

USE OF OCCUPANCY MODELS TO EXAMINE STREAM CONSUMER PREVALENCE
ACROSS A LAND COVER GRADIENT IN THE SOUTHERN APPALACHIANS, USA

by

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(Under the Direction of CATHERINE PRINGLE)

ABSTRACT

Occupancy models were used to identify environmental parameters that best predicted the prevalence of four functionally important focal stream taxa: *Tallaperla* spp. (stonefly), *Cambarus* spp. (crayfish), *Pleurocera proxima* (snail), and *Cottus bairidi* (mottled sculpin). The study was conducted on a landscape scale within the Upper Little Tennessee River Basin (in thirty-seven streams reaches draining catchments between 18-1670 ha, within a 1,130 km² area). The estimated proportion of patches occupied within a reach was used as a measure of focal taxon prevalence and thirty-four models were used to examine the relative association of environmental parameters with taxon occupancy. The prevalence of all four taxa was associated with land cover, and *Tallaperla* was largely absent below a threshold of 85-90% forest cover in the watershed. Occupancy modeling has expanded our understanding of how functionally important stream consumers are influenced by environmental parameters operating at both local and regional watershed extents.

INDEX WORDS: Akaike Information Criterion, *Cambarus*, Consumers, *Cottus bairidi*, Detection, Forest Loss, Habitat, Land-use, Little Tennessee River Basin, Occupancy, *Pleurocera proxima*, Southern Appalachians, Stream Chemistry, *Tallaperla*

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A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2013

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August 2013

DEDICATION

To my family and friends, for your love and support.

ACKNOWLEDGEMENTS

I thank my advisor Catherine Pringle for supporting and encouraging my research. I thank my committee Amy Rosemond, John Maerz, Mary Freeman, Jeff Hepinstall-Cymerman and former committee members Paul Hendrix, Daniel Markewitz, and Brian Kloeppel for their support and key insights on my project. I thank Kristen Cecala, Dave Hung, Cameron Kresl, Lynsey Long, J.R. McMillan, Joe Milanovich, Sakura Evans, Stenka Vulova, Julia Cosgrove, Scott Connelly, John Davis, Sue Dye, Brian Kloeppel, Andrew Mehring, and Meredith Myers for help with long hours performing the field work. I thank Jim Peterson, Kristen Cecala, Mary Freeman, John Maerz, and Marcia Snyder for help with occupancy modeling. I thank all Coweeta researchers, especially Fred Benfield, Ted Gragson, Rhett Jackson, David Leigh, Jason Love, Jack Webster for their collegiality and inspirational research. The Coweeta LTER, Odum School of Ecology at UGA, Warnell School of Forestry and Natural Resources at UGA, the University of Georgia, and U.S. Forest Service provided key financial, intellectual, and logistic support. Finally, I thank the Pringle, Rosemond, and Maerz lab groups for feedback, support, and manuscript review. I thank John Davis, Andrew Mehring, Tom Barnum, and Marcia Snyder for their support and review of my work. Finally, I'd like to thank my parents John and Linda, sister Kristan, wife Jennifer, and son Jack for their patience and loving support.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

OVERVIEW

This introduction and literature review provides background information and relevant studies about key concepts for my thesis, and helps place my work in context. I begin with an overview of human impacts on natural systems, to emphasize the large scope and intensity of the human footprint on natural systems, and the critical need to understand and ameliorate our impact on the natural world. I continue with a discussion of how local environmental conditions for stream organisms are influenced by interrelating processes occurring on multiple scales, and the importance of considering the influence of larger scale processes on local habitat conditions. I then discuss the important roles consumers play in stream systems, followed by an explanation for why I picked four particular stream consumer taxa to study. Finally, I explain why I chose to use occupancy modeling in my research, in order to correct for a common problem in biological studies: an inability to detect organisms with 100% certainty in the field.

HUMAN IMPACTS ON NATURAL SYSTEMS

Humans have had a tremendous impact on the planet (Riley and Jeffries 2004, Diamond 1997, Reisner 1986), worldwide ecosystems are failing (Tolba *et al.* 1992), and we are facing a loss of biodiversity (Barbault and Sastrapradja 1995, Wilson 1992). As human populations grow, people alter their environments more significantly. Humans impact natural systems by changing their surroundings, including: (1) control of fresh water through dams, reservoirs, canals, diversions, and ditches; (2) alteration of the natural landscape through timber harvest and

agriculture; (3) construction of road systems and buildings; (4) alteration of nutrient cycling regimes through agriculture runoff, mining runoff, thermal pollution, and smog (Riley and Jeffries 2004, Murdoch and Cheo 2001). An overview of the myriad ways in which humans impact natural systems is given (Table 1.1).

Agriculture degrades stream systems by increasing sediment loads (Sovell *et al.* 2000, Martin *et al.* 2005, Knox 2006), nutrient (Carpenter *et al.* 1998), and pesticide levels through runoff (D'Arcy and Frost 2001, Allan 2004), with strong effects on biological communities and channel geomorphology. Increase in nutrient levels can result in greater algal production (Carpenter *et al.* 1998); however, greater suspended sediments can decrease autotrophic communities. Increased sediment loads can bury gravel beds, negatively impacting fish and stream insect reproduction (Burkhead and Jelks 2001). Increased pesticide levels can also result in lesions, increased fish kill levels and other detrimental effects on aquatic populations (Relyea and Hoverman 2006). The combined effects of agriculture can result in a shift in the community to more tolerant species, often with lower biodiversity (DeLong and Bresven 1998, Wang *et al.* 2003). If row crops or livestock are allowed along stream banks, bank stability decreases, more bank failure occurs, and a higher sediment load is added to the stream systems (Agouridis *et al.* 2005). In addition, stream temperature increases due to lack of shading (Bourque and Pommeroy 1997), and the stream receives fewer leaf litter inputs. A summary of effects of agriculture on stream systems is provided (Table 1.2).

Water diversion, as well as damming, has serious implications for stream dynamics (Pringle *et al.* 2000, Frothingham *et al.* 2002, Hooke 2006). Dams catch sediment upstream, resulting in sediment paucity downstream, and increased scouring activities. Dams also alter the seasonal hydrograph, timing of floods, and the number of flood events (Graf 2006). Decreases in

streamside vegetation can compound the effects of water diversion, and result in increased runoff and flashiness to storm hydrographs (Paul and Meyer 2001, Walsh *et al.* 2005). Finally, dams alter the composition of biological communities, as the passage of migratory organisms (*e.g.* fish) is blocked, and the temperature and oxygen levels, channel morphology, and other environmental conditions are altered (Pringle *et al.* 2000)

Human development often causes changes in the fluvial geomorphology of stream systems (Brierley *et al.* 1999, Frothingham *et al.* 2002). Changes to water flow or sediment budget alter the functional relationships between the floodplain and channel, modifying channel geomorphology. Sinuosity, bed roughness, channel width, and other instream measurements are affected by changes to fluvial geomorphology caused by altered water and sediment flows (Hooke 2006). Increases in impervious surface areas and other modifications associated with development consistently lead to altered channel morphology, a flashier hydrograph, elevated nutrients, and an increase in tolerant species, characteristics associated with Urban Stream Syndrome (Paul and Meyer 2001, Walsh *et al.* 2005).

SCALE

Local environmental conditions for fauna reflect the integration of processes occurring at multiple scales. At a particular location, the presence of animals reflects proximate conditions meeting individual needs such as food availability, shelter, and microclimate (Morris 1987). Microclimate conditions are shaped by processes occurring both locally and at larger spatial extents. For example, human agriculture and residential development has decreased the amount of forest, which alters the flow of water and nutrients within watersheds (Allan 2004, Webster *et al.* 2012). Riparian vegetation in particular mediates the flow of nutrients and water into streams, as well as stabilizes banks, limits light inputs, and provides leaf litter and woody debris

inputs (Allan 2004). Within watersheds stream chemistry is determined by in-stream processes as well as flow of water and nutrients from surrounding terrestrial and hyporheic linkages (Poole 2010). When studying stream organisms, it is important to understand the relative importance of fine-scale versus larger-scale processes on local conditions, to better understand what environmental factors are important determinants in the distribution and abundance of a given taxon. It is important to include study of larger scale factors when considering the local suitability of habitat for stream consumers to avoid overlooking important influences on the system.

CONSUMERS

Human impacts on stream systems lead to modifications of the physical environment, extirpation of species including consumers, and disruption of food web linkages, which impacts consumers as they have central roles in many stream food webs (Mooney *et al.* 2009). Consumers play important roles in ecosystems beyond their roles as predators and prey in stream systems (Wallace and Webster 1996). In addition, consumers influence community composition of prey populations (Hillebrand *et al.* 2002, Davic and Welsh 2004), nutrient cycling within ecosystems (Wallace *et al.* 1982, Hood *et al.* 2005, Evans-White and Lamberti 2006), top-down and bottom-up influences (Rosemond *et al.* 1993, Pace *et al.* 1999, Nystrom *et al.* 2003), and physical structure present through activities as ecosystem engineers (Flecker *et al.* 1999, Nogaro *et al.* 2009). Grazers can have strong effects on algal biomass and community composition (Rosemond *et al.* 1993, Wallace and Webster 1999). Shredders have an important role in nutrient cycling, downstream transport, and breakdown of coarse particulate organic matter to fine particulate organic matter bioavailable to other feeding guilds (Wallace *et al.* 1982, Wallace and Webster 1999). Filter feeders enable recapture of fine particular matter which would

otherwise pass downstream, and provide an additional food resource through their feces (Wallace and Merritt 1980, Wallace and Webster 1999). Thus, consumers have a central role in structuring stream ecosystems.

SELECTION OF FOCAL TAXA

The four focal taxa (*Tallaperla* spp., *Cambarus* spp., *Pleurocera proxima*, and *Cottus bairdi*) were chosen because of their functional importance and prevalence in the Southern Appalachians. Common taxa are often influential within ecosystems (Schmitz 2010, Gaston 2010). These taxa are influential within ecosystems as consumers: *Tallaperla* as shredders (O'Hop *et al.* 1984), *Cambarus* as omnivores and shredders (Schofield *et al.* 2001, Creed and Reed 2004), *P. proxima* as grazers and shredders (Dillon and Robinson 2009), and *C. bairdi* as benthic insectivores (Grossman *et al.* 2006). As such, each taxon chosen has a different realized niche because of feeding and habitat preferences.

Tallaperla (Insecta: Plecoptera: Pteronarcyioidea: Peltoperlidae) was selected as a focal taxon from a suite of possible macroinvertebrates because: (1) they are a key shredder critical to leaf breakdown in southern Appalachian ecosystems, and shredders are expected to be more negatively affected by changes in land use (particularly loss of forest cover and reduced detritus inputs) than other groups (Benfield personal communication); (2) they are semivoltine and can be found in streams year round whereas many macroinvertebrates are in winged and terrestrial forms during summer and thus cannot be found in streams; (3) one species of *Tallaperla* dominates (*Tallaperla maria*), accounting for approximately 85% of individuals sampled from Coweeta headwater streams (Wallace unpublished data). All species are very similar morphologically (requires microscope identification) and appear to be functionally equivalent in their roles in stream food webs and ecosystem function (Wallace personal communication); (4)

they are characterized by a very distinctive morphology that enables rapid field identification to genus; most macroinvertebrates require microscope identification to genus.

Crayfish (*Cambarus* spp.; Crustacea: Decapoda: Astacidea: Astacoidea: Cambaridae) were selected as a focal taxon because: (1) they are important in decomposition, nutrient cycling, predator/prey dynamics, and in leaf processing (Schofield *et al.* 2001) since their shredding and chewing activities make more organic material available for other stream organisms; (2) they are indicators of water quality, and are particularly sensitive to siltation and water contamination by pollutants; (3) the southern Appalachians are a hotspot for crayfish species diversity (Crandall and Buhay 2008). However, little is known about individual crayfish species distribution with respect to land use/forest cover.

Snails (*Pleurocera proxima*; Gastropoda: Cerithioidea: Pleuroceridae) were selected as a focal taxon because: (1) they are key algal grazers, and an important prey resource for crayfish in stream ecosystems; (2) as forest canopy is reduced, snails are expected to increase in abundance due to increased light and algal biomass (Allan *et al.* 1997, Dye 2005), while the other focal taxa are expected to be negatively affected by loss of forest canopy; (3) snails feed on autochthonous resources (algal and epilithon) largely ignored by our other focal taxa.

Sculpin (*Cottus bairdi*; Actinopterygii: Scorpaeniformes: Cottoidea: Cottidae) were selected as a focal taxon because: (1) they inhabit a key stream microhabitat, cobble/gravel riffles; (2) watershed disruption through human activities (*e.g.* road construction, logging, agriculture, new home construction) increase the sediment load into stream systems: sculpin presence indicates that riffles have not been buried by sediment; (3) extirpation of sculpin from sampled reaches (if detected in future studies) would indicate loss of habitat due to sediment inputs; (4) sculpin are highly territorial and have one of the lowest movement rates recorded for

stream fishes (Petty and Grossman 2004), so are ideal for the occupancy sampling protocol we use in this study.

OCCUPANCY MODELING

A common problem in the biological sciences is an inability to detect focal taxa of interest with 100% certainty when conducting field studies, which has the potential to bias study results. MacKenzie *et al.* (2002) developed an occupancy model framework to address this uncertainty by sampling on multiple days in order to estimate detection probability. This framework allows one to correct observed occupancy frequency by detection probability in order to account for incomplete detection of focal taxa (MacKenzie *et al.* 2006) as:

$$P(d) = P(d|\Psi)*\Psi,$$

where $P(d)$ is the proportion of patches where a taxon was detected, Ψ is the true proportion of patches occupied by a taxon, and $P(d|\Psi)$ was the probability of detecting the taxon at a patch, given it was present. This occupancy modeling framework has been useful for a subset of field studies by accounting for incomplete detection of focal taxa. Although the occupancy model approach has been used extensively for salamanders (Russell *et al.* 2004, Grant *et al.* 2009, Price *et al.* 2011, Cecala 2012) and fish (Albanese *et al.* 2007, Wenger and Freeman 2008), occupancy models have rarely been used to study stream invertebrates, and I am unaware of any studies that have previously used occupancy models for stoneflies, crayfish, or snails.

THESIS

This thesis examines the prevalence of four stream focal taxa: *Tallaperla* spp. (stonefly), *Cambarus* spp. (crayfish), *Pleurocera proxima* (snail), and *Cottus bairdi* (mottled sculpin) in thirty-seven streams across a gradient of land use in the southern Appalachians, USA. I was interested in the relative influence of processes occurring at local versus larger scales on the

prevalence of these four common, functionally important taxa, with focus on effects associated with conversion of forest to agricultural, residential, and urban land use. I used occupancy models to evaluate which environmental parameters (*e.g.* land cover, water chemistry, and habitat parameters) best predict the observed distribution data. From a conservation perspective, I sought to identify a limited number of environmental parameters useful for predicting the prevalence of each taxon, and to investigate the influence of processes influenced by human land use and occurring at different spatial extents on prevalence of each taxon. The occupancy rate of each taxon was affected by both local and larger-scale processes, highlighting the importance of considering processes at multiple scales when examining the factors influencing the prevalence of taxa of interest. I concluded that maintaining forest cover within the Little Tennessee River basin is a conservation priority to ensure the persistence of stream consumers.

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Table 1.1: Global changes and implications (modified from Riley and Jeffries 2004)

Global change trend	Implications
Land cover changes	Large areas of the planet have been modified by humans. The area devoted to croplands has increased more than 5 times since 1700 on a global basis (Meyer and Turner 1992). Turner <i>et al.</i> (1990) estimate that half the surface of the earth (excluding permanent ice fields) has been transformed or exploited by humans.
Introduction of alien species	The distributions of species have been and continue to be dramatically transformed by human activities, both intentionally and unintentionally. In some countries, exotic plants constitute more than 25% of the flora (Heywood 1989).
Increased application of nutrients by humans	It is estimated that N fixation through human activities (fertilizer production, cultivation of N-fixing plant species, and industrial by-products) now exceeds N fixation from all combined natural sources (Vitousek 1994). Application of nitrogen fertilizer has more than doubled since 1970 to 80 Tg yr ⁻¹ in 1990, and is expected to increase at least 130 Tg yr ⁻¹ by 2050 (Matson <i>et al.</i> 1998).
Temperature changes	Computer models suggest substantial changes in surface temperatures around the globe, with most areas experiencing an increase in temperature of up to several degrees centigrade (Rind <i>et al.</i> 1990).
Changes in precipitation and evapotranspiration	Computer models suggest that the many effects of increasing greenhouse gas concentrations in the atmosphere may lead to substantial changes in the amount and timing of precipitation and to changes in water balance in different regions of the globe (Manabe and Wetherald 1986; Rind <i>et al.</i> 1990; Loaiciga <i>et al.</i> 1995).
River channelization (<i>e.g.</i> , dikes or deepening of channels)	Very few rivers near human settlement (as well as elsewhere) have not been channelized (<i>e.g.</i> , 4,500 km of embankments on the Mississippi River) to alter their hydrology to be more favorable for certain human activities (<i>e.g.</i> , flood control, drainage) (Ward 1978). Due to the prominent role water plays in transporting subsidies between systems, these changes in the relationship of a river to its basin is particularly important.
Human population growth	The explosion of the human population, apart from the many effects listed in this table, has also had a substantial effect on subsidies simply by virtue of our biomass and the diversion of subsidies needed to support that biomass. Even if each human were to consume a minimum amount of carbon and nutrients, the four- to fivefold increase of humans in this century alone (Smil 1997; Ojima <i>et al.</i> 1994) represents a considerable rerouting of resources through human biomass. Our omnivorous habit and mobility lead us to be important vectors in moving carbon and nutrients across system boundaries (<i>e.g.</i> , fishing reroutes marine and freshwater materials through terrestrial systems).
Dam construction	Dams substantially alter the shape and function of rivers. Few major rivers in developed countries do not have dams, and substantial dam

	building continues in developing countries. From 1950 to 1986, more than 36,000 large dams (> 15 m high) had been constructed or were under construction in the world (Goudie 1993).
Water diversion and irrigation	Irrigation reroutes the flow of water (and thus of subsidies), thereby establishing subsidy flows that previously did not exist (<i>e.g.</i> , river to non-riparian terrestrial systems) and modifying existing ones (<i>e.g.</i> , upstream to downstream or river to floodplain). The amount of irrigated cropland in the world has increased by 2,400% since 1700 (Meyer and Turner 1992). In 1985, approximately 2,710 km ³ of water per year was withdrawn from rivers for irrigation, of which the majority (approximately 2,340 km ³ yr ⁻¹) was consumptive use (lost as evapotranspiration or seepage) (L'vovich and White 1990).
Harvesting (<i>e.g.</i> , logging, cropping, fishing, etc.)	Although we apply nutrients and carbon to many systems, we also remove large fractions of these potential subsidies through harvesting activities (<i>e.g.</i> , 15-35 kg P ha ⁻¹ is removed in harvesting cereal crops; Smil 1997). Inasmuch as harvest and application of nutrients and carbon are never balanced spatially or temporally, these activities have the potential to dramatically shift pools of subsidies. Harvesting of organisms also alters the composition of communities, thereby altering food web structure.
Altered transport of subsidies by rivers	Transport of subsidies and sediment via river flow to the oceans has been substantially altered due to a number of factors throughout the world (McIntyre 1992; Howarth <i>et al.</i> 1996). Of particular concern are the changes in subsidy delivery to coastal margins.
Loss of ozone and increase in UV-B exposure	As a result of the atmospheric ozone depletion, solar UV-B reaching the surface of the earth is increasing (Rozema <i>et al.</i> 1997). This increase is not distributed evenly over the surface of the earth (Mathews and Keep 1993). UV-B has substantial effects on organisms, through the susceptibility of organisms to the deleterious effects of UV-B exposure varies considerably among species (Rozema <i>et al.</i> 1997).
Use of human-manufactured biocides in the environment and toxic waste	Pesticides and herbicides, by definition, alter the species composition of ecosystems. Although several classes of low-persistence biocides have been developed (after the recognition of the deleterious effects of DDT), contamination of nontarget ecosystems continues (Brown <i>et al.</i> 1990). Global consumption of pesticides exceeded 150,000 metric tons in 1980 (Brown <i>et al.</i> 1990). Discharge of many toxic materials into the environment is decreasing in most developed countries, but a considerable legacy of previous practices will persist (<i>e.g.</i> , Schulz-Bull <i>et al.</i> 1995; Dahlgaard 1996; Holm 1996), and controls on toxic waste are less stringent in many developing countries.
Enhanced levels of carbon in the atmosphere	Carbon dioxide concentrations in the atmosphere have increased by more than 25% during the last century (Ojima <i>et al.</i> 1994). This increase has substantial implications for plant physiology specifically and carbon metabolism in general, as well as numerous effects listed in this

	table.
Acid deposition	Several important elements may be transported long distances and deposited as acidic precipitation (acid rain). This deposition has many consequences, including deleterious effects. In some cases these elements act as subsidies. Although rates of acid deposition from the atmosphere appear to be decreasing in some regions, recovery of aquatic systems is not uniform (Stoddard <i>et al.</i> 1999). There is also concern over acid precipitation in rapidly developing countries.
Enhanced extinction rates	Current data suggest that extinction rates are increasing, and this increase is projected to continue (<i>e.g.</i> , Lovejoy 1980; Simberloff 1986). We may expect alterations in many susceptible food webs resulting from the loss of constituent species alone.
Alteration of global circulation patterns	Some global climate model simulations support the suggestion that El Niño/Southern Oscillation events may become more frequent with global warming (<i>e.g.</i> , Timmermann <i>et al.</i> 1999).
Genetic engineering of organisms	Genetic engineering has the potential to alter the effects of land use changes through changes in carbon metabolism and nutrient use efficiency.

Table 1.2: Agricultural impacts on stream systems (modified from Allan 2004)

Environmental Factor	Effects	References
Sedimentation	Increases turbidity, scouring and abrasion; impairs substrate suitability for periphyton and biofilm production; decreases primary production and food quality causing bottom-up effects through food webs; in-filling of interstitial habitat harms crevice-occupying invertebrates and gravel-spawning fishes; coats gills and respiratory surfaces; reduces stream depth heterogeneity; leading to decrease in pool species	Burkhead & Jelks 2001 Hancock 2002 Henley et al. 2000 Quinn 2000 Sutherland et al. 2002 Walser & Bart 1999 Wood & Armitage 1997
Nutrient enrichment	Increases autotrophic biomass and production, resulting in changes to assemblage composition, including proliferation of filamentous algae, particularly if light also increases; accelerates litter breakdown rates and may cause decreases in dissolved oxygen and shift from sensitive to more tolerant, often non-native species	Carpenter et al. 1998 Delong & Brusven 1998 Lenat & Crawford 1994 Mainstone & Parr 2002 Niyogi et al. 2003
Hydrological alteration	Alters runoff-evapotranspiration balance, causing increases in flood magnitude and frequency, and often lowers base flow; contributes to altered channel dynamics, including increased erosion from channel and surroundings and less-frequent overbank flooding; runoff more efficiently transports nutrients, sediments, and contaminants, thus further degrading in-stream habitat; strong effects from drainage systems and soil compaction in agricultural catchments	Allan et al. 1997 Paul & Meyer 2001 Poff & Allan 1995 Walsh et al. 2001 Wang et al. 2001
Riparian clearing/ canopy opening	Reduces shading, causing increases in stream temperatures, light penetration, and plant growth; decreases bank stability, inputs of litter and wood, and retention of nutrients and contaminants; reduces sediment trapping and increases bank and channel erosion; alters quantity and quality of dissolved organic carbon reaching streams; lowers retention of benthic organic matter owing to loss of direct input and retention structures; alters trophic structure	Bourque & Pomeroy 2001 Findlay et al. 2001 Gregory et al. 1991 Gurnell et al. 1995 Lowrance et al. 1984 Martin et al. 1999 Osborne & Kovacic 1993 Stauffer et al. 2000

CHAPTER 2

USE OF OCCUPANCY MODELS TO EXAMINE STREAM CONSUMER PREVALENCE ACROSS A LAND COVER GRADIENT IN THE SOUTHERN APPALACHIANS, USA¹

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Pringle. To be submitted to Diversity and Distributions.

ABSTRACT

Aim We used an occupancy modeling approach to identify environmental parameters that best predicted the prevalence of four functionally important focal stream taxa: (1) *Tallaperla* spp. (stonefly); (2) *Cambarus* spp. (crayfish); *Pleurocera proxima* (snail); and (4) *Cottus bairdi* (mottled sculpin). While an occupancy modeling approach has been used extensively for salamanders and fish, it has rarely been used to examine the prevalence of stream invertebrates and we are unaware of any studies that have previously used this approach to examine the prevalence of stoneflies, crayfish or snails.

Location Little Tennessee River basin, southern Appalachians, USA (in 37 stream reaches draining catchments between 18-1670 ha, within a 1,130 km² area).

Methods We used the estimated proportion of patches occupied within a stream reach as a measure of focal taxon prevalence and evaluated the fit of thirty-four models to examine the relative association of environmental parameters with taxon occupancy.

Results At the watershed level, the prevalence of all four taxa was associated with land cover, with *Tallaperla* largely absent below a threshold of 85-90% forest cover in the watershed. As forest cover is converted to other land cover types within watersheds, our findings suggest that corresponding decreases in leaf litter food resources cause decreases in abundance and extirpation of this taxon which is an important leaf shredder. Prevalence of *Cambarus* spp. and *Cottus bairdi* was related to local habitat factors and *Pleurocera proxima* was related to water chemistry.

Main conclusions Prevalence of our taxa was linked to parameters reflecting both local and larger-extent processes, highlighting the importance of considering regional factors (*e.g.* land cover in a watershed) in determining local conditions for stream organisms.

Keywords Appalachians, consumers, forest, habitat, land cover, occupancy models, stream chemistry

INTRODUCTION

Across a landscape, variation in the prevalence of stream organisms among reaches reflects the integration of processes occurring at various extents from local to landscape. Locally, the occurrence of animals within a patch depends on proximate conditions such as microclimate, food availability, or the presence of shelter (Morris 1987). However, factors shaping these local conditions are influenced by processes occurring at broader spatial extents. For example, at large spatial extents humans have increased the amount of land used for agriculture, residential developments, and urban centers (Sovell 2000, Allan 2004), decreasing the amount of forest cover and altering the flow of water, nutrients, and other solutes within watersheds (Allan 2004, Webster *et al.* 2012). Within watersheds, flow of nutrients and water from surrounding terrestrial and hyporheic linkages, as well as in-stream physical and biological processes help determine stream chemistry (Poole 2010). More locally, riparian vegetation stabilizes channel morphology, mediates the flow of nutrients and water into stream systems, decreases light penetration, and increases leaf standing stocks and large woody debris available for stream consumers (Allan 2004). While the relationship between local and landscape processes may be intuitive and well-understood, highlighting the interdependence and interaction of local and landscape processes is important. With rapid human alteration of landscapes, there is great urgency to understand the consequences of those effects and to inform management. Focusing on local parameters affecting stream organisms may fail to identify larger extent processes influencing local suitability of habitat, when there is a spatial hierarchy of processes

affecting the system. Ultimately, the goal is to identify the processes that best predict the distribution and abundance of species or entire communities.

Regional landscapes in the southern Appalachians are changing, driven by high population growth and limited zoning restrictions on human development in steep terrain (Gragson & Bolstad 2006). Exurban pressures from surrounding metropolitan areas including Atlanta and Asheville have contributed to high population growth rates; in the 1980s and 1990s the population growth rate in the region was double the national average (Pollard 2005). Historically urban, residential, and agricultural development primarily occurred in valleys; however, recent residential development has increased along mountainsides due to an influx of vacation home owners, resulting in a quintupling of second homes recorded from 1970 to 2000 (U.S. Census Bureau, 1900-2000, Webster *et al.* 2012, Kirk *et al.* 2012). These increases in mountainside human land-use and additional regional conversion of forested land cover to urban, residential, and agricultural land-use has enhanced potential human impacts on adjoining streams, and offer an opportunity to investigate the influence of human land-use on environmental processes occurring at different extents within a spatial hierarchy in the southern Appalachians.

We selected sites along a gradient of land cover from heavily forested watersheds to increasingly agricultural, residential, and urban dominated watersheds within the upper Little Tennessee River basin. Over a large spatial extent, we examined sites at different stages of development along the land cover development trajectory, using a space-for-time framework to capture much of the variability in regional land cover during a short sampling period (Pickett 1989, Fukami & Wardle 2005, Carter *et al.* 2009). The objectives of the study were to: (1) investigate the relationships of local and watershed factors affected by human land use to the

prevalence of stream organisms, (2) to evaluate the relative performance of models using local and landscape factors to predict the observed prevalence of our focal taxa, and (3) to identify a limited number of environmental parameters linked to stream consumer prevalence that could be quickly assessed given limited conservation budgets. We focused on effects of land cover, habitat, and water chemistry on four focal stream consumers within the Little Tennessee River Basin: *Tallaperla* spp. (stonefly), *Cambarus* spp. (crayfish), *Pleurocera proxima* (snail), and *Cottus bairdi* (mottled sculpin), that were expected to influence the prevalence of taxa based on the life history and environmental niche of each taxon.

METHODS

Site Description

The Little Tennessee River originates in northeast Georgia, flows through southwestern North Carolina, and empties into the Tennessee River in eastern Tennessee. Monthly air temperature means range from 3 to 22° C, and mean annual precipitation ranges from 180 - 250 cm (Swift *et al.* 1988). Soils are generally classified as immature Inceptisols or older weathered Ultisols. Our study region was predominately forested (approximately 80% forest cover over the 1,130 km² region, Webster *et al.* 2012) but a mix of forest, agriculture, urban, commercial, and other land cover occur. Thirty-seven study reaches were selected in the upper Little Tennessee River basin in the Blue Ridge Physiographic Province (Figure 2.1). Our study reaches are a wadeable subset (first and second Strahler stream order) of fifty-eight reaches/watersheds that were selected to be representative of different land-use trajectories within the region and accessible (Webster *et al.* 2012). Although stream reaches were not randomly selected, they

were selected with no prior knowledge of stream chemistry, habitat, or the presence/absence of our focal taxa from a stratified database of accessible streams with various land-covers.

Selection of focal taxa

Our four focal taxa (*Tallaperla* spp., *Cambarus* spp., *Pleurocera proxima*, and *Cottus bairdi*) were chosen based on both their functional importance and their prevalence in the southern Appalachians, as common taxa are often influential in ecosystem function (Schmitz 2010, Gaston 2010). These focal taxa are important because of their consumer activities: *P. proxima* as grazers and shredders (Dillon & Robinson 2009), *Tallaperla* as shredders (O'Hop *et al.* 1984), *Cambarus* as omnivores and shredders (Schofield *et al.* 2001, Creed & Reed 2004), and *C. bairdi* as benthic insectivores (Grossman *et al.* 2006). Additional considerations informed our selection of these taxa. The shredding stonefly, *Tallaperla* (Insecta: Plecoptera: Pteronarcyioidea: Peltoperlidae), is found throughout the Appalachians and is detectable during the summer when many other insect taxa are in winged adult form and absent from streams (O'Hop *et al.* 1984, Huryh 1986). In highly forested streams *Tallaperla* is important in leaf decomposition, and represents a substantial percentage of insect biomass (Woodall & Wallace 1972, Stout *et al.* 1993, Hutchens & Wallace 2002). The omnivorous crayfish, *Cambarus* (Crustacea: Decapoda: Astacidea: Astacoidea: Cambaridae), is a leaf shredder that contributes substantially to leaf decomposition (Schofield *et al.* 2001), is found throughout the eastern and central U.S., and is the most widely distributed and prevalent crayfish genus in the Little Tennessee River basin (Simmons & Fraley 2010). The insectivorous sculpin, *Cottus bairdi* (Actinopterygii: Scorpaeniformes: Cottoidea: Cottidae), is found throughout the Appalachian, Great Lake, Rocky Mountain, and northern Cascade states. *C. bairdi*, is the most common fish in the southern Appalachians and displays high territorial fidelity (Grossman *et al.* 2006, Petty &

Grossman 2007), which makes it ideal for occupancy modeling. The snail, *Pleurocera proxima* (Gastropoda: Cerithioidea: Pleuroceridae), is an important stream grazer common in southern Appalachian streams from Georgia to Virginia, has limited dispersal ability, and can significantly regulate nutrient cycling and algal community structure and biomass (Dillon & Robinson 2009). By focusing on four common taxa we were able to rapidly assess patch occupancy, enabling us to sample a large number of streams and a relatively large spatial extent. Our choices of an insect, crustacean, gastropod, and fish reflect an interest in examining the effects of environmental factors on organisms representing different evolutionary trajectories, to see if there are any unifying trends among diverse taxa.

Field Sampling

Field sampling of focal taxa within the Little Tennessee River Basin took place in thirty-seven stream reaches between May - July 2009. Sampled reaches all drained an area less than 17 km², and land cover varied among these reaches (Table 2.1). For each reach, we designated a 150 m reach generally upstream of any nearby road crossing that was surveyed for focal taxa. In each reach, thirty-one 1 m² patches were delineated, each located 5 m upstream from the previous patch. We used two different techniques to detect animals (following Mattfeldt & Grant 2007). First, we actively surveyed each patch by turning cover objects and searching leaf litter. Second, we used rectangular leaf litter bags (25 by 40 cm) constructed with 1 cm² plastic mesh. Bags are attractants, but animals can move freely in and out of the bags. At each reach we collected adjacent streamside leaf litter or litter from the nearest upstream source to fill each bag. One litter bag was placed within each patch in shallow water near the riverbank, and allowed to sit for 48 hours before our first sampling. Litter bags were held in place by using a

large piece of cobble as a weight. During field sampling, the presence/absence of rhododendron adjacent to each patch was noted, in order to calculate the percent rhododendron for each reach.

To estimate probabilities of detection and occupancy, we surveyed each patch daily for three consecutive days. On each day, we actively surveyed the patches and checked leaf litter bags. We checked leaf-litter bags by placing them in a bin and pouring water through the litter bag before gently agitating the litter bags to dislodge animals. Water and any dislodged organisms were filtered through a dip-net for increased detection. On the first and second day, we returned litter bags to the same reach location and returned all organisms into the litter bag. Releasing animals into the litter bags was essential because the failure to capture animals in a bag on a subsequent day would be the result of animals voluntarily leaving the bag and not because we had displaced the animal from the bag. Following sampling on the third day, we removed all litter bags from the reach.

Additional data sources

We used previously collected water chemistry and land cover data (described in Webster *et al.* 2012). Reaches were sampled in June 2009 over three day periods of stable weather and discharge. Field measurement was made of conductivity (YSI Model 30), while calcium, nitrogen, and phosphorous, laboratory analysis was performed from one to four liter stream samples collected in the field (methods in Webster *et al.* 2012). Total dissolved phosphorous was determined by persulfate in-line UV digestion with a Lachat QuickChem FIA+ instrument, total dissolved nitrogen was determined with a Shimadzu TOC-VCPH TN analyzer, and calcium concentration was determined with a PerkinElmer Analyst300 Atomic Absorption Spectrometer. Field measurements were made of large woody debris greater than 10 cm, pebble count (median from 100 pebbles), percent pool, percent riffle, channel width, and slope (methods adapted from

Jackson *et al.* 2001). Visual assessment of study reaches classified riparian zones as: no forested riparian zone (occasional or no trees), single tree riparian zones less than 3 meters in width, narrow forested riparian zone 3-10 meters in width, or riparian forest greater than 10 meters in width. Watershed drainage area was calculated and land cover data was classified into forest, residential, and agricultural classes from 2006 NASA Landsat Thematic Mapping Imagery after delineation of watershed boundaries (Webster *et al.* 2012).

Statistical analysis

We used detection probabilities to estimate the proportion of patches in each study reach that were occupied by each focal taxon, with the assumption that the estimated proportion of patches occupied was a measure of taxon prevalence in each reach. We then fit occupancy models relating covariates to the proportion of patches occupied by each focal taxon (MacKenzie *et al.* 2003). Since biota are detected with less than 100% certainty, this had the potential to confound our models of taxon prevalence. To account for this incomplete detection, we fit occupancy models as:

$$P(d) = P(d|\Psi)*\Psi,$$

where $P(d)$ is the proportion of patches where a taxon was detected, Ψ is the true proportion of patches occupied by a taxon, and $P(d|\Psi)$ was the probability of detecting the taxon at a patch, given it was present (MacKenzie *et al.* 2003). We assumed that differences in detection among reaches was relatively minor, with the same personnel performing standardized techniques with consistent effort.

Taxon-specific occupancy (Ψ) was modeled as a logit linear function of landscape-level characteristics, water chemistry, and habitat (detailed below) and the probability of detection $P(d|\Psi)$ was assumed constant. We used Markov Chain Monte Carlo (MCMC) as implemented in

WinBUGS software, Version 1.4 (Lunn *et al.* 2000) to fit models. Models were fit using 500k iterations, 200k iteration burn in (*i.e.*, the first 200k MCMC iterations were dropped), and diffuse priors. The number of iterations needed for convergence was estimated using the Gelman and Rubin diagnostic test (Gelman & Rubin 1992) based on three Markov chains derived from 500,000 iterations of the global model for each taxon. The Gelman and Rubin diagnostic test was conducted using CODA analysis in program R (Plummer *et al.* 2006, R Development Core Team 2010). For each taxon, goodness-of-fit (GOF) was assessed for the global models using a simple discrepancy measure and 1000 simulated data points (Gelman *et al.* 1996). This method compares deviances of simulated and observed data and fit is considered adequate when the GOF statistic is close to 0.5. After detecting a large site effect, additional models were tested using site-specific habitat parameters (slope, riparian buffer, average channel width, large woody debris frequency, percent pool, percent riffle, and median pebble size) to attempt to reduce the unexplained site effect and improve model performance. Models were fit using 1,000k iterations, 500k iteration burn in, and diffuse priors, based on Gelman and Rubin diagnostic test results.

Prior to analyses we performed data transformations to normalize data and adhere to model assumptions. Watershed land cover measures of percent forest, percent agriculture, percent urban, as well as percent rhododendron, percent pool, and percent riffle in a reach were arcsine transformed. All covariates that were not categorical or percent data were z score standardized to a mean of zero and a standard deviation of one. To avoid multicollinearity, we ran Pearson correlations on all pairs of predictor parameters prior to modeling. Preliminary evaluation of model fit indicated that the data for each taxon were overdispersed. To account for the overdispersion, we included random effects that corresponded to study reaches. The random

effects were assumed to be normally distributed with mean of zero. The random effect variance was counted as an additional parameter in the calculation of Akaike Information Criteria (Akaike 1973) with small sample bias adjustment (AICc; Hurvich and Tsai 1989), discussed below.

We used an information-theoretic approach (Burnham & Anderson 2002) to evaluate the relative fit of candidate models relating the proportion of patches occupied to environmental parameters. We developed a set of thirty-four models representing hypotheses about the relative influence of landscape-level features, water chemistry, and reach habitat on taxon occupancy. We then evaluated the relative fit of the candidate models using AICc and by calculating Akaike weights (w) that can range from '0' to '1', with the best-approximating model having the greatest Akaike weight (Akaike 1973; Burnham & Anderson 2002). Because the MCMC methods produce a distribution of AICc values, we used the mean AICc from the 300k or 500k iterations for all inferences (Fonnesbeck & Conroy 2004). The ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham & Anderson 2002). Thus, we expressed model selection uncertainty by constructing a confidence set of models, which is analogous to the confidence interval of a mean, by including models with Akaike weights that were within 10% of the best approximating model weight. This is similar to the general rule-of-thumb (*i.e.* 12%) suggested by Royall (1997) for evaluating strength of evidence. The precision of parameter estimates was estimated by computing 95% credible intervals (Congdon 2001), which are analogous to 95% confidence intervals. We also calculated scaled odds ratios (Hosmer & Lemeshow 2000) for each predictor parameter to facilitate interpretation. The odds ratio scalars corresponded to what we believed were relevant unit changes in the predictors.

RESULTS

We examined potential correlations among covariates before model construction. Since percent forest, percent agriculture, and percent urban cover in a watershed were highly correlated (Pearson correlation $r < -0.90$), we never used more than one in our models. Percent forest in the watershed was negatively correlated with total nitrogen ($r = -0.81$), conductivity ($r = -0.76$), and calcium ($r = -0.75$). However, since we wanted to focus on expected effects of both land cover and water chemistry on focal taxa, we performed our analyses while aware of the correlations. AIC approaches are generally robust to collinearity as parameter estimates remain unbiased although sampling variances increase (Burnham & Anderson 2002, Freckleton 2011). Remaining correlations were relatively small ($|r| < 0.45$). The global (all parameter) occupancy models had goodness of fit (GOF) statistics ranging from 0.44 – 0.57, indicating that there was adequate model fit. Therefore, we assumed that the fit was adequate for candidate occupancy models (following Burnham & Anderson 2002).

Tallaperla

Tallaperla detection probability was relatively high and averaged 54% for a single sample day and 90% for detecting this taxon on at least one of three days. The best approximating *Tallaperla* occupancy model included percent forest cover in the watershed and total nitrogen ($w = 0.93$), and was 35.9 times more likely than the next best model that included percent forest cover in the watershed, conductivity, calcium, total nitrogen, and total dissolved phosphorous ($w = 0.03$) (Table 2.2a). Therefore, our confidence set contained only the best approximating model. *Tallaperla* occupancy was positively related to percent forest cover in the watershed and negatively related to total nitrogen (Table 2.3). *Tallaperla* were largely restricted to watersheds containing forest cover above a threshold of approximately 85-90% (Figure 2.2).

However, the parameter estimate for total nitrogen was imprecise and the confidence intervals were wide and included zero (no effect). We estimate that *Tallaperla* occupancy rates were, on average, 1.18 times greater with each 10% increase in percent forest cover in the watershed.

Cottus bairdi

C. bairdi detection probabilities were relatively high and averaged 54% for a single sample day and 90% for three sample days. The best approximating occupancy model for *C. bairdi* contained percent forest cover in the watershed and median pebble size ($w = 0.19$). There was no clearly best supported candidate model for *C. bairdi*, as the confidence model set ($w > 0.04$) contained seven additional models that contained percent forest cover in the watershed and/or various habitat parameters (Table 2.2b). The parameter estimates for these effects were all imprecise, with wide confidence limits that included zero. Therefore, we present parameter estimates for two of the best models. *C. bairdi* occupancy was positively related to pebble size and percent forest in the watershed, although the confidence interval for forest barely overlapped zero (Table 2.4). An additional relatively precise model contained channel width, although the confidence interval overlapped zero. We estimate that *C. bairdi* occupancy rate was 1.16 times greater for each 10% increase in forest and 1.17 times greater for each 10% increase in median pebble size.

Cambarus

Cambarus detection probabilities averaged 59% for a single day and 93% for three days. The best *Cambarus* occupancy model contained percent agricultural cover in the watershed and large woody debris per meter ($w = 0.92$) and was 14.3 times more likely than the next best model that only included large woody debris per meter ($w = 0.06$) (Table 2.2c). These two models compromised the confidence set. Large woody debris per meter was positively related to

Cambarus occupancy in both models and the parameter estimates were relatively precise (Table 2.5). We estimate that *Cambarus* occupancy was, on average, 1.2 times greater with each 10% increase in large woody debris. *Cambarus* occupancy was negatively related to agricultural cover in the watershed, but the parameter estimates were imprecise.

Pleurocera proxima

The probability of detecting *P. proxima* was greatest among all four taxa and averaged 65% for a single day and 96% for three days. The best approximating *P. proxima* occupancy model contained the parameter calcium concentration ($w = 0.24$), and was only slightly better supported than the second best model that contained percent forest cover in the watershed ($w = 0.15$) (Table 2.2d). There was no clearly best supported candidate model for *P. proxima*, as the confidence model set ($w > 0.02$) contained seven additional models that contained calcium concentration or percent forest cover in the watershed in various combinations with the water quality parameters conductivity, total nitrogen, and total dissolved phosphorous. The parameter estimates for these effects were all imprecise, with wide confidence limits that included zero. Therefore, we report parameter estimates for the two best approximating models. Calcium concentration was positively related to *P. proxima* occupancy, whereas percent forest cover in the watershed was negatively related (Table 2.6). We estimate that *P. proxima* occupancy rate was, on average, 2.49 times greater with each 0.85 increase in calcium concentration. Conversely, we estimate that *P. proxima* occupancy rate was, on average, 1.21 times lower with each 10% increase in percent forest cover.

DISCUSSION

Our results suggest that prevalence of stream consumers reflected local conditions influenced by the integration of natural processes occurring on multiple spatial extents, and

impacted by human development. Organism prevalence was most closely linked to environmental parameters operating at different spatial extents for each taxon (Table 2.7). *Tallaperla* prevalence was positively associated with forest cover at the watershed level, *C. bairdi* and *Cambarus* prevalence were associated with increased forest cover at the watershed level and habitat covariates at the local level, while *P. proxima* prevalence was negatively associated with forest cover at the watershed level and positively associated with water chemistry (influenced by local to watershed processes). If we had focused solely on local parameters, we would have failed to identify larger extent processes (*i.e.* watershed land cover and water chemistry) influencing local suitability of habitat for stream consumers.

Notably, prevalence of focal taxa ranging from insects, crustaceans, gastropods to fish shared an association with land cover at the watershed level (Figure 2.3). The strong predictive performance of occupancy models that included land cover in a watershed shows the influence of processes occurring at large spatial extents on local conditions and the resulting prevalence of stream consumers. The rapid human population growth in the Little Tennessee River basin and corresponding loss of forest land cover to agricultural, residential, and urban land use in the region has potentially serious effects on stream consumers. Increased human land use within watersheds can negatively impact stream ecosystems and biological communities through increased sedimentation, nutrient enrichment, contaminant pollution, hydrologic alteration, riparian zone clearing, loss of large woody debris, and other effects (Allan 2004). Since our focal stream consumers are important in ecosystem processes and as predators and prey within food webs, decline or extirpation of these stream consumers would likely alter stream ecosystem and food web dynamics within the Little Tennessee River basin. Regional development trends are expected to decrease forest cover which would maintain or enhance habitat for *P. proxima*,

so as a conservation priority we recommend maintaining forested land cover within Little Tennessee River basin watersheds in order that populations of *Tallaperla*, *C. bairdi*, and *Cambarus* persist and remain common.

Tallaperla prevalence was positively and most closely associated with percent forest in a watershed, intimating the influence of larger extent processes on local stream conditions for *Tallaperla*. Below a threshold of approximately 85-90% forest cover in a watershed, *Tallaperla* were largely absent. At the local level, *Tallaperla* are good indicators of standing biomass in streams as leaf litter and associated microbial communities are necessary for food (Woodall & Wallace 1972), and standing leaf biomass is impacted by the amount of forested habitat within a watershed (Huckins & Burgess 2004). Our results suggest that as forests are converted to other land cover types within watersheds, corresponding decreases in leaf litter inputs negatively affect *Tallaperla*, and below a threshold level extirpation results. Although we are the first to detect a threshold level of forest cover in a watershed for *Tallaperla* persistence, other landscape studies have found a positive association of *Tallaperla* with forested watersheds. Huryn *et al.* (2002) categorized seventeen streams in Maine as forest, wetland, agricultural, and urban catchments based on GIS land cover data, and found that while *Tallaperla* had high prevalence in forest streams *Tallaperla* were absent from the other catchments. Hagen *et al.* (2006) examined taxonomic richness and macroinvertebrate densities for twelve streams in North Carolina and Georgia assigned to forest and different agricultural classes based on riparian zone activity; *Tallaperla* had high prevalence in forest streams, and decreased in prevalence as agriculture increased.

Our models show that *C. bairdi* occupancy rate was positively related to percent forest cover in a watershed, and to local habitat factors. Forested watersheds with larger channel

widths are often high-quality streams for fish, with more food and habitat resources. Reach-level studies found that mottled sculpin population dynamics were closely associated with availability of benthic macroinvertebrate prey in three reaches in the Coweeta Creek drainage, North Carolina (Grossman *et al.* 2006, Petty and Grossman 2007). At the local level, *C. bairdi* are likely sensitive to sediment inputs from human development as sediment covers cobble/gravel spawning habitat and decreases macroinvertebrate prey (Wood & Armitage 1997, Schofield *et al.* 2004); larger median pebble size indicates quality habitat remains. On a landscape level, Scott (2006) examined fish communities, the effects of watershed land cover, and land-use legacies in thirty-six streams in the Little Tennessee River and neighboring French Broad River basins. *C. bairdi* was grouped with sixteen other endemic highland species; analysis showed that endemic highland fish relative prevalence was positively related to forest cover, negatively related to urbanization intensity, and negatively impacted by loss of forest cover from the 1970s to 1990s (Scott 2006).

We had good model support for a negative relationship between agricultural cover in a watershed and *Cambarus* occupancy rate, and a positive relationship to the local habitat factor large woody debris per meter. Large woody debris likely serve as refuges from predators and enhance local environmental conditions. Other studies similarly show an association of *Cambarus* with local habitat features. In five Virginia stream reaches Miller (1985) found higher density of *Cambarus* associated with small boulders and large cobbles, which are refuges from predators. Fish predation decreased prevalence of *Cambarus*, and crayfish density in fishless pools was higher than in pools with fish in four Kentucky streams (Englund 1999). Further study of the environmental and competitive factors that determine presence/absence as well as density of different species of *Cambarus* in different stream reaches is recommended. Although

Cambarus bartonii dominates headwater streams seven *Cambarus* species are located in the Little Tennessee River basin (Cooper 2004).

While increased *P. proxima* prevalence was associated with higher stream calcium concentrations, it was also detected in streams with extremely low levels (< 1 mg Ca/L). In contrast, previous studies have found that spatial distribution of pulmonate snails is often limited by available calcium and sufficient alkalinity (Shoup 1943, Dillon & Benfield 1982, Dillon 1984, Lodge *et al.* 1987, Hunter 1990, Hury *et al.* 1995). Similar to our study, Dillon & Benfield (1982) found that over a large region in south Virginia and northwest North Carolina *P. proxima* was unique in persisting in rivers and streams with extremely low alkalinity and total hardness, conditions that excluded other gastropods. Low calcium levels and cold stream temperatures suggest that headwater streams in the Little Tennessee River basin are metabolically stressful environments for gastropods, and many gastropods in cold, oligotrophic systems are stress-tolerant (Dillon 2000). Our study reaches were restricted to first and second order streams, where *P. proxima* populations have previously been found to have highest prevalence (Dillon 1984, Dillon and Robinson 2009).

One concern with use of space-for-time frameworks is an inability to distinguish historical legacies from current conditions, with potential to mistakenly attribute environmental effects to current instead of historical factors (Harding *et al.* 1998, Carter *et al.* 2009). Historical legacies impact this study, but different legacies among watersheds are minimized by consistent region-wide trends: hunting/gathering and small-scale agriculture in the pre-European period, increasing agriculture through the 1800s until 1950, clear-cut logging leading to the elimination of almost all old growth forest in the 1920s and 1930s, and residential development accelerating in the 1960s and 1970s (Swank & Crossley 1988, Gragson & Bolstad 2006). By sampling thirty-

seven watersheds we hoped to dampen the effects of potential outliers, such as an unusual historical footprint within an individual watershed. In addition, we included a random effect term in our models to help account for differences among watersheds.

In conclusion, findings presented here highlight the association between prevalence of stream consumers and land-cover in a watershed, as well as the importance of assessing large-scale processes which impact local habitat suitability for stream organisms. In addition, the occupancy modeling approach was effective in evaluating factors influencing the prevalence of selected freshwater macroinvertebrate taxa. Although the occupancy model approach has been used extensively for salamanders (Russell *et al.* 2004, Grant *et al.* 2009, Price *et al.* 2011, Cecala 2012) and fish (Albanese *et al.* 2007, Wenger & Freeman 2008, Kirsch 2011), occupancy models have rarely been used to study stream invertebrates, and we are unaware of any studies that have previously used occupancy models for stoneflies, crayfish, or snails. This modeling approach has expanded our understanding of how stream consumers important to ecosystem function are influenced by a mix of local and watershed environmental parameters within reaches of the Little Tennessee River basin of the southern Appalachians.

ACKNOWLEDGEMENTS

This study was part of the Coweeta Long Term Ecological Research study funded by National Science Foundation DEB0823293. It was supported by the Odum School of Ecology and the Warnell School of Forestry and Natural Resources at the University of Georgia. D. Hung, C. Kresl, L. Long, J. McMillan, J. Milanovich, S. Evans, S. Vulova, J. Cosgrove, and others provided critical field work. F. Benfield, D. Leigh, M. Valett, and J. Webster led collection of stream chemistry data. J. Hepinstall-Cymerman determined land cover in each

watershed. J. Chamblee, K. Love, and R. Benson produced the study area graphic. The USDA Forest Service provided key logistical support. M. Freeman, M. Snyder, S. Wenger, and the Pringle lab provided valuable comments on the manuscript.

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BIOSKETCH

John Frisch is an ecologist interested in the environmental factors and human impacts influencing the distribution of stream consumers in the southern Appalachians. Author contributions: J.F., C.P., and J.M. led the writing; J.M. and K.C. helped design the study; J.F., K.C., and C.J. collected the data; J.F. and J.P. analyzed the data; J.F., C.P., J.M., and T.G. conceived the idea.

Table 2.1. Statistics for parameters included in occupancy models quantified from surveys of 37 sites within the Little Tennessee River basin. SD is standard deviation, Min. is minimum value, Max. is maximum value.

<u>Characteristic</u>	<u>Mean</u>	<u>SD</u>	<u>Min.</u>	<u>Max.</u>
Forest (%) in watershed (FOREST)	88.56	15.55	43.2	100
Agriculture (%) in watershed (AGRIC)	3.96	6.29	0	29.2
Urban (%) in watershed (URBAN)	5.87	9.80	0	40.7
Rhododendron (%) at site (RHODODENDRON)	45.87	46.24	0	100
Watershed Drainage Area (km ²) (DRAIN)	2.74	3.99	0.18	14.38
Conductivity (μS/cm) at site (COND)	26.91	12.84	9.3	63.5
Calcium (mg/L) at site (CA)	1.46	0.84	0.26	3.15
Total Dissolved Nitrogen (mg/L) at site (TDN)	0.14	0.12	0.02	0.52
Total Dissolved Phosphorous (mg/L) at site (TDP)	0.007	0.004	0.003	0.02
Slope at site (SLOPE)	0.04	0.03	0.001	0.2
Channel Width (m) at site (CHANNEL WIDTH)	3.04	1.32	0.78	6.96
Large Woody Debris Frequency (No./m) at site (LWD)	0.06	0.11	0	0.5
Pool (%) at site (POOL)	5.64	9.00	0	46.00
Riffle (%) at site (RIFFLE)	58.21	35.12	0.53	99.24
Median Bed Particle Size (mm) at site (PEBBLE)	35.95	20.6	5.0	85.5

Table 2.2. Predictor parameters, number of parameters (K), ΔAICc , and Akaike weights (wi) for best performing occupancy models (i). Akaike weights are interpreted as relative plausibility of candidate models a) *Tallaperla* b) *Cottus bairdi* c) *Cambarus* d) *Pleurocera proxima*. Models with Akaike weights (wi) less than .04 are considered highly improbable and were omitted, except when they were the second best model (Table 2.2a).

Table 2.2a.

<i>Tallaperla</i> candidate model	-2LogL	K	ΔAICc	wi
FOREST TDN	2006.37	5	0.00	0.933
FOREST COND CA TDN TDP	2004.33	8	7.16	0.026

Table 2.2b.

<i>Cambarus</i> candidate model	-2LogL	K	ΔAICc	wi
AGRIC LWD	3687	5	0.00	0.919
LWD	3695	4	5.31	0.064

Table 2.2c.

<i>Cottus bairdi</i> candidate model	-2LogL	K	ΔAICc	wi
FOREST PEBBLE	1401	5	0.00	0.189
FOREST	1404	4	0.31	0.161
RHODODENDRON	1405	4	1.31	0.098
CHANNEL WIDTH	1403	5	2.00	0.069
SLOPE	1406	4	2.31	0.059
RIPARIAN CODE	1406	4	2.31	0.059
FOREST LWD PEBBLE	1401	6	2.86	0.045
FOREST PEBBLE	1404	5	3.00	0.042

Table 2.2d.

<i>Pleurocera proxima</i> candidate model	-2LogL	K	Δ AICc	wi
CA	1711.34	4	0.00	0.243
FOREST	1712.33	4	0.99	0.148
FOREST TDP	1710.25	5	1.59	0.110
FOREST CA	1710.32	5	1.66	0.106
COND CA TDN TDP	1704.43	7	1.70	0.104
FOREST COND CA TDN TDP	1701.72	8	2.27	0.078
TDN	1714.56	4	3.21	0.049
FOREST TDN	1712.23	5	3.57	0.041

Notes: FOREST is percent forest in a watershed; AGRIC is percent agriculture in a watershed; RHODODENDRON is percent rhododendron in a reach; TN is total dissolved nitrogen; COND is conductivity; CA is calcium; TDP is total dissolved phosphorous; LWD is large woody debris per meter; PEBBLE is median pebble size; CHANNEL WIDTH is channel width

Table 2.3. Parameter estimates, standard deviation (SD), lower and upper 95% credible intervals, and scaled odds ratios (OR) for the best *Tallaperla* occupancy model. The random effect is an estimate of the extra binomial variance.

Parameter	Estimate	SD	Lower	Upper	Scaled	
					Scalar	OR
<i>Occupancy(Ψ)</i>						
Intercept	-2.358	1.271	-4.877	0.072		
Forest	1.668	0.840	0.102	3.346	0.10	1.18
Total Nitrogen	-2.104	1.604	-5.247	1.037	0.10	0.81
Random effect	3.539	0.349	2.716	3.983		
<i>Detection (p)</i>						
Intercept	0.163	0.061	0.043	0.282		

Table 2.4. Parameter estimates, standard deviation (SD), lower and upper 95% credible intervals, and scaled odds ratios (OR) for the confidence set of *Cottus bairdi* occupancy models. The random effect is an estimate of the extra binomial variance.

Parameter	Estimate	SD	Lower	Upper	Scalar	Scaled OR
<u>Best occupancy model</u>						
<i>Occupancy (Ψ)</i>						
Intercept	0.931	1.253	-1.511	3.340		
Forest	1.495	0.991	-0.481	3.354	0.10	1.16
Pebble	1.573	0.570	0.472	2.709	0.10	1.17
Random effect	3.074	0.550	1.979	3.949		
<i>Detection (p)</i>						
Intercept	0.197	0.104	0.168	0.234		
<u>Additional occupancy model</u>						
<i>Occupancy (Ψ)</i>						
Intercept	-0.759	0.621	-1.958	0.459		
Channel Width	0.505	0.587	-0.701	1.661	0.10	1.05
Random effect	3.428	0.416	2.467	3.977		
<i>Detection (p)</i>						
Intercept	0.195	0.100	0.166	0.228		

Table 2.5. Parameter estimates, standard deviation (SD), lower and upper 95% credible intervals, and scaled odds ratios (OR) for the confidence set of *Cambarus* occupancy models. The random effect is an estimate of the extra binomial variance.

Parameter	Estimate	SD	Lower	Upper	Scalar	Scaled OR
<u>Best occupancy model</u>						
<i>Occupancy (Ψ)</i>						
Intercept	2.901	0.561	1.908	4.140		
Agriculture	-1.638	1.498	-4.536	1.372	0.10	0.85
Large Woody Debris	1.612	0.821	0.218	3.435	0.10	1.17
Random effect	1.899	0.525	1.108	3.179		
<i>Detection (p)</i>						
Intercept	0.355	0.053	0.332	0.380		
<u>Second best occupancy model</u>						
<i>Occupancy (Ψ)</i>						
Intercept	2.774	0.581	1.794	4.077		
Large Woody Debris	1.862	0.838	0.408	3.664	0.10	1.20
Random effect	2.099	0.534	1.273	3.395		
<i>Detection (p)</i>						
Intercept	0.354	0.051	0.331	0.337		

Table 2.6. Parameter estimates, standard deviation (SD), lower and upper 95% credible intervals, and scaled odds ratios (OR) for the two best *Pleurocera proxima* occupancy models. The random effect is an estimate of the extra binomial variance.

Parameter	Estimate	SD	Lower	Upper	Scalar	Scaled OR
<u>Best occupancy model</u>						
<i>Occupancy(Ψ)</i>						
Intercept	-3.070	1.106	-5.205	-0.843		
Calcium	1.074	0.439	0.166	1.907	0.85	2.49
Random effect	3.664	0.266	3.019	3.989		
<i>Detection (p)</i>						
Intercept	0.620	0.064	0.494	0.746		
<u>Second best occupancy model</u>						
<i>Occupancy(Ψ)</i>						
Intercept	0.785	1.255	-1.695	3.194		
Forest	-1.916	0.902	-3.606	-0.146	0.10	0.83
Random effect	3.687	0.252	3.068	3.990		
<i>Detection (p)</i>						
Intercept	0.623	0.064	0.497	0.750		

Table 2.7. Parameters that influence prevalence of focal taxa, with the scale of the parameter. + represents a positive association with increased prevalence, - represents a negative association with increased prevalence, and a blank represents no association.

Taxon	Watershed scale	Watershed to local scale	Local Scale
	Forest Cover	Water Chemistry	Habitat Covariate
<i>Tallaperla</i>	+		
<i>C. bairdi</i>	+		+
<i>Cambarus</i>	+		+
<i>P. proxima</i>	-	+	

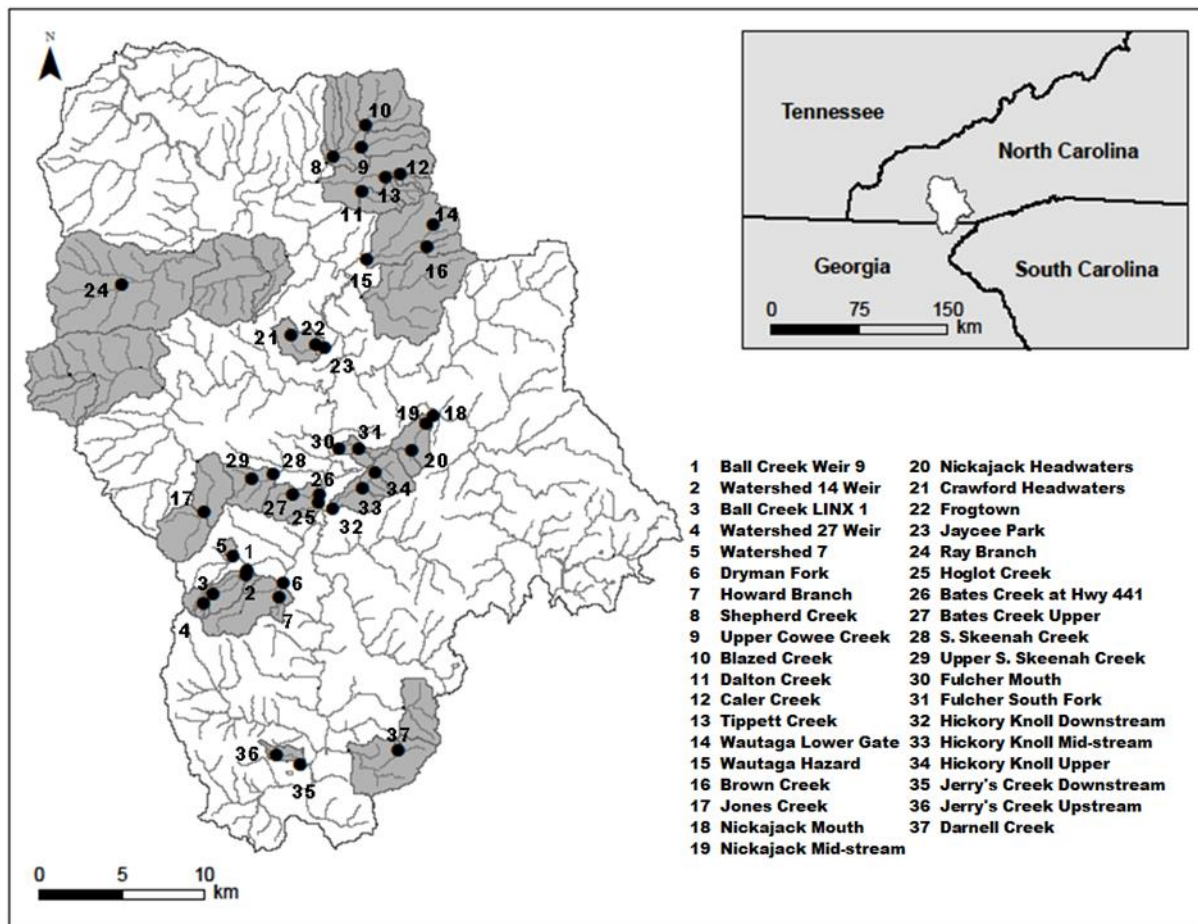


Figure 2.1. Location of study sites within the Little Tennessee River basin, Georgia and North Carolina (1,130 km²).

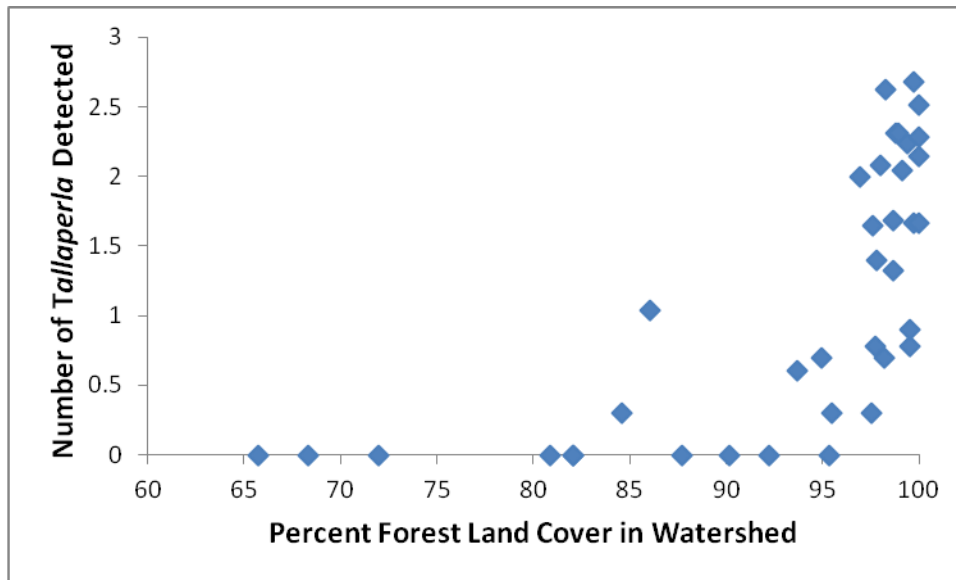


Figure 2.2. Number of *Tallaperla* detected by percent forest land cover in a watershed. A threshold occurs at approximately 85-90% forest cover in a watershed, below which *Tallaperla* are not detected. Please note that the y-axis has been log transformed, after all values were increased by one to avoid undefined log transformations.

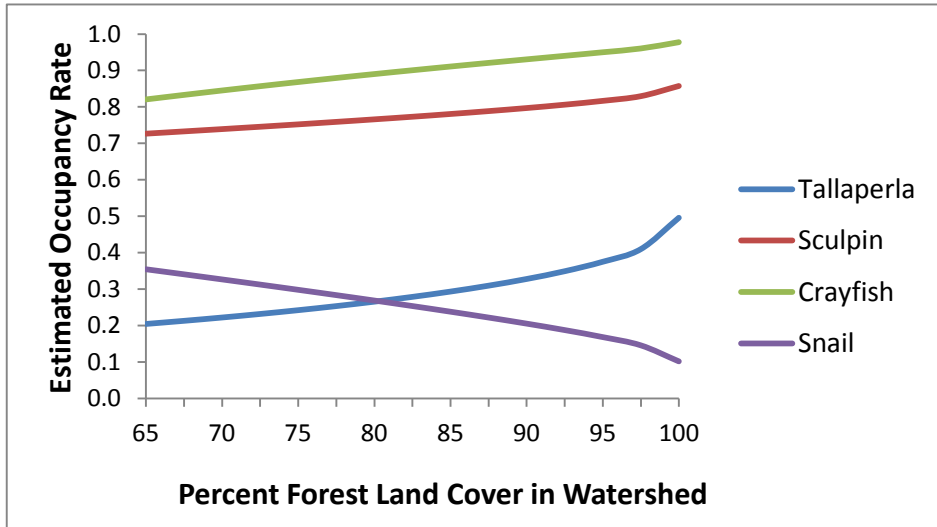


Figure 2.3. The relationship between predicted occupancy rate of the four focal taxa and percent forest land cover in a watershed. The figure was generated using parameters estimated by occupancy models after inverse log transformation.

CHAPTER 3

GENERAL CONCLUSIONS

The objective of my thesis was to investigate the effects of local and watershed scale factors influenced by human land use on the prevalence of stream organisms. I focused on the effects of land cover, habitat, and water chemistry on four focal stream consumers within thirty-seven streams within the Little Tennessee River Basin: *Tallaperla* spp. (stonefly), *Cambarus* spp. (crayfish), *Pleurocera proxima* (snail), and *Cottus bairdi* (mottled sculpin) that are important in regional stream ecosystems. Given limited conservation budgets, my goals were to identify a limited number of environmental parameters linked to stream consumer prevalence that could be quickly assessed in stream systems, and to investigate the importance of processes occurring at various scales.

One difficulty in performing field studies is an inability to detect organisms of interest with 100% certainty. When studies are designed without taking into account incomplete detection, problems with the observed data set have the potential to bias study results. The MacKenzie approach to this issue is to sample on multiple days in order to correct occupancy frequency by detection probability within an occupancy model framework, in order to account for incomplete detection of focal taxa. This approach has become increasingly popular in studies in streams, after fish and salamander studies pioneered the approach, and was the approach that I used in my study. Occupancy models have rarely been used to study stream invertebrates, and I am unaware of any studies that have previously used occupancy models for stoneflies, crayfish, or snails. I focused on land cover, habitat, and water chemistry parameters that were expected to

influence the prevalence of our focal taxa, with predictions based on each taxon's respective life history and environmental niche.

Local habitat conditions for stream organisms reflect the integration of processes occurring from local to landscape scales. At the local level, the occurrence of animals depends on proximate conditions such as microclimate, food availability, and shelter. However, these microhabitat conditions are influenced by processes occurring at larger spatial scales. At large spatial extents the loss of forest cover from human development alters the flow of water and resources within watersheds. In watersheds the exchange of water and nutrients with terrestrial and hyporheic linkages, as well as local processes, help determine stream chemistry. At a site, riparian vegetation decreases light penetration, provides leaves and large woody debris, and mediates the flow of water and nutrients. With rapid human development of landscapes, there is a critical need to understand the consequences of these processes occurring at varying scales, and to inform management interested in conserving natural resources.

Intense human population growth within the southern Appalachians suggest the region as a natural location to study the impacts of development on biological systems. Expanding exurban pressures from neighboring communities (*e.g.* Atlanta and Asheville) have helped contribute to high regional growth. Although historically urban, residential and agricultural development primarily has occurred in valleys, more recent residential development has occurred along mountainsides in the form of second homes. Increases in mountainside land use and regional loss of forested cover has enhanced potential human impacts on adjoining streams.

By using the occupancy modeling approach, it was possible to evaluate the relative influence of various environmental parameters reflecting processes occurring on different scales on the observed prevalence of the four focal taxa. The prevalence of the stream consumers was

strongly related to the percent forest and agricultural cover within a watershed. *Tallaperla* and *C. bairdi* had higher prevalence with greater forest cover, *Cambarus* had greater prevalence with lower agricultural cover, but *P. proxima* had higher prevalence in watersheds with lower forest cover. The importance of land-use within a watershed shows the influence of processes occurring at large spatial extent on local habitat conditions and the prevalence of stream consumers. In addition, the relationship between forested land cover and the prevalence of functionally important stream consumers is an important development consideration for municipal planners. *C. bairdi* and *Cambarus* prevalence were both related to local habitat conditions, which shows the importance of the local environmental for the prevalence of these taxa. Finally, *P. proxima* was positively associated with increased calcium concentrations, an element of water chemistry, which reflects both local and larger scale processes.

While our study was effective in linking observed occupancy probability of the four focal taxa to specific environmental parameters, this was a correlational study. We relied on available literature and our knowledge of the biology of each taxon to infer the influence of a linked environmental parameter to the resulting change in occupancy of a focal taxon. It would be beneficial to test the observed statistical relations by performing manipulative experiments, to determine causality and assess the mechanisms responsible for observed relationships.

In conclusion, findings presented here indicate the effectiveness of an occupancy modeling approach in evaluating factors influencing the prevalence of selected freshwater macroinvertebrate taxa. Although these occupancy modeling techniques have been well-established for vertebrates, my use of occupancy models represents a novel approach for stream invertebrates. This approach has expanded our understanding of how *Tallaperla*, *C. bairdi*, *Cambarus* and *P. proxima* are influenced by a mix of local- and watershed-scale environmental

parameters within reaches of the Little Tennessee River basin, and highlighted the importance of land-cover for the prevalence of four stream consumers. As a conservation priority, I recommend maintaining forested land cover within Little Tennessee River basin watersheds in order that populations of stream consumers persist and remain common.