, and have fewer species, and species apparently more adapted to human-dominated landscapes. More forested streams in the montane Blue Ridge landscapes have more species, and more of those adapted to relatively pristine conditions. Three main forms of riparian forest

conservation exist: policy, management, and land protection. These forms are interlinked, especially in riparian zones where more than one may come into play e.g., Best Management Practices, zoning, and GAP status of public lands.

Policy is a powerful tool for riparian conservation as it may be applied over many kilometers of streams and across jurisdictional boundaries. Many local governments of Southeastern US do not strictly mandate protection of low-order streams and riparian forests. Currently, the average stream buffer width in public properties ranges from 12-20m which is insufficient to meet life history needs of amphibians (Lee et al. 2004). Clean Water Act does not protect intermittent streams that do not have a “significant nexus” to navigable waterways; consequently be degraded due to urbanization, industrial development and agriculture (Elmore & Kaushal 2008). Other federal environmental laws (Pollution Prevention Act, Resource Conservation and Recovery Act, Wild and Scenic River Act, National Environmental Policy Act) provide riparian protections on a case by case basis but are not designed to maintain biodiversity. Policy reformations that might help conserve salamander habitat include 1) strengthening riparian zoning laws: exclusion of riparian zones from development, crop-production, intensive logging, and over grazing (Ekness & Randhir 2007); 2) regulating land-uses in the uplands to sustain upland habitat use by salamanders , TMDL regulations for local land-uses, and to enhance terrestrial connectivity among low-order streams; 3) restricting recreational activities and development of vacation homes in riparian zones and headwaters (Baldwin & Demaynadier 2009); 4) clustering development to minimize the road construction; and prevention of stream impoundments. Management activities including forestry Best

Management Practices, eradication of invasive species, bank stabilization, erosion and sediment controls, introduction of mix-aged native woody and understory species including some perennials to riparian zones, and restoration of historical geomorphology of degraded streams can have positive cumulative effects if implemented over great enough spatial scales (Aust 1994).

Conservation efforts involving multiple stakeholders and landowners such as the Conservation Reserve Program, National Conservation Buffer Initiative, and Integrated River Basin Management can be promoted for conservation of riparian forests. Such programs provide incentives to the landowners and equip them with the best available knowledge and tools necessary to make conservation-driven while encouraging ecofriendly agricultural practices: delineation of pesticide- and fertilizer-free zones; conservation tillage, erosion control and soil management; landscaping with native vegetation; and prevention of stream impoundments (Lee et al. 2004).

Conservation easements are a rapidly growing form of land protection in the US (Hollingshead 1996). Riparian forest conservation could become a top priority among land trusts in easement purchases, i.e., modifying easement to ensure preservation of riparian forests; prioritizing easement purchases in stream-embedded undeveloped private lands adjoining public conservation lands; and purchasing easements to protect headwater streams as patch reserves to facilitate overland dispersal and metapopulation dynamics (Olson et al. 2007; Rissman et al. 2007). The management level of the protected riparian buffers in both ecoregions should be uplifted from GAP III to GAP I where stream buffers are declared as zero-extraction zones with reestablishment of historical

disturbance regimes and ecosystem processes (flood-pulses, geomorphic channel processes, and supply of terrestrial and in-stream woody debris).

Benefits of protecting riparian zones extends beyond amphibian conservation, and include maintenance of water quality, discharge, and productivity; moderation of stream microclimate and dissolved oxygen; improved soil water infiltration, nutrient and sediment retention and downstream supply of inorganic nutrients and organic matter; bioremediation of toxic compounds; stabilization of stream channel and bank; serve as river corridors facilitating dispersal for multiple taxa; and sustain aquatic biodiversity. The Blue Ridge and Piedmont riparian forests are home to a number of rare and threatened species of reptiles (bog turtle, timber rattlesnake), small mammals (Indiana Bat), birds (Cerulean warbler), and flora (Apalachicola wild Indigo); persistent of these organisms are dependent on intact riparian zones.

Table 2.1: Habitat variables estimated in the wet channel, riparian zone and the methods of estimations. The second column refers to the methods performed at each sampling location. The average was calculated from the multiple measurements/estimations taken at a certain sampling location for a given habitat characteristic.

Habitat characteristics	Techniques, instruments used for measurements/ estimations
Stream velocity (m ³ /s)	100 random points using a flow meter.
Water depth	100 random points using a top-set wading rod
Streambed heterogeneity (organic and inorganic streambed substrates)	The zigzag method was used (Bevenger & King 1995). The type of substrates was recorded. The percent cover at the streambed of each substrate type was calculated subsequently. Based on the
Composition of inorganic substrates	The intermediate axis of particles was measured. Inorganic particles too large to pick up were measured on the streambed using the meter stick. If the substrate is bedrock, record as 999 mm
Organic substrates (e.g., detritus, animal inputs, leaves, wood, or aquatic vegetation)	Substrates were assigned to one of five categories according to size and composition: fine particulate organic matter (FPOM), coarse particulate organic matter (CPOM), fine woody debris (FWD), large woody debris (LWD), or aquatic vegetation (AV)
Particle size ratio of the Stream substrate	d_{84}/d_{50} , where d_i indicates the particle size larger than the i th percentile of particles. Length measurements of the intermediate axis of the streambed particles were used (Wolman 1954).
Streambed embedness	The depth of the sediments deposited on the streambed was measured at 50 random points.
Bank complexity	Assessed at 10 random locations of both stream banks on a scale of 0-10, 0 for lowest heterogeneity and 10 for the highest. Presence of undercut banks, presence of littoral vegetation, moss cover and roots of woody plants were considered as the metrics of heterogeneity.
Water quality parameters: Water temperature, turbidity, pH, conductivity, and dissolved oxygen	10 random locations in the wet channel using the 6-series multiparameter water quality sondes (YSI Incorporated)
Percent canopy cover	10 points (at every 10 th meter), at four cardinal directions per point with a spherical densitometer (concave Model C, Forestry Suppliers Inc.).
Canopy height	Using a clinometer on 10 woody tree species of the overstory layer at each bank, along the riparian transect.
Percent litter cover	Estimated at five, 5x5m litter quadrats placed at every 10 th meter, at each bank, along each riparian transect.
Litter depth	metric ruler at five random points inside all 5X5m litter quadrats, at both banks.
Topsoil thickness (A horizon)	metric ruler at five random points at each bank, along the riparian transect. A soil auger was used to excavate a soil profile.
Basal Area	cruising prism (BAF 10, Forestry Suppliers Inc.) at five points with 20m gaps, at each bank, along each riparian transect.

Table 2.2: Response of adult and larval stream Plethodontids to four riparian land-uses and percentage relative abundance of each species across the four land-uses. Analysis was based on a one-way ANOVA where the response variable was relative abundance of each species different riparian land-uses. Larvae of *D. fuscus* and *D. ocoee* were grouped as *D. fuscus* larvae. All larval species from genus *Eurycea* were also grouped. The relative abundance of 9 species among adults and 5 species/genera among larvae differed significantly among the riparian land-use types. ¹highly significant, $p < 0.0001$; ²marginally significant $p \approx 0.05$

Species Name	F (adults)	F (larvae)	Percent relative abundance of adults							Percent relative abundance of larvae							
			Blue Ridge				Piedmont			Blue Ridge				Piedmont			
			Forest	Residential	Agriculture		Forest	Residential	Agriculture	Urban	Forest	Residential	Agriculture		Forest	Residential	Agriculture
<i>D. quadramaculatus</i>	25.10 ¹	2.15 ¹	18.7	0	5.5	8.6	10.0	0	0	30	10.0	0	10.4	0	0	0	
<i>D. marmoratus</i>	29.00 ¹	19.71 ¹	4.8	0	3.6	0	0	0	0	11.7	4.0	0	4.2	0	0	0	
<i>D. monticola</i>	49.47 ¹	22.84 ¹	27.7	1.5	0	0	0	0	0	26.9	0	0	15.3	0	0	0	
<i>D. ocoee</i>	28.61 ¹	1.27	21.0	0	0	0	0	0	0	9.5	70.6	65.3	46.5	78.8	69.6	6.5	
<i>D. fuscus</i>	1.05		13.0	69.5	63.8	67.3	68.5	63.3	64.7								
<i>E. wilderae</i>	26.65 ¹		4.2	3.1	0	0	0	0	0								
<i>E. gluttolineata</i>	2.90 ²	1.37	1.9	11.5	9.0	4.7	5.4	3.9	3.2	8.9	24.5	34.7	17.8	16.7	21.1	27.8	
<i>E. cirrigera</i>	0.67		4.9	14.5	18.2	15.5	21.2	33.0	27.5								
<i>P. ruber</i>	8.17 ¹	4.28 ¹	1.1	0	0	0.8	0.8	0	4.9	1.8	0	0	1.0	1.3	0.9	4.9	
<i>P. montanus</i>	7.59 ¹		1.5	0	0	0.8	0	0	0								
<i>G. porphyriticus</i>	4.90 ¹	4.90 ¹	1.2	0	0	2.2	0.8	0	0	11.1	0.8	0	5.0	3.0	8.2	6.5	

Table 2.3: Model parameters chosen from the stepwise multiple regression analyses on the PCs (as predictor variables representing habitat variables) selected from PCA to predict the species richness and Shannon Index among adult and larval salamanders of Blue Ridge and Piedmont. All response variables were square-root transformed. The PCs correspond to the model parameters. AIC scores, coefficient of determination (r^2), and the P values were used to select the model with best predictability. All the presented models with outlined parameters (PCs) were significant when $P < 0.05$.

Response variable	Blue Ridge Ecoregion			Piedmont Ecoregion		
	PCs	r^2	F ratio	PCs	r^2	F ratio
Adult species richness	1, 2, 3, 5, 6, 8	0.84	20.03	1, 2, 4, 8, 11	0.41	9.15
Adult Simpson Index of diversity	1, 2, 3, 5, 6, 8	0.79	14.22	1, 2, 3, 5, 8, 6,	0.79	14.22
Larvae species richness	1, 2, 3, 5, 6, 8	0.88	31.40	1, 2, 4, 8, 11	0.41	13.35
Larvae Simpson Index of diversity	1, 3, 5, 6, 8	0.89	39.03	1, 4, 9, 11	0.30	7.15

Table 2.4: Degree of protection provided by national protected area network (USGS Protected Area Database) to stream buffer zones of different widths: 140m (Olson et al. 2007) and 240m (Semlitsch and Bodie 2003). The surface area under each landownership category and degree of land management based on GAP status (USGS GAP analyses) is provided. The parenthetical values correspond to the percentage cover of stream buffers within each landownership category and GAP status category calculated as a fraction of total protected land area within the two ecoregions. Percent values for protected and unprotected buffers were calculated as a fraction of the land area of each ecoregion.

Land stewardship categories	Land area (Km ²) and percent coverage			
	Blue Ridge		Piedmont	
	140m buffer	240m buffer	140m buffer	240m buffer
Landowner				
Federal	4030 (82.5)	8068 (81.6)	1345 (55.9)	2576 (56.2)
Jointly owned	1 (0.02)	2 (0.02)	2 (0.1)	3 (0.1)
Local government	80 (1.6)	174 (1.8)	50 (2.1)	0 (0)
Native American	69 (1.4)	131 (1.3)	0 (0)	95 (2.1)
Non-governmental organization	15 (0.3)	33 (0.3)	69 (2.9)	118 (2.6)
Private	422 (8.6)	892 (9.0)	599 (24.9)	1117 (24.4)
State	262 (5.4)	571 (5.8)	323 (13.4)	638 (13.9)
Unknown landowner	9 (0.2)	18 (0.2)	17 (0.7)	37 (0.8)
Total area of protected buffers	4886 (29.1)	9888 (29.3)	2405 (4.0)	4585 (3.8)
Total area of unprotected buffers	12245 (70.9)	22422 (70.7)	54526 (96.0)	104144 (96.2)
Required land acquisition for fee-simple or easement purchases to protected 50% the riparian buffers	3500	7200	25000	53000
Required land acquisition for fee-simple or easement purchases to protected 70% the riparian buffers	6900	14000	40000	11000
GAP (land management) status				
Disturbances proceed/mimicked	1036 (21.2)	1970 (19.9)	55 (2.3)	110 (2.4)
Disturbances suppressed	548 (11.2)	1106 (11.2)	283 (11.8)	551 (12.0)
Managed for multiple uses	2930 (60.0)	6028 (61.0)	1464 (60.9)	2818 (61.5)
No known mandate for protection	373 (7.6)	785 (7.9)	602 (25.1)	1101 (0.1)

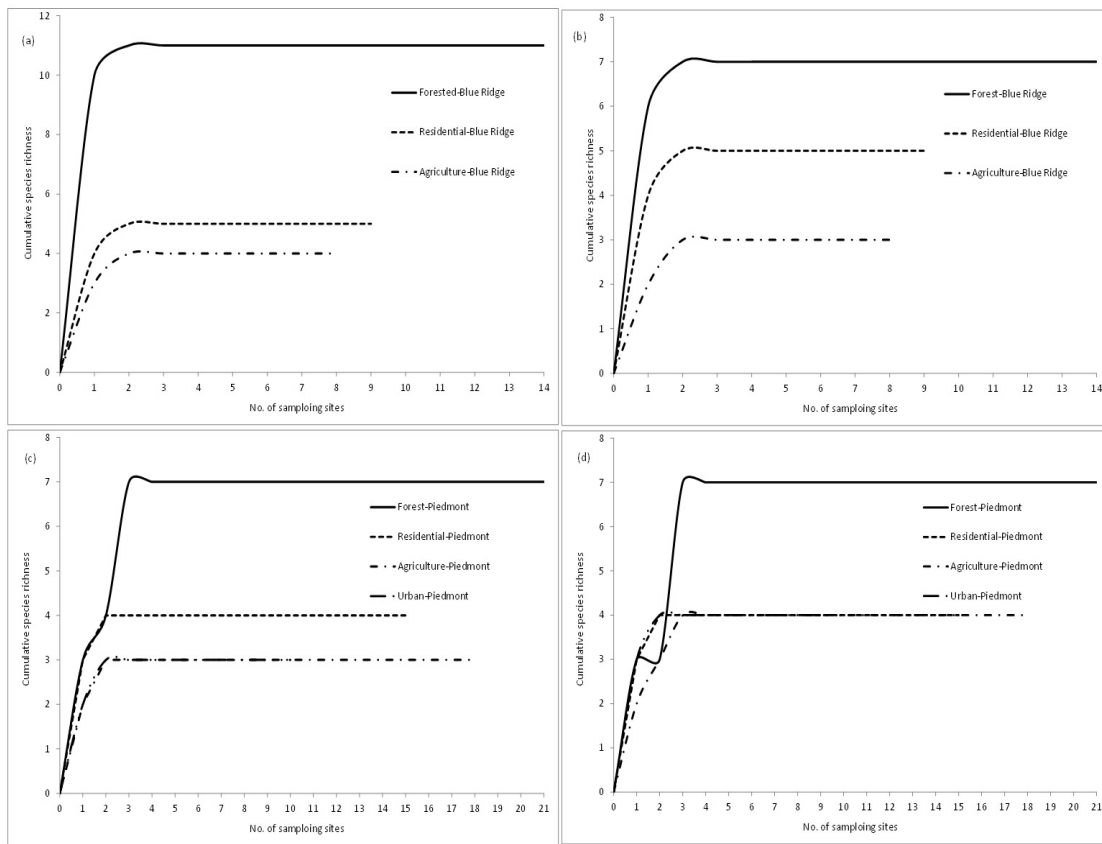


Figure 2.1: Species accumulation curves: (a) adults of the Blue Ridge streams, (b) larvae of the Blue Ridge streams, (c) adults of the Piedmont streams (d) larvae of the Piedmont streams

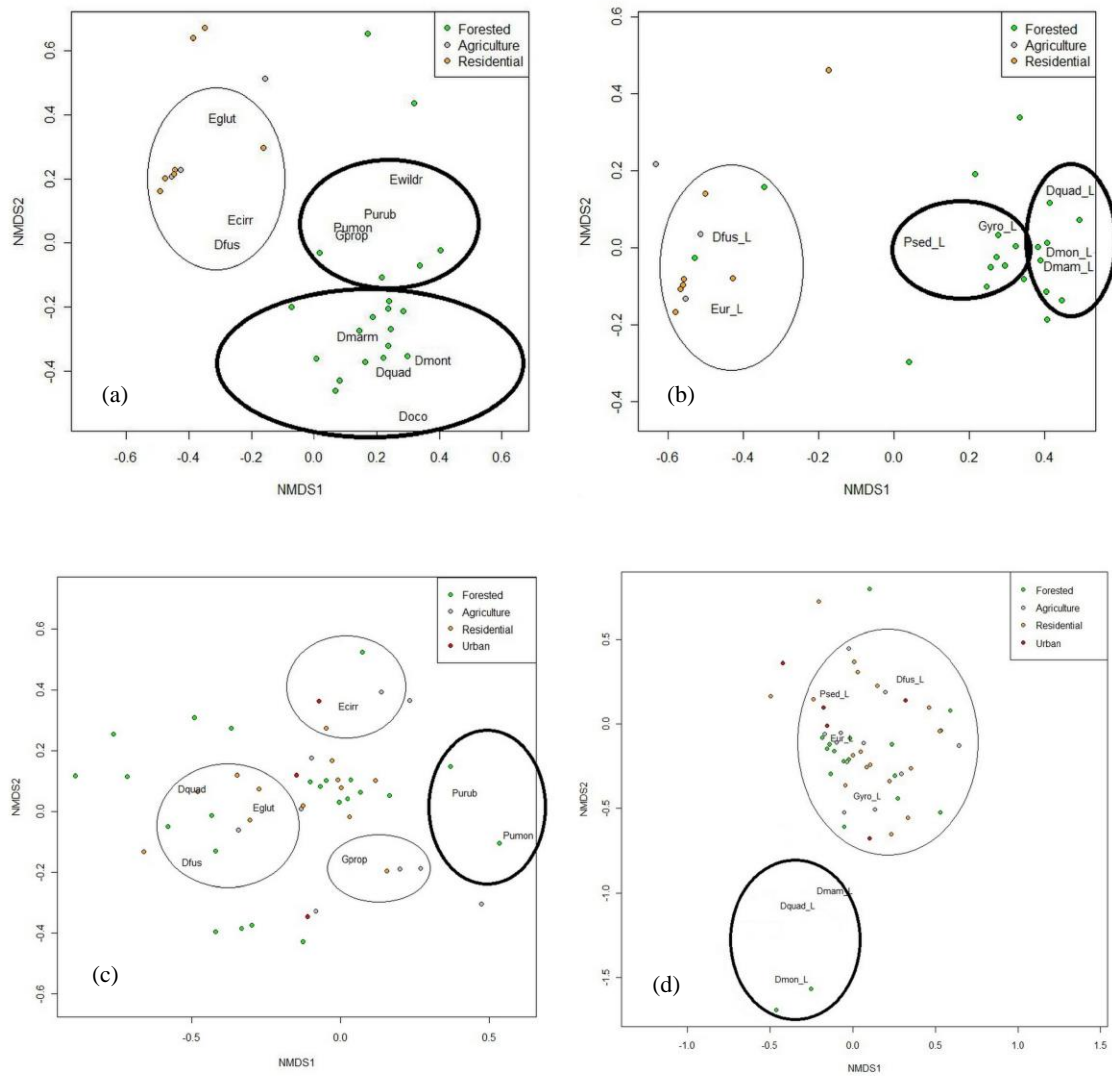


Figure 2.2: NMDS ordinations of salamander assemblages at Blue Ridge and Piedmont Ecoregions. The closer the euclidean distance between the species scores and the site scores in the ordination space, the stronger the ecological association among species recorded and the sites surveyed. (a) adults of Blue Ridge ecoregion, (b) larvae of Blue Ridge ecoregion, (c) adults of Piedmont ecoregion, (d) adults of Piedmont ecoregion; thick circles: disturbance avoiders. Motel-Carlo simulations with 1000 iterations revealed that our NMDS ordination plots are substantially different from random ordinations. Thin circles: disturbance tolerators; Species legend: adults- Ecirr: *E. cirrigera*, Eglut: *E. guttolineata*, Ewldr: *E. wilderae*, Dfus: *D. fuscus*, Dmont: *D. monticola*, Dmarm: *D. marmoratus*, Doco: *D. ocoee*, Dquad: *D. quadramaculatus*, Purub: *P. ruber*, Pmon: *P. montanus*, Gprop: *G. porphyriticus*, Larvae: Dmon_L: *D. monticola*, Dmam_L: *D. marmoratus*, Dquad_L: *D. quadramaculatus*, Dfus_L: *D. fuscus*, Eur_L: *Eucrycea*, Psed_L: *Pseudotriton*, Gyro_L: *G. porphyriticus*.

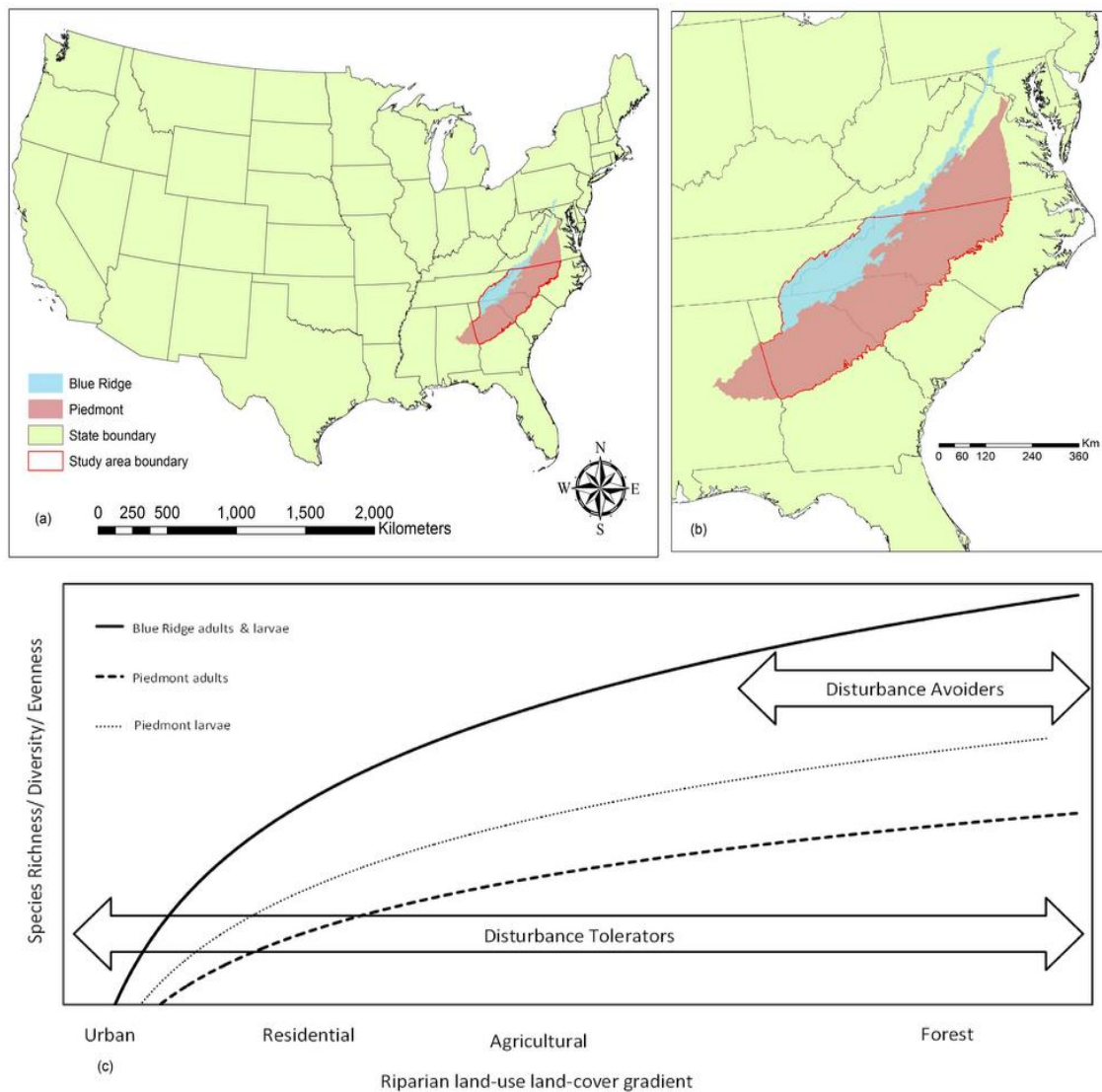


Figure 2.3: The study site and the salamander response groups (a), (b) Study site: Blue Ridge and Piedmont ecoregions in the conterminous US and in the southeastern US. (c) A diagrammatic representation on salamander segregation (based on species richness, diversity and evenness) across the riparian land-use and land-cover gradient in Blue Ridge and Piedmont ecoregions.

CHAPTER THREE

RIPARIAN LAND-USE CONDITIONS INFLUENCE COMPETITION FOR MICROHABITATS AND SPACE BETWEEN A GENERALIST AND SPECIALIST SALAMANDER IN A STREAM ECOSYSTEM

Introduction

A community is an assemblage of species interacting through biological processes such as competition, predation, mutualism, and facilitation, mediated by environmental conditions (Menge & Sutherland 1976; Connell 1978, 1980; Bruno et al. 2003). The species possessing greater competitive ability for a given habitat becomes the superior competitor for that particular habitat, but could become the subordinate species in another habitat with contrasting environmental conditions (May 1974; MacArthur 1984). Interspecific competition has been studied in a multitude of ecosystems and taxa based on both manipulated experiments and field observations: e.g., sessile invertebrates in the coastal intertidal ecosystems (Connell 1961; Navarrete & Castilla 1990), arboreal lizards (Pacala & Roughgarden 1982), granivorous desert fauna (Brown & Davidson 1977), terrestrial amphibians (Fraser 1976b, a; Hairston 1980b; Hairston 1980a), and wetland fauna (Morin 1983; Wissinger et al. 1996). Interspecific competition has also been substantially researched in the context of other ecological and evolutionary processes: predation (Peterson 1982), mutualism (Cushman & Addicott 1989), facilitation (Callaway & Walker 1997), productivity (Tilman et al. 1997a; Tilman et al. 1997b), parasitism (Settle & Wilson 1990), herbivory (Hairston et al. 1960) and disturbances (Dayton 1971).

Disturbances with an intermediate frequency and intensity increase community diversity by maintaining the community at a non-equilibrium status, preventing resource monopolization by competitively dominant species, and promoting the establishment of fast-colonizing, competitively-subordinate species (Connell 1978; Molino & Sabatier 2001). By contrast, human-induced disturbances exceeding background intensity, frequency, and extent have resulted in negative impacts on ecosystem processes and community diversity. Anthropogenic impacts have widespread influences on ecosystems, in particular freshwater systems and have resulted in global declines of many taxa, including amphibians, yet much remains unknown about ecological mechanisms for these declines in a community ecological context (Collins & Storfer 2003; Allan 2004). Interspecific competition needs to be explored in the context of environmental stresses such as anthropogenic disturbances. In this research, we focused on interspecific competition among Plethodontid salamanders occupying streams of Blue Ridge ecoregion of the Southeastern US under different levels of anthropogenic riparian land-use.

Of the limited number of studies on interspecific competition of stream plethodontids occupying the Blue Ridge (Krzysik 1979; Hairston 1980b; Hairston 1980a; Krzysik 1980; Hairston 1986, 1996; Bruce 2011), most are field-based without a response surface-based design, and hence lacked a greater control over confounding variables. Existing studies focused mostly on desmognathines with high similarity in natural history and body morphology (Hairston 1986; Roudebush & Taylor 1987b, a). Given the general consensus that large body size contributes to competitive superiority (Goulden et al.

1982; MacIsaac & Gilbert 1989), desmognathines with longer snout-vent length and larger girth have been proposed as competitively dominant (Hairston 1980b). Bruce (2011) described complete niche segregation among desmognathines based on microhabitat preferences and body size in stream habitats, where large-bodied species were considered primarily aquatic occupying stream channel and small-bodied species riparian and occupying stream banks. But, recent reviews of the literature suggested that there can be a greater degree niche overlap among desmognathines with dissimilar natural history strategies and morphology (Lannoo 2005; Wells 2007). A conservation concern is that large-bodied species may be more vulnerable to decline following disturbances than small-bodied species (Mazerolle 2001; Delgado-Acevedo & Restrepo 2008); large-sized, dominant species could be adversely impacted by anthropogenic disturbances relieving subordinate species from competition (Lytle 2001). Recognizing knowledge gaps in community ecology of desmognathines and how those might be influenced by environmental changes, we investigated disturbance-mediated interspecific competition between two sympatric desmognathine species that are different in body sizes and natural history, Black-belled salamander (*Desmognathus quadramaculatus*) and northern dusky salamander (*D. fuscus*) in experiments simulating stream and riparian land-use conditions (forested, agricultural and urban). As part of a concurrent field study of salamander occupancy patterns, we surveyed multiple stream habitats associated with differential riparian land-use types (forested, agricultural and urban) in the Southern Blue Ridge ecoregion to record relative abundance and microhabitat use of the two focal species in field conditions.

We used two different species with distinct life histories and habitat use so that our findings might be broadly applicable to sympatric species with differential sensitivity to disturbances. The black-bellied salamander is a habitat specialist (forested streams); large-bodied (SVL 110mm), slow-growing species with a lifespan of approximately 10 years, and accounts for the greatest animal biomass in low-order streams and contributes to stream trophic interactions via predating macroinvertebrates (Peterman et al. 2008). Northern dusky salamander is a habitat generalist (forest and non-forest streams); fast-growing and small-bodied, (SVL: 40mm) with a lifespan greater than two years (Petranka 1998; Lannoo 2005). Our specific objectives were: (1) investigate the variation in relative abundance and microhabitat use of the focal species across streams associated with differential land-use types; (2) investigate competition for microhabitats between the two species, and determine whether black-bellied salamanders are competitively superior over northern dusky salamanders for microhabitats in streams representing differential riparian land-use (we hypothesized that large-bodied black-bellied salamanders would dominate microhabitat use in forested streams and that they will be less dominant in the non-forest streams); (3) determine the change in the activity area of the two focal species (competition for space) in co-occurrence and isolation in stream habitats representing differential riparian land-uses (if black-bellied salamanders are competitively superior for space, then we expected the activity area of northern dusky salamanders to decrease when co-occurring); and (4) to determine the change in distance to the nearest heterospecific neighbor (DNN) between the two focal species in streams associated with differential

riparian land-uses (we hypothesized the DNN would differ substantially among different stream types).

Methods

Field survey

We surveyed 40 low-order stream reaches distributed across forested, agricultural and urban riparian areas in the Blue Ridge ecoregion, for the focal species. To select spatially independent stream reaches, we used a VisualBasic query (SC Department of Natural Resources; ArcGIS 10, ESRI) which cross-examined all potential sampling sites based on the percentage of the shared drainage area and selected those that shared no more than half of the same drainage. We conducted a survey comprised of three passes along a 100 m stream reach at each sampling point during which the wet channel and the stream banks were searched using dip nets, kick nets and bottom set nets. We overturned all movable cover objects in the wet channel and stream banks including rocks and logs, and scrutinized surfaces of woody debris, leaf litter, moss, and understory vegetation (Heyer et al. 1994; Dodd 2010). The surveys were conducted daily from 0800 to 1800 h, during April to July for two consecutive years (2010, 2011). We recorded the abundance of the focal species and the microhabitat type each individual was found (channel bottom, stream-bank interface, and stream bank). In addition, we assessed the stream substrate heterogeneity at each sampling reach (Bevenger & King 1995). We used those environmental characterizations in experimental stream simulations.

Overview of the experimental methods

We employed a laboratory-based experimental design to investigate interspecific competition between the two salamanders in the context of riparian land-use. The experiment was conducted at the Aquatic Animal Research Laboratory (AARL) of Clemson University, SC. We simulated three riparian land-use conditions in artificial streams: forested, agricultural and urban. The forested stream represented the least disturbed habitat. Agricultural and urban simulations were constructed to re-create within-stream conditions (e.g., sedimentation, degree of heterogeneity) associated anthropogenic disturbances in the riparian zone (described in detail below). We used wild-caught adults of both species captured from Blue Ridge streams for our experiment. Prior to recording observations, we acclimatized the animals to experimental units and food for a week. Experiments were replicated 6 times.

Experimental Design

We conducted this experiment in artificial streams (hereafter referred to as EU, abbreviation for experimental units). EUs were rectangular fiberglass tubs 1.8 m in length, 0.53 m in width, and 0.38 m in depth. We used two EUs to temporarily and separately house the experimental animals. We collected water and substrates i.e., sand, rocks, gravel, and coarse woody debris (CWD) from streams associated with the three focal riparian land-uses located within the Blue Ridge ecoregion.

Using the collected substrate material, we constructed EUs to closely resemble the morphology of stream channels and stream banks that we observed during the field survey. Riparian land-use has a strong impact on the wet channel and stream bank habitat structure, substrate composition and availability, and channel morphology (Allan 2004; Allan & Castillo 2007). We constructed the forested EU to have the most heterogeneous wet channel habitat and stream bank structure with the highest diversity of substrate types including, large to medium sized rocks (40%), coarse gravel (15%), and abundant supply of woody debris and leaf litter (45%). We arranged the urban EU to have the most homogenous stream habitat and stream bank structure with sand, silt, mud (90%) and fine gravel (10%) as substrate materials. We arranged the agricultural EU with intermediate structural complexity in the bank and the in-stream habitat with an intermediate extent of substrate diversity containing coarse gravel (10%), a few partially or fully embedded small rocks (10%), sand (75%), and scarce amount of leaf litter (5%) but no woody debris. In all EUs, substrates were laid to a height of no more than 80 mm and water was filled to a depth of 100 mm above the substrate. Roudebush and Taylor (1987a) used similar EUs for their experiment on desmognathines. We kept all EUs under fluorescent lights from 0700-2000 h and in dark for the remainder of the diel cycle. This approximately simulated the day-light exposure for these species in their habitats during their summer active periods.

Each replication of our experiment had three phases (Fig. 1); two of species isolation and one of co-occurrence. In the first phase, we introduced both species (six individuals from each species) simultaneously to the EUs, and recorded observations. In

the second phase, we removed northern dusky salamanders and retained black-bellied salamanders in EUs. In the third phase, we reintroduced northern dusky salamanders and removed black-bellied salamanders. Each phase lasted five days; a single replication lasted 15 days. The number of individuals of each species was determined based on the density of each species in forested streams during that we observed during the field survey.

Maintenance of Experimental Units

Air temperature was maintained at 23°C, approximating the average summer temperature of the southern Blue Ridge (based on average summer temperature in GA, NC, and SC; National Weather service and NOAA 2012; <http://www.weather.gov>). We aerated all EUs continuously and recorded dissolved oxygen, water temperature, pH, water depth, nitrate concentration, and ammonia concentration daily and assessed those measures for departures from comparable field conditions. Before each experimental phase, we exchanged the water in the EU with new water collected from equivalent field sites. We introduced fresh substrates in the beginning of each replication to eliminate effects of body secretions from the experimental animals. Throughout the experiment, the animals were fed three times a week with live invertebrates including crickets, earthworms, and black worms. In the event of death of a salamander, it was immediately replaced with a similar sized individual from the same species.

Observations recorded

We made observations daily in 1.5-hour intervals from 0900 h to 0200 h, and each observation session lasted 20 min EU⁻¹. We recorded a total of 60 observation sessions per phase for each EU (12 observation sessions day⁻¹ * 5 days phase⁻¹), and recorded (1) aggressive behavior, (2) microhabitat occupancy, and (3) spatial occurrence. If a particular individual was not detected during a given session, we omitted all data from that session to maintain equal number of observations across all treatments.

We observed all the individuals for a repertoire of aggressive behaviors elicited by plethodontids in their natural habitats: gape display, snout-pressing, lunging, trunk arching, tail swinging, all-trunk-raised display, tail-raised display, tail arching, seizing by limbs/body/tail, and head swinging/jerking (Jaeger & Schwarz 1991; Jaeger & Forester 1993). To record microhabitat occupancy, we noted individuals' location as stream channels, stream banks, or bank-channel interface. To record spatial occurrence, we calibrated the perimeter of each EU in centimeters, and recorded the position of each salamander as Cartesian coordinates (Fig. 2). We used these coordinates to determine the species activity area via the minimum convex polygon (MCP) method, and to calculate DNN.

We trained 42 undergraduates to make observations. Our training goals were (1) accurately identify species, (2) detect all individuals, and (3) reduce inter-observer variability. Training for accurate identification included teaching main distinguishing characteristics using museum specimens, color photographs, and live specimens in the field. Increasing detectability and reducing inter-observer variability included training to

locate partially exposed animals in the field, and doing the same in EUs before each experiment. Undergraduates worked alone with periodic supervision.

Statistical analyses for the field survey

We used a one-way ANOVA to test for any significant differences in the relative abundance of the focal species across the three riparian land-use types (riparian land-use type as predictor variable and the relative abundance as the response variable); followed by a Student's *t* test to determine which riparian land-use type hosted the highest relative abundance for each focal species. We used a nested ANOVA to determine differences in microhabitat use by focal species across different riparian land-uses (riparian land-use type as the main predictor variable, microhabitat type as the nested variable and relative abundance at each microhabitat type as the response variable), followed with LSmeans contrast tests to reveal significant differences in microhabitat occupancy within each riparian land-use type.

Spatial and statistical analyses for the experiment

Using the Cartesian coordinates for animal locations within the EUs, we calculated the MCP for all three phases (objective 2) and DNN for all individuals for the species co-occurrence phase (objective 3) for each observation session across all land-use simulations (Ryti & Case 1992; Southwood & Henderson 2000). We calculated the frequency (percent of counts) of black-bellied and northern dusky salamanders at each microhabitat in each phase based on the total number of occasions a given species was

recorded at stream banks, bank-channel interface, and stream channels during the observation sessions (eq. 1, 2, and 3; objective 1).

Frequency a certain species was recorded in stream banks = $\frac{(\text{No. of times recorded at stream banks})}{(\text{Total No. of times recorded at all microhabitats})} \times 100\%$ eq.1

Frequency a certain species was recorded in bank-channel interface = $\frac{(\text{No. of times recorded at bank-channel interface})}{(\text{Total No. of times recorded at all microhabitats})} \times 100\%$ eq.2

Frequency a certain species was recorded in stream channel = $\frac{(\text{No. of times recorded at stream channel})}{(\text{Total No. of times recorded at all microhabitats})} \times 100\%$ eq.3

To test competition for microhabitat use as mediated by riparian land-use, we ran a three-way chi-square contingency test. The land-use type and the species present (either species present, black-bellied salamanders only, or northern dusky salamanders only) were considered predictor variables and the frequency at each microhabitat type was used as the variable responding to interspecific competition.

To test if black-bellied salamanders were competitively dominant over northern dusky salamanders, we ran two-way chi-square contingency tests for each riparian land-use type. We used average frequency of northern dusky salamanders at each microhabitat in isolation and co-occurrence as the dependent variable and presence-absence of black-

bellied salamanders as the independent variable for all three riparian land-use simulations. To test the effect of the day and time of observations on microhabitat occupancy, we ran an ordinal logistic regression for all EUs where day and time of observations and species present were the independent variables and frequency at each microhabitat was the predictor variable.

To determine the change in species activity area in response to riparian land-use and presence of heterospecifics (objective 2), we used a two-way repeated-measures MANOVA. We used repeated metrics of MCP in each observation session as dependent variables, and riparian land-use type and species present as independent variables. We also conducted a one-way repeated-measures MANOVA separately for each EU to investigate change in activity area of northern dusky salamanders with respect to presence/absence of black-bellied salamanders.

To investigate the change in DNN in response to riparian land-use type and presence of heterospecifics (third objective), we used a two-way repeated-measures MANOVA. We used repeated measurements on average DNN in each observation day for each species as continuous dependent multivariate variables, and the riparian land-use type and species present as independent variables. We also conducted a one-way repeated-measures MANOVA to separately investigate change in average DNN at each EU due to competition. We set alpha at 0.05, and performed statistical analyses in JMP 10 (SAS Institute Inc., NC) and spatial analyses in ArcGIS 10.0 (ESRI, CA).

In the following sections, we use the term “EU” to refer specifically to our experimental units. We use the word “stream” to refer to stream ecosystems and habitats in general.

Results

Field survey on relative abundance and microhabitat use across different riparian land-uses

We noted dissimilar responses of the focal species to riparian land-uses (Table 1). The relative abundance of black-bellied salamanders differed significantly among the three riparian land-uses (ANOVA: $F=25.10$, $p<0.05$) whereas that of northern dusky salamanders did not differ significantly among riparian land-uses (ANOVA: $F=1.05$, $p>0.05$). The relative abundance of black-bellied salamanders was higher in the forested streams than in the agricultural and the residential streams (Student's t test: $t=1.99$, $p<0.05$). Microhabitat use was also different between the focal species across riparian land-uses. Microhabitat occupancy of black-bellied salamanders varied significantly across the three riparian land-uses (Nested ANOVA: $F=55.82$, $p<0.05$) whereas no significant difference was observed in microhabitat use of northern dusky salamanders across different riparian land-uses ($F=1.03$, $p>0.05$). We noted that black bellied salamanders, when in forested streams, mostly occupied the channel bottom (LSmeans contrast test: $F=273.70$, $p<0.05$), but when in non-forested streams occupied stream banks and bank-channel interfaces ($F=15.41$, $p<0.05$). The northern dusky salamanders

were predominantly associated with stream banks across all the riparian land-uses ($F=38.10$, $p<0.05$).

Experimental evidence: Competition for microhabitat use

Both riparian land-use and land-use type (3-way $\chi^2=862.57$, $p<0.05$) and the presence of a heterospecific (3-way $\chi^2=397.80$, $p<0.05$) had a significant influence on microhabitat selection, indicating that these two sympatric species compete for microhabitats and this interspecific competition can be affected by riparian land-use. The two-way chi-square test suggested that black-bellied salamanders are competitively superior, excluding northern dusky salamanders from microhabitats in the channel bottom and bank-channel interface in forested (Fig 3a; $\chi^2=17.19$, $p<0.05$) and agricultural (Fig 3b; $\chi^2=18.27$, $p<0.05$) settings, but not in urban settings. Urban microhabitat use by northern dusky salamanders was not influenced by presence of black-bellied salamanders ($\chi^2=1.38$, $p>0.05$), indicating lack of competitive dominance of the black-bellied salamanders for microhabitat use in urban streams. Further, we observed that when both species were in the urban setting, where there is little heterogeneity in the stream channel, they preferred the stream banks (Fig 3c).

We noted that microhabitat type apparently preferred by black-bellied salamanders changed when in different riparian land-use settings (forested: channel bottom, agriculture: bank-channel interface, urban: stream banks) whereas that of northern dusky remained consistent (stream banks) across all simulated stream habitats (Fig 3). Ordinal logistic regression results did not indicate significant effects of the day of

observation and the time of observations on the microhabitat use of salamanders ($\chi^2=377.71$, $p>0.05$); observed differences in microhabitat use can be attributed to simulated stream type and presence/absence of the conspecific.

Experimental evidence: Change in the species activity area

The two-way repeated-measures MANOVA suggested that presence of the heterospecifics ($F=8.29$, $p<0.05$) and riparian land-use type ($F=87.97$, $p<0.05$) significantly influenced the activity area for both focal species. Black-bellied salamanders showed competitive dominance for activity area in forested and agricultural settings; when we ran separate one-way repeated-measures MANOVA, activity areas of northern dusky salamanders were significantly smaller when co-occurring and larger when in isolation in forested ($F=1683.02$, $p<0.05$) and agricultural treatments ($F=4408.99$, $p<0.05$). In the urban EU, the activity area of northern dusky salamanders did not change significantly between isolation and co-occurrence ($F=0.09$, $p>0.05$) indicating the lack of competitive dominance for space of black-bellied salamanders in an urban context.

We noted the greatest and least change in the activity area between isolation and co-occurrence for black-bellied salamanders in urban and forested EUs, respectively. Northern dusky salamanders showed the least change between isolation and co-occurrence in the activity area in the urban EU while their changes in the activity area at forested and agricultural EU were equally large (Fig. 4).

Experimental evidence: Distance to the nearest heterospecific neighbor

One-way repeated-measures MANOVA indicated that the DNN was significantly different among three riparian land-use types ($F=37111.02$, $p<0.05$). The DNN was shortest in urban EU and farthest in the forested EU. The DNN for animals in the forested EU was 5 times greater than for those in the urban EU. The DNN of the agricultural EU was intermediate, yet animals tended to be spaced at greater distances. DNN in the agricultural setting was more similar to that of the forested EU ($\Delta 44$ mm) than to the DNN of the urban EU ($\Delta 110$ mm; Table 2).

Observations of behavioral types

Of 360 observation sessions during co-occurrence phases, we observed only 4 instances of aggression, all by black-bellied salamanders and all directed towards northern dusky salamanders, rather than conspecifics. We observed three instances of non-fatal aggression, and one in which a black-bellied salamander killed and ate a northern dusky salamander. During the three instances of non-fatal aggression, black-bellied salamanders invaded microhabitats occupied by northern dusky salamanders. Upon invasion, the resident northern dusky salamanders left. The aggression behavior of black-bellied salamanders can best be described as lunging and jerking, and the response by northern dusky salamanders as retreating and yielding. The predation event involved a black-bellied salamander that lunged at a northern dusky salamander, grabbed it below its' head, held it for approximately five minutes, and ingested it head-first. Since sample size of aggressive interactions was low, we did not conduct statistical analyses. Apart

from aggression, we noted that black-bellied salamanders actively dug holes in the banks of the urban stream using their snout and forelimbs. On the contrary, we never observed northern dusky salamanders dig; they used existing crevices.

Discussion

Our study showed that black-bellied salamanders might be competitively superior over northern dusky salamanders for use of microhabitats and space in forested and agricultural stream conditions, but not in urban settings. We observed a reversal of competitive superiority from black-bellied salamanders to northern dusky salamanders in urban stream conditions. Although black-bellied salamanders retained their dominance in agricultural EUs, we observed that they changed microhabitat use and activity area in the absence of northern dusky salamanders (Fig. 3, 4). We inferred that competitive dominance of the black-bellied salamanders is limited to forested and agricultural streams, but may be strongest when in more natural, forested systems. Competition and thus community composition may be influenced by environmental conditions.

Generalizing from an experimental setting to real ecosystems, we suspect that anthropogenic disturbances in the riparian zone can alter competitive interactions among stream-dwelling salamanders, and those influences may increase as degree of disturbance increases (i.e., conversion of riparian forests to agriculture, and to urban). Our field survey revealed similar patterns in microhabitat use across different land-uses, to those observed during the experiment. Additionally, field surveys provided the insight that there was pronounced reduction in the abundance of black-bellied salamanders in non-

forest streams possibility indicating long-term effects of reversal of competitive superiority.

Competition for microhabitats and activity area

We observed a marked change in competition for microhabitats and species activity area between the focal species across riparian land-use types. The shift in microhabitat use of black-bellied salamanders was notable in that they moved from stream channel in the forested EU towards stream banks in non-forest EUs. In the absence of black-bellied salamanders, northern dusky salamanders shifted from stream banks to stream channel in the forested EU and to the bank-channel interface in the agricultural EU. We noted a marked increase in activity area among northern dusky salamanders in isolation at forested and agricultural EUs. Such observations further supported that black-bellied salamanders are competitively superior to northern dusky salamanders in forested and agricultural streams. Black-bellied salamanders are highly territorial, defending their refugia and foraging sites (Southerland 1986a; Bruce 1988; Petranka 1998; Raffaelli 2005) which may explain the limited activity area for northern dusky salamanders in the co-occurrence treatment, in forest and agricultural EUs. The average territory size of black-bellied salamanders in their native habitat (1000 m^2) far exceeds that of northern dusky salamanders (50 m^2) indicating that the former has evolved to defend more physical space (Hairston 1986; Southerland 1986a; Raffaelli 2005; Bruce 2011).

In relatively pristine streams, large-bodied desmognathines occupy stream channels and small-bodied desmognathines primarily stream banks (Bruce et al. 2000), an observation substantiated by our field survey. Desmognathines are highly susceptible to desiccation hence seek refuge with minimum ambient exposure (Foster et al. 2002) and maximum contact with fast-flowing highly-oxygenated water (Feder 1983). Retention of water during low-discharge, continuous nutrient supply, and less fine sediment contribute to making stream channels better habitats (Allan 2004); consequently, there are benefits to be obtained for dominant large-bodied desmognathines competitively excluding small-sized salamanders from the stream channel.

Previous in-situ studies on microhabitat use of desmognathines provide field-based evidence similar to our results. Large-bodied shovel-nosed salamanders (*D. marmoratus*) are found mostly in stream channels. Medium sized black mountain dusky (*D. welteri*) and seal salamanders (*D. monticola*) occur both in stream channels and the bank-channel interface. Small-sized species such as Ocoee (*D. ocoee*) and seepage salamanders (*D. aeneus*) inhabit stream banks (Organ 1961; Hairston 1986; Bruce et al. 2000). Organ (1961) and Means (1975) considered niche diversification under competitive pressure as the mechanism of size-related distribution of desmognathines. Alternatively, Tilley (1968) and Hairston (1996) suggested avoidance of larger, ancestral predatory species by recently-evolved smaller species.

Our findings suggested strong differences for habitat selection under co-occurrence in forested EU; the difference in habitat selection in co-occurrence diminished as riparian land-use became more intense. Hence, niche overlap may differ substantially

across riparian land-uses. Partial niche segregation and interspecific completion have been observed among other amphibian species: overlapped food and breeding niches among *Triturus* newts in wetlands (Jehle et al. 2000), microhabitat use among larval ambystomatid salamanders and anurans (Wilbur 1972; Morin 1983), use of the forest floor and nesting sites by terrestrial plethodontids (Hairston 1996), use of cover objects, substrate interstice, and riparian uplands among desmognathines (Krzysik 1979; Southerland 1986a, c, b; Roudebush & Taylor 1987a, b) and drainage occupancy by northern and southern dusky salamanders in Florida (Means 1975).

Despite the observed shift in microhabitat occupancy of northern dusky salamanders between co-occurrence and isolation at forest and agricultural EUs, they retained a preference for stream banks in isolation. Absence of complete shift in microhabitat use by northern dusky salamanders may be attributed to carry-over effects of chemically-mediated territorial markings by black-bellied salamanders in stream channels (Roudebush & Taylor 1987b). Plethodontids use pheromones and allomones to mark territories on substrates (Southerland 1986a; Jaeger et al. 1998; Ransom & Jaeger 2006). Although not clearly demonstrated, we suspect that subordinate species may refrain at least for a period of time from occupying areas vacated by dominant species.

We observed marked change in microhabitat use of black-bellied salamanders, dominant in forested settings, between isolation and co-occurrence in non-forest EUs. Non-forest streams have lower substrate heterogeneity and fewer refugia for aquatic fauna (Moore & Palmer 2005). Woody debris provides cover and foraging substrate for salamanders (Corn & Bury 1989), and contributes to channel stability, heterogeneity, and

productivity (Gurnell et al. 2006). Given lack of multiple primary and secondary refugia and foraging sites in non-forest stream channels, black-bellied salamanders are forced to seek alternative microhabitats in stream banks (Petranka 1994; Naiman & Décamps 1997). Deforestation of riparian forests can deprive streams of woody debris and organic matter while facilitating upland erosion and smothering channel bottom interstices (Dudgeon et al. 2006; Allan & Castillo 2007); our results support that for at least black-bellied salamanders, lack of stream channel heterogeneity may have conservation implications.

The remarkable reversal of competitive superiority from black-bellied salamanders in least-impacted forested experimental conditions to northern dusky salamanders in highly-impacted urban conditions may be attributed to multiple factors. Northern dusky salamanders are well adapted to inhabit moisture-deprived stream banks (Orser & Shure 1972, 1975; Petranka 1998) and, as we observed are less likely to dig than black-bellied salamanders. Crevices in our simulated urban stream banks were fewer in number, smaller in size and suitable for small-bodied northern dusky salamanders (Krzysik 1979). These crevices were not sufficiently large to accommodate black-bellied salamanders and they constructed crevices. Energy expended digging burrows through compact soil could cost black-bellied salamanders and might explain, at least in part, their low occurrence in urban streams. The urban runoff and biologically hazardous pollutants in urban streams may induce a physiological stress for black-bellied salamanders since the larger body of this species may have increased the level of exposure to pollutants (Pickett et al. 1997; Homan et al. 2006; Booth et al. 2007a; Booth

et al. 2007b). Moreover, as a primarily aquatic salamander, black-bellied salamanders do not possess physiological and anatomical adaptations to xeric conditions, such as would occur in more open urban stream banks (Southerland 1986c, b) and they might limit the production of skin secretions that serve as territorial cues, to preserve water when in xeric conditions (Wingfield et al. 1997).

There are several analogous studies in which dramatic alterations of competitive dominance and other community interactions following disturbances have been observed. In coastal Californian streams, blackflies thrived following physical disturbances, and dominated streambed use over net-spinning caddis flies (Hemphill & Cooper 1983). In the Southwestern US, mosquitofish dominated Sonoran topminnows by predation and competitive displacement under low-frequency disturbance regimes, yet with increased frequency of flashfloods, mosquitofish lost competitive superiority (Meffe 1984). Sredl and Collins (1992) noted that alterations in the habitat structure driven by disturbances affected competition and predation among wetland amphibians. Disturbances with intermediate frequency and intensity accentuate the establishment of competitively superior species and promote colonization by competitively inferior species leading to species coexistence (Connell 1978; Resh et al. 1988). Environmental harshness and unpredictability are regarded as primary ecological determinants of competition (Callaway & Walker 1997), yet may not always favor the species that is dominant in a natural setting. In our study, we observed that the smaller species competitively displaced the larger species in the urban treatment, despite a wealth of literature suggesting that larger body size conveys advantage in salamanders (Hairston 1996; Bruce 2011).

Instances of competitive displacement of large-sized species by smaller species are few in the scientific literature; however Means (1975) reported competitive exclusion of large-bodied southern dusky salamanders (*D. auriculatus*) by smaller congeneric northern dusky salamanders.

Aggressive behavior and predation

The number of instances of aggression and predation we noted in our experiment was low compared to multiple agonistic behavioral types that plethodontids are known to display (Jaeger & Forester 1993). Speckled black salamanders (*Aneides flavipunctatus*) display 12 threat postures (Staub 1993). Jaeger and Schwarz (1991) described five all-trunk-raised gradual threat displays in red-backed smaller salamanders such as Allegheny mountain dusky salamanders (*D. salamanders* (*Plethodon cinereus*)). Black-bellied salamanders have been observed preying on *ochrophaeus*) and relatively larger species such as seal and northern slimy salamanders (*P. glutinosus*). However, similar to our study, (Southerland 1986a) did not observe aggression among four species of stream-associated desmognathines in an experimental setting.

Active threat displays and physical combats are energetically expensive (Marler & Moore 1988) and to avoid such cost, animals may use morphology and body asymmetry as signals (Mathis & Britzke 1999). Black-bellied salamanders collected for our experiment were twice as large as northern dusky salamanders in snout-vent length and this prominent difference could have sufficed. Black-bellied salamanders produce a secretion that has been observed to repel sympatric salamanders; this may have also

served as an unobserved communication mechanism (Southerland 1986a, b). Another possible reason for lack of observation of aggressive behavior is familiarity. Jaeger (1981) noted that plethodontid salamanders are less aggressive towards neighboring conspecifics. Although this has not been demonstrated between our species, scarcity of aggression in our experiment may be a result of “dear enemy recognition”.

Distance to the nearest heterospecific neighbor

We noted that the average DNN between black-bellied and northern dusky salamanders decreased as a function of riparian land-use type. The greatest difference was between forested and urban conditions, with the longest DNN in the forested EU and shortest in the urban EU. Agricultural influence on nearest heterospecific distances appeared intermediate, as average DNN of the agricultural EU was shorter than that of the forest EU. In the forested EU, the availability and diversity of microhabitats were high throughout the stream habitat which we believe facilitated establishment of larger, relatively exclusive activity areas for both species, increasing the DNN. Decreased availability of microhabitats and concentration of the available refugia in stream banks in non-forest EUs could explain decreased DNN, as both species aggregated in stream banks and the bank-channel interface. Although we did not measure, both species may have been physiologically stressed due to environmental harshness in urban and agricultural settings and unable to defend extensive territories (Powell et al. 2000). Similar relationships between DNN and competition have been recorded between red-backed and northern dusky salamanders, and red-backed and southern two-lined

(*Eurycea cirrigera*) salamanders (Jaeger et al. 1998). Also, the home range of seal salamanders expanded in response to decreasing cover density to aggregate resources leading to increased distance between conspecifics and congeners (Jaeger et al. 1998).

Conclusion

Environmental conditions appear to have influenced interspecific competition for space and microhabitat refugia, for two salamander species occupying overlapping ranges in the Southeastern United States. In stream simulations representing natural, forested settings, black-bellied salamanders appeared to have excluded northern dusky salamanders from the stream channel microhabitats. In simulated agricultural stream conditions, black bellied salamanders shifted their activity to, and competitively displaced northern dusky salamanders from the bank-channel interface. In the urban stream setting, competitive advantage appeared to reverse, and northern dusky salamanders excluded black-bellied salamanders from the only microhabitat where refugia were available, the stream banks. Our research indicates that increasing anthropogenic disturbances in stream systems may markedly affect interspecific competition, microhabitat use, spatial occupancy and interspecific neighbor distance. More research on stress response would clarify to what degree, if any, the environment induces physiological changes. As important microhabitats may become more or less available to given species under varying land-use conditions, community interactions change. Such alterations in community interactions need be taken into consideration in biodiversity conservation and natural resource management. Altered community

interactions may result in shifts in community composition with disturbance-adapted species becoming more prevalent (McKinney 2002a). Consequently, anthropogenic disturbances can reduce beta diversity leading to biotic homogenization (McKinney & Lockwood 1999), a process noted for stream fish assemblages of Southern Appalachian Mountains (Scott 2006) and in the Pacific Northwest where synanthropic birds capitalized on the expansion of urban and agricultural land-cover types (Hepinstall et al. 2008). Should urban expansion continue to convert forested riparian areas, we concur with others that stream salamander communities could likewise simplify (Barrett & Guyer 2008; Barrett et al. 2010b; Barrett et al. 2010c).

Table 3.1: Abundance of the black-bellied and northern dusky salamanders at three riparian land-uses and percent occurrence of each focal species at different stream microhabitat types. The abundance of each species indicates the total number of individuals recorded at the three riparian land-use types. Percent occurrence indicates the number of individuals recorded of a certain species at each microhabitat type, within a given riparian land-use type, as a percentage of the total number of individuals of the same species found at that particular riparian land-use type.

Riparian Land-uses	Percent occurrence of black-bellied salamanders at each microhabitat type					Abundance of black-belled salamanders	Percent occurrence of northern-dusky salamanders at each microhabitat type					Abundance of northern dusky salamanders
	Channel bottom	Stream bank	Bank-channel interface				Channel bottom	Stream bank	Bank-channel interface			
Agricultural	17	25	58	12	2	81	17			137		
Forested	87	2	11	460	0	83	16			269		
Residential	0	100	0	7	2	85	13			122		

Table 3.2: Average distance to the nearest heterospecific (DNN) between black-bellied salamanders and northern dusky salamanders in three differential artificial stream types with simulated riparian land-use and land cover types.

Riparian land-use land-cover type	Distance to the nearest heterospecifics \pm standard deviation (mm)
Forested	191 ± 0.9
Agricultural	147 ± 1.1
Urban	37 ± 1.4

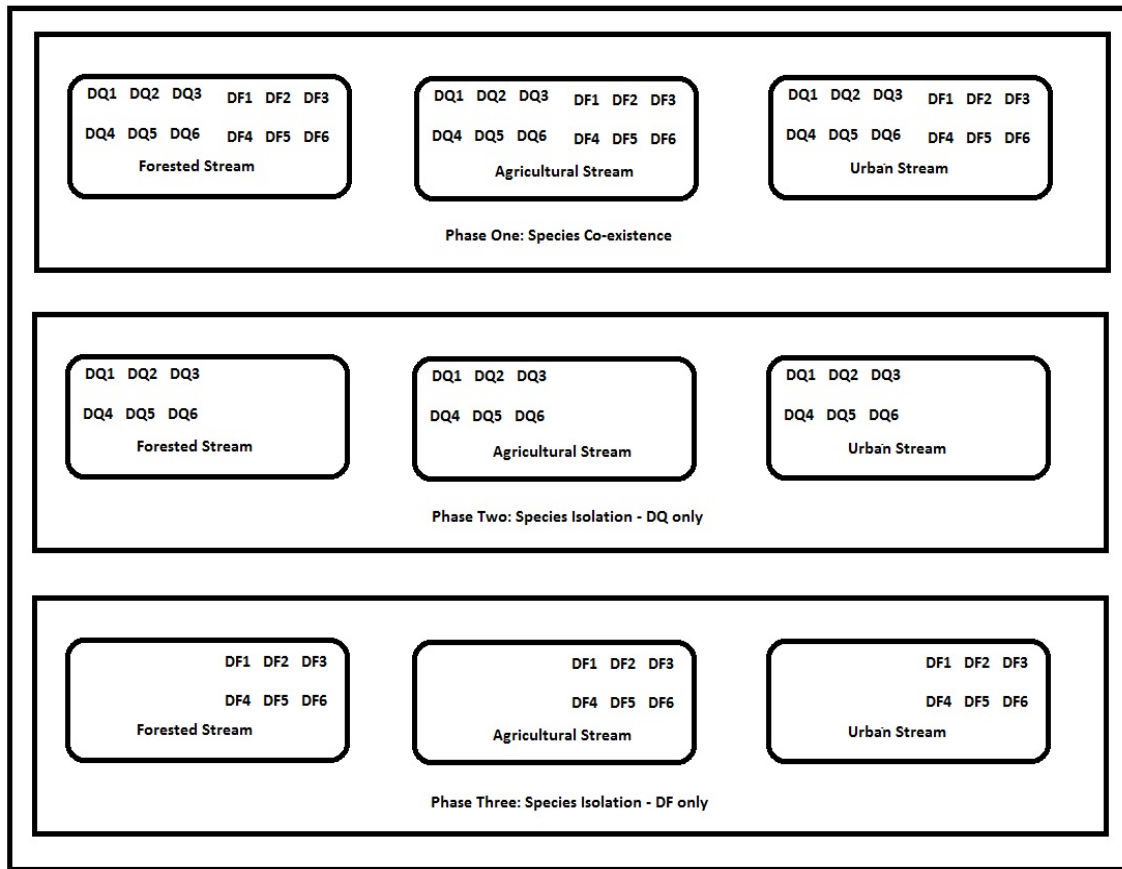


Figure 3.1: The design for the artificial stream experiment with all 3 phases of a single replication; there were 3 replications for each land-use type (forested, agricultural, and Urban) with different individuals of the same species; DQ- *Desmognathus quadramaculatus*, DF- *Desmognathus fuscus*. The numbers 1-6 correspond to the six individuals of each species.

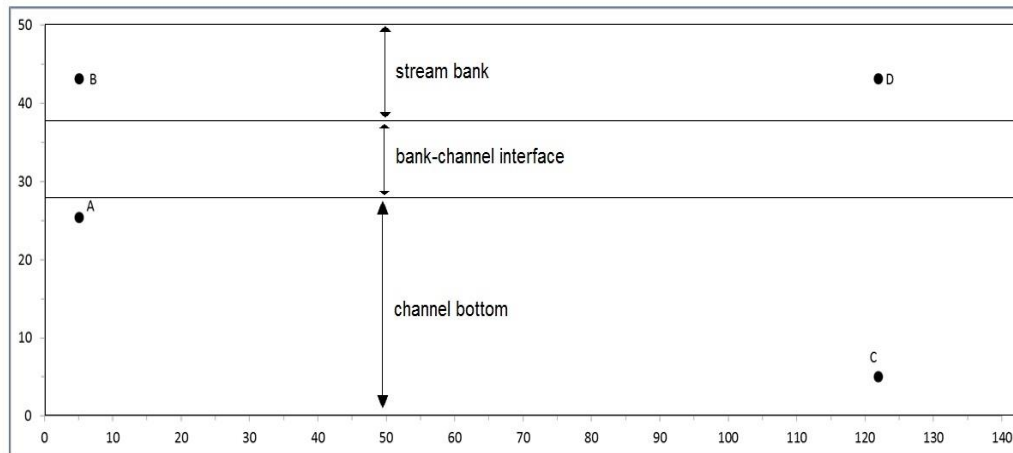


Figure 3.2: The top view of the artificial streams with the perimeter of the artificial streams calibrated in centimeters producing a Cartesian grid to record the point occurrences of salamanders during each observation session. The position of salamanders during the observation session was recorded as a Cartesian coordinate. For example, the positions inside the artificial stream represented by the black circles A, B, C, and D correspond to the following point coordinates (5, 25), (5, 43), (122, 43), and (122, 5), respectively.

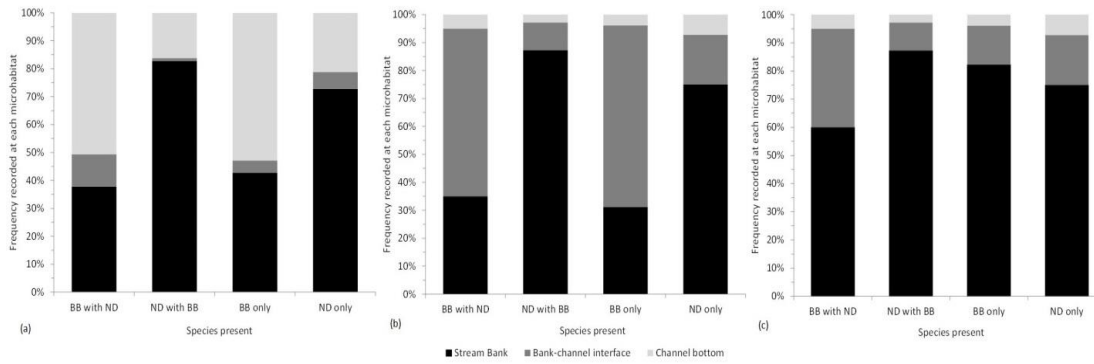


Figure 3.3: Microhabitat use of black-bellied salamander (BB) and northern dusky salamander (ND) in stream habitats associated with differential riparian land-use land-cover types: forested (a), agricultural (b), and urban (c). X-axis is plotted with different phases of species presence: first two columns of each graph represented species co-occurrence and the other columns represented species isolation. Y-axis is plotted with percent frequency of occurrence of each focal species at the 3 microhabitat types when isolated and co-occurring with the heterospecific.

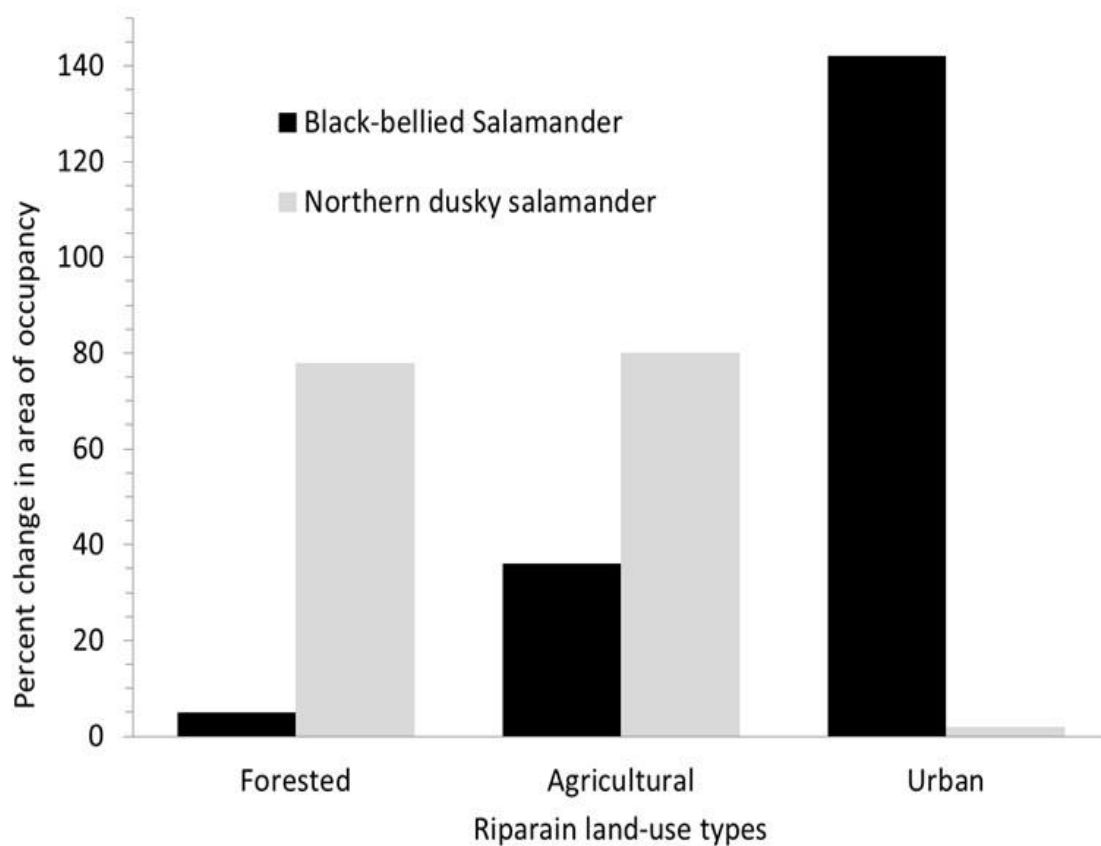


Figure 3.4: Change in the area of occupancy in all riparian land-use types for black-bellied (black) and northern dusky (grey) salamanders from co-occurrence to isolation as a percentage of the area occupied in co-occurrence.

$$\text{Change in range of occupancy} = \frac{(\text{area occupied in isolation} - \text{area occupied in co-occurrence})}{\text{area occupied in co-occurrence}} \times 100\%$$

CHAPTER FOUR

IMPORTANCE OF CURRENT AND HISTORICAL LAND-USE IN STRUCTURING THE COMMUNITY: EVIDENCE FROM SALAMANDER OCCUPANCY IN STREAMS OF BLUE RIDGE AND PIEDMONT ECOREGIONS

Introduction

Increasing human populations and their demand for natural resources worldwide have resulted in a diverse array of transient and permanent land-cover transformations including farming, animal husbandry, and settlements (Ellis et al. 2010). Geo-climatic processes and ecological disturbances (erosion, channel shifts, flooding, wildfire, and wind storms) have substantial impacts on community composition (Dayton 1971; Foster et al. 2003). Yet, anthropogenic disturbances, primarily land-uses, are characterized by higher recurrence intervals and intensity, persistence, and spatial extensiveness; hence their impacts compound and surpass those of “natural” disturbances (Theobald et al. 1997; Foster et al. 2003). Land-uses are considered the leading cause of habitat loss, fragmentation and drastic modifications in the landscape structure of terrestrial and aquatic biomes (Ramankutty & Foley 1999). Landscape alterations change habitat complexity, habitat availability, resource distribution, microclimate, and disturbance regimes, ultimately influencing species distribution, community composition, their life and histories and physiology (Sisk 1998; Turner 2005a). Land uses leave historical legacies that may combine with current conditions to influence organisms. Distributions of many species have been shown to be influenced by current and historical land use

(Foster et al. 2002; Scott 2006); understanding these effects can inform conservation and restoration strategies, particularly for taxa in global decline (Dobson et al. 1997a).

Intensive agriculture, real estate development, urbanization, and lumbering are widespread land-use types that have resulted major changes in landscape structure and patterns of biodiversity in North America (Houghton 1994; McKinney 2002, 2008; Trombulak and Baldwin 2010). Temperate deciduous forests are among the most altered biomes due to their suitability for agriculture and development (Ellis et al 2010). Many studies have shown adverse impacts of current land-uses on biodiversity and ecosystem services: impeded dispersal and migration, species extinctions and population declines, biotic homogenization and invasions by weedy and cosmopolitan species, reduced habitat heterogeneity, suppression of historical disturbances, low resilience and resistance to perturbations (Wilson 1988; McKinney & Lockwood 2001; Soberon & Peterson 2009). Other analyses have emphasized dramatic historical land-uses changes (Foster et al. 1998; Brown et al. 2005; Theobald 2005; Foster 2006; Theobald & Romme 2007). However, impacts of historical land-uses on communities have not been adequately investigated, particularly for taxa of high conservation concern (Delcourt & Delcourt 1998; Foster et al. 1998; Harding et al. 1998; Scott et al. 2002; Hicks & Pearson 2003; Foster 2006; Price et al. 2006).

Species responses to land-uses depend on their adaptive traits, habitat preferences, and other niche dimensions. Different types of historical land-uses may induce differential environmental selection forces (McKinney 2002a; Vellend 2004). North America has a spatially diverse land-use history, with different land uses dominating

different areas at different periods of history. In the Southeastern United States Blue Ridge regions were heavily deforested in the late 19th and early 20th centuries and today have largely redeveloped tree cover; Piedmont areas were intensively farmed with row crops during the same period and now are dominated by urban and exurban development (Sisk 1998; Turner 2005a). It is important to analyze influences of current and historical land-uses on species loss and population decline. Knowledge about the effects of land-use history on community composition and regional biodiversity may contribute to ecological restoration and conservation planning (Black et al. 1998; Foster et al. 2003).

In this study, we focused on the relationship of the distribution and diversity of stream-associated plethodontid (family Plethodontidae) salamanders to historical and current land-use in the watershed (landscape scale) and riparian zone (local scale) in the Blue Ridge and Piedmont ecoregion of the Southeastern US. We compared the impacts of both current and historical land-uses on stream salamanders. Because amphibians are sentinels of environmental degradation, we focused on stream-dwelling plethodontids, a regionally-diverse amphibian taxon (Mitchell and Gibbons 2010). Our specific objectives were to: (1) comparatively assess the impacts of historical and current land-use conditions at riparian (local) and watershed (landscape) scale on diversity of plethodontids; and (2) determine different current and historical land-cover features that elicit species-specific responses and influence community structure of plethodontids.

Methods

Study area

The two ecoregions are in the Southeastern US (SC, NC, and GA; Fig. 1) and have undergone historical (17th-19th centuries) crop-farming, but differed in extent of forest loss and land-cover transitions. The Piedmont underwent extensive cotton farming and recovered substantial forest cover after abandonment becoming widely urbanized during the late 20th century. The Blue Ridge was widely deforested for timber during the late 19th and early 20th centuries; row crop agriculture was most common in coves with slopes remaining forested or with partially open rough pasture (Wear 2002; Jackson et al. 2005; Galang et al. 2007). The Piedmont (elevation: 300-600m, annual rainfall: 1300mm, winter/summer temperature 4/25°C) consists of irregular plains and low hills; mixed mesic-dry deciduous-evergreen forests are dominated by oak-hickory-pine forests; and moderate-gradient streams with cobbles-gravel substrates (US Environmental Protection Agency 2002). The Blue Ridge (elevation: 600-1600m, annual rainfall: 1600mm, winter/summer temperature 0.56/22°C) is characterized by steep slopes and narrow valleys; enriched with headwater streams with a high channel gradient and bedrock and boulder-laden substrates; and montane mesic forests dominated by oak-hickory communities (US Environmental Protection Agency 2002). Both ecoregions have a rich diversity of amphibians (\approx 100 species of salamanders and \approx 40 species of anurans), particularly aquatic salamanders (Dorcas & Gibbons 2008; Mitchell & Gibbons 2010).

Field survey

We surveyed 35 and 66 stream reaches with watersheds $<25\text{Km}^2$, randomly distributed within the Blue Ridge and Piedmont, respectively. At all sites, we surveyed a 100m-stream segment both in-channel and up to a 1m width in the stream banks. All surveys were diurnal (0800-1800h) conducted during mid-spring to mid-summer (April-July) for two consecutive years (2010-2011). We actively searched the stream channel, undercut banks, and stream banks; we overturned movable rocks and woody debris; searched through gravel, cobbles, pebbles and leaf litter, and captured salamanders using bottom set-nets and aquarium nets. At each site, we did three passes to increase detectability of salamanders (Heyer et al. 1994; Dodd 2010). All captured salamanders were identified to species level using standard field guides and keys (Petranka 1998; Mitchell & Gibbons 2010), abundance recorded, and released back to the site of capture. We used a VisualBasic query (SC Department of Natural Resources; ArcGIS 10, ESRI) to select spatially-independent sampling points which cross-examined all potential sampling sites located within the same drainage for spatial autocorrelation. Use of multiple passes to capture salamanders and a well-trained crew improved detectability; species accumulation curves with a long asymptote (Fig. 2) suggest a successful detection. (Mitchell & Gibbons 2010). We excluded point endemics from analyses since distribution of these species might be limited by biophysical filters unrelated to land-uses. Landscape-scale research focusing on species with ecoregion-wide distribution is a reasonable approach to examine the effects of land-uses at different spatial and temporal

scales since such methods account for all potential filters that determine species distribution and abundance (Olson et al. 2001; Abell et al. 2008).

Statistical and geospatial analyses

We assessed current land-use status from the National Land Cover Dataset 2006 (USGS Land Cover Institute) and historical land use from historical aerial photographs (1940-1960, USGS Earth Resources Observation and Science Center) which were georeferenced and joined in mosaics. We used a total of ≈ 600 photographs, 5-6 images were used per sampling location to increase the accuracy of our land-cover classification. Photos were interpreted manually for land uses, based on Anderson Level I system (urban, agriculture including rangelands, forests, open water, wetlands and barren lands) (Anderson 1976). ArcEditor was used to delineate land-use polygons which were converted to raster format for subsequent analysis. We quantified percentage of each land-use type at two spatial scales (Table 1): (1) local scale- 500m riparian zone from the wet channel and (2) landscape scale- subwatershed area delineated based on the USGS National Elevation Dataset (1/3 arc-seconds), using the hydrology toolbox.

We calculated the Simpson Index (SI) and species richness as indicators of species diversity for the sampling sites. SI combines number of species present with the relative abundance, indicates evenness of species distribution and less sensitive to sample size and variability species richness across different communities (Krebs 1999). All analyses were done separately for the two ecoregions.

We performed factor analyses (FA) with varimax rotation via the principle component method for all separately for land-use variables (Table 1). Factor analysis is an eigenvector-based multivariate technique that reduces interrelated predictor variables into fundamental variables (i.e., factors) that concentrate the dispersed information of the original dataset into an underlying pattern (McCune et al. 2002). We extracted factors that explain more than 80% of the variability in percent historical and current land-uses within watersheds and riparian zones. Depending on the eigenvalues, we named each factor with respect to the land-use variable that best represented each factor. Afterward, we ran a multiple step-wise regression ($\alpha=0.05$, mixed model method of forward selection and backward elimination) where species richness and SI were considered response variables and factors were considered predictor variables. Model components with the lowest AIC score were chosen to explain the mechanisms driving the diversity of salamanders with respect to historical and current and-uses.

To assess how individual species of plethodontids respond to different historical and current land-uses, we ran a redundancy analysis (RDA). RDA is an ordination technique based on a direct gradient analysis that relates community composition to environmental or other explanatory variables (Llopiz & Cowen 2009). We adopted this multivariate statistical approach to include relative abundance of each species as multiple response variables elicited by land-uses (Ter Braak & Prentice 1988). Using Pearson Correlation tests, we tested for assumption of linear relationship between response and predictor variables as well as the multicollinearity among land-use data. Only the land-use variables with low multicollinearity were used for the RDA. Abundance data were

squareroot transformed to reach multivariate normality. We ordinated the species matrix by reciprocal averaging; this ordination was constrained by multiple linear regressions on the land-use variables. We centered axis scores and standardized them to unit variance and optimized species scores for axis scaling. We constructed separate ordination plots for each ecoregion using the two constrained RDA axes that accounted greatest variability based on the eigenvalues, and used percentage current and historical land-use as environmental vectors. We performed a Monte Carlo permutation test (500 iterations, $\alpha=0.05$) to assess whether the relationships derived between land-use factors and abundance of individual species were random. We used JMP Pro 10.0 (SAS Inc., NC) and Project R 3.0 (R core Team, Austria) for statistical analyses and ArcGIS 10.0 (ESRI, Canada) for geospatial analyses.

Results

We found 11 species (4 genera) of stream-associated plethodontids in our field survey: *Desmognathus fuscus* (Northern Dusky salamander), *D. marmoratus* (Shovel-nosed salamander), *D. monticola* (Seal salamander), *D. ocoee* (Ocoee salamander), *D. quadramaculatus* (Black-bellied salamander), *Eurycea cirrigera* (Southern Two-lined salamander), *E. guttolineata* (Three-lined salamander), *E. wilderae* (Blue-ridge Two-lined salamander), *Pseudotriton ruber* (Red salamander), *P. montanus* (Mud salamander), and *Gyrinophilus porphyriticus* (Spring salamander). All the above species were recorded in the Blue Ridge whereas only seven were found in the Piedmont (*Desmognathus fuscus*,

D. quadramaculatus, *Eurycea cirrigera*, *E. guttolineata*, *Pseudotriton ruber*, *P. montanus*, and *Gyrinophilus porphyriticus*).

Impacts of current and historical land-use on the diversity of plethodontids

Among land-uses of the Blue Ridge, The first two factors derived from all spatial-temporal scales explained >80% of the variability (Table 2). The factors derived across all the spatial-temporal scales for both ecoregions represented the extent of forest cover, open water, urban land-cover, and agricultural land-cover. Percent land-cover of wetlands, barren lands, and grasslands did not have substantial loadings on the factors in either ecoregion.

Both current and historical land-uses at riparian and watershed scale were important model components in predicting species richness and SI (multiple stepwise regression, Table 3). Land-use history had a higher impact on the species richness and SI in the Piedmont than in the Blue Ridge. According to the optimal regression model, current riparian urban development and forest-cover, and historical watershed land-cover (forest, agriculture, and urbanization) seemed to be important model parameter to predict both Simpson index and species richness in the Blue Ridge. Similarly, historical land-uses and land-cover types at watershed scale i.e., urbanization, agriculture, and forest-cover were important in predicting the species richness and SI in the Piedmont. Current agricultural land-cover was an important parameter in predicting the SI in the Piedmont.

Impacts of current and historical land-use on plethodontid community structure and species-specific responses

Through testing the assumptions, we ensured lower multicollinearity among most of the percent land-use variables and linear relationship between the predictor and response variables. The selected land-use variables explained 70% and 60% of the variability of the relative abundance of stream salamanders of the Blue Ridge and Piedmont, respectively. The first two RDA axes cumulatively explained >85% of the variability of the species abundance (Blue Ridge: 95%; Piedmont: 87%). We also found a non-random relationship between the percent land-uses and the species abundance (Blue Ridge: Pseudo $F = 4.41$, $p > 0.05$; Piedmont: Pseudo $F = 4.41$, $p \approx 0.05$). The variation inflation factor (VIF) was < 10 for riparian land-use variables and ≈ 20 for those at the watershed scale. For the Blue Ridge, the first RDA axis highly correlated with the current riparian and watershed forest-cover (intersect correlations, $R = 0.8-0.9$) whereas the second axis highly correlated with the historical watershed agricultural and forest cover ($R \approx 0.7$). In the Piedmont, all RDA axes highly correlated with historical land-uses than with current land-uses: axis one with watershed-scale agricultural and urban cover as well as riparian-scale agricultural and forest cover ($R = 0.7-0.8$); axis 2 with watershed forest cover ($R \approx 0.6$). The vector lengths of RDA revealed similar results (Fig. 2). For Blue Ridge current land-use variables, i.e., forest cover at watershed and riparian scale were the most important variables, closely followed by historical riparian forest and agricultural cover; historical urban development at riparian scale was the least important vector. Comparatively dissimilar patterns were observed in the Piedmont: historical

agriculture and forest cover at both riparian and watershed scale were the most important; the least impactful vectors were current riparian percent of urban and agriculture.

Species distribution across along each land-use variable and RDA axes differed between the two ecoregions (Fig. 2). In Blue Ridge, *D. quadramculatus*, *D. ocoee*, *D. monticola* and *D. marmoratus* had higher weighted averages on the current watershed and riparian forest cover; those species ranks ranked in the same pattern along the historical riparian and watershed forest cover. Species with moderately-high weights on the forest cover variables were *G. porphyriticus*, *P. ruber* and *P. montanus*; the rest (*D.fuscus*, *E. cirrigera*, and *E. guttolineata*) had lowest weighted averages over forest cover variables. All species ordinated between the plot origin and vector endpoints indicating all salamanders are positively associated with the forest cover. All *Desmognathus* species except *D. fuscus* and all *Spelerpini* (subfamily *Spelerpinae*) but *E. cirrigera* and *E. guttolineata* ordinated in close proximity to each other. In the Piedmont, *D. quadramculatus* had the highest weighted averages while *G. porphyriticus*, *P. ruber* and *P. montanus* had moderately-high weights on the historical forest cover vectors at both riparian and watershed scales. All the above four species had very low weighted averages on the historical urban land-cover, and low weighted averages on current and historical agricultural land-cover at both watershed and riparian scales. Species with lowest weighted averages on all forest cover variables were: *D.fuscus*, *E. cirrigera*, and *E. guttolineata*. The ordination resulted similar patterns as in the Blue Ridge: *D. quadramculatus*, *G. porphyriticus*, *P. ruber* and *P. montanus* ordinated as a single cluster; another cluster contained *D.fuscus*, *E. cirrigera*, and *E. guttolineata*.

Discussion

We recorded all wide-ranging stream-associated plethodontids of the Southern Blue Ridge (11 species) and Piedmont (07 species) during our survey (Mitchell & Gibbons 2010).

Impacts of historical and current land-uses on stream plethodontids

We noted a striking difference and similarities in the influence of historical and current land-uses to predict species distribution between the two ecoregions (Table 3, Fig. 2). Both current and historical land-uses were equally important predictors of species richness at the Blue Ridge while only historical land-use variables were importance at the Piedmont. SI, an index of diversity which composites evenness and relative abundance, showed that both current and historical land-uses are driving forces of diversity of plethodontids across both ecoregions. Our results in the RDA was complementary to those of the regression model; Five historical and four current metrics of land-uses influenced the species distribution in Blue Ridge whereas five historical and two current land-use variables drove the species assembly in Piedmont. We concluded that both historical and current land-uses at local (riparian) and landscape (watershed) scale are critical determinants of the stream salamander community; historical land-uses became more critical in the Piedmont where more intensive, widespread, and prolonged land-use legacies prevailed (Richter et al. 2000).

The differences in determinants of species composition can be attributed to the land-use histories of the two ecoregions. Both the Blue Ridge and Piedmont were subjected to historical (since early 1700s) row-crop agriculture (cotton, corn, wheat, tobacco); farming was mostly extensive across time and space in Piedmont (Aiken 1973; Brender 1974; Harding et al. 1998; Conroy et al. 2003). The farming at Blue Ridge was relatively short-lived and spatially limited since the high topographical relief increased the soil erosion in open croplands rendering mountainous farmlands unproductive (Price & Leigh 2006; Ellis et al. 2010). Further, the physiographic complexity precluded certain parts of Blue Ridge from row-crop cultivation due to limited accessibility (Price & Leigh 2006). The Blue Ridge forests recovered after the abandonment of farms and settlements where these montane landscapes were protected under federal or state jurisdiction limiting anthropogenic disturbances. Urbanization and infrastructure development (particularly the transportation network) followed a rapid transition after the long legacy of farming in Piedmont (Pearson et al. 1999; Brown et al. 2005; Theobald & Romme 2007). The long legacy of agriculture might play a larger role in structuring the current species richness and community composition of stream salamanders in the Piedmont while species richness in Blue Ridge streams were driven by both current and historical land-uses, indicating the mixed effects of relatively brief episodic disturbances, fast rebound of forests and conservation efforts (Boring et al. 1981; Price & Leigh 2006). We noted that predictors of SI of the Piedmont was limited to riparian land-uses. This shows that riparian land-uses can surpass the impact of those at watershed. Further, buffering function of Riparian forests could mitigate disturbances induced by watershed-wide

deforestation. High diversity of stream fauna have been observed with riparian protection despite high extents of imperviousness and deforestation in the watershed (Semlitsch & Bodie 2003; Moore & Palmer 2005; Crawford & Semlitsch 2007).

Agriculture and urbanization across local and landscape scales primarily result in loss of forest cover and vegetation complexity, increased impervious surfaces, channelization, impoundments, and altered matter and energy dynamics, lead to multiple modifications in biological, chemical and physical processes in stream ecosystems (Angermeier 2000; Baron et al. 2002; Scott et al. 2002). Such alterations cascade into multiple ecological impacts, i.e., upland erosion and increased sediment loads; modified channel morphology, discharge and thermal regimes; increased channel incision and stream aggradation; limited supply of woody debris and allochthonous organic matter; substrate embedment, smothered littoral zone, reduced interstices and habitat homogenization; altered light exposure and primary productivity; and increased non-point source pollution with nutrients, heavy metals, oils, agrochemicals, and urban effluvia (Baron et al. 2002; Moore & Palmer 2005; Ambers et al. 2006; Dudgeon et al. 2006; Gardiner et al. 2009). Such impacts can last in stream habitats after the recovery of natural land-cover leading to biotic homogenization (Scott et al. 2002; Scott 2006). Species-poor streams in our study with both land-use legacies and current urbanization, particularly those of Piedmont, may be still recovering in terms of microhabitat structure and stream geomorphology. Existing records on presence of fine sediments; decrease in the streambed particle size; higher bankfull width/depth ratio and wetted width at baseflow, eroded gullies and absence of topsoil, channel incision and aggradation in

historically-impacted watersheds in our study area validate our assertions (Jackson et al. 2005; Ambers et al. 2006; Price & Leigh 2006). It may take a minimum of 75-100 years for piedmont watersheds to stabilize soil erosion and to export the current sediment load (Trimble 1974; Ambers et al. 2006) and longer for species to recolonize and reach stable populations (Detenbeck et al. 1992; Petranka et al. 1993; Hicks & Pearson 2003).

The current riparian land-cover factor representing percent coverage of forests and urban lands was the common denominator for models predicting species richness and SI at Blue Ridge. This indicated the influence of the local-scale forest and urban land-cover over the community structure of stream plethodontids. Unsustainable land-uses are the primary causes of biodiversity loss worldwide, including the Southeastern US where aquatic ecosystems are endangered due to land development (Noss et al. 1995). Our inferences are comparable to many studies regarding impacts of current land-uses: low diversity of macroinvertebrates and Index of Biotic Integrity associated with watershed forest loss (Lammert & Allan 1999); biotic homogenization of anurans along an agroforestry gradient (Wanger et al. 2010); declining stream fish diversity and increased similarity of functional traits in urbanized watersheds (Helms et al. 2005); increased abundance of exotics and human commensals following exurban development (Hansen et al. 2005); positive association of pond-breeding anuran diversity with upland forests and emergent wetlands and declining diversity with watershed urbanization (Knutson et al. 1999; Semlitsch 2000; Calhoun et al. 2003; Semlitsch & Bodie 2003; Baldwin et al. 2006; Baldwin & Demaynadier 2009; Howard et al. 2012); and low diversity and developmental lag of aquatic salamanders with urbanization in the watershed and riparian

zone (Barrett & Guyer 2008; Barrett et al. 2010a; Price et al. 2011; Price et al. 2012). The number of investigations focusing on temporal scale of land-use status is limited: declining stream fish and aquatic macroinvertebrate diversity due to historical agriculture (Harding et al. 1998); limited distribution of stream salamanders given long-term urbanization (Price et al. 2006; Price et al. 2012); increased exotic plant invasions in historically deforested watersheds (Kuhman et al. 2010); and declining populations of birds and arthropods due to three-decade history of intensive agriculture. .

The species clustering (fig. 2) in the ordination plots corresponded to their natural and life histories (Martof et al. 1989; Conant & Collins 1998; Petranka 1998; Lannoo 2005; Mitchell & Gibbons 2010). *D. fuscus*, *E. cirrigera* and *E. glutolineata* ordinated together and are small-bodied (snout-vent length \approx 40-50 mm), with shorter aquatic larval periods and semi-aquatic short-lived adult stages. Adults occupy a range of microhabitats within the riparian zone, undercut banks and the wetted channel and associate many substrate types as refugia. These species showed the lowest association with current and historical forest cover. The rest of the species (except *D. ocoee*) are medium to large bodied (snout-vent length \approx 80-100mm), with prolonged larval stages and long-lived largely-aquatic adult stages. Adults have narrow microhabitat preferences. These species ordinated together and showed relatively high affinity with the current and historical forest cover and negatively associated streams with historic and current non-forest land-cover. These land-use associations were consistent across both ecoregions. The larger body size, longevity, and narrow habitat preference might be a liability at changing habitat conditions (Bruce 1996, 2009; 2011). On the other hand, small-bodied habitat

generalists have smaller energy requirements, are adapted for many stream-associated refugia, and have shorter generation times enabling evolution of adaptations for changing habitats (Bruce 1982, 2005, 2007). Consequently, land-uses may have relieved small-bodied plethodontids from competition with large-bodied species; previous studies have shown that the large-bodied salamanders are competitively dominant over small-bodied salamanders in forested streams. Analogous evidence for amphibians and other taxa indicates that large-bodied, long-lived, habitat specialists with longer generation times might be more susceptible to anthropogenic disturbances (Rabinowitz et al. 1986; Gaston & Blackburn 1995; Lips et al. 2003; Cooper et al. 2008).

Use of multivariate methods

We used a multivariate approach in this study. Multivariate tests enable the optimal usage of the original dataset, investigate joint relationships among intercorrelated variables and analyses of multiple response and predictor variables simultaneously (McCune et al. 2002). Further, variable reduction methods such as FA allow exploratory data analyses which can subsequently lead to construction of descriptive models (James & McCulloch 1990); FA has been used in other studies involving analyses of multiple land-use variables (Riitters et al. 1995; Xiubin 1996; Wayland et al. 2003). The RDA is an ordination technique used to interpret the association between species abundance and community assembly composition with environmental variables (Allen et al. 2006b; Llopiz & Cowen 2009) where the species data is analyzed as a multivariate regression-type function of the ordination axes which are linearly constrained by the environmental

predictor variables. Being a canonical ordination method, RDA underscores the predictor variables that influence species data while neglecting other variables that do not affect species data (Ter Braak 1986; Ter Braak & Prentice 1988; Ter Braak 1994; Ter Braak & Verdonschot 1995).

Conclusive Remarks

Our study indicated the importance of both historical and current land-uses at local and landscape scale in shaping community structure of stream dwelling salamanders. . Ecological interpretation of mechanisms driving species assembly should be done with caution since land-use legacies could be responsible for current patterns of species distribution that cannot be attributed to other biogeographic filters. Our study adds to the growing understanding that conservation actions should consider land-use past as well as present. Of particular interest for stream systems and amphibians are restoration efforts and species reintroductions. , Such actions may require restoration efforts to mitigate legacy impacts including soil erosion, river bank destabilization, channel incision and loss of topsoil. We emphasize the necessity for policy actions to sustainably manage the watersheds and riparian zones to safeguard future stream biodiversity from the “ghost of the land-use past”(Harding et al. 1998).

Table 4.1: A brief description of the four spatial and temporal scales under which different land-use and land cover types were categorized. The data sources for geospatial analyses are also provided.

Spatial and temporal extents of land- uses	Description
Current riparian	Percent coverage of each land-use types (based on USGS NLCD 2006) according to the Anderson level I classification within the riparian scale of the sampling reach (500 m-radius from the sampling point)
Current watershed	Percent coverage of each land-use types (based on USGS NLCD 2006) according to the Anderson level I classification within the watershed scale of the sampling reach
Historical riparian	Percent coverage of each land-use types (based on aerial photographs from 1940-60) according to the Anderson level I classification within the riparian scale of the sampling reach (500 m-radius from the sampling point)
Historical watershed	Percent coverage of each land-use types (based on aerial photographs from 1940-60) according to the Anderson level I classification within the watershed scale of the sampling reach

Table 4.2. Results of the factor analyses and representation of each factor to the land-use variables based on loadings and eigenvalues. Separate analyses were done to different spatial-temporal land-use (LU) and land-cover (LC) regimes to extract independent fundamental variables that underlie extents of different land-use types.

Blue Ridge ecoregion				
Spatial and temporal extents of land-uses	Factors derived	Variability explained	Most representative LULC variables of each factor	Factor name
Current riparian	Factor 1	45.21	Forest-cover urban LC	Current riparian LC (forest-urban)
	Factor 2	35.22	Agricultural LC	Current riparian agricultural LC (farmland)
Current watershed	Factor 1	51.60	Forest-cover Urban LC	Current watershed LC (forest-urban)
	Factor 2	28.60	Agricultural LC	Current watershed agricultural LC (farmland)
Historical riparian	Factor 1	60.58	Forest-cover Urban LC Agricultural LC	Historical riparian LC (forest-urban-farmland)
	Factor 2	25.30	Open water LC	Historical riparian openwater (reservoirs)
Historical watershed	Factor 1	53.56	Forest-cover	Historical watershed LC (forest-farmland)
	Factor 2	38.10	Urban LC Agricultural LC	Historical watershed LC (urban-farmland) factor
Piedmont ecoregion				
Current riparian	Factor 1	41.40	Forest-cover Urban LC	Current watershed LC (forest-urban)
	Factor 2	35.20	Agricultural LC	Current riparian agricultural LC (farmland)
Current watershed	Factor 1	45.87	Agricultural LC Urban LC	Current watershed LC (farmland-urban)
	Factor 2	33.00	Forest-cover	Current watershed forest-cover
Historical riparian	Factor 1	46.40	Agricultural LC Forest-cover	Historical riparian LC (forest-farmland)
	Factor 2	28.80	Urban LC	Historical riparian urban LC factor
Historical watershed	Factor 1	45.12	Forest-cover Agricultural LC	Historical watershed (forest-farmland) LC
	Factor 2	33.31	Urban LC	Historical watershed urban LC

Table 4.3. Results of the multiple stepwise regression to predict the species richness and Simpson index of stream salamander community in response to historical and current land-uses at riparian and watershed scale. The factors derived from the factor analyses were used to represent independent, fundamental land-use predictor variables. All the optimal models presented below were significant ($p < 0.05$) at predicting species diversity indices.

Predictor variable	Blue Ridge ecoregion		Piedmont ecoregion	
	Model components	F ratio	Model components	F ratio
Species richness	Current riparian LC (forest-urban) factor	11.98	Historical riparian LC (forest-urban-farmland) factor	7.18
	Historical watershed LC (forest-farmland) factor		Historical watershed urban LC factor	
Simpson index	Current riparian LC (forest-urban) factor	4.9	Current riparian agricultural LC (farmland) factor	2.33
	Historical watershed LC (urban-farmland) factor		Historical riparian LC (forest-urban-farmland) factor	

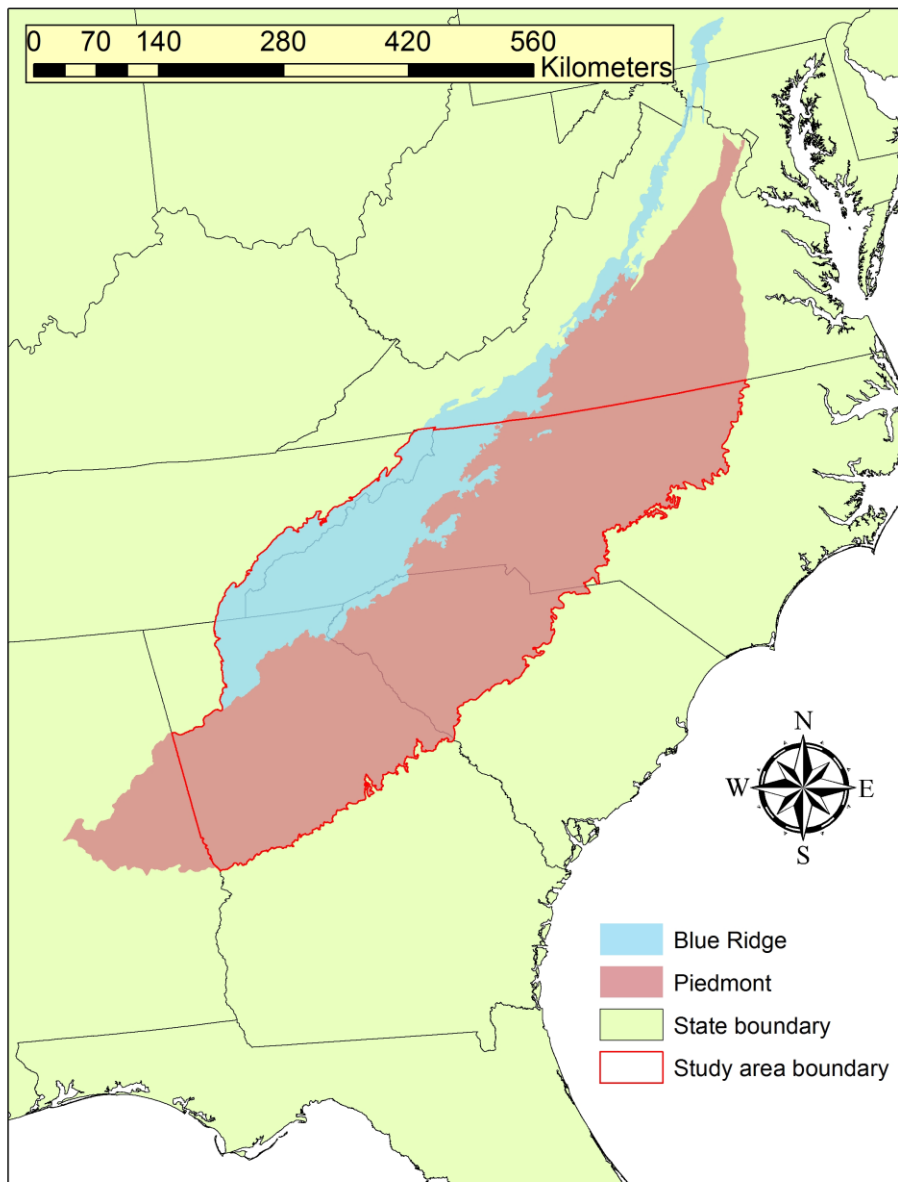


Figure 4.1: Study area: Blue Ridge and Piedmont ecoregions of the southeastern United States. The field survey was limited to the states of North Carolina, South Carolina, and Georgia. Map developed based on shapefiles available from the Environmental Protection Agency (EPA) Western Ecology Division. URL: http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm#Level%20III

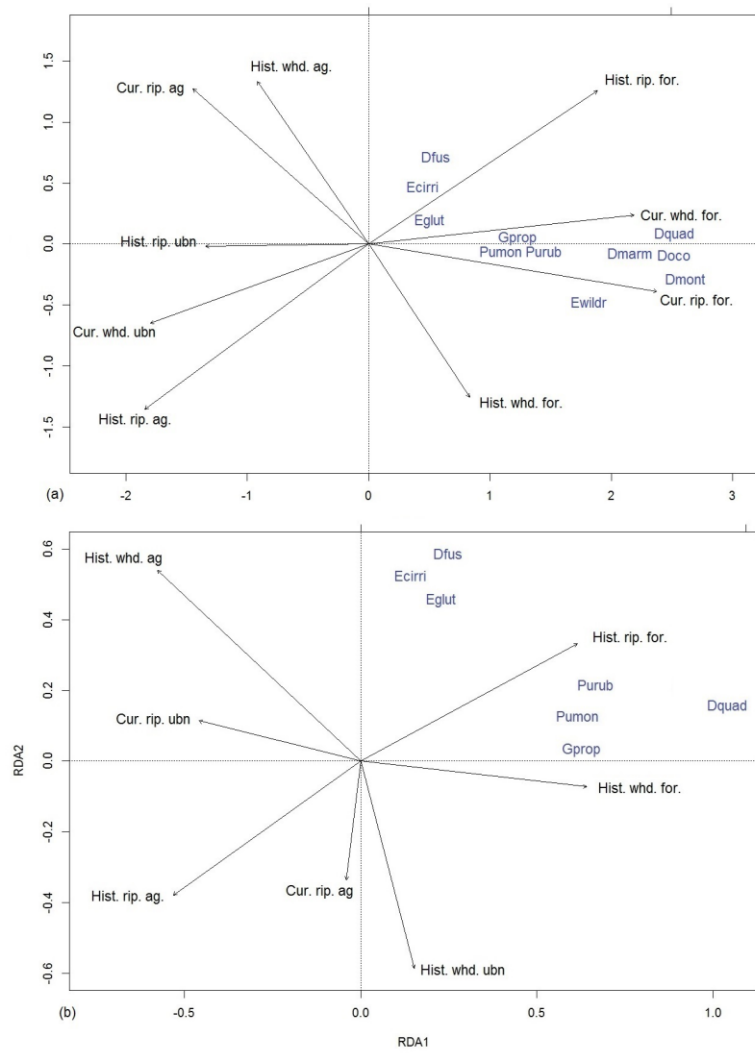


Figure 4.2: Ordination plots for redundancy analyses (RDA) for (a) Blue Ridge and (b) Piedmont. The vectors represent percent historical and current land-use cover at riparian and watershed scale. The name of the vector is labelled at the arrowhead. Species scores are labeled with species names. Species legend: adults- Ecirr: *E. cirrigera*, Eglut: *E. guttolineata*, Ewldr: *E. wilderae*, Dfus: *D. fuscus*, Dmont: *D. monticola*, Dmarm: *D. marmoratus*, Doco: *D. ocoee*, Dquad: *D. quadramaculatus*, Purub: *P. ruber*, Pmon: *P. montanus*, Gprop: *G. porphyriticus*. Land-use legend: Hist: historical; Cur: current; rip: riparian; whd: watershed; for: forested; ag: agricultural; for: forest; ubn: urban

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